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## Basal Archosaurs: Phylogenetic Relationships and Functional Implications

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## BASAL ARCHOSAURS: PHYLOGENETIC RELATIONSHIPS AND FUNCTIONAL IMPLICATIONS

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**ABSTRACT**—Archosaurs first appeared in the Middle Triassic and within a short interval of time came to dominate all faunas of large vertebrates for the remainder of the Mesozoic. It is widely held that shortly after archosaurs first appeared the group split into two clades, now termed “Pseudosuchia” and “Ornithosuchia.” Each clade independently evolved a rotary-style ankle design (“crocodile-normal” and “crocodile-reversed,” respectively) and each independently evolved from semi-erect to erect limb posture. Erect posture, in turn, has been identified as the key adaptation (possibly associated with locomotor stamina) that resulted in the archosaurian radiation.

These hypotheses are examined in light of a numerical cladistic analysis of basal archosaurs. Contrary to previous schemes, Archosauria is divided into Crurotarsi and Ornithodira. Crurotarsi (Suchia + Ornithosuchidae + Parasuchia) is characterized by the rotary crurotarsal ankle joint and other postcranial synapomorphies; this style of ankle joint thus appears to have evolved once rather than twice. Ornithodira is divided into Pterosauria and Dinosauromorpha. Pterosaurs, therefore, occupy a basal position within Ornithodira and do not constitute the sister-group to Dinosauria as has been suggested. The supposed pterosaur precursor, *Scleromochlus*, is reexamined and its proximity to Pterosauria is questioned.

The analysis underscores the perils of employing functional constructs, such as ankle “types,” rather than character data in phylogeny reconstruction. Current scenarios for the evolution of upright posture in archosaurs—either as an “improvement” in design or as a correlate of locomotor stamina—are not supported by the cladistic pattern. Erect archosaurs coexisted for millions of years alongside more abundant sprawling or semi-erect rhynchosaurs and synapsids and radiated only after their demise. Osteological features associated with locomotor stamina in living tetrapods do not appear to be strongly correlated with erect posture among archosaurs. Once erect posture had been achieved in archosaurs, however, it may have promoted the evolution of bipedal locomotion, which appears at about the same time. Bipedal locomotion, in turn, may have permitted more extensive modification of the forelimbs, which in a short interval of time were fashioned as wing supports for powered flight in pterosaurs.

### INTRODUCTION

Archosaurs include familiar forms, such as crocodiles, pterosaurs, and dinosaurs, as well as a variety of less familiar forms that went extinct before the end of the Triassic, including the gavial-like phytosaurs, armored aetosaurs, and a variety of quadrupedal and bipedal rauisuchians and dinosaur precursors. Although several monophyletic groups have long been recognized, the phylogenesis of these groups during the Triassic has remained mysterious and conjectural for more than a century.

Owen (1859) coined the term “Thecodontia” for various Triassic archosaurian remains, and the group later came to be regarded as the “basal stock” from which all later archosaur clades arose (Watson, 1917; Huene, 1922; Kuhn, 1933; Romer, 1966, 1972a; Charig, 1976). A “basal stock,” by definition, is a paraphyletic assemblage because it excludes some of the descendants. “Thecodonts,” for example, are archosaurs that lack the modifications of particular descendant clades (crocodiles, pterosaurs, dinosaurs including birds).

Traditional systematists have long been aware of “the-codont” paraphyly and on occasion have considered the maintenance of “Thecodontia” an admission of ignorance about phylogenetic relationships: “The Order Thecodontia may ultimately be seen to be a largely artificial grouping of distantly related forms” (Cruickshank, 1979:169). Maintenance of the group has served as a convenient cover for the absence of phylogenetic resolution (Gauthier, 1984, 1986; Benton and Clark, 1988; Novas, 1989; Sereno and Arcucci, 1990).

### Archosaurian Classification

Traditional classification of archosaurs is concerned primarily with subdivision according to adaptive or locomotor grades. By the early twentieth century, “the-codonts” were subdivided into the lower and higher paraphyletic grades, “Proterosuchia” and “Pseudosuchia,” respectively (Kuhn, 1933; Huene, 1922; Hughes, 1963; Romer, 1956, 1966, 1972a,b,c; Reig, 1970; Charig and Reig, 1970; Charig, 1976; Charig and Sues, 1976; Bonaparte, 1982). “Proterosuchians”

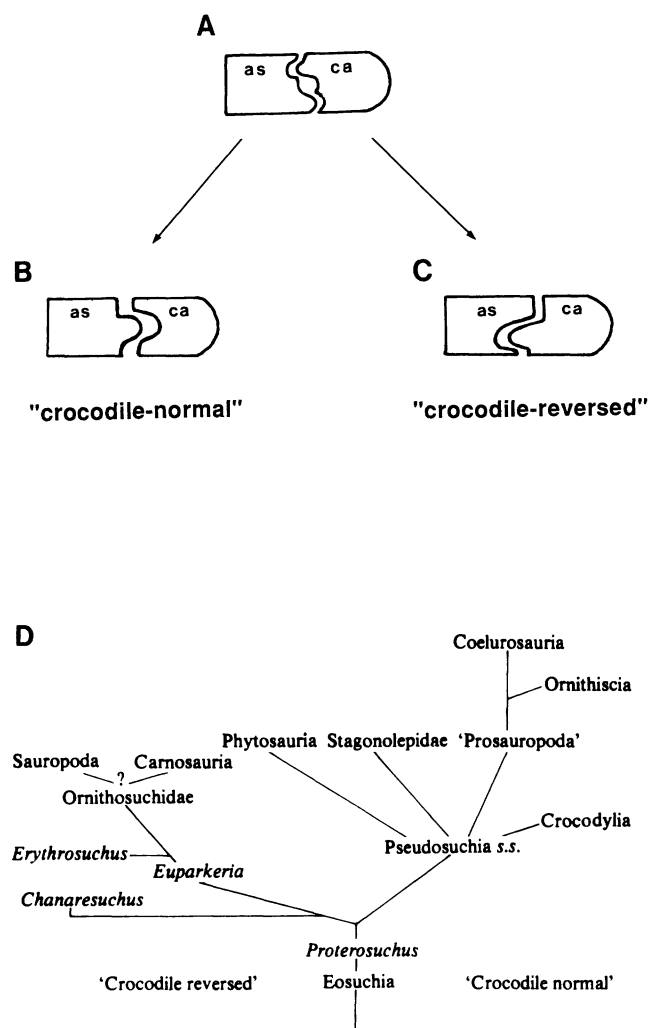


FIGURE 1. Diphyletic origin of crurotarsal ankle joints among archosaurs (after Cruickshank, 1979). Left proximal tarsals in *Proterosuchus* (A), “crocodile-normal” archosaurs (B), and “crocodile-reversed” archosaurs (C). D, Phylogenetic tree depicting the divergence of “reversed” and “normal” crurotarsal archosaur clades from proterosuchian grade ancestors (from Cruickshank, 1979). Abbreviations: as, astragalus; ca, calcaneum.

included the semi-aquatic proterosuchids and the larger-bodied erythrosuchids and, more recently, the semi-aquatic proterochampsids (Romer, 1972b). “Pseudosuchians” were regarded as the more “unspecialized,” “mainline” archosaurs in the Triassic that gave rise to all descendant archosaurian clades. Phytosaurs and aetosaurs have been generally, but not always, classified as separate suborders on the basis of their divergent skeletal modifications, and recently “ornithosuchians” have joined this list (Chatterjee, 1982). Most recently, Carroll (1988) has abandoned “Pseudosuchia” as well as any other hierarchical arrangement of basal archosaurs, with “thecodont” suborders listed serially.

Discovery of the small-bodied Middle Triassic forms, *Lagosuchus* and *Lagerpeton*, represented a turning point in archosaurian systematics. Their close relationship with dinosaurs (Romer, 1971, 1972a,b,c; Bakker and Galton, 1974; Bonaparte, 1975a) constituted the first hypothesis that clearly allied a particular “thecodont” group with an apomorphic descendant clade and pre-saged the subsequent disbanding of “Thecodontia” by cladists.

### The Archosaurian Ankle

Krebs (1963, 1965) was the first to recognize that the unusual crurotarsal ankle joint of extant and fossil crocodilians was also present in Triassic “pseudosuchian” archosaurs. On the basis of the ankle joint, Krebs (1974) united “pseudosuchians” and crocodylomorphs as Suchia and suggested an ancient origin for the group separate from known “proterosuchians.” At about the same time, Walker (1964) and Bonaparte (1972) described the ornithosuchid ankle and soon thereafter Chatterjee (1978) described the crurotarsal ankle in phytosaurs. Chatterjee proposed the terms “crocodilian-normal” and “crocodilian-reversed” to describe the ankle joint in typical “pseudosuchians” and ornithosuchids, respectively. The former is designed as in extant crocodilians, with a “peg” on the astragalus and a “socket” on the calcaneum, whereas the latter reverses the positions of “peg” and “socket.”

Variation in archosaurian ankle morphology was described in more detail in an influential paper by Cruickshank (1979). Cruickshank proposed a basal split within archosaurs (Fig. 1), with each lineage independently acquiring a crurotarsal ankle joint and each gradually “improving” in locomotor function from sprawling through semi- and fully-erect postures, as suggested earlier by Bakker (1971) and Charig (1972): “The attraction of a study of this sort is that it deals with a structure which had a limited number of pathways open to it: in fact there seems to have been only two (Fig. 1) and [sic] involved the elaboration of the ankle joint in similar but contrasting ways. It seems to be possible to follow the archosaur lineages demonstrating these two analogous ankle mechanisms in a phylogenetic manner (Fig. 2). The results of the study confirm in part that the story is straightforward and that one lineage can be shown to lead from the proterosuchian sprawler to the crocodilian semi-improved state to the ‘dinosaur’ fully improved biped (ref. 3, p. 152) (‘crocodile normal’). At the same time there would seem to be a separate and parallel line which, starting also with the proterosuchian sprawler, led through other intermediate (semi-improved) groups to the ornithosuchids and hence possibly to the carnosaurs and sauropods (Fig. 2) (‘crocodile reversed’)” (Cruickshank, 1979:168–169). Since 1979, the independent origin of crocodile-normal and crocodile-reversed ankle joints has served as a central theme in archosaur phylogeny. Several “ankle phylogenies” were proposed, with phylogenetic connections drawn from these two ankle de-

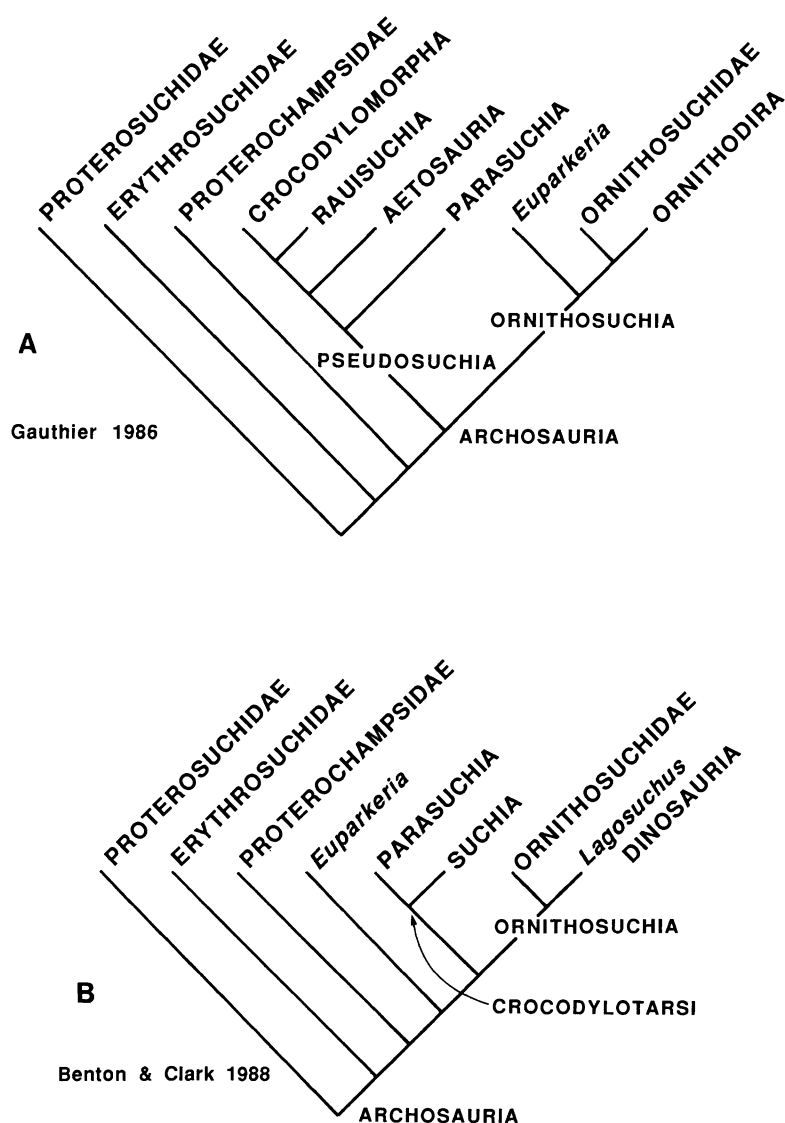


FIGURE 2. Previous cladistic hypotheses for basal archosaurian phylogeny. A, Gauthier (1986); B, Benton and Clark (1988).

signs to presumed primitive and advanced versions (Brinkman, 1981; Chatterjee, 1982; Cruickshank and Benton, 1985; Thulborn, 1980, 1982).

### Recent Cladistic Analyses

The first cladistic analyses followed Cruickshank's scheme to the extent that they support a fundamental division within Archosauria characterized by "crocodile-normal" and "crocodile-reversed" ankle types (Fig. 2; Gauthier 1984, 1986; Benton and Clark, 1988; Novas, 1989). Gauthier named these clades by the older terms "Pseudosuchia" and "Ornithosuchia," respectively. He clearly associated extant crocodiles and birds with each clade and restricted the taxon Archosauria to include only the common ancestor of crocodiles and birds and those fossil forms most closely related to them—the definition of Archosauria fol-

lowed in this analysis and elsewhere (Sereno and Arcucci, 1990). The general configuration of taxa in Gauthier's cladogram is similar to that in Cruickshank's tree. "Pseudosuchia" includes the same taxa (phyosaurs, aetosaurs, crocodylomorphs, and traditional "pseudosuchians") but excludes dinosaurs, as did Cruickshank in a subsequent paper (Cruickshank and Benton, 1985). "Ornithosuchia" includes *Euparkeria*, ornithosuchids, and dinosaurs (including birds). This cladistic division has gained currency in the literature (Gauthier and Padian, 1985; Gauthier et al., 1988, Gauthier et al., 1989), although Benton prefers "Crocodylotarsi" over the older term "Pseudosuchia" (Benton and Clark, 1988; Benton, 1990a).

Sereno and Arcucci (1990; also Sereno, 1989, 1990) have argued that neither "Pseudosuchia" nor "Ornithosuchia" is monophyletic and that preoccupation with "ankle types" has obfuscated important character vari-

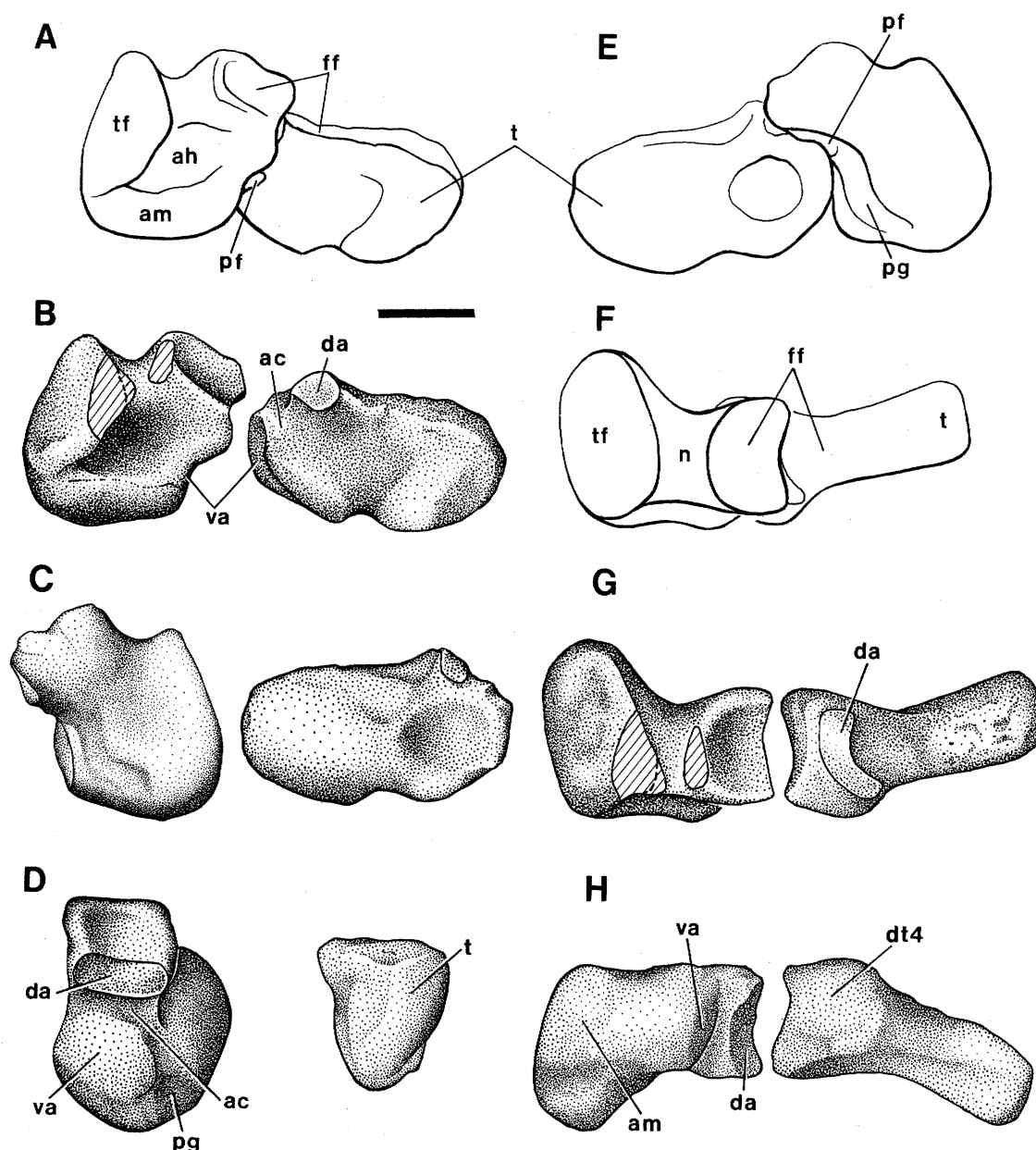


FIGURE 3. *Proterosuchus vanhoepeni* (Haughton, 1924). Left astragalus and calcaneum (MCZ 4301, cast of NM C3016). A, E, F, Astragalus and calcaneum in natural articulation in anterior (A), posterior (E), and dorsal (F) views. B–D, G–H, Astragalus and calcaneum disarticulated in anterior (B), posterior (C), lateral (D), dorsal (G), and ventral (H) views. Scale bar equals 1 cm. Abbreviations: ac, astragalocalcaneal canal; am, articular surface for metatarsals 1 and 2; ah, anterior hollow; da, dorsal articulation; dt4, articular surface for distal tarsal 4; ff, fibular facet; n, notch; pf, perforating foramen; pg, posterior groove; t, tuber; tf, tibial facet; va, ventral articulation.

ation. They proposed a basal split within Archosauria that recognizes the monophyly of crurotarsal archosaurs, and this is developed in more detail here.

#### MATERIALS

Fossil archosaur materials were examined in several collections, which are abbreviated as follows: AMNH, American Museum of Natural History, New York;

BMNH, British Museum (Natural History), London; FMNH, Field Museum of Natural History; GPIT, Institut und Museum für Geologie und Paläontologie, Universität Tübingen, Tübingen; ISI, Indian Statistical Institute, Calcutta; L, Manchester Museum, Manchester; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; NM, National Museum, Bloemfontein; PVL, Instituto Miguel Lillo, Tucumán; UMCZ, University of Cam-

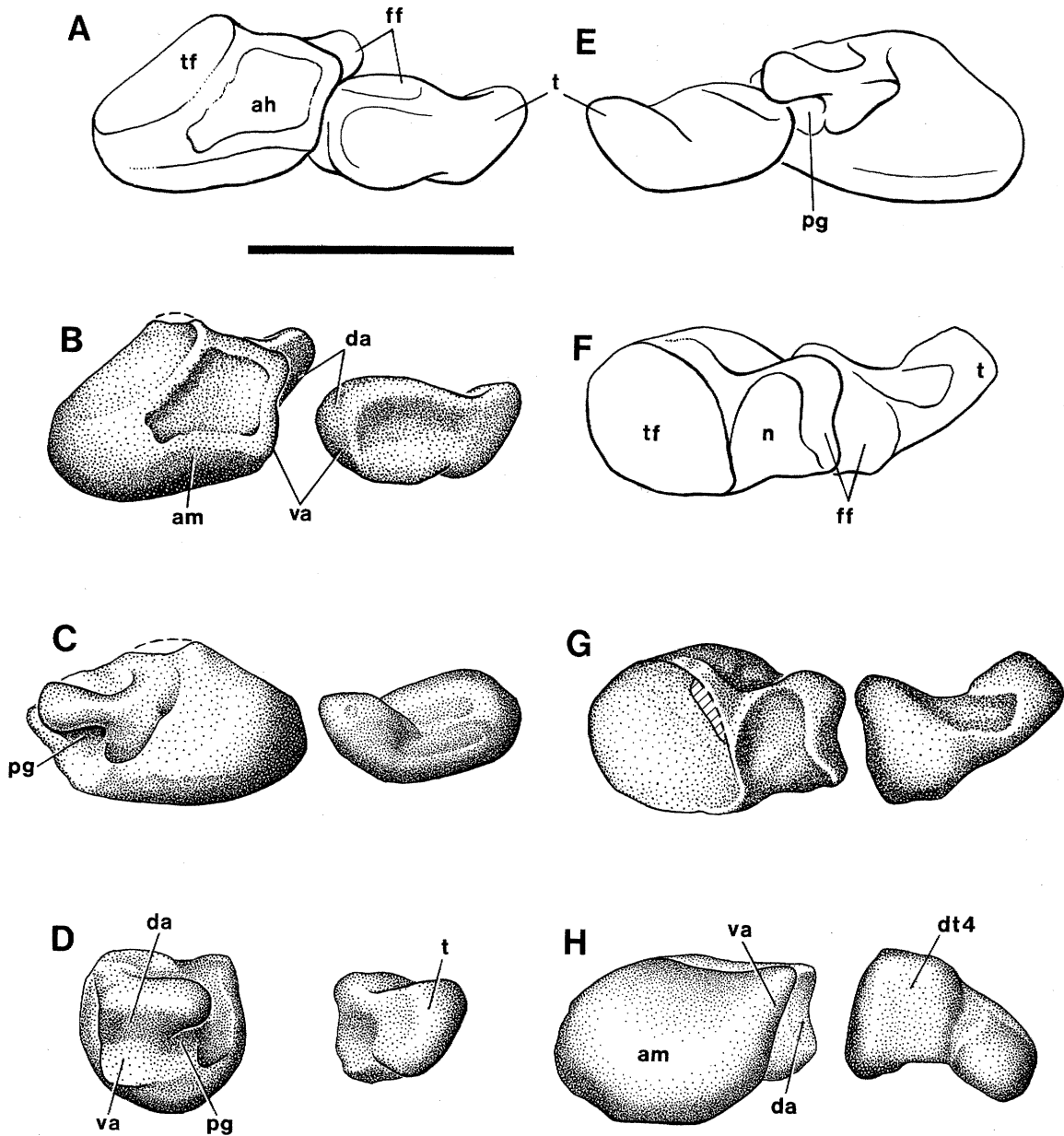


FIGURE 4. *Euparkeria capensis* Broom, 1913. Left astragalus and calcaneum (UMCZ T692). A, E, F, Astragalus and calcaneum in natural articulation in anterior (A), posterior (E), and dorsal (F) views. B–D, G–H, Astragalus and calcaneum disarticulated in anterior (B), posterior (C), lateral (D), dorsal (G), and ventral (H) views. Scale bar equals 1 cm. Abbreviations as in Figure 3.

bridge, Museum of Zoology, Cambridge; USNM, National Museum of Natural History, Washington, D.C.

The figures of the proximal tarsals (Figs. 3–9) were drawn by the author with a camera lucida. The disarticulated views of the tarsals were drawn after the tarsals had been separated from natural articulation in the plane of view. The figures of *Scleromochlus taylori* were drawn by the author with a camera lucida from new latex peels that were made from the original natural molds.

## OUTGROUP RELATIONSHIPS

### *Euparkeria* + Proterochampsidae + Archosauria

“Proterosuchian” archosaurs are regarded as a paraphyletic grade by all recent cladistic analyses. Several cranial and postcranial synapomorphies suggest that erythrosuchids are more advanced than proterosuchids (Paul, 1984; Gauthier, 1984, 1986; Gauthier et al., 1988; Benton and Clark, 1988; Sereno, 1989, 1990; Sereno and Arcucci, 1990). Opinion differs, however,

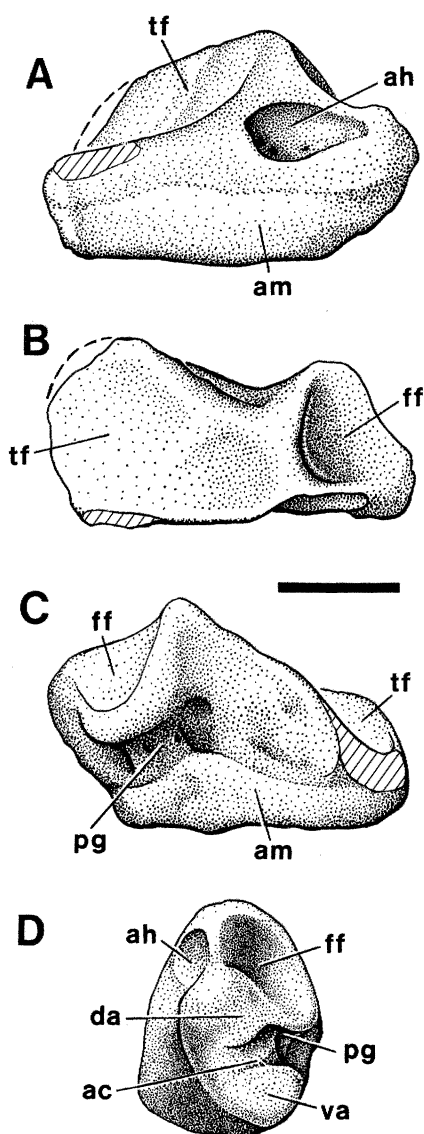


FIGURE 5. *Chanaresuchus bonapartei* Romer, 1972b. Left astragalus (MCZ 4035) in anterior (A), dorsal (B), posterior (C), and lateral (D) views. Scale bar equals 1 cm. Abbreviations as in Figure 3.

on the phylogenetic position of *Euparkeria* and Proterochampsidae. Gauthier (1984; also Gauthier et al., 1988; Gauthier et al., 1989) regarded proterochampsids as the sister-taxon to Archosauria with *Euparkeria* included within Archosauria as a basal "ornithosuchian."

In the present analysis, Proterochampsidae and *Euparkeria* are employed as successive outgroups to Archosauria, following Sereno and Arcucci (1990; see also Sereno, 1989, 1990). Benton and Clark (1988) also positioned these two taxa outside Archosauria, but their relative positions were reversed. The following synapomorphies unite *Euparkeria*, Proterochampsidae, and Archosauria:

- 1) dorsal body osteoderms;
- 2) interclavicle with reduced, tablike lateral processes;
- 3) femoral shaft with marked sigmoid curvature;
- 4) loss of bony astragalocalcaneal canal;
- 5) absence of ossification of distal tarsals 1 and 2;
- 6) pedal digit IV significantly shorter than III.

Gauthier et al. (1988) listed synapomorphies 3 and 5 and Benton and Clark (1988) listed synapomorphies 3 and 4 for the same group. Benton and Clark (1988) listed the presence of dermal armor (synapomorphy 1) but suggested that each osteoderm pair corresponded with a single underlying vertebra. This particular dermal armor pattern, however, only characterizes crurotarsal archosaurs (and possibly *Euparkeria*) and is absent in proterochampsids and unknown in pterosaurs and dinosauromorphs.

The reduction of the lateral processes of the interclavicle (synapomorphy 2) was used previously at a less inclusive level as an archosaur synapomorphy by Gauthier et al. (1988), but in this analysis it applies to a more inclusive taxon due to the position of *Euparkeria* outside Archosauria and the presence of the apomorphic state in *Doswellia* (Weems, 1980). The condition in the outgroup Erythrosuchidae remains unknown; the identification of asymmetrical fragments as possible interclavicles in *Shansisuchus* (Young, 1964a) is not convincing. The absence of ossification of distal tarsals 1 and 2 (synapomorphy 5), on the other hand, was listed at a more inclusive level including erythrosuchids (Benton and Clark, 1988; Gauthier et al., 1988). Although erythrosuchids have been reported to lack an ossified distal tarsal 1 (Cruickshank, 1978) and thus appear to exhibit the apomorphic condition, the referral of this pedal material to *Erythrosuchus* is probably incorrect (Parrish, pers. comm.). The absence of distal tarsal 1, however, has been reliably reported in *Euparkeria* (Ewer, 1965), proterochampsids (Romer, 1972b), and archosaurs (Sereno and Arcucci, 1990) but the bone is clearly present in *Proterosuchus* (Cruickshank, 1972; Carroll, 1976). The absence of distal tarsal 1, therefore, is applied at this time only to *Euparkeria*, proterochampsids, and archosaurs but may eventually also characterize erythrosuchids. Distal tarsal 2 is ossified plesiomorphically among archosauriforms (Cruickshank, 1972; Carroll, 1976), but as with distal tarsal 1 the condition in erythrosuchids is unknown. In *Euparkeria*, proterochampsids, and archosaurs, distal tarsal 2 remains unossified. Very rarely this tarsal reappears among fossil crocodylians (Schaeffer, 1941), but it remains cartilaginous in extant forms (Brinkman, 1981). The isolated report of an ossified distal tarsal 2 in the ornithischian *Heterodontosaurus* (Santa Luca, 1980) is due to misinterpretation of a crack passing through distal tarsal 3.

Sereno and Arcucci (1990:24) reported the presence of an antorbital fossa on the maxilla and lacrimal in proterochampsids as found in *Euparkeria* and archosaurs but noted the likelihood that this would eventually characterize a more inclusive taxon including

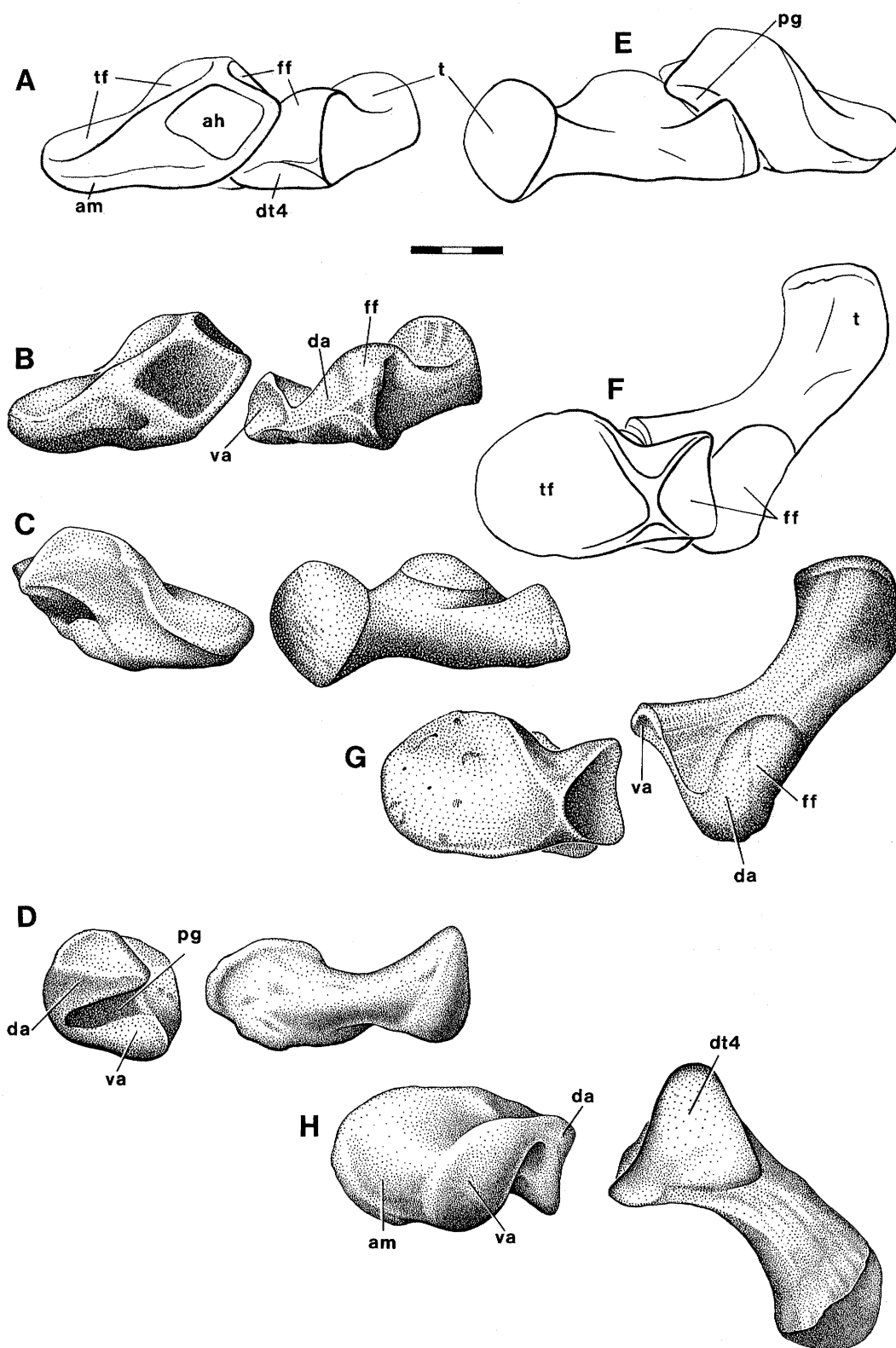


FIGURE 6. *Rutiodon* sp. Left astragalus and calcaneum (USNM 18313). A, E, F, Astragalus and calcaneum in natural articulation in anterior (A), posterior (E), and dorsal (F) views. B–D, G–H, Astragalus and calcaneum disarticulated in anterior (B), posterior (C), lateral (D), dorsal (G), and ventral (H) views. Scale bar equals 3 cm. Abbreviations as in Figure 3.

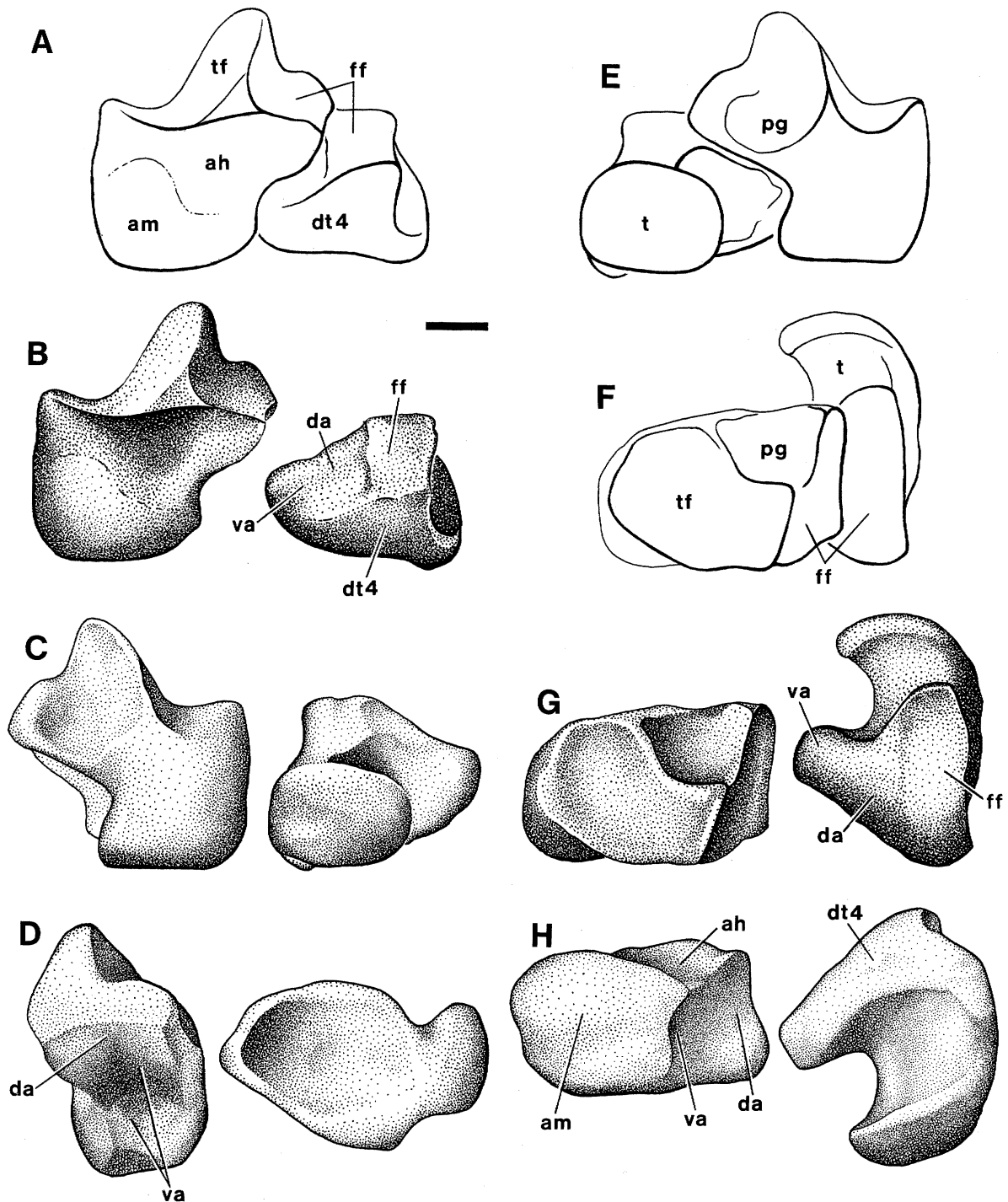


FIGURE 7. *Riojasuchus tenuiceps* Bonaparte, 1969. Left astragalus and calcaneum (PVL 3827). A, E, F, Astragalus and calcaneum in natural articulation in anterior (A), posterior (E), and dorsal (F) views. B–D, G–H, Astragalus and calcaneum disarticulated in anterior (B), posterior (C), lateral (D), dorsal (G), and ventral (H) views. Scale bar equals 1 cm. Abbreviations as in Figure 3.

erythrosuchids (e.g., *Shansisuchus*, Young, 1964a:fig. 10A). Previous studies assumed that an antorbital fossa occurred only in *Euparkeria* and archosaurs (Gauthier, 1984, 1986; Gauthier et al., 1988).

Numerous additional characters listed by Benton and Clark (1988:332, group B) and Gauthier et al. (1988: 204, node 11) to unite *Euparkeria*, Proterochampsidae, and Archosauria are here considered problematic:

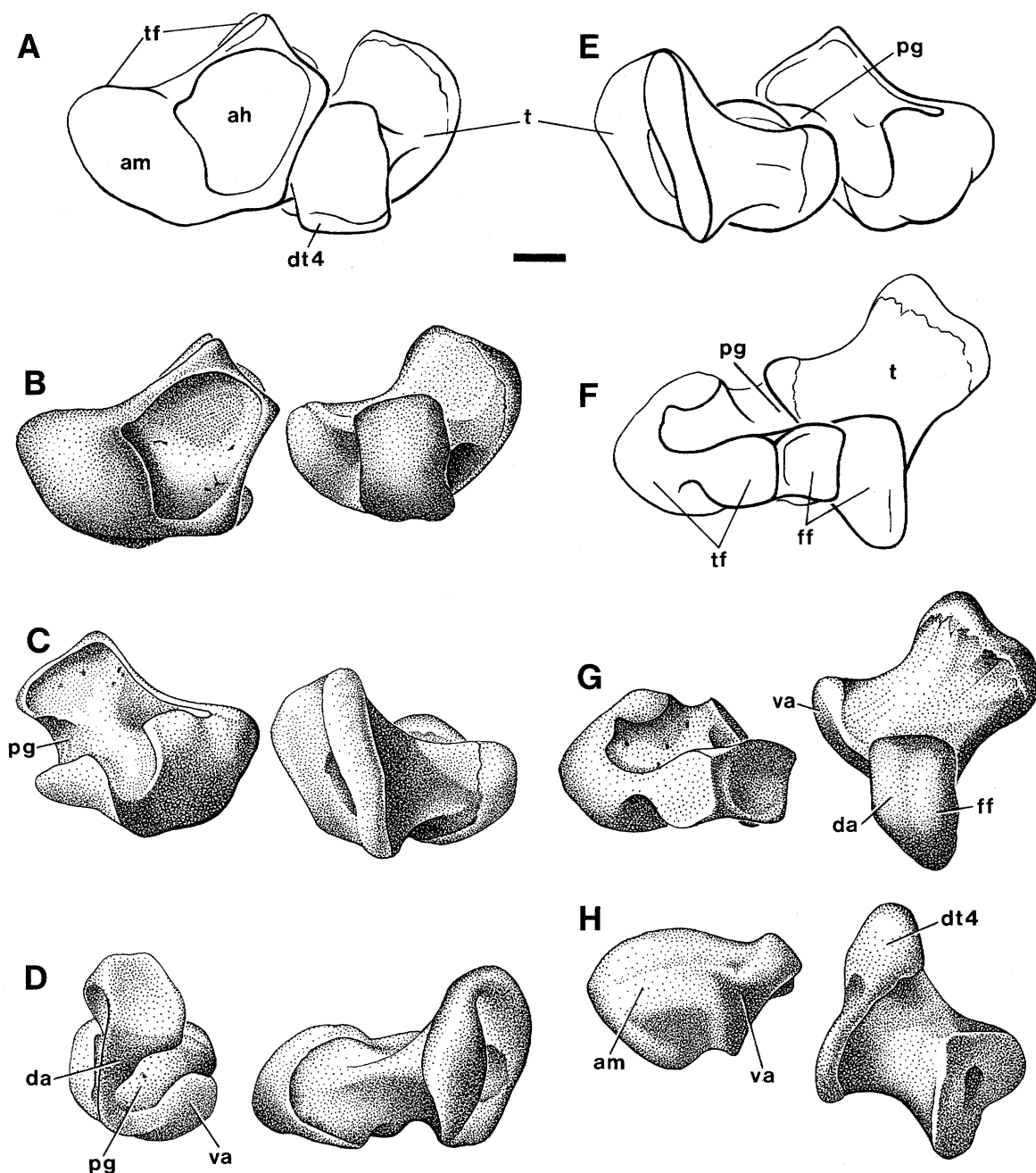


FIGURE 8. *Crocodylus acutus*. Left astragalus and calcaneum (FMNH 22030). A, E, F, Astragalus and calcaneum in natural articulation in anterior (A), posterior (E), and dorsal (F) views. B–D, G–H, Astragalus and calcaneum disarticulated in anterior (B), posterior (C), lateral (D), dorsal (G), and ventral (H) views. Scale bar equals 1 cm. Abbreviations as in Figure 3.

the absence of a parietal foramen, a well-developed otic notch, thecodont dentition, absence of postaxial cervical intercentra, ribs all single-headed or two-headed, reduced humeral epicondyles, medial two digits of manus and pes more robust than lateral two, absence of the femoral intertrochanteric fossa, reduction in the posterior projection of the femoral distal condyles, “crocodiloid tarsus,” and hind-limbs positioned under

the body. Several of these characters have broader distributions. “Thecodont” dentition, absence of a parietal foramen, and presence of two-headed ribs, for example, all occur in the immediate outgroup Erythrosuchidae (Young, 1964a; Charig and Sues, 1976). The humeral epicondyles indeed appear to be reduced in the ingroup (*Euparkeria*, Proterochampsidae, and Archosauria) as compared to the condition

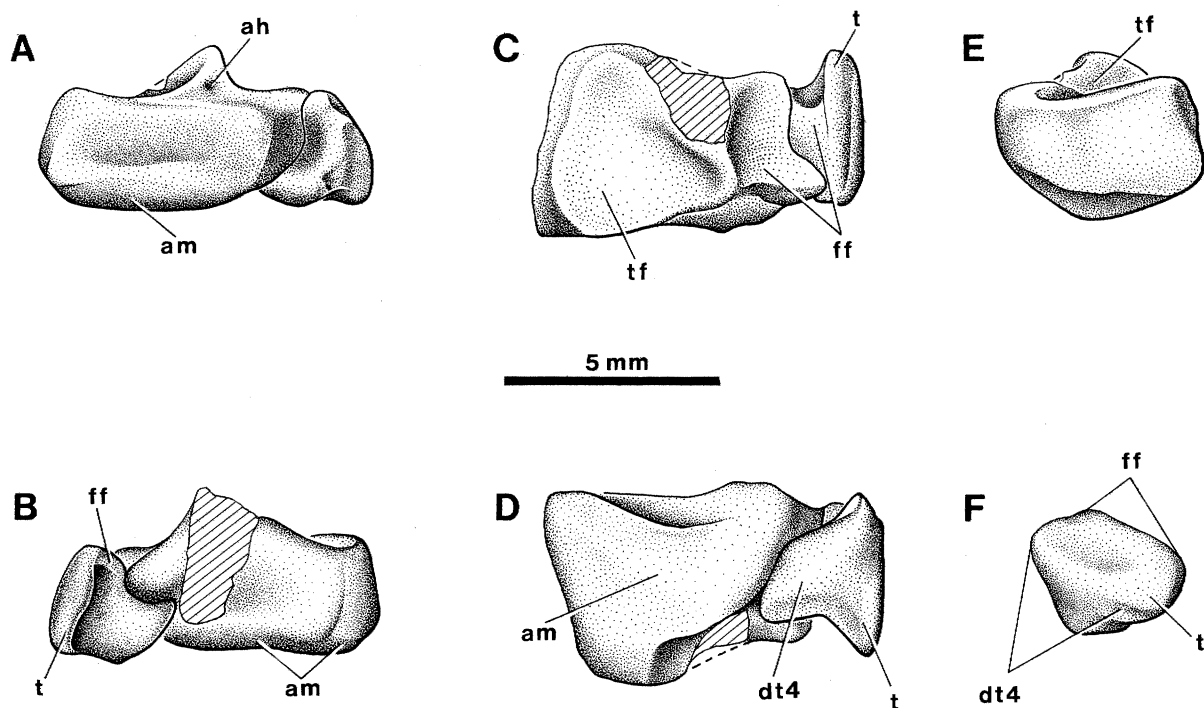


FIGURE 9. *Lagosuchus talampayensis* Romer, 1971. Left astragalus and calcaneum (PVL 3870). A–D, Astragalus and calcaneum in natural articulation in anterior (A), posterior (B), dorsal (C), and ventral (D) views. E, Astragalus in medial view. F, Calcaneum in lateral view. Abbreviations as in Figure 3.

in the heavy-bodied erythrosuchids, but they are not any narrower relative to the width of the proximal end or minimum shaft diameter. Several characters do not appear to describe any observable character variation in basal archosauromorphs: erythrosuchids do not appear to have a deep femoral intertrochanteric fossa as in *Proterosuchus* (Cruickshank, 1972), the posterior projection of the femoral distal condyles does not appear to vary in any systematic or measurable fashion, and the meaning of “crocodiloid tarsus” is unclear.

#### Proterochampsidae + Archosauria

Proterochampsids and archosaurs are united by the following synapomorphies (Sereni and Arcucci, 1990):

- 1) Postaxial intercentra absent;
- 2) contiguous crural facets on astragalus.

Postaxial intercentra have been recorded in *Proterosuchus* (Cruickshank, 1972), Erythrosuchidae (Hughes, 1963; Tatarinov, 1961; Charig and Sues, 1976), and *Euparkeria* (Ewer, 1965). The most complete information is available for *Euparkeria*, in which intercentra occur between all of the presacral centra. In contrast, no intercentra are present in any part of the postaxial column in proterochampsids (e.g., *Chanaresuchus* MCZ 4035, 4037, PVL 4575; *Gualosuchus* PVL 4576) or among archosaurs (synapomorphy 1). Gauthier (1986) and Gauthier et al. (1988) also used the absence of postaxial intercentra for a similar group, although their inclusion of *Euparkeria* within Archo-

sauria resulted in an equivocal distribution for this character.

The articular facets on the astragalus for the crus are separated by a flat nonarticular surface in Archosauriformes, plesiomorphically, as seen in *Proterosuchus* (Fig. 3F–G), *Euparkeria* (Fig. 4F–G), and apparently also in erythrosuchids (Young, 1964a). In contrast, the crural facets in proterochampsids (Fig. 5) and archosaurs (Figs. 6–9) are positioned side by side, separated only by a bony crest. The contiguous position of the crural facets in proterochampsids and archosaurs is not an allometric consequence of small size, as it occurs both in small-bodied forms, like *Chanaresuchus* and *Gracilisuchus* (PVL 4597), and in large-bodied dinosaurs.

#### TERMINAL TAXA

Seven archosaurian terminal taxa were chosen for cladistic analysis. These taxa (Suchia, Parasuchia, *Ornithosuchus longidens*, *Riojasuchus tenuiceps*, *Scleromochlus taylori*, Pterosauria, Dinosauria) are defined and diagnosed below. Supraspecific terminal taxa are defined by listing included taxa; the common ancestor and any additional taxa most closely related to those listed are included by definition within the taxon. Apomorphies supporting the monophyly of terminal taxa are lettered sequentially and discussed individually, with the exception of Pterosauria (autapomorphies listed only in the text). Characters,

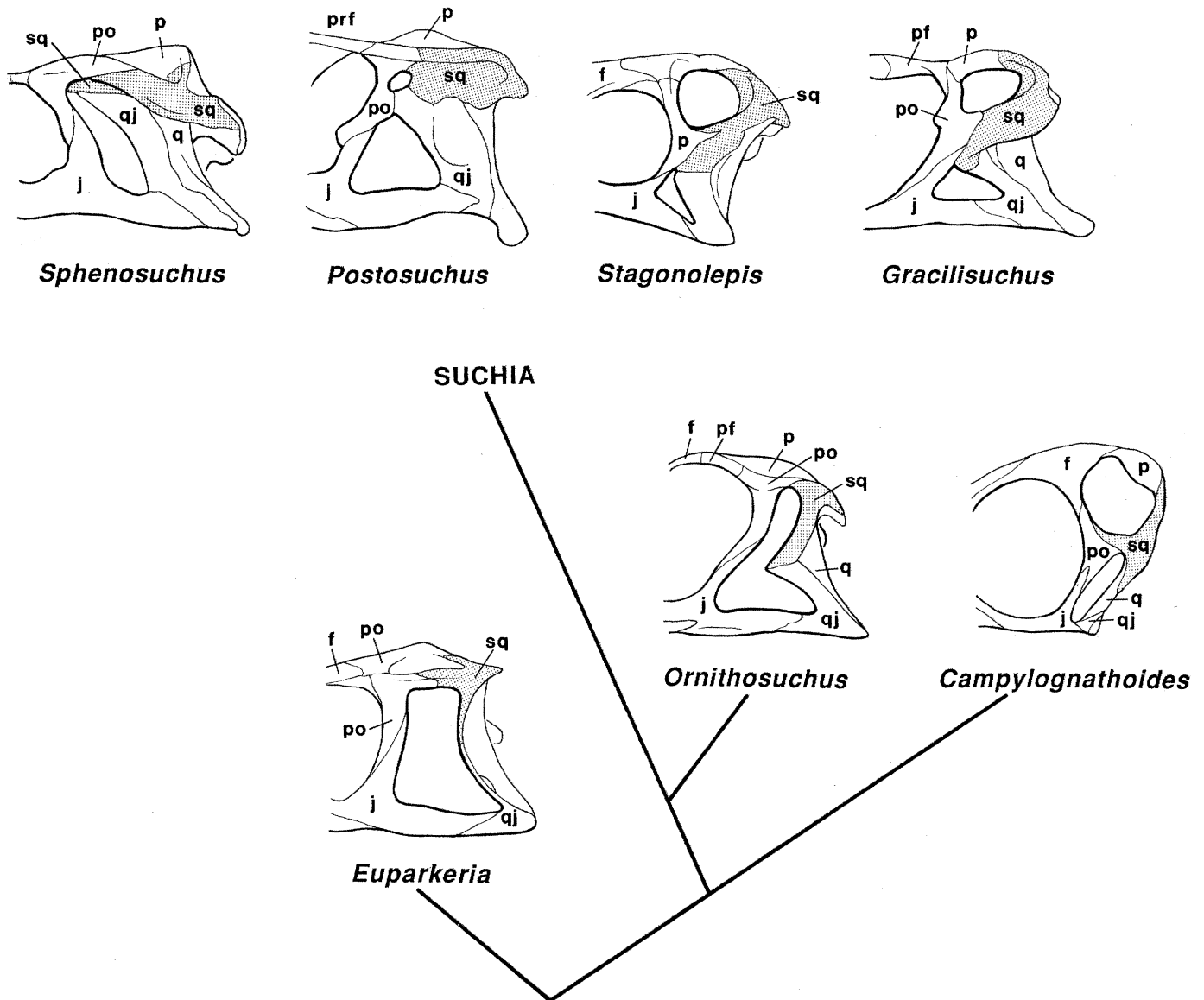


FIGURE 10. Phylogenetic diagram showing the shortened postorbital-squamosal temporal bar (character A) among suchians as compared to that in three proximate outgroups. Abbreviations as in Figure 11.

character states, and character state distributions are compiled in an autapomorphy matrix in the Appendix under the heading Terminal Taxa. Assumptions (such as character reversal within a terminal taxon) and missing data are indicated in this matrix.

#### Suchia Krebs, 1974

**Definition**—Suchia includes *Gracilisuchus stipanicorum*, Aetosauria, Rauisuchia, Poposauridae, Crocodylomorpha, and all descendants of their common ancestor.

**Recorded Temporal Range**—Ladinian (Middle Triassic) to Recent.

Suchia was coined by Krebs (1974) to unite traditional “pseudosuchians” and crocodylomorphs, and

the term has been applied to a clade of crurotarsal archosaurs of similar, but not identical, composition (Benton and Clark, 1988). This cladistic usage is followed here. The predominantly quadrupedal suchians are united by a single cranial synapomorphy, which was listed previously for this group by Benton and Clark (1988:333).

(A) Postorbital-squamosal temporal bar anteroposteriorly short with subtriangular laterotemporal fenestra (Fig. 10). In most basal archosaurs the laterotemporal fenestra is relatively tall with its posterodorsal and posteroventral corners bounded by L-shaped processes of the squamosal and quadratojugal, respectively. In Suchia, in contrast, the squamosal lacks a discernible ventral process and borders very little, if any, of the laterotemporal fenestra. This condition is

present without exception in all major suchian taxa, including *Gracilisuchus* (Romer, 1972c), Aetosauria (Walker, 1961), Rauisuchia (Chatterjee, 1985), and Crocodylomorpha (Crush, 1984; Walker, 1990). *Prestosuchus chiniquensis* (Barbarena, 1978) lacks this modification of the laterotemporal fenestra and thus is not included in Suchia. The concordance between *Prestosuchus* and Suchia in aspects of the postcranium suggests a close relationship.

Numerous additional synapomorphies given by Benton and Clark (1988) and by Gauthier (1986; for an equivalent unnamed taxon) are not supported in this analysis as suchian synapomorphies as discussed below. Five of the eight characters listed by Benton and Clark (1988:310-311) are also listed as "ornithosuchian" synapomorphies and thus have an equivocal distribution on their tree; they could just as well be interpreted as archosaurian synapomorphies with reversal to the plesiomorphic condition in phytosaurs. Some of the characters have broader distributions than Suchia alone. Reduction of pedal digit V to a length shorter than digit I, for example, is difficult to support as a suchian synapomorphy since the same length disparity occurs in the archosaurian outgroups *Euparkeria* (Ewer, 1965) and proterochampsids (Romer, 1972b). Several suchians retain phalanges in digit V (e.g., *Stagonolepis*, *Ticinosuchus*, *Saurosuchus*), and this digit appears to be as long as that in *Euparkeria*. Absence of the septomaxilla, another proposed suchian synapomorphy, may be plesiomorphic rather than apomorphic; this bone has not been reported in any basal archosaurs except phytosaurs (see character S). Absence of a "pubo-ischiadic plate" is difficult to assess without further clarification. A puboischiadic symphysis is always present but varies in the extent to which it floors the pelvic girdle (the thin medial margin of the plate is frequently broken away); many suchians retain a broad puboischiadic plate (e.g., *Stagonolepis*, Walker, 1961). Finally, an "advanced crocodile-normal tarsus" is a character complex or functional concept that must be expressed as anatomical features to be meaningfully employed in cladistic analysis.

Other synapomorphies listed by Gauthier (1986:42) in support of a similar group (Aetosauria + Rauisuchia + Crocodylomorpha) are also problematic, such as the absence of a separate postparietal and the presence of osteoderms on the ventral aspect of the tail. The postparietal is absent in many archosaur clades besides Suchia, such as phytosaurs, ornithosuchids, and ornithodirans. In addition, Romer (1972c) reported a postparietal in the suchian *Gracilisuchus*. Likewise, ventral caudal armor is substantial only among aetosaurs and non-sphenosuchian crocodylomorphs, which have parasagittal rows of ventral plates (Walker, 1961; Colbert and Mook, 1951). Although a short, single row of small ventral ossicles has been reported in the suchian *Ticinosuchus* (Krebs, 1965), other suchians show no sign of ventral caudal armor, such as *Gracilisuchus* and sphenosuchid crocodylomorphs (Huene, 1921; Crush, 1984). Ventral armor plates also occur among

phytosaurs (Fraas, 1896:fig. 10; Gregory, 1962), a proximate suchian outgroup.

### *Ornithosuchus longidens* (Huxley, 1877)

**Hypodigm**—*Ornithosuchus longidens* is based on fossils discovered in sandstone quarries in the nineteenth century along the northern coast of Scotland (Walker, 1964).

**Recorded Temporal Range**—?Carnian (Late Triassic; Olsen and Sues, 1986).

Minor cranial ornamentation distinguishes *O. longidens* from other ornithosuchids. The preserved portion of the postcranium does not exhibit discernible autapomorphies.

(B) Maxilla with free posterior prong (Fig. 11A). An unusual prong-shaped process of the maxilla projects posteriorly from the alveolar margin and is present in the holotype specimen (Elgin Museum EM 1R; Walker, 1964:64).

(C) Postorbital with strong central horizontal crest (Fig. 11A). The postorbital is ornamented by a well-defined rugose ridge passing posteriorly from the dorsal orbital margin and overhanging the ventral process of the postorbital. This feature is absent in *Riojasuchus*, some suchians, phytosaurs, and basal ornithodirans but occurs in parallel in proterochampsids (e.g., *Chanaresuchus*; Romer, 1972b) and some suchians (e.g., *Postosuchus*; Chatterjee, 1985).

(D) Ventral margin of posterior lower jaw concave and elevated (Fig. 11A). The posterior end of the lower jaw of *O. longidens* has an unusual ventral margin that is concave, rather than convex, and the posterior end of the lower jaw is truncated abruptly.

(E) Surangular foramen positioned near surangular-angular suture (Fig. 11A). The surangular foramen lies near the ventral margin of the surangular under the jaw articulation. In most archosaurs the foramen lies closer to the dorsal margin of the surangular under a prominent surangular ridge.

The skull reconstruction of *O. longidens* (Fig. 11) differs from that in Walker (1964) as a result of further preparation of the cranial remains. The posterolateral process of the premaxilla overlaps the anteroventral extremity of the nasal, excluding the maxilla from the border of the external naris (BMNH R3143), and the arched central portion of the palate is visible in lateral view through the antorbital fenestra (Fig. 11A; BMNH 2409). A pair of small pits on the premaxillary palate accommodate the tip of the small, procumbent anterior dentary tooth (Fig. 11D). The vomera do not appear to have been coossified and are dislodged slightly from natural articulation in BMNH R2409. The posterior extremities of the vomera are not preserved in any specimen but their form and position may be inferred from articular surfaces on the anterior end of the pterygoids; the vertical, tongue-shaped anterior process of the pterygoid is concave laterally for contact with the vomer and flat medially where it is closely appressed to its opposite (Walker, 1964:fig. 3i, l, m).

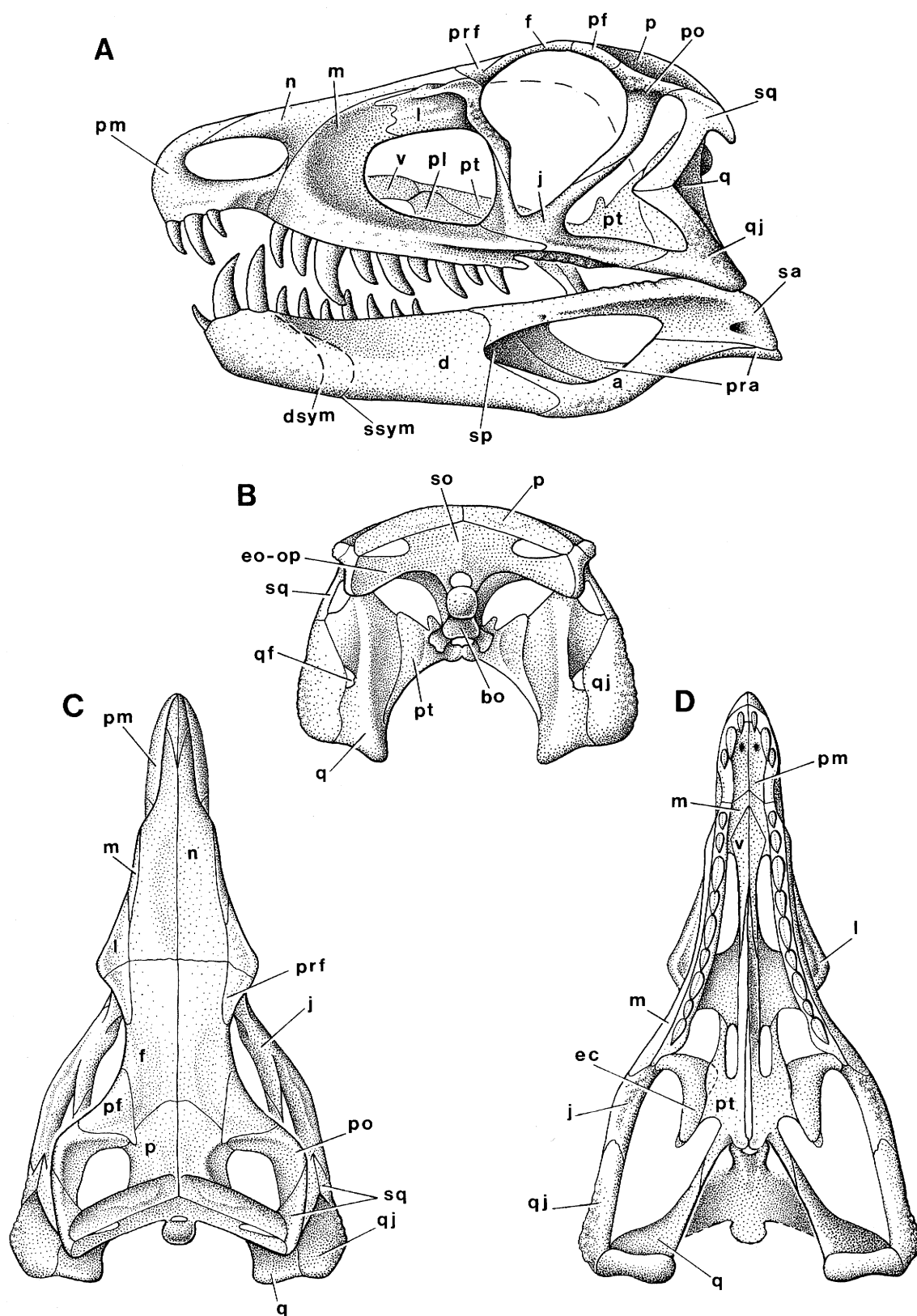


FIGURE 11. *Ornithosuchus longidens* (Huxley, 1877). A, Skull with lower jaws in lateral view; B–D, skull in posterior (B), dorsal (C), and ventral (D) views (modified from Walker, 1964). Abbreviations: a, angular; ar, articular; bo, basioccipital; d, dentary; dsym, dentary symphysis; ec, ectopterygoid; eo, exoccipital; f, frontal; j, jugal; l, lacrimal; m, maxilla; n, nasal; op, opisthotic; p, parietal; pf, postfrontal; pl, palatine; pm, premaxilla; po, postorbital; pra, prearticular; prf, prefrontal; pt, pterygoid; q, quadrate; qf, quadrate foramen; qj, quadratojugal; sa, surangular; so, supraoccipital; sp, splenial; sq, squamosal; ssym, splenial symphysis; v, vomer.

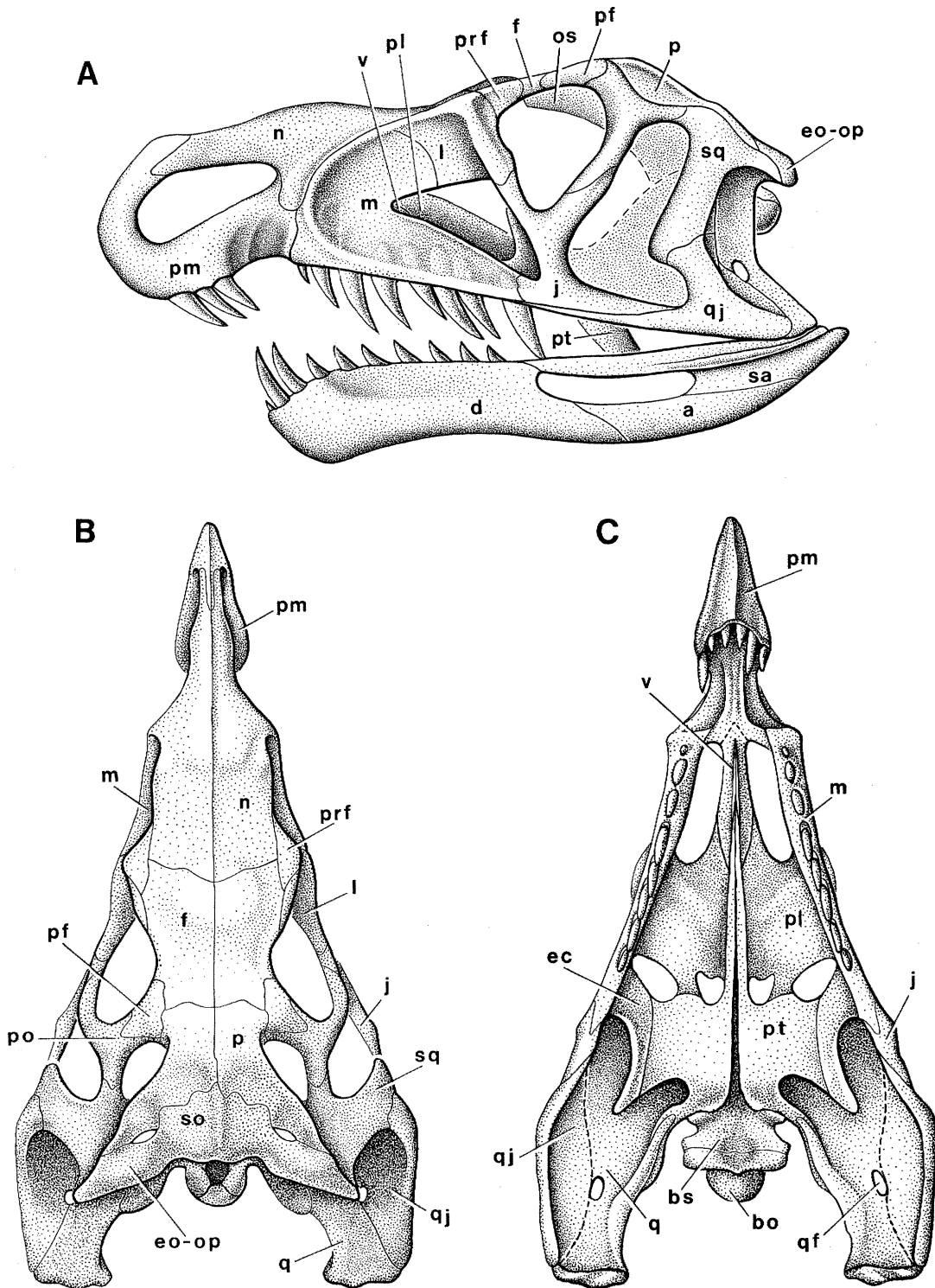


FIGURE 12. *Riojasuchus tenuiceps* Bonaparte, 1969. A, Skull with lower jaws in lateral view; B–C, skull in dorsal (B) and ventral (C) views (modified from Bonaparte, 1972). Abbreviations: bs, basisphenoid; os, orbitosphenoid. Other abbreviations as in Figure 11.

The vomera appear to be somewhat longer than previously shown, based on available material. Slight postmortem transverse compression of the posterior palate in BMNH R2409 has eliminated the narrow

interpterygoid vacuity and overlapped the short posteromedial processes that would otherwise separate the posterior half of the pterygoids (Fig. 11D). A laterosphenoid ossification is partially preserved in BMNH

R3562 contacting the ventral surface of the frontal and would be visible in the orbit in lateral view of the cranium.

### *Riojasuchus tenuiceps* Bonaparte, 1969

**Hypodigm**—*Riojasuchus tenuiceps* is based on skeletal remains discovered in the sandstone cliffs of the Los Colorados Formation in northwestern Argentina (Bonaparte, 1972).

**Recorded Temporal Range**—Norian (Late Triassic).

The following seven autapomorphies distinguish the species.

(F) Large overhanging anterior snout and external naris (Fig. 12A). The anterior snout is expanded relative to the remainder of the cranium such that the fossa around the external naris is subequal in area to the antorbital fossa. The enlarged, overhanging anterior snout and external naris are positioned anterior to the end of the lower jaw, in contrast to the condition in *O. longidens*. *Venaticosuchus rusconii* may also have an expanded overhanging snout, but this region of the type and only specimen is not well preserved (Bonaparte, 1975b:fig. 1B).

(G) Deep antorbital fossa extending to ventral margin of maxilla (Fig. 12A). In other basal archosaurs including the ornithosuchids *O. longidens* and *V. rusconii*, the ventral margin antorbital fossa is separated from the alveolar margin by a narrow external surface. In *R. tenuiceps*, the antorbital fossa reaches the ventral margin of the maxilla.

(H) Narrow jugal bar between the antorbital and laterotemporal fenestrae (Fig. 12A). In nearly all archosaurs, the orbit extends near the ventral margin of the cranium and is bordered ventrally by an anteroposteriorly elongate ramus of the jugal. In *R. tenuiceps*, in contrast, antorbital and laterotemporal fenestrae extend beneath the orbit; the ramus of the jugal beneath the orbit is extremely compressed anteroposteriorly such that its long axis runs dorsoventrally rather than anteroposteriorly.

(I) Occiput sloping 20 degrees above horizontal (Fig. 12A–B). The plane of the occiput is set at a very low angle in *R. tenuiceps*, about 20 degrees above the horizontal. In *O. longidens* and other basal archosaurs, the occiput angles at least 50 degrees above the horizontal.

(J) Atlantal neural arch bases contact in midline. Unlike any other basal archosaur, the bases of the atlantal neural arches in *R. tenuiceps* contact each other in the midline, separating the atlantal intercentrum from the odontoid process of the atlas (Bonaparte, 1972:fig. 5B–C).

(K) Slender radial and ulnar shafts (Fig. 13). The postcranial skeleton is characterized by an unusually delicate forearm, in which the shafts of the radius and ulna are comparable in diameter to the most robust metacarpals. The distal ends of the radius and ulna are separated by the intermedium in natural articulation (PVL 3827). The bones of the forearm in *O. longidens*

(Walker, 1964:fig. 10) and other basal archosaurs are more robust than in *R. tenuiceps*.

(L) Distal tarsal 3 transversely compressed (Fig. 14A). In *R. tenuiceps* distal tarsal 3 is transversely compressed, with height greater than width. The tarsal articulates distally only with metatarsal 3, and the broad lateral surface articulates against distal tarsal 4. A similar condition is not known elsewhere among archosaurs, in which the bone is dorsoventrally flattened (Fig. 14B–C). Distal tarsal 3 may not be preserved in *O. longidens*.

The cranial reconstruction of *R. tenuiceps* has been modified from Bonaparte (1972:figs. 2–4) by addition of the palate and braincase in lateral view of the skull and alteration of some sutures and the shape of the palatal fenestrae. One premaxillary tooth and one anterior dentary tooth are restored. The carpus and manus are poorly known among basal archosaurs but are partially preserved in *R. tenuiceps* (Fig. 13). The relatively large size and shape of the proximal carpals are unusual. The cuboid radiale and tabular ulnare are elongate proximodistally and exhibit a narrowed, shaftlike midsection that bears a striking resemblance to the condition in Crocodylomorpha. Elongation of the proximal carpals may ultimately characterize a more inclusive group than Crocodylomorpha. In *R. tenuiceps* metacarpal 1 is robust with asymmetrical distal condyles. Metacarpal 5, preserved in posterior view of the manus (Fig. 15B), is dorsoventrally compressed with a transversely broad shaft. Previously, the rudimentary terminal phalanx of digit V was misinterpreted as metacarpal 5, and the manus was reconstructed with an extremely reduced digit V (Bonaparte, 1972:figs. 15–16).

### *Parasuchia* Huxley, 1875

**Definition**—*Parasuchia* includes the genera *Angistorhinus*, *Francosuchus*, *Myrstriosuchus*, *Nicrosaurus*, *Parasuchus*, *Rutiodon*, and all descendants of their common ancestor.

**Recorded Temporal Range**—Carnian to Norian (Late Triassic).

Although phytosaurs have long been recognized as a monophyletic group, a thorough list of synapomorphies for the group has never been assembled. Romer (1956) and Gregory (1962) outlined general phytosaurian characters and several of these, with modification, are described below.

(M) Dorsoventrally compressed skull with occiput twice as wide as tall (Fig. 15). In phytosaurs the width of the occiput equals or exceeds twice its height (Case, 1922; Chatterjee, 1978; Gregory, 1962; Westphal, 1976), a proportion that is unique among archosaurs. The skull in the advanced phytosaur *Rutiodon* (= *Mauchaeroprotopus*, Colbert, 1947) appears to have secondarily gained somewhat taller skull proportions.

(N) Elongate premaxillary rostrum (Fig. 15). Unlike the elongate crocodilian snout, which is composed principally of the maxilla and nasal and has a subter-

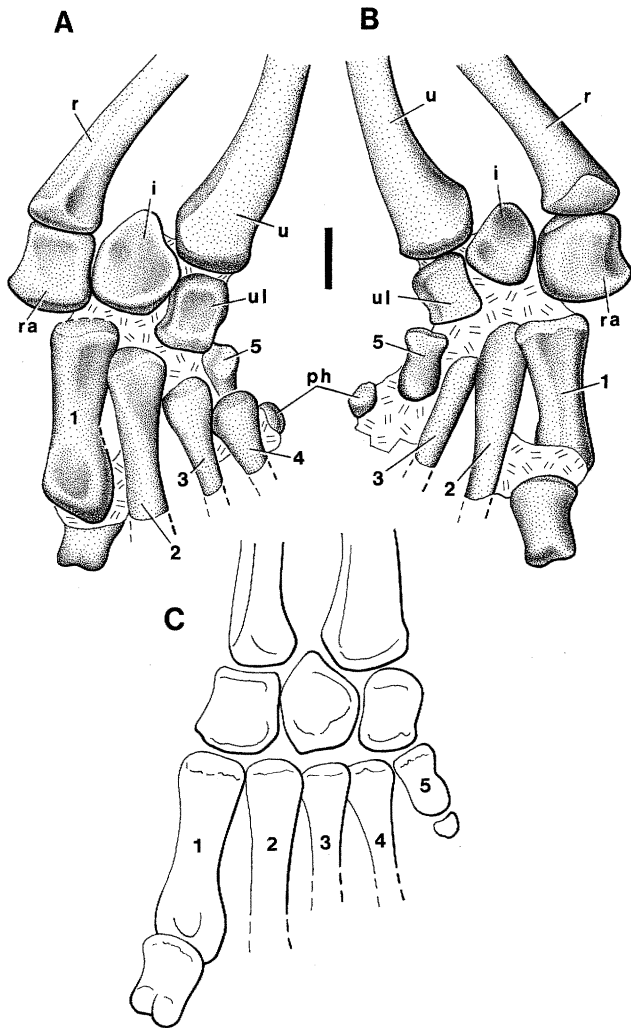


FIGURE 13. *Riojasuchus tenuiceps* Bonaparte, 1969. Left carpus and manus (PVL 3827): **A**, anterior view; **B**, posterior view; **C**, reconstruction of preserved portion of carpus and manus in anterior view. Scale bar equals 1 cm. Abbreviations: 1-5, first through fifth metacarpals; i, intermedium; ph, terminal phalanx, digit V; r, radius; ra, radiale; u, ulna; ul, ulnare.

minimal external naris, the phytosaurian rostrum is constructed nearly entirely of the premaxilla and extends far anterior to the external naris. Prenarial length equals or exceeds postnarial length, a condition unique among archosaurs.

(O) Piscivorous snout (Fig. 15). Modifications in the snout for piscivory include the slender dorsoventral and transverse proportions of the snout end, the slender lower jaw with parallel dorsal and ventral margins, less densely spaced, procumbent (anteriorly and laterally) premaxillary teeth, and a downturned tip of the rostrum. This identical suite of characters has reappeared many times (e.g., teleosts, crocodilians, pterosaurs) and is always associated with piscivory in extant forms. Therefore, these modifications are considered correlated.

(P) Dorsal orientation of external naris and orbit (Fig. 15A, C). The external naris and orbit are directed more dorsally than in other basal archosaurs. Proterochampsids, an archosaurian outgroup, also exhibit low, elongate skull proportions and also are presumed to be aquatic piscivores.

(Q) Subtriangular quadratojugal (Fig. 15A). Among archosaurs plesiomorphically, the quadratojugal is L-shaped and forms the posteroventral corner of the laterotemporal fenestra. In phytosaurs the quadratojugal is subtriangular. Despite the large size of the laterotemporal fenestra, the quadratojugal forms very little of its border. In some specimens of *Rutiodon* (Colbert, 1947), the quadratojugal appears to form proportionately more of the posterior border of the laterotemporal fenestra than in other phytosaurs, but it remains distinctly subtriangular.

(R) Nasal anteriorly extended (Fig. 15C). The nasal among phytosaurs forms all of the lateral margin of the external naris and extends anterior to this opening (Camp, 1930; Westphal, 1976; Chatterjee, 1978). In other archosaurs, the ventrolateral process of the nasal usually terminates at the posterior end of the external naris.

(S) Paramedian "septomaxilla" (Fig. 15C). The presence and form of the septomaxilla in phytosaurs are interpreted in this analysis as apomorphic. Usually the presence of the element is considered plesiomorphic within Archosauria with parallel losses accounting for the absence of the element in archosaurian subgroups (Gauthier, 1986; Benton and Clark, 1988), but here the homology of the element is questioned. In primitive diapsids such as *Petrolacosaurus* (Reisz, 1981), the septomaxilla is ossified as a small thin plate. As in extant squamates, the septomaxilla is positioned on the floor of the nasal passage in the adult, contacting the premaxilla and maxilla, and during development it replaces the roof of the cartilaginous nasal capsule over Jacobson's organ (Jollie, 1960). The shape of the septomaxilla varies in squamates, but the element never achieves broad external exposure as in some basal synapsids. In phytosaurs, in contrast, the element identified as a septomaxilla in several taxa is a deep bone, sutured to its opposite in the midline with broad dorsal exposure (Camp, 1930:fig. 22). It contributes to the roof, rather than the floor, of the nasal passage and forms most, or all, of the internarial septum. There is no contact with the maxilla. Instead, it broadly underlaps the nasal posteriorly and inserts into the premaxilla anteriorly. Given its unusual form and position and the fact that an ossified septomaxilla has not been recorded in any other archosaur or in several successive archosaurian outgroups, the bone in question is regarded here as a parasuchian synapomorphy.

(T-V) Premaxillary-palatine contact; secondary palatal shelves; small postpalatine opening (Fig. 15D). The deeply arched phytosaur palate is unusual among archosaurs in several regards. First, the palatine forms the entire lateral margin of the relatively small internal naris and extends anterior to this opening to contact

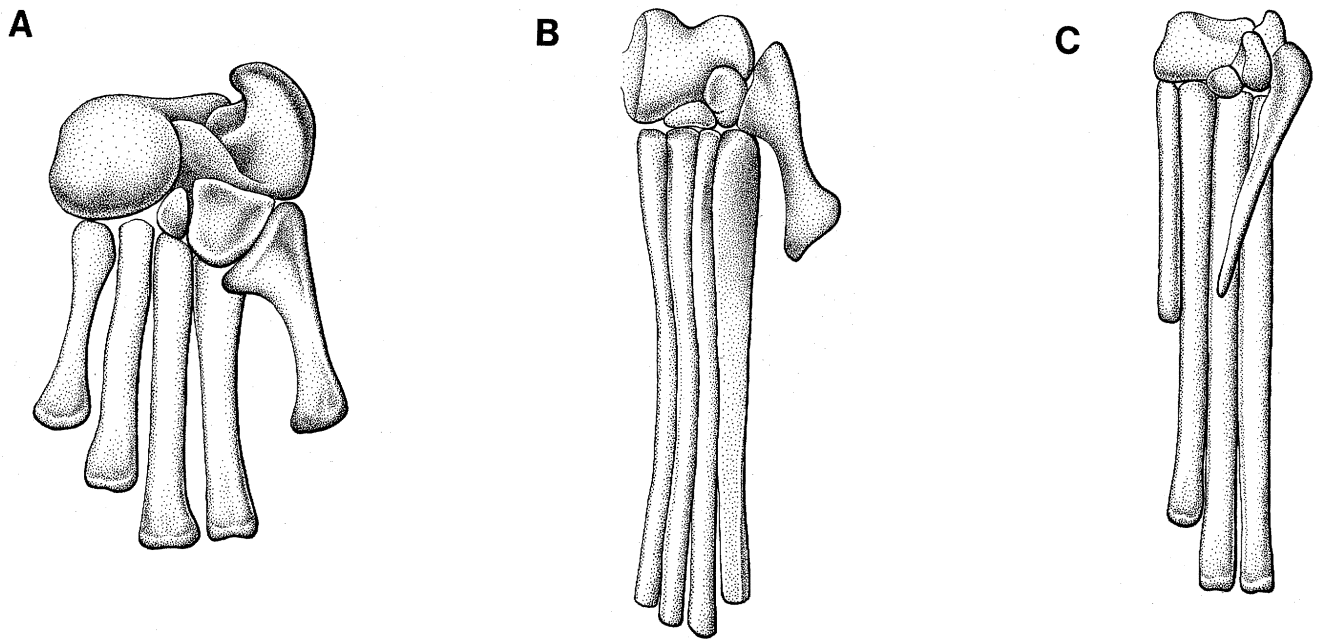


FIGURE 14. Restoration of the tarsus (distal view) and metatarsus (ventral view) in **A**, *Riojasuchus tenuiceps*, **B**, a Middle Jurassic pterosaur from Mexico (Fastovsky et al., 1987), and **C**, *Lagosuchus talampayensis*.

the premaxilla (Camp, 1930; Chatterjee, 1978), a configuration that also occurs among pterosaurs (Wellnhofer, 1978, 1985). The maxilla thus is effectively excluded from the margin of the internal naris. Second, a crest of bone extends along the length of the palatine and presumably formed the bony lateral margin of a fleshy secondary palate. Third, the postpalatine fenestra is reduced to a narrow slit or foramen in phytosaurs, although this may be correlated with the development of a long secondary palate; the postpalatine opening in other basal archosaurs tends to be as large as, or larger than, the internal naris.

(W–X) Crescentic coracoid; enlarged interclavicle. The platelike phytosaur coracoid is crescentic in lateral view because the anterior margin is deeply notched. Presumably this embayment is confluent with the coracoid foramen, because a separate canal for the latter is not present. The interclavicle is large, both in length and width. It equals the scapulocoracoid in length and exceeds the length of all long bones except the femur (Chatterjee, 1978). The maximum width of the interclavicle is comparable to the maximum width of the scapular blade.

#### *Scleromochlus taylori* Woodward, 1907

**Hypodigm**—*Scleromochlus taylori* is a small-bodied gracile archosaur known from a series of natural molds discovered in sandstone quarries (Lossiemouth Sandstone Formation) near Elgin, Scotland (Figs. 16, 17, 18B; Woodward, 1907; Huene, 1914).

**Recorded Temporal Range**—?Carnian (Late Triassic; Benton and Walker, 1985; Olsen and Sues, 1986).

*S. taylori* has long been viewed as an ancestor or

close relative of pterosaurs (Huene, 1914; Gauthier, 1984, 1986; Padian, 1984). At least two autapomorphies in the available skeletal impressions, however, bar it from direct ancestry or designation as a “metataxon” (Gauthier, 1984:117).

(Y) Low subtriangular skull twice as broad across the orbits as deep (Fig. 16). Although the available impressions of the skull in *S. taylori* are flattened post-mortem, the low proportions of the skull are shown by the relatively short quadrate (BMNH R3556), the broad proportions of the skull roof, and the uniformly broad separation of the mandibular rami in many specimens (BMNH R3146, R3556, R3557). The skull is approximately twice as broad across the orbits as deep. Other archosaurs with similar cranial proportions (proterochampsids, phytosaurs) are piscivorous with an elongate snout and long mandibular symphysis. The narial portion of the skull in *S. taylori*, in contrast, is short and tapered, and the mandibular symphysis is restricted to the anteriormost tips of the mandibular rami. In dorsal view, the skull is broad and subtriangular, unlike the deeper skull in Pterosauria.

(Z) Maxilla with raised anterior margin of antorbital fossa (Fig. 16B). The anterior margin of the antorbital fossa is thickened into a low ridge, which diminishes toward the dorsal margin of the fossa (BMNH R3146, R3556). A similar cranial ornamentation is not known elsewhere among basal archosaurs.

#### Pterosauria Owen, 1842

**Definition**—Pterosauria includes the genera *Anurognathus*, *Campylognathoides*, *Dimorphodon*, *Dorygnathus*, *Eudimorphodon*, *Peteinosaurus*, *Preondactylus*,

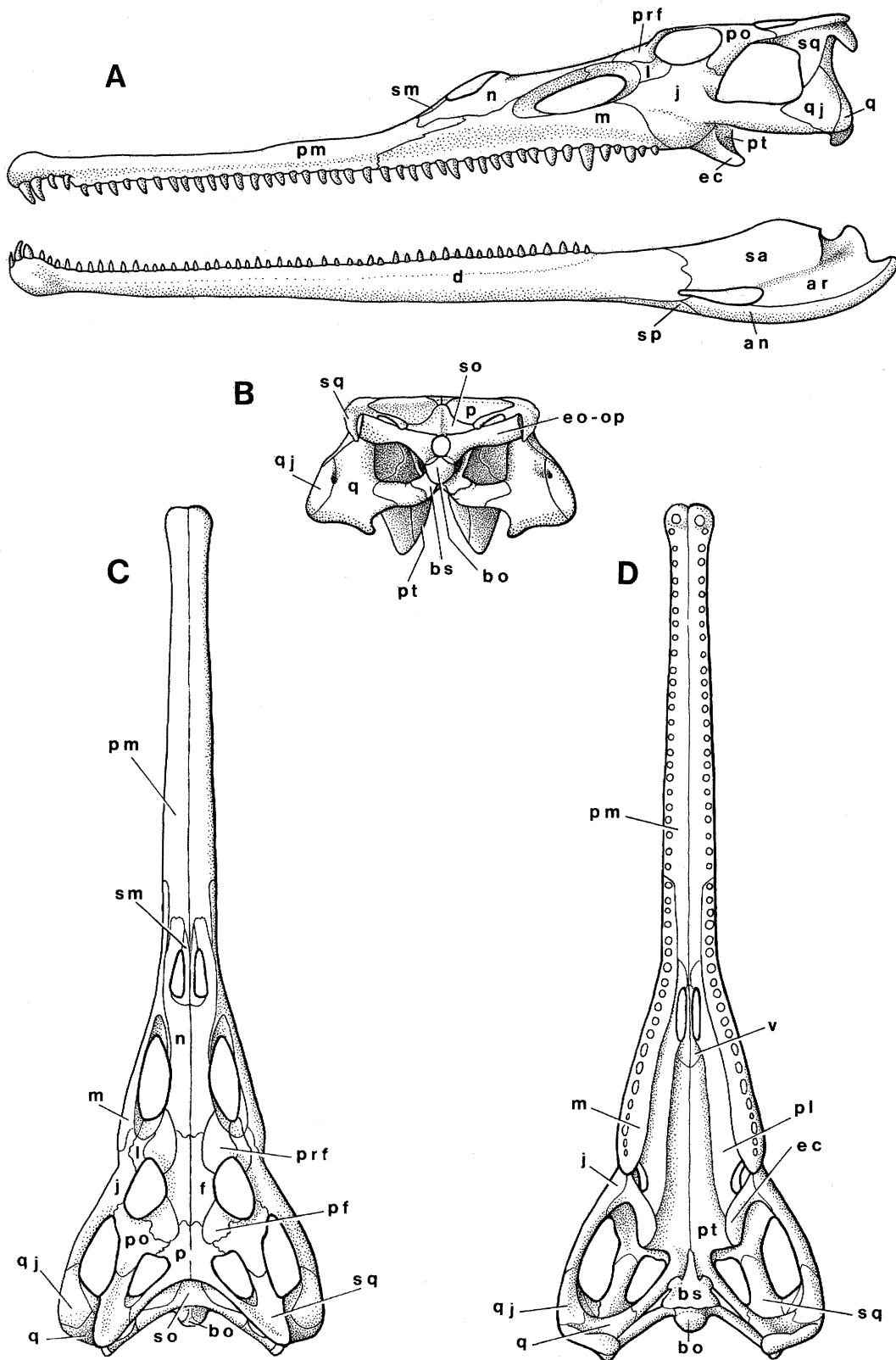


FIGURE 15. *Parasuchus hislopi* Lydekker, 1885. A, Skull with lower jaws in lateral view; B–D, skull in posterior (B), dorsal (C), and ventral (D) views (after Chatterjee, 1978). Abbreviations: sm, “septomaxilla.” Other abbreviations as in Figures 11 and 12.

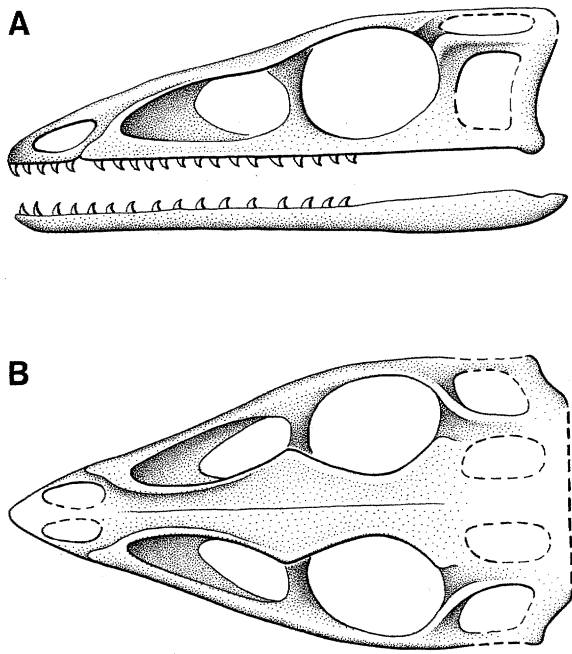


FIGURE 16. *Scleromochlus taylori* Woodward, 1907. A, Reconstruction of skull and lower jaws in lateral view; B, reconstruction of skull in dorsal view (based on BMNH R3146, R3556, R3557).

*Rhamphorhynchus*, *Scaphognathus*, *Pterodactyloidea*, and all descendants of their common ancestor.

**Recorded Temporal Range**—Carnian (Late Triassic) to Maastrichtian (Late Cretaceous).

Pterosaurs were among the first archosaurs to be described in detail, and the monophyly of these highly modified, volant archosaurs is uncontroversial. Numerous synapomorphies from all parts of the cranial and postcranial skeleton indicate the common ancestry of all currently known pterosaurs. Romer (1956) provided the most complete diagnosis of Pterosauria currently available, and most of his characters are also present in the basal pterosaurs described recently from the Upper Triassic of Italy (Wild, 1978, 1983). A few of the pterosaurian synapomorphies listed below have been modified beyond recognition in the advanced pterosaur clade *Pterodactyloidea*. Their status as pterosaurian synapomorphies presumes that rhamphorhynchoid pterosaurs constitute a paraphyletic group with some taxa more closely related to *Pterodactyloidea* than others. Rhamphorhynchoid paraphyly, however, has yet to be established by cladistic analysis.

Pterosaurs are volant archosaurs characterized by approximately 40 skeletal synapomorphies (not lettered individually for reasons of space, but discussed below). Cranial synapomorphies include a proportionately large skull (at least half of presacral vertebral column length), piscivorous snout, external naris displaced posterior to the premaxillary tooth row, elon-

gate premaxillary posterodorsal process that extends posterior to the external naris and contacts the frontal, maxilla that forms approximately one-third of the border of the external naris, maxilla that lacks an antorbital fossa, absence of quadratojugal-squamosal contact, absence of an otic notch, internal naris displaced posteriorly relative to the palatal bones, premaxilla-palatine contact that excludes the maxilla from the border of the internal naris, and absence of an external mandibular fenestra (Fig. 19).

Postcranial synapomorphies directly related to flight function include the extreme hollowing and pneumatization of the skeleton, strut-shaped coracoid with coracosternal joint, glenoid socket facing laterally, broadly arched median sternal plate with hatchet-shaped ventral spine toward anterior end, elongate forelimb, elongate forearm and metacarpus, pteroid bone, and modifications of the fourth digit associated with wing support (Fig. 18A).

Other postcranial synapomorphies not necessarily associated with flight function include procoelous cervicals, elongate posterior cervicals (sixth through ninth cervicals; relative to mid dorsal length), addition of two sacral vertebrae (four sacrals), elongate middle and

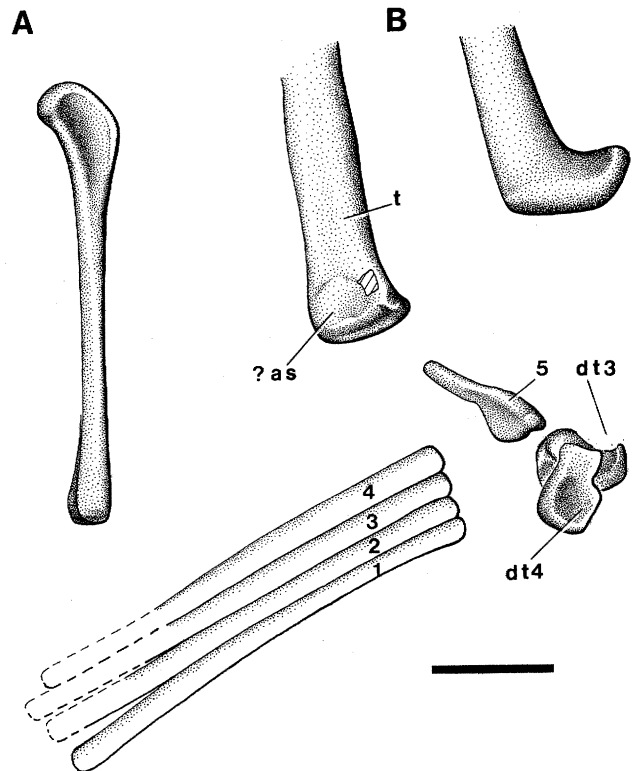


FIGURE 17. *Scleromochlus taylori* Woodward, 1907. A, Left humerus in medial view (BMNH R4823); B, partially articulated right hind limb (BMNH R3557) with proximal femur in anterior view, distal tibia in anterior view, distal tarsals in oblique proximal view, and metatarsus in anterior view. Scale bar equals 5 mm. Abbreviations: 1–5, first through fifth metatarsals; as, astragalus; dt, distal tarsal; t, tibia.

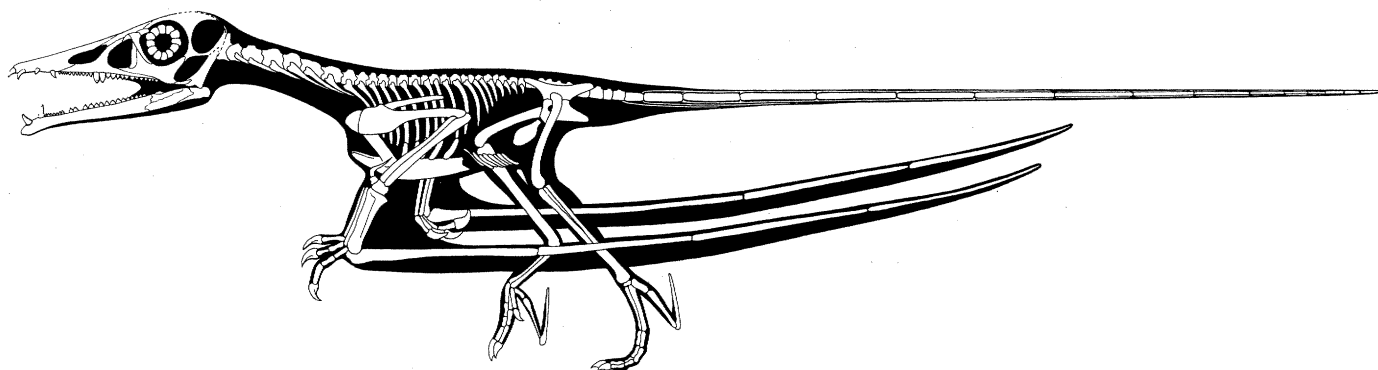
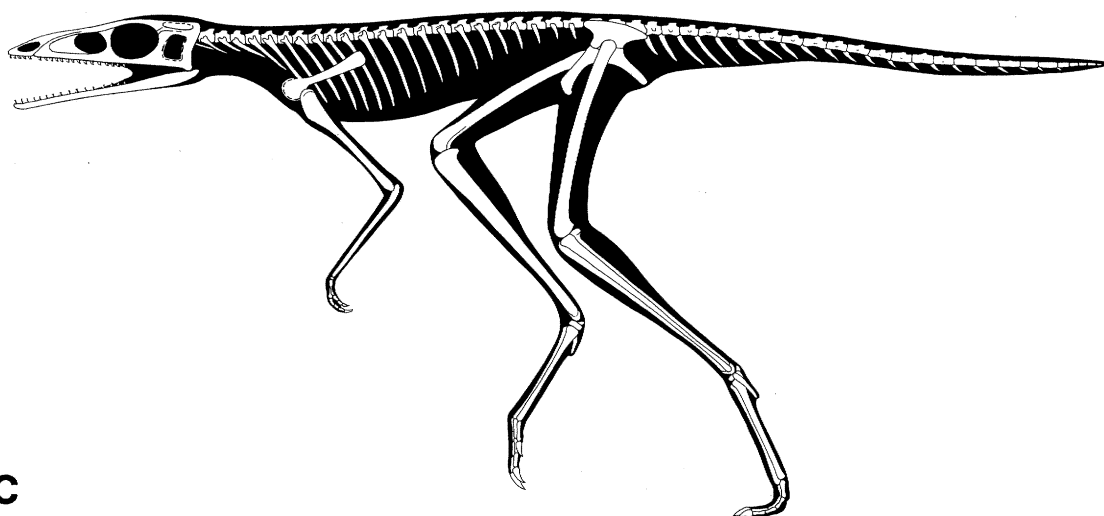
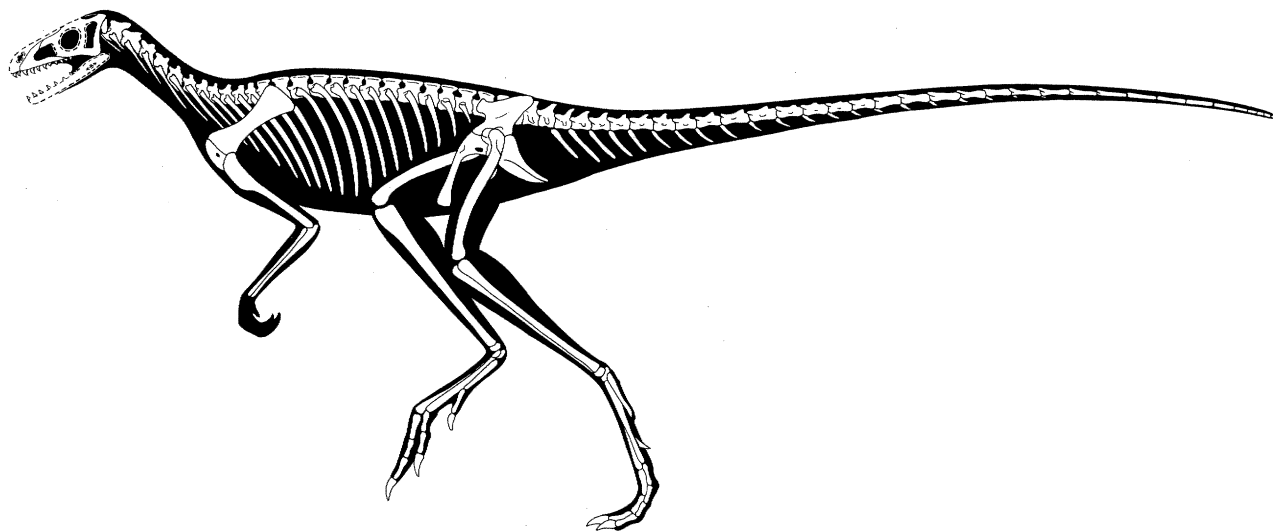
**A****B****C**

FIGURE 18. Skeletal reconstructions of basal ornithodirans. **A**, *Eudimorphodon ranzii* (based on MCSNB 2888 and exemplar Milano; Wild, 1978). **B**, *Scleromochlus taylori* (based on BMNH R3556, R3557). **C**, *Lagosuchus talampayensis* (based on PVL 3870, 3871).

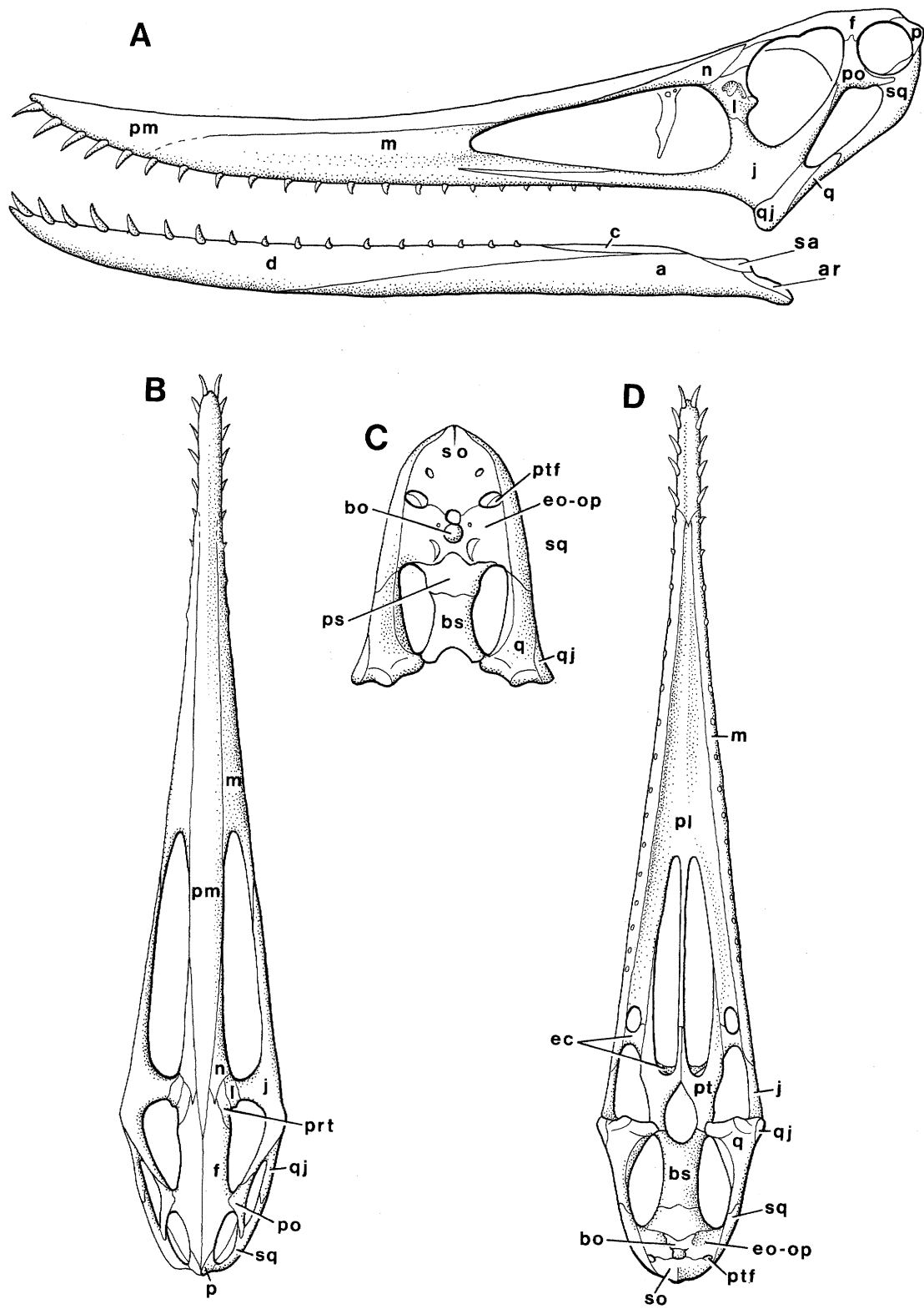


FIGURE 19. *Araripesaurus santanae* Wellnhofer, 1985. A, Skull with lower jaws in lateral view; B–C, skull in dorsal (B) and ventral (C) views (redrawn from Wellnhofer, 1985). Abbreviations: c, coronoid; ptf, posttemporal fenestra. Other abbreviations as in Figures 11 and 12.

distal caudal centra that are more than five times longer than high, and middle and distal caudal zygapophyses and haemal arches extended as narrow intertwining rods. Synapomorphies in the pectoral girdle and forelimb include the absence of the coracoid foramen, humerus with saddle-shaped proximal articular surface, bowed humeral shaft, anteroposteriorly broad deltopectoral crest with concave dorsal margin, only two proximal carpals (often fused) with cup-shaped proximal articular surfaces for the radius and ulna, metacarpal 1 subequal in length to metacarpals 2 and 3, elongate penultimate manal and pedal phalanges, and absence of manal digit V. The pelvic girdle and hindlimb are characterized by a slender preacetabular process equalling or exceeding the length of the postacetabular process, pubis and ischium fused along adjacent margins, paired prepubic element with median symphysis, femoral articular head hemispherical and offset by constriction of the shaft distal to the head, splintlike dorsal fibula coossified with tibia, tibia and proximal tarsals usually coossified as a tibiotarsus, elongate metatarsal 1 only slightly shorter than metatarsals 2–4, and elongate phalanges on pedal digit V that exceed the length of metacarpal 5 (Fig. 18A).

As seen in the above character lists, modifications directly related to flight function comprise only a small proportion of all skeletal synapomorphies. Dense lamellar bone is kept to a minimum to reduce weight, and long bones are hollow cylinders with wall thickness only a small fraction of cross-sectional diameter. Many skeletal elements are pierced by pneumatic foramina, presumably for passage of respiratory diverticulae (Seeley, 1870). Besides lightweight construction, the pectoral girdle and forelimb are modified as the principal skeletal support for the wing. As in birds more advanced than *Archaeopteryx*, the coracoid in pterosaurs forms a rigid strut to maintain the distance between the glenoid and sternum. As in the avian shoulder girdle, the long axes of coracoid and scapula intersect at approximately a right angle. The glenoid faces laterally, rather than posteroventrally, allowing the humerus greater freedom of rotation and posterodorsal-anteroventral excursion during the flight stroke (Padian, 1983b). A broad, gently arched sternal plate with ventral keel provided attachment for flight musculature.

The pterosaur forelimb is proportionately elongate when compared to the forelimbs in other archosaurian subgroups. The lengths of the humerus and forearm, for example, equal or exceed measures of respective hind-limb elements, whereas in other archosaurs hind-limb lengths always exceed forelimb lengths, plesiomorphically. Likewise, in pterosaurs, metacarpal and manal lengths (excluding wing phalanges) are subequal to metatarsal and pedal lengths, respectively, whereas in other basal archosaurs pedal lengths are always greater. The carpus and manus are modified to provide nearly all of the bony support for the wing membrane. The slender rod-shaped pteroid bone, which is apparently a modified carpal, is unique to pterosaurs. Ar-

ticulating proximally on the anterior margin of the carpus, the pteroid is directed medially along the anterior margin and, presumably, controlled the precise angulation of the anterior margin of the wing base. The fourth digit in the manus, the so-called flight finger, is greatly lengthened, with metacarpal 4 and digit IV exceeding the length of the other metacarpals and digits, respectively. In other archosaurs, metacarpal 3 and digit III are longer. In pterosaurs, metacarpal 4 is unique with regard to its exceedingly robust proportions, dorsoventrally flattened proximal shaft, and hemicylindrical and asymmetrical distal condyles. The phalanges of digit IV are also unique in their extreme lengths, simplified interphalangeal articulations, and absence of a horn-covered terminal ungual (Fig. 18A).

A large number of pterosaurian features do not bear any obvious relation to flight function. In most pterosaurs, the snout is designed for piscivory, which appears to constitute the ancestral pterosaur condition. The premaxilla tapers to a slender snout tip, the premaxillary teeth are spaced and anteriorly and laterally procumbent, and the lower jaw is slender and parallel-sided, the same suite of characters that occur in other piscivorous tetrapods. The external naris in pterosaurs is retracted, in contrast to the condition in other basal archosaurs, plesiomorphically. Retraction of the external naris in pterosaurs is shown by the relative position of the premaxillary tooth row, which is located anterior to the external naris (Fig. 19A, B). The extremely short-snouted pterosaur, *Anurognathus*, appears to be the only exception. Three additional aspects of the snout are apomorphic for Pterosauria. By comparison to other archosaurs, the posterodorsal process of the premaxilla is hypertrophied, comprising most of the internarial septum and extending posteriorly beyond the external naris to contact the frontal. The maxilla in pterosaurs forms at least one third of the margin of the external naris, in contrast to other archosaurs, in which the maxilla either is excluded entirely by premaxillary-nasal contact or makes a very short contribution. Although a shallow antorbital fossa may occur in at least some pterosaurs on the lacrimal and jugal (Witmer, 1987), the fossa is absent on the maxilla unlike other basal archosaurs.

The primitive archosaurian quadratojugal is L-shaped, with perpendicular anterior and dorsal rami that form the posteroventral corner of the laterotemporal fenestra. The dorsal ramus extends along the anterior margin of the quadrate shaft, suturing with the anteroventral process of the squamosal, as preserved in a wide variety of primitive archosaurs. In pterosaurs, in contrast, the dorsal ramus of the quadratojugal is reduced and does not contact the squamosal. The anterior ramus of the pterosaur quadratojugal appears to be the stronger of the two, extending to the anteroventral corner of the laterotemporal fenestra. Although the primitive pterosaur *Eudimorphodon* has been reconstructed with a short, slender quadratojugal (Wild, 1978:fig. 1b), the preserved position of the element suggests that it did reach the antero-

ventral corner of the laterotemporal fenestra (Wild, 1978:fig. 1a; Wellnhofer, 1978:fig. 2).

The occiput, palate, and lower jaw are poorly preserved among pterosaurs owing to the very delicate construction of the skull. Available information suggests that there are several apomorphic features in both regions. In contrast to other archosaurs, pterosaurs apparently do not have an otic notch formed between the quadrate shaft and the lateral ends of the squamosal and paroccipital processes, as seen in lateral view of the skull in several species (Wellnhofer, 1978). The configuration of the palate in primitive pterosaurs such as *Campylognathoides* (Wellnhofer, 1974) and pterodactyloids (Wellnhofer, 1978) suggests that the internal naris has shifted posteriorly. The relatively posterior position of the internal naris is suggested by its relation to the palatine, which excludes the maxilla from its lateral margin (as in phytosaurs) and extends anteriorly to contact its opposite in the midline anterior to the internal nares. The posteriorly positioned internal naris is in close proximity to the postpalatine fenestra, with only a narrow intervening bar formed by the pterygoid and palatine. The lower jaw apparently lacks an external mandibular fenestra (Fig. 19A; *Eudimorphodon*, Wild, 1978).

#### Dinosauromorpha Benton, 1985

**Definition**—Dinosauromorpha includes *Lagerpeton chanarensis*, *Lagosuchus talampayensis*, *Pseudolagosuchus major*, Dinosauria (inc. Aves), and all descendants of their common ancestor.

**Recorded Temporal Range**—Ladinian (Middle Triassic) to Recent.

The taxon Dinosauromorpha was originally coined by Benton (1985) for the same group of archosaurs that were termed "Ornithosuchia" by Gauthier (1984, 1986). However, no diagnosis for Dinosauromorpha was proposed, and more recently Benton and Clark (1988) have dropped the term in favor of "Ornithosuchia." Dinosauromorpha is here defined to include ornithodirans more closely related to the dinosaur-avian clade than to pterosaurs. Dinosauromorph monophyly counters previous assertions that pterosaurs are more closely related to dinosaurs than is *Lagosuchus* (Gauthier, 1984; Gauthier and Padian, 1985). The character evidence supporting this alternative pterosaur-dinosaur clade (termed "Ornithotarsi" by Gauthier [1984:175–182]) is weak and problematic (Serenó and Novas, 1990). Synapomorphies supporting dinosauromorph monophyly are listed below. A few of these are unknown in the basal dinosauromorph *Lagerpeton*, but the branching sequence within Dinosauria is not discussed (see Sereno and Novas, 1990).

(AA) Cervical column following strong sigmoid curve with dorsal offset of the anterior face of centrum present as far posteriorly as the ninth or tenth presacral (Fig. 20). In all archosaurs and immediate archosaur outgroups, elevation of the anterior cervical column is achieved by dorsal offset of the anterior articular face

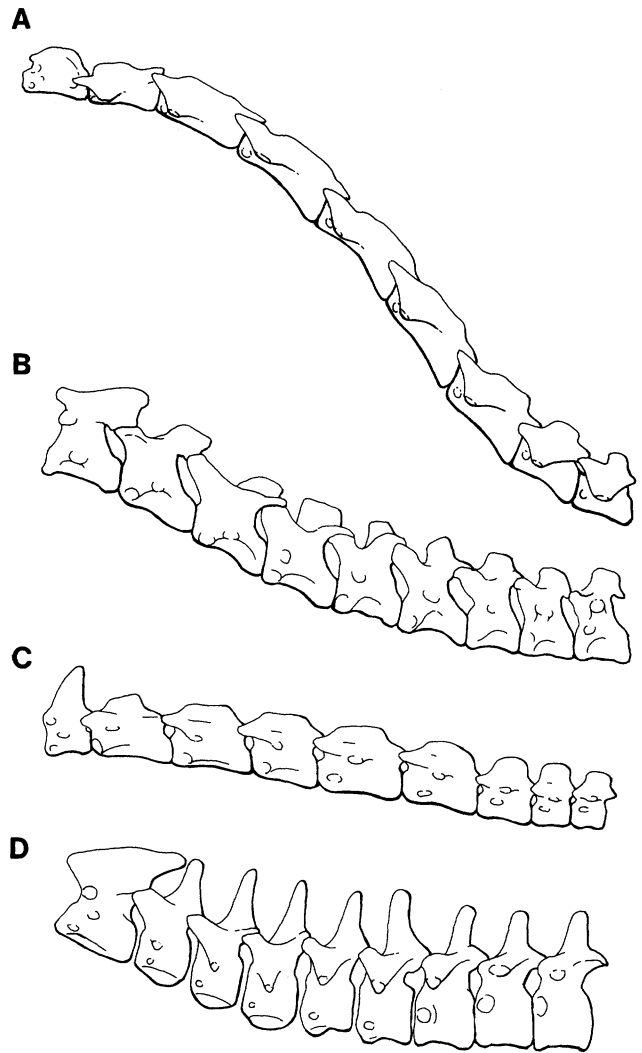


FIGURE 20. Reconstructions of the cervical vertebral column in basal archosaurs. A, *Coelophysis bauri* (after Colbert, 1989). B, *Lagosuchus talampayensis* (based on PVL 3870). C, Basal pterosaur (composite based on *Dimorphodon*, *Eudimorphodon*, and *Rhamphorhynchus*; Padian, 1983a; Wellnhofer, 1978; Wild, 1978). D, *Riojasuchus tenuiceps* (after Bonaparte, 1972).

(relative to the posterior face, held in a vertical plane). Dorsal offset of the anterior articular face appears to be limited to the axis and the succeeding four cervical centra in proterochampsids, ornithosuchids (Bonaparte, 1972), phytosaurs (Camp, 1930), *Gracilisuchus*, rauisuchians, poposaurids, and Crocodylomorpha. In the immediate archosaur outgroup Proterochampsidae, for example, the second through the fourth cervicals are weakly parallelogram-shaped in lateral view. A well-preserved articulated cervical series in *Chanaresuchus* (MCZ 4037) shows noticeable dorsal offset of the anterior articular face in the second through the fifth cervical centra (fourth centrum lacking) with slight asymmetry maintained in the sixth cervical. The seventh cervical is symmetrical in lateral view. In another

proterochampsid, *Gualosuchus* (PVL 4576), dorsal offset of the anterior centrum face is weak in the anterior cervicals and absent by the fifth cervical vertebra. Significant dorsal offset of the anterior centrum face thus does not appear to occur beyond the sixth cervical in proterochampsids. Similarly, in the phytosaur *Rutiodon*, elevation of the anterior cervical column is limited to the second through the fifth cervicals (Camp, 1930). The sixth centrum appears symmetrical. In the ornithosuchid *Riojasuchus*, dorsal offset of the anterior centrum face occurs in the second through the fourth cervicals, is present but subtle in the fifth cervical, and is absent in the sixth cervical (Fig. 20D; PVL 3827). In a second individual (PVL 3828), the anterior face appears to be slightly offset in the sixth cervical. The seventh cervical in this specimen is broken, and the eighth is symmetrical without elevation of the anterior face. In pterosaurs the cervical centra are strongly procoelous. The intervertebral articular surfaces suggest that the cervical series was very flexible and capable of elevating the skull above the axis of the dorsal column. Individual cervical centra, however, do not show significant elevation of the anterior articular face along the cervical column (Fig. 20C) as preserved in the basal pterosaurs *Eudimorphodon* (Wild, 1983) and *Campylognathoides* (Wellnhofer, 1974) and in the pterodactyloids *Dsungaripterus* (Young, 1964b) and *Pteranodon* (Howse, 1986).

In Dinosauromorpha, in contrast, elevation along the cervical series is more marked and begins posteriorly at the ninth or tenth presacral vertebra (Fig. 20A, B). In *Lagosuchus* (PVL 3870, 3872, 4672), the most basal dinosauriform in which the neck is preserved, the centra are parallelogram-shaped, with subparallel anterior and posterior articular faces, from the axis to the sixth or seventh presacral. The eighth, ninth, and apparently the tenth presacral also appear to contribute to the elevation of the cervical column, but in these vertebrae the centra are weakly trapezoidal, rather than parallelogram-shaped. The dorsally convergent articular faces deflect the axis of the vertebral column from a horizontal to an anterodorsal direction at the base of the neck. Then the parallelogram-shaped centra of the middle and anterior cervicals extend the neck along this anterodorsal axis, with the articular surfaces canted at approximately 10 or 15 degrees from the vertical.

In herrerasaurids, anterior and middle cervical centra show elevation of the anterior face but posterior cervicals are poorly preserved. Saurischians consistently exhibit the dinosauromorph apomorphy, showing marked elevation in the anterior and mid-cervicals with parallelogram-shaped or trapezoidal centra back to the eighth or ninth cervical vertebra (*Allosaurus*, Madsen, 1976; *Deinonychus*, Ostrom, 1969; *Dilophosaurus* UCMP 77270; *Gallimimus*, Osmólska et al., 1972; *Massospondylus*, Cooper, 1981). Some ornithischians show strong elevation of the neck which appears to extend back to the eighth, or possibly the ninth, cervical (e.g., *Heterodontosaurus*, Santa Luca, 1984), but most ornithischians resemble other basal archos-

saurs, with elevation of the proximal centrum face restricted to the anterior five or six cervicals (e.g., *Hypsilophodon*, Galton, 1974; *Psittacosaurus*, Sereno, 1987).

Thus there is significant variation and important missing information within Dinosauromorpha with regard to neck curvature. In addition, centrum shape and the relative positions of anterior and posterior articular surfaces are difficult to measure with precision, and centrum edges are often rounded. Furthermore, disparity in dorsoventral diameter between anterior and posterior articular surfaces and postmortem distortion can easily influence interpretation of the orientation and relative position of the articular surfaces. This synapomorphy is supported here with these serious caveats. Previously, Bonaparte (1975a) and Gauthier (1984, 1986) drew attention to this aspect of the neck, the former citing "zonation" in the presacral column and the latter using an "S-shaped" birdlike neck as an ornithodiran (rather than dinosauromorph) synapomorphy. Gauthier (1986:43) also listed "centra steeply inclined in at least the first four postatlantal cervicals" as a synapomorphy for "Ornithosuchia" (including *Euparkeria*).

(BB) Forelimb 50 percent or less hind-limb length (Fig. 18C). In most basal archosaurs, the forelimb ranges from approximately 60 to 75 percent of hind-limb length, with limb length estimated by summation of pro-, epi-, and third metapodial lengths (e.g., *Chanaresuchus*, PVL 4375; *Aetosauroides*, PVL 2073). Although forelimb and hind-limb long bones from a single individual are known in only a few basal archosaurs, the percentage interlimb disparity given above also obtains in most comparisons between corresponding limb segments.

In Dinosauromorpha, in contrast, forelimb length is less than half hind-limb length in most basal forms. In *Lagosuchus*, the length of the proximal segments of the forelimb is 55 percent that of the hind-limb (humerus + radius/femur + tibia; PVL 3870). The length of the radius, however, is only 44 percent of that of the tibia, and the long metatarsus and pedal phalanges would probably result in a forelimb length about 45 percent that of the hind-limb if the manus were known. The length of the forelimb is approximately 50 percent of hind-limb length in the basal dinosaur *Herrerasaurus*, about 35 percent in the basal ornithischian *Lesothosaurus* (Thulborn, 1972), about 35 to 45 percent in the basal theropods *Coelophysis* and *Syntarsus* (Cooper, 1981; Colbert, 1989), and about 50 to 58 percent in the basal sauropodomorphs *Massospondylus* and *Plateosaurus* (Cooper, 1981:table 9). *Scleromochlus* also has a proportionately short forelimb and may eventually be allied with Dinosauromorpha (see below).

(CC) Astragalus with acute anteromedial corner (Fig. 9C–D). In Archosauria plesiomorphically, the distal articular surface of the astragalus is subrectangular in distal view. In Dinosauromorpha, in contrast, the anteromedial corner of the astragalus is prominent with anterior and lateral margins that form an acute angle

(less than 90 degrees) in distal view (*Lagerpeton*, PVL 4619; *Pseudolagosuchus*, *Herrerasaurus*, *Dilophosaurus*, *Liliensternus*, *Riojasaurus*, Novas, 1989). This synapomorphy was first recognized by Novas (1989: 685), who used it to unite *Lagosuchus* and Dinosauria. It also occurs in *Lagerpeton*.

(DD) Distal articular surface of calcaneum with transverse width 35 percent or less that of astragalus (Fig. 9D). In most archosaurs and archosaurian outgroups, the maximum transverse width of the distal articular surface of the calcaneum is 50 percent or more that of the astragalus. The relatively large contribution of the calcaneum to the distal articular surface of the proximal tarsus obtains regardless of structural variation in the ankle joint. In primitive archosauromorphs like *Proterosuchus*, the calcaneal distal articular surface is approximately 60 percent that of the astragalus (Fig. 3H; MCZ 4301, cast of NM C3016). In *Euparkeria* the calcaneal distal articular surface is approximately 50 percent that of the astragalus (Fig. 4H). In *Suchia*, *Parasuchia*, and *Ornithosuchidae*, a relatively large distal articular surface obtains even though the calcaneum has become functionally united with the distal tarsus and pes (Figs. 6H, 7H). In these archosaurs, it is sometimes difficult to measure only that part of the astragalar distal surface that contacts the distal tarsus and metatarsus (i.e., the medial distal tarsal and proximal end of metatarsal 1) because of the smooth junction with the adjacent rotational surface for the calcaneum. Nevertheless, overestimating the distal articular surface for the distal tarsus and first metatarsal would only reduce the relative size of the calcaneal distal surface and thus favor an apomorphic interpretation. But the calcaneal surface still measures over 50 percent of the distal articular surface in these forms (50–60 percent in *Neoaeosauroides* (PVL 3525) and *Typothorax* (MCZ 1488); 70–80 percent in *Parasuchus* (ISI R42) and *Rutiodon*; Fig. 6H). In *Riojasuchus* (Fig. 7H) the transverse dimension of the distal articular surface on the calcaneum exceeds that of the astragalus, and in those pterosaurs with separate proximal tarsals, astragalar width is typically only slightly greater than that of the calcaneum (Wellnhofer, 1978). The large distal calcaneal surface in *Suchia*, *Parasuchia*, and *Ornithosuchidae* cannot be explained as a functional necessity of the crurotarsal joint since some advanced members within *Suchia* show the apomorphic condition (35 percent in *Crocodylus acutus*; Fig. 8H).

In Dinosauromorpha, the maximum width of the distal articular surface of the calcaneum never exceeds 35 percent that of the astragalus, as in the basal forms *Lagerpeton*, *Lagosuchus* (Fig. 9D), and *Pseudolagosuchus*. In the latter two forms, the small, oval distal articular surface on the calcaneum must be distinguished from the adjacent nonarticular distal surface on the calcaneal tuber to observe this character. In dinosaurs, the maximum transverse width of the distal articular surface of the calcaneum is approximately 30 percent or less that of the astragalus, as seen in her-

rerasaurids (PVL 2045; Novas, 1989), prosauropods (Huene, 1926; Cooper, 1981), sauropods (Zhang, 1988), and theropods (Huene, 1934; Welles, 1984; Madsen, 1976). The basal ornithischian *Pisanosaurus* has a disc-shaped calcaneum with a very narrow distal articular surface whereas other ornithischians have a calcaneal width 40 to 50 percent that of the astragalus (e.g., *Hypsilophodon*, Galton, 1974; *Psittacosaurus*, Sereno and Chao, 1988). The general ornithischian condition is considered a reversal in light of the narrow calcaneal proportions in all other dinosaurian clades. Relative expansion of the astragalar distal articular surface with corresponding reduction of the calcaneal distal articular surface in dinosauromorphs was recognized previously by Bonaparte (1975a) and Novas (1989). Gauthier (1986) listed this synapomorphy for a more inclusive group including pterosaurs.

(EE) Distal tarsal 4 with articular surface for metatarsal 5 limited to half of its lateral surface. Most basal archosaurs including pterosaurs (Fig. 15B) have a broad facet on distal tarsal 4 for metatarsal 5, which occupies most, or all, of the lateral surface of the tarsal. In Dinosauromorpha, the articular facet for metatarsal 5 is limited to half or less of the lateral surface of distal tarsal 4, with nonarticular surfaces anterior and posterior to the facet (e.g., *Coelophysis*, Padian, 1986).

(FF) Metatarsal 5 with articular surface for distal tarsal 4 oriented parallel to shaft axis; “hooked” proximal end absent (Fig. 15C). In most archosaurs and immediate archosaurian outgroups, metatarsal 5 diverges posterolaterally from the median axis of the metatarsus at an angle of approximately 20 to 40 degrees. This angle of divergence and the “hooked” proximal end of the metatarsal are clearly absent in Dinosauromorpha, and the absence of these features appears to be due to reorientation of the articular facet at the proximal end of metatarsal 5.

The angle of articulation between metatarsal 5 and distal tarsal 4 is relatively constant in basal archosaurs, with a mediolateral inclination of approximately 50 to 60 degrees to the axis of the third metatarsal in *Euparkeria* (Ewer, 1965), *Riojasuchus* (Fig. 15A), pterosaurs (Fig. 15B; Wellnhofer, 1978; Padian, 1983a), and the basal dinosauromorphs *Lagerpeton* and *Lagosuchus* (Fig. 15C). The facet in *Proterosuchus* (Carroll, 1976) and *Saurosuchus* (Sill, 1974) may have a lower angle of inclination, but the natural position of distal tarsal 4 in these specimens is open to interpretation. In most basal archosaurs, the opposing articular surface on metatarsal 5 is set at an angle to the shaft, resulting in net deflection of the shaft from 20 to 40 degrees from the axis of metatarsal 3. A divergent metatarsal 5 with a “hooked” proximal end is preserved in many archosaur taxa, including those that have undergone substantial reduction of digit V. In *Alligator*, for example, the fifth metatarsal has a divergent long axis and a proximal process that gives a “hooked” appearance to the proximal end even though it is very reduced and positioned more on the ventral, than lateral, side of the tarsus (Schaeffer, 1941; Brink-

man, 1980). Metatarsal 5 is also divergent and hooked in *Riojasuchus*, *Gracilisuchus* (PVL 4597), and *Chanaresuchus* despite previous reconstructions that position metatarsal 5 subparallel to the other metatarsals (Bonaparte, 1972:fig. 20; Romer, 1972b:fig. 2f; Romer, 1972c:fig. 9d). The divergence of metatarsal 5 is also maintained in the digitigrade pes in basal pterosaurs despite the modified function of the elongate fifth digit (Figs. 14B, 18A; Wellnhofer, 1978).

In Dinosauromorpha, on the other hand, the axis of the shaft of metatarsal 5 is subparallel to, or deflected slightly behind, the metatarsal bundle (metatarsals 1–4). In *Lagosuchus* (Fig. 15A) and *Lagerpeton*, metatarsal 5 is preserved in natural articulation, lodged against a notch on the posterolateral aspect of distal tarsal 4 in close association with the base of metatarsal 4 (Romer, 1971; Bonaparte, 1975a). The report of an unusual, reduced metatarsal 5 in a referred specimen of *Lagerpeton* (Arcucci, 1986:fig. 5) is the result of misinterpretation of a small bone fragment glued to the lateral side of metatarsal 4. In the primitive theopod *Coelophysis* (Padian, 1986:fig. 5F), the posterolateral aspect of the lateral distal tarsal is notched as in *Lagosuchus* and *Lagerpeton*, and it must also have accommodated the principal articulation of the fifth metatarsal (contra Padian, 1986:52). A similar but shallower notch is present on distal tarsal 4 in *Deinonychus* (Ostrom, 1969). In prosauropods the paddle-shaped metatarsal 5 articulates on the posteroventral margin of the lateral distal tarsal and its shaft parallels the other metatarsals (Young, 1941). Among ornithischians, the fifth metatarsal is very short and lacks any sign of a medial process. Its articulation against the posteromedial aspect of the lateral distal tarsal is well established (e.g., *Heterodontosaurus*, Santa Luca, 1984; *Psittacosaurus*, Osborn, 1924) and is consistent with the apomorphic dinosauromorph condition.

(GG) Mid-shaft diameters of metatarsals 1 and 5 less than those of metatarsals 2–4 (Fig. 14). Metatarsals 1 and 5 in the primitive archosaur pes are quite robust, with minimum shaft diameters subequal to, or greater than, those of the three central metatarsals, as seen in *Euparkeria* (Ewer, 1965), aetosaurs (Walker, 1961), rauisuchians (Sill, 1974), phytosaurs (Chatterjee, 1978), and pterosaurs (Fig. 14B; Wellnhofer, 1978; Wild, 1978). In *Scleromochlus*, the slender shafts of the elongate metatarsals are approximately equal in cross section and length, except for the short fifth metatarsal which has a stout beveled base (Fig. 17B). There are several exceptions in which one or the other outside metatarsal is reduced in taxa outside Dinosauromorpha. In proterochampsids (Romer, 1972b), the second metatarsal is enlarged and thus achieves a greater shaft diameter than the first. Metatarsal 1, nevertheless, has a shaft diameter subequal to or greater than that of metatarsals 2 and 3, respectively. In *Riojasuchus*, minimum shaft diameter of metatarsal 1 appears to be slightly less than that of the central metatarsals. A more robust metatarsal 1, however, occurs in the closely related taxon *Ornithosuchus* (Walker, 1964). Among

suchians, the first metatarsal is shown as very slender in *Postosuchus* (Chatterjee, 1985) but the pes was not found in articulation. In *Crocodylus*, metatarsal 5 is greatly shortened and spur-shaped, preventing a reliable measurement of shaft diameter. Metatarsal 1, however, remains more robust than adjacent metatarsals (Romer, 1956).

In Dinosauromorpha, in contrast, the outside metatarsals have reduced minimum shaft diameters or are absent altogether. The pes is functionally tridactyl. Metatarsal 1 is usually stronger than metatarsal 5, but its minimum shaft diameter is also less than the central three, as seen in the basal taxa *Lagerpeton* (Romer, 1971), *Lagosuchus* (Fig. 14C), and in Dinosauria plesiomorphically (*Herrerasaurus*, Reig, 1963). In prosauropods, metatarsal 1 is flattened strongly against metatarsal 2 and does not equal the latter in robustness (Cooper, 1981:fig. 72j; Young, 1941). Sauropods, uniquely among dinosaurs, show approximately equally robust shaft diameters across the metatarsus (Zhang, 1988); this condition must be considered a reversal, rather than a symplesiomorphy (contra Cruickshank, 1975), given the condition in sauropod outgroups.

## INGROUP RELATIONSHIPS

Cladistic analysis of 36 characters in seven terminal taxa supports six clades. Archosauria is divided into Crurotarsi and Ornithodira, the former including Parasuchia and an unnamed sister-clade composed of Ornithosuchidae and Suchia and the latter divided into Pterosauria and Dinosauromorpha. The position of *Scleromochlus* is left unresolved within Ornithodira.

Ingroup clades are defined phylogenetically by listing included taxa. The common ancestor and any additional taxa most closely related to those listed are included by definition within the clade (as with definitions of terminal taxa). Synapomorphies are numbered and discussed individually under each clade, with characters, character states, and character state distributions compiled in the Appendix under the heading Ingroup Clades.

### Archosauria Cope, 1869

**Definition**—Archosauria includes two clades, Crurotarsi and Ornithodira, and all descendants of their common ancestor.

**Recorded Temporal Range**—Ladinian (Middle Triassic) to Recent.

(1) Palatal teeth on pterygoid, palatine, and vomer absent (Figs. 11–13, 19). Palatal teeth are present in all archosauriform outgroups (*Proterosuchus*, *Euparkeria*, proterochampsids) except erythrosuchids. In light of other character evidence, palatal teeth must have been lost independently in erythrosuchids and archosaurs (Otschev, 1975). Contrary to recent reports (Gauthier et al., 1988:176), erythrosuchids lack vomerine teeth and archosaurs lack palatal teeth altogether (Ben-

ton and Clark, 1988; minute palatal teeth were recently reported in the prosauropod *Massospondylus* by Attridge et al. (1985) but are problematic).

(2) Calcaneal tuber directed more than 45 degrees posterolaterally (Figs. 6–9). Among archosaurian outgroups (proterochampsids, erythrosuchids, *Euparkeria*, *Proterosuchus*), the axis of the tuber typically angles between 20 and 40 degrees from the transverse axis of the ankle joint. Among archosaurs, in contrast, the tuber is more strongly deflected posteriorly, angling from 45 to 90 degrees from the transverse axis of the ankle joint. Phytosaurs have a lower angle of divergence (45 to 55 degrees) than occurs in other archosaurs (60 degrees or more). It is possible that an angle of divergence of 60 degrees or greater is apomorphic for Archosauria, with reversal to a less acute angle in the sprawling phytosaurs and crocodilians. In either case, posterior deflection of the tuber by at least 45 degrees appears to have occurred in the common archosaurian ancestor.

(3) Calcaneum with contiguous articular surfaces for fibula and distal tarsal 4 (Fig. 21). Among basal archosauriforms such as *Proterosuchus*, the body of the calcaneum is plate-shaped and oriented vertically. A nonarticular anterior surface separates the dorsal articulation with the fibula from the ventral articulation with distal tarsal 4. This broad separation of fibular and distal tarsal articular surfaces also occurs in erythrosuchids (Young, 1964a), *Euparkeria*, and proterochampsids. In archosaurs the articular surfaces on the calcaneum for the fibula and distal tarsal 4 join antero-ventrally along a rounded edge without any intervening nonarticular space.

### Crurotarsi Sereno et Arcucci, 1990

**Definition**—Crurotarsi includes Parasuchia, Ornithosuchidae, *Prestosuchus*, Suchia, and all descendants of their common ancestor.

**Recorded Temporal Range**—Ladinian (Middle Triassic) to Recent.

(4) Proximal humerus strongly arched under inner tuberosity (Fig. 22). The medial margin of the humerus under the inner trochanter is nearly straight, rather than strongly arched, in pterosaurs (Wellnhofer, 1978), dinosauriforms (Bonaparte, 1975a; Reig, 1963; Wild, 1978), and basal archosauriforms (Ewer, 1965; Romer, 1972b; Young, 1964a). In crurotarsal archosaurs, on the other hand, the medial margin of the humerus is strongly arched with a prominent inner tuberosity. The margin under the tuberosity often approaches a horizontal inclination, as seen in anterior or posterior views of the humerus. This arched medial contour of the proximal humerus occurs in both facultative and obligate quadrupeds, including phytosaurs (Colbert, 1947; Chatterjee, 1978), ornithosuchids (Bonaparte, 1975b), aetosaurs (*Typothorax*, AMNH 19337; Bonaparte, 1972; Sawin, 1947; Walker, 1961), and rauisuchians (Chatterjee, 1985). The strongly arched margin, however, is absent in the elongate spheosuchian humerus

(Bonaparte, 1972; Whetstone and Whybrow, 1983) and is somewhat reduced in extant crocodilians.

(5) Anterior trochanter of fibula robust and knob-shaped (Figs. 6–9). The fibular trochanter is developed either as a low vertical crest or as an oval rugosity in dinosauriforms (Bonaparte, 1975a; Colbert, 1970) and basal archosauriforms (Romer, 1972b; Ewer, 1965; Young, 1964a). In pterosaurs the trochanter is apparently absent (Wellnhofer, 1978). In crurotarsal archosaurs, in contrast, the fibula frequently appears crooked in lateral or medial view due to the presence of a robust anterior trochanter that bulges from the shaft. The crooked fibula is present in phytosaurs (Chatterjee, 1978), ornithosuchids (Bonaparte, 1972; Walker, 1964), aetosaurs (Walker, 1961; Sawin, 1947), rauisuchians (Dutuit, 1979; Sill, 1974), and primitive crocodylomorphs (Whetstone and Whybrow, 1983; *Saltoposuchus*, SMNS 12596). Exceptions among crurotarsal archosaurs include *Gracilisuchus* (Romer, 1972c), the rauisuchian *Postosuchus* (Chatterjee, 1985), and extant crocodiles, in which the trochanter is reduced to a low rugosity. Although the absence of a robust trochanter in *Gracilisuchus* may be due to its small body size, a simple allometric relation between body size and a robust trochanter does not hold; large-bodied forms such as *Postosuchus*, extant crocodiles, and dinosaurs exhibit only a low rugosity or welt.

(6) Distal end of fibula wider than proximal end (Fig. 21). In pterosaurs (Wellnhofer, 1978), dinosauriforms (Bonaparte, 1975a; Colbert, 1970) and archosaurian outgroups (Romer, 1972b; Young, 1964a:figs. 32, 48), the maximum width of the proximal end of the fibula is subequal to, or exceeds, that of the distal end. In contrast, the maximum width of the distal end is greater than that of the proximal end in crurotarsal archosaurs, such as phytosaurs (Chatterjee, 1978), ornithosuchids (Bonaparte, 1972), aetosaurs (*Typothorax*, AMNH 19338 and MCZ 1488; Walker, 1961; Bonaparte, 1972), and rauisuchians (Dutuit, 1979; Chatterjee, 1985). Among crocodylomorphs, proximal and distal ends of the fibula are subequal in width (e.g., Whetstone and Whybrow, 1983), rather than broader distally, as in most crurotarsal archosaurs.

(7) Hemicylindrical calcaneal condyle for articulation with fibula (Figs. 6–8, 23B, C). Crurotarsal archosaurs have a specialized articulation between the fibula (crus) and calcaneum (tarsus), from which the name of the group is derived. The distal end of the fibula articulates against a hemicylindrical articular condyle on the calcaneum. The condyle extends along an arc of approximately 85 degrees and exceeds in antero-posterior width the adjacent fibular facet on the astragalus. The calcaneal condyle extends medially under the dorsal process of the astragalus at a low angle, forming a continuous rotary articulation with the astragalus and fibula. The rotary fibulocalcaneal crurotarsal articulation does not occur elsewhere among tetrapods.

(8) Astragalus with flexed tibial articular surface (Figs. 6–8). In ornithodiran archosaurs and immediate ar-

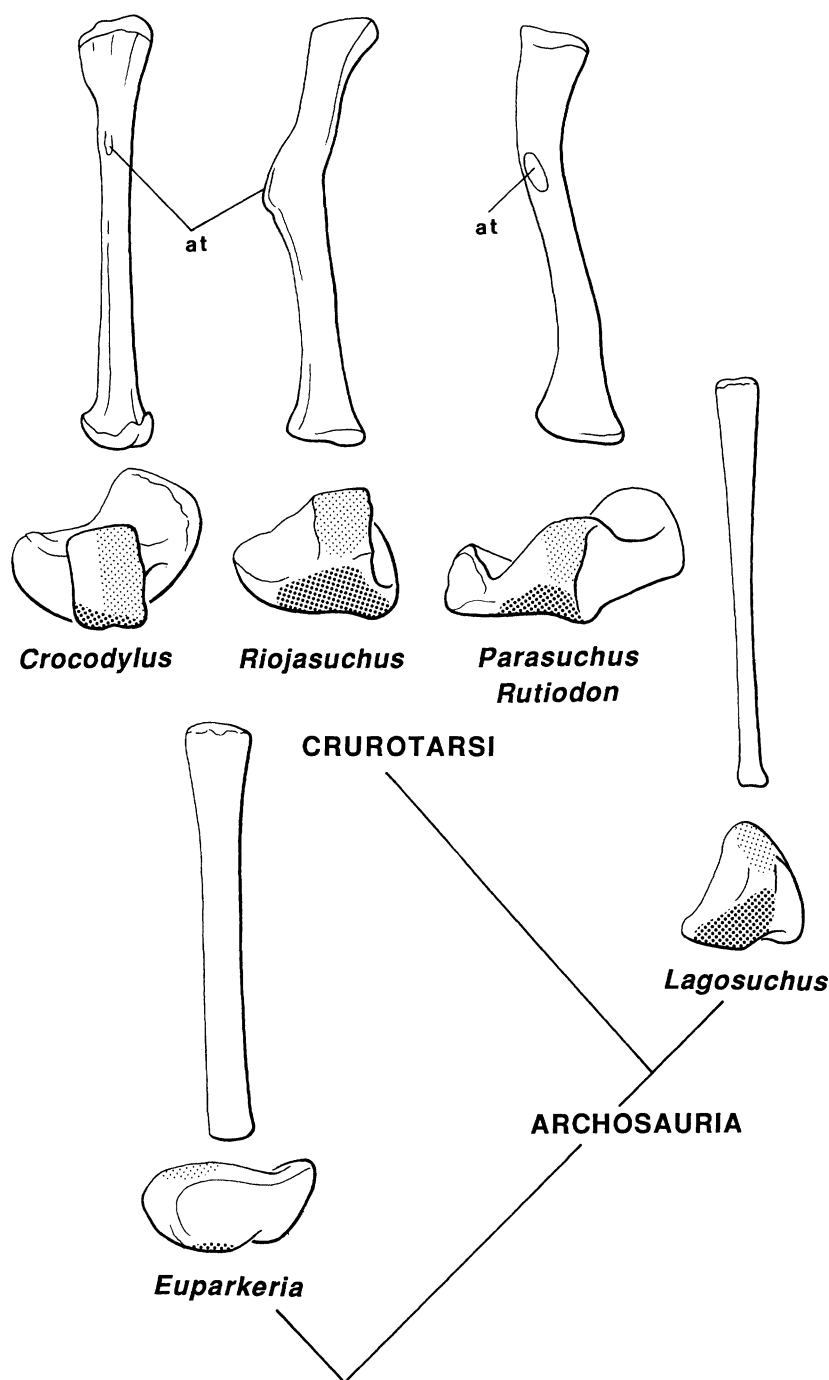


FIGURE 21. Phylogenetic diagram showing the left fibula (lateral view) and left calcaneum (anterior view) in crurotarsal archosaurs and successive outgroups. The apomorphic condition in Crurotarsi involves the robust anterior trochanter of fibula (character 5) and the adjacent positions of fibular and distal tarsal 4 facets (character 3). Light stippling marks the fibular facet, and dark stippling marks the articular surface for distal tarsal 4. Abbreviations: at, anterior trochanter of fibula.

chosaurian outgroups, the tibial facet on the astragalus is concave and the posteromedial portion of the tibial facet is visible in anterior, rather than posterior, view (e.g., *Lagosuchus*, *Chanaresuchus*, *Euparkeria*, erythrosuchids, and *Proterosuchus*). In crurotarsal archosaurs, in contrast, the tibial facet on the astragalus is

divided into two parts: a posteromedial part, which is concave and faces proximally, and an anterolateral part, which is flatter and faces proximally, medially as well as anteriorly.

The curving, flexed surface of the tibial facet in these forms has been described as “saddle-shaped” (Parrish,

1986:23) and the tibioastragalar articulation as a “screw-joint” (Gauthier and Padian, 1985; Gauthier, 1986). These terms are useful approximate descriptions, but the tibial facet does not conform to either a symmetrical “saddle” or “screw” contour. The degree of flexure of the tibial articular surface varies among crurotarsal archosaurs and is more subtly expressed in phytosaurs, extant crocodilians and a few extinct suchians such as “*Mandasuchus*.” All crurotarsal archosaurs that preserve the astragalus, nevertheless, show this flexure, the presence of which is best judged in anterior or posterior views of the astragalus: in crurotarsal archosaurs the concave posteromedial portion of the tibial facet is visible in posterior view of the astragalus, rather than in anterior view as in other archosaurs; the flat anterolateral portion of the tibial facet, on the other hand, is broadly exposed in anterior view of the astragalus (with the opposing tibial surface broadly exposed in posterior view of the distal end of the tibia).

The distribution of the flexed tibioastragalar joint among archosaurs, particularly in *Parasuchia* and *Euparkeria*, has not been clarified. Gauthier (1984, 1986) and Gauthier and Padian (1985) listed “screw joint” tibio-astragalar articulation” as a synapomorphy for aetosaurs, rauisuchians, and crocodylomorphs, and Gauthier (1986) suggested the independent appearance of the same character in ornithosuchids. Parrish (1986: 23) noted the same distribution and added that the “tibial facet in phytosaurs and proterosuchids is flat or very gently saddle-shaped.” The tibial facet of *Euparkeria* has not been compared in detail, although Parrish (1986:23) noted that the rather flat surface resembled that in crocodilians. In phytosaurs, the divided tibial facet on the astragalus is well preserved in *Rutiodon* (Fig. 6) and *Parasuchus* (ISI R43) and, as in other crurotarsal archosaurs, the posteromedial portion of the articular facet is concave and depressed and is visible in posterior, rather than anterior, view of the astragalus. A flexed tibial facet, on the other hand, is clearly absent in *Euparkeria* (Fig. 4).

(9) Robust calcaneal tuber with shaft wider than high (Figs. 6–8). The tuber is absent or reduced in Pterosauria and Dinosauromorpha and appears to be taller than wide in *Lagosuchus* (Fig. 9). In the archosaur outgroup *Euparkeria*, the shaft of the tuber is thickened by a ridge of bone along its posteroventral margin, and as a result the maximum height and width of the shaft are subequal. In a second specimen (GPIT 8694), however, the tuber is taller than wide. In more distant outgroups, the tuber is subtabular in form and in every case shaft height is greater than shaft width (e.g., *Shanisuchus*, Young, 1964a; *Proterosuchus* (Fig. 3); *Notoesuchus*, Carroll, 1976). In all crurotarsal archosaurs, in contrast, the calcaneal tuber is flattened dorsoventrally such that the transverse width of the narrowest portion of the shaft is greater than its height. These proportions obtain in suchians, ornithosuchids (*Riojasuchus*, *Ornithosuchus*) and phytosaurs (*Parasuchus*, ISI R43; *Rutiodon*, AMNH 3001 and Fig. 6).

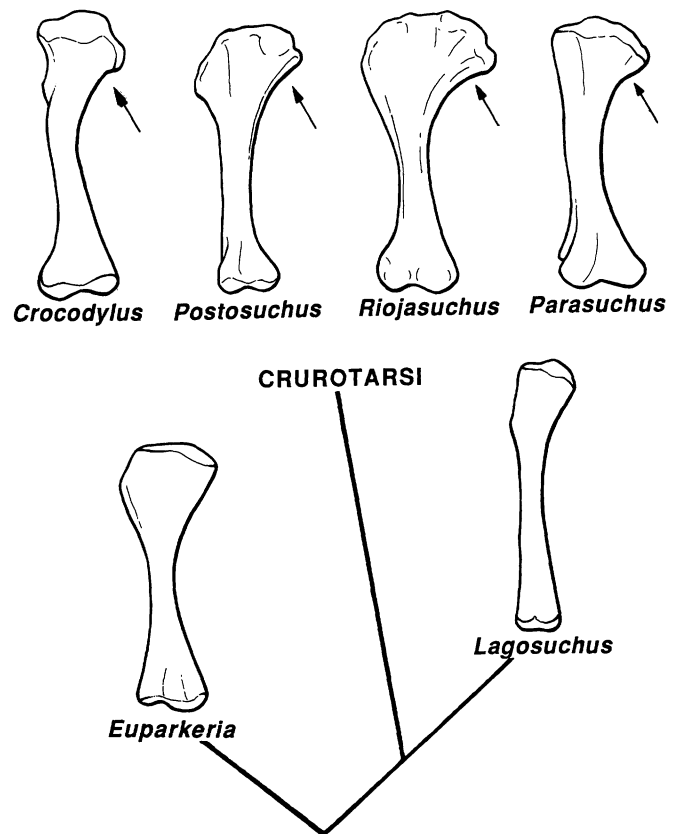


FIGURE 22. Phylogenetic diagram comparing the left humerus in crurotarsal archosaurs with that in two outgroups. Crurotarsal archosaurs show an arched medial margin distal to a prominent medial tuberosity (arrows point to character 4).

(10) Calcaneal tuber with flared distal end. There is no distal expansion of the tuber in dinosauromorphs like *Lagosuchus* that retain the tuber or among archosaur outgroups such as *Euparkeria* and *Proterosuchus* (Figs. 3–4). Among erythrosuchids, the tuber thickens distally but lacks a strong distal flare. Crurotarsal archosaurs are easily distinguished by the distal flare of the tuber on dorsal, ventral, and medial margins. In some aetosaurs (e.g., *Typothorax*), rauisuchians (e.g., *Fasolosuchus*), and crocodylomorphs (e.g., *Crocodylus*; Fig. 8), the lateral margin also forms a prominent rim. In all crurotarsal archosaurs, the broad distal end of the calcaneal tuber provides a broad, smooth surface for the tendon of the gastrocnemius muscle.

(11) Ventral astragalocalcaneal articulation larger than dorsal articulation (Fig. 23). The primitive diapsid astragalocalcaneal articulation is divided into “dorsal” and “ventral” articulations by the astragalocalcaneal canal. This terminology is retained here due to current usage even though these articulations are not necessarily “dorsal” (proximal) or “ventral” (distal) to one another. The condition among the immediate outgroup Ornithodira is impossible to assess due to trans-

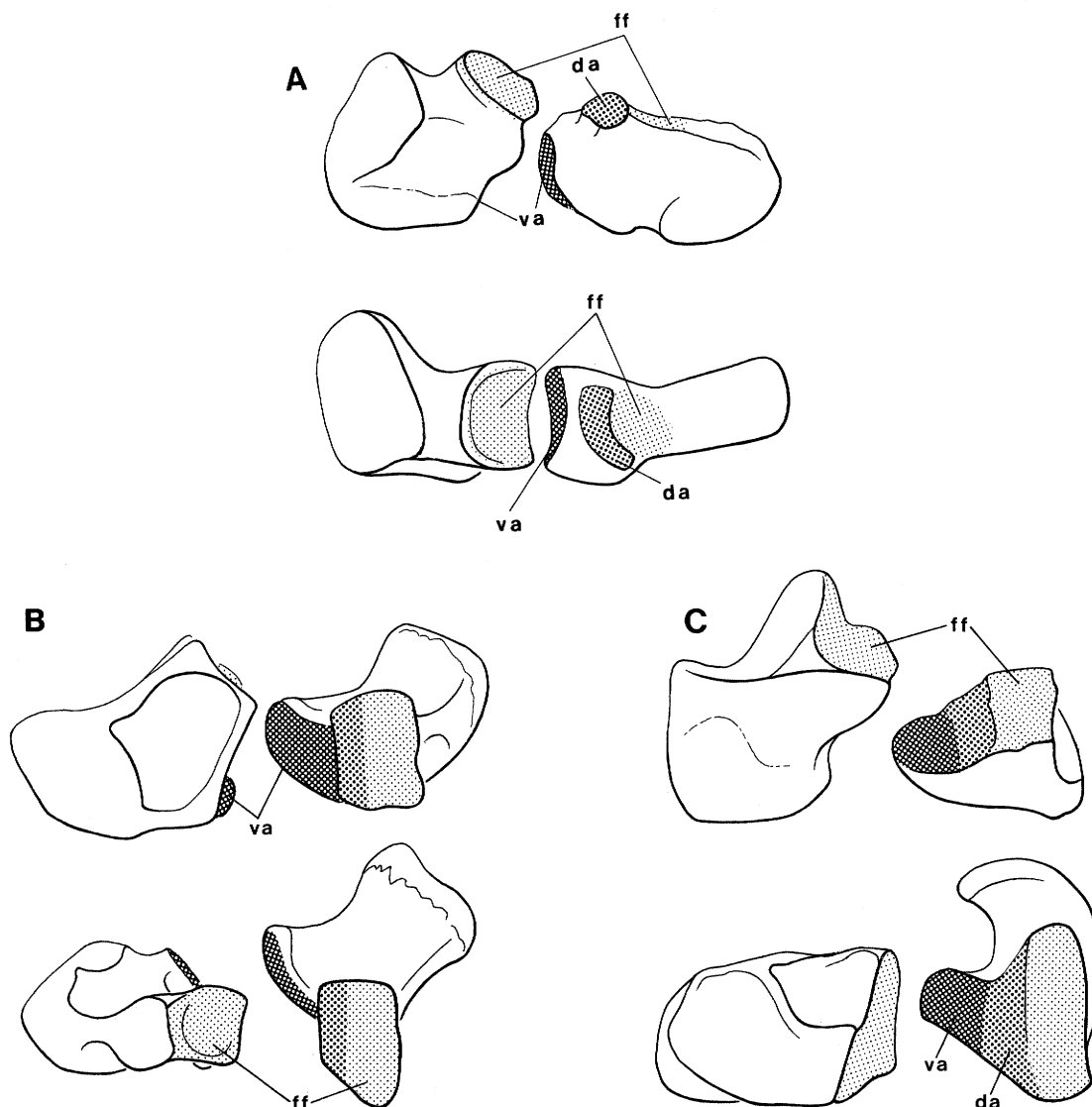


FIGURE 23. Homologies of the fibular facet and the dorsal and ventral astragalocalcaneal articulations in archosaurs. A–C, Left astragalus and calcaneum in anterior and dorsal views in *Proterosuchus vanhoepeni* (A), *Crocodylus acutus* (B), and *Riojasuchus tenuiceps* (C). Light stippling marks the fibular facet, medium stippling the dorsal astragalocalcaneal articulation, and dark stippling the ventral astragalocalcaneal articulation. Abbreviations as in Figure 3.

formation of the astragalocalcaneal articulation. The astragalocalcaneal articulation is reduced in size and shows no indication of separate dorsal and ventral facets (i.e., there is no posterior astragalar groove). In the archosaurian outgroups *Chanaresuchus* and *Euparkeria*, on the other hand, a posterior astragalar groove is present and partially divides the articulation into dorsal and ventral articulations (Figs. 4C–D, 5C–D). In these taxa the portion of the astragalocalcaneal articulation corresponding to the ventral articulation does not extend to the posterior margin of the astragalus. This plesiomorphic condition is clearly visible in distal view of the astragalus in *Proterosuchus* (Fig. 3H) and various archosauriform outgroups, in which the ven-

tral astragalocalcaneal articular surface is small and limited to the anterior half of the astragalus.

In the crurotarsal clades Suchia and Parasuchia, in contrast, the ventral astragalocalcaneal articulation is much larger than the adjacent dorsal astragalocalcaneal articulation (Figs. 6H, 8D, H). The relative enlargement of the ventral articulation is easily seen in ventral view of the astragalus; the ventral astragalocalcaneal articular surface extends farther posteriorly than the dorsal astragalocalcaneal articular surface and reaches the posterior margin of the astragalus. In Ornithosuchidae, the astragalocalcaneal articulation is too transformed for accurate comparison; the astragalocalcaneal articulation forms a single articular surface that

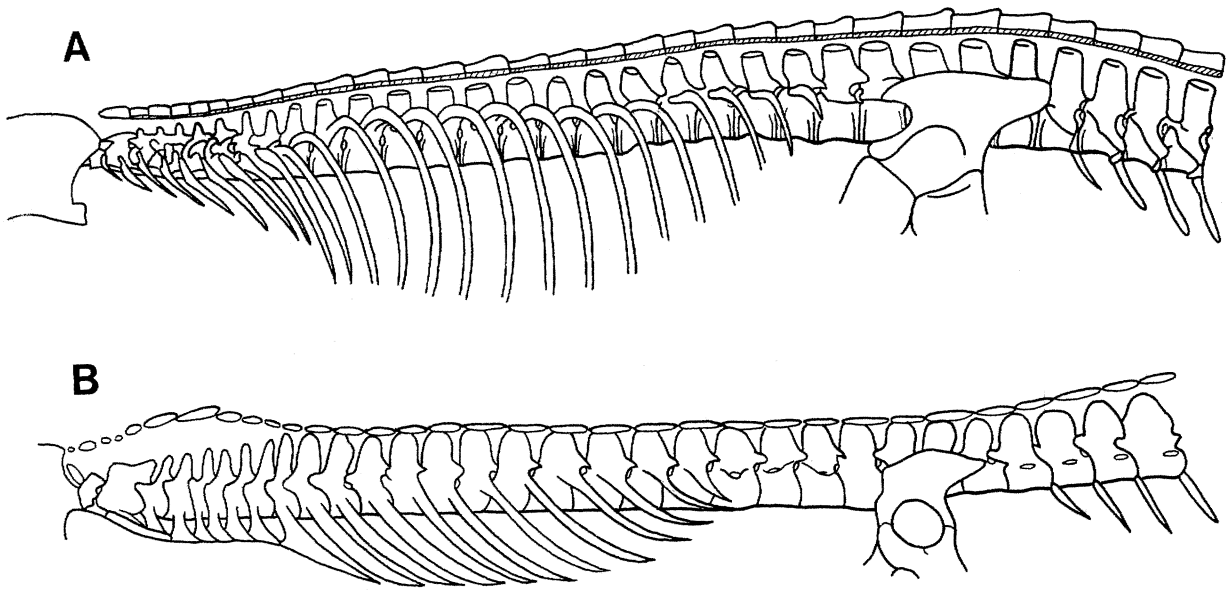


FIGURE 24. *Stagonolepis robertsoni* Agassiz, 1844 and *Melanosuchus niger*. Lateral view of the postcranial skeleton showing the one-to-one relationship between axial segments and the overlying osteoderm rows. A, *Stagonolepis robertsoni* (modified from Walker, 1961). B, *Melanosuchus niger* (MCZ 17726; after Ross and Mayer, 1984).

is not subdivided by the posterior astragalar groove (Fig. 7H). The enlarged ventral articulation, therefore, is most parsimoniously interpreted as a synapomorphy for Crurotarsi, but the condition in ornithosuchids and other archosaurs is too transformed for comparison.

(12) Single paramedian osteoderm pair per cervicodorsal vertebra (Fig. 24). Dermal armor is absent plesiomorphically in Pterosauria and Dinosauriformia and, therefore, the plesiomorphic condition in the first outgroup (Ornithodira) is unknown. Among archosaurian outgroups, the proterochampsids *Chanaresuchus*, *Gualosuchus*, and a third undescribed form (Arcucci, pers. comm.) have only a single median osteoderm row with several scutes per cervicodorsal vertebra. Paramedian rows of osteoderms are present in *Euparkeria* and possibly also in the proterochampsid *Cerritosaurus*. Although Ewer (1965:415) specifically mentioned that scute pairs and vertebrae are not precisely aligned in *Euparkeria*, the number of scute pairs and underlying vertebrae are nearly the same, and the scutes appear to be positioned in succession over the neural spines.

In crurotarsal archosaurs, a single pair of osteoderms is positioned over the midline, articulating with the neural spines of the cervicodorsal vertebrae. The one-to-one relationship between scute pair and vertebral segment is present in nearly all crurotarsal archosaurs that preserve articulated armor, including phytosaurs (Chatterjee, 1978), ornithosuchids (Walker, 1964; Bonaparte, 1972), and suchians (Walker, 1961; Bonaparte, 1972; Long and Ballew, 1985). The relative position of the armor plates to the vertebral segments is best observed in radiographs of extant crocodilians,

which show the scute pairs in intervertebral position spanning the gap between the neural spines (Ross and Mayer, 1984). *Gracilisuchus*, *Prestosuchus*, and the rauisuchians *Ticinosuchus* and *Saurosuchus* are exceptions to this dominant pattern; they have paramedian scute rows over most or all of the cervicodorsal vertebrae, but the small size of the scute permits at least two or three scutes per neural spine. An undescribed rauisuchian from the Triassic of Germany, however, shows the apomorphic condition, with paired large osteoderms for each vertebral segment (Wild, pers. comm.). Some crurotarsal archosaurs, such as *Rauisuchus* or *Postosuchus*, may not have had scute rows, but well-preserved articulated remains of these taxa are not known.

Even if *Euparkeria* has one-to-one correspondence between osteoderm pairs and cervicodorsal vertebrae, it is still most parsimonious to interpret the condition in Crurotarsi as synapomorphic with some variation in Suchia. This synapomorphy, however, is equivocal on the most parsimonious tree due to the absence of information in Ornithodira; the synapomorphy may just as well apply to the more inclusive taxon Archosauria.

#### ?Suchia + Ornithosuchidae

Suchia and Ornithosuchidae may constitute a monophyletic clade within Crurotarsi, but supporting character evidence is weak.

**Recorded Temporal Range**—Ladinian (Middle Triassic) to Recent.

(13) Pubis longer than ischium and at least three

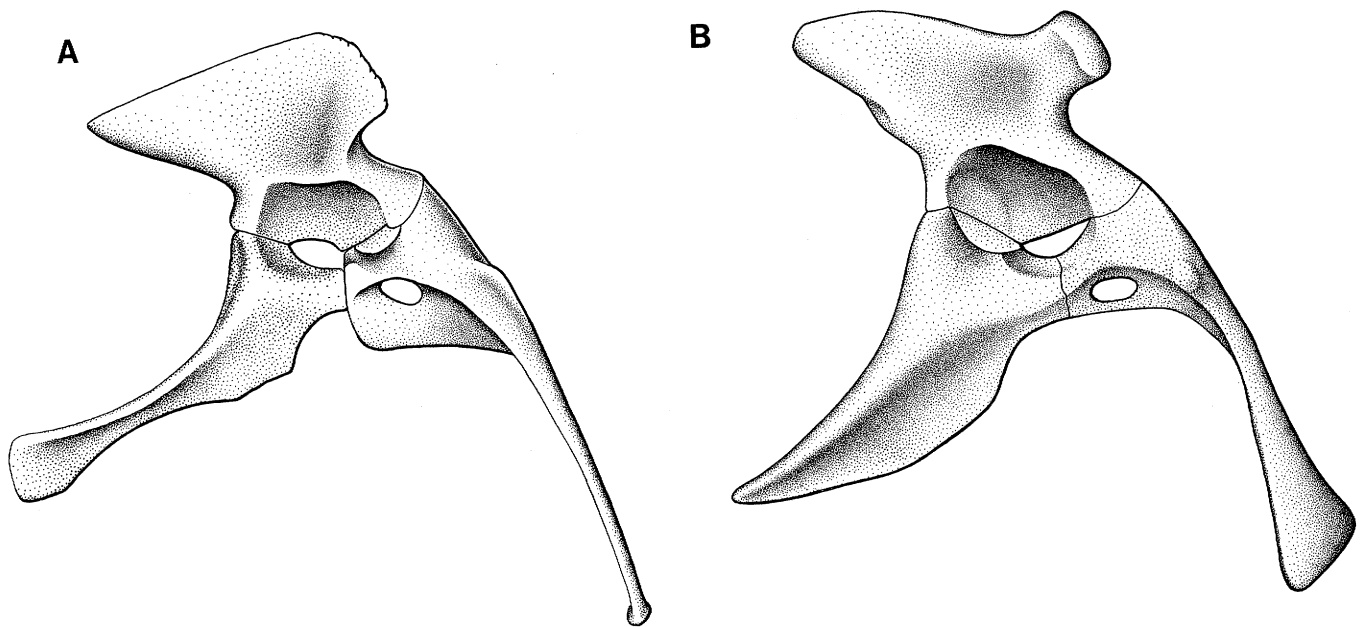


FIGURE 25. *Ornithosuchus longidens* (Huxley, 1877) and *Lagosuchus talampayensis* Romer, 1971. A–B, Pelvic girdle in lateral view showing the development of articular surfaces in the acetabulum in archosaurs: A, *Ornithosuchus longidens* (after Walker, 1964) and B, *Lagosuchus talampayensis* (based on PVL 3870, 3871). Abbreviations: ant, antitrochanter; par, pubic articular recess.

times anteroposterior diameter of acetabulum (Fig. 25). In the immediate outgroups to the suchian-ornithosuchid clade (Parasuchia, pterosaurs, and the basal dinosauromorph *Lagerpeton*), the maximum lengths of the pubis and ischium are subequal, and pubic length is only one and one-half times the diameter of the acetabulum. Within Dinosauromorpha, the pubis independently achieves a relative length equal to that in the suchian-ornithosuchid clade.

Suchians (e.g., *Gracilisuchus*, Bonaparte, 1975b) and ornithosuchids (Bonaparte, 1972; Walker, 1964) have proportionately long pubes. Notable exceptions among suchians include aetosaurs and some advanced crocodylians, which show subequal pubic and ischial lengths and pubic length that falls short of three times acetabulum diameter (Sawin, 1947; Casamiquela, 1961, 1967; Walker, 1961; Parrish, 1986). The pubis in *Stagonolepis* is proportionately longest among aetosaurs (Walker, 1961), but the pelvic reconstruction is based on elements from three individuals and may not show accurate proportions. Lengthened pubic proportions nonetheless are interpreted here tentatively as plesiomorphic for Suchia and thus synapomorphic for Suchia and Ornithosuchidae.

Similar characters have been employed by previous authors in support of different groups to express proportional changes in the pelvic girdle. Gauthier (1986) listed “prominently triradiate pelvis with pubis length at least three times width of acetabulum” for a group including dinosauromorphs and ornithosuchids. Benton and Clark (1988) used the character “pubis is longer than the ischium” to diagnose Suchia, indicating a

parallel condition in Ornithosuchidae. The present analysis indicates lengthened pubic proportions appear to have reversed twice in Suchia (some aetosaurs, advanced crocodylomorphs) and to have evolved in parallel among dinosauromorphs more advanced than *Lagerpeton*. The character is tentatively interpreted as synapomorphic for Suchia plus Ornithosuchidae.

(14) Posterior pubic acetabular margin recessed (Fig. 25). Pterosaurs and basal dinosauromorphs (*Laterpeton*, *Lagosuchus*) lack any differentiation of the pubic border of the acetabulum. In herrerasaurs (e.g., PVL 2558), the acetabular surface tapers in width toward the ischium, but there is no marked division of the border into an articular anterior part and recessed posterior part. All archosaur outgroups, including proterochampsids, *Euparkeria*, and erythrosuchids, show no differentiation of the pubic acetabular surface.

In suchians and ornithosuchids, in contrast, the smooth cupped acetabular surface on the pubis is restricted to the anterior half of its acetabular margin. The posterior half of the pubic acetabular margin is recessed, resulting in a nonarticular gap along the ventral acetabular margin between the articular surfaces of the pubis and ischium (Fig. 25A). The recessed pubic margin occurs in aetosaurs (Bonaparte, 1972; Walker, 1961), rauisuchians (Chatterjee, 1985), and some basal crocodylomorphs (*Terrestriisuchus*, BMNH P72/1; Crush, 1984). In advanced Crocodylomorpha, the pubis is excluded from the acetabulum and therefore is not informative with regard to this character.

The condition among phytosaurs appears to be intermediate or variable. The phytosaur *Parasuchus* ap-

pears to show the plesiomorphic condition in available published illustrations (Chatterjee, 1978). *Rutiodon* appears intermediate, showing a narrow posterior contribution to the acetabulum that is continuous with the ischial acetabular surface (MacGregor, 1906). The posterior margin is recessed in *Machaeroprotopus* (MCZ 2167, cast; Camp, 1930), similar to that in *Suchia* and *Ornithosuchidae*. This suchian-ornithosuchid synapomorphy may eventually include *Parasuchia* and thus lend support to the monophyly of *Crurotarsi* (Serenó, 1990).

### Ornithosuchidae Huene, 1914

**Definition**—*Ornithosuchidae* includes the genera *Ornithosuchus*, *Riojasuchus*, *Venaticosuchus*, and all descendants of their common ancestor.

**Recorded Temporal Range**—Carnian to Norian (Late Triassic).

Although *Venaticosuchus* is known only from a fragmentary skull, the abbreviate lower jaws and overhanging anterior snout suggest a closer relationship with *Riojasuchus* than with *Ornithosuchus*. *Ornithosuchidae* is defined here to include these three genera, their putative common ancestor, and any fossil forms more closely related to them than to other archosaurs.

(15) Two-tooth, arched diastema (Figs. 11A, 12A). When the upper and lower jaws are brought into occlusion in ornithosuchids, two large anterior dentary crowns insert into a diastema between the premaxilla and maxilla. Two curved depressions on the lateral wall of the diastema are fitted to the medial sides of each crown (*Ornithosuchus*, BMNH R3143). In *Riojasuchus*, the second crown was broken away during preparation and was not included in the original restoration (Bonaparte, 1972). The enlarged caniniform dentary crowns in *Ornithosuchus* and *Riojasuchus* are preceded by a very short procumbent first tooth. No other basal archosaurs exhibit this dental configuration.

(16) Nasal-prefrontal contact reduced or excluded by frontal-lacrimal contact (Figs. 11C, 12C). In rauisuchians (Chatterjee, 1985), aetosaurs (Walker, 1961), *Gracilisuchus* (Romer, 1972c), pterosaurs (Wellnhofer, 1985), and Dinosauriforma, sutural contact between the nasal and prefrontal separates the frontal from the lacrimal. In ornithosuchids, on the other hand, the nasal and prefrontal either contact at a point with the lacrimal and frontal (*Ornithosuchus*) or are separated by lacrimal-frontal contact (*Riojasuchus*). The condition is unknown in *Venaticosuchus*.

(17) Palatine-pterygoid fenestra (Figs. 11D, 12C). In *Ornithosuchus* and *Riojasuchus*, an additional palatal fenestra is present between the palatine and pterygoid. This fenestra is not known in other archosaurs.

(18) Dentary-splenic symphysis over 30 percent of total lower jaw length (Fig. 11A). Most basal archosaurs restrict the mandibular symphysis to the anterior ends of the dentaries. Phytosaurs (Chatterjee, 1978) and some long-snouted crocodilians have exception-

ally long symphyses, but this condition is clearly correlated with the extreme elongation of upper and lower jaws. In this analysis, therefore, *Parasuchia* is scored as if the condition were unknown. Some short-snouted basal crocodylomorphs, however, do exhibit an extensive dentary-splenic symphysis similar to that in ornithosuchids (e.g., *Saltoposuchus*, Sereno and Wild, in review), but this condition must have arisen independently in light of the parsimony analysis. In ornithosuchids, the anterior third of the lower jaws is in mutual contact, forming an unusually extensive symphysis involving both the dentary and splenic. The robust symphysis is preserved in articulation in *Ornithosuchus* (BMNH R3143), and the broad symphyseal surface is visible in disarticulation in *Riojasuchus* (PVL 3827). Strengthening of the symphysis may be functionally related to the overhanging snout and prominent caniniform anterior dentary teeth.

(19) Ventral astragalocalcaneal articulation with astragalus concave and calcaneum convex (Figs. 7, 23). Among archosaurs the ventral astragalocalcaneal articulation occurs in four states: flat (*Proterosuchus*), concavoconvex with the calcaneum concave (*Parasuchia* and all suchians except extant crocodylomorphs), saddle-shaped with the calcaneum concave both dorsoventrally and mediolaterally (*Crocodylia*), and concavoconvex with the calcaneum convex (*Ornithosuchidae*).

The ornithosuchid concavoconvex ventral articulation—the so-called “crocodile-reversed” configuration—can be interpreted in two ways. First, as coded in this analysis, the medial portion of the cone-shaped medial process of the calcaneum can be considered the homologue of the separate ventral articulation seen in other archosaurs and among diapsids plesiomorphically. Available topological evidence favors this interpretation despite the absence of a discrete division into dorsal and ventral articulations in ornithosuchids: the convex, medially projecting “tuber” on the calcaneum is in the same position as the concave calcaneal flange in other archosaurs (medial to the calcaneal condyle); and the broad groove on the posterior aspect of the astragalus in ornithosuchids terminates ventrally in the middle of the astragalocalcaneal articulation, closely resembling the posterior groove in other basal archosaurs and archosauriforms that leads to the astragalocalcaneal canal (separating dorsal and ventral articular facets; Figs. 7, 23C).

Alternatively, the medial part of the astragalocalcaneal articulation in ornithosuchids can be viewed as a neomorph—a novel extension (“peg”) of the calcaneum into a novel hollow (“socket”) on the astragalus without any relation to the ventral facet in phytosaurs, suchians, or basal archosauriforms. In this view, the medial portion of the cone-shaped calcaneal surface constitutes an “elongation of the wheel-shaped articular surface of the calcaneum and loss of the ventral flange [i.e., articulation]” (Brinkman, 1981:12). The medial cone-shaped process of the calcaneum, however, is topologically in the position of the ventral ar-

TABLE 1. Presacral centrum lengths (in mm) in the basal archosaurs *Chanaresuchus* (PVL 4647), *Gualosuchus* (PVL 4576), *Riojasuchus* (PVL 3828), and *Lagosuchus* (PVL 3872). Axial centrum length does not include the axial intercentrum. Parentheses indicate estimates.

Presacral no.	<i>Chanaresuchus</i>	<i>Gualosuchus</i>	<i>Riojasuchus</i>	<i>Lagosuchus</i>
2	11.3	10.0	23.8	(5.0)
3	11.8	11.1	22.7	5.3
4	11.3	11.0	22.5	5.2
5	11.1	11.0	22.5	5.1
6	10.9	11.2	22.5	4.7
7	10.2	10.5	22.4	4.1
8	9.8	10.0	21.0	3.6
9	10.2	9.9	20.8	3.6
10	10.3	11.0	—	3.8
11	10.7	10.0	—	4.2
12	10.5	11.0	—	4.4
13	11.0	11.0	—	4.4
14	11.6	11.0	—	4.5
15	11.7	11.3	—	4.5
16	12.2	(11.5)	23.8	4.6
17	12.1	11.3	23.8	4.8
18	13.3	—	21.8	4.9
19	12.7	13.1	21.5	5.2
20	13.1	12.6	23.8	5.1
21	13.1	12.9	—	5.0
22	13.9	—	—	—
23	13.8	—	—	—
24	13.9	—	—	—
25	13.0	—	—	—

tication (medial to the calcaneal condyle and medial to the posterior astragalar groove) and thus appears to be most reasonably interpreted as a transformation of the latter.

(20) Laterally compressed pedal unguals. In most basal archosaurs the pedal unguals are not strongly laterally compressed and lack sharp dorsal keels. Pterosaurs may constitute an exception, but the cross-sectional shape of the pedal claws is difficult to determine from the literature. In comparison the pedal unguals in *Ornithosuchus* and *Riojasuchus* are sickle-shaped, with very narrow deep proportions particularly in the unguals of the inner digits. These unguals are many times taller than wide and project well above the dorsal surface of the penultimate phalanx.

### Ornithodira Gauthier, 1986

**Definition**—Ornithodira includes Pterosauria, *Scleromochlus*, Dinosauromorpha (including birds), and all descendants of their common ancestor.

**Recorded Temporal Range**—Ladinian (Middle Triassic) to Recent.

(21) Anterior cervical centrum length longer than mid-dorsal length (Fig. 20). In most basal archosaurs the postaxial cervical centra are subequal or shorter in length than an average mid-dorsal centra (Table 1).

Notable exceptions occur in basal crocodylomorphs (*Terrestriusuchus*, Crush, 1984; *Lewisuchus*, Romer, 1972d) and in an undescribed proterochampsid (Arcucci, pers. comm.), which have independently lengthened the anterior cervicals.

In basal ornithodirans, in contrast, the lengths of cervical centra C3–5 exceed the length of an average mid-dorsal centrum and are approximately 30 percent longer than centra at the base of the neck (C9–10). This relative elongation of the anterior neck is preserved in Pterosauria, *Lagosuchus*, and the basal dinosaur *Herrerasaurus*, but is reversed in several dinosaurian subgroups. In many ornithischians and some theropods, the anterior cervical centra are not proportionately longer than posterior cervical or mid-dorsal centra (e.g., *Hypsilophodon*, Galton, 1974; *Psittacosaurus*, Sereno, 1987; *Dilophosaurus*, UCMP 77270). Likewise, some theropods and most sauropodomorphs have lengthened the mid and posterior cervical centra such that all of the postaxial centra are roughly equal in length and longer than an average mid-dorsal centrum (e.g., *Plateosaurus*, Huene, 1926). The small enigmatic form *Scleromochlus* is another exception and has short cervical centra that do not change significantly in length along the cervical series. Elongation of the anterior neck, nevertheless, is regarded here as an ornithodiran synapomorphy based on the condition in pterosaurs and basal dinosauromorphs.

(22) Dorsal body armor absent. Crurotarsi, proterochampsids, and *Euparkeria* are all characterized by dorsal dermal armor. In contrast, basal ornithodirans such as pterosaurs, *Scleromochlus*, *Lagerpeton*, *Lagosuchus*, and basal Dinosauria show no sign of such armor. Within Dinosauria, dorsal body armor has reappeared several times (e.g., *Ceratosaurus*, Thyrophora) but is absent in nearly all other taxa.

(23) Interclavicle absent. Most basal archosaurs have an ossified interclavicle as preserved in Suchia, Parasuchia, Ornithosuchidae, and *Euparkeria*. No such element has ever been reliably reported in pterosaurs or dinosauromorphs. In the prosauropod dinosaur *Masospondylus* (Cooper, 1981), the bone identified as the interclavicle is actually the clavicle, as correctly identified by Huene (1926) in the closely related genus *Plateosaurus* and preserved in articulation (SMNS unnumbered). Among birds, the ventral process of the furcula, the hypocleideum, has on occasion been considered the homologue of the interclavicle (Bellairs and Jenkin, 1960), and it occurs early in the history of the group (e.g., Sanz et al., 1988). This homology, however, is untenable because the hypocleideum is not a separate ossification and an interclavicle is absent in *Archaeopteryx*, dinosaurs, and basal ornithodirans.

(24) Clavicles rudimentary or absent. Slender ossified clavicles are preserved in most crurotarsal archosaurs (phytosaur, suchians) and archosaurian outgroups (e.g., *Euparkeria*). Although coossified clavicles (i.e., the furcula) occur in avian ornithodirans and in some theropods, many well preserved skeletons of pterosaurs and dinosauromorphs lack any trace of this

ossification. Because rudimentary clavicles occur sporadically among dinosaurs (*Segisaurus*, Camp, 1936; *Massospondylus*, Cooper, 1981; *Plateosaurus*, Huene, 1926; *Psittacosaurus*, Sereno, 1987; *Protoceratops*, Brown and Schlaikjer, 1940), the clavicle presumably was present but unossified in many dinosaurs. The well developed avian furcula, in particular, is here considered a reversal of the reduced condition that obtains in most ornithodirans.

(25) Subrectangular deltopectoral crest (Fig. 22). In most basal archosaurs the deltopectoral crest is crescentic, with a rounded proximal corner and an apex along the external margin of the crest that is positioned within the proximal 25 percent of the humerus. This condition obtains in phytosaurs, most suchians, proterochampsids, and *Euparkeria*, with the apomorphic subrectangular crest appearing independently from that in Ornithodira in the heavy-bodied erythrosuchids (Young, 1964a) and, in a modified form, among extant crocodilians.

The shape of the deltopectoral crest in Ornithodira is typically subrectangular with rounded external corners proximally and distally, as seen in the primitive pterosaurs *Eudimorphodon* and *Campylognathoides* (Wild, 1978; Wellnhofer, 1978), *Lagosuchus*, and Dinosauria. The proximal corner is located very near the level of the head of the humerus. The distal corner, or apex, is displaced down the shaft away from the head of the humerus by a distance greater than 25 percent of the maximum length of the humerus.

Exceptions among ornithodirans include *Scleromochlus* and pterosaurs. In *Scleromochlus*, the slender humerus has a small subtriangular crest positioned within the proximal quarter. In pterosaurs, the deltopectoral crest is hypertrophied. Some primitive forms such as *Eudimorphodon* retain a subrectangular profile, which is assumed to be plesiomorphic within Pterosauria. In other pterosaurs (*Peteinosaurus*, Wild, 1978; *Dimorphodon*, Padian, 1983a), the deltopectoral crest is constricted near its attachment with the shaft.

(26) Femoral shaft bowed anteriorly along at least 80 percent of femoral length. In basal archosauriforms such as erythrosuchids, *Euparkeria*, and proterochampsids, the femoral shaft is sinuous in lateral view when the principal axis of the femur is held vertically. The proximal end is directed anteriorly and the distal condyles are deflected posteriorly to about the same degree. The sinuous curve of the femoral shaft is not symmetrical, but rather the distal anteriorly bowed portion of the shaft accounts for a greater share of femoral length. In *Chanaresuchus* (PVL 4575), for example, approximately 60 percent of the distal portion of the femur is bowed anteriorly; in modern crocodilians the same portion of the shaft accounts for approximately 70 percent of femoral length. In the ornithosuchid *Riojasuchus*, the anteriorly bowed portion of the shaft appears to account for 80 percent of femoral length in one specimen (PVL 3828) but perhaps only 70 percent in another (PVL 3827). With some variation in the strength of curvature, the anteriorly bowed

distal portion of the femoral shaft accounts for approximately 60–70 percent of femoral length in Crurotarsi and basal archosauriforms. The long-limbed, cursorial crocodylomorph *Terrestriisuchus* and close relatives are notable exceptions with shafts that are gently bowed along nearly their entire lengths.

Among ornithodirans, the anteriorly bowed distal portion of the shaft is proportionately greater and accounts for at least 80 percent of the femoral length. Shaft curvature was estimated with the transverse axis of the two principal distal condyles held perpendicular to the plane of view. The bowed shaft form occurs in pterosaurs, *Lagerpeton*, *Lagosuchus*, *Pseudolagosuchus*, and Dinosauria, and may indicate a more strictly parasagittal orientation of the femur during locomotion (Gauthier and Padian, 1985). In pterosaurs and some dinosaurian subgroups, the anteriorly bowed femoral shaft is more striking. Measurement of shaft curvature, however, is beset with orientation error and postmortem distortion (Sereno and Arcucci, 1990). A slight shift in the angle of view can result in a different measurement of shaft curvature.

The lack of consensus regarding the form of the femoral shaft highlights these problems. First Gauthier (1984:180) used “dorsal arc of the entire femoral shaft” to support a group including pterosaurs and dinosaurs but later used the same as a synapomorphy of Dinosauria alone (1986:46). Subsequently, Benton and Clark (1988:334) applied the same character to the more inclusive group “Ornithosuchia.”

(27) Tibia subequal or longer than femur (Fig. 18). In most basal archosaurs including phytosaurs, aetosaurs, *Gracilisuchus*, and most other suchians, femoral length exceeds tibial length. Despite some homoplasy within Suchia and Ornithodira, tibial length equal to or greater than femoral length is most parsimoniously interpreted as an ornithodiran synapomorphy. Apomorphic proportions occur among the ornithodirans in *Scleromochlus*, pterosaurs, *Lagosuchus*, *Lagerpeton*, *Staurikosaurus*, basal ornithischians (*Lesothosaurus*, *Scutellosaurus*, *Heterodontosaurus*, *Psittacosaurus*), and basal theropods (*Lilliensternus*, *Coelophysis*). *Herrerasaurus* (Reig, 1963), Sauropodomorpha (Cooper, 1981), and large-bodied theropods and ornithischians, in contrast, have reverted to a primitive tibial/femoral ratio less than one. In many of these cases, reversal to the plesiomorphic condition is an allometric consequence of increase in body size; small-bodied ornithischians and theropods invariably show the apomorphic condition.

(28) Posterior groove on astragalus absent (Fig. 9). In basal archosauriforms such as *Proterosuchus*, an incised groove (presumably accommodating vascular structures in life) on the posterior aspect of the astragalus leads to the perforating foramen between the astragalus and calcaneum (Fig. 3A, C–D). Although the foramen is absent in Archosauria, the posterior groove is retained in all crurotarsal archosaurs including extant crocodilians. In Ornithodira, in contrast, there is no trace of a posterior groove on the posterior aspect

of the astragalus, as preserved in Pterosauria, *Lagerpeton*, *Lagosuchus*, and Dinosauria.

(29) Calcaneal tuber rudimentary or absent (Fig. 9). In Crurotarsi and immediate archosaurian outgroups, the calcaneum is always characterized by a substantial tuber. The calcaneal tuber in Ornithodira is either extremely rudimentary (*Lagosuchus*, *Herrerasaurus*, Prosauropoda) or absent (Pterosauria, Ornithischia, Theropoda). The calcaneum in *Scleromochlus* is unknown.

(30) Distal tarsal 4 subequal in transverse width to distal tarsal 3 (Fig. 9). In basal archosauriforms and most basal archosaurs (e.g., *Euparkeria*, *Chanaresuchus*, *Riojasuchus*, *Gracilisuchus*, *Crocodylus*), distal tarsal 4 is a large pyramidal bone, several times the volume of distal tarsal 3 that articulates against the broad base of metatarsal 5. In ornithodirans in contrast, distal tarsal 4 is reduced in size and is subequal in transverse width to distal tarsal 4, as seen in pterosaurs (Padian, 1983a), *Scleromochlus*, *Lagosuchus*, and dinosaurs.

(31) Compact metatarsus with proximal third of metatarsals 1–4 shafts closely appressed (Fig. 14). Crurotarsal archosaurs and archosaur outgroups are characterized by a spreading metatarsus for plantigrade locomotion. The digitigrade pes in sphenosuchian crocodylomorphs is unusual among crurotarsal archosaurs and is considered an independent acquisition (Sereni and Wild, in review).

Ornithodirans are characterized by a digitigrade pedal posture in which only the phalanges contact the substrate. The proximal third of the shafts of all metatarsals but the fifth are flattened and bound together by ligaments. Except for large-bodied thyreophorans (Stegosauria and Ankylosauria), the shafts of metatarsals 1–4 are bound immovably and the pes is digitigrade in all dinosaurs including birds. This character was used previously to support Ornithodira (Gauthier, 1986:43) but the form of the metatarsus and the posture of the pes were listed as two separate characters.

(32) Metatarsals 2–4 elongate with metatarsal 3 more than 50 percent tibial length (Fig. 14). The ratio of metatarsal 3 to tibial length in ornithodiran outgroups apparently never achieves 50 percent even in those forms that have independently acquired a tibia/femur ratio less than one. In Ornithodira the median three metatarsals are proportionately elongate relative to the crus as seen in *Scleromochlus*, Pterosauria, and nearly all dinosaurs. Several dinosaur subgroups that have tibiae shorter than femora maintain metatarsal 3 length that is at least 50 percent of tibial length (e.g., *Herrerasaurus*, *Dilophosaurus*, some prosauropods; Reig, 1963; Cooper, 1981; Welles, 1984).

### ***Scleromochlus* and Pterosauria**

*Scleromochlus* has long been considered to be most closely related, or ancestral, to Pterosauria (Huene, 1914), and recently several synapomorphies have been offered to substantiate this hypothesis (Gauthier, 1984,

1986; Padian, 1984). Because *Scleromochlus* is a small form preserved only as natural molds in sandstone, many details are unavailable. Evidence summarized below from new latex peels from the natural molds supports *Scleromochlus* as an ornithodiran but casts some doubt on its proximity to pterosaurs.

Placement of *Scleromochlus* as an archosauriform is confirmed by the presence of a smooth, recessed antorbital fossa (BMNH R3146, R3556, R3557) and the absence of intercentra in the postaxial vertebral column (BMNH R3556, R3914). *Scleromochlus* exhibits a number of ornithodiran synapomorphies (absence of osteoderms, femoral shaft bowed along nearly all of its length, tibial length exceeding femoral length, metatarsal 3 length exceeding 50 percent of tibial length, compact metatarsus with closely appressed metatarsal shafts) but lacks any synapomorphies shared by crurotarsal archosaurs (parasagittal paired dorsal osteoderms, arched medial trochanter on the humerus, robust fibular anterior process, and characters related to the crurotarsal ankle joint). Notably *Scleromochlus* lacks two ornithodiran synapomorphies—elongate anterior cervical centra (BMNH R3556) and a subrectangular deltopectoral crest. Neither is easily attributed to allometric consequences of small body size since both are present in small-bodied *Lagosuchus*. The particular position of *Scleromochlus* within Ornithodira is less certain. In the present analysis, four potential synapomorphies could unite *Scleromochlus* and Pterosauria.

(33) Skull more than 50 percent presacral column length (Fig. 18A). The length of the skull in *Scleromochlus* and Pterosauria is always more than half of the length of the neck and trunk (measured from the atlas to the sacrum). In basal dinosauiromorphs and most other archosauriforms, the skull is proportionately shorter relative to presacral length except in long-snouted aquatic piscivores (proterochampsids, phytosaurs, and some crocodilians). Skull length is typically one third of the presacral length in larger-bodied forms and somewhat less than half of the presacral length in smaller forms such as *Euparkeria* (Ewer, 1965). In *Scleromochlus*, skull length is 55 to 60 percent of the length of the presacral column (BMNH R3146, R3556). In pterosaurs, the skull is usually proportionately longer at about 70 percent or more of the presacral column. *Scleromochlus* and pterosaurs, therefore, share a disproportionately large skull. Skull shape, however, is very different; pterosaurs have a deep skull in lateral view whereas in *Scleromochlus* the skull is twice as broad as tall.

(34) Length of scapula is less than 75 percent of humeral length (Fig. 18A). In most basal archosaurs the scapula is subequal in length to or longer than the humerus. In *Scleromochlus* and the basal pterosaurs *Dimorphodon* (Padian, 1983a:fig. 21) and *Campylognathoides* (Wellnhofer, 1974:figs. 6–7), the scapula is very short, measuring no more than 65 percent of humeral length. In other basal pterosaurs, such as *Eudimorphodon* (Wild, 1978:figs. 2, 8) and *Peteinosaurus*

(Wild, 1978:fig. 14), the scapula is slightly longer, measuring approximately 75 percent of humeral length.

(35) Fourth trochanter absent. Among basal archosaurs, only *Scleromochlus* and pterosaurs lack a fourth trochanter on the proximal shaft of the femur. In *Scleromochlus* (BMNH R3556, R3557) the shaft of the femur is well exposed without any development of a trochanter.

(36) Metatarsal 1 length is at least 85 percent of metatarsal 3 length (Fig. 17B, Table 2). Metatarsal 1 is significantly shorter than metatarsals 2–4 in most basal archosaurs including the basal dinosauiromorphs *Lagerpeton* and *Lagosuchus*. In *Scleromochlus* (BMNH R3556) and all pterosaurs, in contrast, metatarsal 1 is very elongate, nearly equalling the length of metatarsals 2–4 (Wild, 1978; Wellnhofer, 1978). Sphenosuchian crocodylomorphs are the only other archosaurs with a first metatarsal of comparable length (Colbert and Mook, 1951; Crush, 1984). Although Gauthier (1984) and Padian (1984) drew attention to the elongate proportions of the metatarsus, only the length of metatarsal 1 relative to metatarsals 2–4 is here considered synapomorphic.

Ten additional synapomorphies proposed recently to unite *Scleromochlus* and pterosaurs are not supported by examination of available specimens. Padian (1984:165) listed “head with very large fenestrae, long straplike scapula,” “short, deep, trapezoidal pelvis,” “four elongated closely appressed metatarsals,” “splintlike fibula,” and coossification of proximal tarsals “to each other and to the tibia.” Regarding the cranial openings, standard negative allometry of the orbit with increasing body size suggests that there is nothing unusual about the size of the orbit in a form as small as *Scleromochlus*. The antorbital and temporal fenestrae and the external nares are not unusually large. The scapular blade is not long and strap-shaped, but rather is remarkably short and expands to a distal width approximately twice its proximal width (well preserved in BMNH R3914). The pelvis is triradiate, rather than trapezoid, in lateral view and does not resemble that in pterosaurs in any special way. The distal end of the fibula is not preserved in any specimen; the distal end of the fibula may not have been fused to the tibial shaft because the preserved distal shaft of the fibula is rod-shaped rather than splintlike (BMNH R3556, R4823). Finally, the form of the proximal tarsals is not shown in the natural molds; whether the tibia and proximal tarsals are coossified is a matter of conjecture. Gauthier (1984:117) provided additional characters to link *Scleromochlus* and pterosaurs, including “characteristic metatarsal/tibia/femur ratio,” “‘pterosaur’ 4th distal tarsal,” and “coossified 2nd and 3rd distal tarsals.” But no particular hind-limb ratio was specified, and elongate epipodial proportions are plesiomorphic within Ornithodira. A “pterosaur” distal tarsal 4 is not a character but rather an unsubstantiated claim that such a character might exist. And no evidence has been presented that the medial distal tarsal in *Scleromochlus* or in pterosaurs represents both distal tarsals 2 and 3,

TABLE 2. Skull and limb-bone length (in mm) of *Scleromochlus taylori*. Forelimb measurements from BMNH R3556; all other measurements from BMNH R3557.

Skull	31	Metacarpal 3	3
Humerus	21	Femur	33
Ulna	18	Tibia + astragalus	35
Digit III	6	Metatarsal 1	19

rather than just distal tarsal 3, as in archosaurs plesiomorphically (Romer, 1956).

Although four synapomorphies are described above that support a sister-taxon relationship between *Scleromochlus* and Pterosauria, an equal number of features unite *Scleromochlus* with Dinosauiromorpha and at basal nodes within this group: The length of the forelimb is less than 50 percent of hind-limb length, the femoral head projects medially perpendicular to the shaft axis rather than anteromedially, the distal tibia is transversely expanded with a subrectangular end, the astragalus appears to be characterized by a broad ascending flange as in dinosaurs, and metatarsal 5 is reduced and appears to lack the strong lateral deflection of the digit.

The interpretation of the tarsus has been a point of controversy. Two tarsal elements, one overlapping the other, are distarticulated a short distance from the crus and metatarsus (Fig. 17B; BMNH R3557). These were first identified by Woodward (1907) and Huene (1914) as the astragalus and calcaneum and later by Padian (1984; incorrectly labelled BMNH R3556) as the medial and lateral distal tarsals. The best exposed element indeed does resemble a left crurotarsal calcaneum in lateral view, but this resemblance must be misleading because the bone clearly belongs to the right tarsus. The bone thus is best identified as distal tarsal 4 as suggested by Padian. The second disc-shaped element thus probably represents distal tarsal 3. A subtle raised lip on the anterior side of the distal end of the tibia may indicate the dorsal margin of a broad astragalar ascending process. If this interpretation is correct, the astragalus would form a cap over the distal end of the tibia, thus accounting for the absence of a separate astragalar ossification in partially articulated remains that preserve all other bones of the tarsus and metatarsus. The subrectangular distal articular surface of the tibiotarsus is subcylindrical, rather than spool-shaped as in pterosaurs, with no development of separate distal condyles.

The bound metatarsus is composed of four elongate metatarsals (1–4) and a short metatarsal 5 with a stout base (Fig. 17B). Metatarsal 5 is preserved in place in BMNH R3556, exposing a beveled proximal articular surface for the lateral distal tarsal. It nearly parallels the other metatarsals in BMNH R3556 but is more divergent in BMNH R5589. The natural orientation of metatarsal 5 thus is scored as unknown in the data matrix. Several phalanges and unguals are preserved but the phalangeal formula cannot be determined.

## PHYLOGENETIC RESULTS

### Archosaurian Phylogeny

A single shortest tree (Figs. 26A, 27) resulted from parsimony analysis of skeletal data in basal archosaurs and archosaur outgroups (36 characters, 9 taxa, 42 steps, C. I. 0.88; see Appendix). The principal phylogenetic conclusions are as follows.

(1) Archosaurian monophyly is supported by only three unequivocal skeletal synapomorphies: the loss of palatal teeth, posterior orientation of the calcaneal tuber, and a new configuration of the articular facets on the calcaneum. The broad range of archosaurian synapomorphies in current cladistic literature may be more indicative of a strong belief that this group must be monophyletic than of abundant supporting evidence. These characters (e.g., antorbital fossa, parietal occipital processes, pterygoids meeting along midline, exoccipital-opisthotic coossification, presence of an otic notch, thecodont tooth implantation, absence of cervical intercentra, spine tables, short lateral processes on the interclavicle, etc.; Gauthier, 1984, 1986; Gauthier et al., 1988; Benton and Clark, 1988) either have an equivocal distribution or diagnose more inclusive groups than Archosauria.

(2) Archosauria is composed of two subclades, Crurotarsi and Ornithodira, which include extant crocodilians and birds, respectively, and their fossil archosaurian relatives. The monophyly of crurotarsal archosaurs (Suchia, Ornithosuchidae, Parasuchia) is supported by seven unequivocal synapomorphies in the forelimb and hind-limb, including a hemispherical (crurotarsal) articulation in the ankle that is unique among tetrapods (Serenó, 1989; Sereno and Arcucci, 1990). Ornithodira is supported by 10 unequivocal girdle and limb synapomorphies. Four are newly proposed for this clade (26, 28–30; see Appendix) and six (22–24, 27, 31, 32) were used previously in nearly the same form by Gauthier (1986:43), who first explicitly recognized this clade.

Previous character lists for Ornithodira appear to be inflated. The 15 or 16 additional synapomorphies listed by Gauthier (1986) and several more by Benton and Clark (1988:334) appear to be either inconsistent with available fossil materials and the primary literature or redundant. As an example of the former, Benton and Clark (1988:334) cited the longer length of the pubis in support of Ornithodira when these conditions are variable in basal ornithodirans (pterosaurs, *Lagerpeton*, *Lagosuchus*, and Dinosauria). Character redundancy has occurred when relative size measures are not specified; both “astragalus transversely widened” and “calcaneum reduced” have been listed as ornithodiran synapomorphies (Gauthier, 1986:43). Redundancy also occurs when functional constructs or postures are used along with the characters upon which they are based; for example, both “pes digitigrade” and “metatarsals elongate and closely appressed” have been listed as ornithodiran synapomorphies (Gauthier, 1986:43).

The group name “Ornithodira” was coined for the supposed apomorphic “S-shaped” neck or “regionalized” presacral column in this archosaurian clade (Bonaparte, 1975a; Gauthier, 1984, 1986; Benton and Clark, 1988). In the present analysis, there are no unequivocal synapomorphies in the ornithodiran cervical column. The anterior cervical column in pterosaurs, *Scleromochlus*, and many dinosaurs is not elevated any more than in other basal archosaurs, and the elongation of the anterior cervicals (C3–5; synapomorphy 21) is equivocal as an ornithodiran synapomorphy due to the short cervical centra in *Scleromochlus*.

(3) Crurotarsi is composed of three taxa, Parasuchia, Ornithosuchidae, and Suchia. The monophyly of both Parasuchia and Ornithosuchidae is strongly supported whereas suchians (*Gracilisuchus stipanicorum*, Aetosauria, Rauisuchia, Poposauridae, and Crocodylomorpha) are united by only a single cranial synapomorphy. The interrelationships of Parasuchia, Ornithosuchidae, and Suchia are problematic. Only two synapomorphies of the pelvic girdle provide resolution within Crurotarsi, uniting Ornithosuchidae and Suchia (synapomorphy 13, relative lengthening of the pubis; synapomorphy 14, recessed posterior portion of the pubic acetabular margin). Both characters exhibit some homoplasy or variability within or outside the clade. The single apomorphy shared by Ornithosuchidae and Parasuchia (synapomorphy 18, extensive dentary-splenic symphysis) is considered a parallelism; the extensive symphysis is an unusual feature in the short-snouted ornithosuchids but in phytosaurs it is surely correlated with their narrow piscivorous snout. There are no unequivocal apomorphies shared by the so-called “crocodile-normal” archosaurs, Suchia, and Parasuchia (contra Gauthier, 1984, 1986; Benton and Clark, 1988).

(4) Ornithodira is composed of two taxa, Pterosauria and Dinosauria, and the reputed pterosaurian ancestor *Scleromochlus*. Character evidence for the monophyly of these taxa is strong. Pterosauria is characterized by approximately 40 synapomorphies, many of which do not appear to be related to flight function. Dinosauria monophyly is supported by seven synapomorphies (characters AA–GG; see Appendix). A previous suggestion that pterosaurs, rather than *Lagerpeton* or *Lagosuchus*, are closer to Dinosauria (Gauthier, 1984) thus appears unlikely. At least two autapomorphies characterize *Scleromochlus*, which previously had been considered either a pterosaurian ancestor or “metataxon” (Gauthier, 1984, 1986).

Whether *Scleromochlus* is closer to Pterosauria or Dinosauria is uncertain due to conflicting character distributions and missing data. In this analysis, *Scleromochlus* and Pterosauria share four synapomorphies, two of which are new (short scapula, absence of the femoral fourth trochanter). Ten additional synapomorphies have been postulated to unite *Scleromochlus* and pterosaurs (Gauthier, 1984; Padian, 1984) but these are either inconsistent with the natural molds or are not preserved. The relationships of *Scleromo-*

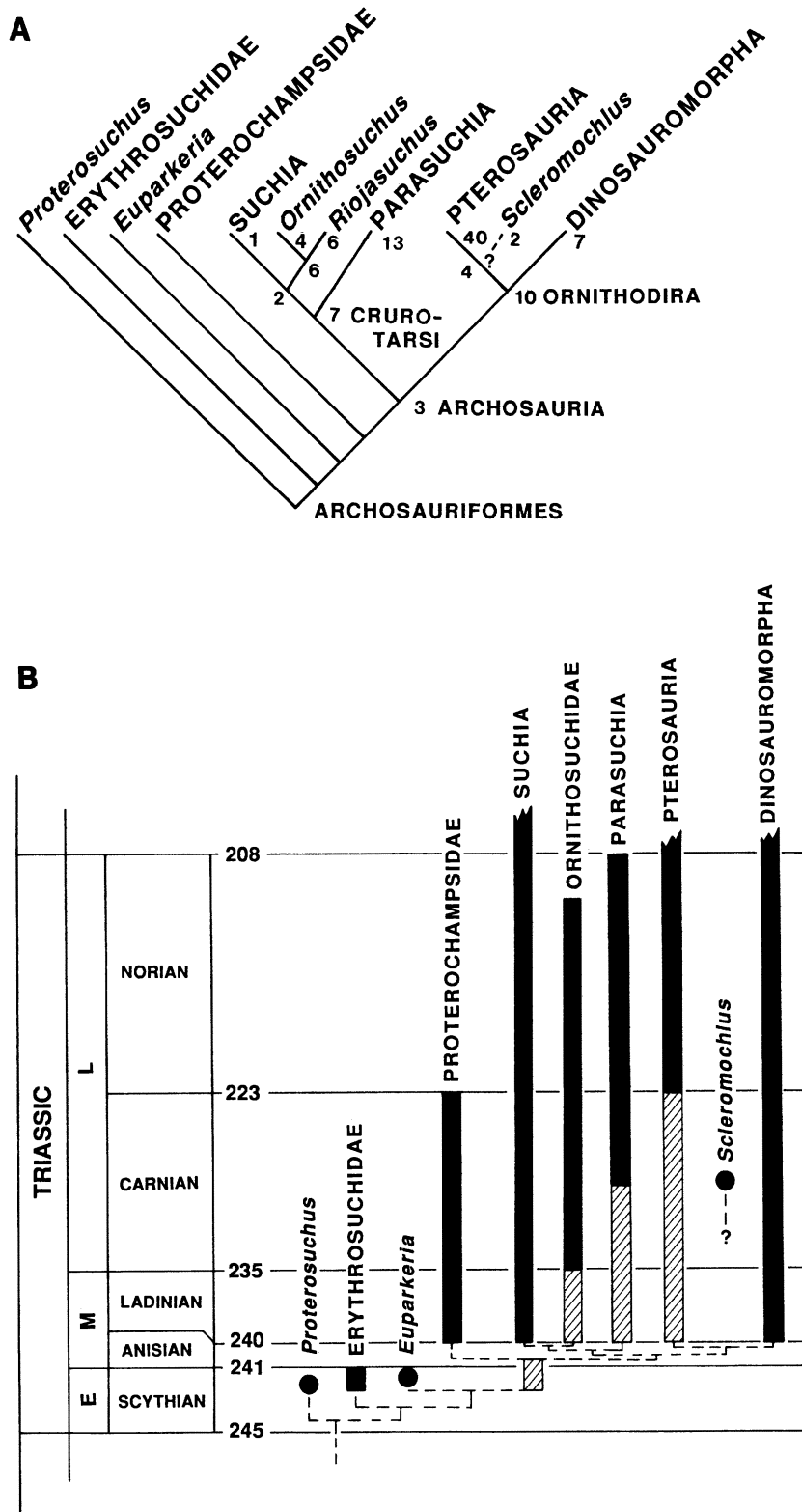
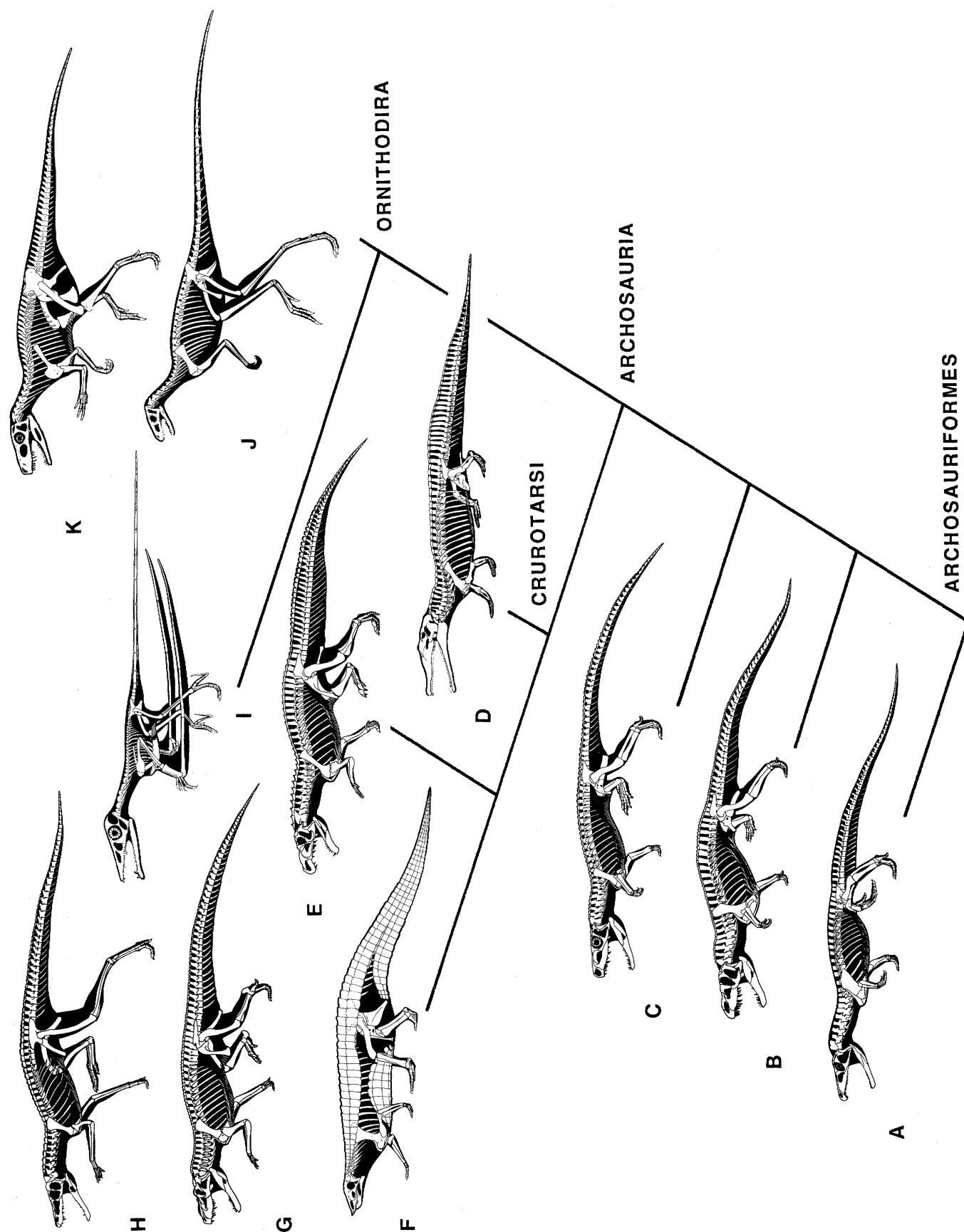


FIGURE 26. Phylogeny and biochronology of Archosauriformes. **A**, Cladogram showing number of autapomorphies supporting each terminal taxon and the number of unequivocal synapomorphies at each internal node. **B**, Biochronology based on cladogram and recorded temporal range with time scale following Harland et al. (1990).



*chilus* within Ornithodira are uncertain. Some evidence even raises a question as to its status as an ornithodiran.

(5) The principal lineages of early archosaurs appear to have radiated over a short period of time during the Middle Triassic (Anisian, Ladinian), based on known stratigraphic ranges and the current geological time scale (Harland et al., 1990). The presence of suchians and dinosauromorphs in the Ladinian (Los Chañares, Monte San Giorgio, Manda faunas) suggests that their sister-taxa Ornithosuchidae, Parasuchia, and Pterosauria must have diverged within or before the Ladinian. The most significant unsampled lineages pertain to parasuchians and pterosaurs during the Carnian. Divergence times for basal archosaurian clades are only approximations given the absence of radiometric dates for Triassic terrestrial faunas.

### “Pseudosuchia” vs. “Ornithosuchia”

By the late 1970s, a broad consensus emerged that archosaurs could be split into two clades, each acquiring a divergent crurotarsal ankle design—“crocodile-normal” and “crocodile-reversed” (Chatterjee, 1978, 1982; Cruickshank, 1979; Brinkman, 1981). Gauthier (1984, 1986) restructured this basal split to include the two extant descendant clades, crocodiles and birds. As he remarked, “Chatterjee’s divisions [Pseudosuchia, Ornithosuchia] represent a broad consensus that emerged as an outgrowth and refinement of Krebs’ (1963, 1965) and Bonaparte’s (1975a) observations that archosaurian ankle joints are organized according to two different morphological plans. The conceptual basis for the groups proposed here differs from that of previous workers, because Ornithosuchia and Pseudosuchia are here applied to strictly monophyletic taxa” (Gauthier, 1984:107–108).

The monophyly of these clades is challenged by the present analysis. *Euparkeria* appears to represent an archosaurian outgroup, and ornithosuchids are more parsimoniously placed with other crurotarsal archosaurs in Crurotarsi on the basis of seven unequivocal synapomorphies. Reconstituting “Ornithosuchia” (sensu Gauthier) by placing ornithosuchids as the sister-taxon to Ornithodira requires eight additional steps, given the data matrix in the Appendix. Including *Euparkeria* in this assemblage requires 12 additional steps. Unless the data are seriously flawed, the monophyly of “Pseudosuchia” and “Ornithosuchia” cannot be maintained.

The characters supporting “Pseudosuchia” and

“Ornithosuchia” are equivocal at best. Most of the synapomorphies listed for “Pseudosuchia” by Gauthier (1986) and Benton and Clark (1988) were acknowledged to occur in “ornithosuchians” by the same authors and have equivocal distributions on their cladograms. The key remaining character, the “crocodile-normal ankle joint,” is not a character but rather a character complex. The only difference between “crocodile-normal” and “crocodile-reversed” ankle joints is the form of the ventral astragalocalcaneal articulation, a multistate character (synapomorphy 19) that lends no support to “pseudosuchian” monophyly.

Supposed “ornithosuchian” synapomorphies are also equivocal or poorly defined (Serenó and Arcucci, 1990). Eight out of 12 “ornithosuchian” synapomorphies listed by Benton and Clark (1988) have equivocal distributions on their phylogeny with equally parsimonious alternative interpretations. Many “ornithosuchian” features are functional constructs, rather than discrete characters, such as “modifications in the hind limb and girdle correlated with semi-erect gait” and “crocodile-reversed ankle joint” (Gauthier, 1986:43). Other proposed synapomorphies are composite characters that are not supported by the literature or specimen examination, such as “first metatarsal with offset distal condyles, and pollex directed medially and bearing enlarged ungual” (Gauthier, 1986:43; see Sereno and Arcucci, 1990). Some are ontogenetic characters that cannot be verified in the majority of fossil forms, such as “anterior trochanter on femur appears early in post-hatching ontogeny” (Gauthier, 1986:43). Finally, some are proportions that are not specified exactly enough to test, such as “fifth metatarsal gracile” (Gauthier, 1986:43). Metatarsal 5 does not appear to be any less robust in ornithosuchids than in pterosaurs or a wide range of other basal archosaurs (Fig. 14).

### Ankle “Types”

After Cruickshank (1979) divided archosaurs into “crocodile-normal” and “crocodile-reversed” clades on the basis of ankle form, many additional ankle “types” were proposed to accommodate “primitive,” “primitive-intermediate,” “incipient,” “fully-developed,” and “vestigial” conditions of the “normal” and “reversed” patterns (Table 3). In traditional analyses ankle form has been accorded special significance and the transformation between “normal” and “reversed” patterns has been regarded as implausible. In previous cladistic schemes, ankle “types” have been used as if they represent discrete, non-overlapping character data.

FIGURE 27. Archosauriform phylogeny. A, *Proterosuchus vanhoepeni* (from Parrish, 1986). B, *Vjushkovia triplicostata* (from Parrish, 1986). C, *Euparkeria capensis* (from Parrish, 1986). D, *Rutiodon* sp. (from Parrish, 1986). E, *Riojasuchus tenuiceps* (from Parrish, 1986). F, *Stagonolepis robertsoni* (modified from Walker, 1961). G, *Saurosuchus galilei* (from Parrish, 1986). H, *Pseudhesperosuchus jachaleri* (from Parrish, 1986). I, *Eudimorphodon ranzii*. J, *Lagosuchus talampayensis*. K, *Herrerasaurus ischigualastensis*. (I–K original.)

TABLE 3. Proposed ankle types and locomotor postures/gaits in basal archosaurs. Data on postures and gaits from Walker (1970), Bakker (1971), Charig (1972), Bakker and Galton (1974), Brinkman (1979), Bonaparte (1984), Crush (1984), and Parrish (1986, 1987).

Ankle type	Original author
Primitive mesotarsal	Chatterjee, 1982
Modified primitive mesotarsal	Cruickshank and Benton, 1985
Duplex	Thulborn, 1980
Crocodile-normal	Chatterjee, 1978
Fully developed crocodile-normal	Gauthier, 1986
Crocodile-reversed	Chatterjee, 1978
Advanced mesotarsal	Chatterjee, 1982
Advanced mesotarsal normal	Chatterjee, 1982
Advanced mesotarsal reversed	Chatterjee, 1982

Posture/Gait	Taxa
Sprawling	<i>Proterosuchus</i> , erythrosuchids, phytosaurs, aetosaurs, ?proterochampsids
Semi-erect	<i>Euparkeria</i> , phytosaurs, some rauisuchians and ornithosuchids, crocodilians
Erect gait	Basal crocodylomorphs, rauisuchians, ornithosuchids, aetosaurs, dinosaurs

A “crocodile-normal” ankle joint, however, does not specify an anatomical feature as does a character such as a “calcaneal tuber.” Rather, it represents a character complex involving many features.

When ankle structure is coded as discrete character data as in this study, the only difference between “crocodile-normal” and “crocodile-reversed” ankle joints is the configuration of the ventral astragalocalcaneal articulation; it is concavoconvex in both, but the polarity of the articular surfaces on the astragalus and calcaneum is reversed. Because this articulation is planar in archosaurian outgroups, it is interpreted here as an unordered multistate character (synapomorphy 19). Despite the attention given to this articulation, its transformations do not unequivocally support any of the major clades of basal archosaurs on the most parsimonious tree. Both “normal” and “reversed” ankle designs, to the contrary, exhibit striking modifications that do not occur among ornithodirans or archosaurian outgroups (synapomorphies 7–10). The hemicylindrical calcaneal condyle, in fact, is unique among tetrapods and constitutes important evidence supporting Crurotarsi. The phylogenetic significance of these and other characters in the ankle has been overlooked due to efforts to shoehorn character variation into non-overlapping ankle “types.”

### Crurotarsi?

Both “Ornithosuchia” and, particularly, “Pseudosuchia” have been applied historically to various archosaur assemblages. “Ornithosuchia” was originally coined for a few ornithosuchids and *Euparkeria* (Chatterjee, 1982). “Pseudosuchia” is a much older term that eventually subsumed a paraphyletic middle grade of archosaurs that pointedly excluded crocodilian descendants. These terms have recently been redefined phylogenetically, as archosaurs more closely related to extant birds and crocodilians, respectively (Gauthier, 1984, 1986). If, as accepted in this work, Archosauria is defined as the most recent common ancestor of birds and crocodiles and all of their descendants (Gauthier, 1984, 1986), then “Ornithosuchia” and “Pseudosuchia” could also be applied to the phylogenetic scheme presented in this work; “Pseudosuchia” would encompass all crurotarsal archosaurs, and a new name for this clade would be redundant. Thus, is the taxonomic designation Crurotarsi Sereno et Arcucci, 1990 necessary?

Recent cladistic redefinition of “Ornithosuchia” and “Pseudosuchia” as monophyletic clades has significantly altered traditional usage of these terms. “Pseudosuchia” was recast to include, rather than exclude, crocodilians, and “Ornithosuchia” now subsumes all ornithodirans (including birds), rather than just a small subset of Triassic forms. These phylogenetic definitions are now in use in cladistic discussions of archosaurian phylogeny.

In the present review, however, ornithosuchids are united with other crurotarsal archosaurs and, thus, are removed from “Ornithosuchia,” as defined by Gauthier. Following his definition, ornithosuchids would then be regarded as “pseudosuchians.” Removing ornithosuchids from “Ornithosuchia,” in addition, creates taxonomic redundancy. “Ornithosuchia” was defined phylogenetically as a stem-based taxon (de Queiroz and Gauthier, 1990) that includes all archosaurs close to birds (Gauthier, 1986:42); it would thus supplant as a senior synonym the now widely recognized stem-based taxon Ornithodira.

To complicate matters further, Benton (in Benton and Clark, 1988; Benton, 1990a) has proposed the term “Crocodylotarsi” to replace Gauthier’s “Pseudosuchia.” “Crocodylotarsi,” apparently, is an apomorphy-based taxon that refers to the presence of a functional complex (the so-called “crocodile-normal” ankle joint). This apomorphy specifically excludes ornithosuchids, according to Benton. The new scheme presented here, however, questions the utility of ankle “types” as apomorphies and places ornithosuchids among other crurotarsal archosaurs. The use of “Crocodylotarsi” to encompass all crurotarsal archosaurs, rather than a subset, would only engender confusion.

A preferable nomenclatorial solution for archosaurian systematics is to subdivide Archosauria into Ornithodira and Crurotarsi, the latter constituting a stem-based taxon that unites all crurotarsal archosaurs including extant crocodilian descendants.

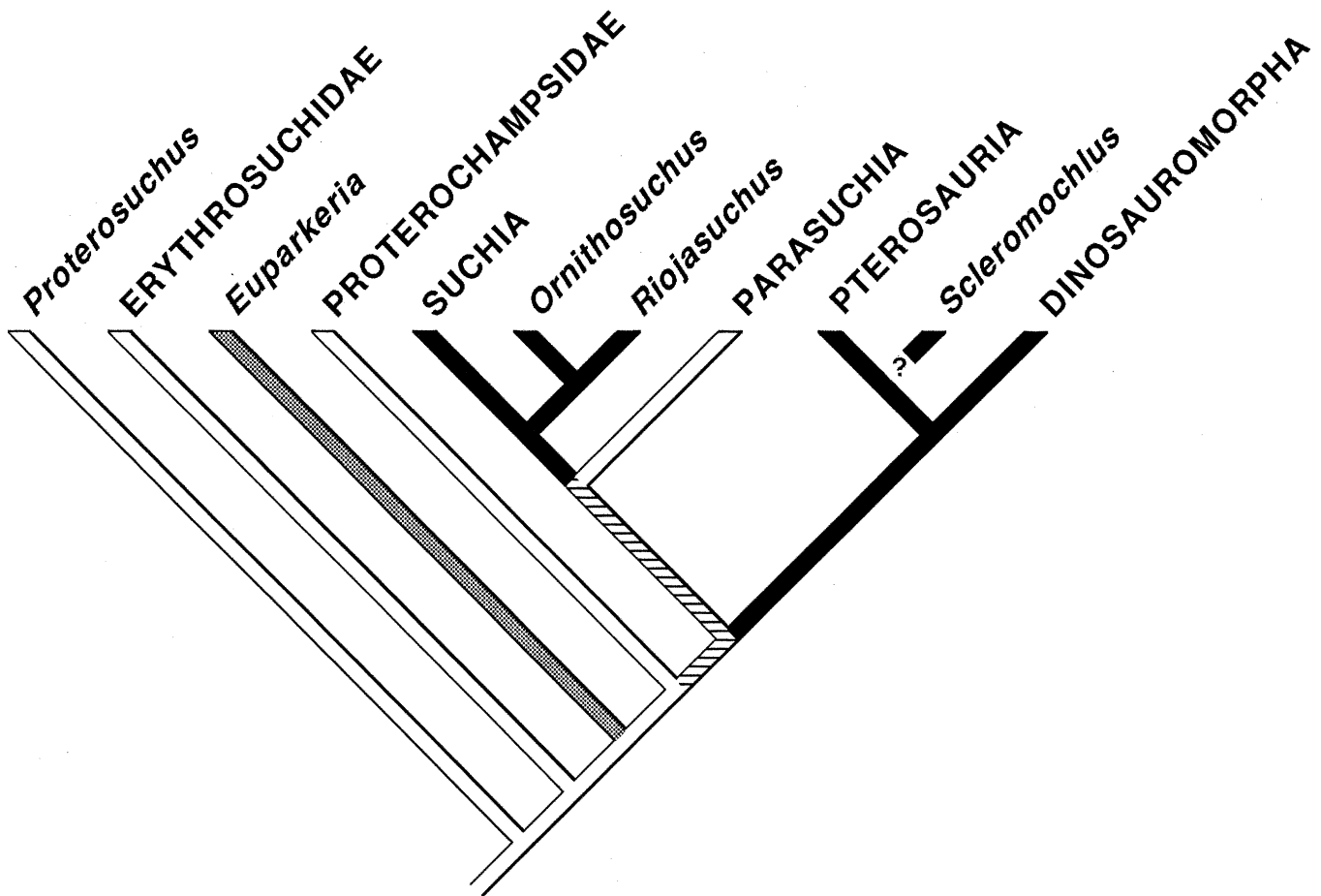


FIGURE 28. Evolution of locomotor posture superimposed on the most parsimonious tree based on skeletal morphology. Terminal branches indicate states of terminal taxa. Open = sprawling; stippled = semi-erect; solid = erect; cross-hatched = equivocal.

## EVOLUTION OF LOCOMOTOR FUNCTION

### Postural Transformation

Most studies of locomotor function among archosaurs have maintained, either explicitly or implicitly, that locomotor posture has gradually transformed from sprawling through semi-erect to fully-erect postures during the course of archosaurian phylogeny (Bakker, 1971; Charig, 1972; Cruickshank, 1979; Parrish, 1986). A sprawling posture appears to be primitive for Archosauriformes, given the pelvic and hind-limb morphology present in the basal archosauriform *Proterosuchus* and various archosauriform outgroups (Protosauria, Choristodera, *Trilophosaurus*). A transformation from sprawling to a more erect posture thus must have occurred within Archosauriformes at least once given the erect posture of many later archosaurs.

Inference of locomotor posture from fossil materials has some serious limitations. Except for the postural extremes—semi-aquatic sprawlers and fully erect cursors—more than a single locomotor posture has been

postulated for several archosaurian subgroups (Table 3). Much of the problem lies with the necessary, but arbitrary, division of locomotor postures into three grades—sprawling, semi-erect and fully erect—and the absence of any modern analogue for terrestrial semi-erect forms such as *Euparkeria* or possibly the ornithosuchid *Riojasuchus*. Furthermore, the assignment of a particular posture implies that a given tetrapod is capable of only a single locomotor posture. Living crocodilians and lepidosaurs, however, demonstrate that locomotor posture can vary with speed, growth stage, and body size; “sprawlers” may exhibit true sprawling locomotion only at very slow speeds, and at least some semi-erect crocodilians are capable of a full gallop (Webb and Gans, 1982).

Presumed locomotor postures for various archosaurian clades, nevertheless, can be plotted on the cladogram for Archosauria to examine the evolution of locomotor posture (Fig. 28). Judging from the cladogram, transitions toward more erect posture are as common as transitions toward lower posture; phytosaurs, advanced crocodilians, and possibly proterochampsids

all appear to have lowered their posture as an adaptation to a semi-aquatic mode of life (Parrish, 1986). Sequential transformation from sprawling through an intermediate semi-erect posture to an erect posture (or the reverse) is not apparent; direct transitions between sprawling and erect postures, it seems, may have occurred. Finally, erect posture may not have arisen independently in three or four archosaurian clades (e.g., Benton, 1990b) but rather only once in the ancestral archosaur.

Thus three common suppositions about the evolution of erect posture in archosaurs can be questioned by the sequence of presumed locomotor postures in archosaurian phylogeny. First, evidence of sequential transformation through an intermediate semi-erect stage (if indeed such a functional state is recognizable in fossil forms) is not obvious; erect posture, it seems, may have arisen from sprawling precursors. Second, trends toward more erect posture among Triassic archosaurs do not necessarily predominate; transitions to more erect posture may not outnumber transitions toward sprawling posture. Third, the widespread belief that erect posture evolved in parallel in Crurotarsi and Ornithodira (Cruickshank, 1979; Chatterjee, 1982; Parrish, 1986), or independently within subgroups of these clades (Benton, 1990b), is not the only possible, or even probable, interpretation. Judging from the pattern of locomotor postures, the common archosaurian ancestor may have been erect, with reversion to a sprawling posture in the semi-aquatic phytosaurs. Variation in hip joint (closed, open, buttress, pillar) or foot posture (plantigrade, digitigrade) in erect archosaurs does not necessarily indicate that erect posture arose independently in each subgroup (contra Bonaparte, 1984; Benton, 1990b:295–296). Erect ankylosaurid dinosaurs evolved a pillar-style hind-limb with a near horizontal, closed acetabulum, but this condition is clearly derived from the inturned femur and vertical, open acetabulum of erect ankylosaurian outgroups. The antecedent condition for erect archosaurian clades must be established; it is not enough to postulate independent origins of erect posture on the basis of differences in hip or ankle joint design.

### **“Improvement” in Locomotor Design**

Radiations and faunal replacements are often explained in terms of competitive advantage, with the success of one taxon over others due to a key innovation or adaptation (Benton, 1987; Nitecki, 1988). In archosaurian phylogeny, the transition from primitive sprawlers to advanced erect forms is commonly regarded as the principal “improvement” that culminated in the replacement of semi-erect non-mammalian synapsids and rhynchosaurs by erect dinosaurs at the end of the Triassic (Bakker, 1971, 1986; Charig, 1972, 1984; Bonaparte, 1982). Charig (1972:121) remarked that “the most important characteristic of the archosaurs, to which they owed their dominant position in the land faunas of the Mesozoic, was their de-

velopment of greatly improved methods of locomotion.” Bakker (1971) explained the competitive advantage of erect dinosaurs in terms of locomotor efficiency; less energy was required to maintain an erect posture owing to the more direct transmission of weight through the limbs. Parrish (1986:32) suggested that erect gait may have “increased maneuverability on land.” Recently, Carrier (1987:337) argued that the evolution of stamina in erect forms is the key adaptation; the radiation of erect ornithomirids, he suggested, “may in large part be founded in an early ability to breathe during running.”

The supposed mechanical superiority of erect posture, however, is not evident in studies on extant tetrapods. An erect parasagittal gait is not more efficient than a sprawling gait at slow speeds (Bakker, 1972; Taylor, 1973; Bennett, 1985). Nor does an erect gait entail a speed advantage over short distances. Likewise, it has not been demonstrated that an erect gait permits greater maneuverability in terrestrial habitats. Finally, although erect posture is associated with stamina and endothermy in present-day mammals and birds (Bakker, 1971; Carrier, 1987), the evidence for correlated evolution of these physiological features with erect posture in early archosaurs is weak. First, as Carrier noted, extant crocodilians are ectothermic and lack appreciable stamina despite their erect crocodilian ancestors. Other osteological correlates of erect posture and stamina, according to Carrier (1987), include bipedal posture, increased size of transverse processes in trunk vertebrae, and increased lateral stability of the trunk by addition of vertebrae to the sacrum and by anterior expansion of the ilium. However, many erect basal archosaurs, dinosaurs, and primitive mammals are obviously not bipedal. Likewise, long transverse processes in the trunk vertebrae also occur in sprawling or semi-erect archosaur outgroups (e.g., proterochampsids, *Euparkeria*; Romer, 1972b; Ewer, 1965). Many erect basal archosaurs have not added vertebrae to the sacrum or expanded the anterior blade of the ilium.

Competitive scenarios for the evolutionary success of erect archosaurs over less erect forms also contradict evidence from the fossil record, which suggests that erect archosaurs arose and persisted alongside sprawling and semi-erect forms for most of the Middle and Late Triassic. The dinosaurian radiation at the end of the Triassic postdates the extinction of non-mammalian synapsids and of rhynchosaurs and thus appears to be an opportunistic, rather than competitive, replacement (Benton, 1983, 1987). Erect dinosaurs and mammals have dominated large-bodied terrestrial faunas since the Triassic, but we as yet have no satisfactory explanation for this historical pattern.

### **Bipedalism and the Evolution of Powered Flight**

All bipeds have an erect posture with parasagittal motion of the hind-limbs. Erect posture, indeed, may be a functional prerequisite for bipedalism; obligate

bipeds must balance the body principally over a single leg support during locomotion (Gatesy and Biewener, 1991), and this may be difficult or impossible to maintain with wide-tracking sprawling or semi-erect postures. Bipedalism, in turn, may be a functional prerequisite for achieving powered flight from the ground up; the forelimbs of a biped are freed from the functional constraints of quadrupedal locomotion. Powered flight evolved twice among archosaurs, in pterosaurs and birds, and in both cases the outgroups and basal members of the volant clades were obligate bipeds. Basal "rhamphorhynchoid" pterosaurs (Fig. 18A) and the primitive bird *Archaeopteryx* (as well as their respective outgroups, basal dinosauromorphs and theropods) are obligate bipeds during terrestrial locomotion, with erect bipedal posture, cursorial hind-limb proportions, a digitigrade pes, and stiff balancing tail (Padian, 1983b). The phylogeny of basal archosaurs (Figs. 26–28) suggests that the initial appearance of obligate bipedalism and powered flight may have been closely associated. Obligate bipedalism first arose among tetrapods in ornithodiran ancestors sometime during or before the Middle Triassic (Fig. 26B). Pterosaurian remains are not known prior to the Norian but their lineage must have extended back to the Middle Triassic (Fig. 26B). By the end of the Middle Triassic, the presence of small-bodied, bipedal dinosauromorphs such as *Lagosuchus* (Fig. 18C) indicates that basal ornithodirans had already split into two clades—one that included *Lagosuchus* and would lead to dinosaurs and their avian descendants and a second that gave rise to pterosaurs, the first vertebrates capable of powered flight.

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# APPENDIX

## TERMINAL TAXA

### Character List and Taxon-Character-State Matrix

The coding and distribution of 33 characters used to diagnose six of the seven archosaur terminal taxa are given below. See text for the 40 synapomorphies used to diagnose Pterosauria.

#### Suchia

- A. Laterotemporal fenestra shape: subrectangular with substantial postorbital-squamosal bar (0); subtriangular with short postorbital-squamosal bar (1).

#### *Ornithosuchus longidens*

- B. Maxilla with free posterior prong: absent (0); present (1).  
C. Postorbital crest: absent (0); present (1).  
D. Ventral margin of posterior end of lower jaw: convex (0); concave and elevated (1).  
E. Surangular foramen location: above (0) or adjacent to (1) the surangular-angular suture.

#### *Riojasuchus tenuiceps*

- F. Anterior snout and external narial form: small (0); large and overhanging (1).  
G. Antorbital fossa ventral margin position: dorsal to (0) or coincident with (1) the ventral margin of maxilla.  
H. Jugal bar shape between antorbital and laterotemporal fenestra: anteroposteriorly elongate (0); dorsoventrally deep (1).  
I. Occiput orientation: 50 degrees (0) or only 20 degrees (1) above the horizontal.  
J. Atlantal neural arch bases: separated (0) or sutured (1) in the midline.  
K. Radial and ulnar shaft dimensions: robust and in mutual contact distally (0); slender and separated distally (1).  
L. Distal tarsal 3 dimensions: dorsoventrally compressed (0); transversely compressed (1).

#### Parasuchia

- M. Occiput dimensions: height twice width (0); height subequal or less than half width (1).  
N. Premaxillary rostrum length: short (0); elongate with prenasal length equal to or exceeding postnasal length (1).  
O. Piscivorous snout: absent (0); present (1).  
P. Principal orientation of external naris and orbit: lateral (0); dorsal (1).  
Q. Quadratojugal shape: L-shaped (0); subtriangular (1).  
R. Nasal anterior extension: between (0) or anterior to (1) external naris.  
S. Paramedian "septomaxilla": absent (0); present (1).  
T. Premaxillary-palatine contact: absent (0); present (1).  
U. Palatine secondary palatal shelves: absent (0); present (1).  
V. Postpalatine fenestra size: moderate (0); very small (1).  
W. Coracoid shape: subcircular (0); crescentic (1); strut-shaped (2).  
X. Interclavicle size: slender (0); long and broad (1).

#### *Scleromochlus taylori*

- Y. Skull proportions at mid length: width subequal to height (0); width twice height (1).  
Z. Raised maxillary margin of antorbital fossa: absent (0); present (1).

#### Dinosauromorpha

- AA. Centrum shape in presacals 6–9 (or 10): subrectangular (0); parallelogram-shaped (1).  
BB. Forelimb/hind-limb ratio: more than 0.5 (0); 0.5 or less (1).  
CC. Astragalar anteromedial corner shape: obtuse (0); acute (1).  
DD. Size of distal articular surface of calcaneum: transverse width more (0) or less (1) than 35 percent of that of the astragalus.  
EE. Articular facet size for metatarsal 5 on distal tarsal 4: more than (0) or less than (1) half of lateral surface of distal tarsal 4.  
FF. Orientation of articular surface for distal tarsal 4 on metatarsal 5: angling 20 to 40 degrees (0) or subparallel (1) to shaft axis.  
GG. Metatarsal 1 and 5 mid-shaft diameters: subequal or greater than (0) or less than (1) those of metatarsals 2–4.

Taxon	Characters						
	E	J	O	T	Y	DD	
Suchia	10000	00000	00000	00000	00000	00000	000
<i>Ornithosuchus</i>	01111	00000	?0000	00000	00000	00000	?00
<i>Riojasuchus</i>	00000	11111	11000	00000	000?0	00000	000
Parasuchia	00000	00000	00111	11111	11111	00000	000
Pterosauria	00000	00000	X0000	00001	002X0	0000X	000
<i>Scleromochlus</i>	?000?	000??	?0000	0????	???X1	101??	?10
Dinosauromorpha	00000	00000	00000	00000	000X0	01111	111

Character-state abbreviations: 0 = plesiomorphic state; 1 = apomorphic state; 0 = plesiomorphic state for clade with some ingroup variation; 1 = apomorphic state for clade with some ingroup variation; X = unknown as a result of transformation; ? = not preserved/unknown.

## INGROUP CLADES

## Character List and Taxon-Character-State Matrix

The coding and distribution are shown below for 36 characters in seven archosaur taxa and in two proximate outgroups. All characters but one are binary, and all character-state transformations are considered equally probable. The data matrix was subjected to parsimony analysis using the branch-and-bound algorithm in PAUP (Swofford, 1985). A single most parsimonious tree was determined with a length of 42 steps and a consistency index of 0.88.

1. Palatal teeth (pterygoid, palatine, vomer): present (0); absent (1).
2. Calcaneal tuber orientation: less (0) or more (1) than 45 degrees posterior deflection.
3. Calcaneal facets for fibula and distal tarsal 4: separated (0); contiguous (1).
4. Medial margin of proximal humerus: weakly (0) or strongly (1) arched.
5. Fibular anterior trochanter: crest-shaped, low (0); knob-shaped, robust (1).
6. Fibular distal end width: subequal or less (0) or greater (1) than proximal end.
7. Astragalar tibial facet: concave (0); flexed (1).
8. Hemicylindrical calcaneal condyle: absent (0); present (1).
9. Calcaneal tuber shaft proportions: taller than broad (0); broader than tall (1).
10. Calcaneal tuber distal end: rounded (0); flared (1).
11. Ventral astragalocalcaneal articular facet size: small (0); large (1).
12. One-to-one alignment between dorsal body osteoderms and vertebrae: absent (0); present (1).
13. Pubis length: shorter (0) or longer (1) than ischium.
14. Pubic acetabular margin, posterior portion: continuous with anterior portion (0); recessed (1).
15. Two-tooth diastema: absent (0); present (1).
16. Nasal-prefrontal contact: present (0); very reduced or absent (1).
17. Palatine-pterygoid fenestra: absent (0); present (1).
18. Dentary-splenial mandibular symphysis length: distally positioned (0); present along one-third of lower jaw (1).
19. Astragalocalcaneal ventral articular surface: flat (0); concavoconvex with concavity on calcaneum (1); concavoconvex with concavity on astragalus (2).
20. Pedal ungual depth: shallow (0); deep (1).
21. Cervical 3–5 centrum length: shorter (0) or longer (1) than mid-dorsal.
22. Dorsal body osteoderms: present (0); absent (1).
23. Interclavicle: present (0); absent (1).
24. Clavicle: present (0); rudimentary or absent (1).
25. Deltopectoral crest: crescentic (0); subrectangular (1).
26. Femoral shaft curvature: 50 percent of shaft (0) or at least 80 percent of shaft (1) bowed anteriorly.
27. Tibia length: shorter (0) or subequal or longer (1) than femoral length.
28. Astragalar posterior groove: present (0); absent (1).
29. Calcaneal tuber: present (0); rudimentary or absent (1).
30. Distal tarsal 4 transverse width: broader than (0) or subequal to (1) distal tarsal 3.
31. Metatarsal 1–4 shaft configuration: spreading (0); compact (1).
32. Metatarsal 2–4 length: less (0) or more (1) than 50 percent tibial length.
33. Skull length: less (0) or more (1) than 50 percent presacral column length.
34. Scapula length: more (0) or less (1) than 75 percent of humerus length.
35. Fourth trochanter: present (0); absent (1).
36. Metatarsal 1 length: 50–75 percent (0) or 85 percent or more (1) of metatarsal 3 length.

Taxon	Character							
	5	10	15	20	25	30	35	
<i>Euparkeria</i>	00000	00000	00000	00000	00000	00000	00000	0
Proterochampsidae	00000	00000	00000	00000	00??0	00000	00000	0
<i>Suchia</i>	11111	11111	11110	00010	00000	00000	00000	0
<i>Ornithosuchus</i>	11111	11111	X1111	11121	00000	10000	00000	0
<i>Riojasuchus</i>	11111	11111	X1111	11121	00??0	10000	00000	0
<i>Parasuchia</i>	11111	11111	11000	001?0	00000	00000	00100	0
Pterosauria	1XX00	XXXXX	XX000	000X0	11111	11111	11111	1
<i>Scleeromochlus</i>	???00	0????	?X0??	??0??	01??0	11??1	11111	1
Dinosauromorpha	11100	00000	XX000	000X0	11111	11111	11000	0

Character-state abbreviations: 0 = plesiomorphic state; 1 = apomorphic state; 0 = plesiomorphic state for clade with some ingroup variation; 1 = apomorphic state for clade with some ingroup variation; X = unknown as a result of transformation; ? = not preserved/unknown.

### Synapomorphies

The character numbers and corresponding states listed below specify the apomorphic condition (1) except for multistate character 19, in which the apomorphic conditions (1, 2) are indicated parenthetically after the character number. Character state reversals are indicated by a negative sign preceding the character number, and an asterisk following a character number indicates an equivocal distribution for apomorphic states (which are listed at all possible nodes). To avoid redundancy, only unequivocal synapomorphies are listed in the diagnoses. Multistate characters and/or homoplasies are listed for terminal taxa; all other autapomorphies for terminal taxa are listed above.

Archosauria: 1, 2, 3, 11\*, 12\*, 19(1)\*.

Palatal teeth absent, calcaneal tuber angled more than 45 degrees posteriorly, and contiguous calcaneal facets for fibula and distal tarsal 4.

Crurotarsi: 4, 5, 6, 7, 8, 9, 10, 11\*, 12\*, 19(1)\*.

Strongly arched medial margin of proximal humerus, knob-shaped fibular anterior trochanter, fibular distal end width greater than proximal end, flexed astragalar tibial facet, hemicylindrical calcaneal condyle, broad calcaneal tuber shaft proportions, and calcaneal tuber with flared distal end.

Suchia + Ornithosuchidae: 13, 14.

Pubis longer than ischium and posterior portion of the pubic acetabular margin recessed.

Ornithosuchidae: 15, 16, 17, 18\*, 19(2), 20, 26\*.

Two-tooth diastema, nasal-prefrontal contact very reduced or absent, palatine-pterygoid fenestra, long dentary-splenic mandibular symphysis, concavoconvex astragalocalcaneal ventral articular surface with concavity on astragalus, and deep pedal unguals.

Ornithodira: 21\*, 22, 23, 24, 25\*, 26, 27, 28, 29, 30, 31, 32.

Dorsal body osteoderms absent, interclavicle absent, clavicle rudimentary or absent, femoral shaft bowed anteriorly along at least 80 percent of shaft, tibia subequal or longer than femur, astragalar posterior groove absent, calcaneal tuber rudimentary or absent, distal tarsal 4 transverse width subequal to distal tarsal 3, metatarsal 1–4 shafts closely appressed, and metatarsal 2–4 length more than 50 percent tibia length.

Scleromochlus + Pterosauria: 33, 34, 35, 36.

Skull length more than 50 percent presacral column length, scapula length less than 75 percent of that of humerus, fourth trochanter absent, and metatarsal 1 length 85 percent or more of metatarsal 3.

Suchia: –18\*.

Parasuchia: 18\*, 33.

Pterosauria: 21\*, 25\*.

Scleromochlus: –21\*, –25\*.

Dinosauromorpha: 21\*, 25\*.

### Characters Ordered by Anatomical Region

#### Skull

Skull length: less (0) or more (1) than 50 percent presacral column length.

Two-tooth diastema: absent (0); present (1).

Nasal-prefrontal contact: present (0); very reduced or absent (1).

Palatal teeth (pterygoid, palatine, vomer): present (0); absent (1).

Palatine-pterygoid fenestra: absent (0); present (1).

Dentary-splenic mandibular symphysis length: distally positioned (0); present along one-third of lower jaw (1).

#### Axial skeleton and accessory ossifications

Cervical 3–5 centrum length: shorter (0) or longer (1) than mid-dorsal.

Dorsal body osteoderms: present (0); absent (1).

One-to-one alignment between dorsal body osteoderms and vertebrae: absent (0); present (1).

#### Pectoral girdle and forelimb

Scapula length: more (0) or less (1) than 75 percent of that of humerus.

Interclavicle: present (0); absent (1).

Clavicle: present (0); rudimentary or absent (1).

Deltopectoral crest: crescentic (0); subrectangular (1).

Medial margin of proximal humerus: weakly (0) or strongly (1) arched.

#### Pelvic girdle and hind limb

Pubis length: shorter (0) or longer (1) than ischium.

Pubic acetabular margin, posterior portion: continuous with anterior portion (0); recessed (1).

Femoral shaft curvature: 50 percent of shaft (0) or at least 80 percent of shaft (1) bowed anteriorly.

Fourth trochanter: present (0); absent (1).

Tibia length: shorter (0) or subequal or longer (1) than femur length.

Fibular anterior trochanter: crest-shaped, low (0); knob-shaped, robust (1).

Fibular distal end width: subequal or less (0) or greater (1) than proximal end.

Ventral astragalocalcaneal articular facet size: small (0); large (1).

Astragalar tibial facet: concave (0); flexed (1).

- Astragalocalcaneal ventral articular surface: flat (0); concavoconvex with concavity on calcaneum (1); concavoconvex with concavity on astragalus (2).
- Astragalar posterior groove: present (0); absent (1).
- Calcaneal tuber: present (0); rudimentary or absent (1).
- Hemicylindrical calcaneal condyle: absent (0); present (1).
- Calcaneal tuber orientation: less (0) or more (1) than 45 degrees posterior deflection.
- Calcaneal facets for fibula and distal tarsal 4: separated (0); contiguous (1).
- Calcaneal tuber shaft proportions: taller than broad (0); broader than tall (1).
- Calcaneal tuber distal end: rounded (0); flared (1).
- Distal tarsal 4 transverse width: broader than (0) or subequal to (1) distal tarsal 3.
- Metatarsal 1–4 shaft configuration: spreading (0); compact (1).
- Metatarsal 1 length: 50–75 percent (0) or least 85 percent (1) of metatarsal 3 length.
- Metatarsal 2–4 length: less (0) or more (1) than 50 percent tibial length.
- Pedal ungual depth: shallow (0); deep (1).