THE EARLY EVOLUTION OF ARCHOSAURS: RELATIONSHIPS AND THE ORIGIN OF MAJOR CLADES

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ABSTRACT

Archosaurs have a nearly 250 million year record that originated shortly after the Permian-Triassic extinction event and is continued today by two extant clades, the crocodylians and the avians. The two extant lineages exemplify two bauplan extremes among a diverse and complex evolutionary history, but little is known about the common ancestor of these lineages. Renewed interest in early archosaurs has led to nearly a doubling of the known taxa in the last 20 years.

This study presents a thorough phylogenetic analysis of 80 species-level taxa ranging from the latest Permian to the early part of the Jurassic using a dataset of 412 characters. Each terminal taxon is explicitly described and all specimens used in the analysis are clearly stated. Additionally, each character is discussed in detail and nearly all of the character states are illustrated in either a drawing or highlighted on a specimen photograph. A combination of novel characters and comprehensive character sampling has bridged previously published analyses that focus on particular archosauriform subclades.

A well-resolved, robustly supported consensus tree (MPTs = 360) found a monophyletic Archosauria consisting of two major branches, the crocodylian-line and avian-line lineages. The monophyly of clades such as Ornithosuchidae, Phytosauria, Aetosauria, Crocodylomorpha, and Dinosauria is supported in this analysis. However, phytosaurs are recovered as the closest sister taxon to Archosauria, rather than basal crocodylian-line archosaurs, for the first time. Among taxa classically termed as "rauisuchians," a monophyletic poposauroid clade was found as the sister taxon to a group of paraphyletic "rauisuchians" and monophyletic crocodylomorphs. Hence, crocodylomorphs are well nested within a clade of "rauisuchians," and are not more closely related to aetosaurs than to taxa such as *Postosuchus*. Basal crocodylomorphs such as *Hesperosuchus* and similar forms ("Sphenosuchia") were found as a paraphyletic grade leading to the clade Crocodyliformes. Among avian-line archosaurs, Dinosauria is well supported. A monophyletic clade containing *Silesaurus* and similar forms is well supported as the sister taxon to Dinosauria. Pterosaurs are robustly supported at the base of the avian line.

A time-calibrated phylogeny of Archosauriformes indicates that the origin and initial diversification of Archosauria occurred during the Early Triassic following the Permian-Triassic extinction. Furthermore, all major basal archosaur lineages except Crocodylomorpha were established by the end of the Anisian. Early archosaur evolution is characterized by high rates of homoplasy, long ghost lineages, and high rates of character evolution. These data imply that much of the early history of Archosauria has not been recovered from the fossil record. Not only were archosaurs diverse by the Middle Triassic, but they had nearly a cosmopolitan biogeographic distribution by the end of the Anisian.

INTRODUCTION

Archosauria consists of two extant clades, crocodylians and birds (Gauthier and Padian, 1985; Gauthier, 1986; Benton and Clark, 1988; Benton, 1990a; Sereno and Arcucci, 1990; Sereno, 1991a; Parrish, 1993; Juul, 1994; Cao et al., 2000). However, these clades represent two body-form extremes in a long, complex, evolutionary history dating to the Triassic (Benton, 1990a; Sereno, 1991a; Gower and Sennikov, 2000; Nesbitt, 2003). In the Triassic, non-archosaurian archosauriforms such as *Proterosuchus*, *Erythrosuchus*, and *Euparkeria* represented a new diapsid body plan not present in the Paleozoic. Immediately after the Triassic divergence of the avian and crocodilian lineages, the crocodylian lineage split into several clades that dominated in diversity, numbers, and body forms (Brusatte et al., 2008). During the Triassic, archosauriforms were present on nearly all continents and mastered terrestrial (e.g., dinosaur, "rauisuchian," aetosaur, crocodylomorph), aquatic terrestrial (phytosaur, *Vancleavea*), and aerial (pterosaur) habitats. Furthermore, several clades became herbivorous independently (aetosaurs, ornithischians, sauropodomorphs), whereas most archosaurs remained carnivorous. Following the Triassic, only two lineages remained, the Crocodylomorpha and the Dinosauria.

PREVIOUS WORK

The evolution of studies of basal archosaur relationships has been on the forefront of the transition from "precladistic" methods to modern cladistic practices largely because of the work of Gauthier (1984, 1986) and Gauthier and Padian (1985). Prior to the 1980s, most of the taxa in what we now know as Archosauriformes were classified as a large group called "Thecodontia" (Owen, 1859). It was thought that "Thecodontia" represented a "basal stock" in which Aetosauria, Crocodylia, Sauropodomorpha, Theropoda, Aves, Ornithischia, Pterosauria, and Phytosauria emerged (e.g., Charig, 1976: fig. 2). Through a number of publications, the ankle of "thecodonts" became very important for classification of various groups (Cruickshank, 1979; Chatterjee, 1982; Cruickshank and Benton, 1985), but the relationships among and between "thecodont" groups was not given much thought. A detailed history of precladistic studies was comprehensively reviewed by Sereno (1991a), Juul (1994), and Gower and Wilkinson (1996), including the group Pseudosuchia, and I will not repeat that here.

In the 1980s, cladistic methods reshaped our understanding of basal archosauriform relationships. The works of Gauthier (1984), Benton (1985), Benton and Clark (1988), and Gauthier et al. (1988) showed the following: (1) crocodylians and avians are each others' closest extant relatives, and they shared a common ancestor at some point in the Triassic; (2) many of the "thecodontians" are just outside Archosauria or belong on either the branch that leads to crocodylians or to avians; (3) dinosaurs are monophyletic. However, these studies only provided lists of synapomorphies supporting different clades (Gower and Wilkinson, 1996). Further, the authors did not provide a character matrix in print and almost entirely used suprageneric taxa. The absence of a numerical analysis did not allow the authors to identify weak portions of the tree and to test the homology of the character states. Nonetheless, this great stride in basal archosaur systematics provided a set of identified synapomorphies and a framework for numerical studies in the near future (fig. 1).

In the early 1990s, each study on basal archosaurs (e.g., Sereno, 1991a; Parrish, 1993; Juul, 1994) included both a character list with discrete character states and a character-taxon matrix. The numerical phylogenetic analysis allowed testing of primary homology statements, and this led to the identification of homoplastic character states. However, limits on computing power and the contemporary cladistic methods led to the reliance of suprageneric taxa. The studies by Sereno (1991a), Parrish (1993), and Juul (1994) provided the characters for the next 10 years. Gower and Wilkinson (1996) examined these three numerical studies as well as those from the 1980s and found that a consensus of the major clades of archosauriforms had been reached, but the position of some taxa (e.g., ornithosuchids) remained controversial. Nearly all modern numerical analyses obtained the same "phylogenetic backbone" presented by Gower and Wilkinson (1996) and discussed by Brochu (2001). As demonstrated by Gower and Wilkinson (1996) all phylogenetic hypotheses show the following: (1) proterosuchians, erythrosuchians, *Euparkeria*, and proterochampsians are closely related to but lie outside Archosauria; (2) Archosauria consists of a major split between the crocodylian and avian lineages; (3) phytosaurs, aetosaurs, ornithosuchids, various "rauisuchians," and crocodylomorphs are part of the crocodylian lineage; and (4) pterosaurs, *Marasuchus*, and dinosaurs are part of the avian lineage.

The most recent phylogenetic studies (Bennett, 1996; Benton, 1999, 2004; Nesbitt and Norell, 2006; Irmis et al., 2007a; Nesbitt, 2007; Brusatte et al., 2008) reused the pool of characters provided by previous studies. Furthermore, the usage of suprageneric taxa as terminal taxa continued in most analyses (but see Irmis et al., 2007a). Unfortunately, recent authors did not provide detailed character descriptions or rationale for scoring strategies as did Sereno (1991a), Juul (1994), and Bennett (1996). This led to heavily recycled characters, sometimes compounding scoring errors from the original matrices. Few, if any, new characters have been added to these analyses. For example, Benton's (1999) character list consisted only

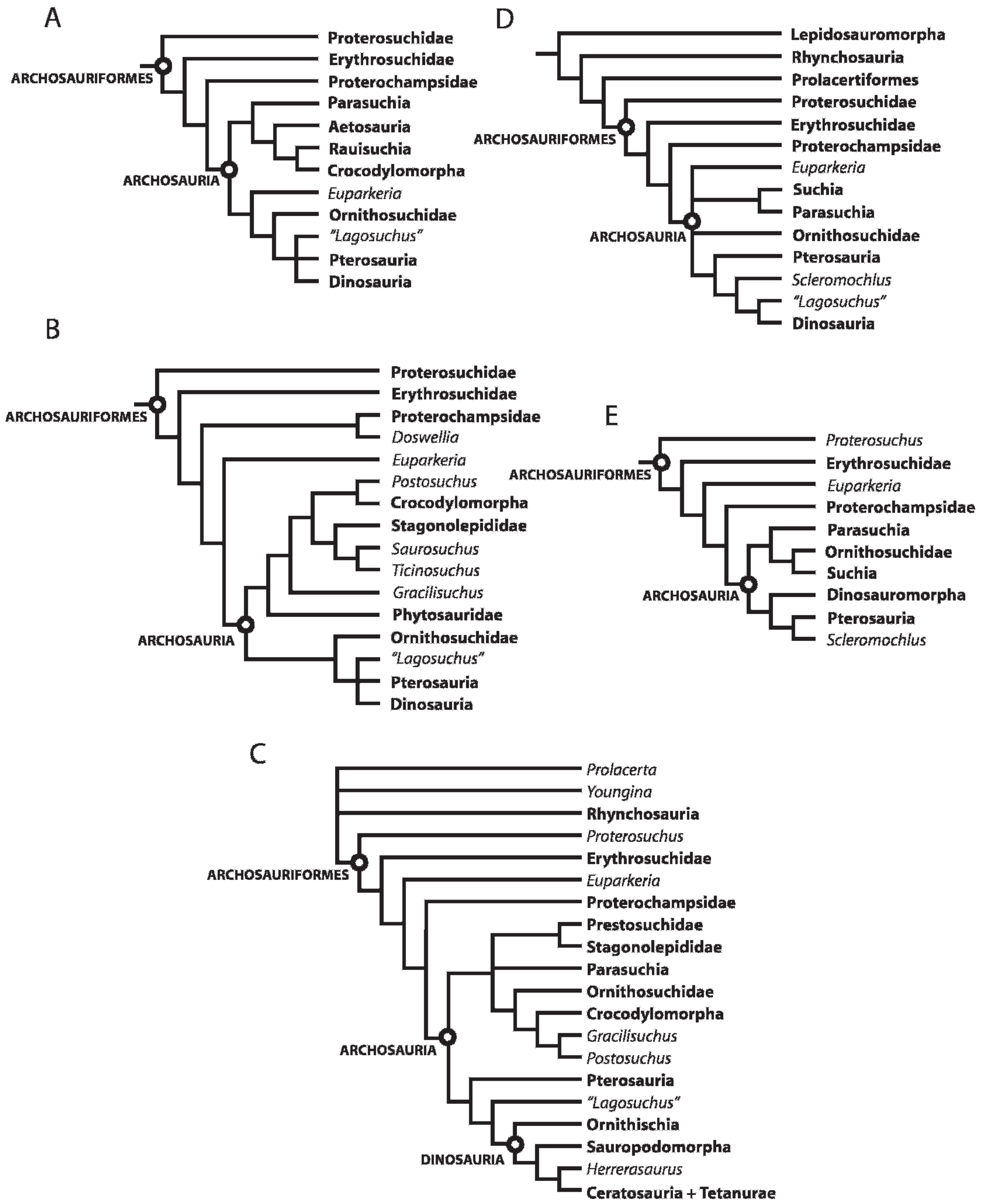


Fig. 1. Phylogenetic relationships of basal Archosauriformes: **A,** Gauthier (1984); **B,** Benton and Clark (1988); **C,** Juul (1994); **D,** Bennett (1996); **E,** Sereno (1991a). Suprageneric taxa are in bold.

of characters previously used in the literature. Benton (2004) and Nesbitt and Norell (2006) added taxa to Benton (1999), yet the relationships of pseudosuchians changed easily when new taxa and characters were added (see fig. 2).

The above briefly summarizes the major basal archosaur analyses and attempts an

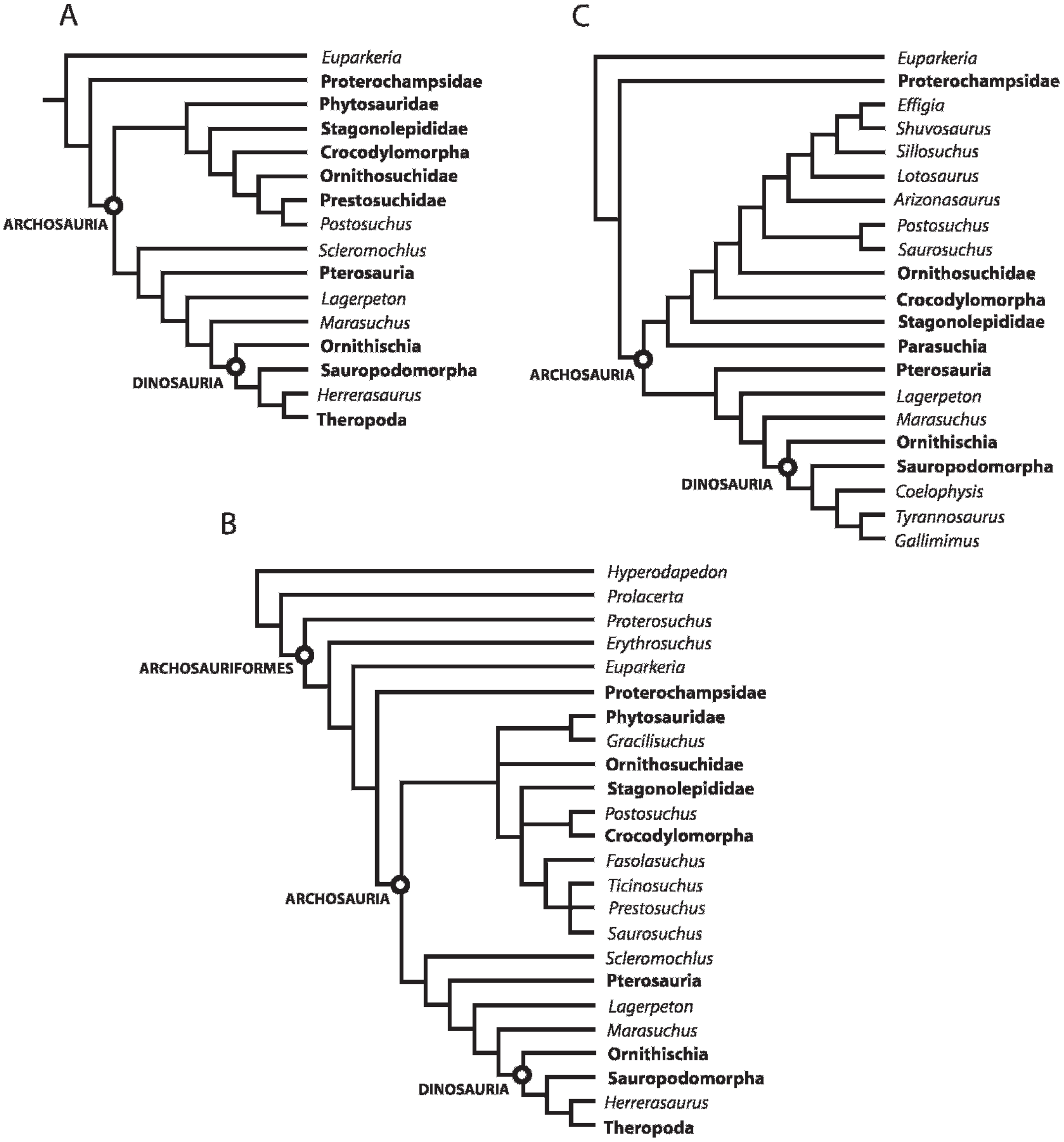


Fig. 2. Phylogenetic relationships of basal Archosauriformes based on the matrix of Benton (1999): **A,** Benton (1999); **B,** Benton (2004); **C,** Nesbitt and Norell (2006); Nesbitt (2007). Suprageneric taxa are in bold.

illustration of our current understanding of the major relationships of basal archosauriform clades. I have identified the following four critical portions of the basal archosaur tree that are controversial: (1) the relationships of non-archosaurian archosauriforms, (2) "rauisuchians," (3) the sister taxon to Crocodylomorpha, and (4) basal avian-line archosaur relationships. Specifically, the controversial relationships in these sections are discussed below.

Non-archosaurian Archosauriforms

Non-archosaurian archosauriforms represent the successive outgroups to Archosauria. Therefore, an understanding of character transformations in non-archosaurian archosauriforms is critical to the optimization of the ancestral character states of Archosauria. Most analyses to date use a suprageneric Proterosuchidae and Erythrosuchidae without providing detailed information on the terminal taxon.

Proterosuchus, by definition (Gauthier et al., 1988), is the basalmost member of Archosauriformes. Prior to the use of numerical analyses, *Proterosuchus* and other potential proterosuchians (Proterosuchidae) were grouped with *Erythrosuchus* and other potential erythrosuchians (Erythrosuchidae) in the Proterosuchia (e.g., Charig and Reig, 1970; Charig and Sues, 1976). Moreover, the proterosuchians were thought to give rise to the sauropodomorphs (Thulborn, 1975), and erythrosuchians were thought to give rise to the rauisuchians (Sill, 1974; Bonaparte, 1982). In the cladistic paradigm, Proterosuchia has been found to be paraphyletic grouping (but see Gower and Sennikov, 1996) in which erythrosuchians (usually *Erythrosuchus* is the only member scored) are found closer to Archosauria than proterosuchians (usually *Proterosuchus* is the only member scored) are to Archosauria (Gauthier, 1986; Benton and Clark, 1988; Juul, 1994; Bennett, 1996; Benton, 2004). Gower and Sennikov (1996) found a monophyletic Proterosuchia in a study utilizing character data only from the braincase of various proterosuchians and erythrosuchians. However, a paraphyletic Proterosuchia was found in a later study using the braincase characters of Gower and Sennikov (1996) in combination with cranial and postcranial characters (Gower and Sennikov, 1997). The monophyly of Proterosuchidae and Erythrosuchidae needs further testing.

The resolution of the sister taxon of Archosauria remains controversial. Both proterochampsians (Sereno, 1991a; Parrish, 1993; Juul, 1994; Benton, 1999, 2004) and *Euparkeria* (Benton and Clark, 1988) were found as the sister taxon to Archosauria. However, Proterochampsia was always scored as a suprageneric taxon, and it is not clear which proterochampsian taxa were scored. Sereno (1991a) cited the following two characters that are present in proterochampsians + Archosauria but not in *Euparkeria*: postaxial intercentra absent and continuous crural facets on the astragalus. However, Sereno (personal commun. in Gower, 1996) stated that *Euparkeria* has continuous crural facets on the astragalus. Therefore, the immediate outgroup to Archosauria remains poorly understood.

New discoveries of Triassic archosauriforms fueled our understanding of the earliest archosaurs. The absolute number of new non-archosaurian archosauriforms has increased slowly with only a handful of new taxa in the last 20 years (e.g., *Tropidosuchus*, Arcucci, 1990; *Sarmatosuchus*, Sennikov, 1994; *Vancleavea*, Long and Murry, 1995). Additionally, the discoveries of new material and more detailed descriptions of previously known non-archosaurian archosauriforms (e.g., *Erythrosuchus*, Gower, 2003) have proven most useful in studies of basal archosauriforms (Nesbitt et al., 2009a).

Rauisuchians

Rauisuchians are pseudosuchian archosaurs from all continents, save Antarctica, during the Triassic (Bonaparte, 1982; Gower, 2000). Rauisuchians represent an important faunal component in the evolution of the Triassic fauna. For example, forms such as *Postosuchus* and *Shuvosaurus* have many similarities to theropod dinosaurs (Nesbitt and Norell, 2006; Brusatte et al., 2008). Generalities regarding the potentially monophyletic clade remain difficult to state because it is unclear whether rauisuchians represent a mono-, para-, or even polyphyletic group (Gower, 2000). It was common for large (2–6 m) carnivorous archosaurs from the Triassic with large skulls, recurved teeth, and elongated limbs to be referred to various subgroups of rauisuchians (e.g., Prestosuchidae, Rauisuchidae, Poposauridae) by Romer (1971b), Sill (1974), and Chatterjee (1985). Rauisuchia and various subgroups have been grouped together based on only a few potential synapomorphies (e.g., additional sacral vertebrae, rugose ridge on ilium, perforate acetabulum) and the fact they did not easily fit into Dinosauria, Aetosauria, Phytosauria, or Crocodylomorpha. An understanding of the interrelationships of rauisuchians is essential to an understanding of the early evolution of

Archosauria, the stability of relationships of taxa within Pseudosuchia, and the identification of the sister taxon of Crocodylomorpha.

The precladistic classification of rauisuchians varied considerably. Huene (1942) coined the term Rauisuchidae for the fragmentary specimens *Rauisuchus* and *Prestosuchus* from the Triassic sequence of Brazil. The more complete remains of *Ticinosuchus* (Krebs, 1965) and *Saurosuchus* (Reig, 1961) solidified the presence of a widespread group of Triassic archosaurs. Krebs (1963, 1965) argued that *Ticinosuchus* and *Rauisuchus* were more closely related to crocodylians than to any other group—a view that was opposed by various workers (e.g., Hughes, 1963; Romer, 1966, 1972b; Bonaparte, 1982) who thought that rauisuchids were proterosuchians. Romer (1966) coined Prestosuchidae for a grouping centered on *Prestosuchus,* but placed *Rauisuchus* and *Saurosuchus* into the Erythrosuchidae. Others presented a different composition of both Prestosuchidae and Rauisuchidae (e.g., Charig, 1967) without justification or a discussion of diagnostic characters. Other than *Ticinosuchus*, most specimens were known from less than 25% of the skeleton.

Chatterjee (1985) described *Postosuchus kirkpatricki* from two relatively complete partial skeletons from the Late Triassic of Texas. Even though Chatterjee (1985) hypothesized that *Postosuchus* was a close relative of carnosaurian theropods, he established a framework for rauisuchian relationships. Chatterjee (1985) allied *Postosuchus* with *Poposaurus gracilis*, *Arizonasaurus*, *Teratosaurus*, and *Bromesgroveia* and placed them into the Poposauridae, whereas, following Bonaparte (1981, 1984), he placed *Rauisuchus*, *Fasolasuchus*, *Prestosuchus*, *Saurosuchus*, *Ticinosuchus* and various other fragmentary forms into Rauisuchidae. Furthermore, Chatterjee (1985) coined Rauisuchia to incorporate Rauisuchidae and Poposauridae. Galton (1985) independently arrived at a similar division in his study of *Bromesgroveia*. Other studies such as Long and Murry (1995) revised the alpha taxonomy of *Postosuchus kirkpatricki,* but did not include a cladistic analysis.

By the mid-1980s, nearly all authors considered rauisuchian taxa part of Pseudosuchia. This classification was followed in early cladistic studies of archosaurs. The first major cladistic studies of Archosauria (Gauthier, 1984, 1986) treated Rauisuchia as a monophyletic clade similar to Aetosauria and Phytosauria. Benton and Clark (1988) used *Prestosuchus* and *Ticinosuchus* to represent Rauisuchidae and *Postosuchus* to represent Poposauridae. Gauthier (1986) found Rauisuchia as the sister taxon of Crocodylomorpha, whereas Benton and Clark (1988) found Poposauridae as the sister taxon to Crocodylomorpha. Benton and Clark (1988) found Aetosauria and Rauisuchidae in a monophyletic group termed Rauisuchia, and Rauisuchia was found as the sister taxon of Poposauridae + Crocodylomorpha.

The shift to numerical analyses tested the monophyly of Rauisuchia, Rauisuchidae, and Prestosuchidae as originally conceived. Parrish (1993) and Juul (1994) included a mixture of species-level and suprageneric taxa of pseudosuchians (fig. 2) and they both found a polyphyletic Rauisuchia. Parrish (1993) and Juul (1994) found that prestosuchids (*Ticinosuchus*, *Saurosuchus*, and *Prestosuchus* in Parrish, 1993) fell outside other traditional rauisuchians and *Postosuchus kirkpatricki* was the approximate sister taxon to Crocodylomorpha. The phylogenetic relationships of Benton and Walker (2002), Benton (2004), and Weinbaum and Hungerbühler (2007) found a paraphyletic grouping of rauisuchians (fig. 3). That hypothesis was supported by three studies of the braincase of pseudosuchians (Gower and Walker, 2002; Gower, 2002; Gower and Nesbitt, 2006).

Most recently, Nesbitt (2003), Nesbitt and Norell (2006), Nesbitt (2007), and Weinbaum and Hungerbühler (2007) focused on taxa variously considered poposaurs, poposaurids, and shuvosaurids (= chatterjeeids). These four studies found a well-supported monophyletic clade of poposaurids with shuvosaurids as the most derived members within the clade.

Even though many recent basal archosaur phylogenies included various rauisuchian taxa, the uncertainty in the relationships led to much confusion in descriptions of new taxa (e.g., Sen, 2005) or redescriptions of existing specimens (e.g., Gebauer, 2004). Furthermore, no explicit phylogenetic defini-

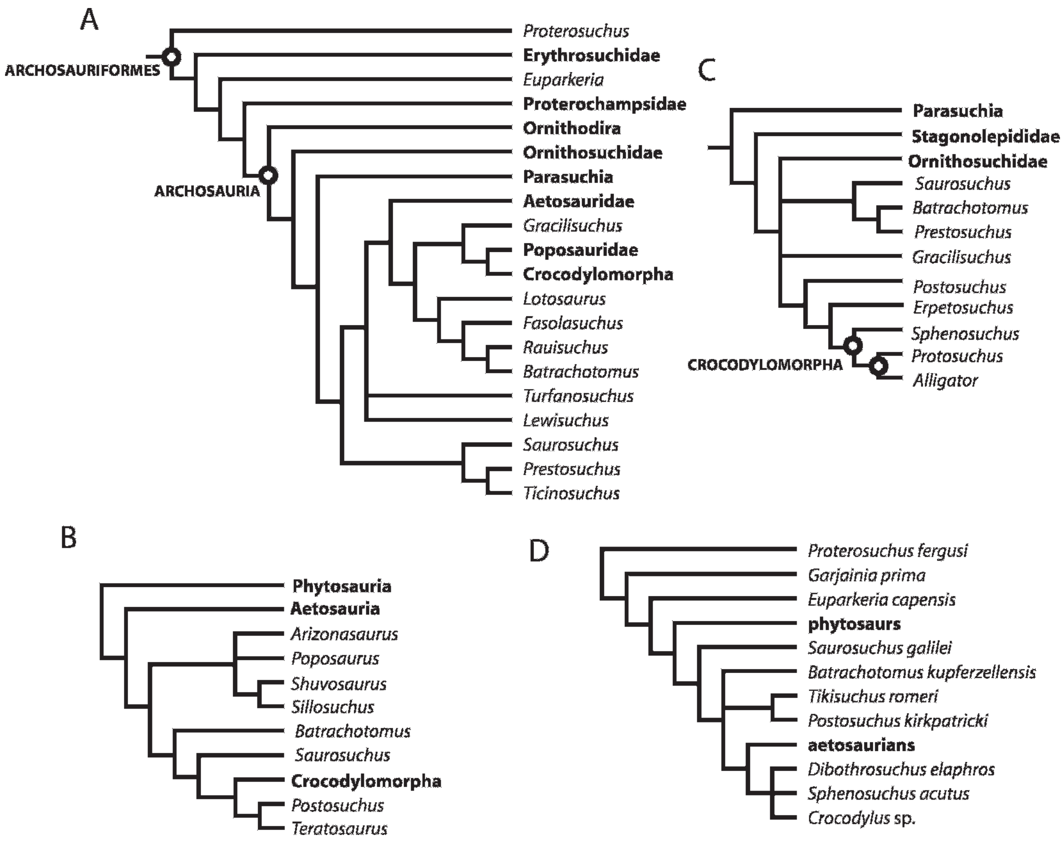


Fig. 3. Phylogenetic relationships of Pseudosuchia with the incorporation of a diversity of "rauisuchians": **A,** Parrish (1993); **B,** Weinbaum and Hungerbühler (2007); **C,** Benton and Walker (2002); **D,** Gower (2002). Suprageneric taxa are in bold.

tions or diagnoses of Poposauria, Poposauridae, Rauisuchia, Rauisuchidae, or Prestosuchidae have been presented to date. Parrish (1993) named a number of poorly supported nodes with a unique taxon composition (e.g., Rauisuchiformes) and (possibly unintentionally) redefined Rauisuchia to include Crocodylomorpha. Confusion of the taxonomic history of "rauisuchians" has prevented some authors from publishing new forms. For example, "*Mandasuchus*" (Charig, 1956) was never fully described and was always considered closely related to *Ticinosuchus* (Parrish, 1993; Sen, 2005), but most of the similarities listed ("ilium is slightly horizontally inclined" attributed to Charig as a personal commun in Juul,1994) cannot be accurately evaluated in the crushed holotype of *Ticinosuchus ferox*.

Fortunately, there is a renewed interest in rauisuchian anatomy and relationships. The number of new "rauisuchian" taxa dramatically increased in the last 10 years and includes the following taxa: *Batrachotomus* (Gower, 1999, 2002; Gower and Schoch, 2009); *Effigia* (Nesbitt and Norell, 2006; Nesbitt, 2007); *Polonosuchus silesiacus* (Sulej, 2005, sensu Brusatte et al., 2009); *Qianosuchus* (Li et al., 2006); *Postosuchus alisonae* (Peyer et al., 2008); *Arganasuchus* (Jalil and Peyer, 2007); and *Yarasuchus* (Sen, 2005). Furthermore, new, more complete specimens of the following important specimens have been found: *Poposaurus* (Weinbaum and Hungerbühler, 2007); *Saurosuchus* (Alcober, 2000); and *Arizonasaurus* (Nesbitt, 2003, 2005a). These studies provided the groundwork for new phylogenetic studies.

Crocodylomorpha

The oldest members of the Crocodylomorpha appear in the fossil record at either the end of the Carnian or the beginning of the Norian (e.g., *Hesperosuchus agilis* and *Trialestes romeri*) as fleet-footed, quadrupedal predators that looked more like an odd theropod dinosaur than members of Crocodylia. The first representatives were small (1–2.5 m in body length). Crocodylomorpha is the only clade of pseudosuchians to survive the Triassic-Jurassic boundary.

The early members of Crocodylomorpha from the Triassic and the Early Jurassic were lumped into the Sphenosuchia prior to explicit phylogenetic analyses. Walker (1970, 1972, 1990) convincingly showed that sphenosuchians were very closely related to Crocodyliforms, and this hypothesis has been validated by cladistic studies. Since the advent of cladistic methodologies, basal crocodylomorph workers have argued whether the Triassic and Jurassic sphenosuchians represent a monophyletic clade or a paraphyletic group that comprises a series of successive sister taxa of Crocodyliformes. A monophyletic Sphenosuchia was found by Sereno and Wild (1992), Wu and Chatterjee (1993), Clark et al. (2000), and Sues et al. (2003), whereas Clark (in Benton and Clark, 1988), Parrish (1991), and Clark et al. (2004) found Sphenosuchia as a paraphyletic assemblage (fig. 4). The dataset of Clark et al. (2000), which originally found a monophyletic Sphenosuchia, was transformed to produce a paraphyletic Sphenosuchia with the addition of new taxa and new characters (Clark et al., 2004). Poor resolution in basal crocodylomorphs is a direct result of often fragmentary specimens and conflicting signals in the postcrania and cranium (as demonstrated by Clark et al., 2004).

Different in-group relationships in studies that find a monophyletic Sphenosuchia demonstrate that outgroup choice is critical to resolution of the debate. Clark (in Benton and Clark, 1988), Parrish (1991), Wu and Chatterjee (1993), and the dataset of Clark et al. (2000) all use real outgroups including *Gracilisuchus*, *Postosuchus*, and an aetosaur. Clark (in Benton and Clark, 1988), Parrish (1991), Wu and Chatterjee (1993), and the dataset of Clark et al. (2000) all found *Postosuchus* (variously labeled as Poposauria/Poposauridae) as the proximal outgroup taxon. Unfortunately, *Postosuchus kirkpatricki* (sensu Chatterjee, 1985) is a chimera of different Triassic archosaurs (Long and Murry, 1995; Weinbaum 2002). On the other hand, Sereno and Wild (1992) used an all (0) outgroup, a strategy deplored by most phylogenetic workers. What then is an appropriate outgroup for Crocodylomorpha?

As pointed out by Clark et al. (2000), rauisuchians are an appropriate proximal outgroup because of the results of Benton and Clark (1988), Parrish (1993), and Juul (1994). Gower and Walker (2002) and Gower (2002) proposed the unique hypothesis that aetosaurs represent the sister taxon of Crocodylomorpha based on synapomorphies in the braincase shared by the aetosaurs (mainly *Stagonolepis*) and crocodylomorphs (mainly *Sphenosuchus* and *Crocodylus*). Gower and Walker (2002) also provided two potential cranial characters uniting the two taxa. Their data were limited to cranial characters; however, the hypothesis represented a clear alternative to a rauisuchian sister taxon. Therefore, the question about the monophyly versus paraphyly of Sphenosuchia may rely on the choice of the proximal outgroup.

Basal crocodylomorph specimens remain rare in fossil collections, and most specimens consist only of vertebrae and partial limb bones (e.g., Parrish, 1991; Long and Murry, 1995). Fortunately, several new taxa are largely complete, and they have doubled the known diversity of basal crocodylomorphs from both the Triassic and the Jurassic. This continuously growing list includes *Dromicosuchus* (Sues et al., 2003), *Litargosuchus* (Clark and Sues, 2002), *Hesperosuchus "agilis"* (Clark et al., 2000), *Kayentasuchus* (Clark and Sues, 2002), *Protosuchus haughtoni* (Gow, 2000), and *Junggarsuchus* (Clark et al., 2004).

Avian-line Archosaurs

Avian-line archosaurs (= Avemetatarsalia of Benton, 1999) consist of pterosaurs, dinosaurs, and a range of intermediate forms. The only surviving members of the clade are

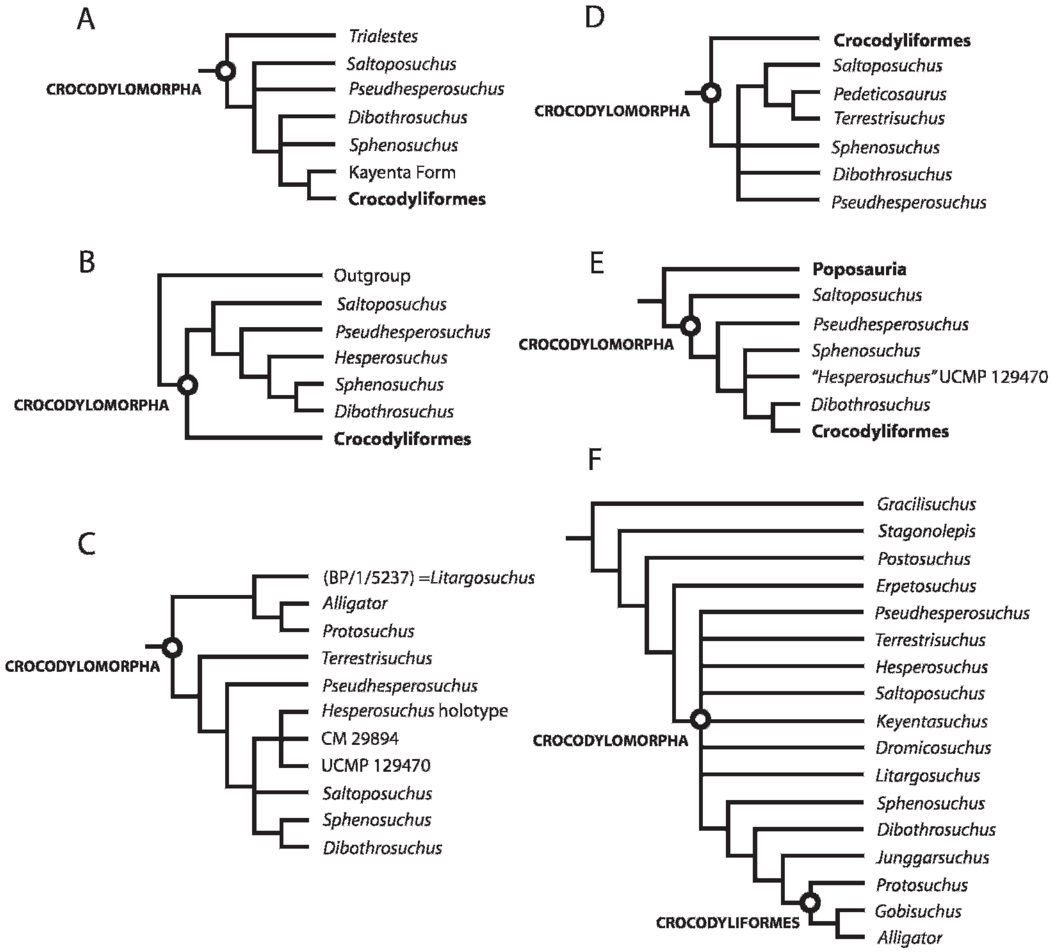


Fig. 4. Phylogenetic relationships of basal Crocodylomorpha: **A,** Clark in Benton and Clark (1988); **B,** Wu and Chatterjee (1993); **C,** Clark et al. (2000); **D,** Sereno and Wild (1992); **E,** Parrish (1991); **F,** Clark et al. (2004). Suprageneric taxa are in bold.

modern birds, one of the most speciose clades of all extant vertebrates (Padian and Chiappe, 1998). Avemetatarsalians first appeared in the Middle Triassic, but they remained a rare component until the origin of the dinosaurs in the Late Triassic. Even in the Late Triassic, avian-line archosaurs were dominated in number of taxa, body types, and overall abundance by the crocodylian-line archosaurs (Irmis et al., 2007a; Brusatte et al., 2008). Many cladistic studies have focused on the origin of Dinosauria and its closest relatives, and these are nearly in complete agreement with each other (Gauthier, 1986; Sereno, 1991a; Juul, 1994; Sereno, 1999; Benton, 1999, 2004; Langer and Benton, 2006; Ezcurra, 2006; Irmis et al., 2007a; Brusatte et al., 2008) (fig. 5).

Beginning with early cladistic studies, pterosaurs were found as the basalmost clade among avian-line archosaurs; this argument was well documented by Padian (1984), Sereno (1991a), Juul (1994), Bennett (1996 in part), and many other studies. Only one study since the cladistic revolution found pterosaurs outside Archosauria (Peters, 2000; but see Hone and Benton, 2007). Pterosaurs share a number of ankle characters and hind limb characters with dinosaurs and their close relatives, but their divergent morphology in the earliest members of the clade has proven difficult when reconstructing charac-

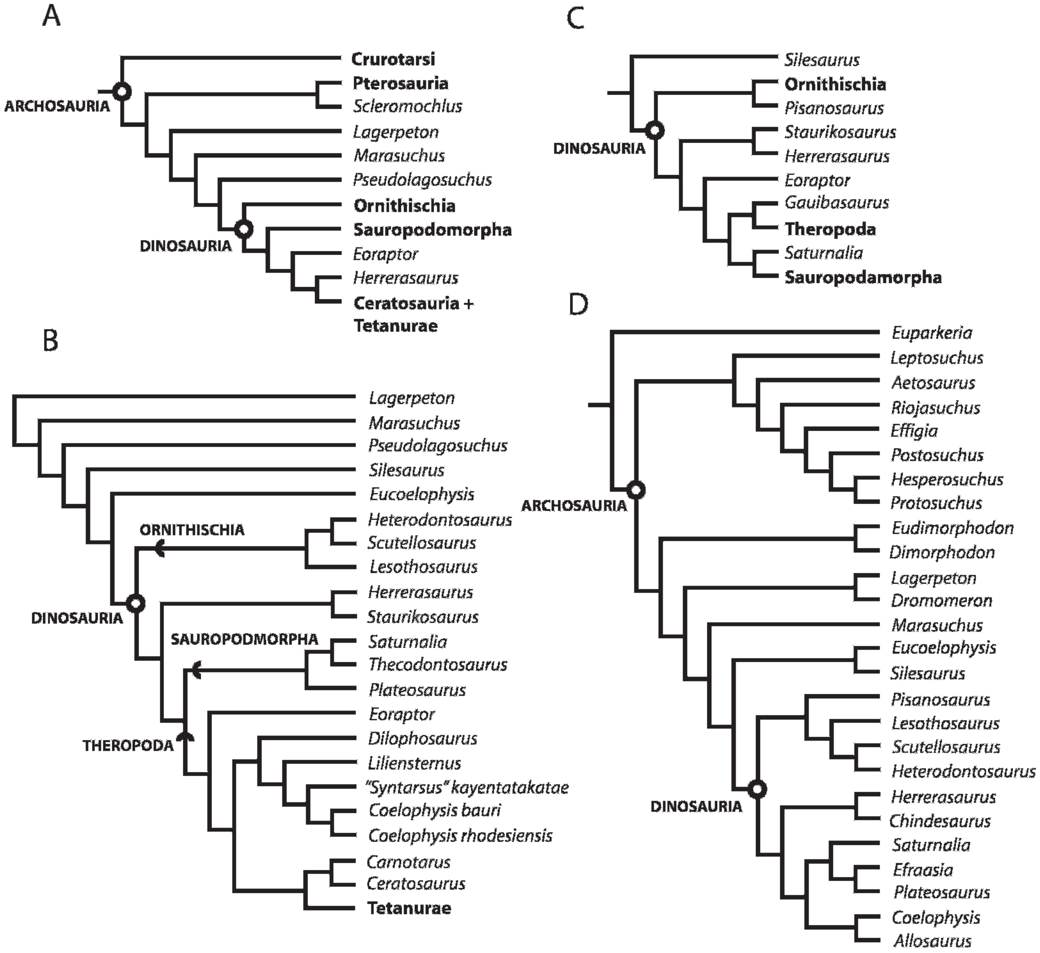


Fig. 5. Recent hypotheses of the phylogenetic relationships of basal Dinosauria: **A,** Novas (1996); **B,** Ezcurra (2006); **C,** Langer and Benton (2006); **D,** Irmis et al. (2007a). Suprageneric taxa are in bold.

ter optimizations at Ornithodira and Archosauria (Bennett, 1996; Padian, 2009). The first pterosaurs appear in the fossil record in the Norian of central Europe (Wild, 1978; Dalla Vecchia, 2003) and Greenland (Jenkins et al., 1994), but the ghost lineage of Pterosauria suggests the clade diverged by the Ladinian (Sereno, 1991a). Further, the oldest pterosaurs (e.g., *Eudimorphodon* and *Austriadactylus*) fall well within the pterosaur clade (Unwin, 2003). This indicates that much of the early history of Pterosauria is missing.

With the exceptions of Irmis et al. (2007a) and Brusatte et al. (2008), authors have treated Pterosauria as a suprageneric taxon in comprehensive phylogenetic analyses (Sereno, 1991a; Bennett, 1996; Benton, 1999). Authors either scored from basal taxa, derived taxa known from complete material, or a combination of both. Unfortunately, the scorings of Sereno (1991a) and Benton (1999) cannot be found in any one taxon of pterosaur. Irmis et al. (2007a) and Brusatte et al. (2008) scored species-level pterosaur taxa and found pterosaurs as the sister taxon to all other avian-line archosaurs.

The controversial taxon *Scleromochlus taylori*, a small-bodied form from the Late Triassic of Scotland, was considered the most primitive pterosaur (Huene, 1914; Padian, 1984; Sereno, 1991a) or the sister taxon to

Pterosauria + Aves (Benton, 1999). Although the taxon is represented by several nearly complete skeletons, all specimens are preserved as external molds and some of the tarsal elements are slightly larger than the grain size of the coarse sandstone in which they are preserved.

Basal dinosauromorphs and dinosauriforms lie closer to Dinosauria than to any other archosaur clade. Once thought of as "advanced thecodontians," *Lagerpeton* and *Marasuchus* from the Middle Triassic of Argentina are known to represent the closest relatives of Dinosauria (Romer, 1971a, 1972a; Bonaparte, 1975; Arcucci, 1986; Sereno and Arcucci, 1994a, 1994b; Novas, 1996). These small-bodied taxa, although not completely known, bear ankle and hind limb synapomorphies found only in Dinosauria (Novas, 1996). Arcucci (1987) described *Pseudolagosuchus*, a larger form from the same fossils beds that produced *Lagerpeton* and *Marasuchus*, and Novas (1996) identified this important taxon as the sister taxon to Dinosauria.

Until recently, it was thought that dinosaurs quickly replaced the "dinosaur precursors" in the Triassic. However, new finds of primitive dinosauromorphs in the southwestern United States (Irmis et al., 2007a; Nesbitt et al., 2009b), reevaluations of purported Triassic dinosaurs (Nesbitt et al., 2007) and new finds of dinosauriforms (Dzik, 2003; Ferigolo and Langer, 2007) have shown that the closest relatives of dinosaurs evolved along with the dinosaurs for much of the Triassic. Furthermore, the bizarre, possibly quadrupedal dinosauriforms *Silesaurus* and *Sacisaurus* bear a suite of classical dinosaurian features, ornithischian dinosaurlike cranial features, and characters not found in any dinosaur. Most authors hypothesized that *Silesaurus* is a non-dinosaurian dinosauriform (Langer and Benton, 2006; Ezcurra, 2006; Nesbitt, 2007; Irmis et al., 2007a).

Owen (1842) conceived Dinosauria as consisting of the theropod *Megalosaurus* and the ornithischians *Hylaeosaurus* and *Iguanodon.* Many early workers were convinced that the different lineages of dinosaurs (e.g., sauropods) arose independently from a "basal stock" of Triassic "thecodontians" (e.g., Thulborn, 1971; Charig, 1976). In a seminal study, Bakker and Galton (1974) cemented Owen's (1842) original concept of Dinosauria and argued for the monophyly of the clade. Since 1974, most workers have agreed that a monophyletic Dinosauria comprises three major lineages, Ornithischia, Sauropodomorpha, and Theropoda and that Sauropodomorpha and Theropoda are sister taxa (Gauthier, 1984, 1986; Gauthier and Padian, 1985; Benton and Clark, 1988; Juul, 1994; Sereno, 1999).

Renewed interest in the origin of Dinosauria has led to the discovery of a greater diversity of basal members of each major dinosaur lineage. This includes the basal saurischians or theropods *Herrerasaurus* (Sereno and Novas, 1992, 1994b; Sereno, 1994; Novas, 1994) and *Eoraptor* (Sereno et al., 1993), the primitive sauropodomorphs *Saturnalia* (Langer et al., 1999) and *Pantydraco* (Yates, 2003; Galton et al., 2007), and the primitive ornithischian *Eocursor* (Butler et al., 2007). Combined with new specimens of basal dinosauromorphs and dinosauriforms, these new finds brought a wealth of anatomical data to the evolution of character states immediately outside of and within Dinosauria. Specifically, these finds helped optimize synapomorphies that can clarify a response to "What makes a dinosaur a dinosaur?" All numerical analyses provided a core set of dinosaurian synapomorphies, many of which overlapped. However, the absence of skulls and hands in the proximal outgroups of Dinosauria has prevented the optimization of many characters at Dinosauria. The new material of basal dinosauriforms, represented by both crania and postcrania, allows further testing of dinosaurian synapomorphies.

OBJECTIVES

This study investigates the evolutionary relationships of basal archosauriforms and places disparate clades of Triassic archosaurs into a comprehensive analysis. Since the advent of basal archosaur phylogenetic studies in the 1980s, the taxonomic sampling has more than doubled. Increasingly, the relationships of several basal archosaur clades (e.g., Dinosauria, Crocodylomorpha, Aetosauria) have been devoid of a larger phylogenetic context, and, thus, the chosen outgroups have affected in-group relationships. Here, all previous basal archosaur studies are combined, from studies examining the evolution of the ankle to studies looking at the relationships of basal crocodylomorphs. I employ rigorous character formulation; previously used characters are critically evaluated and in most cases modified or terminated, and new characters are also added. Nearly every character is fully described and put into a comparative context in an attempt to increase anatomical knowledge of basal archosaurs. Furthermore, each terminal taxon is carefully described. The resultant character list and taxon-character matrix represents a tripling of both character and taxa sampled. This explicit phylogenetic analysis contains scoring strategies and decisions regarding which specimens represent which species-level taxon, along with full synapomorphy lists. This approach records each step in the formulation of my phylogenetic hypothesis from bone features to analyzing phylogenetic trends. My record-keeping provides a framework for reproducing my results in future studies.

I address the following four major questions: (1) What is the sister taxon to Archosauria and what synapomorphies are found in the common ancestor of crocodylians and avians? (2) Are rauisuchians a mono-, para-, or polyphyletic group and what are their closest relatives? (3) What is the sister taxon to Crocodylomorpha? and (4) What characters support a monophyletic Dinosauria?

The answers to these questions provide a testable framework for asking further questions about the early diversification of Archosauria. Questions regarding the split between the crocodylian and avian lineages have important implications for the calibrations of molecular studies of extant archosaurs. Also, understanding the rate at which archosaur lineages evolved in their initial diversification gives insights about the tempo and mode of early archosaur diversification.

In addition, this study attempts to build a framework so that the relationships of incomplete specimens and even isolated specimens can be confidently added to studies of biogeography, abundance, paleoecology, extinction, and morphological rate change. The identification of a specimen is the first step in any evolutionary study, whereas the second and equally important step is putting that specimen into a comparative context. A comprehensive phylogeny is required for both. For example, Nesbitt et al. (2007) tested the identifications of early dinosaurs from the Upper Triassic of the western United States using the latest, most comprehensive diagnosis of Dinosauria, whereas Nesbitt and Stocker (2008) incorporated fragmentary fossils from a single quarry into a phylogenetic context to examine the validity of assemblage comparisons in the Chinle Formation of northern New Mexico. Furthermore, the explicit phylogeny allows the identification of homoplastic characters that may have been previously used to identify fragmentary fossils incorrectly.

TERMINOLOGY

The phylogenetic definition of Archosauriformes is based on ancestry following Gauthier and Padian (1985), Gauthier (1986), Sereno (1991a), and other recent revisions (e.g., Senter, 2005). I present a summary of important taxa tied to phylogenetic definitions in figure 6. The phylogenetic taxonomy accepted here conforms to the most widely used clade names and remains the most logical to facilitate comparisons to previous phylogenetic hypotheses (see tree description for full definitions).

Here, I use Archosauria as first phylogenetically defined by Gauthier and Padian (1985) and Gauthier (1986) and not in the traditional sense of Romer (1966), Benton, and Gower (various works) and Juul (1994). Archosauria (sensu Gauthier and Padian, 1985) is equivalent to crown-group archosaurs and Avesuchia (Benton, 1999). Pseudosuchia (Zittel, 1887–1890, sensu Gauthier and Padian, 1985) is used interchangeably with crocodylian-line archosaurs, and "avian-line archosaurs" is used interchangeably with Avemetarsalia. The term "basal" generally describes the first few branches of a lineage with respect to later, more-derived members. For example, basal archosauriforms refers to non-archosaurian archosauriforms and members of Archosauria extend-

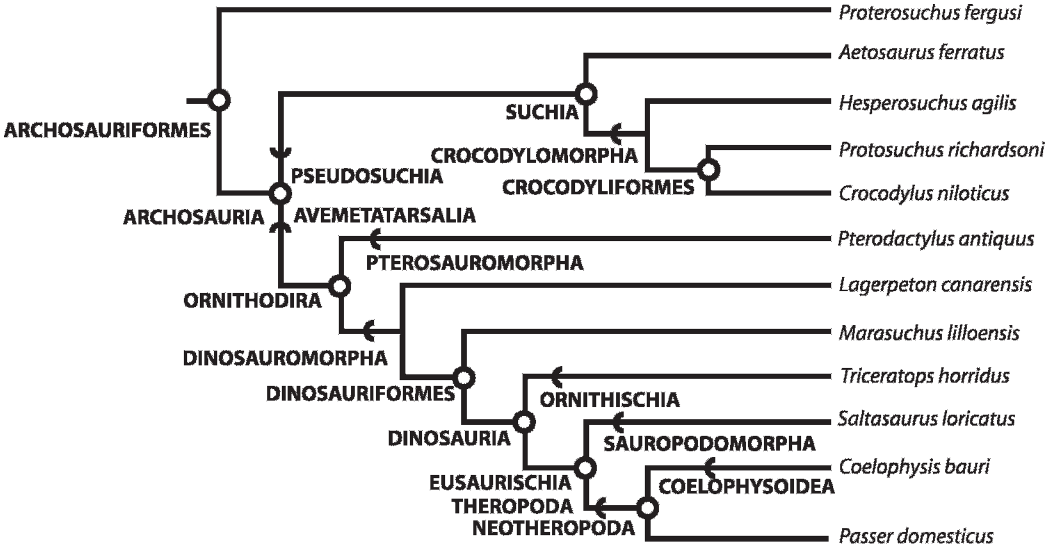


Fig. 6. Archosauriform stem and node clade names used in this study. Circles = nodes; chevrons = stem groups.

ing up into Crocodyliformes and within Dinosauria, whereas basal archosaurs excludes non-archosaurian archosauriforms.

Terms such as “rauisuchian” and “poposaurid” are usually avoided throughout this text because the monophyly of these clades was questioned recently (Gower, 2000). Instead, species-level taxa and specimen numbers are employed for explicitness and to test the monophyly of these groups. When used, the term “rauisuchian” is used in its traditional sense and includes taxa variously considered as members of Rauisuchidae, Prestosuchidae, Poposauridae, and Chatterjeeidae (Gower, 2000).

TERMINAL TAXA

Mesosuchus browni Watson, 1912

AGE: Anisian, Middle Triassic (Rubidge, 2005).

OCCURRENCE: *Cynognathus* Assemblage Zone (B) (Beaufort Group) of South Africa.

HOLOTYPE: SAM 5884, partial skull and partial skeleton.

REFERRED MATERIAL: SAM 6536, complete well-preserved skull and anterior half of the skeleton; SAM 7416, partial postcranial skeleton.

REMARKS: See Nesbitt et al., 2009a.

KEY REFERENCES: Watson, 1912; Broom, 1925; Dilkes, 1998.

Prolacerta broomi Parrington, 1935 (fig. 7E)

AGE: Induan, Early Triassic (Rubidge, 2005).

OCCURRENCE: *Lystrosaurus* Assemblage Zone (Beaufort Group) of South Africa.

HOLOTYPE: UMZC 2003.40, partial skull and mandible.

REFERRED MATERIAL: BP/1/471, complete skull; BP/1/2675, nearly complete skull with postcrania; BP/1/2676, nearly complete skeleton; UCMP 37151, skull; AMNH 9502, postcranial skeleton.

REMARKS: See Nesbitt et al., 2009a.

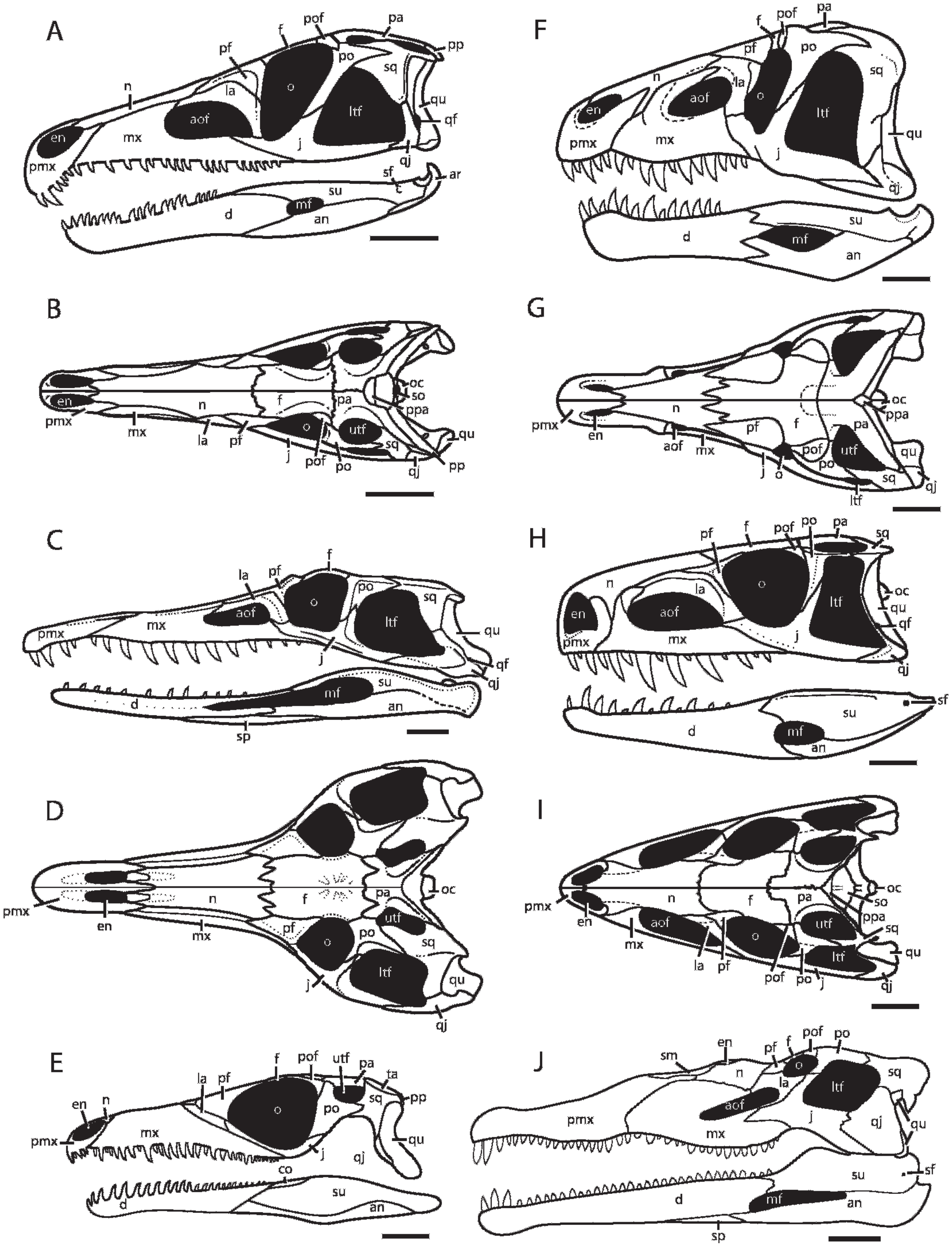
KEY REFERENCES: Parrington, 1935; Camp, 1945; Gow, 1975; Evans, 1988; Colbert, 1987; Gower and Sennikov, 1996; Dilkes, 1998; Modesto and Sues, 2004.

Proterosuchus fergusi Broom, 1903
(fig. 7A–B)

AGE: Induan, Early Triassic (Rubidge, 2005).

OCCURRENCE: *Lystrosaurus* Assemblage Zone (Beaufort Group) of South Africa.

HOLOTYPE: SAM 591, partial skull.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Referred material: TM 201, incomplete skull; RC 96, complete skull; BSP 514, nearly complete skull and anterior cervical vertebrae; NM QR 1484 (also listed as NMC 3016), complete skull and nearly complete articulated skeleton; NM QR 880, complete braincase and partial skull, partial postcrania; AMNH FR 2237, fragmentary postcranial skeleton with nearly complete articulated leg; BP/1/3993, nearly complete skull with braincase.

Remarks: See Nesbitt et al., 2009a.

Key references: Broom, 1903; Cruickshank, 1972, 1979; Gow, 1975; Welman and Flemming, 1993; Welman, 1998.

Erythrosuchus africanus Broom, 1905
(fig. 7F–G)

Age: Anisian, Middle Triassic (Rubidge, 2005).

Occurrence: *Cynognathus* Assemblage Zone (B) (Beaufort Group) of South Africa.

Holotype: SAM 905, incomplete postcranial skeleton.

Referred material: BP/1/ 5207, complete skull; SAM-K1098, maxilla; BMNH R3592, partial skull and skeleton; BMNH R3267a, incomplete postcranium.

Remarks: See Nesbitt et al., 2009a.

Key references: Broom, 1905; Huene, 1911; Charig and Reig, 1970; Cruickshank, 1972; Gower, 1996, 1997, 2003.

Vancleavea campi Long and Murry, 1995

Age: ?Carnian-?Rhaetian, Late Triassic.

Occurrence: Mesa Redondo Member, Chinle Formation, Arizona; Monitor Butte Member, Chinle Formation, Utah; Blue Mesa Member, Chinle Formation, Arizona; Sonsela Member, Chinle Formation, Arizona; Petrified Forest Member, Chinle Formation, Arizona; Owl Rock Member, Chinle Formation, Arizona; "Siltstone Member," Chinle Formation, New Mexico; Bull Canyon Formation, New Mexico; Redonda Formation, New Mexico; Tecovas Formation, Dockum Group, Texas.

Holotype: PEFO 2427, an incomplete postcranial skeleton.

Referred material: GR 138, complete skeleton; GR139, partial disarticulated skeleton.

Remarks: *Vancleavea* stands as one of the most bizarre archosauriforms recorded to date (Nesbitt et al., 2009a). The morphology of *Vancleavea* is unparalleled within Reptilia; it has four unique types of imbricated osteoderms covering the entire body, a short, highly ossified skull, relatively small limbs, and morphological features consistent with a semiaquatic lifestyle. Until recently, the taxon was only represented by a handful of incomplete specimens (Hunt et al., 2002, 2005). However, nearly complete specimens indicate that *Vancleavea* represents one of only few non-archosaurian archosauriforms from Laurasia (Parker and Barton, 2008; Nesbitt et al., 2009a). The long stratigraphic range of *Vancleavea* in the Chinle Formation suggests that it or similar taxa were present for much of the Late Triassic in western North America.

Key references: Long and Murry, 1995; Small and Downs, 2002; Hunt et al., 2002, 2005; Parker and Barton, 2008; Nesbitt et al., 2009a.

Chanaresuchus bonapartei Romer, 1971b
(fig. 7C–D)

Age: Ladinian, Middle Triassic (Rogers et al., 2001).

Occurrence: Chañares Formation, Argentina.

Holotype: UNLR 7 (formerly La Plata Museum 1964-XI-14-12), skull and partial postcranium.

←

Fig. 7. Skull reconstructions of Triassic archosauriform terminal taxa: **A,** *Proterosuchus fergusi* in lateral and **B,** dorsal views; redrawn from Cruickshank (1972); **C,** *Chanaresuchus bonapartei* in lateral and **D,** dorsal views; modified from Romer 1972b; **E,** *Prolacerta broomi* in lateral view; based on BP/1/471; **F,** *Erythrosuchus africanus* in lateral and **G,** dorsal views; redrawn from Gower (2003); **H,** *Euparkeria capensis* in lateral and **I,** dorsal views; redrawn from Ewer (1965); **J,** *Smilosuchus gregorii* in lateral view; based on AMNH FR 3060. See appendix for anatomical abbreviations. Scale bars = 5 cm in A–B, F–G, J, and 1 cm in E, H–I.

REFERRED MATERIAL: PVL 4586, skull; PVL 4575, complete skull and nearly complete postcranial skeleton; PVL 4647, braincase and partial skull; MCZ 4035, complete skull and postcrania; MCZ 4036, skull and most of the postcranium.

REMARKS: See Nesbitt et al., 2009a.

KEY REFERENCES: Romer, 1971b, 1972b; Sues et al., 1976; Arcucci, 1990.

Tropidosuchus romeri Arcucci, 1990

AGE: Ladinian, Middle Triassic (Rogers et al., 2001).

OCCURRENCE: Chañares Formation, Argentina.

HOLOTYPE: PVL 4601, nearly complete articulated skeleton without the distal portions of the forelimbs.

REFERRED MATERIAL: PVL 4602, vertebral column, hind limbs, and partial skull; PVL 4603, complete vertebral column, posterior portion of the skull, osteoderms; PVL 4604, pectoral and forelimb elements; PVL 4605, much of an articulated skeleton including skull; PVL 4606, complete skull, presacral vertebrae, pelvic girdle, and hind limb elements; PVL 4624, hind limb elements.

REMARKS: See Nesbitt et al., 2009a.

KEY REFERENCE: Arcucci, 1990.

Euparkeria capensis Broom, 1913 (fig. 7H–I)

AGE: Anisian, Middle Triassic (Rubidge, 2005).

OCCURRENCE: *Cynognathus* Assemblage Zone (B) (Beaufort Group) of South Africa.

HOLOTYPE: SAM 5867, skull and partial skeleton.

REFERRED MATERIAL: SAM 6050, partial skull; SAM 6047B, vertebrae, femur, pelvis, pectoral girdle; SAM 6049, dorsal, sacral, and caudal vertebrae, right hind limb, and partial pelvic and pectoral girdles; SAM 6047A, skull, vertebrae, and limb fragments; UMCZ T692, articulated foot with astragalus and calcaneum removed for study.

REMARKS: See Nesbitt et al., 2009a.

KEY REFERENCES: Broom, 1913; Ewer, 1965; Gower and Weber, 1998; Senter, 2003.

Parasuchus hislopi (Lydekker, 1885), sensu Chatterjee, 1978

AGE: Late Carnian–early Norian, Late Triassic (Chatterjee, 1978; Lucas, 1998a).

OCCURRENCE: Maleri Formation, near Maleri village, Adilabad district, Andhra Pradesh, India.

NEOTYPE: ISI R 42, nearly complete skull (Chatterjee, 1978: pl. 8) and articulated skeleton (see Chatterjee, 2001).

REFERRED MATERIAL: ISI R 43, most of complete articulated skeleton lacking the forelimbs and the anterior portion of the skull.

REMARKS: *Parasuchus hislopi* had confusing taxonomic history (Chatterjee, 1978) that is continued today (Lucas et al., 2007b). The nondiagnostic holotype was replaced by a neotype (ISI R 42) with approval from the ICZN (Opinion 2045) following the application of Chatterjee (2001). As a result, I score characters only from the two nearly complete skeletons described and illustrated by Chatterjee (1978). The two articulated skeletons represent the most complete phytosaurs known to date. Additionally, *Parasuchus* is important because it has been found as one of the most primitive phytosaurs in phylogenetic analyses of Phytosauria (see Lucas et al., 2007b, for references).

KEY REFERENCE: Chatterjee, 1978.

Smilosuchus gregorii (Camp, 1930), sensu Long and Murry, 1995 (fig. 7J) (= *Machaeroprosopus gregorii* Camp, 1930)

AGE: Early-mid Norian, Late Triassic (Irmis and Mundil, 2008).

OCCURRENCE: Blue Mesa Member of the Chinle Formation, Arizona.

HOLOTYPE: UCMP 27200, complete skull with mandible, eight vertebrae, a femur and osteoderms.

REFERRED MATERIAL: USNM 18313, partial skull, complete mandible, and nearly complete postcranial skeleton; AMNH FR 3060, skull, mandible, pelvis, osteoderms, partial hind limb.

REMARKS: *Smilosuchus* represents one of the largest phytosaurs (skull length >1.5 m) recovered from the Chinle Formation. As with most phytosaur specimens, the holotype of *Smilosuchus* consists of a skull and only fragments of the postcrania. Therefore, I rely on the nearly complete, disarticulated postcranial skeleton with associated skull of USNM 18313 for scoring postcrania. The ankle of USNM 18313 has figured prominently in studies of phytosaur locomotion (Parrish, 1986) and the origin of the "crocodile-normal" ankle type (Sereno, 1991a).

KEY REFERENCES: Camp, 1930; Gregory, 1962; Colbert, 1947; Ballew, 1989; Long and Murry, 1995; Stocker, 2008.

Pseudopalatus pristinus Mehl, 1928

AGE: Mid-late Norian, Late Triassic; most specimens from Petrified Forest National Park, Arizona fall within 30 m of the Black Forest Bed which has been radiometrically dated at 213 ± 1.7 Ma (Riggs et al., 2003).

OCCURRENCE: Petrified Forest Member of the Chinle Formation, Arizona; Bull Canyon Formation of the Dockum Group, New Mexico and Texas.

HOLOTYPE: U. of Mo. 525 VP, nearly complete skull.

REFERRED MATERIAL: UCMP 27235, partial skull and partially articulated postcranium, including much of the pes and manus; UCMP 34249, complete skull; various other isolated *Pseudopalatus pristinus* elements from the Canjilon Quarry (UCMP V2816); UCMP 34253, complete presacral column, sacrals, and anterior caudal vertebrae.

REMARKS: *Pseudopalatus pristinus* occurs throughout the upper half of the Chinle Formation and Dockum Group and stands alone as one of the most completely known derived phytosaurs. As a result, it is constantly cited as biostratigraphically useful (see Lucas, 1998a). Additionally, Zeigler et al. (2002, 2003) proposed that *Pseudopalatus pristinus* represents a sexual morph opposite *Pseudopalatus buceros.* Here, I score material referable to *Pseudopalatus* from the Canjilon Quarry (UCMP V2816), particularly the articulated specimens UCMP 27235 and UCMP 34253 and the complete well preserved skull UCMP 34249.

KEY REFERENCES: Mehl, 1928; Ballew, 1989; Long and Murry, 1995; Hungerbühler, 2002.

Gracilisuchus stipanicicorum Romer, 1972c
(fig. 8C–D)

AGE: Ladinian, Middle Triassic (Rogers et al., 2001).

OCCURRENCE: Chañares Formation, Argentina.

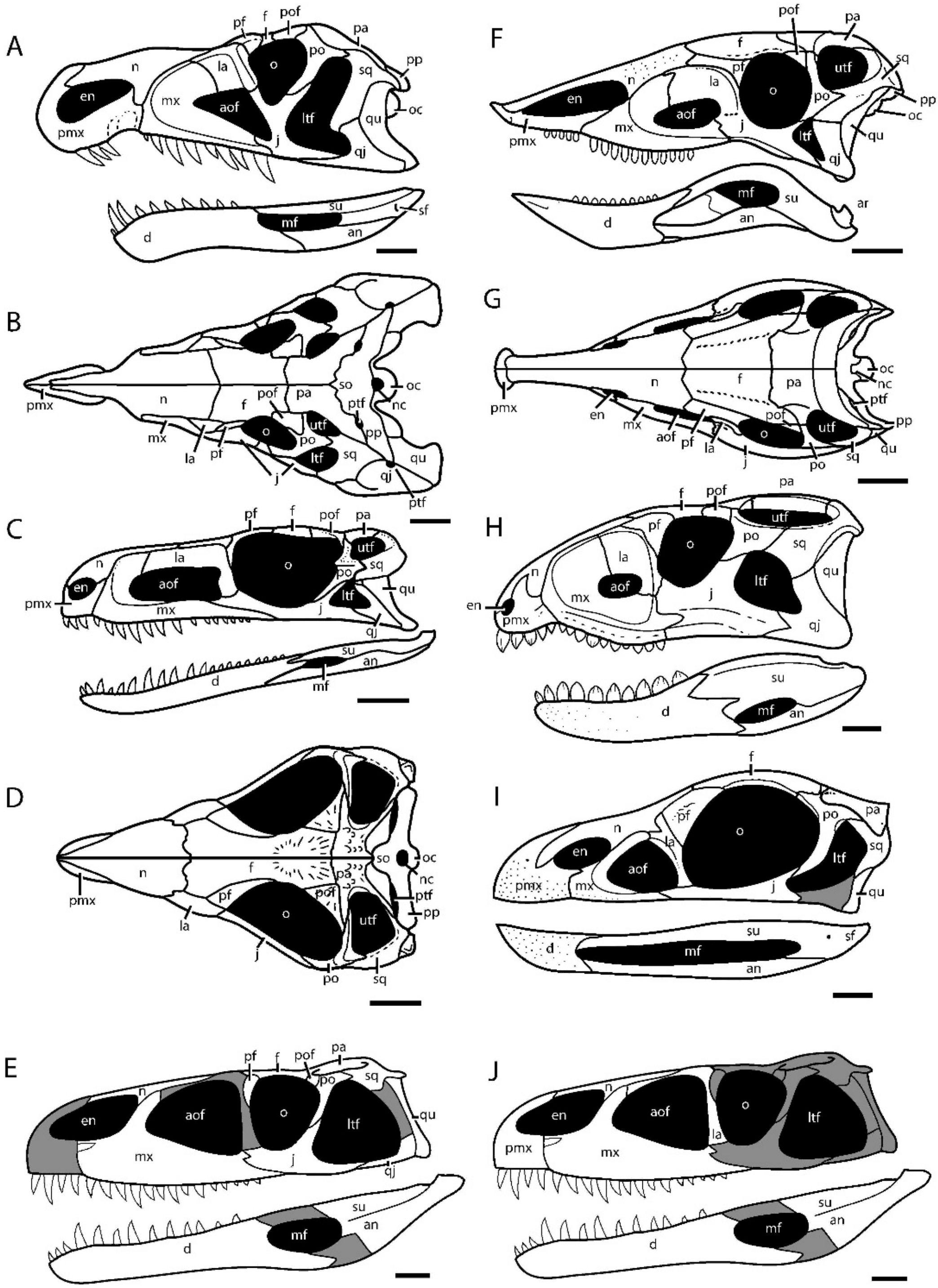
HOLOTYPE: UNLR 08, complete skull, articulated presacral vertebrae and osteoderms, scapula.

REFERRED MATERIAL: MCZ 4116, partially disarticulated skull; MCZ 4117, complete skull; MCZ 4118, partial skull, cervical vertebrae, and osteoderms; PVL 4597, nearly complete skull, presacral vertebrae, osteoderms, sacrum, pelvic girdle, nearly complete hind limb; PVL 4612, nearly complete skull, articulated presacral vertebrae.

REMARKS: *Gracilisuchus* is known from at least five articulated skulls and much of the postcranial skeleton except for the forelimbs. The forelimb assigned to *Gracilisuchus* by Romer (1972c) is too small for the size of the holotype, and Sereno and Arcucci (1994b) considered it part of the undiagnostic holotype of "*Lagosuchus.*" Many of the specimens are either dorsoventrally or mediolaterally crushed. As a result, the articulations and orientations of the posterior skull bones have been hotly debated in the literature (Romer, 1972c; Brinkman, 1981; Parrish, 1993).

Gracilisuchus was first described as an ornithosuchid by Romer (1972c), whereas Brinkman (1981) recognized the completely "crocodile normal" ankle and suggested it was closer to crocodylians. Ever since, *Gracilisuchus* was found in a variety of positions among crocodylian-line archosaurs. Parrish (1993) found *Gracilisuchus* as a close relative of *Postosuchus* and crocodylomorphs, whereas Benton and Clark (1998) found it as a basal suchian. More recently, Benton (2004) found *Gracilisuchus* as the sister taxon to Phytosauridae. *Gracilisuchus* has also been used as an outgroup in phylogenetic analyses of basal crocodylomorph relationships (the dataset of Clark et al., 2000). Until recently, *Gracilisuchus* stood alone as potentially one of the oldest suchians.

KEY REFERENCES: Romer, 1972c; Brinkman, 1981.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Turfanosuchus dabanensis Young, 1973

AGE: Middle Triassic (Young, 1973).

OCCURRENCE: Vertebrate Fossil Bed IV (Kannemeyeriid Zone), lower Kelamayi Formation, Taoshuyuanzi, about 30 km northwest of Turfan Basin, Xinjiang.

HOLOTYPE: IVPP V3237, much of a disarticulated skeleton.

REMARKS: *Turfanosuchus* is one of the oldest archosauriforms with a nearly complete skull and a partial skeleton. The partial skeleton was reassembled, the missing portions were sculpted, and the specimen was encased in plaster and then painted. The processing of the specimen for display purposes concealed details of the skeleton and obscured recognition of which bones were fossils and which were sculpted. For example, Young illustrated a nearly complete right manus and pes (Young, 1973: fig. 2). A recent inspection by me suggests that only the proximal portions of the metatarsals are preserved, whereas the manus and most of the pes are sculpted. Recently, Wu and Russell (2001) described reprepared material including the skull, femur, ilium, pubis, humerus, a newly discovered osteoderm, calcaneum, and astragalus. The specimens were fixed back to the mount after the completion of their study. The morphology of the astragalus could not be confirmed in this study and is not scored here.

The systematic position of *Turfanosuchus* has been debated recently and was included in only in only a few phylogenetic analysis thus far (Parrish, 1993; Dilkes and Sues, 2009). Parrish (1993) found *Turfanosuchus* well nested among crocodylian-line archosaurs. In a point-by-point response to the character scoring of Parrish (1993), Wu and Russell (2001) concluded that *Turfanosuchus* is neither a suchian nor a crurotarsan (= crocodylian-line archosaur in their meaning). Even though the analysis of Parrish (1993) was fraught with problems, Wu and Russell's (2001) detailed discussion of why *Turfanosuchus* is not an archosaur warrants further comment (character number from Wu and Russell, 2001, in parentheses):

(4) Presence of palatal teeth: Even though palatal teeth are present in *Turfanosuchus* and many non-archosaurian diapsids, palatal teeth are present in the archosaur *Eoraptor*. Furthermore, the pterygoid teeth in *Turfanosuchus* are exceedingly small and well spaced; therefore, pterygoid teeth may not be recognized in poorly preserved taxa, disarticulated taxa, or taxa without palates preserved.

(5) Foramina for internal carotid arteries enter the body of the basisphenoid ventral to the basipterygoid processes: The foramina for the entrance of the internal carotid arteries enter ventrally in *Turfanosuchus*, *Euparkeria* (SAM 5867), proterochampsians (e.g., *Chanaresuchus*, PVL 4647), and other non-archosaurian archosauriforms. Previously, it was thought that the internal carotid arteries entered laterally in archosaurs (see Gower and Sennikov, 1996; Gower and Walker, 2002). However, new discoveries, including *Arizonasaurus* (Gower and Nesbitt, 2006), *Qianosuchus* (Li et al., 2006) and *Silesaurus* (Dzik, 2003), showed that a ventral entrance for the internal carotid arteries occurs within Archosauria.

(7) Calcaneal tuber shaft broader than tall: Wu and Russell (2001) confused the measurements of the tuber shaft with the dimensions of the distal end of the tuber. In fact, the shaft of the tuber is wider than tall (contra Wu and Russell, 2001).

(8) Calcaneal tuber not flared distally: The distal end of the calcaneum tuber of *Turfanosuchus* is flared (contra Wu and Russell, 2001).

←

Fig. 8. Skull reconstructions of pseudosuchian archosaur terminal taxa: **A,** *Riojasuchus tenuisceps* in lateral and **B,** dorsal views; redrawn from Sereno (1991a); **C,** *Gracilisuchus stipanicicorum* in lateral and **D,** dorsal views; redrawn from Romer (1971b); **E,** *Arizonasaurus babbitti* in lateral view; redrawn from Nesbitt (2005); **F,** *Stagonolepis robertsoni* in lateral and **G,** dorsal views; redrawn from Walker (1961); **H,** *Revueltosaurus callenderi* in lateral view; based on PEFO 34561. **I,** *Effigia okeeffeae* in lateral view; redrawn from Nesbitt and Norell (2006); **J,** *Xilousuchus sapingensis* in lateral view; based on IVPP V 6026. Shaded areas indicate incomplete preservation. See appendix for anatomical abbreviations. Scale bars = 1 cm.

Most recently, Dilkes and Sues (2009) found *Turfanosuchus* outside Archosauria giving support to the hypothesis of Wu and Russell (2001).

KEY REFERENCES: Young, 1973; Parrish, 1993; Wu and Russell, 2001.

Ornithosuchus longidens (Huxley, 1877), sensu Walker, 1964

AGE: ?Late Carnian, Late Triassic (Lucas and Heckert, 1996).

OCCURRENCE: Lossiemouth Sandstone Formation, various sandstone quarries in the Elgin area, Scotland (see Walker, 1964, for details).

HOLOTYPE: See Walker, 1961, 1964.

REFERRED MATERIAL: See Walker, 1964.

REMARKS: *Ornithosuchus* is one of the few archosaurs from the Late Triassic of Scotland known from both natural molds and preserved remains. The genus-level taxon has a complicated taxonomic history given the poor preservation of the specimens. Walker (1964) reviewed all species of *Ornithosuchus* and concluded that all the material from the Elgin area represents one species-level taxon, *Ornithosuchus longidens*. Walker's concept of *Ornithosuchus* was followed by all subsequent workers. Sereno (1991a) listed five autapomorphies of *Ornithosuchus* that are accepted here.

The relationships of *Ornithosuchus* are as complicated as its taxonomy history. Since the initial description, *Ornithosuchus* was considered an archosaur (in the contemporary usage) with possible affinities with dinosaurs, phytosaurs, and aetosaurs (Newton, 1894; Boulenger, 1903; Huene, 1914; Walker, 1964). In a modern cladistic framework, *Ornithosuchus* (= Ornithosuchidae) was first found as one of the most basal avian-line archosaur clades (Gauthier, 1986; Benton and Clark, 1988), which was subsequently used as a basis to name the avian-line archosaur stem as Ornithosuchia (Gauthier and Padian, 1985). More recent analyses placed *Ornithosuchus* closer to crocodylians than to phytosaurs (Parrish, 1993; Benton, 1999), as the sister taxon of the Suchia (Sereno, 1991a), or within Suchia (Juul, 1994; Irmis et al., 2007a).

KEY REFERENCES: Huxley, 1877; Walker, 1964; Sereno, 1991a.

Riojasuchus tenuisceps Bonaparte, 1967
(fig. 8A–B)

AGE: Norian-?Rhaetian, Late Triassic (Arcucci et al., 2004).

OCCURRENCE: Los Colorados Formation, El Salto, Argentina (Arcucci et al., 2004).

HOLOTYPE: PVL 3827, complete skull, cervical, dorsal, sacral and caudal vertebrae, scapula, coracoid, humerus, distal portion of the radius and ulna, partial manus, ilium, pubis, femur, tibia, fibula, nearly complete pes.

REFERRED MATERIAL: PVL 3828, nearly complete skull, cervical, dorsal, sacral and caudal vertebrae, scapula, coracoid, humerus, ulna, radius, pubis, ischium, ilium, femur, tibia, fibula, calcaneum; PVL 2826 cervical, dorsal, sacral and caudal vertebrae, coracoids, scapula fragments, humerus, ulna, radius, ilium, femur, and tibia; PVL 3814 vertebrae, humerus, and tibia.

REMARKS: *Riojasuchus* is represented by nearly all portions of the skeleton. The well-preserved complete skull was well described by Bonaparte (1971), followed by Sereno (1991a). It is clearly the youngest member of the Ornithosuchidae and apparently represents a late surviving member of the clade.

Sereno (1991a) provided a list of autapomorphies that all differentiate *Riojasuchus* from *Ornithosuchus*. However, autapomorphies I, K, and L have a wider distribution. For example, aetosaurs (e.g., *Aetosaurus*, SMNS 5770) possess a sloping occiput much like that of *Riojasuchus*.

KEY REFERENCES: Bonaparte, 1967; 1971; Sereno, 1991a.

Stagonolepis robertsoni Agassiz, 1844
(fig. 8F–G)

AGE: ?Late Carnian, Late Triassic (Lucas and Heckert, 1996).

OCCURRENCE: Lossiemouth Sandstone Formation, Scotland.

HOLOTYPE: EM 27 R, impression of a segment of a ventral osteoderm.

REFERRED MATERIAL: See Walker, 1961; MCZD 2–4, braincase.

REMARKS: First regarded as a ganoid fish, *Stagonolepis* is one of the better known aetosaurs largely as the result of the work of Huxley (1877) and especially Walker (1961). Although casts produced from sandstone molds represent nearly all the specimens, Walker (1961) laboriously worked to produce a rather complete anatomy of *Stagonolepis*. Details of the pes and other bones are missing because of the preservation of the material. I urge future workers to score characters from the actual casts and molds of the material and not reconstructions of the material, even though it is tempting given Walker's fine work on the Lossiemouth Sandstone archosaurs. Here, I specifically use *Stagonolepis* so that the observations of the braincase by Gower and Walker (2002) could be included in a broader context. Furthermore, I assume all the aetosaur material from the Lossiemouth Sandstone Formation belongs to *Stagonolepis robertsoni*.

KEY REFERENCES: Huxley, 1877; Walker, 1961; Gower and Walker, 2002.

Aetosaurus ferratus Fraas, 1877

AGE: Norian, Middle Keuper, Late Triassic (see Schoch, 2007).

OCCURRENCE: Lower Stubensandstein, Löwenstein Formation, southwest of Stuttgart, Germany.

LECTOTYPE: Specimen 16 (XVI), a nearly complete skull and postcranium that is part of the SMNS 5770 cluster, an assemblage of at least 25 specimens.

REFERRED MATERIAL: SMNS 5771 (type locality and horizon), SMNS 18554 (articulated skeleton lacking skull and pectoral girdle; Blankenhorn Castle near Eibensbach); Middle Stubensandstein from Pfaffenhofen: SMNS 11837 (type of *A. crassicauda*), SMNS 12670 (collection of isolated dorsal plates and a fragment of the ventral osteoderms); SMNS 14882 (articulated tail portion with osteoderms and 14 caudal vertebrae).

REMARKS: *Aetosaurus* was named by Fraas (1877) from an accumulation of at least 24 individuals that lie in almost complete articulation. Although *Aetosaurus* is known from well-preserved articulated material, the extensive osteoderm carapace or other skeletal elements conceal details of the vertebrae, braincase, palate, and pectoral and pelvic girdles. A detailed and useful review of the taxon by Schoch (2007) provided additional information on the skull, variation, and osteoderms. Even though specimens from outside the Lower Stubensandstein have been referred to *Aetosaurus* (Jenkins et al., 1994; Heckert and Lucas, 1998; Small, 1998) only the individuals numbered SMNS 5770 are scored here.

KEY REFERENCES: Fraas, 1877; Huene, 1920; Walker, 1961; Wild, 1989; Schoch, 2007.

Longosuchus meadei (Sawin, 1947),
sensu Hunt and Lucas, 1990

AGE: ?Carnian–early Norian (Lucas et al., 1993).

OCCURRENCE: Otis Chalk area, TMM 31025 (Quarry 1), TMM 31099 (Quarry 2), TMM 31100 (Quarry 3), TMM 31185 (Quarry 3A), TMM 31098 (site 3), TMM 31220 (sites 3, 4) "Pre-Tecovas horizon" (Long and Murry, 1995).

LECTOTYPE: TMM 31185-97 postcrania (formerly 31185-84b). The well-preserved skull TMM 31185-98 belongs to the postcranial skeleton numbered TMM 31185-97 (Sawin, 1947), but because of ICZN rules, it is not part of the lectotype (Parker and Martz, 2010).

REFERRED MATERIAL: TMM 31185-98, skull (formerly part of 31185-84b [Sawin, 1947; Hunt and Lucas, 1990]); TMM 31185-97 (formerly 31185-84a), axial, pelvic and pectoral elements, limb fragments; TMM 31185-84a, appendicular elements axial skeleton, many osteoderms, manus, pes; TMM 31100-435, two-thirds of an articulated tail.

REMARKS: Originally named as a species of *Typothorax* (Sawin, 1947), Hunt and Lucas (1990) renamed the taxon as *Longosuchus meadei* based on the divergent morphology of the TMM specimens with those of *Typothorax coccinarum*. Most elements of the skeleton of *Longosuchus* are known from both articulated and disarticulated specimens and were collected from a limited geographic area near Otis Chalk (see Sawin, 1947). Two exquisitely preserved skulls, one partial and one nearly complete, preserve details of the palate, braincase, and details on the medial side of each preserved element (Sawin, 1947; Parrish, 1994). Furthermore, the specimens preserve manus and pedes in the collected material making *Longosuchus* the most complete, large bodied aetosaur. Unfortunately, many of the bones (e.g., pedes) described by Sawin (1947) are mounted in a reconstruction on display at the Texas Memorial Museum, at the University of Texas at Austin. Based on osteoderms, Lucas (1998b, 1998c) reported *Longosuchus* from the Timesgadiouine Formation of Morocco and Pekin Formation of the Newark Supergroup; none of these specimens is used to score the taxon here.

KEY REFERENCES: Parrish, 1994; Small, 2002; Parker, 2003.

Revueltosaurus callenderi Hunt, 1989 (fig. 8H)

AGE: Middle-late Norian (Parker et al., 2005; most specimens from PEFO fall within 30 m of the Black Forest Bed which was radiometrically dated at 213 ± 1.7 Ma (Riggs et al., 2003).

OCCURRENCE: Bull Canyon Formation, Dockum Group; Petrified Forest Member, Chinle Formation.

HOLOTYPE: NMMNH P-4957, a nearly complete premaxillary tooth.

REFERRED MATERIAL: PEFO 34561, essentially complete skeleton; PEFO 34269, nearly complete skeleton; see Parker et al. (2005) for other specimens.

REMARKS: The original description of *Revueltosaurus* was based on isolated teeth from the Upper Triassic deposits of the American Southwest (Hunt, 1989; Padian, 1990). As described by Hunt (1989), followed by Heckert (2002), *Revueltosaurus* shares an uncanny resemblance to the teeth of early ornithischians. The similarity of teeth of *Revueltosaurus* to ornithischians led to the proliferation of the naming of isolated diagnosable teeth similar to those of ornithischians from other Triassic deposits (Hunt and Lucas, 1994; Heckert, 2002). These isolated teeth formed the basis of our understanding of the early ornithischian record in North America and Europe. Parker et al. (2005) reported a partial skeleton referred to *Revueltosaurus* from the Petrified Forest Member of the Chinle Formation. They demonstrated that *Revueltosaurus* is a pseudosuchian, not a dinosaur. Consequently, *Revueltosaurus* illustrates the difficulty of assigning isolated teeth to a taxon; none of the "ornithischian-like" teeth from the Triassic of southwestern America can be confidently assigned to Ornithischia (Irmis et al., 2007b).

Much of the *Revueltosaurus* cranial and postcranial material originates from a monotypic bonebed. The specimens occur as isolated bones, complete associated specimens, or articulated skeletons. Thus, nearly the entire skeleton of *Revueltosaurus* is known. The phylogenetic position of the new, nearly complete specimens of *Revueltosaurus* have yet to be tested in a broad phylogenetic analysis of basal archosaurs. A full description of the skeleton is underway (Parker et al., in prep.).

KEY REFERENCES: Hunt, 1989; Heckert, 2002; Parker et al., 2005.

Ticinosuchus ferox Krebs, 1965 (figs. 9–10)

AGE: Anisian-Ladinian, Middle Triassic (Rieber, 1973).

OCCURRENCE: "Grenzbitumen" horizon, Monte San Giorgio, Tessin, Switzerland.

HOLOTYPE: PIZ T2817, essentially complete skeleton.

REFERRED MATERIAL: PIZ T2471, six articulated caudal vertebrae with osteoderms; BES 189 at Museo Civico di Storia Naturale, Milano.

REMARKS: *Ticinosuchus* was named by Krebs (1965) based on an essentially complete skeleton found near the Anisian-Ladinian boundary in marine sediments. The skeleton preserves most elements in either articulated or disarticulated state. However, as noted by Krebs (1965), many of the bones are heavily crushed, hidden by other elements, or have poorly preserved surfaces.

This has prevented comparison of individual elements to other pseudosuchian taxa, and many features cannot be scored into phylogenetic analyses. As a result, the phylogenetic position is poorly supported in the few analyses in which it has been included (e.g., Parrish, 1993; Benton, 2004).

I examined the skull region very carefully and have a few comments. Unfortunately,

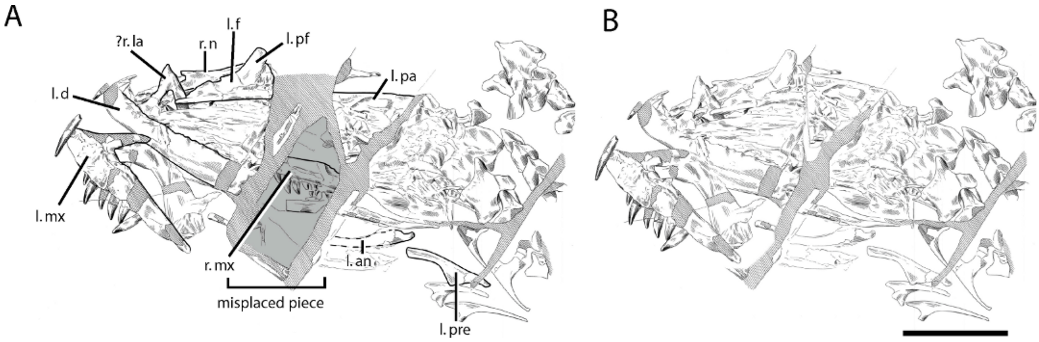


Fig. 9. **A,** The skull of *Ticinosuchus ferox* (PIZ T2817) with highlighted cranial elements (modified from Krebs 1965). The gray ''piece'' actually belongs underneath the piece with the left maxilla. **B,** Corrected skull of *Ticinosuchus* with the incorrectly placed piece removed. See appendix for anatomical abbreviations. Scale bar = 10 cm.

the blocks with skull elements appear to have been reassembled incorrectly. The skull must have been split longitudinally when collected, and a portion of the right side was placed incorrectly posterior to the left side of the skull (see fig. 9). This is apparent because the specimens from the ''Grenzbitumen'' horizon were collected in pieces, then reassembled later (Furrer, personal commun.). The medial surface of the right maxilla is exposed laterally, and there is a large gap between the anterior and posterior portions of the skull. Once this incorrectly placed piece is removed and the anterior and posterior portions of the skull are brought back together, the skull becomes much shorter (see fig. 9). Parts of the skull that were not originally identified include the left frontal and postfrontal in ventral view, the left parietal in lateral view, an upside-down left

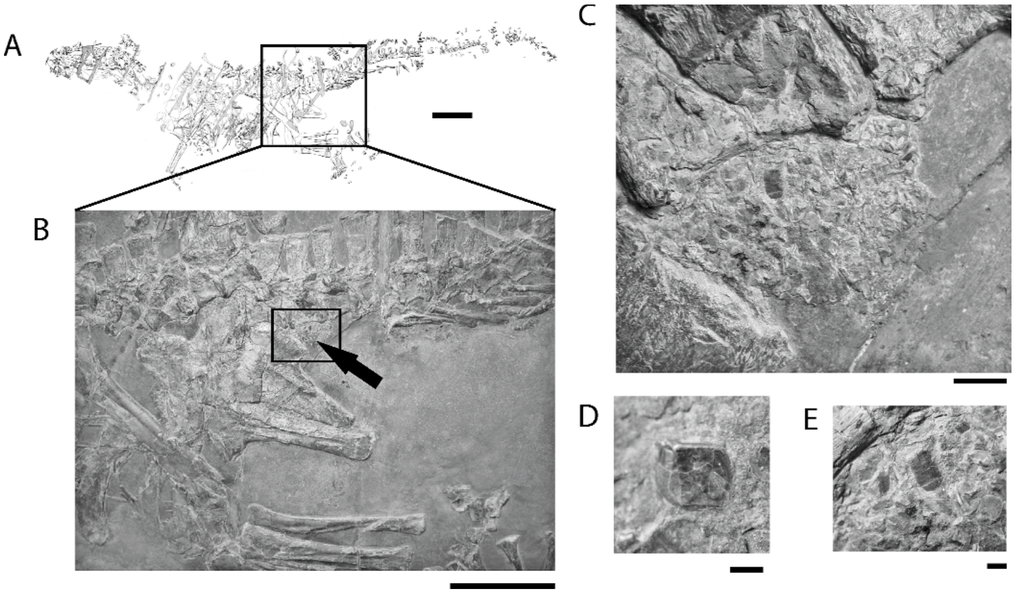


Fig. 10. Gut contents of *Ticinosuchus ferox* (PIZ T2817): **A,** drawing of the skeleton of *Ticinosuchus* (from Krebs, 1965); **B,** close up of the area posterior of the pelvis showing a small mass of scales (arrow); **C,** close up of the accumulation of bone fragments and scales; **D–E,** detailed photograph of fish scales. Scale bars = 10 cm in A–B, 1 cm in C, and 1 mm in D–E.

prearticular in medial view, the impression of the left angular, the left nasal in ventral view, and ?left lacrimal in ?medial view (see fig. 9).

The holotype of *Ticinosuchus ferox* preserves the remains of its last meal (fig. 10), and this represents one of the few examples of prey choice in any Triassic archosaur (see Nesbitt et al., 2006). A small collection of fish scales is present at the base of the tail posterior to the ilium and the proximal portion of the ischium. The three-dimensional structure consists of a tan matrix with randomly oriented fish scales (fig. 10D–E). Even though there are a few fish scales located throughout the matrix in which *Ticinosuchus* is entombed, the abundance of fish scales at the base of the tail far exceeds any other concentration on the slab. It is clear that *Ticinosuchus* included fishes in its diet, and it is unclear to which taxon or taxa the scales belong. Unfortunately, the identity of the fish as either freshwater or marine is not known at this time. The prey choice of *Ticinosuchus* may explain why the seemingly terrestrial carnivore would be found in marine sediments. It is clear that *Ticinosuchus* must have been living close to the shoreline. A similar taxon, *Qianosuchus*, was also found in marine sediments. Therefore, it is possible that *Qianosuchus* may have also lived near the shoreline.

Krebs (1965) described much of the skeleton of *Ticinosuchus* in detail; however, Parrish (1993) discussed a few features of the osteoderms. Parrish (1993) stated that *Ticinosuchus* has only one paramedian pair of osteoderms per vertebral segment. Nevertheless, it is clear from partially articulated segments of osteoderms, the small size of individual osteoderms, and the number of osteoderms preserved that there must be more than one paramedian pair of osteoderms per vertebral segment.

Pinna and Arduini (1978) referred a specimen (BES 189) from the Middle Triassic strata of Besano to *Ticinosuchus*. The specimen consists of partial forelimbs and pectoral girdle, an osteoderm, a tooth, and part of the mandible. The morphology of the osteoderm is consistent with that of *Ticinosuchus*, *Prestosuchus*, and *Saurosuchus*. The other bones do not bear any unique apomorphies for *Ticinosuchus*. Therefore, this taxonomic assignment is not followed. Only PIZ T2817 is scored for *Ticinosuchus*.

KEY REFERENCES: Krebs, 1963, 1965; Pinna and Arduini, 1978.

Qianosuchus mixtus Li et al., 2006

AGE: Anisian, Middle Triassic (Li et al., 2006).

OCCURRENCE: Guanling Formation, Xinmin, Panxian County, southwestern Guizhou Province, China.

HOLOTYPE: IVPP V13899, a skeleton with distal part of forelimbs and posterior end of the tail missing.

REFERRED MATERIAL: IVPP V14300, an incomplete skeleton with nearly complete skull; NMNS 000408/F003877, an incomplete skull.

REMARKS: Li et al. (2006) described *Qianosuchus* from marine sediments from the Anisian of southern China. The taxon is the most completely known early archosaur and one of the most completely documented basal archosaurs to date given that it is represented by two nearly complete skeletons and a crushed skull in ventral view. Even though the specimens are essentially "slab-specimens," the bones are nearly three-dimensionally preserved. *Qianosuchus* awaits a full anatomical description.

Li et al. (2006) hypothesized that *Qianosuchus* was semiaquatic based on tall neural spines of the caudal series, a thinned platelike scapula and coracoid, an elongate neck (the nine cervical vertebrae reaching 75% of the trunk length and, together with the skull, over 120% of the latter) with long and slender cervical ribs, and small-sized dorsal osteoderms in the neck and trunk regions, but absent in the tail region. The authors rightly pointed out that characters one and four are common in marine tetrapods. However, an elongated neck is also present in fully terrestrial archosaurs (e.g., *Arizonasaurus*, MSM 4590; *Effigia,* AMNH FR 30587; *Hesperosuchus agilis*, AMNH FR 6758), and a thinned plate-like scapula and coracoid seem to be an autapomorphy of the taxon with no clear ecological significance. As the authors noted, other features of the skeleton are typical of terrestrial archosaurs. The ecology of this important taxon is unclear because of the ambiguous mix of potentially semiaquatic and terrestrial features and that there are multiple skeletons of *Qianosuchus* from marine deposits.

Qianosuchus possesses an intriguing mix of character states commonly listed as "rauisuchian" and poposauroid apomorphies. *Qianosuchus* clearly bears a crocodylian-normal ankle similar to that of aetosaurs, "rauisuchians," poposauroids, and crocodylomorphs. The taxon has a short pubis and ischium relative to the femur, at least four leaf-shaped osteoderms per vertebra in the presacral series, and typically carnivorous teeth, features found in *Prestosuchus* (UFRGS 0156-T; UFRGS 0152-T; BSP XXV 1-3/5-11/ 28-41/49), *Ticinosuchus* (PIZ T2817), and *Saurosuchus* (PVSJ 32). The elongated cervicals with elongated cervical ribs, the enlarged narial opening, a slot on the anterolateral surface of the maxilla for the posterior process of the maxilla, and the presence of three sacral vertebrae support a close relationship to poposauroids (Nesbitt, 2005). The age, mix of "rauisuchian" and poposauroid character states, and mixed ecological signal makes *Qianosuchus* important to the early radiation of the crocodylian-line archosaurs.

Li et al. (2006) provided the following diagnosis: A medium-sized archosaurian, over 3 m in length, differing from all other archosaurians in having the following combination of derived features: low premaxilla bearing nine daggerlike teeth; posteriorly positioned external naris longer than any other skull opening and mainly enclosed by nasal dorsally and maxilla ventrally; external mandibular fenestra half oval in outline; neural spines in cervical vertebrae 2 to 9 longitudinally very broad, each with five pairs of small osteoderms on its top; neural spines of caudal vertebrae very tall, at least four times the height of the centra and longer than chevrons in midtail region; cervical ribs elongate, most of them over four times length of corresponding centra; scapula plate-like, hatchet shaped in outline.

KEY REFERENCES: Li et al., 2006.

Xilousuchus sapingensis Wu, 1981 (fig. 8J)

AGE: Late Early Triassic (Rubidge, 2005).

OCCURRENCE: Heshanggou Formation, Hazhen commune, Fugu County, northeastern Shensi Province, China (Wu, 1981).

HOLOTYPE: IVPP V 6026, maxillae, premaxilla, lacrimal, nasal, dentary, articular, surangular fragment, splenial, braincase, axis, presacral vertebrae 3–10, primordial sacral two, two distal caudal vertebrae, cervical rib, dorsal rib, clavicle, ungual.

REMARKS: *Xilousuchus sapingensis* Wu, 1981, is one of the most completely known archosauriforms from the Early to Middle Triassic of China. Regardless of the exact age of the Heshanggou Formation, *Xilousuchus* lived along with early archosauriforms such as a *Proterosuchus*-like taxon and *Fugusuchus*, a taxon considered to be more closely related to *Erythrosuchus* than to other archosauriforms (Gower and Sennikov, 1996).

Xilousuchus was named from a single well-preserved partial skull and the anterior portion of the presacral vertebral series. As first described, *Xilousuchus* was referred to the Proterosuchia by Wu (1981), whereas Gower and Sennikov (1996) found it as an erythrosuchian based strictly on the braincase.

Xilousuchus sapingensis differs from all other archosauriforms except *Lotosaurus*, *Ctenosauriscus*, and *Arizonasaurus* in having posterior cervical vertebrae with neural spines that arc anteriorly at the distal end. It differs from *Ctenosauriscus* in having anteroposteriorly expanded neural spines on the midcervical vertebrae. It differs from *Lotosaurus*, but not *Arizonasaurus*, in having a deep pit at the anteroventral margin of the antorbital fossa in the maxilla. *Xilousuchus* differs from *Arizonasaurus* in having a deep pit ventral to the descending process of the opisthotic in the parabasisphenoid, the absence of a divided parapophysis of the posterior cervical vertebrae, and poor development of the posterior centrodiapophyseal lamina in the anterior cervical vertebrae.

KEY REFERENCES: Wu, 1981; Gower and Sennikov, 1996.

Arizonasaurus babbitti Welles, 1947 (fig. 8E)

AGE: Anisian, Middle Triassic (Lucas, 1998a).

OCCURRENCE: Holbrook Member of the Moenkopi Formation, Arizona; Anton Chico Member of the Moenkopi Formation, New Mexico (Schoch et al., 2010).

HOLOTYPE: UCMP 36232, maxilla.

REFERRED MATERIAL: MSM 4590, skull and partial skeleton; see Nesbitt (2003, 2005a) and Schoch et al. (2010) for other specimens.

REMARKS: *Arizonasaurus* represent one of the most completely documented sail-backed archosaurs from the Anisian. Additionally, *Arizonasaurus* is the most common reptile found in the Holbrook and Anton Chico Members of the Moenkopi Formation (Nesbitt, 2005b; Schoch et al., 2010). The holotype and the referred specimen (MSM 4590) share two characters: a uniquely shaped ascending process of the maxilla that is triangular in cross section and a deep pit at the posterior side of the base of the ascending process of the maxilla. Both these characters are present in *Xilousuchus* suggesting that the two taxa are closely related (see below). The partial "lacrimal" described by Nesbitt (2005) is actually the prefrontal.

Nesbitt (2003) found *Arizonasaurus* as a close relative of *Poposaurus* and *Shuvosaurus* (= *Chatterjeea*) within Suchia. Other analyses found a similar position (Nesbitt and Norell, 2006; Irmis et al., 2007a; Weinbaum and Hungerbühler, 2007; Brusatte et al., 2008). Nesbitt (2003, 2005a) hypothesized that *Arizonasaurus* formed a clade with other sail-backed suchians including *Ctenosauriscus*, *Lotosaurus*, *Bromsgroveia*, and *Hypselorhachis*.

Arizonasaurus differs from all other archosaurs except *Xilousuchus*, *Lotosaurus*, *Hypselorhachis*, and *Ctenosauriscus* by the presence of a sail created by the elongation of the neural spines of the presacral vertebrae. It differs from *Xilousuchus* by the absence of a deep pit in the parabasisphenoid ventral to the descending process of the opisthotic. *Arizonasaurus* differs from *Ctenosauriscus* in anteroposteriorly wide neural spines of the midposterior cervical vertebrae. It differs from *Lotosaurus* by the presence of teeth.

KEY REFERENCES: Welles, 1947; Nesbitt, 2003, 2005a; Gower and Nesbitt, 2006; Schoch et al., 2010.

Poposaurus gracilis Mehl, 1915

AGE: Carnian–early Norian, Late Triassic.

OCCURRENCE: Popo Agie Formation, Wyoming; Blue Mesa Member of the Chinle Formation, Arizona; Mesa Redondo Member of the Chinle Formation, Arizona; Tecovas Formation of the Dockum Group, Texas; Monitor Butte Member of the Chinle Formation, southern Utah.

HOLOTYPE: FMNH 357, two dorsal vertebrae, one caudal vertebra, a left ilium, the proximal portion of a left femur, a right femur, distal portion of the ischia.

REFERRED MATERIAL: TTU-P 10419, vertebrae, pelvic elements; TMM 43683-1, vertebrae and nearly complete pelvis; various UCMP elements from A269 (see Long and Murry, 1995); YPM 57100, nearly complete skeleton lacking the skull.

REMARKS: *Poposaurus gracilis* was named from a fragmentary specimen consisting of pelvic elements, the femora, and a few vertebrae (Mehl, 1915). The differences in morphology from other Triassic archosaurs led various authors to identify *P. gracilis* as an ornithischian (Nopsca, 1921), a stegosaur (Huene, 1950), a theropod (Colbert, 1961), and a pseudosuchian (Walker, 1969). New specimens of *P. gracilis* and other closely related taxa confirmed the pseudosuchian affinity of the taxon (Galton, 1977; Long and Murry, 1995; Nesbitt and Norell, 2006; Weinbaum and Hungerbühler, 2007). With the exception of a nearly complete skeleton lacking the skull (Joyce and Gauthier, 2006), nearly all specimens of *P. gracilis* consist of pelvic material, a few vertebrae, and partial limbs (Weinbaum and Hungerbühler, 2007).

The element that was identified as the pubes in the holotype (FMNH 357) is actually the ischium; therefore, the pubis is not represented in the holotype material. The element that was once identified at the pubis bears a large distal expansion (= pubic boot), and this expansion has greatly influenced the interpretation of its relationships in older (Colbert, 1961) and more recent (Weinbaum and Hungerbühler, 2007) studies. Indeed, the ischium bears a greatly enlarged distal expansion. Ironically, new specimens confirm that a large distal expansion (= pubic boot) is present in *P. gracilis* (TMM 43683-1; YPM 57100).

Dawley et al. (1979) described *Heptasuchus*, another "rauisuchian" from the same formation (Popo Agie Formation) as the holotype of *P. gracilis.* Later, Zawiskie and Dawley (2003) hypothesized that the skull of *Heptasuchus* belongs to the body of *P. gracilis.* Although only a few elements (e.g., pubis, ulna) are directly comparable between the unique specimen of *Heptasuchus* and *P. gracilis*, there are important differences between the pubes. Both taxa have a distal expansion of the pubis; however, the distal expansion in *Heptasuchus* is robust and rounded like that of *Batrachotomus* rather than the mediolaterally compressed distal expansion of *P. gracilis* (TMM 43683-1). Furthermore, the preserved portions of the skull of *Heptasuchus* (maxilla, premaxilla, braincase) are much like that of *Batrachotomus* and not much like those of the putative close relatives of *Poposaurus* such as *Arizonasaurus* and *Effigia* (Nesbitt, 2007). Furthermore, it is reasonable to assume that more than two paracrocodylomorph taxa exist in a single assemblage as demonstrated by the cooccurrence of *Postosuchus* and *Poposaurus* in the *Placerias* Quarry (Long and Murry, 1995) and *Postosuchus* and *Shuvosaurus* in the Post (= Miller) Quarry (Long and Murry, 1995). Therefore, the hypothesis that *Heptasuchus* represents the skull of *P. gracilis* is rejected here.

Poposaurus gracilis possesses two autapomorphies: a thick lateral ridge posterior to the acetabulum and a pit on the proximal part of the ischium for reception of the convex ischial peduncle of the ilium (Weinbaum and Hungerbühler, 2007).

KEY REFERENCES: Mehl, 1915; Colbert, 1961; Galton, 1977; Long and Murry, 1995; Weinbaum and Hungerbühler, 2007.

Lotosaurus adentus Zhang, 1975

AGE: Middle Triassic (Zhang, 1975).

OCCURRENCE: Batung Formation, Hunan Province, China (Zhang, 1975).

HOLOTYPE: Unspecified, either IVPP V4880 or V4881.

REFERRED MATERIAL: IVPP V 48013, skull, articulated and disarticulated remains of at least ?10 individuals from a monotypic bonebed (unnumbered).

REMARKS: *Lotosaurus* is a highly specialized archosaur from the Middle Triassic of China with elongated neural spines forming a sail, robust fore- and hind limbs, and a peculiar skull with an edentulous beak. In a preliminary description, Zhang (1975) noted that *Lotosaurus* may be related to other archosaur taxa with elongated neural spines (e.g., *Ctenosauriscus*) and others have followed this line of thought (e.g., Carroll, 1988). Nesbitt (2007) went further and described some of the features *Lotosaurus* shared with taxa such as *Arizonasaurus* and *Effigia* and found *Lotosaurus* to be closely related to these taxa in a position just outside "clade Y" (= Shuvosauridae). As explained by Nesbitt (2007), if *Lotosaurus* is more closely related to *Shuvosaurus* and *Effigia* than to *Arizonasaurus*, the ctenosauriscids (as proposed by Nesbitt, 2005a) would be paraphyletic. A full description of *Lotosaurus* is currently underway.

Lotosaurus differs from all other archosaurs by the combination of a sail formed from the elongation of the neural spines of the presacral vertebrae and the presence of edentulous premaxillae, maxillae, and dentaries.

KEY REFERENCES: Zhang, 1975; Nesbitt, 2007.

Sillosuchus longicervix
Alcober and Parrish, 1997

AGE: Late Carnian, Late Triassic (Rogers et al., 1993, adjusted for the new Triassic timescale of Muttoni et al., 2004).

OCCURRENCE: Ischigualasto Formation, Argentina.

HOLOTYPE: PVSJ 85, postcranium consisting of parts of five cervical vertebrae, the last four dorsal vertebrae, five sacrals, and the first eight caudal vertebrae (the dorsal, sacrals, and caudal vertebrae preserved in articulation), partial right ilium, both pubes (nearly complete), both ischia preserved in articulation, both femora (complete), various pieces of ribs, and indeterminate fragments. Additionally, a partial left coracoid and scapula, the proximal portion of the left humerus, and the proximal portions of both tibiae were also collected with the holotype but not described in the original description.

REMARKS: *Sillosuchus longicervix* was described from an incomplete postcranial skeleton that is poorly preserved and crushed (Alcober and Parrish, 1997). Although rare in the Ischigualasto Formation, other specimens have been found, but await description. The deep pockets on the lateral side of the cervical and the anterior dorsal vertebrae are unparalleled among pseudosuchians. The anteroposteriorly elongate and oval pockets stretch for much of the length of the centrum and only a thin lamina of bone at the midline separates the lateral pockets. Much of the morphology of the pelvis of *Sillosuchus* is very similar to *Shuvosaurus* and *Effigia*. All three taxa share coossified ischia, a dorsally expanded ilium, a thin, anteriorly arching crest dorsal to the supraacetabular crest, anteroposteriorly elongated cervical centra, and four or more sacral vertebrae (Nesbitt, 2007).

The coracoid, part of the scapula, and the proximal portion of the humerus were collected with the holotype, but were not described in the original description. The coracoid bears an elongated postglenoid process like that of *Effigia* (AMNH FR 30587) and *Shuvosaurus* (TTU-P 9001), but does not bear a deep fossa on the dorsal surface of the process as do *Effigia* and *Shuvosaurus*. The scapula is anteriorly expanded into a thin sheet of bone just like that of *Effigia* (AMNH FR 30587). Furthermore, the proximal portion of the head is poorly expanded, and even though the bone is not complete, the proximal portion of the humerus was probably not expanded more than twice the midshaft, another synapomorphy with *Effigia* and *Shuvosaurus* (Nesbitt, 2007). In summary, the undescribed forelimb material of the holotype of *Sillosuchus* is remarkably similar to that of *Effigia* and *Shuvosaurus*. Furthermore, the gracile humerus of *Sillosuchus* suggests that the forelimb of *Sillosuchus* was possibly similar to the short forelimbs of *Effigia*, and it may have had a similar forelimb to hind limb length. Therefore, *Sillosuchus* possibly was another bipedal taxon.

As remarked by Alcober and Parrish (1997), the presence of *Saurosuchus* and *Sillosuchus* in the Ischigualasto Formation, two relatively closely related taxa, adds ambiguity to the identification of isolated specimens of both taxa. For example, Sill (1974) tentatively assigned PVL 2267, an isolated cervical vertebra, to *Saurosuchus*. The presence of deep lateral pockets and anteroposterior elongation of the centrum indicate assignment to *Sillosuchus* rather than *Saurosuchus*. Furthermore, the anteroposteriorly short and dorsally tall cervical vertebrae found with the nearly complete skull of *Saurosuchus* (PVSJ 23) preclude assignment of PVL 2267 to *Saurosuchus*.

Sillosuchus is one of the larger pseudosuchians from the Triassic as indicated by the holotype (femur length = 47 cm) and the larger isolated cervical vertebra (PVL 2267) referable to *Sillosuchus* (see preceding paragraph). Each of the cervicals in the holotype measures about 8 cm long, whereas PVL 2267 measures 20 cm long. The length of PVL 2267 suggests that *Sillosuchus* could have reached an estimated length (from extrapolation of data from the holotype of *Sillosuchus* and *Effigia*) of 9–10 meters. This is further supported by other large isolated elements (PVL 2267; partial left ilium).

Nesbitt (2007) confirmed the hypothesis of Alcober and Parrish (1997) that *Sillosuchus* and *Shuvosaurus* (= *Chatterjeea*) are closely related, and both are closely related to *Poposaurus*.

Sillosuchus longicervix possesses deep pockets (= pneumatic recesses) on the lateral side of both the cervical and dorsal centra and coossified ischia with a highly dorsoventrally compressed distal end that differentiates it from all other archosaurs. *Sillosuchus* also possesses a unique suite of characters including: five coossified sacral vertebrae; small pubic boot; dorsally expanded ilium with a thin, anteriorly arching crest dorsal to the supraacetabular crest (= rim). Alcober and Parrish (1997) listed two characters in the diagnosis: elongated cervical vertebrae and relatively short ischia. The cervical vertebrae of *Sillosuchus* are indeed elongated but proportionally are not more elongated than those of *Shuvosaurus* (= *Chatterjeea*) and *Effigia* (AMNH FR 30587). Furthermore, the short ischia are not complete, and therefore the length cannot be assessed with certainty. That said, the preserved length of the ischia are probably relatively short relative to the pubis.

KEY REFERENCES: Alcober and Parrish, 1997; Nesbitt, 2007.

Effigia okeeffeae Nesbitt and Norell, 2006 (fig. 8I)

AGE: Late Norian–?Rhaetian, Late Triassic (Heckert et al., 2008).

OCCURRENCE: *Coelophysis* Quarry, "siltstone member" of the Chinle Formation, Ghost Ranch, northern New Mexico.

HOLOTYPE: AMNH 30587, nearly complete skull, much of the cervical dorsal, and sacral vertebrae and the first two caudal vertebrae, right pes, left and right femur, left and right tibia, left and right fibula, right and fragments of the left scapula, left and right coracoids, right humerus, right ulna, right radius, right manus, left and right ilium, left and right ischia, right pubis, gastralia, and dorsal ribs.

REFERRED MATERIAL: AMNH FR 30588, femur, ilium, ischium, pubis, sacrum, nearly complete caudal series; AMNH FR 30589, partial skull and cervicals; AMNH FR 30590, proximal part of the femur.

REMARKS: Nesbitt and Norell (2006) named *Effigia* from an articulated skeleton from the *Coelophysis* Quarry in northern New Mexico. The combination of a postcranial skeleton like that of "*Chatterjeea*" and an edentulous, highly apomorphic skull similar to *Shuvosaurus* showed that the skull of *Shuvosaurus* belongs to the body of "*Chatterjeea.*" Furthermore, the skeleton of *Effigia* bears an uncanny resemblance to that of theropods and more specifically, ornithomimids, even though it is more closely related to Crocodylia than Aves (Nesbitt and Norell, 2006). The realization of this convergence led Nesbitt et al. (2007) to critically examine the fossil record of early dinosaurs in North America and to conclude that many of the specimens once thought to be theropods actually belong to close relatives of *Effigia*.

In a superficial review of the taxonomy of *Shuvosaurus*, Lucas et al. (2007c) challenged the difference cited by Nesbitt and Norell (2006) and Nesbitt (2007) separating *Effigia* from *Shuvosaurus*. The two taxa are obviously closely related given their divergent morphology and numerous apomorphies between the two taxa (Nesbitt, 2007). However, the comments of Lucas et al. (2007) must be addressed.

Of the six characters explicitly used to differentiate *Effigia* from *Shuvosaurus* by Nesbitt (2007), Lucas et al. (2007) accepted differences between the maxilla, lacrimal, and squamosal, but stated "the biological significances" of the differences are unknown. It is not clear why Lucas et al. (2007) required an understanding of "biological significance" for a difference to be valid. The absence of a posterior process of the maxilla in *Effigia* represents a genuine difference between the two taxa and nearly all other archosaurs. Furthermore, the squamosal of *Lotosaurus* (IVPP V 48013) also lacks a posterior squamosal process. The premaxillae of *Shuvosaurus* (e.g., TTU-P 9280) apparently lack any posterior process whereas that of *Effigia* has a small tonguelike process. The posterior process of the maxilla of *Effigia* is rather robust, and this suggests that the premaxillae of *Shuvosaurus* genuinely lack this process even though the preservation and preparation of the material of *Shuvosaurus* is poor. The relative sizes of the dentaries cannot be compared at present after the repreparation of the specimen. Prior to the disarticulation of the type skull of *Shuvosaurus* in 2005, the body of the dentary of *Shuvosaurus* extended well past the premaxilla-maxilla articulation, whereas in *Effigia*, the body of the dentary is anterior to and at the premaxilla-maxilla articulation (Chatterjee, 1993; Rauhut, 1997). However, after repreparation, some of the original bone on the posterior portion of the dentary was lost (S.J.N., personal obs.). Therefore, all six characters discussed by Lucas et al. (2007) represent differences between *Effigia* and *Shuvosaurus*.

Furthermore, Lucas et al. (2007) dismissed the differences in the postcrania of the two taxa listed by Nesbitt (2007). These include two characters: the anterior cervical centra have distinct keels (Long and Murry, 1995: fig. 163 A–D), whereas those of *Effigia* lack keels (Nesbitt, 2007: fig. 28D), and difference in the size of the coracoid foramen. Additionally, the only ulna of *Shuvosaurus* (TTU-

P unnumbered) is proportionally much more stout than that of *Effigia*. Unfortunately, limited comparisons can be made at this time because much of the *Shuvosaurus* postcrania remains unprepared. As a result of the discussion presented above, *Effigia* and *Shuvosaurus* are separate terminal taxa here.

Effigia is distinguished from all other suchians except *Shuvosaurus* by the presence of an edentulous premaxilla, maxilla, and dentary, a posteriorly long anterodorsal process of the premaxilla, a long preacetabular process of the ilium that connects to the posterior process by a large thin flange, and a pubic boot that is 33% the length of the pubic shaft. It is distinguished from *Shuvosaurus* by the presence of both a dorsal and posterior process of the maxilla, relatively shorter dentary, the absence of posterior process of the squamosal, a small fossa on the posterolateral side of the squamosal, and the presence of a large pit on the posterior side of the lacrimal (from Nesbitt, 2007).

KEY REFERENCES: Nesbitt and Norell, 2006; Nesbitt, 2007.

Shuvosaurus inexpectatus (Chatterjee, 1993), sensu Nesbitt and Norell, 2006
= *Chatterjeea elegans* Long and Murry, 1995

AGE: Norian, Late Triassic (Lehman and Chatterjee, 2005).

OCCURRENCE: Post (= Miller) Quarry, Cooper Canyon Formation, Dockum Group (Chatterjee, 1985).

HOLOTYPE: TTU-P 9280, disarticulated skull.

PARATYPE: TTU-P 9281, anterior portion of dentries; TTU-P 9282, braincase and other cranial fragments.

REFERRED MATERIAL: TTU-P 9001, much of a postcranial skeleton, hundreds of disarticulated and associated bones from the Post (= Miller) Quarry (material referred to *Chatterjee elegans*).

REMARKS: Chatterjee (1993) named *Shuvosaurus inexpectatus* based on associated bizarre cranial elements from the Post (= Miller) Quarry. Chatterjee (1993) concluded that the large orbits, seemingly pneumatic braincase, and edentulous maxillae, premaxillae, and dentaries of the taxon allied it to ornithomimid dinosaurs. The resultant phylogenetic position indicated that much of the theropod diversity in the Cretaceous was the product of diversification in the Triassic (Rauhut, 1997). However, the absence of coelurosaurian or tetanuran synapomorphies made others (e.g., Rauhut, 2003) question Chatterjee's (1993) original assignment. Long and Murry (1995) named *Chatterjeea elegans* based on distinctive postcranial remains from the same quarry and suggested that *Shuvosaurus* may be the skull of *Chatterjeea*. Nesbitt and Norell (2006) used the articulated skeleton of *Effigia* to demonstrate that the skull of *Shuvosaurus* indeed belongs to the body of *Chatterjeea*. Here, the scorings of *Shuvosaurus* and *Chatterjeea* are combined, and only unambiguous material from the Post (= Miller) Quarry is scored.

Long and Murry (1995) referred material to "*Chatterjeea*" throughout the Chinle Formation and the Dockum Group. Much of the material consists of isolated finds. Given that *Effigia* and *Shuvosaurus* are very similar but distinct taxa, most of these can be assigned only to the clade containing the two taxa.

Shuvosaurus inexpectatus is distinguished from all other suchians except *Effigia* by the presence of an edentulous premaxilla, maxilla, and dentary, a posteriorly long anterodorsal process of the premaxilla, a long preacetabular process of the ilium that connects to the posterior process by a large, thin flange, and a pubic boot that is 33% the length of the pubic shaft. It is distinguished from *Effigia* by the absence of both a dorsal and posterior process of the maxilla, relatively longer dentary, the presence of a posterior process of the squamosal, the absence of a small fossa on the posterolateral side of the squamosal, and the absence of a large pit on the posterior side of the lacrimal.

KEY REFERENCES: Chatterjee, 1993; Long and Murry, 1995; Rauhut, 1997; Nesbitt and Norell, 2006; Nesbitt et al., 2007; Nesbitt, 2007.

Prestosuchus chiniquensis Huene, 1938

AGE: Middle Triassic (Schultz et al., 2000).

OCCURRENCE: Weg sanga, Santa Maria 1 sequence, Santa Maria Formation, Brazil.

HOLOTYPE: BSP XXV 1-3/5-11/ 28-41/49, splenial, anterior portion of the surangular, anterior portion of the angular, prearticular, right partial maxilla, fragmentary dentary, three incomplete cervical vertebrae, fragmentary ribs, one sacral vertebra, two sacral ribs, five anterior caudal vertebrae with chevron bones, 14 middle and posterior caudal vertebrae, right and left scapulocoracoid, interclavicle and clavicle, distal left humerus, right proximal and distal humerus, distal radius, fragmentary ulna, one manual phalanx, incomplete ilium, fragmentary ischia, pubes, and complete left hind limb (including femur, tibia, fibula, ankle, and pes).

REMARKS: Huene (1938) named *Prestosuchus chiniquensis* for a mandible and cranial fragments and much of a postcranial skeleton. For the most part, *P. chiniquensis* was assigned to "Rauisuchia"; furthermore, Parrish (1993) found a clade containing *P. chiniquensis*, *Ticinosuchus*, and *Saurosuchus*. Desojo and Rauhut (2008) presented the following two autapomorphies of *P. chiniquensis*: anterior notch between the scapula and coracoid and longitudinal ridge on the dorsal surface of the ischium. Only the holotype is scored here for this terminal taxon.

KEY REFERENCES: Huene, 1938, 1942; Parrish, 1993; Desojo and Rauhut, 2008.

UFRGS 0156-T

AGE: Ladinian, Middle Triassic, Therapsid assemblage zone (Schultz et al., 2000).

OCCURRENCE: Rosario do Sul, Santa Maria Formation, near Candelaria City, Brazil.

REFERRED MATERIAL: Complete skull, much of the presacral axial column, articulated osteoderms.

REMARKS: UFRGS 0156-T is a very large skull (88 cm) that was assigned to *Prestosuchus chiniquensis* by Barberena (1978) and more recently by Azevendo (1991). Parrish (1993) separated UFRGS 0156-T from *P. chiniquensis* in his phylogenetic analysis and found that no character scores separated the two. Thus, he combined the two in his final hypothesis. I separate *P. chiniquensis* and UFRGS 0156-T as terminal taxa. *P. chiniquensis* and UFRGS 0156-T are both from a similar stratigraphic position near the bottom of the Santa Maria sequence. Parrish (1993) scored characters of the calcaneum and pes of UFRGS 0156-T, but these elements are absent in UFRGS 0156-T.

KEY REFERENCES: Barberena, 1978; Azevendo, 1991; Parrish, 1993.

UFRGS 0152-T

AGE: Middle to Late Triassic.

OCCURRENCE: Santa Maria sequence (see below).

REFERRED MATERIAL: Maxillae, nasals, quadrate, partial quadratojugal, complete braincase, parietal, ectopterygoid, partial pterygoid, jugal, squamosal, anterior portion of the dentary, prearticular, articular, cervical, dorsal, sacral, and caudal vertebrae, osteoderms, scapula, coracoid, humerus, proximal portion of the ulna, complete pelvic girdle, femora, tibia, fibula, calcaneum, pes, chevrons.

REMARKS: UFRGS 0152-T consists of an undescribed archosaur that possesses overlapping elements with both UFRGS 0156-T and *Prestosuchus chiniquensis*. Furthermore, UFRGS 0152-T is indistinguishable from UFRGS 0156-T and *Prestosuchus chiniquensis*. Even though the exact locality is not known, it was collected from the Santa Maria sequence.

Saurosuchus galilei Reig, 1959 (fig. 11D–E)

AGE: Late Carnian, Late Triassic (Rogers et al., 1993, adjusted for the new Triassic timescale of Muttoni et al., 2004).

OCCURRENCE: Ischigualasto Formation, Argentina.

HOLOTYPE: PVL 2062, nearly complete skull, posteriormost portion missing.

REFERRED MATERIAL: PVL 2198, partial maxilla, left ilium, both ischia, nine articulated dorsal vertebrae and fragments, part of the dermal armor, associated ribs and teeth; PVL 2557, two dorsal vertebrae, both sacrals, nine caudal vertebrae, right ilium and ischium, partial pubis, parts of right femur, tibia, fibula, complete right tarsus and foot, associated ribs and chevrons; PVSJ 32, skull and partial skeleton.

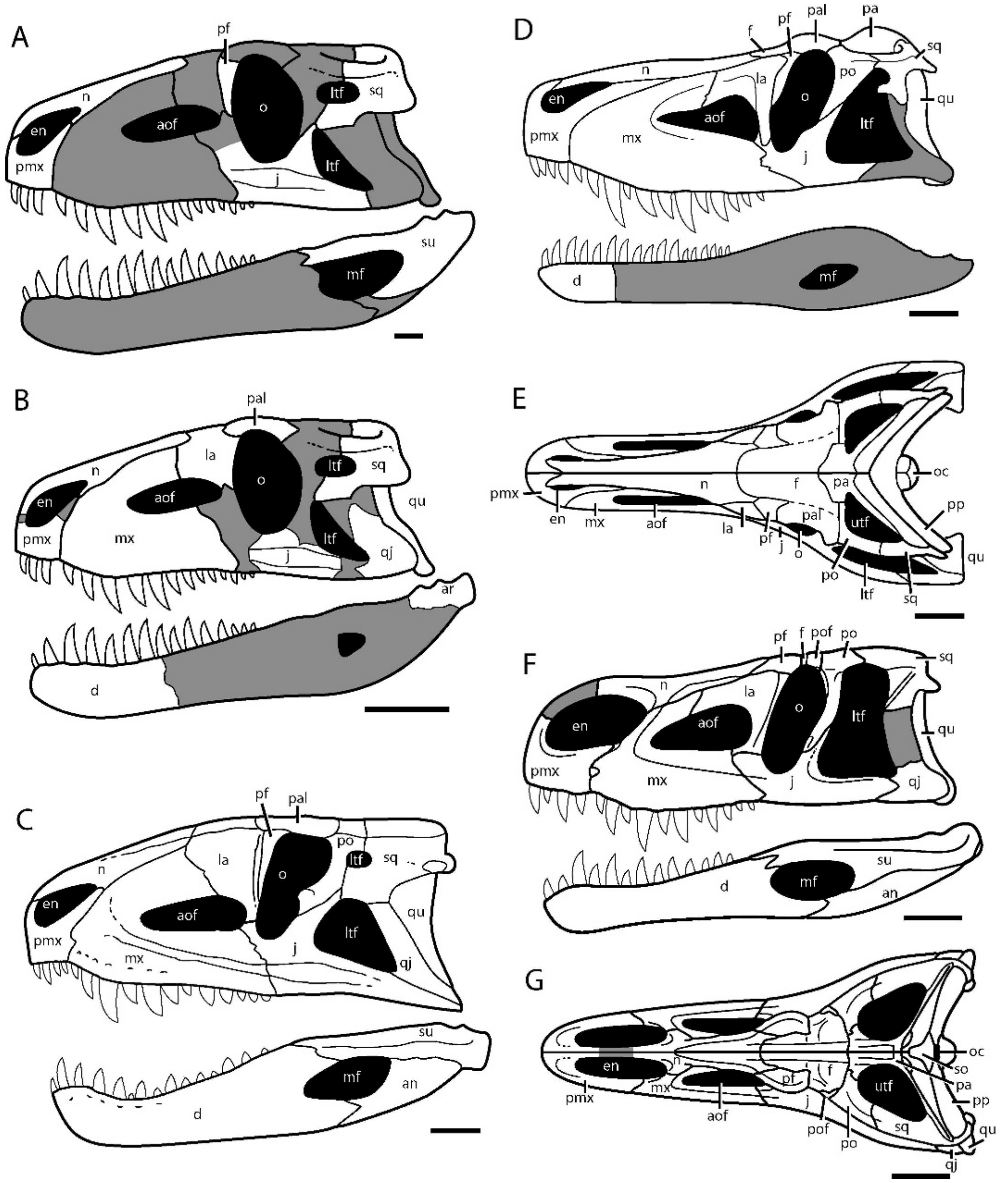


Fig. 11. Skull reconstructions of "rauisuchian" archosaur terminal taxa: **A,** *Rauisuchus triradentes* in lateral view; based on (BSP AS XXV-60-121); **B,** *Polonosuchus silesiacus* in lateral view; redrawn from Sulej (2005); **C,** *Postosuchus kirkpatricki* in lateral view; modified from Chatterjee (1985); **D,** *Saurosuchus galilei* in lateral and **E,** dorsal views; redrawn from Alcober (2000); **F,** *Batrachotomus kuperferzellensis* in lateral and **G,** dorsal views; redrawn from Gower (1999). Shaded areas indicate incomplete preservation. See appendix for anatomical abbreviations. Scale bars = 5 cm in C–G and 1 cm in A–B.

REMARKS: *Saurosuchus galilei* was named from a nearly complete skull (Reig, 1959) from the Ischigualasto Formation, and isolated material from this unit has been referred to the taxon since (Sill, 1974). The holotype represented the first relatively complete skull material of any rauisuchian to date and stands as one of the most complete skulls of a "rauisuchian." Of all the specimens referred to the taxon, only PVSJ 32, a complete skull and presacral vertebral column, can be confidently assigned to *Saurosuchus galilei* because all the autapomorphies of the taxon lie in the skull (see Alcober, 2000). Most of the isolated postcranial material from the Ischigualasto Formation was assigned to *Saurosuchus* without much explanation. Moreover, at least one other large paracrocodylomorph, *Sillosuchus*, is known from the Ischigualasto Formation. The absence of a coherent, supported assignment of the isolated material to *Saurosuchus* has led to confusion. For example, the cervical vertebra (PVL 2472) assigned to *Saurosuchus* belongs to a gigantic specimen of *Sillosuchus* (see above). Furthermore, there are proportional differences between the metatarsals of two pedes (PVL 2557 and PVL 2267) assigned to *Saurosuchus*. Moreover, metatarsal V of PVL 2557 is short and possesses a clear facet for articulation with a phalanx, whereas PVL 2267 possesses a long, tapered metatarsal V without a clear facet for articulation with a phalanx. The ilium found with PVL 2267 shares synapomorphies (e.g., elongated preacetabular process, concave ischial peduncle) with *Sillosuchus* and other poposauroids. Interestingly, the specimens that are possibly referable to *Sillosuchus*, along with the holotype of the taxon, are found in the lowest one-third of the Ischigualasto Formation (Sill, 1974; Alcober and Parrish, 1997), whereas *Saurosuchus* is from the upper two-thirds of the formation. The following examples demonstrate that all the material assigned to *Saurosuchus* may not belong to the taxon. Therefore, I score the cranial material, osteoderm, and axial column from the holotype (PVL 2062) and PVSJ 32 and score a few additional characters from PVL 2198 and the hind limb of PVL 2557.

Saurosuchus was only recently utilized in explicit phylogenetic analyses. It was found closely related to *Prestosuchus* and *Ticinosuchus* by Parrish (1993) and Benton (2004) and to lie outside a clade containing *Postosuchus kirkpatricki*, *Tikisuchus*, *Batrachotomus*, aetosaurs, and crocodylomorphs by Gower and Walker (2002) based on braincase characters. In all analyses, *Saurosuchus* was found as a crocodylian-line archosaur.

The following autapomorphies listed by Alcober (2000) are accepted here: sculptured skull roof and maxilla; ventral process of the lacrimal forms a slender pillar that abuts the jugal laterally; development of a crista on the dorsal supraoccipital; development of a robust, laterally expanded, capitate process of the laterosphenoid.

Alcober (2000) also listed three autapomorphies focused on the frontal and surrounding bones (reduced postfrontal hidden in dorsal view, thickening of the border of the frontal at the level of the orbital fenestra, and presence of a lateral process of the posterolateral frontal). All three of these characters are not unique among crocodylian-line archosaurs once the large bone dorsal to the orbit is reidentified as a palpebral fused to the frontal. A similar frontal-palpebral relationship is found in *Postosuchus kirkpatricki* (TTU-P 9000) and *Polonosuchus silesiacus* (ZPAL Ab III/563).

KEY REFERENCES: Reig, 1959; Sill, 1974; Alcober, 2000.

Batrachotomus kupferzellensis Gower, 1999
(fig. 11F–G)

AGE: Late Ladinian, Middle Triassic, Longobardian (Brunner, 1977, 1980; Urliches, 1989).

OCCURRENCE: Upper Lettenkeuper, Kupferzell, Germany (Brunner, 1977, 1980; Urlichs, 1982).

HOLOTYPE: SMNS 52970, premaxillae, maxillae, nasals, frontal, postfrontals, parietals, squamosals, postorbitals, jugals, quadrates, dentaries, surangulars, articulars, right lacrimal, right prefrontal, left quadratojugal, left ectopterygoid, left prearticular, isolated teeth, three dorsal, a single sacral, three caudal vertebrae, single dorsal osteoderm, right ilium, femora, left tibia, left fibula.

REFERRED MATERIAL: SMNS 80260–80339. See Gower (1999) for crania and Gower and Schoch (2009) for postcrania.

REMARKS: Well-preserved material from different ontogenetic stages and a fully detailed description of the skull (Gower, 1999), the braincase (Gower and Walker, 2002) and postcrania (Gower and Schoch, 2009) make *Batrachotomus* the best represented suchian from the Ladinian and one of the most complete paracrocodylomorphs known from the Triassic. The taxon has served as a basis for comparison with all other paracrocodylomorphs. Unfortunately, *Batrachotomus* lacks good manus material, and much of the pes remains unknown.

Batrachotomus is different from all other suchians (Gower, 1999) and bears one clear autapomorphy: presence of a small depression on the lateral surface on the ventral portion of the postorbital.

KEY REFERENCES: Gower, 1999; Gower and Walker 2002; Gower and Schoch, 2009.

Fasolasuchus tenax Bonaparte, 1981

AGE: Mid-Norian–?Rhaetian, Late Triassic (Arcucci et al., 2004).

OCCURRENCE: La Esquina, La Rioja, Los Colorados Formation, Argentina.

HOLOTYPE: PVL 3850, premaxillae, nasals, fragmentary maxillae and one fragmentary maxilla that includes 10 incomplete teeth, fragmentary pterygoid, unrecognized cranial element, a posterior dentary including the articular, six cervical vertebrae, six dorsal vertebrae, eight caudal vertebrae, incomplete ischium, proximal part of the pubis, complete radius and ulna, right femur, fibula, astragalus and calcaneum, several fragmentary vertebrae, ribs, and osteoderms.

REFERRED MATERIAL: PVL 3851, left maxilla with a few teeth, left dentary with five teeth, articular region, axis, incomplete cervical centra, sacral centra, two sacral vertebrae.

REMARKS: Bonaparte (1981) described *Fasolasuchus* from two associated skeletons from near the top of the Los Colorados Formation in Argentina. The limb bones and the maxilla indicate that *Fasolasuchus* was one of the largest suchians from the Triassic and may have reached 8–10 m in length (extrapolated from comparisons with *Postosuchus* and *Saurosuchus*). Only the articular is present in the two known specimens. Although the articulars do not share any unique morphology, the shape and size are very similar and both bear a medially directed process of the articular with a foramen that pierces it, two character states present in *Arizonasaurus*, *Postosuchus kirkpatricki*, *Polonosuchus*, *Batrachotomus*, *Prestosuchus* (UFRGS 0152-T), *Stagonosuchus*, and *Rauisuchus*. Some of the material described by Bonaparte (1981) such as the nasal could not be located at the time of this study.

KEY REFERENCES: Bonaparte, 1981.

Rauisuchus tiradentes Huene, 1942 (fig. 11A)

AGE: Late ?Carnian–early Norian, Late Triassic (Langer, 2005a), Alemoa local fauna (sensu Barberena et al., 1985, and Azevedo et al., 1990).

OCCURRENCE: Alemoa Member, Santa Maria Formation, Brazil.

HOLOTYPE: BSP AS XXV-60-121, right premaxilla, right nasal, left jugal, right prefrontal/lacrimal, left squamosal, left surangular, right and left splenial, right ectopterygoid, left prearticular, left articular, right pterygoid, isolated teeth, atlas, axis; cervical, dorsal, and caudal vertebrae; ribs, chevrons, right scapula, right coracoid, left pubis, left ilium, right tibia, right fibula, right astragalus, and osteoderms.

REMARKS: *Rauisuchus* was named for a partial, disarticulated skeleton consisting of skull elements and postcranial remains from the Santa Maria Formation, Brazil. According to von Huene (1942), the specimen was found in "Sanga 6" in the Alemoa area. The exact stratigraphic position of the specimen may never be known; however, it was found with other taxa in the "Alemoa local fauna" of Barberena et al. (1985) and Langer (2005a). Langer (2005a, 2005b) considered the "Alemoa local fauna" to correlate with the lower portion of the Ischigualasto Formation. If this correlation holds, *Rauisuchus* would be considered late Carnian because the base of the Ischigualasto Formation is dated at 228 Ma (Rogers et al., 1993). The type of *Rauisuchus tiradentes* is hypothesized to be one individual because all the bones preserving matrix have the same fine red mudstone adhering to them, there are no duplicated elements, and the size of the elements are congruent with those of other rauisuchians.

Other than the original description (Huene, 1942) and Parrish's (1993) scoring of the taxon into his cladistic analysis of pseudosuchians, *Rauisuchus* was largely ignored. *Rauisuchus* differs from all other suchians except *Postosuchus kirkpatricki* and *Polonosuchus silesiacus* in that it has a lateral, rugose ridge on the nasal, a rugose ridge on the dorsal portion of the squamosal, and it has an anteroventral process that splits the lower temporal fenestra into two portions. It differs from *Postosuchus kirkpatricki* and *Polonosuchus silesiacus* in that the axis is parallelogram shaped. *Rauisuchus* has two autapomorphies: ventral margin of the jugal bowed ventrally and ventrally pointed rugose ridge on the posterior portion of the squamosal.

KEY REFERENCES: Huene, 1942; Krebs, 1973; Parrish, 1993.

Polonosuchus silesiacus (Sulej, 2005), sensu Brusatte et al., 2009 (fig. 11B)

AGE: Late Carnian (Dzik and Sulej, 2007).

OCCURRENCE: Krasiejów, Opole, Silesia, Poland (Sulej, 2005).

HOLOTYPE: ZPAL Ab III/563, right and left maxillae, premaxillae, nasals, prefrontals, palatines, quadrates, and fragments of dentary, left jugal, right lacrimal, quadratojugal, squamosal, pterygoid, surangular, articular, fragment of atlas articulated with axis and third cervical vertebra, 12 articulated caudal vertebrae, five caudal osteoderms, and pieces of cervical ribs.

REMARKS: Sulej (2005) first described ZPAL Ab III/563 and assigned it to a new species-level taxon in the genus *Teratosaurus* because of similarities with *Teratosaurus suevicus* (BMNH 38646). In a superficial discussion, Lucas et al. (2007a) rejected all differences between the two taxa of *Teratosaurus* and stated that ZPAL Ab III/563 was referable to *Teratosaurus suevicus.* However, Lucas et al. (2007a) did little to discuss the anatomy of either taxon. Brusatte et al. (2009) showed that there are no clear apomorphies to unite ZPAL Ab III/563 and *Teratosaurus suevicus* exclusive of closely related taxa (e.g., *Postosuchus kirkpatricki*), found that ZPAL Ab III/563 and BMNH 38646 differed extensively, and, therefore, assigned ZPAL Ab III/563 to the new genus *Polonosuchus*. *Polonosuchus* was hypothesized to be closely related to *Postosuchus kirkpatricki* in phylogenetic analyses of basal archosaurs (Weinbaum and Hungerbühler, 2007; Brusatte et al., 2009).

Polonosuchus silesiacus differs from *Postosuchus kirkpatricki* by: ventral margin of the maxilla sinuous and highly convex in outline; first maxillary alveolus approximately equal in size to subsequent alveoli; nasal with bifurcated anterior end, including tapering premaxillary process that contacts the premaxilla; maxillary process of premaxilla terminating anterior to the caudal end of the external naris; absence of fossa on the dorsal surface of the nasal; absence of dorsoventral expansion of the anterior end of the dentary (from Brusatte et al., 2009).

KEY REFERENCES: Sulej, 2005; Brusatte et al., 2009.

Postosuchus kirkpatricki Chatterjee, 1985 (fig. 11C)

AGE: Norian, Late Triassic (Lehman and Chatterjee, 2005).

OCCURRENCE: Post (= Miller) Quarry, Cooper Canyon Formation, Dockum Group (Chatterjee, 1985).

HOLOTYPE: TTU-P 9000, skull and partial skeleton.

PARATYPE: TTU-P 9002, skull and skeleton.

REMARKS: See Nesbitt et al., 2009a.

KEY REFERENCES: Chatterjee, 1985; Long and Murry, 1995; Weinbaum, 2002; Peyer et al., 2008.

Postosuchus alisonae Peyer et al., 2008

AGE: Late Carnian–early Norian (Olsen and Huber, 1997).

OCCURRENCE: Mudstone of Lithofacies Association II sensu Hoffman and Gallagher (1989), south-central region of Durham subbasin of Deep River Basin, Newark Supergroup, West Genlee, Durham County, North Carolina, U.S.A. Equivalent to the lower Sanford Formation (Huber et al., 1993).

HOLOTYPE: UNC 15575, partial skeleton consisting of a few fragmentary cranial bones (nasal, frontal, squamosal, prootic, supraoccipital, left and right opisthotic, articular, angular, prearticular) and isolated teeth. The postcranial skeleton includes seven cervical, one dorsal, and four caudal vertebrae, with associated ribs and chevrons, partial sacral rib, cervical, dorsal, and caudal osteoderms, gastralia, right and partial left coracoid, partial left and right scapulae, interclavicle, clavicle, left and right humeri, radii, and ulnae, nearly complete right and partial left manus, distal ends of left and right pubes, left and right tibiae, fibulae, tarsi, and pedes (Peyer et al., 2008).

REMARKS: Peyer et al. (2008) described a well-preserved partial skeleton of a suchian from the Late Triassic of the Newark Supergroup. The preserved portions of the skeleton are nearly identical to those of *Postosuchus kirkpatricki* except for the one clear autapomorphy stated above. Unfortunately, few comparisons can be made to *Polonosuchus* (ZPAL Ab III/543) because there are few elements that are shared by the known specimens of the two taxa, and those parts that do overlap either support a close relationship between *Postosuchus kirkpatricki*, *Postosuchus alisonae,* and *Polonosuchus* or represent plesiomorphies within Archosauria or more inclusive clades. *Postosuchus alisonae* remains one of only a few Triassic crocodylian-line archosaurs with articulated manus and pedes in the same individual.

Postosuchus alisonae is almost identical to *Postosuchus kirkpatricki* (see Peyer et al., 2008) in the overlapping elements. *Postosuchus alisonae* differs from all known suchians in the presence of a groove in the proximal portion of metacarpal I for contact with metacarpal II (Peyer et al., 2008).

KEY REFERENCES: Peyer et al., 2008.

CM 73372
= *Postosuchus kirkpatricki* Long and Murry, 1995; Weinbaum, 2002; Novak, 2004; Peyer et al., 2008.

AGE: Late Norian–?Rhaetian, Late Triassic (Heckert et al., 2008).

OCCURRENCE: *Coelophysis* Quarry, “siltstone member” of the Chinle Formation, Ghost Ranch, northern New Mexico.

SPECIMEN: CM 73372, articulated postcranial skeleton including hind limbs, pelvis, dorsal, sacral, and caudal vertebrae, portions of the humerus, scapula, ulna, radius, partial manus, osteoderms, ribs, and gastralia.

REMARKS: In a review of *Postosuchus kirkpatricki*, Long and Murry (1995) referred an articulated skeleton from the *Coelophysis* Quarry of New Mexico to *P. kirkpatricki* without specific justification. Weinbaum (2002), Novak (2004), and Peyer et al. (2008) accepted the identification of CM 73372 as *P. kirkpatricki.* Nevertheless, these authors failed to note any synapomorphies unique to *P. kirkpatricki* and CM 73372. All authors noted that the specimen represents a skeletally immature individual because none of the neural sutures are closed (see Brochu, 1996; Irmis, 2007). Weinbaum (2002) and Novak (2004) did note that the preacetabular process of the ilium was much longer than that of *P. kirkpatricki.*

Because there are no clear characters linking *P. kirkpatricki* to CM 73372 to the exclusion of other taxa, it is treated as a separate terminal taxon. CM 73372 differs from *Postosuchus kirkpatricki* and *Rauisuchus* in possessing a concave ventral margin of the ilium. Also, CM 73372 differs from *P. alisonae* in processing an asymmetrical distal end (in distal view) of metatarsal IV. CM 73372 and *Polonosuchus* overlap only in the caudal vertebrae, but do not differ.

KEY REFERENCES: Long and Murry, 1995; Weinbaum, 2002; Novak, 2004; Peyer et al., 2008.

Hesperosuchus agilis Colbert, 1952

AGE: ?Early Norian, Late Triassic (Lucas, 1998a).

OCCURRENCE: Blue Mesa Member, Chinle Formation near Cameron, Arizona (Colbert, 1952).

HOLOTYPE: AMNH FR 6758, portions of the skull including the quadrate, maxillae, dentaries, portion of the premaxilla, part of the nasal, part of the jugal, part of the squamosal, partial braincase (opisthotic, basioccipital), cervical, dorsal, and caudal vertebrae, osteoderms, humerus, ulna, radius, partial radiale, parts of the manus, femora, tibiae, fibulae, partially articulated pes.

REMARKS: Colbert (1952) named *Hesperosuchus* for a partially eroded, articulated specimen from the base of the Chinle Formation that was collected by Barnum Brown. The well-preserved specimen is three-dimensionally preserved, but many of the delicate elements are missing or unidentifiable. Colbert (1952) made a few errors in the identification of elements in his description, but Walker (1970) corrected these mistakes. For example, the "pterygoid" (Colbert, 1952: fig. 9) is actually a sacral rib from the first primordial sacral. Bonaparte (1971) suggested that there are two individuals in the holotype. However, there are no apparent duplications of any of the elements.

Most crocodylomorph-like bones and associated skeletons from the Chinle Formation and Dockum Group have been assigned to *Hesperosuchus* without specific justification (Parrish, 1991; Long and Murry, 1995; Clark et al., 2000). The better preserved specimens from the *Coelophysis* Quarry from the top of Chinle Formation have been separated out as a separate terminal taxon (see below). Here, I score only the holotype for this terminal taxon.

Much of the skeleton of *Hesperosuchus* was eroded before Barnum Brown recovered it in the 1930s. Brown and the AMNH preparators screen-washed thousands of pounds of matrix and recovered bone fragments from the resultant concentrate. Hundreds of bone fragments, teeth, and pieces of the holotype of *Hesperosuchus* were separated. Colbert's (1952) description focused on the material recovered in situ and the obvious bones collected on the surface. However, some of the bones described by Colbert belong to a dinosauromorph (e.g., the elongated metatarsals, one of the humeri), the sacral vertebra belongs to *Vancleavea* (Nesbitt et al., 2009a), and other material collected at the locality represents the remains of fishes, phytosaurs, amphibians, or other archosaurs. Fortunately, the preservation of the holotype of *Hesperosuchus* is unique among the other bones; the weakly weathered or in situ bones are a dark chocolate brown and the weathered bones are orange to yellow, whereas the other fragments are blue, black, tan, or dark grey. Furthermore, the outer surfaces of the bones of the holotype of *Hesperosuchus* are exquisitely preserved. These two factors allow the fragments of *Hesperosuchus* to be separated. As a result, parts of the skull (squamosal, nasal), osteoderms, pelvis, and manus were recovered. Furthermore, the screen-washed material was distributed throughout the fossil vertebrate collections at AMNH. I found parts of the holotype of *Hesperosuchus* with the aetosaurs and parareptiles.

KEY REFERENCES: Colbert, 1952; Walker, 1970; Parrish, 1991; Clark et al., 2000.

Hesperosuchus "*agilis*" Clark et al., 2000

AGE: Late Norian–?Rhaetian, Late Triassic (Heckert et al., 2008).

OCCURRENCE: *Coelophysis* Quarry, "siltstone member" of the Chinle Formation, Ghost Ranch, northern New Mexico.

REFERRED MATERIAL: CM 29894, skull and anterior portion of the skeleton; YPM 41198, partially disarticulated skull, pubis, hind limb.

REMARKS: Clark et al. (2000) described a well-prepared skull and partial skeleton from the *Coelophysis* Quarry at the top of the Chinle Formation and referred the specimen to *Hesperosuchus agilis*. However, the holotype of *Hesperosuchus,* from the Blue Mesa Member, near the base of the Chinle Formation and the specimen from the *Coelophysis* Quarry, from the top of the Chinle sequence, may be separated by as much as 20 million years. Clark et al. (2000) used the following two characters to refer CM 29894 to *Hesperosuchus agilis*: (1) deep anterior end of the dentary; and (2) the configuration of the maxillary tooth row with a rapid increase in size of the anterior teeth from the small, slender first to the very large fourth tooth. The first character is also in *Postosuchus kirkpatricki* (TTU-P 9000) and *Polonosuchus* (ZPAL Ab III/543), and I see little difference between the anterior portions of the dentaries of CM 29894, *Dromicosuchus* (UNC 15574), and *Sphenosuchus* (SAM 3014). The second character does not seem to be unique among

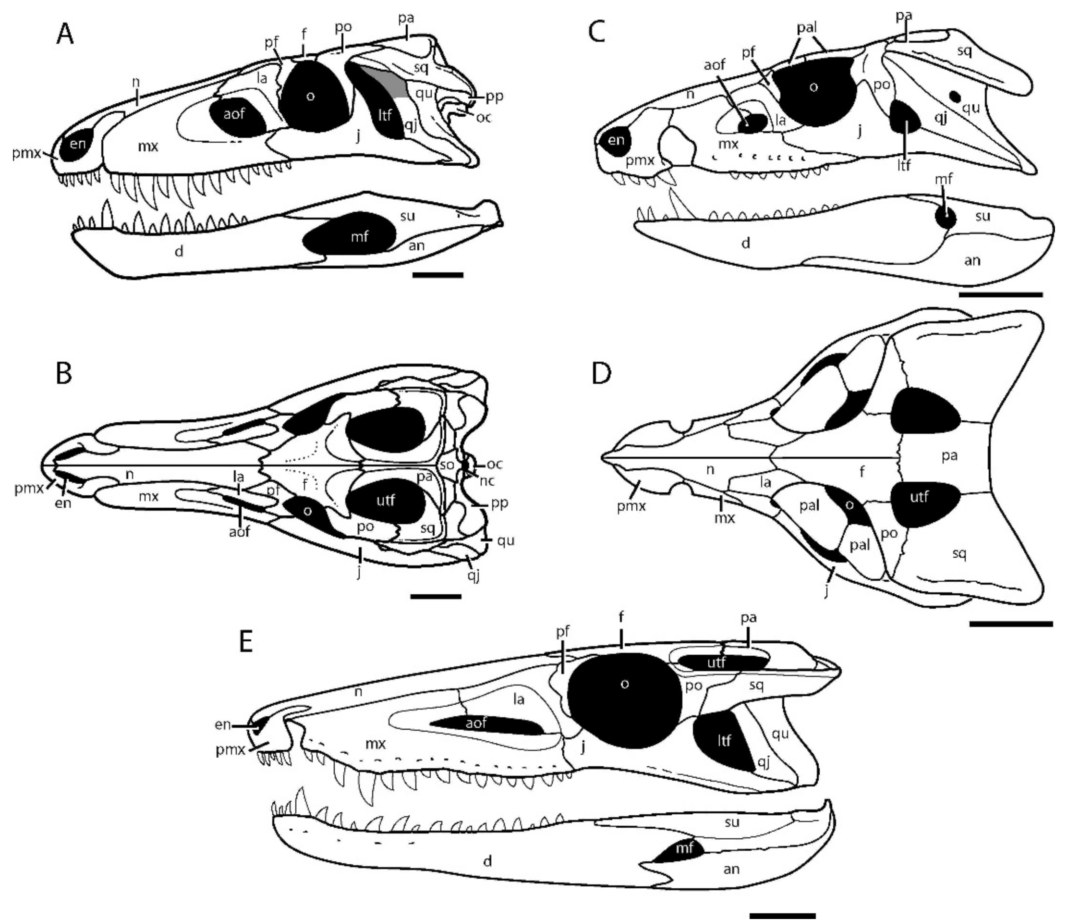


Fig. 12. Skull reconstructions of crocodylomorph archosaur terminal taxa: **A,** *Sphenosuchus acutus* in lateral and **B,** dorsal views; redrawn from Walker (1990); **C,** *Protosuchus richardsoni* in lateral and **D,** dorsal views; modified from Crompton and Smith (1980); **E,** *Dromicosuchus grallator* in lateral view; based on UNC 15574. See appendix for anatomical abbreviations. Scale bars = 1 cm.

suchians. Therefore, CM 29894 cannot be unambiguously assigned to *Hesperosuchus agilis.* CM 29894 and another identical crocodylomorph skull and partial skeleton, YPM 41198, are treated as a separate terminal taxon. Although there are no apparent differences in the holotype of *Hesperosuchus* and CM 29894, no unique characters link the two taxa exclusive of other crocodylomorphs. Therefore, they are treated as separate taxa.

KEY REFERENCES: Clark et al., 2000.

Dromicosuchus grallator Sues et al., 2003
(fig. 12E)

AGE: Late Carnian–early Norian (Olsen and Huber, 1997).

OCCURRENCE: Mudstone of Lithofacies Association II sensu Hoffman and Gallagher (1989), south-central region of Durham subbasin of Deep River Basin, Newark Supergroup, West Genlee, Durham County, North Carolina, U.S.A. Equivalent to the lower Sanford Formation (Huber et al., 1993).

HOLOTYPE: UNC 15574, nearly complete skeleton with complete skull.

REMARKS: See Nesbitt et al., 2009a.

KEY REFERENCE: Sues et al., 2003.

Sphenosuchus acutus Haughton, 1915
(fig. 12A–B)

AGE: Early Jurassic (Olsen and Galton, 1984).

OCCURRENCE: Upper Elliot Formation, South Africa.

HOLOTYPE: SAM 3014, nearly complete skull, cervical vertebrae, pectoral girdle, humeri, tibia, metatarsals.

REMARKS: *Sphenosuchus*, originally described by Haughton (1915), was studied by Walker for over 30 years. From the beginning, *Sphenosuchus* was considered a close relative of crocodylians. In an unprecedented and unparalleled study of a basal archosaur, Walker (1990) disassembled, and in astonishing detail, prepared the entire skull. He revealed particulars of the braincase that united *Sphenosuchus* with crocodyliforms that were later used by Gower and Walker (2002) and Gower (2002) in a braincase study of basal archosaurs. The divergent postcranium of *Sphenosuchus* formed the basis of an argument for a long-limbed clade, Sphenosuchia, at the base of Crocodylomorpha (Sereno and Wild, 1992; Wu and Chatterjee, 1993).

KEY REFERENCES: Haughton 1915; Walker, 1970, 1990; Clark et al., 2000.

Dibothrosuchus elaphros Simmons, 1965

AGE: Early Jurassic, Sinemurian-Pliensbachian stage (Sun and Cui, 1986; Luo and Wu, 1994, 1995).

OCCURRENCE: Zhangjiawa Formation, Lower Lufeng Group, Huangchiatien, Lufeng, Yunnan, China.

HOLOTYPE: CUP 2081, partial jaw and postcranial skeleton.

REFERRED MATERIAL: CUP 2489, partial postcranial skeleton; IVPP V 7907, complete skull and partial postcranium including the cervical vertebrae and osteoderms, humerus, ulna, radius, scapula, coracoid, manus, ilium.

REMARKS: *Dibothrosuchus* was originally described from incomplete skull fragments and partial limb bones by Simmons (1965). Wu and Chatterjee (1993) referred a complete, well-prepared skull and the anterior portion of a skeleton to the taxon, and their referral is accepted here. Like *Sphenosuchus*, *Dibothrosuchus* is known from an articulated skull with a well-preserved braincase, a combination that is rare among basal archosaurs. Although many fragmentary specimens were referred to *Dibothrosuchus*, I score only IVPP V 7907 for this analysis.

KEY REFERENCES: Simmons, 1965; Wu, 1986; Wu and Chatterjee, 1993; Clark et al., 2000.

Terrestrisuchus gracilis Crush, 1984

AGE: ?Rhaetian, Late Triassic (Robinson 1957a, 1957b, Whiteside and Marshall, 2008).

OCCURRENCE: Fissure fills in the Carboniferous limestone of the Pant-y-ffynon Quarry, Cowbridge, Glamorgan, Wales.

HOLOTYPE: BMNH R7557 (formerly P 47/21 and counter part P 47/22).

REFERRED MATERIAL: See Crush, 1984.

REMARKS: *Terrestrisuchus* was named for and based on material collected from fissure fills in a Carboniferous limestone in Wales. The abundant taxon is known from dozens of specimens, from articulated and disarticulated crania, and postcrania. A few of the three-dimensionally preserved bones were prepared out of the matrix and formed the basis of the description by Crush (1984). Although much of the skull was described by Crush (1984), portions of the skull, including much of the braincase, nasals, and premaxilla, remain unknown. Originally, the holotype and referred material were housed at University College, London, but they were transferred to and reside at the Natural History Museum (BMNH).

Soon after *Terrestrisuchus* was named, Benton and Clark (1988) proposed that the taxon may be synonymous with *Saltoposuchus* from the Stubensandstein (Norian) of Baden-Wurttemberg, Germany. Benton and Clark (1988) rightfully criticized the single maxillary character cited by Crush (1984) to separate the two taxa. Sereno and Wild (1992) defended the position that the two taxa should be separated, but as demonstrated by Clark et al. (2000), many of the differences named are noncomparable between the two taxa. Clark et al. (2000) cited a few differences but were unsure in the end whether the taxa were different. Most recently, Allen (2003) suggested that *Terrestrisuchus* was a juvenile of *Saltoposuchus*. Given the uncertainties of the taxonomy of the two taxa, I score only material of *Terrestrisuchus* described by Crush (1984).

KEY REFERENCES: Crush, 1984; Sereno and Wild, 1992; Clark et al., 2000; Allen, 2003.

Litargosuchus leptorhynchus Clark and Sues, 2002

AGE: Early Jurassic (Olsen and Galton, 1984).

OCCURRENCE: Top of the upper Elliot Formation, South Africa (Clark and Sues, 2002).

HOLOTYPE: BP/1/5237, complete skull and much of an articulated postcranium missing the manus and pedes.

REMARKS: The well-preserved, though crushed, skeleton of *Litargosuchus* represents one of the most complete non-crocodyliform crocodylomorphs from Gondwanaland. The skull bears similarities to crocodyliforms, but as in *Kayentasuchus,* it has a mix of "sphenosuchian" and crocodyliform character states. The limb proportions are long relative to the axial column like that of *Terrestrisuchus*. Although incomplete, the ulnare and radiale appear to be the longest of any crocodylomorph. The postcranium has yet to be described formally, but is included in my scoring of the taxon.

KEY REFERENCES: Clark and Sues, 2002.

Kayentasuchus walkeri Clark and Sues, 2002

AGE: Simmurian-Pliensbachian, Early Jurassic (Peterson and Pipiringos, 1979).

OCCURRENCE: Willow Springs, middle of the silty facies of the Kayenta Formation, northern Arizona (Clark and Sues, 2002).

HOLOTYPE: UCMP 131830, partial skull roof, left facial portion, partial mandible, parial ilium, complete femur, and other postcranial elements.

REMARKS: Clark and Sues (2002) named *Kayentasuchus* for an associated skeleton from the Kayenta Formation. The taxon bears a mix of synapomorphies of the non-crocodyliform crocodylomorphs and crocodyliforms. As a result, the incorporation of *Kayentasuchus* into the phylogenetic analysis of Clark et al. (2000) led to a large polytomy at the base of Crocodylomorpha (Clark and Sues, 2002; Clark et al., 2004). *Kayentasuchus* joined an ever-growing list of crocodylomorphs from the Kayenta Formation, including an *Edentosuchus*-like taxon (Clark, 1994), *Eopneumatosuchus colberti* (Crompton and Smith 1980), *Calsoyasuchus valliceps* (Tykoski et al., 2002), and an undescribed protosuchid (TMM 43648-1; Tykoski, 2005).

KEY REFERENCES: Clark and Sues, 2002.

Orthosuchus strombergi Nash, 1968

AGE: Early Jurassic (Olsen and Galton, 1984).

OCCURRENCE: Upper Elliot Formation, Orange River Valley, Qacha's Nek Providence, Lesotho (Nash, 1975).

HOLOTYPE: SAM-K-409, complete skull and nearly complete skeleton missing the caudal region.

REFERRED MATERIAL: SAM-K-4639, skull and mandibles; BP/1/4770, articulated postcranium.

REMARKS: *Orthosuchus* was named for a nearly complete, three-dimensionally prepared skeleton from near the top of the upper Elliot Formation of Lesotho (Nash, 1968, 1975). As mentioned by Clark (in Benton and Clark, 1988), the holotype is dorsoventrally crushed and, as a result, some characters discussed by Nash (1975) are the result of crushing. Between the holotype and the two referred specimens, most of the anatomy of *Orthosuchus* can be scored.

Orthosuchus was found as a crocodyliform more closely related to *Protosuchus* than to *Crocodylus* in all explicit phylogenies of basal crocodyliform relationships (Benton and Clark, 1988; dataset of Pol et al., 2004, 2009). Clark (in Benton and Clark, 1988) listed the following character states that are shared with *Protosuchus*: ventrolateral contact of otoccipital with quadrate relatively broad (Busbey and Gow, 1984); squamosal relatively thick; vomer transversely broad, not rodlike.

KEY REFERENCES: Nash, 1968, 1975; Benton and Clark, 1988.

Protosuchus haughtoni (Busbey and Gow, 1984), sensu Gow, 2000 = *Baroqueosuchus haughtoni* Busbey and Gow, 1984

AGE: Early Jurassic (Olsen and Galton, 1984).

Occurrence: Upper Elliot Formation, South Africa (Gow, 2000).

Holotype: BP/1/4726, posterior portion of a skull.

Referred material: BP/1/4770, complete skull and partial postcranium; SAM-K-8026, complete skull, articulated presacral column and osteoderms, partial forelimb, articulated tail.

Remarks: *Protosuchus haughtoni* is known from an exceptionally well-preserved, three-dimensional skull and partial postcranium. *Protosuchus haughtoni* from South Africa is remarkably similar to *Protosuchus richardsoni* from the Early Jurassic of Arizona (Clark, 1986; Gow, 2000). I score only BP/1/4770 and SAM-K-8026 for this taxon.

Protosuchus haughtoni differs from *P. richardsoni* in the following: (1) a midline ridge and paired ridges lateral to it present on the basisphenoid (these are absent in *P. richardsoni*); (2) junction of maxillae in palate ends well anterior to the maxillary tooth rows; and (3) the large foramen in the maxilla within the anterior notch is not recorded for *P. richardsoni* (Gow, 2000).

Key references: Busbey and Gow, 1984; Gow, 2000.

Protosuchus richardsoni Brown, 1933
(fig. 12C–D)

Age: Hettangian, Early Jurassic (Tanner and Lucas, 2007).

Occurrence: Ward's Terrace, upper half of the Moenave Formation, Arizona.

Holotype: AMNH FR 3016, crushed skull and nearly complete skeleton missing the manus.

Referred material: MCZ 6727, three-dimensionally preserved skull and nearly complete skeleton; UCMP 131827, posterior portion of a skull and disarticulated skeleton; UCMP 130860, complete skull split longitudinally; UCMP 36717, postcranial skeleton.

Remarks: Remains of *Protosuchus richardsoni* are known from a limited number of closely spaced localities along Ward's Terrace in the sandstones of the Moenave Formation in Arizona. The taxon is represented by nearly every skeletal element in extraordinary detail including portions rarely preserved (braincase and palate). *P. richardsoni* forms part of the definition of Crocodyliformes and lies at a critical junction between basal crocodylian-line archosaurs and Crocodylia.

Key references: Brown, 1933; Colbert and Mook, 1951; Crompton and Smith, 1980; Clark, 1986.

Alligator mississippiensis Daudin, 1809

Age: Pleistocene-Recent (Brochu, 1999).

Occurrence: North America.

Specimens: AMNH (herpetology collection) 43316, skull and skeleton; AMNH 40583, articulated skull; AMNH 40584, disarticulated skull.

Remarks: The entire anatomy of *Alligator* has been described in full detail (e.g., Owen, 1850). Additionally, various authors (e.g., Witmer, 1997) used *Alligator* and avians as end members to phylogenetically bracket Archosauria and infer behavior, soft tissue anatomy, and function in basal archosaurs. I use *Alligator* to represent Mesoeucrocodylia.

Dimorphodon macronyx (Buckland, 1829),
sensu Owen, 1870
= *Pterodactylus macronyx* Buckland, 1829

Age: Hettangian-Sinemurian, Early Jurassic (Hallam, 1960).

Occurrence: Lower Lias, Lyme Regis, Dorset, England.

Holotype: BMNH R1034, nearly complete skull and skeleton.

Referred material: BMNH R 1035, much of a skull and skeleton; BMNH 41212, postcrania; YPM 350, partial skeleton; YPM 9182, partial skeleton (see Padian, 1983).

Remarks: *Dimorphodon* is one of the oldest pterosaurs known from well-preserved material. In the most recent pterosaur phylogenies, *Dimorphodon* (or Dimorphodontidae) was found as one of the basalmost taxa either outside Anurognathidae + Pterodactyloidea (Unwin, 2003) or outside Campylognathoididae + Pterodactyloidea (Kellner, 2003). Some of the material assigned to *Dimorphodon* is three-dimensionally prepared, which is rare among basal pterosaurs. This permits unprecedented examination of the ankle, femur, metatarsals, proximal tarsals, humerus, and tibia and fibula (Padian, 1983).

KEY REFERENCES: Buckland, 1829; Owen, 1870; Padian, 1983; Unwin, 1988.

Eudimorphodon ranzii Zambelli, 1973
(fig. 12A)

AGE: Mid-late Norian, Late Triassic (Dalla Vecchia, 2003).

OCCURRENCE: Uppermost part of the Calcare di Zorzino, near Cene, Italy.

HOLOTYPE: MCSNB 2888, complete skull, articulated postcranium missing the caudal region, pelvis, and most of the hind limbs.

REFERRED MATERIAL: MCSNB 8950, articulated skeleton missing the skull and tail; MCSNB 3496, partial skeleton, foot, pelvis.

REMARKS: *Eudimorphodon* was the first pterosaur to be described from the Triassic and was named from a largely articulated specimen including a nearly complete skull. Nearly all pterosaur workers found *Eudimorphodon* within the Campylognathoididae (Kellner, 2003; Unwin, 2003; Dalla Vecchia, 2009; but see Andres et al., 2010), outside Rhamphorhynchidae + Pterodactyloidea. The divergent morphology of the dentition and skull bones, Triassic age, and the relatively derived position within Jurassic pterosaur clades illustrates that much of the early evolution of Pterosauria remains hidden. Here, I score most characters from the holotype, and a few other characters (pelvis, foot, sternum) are scored from MCSNB 8950 and MCSNB 3496.

KEY REFERENCES: Wild, 1978; Dalla Vecchia, 2003; Wellnhofer, 2003.

Lagerpeton chanarensis Romer, 1971a

AGE: Ladinian, Middle Triassic (Rogers et al., 2001).

OCCURRENCE: Chañares Formation, Argentina.

HOLOTYPE: UNLR 06, articulated right hind limb.

REFERRED MATERIAL: PVL 4619, articulated sacrum, pelvis, and partial right and left hind limbs; PVL 4625, articulated vertebral column including dorsal, sacral, and anterior caudal vertebrae, left pelvis, and left femur; PVL 5000, proximal left femur; MCZ 4121, partial right and left femora.

REMARKS: *Lagerpeton* was named for a hind limb (Romer, 1971a), and referred material consists of the pelvic girdle and posterior presacral, sacral, and proximal caudal vertebrae (Bonaparte, 1984; Arcucci, 1986; Sereno and Arcucci, 1994a). In the most recent review of the taxon, Sereno and Arcucci (1994a) provided a detailed description of the hind limb and highlighted synapomorphies shared with dinosauriforms. Therefore, *Lagerpeton* possesses an important mix of plesiomorphic archosaurian character states and derived dinosaurian characters.

Lagerpeton, Dromomeron romeri, and *Dromomeron gregorii* form the Lagerpetidae (Nesbitt et al., 2009b) at the base of Dinosauromorpha. Consequently, most of the unique features of the femur, tibia, and ankle of *Lagerpeton* cited by Sereno and Arcucci (1994a) are now synapomorphies of Lagerpetidae. The thin, aliform ridge for the attachment of the caudifemoralis musculature (= fourth trochanter) differentiates *Lagerpeton* from both *D. romeri* and *D. gregorii*.

KEY REFERENCES: Romer, 1971a, 1972a; Bonaparte, 1984; Arcucci, 1986; Sereno and Arcucci, 1994a.

Dromomeron gregorii Nesbitt et al., 2009b

AGE: ?Carnian–early Norian, Late Triassic (Lucas, 1998a).

OCCURRENCE: Otis Chalk Quarry 3 (TMM 31100), Howard County, Texas; *Placerias* Quarry, Arizona.

HOLOTYPE: TMM 31100-1306, right femur.

Paratypes: TMM 31100-464, right femur; TMM 31100-1308, right femur; TMM 31100-1234, right femur; TMM 31100-764, right femur; TMM 31100-278, right tibia; TMM 31100-1314, left tibia.

REFERRED MATERIAL: UCMP 25815, distal portion of a left femur from the *Placerias* Quarry.

REMARKS: Nesbitt et al. (2009b) described a second taxon of *Dromomeron* from the base of the Dockum Group; *D. gregorii* and *D. romeri* are separated stratigraphically. *D. gregorii* shows that non-dinosaurian dinosauromorphs were present throughout much of the Late Triassic sediments in the southwestern United States. Like *D. romeri, D. gregorii* is currently known only from hind limb material. *D. gregorii* and *D. romeri* are found as sister taxa in a clade with *Lagerpeton* to the exclusion of all other archosaurs in Nesbitt et al. (2009b).

Dromomeron gregorii differs from *Dromomeron romeri* in possessing a distinct ridge for the attachment of the M. caudifemoralis longus (= 4th trochanter), the presence of an anterior trochanter and trochanteric shelf, robust proximal and distal ends of the femora, the intercondylar groove of the distal femur is reduced to a slit in larger specimens (possible autapomorphy), and the lack of an anteromedial concavity on the distal end of the tibia.

KEY REFERENCES: Nesbitt et al., 2009b.

Dromomeron romeri Irmis et al., 2007b

AGE: Mid to late Norian (Litwin et al., 1991; Lucas, 1998a; Heckert et al., 2005; Parker, 2007; Irmis et al., 2007a)

OCCURRENCE: Site 3, Hayden Quarry, Ghost Ranch, Rio Arriba County, New Mexico.

HOLOTYPE: GR 218, left femur.

PARATYPES: A right femur, GR 219, and a left tibia, GR 220, may belong to the same individual as the holotype. Additional material includes GR 221, a partial left femur; GR 234, a complete right femur; GR 222, a complete left tibia; and GR 223, a complete astragalocalcaneum.

REFERRED MATERIAL: GR 235, partial articulated skeleton; GR 236, isolated right tibia (cnemial crest crushed); NMMNH P-35379, complete astragalocalcaneum; AMNH FR 2721, distal portion of a femur; AMNH FR 30648, distal portion of a right tibia; AMNH FR 30649, distal portion of a right tibia.

REMARKS: Irmis et al. (2007a) named and briefly described *Dromomeron romeri*, the first non-dinosaurian dinosauromorph discovered since *Lagerpeton*. The holotype femur bears characters that were thought to be autapomorphies of *Lagerpeton*. The discovery of *Dromomeron* in the Norian of North America, along with non-dinosaurian dinosauriforms and dinosaurs, shows that primitive dinosauromorphs coexisted with dinosaurs. Only hind limb elements are known from this taxon at present.

Dromomeron romeri differs from *Dromomeron gregorii* and all other basal dinosauromorphs in possessing the following autapomorphies: (1) absence of a fourth trochanter; (2) presence of a sharp ridge on the anteromedial edge of the distal end of the femur; (3) presence of a lateral tuberosity on the anterolateral edge of the distal end of the femur; and (4) a large crest on the anteromedial edge of the astragalus and associated anteromedial concavity on the distal tibia.

KEY REFERENCES: Irmis et al., 2007a; Nesbitt et al., 2009b.

Marasuchus lilloensis (Romer, 1971a), sensu Sereno and Arcucci, 1994b
= *Lagosuchus lilloensis* Romer, 1971a

AGE: Ladinian, Middle Triassic (Rogers et al., 2001).

OCCURRENCE: Chañares Formation, Argentina.

HOLOTYPE: PVL 3871, partial articulated skeleton including the posterior portion of the vertebral column (from the last dorsal vertebra to the 25th caudal vertebra), left scapulocoracoid, humerus, radius, ulna, fragmentary right pelvis, left ilium, left pubis, partial right and left hind limbs.

REFERRED MATERIAL: PVL 3870, partial skeleton including the maxilla and partial braincase, vertebral column from the atlas to the anterior caudal vertebrae, articulated pelvis and hind limbs lacking only the distal phalanges and unguals; PVL 3872, partial braincase and articulated vertebral column from the atlas to the ninth presacral vertebra; PVL 4670, articulated anterior caudal vertebrae with chevrons; PVL 4671, articulated anterior caudal vertebrae with chevrons; PVL 4672, articulated vertebral column from atlas to the 17th presacral vertebra.

REMARKS: Romer (1971a, 1972a) described two incomplete long-limbed forms from the Middle Triassic of Argentina, "*Lagosuchus talampayensis*" (UNLR 09) as the genotype and "*Lagosuchus*" *lilloensis* (PVL 3871) as a second species. Sereno and

Arcucci (1994b) demonstrated that the holotype of "*Lagosuchus talampayensis*" (UNLR 09) is not diagnostic, but referred specimens of "*Lagosuchus talampayensis*" as well as "*Lagosuchus*" *lilloensis* (PVL 3871) are diagnosable. Therefore, Sereno and Arcucci (1994b) coined a new genus-level taxon, *Marasuchus*, to replace the nondiagnostic *Lagosuchus*. Subsequent workers followed Sereno and Arcucci (1994b) in this taxonomic usage.

Marasuchus holds a critical phylogenetic position as a proximal outgroup to Dinosauria in a number of studies (Sereno and Arcucci, 1994b; Novas, 1996; Benton, 1999; Irmis et al., 2007a). The anatomy was well documented by Bonaparte (1975) and Sereno and Arcucci (1994b). Unfortunately, most of the skull and the manus are missing. Here, I rely almost exclusively on PVL 3870 and 3871 for scoring.

Rauhut (2003) proposed the following characters autapomorphies of *Marasuchus*: (1) posterior cervical neural spines project anterodorsally; and (2) neural spines of mid- to posterior dorsal vertebrae contact each other dorsally.

KEY REFERENCES: Romer, 1971a, 1972a; Bonaparte, 1975; Sereno and Arcucci, 1994b.

Lewisuchus admixtus Romer, 1972d

AGE: Ladinian, Middle Triassic (Rogers et al., 2001).

OCCURRENCE: Chañares Formation, Argentina.

HOLOTYPE: UNLR 1, posterior portion of the skull, maxilla, dentary, articular (now apparently lost), cervical and dorsal vertebrae, scapulocoracoid, and humerus.

REMARKS: *Lewisuchus* was named by Romer (1972d) based on a partial skull and articulated anterior half of a skeleton. The posterior half of the skull, maxilla, dentary, and postcranium were found in the same nodule, but not articulated (Romer, 1972d). Romer (1972d) argued that the cranial material and postcrania belong to the same individual based on agreement of size and the "thecodont nature" of the material. I agree with Romer's argument and argue that none of the elements is duplicated in the specimen. The maxilla and dentary agree in size and the maxilla differs from those of any other archosauriform from the Chañares assemblage. Furthermore, the maxilla bears a large antorbital fossa that is present on the dorsal process of the maxilla, which is a character present only in archosaurs. The femur described by Romer (1972d) is actually a tibia as observed by Arcucci (1998). The size of the hind limb agrees with the rest of the specimen. Romer (1972d) illustrated and described the posterior portion of a mandible. At the time of this study, these elements seem to be lost.

Romer (1972d) considered *Lewisuchus* a pseudosuchian (at that time, Pseudosuchia was a wastebasket taxon) and made comparisons to "coelurosaurs" (1972 usage), *Hesperosuchus*, and "*Teleocrater*" (a taxon never formally described). Little else was said about the taxon until Parrish (1993) included it in his phylogeny of pseudosuchians. Parrish found it more closely related to crocodylomorphs than to "prestosuchids." This result was a direct result of Parrish (1993) having scored a "crocodile-normal" astragalus for *Lewisuchus*. Arcucci (1998) declared that this astragalus belongs to a much smaller proterochampsian, and her assessment is followed here. Moreover, Arcucci (1997, 1998) stated that *Pseudolagosuchus* and *Lewisuchus* are the same taxon (see below). Hutchinson (2001a) accepted that the two were synonymous.

KEY REFERENCES: Romer, 1972d; Parrish, 1993; Arcucci, 1997, 1998.

Pseudolagosuchus majori Arcucci, 1987

AGE: Ladinian, Middle Triassic (Rogers et al., 2001).

OCCURRENCE: Chañares Formation, near the town of Rio Los Chañares, Departamento Lavalle, Provincia de La Rioja, Argentina.

HOLOTYPE: PVL 4629, complete articulated left femur, tibia, fibula, more poorly preserved astragalus and calcaneum, complete pubis, fragments of presacral vertebrae, and ribs.

REFERRED MATERIAL: PVL 3454, fragment of the distal portion of the femur, distal two-thirds of tibia and fibula articulated with the astragalus, proximal portion of fibula, incomplete metatarsal, two poorly preserved sacral vertebrae connected to both ilia; MACN 18954, three disarticulated vertebrae (probably dorsals), five articulated caudal vertebrae, distal portion of femur, distal portions of articulated tibia and fibula, articulated astragalus and calcaneum; UNLR 53, distal fragments of tibia and fibula, proximal tarsals, and various articulated caudal vertebrae.

REMARKS: *Pseudolagosuchus* was named for a partial articulated pelvic girdle and much of a hind limb by Arcucci (1987). Only the pelvic girdle, hind limb, sacrals, a few dorsal vertebrae, and proximal caudal vertebrae are known from this taxon. Arcucci (1987) recognized that the proximal tarsals were similar to that of *Marasuchus* and dinosaurs, and this was later supported by synapomorphies listed by Novas (1996). Nesbitt et al. (2007) suggested that *Pseudolagosuchus* shares femoral synapomorphies with *Silesaurus* to the exclusion of other avian-line archosaurs.

KEY REFERENCES: Arcucci, 1987; Novas, 1996; Nesbitt et al., 2007.

Asilisaurus kongwe Nesbitt et al., 2010

AGE: Late Anisian (Hancox, 2000; Abdala and Allison, 2005).

OCCURRENCE: Lifua Member of the Manda Beds (Catuneanu et al., 2005), Rahuhu Basin, Tanzania.

HOLOTYPE: NMT RB9, anterior portion of the dentary.

PARATYPES: NMT RB21, anterior cervical vertebra; NMT RB10, left scapulocoracoid; NMT RB11, sacrum; NMT RB12, proximal portion of an ischium; NMT RB13, ilium; NMT RB14, proximal portion of the pubis; NMT RB15, anterior portion of a skull; NMT RB16, proximal portion of the left humerus; NMT RB17, left astragalus; NMT RB18, right calcaneum; NMT RB19, proximal portion of a left femur; NMT RB20, right tibia. Additional material from the type locality referable to *Asilisaurus* is under preparation.

REMARKS: During a recent collection effort in the Manda Beds, the remains of a small dinosauriform were collected (Sidor et al., 2008). The remains were locally abundant, and articulated segments and isolated bones were collected from a handful of localities over a 3 km^2 area. Fragments of the dentary and two complete astragali confirm a close relationship with *Silesaurus*, a non-dinosaurian dinosauriform. *Asilisaurus kongwe* represents the oldest avian-line archosaur yet discovered and shows that many of the basal avian-line archosaur clades were present by the end of the Anisian.

The taxon bears the following unique combination of characters: anterior portion of the dentary tapers to a sharp point, teeth absent from the anterior portion of the dentary, teeth ankylosed into the alveoli, distinctly convex dorsal margin of the dentary, Meckelian groove positioned at the dorsoventral midpoint of the medial surface of the dentary, peg-like teeth with extremely small, and poorly developed serrations.

Eucoelophysis baldwini Sullivan and Lucas, 1999

AGE: Mid to late Norian (Litwin et al., 1991; Lucas, 1998a; Heckert et al., 2005; Irmis et al., 2007b).

OCCURRENCE: Petrified Forest Member, Chinle Formation, New Mexico (Sullivan and Lucas, 1999).

HOLOTYPE: NMMNH P-22298, incomplete postcranial material consisting of two dorsal and four incomplete caudal vertebrae, nearly complete right pubis, partial right ischium, ilium fragment, fragmentary femora, proximal half of the left tibia, incomplete right metatarsals II and IV, complete metatarsal III, phalanges, unidentified bone fragments, and possibly an incomplete left scapulocoracoid.

REFERRED MATERIAL: GR 195, proximal portion of the femur (Irmis et al., 2007a).

REMARKS: The incomplete specimen of *Eucoelophysis* was found in a multitaxic assemblage in the Petrified Forest Member, Chinle Formation, New Mexico. Originally described as a coelophysoid theropod dinosaur by Sullivan and Lucas (1999), *Eucoelophysis* is now considered to be a non-dinosaurian dinosauriform (Nesbitt et al., 2005; Ezcurra, 2006; Irmis et al., 2007a; Nesbitt et al., 2007; Brusatte et al., 2008). In explicit phylogenetic analyses, Ezcurra (2006) found *Eucoelophysis* as the sister taxon to Dinosauria, whereas Irmis et al. (2007a) found *Eucoelophysis* in a clade with *Silesaurus* as the sister taxon to Dinosauria.

The studies of Ezcurra (2006) and Nesbitt et al. (2007) agreed for the most part. However, because the hind limbs were the only elements of *Eucoelophysis* that were definitely associated (within a multitaxic quarry), Nesbitt et al. (2007) considered the hind limbs and metatarsals the only definite material pertaining to the holotype of *Eucoelophysis*. Nesbitt et al. (2007) hypothesized that the pubis does not go to the hind limbs, whereas Ezcurra (2006) scored the pubis as part of *Eucoelophysis* in his data matrix. If the pubis character scores of *Eucoelophysis* are removed, *Eucoelophysis, Silesaurus,* and Dinosauria form a polytomy in Ezcurra's (2006) matrix.

The following autapomorphies were listed by Ezcurra (2006): (1) noninvasive pleurocoels in the dorsal vertebrae; (2) strongly marked U-shaped ischio-acetabular groove in pubis (Sullivan and Lucas, 1999); (3) absence of femoral trochanteric shelf of femur; (4) cnemial crest distinctively offset from the tibial shaft, cranially straight, and without lateral notch; and (5) femoral fourth trochanter reduced. The first character does not occur in any of the vertebrae of *Eucoelophysis*. The second character is present in the pubis, but this element cannot be unambiguously shown to belong to *Eucoelophysis*. *Staurikosaurus* (MCZ 1669), some basal theropods (e.g., *Dilophosaurus,* UCMP 37302), *Sacisaurus* (MCN PV10019), *Lagerpeton* (PVL 4619), basal ornithischians (e.g., *Scutellosaurus*), and basal sauropodomorphs (save *Saturnalia*) all lack a trochanteric shelf. The proximal end of the tibia, including the cnemial crest, is eroded the absence of a posterior notch cannot be assessed. Furthermore, the shaft of the tibia is incomplete; therefore, it cannot be assumed that it is straight. The fourth trochanter of *Eucoelophysis* is reduced relative to other archosaurs. Nesbitt et al. (2007) cited an appressed surface of the tibia as an apomorphy of *Eucoelophysis*.

KEY REFERENCES: Sullivan and Lucas, 1999; Nesbitt et al., 2005; Ezcurra, 2006; Nesbitt et al., 2007.

Sacisaurus agudoensis
Ferigolo and Langer, 2007

AGE: Late Carnian–early Norian (Ferigolo and Langer, 2007).

OCCURRENCE: Santa Maria 2 sequence. Top of the Alemoa Member of the Santa Maria Formation or base of the Caturrita Formation.

HOLOTYPE: MCN PV10041, partial left mandibular ramus.

REFERRED MATERIAL: Dentaries (MCN PV10042, PV10043, PV10044, PV10061, PV10048); MCN PV10050, maxilla; MCN PV10051, postorbital; vertebrae (MCN PV10028, PV10029, PV10032, PV10090, PV10097); MCN PV10033, scapula; MCN PV10100, ilium; pubes (MCN PV10023, PV10024); MCN PV10025, ischium; femora (MCN PV10009, PV10010, PV10011, PV10013, PV10014, PV10015, PV10016, PV10018, PV10019, PV10063, PV10075); MCN PV10020, tibia.

REMARKS: *Sacisaurus* was described by Ferigolo and Langer (2007) from a multitaxic bonebed from the Santa Maria sequence. The holotype was picked from a collection of tens of individuals (counted from femora) as a distinct dentary, and all crania and postcrania were subsequently referred to the taxon (Ferigolo and Langer, 2007). I agree with the authors for most of their assignments because of the similarity of most of the material to *Silesaurus*. However, remains of a basal saurischian dinosaur were found in the same bed among the disarticulated skeletons of *Sacisaurus* (S.J.N., personal obs). An ectopterygoid (MCN PV10049) assigned to *Sacisaurus* appears too large for that taxon and possibly belongs to a saurischian. As described by Ferigolo and Langer (2007), *Sacisaurus* is very similar to *Silesaurus*, a non-dinosaurian dinosauriform.

Ferigolo and Langer (2007) provided the following diagnosis: dinosauriform differing from other known basal members of the group, except *Silesaurus opolensis* and ornithischians, for the presence of an edentulous mandibular rostral portion. This jaw segment differs from that of *S. opolensis* because its front tip is not dorsally curved, and from that of ornithischians because it does not form a typically single (unpaired) predentary, but articulates to its counterpart in the midline.

KEY REFERENCES: Ferigolo and Langer, 2007.

Silesaurus opolensis Dzik, 2003 (fig. 12F)

AGE: Late Carnian (Dzik, 2001).

OCCURRENCE: Krasiejów, Opole, Silesia, Poland.

HOLOTYPE: ZPAL Ab III/361, dentaries, braincase, pterygoid, frontals, quadrate, surangular, nearly complete presacral column, sacrum, caudal vertebrae, scapulocoracoid, radii, ulnae, complete pelvic girdle, and hind limbs.

REFERRED MATERIAL: ZPAL AbIII/362, braincase, cervical, dorsal, sacral, and caudal vertebrae, partial pectoral girdle and forelimb, partial pelvic girdle and hind limbs; ZPAL AbIII/363, associated pelvic girdle; ZPAL AbIII/364, braincase, presacral vertebrae, ribs, partial forelimbs, complete articulated hind limbs.

REMARKS: Since Dzik's (2003) initial description, *Silesaurus* has revolutionized the understanding of the systematics of basal avian-line archosaurs. *Silesaurus* is known from well-preserved material from nearly all parts of the skeleton (Dzik, 2003) except some of the more delicate bones of the skull (Dzik and Sulej, 2007). The material derives from a single horizon in a single locality (Krasiejów) and occurs as both isolated elements and nearly complete skeletons. The well-preserved three-dimensional specimens allow a nearly unparalleled examination of morphological features.

The divergent morphology of *Silesaurus* strongly contrasts with the typical basal dinosaurian and avian-line archosaur bauplan. The elongated forelimbs are proportionally longer than those of basal dinosaurs. The manus is largely missing, but fragments of metacarpals and phalanges suggest the manus was quite small. Furthermore, the dentition closely resembles that of ornithischians, and the anterior portion of the dentary tapers to a sharp point.

The odd mixture of features elsewhere present in herbivorous dinosaurs features has led to controversy concerning the systematic position of *Silesaurus*. Dzik (2003) did not place *Silesaurus* in a phylogenetic analysis, but suggested that it was closely related to, but did not represent, a true dinosaur. Subsequently, Dzik and Sulej (2007) suggested that *Silesaurus* represents a basal ornithischian based on new material. However, this was not based on a phylogenetic analysis either. In explicit phylogenetic analyses, Langer and Benton (2006), Ezcurra (2006), and Irmis et al. (2007a) found *Silesaurus* as the sister taxon to Dinosauria. Given this important systematic position, *Silesaurus* polarizes dinosaurian synapomorphies and is of extreme interest.

Silesaurus differs from all other archosaurs by the combination of the following characters: (1) edentulous anterior portion of the dentary that tapers to a point well above the dental margin; (2) maxillary and dentary tooth crowns expanded above root with small denticles; and (3) femur with notch on the proximal end.

KEY REFERENCES: Dzik, 2003; Ezcurra, 2006; Nesbitt et al., 2007; Irmis et al., 2007a.

Pisanosaurus mertii Casamiquela, 1967

AGE: Late Carnian–early Norian, Late Triassic (Rogers et al., 1993, adjusted for the new Triassic timescale of Muttoni et al., 2004).

OCCURRENCE: Middle portion of the Ischigualasto Formation, Ischigualasto basin, Argentina.

HOLOTYPE: PVL 2577, tooth-bearing elements, vertebrae, incomplete hind limb, impression of the pelvis.

REMARKS: Since its discovery, *Pisanosaurus* was considered the most primitive ornithischian (Casamiquela, 1967; Bonaparte, 1976; Weishampel and Witmer, 1990; Sereno, 1991b; Irmis et al., 2007a; Butler et al., 2007, 2008b). However, questions about the association of the material plagued certainty regarding the validity of the taxon. Our current understanding of the taxon can be better understood only with the discovery of a new specimen. However, *Pisanosaurus* is almost always found as the basalmost member of

Ornithischia (Langer and Benton, 2006; Butler et al., 2007, 2008b; Irmis et al., 2007a) because of the combination of ornithischian synapomorphies and archosaur plesiomorphies, such as the anteroventrally directed pubis.

KEY REFERENCES: Casamiquela, 1967; Bonaparte, 1976; Weishampel and Witmer, 1990; Sereno, 1991b; Irmis et al., 2007a; Butler et al., 2008b.

Heterodontosaurus tucki Crompton and Charig, 1962

AGE: Early Jurassic (Olsen and Galton, 1984).

OCCURRENCE: Clarens Formation (= Cave Sandstone) and upper Elliot Formation, Herschel, Cape Province, South Africa.

HOLOTYPE: SAM-K-337, partial skull.

REFERRED MATERIAL: SAM-K-1332, complete skull and skeleton.

REMARKS: Although *Heterodontosaurus* is only represented by two unambiguous specimens, SAM-K-1332 remains one of the most well-preserved and most complete dinosaurs known to date. Santa Luca (1980) fully described the postcrania of SAM-K-1332, but a full description of the skull has yet to be published.

The phylogenetic position of *Heterodontosaurus*, though highly debated in the literature, is critical to the understanding of early dinosaur and ornithischian relationships. As summarized by Butler et al. (2008b), *Heterodontosaurus* was has been classified as a basal ornithopod, as the sister taxon to Marginocephalia, as the sister taxon to Marginocephalia + Ornithopoda, and as one of the basalmost ornithischians. Most recently, *Heterodontosaurus* was found as a basal ornithischian near *Pisanosaurus* (Butler et al., 2008b). This position better reflects the fossil record of Ornithischia and suggests that some of the "odd" features (e.g., the hand) of *Heterodontosaurus* present in non-ornithischian dinosaurs (e.g., *Herrerasaurus*) may represent plesiomorphies of Dinosauria rather than autapomorphies of *Heterodontosaurus*. A further discussion of these potentially plesiomorphic features were presented by Butler et al. (2008b).

Butler et al. (2008b) provided the following diagnosis of *Heterodontosaurus*: dorsal process of premaxilla does not form contact with nasals; anterior, accessory opening present within the antorbital fossa; squamosal-quadratojugal contact is anteroposteriorly broad; paroccipital processes are very deep dorsoventrally; paired, deep recesses on the ventral surface of the basisphenoid; basisphenoid processes are extremely elongated; cingulum is completely absent on cheek teeth; ischium with elongate flange on lateral margin.

KEY REFERENCES: Crompton and Charig, 1962, Santa Luca et al., 1976; Santa Luca, 1980; Butler et al., 2008b.

Lesothosaurus dianosticus Galton, 1978 (fig. 12B–C)

AGE: Hettangian-Sinemurian, Early Jurassic (Olsen and Galton, 1984).

OCCURRENCE: Upper Elliot Formation, South Africa and Lesotho.

SYNTYPES: BMNH RUB17, mostly disarticulated remains of at least two individuals, one larger than the other, including most of one articulated skull; BMNH RUB 23, partial skull, nearly complete, disarticulated skull; BMNH R11004, partially articulated posterior skull and anterior neck, including the braincase, parietals, right squamosal, right quadrate, posterior portion of the right lower jaw, axis and third cervical, partial postcranium; SAM-PK-K401, partial postcranium, including proximal ischia, partial postcranium, including proximal ischia.

REMARKS: *Lesothosaurus* was first described by Galton (1978) for well-preserved crania and postcrania from the upper Elliot Formation. Sereno (1991a) added further details to Galton's (1978) original description, and assigned other material to the taxon. All basal dinosaur and ornithischians analyses agree that *Lesothosaurus* is one of the basalmost ornithischians. Only Butler et al. (2008b) found heterodontosaurids more basal than *Lesothosaurus* and found *Lesothosaurus* as the sister taxon to all thyreophorans.

Butler (2005) provided the following diagnosis for *Lesothosaurus*: anterior premaxillary foramen present; slot in maxilla for lacrimal present; six premaxillary teeth present; absence of diastema between the premaxillary and maxillary teeth; maxillary teeth lack apicobasally extending ridges on their lingual and labial faces; manual phalanges lacking prominent intercondylar processes; ilium with well-developed supraacetabular flange and ventromedially angling brevis shelf visible in lateral view; dorsal groove on the ischial shaft present; shaft of ischium twists through 90° along its length, forms an elongate symphysis with the opposing ischial blade, and lacks a tab-shaped obturator process; prepubic process short and mediolaterally flattened rather than rodlike and does not extend beyond the end of the preacetabular process of the ilium; postcranial osteoderms absent.

KEY REFERENCES: Thulborn, 1970, 1972; Santa Luca, 1984; Norman et al., 2004; Butler, 2005.

Scutellosaurus lawleri Colbert, 1981

AGE: Simmurian-Pliensbachian, Early Jurassic (Peterson and Pipiringos, 1979).

OCCURRENCE: Silty facies of the Kayenta Formation, Rock Head and other nearby localities (e.g., Gold Spring), northern Arizona (Colbert, 1981).

HOLOTYPE: MNA 175, nearly complete, associated skeleton including the dentition-bearing parts of the skull, cervical, dorsal, sacral, and caudal vertebrae, hundreds of osteoderms, much of the pectoral and pelvic girdles, and portions of the fore- and hind limbs.

REFERRED MATERIAL: MNA 1752, partial disarticulated skeleton; UCMP 130580; UCMP 170829; TMM 43687-16; MCZ 8592; MCZ 8799.

REMARKS: *Scutellosaurus* is one of the better-known basal ornithischians, known from at least 10 partial skeletons. All specimens originate from a small set of localities in the silty facies of the Kayenta Formation. *Scutellosaurus* was consistently found as one of the earliest undoubted members of Thyreophora in phylogenetic analyses of ornithischians (Sereno, 1999; Norman et al., 2004; Butler et al., 2008b). As stated by Irmis et al. (2007b), *Scutellosaurus* is the oldest confirmed ornithischian in North America.

Autapomorphies listed by Butler et al. (2008b) include: dorsal and ventral margins of the preacetabular process of the ilium are drawn out medially into distinct flanges that converge upon one another anteriorly; elongate tail of comprising at least 58 caudal vertebrae.

KEY REFERENCES: Colbert, 1981; Rosenbaum and Padian, 2000; Butler et al., 2008b.

Eocursor parvus Butler et al., 2007

AGE: ?Norian, Late Triassic (Lucas and Hancox, 2001).

OCCURRENCE: Damplaats Farm, Ladybrand District, Free State, Republic of South Africa, upper part of the lower Elliot Formation (Butler et al., 2007).

HOLOTYPE: SAM-PK-K8025, disarticulated partial skeleton including parietal, supraoccipital, basisphenoid, parasphenoid, right dentary, surangular and angular, isolated cheek tooth, fragmentary cervical, dorsal, sacral and caudal vertebrae, scapulae, humeri, radius, six manual phalanges, ilia, ischia, pubes, femora, tibiae, fibulae, right metatarsals II and III, and three pedal phalanges.

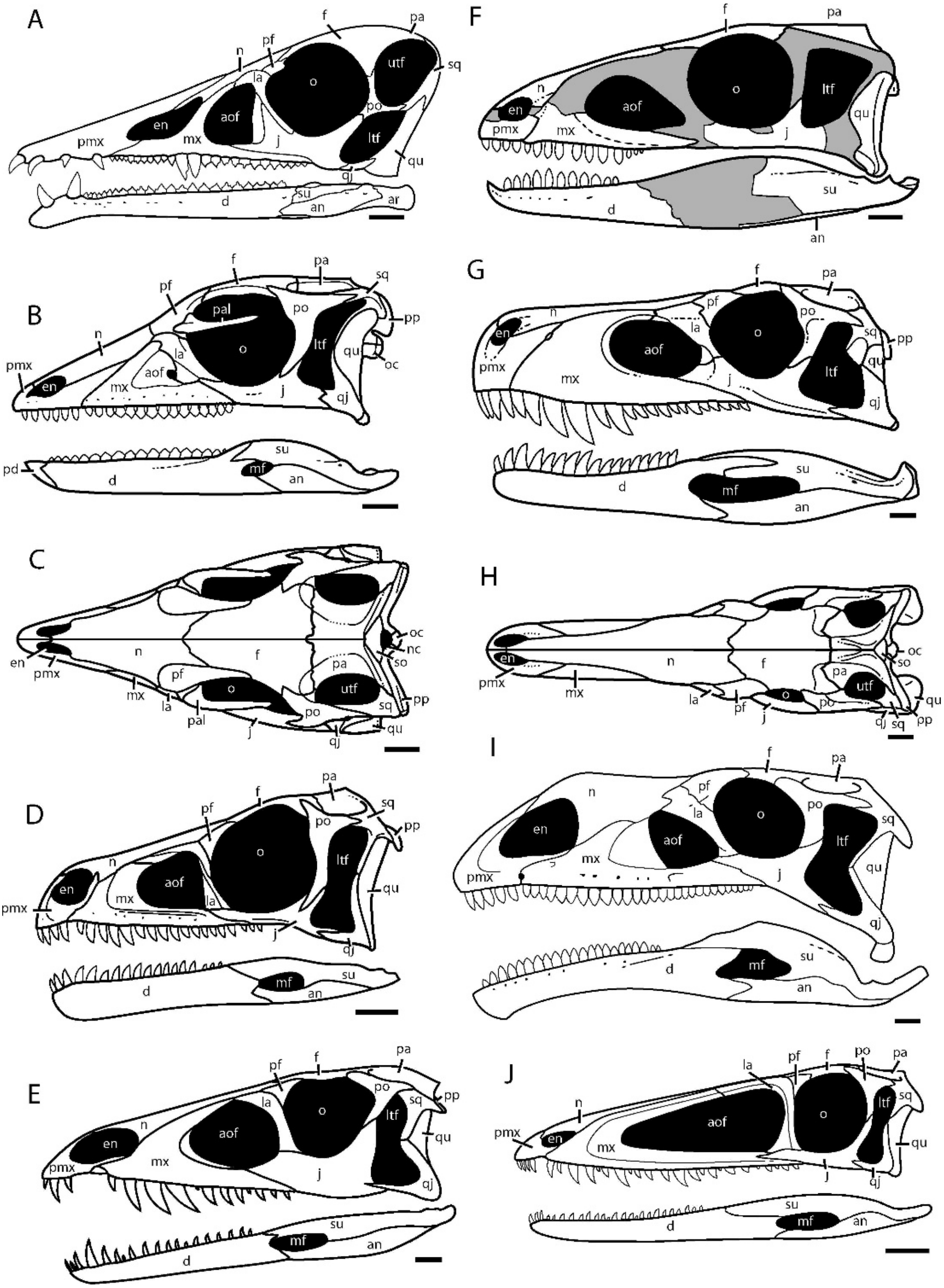
REMARKS: *Eocursor* is known from crania and postcrania from the lower Elliot Formation. This stratigraphic position makes *Eocursor* the earliest most complete ornithischian currently known (Butler et al., 2007). Butler et al. (2007) found *Eocursor* near the base of Ornithischia.

Butler et al. (2007) differentiated *Eocursor* from other ornithischians by: an accessory fossa present on the lateral surface of the basisphenoid, posterior to the canal for the internal carotid artery; maximum transverse expansion of the distal end of the humerus is only 50% of maximum transverse expansion of proximal humerus; and pubic obturator foramen subcircular and enlarged (maximum dorsoventral diameter of foramen is twice the maximum diameter of proximal pubic shaft).

KEY REFERENCES: Butler et al., 2007.

Herrerasaurus ischigualastensis Reig, 1963
(fig. 12G–H)

AGE: Late Carnian, Late Triassic (Rogers et al., 1993, adjusted for the new Triassic timescale of Muttoni et al., 2004).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OCCURRENCE: Ischigualasto Formation, Argentina.

HOLOTYPE: PVL 2566, dorsal, sacral, and caudal vertebrae, ilium, pubis, ischium, right femur, metatarsals, phalanges, left astragalus.

REFERRED MATERIAL: PVSJ 373, well-preserved articulated skeleton, lacking skull and most cervical and caudal vertebrae; PVSJ 407, nearly complete articulated skeleton with skull and mandible.

REMARKS: See Nesbitt et al., 2009a.

KEY REFERENCES: Reig, 1963; Sereno and Novas, 1992; Novas, 1994; Sereno, 1994; Langer and Benton, 2006.

Staurikosaurus pricei Colbert, 1970

AGE: Late Carnian–early Norian, Late Triassic Alemoa local fauna (Langer, 2005a).

OCCURRENCE: Alemoa Member, Santa Maria Formation, Rio Grande do Sul state, Brazil.

HOLOTYPE: MCZ 1669, incomplete skeleton including partial mandibular rami, almost complete vertebral column including six cervical vertebrae, most of the trunk and caudal series, the complete sacrum, two fragments of the scapulocoracoid, a bone fragment of uncertain affinities attributed to the humerus (Galton, 2000), almost complete ilia, pubes, ischia, femora, and the left tibia and fibula.

REMARKS: *Staurikosaurus* was named by Colbert (1970) for a unique specimen from the Triassic Santa Maria sequence in southern Brazil. The age and provenance makes *Staurikosaurus* a very important specimen for answering questions about early dinosaur diversification, relationships, and early evolution. The partially articulated skeleton preserves much of the axial column and pectoral girdle but lacks forelimbs, most of the skull, and the ever-important pes. Unfortunately, the surfaces of the bones are poorly preserved, and the identification of some of the more incomplete elements found with the specimen continue to be debated (see Galton, 2000).

Researchers have generally agreed that *Staurikosaurus* is a dinosaur, but placement within Dinosauria remains controversial. *Staurikosaurus* was found as the sister taxon of *Herrerasaurus* in phylogenetic analyses (Novas, 1992; Sereno, 1999; Rauhut, 2003; Langer, 2004; Langer and Benton, 2006) or suggested as a more basal dinosaurian taxon (Galton, 1977; Brinkman and Sues, 1987). Out of the possible autapomorphies of *Staurikosaurus* listed by Bittencourt and Kellner (2005), none seems to be restricted to the taxon. I agree with Rauhut (2003) that a postacetabular process of the ilium abbreviated and straight posteriorly is an autapomorphy of the taxon.

KEY REFERENCES: Colbert, 1970; Galton, 1977, 2000; Bittencourt and Kellner, 2005.

Saturnalia tupiniquim Langer et al., 1999

AGE: Late Carnian–early Norian, Late Triassic (Langer, 2005b).

OCCURRENCE: Alemoa Member, Santa Maria Formation, Rio Grande do Sul, Brazil.

HOLOTYPE: MCP 3844-PV, a well-preserved, semiarticulated skeleton including most of the presacral vertebral series, both sides of the pectoral girdle, right humerus, partial right ulna, right radius, both sides of the pelvic girdle with the sacral series, left femur, and most of the right hind limb.

REFERRED MATERIAL: MCP 3845-PV, skeleton including the posterior part of the skull with braincase, the natural cast of a mandibular ramus–bearing teeth, presacral series including posterior cervical and anterior trunk vertebrae, both halves of the pectoral girdle, right humerus, right side of

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Fig. 13. Skull reconstructions of basal avian-line archosaur terminal taxa: **A,** *Eudimorphodon ranzii* in lateral view; redrawn from Wild (1978); **B,** *Lesothosaurus dianosticus* in lateral and **C,** dorsal views; redrawn from Sereno (1991a); **D,** *Eoraptor lunensis* in lateral view; redrawn from Sereno et al. (1993); **E,** *Tawa hallae* in lateral view; based on the holotype and referred specimens; **F,** *Silesaurus opolensis* in lateral view; redrawn from Dzik (2003); **G,** *Herrerasaurus ischigualastensis* in lateral and **H,** dorsal views; redrawn from Sereno and Novas (1994); **I,** *Plateosaurus engelhardti* in lateral view; redrawn from Yates (2003); **J,** *Coelophysis bauri* in lateral view; redrawn from Rauhut (2003). Shaded areas indicate incomplete preservation. See appendix for anatomical abbreviations. Scale bars = 1 cm.

the pelvic girdle and most of the right hind limb; MCP 3846-PV, an incompletely prepared skeleton, from which a partial tibia and foot, as well as some trunk vertebrae, are known.

REMARKS: *Saturnalia* is one of the oldest and most completely known sauropodomorphs. Although well described in a series of papers (Langer et al., 1999; Langer, 2003; Langer et al., 2007), much of the material, including the skull, has yet to be fully prepared. *Saturnalia* was found as the basalmost sauropodomorph in all phylogenetic analyses that included the taxon. Thus, it is very important to studies of basal dinosaurs.

KEY REFERENCES: Langer et al., 1999, 2003, 2007; Langer, 2005a; Langer and Benton, 2006.

Eoraptor lunensis Sereno et al., 1993
(fig. 12D)

AGE: Late Carnian, Late Triassic (Rogers et al., 1993, adjusted for the new Triassic timescale of Muttoni et al., 2004).

OCCURRENCE: Ischigualasto Formation, San Juan, Argentina.

HOLOTYPE: PVSJ 512, essentially complete skeleton lacking only the distal caudal vertebrae.

REMARKS: *Eoraptor* remains one of the most controversial basal dinosaurs discovered. It is known from an entire articulated skeleton. Nevertheless, the poor preservation of the surface of the bone, missing details of the skull, crushing of the some of the elements, and covered elements led to conflicting interpretations (compare Sereno et al., 1993, to Langer and Benton, 2006).

Sereno et al. (1993) found *Eoraptor* as the basalmost theropod sister taxon to *Herrerasaurus* + Neotheropoda. Other studies focused on the interrelationships of theropods (e.g., Rauhut, 2003) found *Eoraptor* as the sister taxon to *Herrerasaurus* + Neotheropoda. Most recently, Langer and Benton (2006) found *Eoraptor* as the sister taxon to Eusaurischia. A detailed description of the taxon is currently in progress.

Eoraptor possesses two potential autapomorphies: a leaf-shaped premaxillary and anterior maxillary crowns, and a ventral process of the postorbital flexed sharply anteriorly in the ventral portion (from Rauhut, 2003).

KEY REFERENCES: Sereno et al., 1993; Langer and Benton, 2006; Sereno 2007.

Efraasia minor (Galton, 1973),
sensu Yates, 2003

AGE: Middle Norian, Late Triassic (Yates, 2003).

OCCURRENCE: Middle Löwenstein Formation, Weisser Steinbruch (Quarry), Pfaffenhofen, Germany, lower Löwenstein Formation, Goesel Quarry, Ochsenbach, Germany, (Yates, 2003).

HOLOTYPE: SMNS 11838, dorsal vertebrae, one sacral vertebra, right manus, partial left manus, pubes, right femur, tibia, and fibula, and partial right pes.

REFERRED MATERIAL: SMNS 12188–92, 12354, 12667, 12684, 17928.

REMARKS: In a revision of sauropodomorph taxa from the Triassic of Germany, Yates (2003) assigned the sauropodomorphs from Weisser Steinbrunchh, Pfaffenhofen, Germany, to the taxon *Efraasia*. *Efraasia* represents one of the more plesiomorphic sauropodomorphs (Yates, 2003). Recent phylogenetic analyses of basal sauropodomorph relationships (Yates, 2007; Upchurch et al., 2007) found *Efraasia* diverging before the split of prosauropods (*Plateosaurus*-like taxa) and the lineage leading to Sauropoda.

Efraasia minor possesses two autapomorphies, interbasipterygoid web with a central tubercle and a hypertrophied semilunate-shaped pubic tubercle projecting laterally from the proximal pubis (Yates, 2003).

KEY REFERENCES: Huene, 1908; Galton, 1973; Yates, 2003.

Plateosaurus engelhardti Meyer, 1837
(fig. 12I)

AGE: Middle Norian, Late Triassic (Yates, 2003).

OCCURRENCE: *Plateosaurus* Quarry, upper Löwenstein Formation, Trossingen, Baden-Wurttemberg, Germany.

REFERENCE MATERIAL: SMNS 13200, a nearly complete skull and skeleton. (The original syntypes are not diagnostic [Yates, 2003]).

REFERRED MATERIAL: AMNH FR 6810, disarticulated skull and complete skeleton; AMNH FR various specimens from the *Plateosaurus* Quarry. See Yates (2003). Numerous skeletons from SMNS and GPIT.

REMARKS: *Plateosaurus* is one of the best-known Triassic dinosaurs, and it is represented by hundreds of specimens ranging from nearly complete skeletons to isolated elements. It is unclear which species name, *Plateosaurus engelhardti* or *Plateosaurus longiceps*, should be applied to the *Plateosaurus* Quarry specimens given the incomplete and nondiagnostic syntypes of *Plateosaurus engelhardti* (Meyer, 1837). Here, I follow Yates (2003) and consider all specimens from the *Plateosaurus* Quarry as *Plateosaurus engelhardti.* I score only specimens from the *Plateosaurus* Quarry and have referred to them as *Plateosaurus engelhardti.*

Plateosaurus engelhardti has the following character states: a dorsal end of the lacrimal with a broad, weakly rugose, lateral sheet covering the posterodorsal corner of the antorbital fenestra; short jugal with a dorsoventrally deep suborbital bar; palatine with a centrally located, ventral, peglike process; interbasipterygoid septum deep, filling the whole of the space between the basipterygoid processes, and with paired central processes' stout metacarpal V with a convex proximal articular surface; broad proximal caudal neural spines (proximodistal width greater than 40% of their height); and laterally compressed distal ischial expansions (from Yates, 2003).

KEY REFERENCES: Meyer, 1837; Huene, 1926; Galton, 2000; Yates, 2003.

Tawa hallae Nesbitt et al., 2009c (fig. 12E)

AGE: Middle Norian (Litwin et al., 1991; Lucas, 1998; Heckert et al., 2005; Parker, 2006; Irmis et al., 2007). The HQ has been dated to ~215 to 213 million years ago (Mundil et al., 2008).

OCCURRENCE: Site 2, Hayden Quarry, Ghost Ranch, Rio Arriba County, New Mexico.

HOLOTYPE: GR 241, nearly complete, but disarticulated skull and most of an articulated skeleton.

PARATYPES: see Nesbitt et al., (2009c).

REMARKS: A group of six to seven individuals of *Tawa* skeletons were found in a small area in an extensive multitaxic assemblage. The individuals differ in ontogenetic stage; the smallest fibula is 70% the length of the largest fibula. The well-preserved specimens vary in completeness, from isolated elements to nearly complete articulated skeletons. The skeletons have yet to be completely prepared, and a complete description of this important taxon is underway.

Coelophysis bauri (Cope, 1887),
sensu Colbert, 1989 (fig. 12J)

AGE: Late Norian–?Rhaetian, Late Triassic (Heckert et al., 2008).

OCCURRENCE: *Coelophysis* Quarry, "siltstone member" of the Chinle Formation, Ghost Ranch, northern New Mexico.

HOLOTYPE: AMNH 7224, complete skeleton missing the tail (the tail is reconstructed from other individuals).

REFERRED MATERIAL: AMNH 7223 (see Colbert, 1989) and any coelophysoid material from the *Coelophysis* Quarry, including CM 31374, a complete skull.

REMARKS: *Coelophysis bauri* refers only to the small theropod collected from the *Coelophysis* Quarry at Ghost Ranch. Even though it was cited as represented by a thousand skeletons (Schwartz and Gillette, 1994), few of the original specimens are fully prepared, and all of the specimens were subjected to crushing and distortion. Despite the distortion, *Coelophysis* remains the most completely known basal theropod available for study.

Coelophysis differs from *Eoraptor*, *Herrerasaurus*, and *Staurikosaurus* in the more elongated dorsal vertebrae, five fused sacral vertebrae, dolichoiliacic ilium, presence of a small lateral projection on the distal end of the tibia, and the functionally tridactyl foot with a metatarsal I that is attached to metatarsal II and does not reach the ankle joint. It differs from *Gojirasaurus* in the relatively lower neural spines of the dorsal vertebrae and the significantly smaller size, from *Liliensternus* in the absence of a broad ridge that extends from the posterior end of the diapophyses to the posterior end of the vertebral centra in cervical vertebrae and the smaller size, from *Procompsognathus* in the larger overall size and the lower metatarsal III : tibia ratio, from *Shuvosaurus* in the lack of any of the derived cranial features of the latter taxon, and from the slightly younger, but very similar *Syntarsus* in the lack of a postnasal fenestra. (based on Padian 1986, Colbert, 1989, AMNH 7223 and 7224).

KEY REFERENCES: Colbert, 1989; Rauhut, 2003; Nesbitt et al., 2006.

Dilophosaurus wetherelli (Welles, 1954), sensu Welles, 1970
= *Megalosaurus wetherelli* Welles, 1954

AGE: Simmurian, Early Jurassic (Peterson and Pipiringos, 1979).

OCCURRENCE: Lower portion of the silty facies of the Kayenta Formation, Moenkopi Wash, northern Arizona (Welles, 1984).

HOLOTYPE: UCMP 37302, nearly complete skeleton.

REFERRED MATERIAL: UCMP 37303, premaxilla, maxilla, mandibles, vertebrae, articulated manus; TMM material figured by Tykoski (2005a).

REMARKS: *Dilophosaurus* is one of the best-known early theropods and is known from a variety of material housed at UCMP, TMM, and MNA. All material referable to the taxon originated from the silty facies of the Kayenta Formation on Ward's Terrace. Basal theropod phylogenies placed *Dilophosaurus* as either the basalmost coelophysoid (Gauthier, 1986; Rowe, 1989; Rowe and Gauthier, 1990; Tykoski and Rowe, 2004) or closer to the tetanurans than to coelophysoids (Rauhut, 2003; Smith et al., 2007; Yates, 2007) in a clade containing *Dracovenator*, *Zupaysaurus*, and "*Dilophosaurus*" *sinensis*.

Rauhut (2003) listed the following autapomorphies for *Dilophosaurus*: lacrimal with thickened dorsoposterior rim; cervical neural spines with distinct central "cap"; an anterior and posterior "shoulder"; scapular blade with squared distal margin.

KEY REFERENCES: Welles, 1954, 1970, 1984; Rauhut, 2003.

Allosaurus fragilis Marsh, 1877

AGE: Kimmeridian-Tithonian, Late Jurassic (Foster, 2007).

OCCURRENCE: Morrison Formation, western United States.

NEOTYPE: UUVP 6000, a complete skull and partial skeleton only lacking first caudal vertebra, chevrons, ribs, forearms, and some digits of the pes (Madsen, 1976).

REFERRED MATERIAL: Various materials from UUVP and AMNH.

REMARKS: *Allosaurus* is one of the best Jurassic theropods known to date. The taxon is represented by many articulated and disarticulated elements found throughout the Morrison Formation in North America. *Allosaurus* has been used in many phylogenetic analyses examining the relationships of theropods (e.g., Turner et al., 2007; Rauhut, 2003).

Allosaurus fragilis possesses the following unique characters: distinct "step" in the ventral margin of the jugal, leading to a significant ventral displacement of the posterior part in relation to the anterior portion; neomorphic bone (= antarticular of Madsen, 1976); well-developed notch in the anteroventral margin of the prearticular (Rauhut, 2003).

KEY REFERENCES: Marsh, 1877; Madsen, 1976; Brusatte and Sereno, 2008.

Velociraptor mongoliensis Osborn, 1924

AGE: Campanian, Late Cretaceous (Kielan-Jaworowska and Hurum, 1997).

OCCURRENCE: Djadokhta Formation, Mongolia and China.

HOLOTYPE: AMNH 6515, skull manual digit I.

REFERRED MATERIAL: IGM 100/24, complete skull and a few postcranial elements; IGM 100/25, complete skeleton; IGM 100/976, partial skeleton with a fragmentary skull and partial postcranium; IGM 100/986, fragmentary skeleton consisting of cranial and postcranial fragments; IGM 100/982, nearly completely preserved skeleton.

REMARKS: *Velociraptor* is one of the best-understood maniraptoran theropods from the Cretaceous. It is known from complete skulls and skeletons. *Velociraptor* has been used in many phylogenetic analyses examining the relationships of theropods (e.g., TWiG; Turner et al., 2007) and has been critical to understanding the theropod-bird

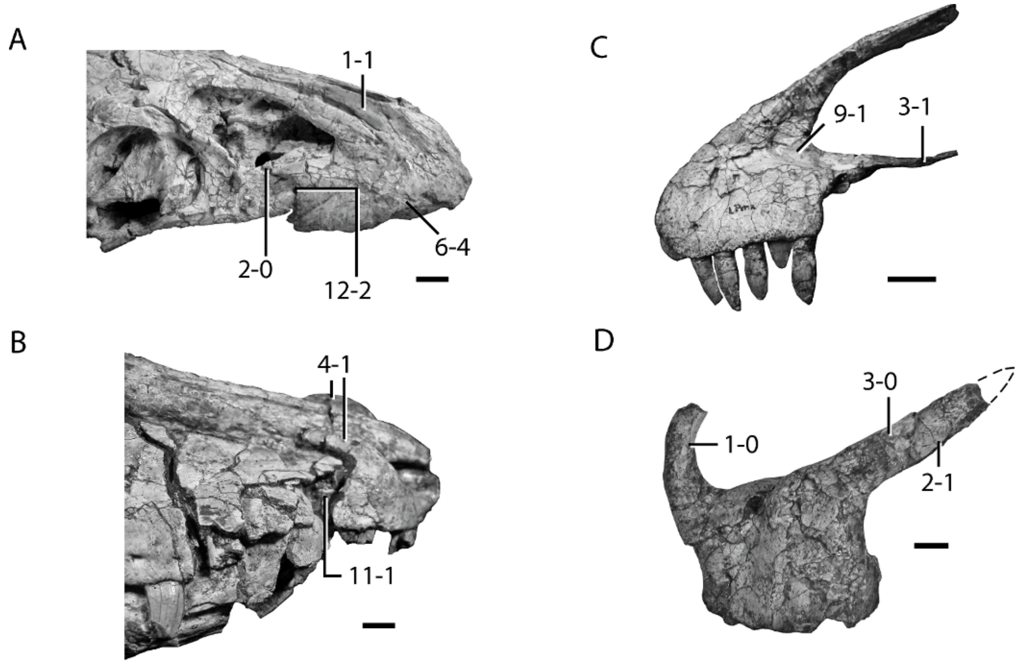


Fig. 14. Premaxillae of archosauriforms: **A,** the skull of *Effigia okeeffeae* (AMNH FR 30587) in right lateral view; **B,** the skull of *Dromicosuchus grallator* (UNC 15574) in right lateral view; **C,** left premaxilla of *Plateosaurus engelhardti* (AMNH FR 6810) in lateral view; **D,** left premaxilla of *Postosuchus kirkpatricki* (TTU-P 9000) in lateral view. Numbers refer to character states. Scale bars = 1 cm.

link (Padian and Chiappe, 1998). Barsbold and Osmólska (1999) present a thorough diagnosis of *Velociraptor* based on the skull.

KEY REFERENCES: Osborn, 1924; Norell and Makovicky, 1997, 1999; Barsbold and Osmólska, 1999.

CHARACTER DESCRIPTIONS

CRANIUM

1. Premaxilla, anterodorsal process (= nasal process), length: (0) less than the anteroposterior length of the premaxilla; (1) greater than the anteroposterior length of the premaxilla (figs. 14, 19) (Nesbitt and Norell, 2006).

Nearly all archosauriforms have a short anterodorsal process of the premaxilla; the process forms the anterior and sometimes the anterodorsal corner of the external naris. In contrast, *Effigia* (AMNH FR 30587) and *Shuvosaurus* (TTU-P 9280) each have an elongated anterodorsal process of the premaxilla that extends posteriorly, dorsal to the external nares (Nesbitt, 2007). The length of the anterodorsal process is measured from the ventral edge of the external naris.

2. Premaxilla, posterodorsal process (= maxillary process, = subnarial process), length: (0) less than or about the same as the anteroposterior length of the premaxilla; (1) greater than the anteroposterior length of the premaxilla (figs. 14, 19) (new).

The posterodorsal process of the premaxilla in most archosauriforms is shorter than or about the same as the anteroposterior length of the premaxilla; however, the length of the posterodorsal process varies widely in archosauriforms. This character attempts to describe the long length of the posterodorsal process of the premaxilla in a subset of suchians. In *Rauisuchus* (BSP AS XXV-60-121), *Saurosuchus* (PVSJ 32), *Postosuchus kirkpatricki* (TTU-P 9000), and *Polonosuchus silesiacus* (ZPAL Ab III/563), the posterodorsal process of the premaxilla is longer than the anteroposterior length of the pre-

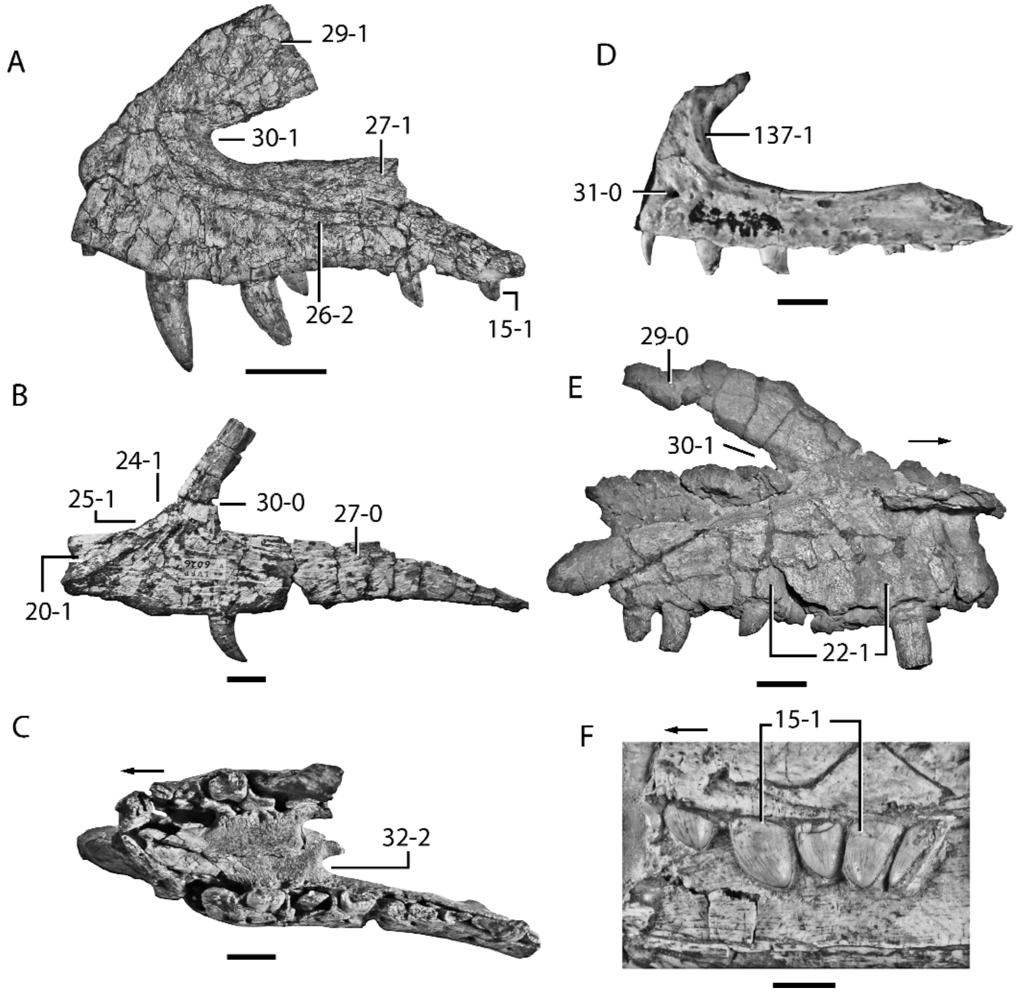


Fig. 15. Maxillae of archosauriforms: **A,** left maxilla of *Postosuchus kirkpatricki* (TTU-P 9000) in lateral view; **B,** left maxilla of *Xilousuchus sapingensis* (IVPP V 6026) in lateral view; **C,** partial maxillae of *Sphenosuchus acutus* (SAM 3014) in ventral view highlighting the palatal processes of the maxillae; **D,** left maxilla of *Euparkeria capensis* (SAM K 6047) in lateral view. The rest of the skull has been removed in the figure for comparison purposes; **E,** left maxilla of *Fasolasuchus tenax* (PVL 3851) in medial view; **F,** close up of the posterior maxillary teeth of CM 29894 (referred to as *Hesperosuchus* "*agilis*"). Numbers refer to character states. Arrow indicates anterior direction. Scale bars = 1 cm in B–D, F and 5 cm in A, E.

maxilla. The length of the posterodorsal process is measured from the ventral edge of the external naris.

3. Premaxilla, posterodorsal process (= maxillary process, = subnarial process): (0) wide, platelike; (1) thin (figs. 14–15, 17, 19–20) (modified from Gauthier, 1986; Rauhut, 2003; Langer and Benton, 2006; Smith et al., 2007).

The maxillary process of the premaxilla broadly contacts the nasal at the posterodorsal portion of the external naris in archosaurs ancestrally (Gauthier, 1986). The posterodorsal process is thin in basal theropods (e.g., *Coelophysis bauri*, CM 31374) and basal sauropodomorphs (e.g., *Plateosaurus*, AMNH FR 6810). This morphology contrasts with that of non-eusaurischian archosauriforms, ornithischians (e.g., *Heterodontosaurus*, SAM-PK-1332), and *Herrerasaurus* (PVSJ 407). As noted by Smith et al. (2007), the exact configuration of the maxillary process of the premaxilla relative to the maxilla and the nasal is variable within Theropoda.

4. Premaxilla, posterodorsal process (=maxillary process, = subnarial process): (0) fits between the nasal and the maxilla or lies on the anterodorsal surface of the maxilla; (1) overlaps anterodorsal surface of nasal; (2) vertical, strongly sutured to maxilla; (3) fits into slot of the nasal. (fig. 14) (modified from Parrish, 1993; Clark et al., 2000; Olsen et al., 2000; Benton and Walker, 2002; Sues et al., 2003; Clark et al., 2004).

This character was originally used to describe the unusual posterior process of the premaxilla in basal crocodylomorphs (Parrish, 1993). In non-archosaurian archosauriforms, non-crocodylomorph crocodylian-line archosaurs, and basal avian-line archosaurs (e.g., *Lesothosaurus*, *Herrerasaurus*), the posterior process of the premaxilla fits between the nasal and the maxilla. In taxa with a short posterior process of the premaxilla (e.g., *Effigia*, inferred for *Arizonasaurus*), the process lies on the anterodorsal edge of the maxilla as with other taxa scored as (0). In the non-crocodyliform crocodylomorphs *Dromicosuchus* (UNC 15574), *Hesperosuchus* "*agilis*" (CM 29894), *Sphenosuchus* (SAM 3014), and *Dibothrosuchus* (IVPP V7907), the posterior process lies on the lateral process of the nasal and not between the nasal and the maxilla (Clark et al., 2000). Crocodyliformes are scored as (2) following Clark et al. (2000). The posterodorsal process fits into a distinct slot within the nasal (state 3) in *Turfanosuchus* (IVPP V 3237) and *Revueltosaurus* (PEFO 33788).

5. Premaxilla, posterodorsal process (= maxillary process, = subnarial process): (0) extends posteriorly to the external naris; (1) restricted to the ventral border of the external naris (figs. 16, 20) (Langer and Benton, 2006).

In non-archosaurian archosauriforms and most crocodylian-line archosaurs, the posterodorsal process of the premaxilla extends posterior to the external naris. Within crocodylian-line archosaurs, *Qianosuchus* (IVPP 13899), *Arizonasaurus* (MSM P4590), *Xilousuchus* (IVPP V 6026), and *Effigia* (AMNH FR 30587), the posterodorsal process of the premaxilla is restricted to the ventral border of the external naris. As discussed by Langer and Benton (2006), the posterodorsal process is restricted to the ventral border of the external naris in basal sauropodomorphs (e.g., *Plateosaurus*, AMNH FR 6810) and basal theropods (*Coelophysis bauri*, CM 31374), whereas the posterodorsal process of *Herrerasaurus* (PVSJ 407) and ornithischians (e.g., *Heterodontosaurus*, SAM-PK-1332) extends posterior to the external naris.

6. Premaxillary teeth, number: (0) 3; (1) 4; (2) 5; (3) 6+; (4) 0 (figs. 14, 17) (Nesbitt and Norell, 2006).

The number of premaxillary teeth is somewhat variable among basal archosauriforms, and this character attempts to support small clades. Premaxillary teeth are absent in *Lotosaurus* (IVPP 48013), *Effigia* (AMNH FR 30587), and *Shuvosaurus* (TTU-P 9280). Only a few basal archosaur taxa have three premaxillary teeth, and this includes *Euparkeria* (SAM 5867), *Heterodontosaurus* (SAM-PK-1332), *Ornithosuchus* (BMNH R3143), *Riojasuchus* (PVL 3827), and *Gracilisuchus* (MCZ 4117). "Rauisuchians" have four premaxillary teeth (e.g., *Postosuchus kirkpatricki*, TTU-P 9000; *Batrachotomus*, SMNS 80260), whereas *Revueltosaurus* (PEFO 34561), *Stagonolepis* (BMNH R4787), *Poposaurus* (YPM 57100), *Xilousuchus* (IVPP V 6026), *Hesperosuchus* "*agilis*" (CM 29894), *Dromicosuchus* (UNC 15574), *Dibothrosuchus* (IVPP V 7907), and *Alligator* have five. Taxa with elongated premaxillae, such as phytosaurs, *Qianosuchus* (IVPP V 13899), and *Proterosuchus* (NM QR 1484) have many (8–25) premaxillary teeth.

7. Premaxilla, teeth: (0) present along entire length of the premaxilla; (1) absent in the anterior portion of the premaxilla (modified from Heckert et al., 1999; Parker, 2007).

Premaxillary teeth in archosauriforms are usually distributed along the length of the premaxilla. The aetosaurs *Aetosaurus* (SMNS 5770 S-4) and *Stagonolepis* (BMNH R4787) do not have premaxillary teeth in the anterior portion of the premaxilla, whereas *Desmato-*

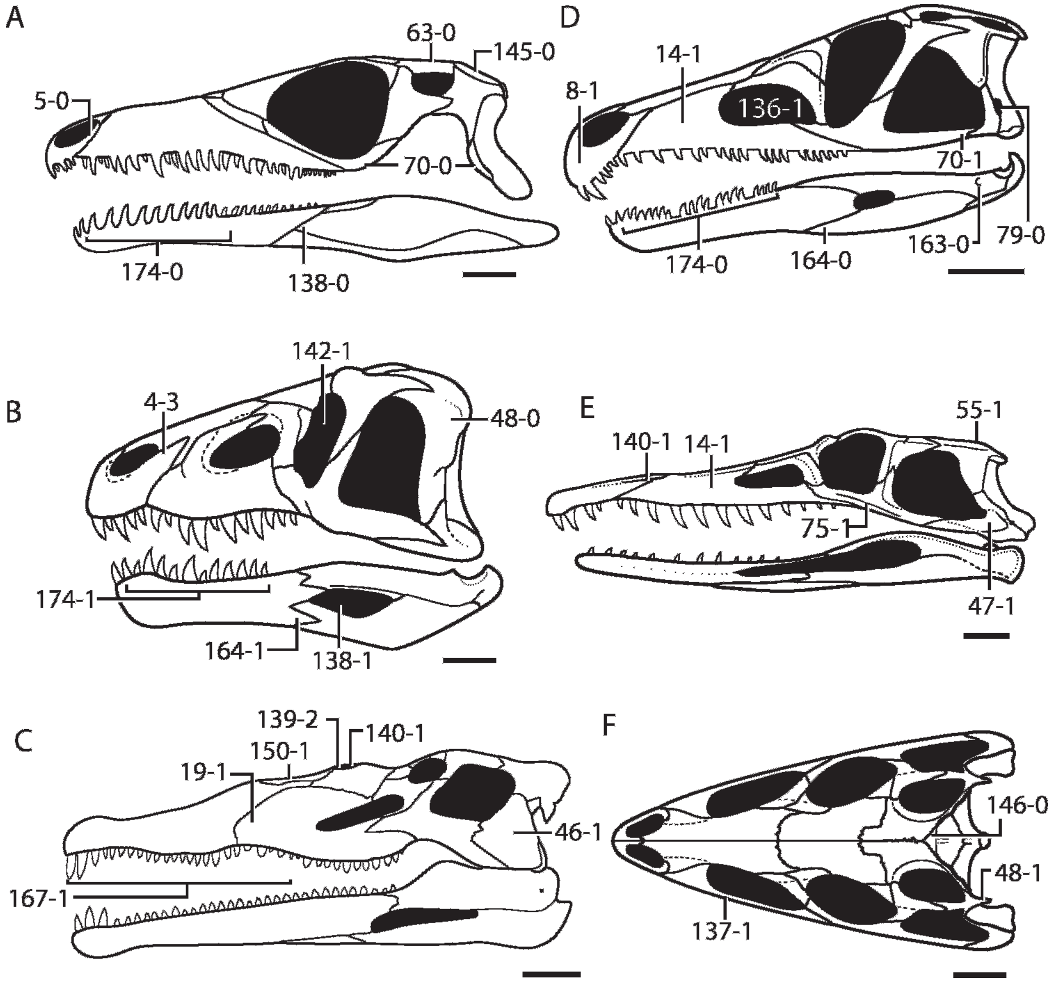


Fig. 16. Skulls of basal archosauriforms in lateral view: **A,** *Prolacerta broomi* in lateral view; **B,** *Erythrosuchus africanus* in lateral view; **C,** *Smilosuchus gregorii* in lateral view; **D,** *Proterosuchus fergusi* in lateral view; **E,** *Chanaresuchus bonapartei* in lateral view; **F,** *Euparkeria capensis* in dorsal view. Numbers refer to character states. Scale bars = 5 cm B–D and 1 cm in A, E, F.

suchus (Small, 2002) does not have premaxillary teeth.

8. Premaxilla: (0) nearly horizontal; (1) downturned (fig. 16) (Gower and Sennikov, 1997).

Gower and Sennikov (1997) cited a downturned premaxilla as a synapomorphy of *Sarmatosuchus* + *Proterosuchus*. They described the following criteria for a downturned premaxilla: (1) the anterodorsal process is directed toward the anterodorsal edge of the posterodorsal process, in lateral view; and (2) the long axis of the palatal process is at a more acute angle to the ventral margin of the premaxilla than is present in taxa without downturned premaxillae (Gower and Sennikov, 1997). I follow these criteria here. The only known Permian archosauriform, *Archosaurus* (PIN 1100/55), has a downturned premaxilla.

Sereno (1991a) used a similar character to describe the premaxillae of *Riojasuchus* and *Ornithosuchus*. Therefore, *Riojasuchus* and *Ornithosuchus* are also scored as (1).

9. Premaxilla, narial fossa: (0) absent or shallow; (1) expanded in the anteroventral

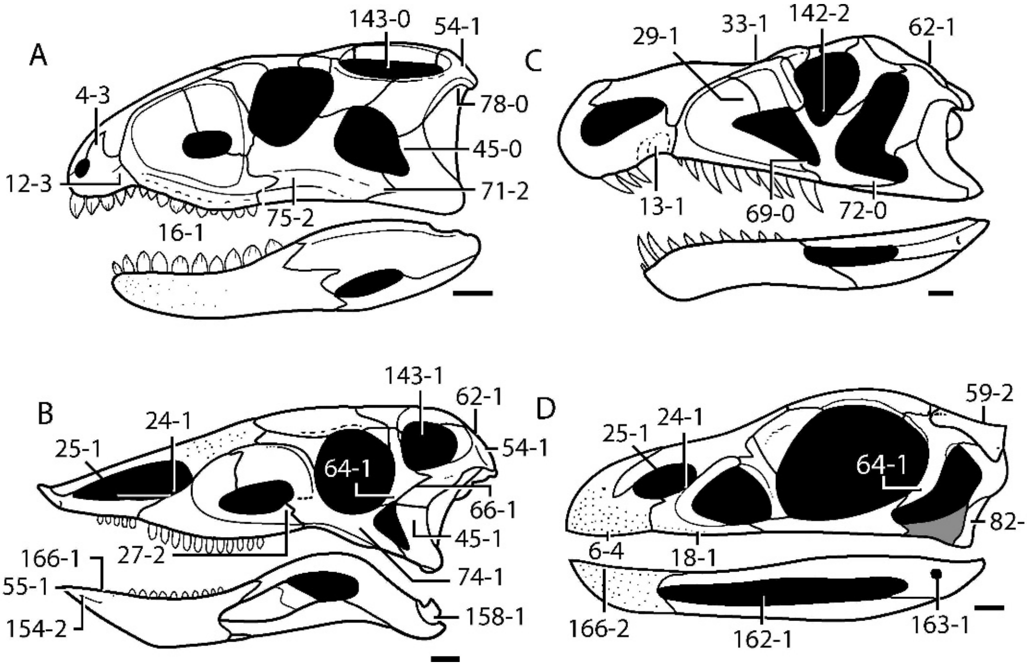


Fig. 17. Skulls of crocodylian-line archosaurs in lateral view: **A,** *Revueltosaurus callenderi* in lateral view; **B,** *Stagonolepis robertsoni* in lateral view; **C,** *Riojasuchus tenuisceps* in lateral view; **D,** *Effigia okeeffeae* in lateral view. Shaded area indicates incomplete preservation. Numbers refer to character states. Scale bars = 1 cm.

corner of the naris (figs. 14, 20) (modified from Sereno, 1999; Langer and Benton, 2006; Irmis et al., 2007a).

Langer and Benton (2006) discussed this character in detail and found that an expanded narial fossa on the anteroventral corner of the naris is found almost exclusively in theropods, *Herrerasaurus* (PVSJ 407), *Eoraptor* (PVSJ 512), and sauropodomorphs. However, even though Langer and Benton (2006) scored the suprageneric ornithischian terminal taxon as (0), a deep narial fossa is present in *Heterodontosaurus* (SAM-PK-1332). The narial fossa described for *Batrachotomus* (Gower, 1999) seems to be an autapomorphy of the taxon.

10. Premaxilla, length: (0) shorter than the maxilla; (1) longer than the maxilla (modified from Sereno, 1991a).

The length of the premaxilla nearly is universally shorter than the maxilla in archosauriforms. However, in phytosaurs (e.g., *Parasuchus hislopi*, ISI R 42) the greatly elongated premaxilla is longer than the maxilla. In some forms such as *Mystriosuchus planirostris*, the premaxilla is at least twice as long as the maxilla (Hungerbühler, 2002).

11. Premaxilla-maxilla, subnarial gap between the elements in lateral view: (0) absent; (1) present (figs. 14, 19) (Gauthier, 1986; Langer and Benton, 2006).

Following Langer and Benton (2006: fig. 4), a subnarial gap between the premaxilla and the maxilla is present in the basal theropods *Coelophysis bauri* (CM 31374) and *Dilophosaurus* (UCMP 37302). The condition in *Eoraptor* (PVSJ 512) is more similar to *Coelophysis bauri* (CM 31374) than to *Herrerasaurus* (PVSJ 407), so I score it as (1). A clear subnarial gap is present in crocodylomorphs (e.g., *Dibothrosuchus*, IVPP V 7907; *Protosuchus richardsoni*, MCZ 6727), *Vancleavea* (GR 138), and *Heterodontosaurus* (SAM-PK-1332). In these taxa, the gap receives an enlarged dentary tooth.

12. Premaxilla-maxilla, subnarial foramen between the elements: (0) absent; (1) present and the border of the foramen is present on

both the maxilla and the premaxilla; (2) present and the border of the foramen is present on the maxilla but not on the premaxilla; (3) present and the border of the foramen is present on the premaxilla but not on the maxilla (figs. 14, 17, 19) (modified from Benton and Clark, 1988; Parrish, 1993; Juul, 1994; Benton, 1999).

Benton and Clark (1988) were the first to use the presence of a slitlike fenestra/foramen between the maxilla and premaxilla to diagnose the clade Rauisuchidae in a phylogenetic context. Parrish (1993) and other basal archosaur workers also termed the opening the *subnarial foramen* in their character lists. The differences in the shape of the gap between the maxilla and the premaxilla, the scoring inconsistencies among the various authors, and the scant distribution of an opening between the maxilla and premaxilla in various archosaurs (see Juul, 1994; Gower, 2000) led Gower (2000) to question the validity of this character as a synapomorphy of a clade of "rauisuchians."

The morphology of the subnarial foramen was reported in a variety of "rauisuchians." Here, I evaluate the distribution of the feature in archosauriforms in order to clarify possible homologies. Some non-archosauriform archosauromorphs (e.g., *Mesosuchus, Prolacerta*), and non-archosaurian archosauriforms (e.g., *Proterosuchus*) possess a large anteriorly directed foramen on the anterior portion of the maxilla. Generally, a similar opening is not present in the same position in *Erythrosuchus* + Archosauria. It is not clear what vessels passed through this opening, but it is possible that they were the same as the elements that passed through the openings between the maxilla and premaxilla in other archosaurs. Juul (1994), followed by Gower (2000), reported a round opening between the maxilla, premaxilla, and nasal in the erythrosuchian *Shansisuchus*; the nasal does not contribute to the opening in any other taxon examined. Juul (1994) reported a similar opening in *Erythrosuchus*; however, in a thorough description of *Erythrosuchus*, Gower (2003) did not find a similar opening. Even though there is not a large opening, the premaxilla of *Erythrosuchus* (BPI 4526) bears a deep groove that originates on the posterior portion at the border of the articulation with the maxilla, dorsal to the premaxillary peg. A similar groove in the premaxilla is present in *Revueltosaurus* (PEFO 34561). As described by Gower (2003), the anterior portion of the maxilla does not have an indentation for an opening between the maxilla and the premaxilla. This also is the case in *Revueltosaurus*; there is no evidence of a foramen in the maxilla alone. However, a foramen between the maxilla and the premaxilla is formed *only* when the two elements are present. In both *Erythrosuchus* and *Revueltosaurus*, the foramen opens anteriorly.

Among crocodylian-line archosaurs, aetosaurs (e.g., *Aetosaurus*, SMNS 5770 S-7; *Longosuchus*, TMM 31185–98) lack any opening between the maxilla and premaxilla. Among other suchians (e.g., "rauisuchians"), the opening between the maxilla and premaxilla is variable. *Effigia* bears an opening between the maxilla and the premaxilla, but there is very little lateral exposure. The condition in *Effigia* is opposite that of *Erythrosuchus* and *Revueltosaurus*; there is no evidence of an opening on the premaxilla, but there is a *posteriorly* directed groove on the maxilla (Nesbitt, 2007). I concur, following Juul (1994) and Gower (2000), that there is no opening between the maxilla and premaxilla in *Prestosuchus* (UFRGS 0156-T). I argue that the two examples of a slitlike gap between the maxilla and premaxilla in both *Luperosuchus* (UNLR 4) and the holotype of *Saurosuchus galilei* (PVL 2062) are taphonomic features resulting from disarticulation and preservation rather than real morphology. The holotype of *Luperosuchus fractus* is poorly preserved, and the nasal is separated from the maxilla for the length of each element. The holotype of *Saurosuchus galilei* (PVL 2062) has a long slit between the maxilla and premaxilla, whereas a newly referred specimen (PVSJ 32; Alcober, 2000) has a long slit on the left side, but the right side has a tightly bound maxilla and premaxilla. The right maxilla of PVSJ 32 is clearly disarticulated because there are numerous cracks displacing the posterior process. The left side of PVSJ 32 illustrates the real morphology of the maxilla-premaxilla contact and indicates that there is no slitlike gap in *Saurosuchus*.

A small foramen shared between the premaxilla and maxilla is present in *Postosu-*

chus kirkpatricki (TTU-P 9000), *Polonosuchus silesiacus* (ZPAL Ab III/563), and *Batrachotomus* (Gower, 1999). The small foramina in *P. kirkpatricki, T. silesiacus,* and *Batrachotomus* are nearly identical to each other; the maxilla and premaxilla *both* form part of the border of the subnarial foramen. Furthermore, a small foramen similar to that of *P. kirkpatricki, T. silesiacus,* and *Batrachotomus* is possibly also found in the basal crocodylomorphs *Dromicosuchus* (UNC 15574) and *Hesperosuchus* (CM 29894). In these crocodylomorphs, a dentary tooth fits in a small foramen in the maxilla and not in the gap between the premaxilla and maxilla. In contrast, a dentary tooth fits into a large gap between the premaxilla and maxilla of *Dibothrosuchus* (Wu and Chatterjee, 1993), and the condition is not clear in *Sphenosuchus* (Walker, 1990). *Rauisuchus* is scored the same as *Postosuchus kirkpatricki* even though the maxilla is not known; half a foramen is present on the well-preserved premaxilla and it is clear that the foramen would open laterally.

It is clear that the multitude of morphologies of the opening between the maxilla and the premaxilla are different among various taxa. The homologies of the different morphologies are not clear, and it is not obvious if the different openings transmit the same vessels and thus, has an underlining homology among archosauromorphs. Therefore, the character states are expanded from past iterations of this character to incorporate the details discussed above.

13. Premaxilla-maxilla, two-tooth diastema between the posterior premaxillary teeth and the anterior maxillary teeth: (0) absent; (1) present (fig. 17) (Sereno, 1991a).

A two-tooth diastema is present in both *Ornithosuchus* (BMNH R3143) and *Riojasuchus* (PVL 3827).

14. Maxilla, facial portion anterior to anterior edge of antorbital fenestra: (0) shorter than posterior portion; (1) equal in length or longer than portion posterior to anterior edge of fenestra (figs. 16, 19–20) (character states reversed from Clark et al., 2000; Olsen et al., 2000; Benton and Walker, 2002; Clark et al., 2004; Sues et al., 2003; Clark et al., 2004).

The facial portion of the maxilla anterior to the anterior edge of the antorbital fossa is much shorter than the length of the posterior portion of the maxilla posterior to the anterior edge of the antorbital fenestra in non-archosaurian archosauriforms, basal avian-line archosaurs, and most non-crocodylomorph crocodylian-line archosaurs. An exception includes *Qianosuchus* (IVPP V 13899) and phytosaurs. Crocodylomorphs (e.g., *Hesperosuchus "agilis,"* CM 29894; *Protosuchus richardsoni*, MCZ 6727) have 50% or more of the length of the maxilla anterior to the anterior edge of the antorbital fenestra (Clark, 1986). A similar condition in theropods is also present (Rauhut, 2003).

15. Maxillary teeth, posterior edge of posterior maxillary teeth: (0) concave or straight; (1) convex (fig. 15) (modified from Sues et al., 2003; Clark et al., 2004).

The posterior edge of archosauriform taxa with carnivorous-like (mediolaterally compressed, recurved, serrated) teeth is either concave or straight posterior margins in the posterior portion of the maxilla. In *Postosuchus kirkpatricki* (TTU-P 9000), *Hesperosuchus "agilis"* (CM 29894), *Dromicosuchus* (UNC 15574), *Litargosuchus* (BP/1/5237), *Kayentasuchus* (UCMP 131830), *Protosuchus richardsoni* (AMNH FR 3024) and *Alligator,* the are either bulbous or have a posterior convex margin on posterior maxillary teeth. The posterior maxillary teeth of phytosaurs (e.g., *Parasuchus hislopi*, ISI R 42) also have convex posterior margins. Ornithischian-like teeth in *Revueltosaurus* (PEFO 34561), aetosaurs (e.g., *Aetosaurus*, SMNS 5770 S-4), *Silesaurus* (ZPAL Ab III/361/26), and sauropodomorphs (e.g., *Plateosaurus*, AMNH FR 6810) are scored as (1).

16. Maxilla, posterior process: (0) articulates ventral to the jugal; (1) articulates into a slot on the lateral side of the jugal (fig. 17) (new).

In most archosauriforms, the maxilla simply articulates ventral to the jugal. *Revueltosaurus* (PEFO 34561) and aetosaurs (e.g., *Desmatosuchus* and *Aetosaurus*) share a complex jugal and maxilla articulation. In these taxa, a small, tapering posterior process of the maxilla fits into a groove in the lateral side of the jugal. Conversely, the jugal has two small, posteriorly tapering processes, one dorsal and one ventral, that project anteriorly into slots in the maxilla.

17. Maxilla, dentition in posterior portion: (0) present; (1) absent (new).

Dentition in the posterior portion of the maxilla is present in most archosaurs. Dentition in the posterior portion of the maxilla of *Orthosuchus* (SAM-PK-409) and *Erpetosuchus* (BMNH R3139) is absent. Edentulous taxa are scored as (?) here.

18. Maxilla, dentition: (0) present; (1) absent (fig. 17) (Nesbitt and Norell, 2006).

In nearly all archosauriforms studied here, the maxillae bear a dentition. *Effigia* (AMNH FR 30587), *Shuvosaurus* (TTU-P 9280), and *Lotosaurus* (IVPP V 48013) have an edentulous maxilla.

19. Maxilla, anterior extent: (0) posterior to the anterior extent of the nasals; (1) anterior to the nasals (fig. 16) (Sereno, 1991a).

In nearly all basal archosauriforms, the anterior end of the nasals lies anterior to the maxilla. However, in phytosaurs (e.g., *Smilosuchus gregorii* USNM 18313), the maxilla stretches well anterior to the nasals. In these forms the nasal and external nares lie completely dorsal to both the antorbital fenestra and the main body of the maxilla.

20. Maxilla, anterolateral surface: (0) smooth; (1) slot for the premaxillary process (fig. 15) (new).

In most archosauriforms, the anterolateral surface of the maxilla is smooth. In contrast, the anterolateral surface of the maxilla bears a distinct slot for the posterodorsal process of the premaxilla in *Arizonasaurus* (UCMP 36232; MSM P4590), *Qianosuchus* (IVPP V 14300), and *Xilousuchus* (IVPP V 6026).

21. Maxilla, ventral portion (ventral to the lacrimal): (0) dorsoventral height greater than mediolateral length; (1) mediolateral length greater than dorsoventral height (new).

In nearly all archosauriforms, the width of the ventral surface of the posterior portion of the maxilla is much less than the height of the posterior process. In contrast, the width of the ventral surface of the posterior process is greater than the height in *Effigia* (30587), *Lotosaurus* (IVPP V 48013), *Erpetosuchus* (BMNH R3139), and *Parringtonia* (BMNH R8646). A wide posterior portion of the maxilla is also present in *Stagonolepis* (Walker, 1961).

22. Maxilla, interdental plates: (0) separate; (1) fused (fig. 15) (new).

The interdental plates are separated in nearly every archosauriform with dentition in the maxilla examined here. In non-archosauriform archosauromorphs (e.g., *Prolacerta*, BP/1/2675; *Mesosuchus*, SAM 6536) and the basalmost archosauriform (*Proterosuchus*, BSP 514), interdental plates are absent. In these taxa, the teeth are ankylosed to the bone of attachment (see character 174). Therefore, the presence of teeth that are free from the bone of attachment (thecodont dentition) seems to coincide with the origin of interdental plates.

Among crocodylian-line archosaurs, only *Postosuchus kirkpatricki* (TTU-P 9000), *Polonosuchus silesiacus* (ZPAL Ab III/563), *Teratosaurus suevicus* (BMNH 38646) and *Fasolasuchus* (PVL 3851) have fused interdental plates. All the interdental plates are fused in *P. kirkpatricki*, *T. suevicus* and *Fasolasuchus* whereas the interdentral plates of *T. silesiacus* are fused in the posterior half of the maxilla. The interdental plates fuse into a continuous sheet of bone that covers the medial side of each alveolus. Taxa without interdental plates are scored as inapplicable.

23. Maxilla, buccal emargination: (0) absent; (1) present (fig. 20) (Butler, 2005; Irmis et al., 2007a; Irmis et al., 2007a).

In most archosauriforms, a buccal margin on the lateral side of the maxilla is absent. Other than ornithischians, *Revueltosaurus* (PEFO 34561) is the only other taxon to have a buccal emargination. According to Butler et al. (2008b), a buccal emargination is present in nearly all basal ornithischians.

24. Maxilla, anterodorsal margin: (0) separated from the external naris by the premaxilla; (1) borders the external naris (figs. 15, 17, 19–20) (modified from Gauthier, 1986; Langer and Benton, 2006).

The anterodorsal margin of the maxilla of most archosauriforms is separated from the external naris by the posterodorsal premaxillary process. However, in the suchians *Arizonasaurus* (UCMP 36232; Nesbitt, 2005a) and *Effigia* (AMNH FR 30587; Nesbitt, 2007) and the aetosaurs *Aetosaurus* (Schoch, 2007), *Desmatosuchus* (TTU-P 9024; Small, 2002), *Stagonolepis* (Walker, 1961), and *Neoaetosauroides* (PVL 4363; Desojo and Baez, 2007) the maxilla creates part of the posterior border of the external naris.

25. Maxilla, anterodorsal margin at the base of the dorsal process: (0) convex or straight; (1) concave (figs. 15, 17, 19) (modified from Langer and Benton, 2006).

Non-archosaurian archosauriforms, *Revueltosaurus* (PEFO 34561), *Gracilisuchus* (MCZ 4117), *Turfanosuchus* (IVPP V 3237), *Riojasuchus* (PVL 3827), "rauisuchians" (*Postosuchus kirkpatricki*, TTU-P 9000; *Saurosuchus*, PVSJ 32), basal crocodylomorphs (*Hesperosuchus "agilis*," CM 29894; *Protosuchus richardsoni*, AMNH FR 3024), basal ornithischians (*Lesothosaurus*, BMNH R8501), and basal theropods (*Coelophysis bauri*, CM 31374) have either straight or convex anterodorsal margins of the maxilla. As scored by Langer and Benton (2006) basal sauropodomorphs have a distinctly concave anterodorsal margin of the maxilla at the base of the dorsal process. In these taxa (e.g., *Plateosaurus*, AMNH FR 6810), the posterodorsal process of the premaxilla separates the maxilla from the external naris. In *Arizonasaurus* (MSM P4590), *Qianosuchus* (IVPP V 13899), *Xilousuchus* (IVPP V 6026), *Lotosaurus* (IVPP V 48013), *Effigia* (AMNH FR 30587), *Batrachotomus* (SMNS 52970), basal pterosaurs (*Eudimorphodon*, MCSNB 2888), and aetosaurs (e.g., *Aetosaurus*, SMNS 5770 S-7), the anterodorsal margin of the dorsal process is concave.

26. Maxilla, lateral surface: (0) smooth; (1) sharp longitudinal ridge present; (2) bulbous longitudinal ridge present (fig. 15, 19) (Gower, 1999; Weinbaum and Hungerbühler, 2007).

Character state (0) applies to a smooth lateral surface of the maxilla in taxa with or without an antorbital fossa. Some taxa with an antorbital fossa may have a slight embankment marking the transition from the antorbital fossa to the lateral surface of the maxilla (e.g., *Saurosuchus*, PVSJ 32). However, this embankment is never raised above the lateral side of the maxilla in taxa scored as (0). Character state (1) and (2) describe ridges that occur at the same location, the transition from the antorbital fossa to the lateral side of the maxilla, but are well raised above/lateral to the lateral surface of the maxilla.

The maxillae of *Postosuchus kirkpatricki* (TTU-P 9000) and *Polonosuchus silesiacus* (ZPAL Ab III/563) share a bulbous ridge (state 2) on the lateral side of the maxilla that extends onto the jugal. The ridge separates the antorbital fossa from the rest of the maxilla. The ridge in *Postosuchus kirkpatricki* (TTU-P 9000) is more bulbous and extends further anteriorly than that of *Polonosuchus silesiacus* (ZPAL Ab III/563).

As discussed by Smith et al., (2007), in *Eoraptor* (PVSJ 512), *Coelophysis bauri* (CM 31374), *Coelophysis rhodesiensis, Syntarsus kayentakatae*, *Zupaysaurus*, *Liliensternus liliensterni*, and a number of other theropods, a distinct raised and sharp ridge on the alveolar border of the maxilla paralleling the tooth row is present (state 1). This horizontal ridge marks the ventral extent of the maxillary antorbital fossa, but also is raised lateral to the alveolar margin.

27. Maxilla, posterior portion ventral to the antorbital fenestra: (0) tapers posteriorly; (1) has a similar dorsoventral depth as the anterior portion ventral to the antorbital fenestra; (2) expands dorsoventrally at the posterior margin of the maxilla (figs. 15, 17, 19) (new).

The posterior portion of the maxilla tapers posteriorly in most saurischians, ornithosuchids (e.g., *Riojasuchus*, PVL 3827), *Xilousuchus* (IVPP V 6026), *Arizonasaurus* (MSM P4590), *Effigia* (AMNH FR 30587), *Prolacerta* (UCMP 37151; Modesto and Sues, 2004), *Gracilisuchus* (MCZ 4117), and *Chanaresuchus* (PVL 4575). In basal ornithischians, *Postosuchus kirkpatricki* (TTU-P 9000), *Batrachotomus* (SMNS 52970; Gower, 1999), *Saurosuchus* (PVSJ 32; Alcober, 2000), *Hesperosuchus* (CM 29894), *Dromicosuchus* (UNC 15574), *Protosuchus* (MCZ 6727), and *Sphenosuchus* (Walker, 1990), the posterior process of the maxilla is rectangular and nearly the same dorsoventral height as the anterior portion of the posterior process. The posteriormost portion of the maxilla expands dorsoventrally relative to the anterior portion ventral to the antorbital fenestra in aetosaurs, *Revueltosaurus* (PEFO 34561), *Proterosuchus* (BPS 514), *Erythrosuchus* (BPI 5207), *Euparkeria* (SAM 5867), *Turfanosuchus* (IVPP

V 3237; Wu and Russell, 2001), and phytosaurs (Ballew, 1989; Hungerbühler, 2002).

28. Maxilla, promaxillary foramen: (0) absent; (1) present (Carpenter, 1992; Rauhut, 2003; Tykoski, 2005b; Smith et al., 2007).

The promaxillary foramen is a small opening located at the base of the dorsal process of the maxilla within the antorbital fossa (Rauhut, 2003). Typically, the promaxillary foramen is hidden in lateral view (Tykoski, 2005b). Rauhut (2003) scored non-archosaurian archosauriforms, crocodylian-line archosaurs, basal avian-line archosaurs, *Herrerasaurus*, *Eoraptor*, *Coelophysis bauri*, *C. rhodesiensis*, and *Torvosaurus* as (0) and nearly all theropods (except the taxa listed above) as (1). Sereno (2007) stated that *Herrerasaurus* also possess a promaxillary foramen with little discussion or justification. Sereno (2007) stated that the large promaxillary foramen in *Herrerasaurus* is clearly visible in lateral view. The basal theropod *Coelophysis bauri* (CM 31374) and closely related taxa (*Liliensternus lilisterni*; Tykoski, 2005b) lack a promaxillary foramen, whereas the feature is present and visible in lateral view in *Dilophosaurus* (Welles, 1984), *Zupaysaurus* (Arcucci and Coria, 2003; Ezcurra, 2006), and "*Syntarsus*" *kayentakatae* (Tykoski, 1998).

29. Maxilla, dorsal (= ascending) process: (0) tapers posterodorsally; (1) remains the same width for its length (fig. 15, 17, 19) (new).

The dorsal process of the maxilla gradually tapers posterodorsally in most archosauriforms. In *Postosuchus kirkpatricki* (TTU-P 9000), *Polonosuchus silesiacus* (ZPAL Ab III/563), *Teratosaurus suevicus* (BMNH R 38646), *Revueltosaurus* (PEFO 34774), aetosaurs (*Aetosaurus*, SMNS 5770), *Riojasuchus* (PVL 3827), and *Prestosuchus* (UFRGS 0152-T; UFRGS 0156-T), the dorsal process of the maxilla maintains the same dorsoventral height posteriorly. In taxa scored as (1), the suture between the lacrimal and the dorsal process of the maxilla is nearly oriented dorsoventrally.

30. Antorbital fenestra, anterior margin: (0) gently rounded; (1) nearly pointed (figs. 15, 19) (modified from Benton and Clark, 1988; Alcober, 2000; Benton and Walker, 2002; Weinbaum and Hungerbühler, 2007).

Many basal archosaur workers previously used this character without discussion. The original wording of the character "antorbital fenestra shape: elliptical or circular (0), triangular, and with elongate narrow anterior point" is open to interpretation and difficult to score. This reformulation focuses on the anterior margin of the antorbital fenestra rather than the opening as a whole. Taxa scored as (0) (e.g., non-archosaurian archosauriforms, aetosaurs, *Herrerasaurus*, *Gracilisuchus*, and *Effigia*) have gently rounded anterior ends of the antorbital fenestra with a radius of curvature similar to the posterior end of the antorbital fenestra. In contrast, the anterior end of the antorbital fenestra is pointed and has a smaller radius relative to the posterior end of the antorbital fenestra in the taxa scored as (1) (e.g., *Postosuchus kirkpatricki*, TTU-P 9000; *Saurosuchus*, PVSJ 32; *Riojasuchus*, PVL 3827). In these taxa, the antorbital fenestra is triangular or wedge shaped. Furthermore, the dorsal process of the maxilla projects posterodorsally 45° or less. Although the antorbital fenestra of *Hesperosuchus "agilis"* (CM 29894), *Dromicosuchus* (UNC 15574), and *Protosuchus* (MCZ 6727) are anteroposteriorly elongated and not triangular as those of *Postosuchus* and *Saurosuchus*, they are scored as (1) because the anterior end of the margin of the antorbital fenestra terminates in a small radius of curvature like those of the other taxa scored as (1).

31. Maxilla, anterolateral surface, large anteriorly opening foramen: (0) present; (1) absent (fig. 15) (Modesto and Sues, 2004; Nesbitt et al., 2009a).

A large anteriorly opening foramen is present on the anterolateral surface of the maxilla, just ventral to the base of the dorsal process, in *Prolacerta* (BP/1/471; Modesto and Sues, 2004), *Proterosuchus* (RC96; Welman, 1998), *Lotosaurus* (131827), and *Euparkeria* (SAM 6049), as well as in non-archosauriform archosauromorphs such as *Protorosaurus* (Modesto and Sues, 2004) and *Mesosuchus* (Dilkes, 1998). A similar opening is not present in the same position in *Erythrosuchus, Vancleavea*, proterochampsians, and nearly all Archosauria. A similar opening between the premaxilla and the maxilla (in suchian taxa such as *Revuelto-*

saurus, S.J.N., personal obs., and *Batrachotomus,* Gower, 1999, and saurischian dinosaurs, Sereno and Novas, 1994, termed the subnarial foramen) may transmit the same vessels as the feature described above but does not seem to be homologous (see character 12).

32. Maxilla, palatal processes: (0) do not meet at the midline; (1) meet at the midline; (2) meet at the midline and expand anteriorly and posteriorly. ORDERED (fig. 15) (modified from Parrish, 1993; Clark et al., 2000; Olsen et al., 2000; Benton and Walker, 2002; Sues et al., 2003; Clark et al., 2004; Nesbitt et al., 2009a).

The palatal process of the maxilla is present in all archosauriforms in this study except for *Proterosuchus*. The structure expands anteromedially from the anteromedial edge of the maxilla on the medial side. The palatal processes of the maxillae do not meet in *Erythrosuchus* (Gower, 2003), *Vancleavea* (Nesbitt et al., 2009a), proterochampsians, and phytosaurs. Gow (1970) reported that there is medial contact of the palatal processes in *Euparkeria*; however, the medial edge of the well-prepared palatal process of SAM 6050 does not have an articular surface, as do other taxa with medial contact of the palatal processes. Gow (1970) did not provide a specimen number, so it is not clear to which specimen he referred; it is likely that he obtained his observations from SAM 6050 because it is the only example of a prepared palatal process. The palatal processes of the maxillae of *Revueltosaurus* (PEFO 34561), *Arizonasaurus* (MSM P4590), *Postosuchus kirkpatricki* (TTU-P 9000), *Polonosuchus silesiacus* (ZPAL Ab III/563), *Fasolasuchus* (PVL 3850), *Batrachotomus* (SMNS 52970), and the crocodylomorphs *Hesperosuchus "agilis"* (YPM 41198), *Sphenosuchus* (SAM 3014), *Dibothrosuchus* (IVPP V7907), *Protosuchus richardsoni* (AMNH FR 3024) and *Alligator* meet at the midline. This is also true of the avian-line archosaurs (e.g., *Allosaurus,* Madsen, 1976; *Silesaurus,* ZPAL Ab III/361/26).

The palatal processes of the maxillae of crocodylians meet at the midline and expand posteriorly to form an extensive secondary palate (Brochu, 2003). Parrish (1993) scored basal crocodylomorphs as having a "secondary palate." Scoring a "secondary palate" in basal archosaurs is difficult given the range of morphologies between that of basal crocodylomorphs and those of crocodylians. Therefore, the ambiguous term "secondary palate" is abandoned for this character state and the actual morphology is described. The palatal processes of the maxillae of crocodylomorphs (*Hesperosuchus "agilis,"* YPM 41198; *Sphenosuchus,* SAM 3014; *Dibothrosuchus,* IVPP V 7907; *Protosuchus richardsoni,* AMNH FR 3024; *Alligator*) expand anteriorly and posteriorly.

33. Nasal-prefrontal, contact: (0) present; (1) absent (fig. 17) (modified from Sereno, 1991a).

Sereno (1991a) cited the absence of nasal and prefrontal contact as a synapomorphy of *Riojasuchus* (PVL 3827) and *Ornithosuchus* (BMNH R 2409, 3562, 3142; Walker, 1964). Here, Sereno's (1991a) observations are confirmed.

34. Nasals, posterior portion at the midline: (0) convex or flat; (1) concave (fig. 21) (new).

The posterodorsal surface of the nasal of most archosauriforms is either flat or slightly convex. Among crocodylian-line archosaurs, this describes *Prestosuchus* (UFRGS T-156), *Saurosuchus* (PVSJ 32), *Aetosaurus* (SMNS 5770), *Revueltosaurus* (PEFO 34561), *Riojasuchus* (PVL 3827), *Effigia* (AMNH FR 30587), *Gracilisuchus* (MCZ 4117), and *Protosuchus richardsoni* (AMNH FR 3024). In contrast, the anterodorsal surface of the nasals is depressed in *Rauisuchus* (BSP AS XXV-60-121), *Postosuchus kirkpatricki* (TTU-P 9000), *Batrachotomus* (SMNS 80260; Gower, 1999), *Dromicosuchus* (UNC 15574), *Hesperosuchus "agilis"* (CM 29894), *Dibothrosuchus* (IVPP V 7907), and *Sphenosuchus* (SAM 3014). In these taxa, an ellipsoid depression is formed at the midline at the posterior portion of the nasals. The depression may be a consequence of a lowered portion of the nasal relative to the raised lateral nasal ridge in *Rauisuchus* (BSP AS XXV-60-121), *Postosuchus kirkpatricki* (TTU-P 9000), and *Batrachotomus* (SMNS 80260; Gower, 1999). However, small lateral ridges present on the posterolateral portion of the nasals in *Sphenosuchus* (SAM 3014) suggest the features are homologous in a subset of "rauisuchians" and crocodylomorphs. The nasal of *Fasolasuchus* (PVL 3580) could not be located (as of 2005). Nevertheless, Bonaparte (1981: fig. 1) showed a depressed region on the posteromedial portion. Therefore, *Fasolasuchus* is scored as (1).

35. Nasal, dorsolateral margin of the anterior portion: (0) smoothly rounded; (1) distinct anteroposteriorly ridge on the lateral edge (figs. 19, 21) (new).

In nearly all archosauriforms (e.g., *Euparkeria*, *Dromicosuchus*), the dorsolateral edge of the nasals is smoothly convex. In contrast, a distinct lateral and rugose ridge is located on the dorsolateral edge of the nasals of *Postosuchus kirkpatricki* (TTU-P 9000), *Batrachotomus* (SMNS 52970), *Polonosuchus silesiacus* (ZPAL Ab III/563), and *Rauisuchus* (BSP AS XXV-60-121). In *Postosuchus kirkpatricki*, *Batrachotomus*, and *Polonosuchus silesiacus,* the rugose ridge continues posteriorly on the lateral margin of the lacrimal, palpebral (*Postosuchus* and *Polonosuchus*), postorbital, and the squamosal.

36. Nasal: (0) does not possess a posterolateral process that envelops part of the anterior ramus of the lacrimal; (1) possesses a posterolateral process that envelops part of the anterior ramus of the lacrimal (fig. 20) (Yates, 2003; Langer and Benton, 2006).

Eusaurischians, and *Eoraptor* (PVSJ 512) have a small posteriorly directed process that invades the lacrimal (Langer and Benton, 2006: fig. 5). This process is located at the dorsal margin of the antorbital fossa. Langer and Benton (2006) scored *Herrerasaurus* (based on PVSJ 407) as (0), and this is followed here.

37. Nasal: (0) does not form part of the dorsal border of the antorbital fossa; (1) forms part of the dorsal border of the antorbital fossa (modified from Sereno et al., 1994; Langer and Benton, 2006; Irmis et al., 2007a).

Langer and Benton (2006) showed that the nasal forms the dorsal border of the antorbital fossa in a variety of basal archosaurs instead of only allosaurids (Sereno et al., 1994). The portions of the maxilla and the lacrimal without an antorbital fossa separate the antorbital cavity from the nasal in taxa scored as (0). This condition is present in crocodylomorphs, *Effigia* (AMNH FR 30587), *Revueltosaurus* (PEFO 34272), phytosaurs (e.g., *Smilosuchus*, USMN 18313), *Riojasuchus* (PVL 3827), basal ornithischians (e.g., *Heterodontosaurus*, SAM-PK-1332), and non-archosaurian archosauriforms with antorbital fenestrae. Although Langer and Benton (2006) stated *Euparkeria* should be scored as (1), a thin portion of the lacrimal in SAM 5207 separates the nasal from the antorbital fossa. The antorbital fossa reaches the nasal in *Aetosaurus* (SMNS 5770 S-7), *Gracilisuchus* (MCZ 4117), *Turfanosuchus* (IVPP V 3237), *Polonosuchus silesiacus* (ZPAL Ab III/563), *Postosuchus kirkpatricki* (TTU-P 9000), *Fasolasuchus* (PVL 3851), *Batrachotomus* (SMNS 52970), and as listed by Langer and Benton (2006), *Eoraptor*, and saurischians.

38. Lacrimal: (0) does not fold over (= overhang) the posterior/posterodorsal part of the antorbital fenestra; (1) folds over (= overhangs) the posterior/posterodorsal part of the antorbital fenestra (fig. 20) (modified from Sereno, 1999; Langer and Benton, 2006).

A "folded over" lacrimal possesses a deep pocket or fossa unobservable in lateral view in the posterodorsal portion of the antorbital fenestra. Langer and Benton (2006) found that state (1), which was previously thought to be only in theropods (Sereno, 1999), is present in all basal saurischians including basal members of Theropoda and Sauropodomorpha. State (0) is present in all other archosauriforms in this study.

39. Lacrimal, height: (0) significantly less than the height of the orbit, and usually fails to reach the ventral margin of the orbit; (1) as high as the orbit, and contacts the jugal at the level of the ventral margin of the orbit (fig. 20) (Rauhut, 2003).

Rauhut (2003) thoroughly discussed this character. The plesiomorphic condition in archosauriforms is to have a lacrimal that is dorsoventrally elongated at the anterior portion and meets the jugal well above the ventral portion of the orbit. In contrast, the lacrimal of *Eoraptor* (PVSJ 512), sauropodomorphs (e.g., *Plateosaurus*, AMNH FR 6810), and theropods (e.g., *Coelophysis bauri*, CM 31374) has an inverted L shape with a dorsoventrally shallow anterior process, and

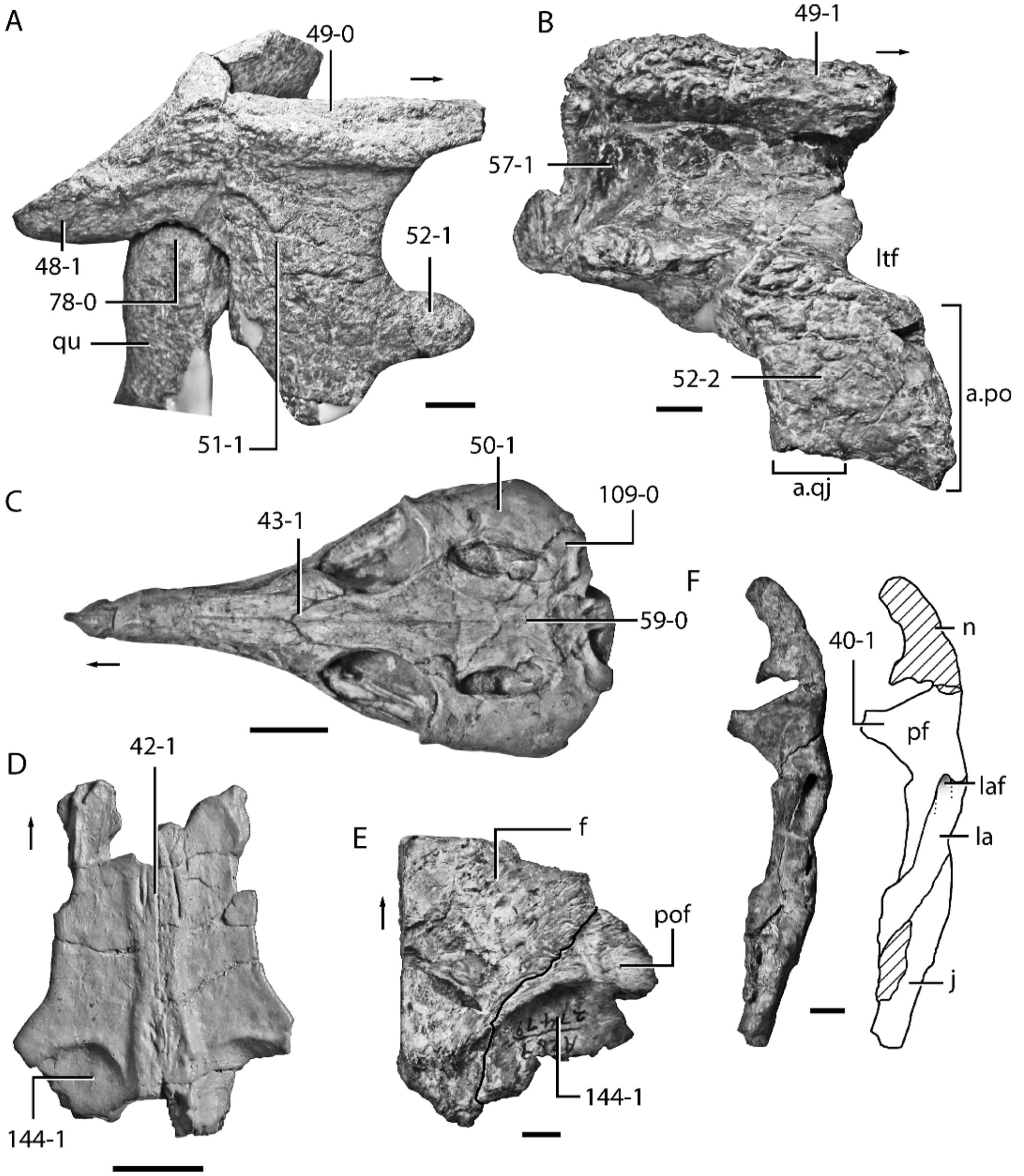


Fig. 18. Cranial character states in archosaurs: **A,** right squamosal and the dorsal portion of the quadrate of *Saurosuchus galilei* (PVSJ 32) in lateral view; **B,** right squamosal of *Postosuchus* (UCMP 27441) in lateral view; **C,** skull of *Litargosuchus leptorhynchus* (BP/1/5237) in dorsal view; **D,** frontals of *Hesperosuchs agilis* (AMNH FR 5867) in dorsal view; **E,** partial right frontal and postfrontal of *Postosuchus* (UCMP 27479) in dorsal view. The suture between the frontal and prefrontal is highlighted; **F,** the prefrontal of *Longosuchus meadei* (TMM 31185-98) posterior view from within the orbit. Arrow indicates anterior direction. Shaded areas indicate incomplete preservation. Numbers refer to character states. See appendix for anatomical abbreviations. Scale bars = 1 cm.

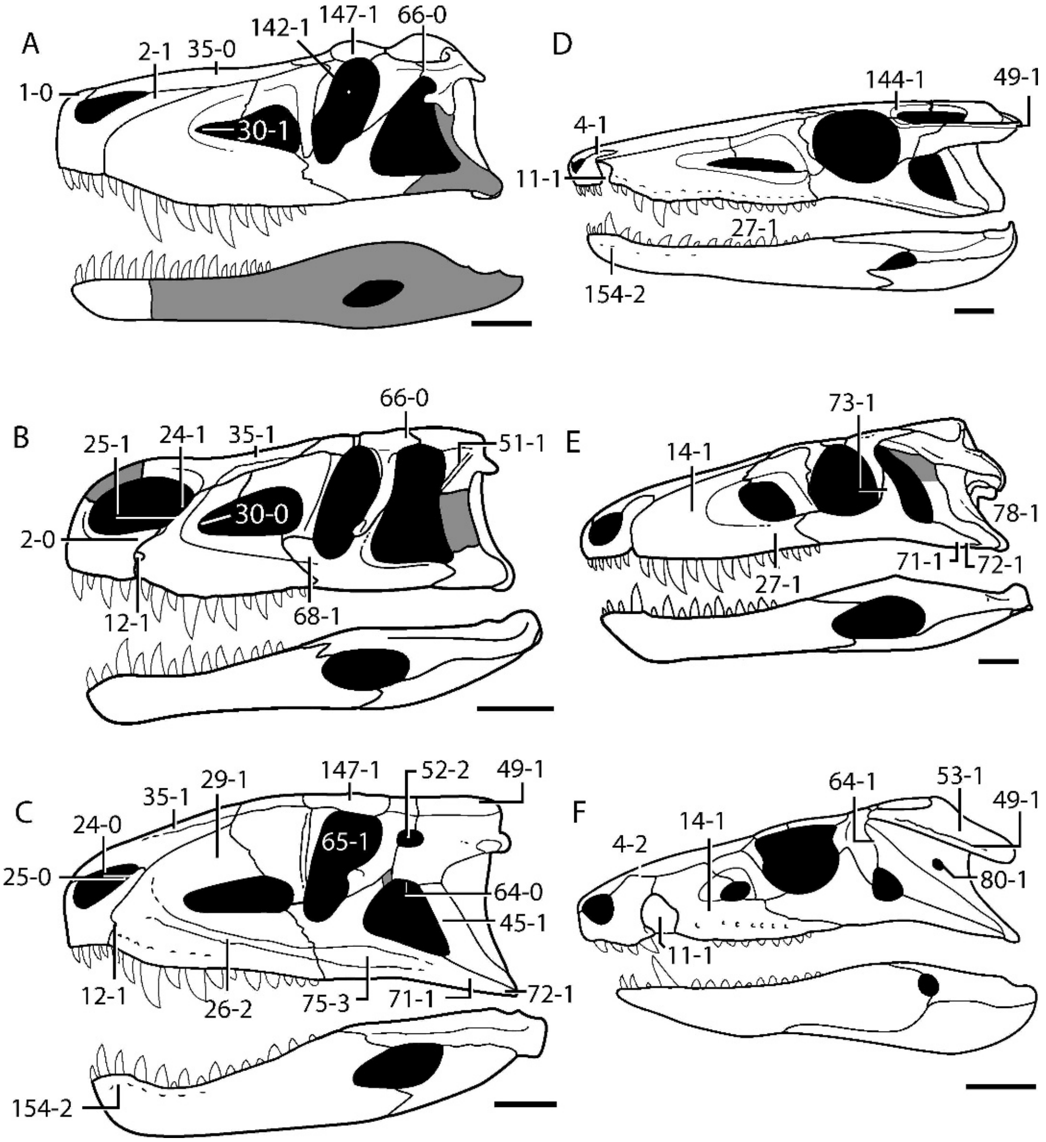


Fig. 19. Skulls of crocodylian-line archosaurs and crocodylomorphs in lateral view: **A,** *Saurosuchus galilei* in lateral in lateral views; **B,** *Batrachotomus kuperferzellensis* in lateral view; **C,** *Postosuchus kirkpatricki* in lateral view; **D,** *Dromicosuchus grallator* in lateral view; **E,** *Sphenosuchus acutus* in lateral view; **F,** *Protosuchus richardsoni* in lateral view. Shaded areas indicate incomplete preservation. Numbers refer to character states. Scale bars = 5 cm in A–C and 1 cm in D–F.

it meets the jugal at the ventral portion of the orbit (Rauhut, 2003). Among crocodylian-line archosaurs, crocodylomorphs also have lacrimals that meet the jugal at the base of the orbit.

The character is essentially equivalent to one used by Gower and Sennikov (1997) (jugal, anterior process: [0] slender and tapering [1] broad and dorsally expanded anteriorly) for basal archosauriform relationships.

40. Prefrontal, ventromedial process: (0) absent; (1) present (fig. 18) (Clark et al., 2000; Olsen et al., 2000; Benton and Walker, 2002; Gower and Walker, 2002; Sues et al., 2003; Clark et al., 2004).

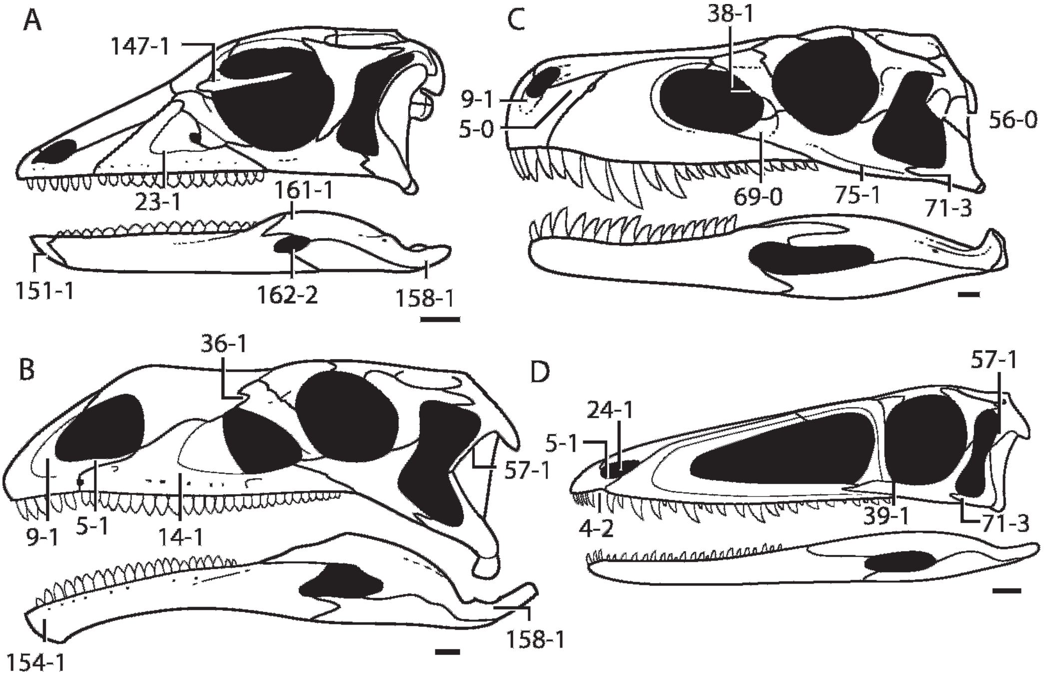


Fig. 20. Skulls of avian-line archosaurs in lateral view: **A,** *Lesothosaurus dianosticus* in lateral view; **B,** *Plateosaurus engelhardti* in lateral view; **C,** *Herrerasaurus ischigualastensis* in lateral view; **D,** *Coelophysis bauri* in lateral view. Numbers refer to character states. Scale bars = 1 cm.

Gower and Walker (2002) used the presence of a ventromedial process of the prefrontal to support a close relationship between aetosaurs and crocodylomorphs. A medial, expanded flange of the prefrontal is clearly present in the crocodylomorphs *Sphenosuchus* (SAM 3014), *Dibothrosuchus* (IVPP V 7907), *Protosuchus richardsoni* (UCMP 131827), and *Alligator*, and in the aetosaurs *Longosuchus* (TMM 31185-98) and *Stagonolepis* (Witmer, 1997). Clark et al. (2000) used a similar character in their analysis of crocodylomorphs (prefrontal not underlying anterolateral edge of frontal to a significant degree [0] or with distinct posterior process underlying frontal dorsal to orbit [1]). A ventromedial process is not present in any other archosauriform studied here.

41. Prefrontal: (0) does not contact the palate; (1) contacts the palate (Wu and Chatterjee, 1993).

In the basal archosauriforms studied here, the prefrontal touches the palate only within crocodylomorphs. Even though examination of this character requires exquisite preservation and meticulous preparation, the prefrontal does not touch the palate in *Sphenosuchus* (SAM 3014; Walker, 1990), whereas the prefrontal touches the palate in *Dibothrosuchus* (IVPP V 7907; Wu and Chatterjee, 1993), *Protosuchus richardsoni* (UCMP 131827), and *Alligator*.

42. Frontal, dorsal surface: (0) flat; (1) with longitudinal ridge along midline (fig. 17) (Wu and Chatterjee, 1993; Clark et al., 2000; Olsen et al., 2000; Benton and Walker, 2002; Sues et al., 2003; Clark et al., 2004).

In the crocodylomorphs *Hesperosuchus* (AMNH FR 6758, CM 29894), *Dromicosuchus* (UNC 15574), *Sphenosuchus* (SAM 3014), and *Dibothrosuchus* (IVPP V 7907), as cited by Clark et al. (2000), a ridge is formed by both frontals. The frontals of *Batrachotomus* (SMNS 52970) and *Postosuchus kirkpatricki* (TTU-P 9000) also have similar ridges. In both *Batrachotomus* and *Postosuchus* there is a ridge on the medial edge of each frontal. When in articulation, the frontals have two parallel ridges separated by a small gap at the midline. The ridge in

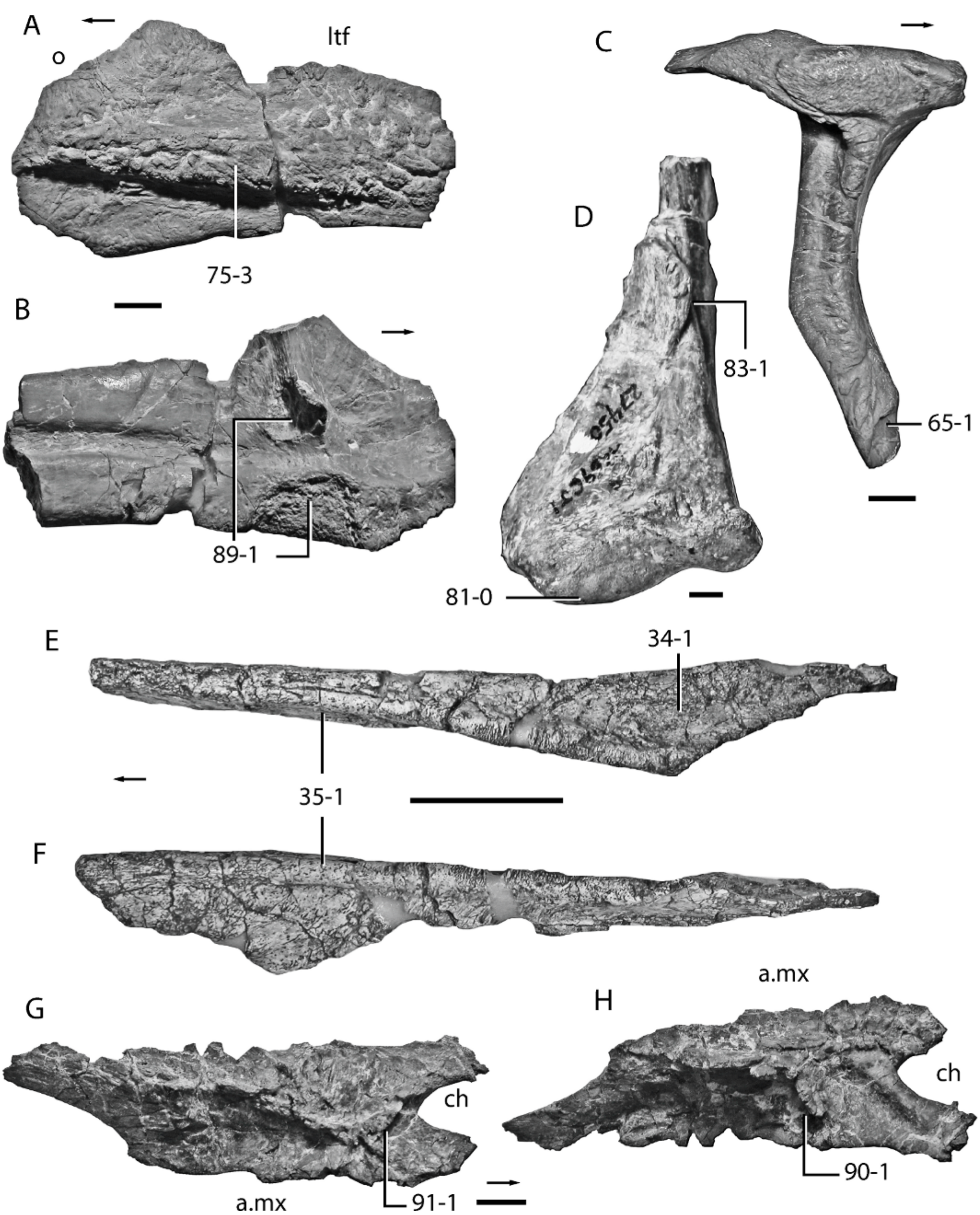


Fig. 21. Cranial character states in archosaurs: **A,** left jugal of *Polonosuchus silesiacus* (ZPAL Ab III/563) in lateral and medial **B,** views; **C,** right postorbital of *Batrachotomus kuperferzellensis* (SMNS 52970) in lateral view; **D,** partial left quadrate of *Postosuchus* (UCMP 27477) in posterior view; **E,** left nasal of *Postosuchus kirkpatricki* (TTU-P 9000) in dorsal and lateral **F,** views; **G,** left palatine of *Polonosuchus silesiacus* (ZPAL Ab III/563) in ventral and dorsal **H,** views. Arrow indicates anterior direction. Numbers refer to character states. See appendix for anatomical abbreviations. Scale bars = 1 cm in A–D, G–H, and 5 cm in E–F.

Batrachotomus (SMNS 52970) is much more robust and developed in comparison with *Postosuchus* (UCMP 27479).

43. Frontal, anterior portion: (0) about as wide as the orbital margin or has a transversely aligned suture with the nasal; (1) tapers anteriorly along the midline (fig. 18) (new).

In most archosauriforms, the frontal meets the nasal in a transverse suture and/or the frontal is about the same mediolateral width as that of the orbital margin. This is apparent in *Euparkeria* (SAM 5867), phytosaurs (e.g., *Smilosuchus*, UCMP 27200), ornithosuchids (e.g., *Riojasuchus*, PVSJ 3827), aetosaurs (e.g., *Aetosaurus* SMNS S-16), *Gracilisuchus* (MCZ 4117), *Qianosuchus* (IVPP V 13899), *Effigia* (AMNH FR 30587), and in basal avian-line archosaurs (e.g., *Plateosaurus*, AMNH FR 6810; *Allosaurus*, Madsen, 1976). The frontals taper anteriorly along the midline in *Postosuchus kirkpatricki* (TTU-P 9000), *Revueltosaurus* (PEFO 34561), *Batrachotomus* (SMNS 52970), *Saurosuchus* (PVSJ 32), *Ticinosuchus* (PIZ T2817), and in crocodylomorphs (e.g., *Hesperosuchus* "*agilis*," CM 29894; *Sphenosuchus*, SAM 3014; *Litargosuchus*, BP/1/5237).

44. Postfrontal: (0) present; (1) absent (Gauthier, 1986; Benton and Clark, 1988; Juul, 1994; Bennett, 1996; Novas, 1996; Benton, 1999; Clark et al., 2000; Olsen et al., 2000; Benton and Walker, 2002; Sues et al., 2003; Clark et al., 2004; Langer and Benton, 2006; Nesbitt, 2007; Irmis et al., 2007a).

Within Archosauromorpha, the postfrontal is present plesiomorphically at the posterodorsal margin of the orbit. This is the case in all archosaur groups except for Crocodylomorpha (Benton and Clark, 1988), Dinosauria (Langer and Benton, 2006), *Effigia* (AMNH FR 30587), and *Shuvosaurus* (TTU-P 9280) and the non-archosaurian archosauriform Proterochampsia. The postfrontal has been scored as absent in *Erpetosuchus* by both Benton and Walker (2002) and Olsen et al. (2000). However, the specimen scored (BMNH R3139) by Benton and Walker (2002) is preserved as a mold; thus, sutures are extraordinarily difficult to discern. Furthermore, a suture between the postfrontal and surrounding bones may not be necessarily expressed as a distinct surface feature. Therefore, it is not clear whether a postfrontal was present or absent in *Erpetosuchus*.

45. Quadratojugal: (0) forms less than 80% of the posterior border of the lower temporal fenestra; (1) more than 80% of the posterior border of the lower temporal fenestra (figs. 17, 19) (modified from Benton and Clark, 1988; Parrish, 1993).

The quadratojugal forms 80% or less of the posterior border of the lower temporal fenestra in most archosaurs. Consequently, taxa scored as (0) have elongated ventral processes of the squamosal, thus making a character measuring the length of a ventral process of the squamosal redundant (Parrish, 1993: char. 39; Clark et al., 2000: 11; Olsen et al., 2000: 11; Benton and Walker, 2002: 11; Sues et al., 2003: 11; Clark et al., 2004: 11). In non-archosaurian archosauriforms, *Saurosuchus* (PVSJ 32), *Prestosuchus* (UFRGS 0156-T), *Revueltosaurus* (PEFO 34561), *Turfanosuchus* (IVPP V 3237), *Gracilisuchus* (MCZ 4117), *Qianosuchus* (IVPP V 13899), *Lotosaurus* (IVPP 131827), and avian-line archosaurs (e.g., *Plateosaurus*, AMNH FR 6810; *Herrerasaurus*, PVSJ 407), the quadratojugal forms less than 80% of the posterior border of the lower temporal fenestra. Taxa scored as (1) include the aetosaurs *Aetosaurus* (SMNS 5770 S-8) and *Desmatosuchus* (Small, 2002), *Postosuchus kirkpatricki* (TTU-P 9002), *Polonosuchus silesiacus* (ZPAL Ab III/563), and *Rauisuchus* (BSP AS XXV-60-121; inferred from the length of the squamosal), and crocodylomorphs (e.g., *Hesperosuchus "agilis,"* CM 29894; *Protosuchus richardsoni*, UCMP 131827). Even though the ventral process of the squamosal of *Batrachotomus* (SMNS 80260) is broken, the preserved length indicates that the quadratojugal would not make up 80% of the posterior border of the lower temporal fenestra. As described above, the taxa scored as (1) have either short processes or do not have ventral processes of the squamosal.

46. Quadratojugal, shape: (0) L-shaped; (1) subtriangular (fig. 16) (Sereno, 1991a).

The quadratojugal of basal archosaurs is L-shaped. Alternatively, the quadratojugal of phytosaurs forms a triangular plate among the squamosal, quadrate, and jugal (Case, 1929; Colbert, 1947; Gregory, 1962; Westphal, 1976; Ballew, 1989; Hungerbühler, 2002). A subtriangular quadratojugal is present in all phytosaur taxa included here.

47. Quadratojugal, lateral surface: (0) without a ridge marking the posteroventral corner of the lower temporal fossa; (1) with a ridge marking the posteroventral corner of the lower temporal fossa (fig. 16) (Nesbitt et al., 2009a).

The main body of the quadratojugals of *Tropidosuchus* (PLV 4604) and *Chanaresuchus* (PVL 4575) has a distinct lower temporal fossa marked by a sharp ridge. All other taxa in this analysis have a nearly smooth quadratojugal without a distinct ridge.

48. Squamosal, posterior end: (0) does not extend posterior to the head of the quadrate; (1) extends posterior to the head of the quadrate (figs. 16, 18) (Nesbitt et al., 2009a).

The squamosals of *Mesosuchus* (SAM 6536), *Prolacerta* (BP/1/471), *Proterosuchus* (BSP 514), and *Erythrosuchus* (BP/1/ 5207) terminate posteriorly just dorsal to the posterior edge of the head of the quadrate. In contrast, the squamosals of *Euparkeria* (SAM 5867), the proterochampsians *Chanaresuchus* (PVL 4586) and *Tropidosuchus* (PVL 4606), and members of crown-group Archosauria (e.g., *Arizonasaurus*, *Herrerasaurus*) have a posteriorly expanded squamosal process that terminates well posterior of the quadrate. This character may be a subdivision the character referred to as the development of the ‘‘archosaur otic notch’’ of Romer (1956) and Gauthier (1984).

49. Squamosal: (0) without distinct ridge on dorsal surface along edge of supratemporal fossa; (1) with distinct ridge on dorsal surface along edge of supratemporal fossa (figs. 18, 19);

= Lateral projecting flange on the squamosal absent (0) or present (1) (Bonaparte, 1982; Parrish, 1993);

= Squamosal not significantly overhanging lateral temporal region (0) or with broad lateral expansion overhanging lateral temporal region (1) (Clark et al., 2000: char. 10; Olsen et al., 2000: 10; Benton and Walker, 2002: 10; Sues et al., 2003: 10; Clark et al., 2004: 10);

= Squamosal overhanging quadrate and quadratojugal laterally: absent (0), present, and contacting the lower temporal fenestra dorsally (1), present, but excluded from the rim of the lower temporal fenestra by postorbital and quadratojugal (2) (Benton and Clark, 1988; Juul, 1994: 74; Benton, 1999: 8).

This character was used in numerous analyses (see above) and in several forms that seem to describe the same morphology. The squamosals of archosauriforms typically do not have a distinct ridge on the dorsolateral margin of the squamosal. This includes *Euparkeria* (SAM 5867), phytosaurs, *Revueltosaurus* (PEFO 34561), aetosaurs, *Turfanosuchus* (IVPP V 3237), *Prestosuchus* (UFRGS 0156-T), *Effigia* (AMNH FR 30587), *Arizonasaurus* (MSM P4590), *Saurosuchus* (PVSJ 32), and avian-line archosaurs. A distinct ridge on the dorsolateral margin of the squamosal is clearly present in *Postosuchus kirkpatricki* (TTU-P 9000), *Polonosuchus silesiacus* (ZPAL Ab III/563), *Rauisuchus* (BSP AS XXV-60-121), and *Batrachotomus* (SMNS 80260). Here, I agree with Parrish (1993) and homologize the dorsally expanded ridge in the taxa listed above with that of the crocodylomorphs *Hesperosuchus ‘‘agilis’’* (CM 29894), *Dromicosuchus* (UNC 15574), *Sphenosuchus* (SAM 3014), *Terrestrisuchus* (BMNH R7591), *Dibothrosuchus* (IVPP V 7907), *Litargosuchus* (BP/1/5237), and crocodyliforms included here. In these taxa, the lateral ridge originates from the same portion of the squamosal, and the lateral edge of the extended portion is rugose. The dorsal margin of the squamosal of *Gracilisuchus* (MCZ 4117) does not have a laterally expanded ridge.

50. Squamosal, transverse length of dorsal exposure: (0) less than the mediolateral width of the upper temporal fenestra; (1) equal to or greater than the mediolateral width of the upper temporal fenestra (fig. 18) (new).

In most basal archosauriforms, the transverse length of the squamosal lateral to the upper temporal fenestra is far less than the maximum transverse width of the upper temporal fenestra. In contrast, the transverse length of the squamosal lateral to the upper temporal fenestra in *Litagrosuchus* (BP/1/ 5237), *Kayentasuchus* (UCMP 131830), *Protosuchus richardsoni* (UCMP 131827; BP/1/ 4746), and *Orthosuchus* (SAM-PK-409) is equal to or greater than the mediolateral width of the upper temporal fenestra.

51. Squamosal: (0) without ridge on lateral side of the ventral process; (1) with ridge on lateral side of the ventral process (fig. 18) (new).

The ventral process of squamosal (if present) is nearly flat and smooth in nearly all archosauriforms except *Batrachotomus* (SMNS 80260), *Saurosuchus* (PVSJ 32), and *Prestosuchus* (UFRGS 0156-T). In these taxa, a ridge on the ventral process originates ventral to the articulation of the parietal and arcs anteroventrally (Gower, 1999).

52. Squamosal, anteroventral process: (0) absent; (1) present and perforates the lower temporal fenestra; (2) present and contacts the postorbital bisecting the lower temporal fenestra. ORDERED (figs. 18, 19) (new).

The ventral process of the squamosal extends ventrally or anteroventrally in basal archosauriforms. In *Prestosuchus* (UFRGS 0152-T) and *Saurosuchus* (PVSJ 32), a small anterior process on the ventral process penetrates the lower temporal fenestra. In *Postosuchus kirkpatricki* (TTU-P 9000; TTU-P 9002), *Polonosuchus silesiacus* (ZPAL Ab III/563), and *Rauisuchus* (BSP AS XXV-60-121), an anterior process on the ventral process contacts the postorbital, and as a result, the process bisects the lower temporal fenestra. The resultant circular opening dorsal to the anteroventral process is formed completely by the squamosal and the postorbital. A sliver of the anteroventral process forms the dorsal border of the lower temporal fenestra in *Postosuchus kirkpatricki, Polonosuchus, Silesiacus*, and *Rauisuchus.*

53. Squamosal, dorsolateral edge: (0) without longitudinal groove; (1) with longitudinal groove (fig. 19) (Clark et al., 2000; Clark and Sues, 2002; Sues et al., 2003; Clark et al., 2004).

The squamosals of *Kayentasuchus* (UCMP 131830), *Protosuchus richardsoni* (UCMP 131827), *Protosuchus haughtoni* (BP/1/4242), *Orthosuchus* (SAM-PK-409), and *Alligator* bear a distinct longitudinal scar on the lateral edge of the squamosal (Clark and Sues, 2002).

54. Squamosal, facet for the paroccipital process on the medial side of the posterior process: (0) mediolaterally thin; (1) rounded and thick (fig. 17) (new).

The facet for the paroccipital process on the medial side of the posterior process of the squamosal is mediolaterally thin in most archosauriforms. In comparison, the same facet is mediolaterally thickened and rounded into a knob in *Revueltosaurus* (PEFO 34561), *Turfanosuchus* (IVPP V 3237), and all aetosaurs known from skull material. Some, non-archosaurian archosauriforms cannot be scored for this character because they do not have separate posterior processes of the squamosal (see character 48); the paroccipital fits directly on the medial side of the body of the squamosal.

55. Squamosal, posterodorsal portion: (0) without upper temporal fossa; (1) with upper temporal fossa (fig. 16) (new).

A distinct shelf or upper temporal fossa lies on the dorsal surface of the squamosal surrounding the upper temporal fenestra in the basal crocodylomorphs *Hesperosuchus* "*agilis*" (CM 29894), *Dromicosuchus* (UNC 15574), *Sphenosuchus* (SAM 3014), *Dibothrosuchus* (IVPP V7907), *Litargosuchus* (BP/1/5237), and *Protosuchus haughtoni* (BP/1/4242), and in proterochampsians (e.g., *Chanaresuchus*, PVL 4586; *Tropidosuchus*, PVL 4606) a rim surrounds the upper temporal fossa.

56. Squamosal, ventral process: (0) wider than one-quarter of its length; (1) narrower than one-quarter of its length (fig. 20) (Yates, 2003; Langer and Benton, 2006).

Yates (2003), followed by Langer and Benton (2006), found that a narrow ventral process of the squamosal is present in sauropodomorphs. I confirm this in *Saturnalia* (MCP 3845-PV), *Plateosaurus* (AMNH 6810), and *Efraasia* (Yates, 2003). However, the distribution of the character outside Sauropodomorpha requires further explanation. Langer and Benton (2006) scored their suprageneric Theropoda as (0). However, the basal theropods *Coelophysis bauri* (CM 31374) and "*Syntarsus*" *kayentakatae* (MNA V2623) have thin ventral processes like that of basal sauropodomorphs, whereas the ventral processes of *Dilophosaurus* (Welles, 1984), *Zupaysaurus* (UNLR 076), and *Allosaurus* (Madsen, 1976) have wide processes. Furthermore, the condition immediately outside Dinosauria remains poorly understood. *Silesaurus* (Dzik and Sulej, 2007: fig. 18A) has a thin ventral process, whereas nearly all crocodylian-line archosaurs have wide ventral processes.

57. Squamosal, deep pit on the posterodorsal corner of the lateral surface: (0) absent; (1) present (fig. 18) (Brusatte et al., 2008).

As described by Brusatte et al. (2008), the squamosals of *Postosuchus kirkpatricki* (TTU-P 9000) and *Polonosuchus silesiacus* (ZPAL Ab III/563) have a deep fossa on the posterodorsal corner of the lateral surface of the squamosal.

58. Parietals, in presumed adults: (0) separate; (1) interparietal suture partially or completely absent (Clark et al., 2000; Olsen et al., 2000; Benton and Walker, 2002; Sues et al., 2003; Clark et al., 2004).

A suture separates the parietals of most basal archosaurs including non-archosaurian archosauriforms, avian-line archosaurs, non-crocodylomorph crocodylian-line archosaurs, and the crocodylomorphs *Dromicosuchus, Hesperosuchus, Terrestrisuchus, Pseudhesperosuchus,* and *Saltoposuchus* (Clark et al., 2000, 2004). In *Sphenosuchus* (SAM 3014), *Dibothrosuchus* (IVPP V 7907), *Junggarsuchus* (IVPP V 14010), *Litargosuchus* (BP/1/5237), *Protosuchus* (MCZ 6727; BP/1/4242), *Orthosuchus* (SAM-PK-409), and *Alligator,* the parietals are completely fused.

In previous analyses, Clark et al. (2000, 2004) had a third character state, "interparietal suture partially obliterated (1)" and ordered the character. Additionally, Clark et al. (2000, 2004) scored *Gracilisuchus* as having an interparietal suture partially obliterated. However, *Gracilisuchus* has a clear interparietal suture (e.g., MCZ 4117) contrary to what was reported originally (Romer, 1972c); therefore it is scored as a (0) here. Other than *Litargosuchus* (BP/1/5237), there are no other examples of "interparietal suture partially obliterated." Thus, the second character state of Clark et al.'s (2000) character 16 is combined with state (2).

59. Parietals, upper temporal fenestrae separated by: (0) broad, flat area; (1) supratemporal fossa separated by a mediolaterally thin strip of flat bone; (2) supratemporal fossa separated by a "sagittal crest" (which may be divided by the interparietal suture) (figs. 17–18) (modified from Clark et al., 2000; Olsen et al., 2000; Benton and Walker, 2002; Sues et al., 2003; Clark et al., 2004).

In most basal archosauriforms, the parietals separate the upper temporal fenestrae by a flat gap. In phytosaurs (e.g., *Smilosuchus*, USNM 18313), some crocodyliforms (*Protosuchus richardsoni*, MCZ 6727), *Gracilisuchus* (MCZ 4117), proterochampsians, and *Doswellia* (Weems, 1980), the area of the parietals between the upper temporal fenestrae is adorned by pits and ridges. *Protosuchus*, *Orthosuchus* (SAM-PK-409), and *Alligator* are scored as (0). *Revueltosaurus* (PEFO 34561) and aetosaurs have deep parietal fossae. However, these fossa are located only on the lateral side of the parietal; thus, they do not form a supratemporal fossa. *Revueltosaurus* and aetosaurs are scored as (0).

The upper temporal fenestrae of *Hesperosuchus "agilis"* (CM 29894), *Dromicosuchus* (UNC 15574), *Batrachotomus* (SMNS 52970), and *Postosuchus kirkpatricki* (TTU-P 9002) are separated by a thin strip of flat bone framed by two thin ridges marking the medial extent of the upper temporal fenestrae. In *Dibothrosuchus* (IVPP V 7907), *Junggarsuchus* (IVPP V 14010), *Sphenosuchus* (SAM 3014), and *Effigia* (AMNH FR 30587), a sagittal crest separates the upper temporal fenestrae at the midline.

60. Parietals, posteroventral edge: (0) extending more than half the width of the occiput; (1) less than half the width of the occiput (fig. 16) (Clark et al., 2000; Clark and Sues, 2002; Clark et al., 2004).

In nearly all archosauriforms, the posteroventral processes of the parietals are expanded laterally to meet the squamosal and supraoccipital/opisthotic ventrally. In stark contrast, the posteroventral edge of the parietals are highly reduced in *Protosuchus* (AMNH FR 3024; BP/1/4770), *Orthosuchus* (SAM-K-409), and other basal crocodyliforms (Clark et al., 2004).

61. Parietals, occipital margin shape: (0) V-shaped in dorsal view; (1) straight in dorsal view (Clark et al., 2000; Clark and Sues, 2002; Clark et al., 2004).

Plesiomorphically in archosauriforms, the lateral processes of the parietals project posterolaterally creating a V-shaped posterior skull table in dorsal view. In contrast, the lateral processes of the parietals of *Dibothrosuchus* (IVPP V 7907), *Sphenosuchus* (SAM 3014), *Kayentasuchus* (UCMP 131830), *Protosuchus* (UCMP 131827; BP/1/4746), *Orthosuchus* (SAM-PK-409), and *Alligator* project laterally creating a straight posterior margin of the skull table.

62. Parietal, posterolateral (= occipital) process: (0) nearly vertical; (1) anteriorly inclined greater than 45° (fig. 17) (modified from Heckert and Lucas, 1999).

The posterolateral process of the parietal is completely or nearly vertical in nearly all archosauriforms studied here. In *Riojasuchus* (PVL 3827), *Ornithosuchus* (BMNH R2409), and aetosaurs (e.g., *Aetosaurus*, SMNS 5770 S-2) the posterolateral processes of the parietals are anteriorly inclined about 45°. In *Aetosaurus* (SMNS 5770 S-8), a set of osteoderms lies on the anteriorly inclined parietals. *Revueltosaurus* (PEFO 34561) has a vertical posterolateral process of the parietal.

63. Parietal foramen: (0) present; (1) absent (fig. 16) (Gauthier, 1984; Benton, 1985; Benton and Clark, 1988; Bennett, 1996; Nesbitt et al., 2009a).

The parietal foramen is absent in *Proterosuchus* (see Welman, 1998) as well as in some specimens of *Prolacerta* (Camp, 1945; Modesto and Sues, 2004). However, the presence of a parietal foramen in *Prolacerta* is variable according to Modesto and Sues (2004); therefore, the character is scored as polymorphic in *Prolacerta*. A parietal foramen is present in *Mesosuchus* (SAM 6536).

64. Quadratojugal-postorbital, contact: (0) absent; (1) present (figs. 17, 19) (Parrish, 1991, 1993).

Observation of this character requires exquisite preservation of the quadratojugal and postorbital. Consequently, this cannot be scored for important basal crocodylomorph taxa such as *Dibothrosuchus* (following Clark et al., 2000), *Terrestrisuchus* (Crush, 1984), and *Dromicosuchus* (Sues et al., 2003). The quadratojugal of *Sphenosuchus* (SAM 3014) is broken as recently interpreted by Clark et al. (2000). However, there is no indication of contact of the quadratojugal on the posterior surface of the well-preserved postorbital. Therefore, *Sphenosuchus* is scored as (0).

Parrish (1991, 1993) scored both *Postosuchus* and *Gracilisuchus* as (1). Repreparation of the holotype of *Postosuchus kirkpatricki* (TTU-P 9000), as well as the identification of new, well-preserved elements (UCMP 27441; Long and Murry, 1995), indicates that the squamosal excludes the quadratojugal from contacting the postorbital (contra Chatterjee, 1985). As reported by Brinkman (1981), the skulls of *Gracilisuchus* are dorsoventrally crushed; thus, in the original and subsequent reconstructions of the taxon (Romer, 1972c; Parrish, 1993), the postorbital is shown to contact the squamosal. Here, I agree with Brinkman (1981) that crushing has artificially forced contact between the two elements and that the quadratojugal and postorbital did not contact in life. Brinkman's (1981) reconstruction of the dorsal orientation of the quadratojugal was too extreme given the preserved length of the quadratojugal and the ventral process of the squamosal versus the length of the postorbital bar. Therefore, the orientation of the quadratojugal and the ventral process of the squamosal would resemble that of *Riojasuchus* (PVL 6827).

Clark et al. (2000) indicated possible quadratojugal-postorbital contact in *Hesperosuchus "agilis"* (CM 29894). Upon further investigation, however, the quadratojugal is incompletely preserved and slightly displaced in CM 29894. Therefore, it is not clear whether there is quadratojugal-postorbital contact in *Hesperosuchus*. In a recent paper, redescribing newly prepared material of *Aetosaurus*, Schoch (2007) described possible quadratojugal-postorbital contact in three of the specimens. These specimens have partially disarticulated skull elements and some are overprepared. However, *Aetosaurus* is scored as (1) here. Furthermore, there is no contact between the quadratojugal-postorbital in the aetosaurs *Desmatosuchus* (Small, 2002) and *Stagonolepis* (Walker, 1961) and in *Revueltosaurus* (PEFO 34561).

Only *Protosuchus richardsoni* (UCMP 130860), *Orthosuchus* (SAM-PK-409), and *Alligator* are scored as (1).

65. Postorbital, ventral termination of the ventral process: (0) tapered; (1) blunt (figs. 19, 21) (modified from Benton and Clark, 1988; Juul, 1994; Benton, 1999; Alcober, 2000; Benton and Walker, 2002).

The ventral process of the postorbital tapers to a point in most archosauriforms.

In contrast, the ventral process of the postorbital of *Postosuchus kirkpatricki* (TTU-P 9000) and *Batrachotomus* (SMNS 80260) terminate in a blunt tab. The tab enters the orbit in both taxa, giving the orbital margin a "stepped" shape. The original formulation of this character by Benton and Clark (1988) focused on the postorbital bar; here I focus on the ventral termination of the postorbital to clarify what is accounting for the "stepped" appearance.

A similar character was also used by Rauhut (2003) and Smith et al. (2007) to describe a similar morphology in Theropoda. According to these authors, *Ilokelesia*, *Abelisaurus*, *Carnotaurus*, *Majungatholus*, *Carcharodontosaurus*, *Giganotosaurus*, and *Tyrannosaurus* have the derived state. The listed theropod taxa share a dorsoventrally elongated orbit with *Batrachotomus* (Gower, 1999) and *Postosuchus* (Chatterjee, 1985).

66. Postorbital-squamosal, contact: (0) restricted to the dorsal margin of the elements; (1) continues ventrally for much or most of the ventral length of the squamosal (figs. 17, 19) (new).

Typically in archosauriforms, a posteriorly directed prong of the postorbital fits into a slot into the anterior portion of the squamosal. This articulation is restricted to the dorsal margin of these elements in non-archosaurian archosauriforms, phytosaurs, *Riojasuchus* (PVL 3827), *Turfanosuchus*, *Gracilisuchus* (MCZ 4117), *Arizonasaurus* (MSM P4590), *Effigia* (AMNH FR 30587), *Batrachotomus* (SMNS 80260), *Saurosuchus* (PVSJ 32), *Prestosuchus* (UFRGS 0156-T), and most avian-line archosaurs (e.g., *Coelophysis bauri*, CM 31374).

The articulation between the two elements is expanded ventrally in *Revueltosaurus* (PEFO 34561), aetosaurs (e.g., *Aetosaurus*, SMNS 5770 S-5) and crocodylomorphs (e.g., *Sphenosuchus*, SAM 3014). With the exception of *Revueltosaurus*, the entire anterior portion of the squamosal terminates on the posterior edge of the postorbital. The condition in *Postosuchus kirkpatricki* (TTU-P 9000), *Rauisuchus* (BSP AS XXV-60-121), and *Polonosuchus silesiacus* (ZPAL Ab III/563) is scored as (1) because the postorbital-squamosal articulation *continues* ventrally even though part of the squamosal attaches to the posterior edge of the squamosal ventral to the dorsal postorbital-squamosal contact; a fenestra separates the two different articulations (see character 52).

67. Postorbital bar: (0) composed both of the jugal and postorbital in nearly equal proportion; (1) composed mostly by the postorbital (new).

In nearly all archosauriforms, the postorbital bar is composed of both the postorbital and the jugal in somewhat equal proportions. In the aetosaurs *Dematosuchus* (TTU-P 9024; Small, 2002), *Stagonolepis* (Walker, 1961), and *Aetosaurus* (SMNS 5770 S-8; Schoch, 2007), *Shuvosaurus* (TTU-P 9280) and *Effigia* (AMNH FR 30587), the postorbital forms nearly the entire posterior border of the orbit. In these taxa the posterodorsal process of the jugal is very short relative to that of other archosauriforms.

68. Jugal, anterior extent of the slot for the quadratojugal: (0) well posterior of the posterior edge of the dorsal process of the jugal; (1) at or anterior to the posterior edge of the dorsal process of the jugal (fig. 19) (new).

The anterior extent of the anterior process of the quadratojugal lies well posterior to the anterior border of the lower temporal fenestra in most archosauriforms. Within Dinosauria, state (0) is present in ornithischians (e.g., *Heterodontosaurus*, SAM-K-1332), sauropodomorphs (e.g., *Plateosaurus*, AMNH FR 6810), *Herrerasaurus* (PVSJ 407), and *Eoraptor* (PVSJ 512). In *Tawa* (GR 241), *Coelophysis bauri* (CM 31374), and *Dilophosaurus* (UCMP 37302), the anterior process of the quadratojugal stretches anteriorly at or to the anterior border of the lower temporal fenestra.

69. Jugal, anterior process: (0) participates in the posterior edge of antorbital fenestra; (1) excluded from the antorbital fenestra by the lacrimal or maxilla (figs. 17, 20) (Clark et al., 2000; Olsen et al., 2000; Benton and Walker, 2002; Sues et al., 2003; Clark et al., 2004; Rauhut, 2003; Langer and Benton, 2006).

This character was used in many phylogenetic analyses of crocodylomorphs, but it is used here for the first time with a more inclusive grouping. Among non-archosaurian archosauriforms, *Proterosuchus* (NM QR 1484) is the only taxon to have the jugal participate in the antorbital fenestra. The jugal enters the antorbital fenestra in *Riojasuchus* (PVL 3827), *Gracilisuchus* (MCZ 4117), and some phytosaurs (e.g., *Mystriosuchus planirostris*; Hungerbühler, 2002). The jugal is clearly excluded from the antorbital fenestra in crocodylomorphs (Clark et al., 2000), *Postosuchus kirkpatricki* (TTU-P 9000), *Qianosuchus* (IVPP V 13899), *Turfanosuchus* (IVPP V 3237), *Saurosuchus* (PVL 2062), *Revueltosaurus* (PEFO 34561), *Aetosaurus* (SMNS 5770 S-16), and *Longosuchus* (TMM 31185-98). The condition is unclear in *Batrachotomus* and *Prestosuchus*.

Among avian-line archosaurs, the jugal clearly enters the antorbital cavity in *Dimorphodon* (BMNH R 1035), *Eudimorphodon* (MCNSB 2888), *Herrerasaurus* (PVSJ 407), the ornithischians included here, *Plateosaurus* (Yates, 2003), and *Efraasia* (Yates, 2003). The jugal does not enter into the antorbital fenestra in *Eoraptor* (PVSJ 512), *Coelophysis bauri* (CM 31394), *Dilophosaurus* (UCMP 37302), and *Allosaurus* (Madsen, 1976).

70. Jugal-quadratojugal, contact: (0) absent; (1) present (fig. 16) (new).

A jugal-quadratojugal contact is present in all archosauriforms plesiomorphically. In this analysis, the lower temporal bar is incomplete only in the outgroups *Mesosuchus* (Dilkes, 1998) and *Prolacerta* (Modesto and Sues, 2004). In these taxa, the posterior process of the jugal tapers, and the quadratojugal is a small bone attached to the lateral side of the quadrate.

71. Jugal, posterior process: (0) lies dorsal to the anterior process of the quadratojugal; (1) lies ventral to the anterior process of the quadratojugal; (2) splits the anterior process of the quadratojugal; (3) is split by the anterior process of the quadratojugal (figs. 17, 19–20) (new formulation).

This character scores how the jugal and the quadratojugal articulate. Within basal archosauriforms (e.g., *Erythrosuchus*, BP/1/5207; *Euparkeria*, SAM 5867; *Chanaresuchus*, PVL 4586), as well as in *Riojasuchus* (PVL 3827), *Batrachotomus* (SMNS 52970), *Arizonasaurus* (MSM P4590), *Qianosuchus* (IVPP V 13899), *Shuvosaurus* (TTU-P 9280), and *Prestosuchus* (UFRGS 0156-T), the jugal lies dorsal to the anterior process of the quadratojugal. In crocodylomorphs (e.g., *Dromicosuchus*, UNC 15574), *Postosuchus kirkpatricki* (TTU-P 9000), *Polonosuchus silesiacus* (ZPAL Ab III/563), and *Gracilisuchus* (MCZ 4117), the posterior portion of the jugal lies ventral to the quadratojugal. The jugal splits the quadratojugal into two processes (dorsal and ventral) in *Revueltosaurus* (PEFO 34561) and *Aetosaurus* (Schoch, 2007). In the previous three states, the jugal terminates in a point posteriorly. In state (3), the posterior portion of the jugal is forked where the anterior process of the quadratojugal splits the jugal into dorsal and ventral portions. This occurs in *Proterosuchus* (NM QR 1484) and in all dinosaurs examined here (Sereno and Novas, 1994).

72. Jugal, posterior termination: (0) anterior to or at the posterior extent of the lower temporal fenestra; (1) posterior to the lower temporal fenestra (figs. 17, 19) (new).

In most archosauriforms, the jugal terminates anteroventral to or at the posterior extent of the lower temporal fenestra. This includes *Euparkeria* (SAM 5867), *Arizonasaurus* (MSM P4590), *Batrachotomus* (SMNS 52970), *Prestosuchus* (UFRGS 0156-T), and most dinosaurs as examples. In contrast, the posterior process of the jugal in crocodylomorphs (e.g., *Sphenosuchus*, SAM 3014; *Alligator*), *Desmatosuchus* (TTU-P 9024), *Postosuchus kirkpatricki* (TTU-P 9000), and *Polonosuchus silesiacus* (ZPAL Ab III/563) lies well posterior of the lower temporal fenestra. State (1) is also in *Erpetosuchus* (AMNH FR 29300), *Gracilisuchus* (MCZ 4117), and *Pseudopalatus* (UCMP 34249).

73. Jugal, posterior border of the postorbital process: (0) concave; (1) convex (fig. 19) (new).

The posterior border of the postorbital process of the jugal is concave in nearly all basal archosauriforms. However, this portion of the jugal is markedly convex in *Sphenosuchus* (Walker, 1990), *Litargosuchus* (BP/1/5237), *Junggarsuchus* (IVPP V14010), and *Protosuchus haughtoni* (Gow, 2000; BP/1/4770).

74. Jugal, long axis of the body: (0) nearly horizontal; (1) anterodorsally inclined (fig. 17) (modified from Heckert and Lucas, 1999; Parker, 2007).

This character is rewritten for clarity from “jugal: not downturned (0) or downturned

(1)" (Heckert and Lucas, 1999). The original formation is vague and does not provide a strict point of reference. The long axis of the body of the jugal in most archosauriforms is horizontally oriented. In contrast, the aetosaurs *Longosuchus* (TMM 31185-98), *Desmatosuchus* (TTU-P 9024), and *Stagonolepis* (Walker, 1961) all have jugals with the long axis of the jugal significantly inclined. The jugals of *Lotosaurus* (IVPP V 131827), *Plateosaurus* (AMNH FR 6810), and *Efraasia* (Yates, 2003) are also anteriorly inclined.

75. Jugal, longitudinal ridge on the lateral surface of the body: (0) absent; (1) present and sharp; (2) present and rounded; (3) present and rounded, restricted to a bulbous ridge (figs. 16, 17, 19–20) (new).

Some archosauriforms (e.g., *Pseudopalatus*, UCMP 34249; *Riojasuchus*, PVL 3827; *Silesaurus*, Dzik, 2003) lack any kind of ridge on the jugal, whereas others have a distinct ridge. The ridge differs throughout Archosauriformes and is split into three morphologies. In *Ornithosuchus* (Walker, 1964), proterochampsians (e.g., *Chanaresuchus*, PVL 4647), *Herrerasaurus* (Sereno and Novas, 1994), and *Coelophysis bauri* (CM 31374), the jugal ridge is sharp. In aetosaurs (e.g., *Aetosaurus*, SMNS 5770), *Revueltosaurus* (PEFO 34561), *Batrachotomus* (Gower, 1999), *Saurosuchus* (PVSJ 32), *Hesperosuchus* "*agilis*" (CM 29894), *Sphenosuchus* (SAM 3014), and *Gracilisuchus* (MCZ 4117), the jugal has a low, rounded ridge dotted with small foramina. The jugals of *Rauisuchus* (BSP AS XXV-60-121), *Polonosuchus silesiacus* (ZPAL Ab III/563), and *Postosuchus kirkpatricki* (TTU-P 9000) have a bulbous ridge that is distinct from that of other archosaurs.

76. Quadrate: (0) does not contact prootic; (1) contacts prootic (fig. 23) (Walker, 1990; Clark et al., 2000; Olsen et al., 2000; Benton and Walker, 2002; Gower and Walker, 2002; Sues et al., 2003; Clark et al., 2004).

The head of the quadrate is separated by the squamosal from the prootic in all archosauriforms with the exceptions of crocodylomorphs and avians. In crocodylomorphs, part of the glenoid where the quadrate articulates is formed by the prootic. A small vertical ridge located near the prootic-paroccipital contact separates the quadrate articular surface from the rest of the prootic as demonstrated by Walker (1990) in *Sphenosuchus* (SAM 3014). An exceptional specimen (e.g., *Sphenosuchus*) or the complete prootic is needed in order to score this character. Quadrate-prootic contact is found in *Hesperosuchus agilis* (AMNH FR 6758), *Dibothrosuchus* (IVPP V 7907), *Kayentasuchus* (UCMP 131830), *Sphenosuchus* (SAM 3014), *Protosuchus richardsoni* (UCMP 130860), and *Alligator*.

77. Quadrate, dorsal head: (0) does not have a sutural contact with the paroccipital process of the opisthotic; (1) has a sutural contact with the paroccipital process of the opisthotic (new).

The head of the quadrate of most archosaurs articulates with the squamosal, or in some, the prootic. However, in phytosaurs (e.g., *Leptosuchus doughtyi*; AMNH FR 4919) the head of the quadrate has an interdigitating suture with the anterior surface of the paroccipital process. Part of the proximal portion of the quadrate attaches to the paroccipital process in *Alligator*, but this condition is not present in any of the other crocodylomorphs included here.

78. Quadrate, head: (0) partially exposed laterally; (1) completely covered by the squamosal (figs. 17–19) (Sereno and Novas, 1994; Juul, 1994; Novas, 1996; Benton, 1999; Langer and Benton, 2006).

As discussed and described by Sereno and Novas (1994) and Langer and Benton (2006), the head of the quadrate is laterally exposed in basal members of Dinosauria and *Lewisuchus* (UNLR 01). Additionally, the head of the quadrate is exposed in *Arizonasaurus* (MSM P4590; Nesbitt, 2005a), *Qianosuchus* (IVPP V 13899), *Turfanosuchus* (IVPP V 3237), *Euparkeria* (SAM 5867), *Saurosuchus* (PVSJ 32), *Batrachotomus* (Gower, 1999), *Revueltosaurus* (PEFO 34561), *Riojasuchus* (PVL 3827), *Proterosuchus* (NM QR 1484), *Chanaresuchus* (PVL 4575), *Tropidosuchus* (PVL 4601), aetosaurs (e.g., *Aetosaurus*, SMNS 5770 S-16), and in avian-line archosaurs examined in this study. When laterally exposed, the articulation of the head of the quadrate with the squamosal is clearly visible at the posterior end of the articulation. The anterior portion of the articulation is somewhat covered in some of the taxa (e.g., *Euparkeria*), whereas the posterior portion is clearly visible. The ventrally concave posterolateral margin of the squamosal frames the quadrate head in taxa scored as (0).

The squamosal, either the body or the ventral process, completely covers the head of the quadrate in taxa scored as (1). The squamosal covers the head of the quadrate in *Vancleavea* (GR 138), *Erythrosuchus* (Gower, 2003), *Postosuchus kirkpatricki* (TTU-P 9000), *Polonosuchus silesiacus* (ZPAL Ab III/563), *Rauisuchus* (BSP AS XXV-60-121), Crocodylomorpha (Benton and Clark, 1988), and *Gracilisuchus* (MCZ 4117).

79. Quadratojugal and quadrate, suture between the elements, foramen: (0) present; (1) absent (fig. 16) (modified from Parrish, 1991; Benton and Walker, 2002).

In most basal archosaurs, a foramen is present between the quadratojugal and quadrate. This is the case in non-archosaurian archosauriforms, *Postosuchus kirkpatricki* (TTU-P 9000), *Polonosuchus silesiacus* (ZPAL Ab III/563), phytosaurs (e.g., *Pseudopalatus*, UCMP 34249), *Batrachotomus* (SMNS 80260), *Desmatosuchus* (Small, 2002), *Stagonolepis* (Walker, 1961), *Arizonasaurus* (MSM P4590), *Prestosuchus* (UFRGS 0156-T), *Saurosuchus* (PVSJ 32), and in most avian-line archosaurs (*Silesaurus*, ZPAL Ab III/361; *Herrerasaurus*, PVSJ 407). In crocodylomorphs included here and *Aetosaurus* (Schoch, 2007), the foramen between the quadratojugal and quadrate is absent.

80. Quadrate, body: (0) without fenestrae; (1) fenestrated (fig. 19) (Clark et al., 2004).

In most basal archosauriforms, the quadrate is a solid bone without any fenestrae. The quadrates of *Protosuchus richardsoni* (UCMP 130860), *Protosuchus haughtoni* (BP/1/4746), *Orthosuchus* (SAM-PK-409), *Junggarsuchus sloani* (Clark et al., 2004), and *Alligator* have fenestrated quadrates. The circular fenestrations are numerous and small.

81. Quadrate, distal articular margin: (0) largely convex with corresponding concave articular surface of the articular; (1) largely concave with corresponding convex articular surface of the articular (fig. 21) (Nesbitt and Norell, 2006).

The quadrates of nearly all archosauriforms consist of a convex articular surface that fits into a corresponding concave surface in the articular. The opposite is true in *Effigia* (AMNH FR 30587) and *Shuvosaurus* (TTU-P 9280). In these taxa, the distal end of the quadrate is mostly concave, whereas the articular is convex (Nesbitt, 2007). *Lotosaurus* (IVPP V 48013) has an intermediate condition where the quadrate is convex anteroposteriorly but concave mediolaterally in posterior view; given that it was still largely convex, it was scored as (0).

82. Quadrate, angled: (0) posteroventrally or vertical; (1) anteroventrally (fig. 17) (Nesbitt, 2007).

The quadrates of most archosauriforms slope posteroventrally. In *Effigia* (AMNH FR 30587), *Shuvosaurus* (TTU-P 9280), *Aetosaurus* (Schoch, 2007), *Stagonolepis* (Walker, 1961), *Desmatosuchus* (Small, 2002), spinosaurids, and ornithomimid theropods (Rauhut, 2003), the quadrate slopes anteroventrally (Nesbitt, 2007).

83. Quadrate, dorsoventrally oriented crest located on the posterior side:(0) absent; (1) present (fig. 21) (new).

The posterior surface of the quadrate is smooth in nearly all archosauriforms. *Polonosuchus silesiacus* (ZPAL Ab III/563) and *Postosuchus kirkpatricki* (TTU-P 9000) have a rugose, dorsoventral crest located on the posterior side of the quadrate just ventral to the quadrate/quadratojugal foramen. This crest slightly arcs medially and creates a concave surface that opens medially.

84. Pterygoid-ectopterygoid, articulation: (0) ectopterygoid ventral to pterygoid; (1) ectopterygoid dorsal to pterygoid (Sereno and Novas, 1994; Novas, 1996; Benton, 1999; Irmis et al., 2007a).

Sereno and Novas (1994) thoroughly discussed this character and their dichotomy remained robust in subsequent analyses. As stated by Sereno and Novas (1994), all three groups of dinosaurs have state (1) ancestrally. The ectopterygoid articulates on the ventral portion of the pterygoid in non-archosaurian archosauriforms and pseudosuchians.

85. Palatine-pterygoid, fenestra: (0) absent; (1) present (Sereno, 1991a).

Following Sereno (1991a), character state (1) is only present in *Ornithosuchus* (BMNH R 3143) and *Riojasuchus* (PVL 3827).

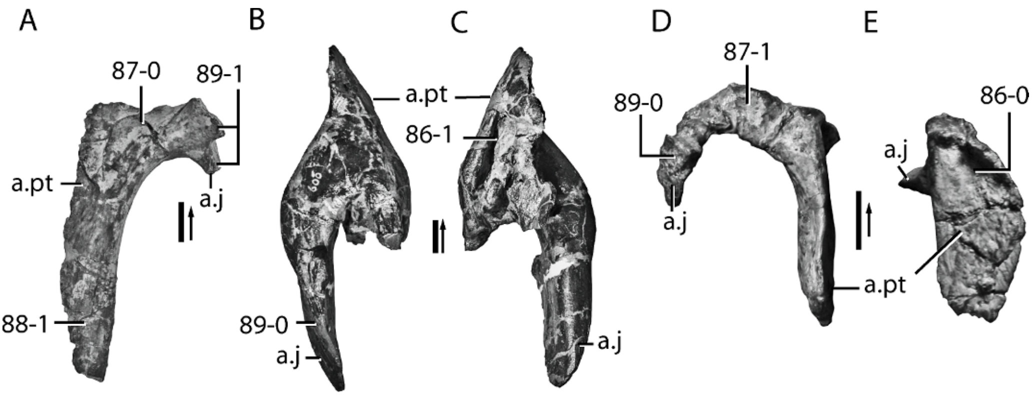


Fig. 22. Archosaur ectopterygoids: **A,** the right ectopterygoid of *Postosuchus kirkpatricki* (TTU-P 9002) in dorsal view; **B,** the left ectopterygoid of *Allosaurus fragilis* (AMNH FR 600) in dorsal and **C,** ventral view; **D,** the left ectopterygoid of *Plateosaurus engelhardti* (AMNH FR 6810) in posterodorsal and ventral **E,** view. Arrow indicates anterior direction. Numbers refer to character states. See appendix for anatomical abbreviations. Scale bars = 1 cm.

86. Ectopterygoid, ventral recess: (0) absent; (1) present (fig. 22) (Gauthier, 1986; Langer and Benton, 2006).

An ectopterygoid recess was cited as a theropod synapomorphy (Gauthier, 1986), and as a character uniting *Eoraptor* with theropods (Sereno, 1999; Langer and Benton, 2006). However, I disagree with Sereno (1999) and Langer and Benton (2006) about the scoring of *Eoraptor* and basal dinosaurs. The ectopterygoid articulates with the dorsal surface of the lateral flange of the pterygoid in dinosaurs (character 84). As a result, the ventral surface of the ectopterygoid has a slight depression for the articulation with the pterygoid. In *Allosaurus* and other tetanurans, there is a distinct recess (possibly pneumatic) *and* a depression for the pterygoid. The ectopterygoids of *Plateosaurus* (AMNH FR 6810), *Eoraptor* (PVSJ 512), *Liliensternus* (MB R. 2175; Rauhut, 2003: fig. 19B), and *Coelophysis* (AMNH FR 7239) possess only a facet for the pterygoid and lack a distinct recess. Yates (2003) described a deep fossa in the ectopterygoid of the basal sauropodomorph *Pantydraco*. This depression is only the articular face with the pterygoid, not a distinct fossa as in *Allosaurus*. Furthermore, any slight disarticulation of the ectopterygoid from the pterygoid may look like a distinct recess; I urge caution when scoring this character.

Langer and Benton (2006) stated that a ventral recess is present in *Sphenosuchus*. However, this slight depression is very different from that of theropods. Therefore, it is scored as (0).

87. Ectopterygoid, body: (0) arcs anteriorly; (1) arcs anterodorsally (fig. 22) (new).

The body of the ectopterygoid connects the jugal with the pterygoid. In non-archosaurian archosauriforms and crocodylian-line archosaurs, the ectopterygoid arches anteriorly between the articulations. In dinosaurs, the ectopterygoid arches anteriorly and dorsally between the articulations. This is true of *Heterodontosaurus* (SAM-PK-1332), *Coelophysis bauri* (CM 31374), and *Plateosaurus* (AMNH FR 6810). This also appears to be the state in *Lewisuchus* (UNLR 01).

88. Ectopterygoid: (0) does not form or forms some of the lateral edge of the lateral pterygoid flange; (1) forms all of the lateral edge of the lateral pterygoid flange (fig. 22) (Dilkes, 1998; Nesbitt et al., 2009a).

The ectopterygoid attaches to only the anterolateral corner of the lateral pterygoid flange in *Mesosuchus* (SAM 6536) and in *Prolacerta* (UCMP 37151), whereas the ectopterygoids of *Proterosuchus* + Archosauria (= Archosauriformes) lie along the entire lateral pterygoid flange.

89. Ectopterygoid: (0) single headed; (1) double headed (figs. 21–22) (Weinbaum and Hungerbühler, 2007).

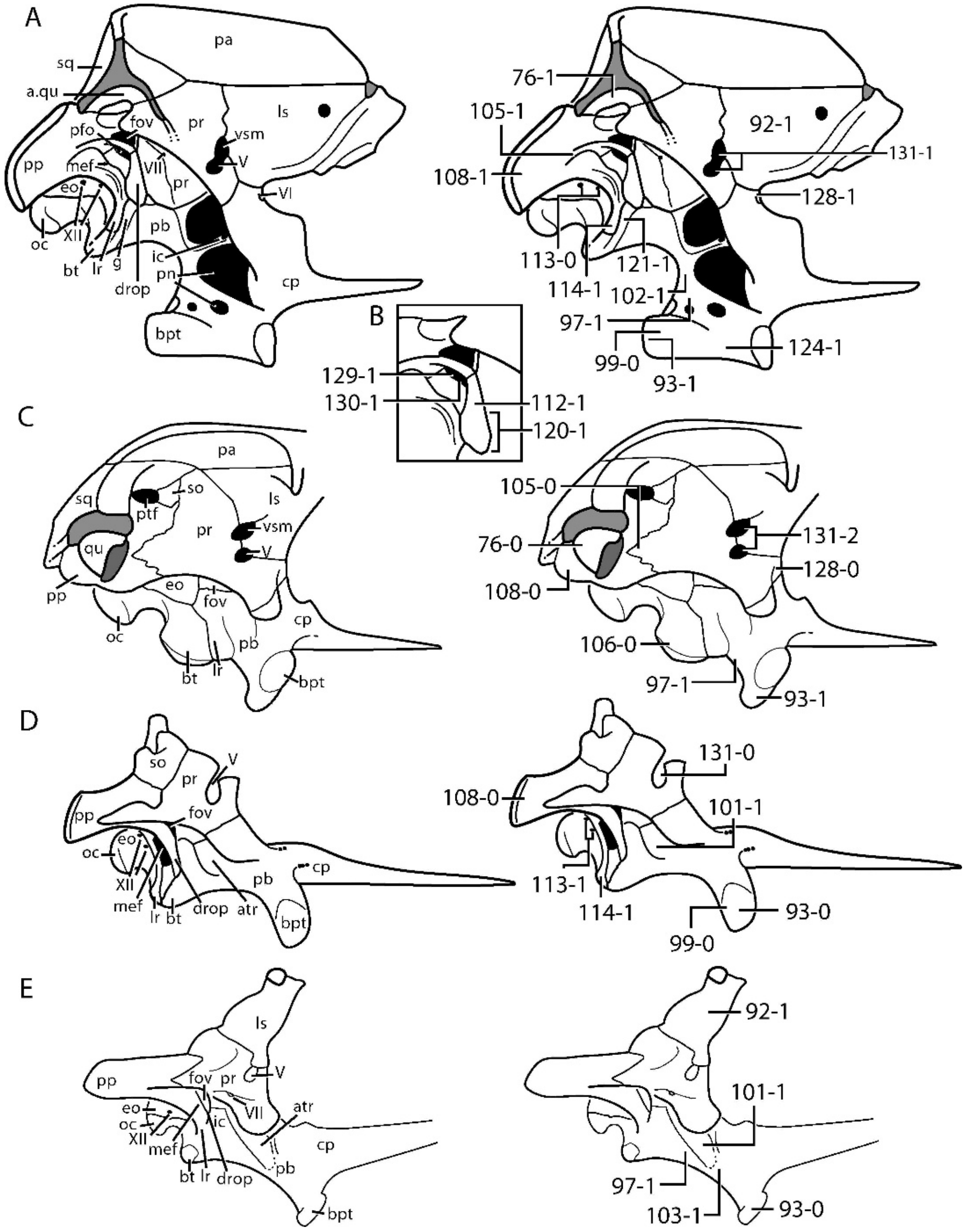


Fig. 23. The braincase of basal archosaurs in lateral view: **A,** reconstruction of the braincase of *Sphenosuchus acutus*; redrawn from Walker (1990); **B,** close-up of the ear region of *Sphenosuchus acutus*; redrawn from Walker (1990); **C,** reconstruction the braincase of *Stagonolepis robertsoni*; redrawn from Walker (1990); **D,** reconstruction the braincase of *Silesaurus opolensis*; redrawn from Dzik (2003); **E,** reconstruction the braincase of *Coelophysis rhodesiensis*; redrawn from Raath (1969). Numbers refer to character states. See appendix for anatomical abbreviations.

As described by Weinbaum and Hungerbühler (2007), the ectopterygoids of most archosauriforms possess a single lateral head that articulates with the jugal into a single socket. In *Postosuchus kirkpatricki* (TTU-P 9002), *Polonosuchus silesiacus* (ZPAL Ab III/563), *Batrachotomus* (Gower, 1999), *Hesperosuchus "agilis"* (YPM 41198), and *Sphenosuchus* (SAM 3014), the head of the ectopterygoid is split into two, a larger ventral head and a smaller posterodorsal head. A well-defined groove splits the two heads; a groove splits two articular facets of the jugal for the ectopterygoid in taxa with state (1). Therefore, this character can be scored if either the medial side of the jugal or the lateral head of the ectopterygoid is visible.

90. Palatine, fossa on the dorsal surface: (0) extends far anteriorly, near the pila postchoanalis; (1) does not extend very far anteriorly along the upper surface of the palatine (fig. 21) (Witmer, 1997; Gower and Walker, 2002).

As discussed by Gower and Walker (2002), Witmer (1997) recognized two basic types of palatine morphology with respect to the extent of the dorsal fossa for attachment of the dorsal part of the M. pterygoideus. The dorsal fossa extends far anteriorly, up to the posterior border of the internal choana in non-archosaurian archosauriforms, phytosaurs (Witmer, 1997b), *Ornithosuchus* (Walker, 1964; Witmer, 1997), *Batrachotomus kupferzellensis* (Gower, 1999), and *Saurosuchus galilei* (Alcober, 2000). The dorsal fossa is shifted more posteriorly, so that there is a flat surface between the posterior edge of the choana and the fossa, and this was cited as present in *Sphenosuchus acutus* (Walker, 1990; Witmer, 1997) and aetosaurians (e.g., *S. robertsoni*, Walker, 1961; Witmer, 1997). The condition is aetosaurs deserves more comment. The palatine is foreshortened in aetosaurs making it difficult to compare to other crocodylian-line archosaurs. Nevertheless, the fossa in *Stagonolepis* is separated from the internal choana by a space much greater than that in *Batrachotomus kupferzellensis* (Gower, 1999). Not all aetosaurs have state (1), as demonstrated by *Longosuchus* (TMM 31185–98); there is a large gap between the choana and the dorsal fossa. The space between the fossa and the internal choana in *Polonosuchus silesiacus* (ZPAL Ab III/543) is great like that of *Sphenosuchus* (SAM 3014) and *Hesperosuchus "agilis"* (YPM 41198). The distribution of this character is more complex in Crocodylomorpha than was stated previously. The palatines of *Terrestrisuchus* (BMNH R7593) and *Protosuchus richardsoni* (UCMP 130860) have a fossa and posterior border of the internal choana that is separated only by a thin ridge.

91. Palatine, posterior margin of the choana: (0) smooth, no raised rim on ventral surface; (1) raised rim defining a fossa around the choana on the ventral surface (= spout of Walker, 1990) (fig. 21) (new).

In most archosauriforms, the ventral margin of the choana is unmarked on the ventral surface of the palatine. This is the condition present in *Euparkeria* (SAM 13664), *Saurosuchus* (PVSJ 32), *Stagonolepis* (Walker, 1961: fig. 3A), *Batrachotomus* (Gower, 1999), and *Plateosaurus* (AMNH FR 6810). In *Polonosuchus silesiacus* (ZPAL Ab III/563), *Sphenosuchus* (SAM 3014), *Dibothrosuchus* (IVPP V 7907), and *Kayentasuchus* (UCMP 131830), the posterior border of the choana is marked by a distinct raised ridge on the ventral surface.

92. Laterosphenoid: (0) absent; (1) present (fig. 23) (Gauthier et al, 1988; Benton and Clark, 1988; Parrish, 1992; Clark, 1993; Juul, 1994; Bennett, 1996; Nesbitt et al., 2009a).

The laterosphenoid of archosauriforms was well described by Clark (1993). An ossified laterosphenoid is clearly absent in *Prolacerta* and present in all archosauriforms examined here. A laterosphenoid is clearly present in the proterochampsian *Chanaresuchus* (PVL 4575).

93. Basipterygoid, processes directed: (0) anteriorly or ventrally at their distal tips; (1) posteriorly at their distal tips (fig. 23) (new).

This character scores the direction of the ventral tips of the basipterygoid processes. The tips point anteriorly in *Silesaurus* (Dzik, 2003), *Marasuchus* (PVL 3870), *Plateosaurus* (AMNH FR 6810), *Coelophysis bauri* (AMNH FR 7239), *Prolacerta* (BPI 2675), *Effigia* (AMNH FR 30587), *Shuvosaurus* (TTU-P 9282), *Charanesuchus* (PVL 4647), and they point posteriorly in *Proterosuchus* (BPI 3993), *Postosuchus kirkpatricki* (TTU-P 9002), *Batrachotomus* (SMNS 80260), *Saur-*

osuchus (PVSJ 32), *Arizonasaurus* (MSM P4590), *Sphenosuchus* (SAM 3014), *Dibothrosuchus* (IVPP V 7907), *Revueltosaurus* (PEFO 34561), aetosaurs (e.g., *Aetosaurus*, SMNS 5770), and phytosaurs (e.g., *Pseudopalatus pristinus*, UCMP 34249; *Smilosuchus*, UCMP 27200). The distribution of this character is not straightforward, but it may support small clades.

94. Prootic, ridge on lateral surface of inferior anterior process ventral to the trigeminal foramen: (0) present; (1) absent (Gower and Sennikov, 1996; Nesbitt et al., 2009a).

Prolacerta (Gow, 1975), *Mesosuchus* (SAM 8552), and *Proterosuchus* (Gow, 1975) are scored as having a ridge on the lateral surface of the inferior anterior prootic process below the trigeminal foramen. Originally, Gower and Sennikov (1996) scored *Euparkeria* as having a small ridge (0), but after examining other *Euparkeria* specimens, Gower and Weber (1998) considered the small ridge a preservational artifact of the specimen originally scored (UMZC T692). Therefore, *Euparkeria* is scored as (1). The character is scored as absent (1) in *Erythrosuchus* (Gower, 1997), *Chanaresuchus* (MCZ 4036), *Vancleavea* (GR 138), and Archosauria. This character cannot be scored in *Tropidosuchus*.

95. Parabasisphenoid, foramina for entrance of cerebral branches of internal carotid artery into the braincase positioned on the surface: (0) ventral; (1) posterolateral; (2) anterolateral (fig. 24) (modified from Parrish, 1993; Gower and Sennikov, 1996; Gower, 2002; Nesbitt et al., 2009a).

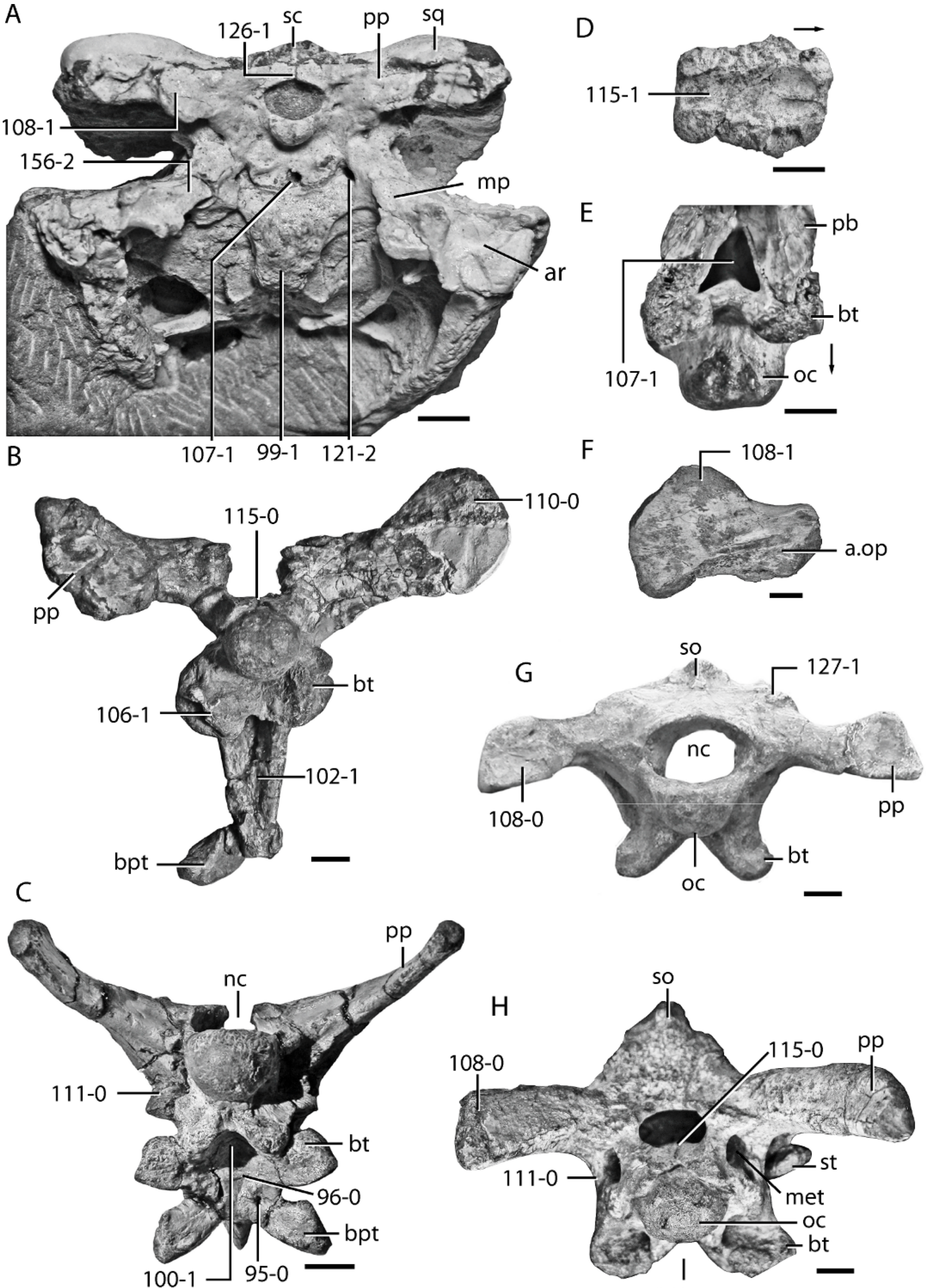
The internal carotids enter the basisphenoid ventrally in *Mesosuchus* (SAM 6536; Dilkes, 1998), *Prolacerta* (BP/1/2675; Evans, 1988), *Proterosuchus* (BP/1/3993; Gow, 1975), *Erythrosuchus* (BMNH R3592; Gower, 1997), *Euparkeria* (UMZC T692; Gower and Weber, 1998), and in the proterochampsians *Tropidosuchus* (PVL 4604) and *Chanaresuchus* (PVL 4647). Parrish (1993) reported that *Proterochampsa* (MCZ 3408) had both a ventral and a lateral entrance, and that is not confirmed nor denied here; however, all other proterochampsian specimens examined by myself have the internal carotids entering from the ventral surface.

Gower (2002) rephrased the original character formation from Parrish (1993) and Gower and Sennikov (1996) in his character set focusing on crocodylian-line archosaur relationships. The wording of Gower (2002) is preferred except for the plesiomorphic entrance of the internal carotids into the braincase. Here, instead of posterior, I use ventral to describe state (0). As explained by Gower (2002), the foramina are located on the lateral surface of the parabasisphenoid just anterior to the notches between the basal tubera and basipterygoid processes in phytosaurs. In phytosaurs, the entrance lies between the notch between the basipterygoid tubera and basitubera (*Pseudopalatus pristinus* UCMP 137319). Gower (2002) hypothesized that this is intermediate between character state (0) and (1), and therefore ordered the character. However, given that the possible crown-group archosaur *Turfanosuchus* (Parrish, 1993; Wu and Russell, 2001), the suchian *Arizonasaurus* (Gower and Nesbitt, 2006), and the dinosauriform *Silesaurus* (Dzik, 2003; Ab III 364/4) have a ventral entrance of the internal carotids, it is not clear that the difference in the entrances of phytosaurs and most suchians are homologous.

Among the dinosauromorphs, the internal carotids enter from the anterolateral portion of the parabasisphenoid like that of suchians. In *Silesaurus* (ZPAL Ab III 364/4), the foramina for the entrance of the cerebral branches of the internal carotid artery into the braincase are positioned on the ventral surface.

96. Parabasisphenoid, plate: (0) present and straight; (1) present and arched anteriorly; (2) absent (fig. 24) (modified from Gower and Sennikov, 1996; Nesbitt et al., 2009a).

The basisphenoid plate is an anterodorsally/posteroventrally compressed plate of bone that lies between the basitubera of the parabasisphenoid (Gower and Sennikov, 1996; Gower, 2002). A plate is not present in *Mesosuchus* (SAM 6536), but it is present in *Prolacerta* (BP/1/2675), *Proterosuchus* (BP/1/3993), and *Erythrosuchus* (Gower and Sennikov, 1996). In these taxa the plate is straight. Here, I score *Tropidosuchus* (PVL 4604), *Chanaresuchus* (PVL 4647), and *Euparkeria* (SAM 5867) as having a parabasi-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sphenoid plate (the basisphenoid/parabasisphenoid plate is scored in *Euparkeria* as absent in Gower and Weber, 1998). In these taxa, a thin lamina of bone connects the basitubera of the parabasisphenoid like that of taxa scored as (0). However, in proterochampsians and *Euparkeria* the thin lamina arcs anteriorly at the midline. In phytosaurs, crocodylian-line archosaurs, and dinosauriforms, a distinct basisphenoid/parabasisphenoid plate is not present. In some phytosaur taxa (e.g., AMNH FR 30646) scored as (2), a ridge created by both the parabasisphenoid and the basioccipital connects the basitubera. A low ridge may be present between the basitubera in taxa; however, this ridge differs from taxa scored as (0) and (1), and thus these features are not considered homologous.

A thin, arched plate of bone is present in *Arizonasaurus* (MSM P4590) and *Xilousuchus* (IVPP V 6026).

97. Parabasisphenoid, orientation: (0) horizontal; (1) more vertical (fig. 23) (Gower and Sennikov, 1996; Nesbitt et al., 2009a).

Mesosuchus (SAM 6536; Dilkes, 1998), *Prolacerta* (BP/1/2675; Evans, 1988), and *Proterosuchus* (BP/1/3993; Gow, 1975) have horizontal basisphenoids; the base of the basitubera and the base of the basipterygoid processes are about the same horizontal level. Verticalized basisphenoids, with the base of the basitubera more dorsal than the base of the basipterygoid processes, are present in *Erythrosuchus* (BMNH R3592; Gower, 1997), *Euparkeria* (UMZC T692), *Tropidosuchus* (PVL 4604), *Chanaresuchus* (PVL 4647), and most of Archosauria (Gower and Sennikov, 1996).

98. Parabasisphenoid, semilunar depression on the lateral surface of the basal tubera: (0) present; (1) absent (Gower and Sennikov, 1996; Nesbitt et al., 2009a).

This character is present in all non-archosaurian archosauriforms including *Chanaresuchus* (PVL 4647). As Gower and Sennikov (1996) reported, this character is absent in crown-group Archosauria.

99. Parabasisphenoid, basipterygoid processes: (0) present; (1) absent (figs. 23–24) (Clark et al., 2000; Olsen et al., 2000; Benton and Walker, 2002; Sues et al., 2003; Clark et al., 2004).

Basipterygoid processes are present in most archosauriforms. In crocodyliforms, the basipterygoid processes are absent (Clark et al., 2000).

100. Parabasisphenoid, recess (= median pharyngeal recess of some authors = hemispherical sulcus = hemispherical fontanelle): (0) absent; (1) present (fig. 24) (modified from Nesbitt and Norell, 2006).

A depression on the ventral surface of the parabasisphenoid is common among basal archosauriforms. Among non-archosaurians, a depression is absent in *Prolacerta* (BPI 2675), *Proterosuchus* (BPI 3993), *Erythrosuchus* (BMNH R3592), *Chanaresuchus* (PVL 4546), and *Euparkeria* (SAM 7696). Phytosaurs (e.g., *Pseudopalatus pristinus*, UCMP 137319) also do not have a recess in the parabasisphenoid. The ornithosuchid *Riojasuchus* (PVL 3827) possesses a shallow recess, as do the aetosaurs *Longosuchus* (TMM 31185–98), *Desmatosuchus smalli* (Small, 2002; Parker, 2005), *Tecovasuchus* (TTU-P 545 Martz and Small, 2006), *Aetosaurus* (SMNS 5770 S-16; Schoch, 2007), *Typothorax* (MCZ 1488), and *Coahomasuchus* (Desojo and Heckert, 2004). Among other crocodylian-line archosaurs, *Arizonasaurus* (MSM P4590), *Shuvosaurus* (TTU-P 9282), and *Effigia* (AMNH FR 30587) have deep and elongated recesses. Alcober (2000) described the deep recess in *Saurosuchus* (PVSJ 32) as the "eustachian foramen," so it is

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Fig. 24. The posterior portion of the braincase of basal archosaurs: **A,** back of the skull of *Protosuchus richardsoni* (UCMP 131827), posterior view; **B,** braincase of *Postosuchus kirkpatricki* (TTU-P 9002), posterior view; **C,** braincase of *Xilousuchus sapingensis* (IVPP V 6026), posterior view; **D,** basioccipital of *Effigia okeeffeae* (AMNH FR 30587), dorsal view; **E,** basiocciptial of *Sphenosuchus acutus* (SAM 3014), ventral view; **F,** paroccipital process of *Postosuchus alisonae* (UNC 14475), anterior view; **G,** braincase of *Lewisuchus admixtus* (UNLR 001), posterior view; **H,** braincase of *Proterosuchus* (NM QR 880), posterior view. Arrow indicates anterior direction. Numbers refer to character states. See appendix for anatomical abbreviations. Scale bar = 1 cm.

unclear whether there is a true opening here for a eustachian tube and whether the recess is subdivided. The fossa is blind in all non-crocodylomorph pseudosuchians observed in this study. The undivided recess is very deep in *Postosuchus kirkpatricki* (TTU-P 9002; UCMP 138843) and *Tikisuchus* (ISI 305). Both *Sphenosuchus* (SAM 3014; Gower, 2002) and *Dibothrosuchus* (IVPP V 7907) have a deep trough like that of *Postosuchus kirkpatricki* (TTU-P 9002), but they also have a deep divided recess entirely within the basioccipital. Only the recess of the parabasisphenoid is scored here. The recess is subdivided in *Batrachotomus* (SMNS 80260; Gower, 2002). The crocodyliforms used here (e.g., *Protosuchus richardsoni*, UCMP 131827) lack a depression in the parabasisphenoid. The depression in the parabasisphenoid of taxa scored as (1) is not homologous with that of the median pharyngeal recess of crocodyliforms (see below).

Among dinosauromorphs, the recess is absent in *Marasuchus* (PVL 3870), but a shallow recess is present in *Silesaurus* (ZPAL Ab III 364/4). Among dinosaurs, basal ornithischians (e.g., *Lesothosaurus*, Sereno, 1991b), *Herrerasaurus* (PVSJ 407), and sauropodomorphs (e.g., *Plateosaurus*, AMNH FR 6810) lack a recess, whereas a recess is clearly present in theropods (e.g., *Coelophysis bauri*, AMNH FR 7239). Rauhut (2003) noted that many theropods with parabasisphenoid recesses have midline subdivisions (e.g., *Coelophysis rhodesiensis*). Witmer (1997) considered this recess pneumatic.

101. Parabasisphenoid, anterior tympanic recess on the lateral side of the braincase: (0) absent; (1) present (fig. 23) (Makovicky and Sues, 1998; Rauhut, 2003).

The presence of an anterior tympanic recess was found as a synapomorphy of Neotheropoda by Rauhut (2003). The recess is located on the lateral side of the basisphenoid just anteroventral to the fenestra ovalis. The recess typically preserves smaller fossae within it suggesting it may be pneumatic (Chure and Madsen, 1996; Witmer, 1997; Makovicky and Sues, 1998; Rauhut, 2003, 2004). Rauhut (2003) scored an anterior tympanic recess absent in dinosauriforms, ornithischians, and *Herrerasaurus* and present in the basal theropods *Dilophosaurus*, *Coelophysis rhodesiensis*, and *Piatnitzkysaurus*, as well as in other theropods. However, the lateral wall of the braincase of *Silesaurus* (ZPAL Ab III/361/4), *Lewisuchus* (Romer, 1972d), *Heterodontosaurus* (SAM-PK-1332), *Eocursor* (SAM-PK-0925), and *Plateosaurus* (AMNH FR 6810) has a feature that I cannot differentiate from that of basal theropods. Therefore, I score these taxa as (1). None of these taxa, though, have smaller "pneumatic" depressions within them.

Among basal archosauriforms and basal crocodylian-line archosaurs, an anterior tympanic recess is not present. As discussed by Gower and Weber (1998), *Euparkeria* does not have an anterior tympanic recess (contra Welman, 1995). *Sphenosuchus* has large pneumatic cavities in the same region (pre- and postcarotid recesses) as do other crocodylomorphs (Walker, 1990). Gower and Weber (1998), followed by Rauhut (2003), rightfully showed that the anterior tympanic recess of theropods is not homologous with that of crocodylomorphs. For a similar interpretation of this character for crocodylomorphs see Clark et al. (2000), character 22. Here, crocodylomorphs are scored as inapplicable.

102. Parabasisphenoid: (0) relatively short dorsoventrally; (1) substantially elongated in the region between the basal tubera and the basipterygoid processes, such that the "median pharyngeal recess" is dorsoventrally extended and troughlike (figs. 23–24) (Parrish, 1993; Gower, 2002).

Character state (1) is clearly present in *Postosuchus kirkpatricki* (TTU-P 9002) and *Tikisuchus* (ISI 305) but absent in aetosaurs, *Batrachotomus* (Gower, 2002), *Saurosuchus* (Alcober, 2000), and *Arizonasaurus* (MSM P4590). Parrish (1993) used this character to unite *Batrachotomus*, *Gracilisuchus*, *Postosuchus*, and *Dibothrosuchus*. Gower (2002) clearly showed that *Batrachotomus* lacks state (1) but explicitly stated that state (1) is not present in any crocodylomorph. Here, I disagree with Gower (2002) and hypothesize that the elongated parabasisphenoid of *Sphenosuchus* (SAM 3014) and *Dibothrosuchus* (IVPP V 7907) is homologous with that of *Postosuchus kirkpatricki* (TTU-P 9002) and

Tikisuchus (ISI 305). These taxa all share a blind trough that is anteroventrally elongated in an identical way. The parabasisphenoid of *Gracilisuchus* (MCZ 4117), although elongated, is not ventrally elongated; therefore, it is scored as (0).

103. Parabasisphenoid, between basal tubera and basipterygoid processes: (0) approximately as wide as long or wider; (1) significantly elongated, at least 1.5 times longer than wide (fig. 23) (Rauhut, 2003; Nesbitt, 2007).

The parabasisphenoids of *Effigia* (AMNH FR 30587) and *Shuvosaurus* (TTU-P 9282) are elongated relative to those of other crocodylian-line archosaurs (Nesbitt, 2007) as well as those of *Coelophysis bauri* (AMNH FR 7239) and *Coelophysis rhodesiensis* (QG 195) (Rauhut, 2003). This character is scored as inapplicable for crocodylomorphs and *Postosuchus kirkpatricki* to avoid the possible correlation with character 102.

104. Basitubera: (0) clearly separated; (1) medially expanded and nearly or completely connected (fig. 24) (new).

The basitubera of nearly all archosauriforms are clearly separated medially by a U-shaped gap. Taxa with a basisphenoid/parabasisphenoid plate are not scored as (1) because the basitubera do not expand medially. In the phytosaurs *Smilosuchus* (UCMP 27200) and *Pseudopalatus* (NMMNH P31292) the basitubera merge medially and are scored (1).

105. Prootic-opisthotic, contact: (0) broad overlap; (1) reduced to a small contact (fig. 23) (modified from Clark et al., 2000; Olsen et al., 2000; Benton and Walker, 2002; Sues et al., 2003; Clark et al., 2004).

Although this character is not quantified, it does represent a discrete change within crocodylian-line archosaurs. In non-archosaurian archosauriforms, basal dinosauromorphs, and most crocodylian-line archosaurs, the posterolateral process of the prootic makes broad contact with the opisthotic, thus forming part of the paroccipital process. This is not true of the crocodylomorph *Sphenosuchus* (fig. 28 of Walker, 1990), where the prootic contacts the opisthotic only on a short surface. Clark et al. (2000) also scored *Dibothrosuchus*, *Protosuchus*, and *Alligator* as (1) for this character, and those scorings are accepted here.

106. Basioccipital, portion of the basal tubera: (0) rounded and anteroposteriorly elongated; (1) bladelike and anteroposteriorly shortened (figs. 23–24) (new).

In most archosauriforms, the basioccipital portion of the basal tubera is rugose, rounded, and anteroposteriorly thick. This is exemplified by *Revueltosaurus* (PEFO 34561), the phytosaur *Smilosuchus* (UCMP 27200), the aetosaur *Stagonolepis* (MCZD 2–4), *Erythrosuchus* (BMNH R3592), and *Herrerasaurus* (PVSJ 409). In *Saurosuchus* (PVSJ 32), *Batrachotomus* (SMNS 80260), *Postosuchus kirkpatricki* (TTU-P 9002), *Hesperosuchus agilis* (AMNH FR 6758), *Sphenosuchus* (SAM 3014), *Dibothrosuchus* (IVPP V 7907), *Protosuchus richardsoni* (UCMP 131827), and *Alligator*, the basioccipital portion of the basal tubera is bladelike and anteroposteriorly shortened compared with that of the other basal archosaur taxa.

107. Basioccipital, deep recess on the ventral surface: (0) absent; (1) present (fig. 24) (new).

In most archosauriforms, the ventral surface of the basioccipital is smooth and does not bear a fossa. In the basal crocodylomorphs *Sphenosuchus* (SAM 3014) and *Dibothrosuchus* (IVPP V 7907), there is a clear recess within the basioccipital that is divided by a lamina located at the midline. This is a different depression than that of the parabasisphenoid recess (= hemispherical sulcus = hemispherical fontanelle) described above. The depression of the parabasisphenoid is restricted to that element. It is clear that a basioccipital recess is not present in aetosaurs (*Aetosaurus*, SMNS 5770), *Saurosuchus* (PVSJ 32), *Arizonasaurus* (MSM P4590), *Batrachotomus* (SMNS 80260), *Postosuchus kirkpatricki* (TTU-P 9002), *Tikisuchus* (ISI 305; Gower, 2002), or the crocodylomorph *Hesperosuchus agilis* (AMNH FR 6758). There is a recess in *Terrestrisuchus* (BMNH P62/20), but it is not clear whether it is subdivided. A foramen in *Protosuchus richardsoni* (UCMP 131827) and *Orthosuchus* (SAM-PK-409) is present in the same position as the opening in *Sphenosuchus* (SAM 3014) and *Dibothrosuchus* (IVPP V 7907). The foramen in *Protosuchus richardsoni*

(UCMP 131827) and *Orthosuchus* is mostly within the basioccipital, but the parabasisphenoid creates a sliver of the anteroventral border. In *Alligator*, a homologous foramen (= median pharyngeal recess) is almost entirely within the parabasisphenoid.

108. Opisthotic, paroccipital processes: (0) no or slight dorsal and ventral expansion distally; (1) markedly expanded dorsally at the distal ends (figs. 23–24) (character states reversed from Clark et al., 2000; Olsen et al., 2000; Benton and Walker, 2002; Sues et al., 2003; Clark et al., 2004).

In most archosauriforms, the paroccipital processes have nearly parallel dorsal and ventral margins or they gradually expand both dorsally and ventrally at their distal ends. This character state is present in non-archosaurian archosauriforms, phytosaurs, aetosaurs (e.g., *Aetosaurus* SMNS 5770 S-5), *Gracilisuchus* (MCZ 4117), *Saurosuchus* (PVSJ 32), *Batrachotomus* (SMNS 80260), *Arizonasaurus* (MSM P4590), *Riojasuchus* (PVL 3827), and basal avian-line archosaurs. In contrast, the distal ends of the paroccipital processes of *Postosuchus kirkpatricki* (TTU-P 9000), *Postosuchus alisonae* (UNC 15575), *Tikisuchus* (Chatterjee and Majumdar, 1987), and the crocodylomorphs *Sphenosuchus* (SAM 3014), *Terrestrisuchus* (Crush, 1984), *Litargosuchus* (BP/1/5237), *Hesperosuchus* (CM 29894), *Dibothrosuchus* (IVPP 7907), *Orthosuchus* (SAM-PK-409), and *Protosuchus richardsoni* (UCMP 131827) have marked dorsally expanded distal ends. In *Alligator*, the paroccipital processes are like those of taxa scored as (0). Clark et al. (2000) used a similar character, but did not differentiate the conditions in *Stagonolepis* and *Gracilisuchus* from those in *Postosuchus* and crocodylomorph taxa such as *Sphenosuchus*.

109. Opisthotic, extent of the lateral margin of the paroccipital: (0) lateral to the upper temporal fenestra; (1) at the margin or medial to the lateral extent of the upper temporal fenestra (fig. 18) (new).

In most archosauriforms, the paroccipital expands to meet the posteromedial portion of the squamosal lateral to the upper temporal fenestra. This is retained in the basal crocodylomorphs *Hesperosuchus* “*agilis*” (CM 29894), *Dromicosuchus* (UNC 15574), *Sphenosuchus* (SAM 3014), and *Dibothrosuchus* (IVPP V7907), whereas in *Litargosuchus* (BP/1/5237), *Kayentasuchus* (UCMP 131830), *Orthosuchus* (SAM-K-409), and *Protosuchus* (AMNH FR 3016), the lateral edge of the paroccipital process is at the margin or medial to the lateral extent of the upper temporal fenestra.

110. Opisthotic, paroccipital processes: (0) directed laterally or dorsolaterally; (1) directed ventrolaterally (fig. 24) (Rauhut, 1997, 2003; Hwang et al., 2004; Smith et al., 2007).

As pointed out by Rauhut (2003), the distal ends of the paroccipital processes of most archosauriforms are laterally or dorsally directed. Among avian-line archosaurs, pterosaurs, *Silesaurus*, and ornithischians also have paroccipital processes that are either laterally or dorsally directed. In saurischians, such as *Herrerasaurus* (PVSJ 407), *Coelophysis bauri* (AMNH FR 7239), and *Plateosaurus* (AMNH FR 6810), the paroccipital processes are directed ventrally at the distal ends.

111. Opisthotic, ventral ramus (= crista interfenestralis): (0) extends further laterally than lateralmost edge of exoccipital in posterior view; (1) covered by the lateralmost edge of exoccipital in posterior view (fig. 24) (Gower, 2002).

As explained by Gower (2002), the ventral ramus of the opisthotic extends further laterally than that of the exoccipital plesiomorphically within archosauriforms. In some aetosaurs (e.g., *Longosuchus*, TMM 31185–97) and crocodylomorphs (Gower, 2002), the ventral ramus of the opisthotic is nearly hidden by the exoccipitals in posterior view. This character cannot be scored for *Revueltosaurus* at present. Among avian-line archosaurs, the ventral ramus of the opisthotic extends further laterally than the lateralmost edge of the exoccipital in sauropodomorphs (e.g., *Plateosaurus*, AMNH FR 6810) and *Herrerasaurus* (PVSJ 407). The ventral ramus of the opisthotic is covered by the lateralmost edge of the exoccipital in posterior view in *Silesaurus* (ZPAL Ab III 364/4) and theropods (e.g., *Dilophosaurus*, UCMP 37302).

112. Opisthotic, distal end of the ventral ramus: (0) does not or barely makes contact with prootic anteroventral to fenestra ovalis; (1) has extended contact with prootic (fig. 23) (Gower, 2002).

In non-crocodylomorph crocodylian-line archosaurs, non-archosaurian archosauriforms, and basal avian-line archosaurs, the opisthotic descends ventrally to rest on the basisphenoid/parabasisphenoid and has little if any contact with the prootic. The process separates the fenestra ovalis from the metotic foramen. In crocodylomorphs, the ventral ramus of the opisthotic meets the prootic on its anterior edge and has a ventrally extended contact (Gower, 2002).

113. Exoccipital, relative positions of the exits of the hypoglossal nerve (XII): (0) aligned in a nearly anteroposterior plane; (1) aligned subvertically (fig. 23) (new).

In nearly all basal archosauriforms there are two exits of the hypoglossal nerve (XII) through the exoccipital. In nearly all archosaurs, the two exits of the hypoglossal nerve are aligned in a nearly anteroposterior plane where one foramen is located posterior of the other. In *Silesaurus* (ZPAL Ab III/364/4) and *Lewisuchus* (UNLR 01), one foramen lies dorsal to the other.

114. Exoccipital, lateral surface: (0) without subvertical crest (= metotic strut); (1) with clear crest (= metotic strut) lying anterior to both external foramina for hypoglossal nerve (XII); (2) with clear crest (= metotic strut) present anterior to the more posterior external foramina for hypoglossal nerve (XII) (fig. 23) (modified from Gower, 2002).

Here, Gower's (2002) original formulation of this character is modified. All the archosaurs examined in this study have two exits for cranial nerve XII. The lateral ridge on the exoccipital is homologized with that of the metotic strut, a feature commonly referred to in theropod dinosaurs (Nesbitt et al., 2009c). Taxa without a distinct lateral ridge on the exoccipital include non-archosaurian archosauriforms, *Arizonasaurus* (MSM P4590; Gower and Nesbitt, 2006), and phytosaurs (*Pseudopalatus prisintus* UCMP 137319 and *Paleorhinus* UCMP 84810). A small change in the angle of the ventral portion of the exoccipital marking the posterior extent of the metotic opening is present in taxa scored as (0). The more posterior exit of XII is posterior to the angle change whereas the more anterior exit of XII is anterior to the angle change. The lateral ridge in taxa scored as (1) and (2) is present at the same location as the change of angle in taxa scored as (0). Furthermore, without exception, the lateral ridge is continued onto the lateral side of the basioccipital.

In taxa scored as (1), both foramina are posterior to a lateral ridge on the exoccipital. This includes crocodylomorphs (Gower, 2000). Originally, Gower (2000) scored aetosaurs the same as crocodylomorphs. However, I did not observe any aetosaur with *both* exits of XII posterior to the lateral ridge in this study. In *Stagonolepis* (MCZD 2–4), *Longosuchus* (TMM 311085-84b), and *Revueltosaurus* (PEFO 34561), one opening of XII lies anterior and the other lies posterior to the lateral ridge. An identical arrangement is also present in *Batrachotomus* (Gower, 2002) and *Postosuchus kirkpatricki* (Gower, 2002). Gower (2002) reported that *Saurosuchus galilei* (PVSJ 32) does not have a lateral ridge; however, *Saurosuchus galilei* is scored as having a lateral ridge. These taxa were scored as (2) here.

Gower (2002) did not consider avian-line archosaurs in his analysis. A lateral ridge on the exoccipital is clearly present in *Lewisuchus* (UNLR 01), *Marasuchus* (PVL 3970, 3872), and *Silesaurus* (ZPAL Ab III/364/4), *Heterodontosaurus* (SAM-K-337), *Coelophysis* (AMNH FR 7239), and *Plateosaurus* (AMNH FR 6810). Both exits of XII are present posterior to the lateral ridge and, thus avian-line taxa are scored as (1).

This character may be correlated with character 111 because a laterally extended lateral ridge on the exoccipital may hide the descending process of the opithotic in posterior view.

115. Exoccipitals: (0) meet along the midline on the floor of the endocranial cavity; (1) do not meet along the midline on the floor of the endocranial cavity (fig. 24) (modified from Gower and Sennikov, 1996; Gower, 2002).

Plesiomorphically among archosauriforms, the exoccipitals meet along the midline preventing the basioccipital from participating in the endocranial cavity (Gower, 2002). As noted by Gower and Sennikov (1996), most taxa scored as (0) have extensive contact along the anteroposterior length of the elements, whereas some non-archosaurian archosauriforms, such as *Vjushkovia triplicostata, Fugusuchus,* and *Xilousuchus*, have midline contact anteriorly but diverge posteriorly. Within Archosauria, many taxa have extensive midline contact of the exoccipitals. Among crocodylian-line archosaurs, crocodylomorphs such as *Hesperosuchus* (AMNH FR 6748), *Sphenosuchus* (SAM 3014) and *Alligator*, *Effigia* (AMNH FR 30587) and *Shuvosaurus* (TTU-P 9280) have large gaps between the exoccipitals, thus exposing the endocranial cavity.

Gower (2002) scored aetosaurs as having state (1) along with crocodylomorphs. Scoring state (1) for aetosaurs needs further discussion. In *Longosuchus* (TMM 31185–98), the exoccipitals meet at the midline. Martz and Small (2006) noted that the exoccipitals do not meet at the midline in *Tecovasuchus* (TTU-P 545). However, the exoccipitals are well ossified to the basioccipital, and the boundary between the elements is unclear. Furthermore, the exoccipitals are very close together whether they are touching or not. In *Desmatosuchus smalli*, the exoccipitals do not touch (Small, 2002). All 15 aetosaur braincases from the *Placerias* Quarry (UCMP V A269) have no gap between the exoccipitals on the dorsal surface of the basioccipital. The condition in *Aetosaurus* and *Stagonolepis* is unclear. In their potentially close relative, *Revueltosaurus* (PEFO 34561), the exoccipitals touch on the midline. Furthermore, in aetosaur taxa where the exoccipitals do not meet, the bases of the exoccipitals are near the midline. This condition contrasts with the highly separated exoccipitals of crocodylomorphs (*Sphenosuchus*, SAM 3014; *Hesperosuchus agilis*, AMNH FR 6758). Thus, the plesiomorphic state in aetosaurs cannot be summarized as state (1).

Among avian-line archosaurs, the exoccipitals meet at the midline in derived pterosaurs (*Pteranodon* YPM 2707), *Marasuchus* (PVL 3872), and *Silesaurus* (Ab III 364/4). The exoccipitals are well separated in *Lesothosaurus* (Sereno, 1991b) and *Heterodontosaurus* (SAM-PK-1332), as well as in *Herrerasaurus* (PVL 407), *Plateosaurus* (AMNH FR 6810), and *Coelophysis bauri* (AMNH FR 7239).

This character can be scored from a disarticulated basioccipital. Taxa that are scored as state (0) have flat exoccipital surfaces that meet at an anteroposteriorly oriented ridge. In contrast, in taxa scored as (1), a U-shaped depression separates the exoccipital articular facets of the basioccipital. Slight disarticulation of the exoccipitals can hinder scoring of this character.

116. Pneumatization of bony elements of the middle ear cavity: (0) absent or restricted; (1) well developed (Gower, 2002).

As described by Gower (2002), only crocodylomorphs have state (1) among suchians. *Sphenosuchus* (SAM 3014), *Hesperosuchus agilis* (AMNH FR 6758), *Kayentasuchus* (UCMP 131830), *Dibothrosuchus* (IVPP V 7907), *Protosuchus richardsoni* (UCMP 131827), and *Alligator* have extensive pneumatization of the middle ear cavity (Gower, 2002).

117. Vestibule, medial wall: (0) incompletely ossified; (1) almost completely ossified (Gower, 2002).

Gower (2002) found that the medial wall of the vestibule is completely ossified in nearly all suchians. Later, Gower and Nesbitt (2006) scored *Arizonasaurus* as (0). However, after a careful inspection of taxa with completely ossified medial walls of the vestibule, it is clear that the larger specimen of *Arizonasaurus* (MSM P4647) has a completely ossified medial wall. Therefore, *Arizonasaurus* is scored as (1) here. Furthermore, the absence of complete ossification of the medial wall in a smaller specimen of *Arizonasaurus* (MSM P4590) supports Gower and Weber's (1998) hypothesis that this character is somewhat problematic given the absence of ontogenetic data in basal archosaurs.

Effigia (AMNH FR 30587) and *Shuvosaurus* (TTU-P 9280) both have fully ossified medial walls of the vestibule. This character cannot be scored for *Marasuchus*, and the medial wall seems to be unossified in *Silesaurus* (ZPAL Ab III 361/35) as well as in *Plateosaurus* (AMNH FR 6810).

118. Lagenar/cochlea recess: (0) absent or short and strongly tapered; (1) present and elongated and tubular (Gower, 2002).

The lagenar/cochlea recess is located just anterior to the ventral ramus of the opisthotic and posterior to the opening of cranial nerve VII in a typically unossified gap

(Gower, 2002). A well-defined recess for the lagena/cochlea is absent in phytosaurs and non-archosaurian archosauriforms (Gower, 2002). In crocodylian-line archosaurs, the recess is elongated and tubular, terminating in a blind fossa well ventral of the contact between the exoccipital and the basioccipital. In avian-line archosaurs, the character cannot be scored in pterosaurs or *Marasuchus*, but it is elongated and tubular in *Silesaurus* (ZPAL Ab III 361/35) and *Plateosaurus* (AMNH FR 6810).

119. Crista vestibuli: (0) absent; (1) present (Gower, 2002).

As pointed out by Gower (2002), this character is very difficult to score given the paucity of well preserved and described braincase material for basal archosaurs. Nevertheless, it remains a clear synapomorphy within Crocodylomorpha.

120. Lagenar/cochlear prominence: (0) absent; (1) present (fig. 23) (Gower, 2002).

Walker (1990) reported a cochlear prominence, an external feature present on the prootic and opisthotic, in crocodylomorphs. Here, the bone is thickened on the lateral surface covering the lagenar/cochlear recess. State (1) is present in crocodylomorphs (Gower, 2002).

121. Eustachian tubes: (0) not enclosed by bone; (1) partially enclosed by bone; (2) fully enclosed by bone. ORDERED (figs. 23–24) (Gower, 2002).

Eustachian tubes are not enclosed by bone in non-crocodylomorph crocodylian-line archosaurs, non-archosaurian archosauriforms, and basal avian-line archosaurs (Gower, 2002). A small groove/channel at the lateral junction of the basioccipital and the parabasisphenoid in *Sphenosuchus* (SAM 3014) and *Dibothrosuchus* was previously hypothesized to house the eustachian tubes (Walker, 1990; Gower, 2002; Wu and Chatterjee, 1993). A similar channel is present in *Postosuchus kirkpatricki* (TTU-P 9000; UCMP 138842), and given the similarity in position and morphology with that of *Sphenosuchus* and *Dibothrosuchus* (IVPP V 7907), *Postosuchus* is scored as (1). *Protosuchus richardsoni* (UCMP 131827), *P. haughtoni* (BP/1/4242), *Orthosuchus* (SAM-K-409), and *Alligator* are scored as (2) because the eustachian tubes are fully enclosed by bone.

122. External foramen for abducen nerve: (0) between parabasisphenoid and prootic; (1) within prootic only; (2) within parabasisphenoid only (Gower, 2002).

The abducens nerve exits between the parabasisphenoid and prootic in a number of non-archosaurian archosauromorphs including *Prolacerta* (BP/1/2675), *Proterosuchus* (BP/1/3993), and *Euparkeria* (Gower, 2002). Gower and Sennikov (1996) suggested the external foramen for the abducens nerves passing through the prootic represented a potential synapomorphy only for erythrosuchians (*Erythrosuchus*, *Vjushkovia triplicostata*, *Shansisuchus*) and *Xilousuchus*. State (1) is also present in *Arizonasaurus*. In *Revueltosaurus* (PEFO 34561), and possibly in the aetosaurs *Tecovasuchus* (TTU-P 9222) and *Typothorax coccinarum* (TTU-P 9214), the external foramen for the abducens nerves only passes through the parabasisphenoid as in crocodylomorphs (Gower, 2002).

In *Plateosaurus* (AMNH FR 6810), the external foramen for the abducen nerves passes through the prootic only. This seems to also be the case in the theropod *Piatnitzkysaurus* (PVL 4073; Rauhut, 2004) and the basal dinosauriform *Silesaurus* (ZPAL Ab III 364/4).

This character is difficult to score given that archosaurs tend to nearly obliterate the suture between the parabasisphenoid and the prootic and because of the difficulty in examining the anterior side of the dorsal sellum.

123. Parabasisphenoid, external foramina for passage of abducens nerves: (0) on the underside of a horizontal surface; (1) on the anterior of a more vertical, upturned process (Gower, 2002).

In nearly all archosaurs, the external foramina for passage of the abducens nerves lies on the anterior surface of a vertically upturned process (= dorsum sellae). This is also true of basal dinosauriforms. I disagree with Gower (2002) for scoring *Batrachotomus* as (0). The condition in *Batrachotomus* is unknown because the external foramina for passage of the abducens nerve cannot be located with confidence.

124. Basipterygoid processes: (0) of moderate size; (1) markedly enlarged (fig. 23) (Gower, 2002; Clark et al., 2004).

As stated by Gower (2002), the basitubera are usually about the same size if not bigger than the basipterygoid processes within Archosauriformes. In non-crocodyliform crocodylomorphs, the basipterygoid processes are enlarged relative to the plesiomorphic condition. This character is equivalent to "basipterygoid processes simple, without large cavity (0) or greatly expanded, with large cavity (1)" of Clark et al. (2000). Clark et al. (2000) scored all crocodylomorphs except *Pseudhesperosuchus* as having state (1). Crocodyliforms do not have basipterygoid processes, and so they are scored as inapplicable.

125. Exit of cranial nerve VII: (0) small, only slightly larger than cranial nerve XII; (1) large (new).

In nearly all archosauriforms, the exit of the facial nerve (VII) is a small foramen that pierces the prootic just ventral to the crista prootica (see Gower and Sennikov, 1996; Gower and Weber, 1998; Gower, 2002; Gower and Walker, 2002; Dzik, 2003; Gower and Nesbitt, 2006). However, in *Postosuchus alisonae* (UNC 15575) and *Postosuchus kirkpatricki* (TTU-P 9000), the exit of the facial nerve is very large relative to that of closely related taxa. Even though the vague terms small and large are used in these character states, the great size of the opening in *Postosuchus* relative to that of other closely related taxa is remarkable. The size of the exit of the facial nerve in *Postosuchus* rivals that in size of the opening for the trigeminal nerve.

126. Supraoccipital: (0) excluded from dorsal border of foramen magnum by mediodorsal midline contact between opposite exoccipitals; (1) contributes to border of foramen magnum (fig. 24) (Gower, 2002).

The supraocciptial is excluded from the dorsal border of the foramen magnum by the exoccipitals in *Erythrosuchus* (Gower, 1997), *Proterosuchus* (BP/1/3993), *Prolacerta* (BP/1/2675), and possibly *Mesosuchus* (Dilkes, 1998). In *Euparkeria* and most basal archosaurs, the supraoccipital participates in the foramen magnum (Gower, 2002). Among dinosauromorphs, it is unclear in *Marasuchus* (PVL 3870); the supraoccipital participates in the foramen magnum in *Silesaurus* (ZPAL Ab III 364/4), *Coelophysis bauri* (AMNH FR 7239), *Herrerasaurus* (PVL 407), and *Heterodontosaurus* (SAM-PK-1332). This character is difficult to score in many taxa because the suture between the supraoccipital and the exoccipitals is often obliterated.

127. Supraoccipital, rugose ridge on the anterolateral edges: (0) absent; (1) present (fig. 24) (new).

The anterolateral surface of the supraoccipitals of nearly all archosauriforms in this study is smooth. In *Lewisuchus* (UNLR 01) and *Silesaurus* (ZPAL Ab III/364/4), the anterolateral surface bears a dorsolateral oriented rugose ridge on each side of the midline.

128. Pila antotica: (0) ossified mainly by prootic and laterosphenoid, such that laterosphenoid-parabasisphenoid contact is absent; (1) ossified largely by laterosphenoid and parabasisphenoid, with contact occurring between these two elements anterior to the trigeminal foramen in the adult braincase (fig. 23) (Gower, 2002).

Here, I keep the character formulation presented by Gower (2002). However, the character essentially scores the presence or absence of laterosphenoid and parabasisphenoid contact. As discussed by Gower (2002), the prootic separates the laterosphenoid from the parabasisphenoid in taxa scored as (0). Therefore, taxa in which the prootics contact at the midline at the anterior portion of the endocranial cavity can be scored as (0) because the prootic separates the laterosphenoid from the parabasisphenoid. Here, only crocodylomorphs are scored as (1).

129. Perilymphatic foramen: (0) with an incompletely ossified border; (1) border entirely ossified such that the ventral ramus of the opisthotic forms a perilymphatic loop incorporating a loop closure suture with itself (fig. 23) (Gower, 2002).

Gower (2002) used the presence of state (1) to suggest a close relationship of aetosaurs and crocodylomorphs to the exclusion of rauisuchians (*Batrachotomus* was the only "rauisuchian" taxon scored for this character). Poor preservation, absence of access within the metotic foramen, and poor preservation in this delicate region hampers the scoring of this character in most taxa. Even though this character requires extraordinary preservation to score, the presence of state (1) in crocodylian-line archosaurs is a potential synapomorphy (Gower and Walker, 2002). Therefore, I retain this character. In avian-line archosaurs, *Silesaurus* (ZPAL Ab III/364/4) has an incompletely ossified border, whereas *Dilophosaurus* (UCMP 16468) apparently has an ossified border.

130. Perilymphatic foramen: (0) in a medial position and oriented so as to transmit the perilymphatic duct out of the otic capsule in a posteromedial or posterior direction; (1) foramen positioned more laterally so that the perilymphatic duct is transmitted posterolaterally/laterally and the foramen is at least partly visible in lateral view (fig. 23) (Gower, 2002).

This character can be scored from the orientation of the opisthotic (Gower, 2002). This character was used by (Gower, 2002) to hypothesize a sister-group relationship between aetosaurs and crocodylomorphs. After examining the braincase of *Stagonolepis* (MCZD 4-2), I cannot score the taxon as (1) as it appears the braincase is slightly compressed. The orientation of the descending process of the opisthotic (mediolaterally) is like that of other non–crocodylian-line archosaur. Therefore, the foramen cannot be oriented laterally. In *Sphenosuchus* (SAM 3014) and *Alligator*, the perilymphatic foramen faces laterally.

131. Foramen for trigeminal nerve and middle cerebral vein: (0) combined and undivided; (1) at least partially subdivided by prootic; (2) fully divided (fig. 22) (modified from Gower and Sennikov, 1996; Gower, 2002).

Partially subdivided openings for the trigeminal nerve and middle cerebral vein are present in *Batrachotomus* (SMNS 80260) and basal crocodylomorphs (Gower, 2002). In taxa scored as (1) here (e.g., *Batrachotomus* and *Sphenosuchus*), the foramen is partially subdivided by bony prongs that penetrate the foramen, but both the trigeminal nerve and middle cerebral vein exit through the same opening. In *Stagonolepis* (MCZD 4-2; Walker, 1990), *Longosuchus* (TMM 31185–98), and *Desmatosuchus smalli* (Small, 2002; Parker, 2005), the trigeminal nerve and middle cerebral vein exit through separate foramina. The posterior border of the foramen for the middle cerebral vein is present on the prootic. Furthermore, a thin bridge of bone in all three aetosaur examples separates the two foramina.

Among dinosauriforms, *Silesaurus* (ZPAL Ab III/364/4) has a single foramen, as do ornithischians. According to Rauhut (2003), the middle cerebral vein exits through a separate foramen than the trigeminal nerve in *Plateosaurus*, *Massospondylus*, *Dilophosaurus*, and *Allosaurus,* but not in *Coelophysis rhodesiensis*, *Coelophysis bauri* (CM 29894), or ornithischians.

132. Foramen or groove passing above and into the dorsal end of the metotic foramen: (0) absent; (1) present (Gower, 2002).

Gower (2002) presented this character to unite a subset of pseudosuchians including *Postosuchus kirkpatricki*, *Batrachotomus*, and extant crocodylians (e.g., *Crocodylus*). As described by Gower (2002), this opening may be a discrete passage for the posterior cerebral/cephalic vein. Furthermore, this character is difficult to score because the location of the foramen requires exceptional preservation. A groove in *Sphenosuchus* (SAM 3014) is located in the same position as the foramen in *Postosuchus kirkpatricki* and *Batrachotomus* (Gower, 2002), and these features may be homologous. However, Gower (2002) scored *Sphenosuchus* as absent. Here, I suggest the condition in *Dibothrosuchus* (IVPP V 7907) is not clear even though it was scored as (0) by Gower (2002). Aetosaurs lack any groove or foramen (Gower, 2002), and I confirmed this with an exquisitely preserved aetosaur braincase from the *Placerias* Quarry (UCMP 27414). Furthermore, *Arizonasaurus* (MSM P4590) has a small foramen in the same place as *Batrachotomus* (scored as [0] in Gower and Nesbitt, 2006).

133. Auricular recess: (0) largely restricted to prootic; (1) extends onto internal surface of epiotic/supraoccipital (Gower, 2002).

The auricular recess is almost exclusively restricted to the prootic in non-archosaurian archosauriforms and phytosaurs (Gower, 2002). In suchians, the auricular recess extends onto the internal surface of the epiotic/supraoccipital (Gower, 2002). This is also the case in dinosauromorphs including *Marasuchus* (PVL 3872), *Lewisuchus* (UNLR 01), and *Silesaurus* (ZPAL Ab III 364/4).

This character cannot be scored in taxa where the prootic and epiotic/supraoccipital have coossified. This is the case in *Plateosaurus* (AMNH FR 6810). Even though *Arizonasaurus* was scored as (0) by Gower and Nesbitt (2006), a reexamination of braincases (MSM P4590, P4647) indicates that the suture between the prootic and epiotic/supraoccipital cannot be discerned.

134. Skull length: (0) less than 50% of length of the presacral vertebral column; (1) more than 50% of the length of the presacral vertebral column (Sereno, 1991a; Benton, 1999).

Sereno (1991a) used this character to unite *Scleromochlus* and pterosaurs. Here it is found in pterosaurs only because *Scleromochlus* is not included.

135. Skull length: (0) longer than two-thirds of the femoral length; (1) shorter than two-thirds of the femoral length (Gauthier, 1986).

Langer and Benton's (2006) description of this character is detailed and complete; therefore, little can be added. I agree with their interpretations and score sauropodomorphs as (1).

136. Antorbital fenestra: (0) absent; (1) present (Juul, 1994; Gower and Sennikov, 1997; Dilkes, 1998; Nesbitt et al., 2009a).

The presence of an antorbital fenestra supports *Proterosuchus* + Archosauria in analyses by Benton and Clark (1988), Gauthier et al. (1988), and Juul (1994). The easily recognizable feature is present in all archosauriforms ancestrally. To score this character confidently, the lacrimal should also be present in the taxon being scored.

137. Antorbital fossa: (0) restricted to the lacrimal; (1) restricted to the lacrimal and dorsal process of the maxilla; (2) present on the lacrimal, dorsal process of the maxilla and the dorsal margin of the posterior process of the maxilla (the ventral border of the antorbital fenestra). ORDERED (figs. 15–16) (Nesbitt et al., 2009a).

The antorbital fossa of *Proterosuchus* (BSP 514) is restricted to the lacrimal. In *Erythrosuchus* (BP/1/ 5207), the antorbital fossa expands onto the anterodorsal portion of the posterior process of the maxilla. This differs from the condition in archosaurs where the antorbital fossa is located on nearly the entire dorsal margin of the posterior process of the maxilla. A similar fossa is present on the dorsal surface of the maxilla of *Shansisuchus* (Young, 1964). Therefore, *Erythrosuchus* is scored as state (1). In the proterochampsians *Chanaresuchus* (PVL 4575) and *Tropidosuchus* (PVL 4604), and as observed by Sereno and Arcucci (1990), *Gualosuchus* (PVL 4576) and *Proterochampsa* (MCZ 3408), the antorbital fossa expands onto the lacrimal and onto the dorsal process of the maxilla. As with proterochampsians, *Euparkeria* (SAM 5867) has a similar arrangement of the antorbital fossa. Within phytosaurs, the antorbital fossa is present on the dorsal process of the maxilla and the lacrimal in the primitive phytosaurs *Parasuchus* (Chatterjee, 1978) and '*Paleorhinus*' *scurriensis* (TTU-P 00539; Langston, 1949; Stocker, 2010) but absent on the maxilla and lacrimal in *Smilosuchus* (UCMP 27200) and *Pseudopalatus pristinus* (NMMNH 31292). In aetosaurs (*Aetosaurus*, SMNS 5770), *Riojasuchus* (PVL 3827), *Gracilisuchus* (MCZ 4117), *Turfanosuchus* (IVPP V 3237), *Ticinosuchus* (PIZ T2817), "rauisuchians," crocodylomorphs, and dinosauriforms (e.g., *Silesaurus* ZPAL Ab III/361/26; *Herrerasaurus* PVSJ 407), the antorbital fossa is located on the lacrimal, the dorsal process of the maxilla, and nearly the entire dorsal margin of the posterior process of the maxilla.

138. Lateral (=external) mandibular fenestra: (0) absent; (1) present (fig. 16) (Benton and Clark, 1988; Juul, 1994; Bennett, 1996; Nesbitt et al., 2009a).

A lateral mandibular fenestra is present in nearly all archosauriforms plesiomorphically as indicated in the analysis by Juul (1994). A lateral mandibular fenestra has been reported to be small or absent in *Proterosuchus* (Charig and Reig, 1970; Cruickshank, 1972). Welman and Flemming (1993), confirmed by Juul (1994), and Welman (1998), showed that the well-preserved specimens of *Proterosuchus* have a small lateral mandibular fenestra. However, given the small size of the opening, the presence of this character in *Proterosuchus* deserves more discussion. The small fenestra forms at the junction of the dentary, angular, and surangular in *Proterosuchus* (RC 96, TM 201; Welman, 1998). Here, the mandibular elements do not have a distinct concave region forming an edge as in *Erythrosuchus* + Archosauria. However, though there are differences, the lateral mandibular fenestra occupies the same area and is composed of the same elements in both *Proterosuchus* and other archosauriforms. The small gap may be a consequence of the slight disarticulation of the mandibular elements, but a lateral mandibular fenestra is clearly present in QR 1484 (listed as NMC 3014 in fig. 3 of Welman, 1998). Therefore, *Proterosuchus* is scored as having a lateral mandibular fenestra. The presence or absence of a lateral mandibular fenestra is difficult to determine in isolated mandibular elements of taxa near the base of Archosauriformes. It is unclear whether *Vancleavea* has a lateral mandibular fenestra. If present, it is very small like that of *Proterosuchus*.

Pterosaurs have been cited as lacking a lateral (or external) mandibular fenestra (Bennett, 1996). A lateral mandibular fenestra is clearly absent in the holotype of *Eudimorphodon* (Wild 1978). However, a mandibular fenestra is clearly present in a specimen referred to *Eudimorphodon* sp. (BPS 1994 I 51; Wild, 1993) and *Dimorphodon* (BMNH R1034) (S.J.N., personal obs.).

139. External nares, position: (0) terminal (at the anterior part of the skull); (1) nonterminal, posterior rim of nares anterior of anterior rim of antorbital fenestra; (2) nonterminal, posterior rim of nares posterior of anterior rim of antorbital fenestra. ORDERED (fig. 16) (Hungerbühler, 2002).

In nearly all archosauriforms, the nares are positioned on the anterior portion of skull dorsal to the body of the premaxilla. In phytosaurs, the nares open dorsally and are located on the surface of the skull table. Hungerbühler (2002) and Stocker (2008) found that the most basal phytosaurs (e.g., *Paleorhinus*; TMM 31025–172) have dorsally oriented nares where the posterior rim of nares is in front of the anterior rim of the antorbital fenestra, whereas other phytosaurs (*Smilosuchus*, USNM 18313; *Pseudopalatus,* UCMP 34249) have the posterior rim of the nares posterior to the anterior rim of the antorbital fenestra.

140. External nares, directed: (0) laterally; (1) dorsally (fig. 16) (modified from Sereno, 1991a; Nesbitt et al., 2009a).

The external nares of non-archosauriform archosauromorphs, *Proterosuchus* (NM QR 1484), *Erythrosuchus* (BP/1/5207), *Euparkeria* (SAM 5867), and most basal members of the Archosauria opens laterally. Alternatively, the external nares of proterochampsians (e.g., *Chanaresuchus*, PVL 4586; *Tropidosuchus*, PVL 4601), *Vancleavea* (GR 138), and phytosaurs (Camp, 1930) open dorsally. This character was suggested to correlate with an aquatic and semiaquatic lifestyle (Sereno, 1991a).

141. Posttemporal opening, mediolateral width: (0) equal to or greater than half the diameter of the foramen magnum; (1) less than half the diameter of the foramen magnum or absent (modified from Sereno and Novas, 1994; Novas, 1996; Benton, 1999).

This character replaces "post-temporal opening fenestra (0) or foramen (1)" of Benton (1999) because of the arbitrary distinction between a small fenestra and a large foramen. Sereno and Novas (1994) described the relative size of the posttemporal opening compared to the foramen magnum, and that division is used here. Sereno and Novas (1994) reported that the posttemporal opening is larger than half the foramen magnum in pterosaurs, *Saurosuchus*, *Gracilisuchus*, aetosaurs, ornithosuchids, and phytosaurs and reduced in dinosaurs, proterochampsians, and *Sphenosuchus*. A posttemporal opening is absent in crocodylomorphs (Sereno and Novas, 1994).

142. Orbit, shape: (0) circular or elliptical; (1) tall and narrow (the "keyhole-shaped orbit"; maximum width is less than half the maximum height); (2) with distinct ventral point surrounded by V-shaped dorsal processes of jugal (figs. 16–17, 19) (Benton and Clark, 1988; Parrish, 1993; Gower, 2000; Benton and Walker, 2002).

The orbital shape in most archosauriforms is rounded or slightly elliptical. This includes aetosaurs (e.g., *Aetosaurus*, SMNS 5770), *Revueltosaurus* (PEFO 34561), *Gracilisuchus* (MCZ 4117), crocodylomorphs (e.g., *Dromicosuchus* UNC 15574), and phytosaurs (e.g., *Smilosuchus*, UCMP 27200). Benton and Clark (1988) diagnosed Rauisuchidae with a "keyhole-shaped orbit." Although "keyhole-shaped orbit" does describe a subset of suchians, this character is better described by the ventral process of the postorbital invading the orbit in another character described above. However, *Saurosuchus* (PVL 2062) and *Prestosuchus* (UFRGS 0156-T) do not have jugals that invade the orbit, but they have a similarly tall and narrow orbit like that of *Postosuchus kirkpatricki* (TTU-P 9000) and *Batrachotomus* (Gower, 1999). The taxa scored as (1) have a ventral orbital radius of curvature that is less than that of the dorsal orbital radius of curvature. The shape of the orbit of *Erythrosuchus* (BP/1/5207) and those of some theropods (Rauhut, 2003; Hwang et al., 2004) is convergent with that of a subset of suchians. The ornithosuchids *Riojasuchus* (PVL 3827) and *Ornithosuchus* (BMNH R3142) have unique V-shaped dorsal processes of the jugal that create an inverted teardrop shape for the orbit and are thus scored as (2).

143. Supratemporal fenestra, position: (0) dorsally exposed; (1) lateral exposed (fig. 17) (Long and Murry, 1995; Heckert and Lucas, 1999; Parker, 2007).

In nearly all diapsids, the supratemporal fenestrae are dorsally oriented. In the aetosaurs *Longosuchus* (TMM 31185–98), *Aetosaurus* (SMNS 5770), *Stagonolepis* (Walker, 1961), *Neoaetosauroides* (Desojo and Baez, 2007), *Aetosauroides* (Casamiquela, 1961), and *Desmatosuchus* (Small, 2002), the supratemporal fenestrae open more laterally than dorsally. The supratemporal fenestrae open dorsally in *Revueltosaurus* (Parker et al., 2005). In some specimens, dorsally oriented supratemporal fenestrae can be observed in lateral view. However, these are still scored as opening dorsally here.

144. Supratemporal fossa: (0) absent anterior to the supratemporal fenestra; (1) present anterior to the supratemporal fenestra (figs. 18–19) (modified from Gauthier, 1986; Novas, 1996).

In its original formulation, Gauthier (1986) used this character to diagnose Dinosauria and focused on those elements the supratemporal fossa was present on. The character is rewritten here in order to test the homology of the extension of the supratemporal fossa anterior to the supratemporal fenestra regardless of which element is anterior to the supratemporal fenestra. Furthermore, in the original form, Gauthier (1986) scored the entire supratemporal fossa as extensive or not extensive. In this vague wording, the presence of the supratemporal fossa in different regions cannot be evaluated. Additionally, it is not clear what constitutes extensive in character state (0) versus state (1).

The supratemporal fossa is present anterior to the supratemporal fenestra in Dinosauria, but absent in the close relative *Silesaurus* (ZPAL Ab III/361) (contra Langer and Benton, 2006). Among crocodylian-line archosaurs, crocodylomorphs (e.g., *Hesperosuchus*, *Sphenosuchus*, *Protosuchus*) possess a supratemporal fossa anterior to the supratemporal fenestra. *Postosuchus kirkpatricki* (TTU-P 9000; UCMP 27479) and *Batrachotomus* (SMNS 52970) also possess a supratemporal fossa anterior to the supratemporal fenestra. Nevertheless the supratemporal fossa of *Postosuchus* lies entirely on the postfrontal. Conversely, all the other taxa scored as (1) lack a postfrontal; instead, the supratemporal fossa is located on the frontal.

145. Supratemporals: (0) present; (1) absent (fig. 16) (Gauthier, 1984; Benton, 1985a; 1990; Benton and Clark, 1988; Bennett, 1996; Gower and Sennikov, 1997; Dilkes, 1998; Nesbitt et al., 2009a).

The supratemporal element lies between the squamosal and the parietal on the posterior margin of the skull roof. Supratemporals are present in *Mesosuchus* (Dilkes, 1998), a number of *Prolacerta* specimens (Modesto and Sues, 2004), and in *Proterosuchus*. Supratemporals are not present in *Erythrosuchus* + Archosauria. As noted by Gauthier (1984) and Modesto and Sues (2004), the presence or absence of supratemporals should be based on nearly complete, articulated skull material because the supertemporals may be easily lost during fossilization. For example, Modesto and Sues (2004) listed *Prolacerta* with or without supratemporals preserved. A facet for the supratemporal on the parietal may indicate the presence of the element in incomplete specimens, but care must be taken when scoring this character.

146. Postparietals: (0) present; (1) absent (fig. 16) (modified from Juul, 1994; Bennett, 1996; Dilkes, 1998; Nesbitt et al., 2009a).

Postparietals are present in *Proterosuchus* (BSP 514), *Erythrosuchus* (BP/1/ 5207), *Shan-*

sisuchus (Young, 1964), and *Euparkeria* (Ewer, 1965), but they are not in *Prolacerta* (UCMP 37151), *Mesosuchus* (Dilkes, 1998), and Archosauria. The condition in *Trilophosaurus* (various TMM specimens) is difficult to determine given the preservation of the cranial material at the posterior portion of the skull. As explained by Juul (1994), the postparietals of *Proterosuchus* (BSP 514), *Erythrosuchus* (BP/1/ 5207), *Euparkeria* (Ewer, 1965), and *Shansisuchus* (Young, 1964) are fused into one element, whereas they remain two elements in *Youngina* (Romer, 1956) and *Petrolacosaurus* (Carroll, 1988).

Juul (1994) also highlighted the presence of the postparietal in a number of other archosauriform groups including phytosaurs (Westphal, 1976), *Longosuchus* (originally referred to *Typothorax* by Sawin, 1947), *Gracilisuchus* (Romer, 1972c), and *Prestosuchus* (UFRGS 0156-T; Barberena, 1978). However, I failed to find a separate ossification between the parietals in my examination of these specimens. In his review of phytosaur osteology, Westphal (1976) cited Camp (1930) for the presence of a postparietal in phytosaurs. Camp (1930) reported the postparietal (= interparietal of Camp, 1930: fig. 29) and made this observation from UCMP 27200 (the holotype of *Machaeroprosopus gregorii* [= *Smilosuchus gregorii*]). However, much of what Camp (1930) identified as the postparietal is actually the supraocciptial; Camp (1930) mistook cracks as sutures deliminating a separate ossification dorsal to the foramen magnum. The posterior dorsal portion of the skull roof of *Prestosuchus* (UFRGS 0156-T) is poorly preserved, and no clear suture can be found. As with *Vancleavea*, *Gracilisuchus* possesses a small posteriorly pointed prong at the midline. In *Gracilisuchus* (MCZ 4117), this peg is the dorsal exposure of the supraoccipital peg. The posteromedial corners of the parietals dorsally overlap the peg. Therefore, *Gracilisuchus* does not have a postparietal.

147. Palpebral(s): (0) absent; (1) present (figs. 19–20) (new).

This character may be hard to score given the erratic distribution of the element. Currently, palpebrals are known in suchians and have not been found in the many well-preserved skulls of phytosaurs or the many well-preserved skulls of *Euparkeria* or proterochampsians. Taxa known from disarticulated and incomplete orbital regions should be scored as unknown. At this point, *Aetosaurus* (Schoch, 2007), *Neoaetosauroides* (Desojo and Baez, 2007), *Saurosuchus* (PVSJ 32), *Postosuchus kirkpatricki* (TTU-P 9000), *Postosuchus alisonae* (UNC 15575), *Polonosuchus silesiacus* (ZPAL Ab III/563), *Hesperosuchus ''agilis''* (Clark et al., 2000), *Junggarsuchus sloani* (Clark et al., 2004), and crocodyliforms can be scored as having palpebral(s) among non-crocodyliform crocodylian-line archosaurs.

148. Palpebral(s) size: (0) roughly the same; (1) one dominant palpebral that is at least twice the size of the other (fig. 25) (new).

The three palpebrals in the orbit of *Aetosaurus* are all nearly the same size although the anteriormost palpebral is usually 10%–20% larger than the others (Schoch, 2007). In spite of the variation in the size of the anterior palpebral of *Aetosaurus,* it is never dominant or nearly twice the size of the other palpebrals. In *Neoaetosauroides* (PVL 5698), one preserved palpebral is located in the anterior portion of the orbit. The single bone is rather small and is proportional to the anteriormost palpebral element of *Aetosaurus*.

The total number of palpebrals in the orbit of *Postosuchus kirkpatricki* (TTU-P 9000) and *Hesperosuchus* is not clear (they both clearly have at least a single palpebral though). However, it is evident that the single palpebrals of *Postosuchus* and *Hesperosuchus* are large and dominate in size over other potential palpebrals. If the triangular bone of *Postosuchus* is composed of three palpebrals, it is clear that the large, circular palpebral dominates in size. Likewise, if *Hesperosuchus* had a second or third palpebral, it would be overshadowed in size by the large circular palpebral. This character hypothesizes the homology between the large, circular palpebral element of *Postosuchus* with that of *Hesperosuchus*, *Junggarsuchus*, and crocodyliforms.

149. Palpebral(s): (0) separated from the lateral edge of the frontals; (1) extensively sutured to each other and to the lateral margin of the frontals (fig. 25) (Pol and Norell, 2004; Pol et al., 2009).

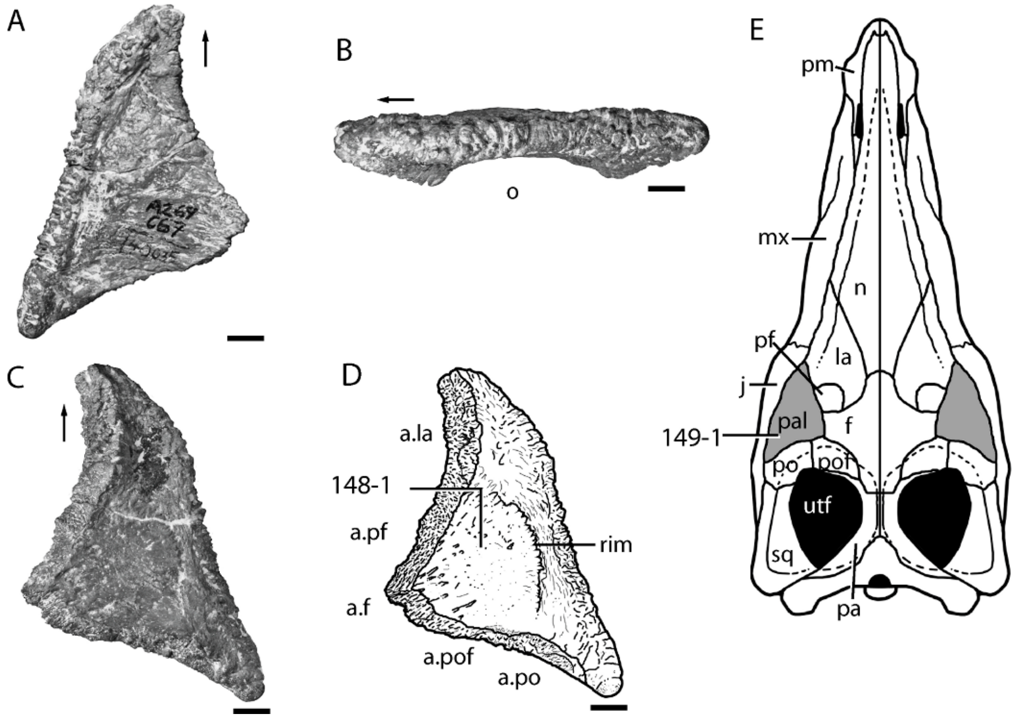


Fig. 25. Photographs of the palepbral of *Postosuchus* (UCMP 140035) in **A,** dorsal, **B,** lateral, and **C,** ventral views. A line drawing of the ventral view of UCMP 140035 is presented in **D,** highlighting the complex articular surfaces and the large circular element in the center of the palpebral; **E,** reconstruction of dorsal view of *Postosuchus kirkpatricki* by Chatterjee (1985) illustrating the palpebral and its relationship to other skull bones. The gray color highlights the palpebral in the reconstruction. Arrow indicates anterior direction. Numbers refer to character states. See appendix for anatomical abbreviations. Scale bars = 1 cm.

Postosuchus kirkpatricki (TTU-P 9000), *Postosuchus alisonae* (UNC 15575), *Saurosuchus* (PVSJ 32), and *Polonosuchus silesiacus* (ZPAL Ab III/563), as well as some crocodyliforms, have palpebrals that are fully integrated into the skull table. The palpebral forms a distinct suture with the frontal, prefrontal, and postfrontal. *Aetosaurus* (SMNS 5770) is scored as (0) because the palpebral elements are not sutured to the frontal even though the palpebral elements are sutured together. Furthermore, taxa that have not been found with palpebrals can be scored because the lateral sides of the frontal, prefrontal, and postfrontal bear distinct articular facets in taxa scored as (1).

150. Separate ossification anterior to the nasals surrounded by the premaxilla: (0) absent; (1) present (fig. 16) (modified from Sereno, 1991a).

This above character is rewritten to incorporate Sereno's (1991a) character "septomaxilla, present or absent." The term *septomaxilla* for the structure in phytosaurs is abandoned because it assumes homology among the structure of phytosaurs and other amniotes with septomaxillae (Stocker, 2008). The phylogenetic position of phytosaurs previously found (Gauthier, 1984; Benton and Clark, 1988; Sereno, 1991a; Parrish, 1993; Juul, 1994) within archosauriforms suggests that the "septomaxilla" of non-archosauriform amniotes and the "septomaxilla" of phytosaurs are not homologous. Phytosaurs, *Prolacerta* (UCMP 37151), and *Proterosuchus* are scored as (1).

151. Predentary: (0) absent; (1) present (fig. 20) (Sereno, 1986; Butler et al., 2007, 2008b).

The presence of a predentary was long cited as a synapomorphy of Ornithischia (e.g., Norman, 1984; Gauthier, 1986; Sereno, 1986, 1999; Butler, 2005; Butler et al., 2007; 2008b). The predentary is a separate, single ossification that lies anteriorly between the dentaries in ornithischians.

Ferigolo and Langer (2007) argued that the edentulous "beak" of *Sacisaurus* and *Silesaurus* is homologous with the predentary of ornithischians. The authors hypothesized that the predentary originated from the paired dentaries of archosaurs and cite examples of an independent origination of the structure on the anterior portion of the dentary in extinct birds and teleosts. *Sacisaurus* and *Silesaurus* do have an anterior dentary that is predentary-like, have an anteriorly tapering tip, and anterior portion of the dentary is edentulous. In *Sacisaurus* and *Silesaurus*, the anterior portion of the dentary is not a separate ossification separated from the rest of the dentary by a suture. The suture is not present on the exposed medial surfaces (Ferigolo and Langer, 2007: fig. 3I). The suture reported by Ferigolo and Langer (2006) in MCN PV10061 does not extend to the ventral margin. This also is the case in MCN PV10042. In the largest specimen, MCN PV10041 (holotype), there is no trace of the suture (S.J.N., personal obs). Instead, there is a foramen at the ventral extent of the hypothesized suture in the other dentaries. The preceeding evidence suggests that there is no suture between the anterior portion of the dentary and the rest of the dentary. Therefore, *Silesaurus* and *Sacisaurus* are not scored as having a predentary. Furthermore, aetosaurs also have a similar anterior end of the dentary and it is clear that the tapering anterior end is composed solely of the dentary (Long and Murry, 1995; Parker, 2007).

152. Anterior half of the dentary, position of the Meckelian groove: (0) dorsoventral center of the dentary; (1) restricted to the ventral border (fig. 27) (new).

In most archosauriforms, the Meckelian groove is located in the dorsoventral center of the medial side of the dentary. Examples of taxa with this morphology include *Erythrosuchus* (BMNH R2790), *Arizonasaurus* (MSM P4590), and *Longosuchus* (TMM 31185–98). In *Silesaurus* (ZPAL Ab III/437/1), *Lewisuchus* (UNLR 01), *Sacisaurus* (MCN PV 10048), and in the ornithschians *Eocursor* (SAM-PK-0925) and *Lesothosaurus* (Sereno, 1991a), the Meckelian groove is restricted to the ventral border of the dentary. Taxa with articulated splenials are difficult to score for this character.

153. Dentary, anterior extent of the Meckelian groove: (0) ends well short of the dentary symphysis; (1) present through the dentary symphysis (fig. 27) (new).

In most archosauriforms examined here, the Meckelian groove terminates well short of the dentary symphysis. Examples of taxa with this condition include *Erythrosuchus* (BMNH R2790), *Arizonasaurus* (MSM P4590), and *Longosuchus* (TMM 31185–98). The Meckelian groove continues through the symphysis in *Silesaurus* (ZPAL Ab III/437/1) and *Sacisaurus* (MCN PV 10048).

154. Dentary, dorsal margin of the anterior portion compared to the dorsal margin of the posterior portion: (0) horizontal (in the same plane); (1) ventrally deflected; (2) dorsally expanded (figs. 17, 19–20, 27) (new).

The dorsal margin of the anterior portion of the dentary of carnivorous archosauriforms (with recurved, mediolaterally compressed, and serrated teeth) is typically in the same horizontal plain as the posterior portion of the dentary. Exceptions among carnivorous archosauriforms include *Hesperosuchus agilis* (AMNH FR 6758), *Polonosuchus silesiacus* (ZPAL Ab III/563), and *Postosuchus kirkpatricki* (TTU-P 9000) where the anterior portion is dorsally expanded. Additionally, the anterior margin of the dentary is dorsally expanded in aetosaurs (*Aetosaurus*, SMNS 5770; *Longosuchus*, TMM 31185–98) as well as in *Silesaurus* (ZPAL Ab III/437/1). A ventral deflection of the anterior portion of the dentary was used in many phylogenetic analyses of sauropodomorphs (e.g., Sereno, 1999; Yates, 2003). *Plateosaurus* (AMNH 6810) is the only taxon scored as (1) here.

155. Dentary, anterior extremity: (0) rounded; (1) tapers to a sharp point (figs. 17, 27) (new).

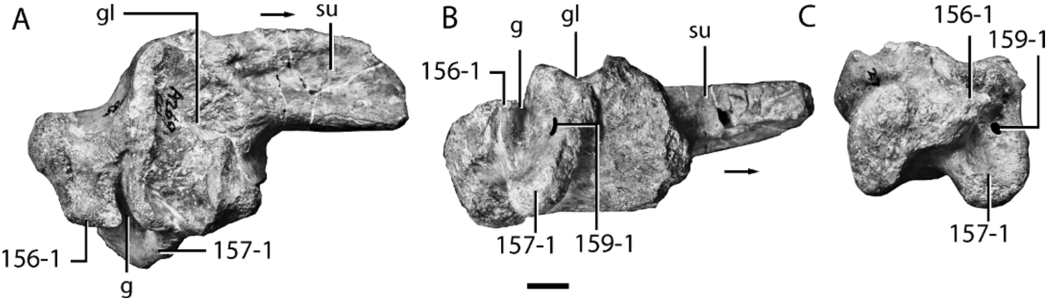


Fig. 26. The articular-partial surangular of *Postosuchus* (UCMP 27485) in **A,** dorsal, **B,** medial, and **C,** posterior views. A foramen passing through the medial process is highlighted. Arrow indicates anterior direction. Numbers refer to character states. See appendix for anatomical abbreviations. Scale bar = 1 cm.

The anterior margin of the dentary of most archosauriforms is rounded. In aetosaurs (e.g., *Aetosaurus* SMNS 5770), *Silesaurus* (ZPAL Ab III/437/1), *Sacisaurus* (MCN PV10041), and *Asilisaurus kongwe* (NMT RB9), the anterior end of the dentary tapers to a point. In *Silesaurus*, the tip arcs dorsally (Dzik, 2003).

156. Articular: (0) without dorsomedial projection posterior to the glenoid fossa; (1) with dorsomedial projection separated from glenoid fossa by a clear concave surface; (2) with dorsomedial projection continuous with the glenoid fossa. ORDERED (figs. 24, 26) (Clark et al., 2000; Olsen et al., 2000; Benton and Walker, 2002; Sues et al., 2003; Clark et al., 2004).

The articular of most archosauriforms lacks a dorsomedially projecting process on the medial side of the articular. In these taxa,

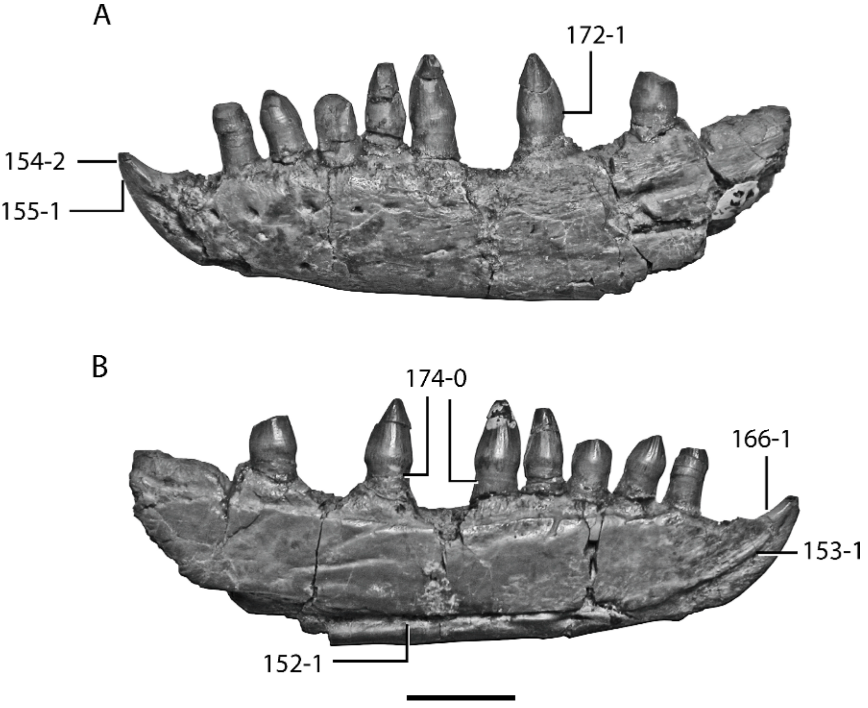


Fig. 27. Left dentary of *Silesaurus opolensis* (ZPAL Ab III/437/1) in **A,** lateral, and **B,** medial views. Numbers refer to character states. Scale bar = 2 cm.

the area posterior to the glenoid is concave. *Postosuchus kirkpatricki* (TTU-P 9000; UCMP 27490), *Batrachotomus* (SMNS 80260; Gower, 1999), *Arizonasaurus* (MSM P4590; Nesbitt, 2005a) (broken in *Polonosuchus silesiacus*, ZPAL Ab III/563 and *Fasolasuchus*, PVL 3851), *Stagonolepis* (Walker, 1961), and *Longosuchus* (TMM 31185–98) possess a small dorsomedially projecting process. The dorsomedial process in these taxa is separated from the glenoid by a large concave surface. Gower (1999) termed this process the retroarticular process. In *Hesperosuchus "agilis"* (CM 29894), *Dromicosuchus* (UNC 15574), *Sphenosuchus* (SAM 3014), *Terrestrisuchus* (Crush, 1984), and *Protosuchus richardsoni* (UCMP 131827), a distinct fingerlike process projects dorsomedially posteromedial to the glenoid. Crocodylomorphs lack a distinct gap between the process and the glenoid. The dorsomedially projecting process is more elongated in crocodylomorphs relative other taxa scored as (1). The process is hypothesized to be homologous between taxa scored as (1) and (2).

157. Articular, ventromedially directed process: (0) absent; (1) present (fig. 26) (new).

In general, the articulars of archosauriforms do not possess medial processes. *Postosuchus kirkpatricki* (TTU-P 9000), *Postosuchus alisonae* (UNC 15575) *Batrachotomus* (SMNS 80260), *Arizonasaurus* (MSM P4590), *Polonosuchus silesiacus* (ZPAL Ab III/563), *Fasolasuchus* (PVL 3851), *Stagonosuchus* (GPIT/RE/3831), *Rauisuchus* (BSP AS XXV-60-121), *Hesperosuchus* (UCMP 129470), *Sphenosuchus* (Walker, 1990) and *Dromicosuchus* (UNC 15574) all have tonguelike ventromedial processes. In the taxa scored as (1), a foramen passes through the ventromedial process. Gower (2000) noted that phytosaurs also possess ventral processes and they are also scored as (1).

158. Articular, glenoid of the mandible located: (0) level with dorsal margin of the dentary; (1) well ventral of the dorsal margin of the dentary (figs. 17, 20) (modified from Gauthier, 1986; Langer and Benton, 2006).

In most archosauriforms, the articular facet of the mandible is located at the dorsal margin of the mandible (e.g., *Riojasuchus*, PVL 3827; *Euparkeria*, SAM 5867; *Herrerasaurus,* PVSJ 407). Among basal archosauriforms, ornithischians (e.g., *Heterodontosaurus*, SAM-PK-1332), sauropodomorphs (*Plateosaurus*, AMNH FR 6810), *Silesaurus* (Dzik, 2003), and aetosaurs (*Longosuchus*, TMM 31185–98) have an articular facet of the mandible located near the ventral margin of the mandible. Additionally, taxa scored as (1) generally have surangulars in which the dorsal margin arcs dorsally to meet the dentary. This is, however, not always the case (e.g., *Herrerasaurus*).

159. Articular, foramen on the medial side: (0) absent; (1) present (fig. 26) (new).

In non-archosaurian archosauriforms, the medial side of the articular lacks a foramen. The foramen is present posteromedial to the glenoid in *Euparkeria* (Ewer, 1965), *Revueltosaurus* (PEFO 34561), and paracrocodylomorphs. In *Hesperosuchus "agilis"* (CM 29894), *Dromicosuchus* (UNC 15574), *Sphenosuchus* (SAM 3014), *Postosuchus kirkpatricki* (TTU-P 9000), *Postosuchus alisonae* (UNC 15575), *Batrachotomus* (SMNS 80260), and *Polonosuchus silesiacus* (ZPAL Ab III/563), the foramen has a large diameter relative to that of *Arizonasaurus* (MSM P4590), *Revueltosaurus* (PEFO 34561), and phytosaurs (USNM 18313). In basal crocodylomorphs, the foramen was termed the *foramen aerum* by Walker (1990), thus implying its homology with the pneumatic opening in crocodyliforms. However, as discussed by Gower (1999), the foramen in basal crocodylomorphs is not pneumatic. Therefore, the term *foramen aerum* should be abandoned for the structure in basal crocodylomorphs. In taxa scored as (1) for character 157, the foramen pierces through a ventromedial process. In phytosaurs, a small foramen is located medial to the glenoid.

160. Dentary-splenial mandibular symphysis, length: (0) distally positioned; (1) present along one-third of lower jaw (Sereno, 1991a).

Sereno (1991a) cited this character as a synapomorphy of *Riojasuchus* and *Ornithosuchus* and remarked that phytosaurs have character state (1), but did not score it. An anteroposteriorly expanded suture is also present in both *Shuvosaurus* and *Effigia* (Nesbitt, 2007) and in Crocodyliformes (Sereno, 1991a; Nesbitt, 2007).

161. Coronoid process, dorsally expanded: (0) absent; (1) present (fig. 20) (Sereno, 1986,

1999; Butler, 2005; Butler et al., 2008b; Irmis et al., 2007a).

An expanded coronoid process is present on the dorsal margin of the mandible in ornithischians (Sereno, 1986) but not any other taxa scored here.

162. Mandibular fenestra: (0) anteroposterior length more than maximum depth of dentary ramus but less than half the length of the mandible; (1) greater than half the length of the mandible; (2) reduced (anteroposterior length less than maximum depth of dentary ramus) (figs. 17, 20) (Butler, 2005; Nesbitt and Norell, 2006).

The size of the mandibular fenestra is restricted to one-fourth or less than the length of the mandible in every archosauriform in this study except *Effigia* (AMNH FR 30587) and *Shuvosaurus* (TTU-P 9280). In the latter two taxa, the extremely long mandibular fenestra is over half the length of the mandible. Furthermore, the surangular and angular are longer than half the length of the dentary, whereas the dentary is restricted to the one-fourth to one-third the length of the mandible. In ornithischians, the mandibular fenestra is highly reduced (Sereno, 1986, 1999) and are scored as (2).

163. Surangular foramen: (0) present and small; (1) present and large; (2) absent (figs. 16–17) (modified from Clark et al., 2004; Nesbitt, 2007).

A foramen is located on the posterior side of the surangular lateral to the articular in most basal archosauriforms including *Proterosuchus* (BPS 514), *Erythrosuchus* (Gower, 2003), saurischians, and nearly all non-crocodylomorph suchians. The foramen is present in *Revueltosaurus* (PEFO various specimens) and the aetosaurs *Longosuchus* (Parrish, 1994) and *Desmatosuchus* (Small, 2002), but it is not clear whether it is present in *Stagonolepis*. In *Effigia* (AMNH FR 30587) and *Shuvosaurus* (TTU-P 9280), the surangular foramen is large (see Nesbitt, 2007). A foramen does not appear to be present in the crocodylomorphs *Hesperosuchus*, *Dromicosuchus*, *Sphenosuchus*, *Dibothrosuchus*, *Terrestrisuchus*, but it is present in *Junggarsuchus* (Clark et al., 2004).

164. Dentary, posteroventral portion: (0) just meets the angular; (1) laterally overlaps the anteroventral portion of the angular (modified from Nesbitt et al., 2009a).

This character was incorrectly identified as the posteroventral portion of the dentary laterally overlaps the anteroventral portion of the *surangular* in Nesbitt et al. (2009a). However, the posteroventral portion of the dentary laterally overlaps the lateral surface of the angular. The following description corrects the mistake in Nesbitt et al. (2009a). The anteroventral portion of the meets the dentary anterodorsally in *Mesosuchus* (SAM 6536), *Prolacerta* (BP/1/471), and *Proterosuchus* (RC 96). Alternatively, the posteroventral portion of the dentary laterally overlaps the anteroventral portion of the angular in *Erythrosuchus* (BP/1/5207), *Euparkeria* (SAM 6050), in the proterochampsians *Tropidosuchus* (PVL 4601) and *Chanaresuchus* (UPLR 7), and in members of Archosauria.

165. Splenial, foramen in the ventral part: (0) absent; (1) present (fig. 16) (modified from Rauhut, 2003; Langer and Benton, 2006; Smith et al., 2007).

According to several recent phylogenies of basal dinosaurian relationships, a foramen (= mylohyoid foramen) is present through the ventral portion of the splenial in saurischians, but not in ornithischians or the closest relatives of dinosaurs (Rauhut, 2003; Langer and Benton, 2006; Smith et al., 2007). Langer and Benton (2006) reported a foramen in a similar location in *Postosuchus* following Chatterjee (1985) and Long and Murry (1995). A foramen could not be located in the newly reprepared holotype (TTU-P 9000). Therefore, a splenial foramen seems to be restricted to eusaurischians.

166. Dentary teeth: (0) present along entire length of the dentary; (1) absent in the anterior portion; (2) completely absent (figs. 17, 27) (modified from Parrish, 1994; Parker, 2007).

Dentary teeth usually span the entire length of the dentary in archosauriforms. In aetosaurs, (e.g., *Longosuchus* TMM 31185–98), the *Asilisaurus kongwe* (NMT RB9), *Silesaurus* (ZPAL Ab III/361/27), and *Sacisaurus* (MCN PV10041), the anterior end of the dentary does not bear teeth. This is also the case in one unusual crocodyliform, *Macelognathus* (Ostrom, 1971; Göhlich et al., 2005). Dentary teeth are completely absent in *Lotosaurus* (IVPP V 48013), *Effigia* (AMNH FR 30587), and *Shuvosaurus* (TTU-P 9280) among basal archosauriforms.

167. Dentition: (0) generally homodont; (1) markedly heterodont (Parrish, 1993).

Parrish (1993) scored both *Leptosuchus* and *Prestosuchus* as having heterodont dentition. Additionally, Sereno et al. (1993) listed heterodont dentition as an autapomorphy of *Eoraptor*. Phytosaurs have markedly heterodont teeth (see Hungerbühler, 2000). However, as noted by Hungerbühler (2000), the subjective term "heterodonty" to describe a set of teeth is highly ambiguous. Here, homodonty describes the general dentition of carnivorous teeth (recurved, serrated) of most archosauriforms and the herbivorous teeth of sauropodomorphs, ornithischians, aetosaurs, and *Revueltosaurus*. All these taxa have teeth that are generally similar. In contrast, the teeth of phytosaurs differ significantly depending on position (see Hungerbühler, 2000). The two character states are general bins to separate phytosaurs (1) from other basal archosaurs (0). *Eoraptor* is scored as (0); the difference in the teeth lies in the direction and number of serrations per 5 mm, but the general form of the teeth is very similar.

168. Tooth, serrations: (0) absent; (1) present as small fine knifelike serrations; (2) present and enlarged and coarser (lower density) = denticles. ORDERED (modified from Gauthier et al., 1988; Juul, 1994; Dilkes, 1998; Irmis et al., 2007a).

Tooth serrations are absent in the two non-archosauriform archosauromorphs (*Prolacerta*, *Mesosuchus*) used here. Within Archosauriformes, tooth serrations are present in nearly all clades ancestrally. In many forms that are considered carnivorous (e.g., theropods, phytosaurs, basal crocodylomorphs), the serrations form a right angle to the carinae of each tooth edge. Typically, there are 3–7 serrations per millimeter depending on the size of the taxon and tooth position. In contrast, *Revueltosaurus* (PEFO 34561), aetosaurs (*Aetosaurus*, SMNS 5770), ornithischians (e.g., *Lesothosaurus*, BMNH R8501), and sauropodomorphs (*Plateosaurus*, AMNH FR 6810) have much larger serrations (typically 1–2 units per mm), and they are angled about 45° to the carinae of each tooth edge. As a result, the serrations (= denticles) are angled dorsally or antero/posterodorsally. A similar description of the differences in the serrations of typically carnivorous taxa versus taxa with denticles was presented by Butler et al. (2008b).

169. Extensive planar wear facets across multiple maxillary/dentary teeth: (0) absent; (1) present (Weishampel and Witmer, 1990).

Typically, most archosauriforms lack extensive planar wear facets across multiple maxillary or dentary teeth. However, within Ornithischia, extensive planar wear facets are present in *Pisanosaurus* (PVL 3577) and *Heterodontosaurus* (SAM-PK-1332), whereas they are absent in *Lesothosaurus* (BMNH R8501) and *Scutellosaurus* (MNA 175).

170. Medial or lateral overlap of adjacent crowns in maxillary and dentary teeth: (0) absent; (1) present (Sereno, 1986; Butler et al., 2008b).

In most archosauriforms, the tooth crowns do not laterally overlap each other; every tooth crown is well separated from every other tooth crown. In ornithischians (e.g., *Lesothosaurus*, BMNH R8501) and some sauropodomorphs (e.g., *Plateosaurus*, AMNH FR 6810), the anterior and posterior margins of the tooth crowns laterally/medially overlap one another.

171. Tooth crown: (0) not mesiodistally expanded; (1) mesiodistally expanded above root in cheek teeth (Sereno, 1986; Butler et al., 2008b).

In most archosauriforms, the base of the crown is mesiodistally the widest between the root and the crown. In contrast, the tooth crowns are mesiodistally expanded in ornithischians (e.g., *Lesothosaurus*, BMNH R8501), sauropodomorphs (e.g., *Plateosaurus*, AMNH FR 6810), *Revueltosaurus* (PEFO 34561), and aetosaurs (e.g., *Aetosaurus*, SMNS 5770). This character was used to assign *Revueltosaurus* to Ornithischia (Hunt, 1989), but was shown by Parker et al. (2005) to have a much wider distribution.

172. Moderately developed lingual expansion of crown (= cingulum) on maxillary/dentary teeth: (0) absent; (1) present (fig. 27) (Sereno, 1986; Butler et al., 2008b).

In most basal archosauriforms, the lingual side is nearly flat. However, in some ornithischians (e.g., *Heterodontosaurus*, SAM-PK 1332) and in *Sacisaurus* (Ferigolo and Langer, 2007: fig. 3J), there is a moderately developed lingual expansion of the crown. As explained by Irmis et al. (2007b), the term *cingulum* should not be used because it is not morphologically homologous with the similarly named structure in mammalian teeth (a distinct ridge), and it is better described as above. The presence of a lingual expansion of the crown was cited by Parker et al. (2005) and Irmis et al. (2007b) as a potential character to assign isolated teeth from the Triassic to ornithischians. However, the presence of a lingual expansion of the crown in the non-ornithischian dinosauriform *Sacisaurus* (Ferigolo and Langer, 2007) negates that hypothesis. Here, I score *Pisanosaurus* (PVL 3577) as having a lingual expansion of the crown.

173. Maxillary and dentary crowns, shape: (0) apicobasally tall and bladelike; (1) apicobasally short and subtriangular (Sereno, 1986; Butler et al., 2008b).

In archosauriforms, the maxillary and dentary crowns are typically tall and bladelike. In ornithischians, the teeth are short and typically subtriangular, and the scorings of Sereno (1986) and Butler et al. (2008b) are followed here.

174. Tooth implantation: (0) free at the base of the tooth; (1) teeth fused to the bone of attachment at the base (figs. 16, 27) (modified from Gauthier, 1984; Benton and Clark, 1988; Benton, 1990a; Bennett, 1996; Nesbitt et al., 2009a).

The tooth implantation of basal archosauriforms was discussed in great detail (Romer, 1956; Hughes, 1963; Charig and Sues, 1976; Gauthier et al., 1988; Benton and Clark, 1988). The terms *thecodont* and *subthecodont* were confused in the literature in reference to basal archosaur dentition, and both terms were used interchangeably to describe the same taxon and condition. Gauthier et al. (1988) first used the depth of the tooth sockets to score this character for basal archosauriforms. However, as explained by Juul (1994), the depth of the socket is difficult to determine and compare.

The confusion of thecodont versus subthecodont dentition may be related to different authors' interpretations (Bennett, 1996). However, there is a clear difference between the dentition of *Prolacerta* (BP/1/2675) and *Proterosuchus* (BP/1/3773), and *Erythrosuchus* + Archosauria. Here, ideas associated with thecodont versus subthecodont are abandoned. Instead, differences of how the base of each tooth attaches to the tooth-bearing element are explored. The bases of the teeth of *Prolacerta* (UCMP 37151) and *Proterosuchus* (BSP 514) are firmly attached to the tooth-bearing element by small ridges of bone that completely surround each tooth. In lateral view, the teeth have flared bases. In contrast, the bases of the teeth of *Erythrosuchus* + Archosauria are free from a bony attachment. The bases of these teeth are not flared. Furthermore, most members of erythrosuchians + Archosauria also have interdental plates between teeth; interdental plates are not present outside this clade within Archosauromorpha. Silesaurids (e.g., *Asilisaurus*, *Silesaurus*) are the only crown-group archosaurs to be scored as (0) (Nesbitt et al., 2010).

175. Palatal teeth present on palatal process of the pterygoid: (0) present; (1) absent (Juul, 1994; Gower and Sennikov, 1997; Nesbitt et al., 2009a).

176. Teeth on transverse processes of pterygoids: (0) present; (1) absent (Gauthier, 1984; Juul, 1994; Bennett, 1996; Gower and Sennikov, 1997; Nesbitt et al., 2009a).

Palatal teeth are in a variety of archosauromorphs and even in members within the archosaur crown group (e.g., *Eoraptor*; Rauhut, 2003). Palatal teeth are present in *Prolacerta* (Camp, 1945; Gow, 1975; Modesto and Sues, 2004), *Mesosuchus* (Dilkes, 1998), *Proterosuchus* (Haughton, 1924; Welman, 1998), *Euparkeria* (Ewer, 1965), and all proterochampsians (Romer, 1971b; Arcucci, 1990). Palatal teeth are absent in *Erythrosuchus* and other erythrosuchians (Parrish, 1992; Gower, 2003) and most members of Archosauria, and the absence of palatal teeth was used to diagnose the clade (Gauthier, 1984; Gauthier et al., 1988; Benton and Clark, 1988; Sereno, 1991a; Juul, 1994). The presence/absence of palatal teeth anywhere on the palate was used previously (Benton and Clark, 1988; Sereno, 1991a; Juul, 1994; Benton, 1999). However, as discovered by Juul (1994), incorporating characters examining the presence/absence of palatal teeth on certain regions of the pterygoid provides phylogenetic information. *Prolacerta* and *Proterosuchus* both have a row of palatal teeth on the transverse process of the pterygoids, whereas other taxa closer to Archosauria (and within) do not have palatal teeth here. Palatal teeth on the palatal process are retained by the non-archosaurian archosauromorphs *Prolacerta*, *Proterosuchus*, proterochampsians, *Doswellia*, and *Euparkeria*, and the crown-group archosaurs *Turfanosuchus* (Wu and Russell, 2001) and *Eoraptor* (Rauhut, 2003).

In nearly all of the taxa with palatal teeth, it is unclear whether vomerine teeth are present; in most specimens, this area is poorly preserved or covered by the dentaries. *Euparkeria* (SAM 6050) has vomerine teeth (Gow, 1970). Examination of the vomer in newly discovered specimens may provide an additional character.

Axial Skeleton

177. Postaxial intercentra: (0) present; (1) absent (Gauthier, 1984; Benton and Clark, 1988; Sereno, 1991a; Parrish, 1993; Juul, 1994; Bennett, 1996; Nesbitt et al., 2009a).

The presence of intercentra was long cited as a character in basal archosaur phylogenies, but the distribution of intercentra within non-archosaurian archosauriforms remains controversial. Sereno (1991a) listed the absence of intercentra as a synapomorphy of proterochampsians + Archosauria because Sereno (1991a) listed *Euparkeria* as having intercentra in all presacral vertebrae. However, there are only two specimens of *Euparkeria* (SAM-PK-6047A, SAM-PK-6047B) that preserve intercentra. In these specimens, intercentra are not found between each of the vertebrae, but sporadically throughout the presacral column (Ewer, 1965). Intercentra are apparently absent in all other specimens even though some may have been prepared away. The intercentra of SAM-PK-6047A are very small in comparison with those of *Mesosuchus* (SAM-PK-6046). Furthermore, the ventral portion of the anterior and posterior articular surfaces of the centra of *Euparkeria* are not beveled and do not have facets for intercentra as they do in the dorsal vertebrae of *Erythrosuchus, Sarmatosuchus* (Gower and Sennikov, 1996), and *Proterosuchus*. The small size and the apparent absence of ossification of some of the intercentra in the column of *Euparkeria* may suggest that closely related taxa that have been scored as lacking intercentra, may indeed have very small intercentra. *Euparkeria* is scored as polymorphic for this character. Benton and Clark (1988) used the absence of intercentra to support the clade proterochampsians + *Euparkeria* + Archosauria (the crown group). Intercentra are present in *Prolacerta* (Gow 1975), *Proterosuchus* (NM QR 1484; Cruickshank, 1972), and *Erythrosuchus* (Gower, 2003).

178. Atlantal articulation facet in axial intercentrum, shape: (0) saddle shaped; (1) concave with upturned lateral borders (fig. 28) (modified from Gauthier, 1986; Langer and Benton, 2006).

In non-archosaurian archosauriforms, crocodylian-line archosaurs, and ornithischians, the anterior articulation of the axial intercentrum is saddle shaped, concave anteroposteriorly, and convex mediolaterally (Langer and Benton, 2006). In contrast, saurischians have a concave articulation facet, with upturned lateral borders. Thus, saurischians are scored as (1) following Langer and Benton (2006).

179. Axis, dorsal margin of the neural spine: (0) expanded posterodorsally; (1) arcs dorsally, where the anterior portion height is equivalent to the posterior height (fig. 28) (new).

In most archosauriform taxa, the neural spine of the axis is anteroventrally slanted where the anterodorsal corner is much lower than the posterodorsal height. In some ornithodiran taxa (e.g., *Marasuchus*, PVL 3870; *Lewisuchus*, UNLR 01; *Coelophysis bauri*, AMNH FR 7224), the neural spine of the axis arcs dorsally, where the anterodorsal height is or nearly is equivalent to the posterior height.

180. Axis, ventral surface: (0) possesses a midline keel; (1) possesses two paramedian keels (fig. 28) (new).

Plesiomorphically, most archosauriforms bear a midline keel on the ventral side of the axis. In *Postosuchus kirkpatricki* (TTU-P 9002), *Postosuchus alisonae* (UNC 15575), *Polonosuchus silesiacus* (ZPAL Ab III/563), *Rauisuchus* (BSP AS XXV-60-121), the axis vertebra has two paramedian keels separated by a shallow fossa. *Saurosuchus* (PVSJ 32), *Batrachotomus* (SMNS 80322), *Ticinosuchus* (PIZ T2817), *Fasolasuchus* (PVL 3850), UFRGS 156-T, and *Arizonasaurus* (MSM P4590) as well as the crocodylomorphs *Hesperosuchus* (AMNH FR 6758) and *Protosuchus richardsoni* (AMNH FR 3024) possess a single midline ventral keel on the axis.

181. Cervical 3–5 centrum length: (0) shorter or the same length as the middorsal; (1) longer than middorsal (Sereno, 1991a; Nesbitt et al., 2009a).

The anterior cervical vertebrae of many basal archosaurs are marginally the same length as the middorsal vertebrae, whereas the length of the anterior cervicals is longer than that of the middorsal vertebrae in dinosauromorphs (Sereno, 1991a). However, given the increased taxon sampling since Sereno's (1991a) discussion, this character needs further discussion.

Among basal archosauriforms, and their closest relatives, the anterior cervical vertebrae are longer in *Prolacerta* (BP/1/2675), *Proterosuchus* (NM QR 1484), and *Vancleavea* (PEFO 33978). Within Proterochampsia, *Chanaresuchus* (PVL 4647), and *Gualosuchus* (PVL 4576) have short anterior cervicals, whereas *Tropidosuchus* (PVL 4601) has anteroposteriorly elongated cervicals relative to the middorsal vertebrae. Phytosaurs (e.g., *Parasuchus*; Chatterjee, 1978), *Riojasuchus* (PVL 3827), *Revueltosaurus* (PEFO 34561), aetosaurs (e.g., *Longosuchus*; Sawin, 1947), *Postosuchus kirkpatricki* (TTU-P 9000), *Saurosuchus* (PVSJ 32), *Ticinosuchus* (PIZ T2817), and *Prestosuchus* (UFRGS 0156-T) have cervicals that are shorter or the same length as the middorsals. In *Gracilisuchus* (UNLR 08), *Arizonasaurus* (MSM P4590), *Effigia* (AMNH FR 30587), and basal crocodylomorphs (e.g., *Hesperosuchus agilis*, AMNH FR 6758; *Dromicosuchus,* UNC 15574), the anterior cervicals are elongated relative to the middorsals.

182. Cervical vertebrae, deep recesses on the anterior face of the neural arch, lateral to the neural canal (= prechonos of Welles, 1984): (0) absent; (1) present (fig. 28) (new).

There are deep recesses on the anterior face of the neural arch just lateral to the neural canal in basal neotheropods such as *Coelophysis bauri* (AMNH 7224) and *Dilophosaurus* (UCMP 37302). The deep fossae are framed by the centroprezygapophyseal lamina (sensu Wilson, 1999) and a unnamed lamina that borders the neural canal laterally. In theropods more closely related to avians (e.g., *Allosaurus*, Madsen, 1976), the recess transforms into a group of small foramina, the hallmark of pneumaticity (Britt, 1993). Similar depressions are present in sauropods (Wilson, 1999) and the ?erythrosuchid *Guchengosuchus* (IVPP V 8808; Peng, 1991).

183. Third cervical vertebra, centrum length: (0) subequal to the axis centrum; (1) longer than the axis centrum (Gauthier, 1986; Langer and Benton, 2006).

According to Langer and Benton (2006), the third cervical vertebra is longer than the axis in saurischians (e.g., *Herrerasaurus*, PVSJ 407; *Coelophysis bauri*, AMNH FR 7224) and in *Lewisuchus* (UNLR 01). Their scorings are followed here with the exception of *Eoraptor*. I could not get an accurate measurement of the axis and the third cervical. Similarly, the third cervical vertebra of *Dimorphodon* (Sereno, 1991a), *Asilisaurus kongwe* (e.g., NMT RB21), *Prolacerta* (BP/1/2675), *Qianosuchus* (IVPP V 14399), and *Xilousuchus* (IVPP V 6026) is longer than the axis.

184. Anterior to middle cervical vertebrae, diapophysis and parapophysis: (0) well separated; (1) nearly touching (new).

The diapophysis and parapophysis in anterior cervical vertebrae in most archosauriforms are well separated. In a few taxa with elongated cervicals (e.g., *Xilousuchus*, IVPP V 6026), the diapophysis and parapophysis in the anterior cervical vertebrae are very close together; however, the diapophysis and parapophysis quickly diverge from each other in the midcervical vertebrae. Within Dinosauria, the diapophysis and parapophysis in anterior to midcervical vertebrae are nearly touching in neotheropods such as *Dilophosaurus* (UCMP 37302) and *Coelophysis bauri* (AMNH FR 7224).

185. Anterior cervical vertebrae, neural arch, posterior portion ventral to the postzygapophysis: (0) smooth posteriorly or has a shallow fossa; (1) with a deep excavation with

a thin lamina covering the anterior extent on the posterolateral surface (fig. 28) (modified from Langer and Benton, 2006).

As described by Langer and Benton (2006), the neural arches of the anterior cervical vertebrae are smooth plesiomorphically whereas the same region has a deep excavation on the posterolateral surface (= caudal chonos of Welles, 1984) in some dinosaurs. Here, I do not agree with all the scoring of this character by Langer and Benton (2006). They score nearly all saurischians as having state (1). The anterior corner of the excavation tapers to a point anteriorly and is covered laterally by a lamina in only neotheropods (e.g., *Coelophysis bauri,* AMNH FR 7224; *Dilophosaurus*, UCMP 37302), whereas the posterolateral excavation is shallow in all other archosauriforms (e.g., *Vancleavea,* PEFO 33978; *Arizonasaurus,* MSM P4590; Nesbitt, 2005a). The anterior cervical vertebrae of *Effigia* (AMNH FR 30587; Nesbitt, 2007: fig. 28C) is the only exception among nontheropod archosauriforms to be scored as (1). A clear, anteriorly tapering excavation is hidden in lateral view in this specimen.

186. Epipophyses: (0) absent in postaxial anterior cervical vertebrae; (1) present in postaxial anterior cervical vertebrae (fig. 28) (Gauthier, 1986; Novas, 1996; Langer and Benton, 2006).

187. Epipophyses: (0) absent in posterior cervical vertebrae (6–9); (1) present in posterior cervical vertebrae (6–9) (Sereno et al., 1993; Langer and Benton, 2006).

Epipophysis are posterodorsally directed processes that lie on the dorsal surface of the postzygapophyses (Gauthier, 1986; Sereno and Novas, 1994). In some taxa, the posterior termination of the structure is expanded well posterior to the postzygapophyses (e.g., *Heterodontosaurus,* SAM-PK-1332; *Herrerasaurus,* PVL 407; *Dilophosaurus*, UCMP 37302) whereas the epipophyses in other taxa are just dorsal expansions that do not project more posteriorly than the postzygapophyses (*Liliensternus,* MBR. 1275) (Langer and Benton, 2006). The presence of epipophyses was recently reviewed by Langer and Benton (2006) and they concluded that the presence of epipophyses are synapomorphic for dinosaurs because they are clearly absent in *Silesaurus*, *Lewisuchus*, and *Marasuchus*. Furthermore, Langer and Benton (2006) follow Sereno et al. (1993) and noticed that only saurischians (including *Eoraptor* and *Herrerasaurus*) had epipophyses in the posterior cervical vertebrae.

Langer and Benton (2006) state that epipophyses are present in non-dinosaurian archosaurs such as *Batrachotomus*. In fact, they are more common among basal archosauriforms than discussed by Langer and Benton (2006). Epipophyses are present in *Batrachotomus* (Langer and Benton, 2006; Gower and Schoch, 2009), *Revueltosaurus* (Parker et al., in prep.), *Vancleavea* (PEFO 33978), *Mesosuchus* (SAM 8552), *Xilousuchus* (IVPP V 6026), and on the atlantal neural arch of *Effigia* (AMNH FR 30587; Nesbitt, 2007) and *Hesperosuchus* (AMNH FR 6758).

188. Cervical vertebrae, pneumatic features (= pleurocoels) in the anterior portion of the centrum: (0) absent; (1) present as deep fossae; (2) present as foramina. ORDERED (fig. 28) (modified from Holtz, 1994; Rauhut, 2003; Smith et al., 2007).

The presence of pneumatic features have been discussed at length elsewhere (see Britt, 1993; Rauhut, 2003; O'Connor, 2004; O'Connor and Claessens, 2005; Wedel, 2003, 2007; Sereno et al., 2008). In nonsaurischian archosauriforms, clear pneumatic structures are absent in the cervical vertebrae. In contrast, theropods possess pneumatic excavation(s) on the lateral sides of cervical vertebrae (Holtz, 1994; Rauhut, 2003). In coelophysoids (e.g., *Coelophysis bauri*, AMNH FR 7224), blind and deep fossae lie medially to the parapophyses on the anterior part of the centrum. In nearly all other theropods, pneumatic features are present as foramina (Rauhut, 2003).

It was reported by Nesbitt (2007) that *Effigia* and *Shuvosaurus* possess deep excavations (= pleurocoels) on the lateral portion of the cervical centra. However, it is not clear whether the cervical vertebrae assigned to *Effigia* (AMNH FR 30587) and *Shuvosaurus* (TTU-P 9001 = holotype of "*Chatterjeea elegans*") unambiguously belong to those taxa. Both specimens had disarticulated cervical regions when discovered and both were found among the remains of coelophysoids (Nesbitt, 2007; Nesbitt and Chatterjee,

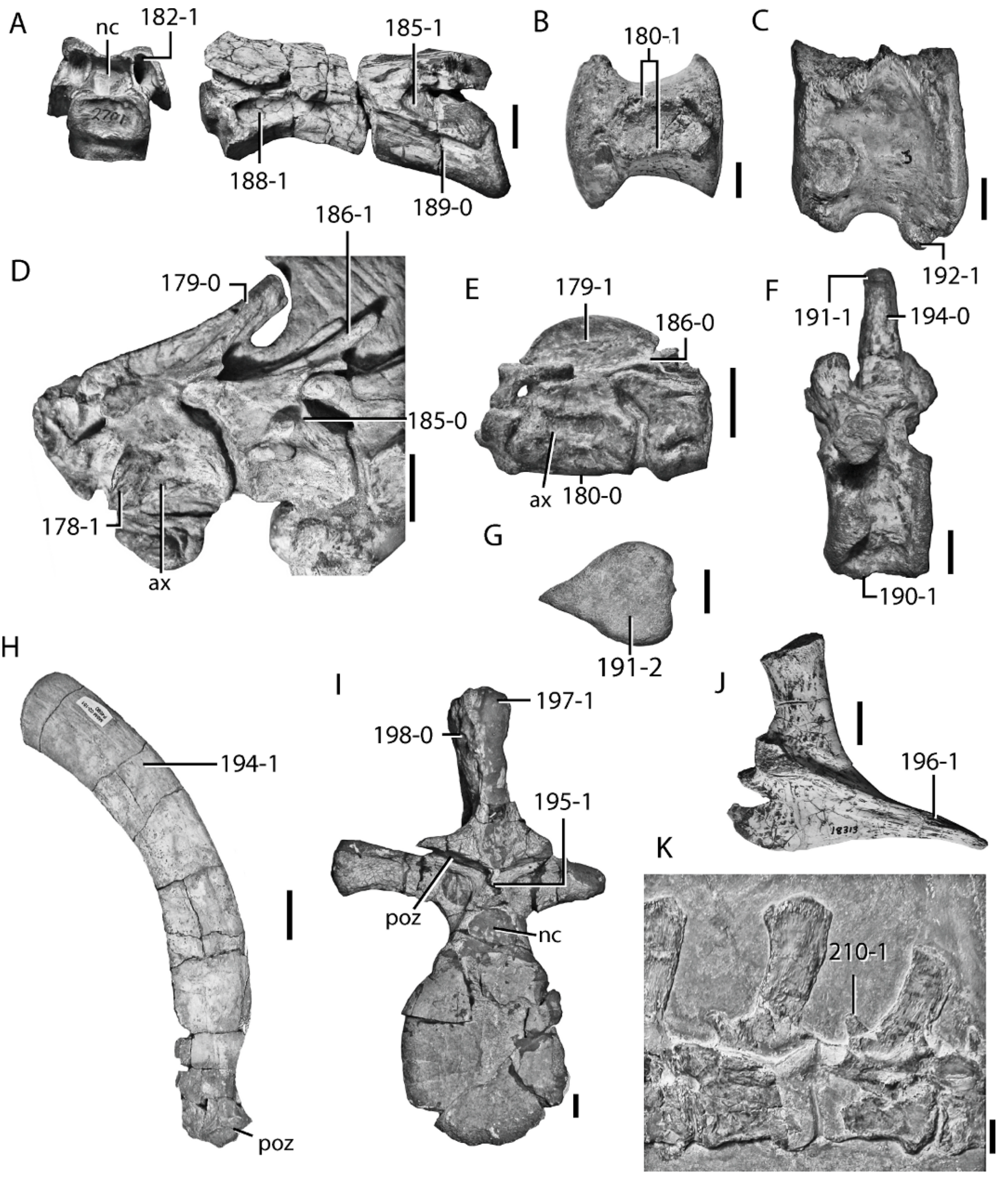


Fig. 28. Vertebrae and ribs of archosauriforms: **A,** anterior cervical vertebra of a coelophysoid (AMNH FR 2701) in anterior (left) and left lateral (right); **B,** axis centrum of *Postosuchus alisonae* (UNC 15575) in ventral view; **C,** anterior cervical vertebra of *Postosuchus alisonae* (UNC 15575) in lateral view; **D,** atlas, axis, and anterior cervical vertebrae of *Heterodontosaurus tucki* (SAM-K-1332) in left lateral view; **E,** atlas and axis of *Lewisuchus admixtus* (UNLR 01) in left lateral view; **F,** posterior cervical vertebra of *Riojasuchus tenuisceps* (PVL 3827) in left lateral view; **G,** posterior cervical neural spine of *Postosuchus alisonae* (UNC 15575) in dorsal view; **H,** posterior cervical neural spine of *Arizonasaurus babbitti* (MSM 4590) in left lateral view; **I,** dorsal vertebra of *Fasolasuchus tenax* (PVL 3850) in posterior view; **J,** cervical rib of *Smilosuchus gregorii* (USNM 18313) in dorsolateral view; **K,** middle caudal vertebrae of *Ticinosuchus ferox* (PIZ T2817) in left lateral view. Anterior direction to the left. Numbers refer to character states. See appendix for anatomical abbreviations. Scale bars = 1 cm.

2008), taxa with excavations on the posterior portion of the cervical centra. *Sillosuchus* (PVSJ 85), a taxon closely related to *Effigia* and *Shuvosaurus* (Nesbitt, 2007), has deep excavations in the cervical and dorsal vertebrae that are very similar to that sauropods and theropod dinosaurs (Alcober and Parrish, 1997; Nesbitt, 2007). In all likelihood, the anterior cervical originally assigned to *Effigia* and *Shuvosaurus* belong to those taxa; it is not unambiguous at this point in time.

189. Cervical vertebrae, rimmed depression on the posterior part of the centrum: (0) absent; (1) present (fig. 28) (modified from Gauthier, 1986; Rauhut, 2003).

The posterior portion of the centrum of the cervical vertebrae of most archosauriforms is free from any depression. A rimmed depression is present in the theropod *Coelophysis bauri* (AMNH FR 7224), *Sillosuchus* (PVSJ 85), and apparently some specimens of *Shuvosaurus* (TTU-P 9001). It is not clear if these depressions are pneumatic in origin even though this has been argued previously (see Britt, 1993).

190. Cervical vertebrae, middle portion of the ventral keel: (0) dorsal to the ventralmost extent of the centrum rim; (1) extends ventral to the centrum rims (fig. 28) (new).

Nearly all basal archosauriforms have keels on the midline of the cervical centra on the ventral surface. In *Riojasuchus* (PVL 3827) and *Ornithosuchus* (BMNH R 3916), the keels are expanded ventral to the centrum rims. *Vancleavea* is also scored as (1).

191. Cervical vertebrae, distal end of neural spines: (0) expansion absent; (1) laterally expanded in the middle of the anteroposterior length; (2) expanded anteriorly, so that the spine table is triangular or heart shaped in dorsal view (fig. 28) (modified from Gauthier, 1984; Juul, 1994; Nesbitt et al., 2009a).

The distal ends of the neural spines of the cervical vertebrae are expanded (= spine tables) in *Euparkeria* (SAM 6047A), *Postosuchus kirkpatricki* (TTU-P 9002), *Riojasuchus* (PVL 3827; Bonaparte, 1971), *Revueltosaurus* (PEFO 34561), aetosaurs (*Desmatosuchus,* MNA V9300), phytosaurs (*Pseudopalatus,* UCMP 34260), but absent in some crocodylian-line archosaurs (e.g., "Clade X" of Nesbitt, 2005, 2007). In taxa scored as (1) or (2), the dorsal surface of the neural spine is flat. Distal expansions of the cervical neural spines are not present in proterochampsians, *Erythrosuchus* (Gower, 2003), *Vancleavea, Proterosuchus* (BP/1/3993), or *Mesosuchus* (SAM 8552). The presence of osteoderms does not coincide with the presence of distal expansions of the neural spines as demonstrated by *Chanaresuchus* (PVL 4575) and other proterochampsians; they have osteoderms, but no distal expansion. Furthermore, distal expansions are not present in some taxa where the dorsal region bears dorsal osteoderms over the entire presacral column (see below). Therefore, the absence of distal expansions does not determine whether a taxon has dorsal osteoderms.

In *Euparkeria* (SAM 6047A), *Riojasuchus* (PVL 3827), and phytosaurs the distal expansions are laterally expanded in the middle of the anteroposterior length of the spine. In dorsal view, the neural spine is oval where the long axis is oriented anteroposteriorly. In *Postosuchus kirkpatricki* (TTU-P 9002), *Postosuchus alisonae* (UNC 15575), *Revueltosaurus* (PEFO 34561), *Batrachotomus* (SMNS 80285), and *Saurosuchus* (PVSJ 32), the neural spine is anteriorly expanded relative to the posterior end. In dorsal view, the neural spine is triangular or heart shaped in dorsal view.

Novas (1994) and Langer and Benton (2006) reported distal expansions in the neural arches of *Herrerasaurus* and *Eoraptor* in the dorsal, caudal, and sacral vertebrae. The features in *Eoraptor* and *Herrerasaurus* contrast with those in *Euparkeria* and *Postosuchus* in that the dorsal and lateral surfaces of the distal expansions of *Eoraptor* and *Herrerasaurus* are rounded and the lateral sides have longitudinal striations. Some of the "spine tables" of the dorsal vertebrae of *Herrerasaurus* also expand anteriorly and posteriorly beyond the anterior and posterior edges of the shaft of the neural spine. A similar pattern occurs in theropods (e.g., *Tyrannosaurus rex*; Brochu, 2003) and avians (S.J.N., personal obs.) as well as the suchian *Effigia* (Nesbitt, 2007). Therefore, dinosaurs are scored as (0) for this character.

192. Middle cervical vertebrae, hypapophyses: (0) absent; (1) present (fig. 28) (new).

Small, ventral projections at the anterior and posterior ends of the ventral keel (= hypapophyses) of the cervical vertebrae are present in *Postosuchus kirkpatricki* (TTU-P 9000, 9002), *Postosuchus alisonae* (UNC 15575; Peyer et al., 2008), and *Rauisuchus* (BSP AS XXV-60-121). This character cannot be scored for *Polonosuchus silesiacus* (ZPAL Ab III/563).

193. Posterior cervical vertebrae, divided parapophyses: (0) absent; (1) present (modified from Weinbaum and Hungerbühler, 2007).

In nearly all basal archosaurs, the parapophysis of the posterior cervical vertebrae is a single unit that attaches to the capitulum of a rib. In the posterior cervicals of *Arizonasaurus* (MSM P4590) and *Poposaurus* (TTU-P 10419 and TMM 31025–177), the parapophysis is divided by a non-articulating gap (Nesbitt, 2005a). It is unclear whether the rib that attaches here is triple headed like that of some of the dorsal ribs erythrosuchians (Parrish, 1992; Gower, 2003).

194. Posterior cervical vertebrae, neural spines: (0) directed dorsally, straight; (1) arc anteriorly (fig. 28) (new).

The neural spines of the posterior cervical vertebrae of nearly all archosauriforms are directed dorsally at their distal margins. In *Arizonasaurus* (MSM P4590), *Xilousuchus* (IVPP V 6036), *Lotosaurus* (IVPP V 48013), and *Ctenosauriscus* (GZG 419-1), the neural spines arc anteriorly at their distal tips.

195. Posterior cervical and/or dorsal vertebrae, hyposphene-hypantrum accessory intervertebral articulations: (0) absent; (1) present (fig. 28) (Gauthier, 1986; Juul, 1994; Benton, 1999; Rauhut, 2003; Langer and Benton, 2006; Weinbaum and Hungerbühler, 2007).

Accessory intervertebral articulations between the dorsal vertebrae (hyposphene-hypantrum) are present in Dinosauria and a number of crocodylian-line archosaurs (Gauthier, 1986; Langer and Benton, 2006). Within Dinosauria, hyposphene-hypantrum articulations are present in *Herrerasaurus*, *Guaibasaurus*, theropods (e.g., *Dilophosaurus*, UCMP 37302), and sauropodomorphs (Rauhut, 2003; Langer and Benton, 2006). Among crocodylian-line archosaurs, *Arizonasaurus* (MSM P4590; Nesbitt, 2007; Weinbaum and Hungerbühler, 2007), *Effigia* (AMNH FR 30587), *Batrachotomus* (SMNS 80296; Gower and Schoch, 2009), *Xilousuchus* (IVPP V 6036), *Poposaurus* (YPM 57100), *Postosuchus alisonae* (UNC 15575), and *Postosuchus kirkpatricki* (TTU-P 9000) as well as in the aetosaur *Desmatosuchus* (MNA V9300; Parker, 2008). In these taxa the hyposphene is a simple, dorsoventrally oriented lamina that is continued ventrally from the ventromedial bases of the postzygapophyses. Furthermore, the hypantrum is just a simple gap between the prezygapophyses.

Eoraptor is scored as unknown here because the intervertebral articulations are not visible in the specimen (PVSJ 512).

196. Cervical ribs: (0) slender and elongated; (1) short and stout (fig. 28) (Gauthier, 1986; Benton and Clark, 1988; Juul, 1994; Benton, 1999).

Plesiomorphically, archosauriforms possess elongated cervical ribs that parallel the cervical vertebrae (Gauthier, 1986). In basal pterosaurs (e.g., *Eudimorphodon ranzii,* MCSNB 2888), phytosaurs (e.g., *Smilosuchus*, USNM 18313), *Postosuchus alisonae* (UNC 15575), *Gracilisuchus* (UNLR 08), in aetosaurs preserving cervical ribs (*Stagonolepis* BMNH R 4789; *Aetosaurus,* SMNS 5770 S-21), and in crocodylomorphs (e.g., *Hesperosuchus*, AMNH FR 6758; *Dromicosuchus*, UNC 15574; Sues et al., 2003) and crocodyliforms (e.g., *Protosuchus richardsoni*, AMNH FR 3024; *Alligator*) the cervicals ribs are very short. Here, a short cervical rib is defined as a rib with an anteroposterior length shorter than the posterior edge of the following centrum. *Arizonasaurus* (MSM P4590), *Qianosuchus* (IVPP V13899) and *Poposaurus* (YPM 57100) have elongated cervical ribs like that of taxa scored as (0).

Langer and Benton (2006) use a similar character (states reversed) to describe the cervical ribs of dinosauromorphs. However, the plesiomorphic state of Langer and Benton (2006), short and directed posteroventrally, is not equivalent to state (0) employed here. Nearly all the taxa scored in Langer and Benton (2006) as (0) and (1) would be scored as (0) here. As described by Langer and Benton (2006), the cervical ribs of ornithischians are short and are scored as (1). Juul (1994) incorrectly states that *Lager-*

peton has slender cervical ribs; the cervical region of *Lagerpeton* is unknown.

197. Dorsal vertebrae, neural spine distal expansion: (0) absent; (1) present with a flat dorsal margin; (2) present with a rounded dorsal margin (fig. 28) (new).

The neural spines of the dorsal vertebrae of *Euparkeria* (SAM 6047B), phytosaurs (e.g., *Smilosuchus*, USNM 18313), *Riojasuchus* (PVL 3827), *Revueltosaurus* (PEFO 34561), aetosaurs (e.g., *Longosuchus*, TMM 31185–98), *Saurosuchus* (PVSJ 32), *Batrachotomus* (Gower and Schoch, 2009), and *Fasolasuchus* (Bonaparte, 1981) expand laterally at the distal end and form a flat surface. This morphology is periodically referred to as a spine table. In *Herrerasaurus* (Novas, 1994), *Eoraptor* (PVSJ 512), and *Heterodontosaurus* (SAM-K-1332) the distal end of the neural spines of the dorsal vertebrae expand, but do not form a flat dorsal surface. Here, the condition in dinosaurs is not considered homologous to that of state (1), but is instead scored as (2).

198. Dorsal vertebrae, neural spines: (0) about the same height as the posterior cervical vertebrae neural spines; (1) 2–5 times taller as the posterior cervical vertebrae neural spines (fig. 28) (new).

The neural spines of the dorsal vertebrae of nearly all archosauriforms are about the same height as the neural spines of the posterior cervical vertebrae. However, the neural spines of the dorsal vertebrae of *Arizonasaurus* (MSM P4590), *Lotosaurus* (IVPP V4880 or V4881), *Ctenosauriscus* (GZG 419-1), and *Hypselorhachis* (Butler et al., 2009) are greatly elongated (Nesbitt, 2003). In these taxa the dorsal vertebrae form a distinctive "sail" (Nesbitt, 2003, 2005a).

199. Middle dorsal vertebrae, diapophyses and parapophyses: (0) close to the body of the midline; (1) expanded on stalks (new).

In most basal archosauriforms the diapophyses and parapophyses are not significantly laterally expanded beyond the neural arch. In contrast, the diapophyses and parapophyses lie together on a laterally expanded transverse process in aetosaurs (e.g., *Desmatosuchus*, MNA V9300), *Revueltosaurus* (PEFO 34561), *Effigia* (AMNH FR 30587), *Shuvosaurus* (TTU-P assorted specimens), and in dinosaurs.

200. Sacral centra: (0) separate; (1) coossified at the ventral edge (new).

The coossification of the sacral centra is common with Archosauria. Most non-archosaurian archosauriforms and many crocodylian-line archosaurs have separate sacral vertebrae. Within crocodylian-line archosaurs, *Arizonasaurus* (MSM P4590), *Poposaurus* (TMM 43683-1), *Effigia* (AMNH FR 30587), *Shuvosaurus* (TTU-P 9280), *Sillosuchus* (PVSJ 85), and *Desmatosuchus* (MNA V9300; Parker, 2008) have coossified sacral centra. Pterosaurs also have coossified sacral centra (Langer and Benton, 2006). Within Dinosauria, the sacral centra are coossified in ornithischians (e.g., *Heterodontosaurus*, SAM-PK-1332; Santa Luca, 1980), some sauropodomorphs (*Sellosaurus gracilis,* SAM 12684; Yates, 2003) and all neotheropods (e.g., *Coelophysis bauri,* AMNH FR 7224; Colbert, 1989) whereas the sacral centra of *Herrerasaurus* (PVL 2566), *Staurikosaurus* (MCZ 1669), and *Saturnalia* (MCP 3944-PV) are not coossified. The sacral centra of *Silesaurus* (ZPAL unnumbered) are not coossified on the ventral margins in any examples. The sacral ribs are shared between vertebrae and as a result, the centra appear to be coossified. However, without the sacral ribs, the centra would not be coossified at all. Thus, *Silesaurus* is scored as (0).

201. Sacral vertebrae, prezygapophyses and complimentary postzygapophyses: (0) separate; (1) coossified (fig. 29) (new).

The prezygapophyses and postzygapophyses of sacral vertebrae remain separated in most basal archosauriforms even if the sacral centra are coossified. However, the prezygapophyses and postzygapophyses are coossified in the sacra of *Arizonasaurus* (MSM P4590), *Poposaurus* (TMM 43683-1), *Effigia* (AMNH FR 30587), *Shuvosaurus* (TTU-P 9001), and *Sillosuchus* (PVSJ 85). Coossification of the prezygapophyses and postzygapophyses also occurs in pterosaurs and neotheropods.

In *Effigia* (AMNH FR 30587) and *Shuvosaurus* (TTU-P 9001) the neural spines are completely coossified into a sheet of bone (Nesbitt, 2007). This is also true of some of the sacral series of *Silesaurus* (ZPAL unnumbered) and in *Coelophysis bauri* (Colbert, 1989).

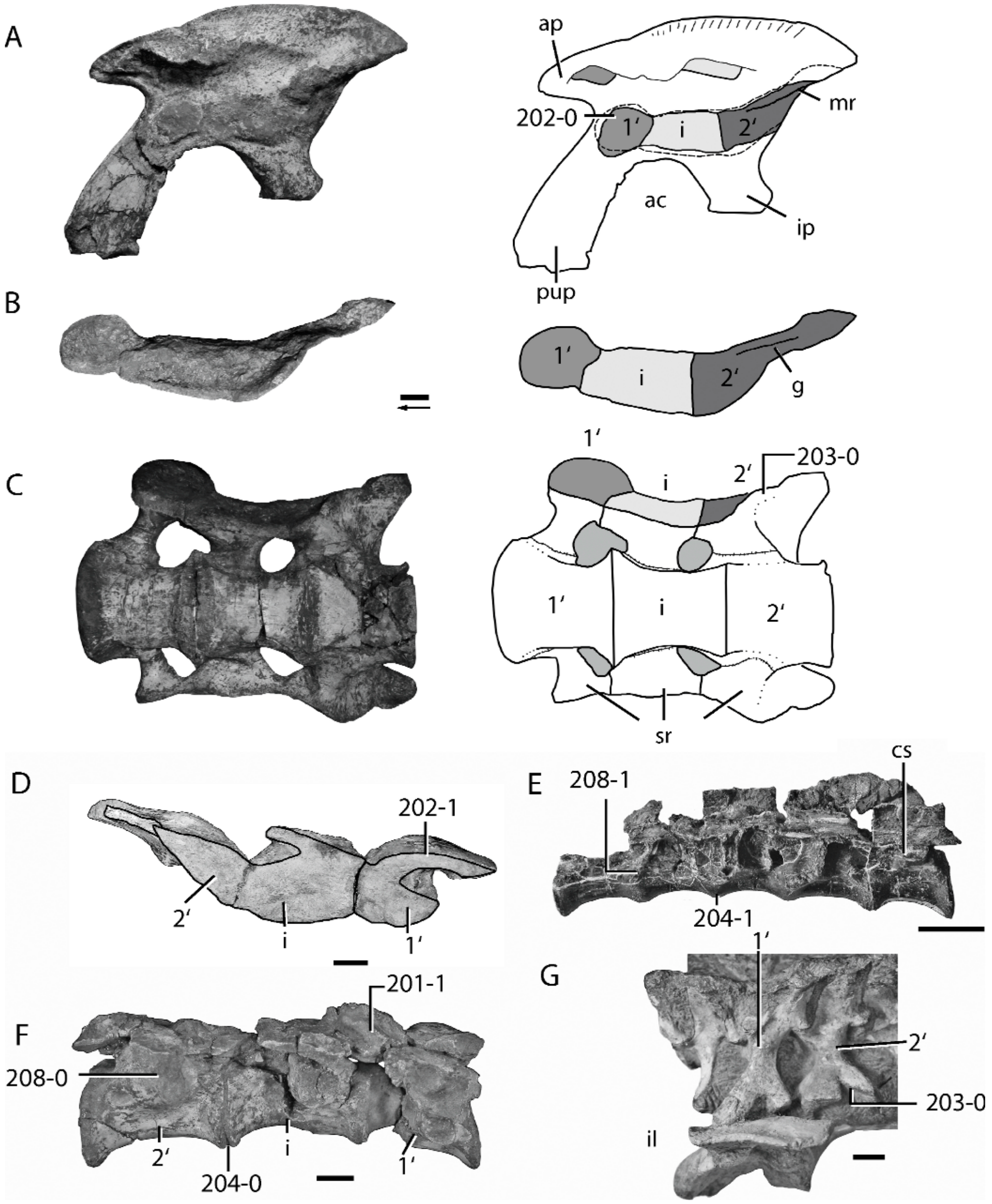


Fig. 29. The sacrum of archosauriforms: **A,** right ilium of *Massospondylus* (BP/1/4934) in medial view; **B,** left sacral ribs of *Massospondylus* (BP/1/4934) in lateral view (reversed); **C,** sacrum of *Massospondylus* (BP/1/4934) in ventral view (reversed); **D,** right sacral ribs of *Arizonasaurus babbitti* (MSM 4590) in lateral view; **E,** coelophysoid sacrum (NMMNH 31661) in left lateral view; **F,** sacrum of *Arizonasaurus babbitti* (MSM 4590) in right lateral view; **G,** sacrum of *Proterosuchus fergusi* (NM QR 1484) in dorsolateral view. Abbreviations: 1′, 1st primary sacral vertebra/rib; 2′, 2nd primary sacral vertebra/rib; i, insertion. Arrow indicates anterior direction. Numbers refer to character states. See appendix for anatomical abbreviations. Scale bars = 1 cm.

202. Primordial sacral one, sacral rib: (0) does not or weakly articulates with anteriorly directed process (= preacetabular process) of the ilium; (1) an anterior process of the rib articulates with the anteriorly directed process of the ilium (fig. 29) (Nesbitt, 2005a, 2007).

The sacral rib of primordial sacral one doesn't or weakly articulates with anteriorly directed process (= preacetabular process) of the ilium in most basal archosaurs including dinosaurs. In non-archosaurian archosauriforms as well as most crocodylian-line archosaurs, the first sacral rib is massive and circular in lateral view (e.g., *Erythrosuchus* BMNH R3592; Gower, 2003). The first sacral rib articulates with the ilium on the dorsal portion of the pubic peduncle in taxa scored as (0). Conversely, the anterodorsal portion of the first primordial sacral rib extends anteriorly to articulate with the anteriorly directed process of the ilium in *Arizonasaurus* (MSM P4590), *Poposaurus* (TMM 43683-1), *Effigia* (AMNH FR 30587), *Shuvosaurus* (TTU-P 9001), *Sillosuchus* (PVSJ 85), and possibly *Lotosaurus* (IVPP V4880 or V4881). This character can be scored from just an ilium because the sacral rib of the primordial sacral leaves a distinct scar on the medial side of the ilium.

203. Second primordial sacral, rib: (0) bifurcated; (1) a single unit (fig. 29) (Dilkes, 1998).

In *Mesosuchus* (SAM-PK-6046), *Prolacerta* (BP/1/2675), and *Proterosuchus* (NM QR 1484) the second sacral rib is bifurcated in dorsal view into a larger anterior portion and a smaller posterior portion. All archosauriforms in this analysis besides *Proterosuchus* have a second sacral rib that is not bifurcated.

204. Sacral vertebrae, centra articular rims: (0) present in sacrum; (1) nearly obliterated (fig. 29) (Nesbitt, 2007).

The centra rims of sacral vertebrae normally expand well ventral of the ventral surface of the body of the centrum in the sacrum of most archosauriforms whether the centra are coossified or not. In *Effigia* (AMNH FR 30587) and *Shuvosaurus* (TTU-P 9001) the centra rims within the sacrum are nearly obliterated; the four sacral vertebrae have been fused into rod similarly in theropods (e.g., *Coelophysis bauri*; Colbert, 1989).

205. Trunk vertebrae: (0) free from the sacrum; (1) incorporated into the sacrum, with their ribs/transverse processes articulating with the pelvis (Sereno et al., 1993; Langer and Benton, 2006).

206. Caudal vertebrae: (0) free from the sacrum; (1) incorporated into the sacrum, with their ribs/transverse processes articulating with the pelvis (Galton, 1976; Langer and Benton, 2006).

207. "Insertion" of a sacral vertebra between the first and second primordial sacral vertebrae: (0) absent; (1) present (new).

These three characters describe the possible homologies of the sacral vertebrae of taxa with more than the primordial two found in basal archosauriforms. As discussed by Langer and Benton (2006), there are two scoring strategies when describing the number and homology of sacral vertebrae: one scores the absolute number of sacral vertebrae (e.g., Gauthier, 1986; Benton, 1990a; Juul, 1994; Novas, 1996; Rauhut, 2003; Irmis et al., 2007b; Smith et al., 2007) and the second parses out the origin of the sacral vertebrae (Sereno et al., 1993; Sereno, 1999; Langer, 2004; Langer and Benton, 2006). Given that sacral vertebrae increased in a number of archosaurian taxa independently (Juul, 1994; Novas, 1996; Rauhut, 2003; Irmis et al., 2007a), the latter strategy is further explored here.

As explained by Langer and Benton (2006), identifying the origin of the sacral vertebrae requires the identification of primordial sacrals one and two. Within archosauriforms, the plesiomorphic state is the presence of two sacral vertebrae (Gauthier, 1984) as evidenced by only two sacral vertebrae in all non-archosaurian archosauriforms, basal dinosauromorphs, and most crocodylian-line archosaurs. These taxa are the key to identifying the primordial sacral vertebrae. Even though Langer and Benton (2006) stated the importance of identifying the primordial sacrals, they did not explicitly state their criteria for identifying the primordial sacral vertebrae in taxa with additional sacral vertebrae.

Langer and Benton (2006) extensively discussed the possible homologies of additional sacral vertebrae other than the primordial two in Dinosauria and close relatives. Nevertheless, Langer and Benton (2006) only suggested that sacral vertebrae are added anterior to or posterior to the two primordial sacrals, and they always assumed the primordial sacral vertebrae are adjacent. Here, I argue that the primordial sacrals do not always have to be adjacent and an additional sacral vertebra is present between primordial one and two in a number of archosaurs.

The morphology of the primordial sacral ribs and their attachment sites on the ilium is essential in identifying the two primordial sacral vertebrae. Sacral vertebrae are defined as vertebrae that contact the ilium by means of a sacral rib or transverse process. The first primordial sacral rib extends laterally to meet the anterior portion of the ilium at the junction of the anterior process (= preacetabular process) and the pubic peduncle in taxa that retain the plesiomorphic condition (e.g., *Euparkeria*). The articular surface of the first primordial sacral rib and the corresponding scar on the ilium are rounded. A small anterior process may articulate with the anterior process of the ilium (see character 202). The second primordial sacral rib is more massive than the first sacral rib and is posterolaterally expanded. In lateral view, the articular surface is teardrop shaped, and this corresponds to a scar on the posteromedial side of the ilium. The more massive anterior portion attaches to the medial side of the ischial peduncle. The posterior portion of the second primordial sacral rib lies ventral to an anteroposteriorly trending ridge located on the medial portion of the posterior process (= posterior ilia wing = postacetabular process) of the ilium. Additionally, the articular surface of the second sacral rib is greater than that of the first sacral rib. The posterior edge of the first primordial sacral rib meets the anterior edge of the second primordial sacral rib. The identification of the two primordial sacral vertebrae can be made from the sacral ribs alone and their corresponding attachment scars on the medial side of the ilium. Ideally, the sacral centra, sacral ribs, and the medial side of the ilium should be used to identify the primordial sacrals.

It appears that the morphology of the first and second primordial ribs remain rather conserved when there are three or more sacral vertebrae in the sacrum. However, any vertebra that lies between the primordial sacral vertebrae is an “insertion”; a sacral vertebra anterior to the first primordial sacral is considered a dorsosacral, and a sacral vertebra posterior to the second sacral vertebrae is considered a caudosacral.

The sacrum of *Arizonasaurus* illustrates a clear example among crocodylian-line archosaurs and the sacra of *Silesaurus* and *Allosaurus* illustrate examples among dinosauromorphs of taxa with an insertion between the primordial sacral vertebrae.

The well-preserved sacrum of *Arizonasaurus* (MSM P4590) consists of three sacral vertebrae and all of the sacral ribs (Nesbitt, 2003, 2005a). Sacral rib one of *Arizonasaurus* corresponds to the first primordial rib of *Euparkeria* and other taxa based on the location of articulation with the ilium and the morphology of the articular facet of the sacral rib. However, sacral rib one of *Arizonasaurus* does not expand proportionally as much posteriorly as that of primordial sacral rib one of *Euparkeria*. Sacral rib three of *Arizonasaurus* expands posteriorly and attaches ventrally to the anteroposteriorly trending medial ridge of the posterior portion of the ilium like that of the second primordial rib of *Euparkeria* (SAM 6049B). Therefore, the third sacral of *Arizonasaurus* is identified as primordial sacral two. Sacral rib three of *Arizonasaurus* does not expand as much anteriorly as that of primordial sacral rib two of *Euparkeria*. Sacral rib two of *Arizonasaurus* is different than both the primordial sacral ribs of *Euparkeria* and other taxa with only the two primordial sacral vertebrae in both shape and connectivity; it does not have the posteriorly elongated flange of primordial sacral rib two and does not articulate at the junction of the anterior process and the pubic peduncle of the ilium. It is clear that sacral rib two of *Arizonasaurus* lies between the posteriorly foreshortened primordial sacral rib one and the anteriorly foreshortened primordial sacral rib two (third sacral rib of *Arizonasaurus*). Furthermore, the articular surface area of the three sacral ribs of *Arizonasaurus* is similar to the articular surface area of the two sacrals of phytosaurs, but the ilia of the two taxa are relatively the same length. Therefore, a sacral vertebra is "inserted" between primordial one and two in *Arizonasaurus*, and this is a reasonable explanation of the shortening of sacral ribs one and three. Among putative close relatives of *Arizonasaurus*, a similar "insertion" of sacral vertebra between primordial one and three is found in *Effigia* (AMNH FR 30587), *Poposaurus* (TMM 43683-1), *Shuvosaurus* (TTU-P 9001), and in *Sillosuchus* (PVSJ 85).

Among other crocodylian-line archosaurs, a similar "insertion" of a third sacral vertebra is possibly present in *Batrachotomus*. There are three sacral vertebrae in *Batrachotomus* (Gower and Schoch, 2009). Even though all sacrals known from *Batrachotomus* are disarticulated, the well-preserved ilia have three distinct sacral rib scars. These scars are very similar to those in the ilia of *Arizonasaurus* in that a circular sacral rib scar lies between the primordial sacral rib scars.

Silesaurus (ZPAL unnumbered) was reported as having four sacral vertebrae (Dzik, 2003; Dzik and Sulej, 2007). However, only three sacral ribs attach to the ilium. *Silesaurus* is unique in that four centra are coossified together by sharing three sacral ribs (see character 208). The three sacral ribs attach in a similar location as the sacral ribs of *Arizonasaurus* and *Batrachotomus*. Conversely, the sacral ribs are much more delicate than those of *Euparkeria* and crocodylian-line archosaurs (see Dzik, 2003; Dzik and Sulej, 2007). Nonetheless, the first sacral rib of *Silesaurus* attaches in the same location as primordial sacral rib one in plesiomorphic forms, whereas the third sacral rib of *Silesaurus* attaches with the anteroposteriorly trending ridge on the medial side of the ilium and is posteriorly elongated as with primordial sacral two of plesiomorphic forms. Therefore, the third sacral of *Silesaurus* is homologous with that of primordial sacral two. Sacral rib two, like that of *Arizonasaurus*, is squeezed between the first and second primordial sacral ribs. Therefore, *Silesaurus* also has an "insertion" in the sacrum.

It is clear from the ilium and sacral ribs of *Allosaurus* (Madsen, 1976) that the taxon has a similar arrangement as *Silesaurus* and *Arizonasaurus*; an additional sacral is present between primordial sacrals one and two. The medial surface of the ilium preserves five sacral rib scars. The position and shape of what Madsen (1976) labeled as sacral rib two corresponds to primordial sacral rib one, whereas what Madsen (1976) labeled as sacral rib four corresponds to primordial sacral rib two. Therefore, the scar labeled as sacral rib three corresponds to an insertion.

As more sacral vertebrae are added to the sacral series, the identification of primordial sacral vertebrae becomes more difficult because the sacral ribs become smaller. As they become smaller, the primordial sacrals lose their identifying characteristics. In the sacrum of the abelisaurid *Carnotaurus sastrei* (MACN 894; Bonaparte et al., 1990), sacral two of Bonaparte et al. (1990) possibly corresponds to primordial sacral one, whereas sacral five of Bonaparte et al. (1990) possibly corresponds to primordial sacral two. Therefore, two vertebrae were inserted between the primordial sacrals.

The identification of dorsosacral and caudosacral vertebrae is possible assuming that my identification of primordial sacrals is correct. Among crocodylian-line archosaurs, *Shuvosaurus* (TTU-P 9001), *Poposaurus* (TMM 43683-1), *Sillosuchus* (PVL 85), *Effigia* (AMNH FR 30587), and *Desmatosuchus* (MNA V9300) have a dorsosacral added into the sacrum. There do not appear to be any crocodylian-line archosaurs that add a caudosacral.

Within Dinosauria, a dorsosacral and a caudosacral appear to be added to the sacra of *Lesothosaurus* (Sereno, 1991b) and *Heterodontosaurus* (SAM-PK-1332), as well as in neotheropods (e.g., *Allosaurus*; Madsen, 1976). The origination of sacral vertebrae in sauropodomorphs has received much attention (Galton, 1976; Yates, 2003; Langer, 2003; Langer and Benton, 2006). It is now clear that some sauropodomorphs add an "insertion" (e.g., *Massospondylus*), whereas others add a caudosacral (e.g., *Saturnalia*).

This new method for identifying the origin of sacral vertebrae is not fully tested. However, I outline a repeatable methodology for identifying the two primordial sacrals. The identification of caudo- and dorsosacrals and insertions is based strictly on the identification of the two primordial sacrals in taxa with more than two sacral vertebrae.

208. Sacral ribs: (0) almost entirely restricted to a single sacral vertebra; (1) shared between two sacral vertebrae (fig. 29) (new).

In most archosauriforms, sacral ribs are almost entirely restricted to a single sacral vertebra. This includes some taxa with at least three sacral vertebrae (e.g., *Batrachotomus*, inferred from the ilium of SMNS 80270; *Desmatosuchus*, MNA V9300; *Arizonasaurus*, MSM P4590). In *Poposaurus* (TMM 43683-1), *Effigia* (AMNH FR 30587), *Shuvosaurus* (TTU-P 9001), *Sillosuchus* (PVSJ 85), *Allosaurus* (Madsen, 1976) and *Silesaurus* (ZPAL unnumbered), the sacral ribs lie between two sacral vertebrae and are shared. The sacral ribs coossify the lateral sides of the articular ends of the sacral centra in *Silesaurus* (ZPAL unnumbered).

209. First primordial sacral, articular surface of sacral rib: (0) circular; (1) C-shaped in lateral view (modified from Langer and Benton, 2006).

The articular surface of the first primordial sacral rib of non-archosaurian archosauriforms and crocodylian-line archosaurs are generally circular. A corresponding circular scar is present on the medial side of the ilium in these taxa. The articular surface of first primordial sacral rib is also circular in *Marasuchus* (PVL 3871), *Pseudolagosuchus* (UNLR 53), and *Silesaurus* (ZPAL unnumbered). *Lesothosaurus* (BMNH RU B.17) and *Eocursor* (SAM-PK-0925) also have a similar arrangement to that of basal dinosauromorphs. In contrast, the anterior margin of the rib of first primordial sacral expands dorsally in saurischians (Langer and Benton, 2006). All together, the sacral rib is C-shaped in lateral view where the posterior side is open. A corresponding C-shaped scar is present on the medial side of the ilium. The simple correspondence between the articular surface of the sacral rib and the scar on the medial side of the ilium allows this character to be scored with just the medial side of the ilium.

210. Middle caudal vertebrae, accessory laminar process on anterior face of neural spine: (0) absent; (1) present (fig. 28) (Benton and Clark, 1988; Juul, 1994; Benton, 1999; Benton and Walker, 2002; Rauhut, 2003; Irmis et al., 2007a).

In most archosauriforms, the anterior edge of the neural spine of the caudal vertebrae is continuous ventrally without interruption. Accessory laminar projections sit on the anteroventral portion of the ventral half of the neural spines in phytosaurs (e.g., *Smilosuchus*, USNM 18313), *Ornithosuchus* (BMNH R3561), *Polonosuchus silesiacus* (ZPAL Ab III/563), *Prestosuchus* (UFRGS 0152-T), *Rauisuchus* (BSP AS XXV-60-121), *Qianosuchus* (IVPP V 14300), *Ticinosuchus* (PIZ T2817), CM 73372, *Saltoposuchus* (SMNS 12596), *Batrachotomus* (SMNS 80339; Gower and Schoch, 2009), and *Terrestrisuchus* (Crush, 1984). As observed in taxa with largely articulated tails, the morphology and location of the anterior laminar process depends on the position within the caudal series. For example, in both *Ticinosuchus* (PIZ T2817) and *Qianosuchus* (IVPP V 14300), the projections lie more distally on the neural spine of the anterior caudal vertebrae than they do on the more posterior caudal vertebrae. Furthermore, the projections on the anterior caudal vertebrae are kinks where the dorsal part of the anterior margin is more strongly inclined posteriorly than the ventral part whereas the anterior projections are located at the base of the neural spine and are triangular in lateral view in the more posterior caudal vertebrae. Anterior projections are present in far more caudal vertebrae in *Ticinosuchus* (caudal 5 to at least caudal 35) compared to *Qianosuchus* (roughly in only 10 midcaudal vertebrae). Given this disparity, only taxa with relatively complete tails can be scored as (0) whereas taxa with any caudal vertebrae with any form of anterior laminar projections are scored as (1). Here, I am the first to record anterior projections in the phytosaur *Smilosuchus* (USNM 18313).

Makovicky (1995) and Rauhut (2003) recognized similar features in the caudal vertebrae of Theropoda. Rauhut (2003) has two characters describing the anterior laminar projections among basal theropods, one describing the kink on the anterior edge of the anterior midcaudal vertebrae (character 123) and one describing an anterior process anterior to the neural spine in midcaudal vertebrae (character 125). As in *Ticinosuchus* (PIZ T2817) and *Qianosuchus* (IVPP V 14300), both of Rauhut's (2003) two distinct characters occur in the same tail in some crocodylian-line archosaurs. This also may be the case in theropods given that both derived states are present or completely absent for both characters in all taxa in Rauhut's (2003) analysis.

211. Distal caudal vertebrae, prezygapophyses: (0) not elongated; (1) elongated more than a quarter of the adjacent centrum (Gauthier, 1986; Rauhut, 2003; Nesbitt, 2007).

The prezygapophyses of the distal caudal vertebrae are short in non-archosaurian archosauriforms, most crocodylian-line archosaurs, and many basal dinosauromorphs. *Effigia* (AMNH FR 30588) and *Shuvosaurus* (TTU-P 9001) have elongated prezygapophyses in the distal caudal vertebrae among crocodylian-line archosaurs. Pterosaurs have elongated caudal prezygapophyses also (Wellnhoffer, 1978). In Dinosauria, ornithischians have short prezygapophyses in the distal caudal vertebrae (e.g., *Heterodontosaurus*; SAM 1332). This is also true of sauropodomorphs (Gauthier, 1986; Sereno, 1999; Rauhut, 2003; Langer and Benton, 2006). Both *Herrerasaurus* (PVL 373) and *Staurikosaurus* (MCZ 1669) have elongated prezygapophyses in the distal caudal vertebrae. Character state (1) is widespread within Theropoda (Rauhut, 2003); elongated caudal prezygapophyses are present in *Coelophysis rhodesiensis* (Raath 1969), *Coelophysis bauri* (AMNH FR 7234), *Dilophosaurus* (Tykoski, 2005a), and most tetanurans, whereas it is absent and *Ceratosaurus* (Madsen and Welles, 2000) and *Coelurus* (YPM 2010).

PECTORAL GIRDLE

212. Forelimb–hind limb, length ratio: (0) more than 0.55; (1) less than 0.55 (Gauthier, 1984; Sereno, 1991a; Juul, 1994; Benton, 1999).

=Humerus + radius: Femur + tibia

The ratio of the length of the forelimb to that of the hind limb has been used repeatedly in most phylogenetic analyses of basal archosaurs. Gauthier (1984) first used this character as an ornithodiran synapomorphy, but stated that avian-line archosaurs have a forelimb–hind limb ratio of 0.5. Gauthier (1984) considered pterosaurs as having a ratio less than 0.5 and thus excluded the elongated manus whereas Sereno (1991a) scored pterosaurs as having a ratio greater than 0.5. Benton (1999) later changed the ratio to greater or less than 0.55.

None of the authors ever defined what was measured in both the hind limb and the forelimb. It was assumed by later authors that the humerus to the distal end of the longest ungual was measured for the forelimb and the femur to the ungual of the longest pedal digit for the hind limb. However, many of the taxa that were scored lack manus material. Here, I include only the total length of the humerus + radius for the forelimb and the femur + tibia for the hind limb. This formulation allows most taxa to be scored and the scoring technique employed here agrees well with the scoring of taxa previously.

213. Clavicles: (0) present and unfused; (1) fused into a furcula (modified from Gauthier, 1986; Sereno, 1991a; Benton, 1999; Benton and Walker, 2002).

Clavicles are present in non-archosaurian archosauriforms and basal crocodylian-line archosaurs. Clavicles are not present in crocodylomorphs (e.g., *Hesperosuchus* "*agilis*," CM 29894; *Protosuchus richardsoni*, AMNH FR 3024) and, therefore, they are scored as inapplicable. Like the interclavicle, the clavicles of the pterosaur *Eudimorphodon* are separate ossifications in a small specimen and incorporated into the sternum (Wild, 1993). All other pterosaurs seem to lack distinct ossifications of the clavicles. Within Dinosauria, clavicles are present, but do not contact in some ornithischians (e.g., *Psittacosaurus*) and are unossified in others (Butler et al., 2008a). The clavicles of some non-sauropod sauropodomorphs (e.g., *Massospondylus*) may contact each other at the midline, but do not fuse (Yates and Vasconcelos, 2005). A furcula (= fused clavicles) is present in nearly all theropods known from complete skeletons including *Coelophysis bauri* (AMNH FR 30647; Rinehart et al., 2007; Nesbitt et al., 2009d) and *Allosaurus fragilis* (UUVP 6102; Chure and Madsen, 1996). This character has been employed by various datasets exploring theropod relationships (e.g., Norell et al., 2001; Clarke, 2004).

214. Interclavicle: (0) present; (1) absent (fig. 30) (Gauthier, 1986; Sereno, 1991a; Juul, 1994; Benton, 1999).

The interclavicle is present in archosauriforms plesiomorphically (Sereno, 1991a) and persists through Pseudosuchia. In Pterosauria, an interclavicle appears to be present in young individuals of *Eudimorphodon* (MCSNB 8950), but fuse to the pectoral elements in larger individuals (Wild, 1993). A distinct interclavicle is not present in all other pterosaurs. Ornithischians and saurischians lack an interclavicle. However, the pectoral girdles in the successive sister taxa to Dinosauria (*Silesaurus*, *Marasuchus*, *Lagerpeton*) do not have the pectoral region completely preserved. As a result, the optimization of this character within Dinosauromorpha is not clear.

215. Interclavicle: (0) T-shaped; (1) anterolateral processes reduced or absent (fig. 30) (modified from Gauthier, 1984; Sereno, 1991a; Gower and Sennikov, 1997; Nesbitt et al., 2009a).

The well-preserved, articulated interclavicle of *Proterosuchus* (NM QR 1484) has long tapering lateral processes. Gower and Sennikov (1997) report that the interclavicle of one erythrosuchian, *Vjushkovia triplicostata* has an interclavicle with reduced lateral processes. To date, no other interclavicle is known in erythrosuchians. As pointed out by Sereno (1991a) the holotype of *Euparkeria capensis* (SAM 5867) possesses short lateral processes as with members of the Archosauria. Although not completely preserved in any proterochampsian, the pectoral girdle of *Tropidosuchus* (PVL 4606) bears two thin clavicles in articulation with short processes of the fragmentary interclavicle (Arcucci, 1990). All archosaurs with an interclavicle are scored as (1).

216. Scapula, length: (0) more than 75% of humerus length; (1) less than 75% of humerus length (Sereno, 1991a).

Sereno (1991a) used this character to unite *Scleromochlus* and Pterosauria. Even though the scapula of pterosaurs is short relative to the humerus, other taxa such as crocodylomorphs (e.g., *Hesperosuchus*, AMNH FR 6758) have short scapulae relative to the humerus.

217. Scapula, entire anterior margin: (0) straight/convex or partially concave; (1) markedly concave (fig. 30) (modified from Gower and Sennikov, 1997; Nesbitt et al., 2009a).

The scapulae of *Mesosuchus* (SAM 6536; Dilkes, 1998), *Prolacerta* (BP/1/2675; Gow 1975), and *Proterosuchus* (NM QR 1484) have wide scapulae that have a partly concave partly convex anterior margin. In contrast, *Erythrosuchus* (BMNH R3267a), *Vancleavea* (GR 138), *Euparkeria* (SAM 5867), *Tropidosuchus* (PVL 4604), *Chanaresuchus* (PVL 4575), and Archosauria have scapulae that have markedly concave anterior margins. Gauthier (1984) had a similar character, scapula 50% taller than wide, to describe erythrosuchians + Archosauria. These two characters cover the same basic observation and both are not used here.

218. Scapula, blade height versus distal width: (0) less than 3 times distal width; (1) more than 3 times distal width (fig. 30) (Sereno, 1999).

In most basal archosauriforms, the distal width of the scapula is about half the height of the blade. In both *Silesaurus*-like taxa and Neotheropoda, the scapula is tall relative to the distal width. Sereno (1999) listed this asa character of Herrerasauridae + Neotheropoda. However, a complete scapula of *Herrerasaurus* is not known and the referred scapula to *Herrerasaurus* (= PVL 53; "*Frenguellisaurus*") is missing the distal extremity. Therefore, state (1) cannot support Herrerasauridae + Neotheropoda at present. Furthermore, *Eoraptor* is scored as (0).

219. Scapula, teardrop-shaped tuber on the posterior edge, just dorsal of the glenoid fossa: (0) absent; (1) present (fig. 30) (new).

In most archosauriforms, the lateral surface of the scapula bears a small scar on the posterior edge of the element just dorsal to glenoid (e.g., *Erythrosuchus*, BMNH R3762a). This scar corresponds to the origin of the scapular head of the M. triceps (Gower, 2003; Gower and Schoch, 2009). In *Prestosuchus* (BSP XXV 1-3/5-11/ 28-41/49), *Batrachotomus* (SMNS 80271), and *Riojasuchus* (PVL 3827) there is a large, distinct a tuber on the anterior edge just dorsal to the glenoid.

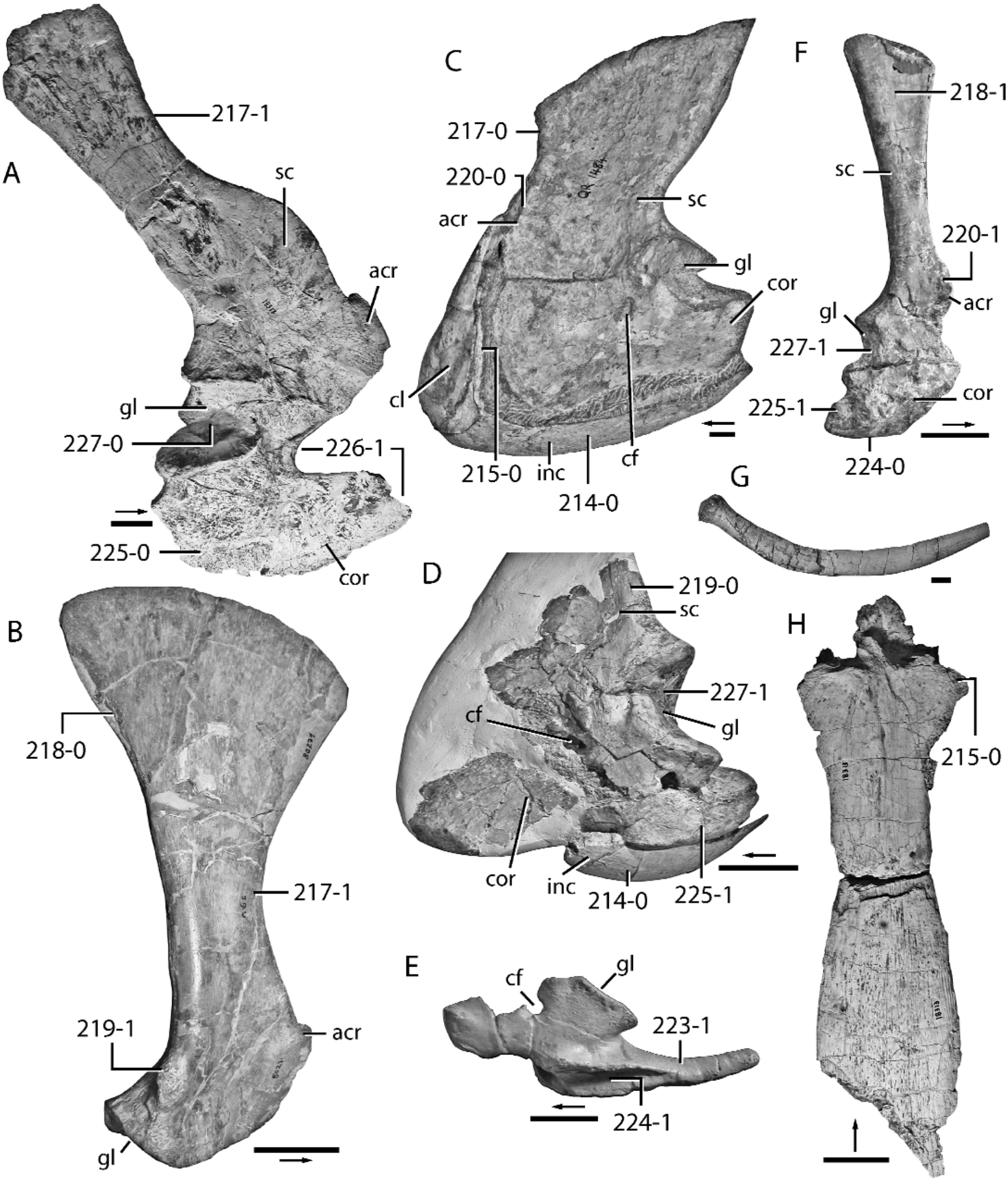


Fig. 30. Examples of pectoral girdle character states of archosauriforms: **A,** right scapulocoracoid of *Smilosuchus gregorii* (USMN 18313) in lateral view; **B,** right scapula of *Batrachotomus kuperferzellensis* (SMNS 80271) in lateral view; **C,** left portion of the pectoral girdle of *Proterosuchus fergusi* (NM QR 1484) in lateral view; **D,** partial left scapulocoracoid of *Postosuchus alisonae* (UNC 14475) in lateral view; **E,** partial left coracoid of *Hesperosuchus agilis* (AMNH FR 6758) in lateral view **F,** right coracoid and scapula of *Lewisuchus admixtus* (UNLR 01) in lateral view; **G,** ?right clavicle of *Postosuchus alisonae* (UNC 14475) in lateral view; **H,** intercalvicle of *Smilosuchus gregorii* (USMN 18313) in dorsal view. Arrow indicates anterior direction. Numbers refer to character states. See appendix for anatomical abbreviations. Scale bars = 5 cm in A–B, D, H and 1 cm in C, E, F.

220. Scapula, acromion process: (0) in the about the same plane as ventral edge of the scapula; (1) distinctly raised above the ventral edge of the scapula (fig. 30) (new).

In the archosauriforms, *Proterosuchus* (NM QR 1484) and *Prolacerta* (BP/1/2675), *Euparkeria* (SAM 6758) and phytosaurs (e.g., *Smilosuchus*, USNM 18313), the anteroventral portion of the scapula is flat. In the scapula of *Erythrosuchus* (Gower, 2003), *Chanaresuchus* (PVL 4575), and nearly all crown-group archosaurs, the acromion process is distinctly raised above the ventral edge of the scapula.

221. Scapulocoracoid, anterior margin: (0) distinct notch between the two elements; (1) uninterrupted edge between the two elements (Parrish, 1993; Benton, 1999).

In many basal archosauriforms, the anterior margin of the junction of the coracoid has a distinct notch. This is usually a consequence of a rounded anterior margin of both the coracoid and the scapula. A scapulocoracoid notch is present in phytosaurs (*Smilosuchus,* USNM 18313), *Euparkeria* (SAM 5867), *Chanaresuchus* (PVL 4575), *Tropidosuchus* (PVL 4604), aetosaurs (e.g., *Aetosaurus*, SMNS 5770 S-2), *Ornithosuchus* (BMNH R 3916), *Revueltosaurus* (PEFO 34561), *Riojasuchus* (PVL 3827), *Prestosuchus* (BSP XXV 1-3/5-11/ 28-41/49), *Saturnalia* (MCP 3845-PV), *Plateosaurus* (AMNH FR 6810), *Silesaurus* (Dzik and Sulej, 2007: fig. 18), and *Allosaurus* (Madsen, 1976). There is no notch in *Postosuchus kirkpatricki* (TTU-P 9000), *Postosuchus alisonae* (UNC 15575), *Hesperosuchus agilis* (AMNH FR 6758), *Dromicosuchus* (UNC 15574), *Dibothrosuchus* (IVPP V 7907), *Sphenosuchus* (SAM 3014), and *Protosuchus richardsoni* (AMNH FR 3024). The anterodorsal corner of the coracoid is "squared-off" in taxa scored as (1). The condition in *Batrachotomus* is not known because all the anterior portions of the coracoids are broken and reconstructed (contra Parrish, 1993).

222. Coracoid: (0) subcircular in lateral view; (1) with postglenoid process (notch ventral to glenoid).

223. Coracoid, postglenoid process: (0) short; (1) elongate and expanded posteriorly only; (2) elongate and expanded anteriorly and posteriorly. ORDERED (fig. 30) (modified from Clark et al., 2004).

The coracoids of *Proterosuchus* (NM QR 1484), *Erythrosuchus* (BMNH R3592), *Chanaresuchus* (PVL 4575), *Euparkeria* (SAM 6049), and phytosaurs (e.g., *Smilosuchus*, USNM 18313) are subcircular in lateral view. In *Revueltosaurus* (PEFO 34561), aetosaurs (e.g., *Longosuchus* TMM 31185-84a), *Riojasuchus* (PVL 3827), rauisuchians (e.g., *Batrachotomus*, SMNS 80271; *Postosuchus alisonae*, UNC 15575), *Effigia* (AMNH FR 30587), and crocodylomorphs (e.g., *Hesperosuchus agilis*, AMNH FR 6758, *Protosuchus richardsoni*, AMNH FR 3024), there is a distinct notch ventral to the glenoid, thus creating a posteriorly projecting process. Furthermore, the postglenoid process is rather short (not expanded much posterior to the posterior lip edge of the glenoid) in the taxa listed except in crocodylomorphs. In crocodylomorphs, the posteromedial edge of the coracoid expands posteromedially to meet the interclavicle at the midline.

Clark et al. (2004) added a forth state "with extremely elongate posteromedial process" from Clark et al. (2000) and scored *Dromicosuchus*, *Sphenosuchus*, *Dibothrosuchus*, *Junggarsuchus* for this character state. *Pseudhesperosuchus, Hesperosuchus,* and *Terrestrisuchus* are scored as (1). However, the differences between the length of the postglenoid process between *Hesperosuchus* and *Pseudhesperosuchus* and *Dromicosuchus* cannot be substantiated. The postglenoid processes of *Dibothrosuchus* (Wu and Chatterjee, 1993) and *Sphenosuchus* (Walker, 1990), however, are marginally longer than that of other non-crocodyliform crocodylomorphs. State (3) of Clark et al. (2004) is not used here.

Here, I have modified the third character state to account for the condition in the crocodyliforms *Protosuchus*, *Orthosuchus*, and *Alligator*. These taxa have an elongated postglenoid process that expands posteromedially and the medial extent of the element expands both anteriorly and posteriorly to form a pendulum shape. *Litargosuchus* (BP/1/5237) is scored as (2).

224. Coracoid, posteroventral edge, deep groove: (0) absent; (1) present (fig. 30) (new).

The posteroventral edge of the coracoid of most archosauriforms tapers to a thin edge. In *Postosuchus kirkpatricki* (TTU-P 9000) and the crocodylomorphs *Hesperosuchus* (AMNH FR 6758), *Dromicosuchus* (UNC 15574), *Terrestrisuchus* (Crush, 1984), *Pseudhesperosuchus* (PVL 3830) and *Sphenosuchus* (SAM 3014), a deep groove is present on the posteroventral edge of the coracoid. In *Postosuchus* and crocodylomorphs, the interclavicle fits into this groove.

225. Coracoid, posteroventral portion: (0) smooth; (1) possesses a "swollen" tuber (= biceps tubercle) (fig. 30) (new).

Among non-archosaurian archosauriforms (*Chanaresuchus*, PVL 4575; *Euparkeria*, SAM 5867) and phytosaurs (*Smilosuchus,* USNM 18313), the coracoid is smooth medially to the glenoid on the lateral surface. In contrast, the coracoid of suchians such as *Revueltosaurus* (PEFO 34561), *Arizonasaurus* (MSM P4590), *Batrachotomus* (SMNS 80271), *Hesperosuchus* (AMNH FR 6758) and dinosauriforms such as *Silesaurus* (ZPAL Ab III/361), *Saturnalia* (= acrocoracoid tubercle of Langer et al., 2007; MCP 3844-PV), and *Heterodontosaurus* (SAM-K-1332; Santa Luca, 1980) have a "swollen" tuber on the posterolateral surface of the coracoid medial to the glenoid. Taxa scored as (1) have a shallow fossa that lies between the tuber and the glenoid. Additionally, a notch is present between the glenoid and the "swollen" tuber on the posterior edge in all taxa scored as (1). The poorly preserved coracoid of *Marasuchus* (PLV 3871) does not preserve the area where the "swollen" tuber would be found; however, a clear notch is present on the posterior edge. Therefore, *Marasuchus* is scored as (1). Furthermore, in the original description of *Lewisuchus*, Romer (1972d: fig. 7) illustrates the coracoid with a broken posterior border. Nevertheless, the posterior border is not broken and it possesses a clear notch and a "swollen" tuber.

226. Coracoid, anterior portion: (0) rounded; (1) distinctly hooked (fig. 30) (modified from Sereno, 1991a).

The anterior portion of the coracoid of most archosauriforms is rounded whereas the anterior portion of the coracoid of phytosaurs is hooked (e.g., *Smilosuchus* USNM V18313). Additionally, phytosaurs lack a coracoid foramen (Sereno, 1991a).

227. Glenoid, orientation: (0) posterolaterally; (1) directed posteroventrally (fig. 30) (Fraser et al., 2002).

The glenoid faces posterolaterally in non-archosaurian archosauriforms (e.g., *Erythrosuchus,* BMNH R3592; *Chanaresuchus,* PVL 4575) as well as phytosaurs (*Smilosuchus,* USNM 18313), *Revueltosaurus* (PEFO 34561), aetosaurs (e.g., *Typothorax*, MCZ 1488), and some rauisuchians (*Batrachotomus,* SMNS 80271). In these taxa, the humerus is oriented more laterally then posteriorly. The glenoid is directed posteroventrally in *Postosuchus kirkpatricki* (TTU-P 9000), *Postosuchus alisonae* (UNC 15575), and basal crocodylomorphs (e.g., *Hesperosuchus agilis*, AMNH FR 6758).

Fraser et al. (2002) cited a posteroventrally directed glenoid as a synapomorphy of Dinosauria. However, a posteroventrally directed glenoid is present in *Marasuchus* (PVL 3870) and *Silesaurus* (ZPAL Ab III/362). Thus, the distribution of character state (1) has a wider distribution among avian-line archosaurs.

228. Coracoid, deep fossa on the posterodorsal edge: (0) absent; (1) present (new).

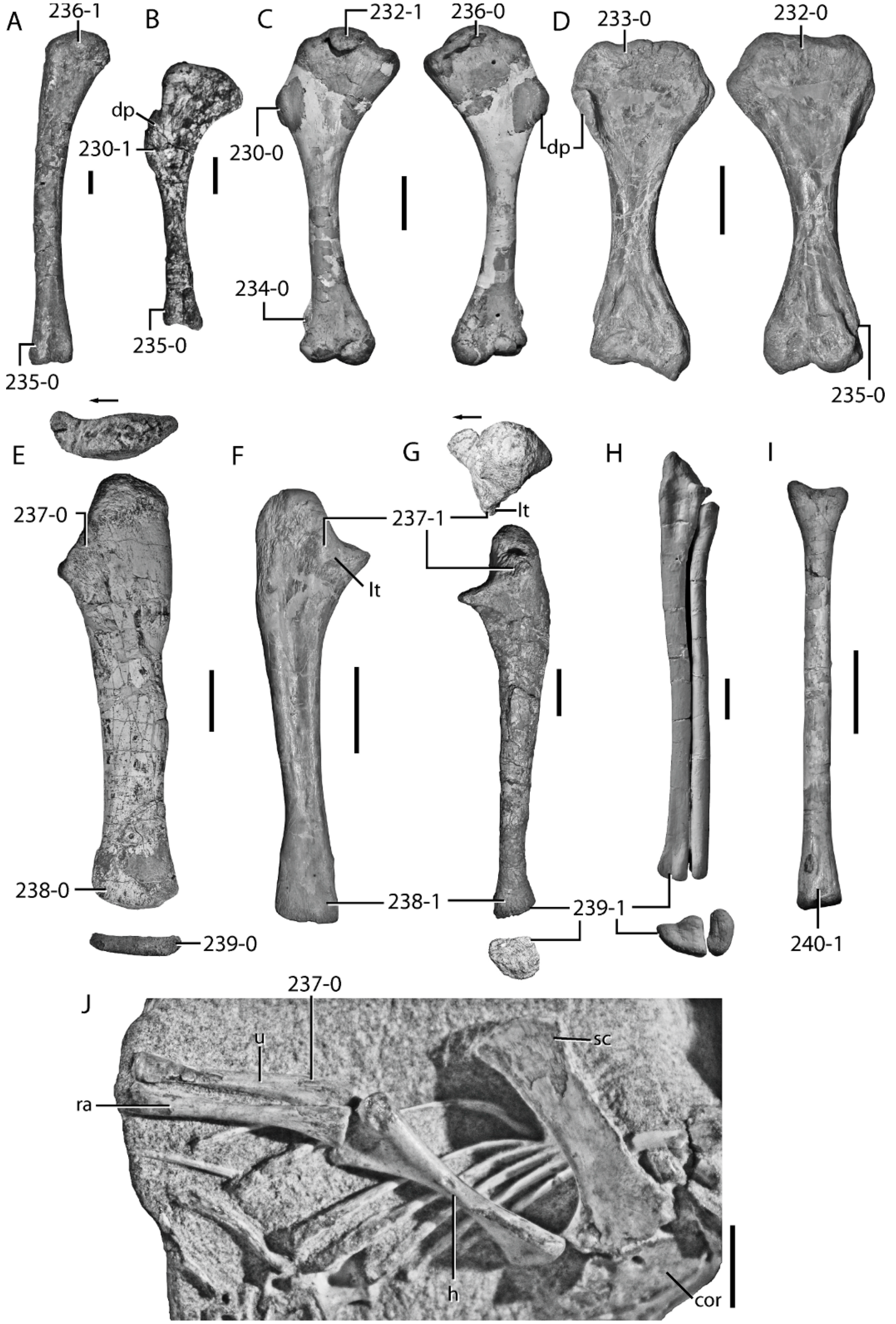
The posterior edge of the coracoid is either rounded or notched (see character 223). The coracoids of *Sillosuchus* (PVSJ 85), *Effigia* (AMNH FR 30587), and *Shuvosaurus* (TTU-P 9001) have an elongated postglenoid process. A deep fossa is located on the dorsal side of the postglenoid process in these forms (Nesbitt, 2007).

229. Coracoid, sharp ridge leading from the glenoid to anteroventral corner: (0) absent; (1) present (new).

The lateral surface of the coracoid of most archosauriforms is smooth. In *Prestosuchus* (UFRGS 0156-T), and a new taxon (= Tanzanian pseudosuchian) there is a sharp ridge leading from the glenoid to anteroventral corner of the coracoid.

FORELIMB

230. Humerus, apex of deltopectoral crest situated at a point corresponding to: (0) less than 30% down the length of the humerus; (1) more than 30% down the length of the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humerus (fig. 31) (modified from Bakker and Galton, 1974; Benton, 1990a; Juul, 1994; Novas, 1996; Benton, 1999).

Langer and Benton (2006) thoroughly discussed the distribution of the character states of this character and find that state (1) is restricted to dinosaurs within Archosauria. Here, I follow the conclusions and scorings of Langer and Benton (2006). Furthermore, the commonly used character "deltopectoral crest on humerus: (0) rounded or pointed (1) subrectangular" is redundant with the character discussed here; a subrectangular deltopectoral crest is a consequence of having a distally elongated crest. *Erythrosuchus* is scored as (1).

231. Humerus, length: (0) longer than or subequal to 0.6 of the length of the femur; (1) shorter than 0.6 of the length of the femur (modified from Novas, 1996; Langer and Benton, 2006).

Langer and Benton (2006) thoroughly discussed the distribution of the character states and find that state (1) is restricted to *Herrerasaurus* (PVSJ 373), *Eoraptor* (PVSJ 512), and neotheropods.

232. Humerus, proximal head: (0) confined to the proximal surface; (1) posteriorly expanded and hooked (fig. 31) (new).

In nearly all archosauriforms, the articular surface of the head of the humerus is confined to the proximal surface of the element. In *Postosuchus kirkpatricki* (TTU-P 9002), *P. alisonae* (UNC 15575), and the crocodylomorphs *Hesperosuchus* (AMNH FR 6758), *Terrestrisuchus* (BMNH R7591b), *Litargosuchus* (BP/1/5237), and *Sphenosuchus* (SAM 3014), the head of the humerus expands posteriorly. The posterior expansion is concave ventral to the articular surface, thus creating a hooked shape.

233. Humerus, proximal articular surface: (0) continuous with the deltopectoral crest; (1) separated by a gap from the deltopectoral crest (fig. 31) (new).

In most archosauriforms, the proximal articular surface is continuous with the dorsal portion of the deltopectoral crest. In most dinosaurs (e.g., *Tawa*), the dorsal portion of the deltopectoral and the proximal surface of the humerus are separated usually by a thin ridge of bone.

234. Humerus, ectepicondylar flange: (0) present; (1) absent (fig. 31) (Benton and Clark, 1988; Gauthier et al., 1988).

Benton and Clark (1988) listed the absence of an ectepicondylar groove as a synapomorphy of archosauriforms whereas in Gauthier et al. (1988) the absence of an ectepicondylar groove is a synapomorphy of *Erythrosuchus* + Archosauria. Even though a groove is not present in *Euparkeria* or proterochampsians, a clear groove is present in phytosaurs (*Smilosuchus*, USNM 18313), aetosaurs (*Stagonolepis,* BMNH R4784; *Aetosaurus,* SMNS 5770 S-5), *Batrachotomus* (SMNS 80275), *Postosuchus kirkpatricki* (TTU-P 9000), *Stagonosuchus* (GPIT/RE/3831), and *Poposaurus* (YPM 57100). In a humerus assigned to the aetosaur *Desmatosuchus* (UCMP A269/32184), the ectepicondylar groove is folded over to create a foramen. An ectepicondylar groove is absent in the crocodylomorphs observed here. Among avian-line archosaurs, an ectepicondylar groove is also present in a humerus (TTM-31000-1329) assigned to the non-dinosauriform dinosauromorph *Dromomeron gregorii* but unknown in any other member.

235. Humerus, distal end width: (0) narrower or equal to 30% of humerus length; (1) greater than 30% of humerus length (fig. 31) (Langer and Benton, 2006).

←

Fig. 31. Forelimb pro- and epipodials of archosauriforms: **A,** left humerus of *Shuvosaurus inexpectatus* (TTU-P unnumbered) in posterior view; **B,** right humerus of *Eocursor parvus* (SAM-PK-0925) in anterior view; **C,** left humerus of *Postosuchus alisonae* (UNC 15575) in posterior (left) and anterior (right) views; **D,** right humerus of *Batrachotomus kuperferzellensis* (SMNS 80275) in anterior (left) and posterior (right) view; **E,** left ulna of *Smilosuchus gregorii* (USNM 18313) in proximal (top), lateral (middle), and distal (bottom) views; **F,** right ulna of *Batrachotomus kuperferzellensis* (SMNS 80275) in lateral view; **G,** left ulna of *Fasolasuchus tenax* (PVL 3850) in proximal (top), lateral (middle), and distal (bottom) views; **H,** left ulna and radius of *Hesperosuchus agilis* (AMNH FR 6758) in medial (top) and distal (bottom) views; **I,** left radius of *Postosuchus alisonae* (UNC 15575) in posterior view. **J,** right forelimb of *Euparkeria capensis* (SAM 5867). Arrow indicates anterior direction. Numbers refer to character states. See appendix for anatomical abbreviations. Scale bars = 5 cm in C–G, I, and 1 cm in A, B, H, J.

As explained by Langer and Benton (2006), the distal width of the humerus is greater than 30% the length of the element in sauropodomorphs.

236. Humerus, proximal portion: (0) expanded more than twice the width of the midshaft of the humerus; (1) expanded less than twice the width of the midshaft of the humerus (fig. 31) (Nesbitt, 2007).

Among archosauriforms, the proximal portion of the humerus is greatly expanded relative to the width of the midshaft. In contrast, the poorly expanded proximal end of the humeri of *Effigia* (AMNH 30587), *Shuvosaurus* (TTU-P 9001) and possibly in *Sillosuchus* (PVSJ 85) are not expanded more than twice that of the midshaft.

237. Ulna, lateral tuber (= radius tuber) on the proximal portion: (0) absent; (1) present (fig. 31) (new).

The proximal portion of the ulna is mediolaterally compressed without a lateral tuber in *Proterosuchus* (NM QR 1484), *Vancleavea* (GR 138), *Euparkeria* (SAM 5867), and phytosaurs (e.g., *Smilosuchus*, USNM 18313). In aetosaurs, *Revueltosaurus* (PEFO 34561), most paracrocodylomorphs, and basal dinosauriforms (e.g., *Marasuchus*, PVL 3870, Dinosauria), a distinct tuber is present on the lateral side of the proximal portion of the ulna.

238. Ulna, distal end in posterolateral view: (0) rounded and convex; (1) squared off where the distal surface is nearly flat (fig. 31) (new).

Among basal archosauriforms, the distal end of the ulna is rounded and convex in posterolateral view in *Proterosuchus* (NM QR 1484), *Vancleavea* (GR 138), *Euparkeria* (SAM 5867), phytosaurs (e.g., *Smilosuchus*, USNM 18313), *Revueltosaurus* (PEFO 34561), and aetosaurs (e.g., *Aetosaurus*, SMNS 5770 S-6). Likewise, all avian-line archosaurs have distal surfaces that are well rounded. The distal end of the ulna is squared off where the distal surface is at nearly a right angles to the shaft surfaces, in *Ticinosuchus* (PIZ T2817), *Fasolasuchus* (PVL 3851), *Batrachotomus* (SMNS 80275), *Postosuchus kirkpatricki* (TTU-P 9002), *P. alisonae* (UNC 15575), *Hesperosuchus agilis* (AMNH FR 6758), *Dromicosuchus* (UNC 15574), *Terrestrisuchus* (BMNH R7562), and *Protosuchus richardsoni* (AMNH FR 3024).

239. Ulna, distal end: (0) anteroposteriorly compressed or rounded; (1) with anterior expansion (fig. 31) (new).

In archosauriforms, the distal end of the ulna typically is anteroposteriorly compressed or rounded. This includes *Proterosuchus* (NM QR 1484), *Erythrosuchus* (SAM 905), *Euparkeria* (SAM 5853), *Revueltosaurus* (PEFO 34561), *Riojasuchus* (PVL 3827), and basal avian-line archosaurs as examples. In contrast, the distal end of the ulna has an expansion on the anterior surface in *Fasolasuchus* (PVL 3851), *Batrachotomus* (SMNS 80275), *Postosuchus kirkpatricki* (TTU-P 9002), *P. alisonae* (UNC 15575), *Hesperosuchus agilis* (AMNH FR 6758), *Dromicosuchus* (UNC 15574), *Terrestrisuchus* (BMNH R7562), *Protosuchus richardsoni* (AMNH FR 3024), and *Alligator*. The anterior expansion tapers to a ridge that extends proximally along the shaft.

240. Radius, distal end: (0) convex; (1) shallow longitudinal groove on the posterior side (fig. 31) (new).

The posterior side of the radius in most archosauriforms is convex and rounded. In *Postosuchus kirkpatricki* (TTU-P 9002), *Postosuchus alisonae* (UNC 15575), *Hesperosuchus agilis* (AMNH FR 6758), and *Revueltosaurus* (PEFO 34561), there is a groove on the posterior side of the radius.

241. Radius, length: (0) longer than 80% of humerus length; (1) shorter than 80% of humerus length (Langer and Benton, 2006).

In most archosauriforms, the humerus and the radius are nearly the same length. The radius is shorter than 80% of humerus in ornithischians, *Saturnalia*, sauropodomorphs, and theropods as detailed by Langer and Benton (2006). However, the radius and the humerus are about the same length in the *Tawa* and *Herrerasaurus* (estimated from PVSJ 407).

242. Proximal carpals (radiale, ulnare): (0) equidimensional; (1) elongate (fig. 32) (Benton and Clark, 1988; Parrish, 1993; Benton and Walker, 2002; Clark et al., 2004).

In most archosauriforms with ossified carpals, the proximal carpals are rounded or cubic. Examples of short proximal carpals include *Proterosuchus* (SAM 160), *Ty-*

pothorax (MCZ 1488), *Riojasuchus* (PVL 3827), *Postosuchus alisonae* (UNC 15575), and *Heterodontosaurus* (SAM-PK-1332). In crocodylomorphs, the proximal carpals are highly elongated and the shafts of the elements resemble those of the limb bones (Benton and Clark, 1988). Elongated proximal carpals are present in *Hesperosuchus* "*agilis*" (CM 29894), *Dromicosuchus* (UNC 15574), *Dibothrosuchus* (IVPP V 7907), *Hesperosuchus agilis* (AMNH FR 6758), *Terrestrisuchus* (BMNH R7557), *Protosuchus richardsoni* (MCZ 6727), and *Orthosuchus* (SAM-K-409).

243. Ulnare, length: (0) shorter than the longest metacarpal; (1) longer than the longest metacarpal (fig. 32) (new).

In crocodylomorphs, the ulnare and radiale are elongated (Benton and Clark, 1988). Within Crocodylomorpha the ulnare and radiale are shorter than the longest metacarpal in *Hesperosuchus* "*agilis*" (CM 29894), *Dromicosuchus* (UNC 15574), *Terrestrisuchus* (Crush, 1984), and *Alligator*. In contrast, the ulnare and radiale are longer than the longest metacarpal in *Dibothrosuchus* (IVPP V 7907), *Orthosuchus* (SAM-K-409), and *Protosuchus richardsoni* (AMNH FR 3024).

244. Pteroid bone: (0) absent; (1) present (Bennett, 1996).

A pteroid bone is a specialized carpal element in pterosaurs. The element articulates with the preaxial carpal (= lateral distal carpal), is directed medially, and controlled the propatagium (Bennett, 2007). A pteroid is present in nearly all pterosaurs including the basal pterosaurs *Eudimorphodon ranzii* (MCSNB 2888) and *Peteinosaurus zambellii* (MCSNB 3359). A pteroid has not been found thus far outside Pterosauria.

245. Longest metacarpal: Longest metatarsal: (0) >0.5; (1) <0.5 (new).

This character attempts to compare the size of the pes with that of the manus. The size of the manus is rather small relative to the pes in most basal archosaurs. Even though the ability to score this character relies on presence of both a complete manus and pes, it can be scored in a variety of basal archosauriforms. Among non-archosaurian archosauromorphs, *Prolacerta* (BP/1/2674), *Proterosuchus* (SAM 140), *Vancleavea* (GR 138) and *Euparkeria* (pes from SAM 5867 scaled to the manus of SAM 13666), the longest metacarpal is longer than 50% of the longest metatarsal. The same is true in phytosaurs (e.g., *Pseudopalatus*, UCMP 27235). The longest metacarpal is longer than 50% the length of the longest metatarsal in most members of Archosauria. Pterosaurs are not scored because of the greatly modified manus. Nevertheless, if the second longest metacarpal is compared to the longest metatarsal, they would be scored as (0) given the proportions in a variety of basal pterosaurs. Among most members of the Archosauria, metacarpal three is usually the longest in the manus whereas metatarsal three is the longest in the pes.

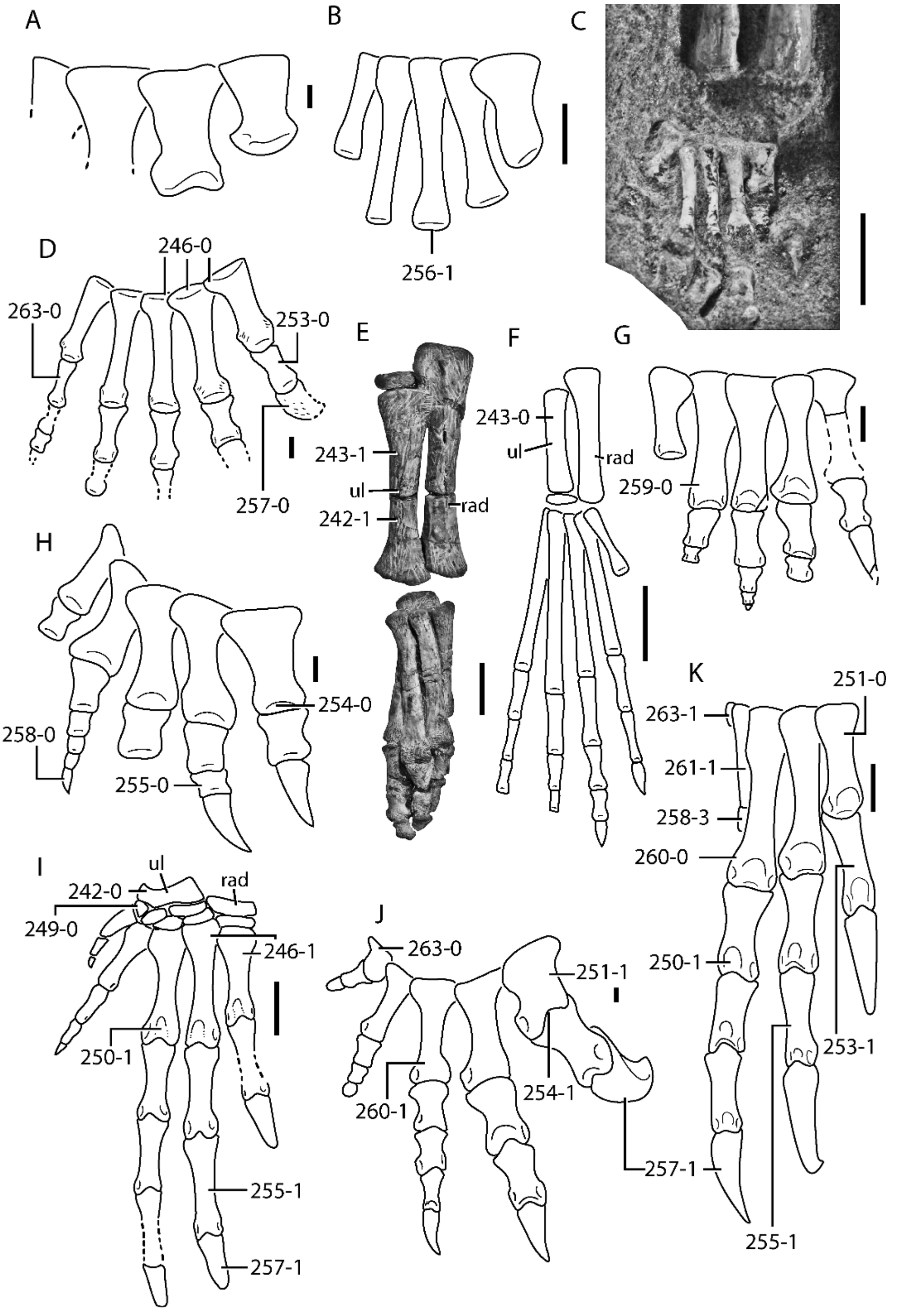
246. Metacarpals, proximal ends: (0) overlap; (1) abut one another without overlapping (fig. 32) (Sereno and Wild, 1992; Clark et al., 2000; Olsen et al., 2000; Benton and Walker, 2002; Sues et al., 2003; Clark et al., 2004).

In most basal archosauriforms, the proximal portions of the metacarpals overlap each other. In this configuration, the contacting surfaces of the metacarpals are imbricated laterally where metacarpal I lies on the anterior/dorsal surface of metacarpal II. Clark et al. (2000), followed by later studies using the same dataset (Clark et al., 2004), scored CM 29894, *Saltoposuchus,* and *Dibothrosuchus* as having abutting metacarpals. However, in these taxa, the metacarpals are imbricated as in *Alligator*.

In avian-line archosaurs, the proximal portions of the metacarpals abut one another in *Herrerasaurus* (PVSJ 373), *Heterodontosaurus* (SAM-PK-1332), and neotheropods examined in this study. Sereno (1999) used a similar character "metacarpals I–III, intermetacarpal articular facets" to unite *Herrerasaurus* and neotheropods.

247. Manual length (measured as the average length of digits I–III): (0) accounts for less than 0.3 of the total length of humerus plus radius; (1) more than 0.3 but less than 0.4 of the total length of humerus plus radius; (2) more than 0.4 of the total length of humerus plus radius. ORDERED (modified from Gauthier, 1986; Langer and Benton, 2006).

248. Medialmost distal carpal: (0) subequal other distal carpals; (1) significantly larger


A
B
256-1
C
D
246-0
263-0
253-0
257-0
E
243-1
ul
242-1
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F
243-0
ul
rad
G
259-0
H
254-0
258-0
255-0
K
251-0
263-1
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258-3
260-0
250-1
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J
263-0
251-1
254-1
260-1
257-1

than other distal carpals (Gauthier, 1986; Langer and Benton, 2006).

The distal carpals are proportionate to the size of the proximal of portion of its metacarpal. Langer and Benton (2006) argue that the enlarged carpal 1 of sauropodomorphs and theropods is homologous. Sauropodomorphs (e.g., *Massospondylus* BP/1/4934) do have an enlarged carpal 1, but this is proportionate with the enlargement of metacarpal I relative to basal members of Dinosauria. In theropods (*Coelophysis*, AMNH FR unnumbered and *Allosaurus* DINO 11541), the carpal capping metacarpal one also caps metacarpal II. This is not the case in sauropodomorphs were a fully formed carpal 2 lies on top of metacarpal II. Here, I suggest that only theropods can be scored as (1). Langer and Benton's (2006) scoring of this is character should not be a eusaurichian synapomorphy and, as a result, this character would not be a character excluding *Herrerasaurus* from Eusaurischia.

249. Distal carpal V: (0) present; (1) absent (fig. 32) (Sereno, 1999; Langer and Benton, 2006).

Langer and Benton (2006) thoroughly described this character and, following Sereno (1999), find that the absence of distal carpal V as a saurischian synapomorphy. However, a juvenile specimen of *Tawa* has distal carpal V, suggesting that (1) either the taxa autapomorphically reevolved a distal carpal V or (2) the distal carpal V may be present in juvenile saurischians, but fused to other distal carpals in more mature individuals.

250. Extensor pits on the proximodorsal portion of metacarpals I–III: (0) absent or shallow and symmetrical; (1) deep and asymmetrical (fig. 32) (modified from Sereno et al., 1993; Langer and Benton, 2006).

Originally, Sereno et al. (1993) used deep extensor pits to unite in *Herrerasaurus* (PVSJ 373) and neotheropods. Later, Sereno (1999) scored *Eoraptor* as (1) and modified the character by including symmetry versus asymmetry to the character. As discussed by Langer and Benton (2006), deep extensor pits are present in *Heterodontosaurus* and basal sauropodomorphs as well. Furthermore, the relative depth and asymmetry of basal dinosaur taxa are difficult to assess as pointed out by Langer and Benton (2006). Nevertheless, Sereno's (1999) character states and scorings are retained here even though this character needs further revision.

251. Metacarpal I, width at the middle of the shaft accounts for: (0) less than 0.35 of the total length of the bone; (1) more than 0.35 of the total length of the bone (fig. 32) (modified from Bakker and Galton, 1974; Langer and Benton, 2006).

252. Digit I with metacarpal: (0) longer than the ungual; (1) subequal or shorter than the ungual (Sereno, 1999; Langer and Benton, 2006).

253. Manual digit I, first phalanx: (0) is not the longest nonungual phalanx of the manus; (1) is the longest nonungual phalanx of the manus (fig. 32) (Gauthier, 1986; Langer and Benton, 2006).

254. Metacarpal I, distal condyles: (0) approximately aligned or slightly offset; (1) lateral condyle strongly distally expanded relative to medial condyle (fig. 32) (modified from Bakker and Galton, 1974, Langer and Benton, 2006; Irmis et al., 2007a).

255. Manual digit II, second phalanx (= 2.2): (0) shorter than first phalanx; (1) longer than first phalanx (fig. 32) (modified from Gauthier, 1986; Langer and Benton, 2006).

256. Metacarpal II: (0) shorter than metacarpal III; (1) equal to or longer than metacarpal III (fig. 32) (Gauthier, 1986; Langer and Benton, 2006; Irmis et al., 2007a).

←

Fig. 32. The right manus of archosauriforms: **A,** *Erythrosuchus africanus* (redrawn from Gower, 2003); **B,** *Vancleavea campi* (based from GR 138); **C,** *Euparkeria capensis* (left manus) (SAM 13666); **D,** *Pseudopalatus* (based from UCMP 27235); **E,** *Dibothrosuchus elaphros* (IVPP V 7907); **F,** *Terrestrisuchus gracilis* (redrawn from Crush, 1984); **G,** *Postosuchus alisonae* (based from UNC 15575); **H,** *Longosuchus meadei* (redrawn from Sawin, 1947); **I,** *Heterodontosaurus tucki* (redrawn from Santa Luca, 1980); **J,** *Plateosaurus engelhardti* (based from AMNH FR 6810); **K,** *Herrerasaurus ischigualastensis* (redrawn from Sereno, 1994). Numbers refer to character states. See appendix for anatomical abbreviations. Scale bars = 1 cm.

257. Manual digits I–III: (0) blunt unguals on at least digits II and III; (1) trenchant unguals on digits I–III (fig. 32) (Gauthier, 1986; Juul, 1994; Benton, 1999; Irmis et al., 2007a).

258. Manual digit IV: (0) five phalanges; (1) four phalanges; (2) one phalanx (fig. 32) (Gauthier, 1986; Benton and Clark, 1988; Sereno et al., 1993; Novas, 1996; Benton, 1999; Irmis et al., 2007a).

259. Metacarpal IV: (0) present; (1) reduced to a nubbin or absent (fig. 32) (Gauthier, 1986).

Metacarpal IV is present in all non-archosaurian archosauriforms, crocodylian-line archosaurs, and nontetanuran avian-line archosaurs. As described by Gauthier (1986) and Rauhut (2003), metacarpal IV is either highly reduced or absent in tetanurans (see Xu et al., 2009, for a different interpretation).

260. Metacarpal IV, length: (0) longest of the metacarpals; (1) about the same length or shorter than metacarpal III (fig. 32) (new).

In *Mesosuchus* (SAM 6046), *Prolacerta* (BP/1/2675), and *Proterosuchus* (SAM 140), metacarpal IV is the longest of the metacarpals in the manus. Alternatively, metacarpal III is longer than or about the same length as metacarpal IV in *Vancleavea* (GR 138), *Euparkeria* (SAM 13666), *Pseudopalatus* (UCMP 27235), *Aetosaurus* (SMNS 5770 S-10), *Ticinosuchus* (PIZ T2817), *Postosuchus kirkpatricki* (TTU-P 9000), *Postosuchus alisonae* (UNC 15575), *Poposaurus gracilis* (YPM 57100), *Hesperosuchus* "*agilis*" (CM 29894) and all avian-line archosaurs sampled in this analysis.

261. Metacarpal IV, shaft width: (0) about the same width as that of metacarpals I–III; (1) significantly narrower than that of metacarpals I–III (fig. 32) (modified from Sereno et al., 1993; Langer and Benton, 2006).

262. Manual digit IV length: (0) less than or equal to 50% of total forelimb length; (1) more than 50% of total forelimb length (Bennett, 1996; Irmis et al., 2007a).

In pterosaurs, manual digit IV is greatly elongated (Bennett, 1996) and only pterosaurs are scored as (1).

263. Manual digit V: (0) possesses one or more phalanges; (1) absent or reduced to a tiny nubbin (fig. 32) (modified from Bakker and Galton, 1974; Langer and Benton, 2006; Irmis et al., 2007a).

PELVIC GIRDLE

264. Ilium, supraacetabular crest (= supraacetabular rim): (0) projects laterally or ventrolaterally; (1) projects ventrally (fig. 34) (Gauthier, 1986).

A supraacetabular crest roofs the acetabulum in all archosauriforms. In nearly all non-archosaurian archosauriforms, crocodylian-line archosaurs, and avian-line archosaurs, the supraacetabular crest projects laterally or ventrolaterally. In *Poposaurus* (FMNH UR 357; YPM 57100), *Effigia* (AMNH FR 30587), *Shuvosaurus* (TTU-P 9001), and *Sillosuchus* (PVSJ 85), the supraacetabular crest projects ventrally at its distal margin. A similar condition is also found in *Coelophysis* (AMNH FR 7224) and *Dilophosaurus* (UCMP 37302). The acetabulum covers the lateral portion of the proximal portion of the femur (Gauthier, 1986) in taxa scored as (1).

265. Ilium, crest dorsal to the supraacetabular crest/rim: (0) absent; (1) present and divides the anterior (= preacetabular) process from the posterior (= postacetabular) process; (2) confluent with anterior extent of the anterior (= preacetabular) process of the ilium (figs. 33–34).

266. Ilium, crest dorsal to the supraacetabular crest/rim: (0) vertical; (1) anterodorsally inclined (figs. 33–34).

267. Ilium, crest dorsal to the supraacetabular crest/rim: (0) thick; (1) thin ridge (fig. 34) (new formulations).

The presence of a crest dorsal to the supraacetabular crest (= rim) has been repeatedly cited as a character uniting various suchian taxa (see review of Gower, 2000) especially taxa traditionally regarded as rauisuchians. The various descriptors (buttress, swelling, supraacetabular crest, rugose ridge) of this feature have led to confusion because they (1) are never described using specific taxa, (2) are vague and later authors have confused the terms when scoring matrices, and (3) only one of them incorporated a wide range of variation. Gower (2000) provided a thorough discussion of the problem and suggested that the

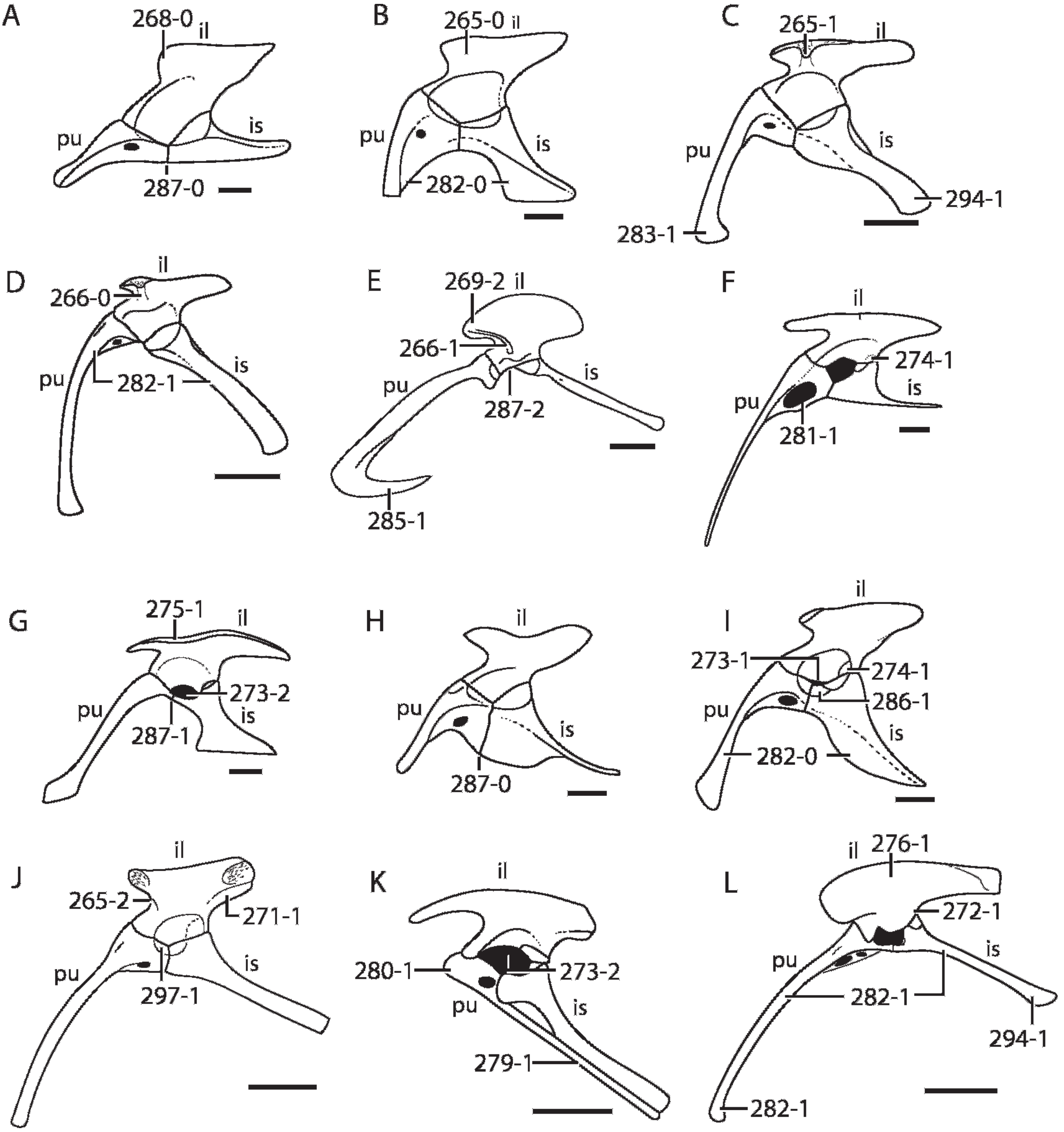


Fig. 33. The pelvic girdle of archosauriforms in lateral view: **A,** *Proterosuchus fergusi* (redrawn from Cruickshank, 1972); **B,** *Chanaresuchus bonapartei* (redrawn from Romer, 1972b); **C,** *Batrachotomus kuperferzellensis* (redrawn from Gower and Schoch, 2009); **D,** *Arizonasaurus babbitti* (redrawn from Nesbitt, 2005a); **E,** *Shuvosaurus inexpectatus* (modified from Long and Murry, 1995); **F,** *Terrestrisuchus gracilis* (redrawn from Crush, 1984); **G,** *Protosuchus richardsoni* (modified from Colbert and Mook, 1951); **H,** *Lagerpeton canarensis* (redrawn from Sereno and Arcucci, 1994a); **I,** *Marasuchus lilloensis* (redrawn from Sereno and Arcucci, 1994b); **J,** *Silesaurus opolensis* (redrawn from Dzik, 2003); **K,** *Lesothosaurus dianosticus* (redrawn from from Sereno, 1991b); **L,** *Coelophysis bauri* (based on AMNH FR 7224). Numbers refer to character states. See appendix for anatomical abbreviations. Scale bars = 5 cm in C–E, J–L, and 1 cm in A, B, F–I.

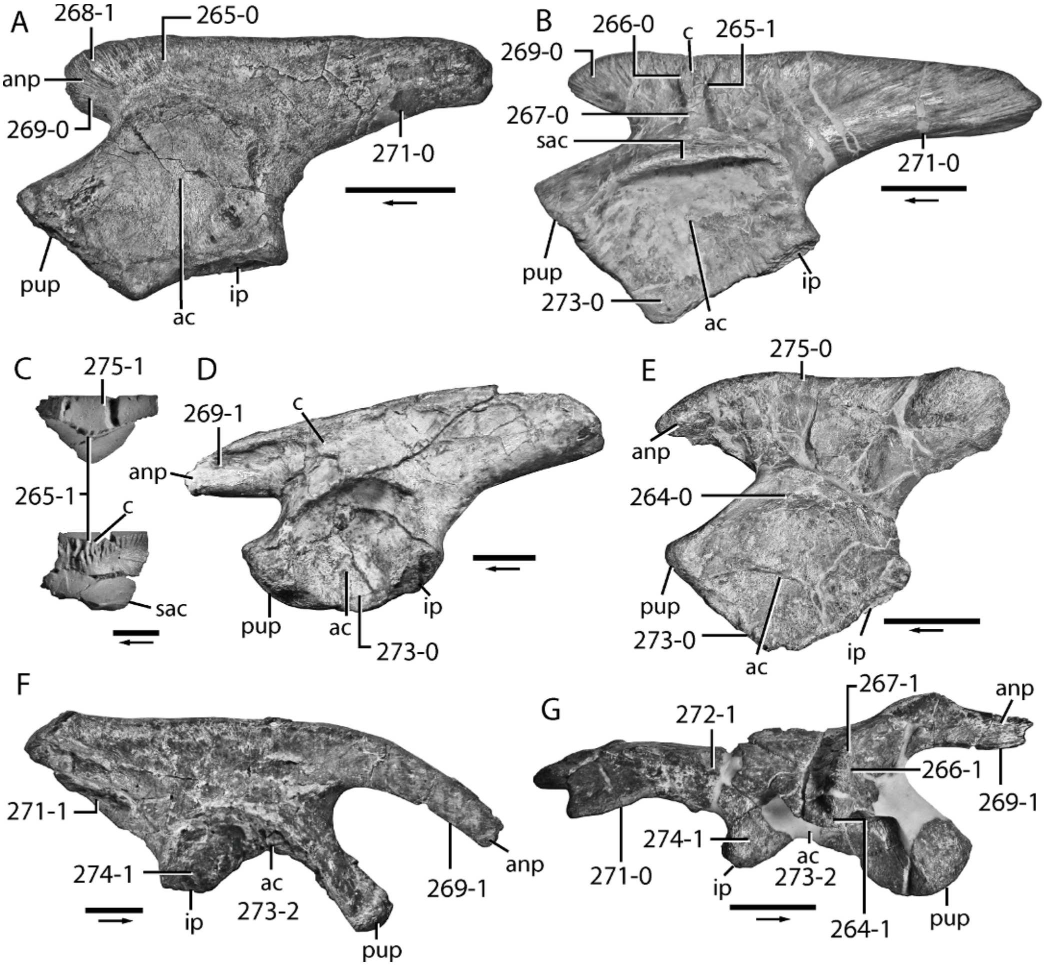


Fig. 34. Archosauriform ilia: **A,** left ilium of Phytosauria (SMNS 52971) in lateral view; **B,** left ilium of *Batrachotomus kuperferzellensis* (SMNS unnumbered) in lateral view; **C,** left ilium fragments of *Hesperosuchus agilis* (AMNH FR 6758) in dorsal (top) and lateral (bottom) views; **D,** left ilium of *Dromicosuchus grallator* (UNC 15574) in lateral view; **E,** left ilium of Aetosauria (UCMP 32422) in lateral view; **F,** right ilium of *Lesothosaurus dianosticus* (SAM 401) in lateral view; **G,** right ilium of *Poposaurus gracilis* (TTU-P 10419) in lateral view. Arrow indicates anterior direction. Numbers refer to character states. See appendix for anatomical abbreviations. Scale bars = 5 cm in A–B, E, G, and 1 cm in C–D, F.

feature must be thoroughly described. A dorsal crest has also been reported in dinosauriforms. Here, the morphology and orientation of the crest dorsal to the supraacetabular crest is discussed and divided into three characters.

Among suchians, a crest dorsal to the supraacetabular crest is present in various forms in *Arizonasaurus* (MSM P4590), *Lotosaurus* (IVPP V V4880 or V4881), *Bromsgroveia* (WARMS G.3), a poposauroid from the Middle Triassic Moenkopi Formation (Nesbitt, 2005b; Schoch et al., 2010), CM 73372, *Postosuchus kirkpatricki* (TTU-P 9002), *Sillosuchus* (PVSJ 85), *Effigia* (AMNH FR 30587), *Shuvosaurus* (TTU-P 9001), *Poposaurus*), *Rauisuchus* (BSP AS XXV-60-121), *Saurosuchus* (PVL 2198), *Batrachotomus* (SMNS 80269), *Dromicosuchus* (UNC 15574), and *Hesperosuchus agilis* (AMNH FR 6758). In these taxa, the dorsal crest separates the anterior (= preacetabular) process from the posterior (= postacetabular) process. The crest of *Dromicosuchus*

(UNC 15574) and *Hesperosuchus agilis* (AMNH FR 6758) expands laterally only at the dorsal margin, which is not as distinct as the vertical, laterally expanded crest in *Postosuchus kirkpatricki* (TTU-P 9002). The crests in *Dromicosuchus* (UNC 15574) and *Hesperosuchus agilis* (AMNH FR 6758) are rugose like that of the dorsal margin of the dorsal crests of *Postosuchus kirkpatricki* and therefore these three taxa are scored as (1).

The crest dorsal to the supraacetabular crest differs in robustness. It is an anteroposteriorly thickened and rounded ridge in *Arizonasaurus* (MSM P4590), CM 73372, *Bromsgroveia* (WARMS G.3), *Postosuchus kirkpatricki* (TTU-P 9002), *Batrachotomus* (SMNS 80269), and *Saurosuchus* (PVL 2198) whereas in *Lotosaurus* (IVPP V4880 or V4881), *Sillosuchus* (PVSJ 85), *Effigia* (AMNH FR 30587), *Shuvosaurus* (TTU-P 9001), and *Poposaurus* (CFMNH 357) it is anteroposteriorly thin. *Dromicosuchus* and *Hesperosuchus agilis* were not scored for this character because their small crests are not like those of taxa scored as (0) or (1).

The crest dorsal to the supraacetabular crest also differs in orientation. It is vertical in *Bromsgroveia, Postosuchus kirkpatricki,* CM 73372, *Batrachotomus,* and *Saurosuchus*, and anteriorly inclined at the dorsal margin in *Lotosaurus, Sillosuchus* (PVSJ 85), *Effigia*, *Shuvosaurus*, *Bromsgroveia*, and *Poposaurus*.

Schoch (2007) reports that a dorsal crest is present in some large specimens of *Aetosaurus* (SAM 5770 S-22), but absent in smaller specimens (SAM 5770 S-20). No other aetosaurs have a crest dorsal to the supraacetabular crest. The "crest" in *Aetosaurus* is nothing more than a rugose region; it is not expanded into a distinct crest like in *Arizonasaurus*.

The ornithosuchids *Riojasuchus* and *Ornithosuchus* and basal dinosauromorphs (e.g., *Marasuchus*, *Silesaurus*, *Herrerasaurus*, *Plateosaurus*) have a crest dorsal to the supraacetabular crest that is confluent with the anterior extent of the anterior (= preacetabular) process of the ilium. All these taxa are scored as not applicable for the second and third supraacetabular crest characters.

268. Ilium, anterior process (preacetabular process) on the dorsal margin: (0) absent; (1) present (figs. 33–34) (Gauthier, 1984; Juul, 1994; Nesbitt et al., 2009a).

A small anteriorly projecting process is present dorsal to the supraacetabular rim in *Erythrosuchus* (BMNH R3592; Gower, 2003), proterochampsians (e.g., *Chanaresuchus*, PVL 4575), *Euparkeria* (Ewer, 1965), and nearly all members of the Archosauria plesiomorphically (see the phylogenetic trees of Gauthier, 1984, and Juul, 1994). The ilium of *Prolacerta* (Gow 1975), *Proterosuchus* (NM QR 1484; Cruickshank, 1972) and non-archosauriform archosauromorphs lack an anteriorly projecting process on the dorsal margin of the ilium. In these taxa, the anterior portion of the dorsal margin of the ilium arc posteriorly. *Vancleavea* (GR 138) lacks an anterior process of the ilium (Nesbitt et al., 2009a).

269. Ilium, anterior (= preacetabular, = cranial) process: (0) short and does not extend anterior to the acetabulum; (1) long and extends anterior to the acetabulum but shorter than the posterior process of the ilium; (2) subequal or longer than the posterior process of the ilium. ORDERED (figs. 33–34) (modified from Galton, 1976; Benton, 1985; Sereno, 1986; Juul, 1994; Gower, 2000; Hutchinson, 2001b; Langer and Benton, 2006; Nesbitt and Norell, 2006; Butler et al., 2008b).

An anterior (= preacetabular) process dorsal to the supraacetabular crest is present in *Erythrosuchus* + Archosauria (see character 268). Plesiomorphically, the anterior process is short and does not expand anterior to the pubic peduncle. This is the case in *Euparkeria* (SAM 6049), proterochampsians (*Tropidosuchus*, PVL 4601), phytosaurs (*Smilosuchus*, USNM 18313), *Gracilisuchus* (PVL 4597), *Turfanosuchus* (IVPP V3237), *Revueltosaurus* (PEFO 34561), *Aetosaurus* (SMNS 5770), *Rauisuchus* (BSP AS XXV-60-121), *Saurosuchus* (PVL 2198), *Arizonasaurus* (MSM P4590), *Batrachotomus* (SMNS unnumbered), *Ticinosuchus* (PIZ T2817), and *Stagonosuchus* (GPIT/RE/3831). The anterior process expands anterior to the pubic peduncle in *Poposaurus* (TMM 43683-1), *Effigia* (AMNH FR 30587), *Shuvosaurus* (TTU-P 9001), *Sillosuchus* (PVL 85), *Typothorax* (MCZ 1488), CM 73372, *Dromicosuchus* (UNC 15574), *Hesperosuchus agilis*

(AMNH FR 6578), *Terrestrisuchus* (BMNH 149-1), and *Protosuchus richardsoni* (AMNH FR 3024). It is worth noting that the anterior process of the aetosaur *Neoaetosauroides* has an elongated anterior process (Desojo and Baez, 2005).

Among avian-line archosaurs, the anterior process is long in pterosaurs, short in non-dinosaurian dinosauromorphs, sauropodomorphs, and elongated in theropods and ornithischians.

270. Ilium, orientation: (0) mainly vertically orientated (0°–20°); (1) ventrolaterally deflected about 45° (modified from Benton and Clark, 1988; Juul, 1994; Benton and Walker, 2002).

The orientation of the ilium has been used as a character since Bonaparte's (1981, 1984) comparison of archosaur pelves. Benton and Clark (1988) first used state (1) to unite aetosaurs and rauisuchians. However, Gower (2000) suggested that the scattered distribution of the character has made the homology of the character unclear. Ventrolaterally deflected ilia are present in the articulated pelvis of a specimen referred to *Postosuchus* (UMMP 7266). The ilia are about 80° ventrolaterally directed. However, the specimen is deformed for three reasons, (1) the sacral ribs have displaced microfactures, (2) one ilium is more ventrolaterally deflected than the other, and (3) a comparably sized ischium in the TTU-P 9000 would be too wide to articulate with the ilium. When these factors are considered, the ilium would be deflected about 40°–60°. In the articulated sacra of *Saurosuchus* (PVSJ unnumbered) and *Postosuchus* (UMMP 7266), the sacral rib facets are ventrolaterally deflected about 45°. This is not to be confused with the orientation of the sacral ribs. For example, in an articulated pelvis of a phytosaur (USNM 18313) the sacral ribs are ventrolaterally deflected, but the articular facets of the sacral ribs are deflected only about 15°. Therefore, the articular surfaces of the sacral ribs, particularly primordial sacral rib one, can be used to determine how much the ilium would be deflected ventrally from disarticulated material.

The sacrals ribs indicate that the ilia of *Arizonasaurus* (MSM P4590), *Batrachotomus* (SMNS 80324), *Stagonosuchus* (GPIT/RE/3831), *Prestosuchus* (BPS XXV 1-3/5-11/ 28-41/49), *Postosuchus kirkpatricki* (TTU-P 9002), CM 73372, and *Hesperosuchus agilis* (AMNH FR 6758) are ventrally deflected about 45° whereas the ilia of *Poposaurus* (YPM 57100), *Sillosuchus* (PVSJ 85), *Effigia* (AMNH FR 30587), and *Shuvosaurus* (TTU-P 9001) have nearly vertical ilia. Aetosaurs also have ventrally deflected ilia (e.g., *Desmatosuchus*, MNA V9300; *Typothorax*, MCZ 1488). Curiously, *Revueltosaurus*, a putative sister taxon of aetosaurs (Parker, 2007) has nearly vertical directed ilia, potentially suggesting that aetosaurs and other crocodylian-line archosaurs scored as (1) may have evolved state (1) independently. Ventrolateral deflection of the ilium is also present in other taxa (e.g., ankylosaur dinosaurs, glyptodonts) with an extensive dorsal carapace formed from osteoderms. As a character measuring the orientation of an element, taphonomic effects should be carefully considered.

271. Ilium, distinct fossa present for the attachment of the caudifemoralis brevis muscle: (0) absent; (1) present as an embankment on the lateral side of the posterior portion of the ilium; (2) present as a deep fossa on the ventral surface of postacetabular part or ilium. ORDERED (figs. 33–34) (modified from Gauthier and Padian, 1985; Gauthier, 1986: Juul, 1994; Novas, 1996; Benton, 1999; Hutchinson, 2001b).

The caudifemoralis brevis muscle attaches to either the lateral or ventral portion of the posterior process of the ilium, just posterior to the acetabulum (Carrano and Hutchinson, 2002). In non-archosaurian archosauriforms and crocodylian-line archosaurs, a muscle scar for the muscle is either very small or absent. In contrast, most dinosaurs have a distinct scar or fossa (= pocket) on either the lateral or ventral side of the ilium. The site and morphology of attachment of the caudifemoralis brevis muscle has been extensively reviewed by Novas (1996) for Dinosauria. Given that *Silesaurus* (ZPAL unnumbered) has a distinct brevis fossa and *Herrerasaurus* (PVL 2566) lacks any kind of brevis fossa, the distribution of the character within dinosaurs character remains to be seen. Furthermore, the basal condition among ornithischians remains unclear. For example, *Heterodonto-*

saurus (SAM-PK-1332) lacks a lateral expression of the brevis fossa whereas *Eocursor* (SAM-PK-0925) has a shallow fossa on the ventral margin of the posterior portion of the ilium, and *Lesothosaurus* (SAM 401) has a distinct lateral scar on the lateral side of the posterior portion of the ilium. Among sauropodomorphs, the basalmost taxon, *Saturnalia* (MCP 3944-PV) has a small brevis fossa whereas *Plateosaurus* (AMNH FR 2107) lacks any kind of brevis fossa. In neotheropods (e.g., *Coelophysis bauri*, AMNH FR 7224; *Dilophosaurus*, UCMP 37302) the attachment of M. caudifemoralis brevis is present as a deep fossa on the ventral surface of postacetabular part or ilium.

272. Ilium, ridge connecting the posterior portion of the supraacetabular rim to the posterior portion of the ilium: (0) absent; (1) present (figs. 33–34) (modified from Langer and Benton, 2006).

A ridge originating from the posterior edge of the supraacetabular rim connects to the posterior portion of the ilium in *Eoraptor* (PVSJ 512), *Coelophysis bauri* (AMNH FR 7224), and *Dilophosaurus* (UCMP 37302).

273. Ilium, ventral margin of the acetabulum: (0) convex; (1) straight; (2) concave (figs. 33–34);

= Waisted area of the ilium between pubic and ischiadic processes (modified from Langer and Benton, 2006).

= Acetabulum: imperforate (0) or extensively perforated (1) (Bakker and Galton, 1974; Gauthier and Padian, 1985; Gauthier, 1986; Juul, 1994; Novas, 1996; Benton, 1999; Fraser et al., 2002; Langer and Benton, 2006).

The ventral margin of the ilium has been used in nearly all basal archosaur phylogenetic datasets. Previous characters focused on the acetabulum being imperforate or perforate. However, these terms are somewhat ambiguous across basal archosaur taxa. Instead, I focus on the ventral margin of the ilium.

In non-archosaurian archosauriforms as well as most crocodylian-line archosaurs, the ischial and pubic peduncles converge at a point ventral to the acetabulum. The resultant shape is convex. In *Qianosuchus* (IVPP V 14300), *Poposaurus* (CFMNH UR 357), *Arizonasaurus* (MSM P4590), *Lotosaurus* (IVPP V4880 or V4881), *Sillosuchus* (PVSJ 85), *Shuvosaurus* (TTU-P 9001), and *Effigia* (AMNH FR 30587), the ventral margin of the ischial peduncle is elongated anteriorly and concave. Therefore, these taxa are scored as (2). Within Crocodylomorpha, the ventral margin of the ilia of *Hesperosuchus agilis* (AMNH FR 6758) and *Dromicosuchus* (UNC 15574) is convex whereas the ventral margin of the ilium of *Dibothrosuchus* (IVPP V 7907), *Kayentasuchus* (UCMP 131830), *Protosuchus richardsoni* (AMNH FR 3024), *Terrestrisuchus* (Crush, 1984), *Orthosuchus* (SAM-PK-409), and *Alligator* is concave.

Among avian-line archosaurs, the ventral margin of the ilium of pterosaurs, *Lagerpeton* (PVL 4619), and *Marasuchus* (PVL 3870; following Novas, 1996) is convex. In *Silesaurus* (ZPAL unnumbered), *Pseudolagosuchus* (PVL 3454), *Asilisaurus kongwe* (NMT RB13), and *Saturnalia* (Langer, 2003), the ventral margin of the ilium is straight. With the exception of *Saturnalia*, all basal dinosaurs have a concave ventral margin of the ilium (Bakker and Galton, 1974; Novas, 1996; Fraser et al., 2002; Langer and Benton, 2006).

274. Ilium, acetabular antitrochanter: (0) absent; (1) present (figs. 33–34) (Sereno and Arcucci, 1994a; Novas, 1996; Benton, 1999; Fraser et al., 2002; Irmis et al., 2007a).

An iliac antitrochanter is defined as a raised surface at the posterior portion of the acetabulum. An acetabular antitrochanter on the ilium is absent in most archosauriforms but present in many disparate archosaur taxa (Fraser et al., 2002). Taxa should be scored only if the ilium is well preserved.

275. Ilium, dorsal margin dorsal to the supraacetabular rim: (0) rounded or sharp; (1) flat (figs. 33–34) (new).

In nearly all archosauriforms, the dorsal margin of the ilium is rounded. In the crocodylomorphs *Hesperosuchus agilis* (AMNH FR 6758), *Dromicosuchus* (UNC 15574), *Terrestrisuchus* (BMNH P72/1), and *Protosuchus* (AMNH FR 3024), the dorsal margin is flat. The dorsal margin of the ilium is also flat in *Coelophysis bauri* (various AMNH specimens) and UCMP 129618, a specimen referred to *Coelophysis* by Padian (1986). The dorsal margin of the ilium of *Coelophysis bauri* (AMNH FR 7224) and *Liliensternus* (MB R. 2175) is rounded.

276. Ilium, dorsal portion: (0) height about the same or shorter than the distance from the dorsal portion of the supraacetabular rim to the pubis-ischium contact; (1) expanded dorsally, height markedly taller than the dorsal portion of the supraacetabular rim to the pubis-ischium contact (new).

In most basal archosauriforms, the height of the region dorsal to the acetabular rim (= acetabular crest) is usually less than height of the acetabulum. In *Effigia* (AMNH FR 30587), *Lotosaurus* (IVPP V 4880 or V 4881), *Shuvosaurus* (TTU-P 9001), and possibly *Sillosuchus* (PVSJ 85), the height of the dorsal portion of the ilium is taller than the height of the acetabulum. Additionally, in theropods (e.g., *Coelophysis bauri*, AMNH FR 7224; *Liliensternus*, MB R. 2175; *Dilophosaurus*, UCMP 37302) the dorsal portion of the ilium is expanded in height.

277. Ilium, ischiadic peduncle orientation: (0) mainly vertical in lateral aspect; (1) well expanded posteriorly to the anterior margin of the postacetabular embayment (Langer and Benton, 2006).

Here, I follow the scoring of Langer and Benton (2006) and score neotheropods as (1).

278. Pubis, length: (0) less than 70% of femoral length; (1) more than 70% or more of femoral length (Novas, 1996).

As described by Novas (1996), the pubis is shorter than 70% of the length of the femur in non-archosaurian archosauriforms, *Lagerpeton* (PVL 4619), and *Marasuchus* (PVL 3870). The pubis is longer than 70% the length of the femur in *Pseudolagosuchus* (PVL 4629), *Silesaurus* (ZPAL Ab III/362), and all dinosaurs plesiomorphically (Novas, 1996). Some suchians also possess an elongated pubis relative to the femur. This includes *Riojasuchus* (PVL 3827), *Gracilisuchus* (PVL 4597), a specimen referred to *Prestosuchus* (UFRGS 152-T), *Poposaurus* (YPM 57100), CM 77372, *Hesperosuchus* (YPM 41198), and *Terrestrisuchus* (BMNH R7562). Aetosaurs (*Aetosaurus*, SMNS 5770) and *Revueltosaurus* (PEFO 34561) possess pubes that are less than 70% of femoral length.

279. Pubis, orientation: (0) anteroventral; (1) rotated posteroventrally to lie alongside the ischium (opisthopubic) (fig. 33) (Sereno, 1986; Butler et al., 2008b).

The pubis projects anteroventrally in nearly all basal archosauriforms other than ornithischians. It projects anteroventrally in *Pisanosaurus* (PVL 3577), whereas it is rotated posteroventrally to lie alongside the ischium in *Heterodontosaurus* (SAM-PK-1332), *Eocursor* (SAM-PK-0925), *Lesothosaurus* (BMNH RUB17), and *Scutellosaurus* (MNA 175).

280. Pubis, prepubic process: (0) absent, anterior margin unexpanded; (1) present, anterior margin expanded into a process (fig. 33) (Sereno, 1986; Butler et al., 2008b).

The prepubic process, an anteriorly expanded process on the anterior portion of the proximal portion of the pubis, is consistently found in all ornithischians except *Pisanosaurus* (Sereno, 1986; Butler et al., 2008b).

281. Pubis, obturator foramen: (0) small; (1) enlarged (fig. 33) (Sereno and Wild, 1992).

The character states used here follow the original character construction of Sereno and Wild (1992). Even though the states are relative terms, it is clear that the obturator opening in *Terrestrisuchus* (BMNH R7557), a pubis assigned to *Saltoposuchus* (SMNS 12596), and a specimen referred to *Hesperosuchus* "*agilis*" from the *Coelophysis* quarry (YPM 41198) is much bigger relative to all basal archosauriforms. Clark et al. (2000) argued that this character was not informative and, at the time, it was not. As noted by Clark et al. (2000), the bone surrounding the obturator foramen is extremely thin and requires exquisite preservation. The status of this character in all other crocodylomorphs is unclear and crocodyliforms lack an obturator foramen altogether. The obturator foramen in *Fasolasuchus* (PVL 3850) is large relative to the proximal portion of the pubis. The taxon is tentatively scored as (1) given that the pubis is incomplete and a relative size of the pubis compared to the size of the obturator foramen cannot be fully assessed. Clearly, the size of the obturator foramen in *Fasolasuchus* is proportionally larger than other non-crocodylomorph crocodylian-line archosaurs. This character cannot be scored in *Postosuchus*, *Rauisuchus*, *Polonosuchus silesiacus* (ZPAL Ab III/563), or CM 73372.

282. Pubis, length: (0) shorter or subequal to the ischium; (1) longer than ischium (fig. 33) (modified from Benton and Clark, 1988; Juul, 1994; Novas, 1996; Benton, 1999; Benton and Walker, 2002).

The length of the pubis versus the ischium varies among basal archosaurs and has been used as a character since Benton and Clark (1988). The length of each element is taken from the acetabular margin to the distal surface of each element. The ischium and pubis are nearly the same length in non-archosaurian archosauriforms and in *Revueltosaurus* (PEFO 34561), aetosaurs, phytosaurs, *Ticinosuchus* (Krebs 1965), *Batrachotomus* (Gower and Schoch, 2009), pterosaurs, *Lagerpeton*, and *Marasuchus* (Novas, 1996). The pubis is clearly longer than the ischium in dinosaurs (e.g., *Coelophysis bauri*, AMNH FR 7224) and a subset of pseudosuchians (e.g., *Poposaurus*, YPM 57100; *Terrestrisuchus*, BMNH P72/1).

283. Pubis, distal end: (0) unexpanded; (1) expanded relative to the shaft (= pubic boot) (fig. 33) (Gauthier, 1986; Sereno and Novas, 1992; Juul, 1994; Benton, 1999; Rauhut, 2003; Langer and Benton, 2006; Nesbitt, 2007).

The clear expansion of the distal margin of the pubis is documented in a number of suchians such as *Postosuchus alisonae* (UNC 15575) and *Arizonasaurus* (MSM P4590) and in dinosaurs such as *Herrerasaurus* (PVL 2566) and nearly all neotheropods. Much controversy has surrounded the presence/absence of an expansion in taxa with smaller expansions. For example, the holotype of *Hesperosuchus agilis* (AMNH FR 6758) bears a small posterior expansion on the distal end of the pubis. Basal archosaur workers have mostly considered crocodylomorphs to lack any expansion at the distal end of the pubis (Juul, 1994). Wu and Chatterjee (1993) scored *Hesperosuchus*, *Saltoposuchus*, *Protosuchus*, and *Alligator* as having a bulge, but considered it different than the condition in *Postosuchus*. They never tested the homology of the conditions in *Postosuchus* and crocodylomorphs. Furthermore, there is no evidence for either *Protosuchus* or *Alligator* having a knob at the distal end of the pubis. In non-archosaurian archosauriforms and clades such as the phytosaurs and taxa such as *Gracilisuchus* (PVL 4597), and *Revueltosaurus* (PEFO 34561), an expansion is scored as (0). Aetosaurs have little or no bulge at the distal end of the pubis. However, there is a clear pubic expansion in *Aetosauroides* (PVL 2073) like that of *Postosuchus* and *Hesperosuchus*.

In basal dinosaurs, the presence of a distal expansion of the pubis has been cited by many basal archosaur workers and was recently commented on by Langer and Benton (2006). They observe a slight bulge in *Plateosaurus*, *Eoraptor*, and *Saturnalia* and score this expansion as homologous to that of *Herrerasaurus* and neotheropods whereas other workers do not consider these taxa to have any expansion (e.g., Gauthier, 1986; Rauhut, 2003). Further, Langer and Benton (2006) distinguish the morphology of the distal expansion of the pubis of *Herrerasaurus* and *Staurikosaurus* from that of other basal archosaurs. They suggest that the pubis is folded medially in *Herrerasaurus* and *Staurikosaurus*. Although I agree the pubic expansion of *Herrerasaurus* (PVL 2566) is unique in having a large triangular expansion and that the lateral margin is inset distally in anterior view, the condition in *Staurikosaurus* (MCZ 1669) is much like that of theropods in which the lateral margin is not inset. Therefore, the divergent morphology of the expansion in *Herrerasaurus* should be considered an autapomorphy of the taxon, but the presence of the distal expansion should be considered homologous to that of neotheropods when scored. Similarly, I do not consider the expansion of the distal portion of the pubis of *Marasuchus* homologous with that of taxa with an expansion. In *Marasuchus* (PVL 3870), the lateral edge gradually arcs posteriorly and does not form a distinct bulge or a distinct lateral process. I follow Sereno and Arcucci (1994b) in considering this character in *Marasuchus* to be an autapomorphy of the taxon. Here, I score all taxa with an expansion as (1).

284. Pubis, expanded distal margin: (0) mediolaterally thick and rounded; (1) mediolaterally thin (fig. 35) (Gauthier, 1986; Juul, 1994; Benton, 1999).

In both crocodylian- and avian-line archosaurs, taxa with an expanded distal end of the pubis can be separated into two distinct

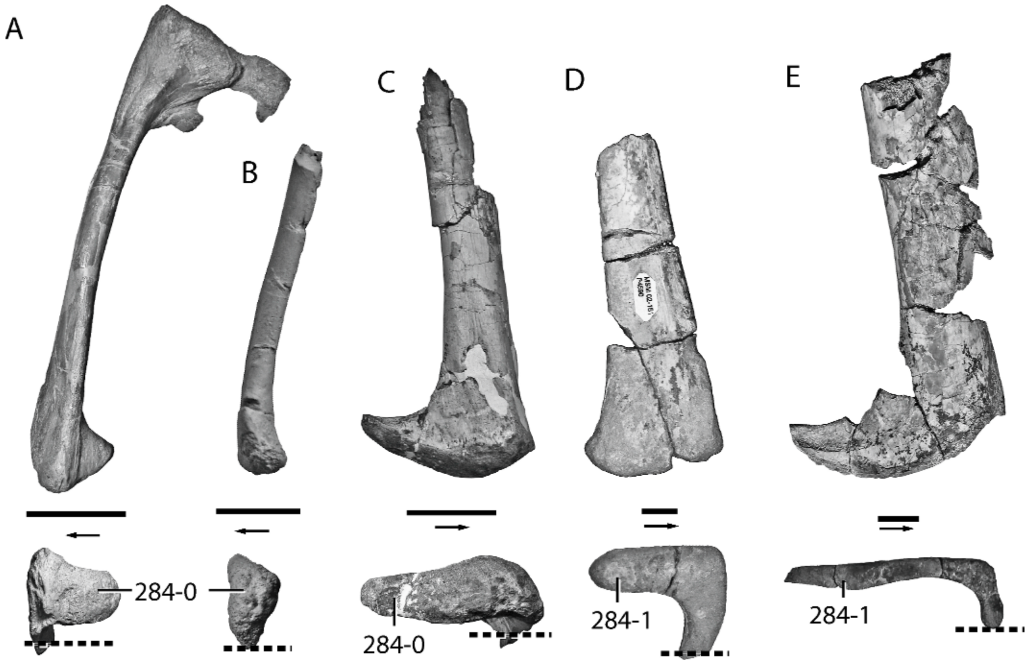


Fig. 35. Distal portion of the pubis of paracrocodylomorphs displaying a posteriorly expanded distal end (283-1): **A–E,** distal end of the pubis in lateral (upper) and distal (lower) views. **A,** *Batrachotomus kuperferzellensis* (SMNS 80279) Note: the plaster surrounding the obturator foramen was erased in this figure; **B,** *Hesperosuchus agilis* (AMNH FR 6758); **C,** *Postosuchus alisonae* (UNC 15575); **D,** *Arizonasaurus babbitti* (MSM 4590); **E,** *Poposaurus gracilis* (TMM 43683-1). Arrow indicates anterior direction and dotted line identifies the midline. Numbers refer to character states. Scale bars = 5 cm in A, C, and 1 cm in B, D–E.

morphologies, a distal expansion that is expanded for the mediolateral length of the distal end or an expansion that largely is restricted to the lateral edge of the distal end of the pubis. Furthermore, taxa scored as (0) have a distal expansion that is rounded and mediolaterally thick whereas the distal expansion is mediolaterally compressed in taxa scored as (1). Generally, in taxa scored as (0), the pubic expansions touch at the midline whereas in taxa scored as (1), the distal expansions are well separated from each other. These shapes can easily be distinguished in ventral view.

In crocodylian-line archosaurs with a distal expansion of the pubis, taxa such as *Prestosuchus* (BSP XXV 1-3/5-11/ 28-41/49), *Batrachotomus* (SMNS 80270), *Postosuchus alisonae* (UNC 15575), and *Hesperosuchus* (AMNH FR 6758) have pubic expansions that are scored as (0). In *Arizonasaurus* (MSM P4590), *Poposaurus* (TMM 43683-1), and *Effigia* (AMNH FR 30587), the distal expansion is restricted to the lateral margin of the pubis and is L-shaped in ventral view.

The dichotomy in the morphology of the distal expansion of the pubis in crocodylian-line archosaurs closely resembles that of dinosaurs. For example, the distal expansion of the pubis in *Eoraptor* (PVSJ 512) and *Saturnalia* (MCP 3844-PV) and other sauropodomorphs are mediolaterally expanded and are rounded in distal view. In contrast, the distal pubic expansions of basal theropods, *Staurikosaurus* (MCZ 1669), and *Herrerasaurus* (PVL 2566) are mediolaterally thin and restricted to the lateral margin of the pubis.

285. Pubis, expanded distal margin: (0) shorter than 33% of the length of the shaft of the pubis; (1) greater than 33% of the length of the shaft of the pubis (fig. 33) (Nesbitt and Norell, 2006; Nesbitt, 2007).

The distal expansion of the pubis of most archosaurs is small, well shorter than 33% of

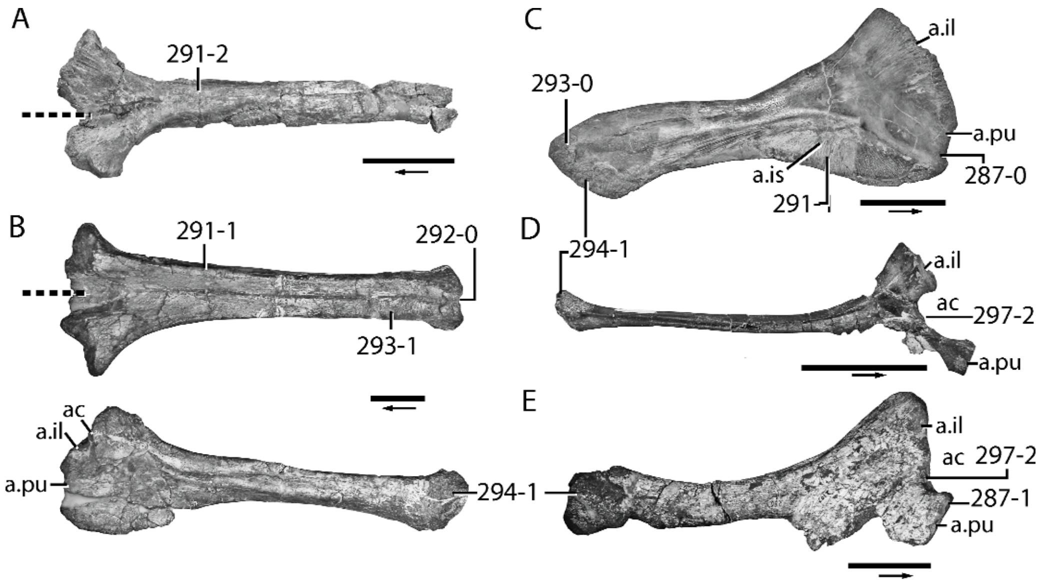


Fig. 36. Archosauriform ischia: **A,** ischia of *Effigia okeeffeae* (AMNH FR 30587) in dorsal view; **B,** ischia of *Postosuchus kirkpatricki* (TTU-P 9000) in dorsal (top) and lateral (bottom) views; **C,** left ischium of *Batrachotomus kuperferzellensis* (SMNS 80268) in medial view; **D,** right ischium of a coelophysoid (NMMNH 29047) in lateral view; **E,** right ischium of *Plateosaurus engelhardti* (AMNH FR 2107) in lateral view. Arrow indicates anterior direction and dotted line identifies the midline. Numbers refer to character states. See appendix for anatomical abbreviations. Scale bars = 5 cm.

the length of the shaft of the pubis. In contrast, the expanded distal ends of the pubes of *Effigia* (AMNH FR 30587) and *Shuvosaurus* (TTU-P 9001) are posteriorly elongated to about 33% the length of the shaft of the pubis.

286. Pubis, proximal portion: (0) articular surfaces with the ilium and the ischium continuous; (1) articular surfaces with the ilium and the ischium separated by a groove or gap (fig. 33) (new).

Among basal archosauriforms, the articular surfaces of the ilium and the ischium are continuous in most clades. *Silesaurus* (Dzik, 2003) and *Asilisaurus kongwe* (NMT RB12) share a deep groove separating the articular surface of the ilium and the ischium. Among dinosaurs, ornithischians have a continuous articular surface for the ilium and ischium (e.g., *Heterodontosaurus*, SAM-K-1332; *Lesothosaurus*, SAM 401) whereas there is a gap between the ischial and iliac articulations in saurischians. Because the ornithischians used in this analysis are scored as (0), the presence of an open acetabulum is not redundant.

287. Ischium-pubis, contact: (0) present and extended ventrally; (1) present and reduced to a thin proximal contact; (2) absent (figs. 33, 36) (modified from Benton and Clark, 1988; Novas, 1996).

The contact between the ischium and pubis is extensive in non-archosaurian archosauriforms, aetosaurs, phytosaurs, basal pterosaurs, and *Lagerpeton* (PVL 4619). In these taxa, the contact between the two elements extends ventrally or ventromedially. In contrast, the contact between the pubis and ischium is restricted to the proximal margins of the elements in the following examples among crocodylian-line archosaurs: ornithosuchids, *Gracilisuchus* (PVL 4597), *Arizonasaurus* (MSM P4590), *Batrachotomus* (SMNS 80270), and *Terrestrisuchus* (BMNH R7562). Among avian-line archosaurs, the ischium and pubis have a reduced contact in *Marasuchus* (PVL 3870), *Pseudolagosuchus* (PVL 4629), *Silesaurus* (ZPAL Ab III/361), and all basal dinosaurs. The ischium and pubis do not contact each other in *Effigia* (AMNH FR 30587), *Shuvosaurus* (TTU-P 9001, other uncatalogued specimens), and *Arizonasaurus* (MSM P4590). This character can be scored from isolated pubes and ischia as long as the anterior portion is well preserved.

288. Pubis, pubic apron, proximal portion: (0) similar anteroposterior thickness as the rest of the pubic apron; (1) thickened process (Nesbitt, 2005a, 2007).

Plesiomorphically, the medial margin of the pubis (= pubic apron) has a relatively similar anteroposteriorly thickness for the length of the element. In *Poposaurus* (TTU-P 10419), *Arizonasaurus* (MSM P4590), *Shuvosaurus* (various TTU-P specimens), and *Effigia* (AMNH FR 30587), an anteroposteriorly thickened process is located at the proximal portion of the pubic apron. The particularly thickened process in *Effigia* (AMNH FR 30587) possesses a distinct platform for articulation with its antimere.

289. Pubis, mediolateral width of distal portion: (0) nearly as broad as proximal width; (1) significantly narrower than proximal width; (2) mediolaterally compressed and not broader than anteroposteriorly deep (Galton, 1976; Novas, 1996; Sereno, 1999; Langer and Benton, 2006).

This character compares the distal width of the pubic apron versus the proximal width in anterior view. In all non-archosaurian archosauriforms, the distal and proximal width of the pubis are similar. This is also true of *Lagerpeton* (PVL 4619), *Marasuchus* (PVL 3870), and possibly basal pterosaurs among avian-line archosaurs. This is the case among phytosaurs, *Revueltosaurus* (PEFO 34561), aetosaurs, *Gracilisuchus* (PVL 4597), and the ornithosuchid *Riojasuchus* (PVL 3827). Among crocodylian-line archosaurs, for example, *Arizonasaurus* (MSM P4590), *Effigia* (AMNH FR 30587), and the crocodylomorph *Hesperosuchus* (YPM 41198), the width of the distal portion of the pubic apron is less than that of the proximal portion. This is also apparent in *Pseudolagosuchus* (PVL 4629), *Silesaurus* (Dzik, 2003: fig. 12D), *Herrerasaurus* (PVL 2566), *Staurikosaurus* (MCZ 1667), and the neotheropod *Coelophysis bauri* (AMNH 7224). Ornithischians are scored as inapplicable because of the divergent morphology of the pubis. Sauropodomorphs (e.g., *Saturnalia* MCP 3844-PV, *Plateosaurus* AMNH FR 6810) have a pubic apron with similar distal and proximal widths. *Allosaurus* and *Velociraptor* are scored as (2) here following Sereno (1999), and *Effigia* and *Shuvosaurus* are also scored as (2).

290. Pubis, lateral side of the shaft: (0) smooth; (1) elongated ridge (new).

In nearly all archosauriforms, the lateral side of the shaft of the pubis is smooth. In contrast, the lateral side of the pubis in both *Effigia* (AMNH FR 30587) and *Shuvosaurus* (various specimens at TTU-P) bears an elongated (50% the length of the element) and sharp ridge.

291. Ischium, medial contact with antimere: (0) restricted to the medial edge; (1) extensive contact but the dorsal margins are separated; (2) extensive contact and the dorsal margins contact each other. ORDERED (fig. 36) (new).

In non-archosaurian archosauriforms, the ischia meet at the midline in a simple contact restricted to the medial edge of the elements. This is also present in phytosaurs, *Revueltosaurus* (PEFO 34561), aetosaurs, *Gracilisuchus* (PVL 4597), *Terrestrisuchus* (BMNH R7562), *Alligator*, *Lagerpeton* (PVL 4619), and *Marasuchus* (PVL 3870). In taxa traditionally referred to as "rauisuchians," the ischia contact each other at the midline in a dorsoventrally expanded contact surface. In *Effigia* (AMNH FR 30587), *Shuvosaurus* (TTU-P 9001), and *Sillosuchus* (PVSJ 85), the entire medial side of the ischia meet and are strongly sutured at the midline (scored as [2]). Unfortunately, the ischia are not known in most basal crocodylomorphs. Among dinosauriforms, the ischia of *Silesaurus* (ZPAL Ab/III 363) and dinosaurs have extensive ischial contact, but the dorsal margins are separated.

Note: The reconstruction of the midline contact between the ischia in *Silesaurus* is incorrect in the reconstruction of Dzik (2003: fig. 12E). Scars on medial side of the ischia indicate that the ischia were in contact along the midline for most of the length of the elements.

292. Ischia, distal margin in dorsal view: (0) midline contact to the distal end; (1) midline gap between the distal ends (fig. 36) (new).

In most archosauriforms, the ischia meet at the midline for most of the length of the elements. Further, the ischia touch at the midline at their posterior termination. This is exemplified in *Euparkeria* (SAM 6049) and *Lagerpeton* (PVL 4619). Alternatively, in *Gracilisuchus* (PVL 4597) and *Ornithosuchus* (BMNH R3561), the ischia diverge distally.

293. Ischium, cross section of the distal portion: (0) platelike; (1) rounded or semicircular; (2) subtriangular (fig. 36) (modified from Sereno, 1999; Langer and Benton, 2006; Irmis et al., 2007a).

The ischium of non-archosaurian archosauriforms is platelike or dorsoventrally thin. This also true of phytosaurs, aetosaurs, *Revueltosaurus* (PEFO 34561), *Gracilisuchus* (PVL 4597), *Ticinosuchus* (PIZ T2817), and *Batrachotomus* (SMNS 80268). Among avian-line archosaurs, the outline of the distal portion of the ischium is platelike in basal pterosaurs, *Lagerpeton* (PVL 4619), *Marasuchus* (PVL 3870), *Silesaurus* (ZPAL Ab III/ 363), and ornithischians. Among crocodylian-line archosaurs, the ischium of *Arizonasaurus* (MSM P4590), *Sillosuchus* (PVSJ 85), *Effigia* (AMNH FR 30587), *Stagonosuchus* (GPIT/RE/3832), *Postosuchus* (TTU-P 9000), ischia assigned to *Saurosuchus* (PVL 2198-3; Sill, 1974), and CM 73372, has a circular outline in distal view. Among avian-line archosaurs, the ischium of *Eoraptor* (PVSJ 512) and theropods has a rounded outline in distal view whereas the ischia have a subtriangular shape in distal view in *Herrerasaurus*, *Saturnalia*, and sauropodomorphs (following the scoring of Langer and Benton, 2006).

294. Ischium, distal portion: (0) unexpanded; (1) expanded relative to the ischial shaft (= ischial boot) (figs. 33, 36) (Smith and Galton, 1990; Holtz, 1994; Hutchinson, 2001b; Rauhut, 2003; Langer and Benton, 2006).

An expansion at the distal end of the ischium is absent in non-archosaurian archosauriforms and many clades of archosaurs. In these taxa, the shaft of the ischium has similar dimensions to its termination. A distal expansion has been well documented in basal dinosaurs (Smith and Galton, 1990; Holtz, 1994; Hutchinson, 2001b; Rauhut, 2003; Langer and Benton, 2006) and seems to be a eusaurischian synapomorphy (see Langer and Benton, 2006). *Asilisaurus kongwe* (Nesbitt et al., 2010) has a large distal expansion and seems to be the only clear example outside Eusaurischia to have state (1).

A distal expansion of the ischium also is present in a number of crocodylian-line archosaurs. This includes *Stagonosuchus* (GPIT/RE/3832), *Poposaurus* (YPM 57100), and, to a lesser extent, *Arizonasaurus* (MSM P4590), *Batrachotomus* (SMNS 80268), *Postosuchus kirkpatricki* (TTU-P 9000), a specimen referred to *Saurosuchus* (PVL 2198-3), *Ticinosuchus* (PIZ T2817), and *Prestosuchus* (BPS 34). The only non-crocodyliform crocodylomorph taxon for which there is a well-preserved ischium, *Terrestrisuchus*, lacks an expansion, as do all crocodyliforms.

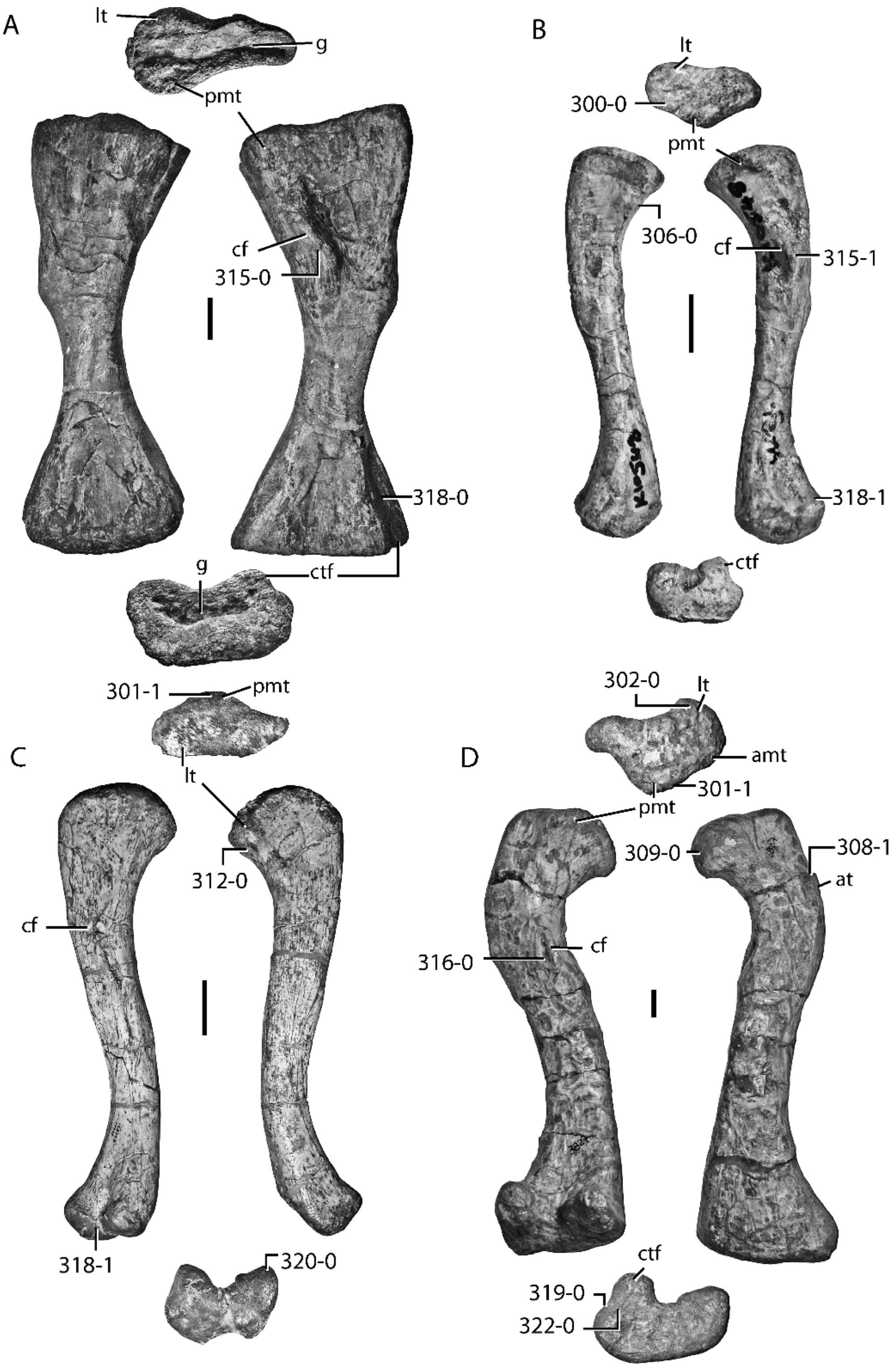
295. Ischium, obturator process: (0) confluent with the pubic peduncle; (1) offset from the pubic peduncle by a notch (Gauthier, 1986; Novas, 1993; Rauhut, 2003).

Rauhut (2003) discussed this character at great length and found that most tetanuran theropods possess state (1). An offset obturator process is absent in all nontetanuran archosauriforms. Here, only *Allosaurus* and *Velociraptor* are scored as (1).

296. Ischium, ventral margin: (0) continuous ventral margin; (1) notch present; (2) abrupt change in angle between the proximal end and the shaft (modified from Sereno et al., 1996; Rauhut, 2003).

In non-archosaurian archosauriforms, most crocodylian-line archosaurs, and nontheropod avian-line archosaurs, the ventral margin of the ischium is continuous. Rauhut (2003) found that a distinct notch on the ventral edge of the ischium is a synapomorphy of neotheropods. Among crocodylian-line archosaurs, *Prestosuchus* (BSP XXV 1-3/ 5-11/ 28-41/49, UFRGS 0152-T) and *Stagonosuchus* (GPIT/RE/3832) bear an abrupt change in angle between the proximal end and the shaft of the ventral margin the ischium.

297. Ischium, proximal articular surfaces: (0) articular surfaces with the ilium and the pubis continuous; (1) articular surfaces with the ilium and the pubis continuous but separated by a fossa; (2) articular surfaces with the ilium and the pubis separated by a nonarticulating concave surface. ORDERED (figs. 33, 36) (modified from Irmis et al., 2007a).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The proximal portion of the ischium articulates with both the ilium and the ischium. In most archosauriform taxa, these two articular facets are connected. In *Marasuchus* (PVL 3870), *Silesaurus* (ZPAL Ab III/362), and *Asilisaurus kongwe* (NMT RB12), the articular facets are still continuous, but a distinct fossa is present on the lateral surface between the two articular facets. In dinosaurs, the ischium is divided into two distinct articular facets, one for the ilium and one for the ischium, separated by a concave surface. This character may be correlated with the opening of the acetabulum. This, however, illustrates not only that the medial wall of the acetabular region of the ilium was lost, but the morphology of the proximal portion of the ischium also changed when the acetabulum became opened laterally.

298. Ischium length: (0) about the same length or shorter than the dorsal margin of iliac blade; (1) markedly longer than the dorsal margin of iliac blade (Juul, 1994; Nesbitt et al., 2009a).

This character measures the length of the ischium versus the length of the dorsal margin of the ilium. The dorsal margin of the ilium remains relatively the same length in archosauriforms and early members of the Archosauria whereas the ischium elongates relative to the dorsal margin of the ilium in taxa close to Archosauria and within it.

Hind Limb

299. Tibia (or fibula)-femur length: (0) femur longer or about the same length as the tibia; (1) tibia longer (modified from Gauthier, 1986; Sereno, 1991a; Juul, 1994; Benton, 1999; Irmis et al., 2007a).

The length of the femur versus the tibia has been used as a character since the beginning of basal archosaur phylogenetics and little can be added to the previous discussions. The femur is consistently longer than the tibia in non-archosaurian archosauriforms and in crocodylian-line archosaurs. Among avian-line archosaurs, the tibia is longer than the femur in basal pterosaurs (e.g., *Preondactylus* 1770 MFSN), *Lagerpeton* (PVL 4619), *Dromomeron* (GR 235), *Marasuchus* (PVL 3870), *Pseudolagosuchus* (PVL 4692), basal ornithischians, *Eoraptor,* and small basal theropods. The tibia is about the same length as the femur in large theropods, nearly all sauropodomorphs, and *Silesaurus* (ZPAL Ab III/362). It may be argued that large body size may be responsible for this pattern; however, the femur/tibia length ratio in the small sauropodomorph *Saturnalia* (MCP 3844-PV) is similar to that of large nonsauropod sauropodomorphs such as *Plateosaurus* (AMNH FR 6810).

300. Femur, proximal portion, anteromedial tuber: (0) absent; (1) small and rounded; (2) offset medially (or posteriorly) relative to the posteromedial tuber; (3) large and "hooked" posteriorly (figs. 37–39) (modified from Gauthier, 1986; Benton, 1999; Clark et al., 2000; Olsen et al., 2000; Benton and Walker, 2002; Sues et al., 2003; Clark et al., 2004).

301. Femur, proximal portion, posteromedial tuber: (0) present and small; (1) present and largest of the proximal tubera; (2) absent (figs. 37–39) (modified from Novas, 1996; Nesbitt, 2005a; Irmis et al., 2007a).

302. Femur, proximal portion, anterolateral tuber: (0) present as an expansion; (1) absent, the anterolateral face is flat (fig. 37, 39) (modified from Sereno and Arcucci, 1994a; Irmis et al., 2007a).

Basal archosaur workers have long examined the proximal portion of the femur,

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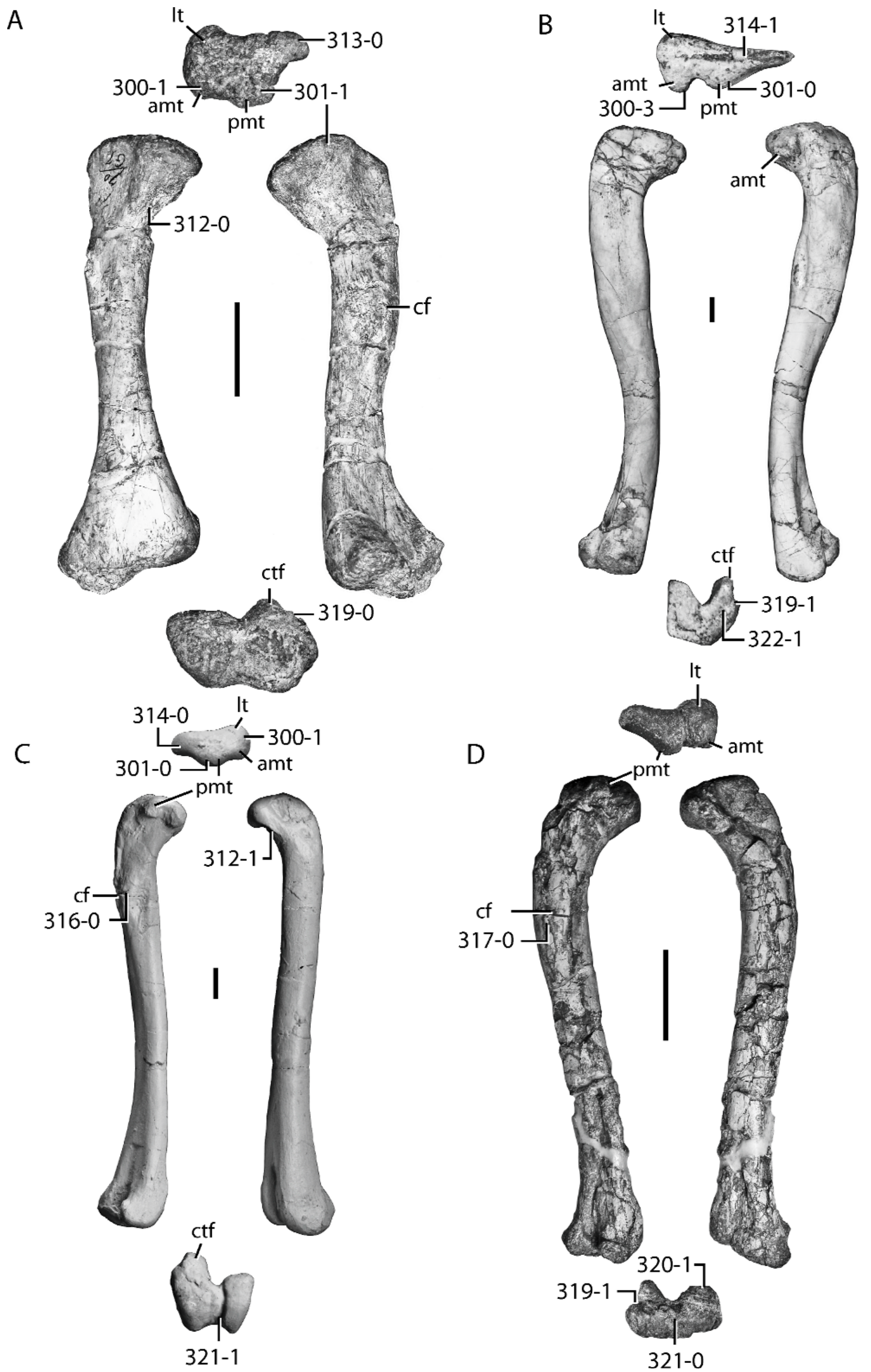
Fig. 37. Archosauriform femora: **A,** right femur of *Erythrosuchus africanus* (BMNH R3592) in proximal (top), dorsal (middle left), ventral (middle right), and distal (bottom) views. Femur orientation following Gower (2003); **B,** right femur of *Euparkeria capensis* (SAM 10548) in proximal (top), anterolateral (middle left), posteromedial (middle right), and distal (bottom) views; **C,** left femur of *Pseudopalatus* (UCMP 122078) in proximal (top), posteromedial (middle left), anterolateral (middle right), and distal (bottom) views; **D,** left femur of *Riojasuchus tenuisceps* (PVL 3827) in proximal (top), posteromedial (middle left), anterolateral (middle right), and distal (bottom) views. Arrow indicates anterior direction. Numbers refer to character states. See appendix for anatomical abbreviations. Scale bars = 5 cm in A,C, and 1 cm in B, D.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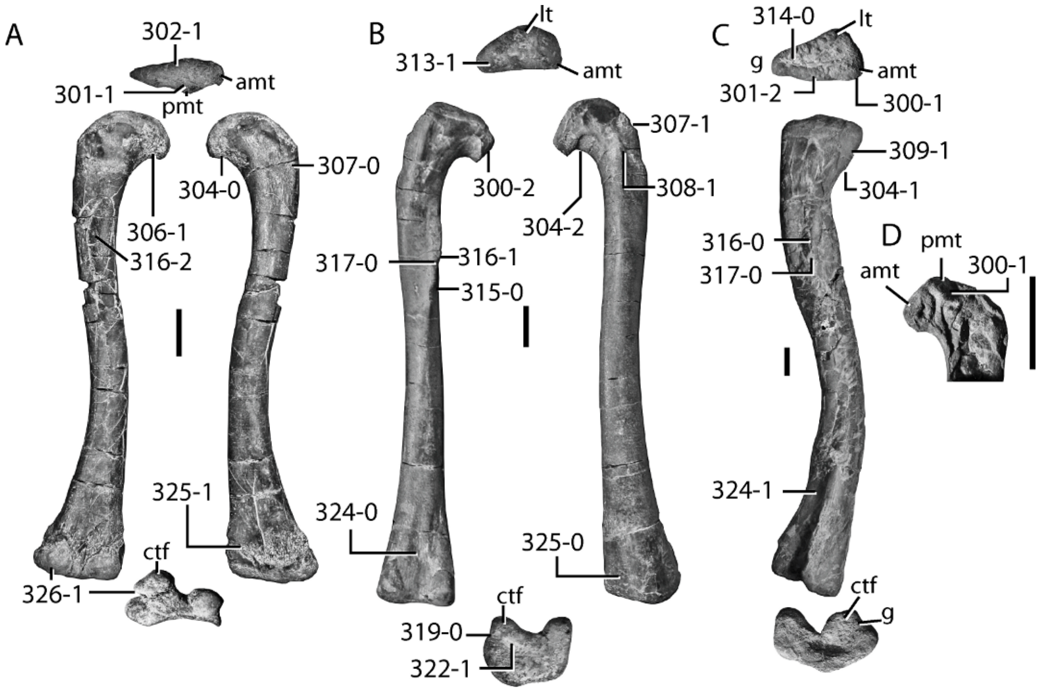

Fig. 39. Avian-line archosaur femora: **A,** left femur of *Dromomeron romeri* (GR 218) in proximal (top), posteromedial (middle left), anterolateral (middle right), and distal (bottom) views; **B,** left femur of the *Tawa hallae* (GR 244) in proximal (top), medial (middle left), lateral (middle right), and distal (bottom) views; **C,** left femur of *Silesaurus opolensis* (ZPAL Ab III 460/1) in proximal (top), posteromedial (middle), and distal (bottom) views; **D,** proximal portion of the right femur of *Dimorphodon macronyx* (YPM 9182) in medial view. Arrow indicates anterior direction. Numbers refer to character states. See appendix for anatomical abbreviations. Scale bars = 1 cm.

particularly in studies focusing on the relationships of dinosaurs and their kin (Bakker and Galton, 1974; Gauthier, 1986; Sereno and Arcucci, 1994a, 1994b; Novas, 1996; Hutchinson, 2001a; Carrano, 2000; Langer, 2003, 2004; Langer and Benton, 2006). Most workers cite an "offset femoral head" as unique dinosaurian character. However, it is unclear which features form the "offset femoral head." As I understand, the "offset femoral head" is an enlarged tuber on the proximal portion of the femur that articulates into the acetabulum. Others have also added a direction as a component to the "offset femoral head." Here, I consider the direction of the long axis of the femoral head a separate character (see below). Given that identification of the features of the dinosaurian "offset femoral head" remains elusive, I have attempted to break the morphology of the proximal portion of the femur into a set of characters describing the tubera present in archosauriforms following the identification criteria of Nesbitt (2005a, 2005b).

The proximal portion of the femur bears two tubera in non-archosaurian archosauriforms and three in nearly all archosaurs. Non-archosaurian archosauriforms have a

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Fig. 38. Archosaur femora in proximal (top), anterolateral (middle left), posteromedial (middle right), and distal (bottom) views: **A,** right femur of *Typothorax* (UCMP 34238); **B,** right femur of Shuvosauridae (TTU-P 3870); **C,** left femur of *Hesperosuchus agilis* (AMNH FR 6758); **D,** left femur of *Postosuchus kirkpatricki* (TTU-P 9000). Arrow indicates anterior direction. Numbers refer to character states. See appendix for anatomical abbreviations. Scale bars = 5 cm in A, 1 cm in B, C, and 10 cm in D.

single anterolateral tuber and a large single medial tuber. These tubera are clearly present in proterochampsians (*Chanaresuchus* MCZ 4035), *Euparkeria* (SAM 6047B), and phytosaurs (e.g., *Pseudopalatus*, UCMP 122078). Therefore, these taxa lack a distinct anteromedial tuber and are scored accordingly. The homology of the tubera on the proximal portion of the femur in taxa with clear internal trochanters (e.g., *Mesosuchus*, *Prolacerta*, *Proterosuchus*) cannot be assessed because the homology of the only tubera is not clear. Therefore, these taxa are scored as unknown.

In all archosaurs, three tubera are present, an anterolateral tuber in the same location as that of non-archosaurian archosauriforms, and two medial tubera, one anteromedial and one posteromedial. Among crocodylian-line archosaurs, in aetosaurs, *Revueltosaurus* (PEFO 34561), ornithosuchids, and *Gracilisuchus* (MCZ 3108) the posteromedial tuber is much larger than the anteromedial tuber. Similarly, among avian-line archosaurs, the posteromedial tuber of *Lagerpeton* and *Dromomeron* (Nesbitt et al., 2009b) is much larger than that of the anteromedial tuber. The large size and position of the posteromedial tuber suggests homology with the single medial tuber of non-archosaurian archosauriforms. Nearly all known basal pterosaur femora are crushed. However, a three-dimensionally preserved femur of *Dimorphodon macronyx* (YPM 9182) preserves two equally sized medial tubera.

In taxa traditionally referred to "rauisuchians" and crocodylomorphs, the two medial tubera are nearly equal in size. This is retained in members of the Crocodylia. The two medial tubera are nearly equal in size in *Marasuchus* (PVL 3870), *Pseudolagosuchus* (UNLR 53), and apparently in ornithischians, *Herrerasaurus* (PVSJ 373), and sauropodomorphs (e.g., *Saturnalia*, MCP 3844-PV; *Plateosaurus,* various AMNH FR specimens). Novas (1996) stated that the posteromedial tuber (= tuber that externally bounds the ligament of the femoral head) is reduced in Dinosauria. Nonetheless, the anteromedial tuber is still not bigger in comparison in the examples he gives. It is only in theropods that the anteromedial tuber expands medially to become much larger than the other proximal tuber among Dinosauria. In neotheropods, the anteromedial tuber is enlarged perpendicular to the long axis of the proximal surface of the femur. Therefore, neotheropods are the only group to have an enlarged femoral head relative to the condition in other archosaur taxa. In *Shuvosaurus* (TTU-P 9280) and *Effigia* (AMNH FR 30588), the anteromedial tuber is enlarged relative to the other tubera, as with theropods. However, the tuber is posteriorly directed at its medial margin, a condition unique among archosaurs. Therefore, *Effigia* and *Shuvosaurus* are the only taxa scored as having an anteromedial tuber that is large and "hooked" posteriorly (state [3]).

The posteromedial tuber appears to be present in nearly all archosaurs, including dinosaurs. In *Silesaurus* (ZPAL Ab III/361/23) and *Eucoelophysis* (NMMNH P 22298), the posteromedial tuber is absent giving the femoral head a triangular shape in proximal view. Nesbitt et al. (2007) and Irmis et al. (2007a) used the character "in proximal view: head of the femur roughly triangular" to describe the femoral head of *Silesaurus* and like forms. However, it is now clear that the triangular shape of the femoral head in dorsal view is the result of a variety of changes including the reduction of the medial tuber.

The anterolateral tuber is present in nearly all archosaurs plesiomorphically as either a bulge (most crocodylian-line archosaurs) or distinct ridge (dinosauriforms). A distinct anterolateral tuber is absent in *Lagerpeton* and *Dromomeron* (Nesbitt et al., 2009b) and in *Shuvosaurus* (TTU-P 9001) and *Effigia* (AMNH FR 30588) (Nesbitt, 2007). In these taxa, the lateral side of the femur is flat.

303. Femur, medial articular surface of the head in dorsal view: (0) rounded; (1) flat/straight (new).

In nearly all archosauriforms, the articular surface of the femur is rounded in dorsal view. In contrast, the same margin in *Silesaurus* (ZPAL Ab III/2063) and *Sacisaurus* (MCN PV 10019) is flat or straight. The flat surface connects the anterolateral and anteromedial tubera in *Silesaurus* and *Sacisaurus*. Furthermore, the flat surface creates part of the triangular shape as described for *Silesaurus* (Dzik, 2003).

304. Femur, ventral to the proximal head: (0) smooth transition from the femoral shaft to the head; (1) notch; (2) concave emargination (fig. 39) (Sereno and Arcucci, 1994a; Novas, 1996).

In non-archosaurian archosauriforms and crocodylian-line archosaurs, the femoral head transitions to the shaft without any interruption. This condition is exemplified by *Euparkeria* (SAM 6047B), *Batrachotomus* (SMNS 52970), and *Marasuchus* (PVL 3870). In contrast, the transition from the femoral shaft to the femoral head is interrupted by a notch in *Silesaurus* (ZPAL Ab III/361/23), *Pseudolagosuchus* (UNLR 53), *Asilisaurus kongwe* (NMT RB19), *Eucoelophysis* (NMMNH P-22298), and *Sacisaurus* (MCN PV 10019). In dinosaurs, the transition from the femoral shaft to the femoral head is interrupted by a concave depression ventral to the head. This feature is present in ornithischians and saurischians.

305. Femur, femoral head orientation (long axis of the femoral head angle with respect to the transverse axis through the femoral condyles Parrish, 1986): (0) anterior (60°–90°); (1) anteromedial (20°–60°); (2) medial (0°–20°) (modified from Benton and Clark, 1988; Hutchinson, 2001a).

The orientation of the femoral head relative to the shaft was used in many phylogenetic analyses of basal archosaurs relationships in several forms. The orientation of the femoral head has contributed to the ambiguous term "offset femoral head" often attributed to taxa included in Pterosauria + Dinosauria (Benton, 1990a; Hutchinson, 2001a). Hutchinson (2001a) reviewed why previous authors have referred to the femoral head condition Pterosauria + Dinosauria as "offset femoral head" and concluded that the femoral head become medially deflected relative to the proximal outgroups and that all associated structures (muscular attachments) rotated with it. However, many basal archosauriforms also have a femoral head directed 45°.

Juul (1994) warned that taphonomic distortion of femora may affect the scoring of taxa. Therefore, only well-preserved femora are scored here. New specimens and a reevaluation of well-preserved basal archosauriform femora have allowed more taxa to be scored accurately. Here, the long-axis of the hemoral head is used to obtain the direction relativ to the distal end. Among archosauriforms, the femoral heads of phytosaurs and *Vancleavea* (GR 138) are directed anteriorly (60°–90°) whereas the femoral heads of *Euparkeria* (SAM 6047B), *Chanaresuchus* (MCZ 4035), and nearly all crocodylian-line archosaurs are directed 45° to the transverse axis through the femoral condyles. Among crocodylian-line archosaurs, Bonaparte (1984) articulated the femoral head with the ilium in *Saurosuchus* and *Fasolasuchus* like that of early dinosaurs (= 90°), but a reevaluation of these specimens confirms a femoral head directed at an angle of 45°. The same angle is also found in basal crocodylomorphs (e.g., *Hesperosuchus*, AMNH FR 6758) and *Alligator*. Among avian-line archosaurs, the femoral head is similar to that of early dinosaurs as exemplified by pterosaurs, *Marasuchus* (PVL 3870), and *Silesaurus* (ZPAL Ab III/361/23). The femur of *Lagerpeton* (PVL 4619) is crushed, but the close relatives *Dromomeron romeri* (GR 218) and *D. gregorii* (TMM 31100-1306) have a femoral head angle about 45° to the transverse axis through the femoral condyles. As described by Carrano (2000), each of the three major dinosaurian lineages turned the head completely medially and these taxa are scored as (2). The wide distribution of taxa scored as (1) indicates that an "interned femoral head" is widespread among basal archosaurs and is not a unique feature in pterosaurs + dinosaurs.

306. Femur, femoral head in medial and lateral views: (0) rounded; (1) hook shaped (figs. 37, 39) (Sereno and Arcucci, 1994a; Irmis et al., 2007a).

In most basal archosauriforms, the shaft of the femur gradually grades into the femoral head. Originally, Sereno and Arcucci (1994a) described the femoral head of *Lagerpeton* as hook shaped and cited the shape as an autapomorphy of the taxon. The hook-shaped femoral head is created by a unique set of two features, a femoral shaft that meets the femoral head at an acute angle and a dorsal surface that is arched nearly 180°. *Lagerpeton* (PVL 4619), *Dromomeron romeri* (GR 218), and *D. gregorii* (TMM 31100-1306) are the only taxa scored as (1) following Sereno and Arcucci (1994a), Irmis et al. (2007a), and Nesbitt et al. (2009b).

307. Femur, dorsolateral margin of the proximal portion: (0) smooth; (1) sharp ridge (= dorsolateral trochanter of some); (2) rounded ridge (= dorsolateral trochanter of some) (fig. 38) (new).

Plesiomorphically in archosauriforms, the dorsolateral margin of the proximal portion of the femur is smooth and featureless. Only the crocodylomorphs *Terrestrisuchus* (BMNH R7562) and *Kayentasuchus* (UCMP 131830; Clark and Sues, 2002: fig. 5) possess a sharp ridge on the dorsolateral margin of the proximal portion of the femur among crocodylian-line archosaurs. Among dinosauriforms, the dorsolateral margin of the femur of *Marasuchus* (PVL 3870) lacks any feature whereas a clear ridge is present in many other dinosauriforms. The small femora of *Silesaurus* (ZPAL Ab III/460/1) bear a sharp ridge whereas the larger specimens of *Silesaurus* bear a rounded ridge (ZPAL Ab III/361/21). The same pattern is present in undescribed *Silesaurus*-like femora from the Otis Chalk Quarries (various specimens with the prefix TMM 31100) of central Texas. Therefore, the presence of a sharp ridge or a rounded ridge may be ontogenetically developed. Nonetheless, the character is still used and taxa showing both states (1) and (2) are scored as polymorphic.

Among dinosaurs, a rounded ridge seems to be consistently present in all ontogenetic stages of *Coelophysis bauri* (AMNH FR, various specimens), a sharp ridge is present in *Liliensternus liliensterni* (MB R.1275; Langer and Benton, 2006) whereas a sharp ridge seems to be present in basal ornithischians such as *Eocursor* (SAM-PK-0925) and the larger *Stormbergia* (SAM-PK-1105). In *Heterodontosaurus* (SAM-PK-1332) and more derived ornithischians, the ridge fuses to the anterior trochanter. The same is also present in tetanuran theropods (Rauhut, 2003). In *Saturnalia* (MCP 3844-PV) and *Plateosaurus* (AMNH FR 2106), a sharp ridge is present in the largest specimens.

308. Femur, anterior trochanter (= M. iliofemoralis cranialis insertion): (0) absent; (1) present and forms a steep margin with the shaft, but is completely connected to the shaft; (2) present and forms a steep margin with the shaft and separated from the shaft by a marked cleft (figs. 37, 39) (Bakker and Galton, 1974; Gauthier, 1986; Novas, 1992; Juul, 1994; Novas, 1996; Benton, 1999; Langer and Benton, 2006; Nesbitt et al., 2009a).

This classic character has been discussed thoroughly in a number of publications (most recently by Langer and Benton, 2006). Here, little can be added except to state that I agree with the character-state distribution described by Langer and Benton (2006). Therefore, only *Dilophosaurus*, tetanurans, and ornithischians are scored as (2) among avian-line archosaurs. The ornithosuchids *Ornithosuchus* and *Riojasuchus* are scored as (1) and the crocodylomorph *Kayentasuchus* is scored as (1). It is worth noting that the anterior trochanter is only present in larger individuals of *Dromomeron gregorii* (Nesbitt et al., 2009b). All other taxa with an anterior trochanter seem to have the feature at all stages of ontogenetic development.

309. Femur, medial articular facet of the proximal portion: (0) rounded; (1) straight (fig. 39) (new).

In basal archosauriforms and crocodylian-line archosaurs, the articular facet of the proximal portion of the femur is rounded in posteromedial view. Among avian-line archosaurs, the same is true except in *Pseudolagosuchus* (UNLR 53), *Asilisaurus kongwe* (NMT RB19), *Sacisaurus* (MCN PV10019), *Eucoelophysis* (NMMNH P-22298), and *Silesaurus* (ZPAL Ab III/2063). In these forms, the medial articular facet of the proximal portion is nearly straight from the notch of the femoral head to nearly the proximal surface.

310. Femur, anterolateral side of the femoral head: (0) smooth, featureless; (1) ventral emargination present (Sereno and Arcucci, 1994a; Irmis et al., 2007a).

The anterolateral surface of the proximal portion of the femur of most basal archosauriforms is smooth and featureless. In *Lagerpeton* (PVL 4619), *Dromomeron romeri* (GR 218), and *D. gregorii* (TMM 31100-1306), there is a distinct ventral emargination on the anterolateral side of the femoral head (Sereno and Arcucci, 1994a: fig. 2a). Some dinosaurs (*Coelophysis bauri*, AMNH FR 30816) have a similar emargination in the same place as taxa scored as (1). However, the extent of the emargination in *Lagerpeton* and *Dromomeron* is unmatched among archosaurs. Further, the feature in some dinosaurs may not be homologous given that *Marasuchus* (PVL 3870), *Silesaurus*-like taxa, and basal ornithischians (*Eocursor* SAM-PK-0925) do not have any ventral emargination on the anterolateral side of the femoral head.

311. Femur, anterior trochanter shelf proximal to the attachment site of the M. caudifemoralis (insertion site for the M. iliofemoralis externus): (0) absent; (1) present (modified from Gauthier, 1986; Rowe and Gauthier, 1990; Novas, 1992, 1996; Langer and Benton, 2006).

The presence or absence of an anterior trochanteric shelf has been fiercely debated in the literature. Novas (1992, 1996) has conclusively shown that an anterior trochanteric shelf is present in dinosauriforms such as *Marasuchus* (PVL 3870), *Pseudolagosuchus* (UNLR 53), *Herrerasaurus* (PVSJ 373), but absent in ornithischians and tetanuran theropods. More recently, Langer and Benton (2006) have shown that an anterior trochanter shelf is also present in the basal sauropodomorph *Saturnalia* and the dinosauriform *Silesaurus* (Dzik, 2003). They also score an anterior trochanter shelf absent in *Staurikosaurus* (MCZ 1889) and *Eoraptor* (PVSJ 512) and score all other sauropodomorphs as (0) (contra Novas, 1996). Nesbitt et al. (2009b) showed that the anterior trochanter shelf develops ontogenetically in the non-dinosauriform dinosauromorph *Dromomeron gregorii*. Moreover, it is clear that small femora of *Silesaurus* (ZPAL Ab III/460/1) lack an anterior trochanter shelf whereas larger specimens (ZPAL Ab III/361/21; ZPAL Ab III/361/23) have a clear anterior trochanter shelf. Therefore, this character may be difficult to assess without comparing adults. The positional data was added to the character because some nonavian archosauriforms have a scar for the insertion of the M. iliofemoralis externus that looks similar to that of a "trochanteric shelf" (e.g., *Erythrosuchus* BMNH R3592; "*Mandasuchus*" BMNH R "11b") but is near midshaft, ventral to the attachment site of the M. caudifemoralis. The anterior trochanter shelf lies dorsal to the attachment site of the M. caudifemoralis in all known avian-line archosaurs.

312. Femur, proximal condylar fold: (0) absent; (1) present (figs. 37–38) (Nesbitt et al., 2006).

The proximal condylar fold (sensu Brochu, 1992) is a straight ridge that connects the medioventral portion of the ventral head with the shaft on the anterolateral surface of the femur. A proximal condylar fold is present in crocodylomorphs (e.g., *Hesperosuchus,* AMNH FR 6758; *Terrestrisuchus,* BMNH R 7337; *Protosuchus* AMNH FR 3024) and in CM 73372, a specimen referred to *Postosuchus kirkpatricki* (Long and Murry, 1995), and *Fasolasuchus* (PVL 3851). The preservation of the proximal portion of the femur must be well preserved to assess the presence/absence of the fold. Nesbitt et al. (2006) used the presence of a proximal condylar fold on the proximal portion of a femoral head that was found in the famous "cannibal" *Coelophysis* (AMNH FR 7224) to show that *Coelophysis* was not a cannibal. A similar lamina is also present in some avian-line taxa (*Coelophysis bauri* AMNH FR 30816; *Lagerpeton* PVL 4619). However, the lamina is arched in these taxa and not straight as in taxa scored as (1).

313. Femur, posterolateral portion (= fossa trochanterica, = posterolateral depression, = facies articularis antitrochanterica) of the head: (0) level with the greater trochanter; (1) ventrally descended (figs. 38–39) (modified from Novas, 1996).

Novas (1996) stated that the presence of a depression on the posterolateral portion of the proximal surface of the femur is present in dinosauriforms. I agree with Novas (1996) in his description and analysis, but add a few observations. The posterolateral depression is present when the anterolateral portion of the proximal surface of the femur is higher proximally than the posterolateral portion. Novas (1996) stated that state (1) was absent in *Lagerpeton* (PVL 4619). However, the specimens are crushed. Nesbitt et al. (2009b) identified a clear fossa trochanterica in both taxa of *Dromomeron*, a close relative of *Lagerpeton*. Nearly all dinosauriforms have a fossa trochanterica except for *Eucoelophysis* (NMMNH P-22298), *Sacisaurus* (MCN PV 10019), and *Silesaurus* (ZPAL Ab III/361/23).

In these taxa, both the anterolateral and posterolateral sides are the same height. Most crocodylian-line archosaurs are scored as (0). Nonetheless, *Effigia* (AMNH FR 30588) and *Shuvosaurus* (TTU-P 9001) both have a clear fossa trochanterica.

314. Femur, proximal surface: (0) rounded and smooth; (1) transverse groove that is straight; (2) transverse groove that is curved. ORDERED (figs. 38–39) (Ezcurra, 2006).

Differences in the morphology of proximal surface of the femora of archosauriforms have been used only once in basal archosaur phylogenetic analyses (Ezcurra, 2006). In non-archosaurian archosauriforms, a straight groove on the proximal surface is present in *Erythrosuchus* (Gower, 2003), in *Chanaresuchus* (MCZ 4035), but not in *Tropidosuchus* (PVL 4601). All other non-archosaurian archosauriforms have a convex, rounded proximal surface of the femur. In crocodylian-line archosaurs, a groove is present in some aetosaurs (e.g., *Aetosauroides* PVL 2073) whereas the dorsal surface is smooth in others (e.g., *Aetosaurus* SMNS 5770 S22). Further, Nesbitt (2005a) noted that the same taxon of aetosaur (*Typothorax coccinarum*) has a groove in small individuals whereas the dorsal surface is smooth in larger individuals (specimens from the Canjilon Quarry, new Mexico). The proximal surface of the femora of *Gracilisuchus* (MCZ 3801), *Riojasuchus* (PVL 3827), *Fasolasuchus* (PVL 3850), CM 73372, *Postosuchus kirkpatricki* (TTU-P 9000), and all crocodylomorphs have a smooth, rounded proximal surface. In contrast, a straight groove is present in *Arizonasaurus* (MSM 4596), *Batrachotomus* (SMNS 52970), *Prestosuchus* (BSP XXV 1-3/5-11/ 28-41/49), *Poposaurus* (CFMNH UR 357), and *Effigia* (AMNH FR 30588).

Most basal avian-line archosaurs have a rounded proximal surface of the femur. Among dinosauriforms, *Eucoelophysis* (NMMNH P-22298), *Sacisaurus* (MCN PV 10019), *Silesaurus* (ZPAL Ab III/361/23, and *Asilisaurus kongwe* (NMT RB19) have a deep straight groove. Basal neotheropods, such as *Coelophysis bauri* (AMNH FR 30816), have a curved groove on the proximal portion of the femur whereas saurpodomorphs, *Saturnalia* (MCP 3844-PV), and *Saurikosaurus* (MCZ 1669) have a faint, straight groove.

I order this character to homologize the presence of a groove.

315. Femur, ridge of attachment of the M. caudifemoralis: (0) bladelike with a distinct asymmetric apex located medially; (1) low and without a distinct medial asymmetrical apex (= fourth trochanter) (figs. 37, 39) (Nesbitt et al., 2009a).

The transition from an internal trochanter in non-archosauriform archosauromorphs, *Proterosuchus*, and erythrosuchians to the fourth trochanter of *Euparkeria*, proterochampsians, and members of the Archosauria has received little attention. Most phylogenetic analyses focus on the presence/absence of the internal trochanter as well as the presence/absence of the fourth trochanter (Benton, 1985; Gauthier, 1986; Sereno, 1991a; Parrish, 1992; Juul, 1994; Benton, 2004) without testing the homology of the two structures. Parrish (1992) suggested that *Erythrosuchus* had both an internal trochanter and a fourth trochanter, but as pointed out by Gower (2003), the area Parrish suggests to be the fourth trochanter was not for the attachment of the M. caudifemoralis, but instead for M. iliofemoralis. Here, the observation made by Gower (2003) is followed. A detailed account of the transition between the internal trochanter and the fourth trochanter is in process (Gower, personal commun.), but a short description is presented below.

The internal trochanter of lizards (Snyder, 1962) and the fourth trochanter of archosaurs both have the caudifemoralis musculature attached to them and this musculature functions to retract the femur. In non-archosauriform archosauromorphs, the internal trochanter lies near the proximal surface of the femoral head whereas the fourth trochanter lies more distally in taxa traditionally considered to have a fourth trochanter (e.g., *Euparkeria* and Archosauria). However, the ridge of attachment in *Erythrosuchus*, a taxon near the traditional transition, has a ridge considered an internal trochanter located in a location similar to where a fourth trochanter would be positioned. Therefore, the wording in the character above concentrates on the morphology of the ridge of attachment rather than the position. Non-archosauriform archosauromorphs, *Proterosuchus* (NM QR 1484), and *Erythrosuchus* (BMNH R 3592) have ridges of attachment that are nearly uniformly thin (= bladelike) and have an asymmetrical apex. In *Euparkeria* (SAM 6047B) and Archosauria, the ridge of attachment in low without a distinct asymmetrical apex. The ridge for the attachment of the M. caudifemoralis in proterochampsians (e.g., *Chanaresuchus* PVL 4575) is expanded and sharp. However, the apex of the ridge is symmetrical anteroposteriorly.

316. Femur, fourth trochanter shape: (0) moundlike and rounded; (1) a sharp flange; (2) absent, no distinct ridge for the attachment of the M. caudifemoralis (figs. 37–39) (Gauthier, 1986; Benton and Clark, 1988; Sereno, 1991a; Juul, 1994; Bennett, 1996; Benton, 1999).

317. Fourth trochanter: (0) symmetrical, with distal and proximal margins forming similar low-angle slopes to the shaft; (1) asymmetrical, with distal margin forming a steeper angle to the shaft (figs. 38–39) (Langer and Benton, 2006).

Basal archosaur workers have long utilized the presence and shape of the fourth trochanter as a phylogenetic character(s). Much of their work will not be repeated here. Nearly all non-archosaurian archosauriforms, and crocodylian-line archosaurs possess a moundlike fourth trochanter that is symmetrical. *Gracilisuchus* has been reported to lack a fourth trochanter (Romer, 1972c; Juul, 1994); nonetheless, a clear, rounded fourth trochanter is present in a femur associated with a *Gracilisuchus* skull (PVL 4597). A distinct ridge for the attachment of the M. caudifemoralis is absent in pterosaurs (Bennett, 1996), *Shuvosaurus* (TTU-P 9001, various specimens), and *Dromomeron romeri* (GR 218), but these taxa do have a scar where the fourth trochanter is located in other taxa. Interestingly, within Lagerpetidae, *Dromomeron romeri* (GR 218) lacks a distinct ridge for the attachment of the M. caudifemoralis, *Lagerpeton* (PVL 4619) has a sharp fourth trochanter, and *Dromomeron gregorii* (TMM 31100-1306) has a moundlike fourth trochanter.

All dinosaurs have a sharp, bladelike fourth trochanter. The shape of the fourth trochanter can be divided into two morphologies, a dorsoventrally symmetrical structure or a dorsoventrally asymmetrical structure where the distal margin forming a steeper angle to the shaft (Langer and Benton, 2006). All theropods have a symmetrical fourth trochanter whereas *Herrerasaurus*, *Staurikosaurus*, *Eoraptor*, ornithischians, and sauropodomorphs have an asymmetrical fourth trochanter (Langer and Benton, 2006).

318. Femur, distal condyles: (0) prominent; (1) not projecting markedly beyond shaft (fig. 37) (Gauthier et al., 1988).

Subsequent workers have ignored this character since its formulation. Juul (1994) considered this character too subjective to score. However, the incompletely explained character states are discussed here. The distal end of the femur of *Prolacerta* (BP/1/ 2676), *Proterosuchus* (NM QR 1484), and *Erythrosuchus* (BMNH R3592) as well as rhynchosaurs and *Trilophosaurus* (Gregory, 1945) expands dorsoventrally (in sprawling orientation) whereas the femora of *Vancleavea* (GR 138), *Euparkeria* (SAM 6047b), proterochampsians, and Archosauria expand little more than the midshaft. Further, the expansion of the distal femora of *Prolacerta* (BP/1/ 2676), *Proterosuchus* (NM QR 1484), and *Erythrosuchus* (BMNH R3592) is restricted to the distal end whereas the femora of *Vancleavea*, *Euparkeria*, proterochampsians and Archosauria expand gradually if there is any expansion.

319. Femur, angle between the lateral condyle and the crista tibiofibularis in distal view: (0) obtuse; (1) about a right angle (figs. 37–39) (Parker and Irmis, 2005).

In non-archosaurian archosauriforms, phytosaurs, ornithosuchids, aetosaurs, *Revueltosaurus* (PEFO 34561) and avian-line archosaurs, the angle between the lateral condyle and the crista tibiofibularis in distal view is obtuse. In these forms, the lateral condyle is semicircular and rounded. In contrast, the angle between the lateral condyle and the crista tibiofibularis in distal view is nearly a right angle in *Effigia* (AMNH FR 30587; Nesbitt, 2007), *Batrachotomus* (SMNS 80278), *Fasolasuchus* (PVL 3850), *Postosuchus* (TTU-P 9000; 9002), and crocodylomorphs (e.g., *Dromicosuchus,* UNC 15574).

320. Femur, medial condyle of the distal portion: (0) tapers to a point on the medial

portion in distal view; (1) smoothly rounded in distal view (figs. 37–38) (new).

In non-archosaurian archosauriforms, aetosaurs, *Revueltosaurus* (PEFO 34561), *Gracilisuchus* (MCZ 3801), *Arizonasaurus* (MSM 4596), and *Prestosuchus* (BPS 34), the medial condyle of the distal portion of the femur tapers to a point medially. In contrast, the medial condyle of the femur is rounded in all avian-line archosaurs, *Fasolasuchus* (PVL 3850), *Postosuchus kirkpatricki* (TTU-P 9001), *Batrachotomus* (SMNS 52970) and all basal crocodylomorphs examined.

321. Femur, distal surface between the lateral and medial condyles: (0) nearly flat or flat; (1) groove separating the medial condyle from the lateral condyle (fig. 38) (new).

The distal surface of the femur is generally convex in most archosauriforms and, thus, there is no groove between the lateral and medial condyles. Among crocodylomorphs, there is no gap in *Dromicosuchus* (UNC 15574) or *Terrestrisuchus* (BMNH R7751), whereas there is a clear gap in *Hesperosuchus agilis* (AMNH FR 6758), *Kayentasuchus* (UCMP 131830), *Litargosuchus* (BP/1/5237), and *Protosuchus* (AMNH FR 3024).

322. Femur, surface between the lateral condyle and crista tibiofibularis on the distal surface: (0) smooth; (1) deep groove (figs. 37–39) (new).

All archosauriforms bear a lateral and medial condyle and a crista tibiofibularis (= fibular condyle of some). A groove is clearly absent in non-archosaurian archosauriforms, phytosaurs, *Revueltosaurus* (PEFO 34561), aetosaurs, *Gracilisuchus* (MCZ 3801), *Riojasuchus* (PVL 3827), and the pterosaur *Dimorphodon* (YPM 9182). In some of the taxa listed above, there is an elevation change between the lateral condyle and the crista tibiofibularis. However, there is no clear groove between the features even when there is an elevation difference (e.g., *Riojasuchus*, PVL 3827). A groove is present in dinosauromorphs, *Effigia* (AMNH FR 30587), *Poposaurus* (YPM 57100), *Fasolasuchus* (PVL 3850), *Postosuchus* (TTU-P 9000; 9002), and crocodylomorphs. Taxa with a deep groove on the surface of the distal articular surface trending parallel with the long axis of the distal surface are scored as (?) because the cartilage cap is not fully ossified as in all the other taxa scored as (0) or (1). These taxa include *Arizonasaurus* (MSM 4596), *Batrachotomus* (SMNS 80278), *Prestosuchus* (BSP XXV 1-3/5-11/ 28-41/49), and *Erythrosuchus* (BMNH R3592).

323. Femur, bone wall thickness at or near midshaft: (0) thickness/diameter >0.3; (1) thin, thickness/diameter >0.2, <0.3; (2) very thin, thickness/diameter <0.2 (new).

The degree of "hollowness" of the femur at the midshaft has yet to be used in a phylogenetic analysis. Here, I used the bone wall thickness/diameter (following Curry and Alexander 1985; Hutchinson, 2001a) near the midshaft of the femur. Not all specimens could be scored for this, given that internal structures of the midshaft had to be examined. In both the scientific literature and the popular literature, various authors have pointed out that pterosaurs and theropods have extremely thin-walled bones. However, from the character scoring here, it is clear that other non-avian-line archosaurs also had thin bone-wall thickness/diameter. For example, the crocodylian-line archosaurs *Poposaurus* and *Terrestrisuchus* are scored as (1). Among basal archosaurs, pterosaurs have the thinnest bone-wall thickness/diameter (Hutchinson, 2001a). These data indicate that ornithischians and sauropodomorphs may have increased the bone-wall thickness/diameter relative to other avian-line archosaurs. The character scoring of this character shows that "hollow" bones are not restricted to theropods and pterosaurs.

324. Femur, distal condyles of the femur divided posteriorly: (0) less than ¼ the length of the shaft; (1) between ¼ and ⅓ the length of the shaft (fig. 39) (new).

In nearly all archosauriforms, the dorsal extent of distal condyles on the posterior side of the femur is restricted to the distal ¼ of the length of the femur. In *Silesaurus* (ZPAL Ab III/460/1), *Sacisaurus* (MCN 10014-PV), possibly *Eucoelophysis* (NMMNH P-22298), and *Asilisaurus kongwe* (Nesbitt et al., 2010), the distal condyles extend between ¼ and ⅓ the length of the shaft. Furthermore, the extended condyles preserve a dorsoventrally elongated fossa between the two features. This character is difficult to assess in *Pseudolagosuchus* (PVL 4629; UNLR 53), but it appears that the taxon should be scored as (0).

325. Femur, anterior surface of the distal portion: (0) smooth; (1) distinct scar orientated mediolaterally (fig. 39) (Nesbitt et al., 2009b).

The anterior surface of the distal end of the femur is nearly flat or concave in most basal archosaurs and *Lagerpeton*. However, there is a ridge that transverses the anterior surface of the distal end of the femora of both *Dromomeron romeri* (GR 218) and *D. gregorii* (best preserved in TMM 31100-1234). The ridge separates finished bone, ventral to the ridge, from unfinished bone, dorsal to the ridge. This muscle scar is hypothesized to be the distal origin for the M. femorotibialis externus based on the extant phylogenetic bracket set up by Hutchinson (2001a), and also the relative position of the linea intermuscularis cranialis, which separates the origins of M. femorotibialis internus and M. femorotibialis externus more proximally (Carrano and Hutchinson, 2002).

326. Femur, crista tibiofibularis (fibular condyle of Sereno and Arcucci, 1994a): (0) smaller or equal in size to the medial condyle; (1) larger than the medial condyle (fig. 39) (modified from Sereno and Arcucci, 1994a; Irmis et al., 2007a).

The size of the crista tibiofibularis consistently remains smaller than the medial condyle in nearly all archosauriforms. In *Lagerpeton* (PVL 4619), *Dromomeron gregorii* (GR 218), and *D. gregorii* (TMM 31100-1306), the crista tibiofibularis is larger than the medial condyle.

327. Femur, anteromedial corner of the distal end: (0) rounded; (1) squared off near 90° or acute >90° (Nesbitt et al., 2009b).

The anteromedial corner of the distal end of the femur of most basal archosaurs is rounded and much greater than 90°. The anteromedial corner of the distal end of the femur is about 90° in all specimens of *Dromomeron gregorii* (TMM 31100-1306), and less than 90° in both *Lagerpeton* (PVL 4619) and *D. romeri* (GR 218). The anteromedial corner of *D. romeri* is much less than 90° because of the anteromedially projecting ridge, an autapomorphy of the taxon (Nesbitt et al., 2009b). However, if the autapomorphic feature is accounted for, the anteromedial corner forms an angle of about 90°.

TIBIA

328. Tibia, proximal portion, cnemial crest: (0) absent; (1) present and anteriorly straight; (2) present and curved anterolaterally (fig. 40) (Benton and Clark, 1988; Juul, 1994; Novas, 1996; Benton, 1999; Irmis et al., 2007a).

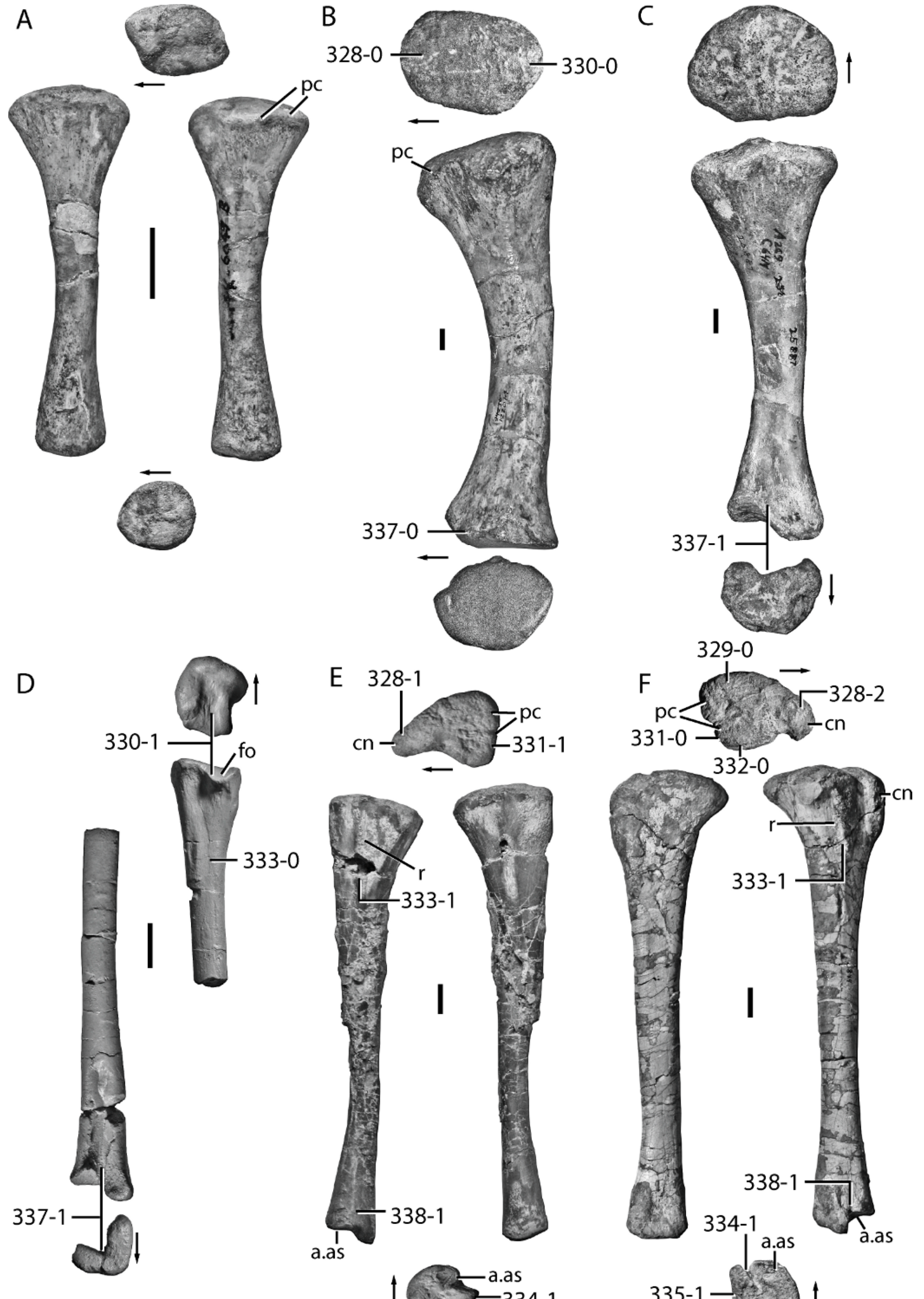
The cnemial crest was named for the tapered anterior portion of the proximal portion of the tibia in Aves (Baumel, 1993). In nearly all basal archosaur phylogenies, a cnemial crest is scored as present in dinosauromorphs but absent in all non-dinosauromorph archosauriforms (e.g., Benton and Clark, 1988; Juul, 1994; Benton, 1999). A precise description of the cnemial crest was given by Novas (1996) and his criteria for identification of the feature is followed here. The proximal portions of the tibiae of *Lagerpeton* (PVL 4619) are poorly preserved so the taxon is scored as unknown, though the close relatives *Dromomeron romeri* (GR 222) and *D. gregorii* (TMM 31100-278) have small, but distinct and straight cnemial crests. Non-dinosaurian dinosauromorphs have straight cnemial crests whereas dinosaurs have cnemial crests that arch anterolaterally.

329. Tibia, proximal surface: (0) flat or convex; (1) concave, the posterior condyles of the tibia are separated from the cnemial crest by a concave surface (fig. 40) (new).

In nearly all archosauriforms, the proximal surface of the tibia is flat or convex. The proximal surface of the tibia of *Coelophysis bauri* (AMNH FR 7246) has a shallow concavity whereas other theropods have a deep concave surface between the posterior condyles and the cnemial crest (e.g., *Allosaurus,* AMNH FR 324). Alternatively, the concavity could be the result of the dorsal expansion of the dorsal extent of the cnemial crest above the posterior condyles.

330. Tibia, proximal surface of the lateral condyle: (0) convex or flat; (1) depressed (fig. 40) (new).

In most non-archosaurian archosauriforms and avian-line archosaurs, the proximal surface of the lateral condyle of the proximal portion of the tibia is either flat or convex. The only exception among the taxa listed above is *Euparkeria*. The proximal surface of the lateral condyle of the tibia of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Euparkeria (SAM 6047B; SAM K 10010) is slightly depressed but not to the same degree as that in crocodylian-line archosaurs. The proximal surface of the lateral condyle bears a well-developed depression in crocodylian-line archosaurs including *Riojasuchus* (PVL 3827), *Batrachotomus* (SMNS 52970), *Poposaurus* (YPM 57100), *Effigia* (AMNH FR 30587), *Postosuchus kirkpartricki* (TTU-P 9002), *Postosuchus alisonae* (UNC 15575), CM 73372, *Saurosuchus* (PVL 2267), *Dromicosuchus* (UNC 15574), *Hesperosuchus agilis* (AMNH FR 6758), *Sphenosuchus* (SAM 3014), and *Protosuchus* (AMNH FR 3024). Aetosaurs and *Revueltosaurus* (Parker et al., 2005) seem to have the same depression, but it is not as deep as that of other crocodylian-line archosaurs.

331. Tibia, lateral (fibular) condyle of the proximal portion: (0) offset anteriorly from the medial condyle; (1) level with the medial condyle at its posterior border (fig. 40) (Langer and Benton, 2006; Irmis et al., 2007a).

Langer and Benton (2006) recently reviewed the location of the lateral condyle relative to the medial condyle of the tibia in basal dinosaurs. For the most part, I agree with their conclusions and scorings. In basal archosauriforms, both condyles are present and nearly all of them have an anteriorly shifted lateral condyle relative to the medial condyle. The tibia of *Pisanosaurus* (PVL 3577) is rather crushed and it appears that the lateral side of the lateral condyle has been somewhat eroded or overpreparation. Even though the lateral condyle is posteriorly pointed, the gap between the two condyles is large and much like that of other taxa with an offset lateral condyle. Therefore, *Pisanosaurus* is scored as (0). The newly described *Dromomeron gregorii* and *D. romeri* both have a lateral condyle that is offset anteriorly relative to the medial condyle. The condition in *Lagerpeton* is not clear given that the proximal portions of both tibiae are crushed.

332. Tibia, lateral margin of the lateral condyle of the proximal portion: (0) rounded; (1) squared off (fig. 40) (new).

In nontheropod archosauriforms, the lateral margin of the lateral condyle of the proximal portion of the tibia is well rounded. In contrast, both the lateral and posterior margin of the lateral condyle in theropods (*Coelophysis bauri* AMNH FR 7246; *Allosaurus* AMNH FR 324) is flat. The result is a squared-off shape of the lateral condyle in dorsal view. *Herrerasaurus* (PVSJ 373), *Staurikosaurus* (MCZ 1889), and the *Tawa* (GR 242) are scored as (1).

333. Tibia, lateral side of the proximal portion: (0) smooth; (1) dorsoventrally oriented crest present (= fibular crest) (fig. 40) (Gauthier, 1986; Rauhut, 2003).

The presence or absence of a crest on the lateral side of the proximal portion of the tibia has been used in theropod phylogenetic studies since the initial work of Gauthier (1986). Since the initial description of the feature, the crest has been recorded in the basal sauropodomorph *Saturnalia* (Langer, 2003), the ornithischian *Heterodontosaurus* (Santa Luca, 1980), *Silesaurus* (Dzik, 2003), and *Sacisaurus* (Ferigolo and Langer, 2007). In these taxa, the crest is located high on the tibial shaft like that of basal theropods (e.g., *Liliensternus liliensterni,* MB R. 2175) rather than more distally in tetanurans.

334. Tibia, posterolateral flange of the distal portion: (0) absent; (1) present and contacts fibula; (2) present and extends well posterior to the fibula (fig. 40) (modified

←

Fig. 40. Archosauriform tibiae: **A,** left tibia of *Euparkeria capensis* (SAM 6047B) in proximal (top), medial (middle left), lateral (middle right), and distal (bottom) views; **B,** right tibia of *Pseudopalatus* (UCMP 122079) in proximal (top), medial (middle), and distal (bottom) views; **C,** left tibia of Aetosauria (UCMP 35887) in proximal (top), posterior (middle), and distal (bottom) views; **D,** left tibia of *Hesperosuchus agilis* (AMNH FR 6758) in posterior (middle left) and distal (bottom) views and right tibia in proximal (top) and posterior (middle right) views; **E,** left tibia of *Silesaurus opolensis* (ZPAL Ab III 361/22) in proximal (top), lateral (middle left), medial (middle right), and distal (bottom) views; **F,** right tibia of *Saturnalia tupiniquim* (MCP 3844-PV) in proximal (top), medial (middle left), lateral (middle right), and distal (bottom) views. Arrow indicates anterior direction. Numbers refer to character states. See appendix for anatomical abbreviations. Scale bars = 1 cm.

from Novas, 1992; Juul, 1994; Benton, 1999; Langer and Benton, 2006; Irmis et al., 2007a).

In non-archosaurian archosauriforms and crocodylian-line archosaurs, the distal end of the tibia does not bear a distinct posterolateral process of the tibia. Among avian-line archosaurs, basal pterosaurs (*Dimorphodon,* YPM 9182), *Lagerpeton* (PVL 4619), and both species of *Dromomeron* (Nesbitt et al., 2009b) do not have a distinct process either. In contrast, *Marasuchus* (PVL 3871), *Pseudolagosuchus* (UNLR 53), *Silesaurus* (ZPAL Ab III/364), and dinosaurs have a distinct process that contacts the fibula on its posteromedial side. Within Dinosauria, *Herrerasaurus* (PVSJ 373), *Staurikosaurus* (MCZ 1667), *Saturnalia* (MCP 3844-PV), other sauropodomorphs (e.g., *Plateosaurus*, AMNH FR 2106), basal theropods (*Coelophysis bauri*, AMNH FR unnumbered), and *Pisanosaurus* (PVL 3577) all have short posterolateral flanges that do not extend well posterior to the fibula. In ornithischians more closely related to *Triceratops* than to *Pisanosaurus* or *Heterodontosaurus*, the posterolateral portion becomes laterally extended and clearly lies posterior to that of the fibula (Langer and Benton, 2006). The condition in *Heterodontosaurus* (SAM-PK-1332) is difficult to assess because the ankle is fused to the fibula and tibia; however, it appears that the fibula is well exposed posteriorly. Therefore, *Heterodontosaurus* is scored as (1). Langer and Benton (2006: character 90) scored *Silesaurus* as the equivalent to state (2). However, the lateral termination of the posterolateral flange is nearly identical to that of *Herrerasaurus* (PVSJ 373) and other taxa scored as (1). Further examination of a nicely preserved ankle of *Silesaurus* (ZPAL Ab III/361/20) confirms that the posterolateral flange does not lie well posterior to the fibular facet. In *Dilophosaurus* (UCMP 37302) and *Allosaurus* (Rauhut, 2003: fig. 49D), the posterolateral flange clearly lies posterior to the fibula.

The astragalus of each of the taxa listed precisely records the extent of the posterolateral flange of the tibia and can be scored even in absence of a distal portion of the tibia.

335. Tibia, posterolateral margin of the distal end: (0) straight or convex; (1) concave (fig. 40) (Irmis et al., 2007a).

The posterolateral margin of the distal portion of the tibia of non-archosaurian archosauriforms and crocodylian-line archosaurs is convex. Among avian-line archosaurs, the posterolateral margin of *Marasuchus* (PLV 3870), *Dromomeron romeri* (GR 222), *Silesaurus* (ZPAL Ab III/364), ornithischians (e.g., *Eocursor* SAM-PK-0925), *Herrerasaurus* (PVSJ 373), *Eoraptor* (PVSJ 512), and *Staurikosaurus* (MCZ 1669) remain convex or straight. In contrast, the posterolateral margin of the distal end of the femur is concave in theropods (*Coelophysis bauri* AMNH FR unnumbered; *Allosaurus* AMNH FR 324) and in *Saturnalia* (MCP 3944-PV Langer and Benton, 2006) and other sauropodomorphs (*Plateosaurus,* AMNH FR 6810). All taxa scored as (1) in Langer and Benton (2006; character 87) have a distinctly acute-angled anteromedial margin of the distal end of the tibia. This observation suggests that the presence of the ridge creates the acute angle. All basal ornithischians have the same ridge; however, the angle of the anteromedial margin is obtuse. Here, this character is used in lieu of Langer and Benton's (2006) character 87 and both this character and Langer and Benton's (2006) character should not be used in the same analysis.

336. Tibia, posterior face of the distal end: (0) rounded surface; (1) distinct proximodistally oriented ridge present (fig. 40) (new).

The anteromedial margin of the distal portion of the tibia of non-archosaurian archosauriforms and crocodylian-line archosaurs is convex. This is also true of *Lagerpeton* (PVL 4619), *Dromomeron romeri* (GR 222), and *Silesaurus* (ZPAL Ab III/364). In dinosaurs, there is a distinct proximodistally oriented ridge present on the anteromedial margin of the tibia. A clear ridge is present in ornithischians (e.g., *Lesothosaurus*, BMNH R 11001), sauropodomorphs (*Riojasaurus*, PVL 3525), and neotheropods (*Liliensternus liliensterni*, MB R.1275). A ridge is not present in *Staurikosaurus* (MCZ 1667), *Chindesaurus* (PEFO 10395), and a possible basal theropod (TTU-P 10072; Nesbitt and Chatterjee, 2008). It appears that *Eoraptor* (PVSJ 512) also lacks the ridge.

337. Tibia, posterior side of the distal portion: (0) smooth and featureless; (1)

dorsoventrally oriented groove or gap (fig. 40) (new).

Plesiomorphically, the distal end of the tibia is round in distal view. This is exemplified by the condition in *Euparkeria* (SAM 6047B) and the phytosaur *Smilosuchus* (USNM 18313). In most crocodylian-line archosaurs, there is a distinct concave region of the posterior side of the distal portion of the tibia. There is no groove on the posterior side of the distal portion in avian-line archosaurs.

338. Tibia, lateral side of the distal portion: (0) smooth/rounded; (1) proximodistally oriented groove (fig. 40) (Novas, 1996).

As described above the distal end of the tibia is round in distal view in *Euparkeria* (SAM 6047B) and the phytosaur *Smilosuchus* (USNM 18313). The lateral side of the distal portion of the tibia is rounded in crocodylian-line archosaurs, basal pterosaurs (*Dimorphodon*, YPM 9182), *Lagerpeton* (PVL 4619), and *Dromomeron romeri* (e.g., GR 222). In *Marasuchus* (Sereno and Arcucci, 1994b: fig. 12), *Pseudolagosuchus* (Novas, 1996: fig. 4D), *Silesaurus* (ZPAL Ab III/364), and all dinosaurs plesiomorphically, there is a distinct proximodistally oriented groove on the lateral side marking the division between the anterior portion that articulates with the anterior ascending process of the astragalus from the portion that lies posterior to the ascending process. In ornithischians and theropods, the groove moves laterally and posteriorly as a result of other changes in the distal portion of the tibia. However, a slight homologous groove is still present in basal members of each large clade.

Outside dinosauriforms, proterochampsians (*Chanaresuchus*, PVL 4647; *Tropidosuchus*, PVL 4601) are the only other taxon to possess a proximodistally oriented groove.

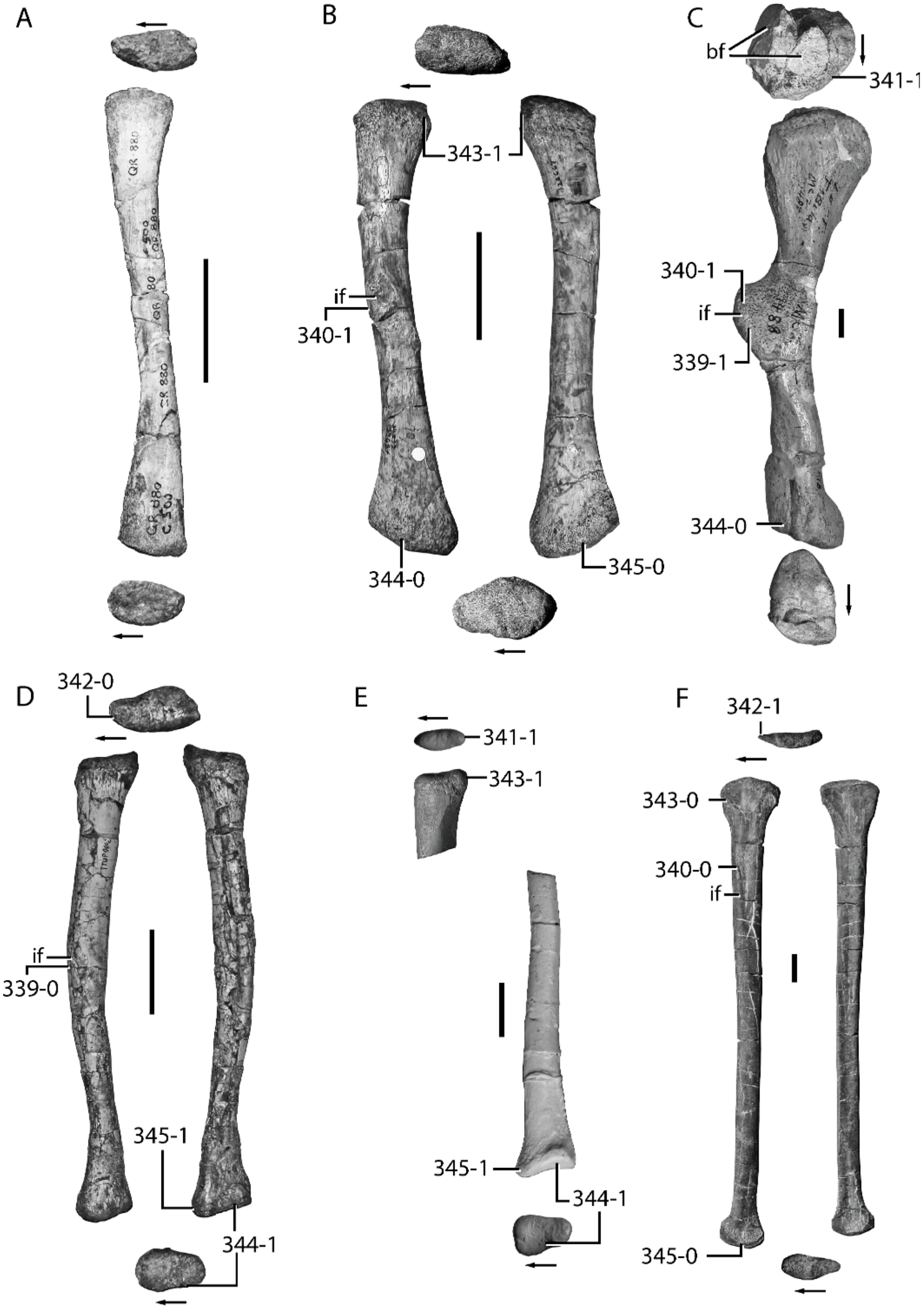
339. Fibula, attachment site for the M. iliofibularis, form: (0) crest shaped, low; (1) knob shaped, robust (fig. 41) (Sereno, 1991a).

340. Fibula, attachment site for the M. iliofibularis, location: (0) near the proximal portion; (1) near the mid point between the proximal and distal ends (fig. 41) (modified from Sereno, 1991a).

The insertion site of the M. iliofibularis is located on the fibula and present in nearly all diapsids, as described by Parrish (1993). Sereno (1991a) was first to use the development of the ridge for the attachment of the M. iliofibularis and hypothesized that a robust ridge is present in phytosaurs, ornithosuchids, some "rauisuchians," aetosaurs, and basal crocodylomorphs. In response, Parrish (1993) cited numerous exceptions among crocodylian-line archosaurs (e.g., *Terrestrisuchus*, *Gracilisuchus*) and suggested that (1) the character is related to size because the small aetosaur *Aetosaurus* lacks a robust attachment site, and (2) a robust attachment site for the M. iliofibularis is present in the large erythrosuchian *Vjushkovia triplicostata* (Parrish, 1993). The two reasons that Parrish (1993) discussed for dismissing Sereno's (1991a) character are welcomed, but oversimplified. The exceptions listed by Parrish (1993), as well as Sereno (1991a) in the original formulation can also be interpreted as autapomorphies.

Here, I divide Sereno's (1991a) character into two, one examining the position and one examining the morphology of attachment site for the M. iliofibularis. A robust, tablike attachment site is found in phytosaurs (e.g., *Smilosuchus,* USNM 18313), ornithosuchids (e.g., *Riojasuchus,* PVL 3827), *Revueltosaurus* (PEFO 34561), and aetosaurs (e.g., *Aetosaurus,* SMNS 5770 S-4; *Typothorax,* MCZ 1488). I argue that the condition in "rauisuchians" is more like that of taxa scored as (0). Further, the attachment site is elongated, though is not developed into a knob but rather an elongated crest (e.g., *Fasolasuchus,* PVL 3850; *Postosuchus alisonae*, UNC 15575). Sereno (1991a) stated that *Saltoposuchus* (SMNS 12596) possesses a robust ridge. However, the attachment site for the M. iliofibularis is actually proximally located and present as a low ridge. The strong bend in the fibula of *Saltoposuchus* (SMNS 12596) seems to be the result of preservation and not of a large attachment site at the midshaft of the element. The attachment site for the M. iliofibularis of *Saltoposuchus* is identical to that of other crocodylomorphs such as *Hesperosuchus* (AMNH FR 6758), *Dromicosuchus* (UNC 15574), and *Protosuchus richardsoni* (AMNH FR 3024).

The position of the attachment site for the M. iliofibularis varies among archosauri-


A
B
343-1
if
340-1
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345-0
C
bf
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340-1
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339-1
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forms. In most archosauriforms the attachment site is located in the proximal third of the fibula. Among crocodylian-line archosaurs, *Revueltosaurus* (PEFO 34561), *Aetosaurus* (SMNS 5770 S-4), *Gracilisuchus* (PVL 4597), *Ticinosuchus* (PIZ T2817), and "*Mandasuchus*" (BMNH R "11b"), the attachment site is located in the proximal third of the fibula. In phytosaurs, ornithosuchids, and many "rauisuchians" (e.g., *Fasolasuchus,* PVL 3850; *Postosuchus alisonae*, UNC 15575; *Batrachotomus,* SMNS 52970), the attachment site is at the midshaft. As stated above, the attachment site is located in the proximal third of the shaft in crocodylomorphs.

Parrish (1993) declared that a distinct attachment site was absent in avian-line archosaurs (= Ornithodira in his terms). Although the crest may be absent in pterosaurs (Wellnhofer, 1978; Sereno, 1991a) a small, dorsally placed attachment site is present in *Dromomeron romeri* (GR 235), *Silesaurus* (ZPAL Ab III/361/18), and in basal Dinosauria (e.g., *Saturnalia,* MCP 3944 PV; *Herrerasaurus,* PVSJ 373).

341. Fibula, proximal end in proximal view: (0) round or slightly elliptical; (1) mediolaterally compressed (fig. 41) (new).

Plesiomorphically in archosauriforms, the proximal portion of the fibula is mediolaterally compressed in *Proterosuchus* (NM QR 880), *Erythrosuchus* (BMNH R3592), *Vancleavea* (GR 138), and proterochampsians (e.g., *Chanaresuchus* MCZ 4035). Like that of basal archosauriforms, avian-line archosaurs have a mediolaterally compressed proximal portion of the fibula. In *Euparkeria*, phytosaurs (*Smilosuchus* USNM 18313), *Riojasuchus* (PVL 3827), *Revueltosaurus* (PEFO 34561), *Aetosaurus* (SMNS 5770 S-22), *Prestosuchus* (BSP XXV 1-3/5-11/ 28-41/49), *Fasolasuchus* (PVL 3851), and *Batrachotomus* (SMNS 52970), the proximal portion of the fibula is round in proximal view. In contrast, the proximal portion of the fibula of *Poposaurus* (YPM 57100), *Effigia* (AMNH FR 30587), *Shuvosaurus* (TTU-P 9001, various specimens), *Postosuchus alisonae* (UNC 15575), *Postosuchus kirkpatricki* (TTU-P 9002), CM 73372, and crocodylomorphs (e.g., *Hesperosuchus*, AMNH FR 6758; *Protosuchus*, AMNH FR 3024) are distinctly mediolaterally compressed.

342. Fibula, anterior edge of the proximal portion: (0) rounded; (1) tapers to a point and arched anteromedially (fig. 41) (new).

In non-archosaurian archosauriforms and crocodylian-line archosaurs, the anterior portion of the proximal portion of the fibula is rounded. Among avian-line archosaurs, the condition in basal pterosaurs is unknown whereas the anterior margin of the fibula is rounded in *Dromomeron romeri* (GR 235) and *Marasuchus* (PVL 3870). In *Silesaurus* (ZPAL Ab III/361/18) and dinosaurs (e.g., *Herrerasaurus*, PVSJ 373; *Saturnalia*, MCP 3844-PV), the anterior margin of the proximal portion of the fibula tapers to a point and arches anteromedially.

343. Fibula, proximal portion in lateral view: (0) symmetrical or nearly symmetrical; (1) posterior part expanded posteriorly (fig. 41) (new).

In lateral view, the fibula of basal archosauriforms such as *Proterosuchus* (NM QR 880) and *Vancleavea* (GR 138) is nearly anteroposteriorly symmetrical. In contrast, the proximal portion of the fibula in lateral view is distinctly asymmetrical in proterochampsians (*Chanaresuchus* MCZ 4035), phytosaurs (*Smilosuchus* USNM 18313), and nearly all crocodylian-line archosaurs and avian-line archosaurs (e.g., *Silesaurus*,

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Fig. 41. Archosauriform fibulae: **A,** left fibula of *Proterosuchus fergusi* (NM QR 880) in proximal (top), lateral (middle), and distal (bottom) views; **B,** left fibula of *Pseudopalatus* (UCMP 122661) in proximal (top), lateral (middle left), medial (middle right), and distal (bottom) views; **C,** left fibula of *Typothorax* (MCZ 1488) in proximal (top), lateral (middle), and distal (bottom) views; **D,** left fibula of *Postosuchus kirkpatricki* (TTU-P 9002) in proximal (top), lateral (middle left), medial (middle right), and distal (bottom) views; **E,** right fibula of *Hesperosuchus agilis* (AMNH FR 6758) in proximal (top) and medial (middle left) views and the left distal end of the fibula in medial (middle right) and distal (bottom) views; **F,** left fibula of a *Tawa hallae* (GR 242) in proximal (top), lateral (middle left), medial (middle right), and distal (bottom) views. Arrow indicates anterior direction. Numbers refer to character states. See appendix for anatomical abbreviations. Scale bars = 5 cm in A–B, D, and 1 cm in C, E–F.

ZPAL Ab III/361/18). The asymmetry is a result of the proximoposterior edge tapering to a rounded point.

344. Fibula, medial face of the distal portion: (0) smooth; (1) banked with an articular facet that articulates with the astragalus (fig. 41) (new).

The medial side of the distal portion of the fibula articulates with the proximolateral side of the astragalus in archosauriforms. For the most part, the medial side is smooth in archosauriforms. This is the plesiomorphic condition in crocodylian-line archosaurs as it is present in *Revueltosaurus* (PEFO 34561), aetosaurs (*Typothorax*, MCZ 1488), *Riojasuchus* (PVL 3827), and the "rauisuchians" *Effigia* (AMNH FR 30587), *Poposaurus* (YPM 57100), *Saurosuchus* (PVL 2557), *Ticinosuchus* (PIZ T2817), and *Batrachotomus* (SMNS 52970). In contrast, in *Fasolasuchus* (PVL 3851), *Postosuchus kirkpatricki* (TTU-P 9002), *Postosuchus alisonae* (UNC 15575), CM 73372, *Hesperosuchus agilis* (AMNH FR 6758), *Protosuchus richardsoni* (AMNH FR 3024), and *Alligator*, the medial side of the distal end of the fibula has a banked articular facet that contacts the astragalus.

345. Fibula, distal end in lateral view: (0) angled anterodorsally (asymmetrical); (1) rounded or flat (symmetrical) (fig. 41) (new).

The distal end of the fibula in lateral view of most non-archosaurian archosauriforms remains symmetrical whereas that of phytosaurs (*Smilosuchus,* USNM 18313), *Revueltosaurus* (PEFO 34561), aetosaurs (*Typothorax*, MCZ 1488), *Ticinosuchus* (PIZ T2817), *Batrachotomus* (SMNS 52970), and *Saurosuchus* (PVL 2557), *Fasolasuchus* (PVL 3851), *Postosuchus kirkpatricki* (TTU-P 9002), *Postosuchus alisonae* (UNC 15575), CM 73372, *Hesperosuchus agilis* (AMNH FR 6758), and *Protosuchus richardsoni* (AMNH FR 3024), the distal end is angled anterodorsally which makes the distal end asymmetrical anteroposteriorly. Alternatively, the distal end of the fibula remains flat in *Qianosuchus* (IVPP 14300), and *Shuvosaurus* (TTU-P 9001). Among avian-line archosaurs, only *Marasuchus* (PVL 3871; Novas, 1996: fig. 9A) seems to have an anterodorsally angled distal portion of the fibula. Taxa scored as (1) have an overall S-shape of the fibula whereas taxa scored as (0) have a much straighter fibular shaft.

346. Tarsals 1 and 2: (0) ossified; (1) absent (Gauthier, 1984; Sereno, 1991a; Gower, 1996; Benton, 2004; Nesbitt et al., 2009a).

Gauthier (1984) used this character to separate non-archosauriform archosauromorphs and *Proterosuchus* (tarsals 1–4 ossified) from *Euparkeria*, proterochampsians, and members of the Archosauria (tarsals 3 + 4 ossified only). Sereno (1991a) followed this but restricted most of his discussion to the presence/absence of tarsal 1. Tarsal 1 and 2 are both either ossified or absent in basal archosaurs. However, Gauthier (1984) and Sereno (1991a) report that tarsal 2 is present in some fossil crocodylians and in old, mature crocodiles. Gower (1996) clarified Sereno's (1991a) doubts about the presence/absence of tarsal 1 in *Erythrosuchus*; Gower (1996) conclusively showed that *Erythrosuchus* has only tarsals 3 and 4. Basal dinosaurs retain two tarsals (3 and 4).

347. Distal tarsal 4, transverse width: (0) broader than distal tarsal 3; (1) subequal to distal tarsal 3 (fig. 42) (Sereno, 1991a; Juul, 1994; Benton, 1999).

The transverse width of distal tarsal 4 is much greater than the transverse width of distal tarsal 3 in non-archosaurian archosauriforms and crocodylian-line archosaurs (Sereno, 1991a). New information from the non-archosaurian archosauriform *Erythrosuchus* (Gower, 1996), and the crocodylian-line archosaurs *Revueltosaurus* (PEFO 34561), *Typothorax* (MCZ 1488), *Effigia* (AMNH FR 30587), *Postosuchus alisonae* (UNC 15575), and *Hesperosuchus* (AMNH FR 6758) continues to support Sereno's (1991a) conclusion. In basal pterosaurs (Wild, 1978; Padian, 1983) and dinosauromorphs, distal tarsal 4 has a similar transverse width as the transverse width of distal tarsal 3 (Sereno, 1991a).

348. Distal tarsal 4, size of articular facet for metatarsal V: (0) more than half of lateral surface of distal tarsal 4; (1) less than half of lateral surface of distal tarsal 4 (fig. 42) (Sereno, 1991a; Novas, 1996; Benton, 1999).

As stated by Sereno (1991a), the articular facet for metatarsal V on the ventrolateral side of distal tarsal 4 covers more than 50% of the lateral surface in non-archosaurian archosauriforms, pterosaurs, and crocodylian-line archosaurs. In contrast, the articular facet for metatarsal V on the ventrolateral

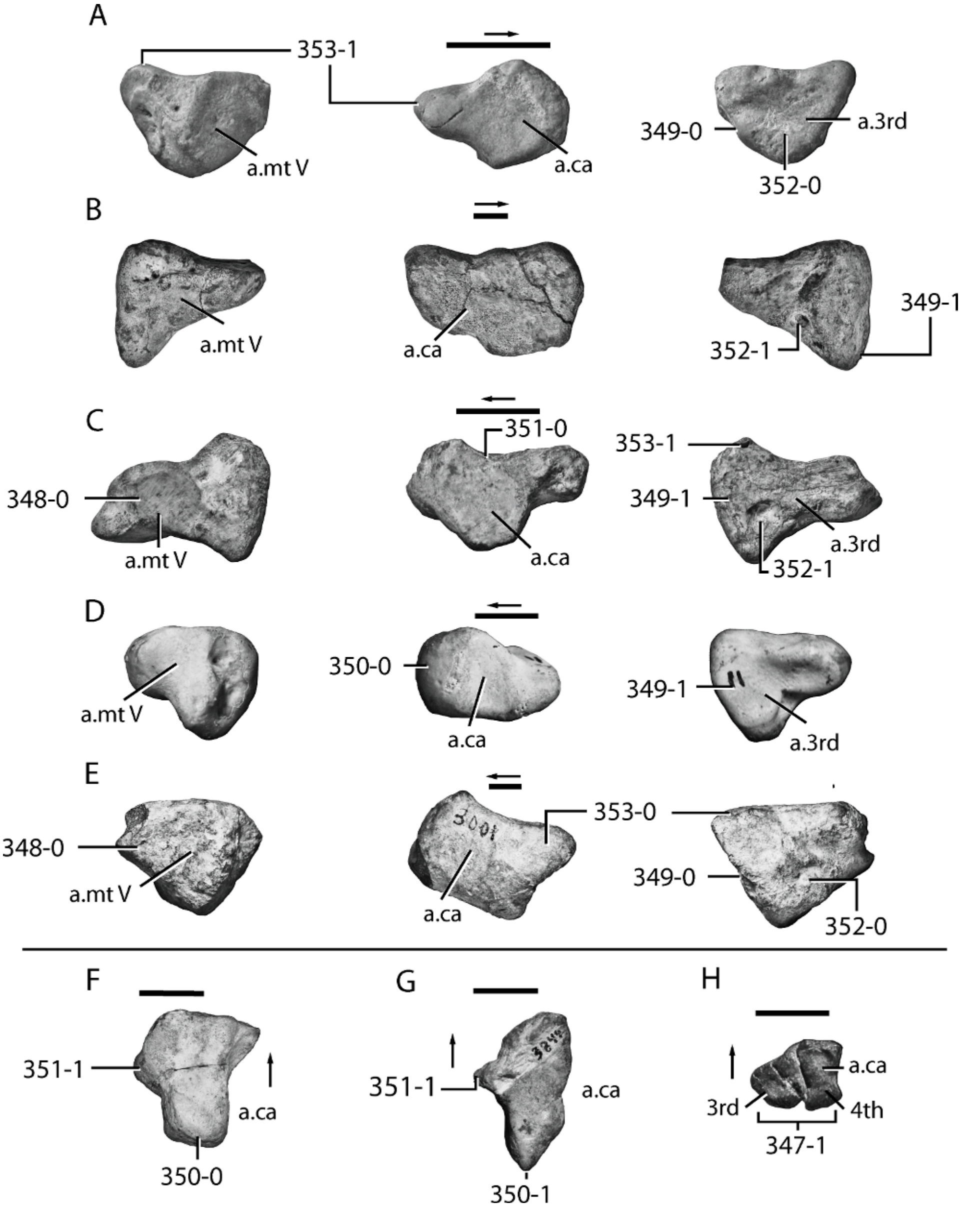


Fig. 42. Fourth distal tarsal of archosauriforms: **A–E,** elements in lateral (left), proximal (middle), and medial (right) views; **A,** right 4th distal tarsal of *Revueltosaurus callenderi* (PEFO 34561); **B,** right 4th distal tarsal of *Postosuchus alisonae* (UNC 15575); **C,** left 4th distal tarsal of *Hesperosuchus* ''*agilis*'' (YPM 41198); **D,** left 4th distal tarsal of *Alligator mississippiensis* (AMNH unnumbered); **E,** left 4th distal tarsal of Phytosauria (AMNH FR 3001); **F,** right 4th tarsal of *Coelophysis* (UCMP 129618) in dorsal view; **G,** right 4th tarsal of *Saturnalia tupiniquim* (MCP 3844-PV) in dorsal view; **H,** right tarsals of *Dimorphodon macronyx* in dorsal view. Scale bars = 1 cm.

side of distal tarsal 4 covers less than 50% of the lateral surface in dinosauromorphs (Sereno, 1991a).

349. Distal tarsal 4, posteroventral portion: (0) tapers to point or poorly ventrally expanded; (1) ventrally expanded into a small process (fig. 42) (new).

The posterior portion of distal tarsal 4 thickens posteriorly in most non-archosaurian archosauriforms (e.g., *Erythrosuchus*, BMNH R 3592; Gower, 1996), crocodylian-line archosaurs, and dinosauromorphs. This posterior expansion has been referred to as a peg by Gower (1996) for *Erythrosuchus* or a heel (Sereno and Arcucci, 1994a: fig. 4) by Sereno and Arcucci (1994a) for *Lagerpeton*. In the taxa listed above, the posterior portion of distal tarsal 4 expands dorsally into a small mound. The posterior expansion is confined to a dorsal expansion in non-archosaurian archosauriforms, phytosaurs, *Revueltosaurus*, aetosaurs, and non-saurischian dinosauromorphs. These taxa are scored as (0) for this character. In contrast, the posteroventral portion of distal tarsal 4 is ventrally expanded in *Effigia* (AMNH FR 30587), *Postosuchus alisonae* (UNC 15575), *Saurosuchus* (PVL 2557), *Prestosuchus* (BSP XXV 1-3/5-11/ 28-41/49), CM 73372, *Terrestrisuchus* (BMNH P47/21a), *Hesperosuchus* (YPM 41198), and *Protosuchus richardsoni* (AMNH FR 3024). In these taxa, the articular facet for metatarsal V extends to the ventral portion of the process.

350. Distal tarsal 4, posterior prong: (0) blunt; (1) pointed (fig. 42) (Langer and Benton, 2006).

Novas (1994, 1996) followed by Langer and Benton (2006) noticed the posterior (= posteromedial) end of the distal tarsal 4 in blunt in proximate outgroups of Dinosauria whereas some dinosaurs possess a pointed posterior end. Langer and Benton (2006) scored ornithischians and theropods as (0), and *Herrerasaurus* (PVSJ 373) and sauropodomorphs as (1). I agree with their scoring here.

351. Distal tarsal 4, medial side: (0) without a distinct medial process present in the anteroposterior middle of the element; (1) with a distinct medial process present in the anteroposterior middle of the element (fig. 42) (new).

In saurischians, a distinct, medially projecting process is present on the medial side of distal tarsal 4. This process is located in the middle of the anterior and posterior extent of the element. A medial process is not present in non-archosaurian archosauriforms, crocodylian-line archosaurs, and non-saurischian dinosaurs.

352. Distal tarsal 4, medial side: (0) without foramen/foramina; (1) with foramen/foramina (fig. 42) (new).

This character can be scored only if distal tarsal 4 is well preserved. In taxa such as *Fasolasuchus* (PVL 3850), CM 73372, *Hesperosuchus "agilis"* (YPM 41198), *Poposaurus gracilis* (YMP 57100), Effigia (AMNH FR 30587), and *Alligator*, there are small foramina at the ventral portion of the medial side of distal tarsal 4. Similar foramina are not present in *Euparkeria* (UMCZ T692) and *Revueltosaurus* (PEFO 34561) or any avian-line archosaur examined.

353. Distal tarsal 4, proximal surface: (0) flat; (1) distinct, proximally raised region on the posterior portion (= heel of Sereno and Arcucci, 1994a, 1994b) (fig. 42) (new).

Plesiomorphically, the proximal surface of distal tarsal 4 is flat in non-archosaurian archosauriforms as exemplified by *Proterosuchus* (AMNH FR 2237) and *Euparkeria* (UMCZ T692). The same is also present in the phytosaurs *Pseudopalatus* (UCMP 27235) and a specimen referred to *Smilosuchus* (AMNH FR 3001). In the only basal pterosaur with a well-preserved distal tarsal 4, *Dimorphodon* (YPM 9182), the surface is flat (Padian, 1983). A posterior heel is clearly present in *Revueltosaurus* (PEFO 34561), *Riojasuchus* (PVL 3827), CM 73372, *Fasolasuchus* (PVL 3851), *Effigia* (AMNH FR 30587), *Postosuchus alisonae* (UNC 15575), *Hesperosuchus "agilis"* (YPM 41198) and *Hesperosuchus agilis* (AMNH 6758), *Alligator,* and two avian-line archosaurs, *Lagerpeton* (PVL 4619) and *Marasuchus* (PVL 3870). Distal tarsal 4 is flat in dinosaurs (Novas, 1996).

354. Astragalus, ridge separating the tibial facet from the posterior edge (= astragalar ridge): (0) thick; (1) thin lamina (fig. 43) (new).

The astragalar ridge (sensu Brochu, 1992) is located at the posterior edge of the tibial

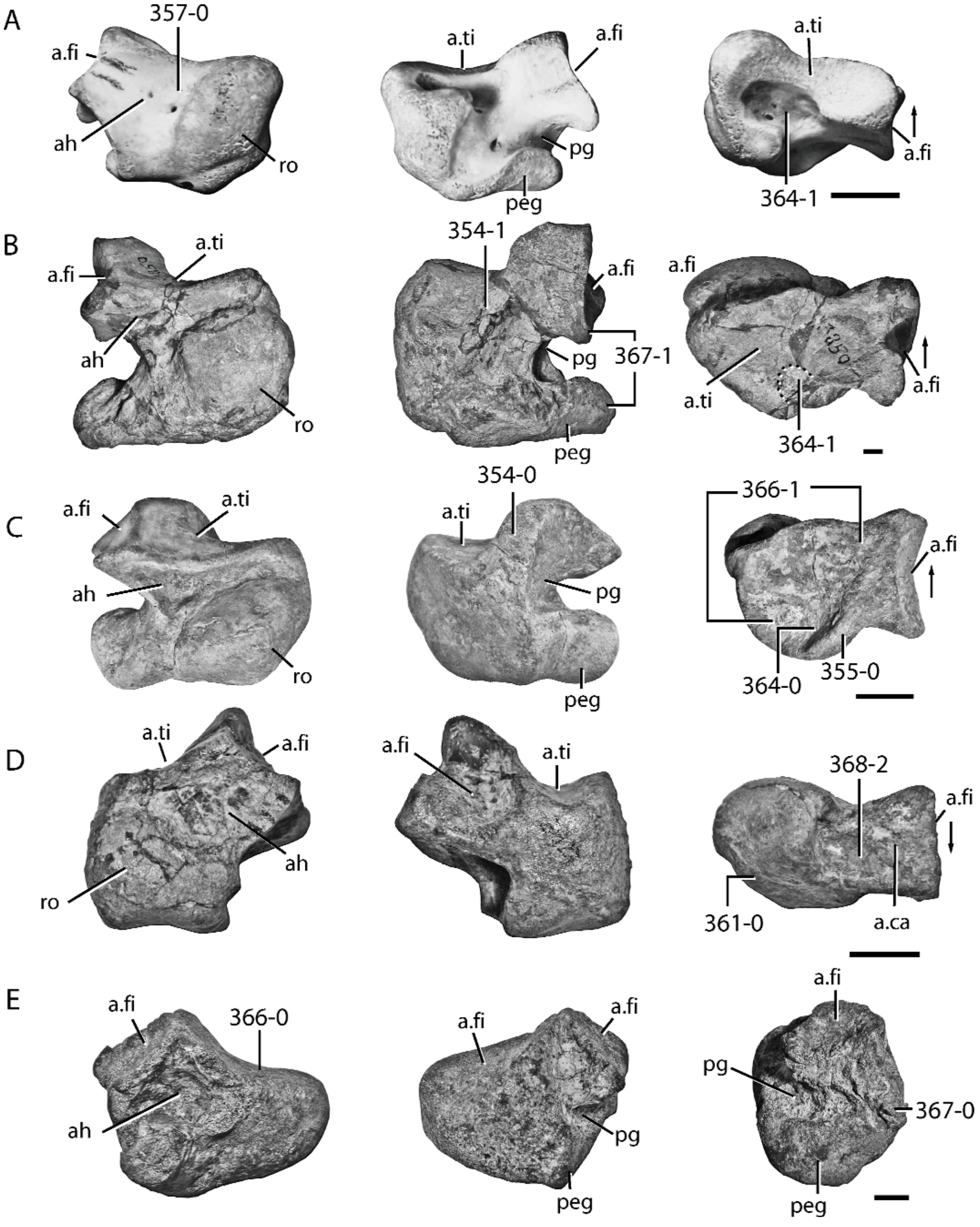


Fig. 43. Astragali of archosauriforms: **A,** right astragalus of *Alligator mississippiensis* (AMNH FR unnumbered) in anterior (left), posterior (middle), and proximal (right) views; **B,** right astragalus of *Fasolasuchus tenax* (PVL 3850) in anterior (left), posterior (middle), and proximal (right) views; **C,** right astragalus of *Effigia okeeffeae* (AMNH FR 30587) in anterior (left), posterior (middle), and proximal (right) views; **D,** left astragalus of *Riojasuchus tenuisceps* (PVL 3827) in anterior (left), posterior (middle), and distal (right) views; **E,** right astragalus of *Pseudopalatus* (UCMP 27235) in anterior (left), posterior (middle), and lateral (right) views. Arrow indicates anterior direction. Numbers refer to character states. See appendix for anatomical abbreviations. Scales = 1 cm.

articular facet and continues to meet the fibular facet. Among basal archosauriforms, *Euparkeria* (UMCZ T692), *Chanaresuchus* (MCZ 4035) and possibly *Erythrosuchus* (BMNH R3592), the astragalar ridge is robust. This is similar to phytosaurs (USNM 18313), *Effigia* (AMNH FR 30587), *Riojasuchus* (PVL 3827), *Revueltosaurus* (PEFO 34561), aetosaurs (e.g., *Typothorax* MCZ 1488), *Prestosuchus* (BSP XXV 1-3/5-11/ 28-41/49), *Saurosuchus* (PVL 2557), and *Gracilisuchus* (PVL 4597). In *Fasolasuchus* (PVL 3850), *Postosuchus kirkpatricki* (TTU-P 9000), CM 73372, *Tikisuchus* (ISI R 305), *Hesperosuchus* (YPM 41198; AMNH FR 6758), *Terrestrisuchus* (BMNH P47/21a), and *Protosuchus richardsoni* (AMNH FR 3024), the ridge is distinct and has sharp lamina.

355. Astragalus, dorsally expanded process on the posterolateral portion of the tibial facet: (0) absent or poorly expanded; (1) expanded into a distinct, raised process (= posterior ascending process of Sereno and Arcucci, 1994a) (figs. 43, 46) (modified from Sereno and Arcucci, 1994a).

Plesiomorphically in archosauriforms, a rim surrounds the tibial facet of the astragalus. As described by Sereno and Arcucci (1994a), a distinct raised process is located on the posterolateral portion of the tibial facet in *Lagerpeton* (PVL 4619). Irmis et al. (2007a) also found the same feature in *Dromomeron romeri* (GR 223), and Nesbitt et al. (2009b) used the morphology of the distal end of the tibia to conclude that the feature was present in *Dromomeron gregorii* (TMM 31100-278). A possibly homologous feature is located in the same position in some crocodylian-line archosaurs (e.g., *Effigia*, AMNH FR 30587). However, the process is not well developed in crocodylian-line archosaurs (see Nesbitt et al., 2009b).

356. Astragalus, anterior ascending flange (anterior process): (0) absent; (1) present and less than the height of the dorsoventral height of the posterior side of the of the astragalus; (2) present and greater than the dorsoventral height of the posterior side astragalus. ORDERED (fig. 46) (modified from Gauthier, 1986; Novas, 1992, 1996; Benton, 1999; Rauhut, 2003).

In non-archosaurian archosauriforms, crocodylian-line archosaurs, pterosaurs, *Lagerpeton*, *Dromomeron*, and *Marasuchus*, the anterior portion of the astragalus does not have an anterior process that fits on the anterior face of the tibia. In *Lagerpeton* (PVL 4619), *Dromomeron* (GR 223), and *Marasuchus* (PVL 3870) a small anterior process is present on the anterior edge of the astragalus between the articular facets for the tibia and the fibula. This small pyramidal process could be homologous to the ascending process, but a transitional form between the non-dinosauriform dinosauromorph and dinosauriform, taxa with a clear ascending process, morphology has not been found to date.

In the non-dinosaurian dinosauriform *Silesaurus* (ZPAL Ab/III 361/20) a short anterior ascending process fits into a slot on the anterior face of the distal portion of the tibia. *Pseudolagosuchus* (PVL 3454) has a very short anterior ascending process the fits into a slot on the anteroventral surface of the tibia. In basal dinosaurs, the anterior ascending process fits into a slot on the anterior face of the distal portion of the tibia, and the height of the anterior ascending process is not as tall as the dorsoventral height of the posterior side. *Coelophysis bauri* (AMNH FR 30576) and other basal theropods also have a short anterior ascending process whereas the process is taller than the dorsoventral height of the posterior side astragalus in tetanurans (see Rauhut, 2003; Smith et al., 2007).

Taxa with an anterior ascending process have a depression posterior to the process. This basin (= posterodorsal basin of Novas, 1996) can either be continuous with the other portions of the articular surface for the tibia or can be a separate fossa with a distinct rim (see character 359).

357. Astragalus, anterior hollow: (0) shallow depression; (1) reduced to a foramen (= extensor canal) (figs. 43, 46) (new).

The anterior hollow is located on the anterodorsal portion of the astragalus between the articular facets of the tibia and the fibula. A shallow anterior hollow is present in *Prolacerta* (BPI 2676), *Proterosuchus* (NM C1484), *Vancleavea* (GR 138), *Charanesuchus* (MCZ 4035), *Tropidosuchus* (PVL 4601), *Euparkeria* (UMCZ T692), phytosaurs, and all crocodylian-line archosaurs. An anterior hollow is not present in *Dimorphodon* (YPM 9182), *Lagerpeton* (PVL 4619), and *Dromo-*

meron romeri (GR 223) and is present as a small foramen in *Marasuchus* (PVL 3870) and all dinosauriforms examined here.

358. Articular facet for the astragalus of the calcaneum lies: (0) completely medial to the fibular facet; (1) partially ventral to the fibular facet (fig. 45) (modified from Parrish, 1993).

In most archosauriforms, the articular facet for the astragalus of the calcaneum lies completely medial to the fibular facet of the calcaneum. In *Gracilisuchus* (PVL 4597), *Revueltosaurus* (PEFO 34561), aetosaurs (e.g., *Typothorax*, MCZ 1488), *Ticinosuchus* (PIZ T2817), *Riojasuchus* (PVL 3827), *Qianosuchus* (Li et al., 2006: fig 3E), *Prestosuchus* (BSP XXV 1-3/5-11/ 28-41/49), the articular facet for the calcaneum is completely or nearly completely medial to the fibular facet. In *Effigia* (AMNH FR 30587), *Batrachotomus* (SMNS 90018), *Saurosuchus* (PVL 2557), *Fasolasuchus* (PVL 3850), *Postosuchus kirkpatricki* (TTU-P 9002), CM 73372, *Postosuchus alisonae* (UNC 15575), and crocodylomorphs (*Hesperosuchus agilis*, AMNH FR 6758; *Protosuchus richardsoni*, AMNH FR 3024), there is a deep fossa on the medial side of the fibular facet. The "peg" of the astragalus fits into this fossa.

359. Astragalus, proximal surface: (0) lacks a marked rimmed and elliptical fossa posterior to the anterior ascending process; (1) possesses a marked rimmed and elliptical fossa posterior to the anterior ascending process (fig. 46) (Langer and Benton, 2006).

All taxa with an anterior ascending process of the astragalus (dinosauriforms) have an articular surface that articulates with the tibia posterior to the process. In most forms, this portion of the proximal articular surface is continuous with the other articular surfaces for the tibia. In *Herrerasaurus* (PVL 373), *Saturnalia* (Langer 2003), *Tawa* (Nesbitt et al. 2009c), basal sauropodomorphs, and *Chindesaurus* (PEFO 33982), there is a distinct, rimmed depression fossa posterior to the ascending process. The depression is lined with compact bone and most taxa bear small foramina within the fossa. Taxa lacking an anterior ascending process are scored as inapplicable.

360. Astragalus, dorsolateral margin: (0) overlaps the anterior and posterior portions of the calcaneum equally; (1) the posterior corner of the dorsolateral margin of the astragalus dorsally overlaps the calcaneum much more than the anterior portion (fig. 46) (Nesbitt et al., 2009a).

In non-archosauriform archosauromorphs, *Proterosuchus* (AMNH FR 2237), *Erythrosuchus* (BMNH R3592), *Vancleavea* (GR 138), and the proterochampsians *Tropidosuchus* (PVL 4601) and *Chanaresuchus* (MCZ 4035), the anterior and posterior portions of the dorsolateral margin of the astragalus overlap the calcaneum equally. The posterior portion of the dorsolateral margin of the astragalus dorsally overlaps the calcaneum much more than that of the anterior portion in *Euparkeria* (UMCZ T692), *Dromomeron* (GR 223), *Lagerpeton* (PVL 4619), *Marasuchus* (PVL 3870), *Pseudolagosuchus* (PVL 3454), and other basal dinosaurs, phytosaurs (USNM 18313), and in suchians.

361. Astragalus, anteromedial corner shape: (0) obtuse; (1) acute (figs. 43, 46) (Bonaparte, 1976; Novas, 1989; Sereno, 1991a; Juul, 1994; Novas, 1996; Benton, 1999).

The anteromedial corner of the astragalus is subrectangular or rounded in distal view in nearly all non-dinosauromorphs archosauriforms (Sereno, 1991a). In contrast, the anteromedial corner of the astragalus is pointed and the edges of the anteromedial corner form an acute angle in pterosaurs (*Dimorphodon*, YPM 9182) and all dinosauromorphs (e.g., *Dromomeron* GR 223, *Herrerasaurus* PVSJ 373, *Pisanosaurus* PVL 3577).

362. Astragalus, proximal articular facet for fibula occupies: (0) more than 0.3 of the transverse width; (1) less than 0.3 of the transverse width (fig. 46) (Langer and Benton, 2006).

The articular facet is formed from portions of the astragalus and calcaneum. Plesiomorphically within Archosauriformes, the articular facet for the fibula occupies more than 0.3 of the transverse width of the astragalus. In the dinosauromorphs *Lagerpeton*, *Dromomeron romeri*, *Marasuchus*, *Pseudolagosuchus*, and *Silesaurus*, the articular facet for fibula occupies about 0.5 the transverse length of the astragalus and calcaneum combined. As stated by Langer and Benton (2006), dinosaurs have state (1).

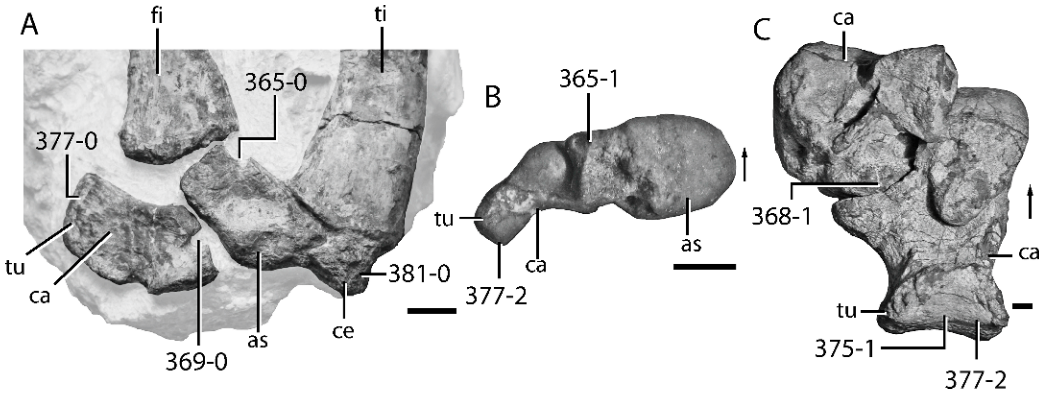


Fig. 44. Articulated ankles of archosauriforms: **A,** right ankle of *Proterosuchus* (AMNH FR 2237) in anterior view. The matrix has been lightened; **B,** left ankle of *Euparkeria capensis* (UMCZ T692) in proximal view; **C,** right ankle of *Fasolasuchus tenax* (PVL 3850) in proximal view. Arrow indicates anterior direction. Numbers refer to character states. See appendix for anatomical abbreviations. Scale bars = 1 cm.

363. Astragalus, posterior groove: (0) present; (1) absent (fig. 46) (Sereno, 1991a; Nesbitt et al., 2009a).

An astragalar posterior groove separates the lateral portion of the astragalus into dorsal and ventral articular surfaces. The dorsal surface articulates with the fibula proximally and the calcaneum distally. The distal surface articulates with the distal portion of the calcaneum. The posterior groove is present in *Mesosuchus* (SAM 6046), *Prolacerta* (BPI 2676), *Proterosuchus* (NM C1484), proterochampsian *Charanesuchus* (MCZ 4035), *Euparkeria* (UMCZ T692), phytosaurs (USNM 18313), and suchians. A groove is apparently absent in the proterochampsian *Tropidosuchus* (PVL 4601). The posterior groove is present in *Marasuchus* (PVL 3870), *Pseudolagosuchus* (PVL 3454), basal sauropodomorphs (e.g., *Coloradosaurus* PVL 3967), and *Herrerasaurus* (PVSJ 373) even though Sereno (1991a) suggests that a posterior groove is absent in all dinosauromorphs. The groove is clearly absent in *Dromomeron* (GR 223), *Lagerpeton* (PVL 4619), theropods and ornithischians.

364. Astragalus, tibial articular surface: (0) continuous articular surface; (1) nonarticular fossa present on the posterior portion (fig. 43) (new).

In nearly all basal archosaurs, the tibia articulates completely with the tibial articular facet of the astragalus. In *Poposaurus* (YPM 57100), *Fasolasuchus* (PVL 3850), CM 73372, *Postosuchus kirkpatricki* (TTU-P 9002), *Postosuchus alisonae* (UNC 15575), *Hesperosuchus "agilis"* (YPM 41198), *Terrestrisuchus* (BMNH P47/21a), *Protosuchus richardsoni* (AMNH FR 3024), *Longosuchus* (TMM 31185-84b), and *Alligator*, a distinct nonarticular fossa is present on the posterior portion of the proximal surface of the astragalus. The tibia of taxa scored as (1) is C-shaped in distal view where the gap in the tibia lies over the proximal fossa.

365. Astragalus, tibial and fibular articulations: (0) separated by a gap (or notch of Gower, 1996); (1) continuous (fig. 44) (modified from Sereno and Arcucci, 1990; Sereno, 1991a; Gower, 1996; Nesbitt et al., 2009a).

In non-archosauriform archosauromorphs, *Proterosuchus* (NM QR 1484), *Shansisuchus* (IVPP field number 56173; Gower, 1996), and *Vancleavea* (GR 138) a clear, nonarticular gap completely separates the articular facet of the tibia and fibula. The presence of a gap in the astragalus of *Erythrosuchus* is not clear because of the poor ossification of the astragalus. Proterochampsians and basal members of the Archosauria all lack a gap. As discussed by Gower (1996), *Euparkeria* does not have a gap between the tibial and fibular facets of the astragalus even though this was cited as a character placing *Euparkeria* outside of proterochampsians + Archosauria in Sereno (1991a).

366. Astragalus, tibial facet: (0) concave or flat; (1) divided into posteromedial and

anterolateral basins (figs. 43, 46) (Sereno, 1991a; Parrish, 1993; Juul, 1994; Benton, 1999).

The articular surface for the tibia on the calcaneum is concave in non-archosaurian archosauriforms (Sereno, 1991a). This morphology can be further confirmed by the distal end of the tibia; in non-archosaurian archosauriforms, the distal articular surface of the tibia is concave. In contrast, the articulation between the astragalus and tibia is more complicated in ornithosuchids, aetosaurs, *Gracilisuchus*, "rauisuchians," and crocodylomorphs. In these taxa, the tibial facet of the astragalus is split into two shallow basins, posteromedial and anterolateral. A raised ridge oriented anteromedially divides the two basins. A corresponding "screw-joint" distal surface (Gauthier, 1986) of the tibia fits into the two basins.

I agree with Sereno (1991a) in his thorough discussion of the character and most scoring decisions except for phytosaurs. Sereno (1991a), followed by others (e.g., Juul, 1994), scored phytosaurs as having a state similar to (1) here (= flexed). Parrish (1993) disagreed with Sereno (1991a) and concluded that phytosaurs have a concave surface. My observations of the tibial facet of the astragalus of *Smilosuchus* (USNM 18313) and *Pseudopalatus* (UCMP 27235) agree with the observations of Parrish (1993) and I score phytosaurs as concave. Further, the distal surface of the tibia of phytosaurs is convex in phytosaurs. That said, I have observed a specimen of a phytosaur (TMM 31100-466, possibly *Paleorhinus* or *Angistorhinus*) from the Otis Chalk quarries that has a weakly flexed tibial facet (see discussion below).

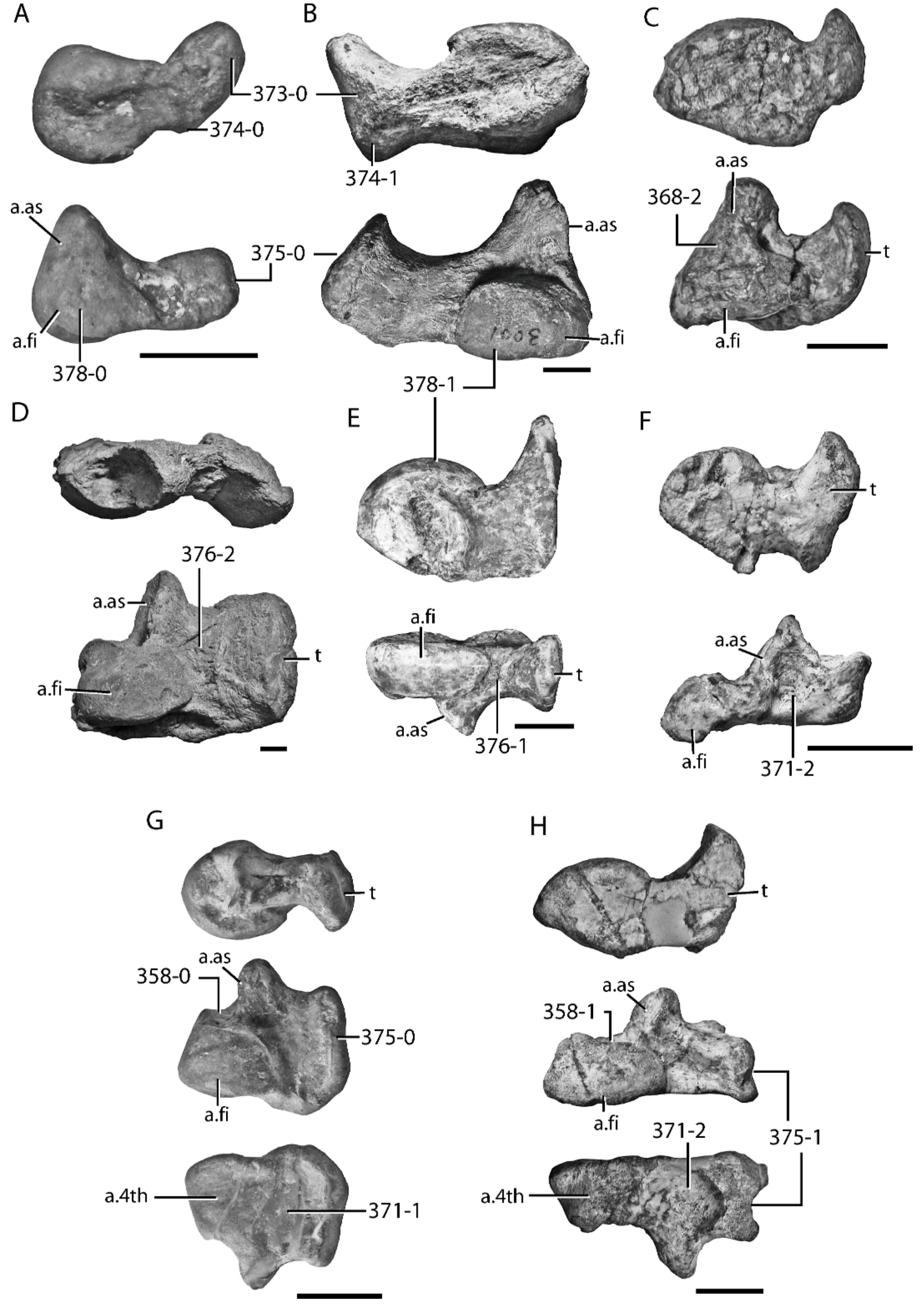
Parrish (1993) observed a "flexed" facet of the astragalus in dinosauromorphs. Here, I expand on his observation. The proximal surface of the astragalus of *Lagerpeton* (PVL 4619) is poorly preserved and it cannot be determined whether the two basins are present. *Dromomeron romeri* (GR 223), a close relative of *Lagerpeton* (Irmis et al., 2007a), has a well-preserved astragalocalcaneum that clearly possesses separate posteromedial and anterolateral basins. Although poorly preserved, the articular facet for the tibia of the astragalus of *Marasuchus* (PVL 3870) appears to possess a deep posteromedial basin. Therefore, among dinosauromorphs, *Dromomeron romeri* and *Marasuchus* are scored as (1). In dinosauriforms, two distinct basins are not present on the tibial facet of the astragalus. The proximal surface of the astragalus is too transformed to be scored in *Silesaurus* and dinosaurs. Basal pterosaurs cannot be scored for this character.

367. Astragalus, articular surface for the calcaneum: (0) stretches from fibular facet of the astragalus to the ventral margin; (1) restricted to the ventral surface of the fibular facet, clearly separated from the ventral margin (fig. 43) (new).

In *Proterosuchus* (NM QR 1484) and *Prolacerta* (BP/1/2676) the articulations of the dorsal portion and ventral portions of the astragalus are clearly separated by a foramen. In *Vancleavea* (GR 138), *Tropidosuchus* (PVL 4601), *Euparkeria* (UMCZ T692), *Smilosuchus* (USNM 18313), *Riojasuchus* (PVL 3827), *Revueltosaurus* (PEFO 34561), and aetosaurs, the articular surface for the calcaneum stretches from fibular facet of the astragalus to the ventral margin. In forms listed above with a "peg," the articular surface for the calcaneum is continuous from ventral to the fibular facet to the "peg." In *Fasolasuchus* (PVL 3850), *Postosuchus kirkpatricki* (TTU-P 9000), *Postosuchus alisonae* (UNC 15575), *Rauisuchus* (BSP AS XXV-60-121), *Hesperosuchus* "*agilis*" (YPM 41198), *Terrestrisuchus* (BMNH R P47/21a), and *Protosuchus* (AMNH FR 3024), the calcaneal articulations are separated into (1) the surface ventral to the fibular facet and (2) the "peg." All avian-line archosaurs are scored as (0) given our knowledge of taxa with disarticulated calcanea and astragali (e.g., *Pseudolagosuchus*, *Dilophosaurus*).

368. Astragalus-calcaneum, ventral articular surface: (0) flat or slightly convex; (1) concavoconvex with concavity on calcaneum; (2) concavoconvex with concavity on astragalus (figs. 43–45) (Sereno, 1991a).

Sereno (1991a) thoroughly discussed the construction of this character and little can be added here. It is important to note that this character examines the ventral articular surface of the articulation between the astragalus and calcaneum. *Prolacerta* (BPI


A
373-0
374-0
a.as
375-0
a.fi
378-0
B
374-1
a.as
a.fi
378-1
C
a.as
368-2
t
a.fi
D
376-2
a.as
t
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E
a.fi
t
a.as
376-1
F
t
a.as
a.fi
371-2
G
t
a.as
358-0
375-0
a.fi
a.4th
371-1
H
t
a.as
358-1
a.fi
371-2
375-1
a.4th

2675) and *Proterosuchus* (NM QR 1484) are scored as (1) whereas *Erythrosuchus*, *Vancleavea*, proterochampsians, and *Euparkeria* (UMCZ T692) are scored as (0). All avian archosaurs are scored as (?). Taxa considered as "crocodile-normal" are scored as (1). This includes *Turfanosuchus* (IVPP V3237), phytosaurs (e.g., *Smilosuchus*, USNM 18313), *Gracilisuchus* (PVL 4597), *Revueltosaurus* (PEFO 34561), aetosaurs (e.g., *Aetosaurus*, SMNS 5770 S-22), *Effigia* (AMNH FR 30587), *Poposaurus* (YPM 57100), "rauisuchians," and crocodylomorphs. *Riojasuchus* (PVL 3827) and *Ornithosuchus* (BMNH R2410), two taxa considered to have a "crocodile-reversed" astragalus-calcaneum articulation, are scored as (2).

369. Astragalus-calcaneum, ossified astragalo-calcaneal canal: (0) present; (1) absent (fig. 44) (Gauthier, 1984; Bennett, 1996; Gower and Sennikov, 1997; Nesbitt et al., 2009a).

An ossified astragalo-calcaneal canal is present when a foramen is formed between the astragalus and calcaneum when the two elements are in articulation. The border of the astragalo-calcaneal canal is present on *both* the calcaneum and astragalus. The border of the astragalo-calcaneal canal on the astragalus may be homologous with the posterior groove of the astragalus in *Euparkeria*, nearly all crocodylian-line archosaurs, and some avian-line archosaurs.

This character has been largely ignored because of taxon selection for archosaur relationships and diapsid relationships; most archosaur phylogenies use *Proterosuchus* as an outgroup whereas diapsid relationships use *Proterosuchus* as a terminal taxon representative of Archosauriformes. Gauthier (1984) showed that non-archosauriform archosauromorphs and *Proterosuchus* (e.g., NM QR 1484) have a clear astragalo-calcaneal canal between the astragalus and calcaneum in articulation whereas *Euparkeria*, proterochampsians, and Archosauria do not have a gap between the two elements. Gower (1996) explicitly showed that *Erythrosuchus* as well as the other erythrosuchians, *Shansisuchus* and *Vjushkovia triplicostata*, also lack an astragalo-calcaneal canal. An astragalo-calcaneal canal is absent in the proterochampsians *Tropidosuchus* (PVL 4601) and *Chanaresuchus* (MCZ 4035) and in *Vancleavea* (GR 138).

370. Astragalus-calcaneum, articulation: (0) free; (1) coossified (fig. 46) (Sereno and Arcucci, 1994a; Irmis et al., 2007a).

In most archosauriforms, save avians and close relatives, the astragalus and calcaneum are separate elements. In pterosaurs (e.g., *Dimorphodon*, YPM 9182), *Lagerpeton* (PVL 4619), and *Dromomeron romeri* (GR 223), the astragalus and calcaneum are coossified. Among basal dinosaurs, the proximal tarsals are coossified in *Heterodontosaurus* (SAM-PK-1332) and coelophysoids (Rowe and Gauthier, 1990; Tykoski, 2005b).

371. Calcaneum, ventral articular surface for distal tarsal 4 and the distal end of the tuber: (0) continuous; (1) separated by a clear gap; (2) separated by a gap with a ventral fossa. ORDERED (fig. 45) (new).

In non-archosaurian archosauriforms, the articular facet for distal tarsal 4 and the tuber is continuous on the ventral surface of the calcaneum. This arrangement is present in *Erythrosuchus* (BMNH R 3592), *Tropidosuchus* (PVL 4601), and *Euparkeria* (UMCZ T692). In these taxa, the ventral surface of the tuber shaft is slightly concave. In phytosaurs (AMNH FR 3001, USNM

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Fig. 45. Calcanea of archosauriforms: **A,** left calcaneum of *Euparkeria capensis* (UMCZ T692) in anterolateral (top) and proximal (bottom) views; **B,** right calcaneum of Phytosauria (AMNH FR 3001) in anterolateral (top) and proximal (bottom) views; **C,** left calcaneum of *Riojasuchus tenuisceps* (PVL 3827) in anterolateral (top) and proximal (bottom) views; **D,** left calcaneum of *Batrachotomus kuperferzellensis* (SMNS 90018) in medial (top) and proximal (bottom) views; **E,** right calcaneum of *Shuvosaurus inexpectatus* (TTU-P 9001) in medial (top) and proximal (bottom) views: **F,** left calcaneum of *Protosuchus richardsoni* (AMNH FR 3024) in lateral (top) and ventral (bottom) views; **G,** left calcaneum of *Revueltosaurus callenderi* (PEFO 34561) in medial (top), proximal (middle), and ventral (bottom) views; **H,** left calcaneum of *Hesperosuchus "agilis"* (YPM 41198) in lateral (top), proximal (middle), and ventral (bottom) views. Arrow indicates anterior direction. Numbers refer to character states. See appendix for anatomical abbreviations. Scale bars = 1 cm.

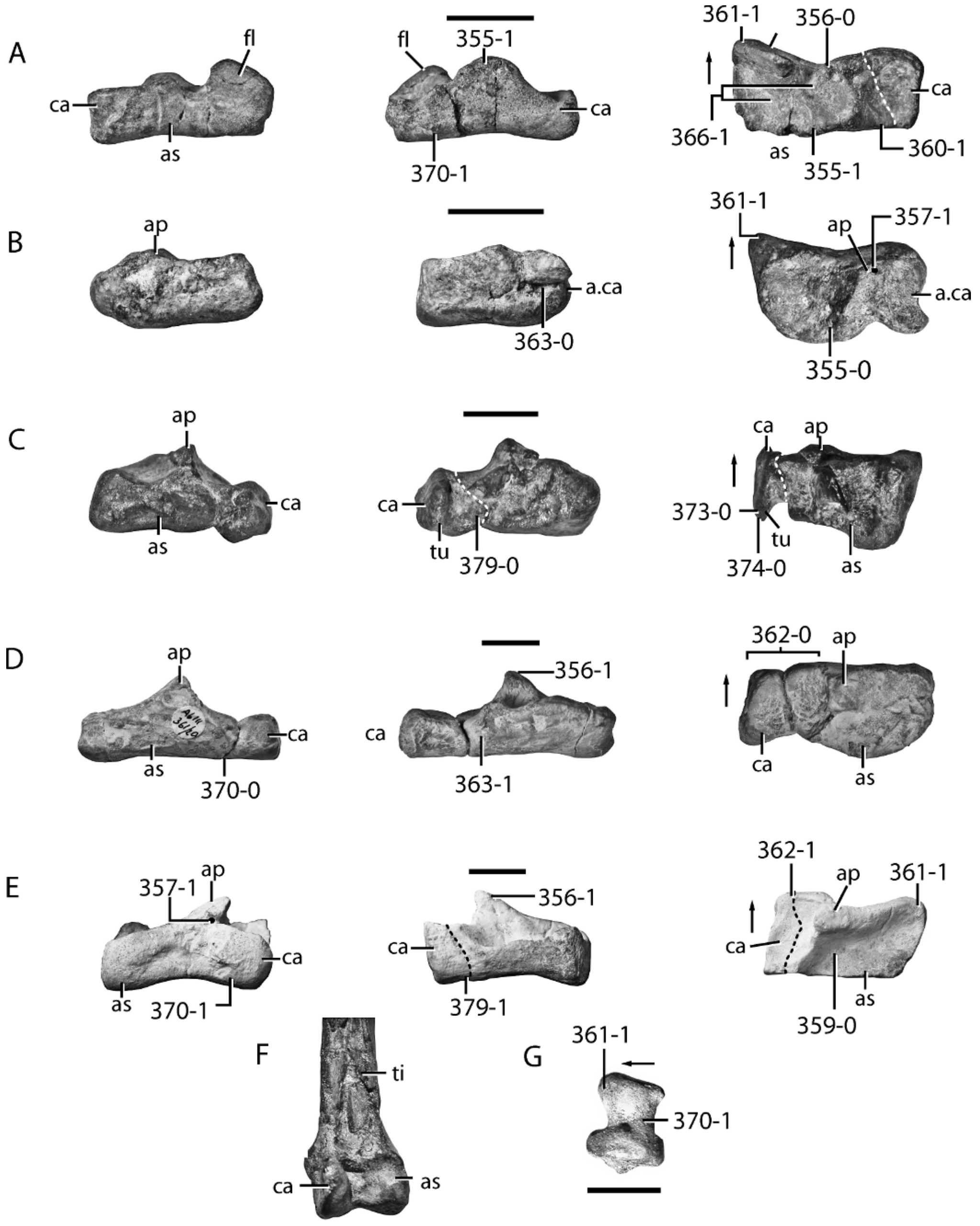

Fig. 46. Proximal ankle elements of avian-line archosaurs: **A–E,** elements in posterior (left), anterior (middle), and proximal (right) views. **A,** right astragalocalcaneum of *Dromomeron romeri* (GR 223); **B,** right astragalus of *Pseudolagosuchus major* (PVL 4629); **C,** left astragalus and calcaneum of *Marasuchus lilloensis* (PVL 3871); **D,** left astragalus and calcaneum of *Silesaurus opolensis* (ZPAL Ab III 361/20); **E,** left astragalus and calcaneum of *Coelophysis bauri* (30576); **F,** right astragalocalcaneum of *Dimorphodon macronyx* (YPM 9182E) in anterior and distal **G,** views. Arrow indicates anterior direction. Numbers refer to character states. See appendix for anatomical abbreviations. Scale bars = 1 cm in A–B, D–E, and 5 mm in C, F–G.

18313) and suchians, the articular facet for distal tarsal 4 and the tuber is separated by clear gap lined with compact bone. A gap is clearly present in *Riojasuchus* (PVL 3827), *Gracilisuchus* (PVL 4597), *Revueltosaurus* (PEFO 34561), all aetosaurs, *Postosuchus kirkpatricki* (TTU-P 9000) and *Shuvosaurus* TTU-P 9001), and crocodylomorphs. *Postosuchus kirkpatricki* (TTU-P 9002), CM 73372, *Prestosuchus* (BSP XXV 1-3/5-11/28-41/49), *Hesperosuchus* "*agilis*" (YPM 41198), *Dromicosuchus* (UNC 15574), *Terrestrisuchus* (BMNH P47/21a), and *Protosuchus richardsoni* (AMNH FR 3024) possess a ventral fossa between the surface for distal tarsal 4 and the tuber. The fossa is walled by two ridges, a lateral ridge connecting the tuber and articular surface for distal tarsal 4, and a medial ridge connecting the tuber from the articular facet with the astragalus. Avian-line archosaurs cannot be scored for this character.

372. Calcaneum, articular facets for the fibula and astragalus: (0) connected by a continuous surface; (1) separated (new).

In non-archosaurian archosauriforms, phytosaurs (*Smilosuchus*, USNM 18313), ornithosuchids (*Riojasuchus*, PVL 3827), and the Tanzanian pseudosuchian, the articular facets of the calcaneum for the fibula and astragalus are connected by a continuous surface. In contrast, the articular facets of the calcaneum for the fibula and astragalus are separated in aetosaurs (e.g., *Longosuchus*, TMM 31185-84a), *Ticinosuchus* (PIZ T2817), *Effigia* (AMNH FR 30587), *Poposaurus gracilis* (YPM 57100), *Batrachotomus* (Gower and Schoch, 2009), *Postosuchus kirkpatricki* (TTU-P 9002), and crocodylomorphs (e.g., *Terrestrisuchus*; Crush, 1984). The condition in avian-line archosaurs is unknown in most taxa although it looks like state (0) in taxa with a disarticulated calcaneum and astragalus.

373. Calcaneum, calcaneal tuber: (0) present; (1) absent (figs. 45–46) (Gauthier, 1986; Sereno, 1991a; Juul, 1994; Benton, 1999).

The calcaneal tuber lies on the lateral portion or the posterior portion of the calcaneum in basal archosauriforms. As discussed by Gauthier (1984) and Sereno (1991a), the calcaneal tuber is present in non-archosaurian archosauriforms and all crocodylian-line archosaurs. Gauthier (1984) reported that a tuber is not present in any ornithodiran archosaurs, whereas Sereno (1991a) considered a highly reduced tuber to be present in *Marasuchus* (PVL 3070), *Herrerasaurus*, and basal sauropodomorphs. Here, I agree with Sereno (1991a) that a small calcaneal tuber is present in some dinosauromorphs, specifically, *Marasuchus* (PVL 3870) and *Pseudolagosuchus* (PVL 4629), but disagree that there is any tuber in *Herrerasaurus* and basal sauropodomorphs. Sereno's (1991a) character (29) homologized taxa with a reduced tuber with taxa with no tuber. This is not followed here. However, the distribution of the presence of a tuber is complicated among avian-line archosaurs. Pterosaurs (e.g., *Dimorphodon*, YPM 9182), *Lagerpeton* (PVL 4619), and close relative *Dromomeron romeri* (GR 223) all clearly lack a calcaneal tuber. Furthermore, a calcaneal tuber is not present in *Silesaurus* (ZPAL Ab III/361/20) or in dinosaurs. Given the complex distribution and that basal avian-line archosaurs (pterosaurs and Lagerpetidae) lack a tuber, the structure in *Marasuchus* and *Pseudolagosuchus* may not be homologous with that of non-archosaurian archosauriforms and crocodylian-line archosaurs.

374. Calcaneum, calcaneal tuber, distal end: (0) rounded and unexpanded; (1) flared, dorsally and ventrally (figs. 45–46) (Sereno, 1991a).

The distal end of the calcaneal tuber of phytosaurs and all crocodylian-line archosaurs is flared relative to that of *Euparkeria*, proterochampsians, *Vancleavea*, and *Proterosuchus* as discussed by Sereno (1991a). The tubera of *Marasuchus* (PVL 3870) and *Pseudolagosuchus* (PVL 4629) are unexpanded.

375. Calcaneum, calcaneal tuber, distal end: (0) without dorsoventrally aligned median depression; (1) with dorsoventrally aligned median depression (figs. 44–45) (Parrish, 1993; Benton, 1999).

The distal end of the calcaneal tuber of most basal archosauriforms as well as some crocodylian-line archosaurs is convex or flat. This includes taxa such as *Erythrosuchus* (Gower, 1996), *Vancleavea* (GR 138), *Euparkeria* (UMCZ T692), *Revueltosaurus* (PEFO 34561), *Aetosaurus* (SMNS 5770), *Riojasuchus* (PVL 3827), *Shuvosaurus* (TTU-P 9001), *Ticinosuchus* (PIZ T2817), and *Batrachotomus* (Gower and Schoch, 2009). In contrast, the distal end of the calcaneal tuber has dorsoventrally aligned median depression in *Fasolasuchus* (PVL 3850), *Postosuchus kirkpatricki* (TTU-P 9002), *Postosuchus alisonae* (UNC 15575), and crocodylomorphs (e.g., *Hesperosuchus* "*agilis*," YPM 41198; *Protosuchus richardsoni*, AMNH FR 3024).

376. Calcaneum, calcaneal tuber, shaft proportions at the midshaft of the tuber: (0) taller than broad; (1) about the same or broader than tall; (2) just short of twice the mediolateral width of the fibular facet (fig. 45) (modified from Sereno, 1991a; Parrish, 1993; Juul, 1994; Benton, 1999; Nesbitt et al., 2009a).

Here, to make the character more rigorous, the shaft proportions are taken between the lateral expansion and fibular facet. The tuber shafts are much taller than broad in *Prolacerta* (BP/1/ BP/1/2676), *Proterosuchus* (AMNH FR 2237), *Erythrosuchus* (BMNH R3592), *Vancleavea* (GR 138), and the proterochampsians *Tropidosuchus* (PVL 4601), and *Chanaresuchus* (MCZ 4036). The cross section of the tuber shafts of these taxa is anteroposteriorly compressed. In *Euparkeria*, phytosaurs, ornithosuchids, and suchians the width and height of the calcaneal tuber shaft is about the same or broader than tall. The shafts of *Euparkeria* and phytosaurs are nearly round in cross section, so they are scored as (1). Taxa such as *Riojasuchus* (PVL 3827), *Ornithosuchus* (BMNH R 2410), *Effigia* (AMNH FR 30587), *Shuvosaurus* (TTU-P 9280), *Poposaurus* (YPM 57100), *Postosuchus kirkpatricki* (TTU-P 9002), CM 73372, *Fasolasuchus* (PVL 3850), *Tikisuchus* (ISI R 301), *Hesperosuchus* (YPM 41198), *Dromicosuchus* (UNC 15574) *Terrestrisuchus* (BMNH P47/21a), and *Protosuchus* (AMNH FR 3024) have tuber shafts that are about the same mediolateral width of the fibular facet of the calcaneum. In these taxa, the distal end of the calcaneal tuber is mediolaterally compressed.

A third state, calcaneal tuber shaft proportions at the midshaft of the tuber just short of twice the mediolateral width of the fibular facet, was added to Sereno's (1991a) original character. A wide calcaneal shaft is present in *Gracilisuchus* (PVL 4597), *Revueltosaurus* (PEFO 34561), all aetosaurs, *Prestosuchus* (BSP XXV 1-3/5-11/ 28-41/49), *Batrachotomus* (SMNS 90018), *Saurosuchus* (PVL 2557), *Ticinosuchus* (PIZ T2817), and *Qianosuchus* (IVPP 143000). In taxa scored as (2), the tuber is also mediolaterally expanded. Most avian-line archosaurs cannot be scored for this character. However, *Marasuchus* and *Pseudolagosuchus* are scored as (2).

377. Calcaneum, calcaneal tuber, orientation relative to the transverse plane: (0) lateral less the 20° posteriorly; (1) deflected between 21°–49° posterolaterally; (2) between 50°–90° posteriorly (fig. 44) (modified from Gauthier, 1984; Sereno, 1991a; Parrish, 1993; Juul, 1994; Benton, 1999; Nesbitt et al., 2009a).

In non-archosauriform archosauromorphs, *Proterosuchus* (AMNH FR 2237), *Erythrosuchus* (BMNH R3592), and *Vancleavea* (GR 138) the calcaneum is directed laterally with a little posterior derivation (no more than 20°). In the proterochampsian *Tropidosuchus* (PVL 4601) and phytosaurs the orientation is about 45°. The orientation of the tuber in the only known *Chanaresuchus* calcaneum (MCZ 4036) is not known. In *Euparkeria,* the extent of the posterior deflection of the tuber has been debated. Gower (1996) suggested that the tuber is nearly lateral whereas Sereno (1991a) and Parrish (1993) claimed that the orientation is near 45°. Articulation of the ankle of *Euparkeria* (UMCZ T692) indicates that the orientation of the tuber must have been posteriorly at least 20°, and this is supported by articulated examples (SAM 5867). The exact range cannot be determined but here it is scored as (1). The tubera of ornithosuchids and suchians projects nearly perpendicular to the long axis of the astragalus.

In the above character, the posterior deflection ranges are not reflective of specific bins based on "breaks" in the data. The bins reflect the uncertainty of rearticulating disarticulated specimens and taphonomic disappearances prior to and after burial.

Most avian-line archosaurs cannot be scored for this character. However, *Marasuchus* and *Pseudolagosuchus* are scored as (2).

378. Calcaneum, articular surface for the fibula: (0) convex; (1) convex and hemicylindrical shaped; (2) concave (fig. 45) (mod-

ified from Sereno, 1991a; Parrish, 1993; Juul, 1994; Novas, 1996; Gower, 1996; Benton, 1999; Nesbitt et al., 2009a).

The fibular facet of the proximal surface of the calcaneum is convex in non-archosaurian archosauriforms and crocodylian-line archosaurs. The hemicylindrical condyle is a feature phytosaurs and suchians share. A hemicylindrical condyle is present when this articulation is (1) convex both anteroposteriorly and mediolaterally and (2) mediolaterally constricted and bordered by a nonarticular surface medially. Hence, ornithosuchids are scored as (0) because I cannot separate the condition in *Riojasuchus* (PVL 3827) from that of *Euparkeria* (UMCZ T692) (contra Sereno, 1991a). This character is not present in any specimen of *Euparkeria.* In criticism of Sereno (1991a), Parrish (1993) reported that this character was present in *Euparkeria* and unknown in proterochampsians. However, Parrish (1993) was mistaken in his interpretation of Sereno's (1991) character. The calcaneum of *Euparkeria* does have a convex articulation with the fibula, yet this articulation does not satisfy the second part of criteria stated above. The articular facet of the calcaneum for the fibula is similar between *Euparkeria* and the proterochampsians *Chanaresuchus* (MCZ 4036) and *Tropidosuchus* (PVL 4601). The articular facet of the fibula is concave in pterosaurs and in most dinosauromorphs (Sereno, 1991a). Novas (1996) explicitly reported that the calcaneum of *Marasuchus* and *Pseudolagosuchus* have a convex, proximal articulation with the fibula and this is followed here.

379. Calcaneum, shape: (0) proximodistally compressed with a short posterior projection and medial process; (1) transversely compressed, with the reduction of these projections (fig. 46) (modified from Langer and Benton, 2006).

Langer and Benton (2006) thoroughly discussed this character. A calcaneum is triradiate when both a medial process and a posterior projection (= calcaneal tuber of Langer and Benton, 2006) are present. The medial process lies ventral to the astragalus in a slight depression in avian-line archosaurs. In *Lagerpeton* (PVL 4619) and *Dromomeron romeri* (GR 223), a medial process of the calcaneum lies ventral to the astragalus even though the proximal tarsals are coossified. A clear medial process is present in *Marasuchus* (PVL 3870), *Pseudolagosuchus* (PVL 4629), *Silesaurus* (ZPAL Ab/III 361/20), *Herrerasaurus* (PVSJ 373), *Guaibasaurus* (MCP 2355-PV), *Saturnalia* (MCP 3844-PV), and sauropodomorphs (Langer and Benton, 2006). In neotheropods (*Coelophysis bauri*, AMNH FR 30576) and ornithischians (e.g., *Lesothosaurus* SAM-PK-1106), the medial process is reduced and there is no posterior projection.

380. Calcaneum, articular surfaces for fibula and distal tarsal IV: (0) separated by a nonarticular surface; (1) continuous (Sereno, 1991a; Juul, 1994; Benton, 1999; Nesbitt et al., 2009a).

Sereno (1991a) used this character to support Archosauria. This character, however, is in need of more description. In the calcaneum, a nonarticular surface composed of finished, compact bone clearly separates the fibular and fourth tarsal facets in nonarchosauriform archosauromorphs, *Proterosuchus*, *Erythrosuchus*, *Vancleavea*, and proterochampsians. Gower (1996) agreed with Sereno (1991a) that there is a nonarticular gap separating the fibular and fourth tarsal facets in *Euparkeria.* However, I agree with Parrish (1993) in that the anterior portion of the calcaneum is no different than that of phytosaurs. In these taxa, the fibular facet is located directly dorsal to the fourth tarsal facet. In contrast, the fibular and the fourth tarsal articular surfaces of phytosaurs and all basal members of the Archosauria are continuous and not separated by finished, compact bone; a thin edge of bone separates the fibular and fourth tarsal articular surfaces in Archosauria. Figure 9 of Sereno (1991a) inaccurately depicts the calcaneum of *Marasuchus* (labeled as *Lagosuchus*) in that the articular surfaces (shaded regions) of the fibula and fourth tarsal should be touching. The difference in the manner in which the fibula attaches to the calcaneum, either on a convex or concave surface, is explored in other phylogenetic characters (Sereno, 1991a; Parrish, 1993; Juul, 1994; Benton, 1999).

381. Centrale: (0) present; (1) absent (completely fused to the astragalus) (Gauthier, 1984; Gower, 1996; Bennett, 1996; Gower and Sennikov, 1997; Benton, 2004; Nesbitt et al., 2009a).

A distinct centrale is present in rhynchosaurs, *Trilophosaurus* (Gregory, 1945: fig. 11), *Prolacerta* (BP/1/ 2676; Gow 1975), and in *Proterosuchus* (NM QR 1484; see discussion in Gower, 1996). In some of these (rhynchosaur PVSJ 679 and *Proterosuchus* NM QR 1484), the centrale (the lateralmost proximal tarsal; Gower, 1996) has partly fused with the astragali whereas the elements are completely separated in *Trilophosaurus* and *Prolacerta*. A partially fused or independent centrale is absent in *Erythrosuchus* (Gower, 1996), *Euparkeria*, *Vancleavea*, proterochampsians, and Archosauria.

382. Metatarsus, configuration: (0) metatarsals diverging from ankle; (1) compact metatarsus, with metatarsals II–IV tightly bunched for half of the length (figs. 47–48) (Gauthier 1986; Benton and Clark 1988; Sereno 1991a; Juul 1994; Benton 1999).

Gauthier (1986) first noticed that the metatarsals of avian-line archosaurs are closely appressed for most of the length of the elements and subsequent authors followed this. Sereno (1991a) realized that some suchians (not listed) also have compact metatarsals, but works such as those by Juul (1994) and Benton (1999) did not consider the metatarsus to be compact in any suchian. However, the compact metatarsals of crocodylomorphs such as *Terrestrisuchus* (BMNH R7551) and *Protosuchus* (AMNH FR 3024) cannot be differentiated from the condition in avian-line archosaurs. Here, I more rigorously define a compact metatarsus as metatarsal II–IV contacting each other for at least the proximal half of the elements.

383. Longest metatarsal: (0) shorter than 50% of tibial length; (1) longer than 50% of tibial length (modified from Sereno, 1991a; Juul, 1994; Benton, 1999).

The metatarsals of avian-line archosaurs are elongated relative to those of all other archosauriforms. Sereno (1991a) discusses the character and his views are followed here. Since Sereno's (1991a) original formulation, later workers have also included metatarsals II and IV. However, in some taxa, metatarsals II and IV are about 50% the length of the tibia or less. In order to make the character applicable to more basal archosauriform taxa, I replace "metatarsal III" to "longest metatarsal" as the new comparison for the measurement; metatarsal III is the longest metatarsal in archosaurs, but metatarsal IV is longest in many basal archosauriforms (see character 393).

384. Metatarsals, midshaft diameters: (0) I and V subequal or greater than II–IV; (1) I and V less than II–IV (figs. 47–48) (Sereno, 1991a; Juul, 1994; Novas, 1996; Benton, 1999).

Sereno (1991a) discussed this character thoroughly and little can be added.

385. Metatarsal I: (0) reaches the proximal surface of metatarsal II; (1) does not contact the ankle joint and attaches onto the medial side of metatarsal II (fig. 48) (modified from Gauthier, 1986; Rauhut, 2003).

Plesiomorphically in archosauriforms and Dinosauria, metatarsal I always reaches the proximal surface of metatarsal II. In theropods, metatarsal I attaches to the side of metatarsal II (Gauthier, 1986).

386. Metatarsal I, anteromedial portion of the shaft: (0) smooth or slight ridge; (1) distinct, rugose ridge present (fig. 47) (new). In all archosauriforms, save phytosaurs, the anteromedial portion of the shaft of metatarsal I is smooth or has a small ridge. In the phytosaurs *Smilosuchus* (USNM 18313) and *Pseudopalatus* (UCMP 27235), there is a distinct, bulbous ridge on the anteromedial portion of metatarsal I.

387. Metatarsal I, length, relative to length of metatarsal III: (0) 0%–84%; (1) 85% or more (fig. 48) (Sereno, 1991a; Benton, 1999).

Sereno (1991a) originally used this character to support *Scleromochlus* + Pterosauria and also noted that crocodylomorphs have state (1). Here, that scoring is followed.

388. Metatarsal II midshaft diameter: (0) less than or equal to the midshaft diameter of metatarsal I–IV; (1) more than the midshaft diameter of metatarsal I (fig. 47) (Nesbitt et al., 2009a).

Metatarsal II of *Proterosuchus* (NM QR 1484), *Erythrosuchus* (BMNH R3592), *Euparkeria* (UMCZ T692) and members of the Archosauria (e.g., *Lagerpeton*, PVL 4619; *Marasuchus*, PVL 3871; *Postosuchus*, UNC 15575; *Aetosaurus*, SMNS 5770) has a midshaft diameter that is smaller or about the same as metatarsal I. In contrast, metatarsal II has a much larger midshaft diameter than

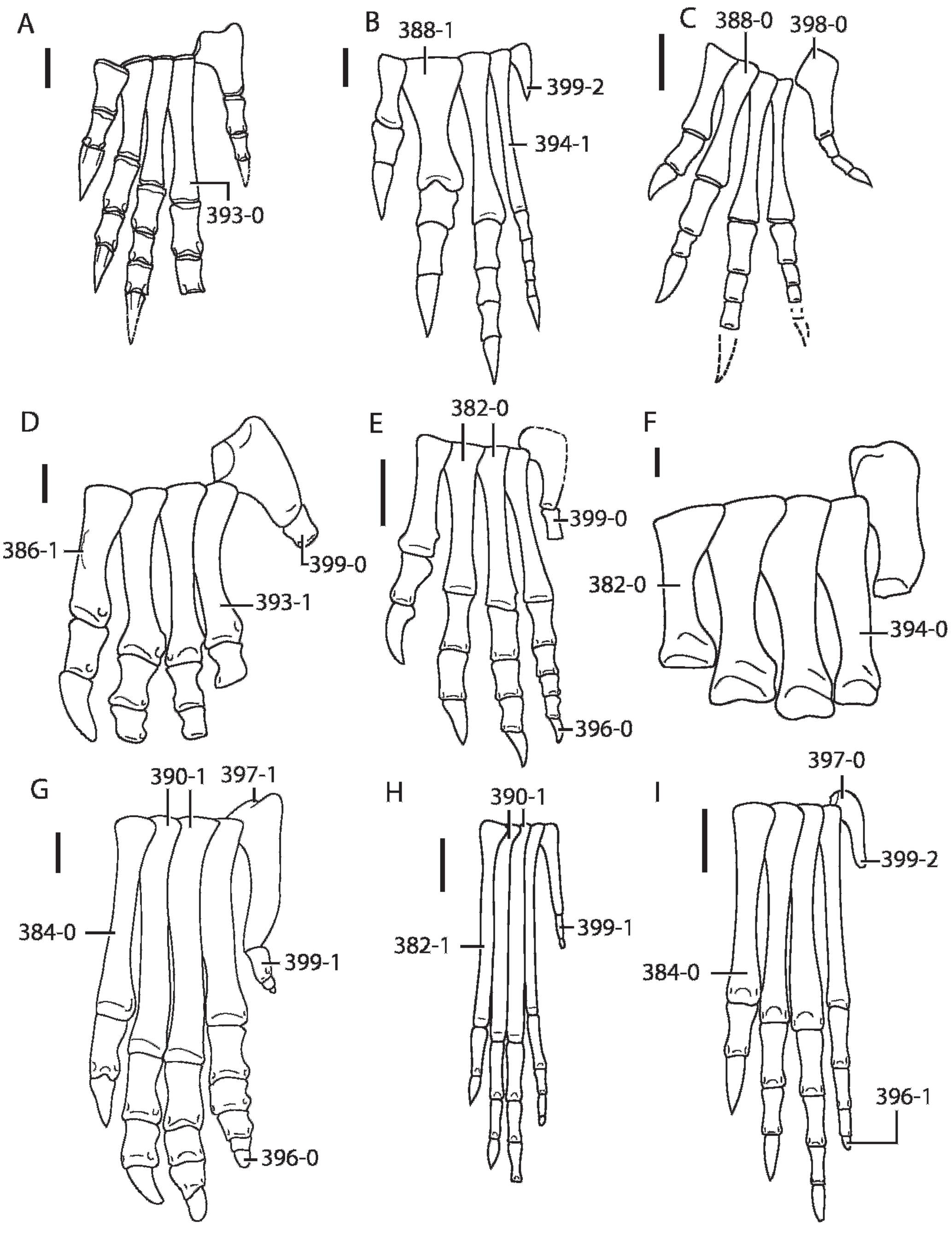

Fig. 47. The left pes of archosauriforms in anterior/dorsal view: **A,** *Proterosuchus fergusi* (redrawn from Cruickshank, 1972); **B,** *Chanaresuchus bonapartei* (redrawn from Romer, 1972b); **C,** *Euparkeria capensis* (redrawn from Ewer, 1965); **D,** *Pseudopalatus* (based on UCMP 27235); **E,** *Aetosaurus ferratus* (based on SMNS 5770 S-22); **F,** *Saurosuchus galilei* (based on PVL 2557); **G,** *Postosuchus alisonae* (based on UNC 15575); **H,** *Terrestrisuchus gracilis* (redrawn from Crush, 1984); **I,** *Protosuchus richardsoni* (based on AMNH FR 3024). Numbers refer to character states. See appendix for anatomical abbreviations. Scale bars = 1 cm.

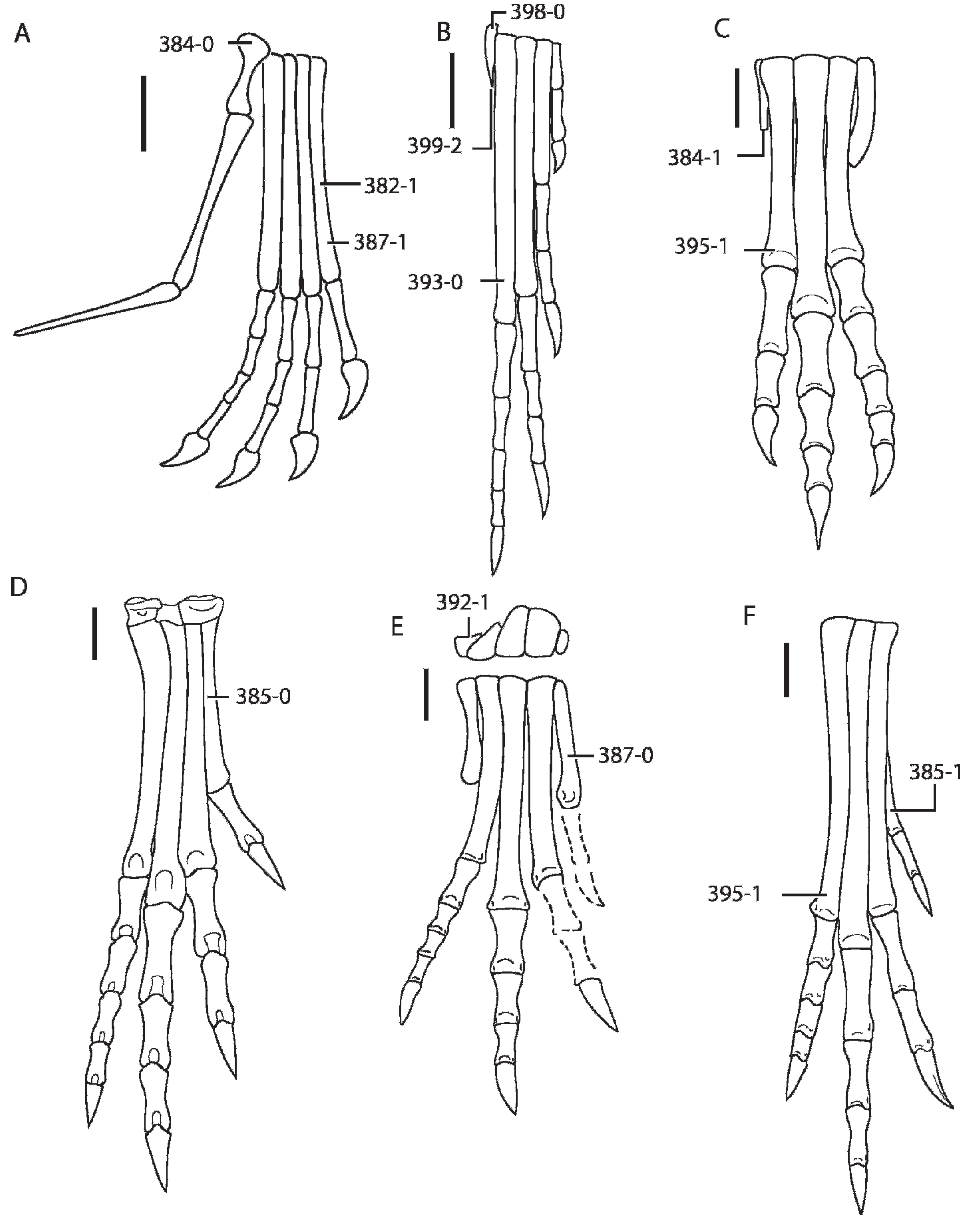

Fig. 48. The right pes of avian-line archosaurs in anterior/dorsal view: **A,** *Dimorphodon macronyx* (modified from Arthaber, 1919); **B,** *Lagerpeton canarensis* (redrawn from Sereno and Arcucci, 1994a); **C,** left pes of *Silesaurus opolensis* (redrawn from Dzik, 2003); **D,** *Heterodontosaurus tucki* (redrawn from Santa Luca, 1980); **E,** *Saturnalia tupiniquim* (redrawn from Langer, 2003); **F,** *Coelophysis bauri* (based on MNA 3320). Numbers refer to character states. See appendix for anatomical abbreviations. Scale bars = 1 cm.

that of metatarsal I in *Tropidosuchus* (PVL 4601) and *Chanaresuchus* (MCZ 4035; Romer, 1972b).

389. Metatarsal III, proximal end: (0) does not back to the ventral side of metatarsals II and IV; (1) backs metatarsals II and IV posteroventrally, resulting in a T-shaped proximal profile ("antarctometatarsus") (Carrano et al., 2002; Tykoski, 2005a).

Tykoski (2005a) described this character thoroughly and found that in all neotheropods the proximal end of metatarsal III backs metatarsals II and IV posteroventrally, resulting in a T-shaped proximal profile in proximal view.

390. Metatarsal III: (0) longer than metatarsal II; (1) subequal to metatarsals II (fig. 47) (new).

In most archosauriforms, metatarsal III is longer than metatarsal II. This is clearly the case in non-archosaurian archosauriforms, avian-line archosaurs, phytosaurs, aetosaurs, ornithosuchids, *Prestosuchus* (BSP XXV 1-3/ 5-11/ 28-41/49), and *Ticinosuchus* (PIZ T2817). In *Effigia* (AMNH FR 30587), *Shuvosaurus* (TTU-P 9001), *Postosuchus alisonae* (UNC 15575), CM 73372, *Saurosuchus* (PVL 2557), *Terrestrisuchus* (BMNH R 7557), *Protosuchus* (AMNH FR 3024), and *Alligator* metatarsals II and III are about the same length.

This character cannot be scored for *Sphenosuchus* (SAM 3014). Walker (1990) identified three bundled metatarsals as metatarsal I–III from the left pes. However, the assignment of metatarsal I by Walker (1990) to the metatarsal with the smallest diameter out of the metatarsals is inconsistent with that of other crocodylomorphs. Metatarsal I has the largest diameter whereas metatarsal IV has the smallest diameter of the metatarsals in crocodylomorphs (e.g., *Terrestrisuchus*, *Protosuchus*, *Alligator*). Therefore, the group of metatarsals identified as left metatarsals I–III by Walker (1990), are actually metatarsals II–IV from the right side.

391. Metatarsal IV, distal articulation surface: (0) broader than deep (nearly symmetrical); (1) broad as deep or deeper than broad (asymmetrical) (modified from Sereno, 1999; Langer and Benton, 2006).

Sereno (1999), followed by Langer and Benton (2006), suggested that having a mediolaterally compressed distal end of metatarsal IV is synapomorphic for theropods and, as Langer and Benton (2006) showed, for *Saturnalia*, *Pisanosaurus*, and basal ornithopods as well. Although true, the differences in the depth versus the width of the distal end of metatarsal IV remain subject to subtle distortion among basal dinosaurs. Instead, I focus on the larger morphological difference among dinosaurs and other basal archosaurs. The distal surface of metatarsal IV of dinosaurs is mediolaterally constricted anteriorly and relatively expanded posteriorly. As a result, the distal articular surface is triangular. Conversely, in most non-dinosauriform archosauriforms, the distal surface of metatarsal IV is more symmetrical and rectangular in distal view. Among crocodylian-line archosaurs, *Effigia* (AMNH FR 30587), *Shuvosaurus* (TTU-P 9280), CM 73372, *Postosuchus alisonae* (UNC 15575) also have a clearly asymmetrical distal surface of metatarsal IV. *Pseudolagosuchus* (UNLR 53) and *Silesaurus* (ZPAL Ab III/ 364) also have an asymmetrical distal surface of metatarsal IV whereas the distal surface is symmetrical in *Marasuchus* (PVL 3870) and *Lagerpeton* (PVL 4619).

392. Metatarsal IV, proximal portion, possesses an elongated lateral expansion that overlaps the anterior surface of metatarsal V: (0) absent; (1) present (fig. 48) (Sereno, 1999; Langer and Benton, 2006).

Langer and Benton (2006) described this character exhaustively and concluded that state (1) is present in sauropodomorphs and *Herrerasaurus* exclusively. This is followed here.

393. Metatarsal IV: (0) longer than metatarsal III; (1) about the same length or shorter than metatarsal III (figs. 47–48) (modified from Bennett, 1996; Gower and Sennikov, 1997; Nesbitt et al., 2009a).

This classically formulated character has been used to quantify the differences of the pes of basal archosauromorphs and members of the Archosauria. Originally, the formulation of this character examined the complete length (metatarsal + phalanges) of digit 4 compared to digit 3 (Gauthier, 1984; Sereno, 1991a). The fourth digit of non-archosauriform archosauromorphs (e.g., rhynchosaurs, *Trilophosaurus*, *Prolacerta*) is the longest in the pes whereas digit 3 is longest in *Euparkeria* (UMCZ T692) and all the archosaurs that could be scored (Gauthier, 1984). Gower and Sennikov (1997) simplified the character by examining the length of metatarsal IV with metatarsal III. Gower and Sennikov's (1997) simplification is followed here because (1) more taxa can be scored (few taxa possess a complete pes) and (2) there are no taxa observed by me that have a longer metatarsal III, but a longer pedal digit 4 (metatarsal IV + phalanges).

Having a longer metatarsal III than metatarsal IV has a nearly uniform distribution among crocodylian-line archosaurs whereas the basal members of the avian-line retain state (0). *Riojasuchus* (PVL 3827), the two aetosaurs *Aetosaurus* (SMNS 18554) and *Typothorax* (MCZ 1488), *Postosuchus alisonae* (UNC 15575), and *Alligator* all have a longer metatarsal III than metatarsal IV. Among avian-line archosaurs, pterosaurs (Wellnhofer, 1978; Wild, 1978), *Silesaurus* (ZPAL Ab III/364; Dzik, 2003), and members of the Dinosauria all have metatarsal III longer than metatarsal VI. In *Lagerpeton* (PVL 4619; Sereno and Arcucci, 1994a) metatarsal VI is clearly longer than it is than metatarsal III whereas the metatarsal IV and III are nearly the same length (metatarsal IV is reported shorter than III in Sereno and Arcucci, 1994b: table 5) in *Marasuchus*. Additionally, in the proterochampsian *Tropidosuchus* (PVL 4601), metatarsal IV is longer than that of metatarsal III at first glance; however, metatarsal IV is about the same length as metatarsal III when measured. Although these exceptions show that this character is not as straightforward as previously thought, the character may prove to be useful in determining relationships.

394. Metatarsal IV: (0) nearly the same midshaft diameter as metatarsal III; (1) reduced where the midshaft diameter is less than metatarsal III (fig. 47) (Nesbitt et al., 2009a).

Although not rigorously defined, this character attempts to highlight the difference between metatarsal IV of the proterochampsians *Tropidosuchus* (PVL 4601) and *Chanaresuchus* (MCZ 4035; Romer, 1972b). Metatarsal IV of these taxa is reduced in diameter relative to metatarsals I–III. Metatarsal IV has a midshaft diameter comparable to that of metatarsal II and III in members of the Archosauria, *Euparkeria* (UMCZ T692), *Proterosuchus* (NM QR 1484), and *Erythrosuchus* (BMNH R3592).

395. Metatarsal IV length: (0) longer than metatarsal II; (1) subequal to metatarsal II (fig. 48) (modified from Gauthier, 1986).

Typically, metatarsal IV is longer than metatarsal II in most basal archosauriforms (Gauthier, 1986). In dinosauriforms, to the exclusion of *Marasuchus* (PVL 3870), the length of metatarsal IV is subequal to that of metatarsal II, giving the metatarsus the traditional "tridactyl" appearance. A similar change is present in the relative lengths of metatarsals II and IV among crocodylian-line archosaurs. Metatarsal IV of *Revueltosaurus* (PEFO 34561), *Aetosaurus* (SMNS 5770 S-22), *Gracilisuchus* (PVL 4529), and *Riojasuchus* (PVL 3827) is clearly longer than metatarsal II. It is clear that most "rauisuchians" and crocodylomorphs have to be scored as (1).

396. Pedal digit IV, number of phalanges: (0) five; (1) four or fewer (fig. 47) (Parrish, 1993).

In nearly all archosauriforms, five phalanges are present on pedal digit IV. In the crocodylomorphs, *Terrestrisuchus* (BMNH R 7557), *Protosuchus* (AMNH FR 3024), and *Alligator* there are four or fewer phalanges on pedal digit IV. The only known specimen of *Pseudhesperosuchus* (PVL 3830) was scored as (1) by Parrish (1993); however, the pes of *Pseudhesperosuchus* is unknown.

397. Metatarsal V, dorsal prominence separated from the proximal surface by a concave gap: (0) absent; (1) present (fig. 47) (new).

The dorsal exposure of metatarsal V either contacts distal tarsal 4 completely or has a posterior lateral flange that does not participate in the articular surface with tarsal 4. The nonarticular gap is concave in taxa scored as (1). A gap on the dorsal surface of metatarsal V is present in CM 73372, *Postosuchus kirkpatricki* (TTU-P 9000), *Postosuchus alisonae* (UNC 15575), *Prestosuchus* (BSP XXV 1-3/5-11/ 28-41/49), *Saurosuchus* (PVL 2557), and *Batrachotomus* (90018). Nearly the entire dorsal surface of metatarsal V articulates with distal tarsal 4 in taxa scored as (0). Aetosaurs (*Aetosaurus*, SMNS 6770 S-22), crocodylomorphs (*Hesperosuchus agilis*, AMNH FR 6758), *Riojasuchus* (PVL 3827), *Gracilisuchus* (PVL 4529), *Revueltosaurus* (PEFO 34561), and phytosaurs (*Pseudopalatus*, UCMP 27235) lack a dorsal prominence.

398. Metatarsal V, "hooked" proximal end: (0) present; (1) absent, and articular face for distal tarsal 4 subparallel to shaft axis (figs. 47–48) (Sereno, 1991a; Juul, 1994; Benton, 1999).

Sereno (1991a) discusses this character in depth and concluded that all dinosauromorphs have state (1) and that all other archosauriforms are scored as (0). His conclusions are followed here except for a few exceptions. *Gracilisuchus* (PVL 4529), *Ornithosuchus* (BMNH R 2410), and *Riojasuchus* (PVL 3827) seem to lack a "hooked" proximal end of metatarsal V.

399. Metatarsal V, phalanges: (0) present and "fully" developed first phalanx; (1) present and "poorly" developed first phalanx; (2) without phalanges and metatarsal tapers to a point. ORDERED (figs. 47–48) (modified from Gauthier, 1984; Parrish, 1993).

Plesiomorphically within archosauriforms, metatarsal V bears phalanges ranging in number from three to none. The first phalanx of metatarsal V is similar to other first phalanges of the other digits in that the proximal surface is fully concave, the distal articular ridges are similar sizes and the lateral sides bear ligament pits (= fully developed). Among non-archosaurian archosauriforms, the proterochampsians *Chanaresuchus* (PVL 4575) and *Tropidosuchus* (PVL 4601) have a very reduced metatarsal V without phalanges whereas all others seem to possess the plesiomorphic condition.

A splintlike metatarsal V without phalanges is present in most avian-line archosaurs. *Herrerasaurus* (PVSJ 373) and sauropodomorphs retain at least one phalanx that is poorly developed. A fully developed first phalanx of metatarsal V is present in one of the few examples of a phytosaur pes (*Pseudopalatus* UCMP 27235). Among suchians, scoring of this character has been inconsistent in the literature. All non-crocodyliforms suchians with pedal material possess an articular facet on the distal end of metatarsal V. In *Aetosaurus* (SMNS 18554), *Neoaetosauroides* (PVL 3525), *Typothorax* (MCZ 1488), *Saurosuchus* (PVL 2557), *Riojasuchus* (PVL 3827), *Ticinosuchus* (PIZ T2817), and *Prestosuchus* (BSP 32), metatarsal V bears phalanges and the first phalanx is fully developed (see above). Parrish (1993) scored *Gracilisuchus* as having a tapering metatarsal V; however, metatarsal V clearly does not taper and bears a fully developed first phalanx in specimen PVL 4597. In *Postosuchus alisonae* (UNC 15575), *Hesperosuchus* "*agilis*" (YPM 41198), and *Terrestrisuchus* (BMNH R 7557) metatarsal V bears a facet and at least one phalanx. The first phalanx of these three taxa is poorly developed, the proximal end is convex and the distal end has very shallow lateral ligament pits. In *Postosuchus alisonae* (UNC 15575), metatarsal V has three phalanges that are highly reduced where the third phalanx is just a rounded speck of bone. *Protosuchus* (AMNH FR 3024) and all other crocodyliforms have a tapered metatarsal V without phalanges.

Taxa with an articular facet on the distal end of metatarsal V bear phalanges in all cases studied. On the other hand, phalanges are not present in taxa with splintlike metatarsal V. Therefore, a taxon can be scored if metatarsal V is tapered or bears an articular distal portion.

400. Pedal unguals: (0) weakly mediolaterally compressed, rounded or triangular in cross section; (1) dorsolaterally compressed; (2) strongly mediolaterally compressed, with a sharp dorsal keel (fig. 49) (modified from Sereno, 1991a).

In basal archosauriforms, the unguals of the pes are simple, weakly mediolaterally compressed structures. This is present in *Euparkeria* (SAM 8039), *Proterosuchus* (SAM-PK-140), *Tropidosuchus* (PVL 4606), and avian-line archosaurs. In strict contrast, the pedal unguals of *Poposaurus* (YPM 57100), *Effigia* (AMNH FR 30587), and *Shuvosaurus* (TTU-P various specimens) are dorsoventrally compressed and "hoof-like." As described by Nesbitt (2007), the pedal unguals originally assigned to *Shuvosaurus* by Long and Murry (1995) are actually those of phytosaurs. The single known articulated pes of *Shuvosaurus* (TTU-P unnumbered) has an

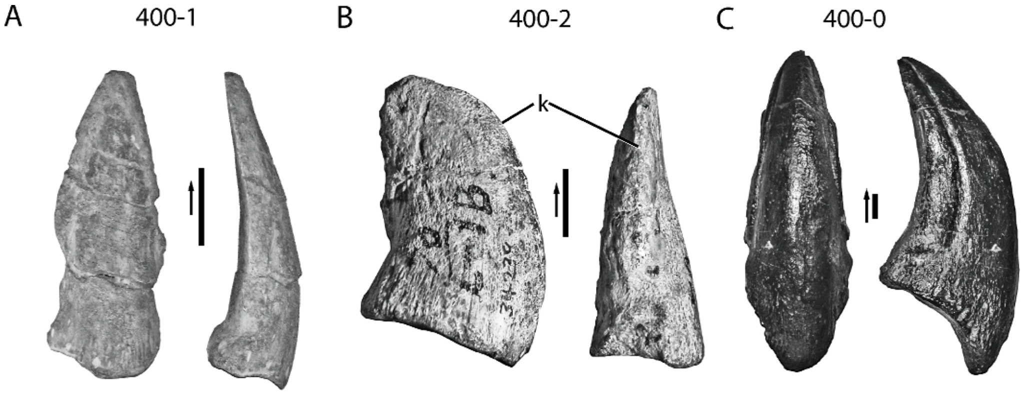

Fig. 49. Pedal unguals of archosauriforms: **A,** *Effigia okeeffeae* (AMNH FR 30587) in dorsal (left) and lateral (right) views; **B,** *Pseudopalatus* (UCMP 34239) in dorsolateral (left) and dorsal (right) views; **C,** *Allosaurus fragilis* (AMNH FR 324) in dorsal (left) and lateral (right) views. Arrow indicates anterior direction. Numbers refer to character states. See appendix for anatomical abbreviations. Scale bars = 1 cm.

ungual like that of *Effigia*. Similarly, the unguals of *Silesaurus* (ZPAL Ab III/364) are dorsoventrally compressed.

Sereno (1991a; character 20) hypothesized that the strongly mediolaterally compressed unguals in *Ornithosuchus* and *Riojasuchus* represented a synapomorphy uniting the two taxa. However, a similar morphology is present in phytosaurs (*Smilosuchus*, USNM 18313; *Pseudopalatus*, UCMP 27235; apparently in *Parasuchus*, Chatterjee, 1978), *Saurosuchus* (PVL 2557), *Ticinosuchus* (PIZ T2817), and the aetosaurs *Aetosaurus* (SMNS 5770 S-22) and *Typothorax* (MCZ 1488). Although this character is vaguely worded, it attempts to qualify the large differences among the unguals of basal archosaurs.

OSTEODERMS

401. Osteoderms, dorsal to the vertebral column: (0) absent; (1) present (Gauthier, 1984; Benton and Clark, 1988; Sereno, 1991a; Juul, 1994; Bennett, 1996; Dilkes, 1998; Benton, 1999; Nesbitt et al., 2009a).

The presence of osteoderms has been used by nearly all basal archosaur phylogenies, although the formulations of the characters have varied. Non-archosauriform archosauromorphs including *Mesosuchus*, *Prolacerta*, and *Proterosuchus* lack osteoderms. Huene (1911) and most recently, Gower (2003) reported the presence of two osteoderms in *Erythrosuchus* (BMNH R3592). The osteoderm attached to the side of the caudal series of BMNH R3592 (Gower, 2003: fig. 27B) is poorly preserved and few fine details cannot be observed. A close inspection could not identify typical features (weaved bone surface, compact outer surface, small channels for blood vessels) of bony osteoderms in this specimen. The second specimen is well preserved and fine features can be evaluated (Gower, 2003: fig. 36). The edges of the element are incomplete, exposing a spongy interior not typical of osteoderms and a cross section of the very thin compact external surface. The thin compact outer surface differs from the typical thick, compact, and laminar external surface of other osteoderms. The external surface has a pattern similar to other osteoderms, but cannot be differentiated from other bony elements covered in a hard covering (e.g., claw). Even if these two specimens represent osteoderms, it is clear that *Erythrosuchus* did not have many osteoderms and certainly did not have paramedian or a single row of osteoderms dorsal to the vertebrae; none of the articulated presacral vertebrae have associated or articulated osteoderms.

Vancleavea (GR 138), the proterochampsians *Chanaresuchus* (PVL 4575) and *Tropidosuchus* (PVL 4601), *Euparkeria* (SAM 5867), phytosaurs, and most crocodylian-line archosaurs bear osteoderms dorsal to the neural spines of the vertebrae. Osteoderms

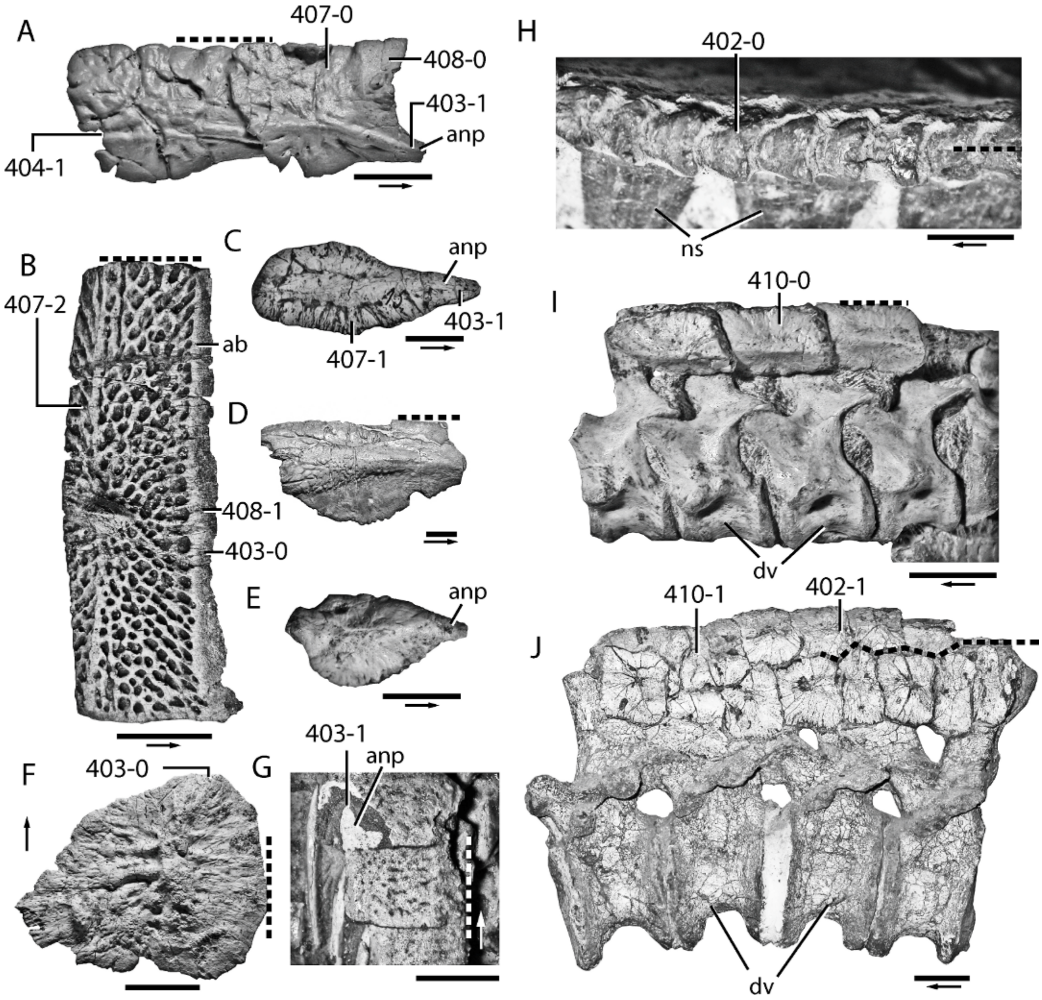

Fig. 50. Osteoderms of archosauriforms: **A,** two articulated, presacral, and dorsal osteoderms of *Hesperosuchus agilis* (AMNH FR 6758) in dorsal view; **B,** Aetosauria presacral dorsal osteoderm (AMNH FR 19331) in dorsal view; **C,** presacral dorsal osteoderm of *Rauisuchus triradentes* (BSP AS XXV-60-121) in dorsal view; **D,** presacral dorsal osteoderm of *Batrachotomus kuperferzellensis* (SMNS unnumbered) in dorsal view; **E,** presacral dorsal osteoderm of *Euparkeria capensis* (SAM 6047B) in dorsal view; **F,** presacral dorsal osteoderm of *Smilosuchus gregorii* (USNM 18313) in dorsal view; **G,** presacral dorsal osteoderms of *Protosuchus richardsoni* (UCMP 36717) in dorsal view; **H,** presacral dorsal osteoderms of *Chanaresuchus bonapartei* (PVL 4575) in dorsolateral view; **I,** presacral dorsal osteoderms of *Euparkeria capensis* (SAM 6047) in lateral view; **J,** presacral dorsal osteoderms of a referred specimen of *Prestosuchus* (UFRGS 0156-T). Arrow indicates anterior direction and dotted line identifies the midline. Numbers refer to character states. See appendix for anatomical abbreviations. Scale bars = 5 cm in B, F, J, and 1 cm in A, C–E, G–I.

are absent in *Arizonasaurus* (MSM P4590), *Poposaurus* (YPM 57100), *Effigia* (AMNH FR 30587), *Shuvosaurus* (TTU-P 9001), *Sillosuchus* (PVSJ 85), and avian-line archosaurs plesiomorphically. Only taxa that have much of the presacral vertebral column should be scored because it may be difficult to determine whether osteoderms are present or absent in fragmentary specimens.

402. Postaxial osteoderms, arrangement dorsal to the vertebral column: (0) a single median row; (1) in paramedian row(s)

(fig. 49) (modified from Gauthier, 1986; Benton and Clark, 1988; Sereno, 1991a; Parrish, 1993; Juul, 1994; Benton, 1999).

In nearly all taxa with osteoderms, the osteoderms are arranged in one or more paramedian rows dorsal to the vertebral column. Alternatively, the proterochampsians *Chanaresuchus* (PVL 4575) and *Tropidosuchus* (PVL 4601) possess a single row of osteoderms dorsal to the vertebral column. *Vancleavea* cannot be scored for this character. Postaxial is specified because in taxa with articulated osteoderms (e.g., *Dibothrosuchus*, IVPP 7907), the first osteoderm is unpaired whereas all of the remaining osteoderms are paired.

403. Osteoderms, presacral, dorsal, anterior edge: (0) straight or rounded; (1) with distinct anterior process (= leaf shaped) (fig. 49) (Clark et al., 2000; Olsen et al., 2000; Benton and Walker, 2002; Sues et al., 2003; Clark et al., 2004).

The anterior edge of the presacral osteoderms in *Vancleavea* (GR 138) has a distinct anterior process. In *Euparkeria* (SAM 6047B), the lateral and medial edges converge anteriorly to form an anterior apex whereas the anterior edge of the dorsal osteoderms is unknown in proterochampsians. The anterior edge of phytosaur (*Smilosuchus*, USNM 18313) osteoderms is rounded. The previously listed taxa indicate the diversity of the morphology of osteoderms and illuminate the difficulties in grouping the anterior edge morphology of osteoderms among basal archosauriforms. Among crocodylian-line archosaurs the anterior edge is nearly straight in *Erpetosuchus* (BMNH R3139), *Revueltosaurus* (PEFO 34561), and all aetosaurs (Parker, 2007), as well as in the ornithosuchids *Riojasuchus* (PVL 3827) and *Ornithosuchus* (BMNH R3562). The morphology of the anterior edge of the osteoderms of *Gracilisuchus* is not clear at the present time, but it possible that in one specimen of *Gracilisuchus* (MCZ 4118), the anterior edge is rounded or straight like that of ornithosuchids. In *Ticinosuchus* (PIZ T2817), *Prestosuchus* (UFRGS 156-T, UFRGS 0152-T), *Saurosuchus* (PVSJ 32), *Batrachotomus* (Gower and Schoch, 2009: fig. 6H), *Rauisuchus* (BSP AS XXV-60-121), *Postosuchus kirkpatricki* (TTU-P 9002), *Postosuchus alisonae* (UNC 15575), *Hesperosuchus* (AMNH FR 6758), *Dromicosuchus* (UNC 15574), *Saltoposuchus* (SMNS 12596), *Kayentasuchus* (UCMP 131830; Clark and Sues, 2002), and *Protosuchus richardsoni* (AMNH FR 3024), there is a distinct anterior process anterior to the keel of the osteoderm. In *Protosuchus* and *Orthosuchus*, there is no keel on the osteoderm and the distinct anterior process is located on the lateral edge of the osteoderm.

404. Osteoderms, presacral, paramedian: (0) flat or weakly arched; (1) with distinct longitudinal bend near lateral edge (fig. 49) (Clark et al., 2000; Olsen et al., 2000; Benton and Walker, 2002; Sues et al., 2003; Clark et al., 2004).

The presacral osteoderms of *Euparkeria* (SAM 6047B), *Batrachotomus* (Gower and Schoch, 2009: fig. 6H), *Rauisuchus* (BSP AS XXV-60-121), *Postosuchus kirkpatricki* (TTU-P 9002), *Postosuchus alisonae* (UNC 15575), *Gracilisuchus* (MCZ 4118), and non-crocodyliform crocodylomorphs (e.g., *Kayentasuchus*, UCMP 131830; Clark and Sues, 2002; *Hesperosuchus*, AMNH FR 6758) have a distinct ventral bend. In *Orthosuchus* (SAM-K-409), *Protosuchus* (AMNH FR 3024), and *Alligator*, the dorsal osteoderms are weakly arched. The osteoderms of *Ornithosuchus* (BMNH R 3562), *Riojasuchus* (PVL 3827), *Revueltosaurus* (PEFO 34561), all aetosaurs, and phytosaurs are nearly flat or slightly arched. The osteoderms of *Ticinosuchus* (PIZ T2817), *Saurosuchus* (PVSJ 32), and *Prestosuchus* (UFRGS 156-T, UFRGS 0152-T) seem to be flat ventrally even though they have been scored as (1) by Benton and Walker (2002).

This character could not be scored in *Vancleavea* and is inapplicable in proterochampsians because the osteoderms lie over the midline in a single row.

405. Osteoderms, covering the appendages (= appendicular osteoderms), at least in part: (0) absent; (1) present (Heckert and Lucas, 1999).

This character requires well-preserved specimens for accurate scoring. For example, the articulated specimens of *Aetosaurus* (SMNS 5770) show how the osteoderms cover the limbs and articulate with each other. As these articulated specimens indicate, the appendicular osteoderms are preserved in the skin and quickly become disarticulated after decomposition given that only a few of the *Aetosaurus* specimens have articulated appendicular osteoderms. Disarticulated skeletons of taxa (e.g., aetosaurs) with appendicular osteoderms have abundant rounded osteoderms surrounding the skeleton. Appendicular osteoderms are present in *Revueltosaurus* (PEFO 34561), all aetosaurs, *Vancleavea* (GR 138), and some crocodyliforms.

406. Osteoderms, number of paramedian rows: (0) 1 paramedian pair (2 osteoderms per segment); (1) 2 paramedian pairs (4 osteoderms per segment) (new).

Typically in Archosauriformes, there is only a single paramedian row (2 osteoderms per segment). This is the case in *Euparkeria* (SAM 5867), "rauisuchians" (*Saurosuchus*, PVSJ 32), basal crocodylomorphs (e.g., *Dromicosuchus*, UNC 15574), ornithosuchids (*Riojasuchus*, PVL 3827), and phytosaurs (*Pseudopalatus*, UCMP 27235). In aetosaurs (e.g., *Aetosaurus*, SMNS 5770), there are two distinct rows of paramedian osteoderms (4 osteoderms per segment); the paramedian (more medial row) and the lateral row. It is unclear how many paramedian rows were present in *Revueltosaurus* bears. Benton and Walker (2002) described one specimen of *Erpetosuchus* (NMS 1966.4.3) with two rows of paramedian osteoderms. In *Erpetosuchus*, the second paramedian row starts in the dorsal vertebral series whereas in aetosaurs, the two paramedian rows are present in the entire presacral region.

407. Presacral osteoderms, dimensions: (0) square shaped, about equal dimensions; (1) longer than wide; (2) wider than long (fig. 49) (new).

This character is a first attempt at dividing the dimensions of basal archosauriform osteoderms given the vast diversity in osteoderm shape. In *Vancleavea* (GR 138), *Euparkeria* (SAM 6047B), phytosaurs, *Erpetosuchus* (NMS 1966.4.3), *Gracilisuchus* (MCZ 4118), *Ticinosuchus* (T2817), *Prestosuchus* (UFRGS 156-T, UFRGS 0152-T), and *Saurosuchus* (PVSJ 32), the osteoderms are roughly square in dorsal view, where the mediolateral dimensions are similar to the anteroposterior dimensions. In *Batrachotomus* (Gower and Schoch, 2009: fig. 6H), *Rauisuchus* (BSP AS XXV-60-121), *Postosuchus kirkpatricki* (TTU-P 9002), *Postosuchus alisonae* (UNC 15575), *Hesperosuchus* (AMNH FR 6758), *Dromicosuchus* (UNC 15574), *Saltoposuchus* (SMNS 12596), *Terrestrisuchus* (BMNH R10002), and *Dibothrosuchus* (IVPP 7907) the osteoderms are clearly longer than wide. Alternatively, the osteoderms of *Revueltosaurus* (PEFO 34561), and the paramedian osteoderms of aetosaurs (e.g., *Aetosaurus*, SMNS 5770; *Longosuchus* TMM 31185-98), the cervical osteoderms of *Riojasuchus* (PVL 3827), and all dorsal osteoderms of *Protosuchus* (AMNH FR 3024; BP/1/4770), *Orthosuchus* (SAM-K-409), and basal crocodyliforms are clearly wider than long. In addition, a further parsing of the length vs. width of the paramedian osteoderms has been useful in aetosaur in-group relationships (Parker, 2007).

408. Anterior bar located on the anterior edge of an osteoderm: (0) absent; (1) present (fig. 49) (Heckert and Lucas, 1999; Parker, 2007).

An anterior bar is a smooth strip located along the entire anterior surface of the osteoderm that marks the overlapping surfaces in the proceeding osteoderm. An anterior bar is present on the anterior edge of the paramedian and lateral osteoderms in most aetosaurs including *Stagonolepis* (BMNH R 4799), *Aetosaurus* (SMNS 5770), *Typothorax* (MCZ 1488), and *Longosuchus* (TMM 31185 specimens) as well as in *Revueltosaurus* (PEFO 34561). An anterior lamina is also present in *Protosuchus* (AMNH FR 3024; BP/1/4770), *Orthosuchus* (SAM-K-409), and basal crocodyliforms, but lost in eusuchians. An anterior bar is present in two articulated osteoderms of *Rauisuchus* (BSP AS XXV-60-121), but is absent in all other osteoderms.

409. Ventral carapace in the trunk region: (0) absent; (1) present (Heckert and Lucas, 1999).

A ventral carapace consists of a sheet of osteoderms arranged in multiple rows and columns covering the abdominal region. A ventral carapace is present in all aetosaurs that are known from relatively complete skeletons. This includes *Aetosaurus* (SMNS 5770), *Stagonolepis* (MCGD 2), and *Ty-*

pothorax (MCZ 1488). The ventral osteoderms of these taxa are square shaped and flat with faint sculpturing. Even though the specimens of *Longosuchus* were not found completely articulated (Sawin, 1947), flat, square-shaped osteoderms with faint sculpturing were recovered with the skeletons (Sawin, 1947: fig. 11). Therefore, *Longosuchus* is scored as (1). A ventral carapace is also present in *Protosuchus* (AMNH FR 3024; BP/1/4770) and some other crocodyliforms. *Vancleavea* (GR 138) and *Doswellia* (Weems, 1980; Dilkes and Sues, 2009) are the only known non-archosaurian archosauriforms to have a ventral carapace.

410. Dorsal osteoderms, relation to presacral vertebrae: (0) one to one (includes pairs); (1) more than one osteoderm (fig. 49) (modified from Gauthier, 1986; Benton and Clark, 1988; Sereno, 1991a; Parrish, 1993; Juul, 1994; Benton, 1999).

Sereno (1991a) discussed this well-used character thoroughly (followed by comments from Parrish, 1993), and I agree that *Euparkeria* has a one-to-one ratio between osteoderms and presacral vertebrae. Furthermore, the following taxa are also scored as (0): *Erpetosuchus* (NMS 1966.4.3), aetosaurs, phytosaurs, *Revueltosaurus* (PEFO 34561), CM73372, *Fasolasuchus* (PVL 3850), *Batrachotomus* (Sereno, 1991a), *Postosuchus alisonae* (UNC 15575), *Rauisuchus* (BSP AS XXV-60-121), and crocodylomorphs.

Multiple osteoderms per vertebra are present in *Gracilisuchus* (MCZ 4118), *Ticinosuchus* (PIZ T2817), *Saurosuchus* (PVSJ 32), *Qianosuchus* (IVPP 13899), *Prestosuchus* (UFRGS 156-T, UFRGS 0152-T), and proterochampsians. Even though the vertebrae cannot be observed in *Vancleavea* (GR 138), it is scored as having more than one osteoderm per vertebra because there are far more osteoderms than possible vertebrae.

411. Dorsal osteoderm alignment dorsal to the dorsals (presacrals 10–24): (0) staggered; (1) one to one (new).

In nearly all archosauriforms with osteoderms, the paramedian osteoderms are almost perfect mirror images of each other with a line of symmetry through the midline. The exceptions include *Euparkeria* (SAM 6047A), *Ticinosuchus* (PIZ T2817), "*Prestosuchus*" (UFRGS 156-T, UFRGS 0152-T), and *Saurosuchus* (PVSJ 32). In these forms, the paramedian osteoderms are staggered.

412. Gastralia: (0) forming extensive ventral basket with closely packed element; (1) well separated; (2) absent (new).

A closely packed gastral "basket" is clearly present in *Prolacerta* (BP/1/2675), *Proterosuchus* (NM QR 1484), *Euparkeria* (SAM 5867), phytosaurs (e.g., *Pseudopalatus*, UCMP 27235), *Poposaurus* (YPM 57100), *Hesperosuchus "agilis"* (CM 29894), *Terrestrisuchus* (BMNH R7557), *Sphenosuchus* (SAM 3014), *Protosuchus richardsoni* (AMNH FR 3024), *Effigia* (AMNH FR 30587), *Postosuchus alisonae* (UNC 15575), CM 73372, *Ticinosuchus* (PIZ T2817), *Batrachotomus* (SMNS unnumbered). In avian-line taxa, the gastralia are well separated (e.g., *Eoraptor*, PVSJ 512). Aetosaurs and *Revueltosaurus* (PEFO specimens) seem to lack any gastralia.

PHYLOGENETIC ANALYSIS

METHODS

The matrix was constructed in MorphoBank (O'Leary and Kaufman, 2007). The basal archosauriform matrix was analyzed with equally weighted parsimony using TNT v. 1.0 (Goloboff et al., 2003, 2008). The "New Technology search" option was first used to find all of the tree islands (sectorial search, rachet, and tree-fusing search methods, all with default parameters). Under these settings, replications were run until the minimum length tree was found in 1000 separate replicates. These trees were held in RAM. Second, a heuristic tree search strategy was then conducted performing 1000 replicates of Wagner trees (using random addition sequences, RAS) followed by TBR branch swapping (holding 10 trees per replicate). Zero-length branches were collapsed if they lacked support under any of the most parsimonious reconstructions. Bremer support values were calculated in TNT.

TAXON SAMPLING

The goal of this analysis was to place a wide breadth of basal archosauriforms into a phylogenetic context. The analysis contains taxa at the base of Archosauriformes and stretches up through Crocodyliformes to within Dinosauria. Detailed description of terminal taxa are presented above to clarify which specimens were studied. This is the largest analysis of its kind to date and during the course of this study, 36 institutions were visited in North and South America, Africa, Europe, and Asia. Hundreds of basal archosauriform specimens were examined firsthand. The pterosaur *Eudimorphodon* and the phytosaur *Parasuchus* remain the only taxa not observed firsthand. Fortunately, these two taxa are well described in the literature by Wild (1978) and Chatterjee (1978), respectively.

This study has largely been driven by the discovery of new basal archosauriform taxa in the last 10 years and a renewed interest in the early evolution of Archosauria. The publications of new taxa or specimens clearly demonstrate the growing body of knowledge of basal archosauriform anatomy and relationships. New taxa include *Batrachotomus* (Gower, 1999), *Effigia* (Nesbitt and Norell, 2006), *Polonosuchus* (Sulej, 2005), *Qianosuchus* (Li et al., 2006), *Postosuchus alisonae* (Peyer et al., 2008), *Dromicosuchus* (Sues et al., 2003), *Litargosuchus* (Clark and Sues, 2002), *Kayentasuchus* (Clark and Sues, 2002), *Protosuchus haughtoni* (Gow, 2000), *Silesaurus* (Dzik, 2003), *Sacisaurus* (Ferigolo and Langer, 2007), *Eucoelophysis* (Sullivan and Lucas, 1999; sensu Nesbitt et al., 2007), *Asilisaurus kongwe* (Nesbitt et al., 2010), *Dromomeron romeri* (Irmis et al., 2007a), *Dromomeron gregorii* (Nesbitt et al., 2009b), *Eocursor* (Butler et al., 2007), *Saturnalia* (Langer et al., 2007), and *Tawa hallae* (Nesbitt et al., 2009c) and new taxa account for nearly 20% of the taxa sampled here. Furthermore, new specimens of poorly known taxa include *Poposaurus* (Weinbaum and Hungerbühler, 2007), *Saurosuchus* (Alcober, 2000), *Arizonasaurus* (Nesbitt, 2003; 2005a), *Vancleavea* (Nesbitt et al., 2009a), *Revueltosaurus* (Parker et al., 2005), and *Hesperosuchus* "*agilis*" (Clark et al., 2000), which raises the percentage to nearly 30% of completely new information for basal archosauriform phylogeny.

All taxa in this analysis are represented as species-level taxa and no suprageneric taxa are used. Besides *Alligator*, *Velociraptor,* and *Allosaurus*, nearly all the taxa are from the Triassic and a few are from the Early Jurassic. Essentially, many specimens are known either from a single specimen (e.g., *Polonosuchus*, *Ticinosuchus*, *Dromicosuchus*, *Sphenosuchus*, *Pisanosaurus*) or multiple specimens from the same fossil horizon (e.g., *Mesosuchus*, *Chanaresuchus*, *Lotosaurus*, *Batrachotomus*, *Postosuchus kirkpatricki*, *Euparkeria*, *Silesaurus*, *Coelophysis bauri, Effigia*). Of the remaining taxa, nearly all are restricted to the formations in which they are found (e.g., *Protosuchus richardsoni*, *Pseudopalatus pristinus*, *Lesothosaurus*). Only *Proterosuchus fergusi* of the taxa examined here is clearly from more than one formation. Because most taxa examined effectively represent point occurrences, the monophyly of each taxon is not in doubt. Specimens that were obviously the same species-level taxon were combined later.

In taxa scored with more than one specimen, the criteria for combining specimens into species-level terminal taxa are as follows: the specimens were from the same bonebed (e.g., *Postosuchus kirkpatricki* TTU-P 9000 and TTU-P 9002; *Lotosaurus*; *Batrachotomus*) or the specimens share a unique autapomorphy or set of unique characters (*Smilosuchus*; *Revueltosaurus*; *Proterosuchus*). Some specimens were combined into a species-level terminal taxon after each specimen was incorporated into the phylogeny separately. If the specimens fell into a polytomy together (*Prestosuchus*; *Lewisuchus*/*Pseudolagosuchus*; see discussion), they were combined into a species-level taxon. In any case, every specimen is listed in the terminal taxon designation (see above).

Mesosuchus and *Prolacerta* were chosen as outgroups because they are the closest relatives of archosauriforms in the analysis of Dilkes (1998). Furthermore, these two taxa have been well described, illustrated, and are known from almost every element in the skeleton. In addition, *Proterosuchus fergusi* and *Erythrosuchus africanus* were also used to represent the base of Archosauriformes. *Proterosuchus fergusi* (sensu Welman, 1998) generally represents the Proterosuchidae because it is the best-represented taxon of the clade (Gower and Sennikov, 1997). *Erythrosuchus africanus* (sensu Gower, 2003) generally represents the Erythrosuchidae. The monophyly of this clade is controversial and has been examined only by Parrish (1992) and Gower and Sennikov (1996) in a phylogenetic context. Both of these studies obtain different relationships within Erythrosuchidae, but both obtain *Erythrosuchus* as one of the most-derived members.

I included two proterochampsians, *Chanaresuchus* and *Tropidosuchus,* as representatives of the Proterochampsia. Unexpectedly, the monophyly of the clade has only been suggested (Sues, 1976; Arcucci, 1990), but never been tested in a phylogenetic context; most authors (Benton and Clark, 1988; Sereno, 1991a; Juul, 1994; Benton, 1999, 2004) have used a suprageneric designation without a list of specimens or taxa used.

The monophyly of clades such as Phytosauria, Aetosauria, Ornithosuchidae, and Pterosauria is in little doubt as shown by numerous authors (Benton and Clark, 1988; Ballew, 1989; Sereno, 1991a; Juul, 1994; Parrish, 1994; Benton, 1999, 2004; Hungerbühler, 2002). In each of these clades, at least two exemplar taxa are used and I include three phytosaurs and aetosaurs.

Among crocodylian-line archosaurs, as many taxa traditionally considered as "rauisuchians" as possible were incorporated into this phylogeny to test the monophyly of the group. This includes taxa such as *Batrachotomus*, *Polonosuchus*, *Poposaurus*, *Postosuchus alisonae*, *Postosuchus kirkpatricki*, *Prestosuchus*, *Saurosuchus,* and *Ticinosuchus*. More controversial taxa such as the Middle Triassic *Gracilisuchus* and *Turfanosuchus* were also added. As many non-crocodyliform crocodylomorphs that are not currently under study were added to the analysis following the Clark et al. (2004) dataset. Several crocodyliform taxa (*Alligator*, *Orthosuchus*, *Protosuchus richardsoni*, *Protosuchus haughtoni*) were included in an attempt to provide an accurate and comprehensive representation of character distribution at the node Crocodyliformes.

Among avian-line archosaurs, I include all the available non-dinosaurian dinosauromorphs (e.g., *Lagerpeton*, *Dromomeron*, *Marasuchus*, *Silesaurus*) available to date. Within Dinosauria, the controversial taxa *Herrerasaurus* and *Eoraptor* are included among four unambiguous ornithischians (e.g., Butler et al., 2008b), three unambiguous sauropodomorphs (Yates, 2003), and four unambiguous neotheropods (Rauhut, 2003). *Tawa*, a recently described theropod form from Ghost Ranch, is also added to the matrix (Nesbitt et al., 2009c). These carefully chosen dinosaur taxa represent an accurate and comprehensive representation of character distribution in the basal members of those clades.

In most cases, each specimen was scored independently to prevent chimerical scoring. Nearly all the specimens in this analysis were observed firsthand and the specimen number next to a taxon in the character descriptions indicates personal observations of those specimens. Fifty-seven of the 87 total taxa were scored in person whereas the remaining taxa were scored from detailed drawings, notes, and photographs. I recorded all character scores and, therefore, any mistake is my own and not the result of following others' previous scores. In this study, it was apparent that scoring errors were compiled in the most recent basal archosaur phylogenies. Hence, I scored every character during this study to prevent the repetition of errors of previous scores.

Character Sampling and Methods

Basal archosaurs lie at the critical junction between phylogenetic datasets examining crocodylomorph relationships (e.g., dataset of Clark et al., 2000; Pol et al., 2009), basal dinosaur relationships (e.g., Langer and Benton, 2006), and those of non-archosaurian archosauriforms (e.g., Gower and Sennikov, 1997). As a result, the phylogenetic positions of the outgroup or taxa at the base of the tree in studies examining crocodylomorphs and basal dinosaurs are usually based on a priori assumptions and the relationships are not tested in a broad context. Some authors (e.g., Benton and Clark 1998; Sereno, 1991a; Juul, 1994) have attempted to include many basal archosaur groups and were greeted with some success, but with poor support for many of the relationships. Therefore, the dataset presented here fuses the datasets of basal archosaur (e.g., Juul, 1994), non-archosaurian archosauriforms (e.g., Gower and Sennikov, 1997), basal crocodylomorphs (e.g., Clark et al., 2004), and basal dinosaurs (Langer and Benton, 2006).

The inclusion of characters from the various basal archosaur studies designed to support the relationships of less inclusive clades (e.g., Dinosauria) required the addition and modification of the character states and modification of the characters themselves. I relied on the phylogenetic analyses of Gauthier (1984; 1986), Benton and Clark (1988), Sereno (1991a), Parrish (1993), Juul (1994), Bennett (1996), Gower and Sennikov (1996, 1997), Novas (1996), Benton (1999, 2004), Clark et al. (2000, 2004), Gower (2002), Rauhut (2003), Langer and Benton (2006), and Irmis et al. (2007a) as a base of characters. Other sources were also used and cited where appropriate. As a consequence of the large number of datasets spanning hundreds of taxa, I have revised many previously used characters and have excluded others. Moreover, I have added nearly 100 new characters. In the end, the dataset includes 412 discrete characters sampled from all over the skeleton.

Of the hundreds of previously reported basal archosauriform characters available from the literature, most of the characters were incorporated into my analysis. Modification of the characters ranges from accepting the original formulation (e.g., postfrontal: [0] present or [1] absent) to a complete revision (e.g., rewritten, divided into two or more characters, combined with other characters). In most cases, revisions were completed to incorporate a greater diversity of morphologies whereas clarity and specificity were added to others.

The much-welcomed revisions of basal archosaur characters previous to 1993 by Juul (1994) and the assessment of Sereno (1991a) by Parrish (1993) are generally accepted here unless noted in the character descriptions. However, since these two revisions, some characters were not included here for four main reasons: (1) the character was just listed with no, little, or vague explanations; (2) problems with interpretation of the morphology; (3) characters describing complex shapes of cranial openings; and (4) characters focusing on features that are related to taphonomy instead of actual morphology. Examples of these four categories are shown below:

(1) Characters just listed with no, little, or vague explanations:

Fibula nontapering and calcaneum unreduced (0), or thin, tapered fibula and reduced calcaneum (Juul, 1994: character 49).

The formulation of these kinds of characters are problematic because (1) it uses vague terms such as *nontapered* and *reduced* and (2) it combines the morphology of the fibula and calcaneum together even though they are possibly two discrete changes. The vague terms, in this situation, cannot be assessed for taxa not included in the analysis of Juul (1994). The author's intentions for this character cannot be understood; why some archosaurs are scored as (1) whereas other are scored as (0) is not explained.

Other examples of characters listed with no, little, or vague explanations: Parasphenoid rostum rodlike (0) or a dorsoventrally expanded wedge (1) (Parrish, 1993: character 28); Anterior parts of lateral sides of the dorsal vertebrae smoothly convex (0) or constricted (1) (Parrish, 1993: character 19);

(2) Problems with interpretation of the morphology:

Metacarpal IV and V bases (0) lie more or less in the same plane as the inner metacarpals or (1) lie on palmar surfaces of manual digits III and IV respectively (Gauthier, 1986); As far as I have observed, metacarpals always lie in an arc and never in a single plane (e.g., *Alligator* versus *Herrerasaurus*, PVSJ 373). Moreover, I have not observed any cases where the base of metacarpal IV lies on the palmar surface of metacarpal III and the base of metacarpal V lies on the palmar surface of metacarpal IV. Therefore, this character is excluded.

Other examples of problematic characters describing complex shapes of cranial openings: Intramandibular joint: absent or poorly developed (0), well developed (1) (Juul, 1994: character 73); Jugal-lacrimal articular relation: (0) lacrimal laterally overlaps jugal or (1) jugal laterally overlaps lacrimal (Sereno and Novas, 1994: character 16).

(3) Characters describing complex shapes of cranial openings:

Lower temporal fenestra shape: nontriangular (0), or triangular and reduced in size (1) (Benton and Clark, 1988: character two supporting Suchia). The complex morphology of skull openings is nearly always the product of two or more skull elements and therefore, the morphology of the particular elements can be turned into characters. This better represents statements of homology. In the example above from Benton and Clark (1988), modifications in either the squamosal or the quadratojugal can make a triangular lower temporal fenestra.

Other examples of a problematic characters describing complex shapes of cranial openings: Antorbital fenestra shape elliptical or circular (0), triangular, and with elongate narrow anterior point (Benton and Walker, 2002: character 38).

(4) Characters focusing on features that are related to taphonomy instead of actual morphology:

Prominent rim encircling the distal end of the calcaneum tuber absent (0) or present (1) (Parrish, 1993: character 33). The prominent rim described by Parrish (1993) is a consequence of the transition from compact bone to unfinished bone on the distal end of the calcaneum. This transition occurs in all non-archosaurian archosauriforms as well as most crocodylian-line archosaurs examined by me. However, the "prominent rim" is much more noticeable in well-preserved specimens compared to specimens that are not well prepared, incomplete, or poorly preserved. For example, Parrish (1993) scored *Prestosuchus* as (0) even though a clear "rim" transition from compact to a more spongy bone is present (Parrish, 1993: fig. 3B).

Another example of a similar problematic character: Two prominent ridges on the anterior face of the distal end of the fibula absent (0) or present (1) (Parrish, 1993: character 34).

The new characters derive from all over the skeleton. Many of the new characters stem from parts of the skeleton poorly sampled before. For example, I sampled characters from the ulna and radius whereas ulna and radius characters were previously used only among dinosaurs. The elements of the posterior portion of the skull have also been sparsely represented in previous basal archosaur datasets. Furthermore, I converted a number of observations (e.g., Nesbitt, 2005a) into phylogenetic characters. This includes observations of the femur and the osteoderms. Gower (2002) described 27 basal archosauriform characters from the braincase, a region that had only a handful of characters previously. Moreover, I added 20 more braincase characters (new and from other datasets). Thus, braincase characters consist of 11% of the total number of characters, a tenfold increase. This has been a direct result of the work published in numerous papers by David Gower and the increase of well-prepared specimens and newly discovered taxa. Characters originally used exclusively for theropods also support clades such as Crocodylomorpha—these characters are essentially new for basal archosaurs. For example, Rauhut (2003; character 29) uses the height of the lacrimal stretching from the bottom of the orbit to the top as a theropod character; the same character state is also a character basal crocodylomorphs. Essentially, many of the new characters stem from the discovery of new taxa, which, in turn, calls for a critical reevaluation of previously examined taxa.

Inapplicable scorings were unavoidable in such a large analysis incorporating a diversity of morphology even though inapplicable scores limit the informativeness of the characters (Platnick et al., 1991). Characters were scored as NPA (not presently available) in Morphobank for specimens that did not preserve that portion of the skeleton or where that particular structure is obscured.

A limited number of ratio characters were used. Nearly all of these characters were used previously and were shown to be useful in resolving relationships. Statistical gap scoring (Archie, 1985) was not used previously and is not used here. However, the gaps of most of the previously used ratio characters appear to be clear.

Thirty-six multistate characters were used. Of those, 18 (characters 32, 52, 121, 137, 139, 156, 168, 188, 223, 247, 258, 269, 271, 291, 297, 328, 356, 399) were ordered. The ordered characters represent a range with intermediate stages between two extremes. If the 18 characters are not ordered, the strict consensus remains the same (360 MPTs, tree length = 1276, CI = 0.372, RI = 0.768).

RESULTS

This analysis found 360 equally most parsimonious trees (MPTs) of length 1285

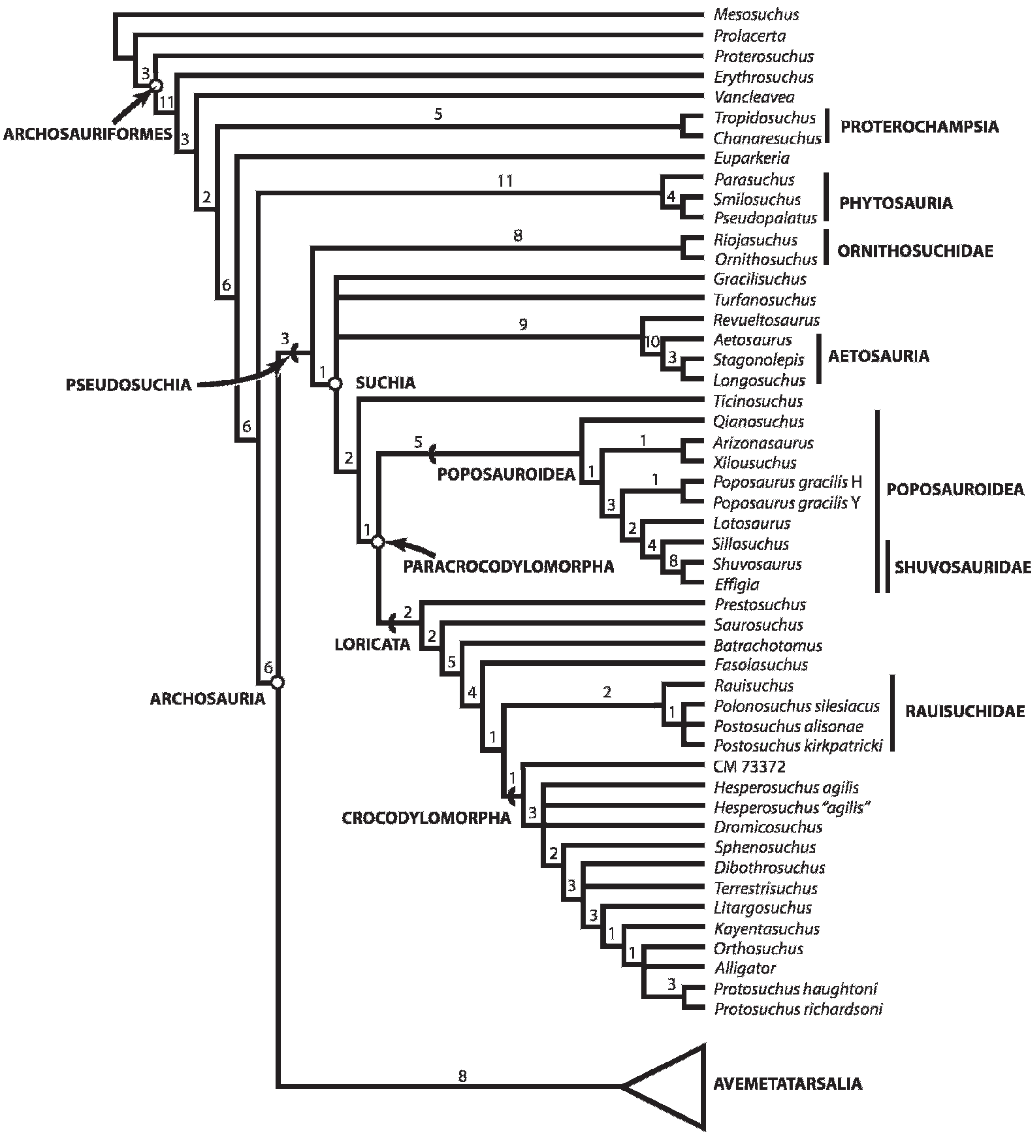

Fig. 51. Archosauriform relationships (77 taxa, 412 characters) highlighting Bremer support values. Consensus of 360 MPTs of length 1285. H = holotype, Y = YPM.

(CI = 0.375; RI = 0.776) in TNT (figs. 51–52). The small number of MPTs reflects the well-resolved topology obtained from 77 taxa and 412 characters. The results of a PTP test (Archie, 1989; Faith and Cranston, 1991) were significant (P < 0.001) indicating the data are not random. The instability in the tree lies at the base of Suchia and the interrelationships of Ornithischia in the strict consensus. The positions of *Gracilisuchus* and *Turfanosuchus* and the clades Aetosauria + *Revueltosaurus* with all other crocodylian-line archosaurs are unresolved in the strict consensus.

The tree is well supported. Bremer supports for monophylectic clades such as

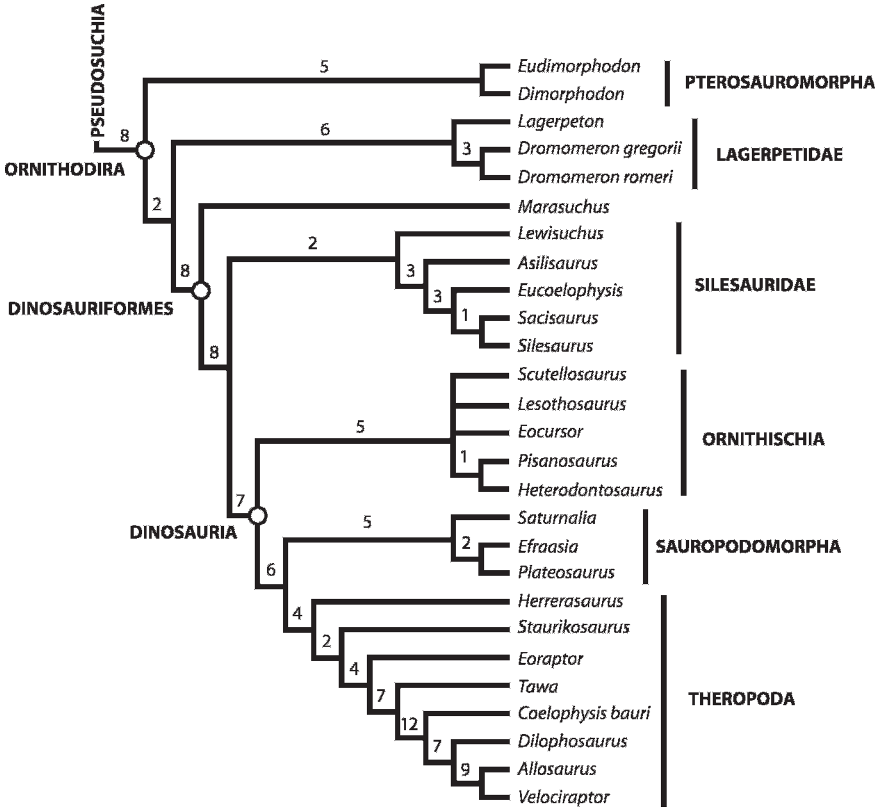

Fig. 52. Avian-line archosaur relationships (77 taxa, 412 characters) highlighting Bremer support values. Consensus of 360 MPTs of length 1285.

Phytosauria, Aetosauria, Ornithosuchidae, Neotheropoda, and Pterosauria are high (5–12). The internal nodes of the crocodylian-line archosaur portion of the tree have Bremer supports ranging from one to four (fig. 51), whereas internal nodes among avian-line archosaur are generally better supported (fig. 52).

I cite only the most important unambiguous synapomorphies (usually CI values higher or equal to 0.33) in the following tree description. Reversals are quite common and are noted throughout. Not all nodes are described. An asterisk denotes character states that appear only once or twice in the tree (high CI values), and hence, represent good synapomorphies for those clades. Potential synapomorphies are listed under accelerated and delayed transformations (ACCTRAN and DELTRAN).

Archosauriformes Gauthier, Kluge and Rowe, 1988

DEFINITION: Node: The least inclusive clade containing *Crocodylus niloticus* Laurenti, 1768, and *Proterosuchus fergusi* Broom, 1903 (new).

TEMPORAL RANGE: Late Permian (*Archosaurus rossicus* Tatarinov, 1960) to Recent (*Crocodylus niloticus* Laurenti, 1768).

SUPPORT: Archosauriformes is a well-supported node recovered here, as found in all basal archosaur phylogenies containing non-archosauriform archosauromorphs, *Proterosuchus,* and other archosaurs (Juul, 1994; Bennett, 1996; Benton, 2004). Archosauriformes is supported by seven unambiguous synapomorphies including: (1) Absence of a parietal foramen (63-1)*. (2) Jugal-quadratojugal contact (70-1)*. (3) Ectopterygoid forms all of the lateral edge of the lateral pterygoid flange (88-1)*. (4) Ossified laterosphenoid present (92-1)*. (5) Antorbital fenestra present (136-1)*. Reversed in *Alligator* and *Vancleavea*. (6) Lateral mandibular fenestra present (138-1)*. Reversed in pterosaurs and *Vancleavea*. (7) Presence of tooth serrations (168-1)*.

Other possible synapomorphies: **ACCTRAN**: Tall and narrow orbit (142-1).

Unnamed Node (*Erythrosuchus* + Archosauria)

TEMPORAL RANGE: Early Triassic (Olenekian, *Xilousuchus sapingensis* Wu, 1981) to Recent (*Crocodylus niloticus* Laurenti, 1768).

SUPPORT: (1) Absence of a large anteriorly opening foramen on the anterolateral surface of the maxilla (31-0) (reversed in *Euparkeria* and *Lotosaurus*). (2) Basipterygoid, processes directed anteriorly or ventrally at their distal tips (93-1). (3) Absence of a ridge on lateral surface of inferior anterior process of the prootic ventral to the trigeminal foramen (94-1)*. (4) Verticalized parabasisphenoid (97-1)*. (5) Absence of supratemporals (145-1)*. (6) Posteroventral portion of the dentary laterally overlaps the anteroventral portion of the angular (164-1)*. (7) Thecodont tooth implantation (174-1)*. (8) Second primordial sacral rib is not bifurcated (203-1). (9) Entire anterior margin of the scapula is concave (217-1)*. (10) Acromion process of the scapula distinctly raised above the ventral edge of the scapula (220-1)*. (11) Distinct notch between the scapulocoracoid on the anterior margin (221-0). (12) Tarsals 1 and 2 absent (346-1)*. (13) Absence of an ossified astragalo-calcaneal canal (369-1)*. (14) Absence of a distinct centrale (381-1)*. (15) Metatarsal IV about the same length or shorter than metatarsal III (393-1)*.

Other possible synapomorphies: **ACCTRAN**: Antorbital fossa restricted to the lacrimal and dorsal process of the maxilla (137-1); absence of a separate ossification anterior to the nasals surrounded by the premaxilla (150-0); absence of teeth on the transverse process of the pterygoid (176-1); anterolateral processes of the interclavicle reduced or absent (215-1); metacarpal IV about the same length or shorter than metacarpal III (260-1); anterior (= preacetabular, = cranial) process on the dorsal margin of the ilium present (268-1). With the exception of the character 268-1 and 150-0, all of these characters were unknown or not applicable to *Vancleavea*. They probably all represent valid apomorphies of *Erythrosuchus* + Archosauria.

Unnamed Node (*Vancleavea* + Archosauria)

TEMPORAL RANGE: Early Triassic (Olenekian, *Xilousuchus sapingensis* Wu, 1981) to Recent (*Crocodylus niloticus* Laurenti, 1768).

SUPPORT: (1) Postparietal(s) absent (146-1). (2) Postaxial intercentra absent (177-1). (3) Ectepicondylar flange of the humerus absent (234-1). (4) Distal condyles of the femur not projecting markedly beyond shaft (318-1)*. (5) Osteoderms present (401-1)*.

Other possible synapomorphies: **ACCTRAN**: Anterodorsal process (= nasal process), length of the premaxilla greater than the anteroposterior length of the premaxilla (1-1); postfrontal absent (44-1); parabasisphenoid plate present and arched anteriorly (96-1); external foramina for passage of abducens nerves on the anterior of a more vertical, upturned process of the parabasisphenoid (123-1); external naris directed dorsally (140-1); orbit circular or elliptical (142-0); ridge of attachment of the M. caudifemoralis low on the proximal portion of the femur and without a distinct medial asymmetrical apex (= fourth trochanter) (315-1). **DELTRAN:** Metacarpal IV about the same length or shorter than metacarpal III (260-1).

Proterochampsia Bonaparte, 1971, sensu Kischlat, 2002

ORIGINAL DEFINITION: Taxa closer to *Proterochampsa* than *Crocodylus* and *Vultur*.

REVISED DEFINITION: Stem: The most inclusive clade containing *Proterochampa barrionuevoi* Reig, 1959, but not *Euparkeria capensis* Broom, 1913, *Erythrosuchus africanus* Broom, 1905, *Passer domesticus* Linnaeus, 1758, or *Crocodylus niloticus* Laurenti, 1768 (new).

TEMPORAL RANGE: Middle Triassic (Ladinian, *Chanaresuchus bonapartei* Romer, 1971b) to Late Triassic (early Norian, *Proterochampa barrionuevoi* Reig, 1959).

SUPPORT: This is the first time the monophyly of the group has been tested. Although I include only two of seven potential proterochampsians (Sues, 1976), this initial attempt aims to build a foundation for future work. The two proterochampsians are supported by seven unambiguous synapomorphies: (1) Lateral surface of the quadratojugal with a ridge marking the posteroventral corner of the lower temporal fossa (47-1)*. (2) Presence of an upper temporal fossa on the posterodorsal portion of the squamosal (55-1)*. (3) Sharp longitudinal ridge on the body of the jugal (75-1). (4) Proximodistally oriented groove on the lateral side of the distal portion of the tibia (338-1). (5) Midshaft diameter of metatarsal II more than the average midshaft diameter of metatarsal I–IV (388-1)*. (6) Metatarsal IV reduced where the midshaft diameter is less than metatarsal III (394-1)*. (7) Metatarsal V tapers to a point and lacks phalanges (399-2).

Other possible synapomorphies: **DELTRAN:** Anterodorsal process of the premaxilla greater than the anteroposterior length of the premaxilla (1-1); posterodorsal process of the premaxilla less than or about the same as the anteroposterior length of the premaxilla (2-0); postfrontal absent (44-1); external naris directed dorsally (140-1).

Unnamed Node (*Euparkeria* + Archosauria)

TEMPORAL RANGE: Early Triassic (Olenekian, *Xilousuchus sapingensis* Wu, 1981) to Recent (*Crocodylus niloticus* Laurenti, 1768).

SUPPORT: Here I include a description of the node of *Euparkeria* + Archosauria because various authors find *Euparkeria* closer to Archosauria than to proterochampsians (Benton and Clark, 1988; Bennett, 1996) or proterochampsians (Sereno, 1991a; Parrish, 1993; Juul, 1994; Benton, 1999, 2004). The following unambiguous characters support *Euparkeria* closer to Archosauria than to Proterochampsia: (1) Foramen on the medial side of the articular (159-1)*. (2) Distal ends of neural spines of the cervical vertebrae laterally expanded (191-1)*. (3) Neural spines of the dorsal vertebrae with a lateral expansion and a flat dorsal margin (197-1). (4) Proximal end of the fibula, in proximal view, rounded or slightly elliptical (341-0). (5) Distal end of the fibula asymmetrical in lateral view (345-0). (6) The posterior corner of the dorsolateral margin of the astragalus dorsally overlaps the calcaneum much more than the anterior portion (360-1)*. (7) Calcaneal tuber shaft proportions about the same or broader than tall (376-1)*.

Other possible synapomorphies: **ACCTRAN:** postaxial osteoderms arranged in paramedian row dorsal to the vertebral column (402-1). **DELTRAN:** External foramina for passage of abducens nerves on the anterior of a more vertical, upturned process of the parabasisphenoid (123-1).

Crurotarsi Sereno and Arcucci, 1990

ORIGINAL DEFINITION: Ornithosuchidae, Parasuchia, Aetosauria, Rauisuchia, Crocodylomorpha, and all extinct descendants that are most closely related to these taxa (Sereno and Arcucci, 1990).

REVISED DEFINITION: Node: The least inclusive clade containing *Rutiodon carolinensis* Emmons, 1856, and *Crocodylus niloticus* Laurenti, 1768 (new).

TEMPORAL RANGE: Early Triassic (Olenekian, *Xilousuchus sapingensis* Wu, 1981) to Recent (*Crocodylus niloticus* Laurenti, 1768).

SUPPORT: (1) Parabasisphenoid plate absent (96-2)*. (2) Semilunar depression on the lateral surface of the basal tubera of the parabasisphenoid absent (98-1)*. (3) Absence of teeth on palatal process of the pterygoid (175-1)*. (4) Cervical ribs short and snout (196-1)*. (5) Ventral articular surface of the astragalus-calcaneum, concavoconvex with concavity on calcaneum (368-1)*. (6) Ventral articular surface for distal tarsal 4 and the distal end of the tuber of the calcaneum separated by a clear gap (371-1)*. (7) Articular surfaces for fibula and distal tarsal IV on the calcaneum continuous (380-1)*.

Other possible synapomorphies: **ACCTRAN**: Calcaneal tuber distal end flared, dorsally and ventrally (374-1); articular surface for the fibula of the calcaneum convex and hemicylindrical shaped (378-1); dorsal osteoderm alignment dorsal to the dorsal vertebrae (presacrals 10~24) one to one (411-1).

Phytosauria Meyer, 1861

ORIGINAL DEFINITION: *Paleorhinus*, Phytosauridae, and all descendants of their closest common ancestor (Doyle and Sues, 1995).

REVISED DEFINITION: Stem: The most inclusive clade containing *Rutiodon carolinensis* (Emmons, 1856) but not *Aetosaurus ferratus* Fraas, 1877, *Rauisuchus tiradentes* Huene, 1942, *Prestosuchus chiniquensis* Huene, 1942, *Ornithosuchus longidens* Huxley, 1877, and *Crocodylus niloticus* Laurenti, 1768 (sensu Sereno, 2005).

TEMPORAL RANGE: Late Triassic (late Carnian, *Parasuchus hislopi, sensu* Chatterjee, 2001, to latest Triassic (?Rhaetian, *Redondasaurus* Hunt and Lucas, 1993).

SUPPORT: (1) Six+ premaxillary teeth (6-3). (2) Premaxilla longer than the maxilla (10-1)*. (3) Facial portion of the maxilla anterior to anterior edge of antorbital fenestra equal in length or longer than portion posterior to anterior edge of fenestra (14-1). (4) Anterior extent of the maxilla anterior to the nasals (19-1)*. (5) Posterior portion of the maxilla ventral to the antorbital fenestra expands dorsoventrally at the posterior margin of the maxilla (27-2). (6) Subtriangular quadratojugal (46-1)*. (7) Dorsal head of the quadrate has a sutural contact with the paroccipital process of the opithotic (77-1)*. (8) External nares nonterminal (139-1+2)*. (9) Separate ossification anterior to the nasals surrounded by the premaxilla present (150-1). (10) Dentary-splenial mandibular symphysis present along one-third of lower jaw (160-1). (11) Markedly heterodont dentition (167-1). (12) Anterior portion of the coracoid distinctly hooked (226-1)*. (13) Ectepicondylar flange of the humerus present (234-0). (14) Attachment site for the M. iliofibularis on the fibula knob shaped or tablike, robust (339-1). (15) Articular surface for the fibula of the calcaneum convex and hemicylindrical shaped (378-1).

Other possible synapomorphies: **ACCTRAN**: External naris directed dorsally (140-1); femoral head orientation anterior (60°–90° degrees) (305-0); medial side of distal tarsal 4 with foramen/foramina (352-1). **DELTRAN:** Foramina for entrance of cerebral branches of internal carotid artery into the braincase positioned on the posterolateral surface (95-1); external naris directed dorsally (140-1); acromion process of the scapula in the about the same plane as ventral edge of the scapula (220-0); distal end of the calcaneal tuber flared dorsally and ventrally (374-1).

Archosauria Cope, 1869
= Avesuchia Benton, 1999

ORIGINAL DEFINITION: A monophyletic taxon composed of the living crocodiles and birds, and of fossil taxa that share their most recent common ancestor (Gauthier and Padian, 1985).

REVISED DEFINITION: Node: The least inclusive clade containing *Crocodylus niloticus* Laurenti, 1768, and *Passer domesticus* Linnaeus, 1758 (sensu Sereno, 2005).

TEMPORAL RANGE: Early Triassic (Olenekian, *Xilousuchus sapingensis* Wu, 1981) to Recent (*Crocodylus niloticus* Laurenti, 1768).

SUPPORT: (1) Palatal processes of the maxilla meet at the midline (32-1)*. (2) Lagenar/cochlea recess present and elongated and tubular (118-1)*. (3) External foramen for abducens nerves within prootic only (122-1). (4) Antorbital fossa present on the lacrimal, dorsal process of the maxilla and the dorsolateral margin of the posterior process of the maxilla (the ventral border of the antorbital fenestra) (137-2)*. (5) Posteroventral portion of the coracoid possesses a "swollen" tuber (225-1)*. (6) Lateral tuber (= radius tuber) on the proximal portion of the ulna present (237-1)*. (7) Longest metacarpal: Longest metatarsal <0.5 (245-1). (8) Anteromedial tuber of the proximal portion of the femur present (300-1)*. (9) Tibial facet of the astragalus divided into posteromedial and anterolateral basins (366-1). (10) Calcaneal tuber orientation, relative to the transverse plane, between 50° and 90° posteriorly (377-2).

Other possible synapomorphies: **ACCTRAN**: Foramina for entrance of cerebral branches of internal carotid artery into the braincase positioned on the anterolateral surface (95-2); acromion process of the scapula distinctly raised above the ventral edge of the scapula (220-1); coracoid with postglenoid process (notch ventral to glenoid) (222-1); proximal surface of distal tarsal 4 with distinct, proximally raised region on the posterior portion (= heel of Sereno and Arcucci, 1994a, 1994b) (353-1). These may represent synapomorphies of Archosauria, but the condition of most of these are either unknown or inapplicable in pterosaurs.

Pseudosuchia Zittel, 1887–1890

ORIGINAL DEFINITION: Crocodiles and all archosaurs closer to crocodiles than to birds (Gauthier and Padian, 1985).

REVISED DEFINITION: Stem: The most inclusive clade containing *Crocodylus niloticus* Laurenti, 1768, but not *Passer domesticus* Linnaeus, 1758 (sensu Sereno, 2005).

TEMPORAL RANGE: Early Triassic (Olenekian, *Xilousuchus sapingensis* Wu, 1981) to Recent (*Crocodylus niloticus* Laurenti, 1768).

SUPPORT: (1) Parabasisphenoid recess (= median pharyngeal recess of some authors = hemispherical sulcus = hemispherical fontanelle) present (100-1)*. (2) Squared off distal end of the ulna (238-1)*. This could also be a synapomorphy of Archosauria, but the basal condition in avian-line archosaurs is not known. (3) Depressed proximal surface of the lateral condyle of the tibia (330-1)*. (4) Dorsoventrally oriented groove or gap on the posterior side of the distal portion of the tibia (337-1)*.

Other possible synapomorphies: **ACCTRAN**: Medial wall of the vestibule almost completely ossified (117-1); pubis longer than ischium (282-1). **DELTRAN**: Coracoid with postglenoid process (notch ventral to glenoid) (222-1). This could also be a synapomorphy of Archosauria, but the basal condition in avian-line archosaurs is not known; pedal unguals strongly mediolaterally compressed, with a sharp dorsal keel (400-2). Also present in phytosaurs.

Ornithosuchidae Huene, 1907–1908

ORIGINAL DEFINITION: *Ornithosuchus*, *Riojasuchus*, *Venaticosuchus*, and all descendants of their common ancestor (Sereno, 1991a).

REVISED DEFINITION: Stem: The most inclusive clade containing *Ornithosuchus longidens* Huxley, 1877, but not *Rutiodon carolinensis* Emmons, 1856, *Aetosaurus ferratus* Fraas, 1877, *Rauisuchus tiradentes* Huene, 1942, *Prestosuchus chiniquensis* Huene, 1942, *Crocodylus niloticus* Laurenti, 1768, or *Passer domesticus* Linnaeus, 1758 (modified from Sereno, 2005).

TEMPORAL RANGE: Late Triassic (Carnian, *Ornithosuchus longidens* Huxley, 1877, to mid-Norian– ?Rhaetian, *Riojasuchus tenuisceps* Bonaparte, 1967).

SUPPORT: The monophyly of Ornithosuchidae has never been contested. However, Sereno (1991a) is the only person to include both *Ornithosuchus* and *Riojasuchus* as separate terminal taxa.

(1) Three premaxillary teeth (6-0). (2) Downturned premaxilla (8-1)*. (3) Two-tooth diastema between the posterior premaxillary teeth and the anterior maxillary teeth between the maxilla and the premaxilla (13-1)*. (4) Nasal-prefrontal contact absent (33-1)*. (5) Posterolateral (= occipital) process of the parietals anteriorly inclined greater than 45° (62-1). (6) Palatine-pterygoid fenestra present (85-1)*. (7) Orbit with distinct ventral point surrounded by V-shaped dorsal processes of jugal (142-2)*. (8) Dentary-splenial mandibular symphysis present along one-third of lower jaw (160-1). (9) Cervical vertebrae, middle portion of the ventral keel extends ventral to the centrum rims (190-1)*. (10) Pubis 70% or more of femoral length (278-1). (11) Anterior trochanter (= M. iliofemoralis cranialis insertion) present and forms a steep margin with the shaft but is completely connected to the shaft (308-1)*. (12) Astragalus-calcaneum, ventral articular surface concavoconvex with concavity on astragalus (368-2)*. (13) Metatarsal V "hooked," proximal end absent (398-1).

Other possible synapomorphies: **ACCTRAN:** Lateral surface of the exoccipital without subvertical crest (= metotic strut) (114-0); primordial trunk vertebrae incorporated into the sacrum, with their ribs/transverse processes articulating with the pelvis (205-1); accessory laminar process on anterior face of neural spine of the midcaudal vertebrae present (210-1); gap at the midline between the distal ends of the ischia (292-1); attachment site for the M. iliofibularis near the midpoint between the proximal and distal ends (340-1). **DELTRAN:** Diapophyses and parapophyses of the middle dorsal vertebrae

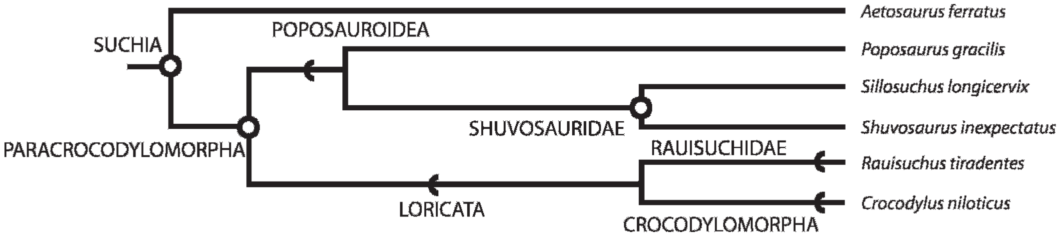

Fig. 53. Proposed taxonomy of basal suchians. Circles = nodes; chevrons = stem groups. See results section.

expand laterally where both diapophyses and parapophyses originate on a transverse process (199-1); attachment site for the M. iliofibularis of the fibula knob shaped or tablike, robust (339-1).

Suchia Krebs, 1974 (fig. 53)

ORIGINAL DEFINITION: Suchia includes *Gracilisuchus stipanicicorum*, Aetosauria, Rauisuchia, Poposauridae, Crocodylomorpha, and all descendants of their common ancestor (Sereno, 1991a).

REVISED DEFINITION: Node: The least inclusive clade containing *Aetosaurus ferratus* Fraas, 1877, and *Rauisuchus tiradentes* Huene, 1942, *Prestosuchus chiniquensis* Huene, 1942, *Crocodylus niloticus* Laurenti, 1768 (new).

SUPPORT: (1) Longitudinal ridge on the body of the jugal rounded and broad (75-2). (2) Articular facets for the fibular and astragalus of the calcaneum separated (372-1)*. (3) Calcaneal tuber, shaft proportions at the midshaft of the tuber just short of twice the mediolateral width of the fibular facet (376-2)*. (4) Articular surface for the fibula of the calcaneum convex and hemicylindrical shaped (378-1)*.

Other possible synapomorphies: **ACCTRAN:** Shallow longitudinal groove on the posterior side of the radius (240-1); medial condyle of the distal portion of the femur tapers to a point on the medial portion in distal view (320-0).

Unnamed Node (*Revueltosaurus* + Aetosauria)

TEMPORAL RANGE: Late Triassic (?Carnian–early Norian, *Aetosauroides scagliai* Casamiquela, 1960, to ?late Norian (*Redondasuchus reseri* Hunt and Lucas, 1991).

SUPPORT: (1) Posterior process of the maxilla articulates into a slot on the lateral side of the jugal (16-1)*. (2) Postorbital-squamosal contact continues ventrally for much or most of the ventral length of the squamosal (66-1). (3) Postorbital bar composed by mostly the postorbital (67-1)*. (4) Posterior process of the jugal splits the anterior process of the quadratojugal (71-2)*. (5) External foramen for abducens nerves within parabasisphenoid only (122-2). (6) Radius length shorter than 80% of humerus length (241-1)*. (7) Osteoderms covering the appendages present (405-1)*. (8) Anterior bar located on the anterior edge of an osteoderm (408-1). (9) Ventral carapace in the trunk area (409-1)*. (10) Gastralia absent or few (412-2)*.

Other possible synapomorphies: **ACCTRAN:** Ventral ramus of the opisthotic covered by the lateralmost edge of exoccipital in posterior view (111-1); foramen for trigeminal nerve and middle cerebral vein fully divided (131-2), unknown in *Revueltosaurus*; palpebral(s) present (147-1), unknown in *Revueltosaurus*. **DELTRAN**: Posterior edge of posterior maxillary teeth convex (15-1); dorsal (= ascending) process of the maxilla remains the same width (29-1); rounded and thick facet for the paroccipital process on the medial side of the posterior process of the squamosal (54-1); middle dorsal vertebrae, diapophyses and parapophyses expand laterally where both diapophyses and parapophyses originate on a transverse process (199-1); presacral osteoderms wider than long (407-1).

Aetosauria Marsh, 1884

ORIGINAL DEFINITION: All crurotarsans more closely related to *Desmatosuchus* than the immediate sister group, recognizing that the sister group may be rauisuchians, prestosuchians, or another suchian taxon (Heckert and Lucas, 2000).

REVISED DEFINITION: Stem: The most inclusive clade containing *Aetosaurus ferratus* Fraas, 1877, and *Desmatosuchus haplocerus* Cope, 1892, than to *Rutiodon carolinensis* Emmons, 1856, *Postosuchus kirkpatricki* Chatterjee, 1985, *Prestosuchus chiniquensis* Huene, 1942, *Poposaurus gracilis* Mehl, 1915, *Crocodylus niloticus* Laurenti, 1768, *Gracilisuchus stipanicicorum* Romer, 1972c, and *Revueltosaurus callenderi* Hunt, 1989 (modified from Parker, 2007).

TEMPORAL RANGE: Late Triassic (?Carnian–early Norian, *Aetosauroides scagliai* Casamiquela, 1960, to ?late Norian (*Redondasuchus reseri* Hunt and Lucas, 1991)

SUPPORT: The monophyly of Aetosauria has never been contested. Here, Aetosauria is supported by the following unambiguous synapomorphies: (1) Premaxilla teeth absent in the anterior portion of the premaxilla (7-1)*. (2) Anterodorsal margin of the maxilla borders the external naris (24-1). (3) Concave anterodorsal margin at the base of the dorsal process of the maxilla (25-1). (4) Quadratojugal forms more than 80% of the posterior border of the lower temporal fenestra (45-1). (5) Straight occipital margin of the parietals in dorsal view (61-1). (6) Posterolateral (= occipital) processes of the parietals anteriorly inclined greater than 45° (62-1). (7) Quadrate angled anteroventrally (82-1). (8) Lateral exposed supratemporal fenestra (143-1)*. (9) Anterodorsal margin of the dentary dorsally expanded (154-2). (10) Anterior extent of the dentary tapers to a sharp point (155-1)*. (11) Glenoid of the mandible located well ventral of the dorsal margin of the dentary (158-1). (12) Dentary teeth absent in the anterior portion (166-1)*. (13) Tooth crown mesiodistally expanded above root in cheek teeth (171-1).

Other possible synapomorphies: **ACCTRAN**: Ventromedial process of the prefrontal present (40-1); absence of an articular foramen on the medial side (159-0); hyposphene-hypantrum accessory intervertebral articulations in the posterior cervical and/or dorsal vertebrae (195-1); ilium ventrolaterally deflected about 45° (270-1); attachment site for the M. iliofibularis of the fibula near the mid point between the proximal and distal ends (340-1). **DELTRAN**: Two paramedian pairs (4 osteoderms per segment) (406-1). The condition is unknown in *Revueltosaurus* at present.

Unnamed Node (*Ticinosuchus* + Crocodyliformes)

TEMPORAL RANGE: Early Triassic (Olenekian, *Xilousuchus sapingensis* Wu, 1981) to Recent (*Crocodylus niloticus* Laurenti, 1768).

SUPPORT: (1) Accessory laminar process on anterior face of neural spine of the middle caudal vertebrae (210-1)*. (2) Extensive medial contact between the ischia but the dorsal margins are separated (291-1)*. (3) Rounded or elliptical outline of the distal portion of the ischium (293-1). (4) Ischium expanded relative to the ischial shaft (= ischial boot) (294-1)*. (5) Ischium length markedly longer than the dorsal margin of iliac blade (298-1). (6) Dorsal osteoderm alignment dorsal to the dorsals (presacrals 10~24) staggered (411-0)*.

Other possible synapomorphies: **ACCTRAN**: Anterior margin antorbital fenestra nearly pointed (30-1); articular with dorsomedial projection separated from glenoid fossa by a clear concave surface (156-1). Unknown in *Ticinosuchus*; ventromedially directed process of the articular present (157-1). Unknown in *Ticinosuchus*; ilium ventrolaterally deflected about 45° (270-1). Also present in aetosaurs; straight transverse groove on the proximal surface of the femur (314-1). Unknown in *Ticinosuchus*. **DELTRAN:** Hyposphene-hypantrum accessory intervertebral articulations in the posterior cervical and/or dorsal vertebrae (195-1). Also in saurischians.

Paracrocodylomorpha Parrish, 1993 (fig. 53)

ORIGINAL DEFINITION: Last common ancestor of Poposauridae and Crocodylomorpha and all its descendants (Parrish, 1993). Later, Weinbaum and Hungerbühler (2007) defined Paracrocodylomorpha as archosaurs more closely related to *Batrachotomus wildi*, *Postosuchus kirkpatricki*, *Saurosuchus galilei*, and *Crocodylus niloticus* than to *Poposaurus gracilis*.

REVISED DEFINITION: Node: The least inclusive clade containing *Poposaurus gracilis* Mehl, 1915, and *Crocodylus niloticus* Laurenti, 1768 (sensu Sereno, 2005).

Temporal Range: Early Triassic (Olenekian, *Xilousuchus sapingensis* Wu, 1981) to Recent (*Crocodylus niloticus* Laurenti, 1768).

SUPPORT: (1) Pubis distal end expanded relative to the shaft (= pubis boot) (283-1)*. Also in saurischians. (2) Metatarsal IV length subequal or shorter than to metatarsal II (395-1).

Other possible synapomorphies: **ACCTRAN**: Posteromedial tuber of the proximal portion of the femur present and small (301-0). **DELTRAN**: Ventromedially directed process of the articular (157-1); ilium ventrolaterally deflected about 45° (270-1); ischiopubis reduced to a thin proximal contact (287-1); straight transverse groove on the proximal surface of the femur (314-1).

Poposauroidea Nopcsa, 1923 (fig. 53)

ORIGINAL DEFINITION: Poposauridae plus all taxa referred to Ctenosauriscidae Weinbaum and Hungerbühler, 2007.

REVISED DEFINITION: Stem: The most inclusive clade containing *Poposaurus gracilis* Mehl, 1915, but not *Postosuchus kirkpatricki* Chatterjee, 1985, *Crocodylus niloticus* Laurenti, 1768, *Ornithosuchus longidens* Huxley, 1877, or *Aetosaurus ferratus* Fraas, 1877 (new).

TEMPORAL RANGE: Early Triassic (Olenekian, *Xilousuchus sapingensis* Wu, 1981) to latest Triassic (late Norian–?Rheatian, *Effigia okeeffeae* Nesbitt and Norell, 2006).

SUPPORT: (1) Anterodorsal process (= nasal process) of the nasal greater than the anteroposterior length of the premaxilla (1-1). (2) Posterodorsal process (= maxillary process, = subnarial process) of the premaxilla restricted to the ventral border of the external naris (5-1). (3) Anterodorsal margin of the maxilla borders the external naris (24-1). (4) Concave anterodorsal margin at the base of the dorsal process of the maxilla (25-1). (5) Foramina for entrance of cerebral branches of internal carotid artery into the braincase positioned on the ventral surface (95-0)*. (6) Cervical ribs slender and elongated (196-0). (7) Distal expansion of neural spines of the dorsal vertebrae absent (197-0). (8) Sacral rib of primordial sacral one articulates with the anteriorly directed process of the ilium (202-1)*. (9) Insertion of a sacral vertebra between the first primordial sacral vertebra (207-1). (10) Concave ventral margin of the acetabulum of the ilium (273-2). (11) Thickened process on the proximal portion of the pubic apron (288-1)*. (12) Distal end of the fibula rounded or flat (symmetrical) (345-1).

Other possible synapomorphies: **ACCTRAN**: Length of the posterodorsal process of the premaxilla less than or about the same as the anteroposterior length of the premaxilla (2-0); anterolateral surface of the maxilla with a slot for the premaxillary process (20-1); anterior margin of the antorbital fenestra gently rounded (30-0); centra 3–5 longer than middorsal (181-1); sacral centra coossified at the ventral edge (200-1); lateral surface of the exoccipital without subvertical crest; forelimb–hind limb length ratio less than 0.55 (212-1); angle between the lateral condyle and the crista tibiofibularis of the femur about 90° in distal view (319-1).

Unnamed Node (*Arizonasaurus* + Shuvosauridae)

TEMPORAL RANGE: Early Triassic (Olenekian, *Xilousuchus sapingensis* Wu, 1981) to latest Triassic (late Norian–? Rhaetian, *Effigia okeeffeae* Nesbitt and Norell, 2006).

SUPPORT: (1) Posterior portion of the maxilla ventral to the antorbital fenestra tapers posteriorly (27-0). (2) Prezygapophyses and postzygapophyses of the sacral vertebrae coossified (201-1)*. (3) Pubis expanded distal margin (= pubic boot) mediolaterally thin (284-1). (4) Ischio-pubis contact absent (287-2)*. (5) Distal pubis mediolateral width significantly narrower than proximal width (289-1). (6) Osteoderms absent (401-0)*.

Other possible synapomorphies: **ACCTRAN**: Accessory laminar process on anterior face of neural spine of the middle caudal vertebrae absent (210-0); prezygapophyses of the distal caudal vertebrae elongated more than a quarter of the adjacent centrum (211-1); articular facet for the astragalus of the calcaneum lies partially ventral to the fibular facet (358-1); calcaneal tuber, shaft proportions at the midshaft of the tuber about the same or broader than tall (376-1). All the ACCTRAN characters are unknown in *Arizonasaurus.* **DELTRAN:** Lateral surface of the exoccipital without subvertical crest (= metotic strut) (114-0).

Unnamed Node (*Arizonasaurus* + *Xilousuchus*)

TEMPORAL RANGE: Early Triassic (Olenekian, *Xilousuchus sapingensis* Wu, 1981) to Middle Triassic (Anisian, *Arizonasaurus babbitti* Welles, 1947).

SUPPORT: (1) Parabasisphenoid plate present and straight (96-0)*. (2) Neural spines of the posterior cervical vertebrae arc anteriorly (194-1). Also present in *Lotosaurus*.

Other possible synapomorphies: **ACCTRAN**: Neural spines of the dorsal vertebrae 2–5 times taller as the posterior cervical vertebrae neural spines (198-1). Unknown in *Xilousuchus*. Also present in *Lotosaurus.* **DELTRAN:** Anterolateral surface of the maxilla with a slot for the premaxillary process (20-1). Also present in *Qianosuchus*.

Unnamed Node (*Poposaurus* + Shuvosauridae)

TEMPORAL RANGE: Middle Triassic (Anisian, Moenkopi shuvosaurid [= chatterjeeid] Nesbitt, 2005b) to latest Triassic (late Norian–? Rhaetian, *Effigia okeeffeae* Nesbitt and Norell, 2006).

Support: (1) Supraacetabular crest (= supraacetabular rim) of the ilium projects ventrally (264-1)*. (2) Anterodorsally inclined crest dorsal to the supraacetabular crest/rim of the ilium (266-1)*. (3) Anterior (= preacetabular, = cranial) process of the ilium long and extends anterior to the acetabulum but shorter than the posterior process of the ilium (269-1). (4) Pedal unguals dorsolaterally compressed (400-1)*.

Other possible synapomorphies: **ACCTRAN**: Anterolateral surface of the maxilla smooth (20-0); sharp longitudinal ridge present on the lateral surface of the maxilla (26-1); palatal processes of the maxilla do not meet at the midline (32-0); posterior end of the squamosal does not extend posterior to the head of the quadrate (48-0); foramen or groove passing above and into the dorsal end of the metotic foramen absent (132-0); anterior extent of the dentary tapers to a sharp point (155-1); ventromedially directed process of the articular absent (157-0); 3–5 cervical centra shorter or the same length as the middorsal (181-0); third cervical vertebra length subequal to that of the axis centrum (183-0); ilium mainly vertically orientated (270-0); medial condyle of the distal portion of the femur smoothly rounded in distal view (320-1). All of these characters except for the last are unknown in *Poposaurus*. **DELTRAN:** Sacral centra coossified at the ventral edge (200-1); accessory laminar process on anterior face of neural spine of the middle caudal vertebrae absent (210-0); prezygapophyses of the distal caudal vertebrae elongated more than a quarter of the adjacent centrum (211-1); distal tarsal 4 ventrally expanded into a small process (349-1); medial side distal tarsal 4 with foramen/foramina (352-1); calcaneal tuber, shaft proportions at the midshaft of the tuber about the same or broader than tall (376-1).

Unnamed Node (*Lotosaurus* + Shuvosauridae)

TEMPORAL RANGE: Middle Triassic (Anisian, Moenkopi shuvosaurid [= chatterjeeid] Nesbitt, 2005b) to latest Triassic (late Norian–?Rhaetian, *Effigia okeeffeae* Nesbitt and Norell, 2006).

SUPPORT: (1) Premaxillary teeth absent (6-4)*. (2) Maxillary dentition absent (18-1)*. (3) Ventral edge surface of the maxilla mediolateral width greater than dorsoventrally length (21-1)*. Also present in *Erpetosuchus*. (4) Ilium expanded dorsally, height markedly taller than the dorsal portion of the supraacetabular rim to the pubis-ischium contact (276-1)*. Also in Neotheropoda. (5) Extensive medial contact between the ischia the dorsal margins contact each other (291-2). (6) Distal portion of the ischium unexpanded (294-0); although there seems to be a slight bulbous expansion in some specimens of *Shuvosaurus*.

Other possible synapomorphies: **ACCTRAN**: Five phalanges on manual digit IV (258-0). Unknown in *Effigia*, *Shuvosaurus*, and *Sillosuchus*; anterolateral tuber of the proximal portion of the femur absent, the anterolateral face is flat (302-1). Unknown in *Lotosaurus*; deep groove between the lateral condyle and crista tibiofibularis on the distal surface (322-1) absent in *Lotosaurus* and unknown in *Sillosuchus*. **DELTRAN:** Subnarial foramen between the premaxilla-maxilla present and the border of the foramen is present on the maxilla but not on the premaxilla (12-2); sharp longitudinal ridge present on the lateral surface of the maxilla (26-1). Also present in *Eoraptor* and coelophysoids; palatal processes of the maxilla do not meet at the midline (32-0); anterior extent of the dentary tapers to a sharp point (155-1); ventromedially directed process of the articular absent (157-0); glenoid of the mandible located well ventral of the dorsal margin of the dentary (158-1); dentary teeth absent (166-2); medial condyle of the distal portion of the femur smoothly rounded in distal view (320-1).

Shuvosauridae Chatterjee, 1993 (fig. 53)

DEFINITION: Node: The least inclusive clade containing *Shuvosaurus inexpectatus* Chatterjee, 1993, and *Sillosuchus longicervix* Alcober and Parrish, 1997 (new).

TEMPORAL RANGE: Late Triassic (?Carnian–early Norian, *Sillosuchus longicervix* Alcober and Parrish, 1997) to latest Triassic (late Norian–?Rhaetian, *Effigia okeeffeae* Nesbitt and Norell, 2006).

SUPPORT: (1) Pneumatic features (= pleurocoels) in the anterior portion of the cervical centrum present as deep fossae (188-1). (2) Rimmed depression on the posterior part of the cervical centrum (189-1)*. (3) Sacral ribs shared between two sacral vertebrae (208-1). (4) Entire anterior margin of the scapula straight/convex or partially concave (217-0). (5) Posteroventral portion of the coracoid smooth (225-0)*. (6) Proximal portion of the humerus expanded less than twice the width of the midshaft of the humerus (236-1)*.

Other possible synapomorphies: **ACCTRAN**: Anterior portion of the frontal tapers anteriorly along the midline (43-1); postfrontal absent (44-1); upper temporal fenestrae separated by a "sagittal crest" (59-2); postorbital bar composed mostly of the postorbital (67-1). Also present in aetosaurs; longitudinal ridge on the body of the jugal absent (75-0); distal articular margin of the quadrate largely concave and corresponding convex articular surface of the articular (81-1); quadrate angled anteroventrally (82-1); basipterygoid processes directed anteriorly or ventrally at their distal tips (93-0); foramina for entrance of cerebral branches of internal carotid artery into the braincase positioned on the anterolateral surface (95-2); parabasisphenoid, between basal tubera and basipterygoid processes significantly elongated at least 1.5 times longer than wide (103-1); paroccipital processes directed ventrolaterally (110-1). Only known in *Shuvosaurus*; exoccipitals do not meet along the midline on the floor of the endocranial cavity (115-1); articular without dorsomedial projection posterior to the glenoid fossa (156-0); foramen on the medial side of the articular absent (159-0); mandibular fenestra length greater than half the length of the mandible (162-1); surangular foramen large (163-1); ectepicondylar flange of the humerus absent (234-1); metatarsal III subequal to metatarsal II (390-1). None of these characters are known in *Sillosuchus*. **DELTRAN:** Primordial trunk vertebrae incorporated into the sacrum (205-1); crest dorsal to the supraacetabular crest of the ilium as a thin ridge (267-1).

Unnamed Node (*Effigia* + *Shuvosaurus*)

TEMPORAL RANGE: Late Triassic (early Norian, *Shuvosaurus inexpectatus* Chatterjee, 1993, sensu Nesbitt and Norell, 2006) to latest Triassic (late Norian–?Rhaetian, *Effigia okeeffeae* Nesbitt and Norell, 2006).

SUPPORT: (1) Middle portion of the ventral keel extends ventral to the centrum rims (190-1). Also in ornithosuchids. (2) Centra articular rims in the sacrum nearly obliterated (204-1)*. (3) Deep fossa on the posterodorsal edge of the coracoid (228-1)*. (4) Expanded distal margin of the pubis (= pubic boot) greater than 33% of the length of the shaft of the pubis (285-1)*. (5) Distal pubis mediolateral width mediolaterally compressed and not broader than anteroposteriorly deep (289-2). (6) Elongated ridge on the lateral side of the shaft of the pubis (290-1)*. (7) Anteromedial tuber of the proximal portion of the femur large and "hooked" posteriorly (300-3)*. (8) Posterolateral portion (= fossa trochanterica, = posterolateral depression, facies articularis antitrochanterica) of the femoral head ventrally descended (313-1). Also in dinosauromorphs.

Other possible synapomorphies: **ACCTRAN**: Diapophyses and parapophyses of the middle dorsal vertebrae expand laterally where both diapophyses and parapophyses originate on a transverse process (199-1); fourth trochanter absent (316-2). **DELTRAN:** Anterior portion of the frontal tapers anteriorly along the midline (43-1); postfrontal absent (44-1); upper temporal fenestrae separated by a "sagittal crest" (59-2); postorbital bar composed by mostly the postorbital (67-1). Also present in aetosaurs; longitudinal ridge on the body of the jugal absent (75-0); distal articular margin of the quadrate largely concave and corresponding convex articular surface of the articular (81-1); quadrate angled anteroventrally (82-1); basipterygoid processes directed anteriorly or ventrally at their distal tips (93-0); foramina for entrance of cerebral branches of internal carotid artery into the braincase positioned on the anterolateral surface (95-2); parabasisphenoid, between basal tubera and basipterygoid processes significantly elongated at least 1.5 times longer than wide (103-1); paroccipital processes directed ventrolaterally (110-1). Only known in *Shuvosaurus*; exoccipitals do not meet along the midline on the floor of the endocranial cavity (115-1); articular without dorsomedial projection posterior to the glenoid fossa (156-0); foramen on the medial side of the articular absent (159-0); mandibular fenestra length greater than half the length of the mandible (162-1); surangular foramen large (163-1); forelimb–hind limb length ratio less than 0.55 (212-1); ectepicondylar flange of the humerus absent (234-1); anterior (= preacetabular, = cranial) process of the ilium subequal or longer than the posterior process of the ilium (269-2); anterolateral tuber of the proximal portion of the femur absent, the anterolateral face is flat (302-1); deep groove between the lateral condyle and crista tibiofibularis on the distal surface of the femur (322-1); mediolaterally compressed proximal end of the fibula (341-1); metatarsal III subequal to metatarsal II (390-1); metatarsal IV distal articulation surface deeper than broad (391-1).

Loricata Merrem, 1820 (fig. 53)

DEFINITION: Stem: The most inclusive clade containing *Crocodylus niloticus* Laurenti, 1768, but not *Poposaurus gracilis* Mehl, 1915, *Ornithosuchus longidens* Huxley, 1877, or *Aetosaurus ferratus* Fraas, 1877 (new).

TEMPORAL RANGE: Middle Triassic (Ladinian, *Prestosuchus chiniquensis* Huene, 1942) to Recent (*Crocodylus niloticus* Laurenti, 1768).

SUPPORT: (1) Four premaxillary teeth (6-1). (2) Ridge on lateral side of the ventral process of the squamosal (51-1)*. (3) Anteroventral process of the squamosal present and perforates the lower temporal fenestra (52-1)*. (4) Orbit tall and narrow (142-1). (5) Attachment site for the M. iliofibularis near the midpoint between the proximal and distal ends of the fibula (340-1). (6) Ventral articular surface of the calcaneum for distal tarsal 4 and the distal end of the tuber separated by a gap with a ventral fossa (371-1)*. (7) Metatarsal V dorsal prominence separated from the proximal surface by a concave gap (397-1).

Other possible synapomorphies: **ACCTRAN**: Paroccipital processes markedly expanded dorsally at the distal ends (108-1); auricular recess extends onto internal surface of epiotic/supraoccipital (133-1); distal end of neural spines of the cervical vertebrae expanded anteriorly so that the spine table is triangular or heart shaped in dorsal view (191-2); distal end of the ulna with anterior expansion (239-1). Unknown in *Prestosuchus* and *Saurosuchus*; attachment site for the M. iliofibularis on the fibula knob shaped or tablike, robust (339-1); articular surface for the calcaneum of the astragalus restricted to the ventral surface of the fibular facet, clearly separated from the ventral margin (367-1). **DELTRAN:** Posterodorsal process (= maxillary process, = subnarial process) of the premaxilla greater than the anteroposterior length of the premaxilla (2-1); anterior margin antorbital fenestra nearly pointed (30-1); pubis length more than 70% or more of femoral length (278-1).

Unnamed Node (*Saurosuchus* + Crocodylifomes)

TEMPORAL RANGE: Middle Triassic (Ladinian, *Batrachotomus kupferzellensis* Gower, 1999) to Recent (*Crocodylus niloticus* Laurenti, 1768).

SUPPORT: (1) Dorsal surface of the frontal with longitudinal ridge along midline (42-1)*. (2) Basioccipital portion of the basal tubera bladelike and anteroposteriorly shortened (106-1)*. (3) Palpebral(s) present (147-1)*. (4) Ilium, crest dorsal to the supraacetabular crest/rim divides the anterior (= preacetabular) process from the posterior (= postacetabular) process (265-1)*. Possibly in specimens referred to *Prestosuchus*. (5) Medial condyle of the distal portion of the femur smoothly rounded in distal view (320-1)*. (6) Articular facet for the astragalus of the calcaneum lies partially ventral to the fibular facet (358-1)*.

Other possible synapomorphies: **ACCTRAN**: Distinct notch between the scapulocoracoid absent (221-1). Unknown in *Saurosuchus*; calcaneal tuber, shaft proportions at the midshaft of the tuber about the same or broader than tall (376-1).

Unnamed Node (*Batrachotomus* + Crocodylifomes)

TEMPORAL RANGE: Middle Triassic (Ladinian, *Batrachotomus kupferzellensis* Gower, 1999) to Recent (*Crocodylus niloticus* Laurenti, 1768).

SUPPORT: (1) Subnarial foramen between the premaxilla-maxilla and the border of the foramen is present on both the maxilla and the premaxilla (12-1). (2) Posterior portion of the nasal at the midline concave (34-1)*. (3) Anterior portion of the frontal tapers anteriorly along the midline (43-1)*. (4) Squamosal with distinct ridge on dorsal surface along edge of supratemporal fossa (49-1)*. (5) Upper temporal fenestrae separated by a mediolaterally thin strip of flat bone (59-1)*. (6) Double-headed ectopterygoid (89-1)*. (7) Foramen for trigeminal nerve and middle cerebral vein at least partially subdivided by prootic (131-1)*. (8) Posttemporal opening absent or less than half the diameter of the foramen magnum (141-1). (9) Supratemporal fossa anterior to the supratemporal fenestra (144-1). (10) Angle between the lateral condyle and the crista tibiofibularis of the femur about 90° in distal view (319-1)*. (11) Paramedian presacral osteoderms with distinct longitudinal bend near lateral edge (404-1)*. (12) Longer than wide presacral osteoderms (407-1). (13) One-to-one (includes pairs) dorsal osteoderms relation to presacral vertebrae (410-0). (14) Dorsal osteoderm alignment dorsal to the dorsal vertebrae (presacrals 10–24) one to one (411-1).

Other possible synapomorphies: **ACCTRAN**: Ventromedial process of the prefrontal present (40-1). Unknown in noncrocodylomorphs paracrocodylomorphs; blunt ventral termination of the ventral process of the postorbital (65-1); posteroventral portion of distal tarsal 4 ventrally expanded into a small process (349-1); thin lamina separating the tibial facet from the posterior edge (= astragalar ridge) of the astragalus (354-1). Unknown in *Batrachotomus*; nonarticular fossa present on the posterior portion of the tibial articular surface of the astragalus (364-1). Unknown in *Batrachotomus*; metatarsal III length subequal to metatarsal II (390-1). Unknown in *Batrachotomus*; metatarsal V has a "poorly" developed first phalanx (399-1). **DELTRAN:** Paroccipital processes markedly expanded dorsally at the distal ends (108-1); foramen or groove passing above and into the dorsal end of the metotic foramen (132-1); auricular recess extends onto internal surface of epiotic/supraoccipital (133-1); articular with dorsomedial projection separated from glenoid fossa by a clear concave surface (156-1); distal end of the ulna with anterior expansion (239-1); posteromedial tuber proximal portion of the femur present and small (301-0).

Unnamed Node (*Fasolasuchus* + Crocodylifomes)

TEMPORAL RANGE: Late Triassic (?Carnian–early Norian, *Rauisuchus tiradentes* Huene, 1942) to Recent (*Crocodylus niloticus* Laurenti, 1768).

SUPPORT: (1) Obturator foramen of the pubis enlarged (281-1)*. Unknown in Rauisuchidae. (2) Proximal condylar fold of the proximal portion of the femur (312-1)*. (3) Rounded and smooth proximal surface of the femur (314-0). (4) Medial face of the distal portion of the fibula banked with an articular facet that articulates with the astragalus (344-1)*. (5) Distal end of the calcaneal tuber with a dorsoventrally aligned median depression (375-1)*.

Other possible synapomorphies: **ACCTRAN**: Facial portion of the maxilla equal in length or longer than portion posterior to anterior edge of fenestra (14-1); posterior edge of posterior maxillary teeth convex (15-1); maxillary interdental plates fused (22-1); quadratojugal forms more than 80% of the posterior border of the lower temporal fenestra (45-1); squamosal without ridge on lateral side of the ventral process (51-0); postorbital-squamosal, contact continues ventrally for much or most of the ventral length of the squamosal (66-1); posterior process of the jugal lies ventral to the anterior process of the quadratojugal (71-1); posterior termination of the jugal posterior to the lower temporal fenestra (72-1); quadrate head completely covered by the squamosal (78-1); fossa on the dorsal surface of the palatine does not extend very far anteriorly along the upper surface of the palatine (90-1); raised rim defining a fossa around the choana on the ventral surface of the palatine (91-1); parabasisphenoid substantially elongated in the region between the basal tubera and the basipterygoid processes, such that the median pharyngeal recess is dorsoventrally extended and troughlike (102-1); small contact between the prootic and the paroccipital process (105-1); ventral ramus of the opisthotic covered by the lateralmost edge of exoccipital in posterior view (111-1); eustachian tubes partially enclosed by bone (121-1); external foramen for abducen nerves within parabasisphenoid only (122-2). Unknown in *Postosuchus kirkpatricki, Postosuchus alisonae*, *Rauisuchus* and *Polonosuchus silesiacus*; perilymphatic foramen border entirely ossified such that the ventral ramus of the opisthotic forms a perilymphatic loop incorporating a loop closure suture with itself (129-1). Unknown in *Postosuchus kirkpatricki, Postosuchus alisonae*, *Rauisuchus, Polonosuchus silesiacus, Dibothrosuchus, Hesperosuchus agilis,* and *Hesperosuchus "agilis"*; perilymphatic foramen positioned more laterally so that duct is transmitted posterolaterally/laterally and the foramen is at least partly visible in lateral view (130-1); distal end of neural spines of the cervical vertebrae laterally expanded in the middle of the anteroposterior length (191-1); teardrop-shaped tuber on the posterior edge, just dorsal of the glenoid fossa of the scapula (possible attachment site of the scapular head of M. triceps) absent (219-0); distinct notch between the scapulocoracoid on the anterior margin (221-1); deep groove on the posteroventral edge of the coracoid (224-1); glenoid oriented posteroventrally (227-1); proximal head of the humerus posteriorly expanded and hooked (232-1); distal pubis mediolateral width significantly narrower than proximal width (289-1); pedal unguals weakly mediolaterally compressed, rounded or triangular in cross section (400-0). With the exception of character states (191-1), (14-1), and (22-1), all characters are unknown in *Fasolasuchus*. **DELTRAN:** Posteroventral portion of distal tarsal 4 ventrally expanded into a small process (349-1); medial side distal tarsal 4 with foramen/foramina (352-1); thin lamina separating the tibial facet from the posterior edge (= astragalar ridge) of the astragalus (354-1); nonarticular fossa present on the posterior portion of the tibial articular surface of the astragalus (364-1); articular surface for the calcaneum of the astragalus restricted to the ventral surface of the fibular facet, clearly separated from the ventral margin (367-1); calcaneal tuber shaft proportions about the same or broader than tall (376-1).

Unnamed Node (Rauisuchidae + Crocodyliformes)

TEMPORAL RANGE: Late Triassic (?Carnian–early Norian, *Rauisuchus tiradentes* Huene, 1942) to Recent (*Crocodylus niloticus* Laurenti, 1768).

SUPPORT: (1) Anterior portion of the dentary dorsally expanded (154-2)*. (2) Distal expansion neural spines of the dorsal vertebrae absent (197-0)*. (3) Mediolaterally compressed proximal end of the fibula (341-1).

Other possible synapomorphies: **DELTRAN:** Posterior edge of posterior maxillary teeth convex (15-1); quadratojugal forms more than 80% of the posterior border of the lower temporal fenestra (45-1); postorbital-squamosal, contact continues ventrally for much or most of the ventral length of the squamosal (66-1); posterior process of the jugal lies ventral to the anterior process of the quadratojugal (71-1); posterior termination of the jugal posterior to the lower temporal fenestra (72-1); quadrate head completely covered by the squamosal (78-1); fossa on the dorsal surface of the palatine does not extend very far anteriorly along the upper surface of the palatine (90-1); raised rim defining a fossa around the choana on the ventral surface of the palatine (91-1); parabasisphenoid substantially elongated in the region between the basal tubera and the basipterygoid processes, such that the median pharyngeal recess is dorsoventrally extended and troughlike (102-1); small contact between the prootic and the paroccipital process (105-1); ventral ramus of the opisthotic covered by the lateralmost edge of exoccipital in posterior view (111-1); eustachian tubes partially enclosed by bone (121-1); supratemporal fossa anterior to the supratemporal fenestra (144-1); deep groove on the posteroventral edge of the coracoid (224-1); glenoid oriented posteroventrally (227-1); proximal head of the humerus posteriorly expanded and hooked (232-1); metatarsal III subequal in length to metatarsals II (390-1); metatarsal V present and has a "poorly" developed first phalanx (399-1); pedal unguals weakly mediolaterally compressed, rounded or triangular in cross section (400-0).

Rauisuchidae Huene, 1936 (fig. 53)

DEFINITION: Stem: The most inclusive clade containing *Rauisuchus tiradentes* (Huene, 1942) but not *Aetosaurus ferratus* Fraas, 1877, *Prestosuchus chiniquensis* Huene, 1942, *Poposaurus gracilis* Mehl, 1915, or *Crocodylus niloticus* Laurenti, 1768 (sensu Sereno, 2005).

TEMPORAL RANGE: Late Triassic (?Carnian–early Norian, *Rauisuchus tiradentes* Huene, 1942, to Norian, *Postosuchus kirkpatricki* Chatterjee, 1985).

SUPPORT: (1) Dorsolateral margin of the anterior portion of the nasal with distinct anteroposterior ridge on the lateral edge (35-1)*. (2) Anteroventral process of the squamosal contacts the postorbital thus bisecting the lower temporal fenestra (52-2)*. (3) Longitudinal ridge on the body of the jugal rounded and restricted to a bulbous ridge (75-3)*. (4) Ventral surface of the axis possesses two paramedian keels (180-1)*.

Other possible synapomorphies: **ACCTRAN**: Facial portion of the maxilla shorter than posterior portion (14-0); bulbous longitudinal ridge present on the lateral surface of the maxilla (26-2); dorsal (= ascending) process of the maxilla remains the same width (29-1); dorsoventrally oriented crest located on the posterior side of the quadrate (83-1); large exit of cranial nerve VII (125-1); palpebral(s) extensively sutured to each other and to the lateral margin of the frontals (149-1); distal end of neural spines of the cervical vertebrae expanded anteriorly, so that the spine table is triangular or heart shaped in dorsal view (191-2). All of these character states are unknown in *Rauisuchus*.

Unnamed Node (*Postosuchus* + *Polonosuchus silesiacus*)

TEMPORAL RANGE: Late Triassic (?Carnian–early Norian, *Polonosuchus silesiacus* Sulej, 2005, to Norian, *Postosuchus kirkpatricki* Chatterjee, 1985).

SUPPORT: (1) Deep pit on the posterodorsal corner of the lateral surface of the squamosal (57-1)*. (2) Hypapophyses in the middle cervical vertebrae (192-1)*.

Other possible synapomorphies: **DELTRAN**: Maxillary interdental plates fused (22-1); bulbous longitudinal ridge present on the lateral surface of the maxilla (26-2); dorsal (= ascending) process of the maxilla remains the same width (29-1); squamosal without ridge on lateral side of the ventral process (51-0); dorsoventrally oriented crest located on the posterior side of the quadrate (83-1); large exit of cranial nerve VII (125-1); palpebral(s) extensively sutured to each other and to the lateral margin of the frontals (149-1).

Crocodylomorpha Walker, 1968 (fig. 53)

ORIGINAL DEFINITION: The most inclusive clade containing *Crocodylus niloticus* (Laurenti, 1768) but not *Poposaurus gracilis* Mehl, 1915, *Gracilisuchus stipanicicorum* Romer, 1972c, *Prestosuchus chiniquensis* Huene, 1942, or *Aetosaurus ferratus* Fraas, 1877.

REVISED DEFINITION: Stem: the most inclusive clade containing *Crocodylus niloticus* Laurenti, 1768, but not *Rauisuchus tiradentes* Huene, 1942, *Poposaurus gracilis* Mehl, 1915, *Gracilisuchus stipanicicorum* Romer, 1972c, *Prestosuchus chiniquensis* Huene, 1942, or *Aetosaurus ferratus* Fraas, 1877 (Sereno, 2005).

TEMPORAL RANGE: Late Triassic (?Carnian–early Norian, *Trialestes romeri* [Reig, 1963]) to Recent (*Crocodylus niloticus* Laurenti, 1768).

SUPPORT: Synapomorphies with CM 73372 removed. (1) Posterodorsal process (= maxillary process, = subnarial process) of the premaxilla less than or about the same as the anteroposterior length of the premaxilla (2-0). (2) Posterodorsal process (= maxillary process, = subnarial process) of the premaxilla overlaps anterodorsal surface of nasal (4-1). (3) Five premaxillary teeth (6-2). (4) Subnarial gap between the premaxilla-maxilla (11-1)*. (5) Nasal forms part of the dorsal border of the antorbital fossa (37-0). (6) Lacrimal as high as the orbit, and contacts the jugal at the level of the ventral margin of the orbit (39-1). (7) Postfrontal absent (44-1)*. (8) Anteroventral process of the squamosal absent (52-0). A distinct anteroventral process in crocodylomorphs may not be recognizable given the modifications of the squamosal. It is possible that the squamosal of crocodylomorphs has an anteroventral process like that of *Postosuchus kirkpatricki*; the dorsal lower temporal fenestra present in taxa such as *Postosuchus kirkpatricki* may be filled in with bone in basal crocodylomorphs. (9) Upper temporal fossa on the posterodorsal portion of the squamosal (55-1). (10) Quadratojugal-quadrate foramen absent (79-1)*. (11) Orbit circular or elliptical (142-0). (12) Articular with dorsomedial projection continuous with the glenoid fossa (156-2)*. (13) Clavicles absent (213-1)*. (14) Postglenoid process of the coracoid elongate and expanded posteriorly only (223-1)*. (15) Ectepicondylar flange of the humerus absent (234-1). (16) Proximal carpals (radiale, ulnare) elongate (242-1)*. (17) Distal carpal V absent (249-1)*. (18) Anterior (= preacetabular, = cranial) process of the ilium long and extends anterior to the acetabulum but shorter than the posterior process of the ilium (269-1). Present in CM 73372. (19) Dorsal margin of the ilium dorsal to the supraacetabular rim flat (275-1)*.

Other possible synapomorphies: **ACCTRAN**: Maxillary interdental plates separate (22-0); palatal processes of the maxilla meet at the midline and expand anteriorly and posteriorly (32-2); ventral termination of the ventral process of the postorbital tapered (65-0); quadrate contacts prootic (76-1); Distal end of the ventral ramus of the opisthotic has extended contact with prootic (112-1); lateral surface of the exoccipital with clear crest (= metotic strut) lying anterior to both external foramina for hypoglossal nerve (XII) (114-1); exoccipitals do not meet along the midline on the floor of the endocranial cavity (115-1); pneumatization of bony elements of the middle ear cavity well developed (116-1); crista vestibuli present (119-1); lagenar/cochlear prominence (120-1); markedly enlarged basipterygoid processes (124-1); pila antotica ossified largely by laterosphenoid and parabasisphenoid, with contact occurring between these two elements anterior to the trigeminal foramen in the adult braincase (128-1); hyposphene-hypantrum accessory intervertebral articulations absent (195-0); proximal articular surface of the humerus separated by a gap from the deltopectoral crest (233-1); distal portion of the ischium unexpanded (294-0); proximal articular surfaces of the ischium articular surfaces with the ilium and the pubis separated by a large concave surface (297-2); ischium about the same length or shorter than the dorsal margin of the iliac blade (298-0); four or fewer phalanges on pedal digit IV (396-1); metatarsal V dorsal prominence separated from the proximal surface by a concave gap absent (397-0). **DELTRAN:** Distal pubis mediolateral width significantly narrower than proximal width (289-1).

Unnamed Node (*Sphenosuchus* + Crocodylifomes)

TEMPORAL RANGE: Late Triassic (Norian, *Hemiprotosuchus leali* Bonaparte, 1969) to Recent (*Crocodylus niloticus* Laurenti, 1768).

SUPPORT: (1) Interparietal suture partially or completely absent (58-1)*. (2) Supratemporal fossa separated by a "sagittal crest" (59-1)*. (3) Occipital margin of the parietal straight in dorsal view (61-1)*. (4) Deep recess on the ventral surface of the basioccipital (107-1)*. (5) Compact metatarsus, with metatarsals II–IV tightly bunched (382-1).

Other possible synapomorphies: **ACCTRAN**: Anterior margin of the antorbital fenestra gently rounded (30-0); ulnare longer than the longest metacarpal (243-1). Unknown in *Sphenosuchus*; concave ventral margin of the acetabulum of the ilium (273-2); sharp ridge on the dorsolateral margin of the proximal portion of the femur (307-1); Unknown in *Sphenosuchus*; angle between the lateral condyle and the crista tibiofibularis in distal view obtuse (319-0). **DELTRAN:** Distal end of the ventral ramus of the opisthotic has extended contact with prootic (112-1); crista vestibuli present (119-1); lagenar/cochlear prominence (120-1); external foramen for abducen nerves within parabasisphenoid only (122-2); markedly enlarged basipterygoid processes (124-1); pila antotica ossified largely by laterosphenoid and parabasisphenoid, with contact occurring between these two elements anterior to the trigeminal foramen in the adult braincase (128-1); perilymphatic foramen border entirely ossified such that the ventral ramus of the opisthotic forms a perilymphatic loop incorporating a loop closure suture with itself (129-1); perilymphatic foramen positioned more laterally, so that duct is transmitted posterolaterally/laterally and the foramen is at least partly visible in lateral view (130-1).

Unnamed Node (*Dibothrosuchus* + Crocodylifomes)

TEMPORAL RANGE: Late Triassic (Norian, *Hemiprotosuchus leali* Bonaparte, 1969) to Recent (*Crocodylus niloticus* Laurenti, 1768).

SUPPORT: (1) Posterior portion of the maxilla ventral to the antorbital fenestra: tapers posteriorly (27-0). (2) Prefrontal contacts the palate (41-1)*. (3) Dorsal margin of the anterior portion of the dentary in the same horizontal plane compared to the posterior portion (154-0). (4) Scapula length less than 75% of humerus length (216-1).

Other possible synapomorphies: **ACCTRAN**: Quadratojugal/postorbital present (64-1). Unknown in *Dibothrosuchus*, *Terrestrisuchus*, *Litargosuchus*, or *Kayentasuchus*; fossa on the dorsal surface of the palatine extends far anteriorly, near the pila postchoanalis (90-0); scapula less than 75% of humerus length (216-1). **DELTRAN**: Hyposphene-hypantrum accessory intervertebral articulations absent (195-0); concave ventral margin of the acetabulum of the ilium (273-2).

Unnamed Node (*Litargosuchus* + Crocodylifomes)

TEMPORAL RANGE: Late Triassic (Norian, *Hemiprotosuchus leali* Bonaparte, 1969) to Recent (*Crocodylus niloticus* Laurenti, 1768).

SUPPORT: (1) Upper temporal fenestrae separated by a broad, flat area (59-0). (2) Posteroventral edge of the parietals less than half the width of the occiput (60-1)*. (3) Supratemporal fossa absent anterior to the supratemporal fenestra (144-0)*. (4) Postglenoid process of the coracoid elongate and expanded posteriorly and anteriorly (223-2)*. (5) Deep groove on the posteroventral edge of the coracoid absent (224-1). (6) Medial contact of the ischia restricted to the medial edge (291-0).

Other possible synapomorphies: **ACCTRAN**: Anterior margin of the antorbital fenestra gently rounded (30-0); anterior extent of the Meckelian groove present through the dentary symphasis (153-1); pubis length less than 70% of femoral length (278-0); presacral osteoderms wider than long (407-0); anterior bar located on the anterior edge of an osteoderm (408-1). **DELTRAN:** Four premaxillary teeth (6-1); Posterior portion of the nasal at the midline flat (34-0); dorsal surface of the frontal flat (42-0); metatarsal V without phalanges and tapers to a point (399-2).

Unnamed Node (*Kayentasuchus* + Crocodylifomes)

TEMPORAL RANGE: Late Triassic (Norian, *Hemiprotosuchus leali* Bonaparte, 1969) to Recent (*Crocodylus niloticus* Laurenti, 1768).

SUPPORT: (1) Posterior portion of the maxilla ventral to the antorbital fenestra has a similar dorsoventral depth as the anterior portion ventral to the antorbital fenestra (27-1). (2) Dorsolateral edge of the squamosal with longitudinal groove (53-1)*.

Other possible synapomorphies: **ACCTRAN:** Quadrate body with fenestrae (80-1); supraoccipital excluded from dorsal border of foramen magnum by mediodorsal midline contact between opposite exoccipitals (126-0); diapophyses and parapophyses of the middle dorsal vertebrae expand laterally where both diapophyses and parapophyses originate on a transverse process (199-1); scapula less than 75% of humerus length (216-1); glenoid directed posterolaterally (227-1); metatarsal V, "hooked" proximal end present (398-0); presacral osteoderms wider than long (407-2); ventral carapace in the dorsal area (209-1). **DELTRAN:** Anterior extent of the Meckelian groove present through the dentary symphasis (153-1).

Crocodyliformes Hay, 1930

DEFINITION: Node: The least inclusive clade containing *Protosuchus richardsoni* Brown, 1933, and *Crocodylus niloticus Laurenti* 1768 (Sereno et al., 2001).

TEMPORAL RANGE: Late Triassic (Norian, *Hemiprotosuchus leali* Bonaparte, 1969) to Recent (*Crocodylus niloticus* Laurenti, 1768).

SUPPORT: (1) Posterodorsal process (= maxillary process, = subnarial process) of the premaxilla vertical, strongly sutured to maxilla (4-2)*. (2) Osteoderms covering the appendages (405-1)*.

Other possible synapomorphies: **ACCTRAN:** Posterior margin of the choana of the palatine smooth, no raised rim on ventral surface (91-0); tooth crown mesiodistally expanded above root in cheek teeth (171-1); dorsolateral margin of the proximal portion of the femur smooth (307-0). **DELTRAN:** Parabasisphenoid relatively short dorsoventrally (102-0).

Ornithodira Gauthier, 1986
= Avemetatarsalia Benton, 1999

ORIGINAL DEFINITION: Pterosauria, *Scleromochlus*, Dinosauromorpha (including birds), and all descendants of their common ancestor (Sereno, 1991a).

REVISED DEFINITION: Node: The least inclusive clade containing *Pterodactylus antiquus* Sömmerring, 1812, and *Passer domesticus* Linnaeus, 1758 (new).

TEMPORAL RANGE: Middle Triassic (Anisian, *Asilisaurus kongwe*) to Recent (*Passer domesticus* Linnaeus, 1758).

SUPPORT: (1) Distal end of neural spines of the cervical vertebrae unexpanded (191-0). (2) Distal expansion neural spines of the dorsal vertebrae absent (197-0). (3) Second phalanx (= 2.2) of manual digit II longer than first phalanx (255-1)*. (4) Trenchant unguals on manual digits I–III (257-1)*. (5) Tibia longer than the femur (299-1)*. (6) Distal tarsal 4 transverse width subequal to distal tarsal 3 (347-1)*. (7) Size of articular facet for metatarsal V less than half of lateral surface of distal tarsal 4 (348-1)*. (8) Anterior hollow of the astragalus reduced to a foramen or absent (357-1)*. (9) Anteromedial corner of the astragalus acute (361-1)*. (10) Compact metatarsus, metatarsals II–IV tightly bunched (at least half of the length) (382-1)*. (11) Osteoderms absent (401-0). (12) Gastralia well separated (412-1)*.

Other possible synapomorphies: **ACCTRAN**: Postfrontal absent (44-1); ectopterygoid articulates with the dorsal surface of the pterygoid (84-1), unknown in basal pterosaurs and lagerpetids; ectopterygoid body arcs anterodorsally (87-1), unknown in basal pterosaurs and lagerpetids; ventral ramus of the opisthotic covered by the lateralmost edge of exoccipital in posterior view (111-1), unknown in basal pterosaurs and lagerpetids; posttemporal opening less than half the diameter of the foramen magnum or absent (141-1), unknown in basal pterosaurs and lagerpetids; articular foramen on the medial side absent (159-0); dorsal margin of the neural spine of the axis arcs dorsally, where the anterior portion's height is equivalent to the posterior height (179-1); third cervical centrum longer than the axis centrum (183-1); posteromedial tuber proximal portion of the femur present and small (301-0); bone wall thickness at or near midshaft of the femur, thickness/diameter >0.2, <0.3 (323-1); mediolaterally compressed proximal end of the fibula (341-1); distal end of the fibula rounded or flat (symmetrical) (345-1); pedal unguals weakly mediolaterally compressed, rounded or triangular in cross section (400-0). **DELTRAN:** Medial condyle of the distal portion of the femur smoothly rounded in distal view (320-1).

Pterosauromorpha Padian, 1997

ORIGINAL DEFINITION: Pterosauria and all ornithodiran archosaurs closer to them than to dinosaurs. (Padian, 1997).

REVISED DEFINITION: Stem: The most inclusive clade containing *Pterodactylus antiquus* Sömmerring, 1812, but not *Passer domesticus* Linnaeus, 1758 (sensu Sereno, 2005).

TEMPORAL RANGE: Late Triassic (Norian, *Eudimorphodon ranzii* Zambelli, 1973) to Cretaceous (Maastrichtian, *Quetzalcoatlus northropi* Lawson, 1975).

SUPPORT: (1) Anterodorsal process (= nasal process) of the premaxilla greater than the anteroposterior length of the premaxilla (1-1). (2) Anterodorsal margin of the maxilla borders the external naris (24-1). (3) Concave anterodorsal margin at the base of the dorsal process of the maxilla (25-1). (4) Skull length more than 50% of length of the presacral vertebral column (134-1)*. (5) Dentition markedly heterodont (167-1)*. (6) Cervical centra 3–5 longer than a middorsal vertebra (181-1). (7) Distal caudal vertebrae prezygapophyses elongated more than a quarter of the adjacent centrum (211-1)*. (8) Postglenoid process of the coracoid elongate and expanded posteriorly (223-1). (9) Pteroid bone present (244-1)*. (10) Manual digit IV length more than or equal to 50% of total forelimb length (262-1)*. (11) Anterior (= preacetabular, = cranial) process of the ilium long and extends anterior to the acetabulum but shorter than the posterior process of the ilium (269-1). (12) Metatarsal I length 85% or more (387-1)*. (13) Metatarsal V dorsal prominence separated from the proximal surface by a concave gap (397-1).

Other possible synapomorphies: **ACCTRAN**: Posterodorsal process (= maxillary process, = subnarial process) of the premaxilla restricted to the ventral border of the external naris (5-1); teeth present on palatal process of the pterygoid (175-0). This is known only in *Eudimorphodon* among pterosaurs; manual digit V absent (263-2); fourth trochanter absent (316-2); bone wall thickness of the femur at or near midshaft very thin, thickness/diameter <0.2 (323-2); proximal surface of distal tarsal 4 flat (353-0); metatarsal IV distal articulation surface deeper than broad (391-1); metatarsal IV subequal to or shorter than metatarsal II (395-1). **DELTRAN:** Length of the posterodorsal process of the premaxilla less than or about the same as the anteroposterior length of the premaxilla (2-0); proximal articular surface of the humerus separated by a gap from the deltopectoral crest (233-1); astragalus-calcaneum coossified (370-1); calcaneal tuber absent (373-1).

Dinosauromorpha Benton, 1985

ORIGINAL DEFINITION: *Lagerpeton chanarensis*, *Lagosuchus talampayensis*, *Pseudolagosuchus major*, Dinosauria (incl. Aves), and all descendants of their common ancestor. (Sereno, 1991a).

REVISED DEFINITION: Stem: The most inclusive clade containing *Passer domesticus* Linnaeus, 1758, but not *Pterodactylus antiquus* Sömmerring, 1812, *Ornithosuchus longidens* Huxley, 1877, *Crocodylus niloticus* Laurenti, 1768 (sensu Sereno, 2005).

TEMPORAL RANGE: Middle Triassic (Anisian, *Asilisaurus kongwe*) to Recent (*Passer domesticus* Linnaeus, 1758).

SUPPORT: (1) Posterolateral portion (= fossa trochanterica, = posterolateral depression, facies articularis antitrochanterica) of the femoral head ventrally descended (313-1)*. (2) Straight cnemial crest (328-1)*. (3) Longest metatarsal longer than 50% of tibial length (383-1)*. (4) Metatarsal V "hooked" proximal end absent, and articular face for distal tarsal 4 subparallel to shaft axis (398-1)*. (5) Metatarsal V without phalanges and tapers to a point (399-2) (reversed in basal Dinosauria).

Other possible synapomorphies: **ACCTRAN**: Cervical ribs slender and elongated (196-1); interclavicle absent (214-1); glenoid directed posteroventrally (227-1); metacarpal II equal to or longer than metacarpal III (256-1); three or two phalanges on manual digit IV (258-2). **DELTRAN**: Radius length shorter than 80% of humerus length (241-1).

Lagerpetidae Nesbitt et al., 2009b

DEFINITION: All taxa more closely related to *Lagerpeton chanarensis* Romer, 1971a, than to *Alligator mississippiensis* Daudin, 1801, *Eudimorphodon ranzii* Zambelli, 1973, *Marasuchus lilloensis* Sereno and Arcucci, 1994b, *Silesaurus opolensis* Dzik, 2003, *Triceratops horridus* Marsh, 1889, *Saltasaurus loricatus* Bonaparte and Powell, 1980, and *Passer domesticus* Linnaeus, 1758.

TEMPORAL RANGE: Middle Triassic (Ladinian, *Lagerpeton chanarensis* Romer, 1971a) to Late Triassic (Norian, *Dromomeron romeri* Irmis et al., 2007a).

SUPPORT: (1) Anterolateral tuber of the proximal portion of the femur absent, the anterolateral face is flat (302-1)*. (2) Femoral head hook shaped in medial and lateral views (306-1)*. (3) Ventral emargination present on anterolateral side of the femoral head (310-1)*. (4) Crista tibiofibularis larger than the medial condyle (326-1)*. (5) Dorsally expanded process on the posterolateral portion of the tibial facet of the astragalus expanded into a distinct, raised process (= posterior ascending process of Sereno and Arcucci, 1994a) (355-1)*. (6) Concave articular surface for the fibula on the calcaneum (378-2).

Other possible synapomorphies: **ACCTRAN:** Acetabular antitrochanter on the ilium present (274-1) scored only in *Lagerpeton*; posteromedial tuber of the proximal portion of the femur present and largest of the proximal tubera (301-1); metatarsal IV longer than metatarsal III (393-0) only scored in *Lagerpeton*. **DELTRAN:** Posterior groove of the astragalus absent (363-1); calcaneal tuber absent (373-1).

Dromomeron Irmis et al., 2007b (*Dromomeron romeri* + *Dromomeron gregorii*)

TEMPORAL RANGE: Middle Triassic (Ladinian, *Lagerpeton chanarensis* Romer, 1971a) to Late Triassic (Norian, *Dromomeron romeri* Irmis et al., 2007a).

SUPPORT: (1) Deep groove between the lateral condyle and crista tibiofibularis on the distal surface (322-1). (2) Distinct scar orientated mediolaterally anterior surface of the distal portion of the femur (325-1)*. (3) Squared off near 90° or acute >90° anteromedial corner of the distal end of the femur (327-1)*.

Dinosauriformes Novas, 1992

ORIGINAL DEFINITION: The most recent common ancestor of *Lagosuchus*, Dinosauria, and all taxa stemming from it (Novas, 1992).

REVISED DEFINITION: Node: The least inclusive clade containing *Passer domesticus* Linnaeus, 1758, and *Marasuchus lilloensis* Romer, 1971a (sensu Sereno, 2005).

TEMPORAL RANGE: Middle Triassic (Anisian, *Asilisaurus kongwe*) to Recent (*Passer domesticus* Linnaeus, 1758).

SUPPORT: (1) Pubis longer than ischium (282-1). (2) Proximal portion of the pubis articular surfaces with the ilium and the ischium separated by a groove or gap (286-1)*. (3) Ischio-pubis contact present and reduced to a thin proximal contact (287-1). (4) Ischium, proximal articular surfaces articular surfaces with the ilium and the pubis continuous but separated by a fossa (297-1). (5) Ischium length markedly longer than the dorsal margin of iliac blade (minus the anterior process) (298-1). (6) Anterior trochanter forms a steep margin with the shaft but is completely connected to the shaft (308-1). (7) Anterior trochanter shelf proximal to the fourth trochanter (insertion site for M. iliofemoralis externus) present (311-1)*. (8) Proximodistally oriented groove on the lateral side of the distal portion of the tibia (338-1)*. (9) Anterior ascending flange (anterior process) of the astragalus present and less than the height of the dorsoventral height of the posterior side of the astragalus (356-1)*.

Other possible synapomorphies: **ACCTRAN:** Posterior groove of the astragalus present (363-0); free astragalus-calcaneum articulation (370-0); calcaneal tuber present (373-0). **DELTRAN:** Basipterygoid processes directed anteriorly or ventrally at their distal tips (93-0); ventral ramus of the opisthotic covered by the lateralmost edge of exoccipital in posterior view (111-1); lateral surface of exoccipital with clear crest (= metotic strut) lying anterior to both external foramina for hypoglossal nerve (XII) (114-1); dorsal margin of the neural spine of the axis arcs dorsally, where the anterior portion height is equivalent to the posterior height (179-1); small posteromedial tuber of the proximal portion of the femur (301-0).

Unnamed Clade (Silesauridae + Dinosauria)

Temporal range: Middle Triassic (Anisian, *Asilisaurus kongwe*) to Recent (*Passer domesticus* Linnaeus, 1758).

Support: (1) Anterior tympanic recess on the lateral side of the braincase present (101-1)*. (2) Auricular recess extends onto internal surface of epiotic/supraoccipital (133-1). (3) Atlantal articulation facet in axial intercentrum, shape concave with upturned lateral borders (178-1)*. (4) Crest dorsal to the supraacetabular crest/rim confluent with anterior extent of the anterior (= preacetabular) process of the ilium (265-2)*. (5) Pubis more than 70% or more of femoral length (278-1)*. (6) Extensive medial contact between the ischia, but the dorsal margins are separated (291-1). (7) Sharp ridge (= dorsolateral trochanter of some) on the dorsolateral margin of the proximal portion of the femur (307-1). (8) Straight transverse groove on the proximal surface of the femur (314-1). (9) Posterolateral flange of the distal portion of the tibia nearly contacts or contacts fibula (334-1)*. (10) Anterior edge of the proximal portion of the fibula tapers to a point and arched anteromedially (342-1)*. (11) Midshaft diameters of metatarsals I and V less than II–IV (384-1)*. (12) Distal articulation surface of metatarsal IV deeper than broad (391-1)*. (13) Metatarsal IV length subequal to or shorter than metatarsal II (395-1).

Other possible synapomorphies: **ACCTRAN:** Distinct fossa present for the attachment of the M. caudifemoralis brevis present as a embankment on the lateral side of the posterior portion of the ilium (271-1); straight ventral margin of the acetabulum of the ilium (273-1); mediolateral width of distal pubis significantly narrower than proximal width (289-1); flat distal tarsal 4 proximal surface (353-0). **DELTRAN:** Ectopterygoid articulates with the dorsal portion of the pterygoid (84-1); ectopterygoid body arcs anterodorsally (87-1); cervical ribs slender and elongated (196-0); rounded or flat distal end of the fibula in lateral view (345-1).

Silesauridae Nesbitt et al., 2010

Definition: Stem: The most inclusive clade containing *Silesaurus opolensis* Dzik, 2003, but not *Passer domesticus* Linnaeus, 1758, *Triceratops horridus* Marsh (1889), and *Alligator mississippiensis* Daudin, 1801–1803.

Temporal range: Middle Triassic (Anisian, *Asilisaurus kongwe*) to Late Triassic (Norian, *Eucoelophysis baldwini* Sullivan and Lucas, 1999).

Support: (1) Exits of the hypoglossal nerve (XII) nearly aligned in a near anteroposteriorly plane (113-1)*. (2) Rugose ridge on the anterolateral edges of the supraoccipital (127-1)*. (3) Cervical centra 3–5 longer than middorsal (181-1)*. (4) Notch ventral to the proximal head of the femur (304-1)*.

Other possible synapomorphies: **ACCTRAN:** Ventral process of the squamosal narrower than one quarter of its length (56-1); teeth fused to the bone of attachment at the base (174-0), unknown in *Lewisuchus*; proximal articular surface of the humerus continuous with the deltopectoral crest (233-0); pedal unguals dorsolaterally compressed (400-1), unknown in *Lewisuchus.* **DELTRAN:** Straight transverse groove on the proximal surface of the femur (314-1).

Unnamed Clade (*Asilisaurus kongwe* + *Silesaurus*)

Temporal range: Middle Triassic (Anisian, *Asilisaurus kongwe*) to Late Triassic (Norian, *Eucoelophysis baldwini* Sullivan and Lucas, 1999).

Support: (1) Anterior extent of the dentary tapers to a sharp point (155-1)*. (2) Dentary teeth absent in the anterior portion (166-1)*. (3) Maxillary and dentary crowns apicobasally short and subtriangular (173-1). (4) Sacral ribs shared between two sacral vertebrae (208-1)*. (5) Straight medial articular facet of the proximal portion of the femur (309-1)*. (6) Distal condyles of the femur divided posteriorly between ¼ and ⅓ the length of the shaft (324-1)*.

Other possible synapomorphies: **ACCTRAN:** Foramina for entrance of cerebral branches of internal carotid artery into the braincase positioned on the ventral surface (95-0); femur longer or about the same length as the tibia/fibula (299-0). **DELTRAN:** Tooth crown mesiodistally expanded above root in cheek teeth (171-1); teeth fused to the bone of attachment at the base (174-0).

Dinosauria Owen, 1842

ORIGINAL DEFINITION: All descendants of the most recent common ancestor of birds and *Triceratops* (Padian and May, 1993).

REVISED DEFINITION: Node: The least inclusive clade containing *Triceratops horridus* (Marsh, 1889) and *Passer domesticus* Linnaeus, 1758 (sensu Sereno, 2005).

TEMPORAL RANGE: Late Triassic (?Carnian–early Norian *Pisanosaurus mertii* Casamiquela 1967) to Recent (*Passer domesticus* Linnaeus, 1758).

SUPPORT: (1) Exoccipitals do not meet along the midline on the floor of the endocranial cavity (115-1)*. Also in Crocodylomorpha and *Effigia* + *Shuvosaurus*. (2) Supratemporal fossa present anterior to the supratemporal fenestra (144-1). (3) Epipophyses present in postaxial anterior cervical vertebrae (186-0)*. (4) Apex of deltopectoral crest situated at a point corresponding to more than 30% down the length of the humerus (230-1)*. (5) Radius shorter than 80% of humerus length (241-1). (6) Proximal articular surfaces of the ischium with the ilium and the pubis separated by a large concave surface (297-2)*. (7) Fourth trochanter a sharp flange (316-1)*. (8) Fourth trochanter asymmetrical, with distal margin forming a steeper angle to the shaft (317-1). (9) Cnemial crest arcs anterolaterally (328-2)*. (10) Distinct proximodistally oriented ridge present on the posterior face of the distal end of the tibia (336-1)*. (11) Proximal articular facet for fibula of the astragalus occupies less than 0.3 of the transverse width of the element (362-1). (12) Concave articular surface for the fibula of the calcaneum (378-2).

Other possible synapomorphies: **ACCTRAN:** Three premaxillary teeth (6-0); premaxillary narial fossa expanded in the anteroventral corner of the naris (9-1); posterior process of the jugal is split by the anterior process of the quadratojugal (71-3); forelimb–hind limb length ratio less than 0.55 (212-1); concave ventral margin of the acetabulum of the ilium (273-2); concave emargination ventral to the proximal head of the femur (304-2); posterior groove of the astragalus absent (363-1); calcaneal tuber absent (373-1). **DELTRAN:** Postfrontal absent (44-1); posttemporal opening absent or less than half the diameter of the foramen magnum (141-1); interclavicle absent (214-1); proximal articular surface of the humerus separated by a gap from the deltopectoral crest (233-1); three or two phalanges on manual digit IV (258-2); calcaneal tuber absent (373-1).

Ornithischia Seeley, 1887

ORIGINAL DEFINITION: Those dinosaurs closer to *Triceratops* than to birds (Padian and May, 1993).

REVISED DEFINITION: Stem: The most inclusive clade containing *Triceratops horridus* Marsh, 1889, but not *Passer domesticus* Linnaeus, 1758, or *Saltasaurus loricatus* Bonaparte and Powell, 1980 (sensu Sereno, 2005).

TEMPORAL RANGE: Late Triassic (?Carnian–early Norian *Pisanosaurus mertii* Casamiquela, 1967) to Late Cretaceous (Maastrichtian, *Triceratops horridus* Marsh, 1889).

SUPPORT: (1) Buccal emargination separated from the ventral margin of the antorbital fossa of the maxilla (23-1)*. (2) Predentary present (151-1)*. (3) Dorsally expanded coronoid process of the mandible (161-1)*. (4) Mandibular fenestra reduced, anteroposterior length less than maximum depth of dentary ramus (162-2)*. (5) Extensive planar wear facets across multiple maxillary/dentary teeth (168-2)*. (6) Medial or lateral overlap of adjacent crowns in maxillary and dentary teeth (170-1). (7) Maxillary and dentary crowns apicobasally short and subtriangular (173-1). (8) Anterior (= preacetabular, = cranial) process of the ilium long and extends anterior to the acetabulum but shorter than the posterior process of the ilium (269-1). (9) Pubis rotated posteroventrally to lie alongside the ischium (opisthopubic) (279-1). (10) Prepubic process present (280-1). (11) Anterior trochanter (= M. iliofemoralis cranialis insertion) forms a steep margin with the shaft and separated from the shaft by a marked cleft (308-2). Unknown in *Pisanosaurus*. (12) Anterior trochanter shelf proximal to the fourth trochanter absent (311-0). Unknown in *Pisanosaurus*. (13) Posterolateral flange of the distal portion of the tibia present and extends well posterior to the fibula (334-2). (14) Transversely compressed calcaneum (379-1).

Other possible synapomorphies: **ACCTRAN:** Facial portion of the maxilla equal in length or longer than portion posterior to anterior edge of fenestra (14-1); palpebral(s) present (147-1); dorsal margin of the neural spine of the axis expanded posterodorsally (179-0); third cervical vertebra subequal in length to the axis centrum (183-0); primordial trunk vertebrae incorporated into the sacrum (205-1); insertion of a sacral vertebra between the first primordial sacral vertebra (207-1); primordial caudal vertebrae incorporated into the sacrum (206-1); proximal portion of the pubis, articular surfaces with the ilium and the ischium continuous (286-0). Unknown in *Pisanosaurus*; posterolateral flange of the distal portion of the tibia extends well posterior to the fibula (334-2); gastralia absent or few (412-2).

Saurischia Seeley, 1887
= Eusaurischia Padian et al., 1999

ORIGINAL DEFINITION: Birds and all dinosaurs that are closer to birds than they are to Ornithischia (Gauthier, 1986).

REVISED DEFINITION: Node: The most inclusive clade containing *Passer domesticus* Linnaeus, 1758, and *Saltasaurus loricatus* Bonaparte and Powell, 1980, but not *Triceratops horridus* (Marsh, 1889) (sensu Sereno, 2005).

TEMPORAL RANGE: Late Triassic (?Carnian–early Norian, *Herrerasaurus ischigualastensis* Reig, 1963) to Recent (*Passer domesticus* Linnaeus, 1758).

SUPPORT: (1) Subnarial foramen between the premaxilla-maxilla where the border of the foramen is present on both the maxilla and the premaxilla (12-1)*. (2) Lacrimal folds over (= overhangs) the posterior/posterodorsal part of the antorbital fenestra (38-1)*. (3) Ventral ramus of the opisthotic covered by the lateralmost edge of exoccipital in posterior view (111-1). (4) Foramen in the ventral part of the splenial (165-1)*. (5) Epipophyses present in posterior cervical vertebrae (cervicals 6–9) (187-1). (6) Hyposphene-hypantrum accessory intervertebral articulations in the posterior cervical and/or dorsal vertebrae (195-1)*. (7) First primordial sacral rib C-shaped in lateral view (209-1)*. (8) Manual length accounts for more than 0.3 but less than 0.4 of the total length of humerus plus radius (247-1). (9) Distal carpal V absent (249-1)*. (10) Manual digit I, first phalanx (1.1) is the longest nonungual phalanx of the manus (253-1)*. (11) Lateral distal condyle strongly distally expanded relative to medial condyle of metacarpal I (254-1). (12) Metacarpal IV shaft width significantly narrower than that of metacarpals I–III (261-1). (13) Distal end of pubis expanded relative to the shaft (= pubis boot) (283-1). (14) Cross section of the distal portion of the ischium subtriangular (293-2). (15) Deep groove between the lateral condyle and crista tibiofibularis on the distal surface of the femur (322-1). (16) Posterior prong of distal tarsal 4 pointed (350-1)*. (17) Distal tarsal 4 with a distinct medial process present in the anteroposterior middle of the element (351-1)*. (18) Astragalus, proximal surface possesses a marked rimmed and elliptical fossa posterior to the anterior ascending process (359-1)*.

Other possible synapomorphies: **ACCTRAN:** Nasal possesses a posterolateral process that envelops part of the anterior ramus of the lacrimal (36-1). Absent in *Herrerasaurus* according to Langer and Benton (2006); nasal forms part of the dorsal border of the antorbital fossa (37-1). Absent in *Herrerasaurus* according to Langer and Benton (2006); lacrimal as high as the orbit, and contacts the jugal at the level of the ventral margin of the orbit (39-1). Absent in *Herrerasaurus*; femur longer or about the same length as the tibia/fibula (299-0); rounded ridge (= dorsolateral trochanter of some) on the dorsolateral margin of the proximal portion of the femur (307-1); proximal portion of metatarsal IV possesses an elongated lateral expansion that overlaps the anterior surface of metatarsal V (392-1); metatarsal V present and has a "poorly" developed first phalanx (399-1).

Theropoda Marsh, 1881

ORIGINAL DEFINITION: Birds and all saurischians that are closer to birds than they are to sauropodomorphs. (Gauthier, 1986).

REVISED DEFINITION: Stem: The most inclusive clade containing *Passer domesticus* Linnaeus, 1758, but not *Saltasaurus loricatus* Bonaparte and Powell, 1980 (sensu Sereno, 2005).

TEMPORAL RANGE: Late Triassic (?Carnian–early Norian, *Herrerasaurus ischigualastensis* Reig, 1963) to Recent (*Passer domesticus* Linnaeus, 1758).

SUPPORT: (1) Posterior edge of posterior maxillary teeth concave or straight (15-0). (2) Parabasisphenoid recess present (100-1). (3) Prezygapophysis of the distal caudal vertebrae elongated more than a quarter of the adjacent centrum (211-1)*. (4) Humerus length shorter than 0.6 of the length of the femur (231-1)*. (5) Metacarpals proximal ends abut one another without overlapping (246-1). Also present in *Heterodontosaurus*. (6) Extensor pits on the proximodorsal portion of metacarpals I–III deep and asymmetrical (250-1). Also present in *Heterodontosaurus.* (7) Metacarpal IV shaft width significantly narrower than that of metacarpals I–III (261-1)*. (8) Mediolaterally thin pubic boot (284-1)*. (9) Lateral (fibular) condyle of the proximal portion of the tibia level with the medial condyle at its posterior border (331-1)*.

Other possible synapomorphies: **ACCTRAN:** Sharp longitudinal ridge on the jugal body (75-1); medial wall of the vestibule almost completely ossified (117-1); clavicles fused into a furcula (213-1). Unknown in *Herrerasaurus*, *Staurikosaurus, Eoraptor*, and *Tawa*; manual length accounts for more than 0.4 of the total length of humerus plus radius (247-2). Absent in *Eoraptor*; bone wall thickness at or near midshaft of the femur, thickness/diameter >0.2, <0.3 (323-1). Unknown in *Herrerasaurus* and *Eoraptor*.

Unnamed Clade (*Eoraptor* + Tetanurae)

TEMPORAL RANGE: Late Triassic (?Carnian–early Norian, *Eoraptor lunesis* Sereno et al., 1993) to Recent (*Passer domesticus* Linnaeus, 1758).

SUPPORT: (1) Distinct embankment on the lateral side of the posterior portion of the ilium for the attachment of M. caudifemoralis brevis (271-1)*. (2) Ridge connecting the posterior portion of the supraacetabular rim to the posterior portion of the ilium (272-1). (3) Ischiadic peduncle of the ilium well expanded posteriorly to the anterior margin of the postacetabular embayment (277-1). (4) Anterior trochanter shelf proximal to the fourth trochanter (insertion site for M. iliofemoralis externus) absent (311-0). This is possibly a juvenile character (Tykoski, 2005b).

Other possible synapomorphies: **ACCTRAN:** Primordial trunk vertebrae incorporated into the sacrum (205-1). **DELTRAN:** Subnarial gap between the premaxilla-maxilla (11-1); nasal possesses a posterolateral process that envelops part of the anterior ramus of the lacrimal (36-1); lacrimal as high as the orbit, and contacts the jugal at the level of the ventral margin of the orbit (39-1); anterior process of the jugal excluded from the antorbital fenestra by lacrimal or maxilla (69-1).

Unnamed Clade (*Tawa hallae* + Tetanurae)

TEMPORAL RANGE: Late Triassic (*Camposaurus arizonensis* Hunt et al., 1998) to Recent (*Passer domesticus* Linnaeus, 1758).

SUPPORT: (1) Anterodorsal process (= nasal process) of the premaxilla length greater than the anteroposterior length of the premaxilla (1-1). (2) Anterior extent of the slot for the quadratojugal of the jugal at or anterior to the posterior edge of the dorsal process of the jugal (68-1*). (3) Cervical centra 3–5 length longer than middorsal (181-1)*. (4) Diapophysis and parapophysis of the anterior to middle cervical vertebrae nearly touching (184-1)*. (5) Neural spine of the anterior cervical vertebrae with a deep excavation with a thin bone lamina covering the anterior extent on the posterolateral surface (185-1)*. (6) Deep fossae in the anterior portion of the cervical centrum (188-1)*. (7) Fourth trochanter symmetrical, with distal and proximal margins forming similar low-angle slopes to the shaft (317-0). (8) Lateral margin of the lateral condyle of the proximal portion of the femur squared off (332-1).

Other possible synapomorphies: **ACCTRAN**: Distal portion of the ischium expanded relative to the ischial shaft (= ischial boot) (294-1). Unknown in *Tawa*; obturator process of the ischium offset from the pubic peduncle by a notch (295-1). **DELTRAN**: Maxillary interdental plates fused (22-1); deep recesses on the anterior face of the neural arch of the cervical vertebrae (182-1); anteromedial tuber of the proximal portion of the femur offset medially (or posteriorly) relative to the posteromedial tuber (300-2); curved transverse groove on the proximal surface of the femur (314-2); fourth trochanter symmetrical, with distal and proximal margins forming similar low-angle slopes to the shaft (317-0); bone-wall thickness at or near midshaft of the femur, thickness/diameter >0.2, <0.3 (323-1); transversely compressed calcaneum (379-1).

Neotheropoda Bakker, 1986

ORIGINAL DEFINITION: *Coelophysis*, Neornithes, their most recent common ancestor and all descendants (Sereno, 1998).

REVISED DEFINITION: Node: The least inclusive clade containing *Coelophysis bauri* Cope, 1889; sensu Colbert et al., 1992, and *Passer domesticus* Linnaeus, 1758 (sensu Sereno, 2005).

TEMPORAL RANGE: Late Triassic (?Carnian–early Norian, *Eoraptor lunesis* Sereno et al., 1992) to Recent (*Passer domesticus* Linnaeus, 1758).

SUPPORT: (1) Thin posterodorsal process (= maxillary process, = subnarial process) of the premaxilla (3-1). Also in Sauropodomorpha. (2) Posterodorsal process (= maxillary process, = subnarial process) of the premaxilla restricted to the ventral border of the external naris (5-1). Also in Sauropodomorpha. (3) Ventral ramus of the opisthotic covered by the lateralmost edge of exoccipital in posterior view (111-1)*. (4) Primordial caudal vertebrae incorporated into the sacrum (206-1). (5) Insertion of a sacral vertebra between the first primordial sacral vertebra (207-1). (6) Medialmost distal carpal significantly larger than other distal carpals (248-1)*. (7) Anterior (= preacetabular, = cranial) process of the ilium subequal to or longer than the posterior process of the ilium (269-2). (8) Deep fossa on the ventral surface of postacetabular part of the ilium for the attachment of the M. caudifemoralis brevis (271-2)*. (9) Ilium expanded dorsally, height markedly taller than the dorsal portion of the supraacetabular rim to the pubis-ischium contact (276-1)*. (10) Proximal surface of the tibia concave, between the posterior condyles and the cnemial crest (329-1)*. (11) Dorsoventrally oriented crest (= fibular crest) on the lateral side of the proximal portion of the tibia (333-1)*. (12) Posterolateral margin of the distal end of the tibia concave (335-1). Also in Sauropodomorpha. (13) Distinct proximodistally oriented ridge present on the anterior face of the distal end of the tibia (336-1). Also in Dinosauria. (14) Posterior prong distal tarsal 4 blunt (350-0). (15) Proximal surface of the astragalus lacks a marked rimmed and elliptical fossa posterior to the anterior ascending process (359-0). (16) Metatarsal I does not reach the proximal surface of metatarsal II and attaches onto the medial side of metatarsal II (385-1)*.

Other possible synapomorphies: **ACCTRAN:** Supraoccipital excluded from dorsal border of foramen magnum by mediodorsal midline contact between opposite exoccipitals (125-0); perilymphatic foramen border entirely ossified such that the ventral ramus of the opisthotic forms a perilymphatic loop incorporating a loop closure suture with itself (129-1). Unknown in *Coelophysis bauri*; rimmed depression on the posterior part of the cervical centra (189-1); metatarsal III backs metatarsals II and IV posteroventrally, resulting in a T-shaped proximal profile (389-1). **DELTRAN:** Primordial trunk vertebrae incorporated into the sacrum (205-1); clavicles fused into a furcula (213-1); metacarpal II equal to or longer than metacarpal III (256-1); distal portion of the ischium expanded relative to the ischial shaft (= ischial boot) (294-1); obturator process of the ischium offset from the pubic peduncle by a notch (295-1).

Unnamed Node (*Dilophosaurus* + Tetanurae)

TEMPORAL RANGE: Early Jurassic (Sinemmurian, *Dilophosaurus wetherelli* Welles, 1954) to Recent (*Passer domesticus* Linnaeus, 1758).

SUPPORT: (1) Promaxillary foramen present (28-1)*. (2) Paroccipital processes directed ventrolaterally (110-1)*. (3) Foramen for trigeminal nerve and middle cerebral vein fully divided (131-1)*. (4) Dorsal margin of the neural spine for the axis expanded posterodorsally (179-1). (5) Pneumatic features (= pleurocoels) in the anterior portion of the cervical centrum present as foramina (188-2)*. (6) Femur longer or about the same length as the tibia/fibula (299-0). (7) anterior trochanter (= M. iliofemoralis cranialis insertion) present and forms a steep margin with the shaft and separated from the shaft by a marked cleft (308-2)*. (8) Posterolateral flange of the distal portion of the tibia extends well posterior to the fibula (334-2)*.

Other possible synapomorphies: **ACCTRAN:** Ectopterygoid ventral recess present (86-1); tall and narrow (“keyhole-shaped”) orbit (142-1); notch present at the ventral margin of the ischium (296-1). **DELTRAN**: Foramen in the ventral part of the splenial (165-1).

Sauropodomorpha Huene, 1932

ORIGINAL DEFINITION: Sauropoda, Prosauropoda, and all saurischians closer to them than to birds (Upchurch et al., 1997).

REVISED DEFINITION: Stem: The most inclusive clade containing *Saltasaurus loricatus* Bonaparte and Powell, 1980, but not *Passer domesticus* Linnaeus, 1758, or *Triceratops horridus* Marsh, 1889 (sensu Sereno, 2005).

TEMPORAL RANGE: Late Triassic (?late Carnian–early Norian, *Saturnalia tupiniquim* Langer et al., 1999) to Late Cretaceous (Maastrichtian, *Alamosaurus sanjuanensis* Gilmore, 1922).

SUPPORT: (1) Ventral process of the squamosal narrower than one quarter of its length (56-1). (2) Skull length shorter than two-thirds of the femoral length (135-1)*. (3) Tooth serrations enlarged and coarser (lower density) = denticles (168-2)*. (4) Width of distal end of the humerus greater than 30% of the length (235-1)*. (5) Distal portion of the ischium expanded relative to the ischial shaft (= ischial boot) (294-1). (6) Posterolateral margin of the distal end of the tibia concave (335-1). Also in Neotheropoda.

Other possible synapomorphies: **ACCTRAN:** Thin posterodorsal process (= maxillary process, = subnarial process) of the premaxilla (3-1). Unknown in *Saturnalia*; posterodorsal process (= maxillary process, = subnarial process) of the premaxilla restricted to the ventral border of the external naris (5-1). Unknown in *Saturnalia*; concave anterodorsal margin at the base of the dorsal process of the maxilla (25-1). Unknown in *Saturnalia*; long axis of the body of the jugal anterodorsally inclined (74-1); metacarpal I width at the middle of the shaft accounts for more than 0.35 of the total length of the bone (251-1). Unknown in *Saturnalia*; digit I with metacarpal subequal or shorter than the ungual (252-1). Unknown in *Saturnalia*; distal pubis mediolateral width of the pubis nearly as broad as proximal width (289-0). **DELTRAN:** Lacrimal as high as the orbit, and contacts the jugal at the level of the ventral margin of the orbit (39-1); tooth crown mesiodistally expanded above root in cheek teeth (171-1); femur longer or about the same length as the tibia/fibula (299-0); rounded ridge (= dorsolateral trochanter of some) on the dorsolateral margin of the proximal portion of the femur (307-1); straight transverse groove on the proximal surface of the femur (314-1); proximal portion of metatarsal IV possesses an elongated lateral expansion that overlaps the anterior surface of metatarsal V (392-1).

DISCUSSION

The general structure of the relationships in this comprehensive analysis agrees with those of previously published analyses. The addition, however, of a wide breadth of taxa and an extensive character list has important effects on the structure of Pseudosuchia, Archosauria, and Dinosauromorpha. Results in common with previous analysis, for the most part, were strengthened and provide a stable framework for future analyses. The discussion is divided into two major sections (previously and novel results) examining the most important results of this hypothesis.

Results previously found: (1) Archosauria comprises two major clades, the crocodylian-line and avian-line archosaurs; (2) *Euparkeria* is found outside Archosauria; (3) the traditional concept of Rauisuchia is paraphyletic; (4) poposauroids are monophyletic and separated from other "rauisuchians"; (5) Sphenosuchia is paraphyletic; (6) pterosaurs lie at the base of Avemetatarsalia; (7) Lagerpetidae is recovered; (8) dinosaurs are monophyletic; (9) *Herrerasaurus* and *Eoraptor* are found as theropods.

Novel findings include: (1) proterochampsians are monophyletic; (2) phytosaurs are the most proximal outgroup to Archosauria; (3) *Gracilisuchus* is one of the most basal suchians; (4) Rauisuchidae is recovered as monophyletic; (5) *Hesperosuchus* and *Hesperosuchus*-like taxa are the basalmost crocodylomorphs; (6) Crocodylomorpha is the sister taxon to Rauisuchidae; (7) "silesaurs" are a monophyletic sister taxon to Dinosauria.

MONOPHYLY OF PROTEROCHAMPSIA

The placement of proterochampsians among archosauriforms has had an unsatisfying history. Once considered close crocodylian relatives (Price, 1946), phytosaur relatives (Walker, 1968), or similar to proterosuchids (Charig and Sues, 1976), proterochampsians are found to be non-archosaurian archosauriforms in cladistic analyses. Further, proterochampsians were considered the sister taxon either to Archosauria (Sereno, 1991a; Parrish, 1993; Juul, 1994; Benton, 1999, 2004) or to *Euparkeria* + Archosauria (Benton and Clark, 1988). However, proterochampsians have been treated as a supra-generic taxon in all previous numerical analyses examining basal archosauriform relationships. Furthermore, only precladistic diagnoses (e.g., Sues, 1976) have hypothesized the monophyly of proterochampsians including *Chanaresuchus*, *Cerritosaurus*, *Gualosuchus*, and *Proterochampsa*. *Doswellia* is the only taxon found closer to proterochampsians than to any other archosauriform (Benton and Clark, 1988; Dilkes and Sues, 2009).

Here, I preliminarily test the monophyly of Proterochampsia and find that the two hypothesized members of the Proterochampsia, *Tropidosuchus* and *Chanaresuchus*, do form a monophyletic group. Proterochampsia is diagnosed by the following unique character states among archosauriforms: lateral surface of the quadratojugal with a ridge marking the posteroventral corner of the lower temporal fossa, midshaft diameter of metatarsal II more than the average midshaft diameter of metatarsals I–IV, and metatarsal IV reduced where the midshaft diameter is less than that of metatarsal III. Other characters that both taxa share, but that are present in other archosaurs include: presence of an upper temporal fossa on the posterodorsal portion of the squamosal, sharp longitudinal ridge on the body of the jugal, a proximodistally oriented groove present on the lateral side of the distal portion of the tibia, and metatarsal V tapers to a point and lacks phalanges.

The analysis presented here finds proterochampsians as the sister taxon to *Euparkeria* + Archosauria, which is a placement similar to previous hypotheses (Benton and Clark, 1988). The proterochampsians are in need of a critical taxonomic and systematic review. Although this is beyond the scope of this paper, the findings here serve as a starting point for future investigations.

THE PHYLOGENETIC POSITION OF PHYTOSAURIA

Phytosaurs are found as the sister taxon of Archosauria for the first time in this comprehensive analysis. In all other analyses (except Bennett, 1996) phytosaurs were found more closely related to Crocodylomorpha than to Aves in a resolved position as either the most basal clade of pseudosuchians (Gauthier, 1984; Benton and Clark, 1988; Sereno, 1991a; Irmis et al., 2007a) or one node closer to Crocodylomorpha than Ornithosuchidae (Parrish, 1993). The position of phytosaurs was unresolved at the base of Pseudosuchia in a number of other analyses (Juul, 1994; Benton, 1999, 2004). However, few unambiguous characters support the basal position of phytosaurs within Pseudosuchia. Below, I summarize and discuss the characters previously cited to support the position of phytosaurs within Pseudosuchia.

TARSAL CHARACTERS: *Crocodile normal crurotarsal ankle joint* (Gauthier, 1984; Benton and Clark, 1988; Parrish, 1993; Juul, 1994). This is one of the most commonly cited characters supporting phytosaurs as closer to crocodylians than to avians. Sereno and Arcucci (1990) and Sereno (1991a) recognized that a "crocodile normal crurotarsal ankle joint" represents a character complex that should be dismantled into several characters (see below). The presence of a "crurotarsal ankle joint" was always considered a character shared among taxa more closely related crocodylians than to avians given the clear absence in *Euparkeria*, proterochampsians, and other non-archosaurian reptiles. Nevertheless, this character cannot be scored in the basal avian-line archosaurs pterosaurs, lagerpetids, *Silesaurus*, and Dinosauria. The condition in *Marasuchus* (Sereno and Arcucci, 1994b) and *Asilisaurus kongwe* is difficult to pinpoint, but it appears that the joint between the astragalus and calcaneum is similar to that of the "crurotarsal ankle joint" of pseudosuchians. As a result, this character cannot be shown as unambiguous support of Phytosauria within Pseudosuchia.

Hemicylindrical condyle on the proximal surface of the calcaneum (Sereno, 1991a; Parrish, 1993; Juul, 1994). Suchians share a hemicylindrical condyle on the proximal surface of the calcaneum, and this character is also present in phytosaurs (e.g., *Smilosuchus*, USNM 18313). The hemicylindrical condyle on the proximal surface of the calcaneum is a mediolaterally constricted articular surface. However, ornithosuchids, which here are found closer to crocodylians than phytosaurs are to crocodylians, lack a hemicylinderical condyle on the proximal surface of the calcaneum. Furthermore, the basal condition among avian-line archosaurs is unknown. The fibular articular surface of the calcaneum of *Marasuchus* resembles that of a hemicylindrical condyle as described by Novas (1996). Furthermore, the basal silesaurid *Asilisaurus* has a clear hemicylinderical condyle on the calcaneum for the fibula (Nesbitt et al., 2010). However, the distribution of this character state is not clear among avian-line archosaurs because the presence or absence of a hemicylindrical condyle is unknown in pterosaurs and lagerpetids do not have a hemicylindrical condyle.

Astragalus with flexed tibial articular surface (Sereno, 1991a; Parrish, 1993). The distribution and identification of a flexed facet for the tibia on the astragalus was observed by both Sereno (1991a) and Parrish (1993). Even though the two authors examined the same feature, they disagreed about the presence of the feature in phytosaurs; Sereno (1991a) stated that phytosaurs (based on USNM 18313) possess a flexed facet, Parrish (1993) that phytosaurs lack a flexed facet (based on USNM 18313). Here, I agree with Parrish's (1993) interpretation and score all phytosaurs used in this analysis as having a simple concave surface (see character 366). However, I have recently observed a weakly flexed tibial facet in an isolated phytosaur astragalus (TMM 31100-466). The astragalus is likely from either *Paleorhinus* or *Angistorhinus*, two primitive members of Phytosauria (Ballew, 1989; Stocker 2010). Even if a flexed tibial facet is the ancestral condition of Phytosauria, my analysis shows that a flexed facet is also present in basal dinosauromorphs (e.g., *Dromomeron romeri*). Therefore, the character cannot unambiguously support phytosaurs as pseudosuchians.

Calcaneal tuber broader than tall (Sereno, 1991a; Juul, 1994). This character is difficult to interpret as originally written by Sereno (1991a). The dimensions of the calcaneal tuber change throughout the length of the element in nearly all taxa with a tuber. Here, I measured the dimensions at the midshaft of the tuber. Additionally, the midshaft of the tuber of phytosaurs and pseudosuchians is round, so that the calcaneal tuber is not clearly taller or broader. Sereno (1991a) scored phytosaurs as having a calcaneal tuber that is broader than tall, and this supported a basal position for this group within Pseudosuchia. The midshaft of the calcaneal tuber of phytosaurs does not differ from that of *Euparkeria*. Furthermore, a calcaneal tuber is not present in pterosaurs, lagerpetids, or dinosaurs. A small spur of bone present on the posterior side of the calcaneum of *Marasuchus* was interpreted as homologous with the calcaneal tuber of suchians by Sereno (1991a), and I follow this interpretation here. The dimensions of the tuber are difficult to interpret, but the tuber of *Marasuchus* appears round in cross section. Once again, this character cannot be shown to unambiguously support phytosaurs within Pseudosuchia.

Calcaneal tuber flaring distally (Gauthier, 1984; Benton and Clark, 1988; Sereno, 1991a; Parrish, 1993; Juul, 1994). The calcanea of phytosaurs, ornithosuchids, and suchians have a calcaneal tuber which flares distally. In these taxa, the distal expansion is much greater than the midshaft dimensions of the calcaneum. The distal end of the calcaneal tuber of *Euparkeria* (UMCZ T692) slightly expands, but clearly not to the same degree as in phytosaurs, ornithosuchids, and suchians. The two avian-line archosaurs interpreted to have a calcaneal tuber, *Marasuchus* and *Pseudolagosuchus*, lack any distal expansion. Therefore, a distally flaring calcaneal tuber represents a potential synapomorphy placing phytosaurs within Pseudosuchia. However, the topology obtained with my character set suggests that phytosaurs evolved a distally flaring calcaneal tuber independently (DELTRAN) or that avian-line archosaurs lost the distally flaring tuber (ACCTRAN).

Ventral astragalocalcaneal articulation larger than dorsal articulation (Sereno, 1991a). This character is not used in my character set, and it was not used subsequently after Sereno (1991a). It is difficult to score and cannot be scored in avian-line archosaurs. The character cannot be shown to represent a synapomorphy placing phytosaurs within Pseudosuchia.

OTHER CHARACTERS: *Short and stout cervical ribs* (Gauthier, 1984; Benton and Clark, 1988; Juul, 1994). The optimization of this character state (character 196-1 here) has a complex distribution. Elongated cervical ribs are present in all other non-archosaurian archosauriforms, poposauroids, and most members of Silesauridae + Dinosauria, whereas short and stout cervical ribs are present in phytosaurs, aetosaurs, *Gracilisuchus*, and non-poposauroid paracrocodylomorphs. Among ornithodirans, the cervical ribs of basal pterosaurs are short and stout, and the character state in lagerpetids and *Marasuchus* is not known. Therefore, the presence of short and stout cervical ribs is not an unambiguous synapomorphy supporting Phytosauria within Pseudosuchia.

Discrete postparietal confined to early juvenile or prehatchling stages (Gauthier, 1984). Postparietals are not present in phytosaurs, avian- and crocodylian-line archosaurs. Therefore, the absence of a postparietal in phytosaurs does not place phytosaurs unambiguously within Pseudosuchia.

Deltopectoral crest extends less than one quarter of the length of the humerus shaft (Benton and Clark, 1988). The deltopectoral crest extends less than one-quarter of the length of the humerus in proterochampsians (e.g., *Chanaresuchus*, PVL 4575) and *Euparkeria* (SAM 5867), as well as in phytosaurs, aetosaurs, basal paracrocodylomorphs, crocodylomorphs, pterosaurs, *Marasuchus*, and silesaurids. The distribution of this character does not support an exclusive relationship of Phytosauria within Pseudosuchia.

One paramedian pair of dorsal osteoderms per cervicodorsal vertebra (Sereno, 1991a; Juul, 1994). *Euparkeria*, phytosaurs, ornithosuchids, and suchians, with the exception of aetosaurs and some crocodyliforms, all bear one paramedian pair of dorsal osteoderms per presacral vertebra. Therefore, the presence of this feature in phytosaurs does not exclusively place phytosaurs as pseudosuchians. Furthermore, if proterochampsians are found closer to Archosauria than *Euparkeria* (e.g., Sereno, 1991a), then the distribution of the presence of one paramedian pair of dorsal osteoderms per cervicodorsal vertebra is still ambiguous. Sereno (1991a) stated that this character is ambiguous at best in his discussion.

Scapulocoracoid notch developed at anterior junction of the scapula and coracoid (Parrish, 1993). Parrish (1993) cited the presence of a scapulocoracoid notch as a character placing phytosaurs within Pseudosuchia. Here, following Sereno (1991a), I did not consider the large hook-shaped coracoid of phytosaurs to be homologous with that of the notch formed between the scapula and the coracoid in taxa such as *Revueltosaurus* and *Prestosuchus*. In phytosaurs, there is no notch between the scapula and the coracoid; the “notch” or hook is within the coracoid only.

Heterodonty, with caniniform anterior teeth and mediolaterally compressed and recurved posterior teeth (Parrish, 1993). This character is difficult to score, and the scoring strategy implemented by Parrish (1993) could not be reproduced. Phytosaurs clearly have a heterodont dentition, but it is far from clear whether the heterodonty in phytosaurs can be homologized with that of any other archosaur group. The character states used by Parrish (1993) can be argued to also be in theropod dinosaurs, *Euparkeria*, and even *Erythrosuchus*.

Proximal humerus strongly arched under inner tuberocity (Sereno, 1991a). The angle of the inner tuberocity of the humerus relative to the shaft is difficult to access in a variety of specimens given the definition of the character states and discussion by Sereno (1991a). Therefore, I did not use this character in my analysis. Here, I agree with the assessment of this character by Parrish (1993) and agree that there is a continuum among archosauriforms. Therefore, this character cannot be shown to represent a synapomorphy linking phytosaurs with other crocodylian-line archosaurs.

Anterior trochanter of the fibula robust and knob shaped (Sereno, 1991a). The distribution of a robust and knob-shaped anterior trochanter of the fibula is widespread near the base of Archosauria. It is possible that this character unites phytosaurs and other crocodylian-line archosaurs, but the distribution in my analysis is ambiguous at present.

Distal end of fibula wider than the proximal end (Sereno, 1991a). As discussed by Parrish (1993), this character is also difficult to score and has a complex distribution. Furthermore, the proximal and distal widths of the fibulae of many archosauriforms are the same or within a few millimeters. Given the ambiguity of the character, it was not used in this analysis. However, the distal width of the fibulae of phytosaurs, *Revueltosaurus*, and aetosaurs are clearly wider than the proximal ends.

Osteoderm sculpture present (Benton, 1999). The scoring of this character cannot be reconciled with the scoring strategy of Benton (1999) and previous authors (Parrish, 1993). The osteoderms of non-archosaurian archosauriforms, such as *Euparkeria* and proterochampsians, also have sculpturing though they are smaller in overall size. Therefore, this is not a unique character supporting phytosaurs within Pseudosuchia.

The discussion of each character demonstrates that nearly all the characters previously listed placing Phytosauria within Pseudosuchia are characters difficult to score or have complex distributions near Archosauria. Furthermore, missing information or unscorable character states among basal avian-line archosaurs prevents a clear understanding of the evolution of these features. The support for phytosaurs as pseudosuchians in previous analyses was weak and relied mainly on ankle character states, characters that sometimes cannot be scored in basal avian-line archosaurs.

My analysis finds a well-supported position of Phytosauria as the sister taxon to Archosauria. Thirteen additional steps are required to place Phytosauria as the basalmost member of Pseudosuchia. This analysis finds 10 unambiguous characters, and three possible additional characters under ACCTRAN, which unite Archosauria to the exclusion of phytosaurs. These character states are distributed rather evenly throughout the body. Specifically in the skull, phytosaurs lack palatal processes of the maxilla that meet at the midline (character 32). In all other archosaurs that I examined, the palatal processes meet at the midline, whereas in phytosaurs, the palatal processes of the maxillae are at least divided by the premaxillae. The maxilla of phytosaurs lacks an antorbital fossa on the dorsolateral margin of the posterior process of the maxilla (the ventral border of the antorbital fenestra). Basal phytosaurs such as *Parasuchus* (Chatterjee, 1978) and '*Paleorhinus' scurriensis* (TTU-P 00539; Langston, 1949; Stocker, 2010) have a clear antorbital fossa on the lacrimal and the dorsal process (= ascending process) of the maxilla as in *Euparkeria* (SAM 5867) . More derived phytosaurs such as *Smilosuchus* (USNM 18313) and *Pseudopalatus* (UCMP 27235) lack an antorbital fossa on any of the elements surrounding the antorbital fenestra (pers. obs.). In Archosauria, the antorbital fenestra lies on the dorsolateral side of the posterior process of the maxilla (character 137). The braincase of phytosaurs bear a very shallow lagenar/cochlear recess, whereas the structure is elongated and tabular in archosaurs (character 118). Furthermore, the external foramen for the abducens nerve (cranial nerve VI) lies at the border between the prootic and the parabasisphenoid in phytosaurs and other non-archosaurian archosauromorphs (character 122). In archosaurs, at least primitively, the external foramen for the abducen nerve lies within the prootic only. The distributions of the two braincase character states, however, are difficult to assess in basal avian-line archosaurs, whereas the derived states are clearly present in suchians and in dinosaurs.

Postcranially, phytosaurs lack several archosaur synapomorphies. The posteroventral portion of the coracoid of phytosaurs is thin and lacks a "swollen" tuber (character 225). In archosaurs, the posteroventral portion of the coracoid possesses a distinct thickened edge and a distinct muscle scar. *Euparkeria* (SAM 6047B) has a slight thickening on the posteroventral portion of the coracoid but lacks the muscle scar. Additionally, under ACCTRAN optimization, phytosaurs lack a coracoid with a postglenoid process (character 222). Phytosaurs, like *Euparkeria,* lack a distinct lateral tuber (= radial tuber) on the proximal portion of the ulna (character 237). Instead, phytosaurs possess a simple convex lateral margin of the ulna. It appears that archosaurs share the presence of short metacarpals relative to metatarsals, even though the character state is not clear in basal avian-line archosaurs. In phytosaurs, *Euparkeria*, and *Proterosuchus*, the longest metacarpal is longer than half the length of the longest metatarsal. The proximal portions of the femora in phytosaurs lack a distinct anteromedial tuber (character 300), whereas all archosaurs have both an anteromedial and posteromedial condyle Under ACCTRAN, it appears that phytosaurs and other non-archosaurian archosauriforms lack a distal tarsal 4 with a distinct, proximally raised region on the posterior portion (character 353) (= heel of Sereno and Arcucci, 1994a, 1994b); this character is present among all basal archosaurs. My analysis found two ankle characters that excluded phytosaurs from Archosauria (tibial facet of the astragalus divided into posteromedial and anterolateral basins [character 366] and calcaneal tuber orientation between 50° and 90° posteriorly relative to the transverse plane [character 377]). Sereno (1991a) and Parrish (1993) debated the presence of the former ankle character in phytosaurs. Here, I find that most phytosaurs lack the two basins but two faint basins may be present in primitive phytosaurs (but see above). The calcaneal tuber orientation of phytosaurs and *Euparkeria* is about 45° posteriorly relative to the transverse plane, whereas the tuber of ornithosuchids, suchians, and the avian-line archosaurs *Marasuchus* and *Pseudolagosuchus* is between 50° and 90° but closer to 90° in most cases.

I have presented a brief discussion of at least 10 characters that exclude phytosaurs from Archosauria. Nearly all the characters used to support phytosaurs outside of Archosauria are characters that were only used here or were used in other more restricted analyses (see Gower, 2002).

Phytosaurs are well supported as the sister taxon of Archosauria by seven unambiguous synapomorphies and three unambiguous synapomorphies (ACCTRAN). Many of the character states supporting Phytosauria + Archosauria were previously cited as characters supporting Archosauria (Gauthier, 1984; Benton and Clark, 1988; Sereno, 1991a; Juul, 1994; Gower and Sennikov, 1997). These include the absence of teeth on the palatal process of the pterygoid (character 175) and continuous articular surfaces for the fibula and distal tarsal IV on the calcaneum (character 380). Other character states include the absence of a parabasisphenoid plate (character 96), absence of a semilunar depression on the lateral surface of the basal tubera of the parabasisphenoid (character 98), and the ventral articular surface for distal tarsal 4 and the distal end of the tuber of the calcaneum separated by a clear gap (character 371). A few characters cited by Sereno (1991a) to support phytosaurs as pseudosuchians are either unambiguous synapomorphies of the crurotarsan node (e.g., cervical ribs short and stout) or ambiguous characters supported under ACCTRAN (e.g., calcaneal tuber distal end flared, dorsally and ventrally, articular surface for the fibula of the calcaneum convex and hemicylindrical, and dorsal osteoderm alignment one to one with the dorsal vertebrae (presacrals 10–24)).

The most interesting outcome of the phylogenetic position of phytosaurs as the sister taxon of Archosauria is that the classic "crocodile normal ankle" is rendered plesiomorphic for Phytosauria + Archosauria

(= Crurotarsi). The synapomorphy "ventral articular surface of the astragalus-calcaneum, concavoconvex with concavity on calcaneum" embodies the concept of the "crocodile normal ankle." Even though this is the only ankle character uniting Phytosauria and Archosauria, it has important implications for biomechanical studies of locomotion in Archosauria and the origin of the mesotarsal ankle.

ARCHOSAURIA

My analysis finds Archosauria composed of the typical archosaur clades found in previous numerical analyses with the exception of phytosaurs. Archosauria consists of one lineage that leads to crocodylians and one that leads to avians. By definition, Archosauria will always consist of these two lineages. However, the node at which the two lineages meet was relatively poorly supported in all previous phylogenetic analyses. With the exception of Gauthier (1984), who found *Euparkeria* within Archosauria, nearly all other basal archosaur workers (e.g., Sereno, 1991a; Juul, 1994; Benton, 1999) presented the following three unambiguous characters to support Archosauria: (1) palatal teeth absent; (2) calcaneal tuber directed more than 45° posterolaterally; and (3) calcaneum with contiguous articular surfaces for fibula and distal tarsal 4. All three of these character states were used in this analysis, but were found supporting Phytosauria + Archosauria as a consequence of the novel finding of Phytosauria outside Archosauria. This study hypothesizes a strongly supported Archosauria, which is supported by 10 unambiguous synapomorphies from throughout the body (discussed above).

GRACILISUCHUS IS A BASAL SUCHIAN

Gracilisuchus was named from a small form from the Middle Triassic Chañares Formation of Argentina by Romer (1972c). *Gracilisuchus* is known from well-preserved skulls and a variety of three-dimensionally preserved postcranial material. However, details of the limb articular ends and the absence of any forelimb material (see description of the *Gracilisuchus* terminal taxon) combined with an unusual mix of plesiomorphic archosaurian features and seemingly derived character states led to a swath of hypothesized phylogenetic positions for the taxon. When first described, Romer (1972c) suggested that *Gracilisuchus* was similar to *Ornithosuchus* because the "skull structure is closely comparable in most regards, as are various postcranial features." Unfortunately, Romer (1972c) did not elaborate on his comparison between the two taxa.

Brinkman (1981) evaluated Romer's (1972c) hypothesis of a close relationship between ornithosuchids and *Gracilisuchus*. He concluded that *Gracilisuchus* does not share any exclusive features with ornithosuchids and suggested that *Gracilisuchus* may be more closely related to crocodylomorphs. Since the onset of numerical phylogenetic analyses, *Gracilisuchus* was found in a variety of positions among pseudosuchians. Even though the position of *Gracilisuchus* was variable in most previous studies, two conclusions are important. The first conclusion is *Gracilisuchus* is always more closely related to Crocodylomorpha than phytosaurs are related to Crocodylomorpha. The second is *Gracilisuchus* was always found as a pseudosuchian. *Gracilisuchus* was found as the sister taxon to *Postosuchus kirkpatricki* near Crocodylomorpha by Juul (1994), as the sister taxon to *Postosuchus kirkpatricki* + Crocodylomorpha by Parrish (1993), and as a basal pseudosuchian by Benton and Clark (1988), Benton (1999), and Benton and Walker (2002). Furthermore, Clark et al. (2004) used *Gracilisuchus* as an outgroup taxon to aetosaurs + *Postosuchus* + Crocodylomorpha in an analysis examining basal crocodylomorph relationships. *Gracilisuchus* was never found as more closely related to ornithosuchids than to any other archosaur in a numerical analysis.

The position of *Gracilisuchus* near *Postosuchus* and Crocodylomorpha obtained by Parrish (1993) and Juul (1994) is supported by a number of incorrectly scored characters. These characters include the mis-scoring of the morphology of the fifth metatarsal of *Gracilisuchus*; the fifth metatarsal is long and posses at least on phalanx (PVL 4597), whereas the fifth metatarsal was scored as tapered and lacking any phalanges by Parrish

(1993) and Juul (1994). *Gracilisuchus* does not have a dorsoventrally aligned groove on the distal end of the calcaneum tuber whereas Juul (1994) scored the groove as present. The lower temporal fenestra of *Gracilisuchus* is shaped like that of *Euparkeria* or *Ornithosuchus* (see skull reconstruction of *Gracilisuchus* in fig. 8) whereas Juul (1994) described the lower temporal fenestra as triangular and reduced. Both Parrish (1993) and Juul (1994) hypothesized that the laterally projecting flange of the squamosal in *Gracilisuchus* is homologous with that of *Postosuchus kirkpatricki* and crocodylomorphs. I agreed with this potential homology and scored the conditions in *Gracilisuchus* and crocodylomorphs as homogous. However, it is found as convergent in this analysis.

My results place *Gracilisuchus* in an unresolved polytomy with *Revueltosaurus* + Aetosauria, *Turfanosuchus*, and *Ticinosuchus* + Paracrocodylomorpha at the base of Suchia. *Gracilisuchus* is found in a variety of positions among basal suchians (fig. 54). This analysis confirms that *Gracilisuchus* is more closely related to Crocodylomorpha than phytosaurs are related to Crocodylomorpha and *Gracilisuchus*, and is at the base of Suchia. If *Turfanosuchus* is removed from my analysis *Gracilisuchus* becomes the sister taxon to Ornithosuchidae (fig. 54). This relationship is supported by five unambiguous synapomorphies including: three premaxillary teeth (6-0) (also in *Euparkeria*); pubis length more than 70% or more of femoral length (278-1); pubis length longer than ischium (282-1); gap at the midline between the distal ends of the ischia (292-1); and metatarsal V "hooked" proximal end absent (398-1). The phylogenetic position of *Gracilisuchus* at the base of Suchia is very important for resolving the relationships of pseudosuchians.

TRADITIONAL RAUISUCHIA/RAUISUCHIDAE IS PARAPHYLETIC

My results show that taxa traditionally considered rauisuchians, poposauroids, poposaurs, poposaurids, and rauisuchids form a monophyletic group only if Crocodylomorpha is included. These results generally agree with previous hypotheses of relationships of pseudosuchians (Gauthier, 1984; Parrish, 1993; Juul, 1994; Weinbaum and Hungerbühler, 2007). A minimum of 56 steps is required to make a monophyletic Rauisuchia (containing Rauisuchidae + Poposauroidea + *Ticinosuchus*) exclusive of Crocodylomorpha. With the exception of Parrish (1993), Benton (2004), and Weinbaum and Hungerbühler (2007), all other authors used either three or fewer "rauisuchians" or composite scorings for suprageneric taxa (e.g., Prestosuchidae) in their analyses. Here, I used nearly all taxa referred to as a "rauisuchian" at the species level. Of the studies that included at least five "rauisuchian" taxa (Parrish, 1993; Benton, 2004; Weinbaum and Hungerbühler, 2007), only Parrish (1993) actually tested the monophyly of the traditional concept of Rauisuchia. He found a polyphyletic Rauisuchia with respect to aetosaurs and crocodylomorphs. However, the tree of Parrish (1993) was not well supported (Gower and Wilkinson, 1996). The tree presented here is well supported given the number of characters and fragmentary taxa. The Bremer support ranges from one to four, and each node is supported by at least two unambiguous synapomorphies.

These results strongly argue that the term Rauisuchia be abandoned for future analyses. Rauisuchia was coined by von Huene (1942) before explicit phylogenetic testing was common, and many fragmentary forms that clearly were not phytosaurs, aetosaurs, or dinosaurs were subsequently assigned to the clade. Rauisuchia should be used only for a monophyletic clade containing Rauisuchidae, Poposauroidea, and other "rauisuchian-like" taxa, but not Aetosauria and Crocodylomorpha.

None of the past numerical studies of basal archosaurs incorporated a variety of "rauisuchian" taxa combined with a large sample of non-crocodyliform crocodylomorphs. Thus, it is difficult to accurately compare previous studies to my results. Nevertheless, a few generalities can be discussed including the position of certain taxa or groups of taxa and the characters previously used to diagnose groups of rauisuchians. Here, the clade Paracrocodylomorpha includes Crocodylomorpha, Rauisuchidae, Poposauroidea (poposauroids are discussed separately below),

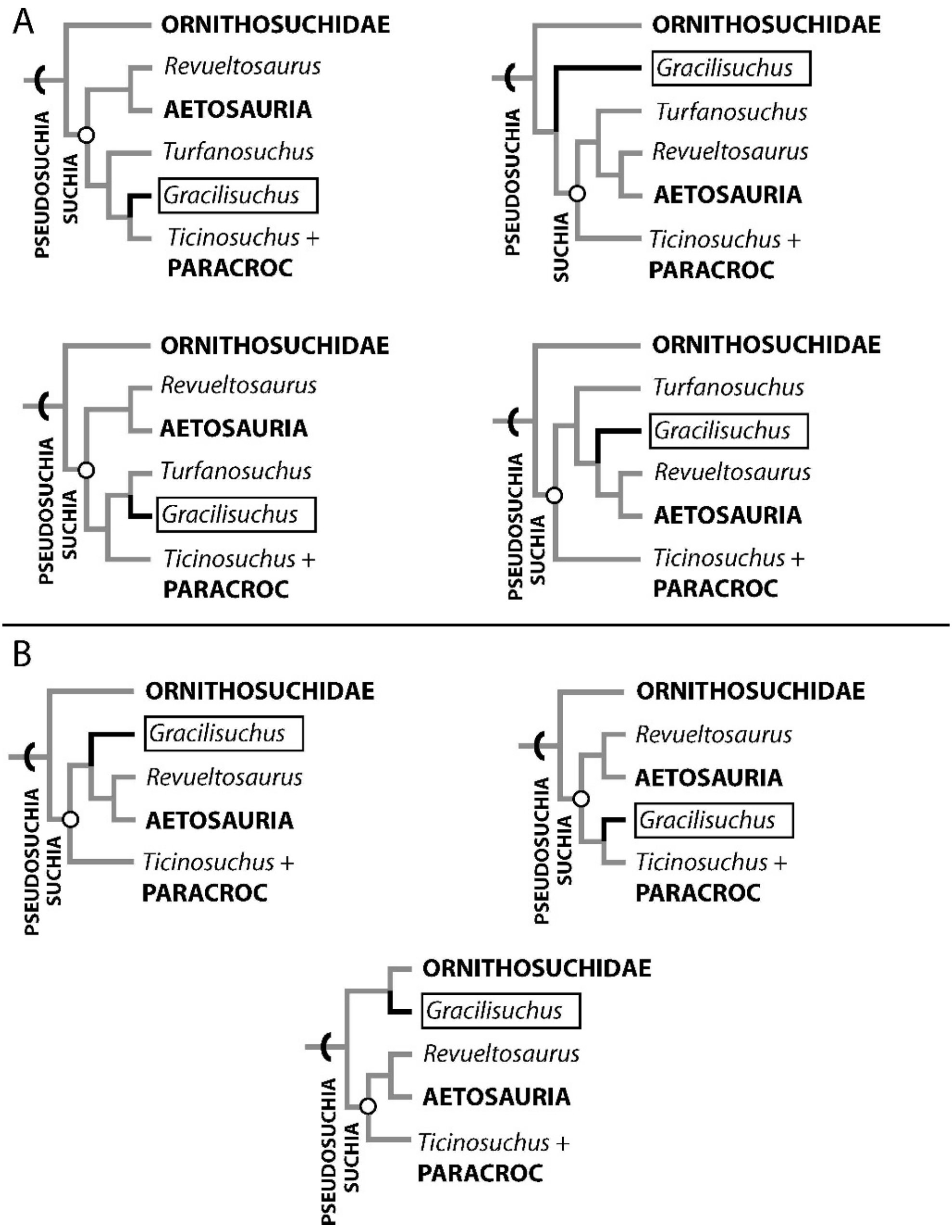

Fig. 54. The possible phylogenetic positions of *Gracilisuchus* at the base of Suchia when *Turfanosuchus* is included (A) and when *Turfanosuchus* is excluded (B).

Fasolasuchus, *Prestosuchus*, *Saurosuchus*, and *Batrachotomus*.

Even though there were a large number of characters suggested to support a "rauisuchian" clade by various authors (e.g., Benton in Benton and Clark, 1988), I concentrated on characters that are used most often and are not obviously plesiomorphic for Suchia, Archosauria, or Archosauriformes. The following characters are composed of character states typically cited as defining a monophyletic clade of a subset of rauisuchians. The original author of the character state and other authors deemed important for this discussion are cited, but a comprehensive list of authors that have used these characters is not included. Most of the characters listed below were incorporated into the phylogenetic analysis in one form or another:

Extra slitlike fenestra between maxilla and premaxilla (Benton and Clark, 1988; Parrish, 1993; Juul, 1994; Alcober, 2000; Gower, 2000). This is one of the most common character states discussed as a potential "rauisuchian" synapomorphy. However, an extra slitlike fenestra between the maxilla and the premaxilla is a difficult character to score given the poor previous definition and descriptions of the slitlike fenestra in most taxa, problems of homology (Gower, 2000), and taphonomic distortion of skulls. A foramen between the maxilla and premaxilla is common to many disparate archosaur groups (see Gower, 2000).

I have interpreted the elongated slit between the premaxilla and the maxilla *Saurosuchus* as a taphonomic artifact (see above). The maxilla-premaxilla articulation in *Saurosuchus* is similar to that of the skull of *Prestosuchus* (UFRGS 0156-T), in which the maxilla and the premaxilla tightly abut each other. In contrast, there is a clear foramen between the maxilla and premaxilla of *Batrachotomus*, *Postosuchus kirkpatricki*, *Polonosuchus*, *Rauisuchus, Fasolasuchus*, and it appears the feature is also present in *Dromicosuchus* and *Hesperosuchus* "*agilis*." In these taxa, the foramen is formed by indentations on both the maxilla and the premaxilla (character 12). Thus, this character state unites a subset (at minimum) of rauisuchians and basal crocodylomorphs.

Movable joint between the maxilla and the premaxilla (Benton and Clark, 1988; Juul, 1994). I did not use this character in my phylogenetic analysis. The definition of a movable joint is unclear, and I could not reproduce the scoring strategy of either Benton and Clark (1988) or Juul (1994). Moreover, the character state describes an inferred function rather than morphology.

Main antorbital fenestra low in front (Benton and Clark, 1988; Juul, 1994; Benton, 1999, 2004; Alcober, 2000). This character is also commonly used to describe a subset of "rauisuchians," but it ranges in its definition from describing the anterior end of the antorbital fenestra to the overall shape of the antorbital fenestra (e.g., triangular; Benton, 1999). Because I did not use general shape characters, I focused on the morphological details of the anterior margin of the antorbital fenestra, which is formed entirely by the maxilla (character 30). The anterior margin of the antorbital fenestra is nearly pointed in *Ticinosuchus*, *Prestosuchus*, *Saurosuchus*, *Fasolasuchus*, *Polonosuchus*, *Postosuchus kirkpatricki*, and the crocodylomorphs *Hesperosuchus* "*agilis*" and *Dromicosuchus*. Therefore, this character state accurately diagnoses a group of rauisuchians and the basalmost crocodylomorphs.

Tall orbit with a "stepped" postorbital bar (Benton and Clark, 1988; Juul, 1994; Benton, 1999; Alcober, 2000). I divided this character state into two characters, one examining the shape of the orbit (character 142) and one examining the termination of the postorbital (character 65). This strategy describes the morphology of the orbit more precisely. Members of the Rauisuchidae, *Saurosuchus*, *Prestosuchus*, and *Batrachotomus* have tall orbits, as do many large archosauriform carnivores. Nevertheless, the tall orbit does characterize a subset of my sampled taxa. Crocodylomorphs have rounded orbits, thus indicating a reversal given the relationships found here. Defining a "stepped" postorbital bar was more difficult than previously thought. *Saurosuchus* is always scored as having a "stepped" postorbital bar. However, the "stepped" postorbital bar in *Saurosuchus* is a consequence of a small hump on the anterodorsal edge of the ventral process of the postorbital, whereas the "stepped" postorbital bar in *Postosuchus kirkpatricki* and *Batrachotomus* is the result of a blunt end of the ventral portion of the postorbital. Therefore, I focused on the morphology of the ventral termination of the postorbital. I scored *Postosuchus kirkpatricki* and *Batrachotomus* as having a blunt ventral termination of the postorbital, whereas the ventral termination of the postorbital is tapered in *Saurosuchus* and *Prestosuchus*.

The shape of the orbit, at some level, does diagnosis a subset of paracrocodylomorphs.

Short descending process of the squamosal and tall quadratojugal that contacts the postorbital (Benton and Clark, 1988; Parrish, 1993; Juul, 1994). This character was broken down into two characters, one describing contribution of the quadratojugal to the posterior border of the lower temporal fenestra (character 45) and the other describing the quadratojugal-postorbital contact (character 64). The quadratojugal forms most of the posterior border (+ 80%) of the lower temporal fenestra in *Postosuchus kirkpatricki*, *Polonosuchus*, and Crocodylomorpha, whereas the quadratojugal forms about 50% of the posterior border of the lower temporal fenestra in other paracrocodylomorphs. Therefore, this character only supports a subset of paracrocodylomorphs (possibly rauisuchids + crocodylomorphs).

As detailed in the character descriptions, quadratojugal-postorbital contact is not present in any non-crocodylomorph paracrocodylomorph and could be confirmed only in the crocodyliforms used in the analysis.

Maxillary-vomer secondary palate (Benton and Clark, 1988; Juul, 1994). The term "secondary palate" is difficult to understand given the large diversity of organisms in which the term is applied. I abandoned the term in the character descriptions and replaced it with a character describing the palatal processes of the maxillae. Plesiomorphically in Suchia, the palatal processes of the maxillae meet at the midline and expand only anteriorly (character 32). This is the condition present in *Saurosuchus*, *Batrachotomus*, *Fasolasuchus*, and *Postosuchus kirkpatricki*. In basal crocodylomorphs (e.g., *Sphenosuchus*), the palatal processes of the maxillae meet at the midline and expand both anteriorly and posteriorly (character 32-2). The size of the palatal processes in crocodylomorphs is only slightly larger than that in non-crocodylomorph suchians. It is not until well within Crocodyliformes that the processes become large and form a significant "secondary palate" (Clark, 1986).

Supraactetabular crest on the ilium (Benton and Clark, 1988; Juul, 1994; Benton, 1999; Gower, 2000). A rugose crest dorsal to the supraacetabular rim of the ilium was cited as a typical rauisuchian feature (Benton and Clark, 1988; Juul, 1994; Benton, 1999; Gower, 2000). A rugose, vertical crest is present in *Saurosuchus*, *Batrachotomus*, *Rauisuchus*, and *Postosuchus kirkpatricki* (but unknown in *Ticinosuchus*), and also in the crocodylomorphs *Dromicosuchus*, *Hesperosuchus agilis,* and somewhat in *Terrestrisuchus*, *Ornithosuchus*, and *Protosuchus richardsoni* (characters 265–267). The homology of this feature with that of poposauroids is not clear given the uncertainty in the optimization of the character state at Paracrocodylomorpha given that the crest is apparently absent in *Prestosuchus*.

Ventrally facing ribs/ilium (Benton and Clark, 1988; Gower, 2000). Although the orientation of the ilium is difficult to score, the sacral ribs of *Prestosuchus* (UFRGS 0152-T), *Batrachotomus*, *Postosuchus kirkpatricki*, *Hesperosuchus agilis*, and *Dromicosuchus* are angled about 45° to horizontal. Therefore, the ilium is oriented at about 45° (see character 270 discussion). The ilia of aetosaurs are also oriented about 45°. However, the ilia of *Revueltosaurus* are nearly vertical (0°–20°), thus indicating that the condition in aetosaurs may be convergent with that of paracrocodylomorphs.

Anterior process of the ventral ramus of the squamosal (Alcober, 2000). This character state was described only by Alcober (2000), but it is important in this analysis uniting *Prestosuchus*, *Saurosuchus*, *Postosuchus kirkpatricki*, *Rauisuchus,* and *Polonosuchus*. In *Prestosuchus* and *Saurosuchus*, the anterior process pierces the lower temporal fenestra (character 52), whereas the anterior process bisects the lower temporal fenestra and contacts the postfrontal in *Postosuchus kirkpatricki*, *Rauisuchus,* and *Polonosuchus*. Therefore, this character state unites Rauisuchidae. A distinct anterior process of the squamosal is not readily apparent in crocodylomorphs because the ventral process of the squamosal is very short in this clade.

In summary, most of the previously used character states considered to represent a possible rauisuchian/rauisuchid clade diagnose a subset of paracrocodylomorphs. Furthermore, many of these characters are present in the crocodylomorphs *Hesperosuchus* and *Dromicosuchus*. Additionally, several of the character states were split into two characters and redefined to incorporate new specimens and observations.

Ticinosuchus: Even though a nearly complete skeleton of *Ticinosuchus* is known, only 49% of my characters could be scored for this taxon. The phylogenetic position of *Ticinosuchus* as the sister-taxon to Paracrocodylomorpha generally agrees with the topology found in previous analyses (e.g., Parrish, 1993). However, it takes only two steps to place *Ticinosuchus* within Paracrocodylomorpha.

Prestosuchus: *Prestosuchus* was one of the first "rauisuchians" to be described. Huene (1942) named two species of the taxon, *P. chiniquensis* and *P. loricatus,* from material collected from the same region in the Santa Maria Formation. Here, I scored only the more complete holotype of *P. chiniquensis*. Furthermore, Barberena (1978) assigned a complete skull and nearly complete presacral vertebral column (UFRGS 0156-T) to *P. chiniquensis*. Parrish (1993) recognized that the holotype of *P. chiniquensis* and UFRGS 0156-T may not necessarily represent the same taxon and scored them as separate terminal taxa. Here, I used the same strategy; the holotype of *P. chiniquensis*, UFRGS 0156-T, and a third specimen (UFRGS 0152-T) were scored separately in the analysis. Each specimen only partially overlaps the other's preserved portions; the holotype (BSP XXV 1–3/5–11/ 28–41/49) contains the lower jaw, a complete hind limb, parts of the vertebrae, a complete pectoral girdle (41% of characters scored), UFRGS 0156-T contains a complete skull and articulated presacral vertebrae with osteoderms (40% of characters scored), and UFRGS 0152-T contains much of a disarticulated skull including a braincase, most of the vertebrae, osteoderms, the pectoral girdle, a complete pelvic girdle, some of the forelimb, and much of the hind limb (64% of characters scored).

All three specimens were found in the Santa Maria Formation and most likely came from its lower portion (Huene, 1942; Barberena, 1978; Schultz et al., 2000). Most of the features these three specimens share represent plesiomorphies within Suchia (e.g., ankle characters, hind limb, pelvic characters). However, the morphology of all three specimens is consistent with one exception: the jugal of the largest specimen (UFRGS 0156-T) bears a sharp ridge on the lateral surface, whereas the jugal of the smallest specimen (UFRGS 0152-T) lacks a ridge. Furthermore, the specimens do share some potential autapomorphies; the absence of overlapping material prevented confirmation in all three specimens. For example, UFRGS 0152-T and UFRGS 0156-T share well-expanded distal ends of the paraoccipital processes and the paraoccipital processes terminate in a semicircular shape in posterior view. The ischia of UFRGS 0156-T and the holotype share a notch on the ventral border of the ischium. However, this character state is also present in *Stagonosuchus*. Therefore, the specimens do not unambiguously represent the same species-level taxon and were not combined a priori.

Originally, I kept each specimen as a separate terminal taxon in the phylogenetic analysis (see taxon scores). The results of the analysis show that all three specimens form a polytomy near the base of Paracrocodylomorpha. In all my MPTs, the three specimens are more closely related to each other than to any other taxon. Because of this, I combined the scorings of all three specimens into a single terminal taxon (85% of the characters scored). The combined *Prestosuchus* terminal taxon fell out in the same topology, as did all three specimens separately; *Prestosuchus* fell out as a paracrocodylomorph closer to Crocodylomorpha than to *Poposaurus*.

Prestosuchids: Prestosuchids, as found by Parrish (1993) and Benton (2004) (*Ticinosuchus* + *Prestosuchus* + *Saurosuchus*), consist of a polyphyletic group in this analysis. I found *Ticinosuchus* as the sister taxon to Paracrocodylomorpha, and *Prestosuchus* and *Saurosuchus* are found as successive sister taxa of *Batrachotomus* + *Fasolasuchus* + Rauisuchidae + Crocodylomorpha, respectively. A monophyletic Prestosuchidae requires a minimum of seven additional steps. The single character state listed by Parrish (1993) to support Prestosuchidae (paramedian plates with anterior articular processes) is present in all paracrocodylomorphs preserved with osteoderms. Parrish (1993) also listed a tentative suite of calcaneal character states (shallow socket for the astragalus, posteriorly facing tuber, slightly swollen distal end of the tuber). However, this suite of character states is also found in *Revueltosaurus*, aetosaurs, *Turfanosuchus*, *Gracilisuchus*, and *Batrachotomus*. Furthermore, Parrish (1993) stated that the collapse of Prestosuchidae required only one extra step in his analysis and suggested that this clade could easily represent a paraphyletic grade. Benton (2004) also listed a single character state (antorbital fenestra triangular with elongated narrow rostral point) to support Prestosuchidae. As discussed in my character descriptions, *Ticinosuchus*, *Saurosuchus*, and *Prestosuchus* share this character state. However, *Postosuchus kirkpatricki*, *Fasolasuchus*, and the basal crocodylomorph *Dromicosuchus* also have the same character state. Therefore, Prestosuchidae should not be used to represent a monophyletic clade uniting *Ticinosuchus, Prestosuchus*, and *Saurosuchus* in cladistic analyses or for comparative purposes.

RAUISUCHIDAE: A small group of taxa traditionally considered "rauisuchians" or rauisuchids compose the clade Rauisuchidae. This clade contains *Rauisuchus* as the sister taxon to a polytomy consisting of *Postosuchus kirkpatricki*, *Postosuchus alisonae,* and *Polonosuchus silesiacus*. These taxa share a number of unique synapomorphies including a dorsolateral margin of the anterior portion of the nasal with distinct anteroposteriorly ridge on the lateral edge (also in *Batrachotomus*), anteroventral process of the squamosal contacts the postorbital thus bisecting the lower temporal fenestra; longitudinal ridge on the body of the jugal rounded and restricted to a bulbous ridge; and ventral surface of the axis possesses two paramedian keels. Furthermore, this clade may share these other unique synapomorphies (e.g., a bulbous longitudinal ridge present on the lateral surface of the maxilla [unknown in *Rauisuchus* and *P. alisonae*], large exit of cranial nerve VII [unknown in *Rauisuchus* and *Polonosuchus*], and palpebral[s] extensively sutured to each other and to the lateral margin of the frontals [unknown in *Rauisuchus*]). The monophyly of *Postosuchus* consisting of *P. kirkpatricki* and *P. alisonae* could not be verified largely because *P. alisonae* and *Polonosuchus silesiacus* lack few overlapping elements. Specifically, *Polonosuchus* is known from much of the skull (but lacks the braincase,) the anterior portions of the cervical and caudal series, whereas *P. alisonae* is known from the braincase, scattered vertebrae, forelimbs, and hind limbs. *P. kirkpatricki* remains the most completely known taxon from this clade (82% scored).

Chatterjee and Majumdar (1987), Gower (2002), and Sulej (2005) hypothesized that *Tikisuchus* is a member of Rauisuchidae. Much of the evidence cited by Chatterjee and Majumdar (1987) was based on plesiomorphies, whereas Gower (2002) and Sulej (2005) cited potential synapomorphies. Here, I did not include *Tikisuchus* because I was not able to see the specimen. However, it remains a potential member of Rauisuchidae.

POSTOSUCHUS KIRKPATRICKI: Confusion has lingered regarding which specimens comprise the holotype and paratype of *P. kirkpatricki* since the initial description by Chatterjee (1985). The work of Long and Murry (1995) and Weinbaum (2002) separated the ischium and ilium from the holotype and assigned them to what is now called *Poposaurus langstoni* (sensu Weinbaum and Hungerbühler, 2007) and separated the postcrania of the smaller paratype of *P. kirkpatricki* and assigned them to what is now known as *Shuvosaurus* (sensu Nesbitt, 2007). Furthermore, the skeleton of the closely related *P. alisonae* served as a checklist for element assignment to *P. kirkpatricki*, and the quarry map of both the holotype and the paratype skeletons (Chatterjee, 1985) confirmed Long and Murry's (1995) and Weinbaum's (2002) concept of *P. kirkpatricki.*

The phylogenetic position of *P. kirkpatricki* found here confirms the hypothesis of Long and Murry (1995) that *P. kirkpatricki* is more closely related to *Rauisuchus*, *Prestosuchus*, *Saurosuchus*, and *Fasolasuchus* than to *Poposaurus*. Interestingly, the position of *P. kirkpatricki* as more closely related to Crocodylomorpha than to any other clade of paracrocodylomorphs (= other "rauisuchians") was common in many previous analyses (e.g., Benton and Clark, 1988; Parrish, 1993; Juul, 1994; Benton, 2004).

POPOSAUROIDS ARE MONOPHYLETIC AND DISTINCT FROM OTHER "RAUISUCHIANS"

Soon after the naming of *Poposaurus* (Mehl, 1915), Nopsca (1923) coined Poposauria, Poposauridae, and Poposauroidea. Unfortunately, these three terms have been used somewhat interchangeably without a specific definition. Furthermore, each author conducting a phylogenetic analysis on basal archosaurs or naming a new "*Poposaurus*-like" taxon has not understood which less-inclusive clade name to use. As a result, various "*Poposaurus*-like" or "rauisuchian" taxa have been grouped into a poorly defined and diagnosed clade and known as either poposaurs or poposaurids. Furthermore, the holotype of *Poposaurus gracilis* consists of only a few vertebrae, an ilium, an ischium, and the proximal portions of the femora. Therefore, comparisons to other taxa are limited.

A small subset of pseudosuchians similar to *Poposaurus* was placed into the Poposauridae starting with Chatterjee (1985). This subset included *Poposaurus*, *Postosuchus kirkpatricki*, *Polonosuchus*, *Arizonasaurus*, and *Bromsgroveia*. Subsequent authors generally accepted this group, but it was not explicitly tested phylogenetically. As the most completely known taxon within Poposauridae, *Postosuchus* was later used in numerical phylogenetic analyses (Benton and Clark, 1988; Parrish, 1993) and in comparative descriptions (e.g., Alcober and Parrish, 1997) to represent Poposauridae. Long and Murry (1995) incisively showed that the ilium assigned to *Postosuchus kirkpatricki* by Chatterjee (1985) did not belong to the taxon and actually belonged to a form very closely related to *Poposaurus*. Therefore, most of the characters shared between *Poposaurus* and *Postosuchus* were not valid. Furthermore, Long and Murry (1995) removed *Postosuchus* from Poposauridae. Nesbitt (2003) was the first to place *Poposaurus* into a phylogenetic analysis and found it grouped with *Arizonasaurus* and *Shuvosaurus* (= *Chatterjeea* of Nesbitt, 2003). This result was later confirmed by Weinbaum and Hungerbühler (2007).

Here, I included all *Poposaurus*-like taxa, most taxa that have been considered poposaur(id)s, and *Poposaurus*. Fortunately, a newly discovered articulated skeleton of *Poposaurus* (YPM 57100) provided missing details for the taxon (Joyce and Gauthier, 2006). The results of my analysis places *Poposaurus* in a clade containing *Qianosuchus*, *Arizonasaurus*, *Xilousuchus*, *Lotosaurus*, *Sillosuchus*, *Effigia*, and *Shuvosaurus* as the sister taxon to Loricata, a clade containing *Prestosuchus*, *Saurosuchus*, *Batrachotomus*, *Fasolasuchus*, *Rauisuchidae*, and Crocodylomorpha. Following Weinbaum and Hungerbühler (2007), the clade containing any taxa closer to *Poposaurus* than to any other archosaur clade is termed Poposauroidea.

The basalmost member of Poposauroidea is *Qianosuchus* from the Middle Triassic of China. Much of the morphology of the skeleton of *Qianosuchus* resembles that of *Ticinosuchus* because it has short pelvic elements and at least four osteoderms per presacral vertebra. *Qianosuchus* shares the following important character states with other poposauroids: anterodorsal process (= nasal process) of the nasal greater than the anteroposterior length of the premaxilla (1-1); posterodorsal process (= maxillary process, = subnarial process) of the premaxilla restricted to the ventral border of the external naris (5-1); anterodorsal margin of the maxilla borders the external naris (24-1); concave anterodorsal margin at the base of the dorsal process of the maxilla (25-1); foramina for entrance of cerebral branches of internal carotid artery into the braincase positioned on the ventral surface (95-0); cervical ribs slender and elongated (196-0); distal expansion of neural spines of the dorsal vertebrae absent (197-0); sacral rib of primordial sacral one articulates with the anteriorly directed process of the ilium (202-1); and insertion of a sacral vertebra between the first primordial sacral vertebra (207-1).

The next grouping of poposauroids, *Arizonasaurus* + *Effigia*, was predicted and termed "Group X" by Nesbitt (2005b) and detailed further by Nesbitt (2007). Of the 10 potential synapomorphies of "Group X" listed (see Nesbitt, 2005a, 2007) to unite this clade, only the following four synapomorphies are unambiguous: loss of osteoderms, ischium-pubis contact absent (= waisted ventral margin of the ilium), fully fused sacral vertebrae, and dorsolaterally thin pubic boot. Some of the other characters listed by Nesbitt (2007) for "Group X" became synapomorphies of Poposauroidea, and the optimizations of a few other characters listed are not clear.

Poposaurus is well nested within Poposauroidea. It shares three exclusive synapomorphies with shuvosaurids including: supraacetabular crest (= supraacetabular rim) of the ilium projects ventrally (264-1), anterodorsally inclined crest dorsal to the supraacetabular crest/rim of the ilium (266-1), and pedal unguals dorsolaterally compressed (400-1). Unfortunately, the skull is known only from a few maxillary fragments and the left and right premaxilla. However, both the maxilla and premaxilla of Poposaurus (YPM 57100) bear teeth.

Recent preparation of the syntypes of *Lotosaurus adentus* has allowed a reevaluation of the phylogenetic position of this important taxon. In my analysis, *Lotosaurus* falls out closer to shuvosaurids than to *Arizonasaurus* (see above), an alternate prediction put forward by Nesbitt (2007) because of the similarity of the skull of *Lotosaurus* to that of *Effigia*. Therefore, some of the features of *Lotosaurus* (e.g., large forelimbs and pectoral girdle) that may have been considered plesiomorphic for pseudosuchians are actually autapomorphic for the taxon. For example, *Lotosaurus* has large forelimbs whereas *Qianosuchus* (humerus only), *Poposaurus,* and shuvosaurids have greatly reduced forelimbs relative to other archosauriforms. The phylogenetic position of *Lotosaurus* outside Shuvosauridae, and the morphology of the skulls of *Effigia* and *Shuvosaurus*, predicts that the currently unknown skull of *Sillosuchus* would be lightly built, have large nasals, and bear edentulous jaws.

Nesbitt (2007) found a clade containing *Sillosuchus*, *Effigia*, and *Shuvosaurus* and termed this potential clade "Group Y." A similar clade uniting *Sillosuchus* and *Shuvosaurus* (= *Chatterjeea*) was suggested by Alcober and Parrish (1997) and shown phylogenetically by Weinbaum and Hungerbühler (2007). This clade is defined above and named Shuvosauridae as suggested by Nesbitt (2007). Of the 11 potential synapomorphies listed by Nesbitt (2007), only two (pneumatic features [= pleurocoels] in the anterior portion of the cervical centrum present as deep fossae [188-1] and sacral ribs shared between two sacral vertebrae [208-1]) optimize at this node. Many other potential synapomorphies were not added to the analysis and a few other potential characters from Nesbitt (2007) optimized at the node containing *Lotosaurus* + *Effigia* (e.g., ilium expanded dorsally, height markedly taller than the dorsal portion of the supraacetabular rim to the pubis-ischium contact [276-1]). Furthermore, I scored parts of the holotype skeleton of *Sillosuchus* (see above) including the pectoral girdle and humerus, two elements found with the holotype, but not described by Alcober and Parrish (1997). The addition of these details led to two additional synapomorphies (posteroventral portion of the coracoid smooth [225-0], and proximal portion of the humerus expanded less than twice the width of the midshaft of the humerus [336-1]).

Effigia and *Shuvosaurus* form a well-supported clade. Many of the potential synapomorphies listed by Nesbitt (2007) support the clade unambiguously, whereas other characters listed were supported only under DELTRAN.

In summary, Poposauroidea is a well-supported clade situated as the sister taxon to Loricata, well within Pseudosuchia in my analysis. The members of the clade present the most extreme body plans in Pseudosuchia, from quadrupedal, sail-backed taxa to bipedal, edentulous taxa. Furthermore, the poposauroid clade is one of the first archosaur clades to appear in the fossil record (*Xilousuchus*) and one of few pseudosuchian clades confirmed to survive to the very end of the Triassic (*Effigia*).

CTENOSAURISCIDS: Nesbitt (2003, 2005a) suggested that *Arizonasaurus*, *Lotosaurus*, *Ctenosauriscus*, *Bromsgroveia*, and *Hypselorhachis* may form a monophyletic clade at the base of "Group X" called Ctenosauricidae. Two aspects of the neurals spines of the presacral vertebrae would unite these forms, a "sail" (except *Bromsgroveia*) formed by dorsally expanded neural spines in the presacral vertebrae and anteriorly arching neural spines in the posterior cervical and anterior dorsal vertebrae (Nesbitt, 2003, 2005a).

In this study, I incorporated only *Arizonasaurus* and *Lotosaurus* into the phylogeny. The much more incompletely known taxa *Ctenosauriscus, Bromsgroveia*, and *Hypselorhachis* were not treated as separate terminal taxa and added into the phylogeny because the only characters that could be scored for each were completely redundant with the scorings of both *Arizonasaurus* and *Lotosaurus*. The results presented here indicate that *Lotosaurus* and *Arizonasaurus* do not form a monophyletic clade. Eleven steps are required to create a monoplyletic ctenosauriscid clade containing *Lotosaurus* and *Arizonasaurus* exclusive of other poposauroids. Therefore, the presence of a ''sail'' in a pseudosuchian does not indicate that a taxon is a ctenosauriscid. My results indicate two equally parsimonious interpretations for the evolution of a ''sail'' in poposauroids: either the ''sail'' is a character lost in both *Poposaurus* and Shuvosauridae independently, or the ''sail'' in *Arizonasaurus* and *Lotosaurus* evolved independently (fig. 55).

However, it is entirely possible that *Ctenosauriscus, Bromsgroveia*, and *Hypselorhachis* form a ctenosauriscid clade with *Arizonasaurus* to the exclusion of *Lotosaurus*. New material of the more fragmentary taxa is required before this idea is testable. Nevertheless, during the course of this study, I was able to include the fragmentary taxon *Xilousuchus* from the late Early Triassic of China. This specimen preserves the posteriormost cervical vertebrae with posteriorly increasingly taller neural spines that arch anteriorly at the dorsal margin, characters found in both *Arizonasaurus* and *Lotosaurus*. Furthermore, the maxilla of *Xilousuchus* shares a deep fossa on the posteroventral side of the dorsal process with the maxilla of *Arizonasaurus*; this is a unique feature (listed as a potential autapomorphy by Nesbitt, 2003, 2005a). *Arizonasaurus* and *Xilousuchus* share a straight parabasisphenoid plate on the ventral surface of the parabasisphenoid (96-0), a character that is unique in Pseudosuchia. These shared features and additional synapomorphies of poposauroids placed *Xilousuchus* as the sister taxon of *Arizonasaurus*. Therefore, there is at least a small clade of ''sail-backed'' poposauroids near the base of Poposauroidea.

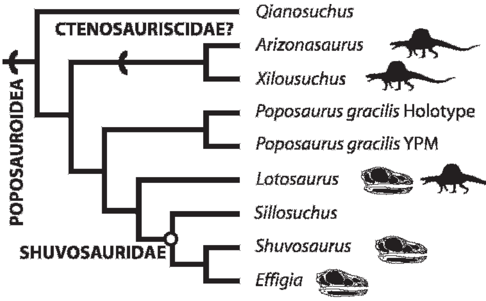

Fig. 55. Relationships of Poposauroidea. The distribution of a ''sail'' (silhouette of the skeleton) and endentulism (drawing of the skull) is complex. A ''sail'' either evolved twice in poposauroids, once in *Arizonsaurus* + *Xilousuchus,* and once in *Lotosaurus* or the ''sail'' was lost independently in *Poposaurus* and Shuvosauridae.

The Sister Taxon of Crocodylomorpha

Crocodylomorphs are paracrocodylomorphs: this analysis finds Rauisuchidae as the sister taxon of Crocodylomorpha. In a broad sense, this result is consistent with many previous results including those of Gauthier (1984), Benton and Clark (1988), Parrish (1993), Juul (1994), Benton and Walker (2002), Irmis et al. (2007a), and Weinbaum and Hungerbühler (2007). The evidence for a sister-taxon relationship between a group of paracrocodylomorphs and Crocodylomorpha is well supported. The following lists of synapomorphies are shared between subclades of paracrocodylomorphs (taxa closer to Crocodylomorpha than to *Poposaurus*) and crocodylomorphs. Furthermore, nearly all these character states unless noted are absent in aetosaurs and *Revueltosaurus*.

The first list presents unambiguous synapomorphies at various nodes in clades closer to Crocodylomorpha than to *Poposaurus*. The optimization of these characters is presented in the tree description. The character states listed below are not necessarily unique to paracrocodylomorphs (taxa closer to Crocodylomorpha than to *Poposaurus*) and crocodylomorphs; some are unique, whereas others are present in other taxa.

(1) Subnarial foramen between the premaxilla-maxilla and the border of the foramen is present on both the maxilla and the premaxilla (12-1).

(2) Posterior portion of the nasal at the midline concave (34-1).

(3) Dorsal surface of the frontal with longitudinal ridge along midline (42-1).

(4) Anterior portion of the frontal tapers anteriorly along the midline (43-1). Also present in *Revueltosaurus*.

(5) Squamosal with distinct ridge on dorsal surface along edge of supratemporal fossa (49-1).

(6) Upper temporal fenestrae separated by a mediolaterally thin strip of flat bone (59-1). The upper temporal fenestrae are separated by a "sagittal crest" in *Sphenosuchus* and *Dibothrosuchus* whereas the upper temporal fenestrae are separated by a broad, flat area in *Litargosuchus* + Crocodyliformes.

(7) Double-headed ectopterygoid (89-1).

(8) Basioccipital portion of the basal tubera bladelike and anteroposteriorly shortened (106-1).

(9) Anterior portion of the dentary dorsally expanded (154-2). The anterior portion of the dentary of *Sphenosuchus* + Crocodyliformes is not dorsally expanded.

(10) Distal expansion of neural spines of the dorsal vertebrae absent (197-0).

(11) Accessory laminar process on anterior face of neural spine of the middle caudal vertebrae (210-1).

(12) Ilium, crest dorsal to the supraacetabular crest/rim divides the anterior (= preacetabular) process from the posterior (= postacetabular) process (265-1). Reversed in some crocodylomorphs (e.g., *Dibothrosuchus*).

(13) Obturator foramen of the pubis enlarged (281-1).

(14) Pubis distal end expanded relative to the shaft (= pubis boot). Reversed in *Terrestrisuchus* + Crocodyliforms (283-1).

(15) Pubis length longer than ischium (282-1).

(16) Proximal condylar fold of the proximal portion of the femur (312-1).

(17) Angle between the lateral condyle and the crista tibiofibularis of the femur about a right angle in distal view (319-1).

(18) Medial condyle of the distal portion of the femur smoothly rounded in distal view (320-1).

(19) Medial face of the distal portion of the fibula banked with an articular facet that articulates with the astragalus (344-1).

(20) Articular facet for the astragalus of the calcaneum lies partially ventral to the fibular facet (358-1).

(21) Ventral articular surface of the calcaneum for distal tarsal 4 and the distal end of the tuber separated by a gap with a ventral fossa (371-1).

(22) Distal end of the calcaneal tuber with a dorsoventrally aligned median depression (375-1).

This second list presents character states that a subset of paracrocodylomorphs (excluding poposauroids) share, but it is unclear where the states optimize within Paracrocodylomorpha (ACCTRAN and DELTRAN).

(1) Anterior margin antorbital fenestra nearly pointed (30-1). Absent in *Batrachotomus* and *Dibothrosuchus* + Crocodyliformes.

(2) Posterior process of the jugal lies ventral to the anterior process of the quadratojugal (71-1).

(3) Posterior termination of the jugal posterior to the lower temporal fenestra (72-1).

(4) Quadrate head completely covered by the squamosal (78-1).

(5) Small contact between the prootic and the paroccipital process (105-1).

(6) Paroccipital processes markedly expanded dorsally at the distal ends (108-1).

(7) Eustachian tubes partially enclosed by bone (121-1).

(8) Supratemporal fossa anterior to the supratemporal fenestra (144-1).

(9) Ventromedially directed process of the articular present (157-1).

(10) Proximal head of the humerus posteriorly expanded and hooked (232-1).

(11) Pubis length more than 70% or more of femoral length (278-1).

(12) Distal pubis mediolateral width significantly narrower than proximal width (289-1).

(13) Posteroventral portion of distal tarsal 4 ventrally expanded into a small process (349-1).

(14) Thin lamina separating the tibial facet from the posterior edge (= astragalar ridge) of the astragalus (354-1).

(15) Nonarticular fossa present on the posterior portion of the tibial articular surface of the astragalus (364-1).

(16) Metatarsal V has a "poorly" developed first phalanx (399-1).

The following list contains character states of Paracrocodylomorpha that are not present in Crocodylomorpha. In my topology, these character states would have to be secondarily lost in Crocodylomorpha. Furthermore, all these character states listed as reversals in Crocodylomorpha are shared between *Revueltosaurus* + aetosaurs and crocodylomorphs. This includes:

(1) Maxillary interdental plates fused (22-1). Maxillary interdental plates are fused in *Fasolasuchus*, *Postosuchus kirkpatricki*, and *Polonosuchus*. The interdental plates of all crocodylomorphs examined here are distinct and not fused.

(2) Anteroventral process of the squamosal present and perforates the lower temporal fenestra (52-1). A distinct anteroventral process in crocodylomorphs may not be recognizable given the modifications of the squamosal in the group relative to other archosaurs. It is possible that the squamosals of crocodylomorphs have an anteroventral process like that of *Postosuchus kirkpatricki*; the "dorsal" lower temporal fenestra present in taxa such as *Postosuchus kirkpatricki* may be filled in with bone in basal crocodylomorphs.

(3) Orbit tall and narrow (142-1). The orbits of non-crocodylomorph paracrocodylomorphs (excluding Poposauroidea) are tall and narrow, whereas the orbits of all crocodylomorphs included in this analysis are nearly circular. Interesting, there are no small taxa with a tall orbit that I examined in Archosauria, whereas big carnivorous taxa (e.g., theropods) have narrow and tall orbits. This may be evidence that body size is correlated with these character states.

(4) Extensive medial contact between the ischia but dorsal margins separated (291-1). The ischia of crocodylomorphs (e.g., *Terrestrisuchus* + Crocodyliformes) only meet at their medialmost edge along the midline. However, this character could not be scored in the basalmost crocodylomorphs including *Hesperosuchus*, *Dromicosuchus*, *Sphenosuchus*, and *Dibothrosuchus*. A few other ischial character states require a reversal somewhere within Crocodylomorpha. However, the ischium is not known in any of the basalmost members of the clade at this time.

(5) Attachment site for the M. iliofibularis near the midpoint between the proximal and distal ends of the fibula (340-1). The attachment site for M. iliofibularis is located in the proximal ⅓ of the fibula in crocodylomorphs.

(6). Metatarsal V dorsal prominence separated from the proximal surface by a concave gap (397-1). Crocodylomorphs lack a dorsal prominence on the proximal portion of metatarsal V.

Thus, there is an overwhelming number of character states that support a much closer relationship between crocodylomorphs and clades of paracrocodylomorphs rather than an aetosaur-crocodylomorph clade. Nevertheless, there is a large morphological "gap" between crocodylomorphs and any other pseudosuchian clade regardless of the sister taxon of Crocodylomorpha. Crocodylomorphs share 19 unambiguous synapomorphies and another 20 possible synapomorphies under ACCTRAN. Furthermore, at least half of these 39 synapomorphies are present only in Crocodylomorpha among crocodylian-line archosaurs.

Aetosaurs are not the sister taxon of Crocodylomorpha: Gower (2002) and Gower and Walker (2002) put forth the hypothesis that aetosaurs are the sister taxon to Crocodylomorpha. Their hypothesis was formed mainly by comparing the braincase morphology of the aetosaur *Stagonolepis*, the loricatan *Batrachotomus*, and the non-crocodyliform crocodylomorph *Sphenosuchus*. Further, they also compared those three taxa to other aetosaurs (e.g., *Longosuchus*), other loricatans (e.g., *Postosuchus kirkpatricki*), and phytosaurs. Gower (2002) and Gower and Walker (2002) found that aetosaurs and *Sphenosuchus* + *Crocodylus* share the following characters: (1) perilymphatic foramen entirely bordered by bone with an associated loop closure in the ventral ramus of the opithotic; (2) posterolateral rather than posterior/posteromedial path of route of the perilymphatic duct out of the otic capsule; (3) external foramina for hypoglossal nerve posterior to a lateral exoccipital ridge; (4) lack of midline contact of the exocciptials on the floor of the endocranial cavity; (5) the relatively elongate region comprised of that part of the exoccipitals and basioccipital posterior to metotic foramen. With the exception of the last character listed (= character 4 of Gower, 2002), all the other character states were tested in this comprehensive matrix, which includes more taxonomic sampling (i.e., the addition of avian-line archosaurs and more pseudosuchians). Character 4 of Gower, 2002, was deleted from the analysis because there seems to be an unbroken continuum in the different lengths of the exoccipitals and basioccipital in basal archosaurs without a clear break in morphologies in the material I examined.

The analysis presented here did not find aetosaurs as the sister taxon of crocodylomorphs. It takes 57 more steps to make aetosaurs (+*Revueltosaurus*) the sister taxon of Crocodylomorpha. If aetosaurs (+ *Revueltosaurus*) are constrained as sister taxa, taxa traditionally considered "rauisuchians" (including poposauroids) form a monophyletic clade as the sister taxon to aetosaurs (+ *Revueltosaurus*) + Crocodylomorpha (fig. 56) in a constrained analysis. This adds 59 more steps to the MPTs.

Some of the features cited by Gower (2002) and Gower and Walker (2002) as synapomorphies of aetosaurs + crocodylomorphs did not unite these two clades when I added other cranial and postcranial characters. However, four of the five characters listed by Gower (2002) to support aetosaurs + crocodylomorphs deserve discussion because I recover different distributions of the character states among archosaurs. The perilymphatic foramen is clearly surrounded by bone in *Stagonolepis* (Gower and Walker, 2002), *Sphenosuchus,* and *Alligator*. However, the only other pseudosuchian taxa that could be scored for this character are *Batrachotomus*, *Arizonasaurus*, *Xilousuchus*, and *Lotosaurus*, which all lack an ossified perilymphatic foramen border. As discussed in the character descriptions, only extremely well-preserved material can be scored for this character because the border of the perilymphatic foramen is easily broken before a specimen is studied. The presence of an ossified border of the perilymphatic foramen is not limited to crocodylian-line archosaurs, the perilymphatic foramen is clearly surrounded by bone in the basal theropod *Dilophosaurus*. Although a perilymphatic foramen entirely bordered by bone is common to both aetosaurs (only *Stagonolepis* could be scored) and crocodylomorphs, the character state does not necessarily support an aetosaur-crocodylomorph relationship exclusive of "rauisuchians" given that the character cannot be scored in many suchian taxa.

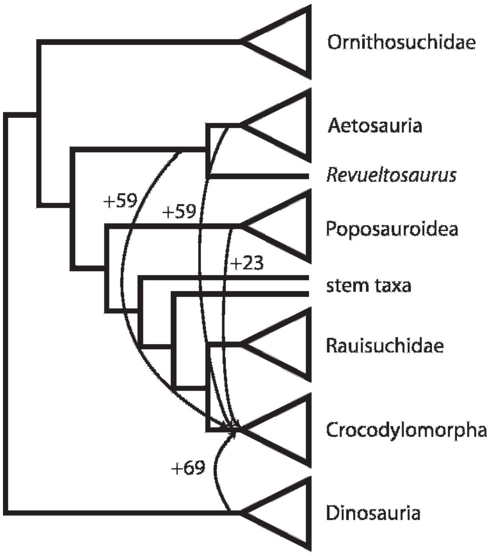

Fig. 56. Different clades previously proposed to be the sister taxon of Crocodylomorpha. The numbers represent how many additional steps it would take to make these clades the sister taxon of Crocodylomorpha.

The orientation of the perilymphatic foramen was listed by Gower (2002) and Gower and Walker (2002) to support an exclusive aetosaur + crocodylomorph clade. However, I disagree with the scoring of perilymphatic foramen as posterolateral in *Stagonolepis*. I did not see any difference in the orientation of the ventral process of the opisthotic of *Stagonolepis* and that of *Postosuchus*, *Arizonasaurus*, phytosaurs, *Turfanosuchus*, *Euparkeria*, or avian-line archosaurs (see above also). In these forms, the ventral process of the opisthotic expands as a thin sheet of bone laterally with a small posterior component. The perilymphatic foramen (or groove), which passes through the opithotic, cannot be oriented laterally if the ventral process of the opisthotic is oriented mediolaterally. In *Sphenosuchus*, the opisthotic expands anteroposteriorly and the perilymphatic foramen exits laterally. Scoring differences between this analysis and Gower (2002) and Gower and Walker (2002) in this character prevent it from uniting aetosaurs and crocodylomorphs.

Gower (2002) and Gower and Walker (2002) hypothesized that having a vertical ridge on the lateral side of the exoccipital and having both hypoglossal foramina posterior to this ridge united aetosaurs and crocodylomorphs exclusive of other clades of pseudosuchians. However, the addition of more archosaurian taxa, specifically avian-line archosaurs, complicated Gower's (2002) character definition and states (character 2 of Gower, 2002). Therefore, the character was rewritten to incorporate the large range of morphology here. In taxa with a lateral ridge on the exoccipital, either both hypoglossal foramina lie posterior to the ridge or one of the hypoglossal foramina is present anterior to the ridge (the other hypoglossal foramen exited posterior to the ridge). As stated by Gower (2002), crocodylomorphs clearly have both hypoglossal exits posterior to the lateral ridge. Among aetosaurs, *Stagonolepis*, *Longosuchus,* and a well-preserved aetosaur braincase from the *Placerias* Quarry (UCMP 27414) have one of the hypoglossal foramina exiting anterior to the ridge, whereas the other hypoglossal foramina posterior to the ridge. This is the same condition in *Postosuchus kirkpatricki* (TTU-P 9002), *Turfanosuchus*, and *Revueltosaurus*. Only one hypoglossal foramen is present in *Batrachotomus*. However, the single hypoglossal foramen opens anterior to the exoccipital ridge. Therefore, this character state does not necessarily unite aetosaurs and crocodylomorphs exclusively. Furthermore, the presence of both hypoglossal foramina exiting posterior to a lateral ridge may be the plesiomorphic state for avian-line archosaurs because it is present in *Marasuchus*, *Silesaurus*, *Lewisuchus*, *Plateosaurus*, *Heterodontosaurus*, and *Coelophysis bauri*. Thus, the arrangement present in crocodylomorphs is much more common in basal archosaurs than previously thought.

Gower (2002) and Gower and Walker (2002) also hypothesized that the lack of midline contact of the exoccipitals on the floor of the endocranial cavity supported an aetosaur and crocodylomorph clade. As detailed in the character descriptions, aetosaurs have exoccipitals that meet at the midline (see above for a further explanation).

After obtaining evidence for a possible aetosaur-crocodylomorph clade based on the braincase, Gower and Walker (2002) suggested two characters within the skull may be further support for the clade. These characters include the dorsal fossa on the palatine is restricted posteriorly and the presence of a ventromedial process (or flange) of the prefrontal. Both characters (40 and 90) were incorporated into the phylogeny here. As described by Witmer (1997), the dorsal fossa is posteriorly restricted in *Stagonolepis* and *Sphenosuchus*, whereas the dorsal fossa nearly reaches the internal choana in *Ornithosuchus* and *Batrachotomus* (Gower, 1999; Gower and Walker, 2002). However, the pattern of character distribution is much more complicated when more taxa are added to the analysis. For example, *Polonosuchus silesiacus* has a state similar to that in *Sphenosuchus*, whereas the crocodylomorphs *Terrestrisuchus* and *Protosuchus richardsoni* have a state similar to that of *Batrachotomus* (see above for more details). Therefore, the character state shared by *Stagonolepis* and *Sphenosuchus* appears to not represent a character supporting aetosaurs and crocodylomorphs as an exclusive clade.

The presence of a ventromedial process (or flange) of the prefrontal is clearly present in all crocodylomorphs with this portion of the prefrontal preserved in my analysis. It is also clearly preserved in *Stagonolepis* and *Longosuchus* among aetosaurs. However, as detailed in the character descriptions, this process is very thin and easily broken off. Therefore, I am not confident that this feature is absent in taxa such as *Postosuchus kirkpatricki* or *Polonosuchus silesiacus* although it is clearly absent in *Saurosuchus*. The presence of a ventromedial process of the prefrontal is clearly present in aetosaurs and crocodylomorphs, but the analysis here suggests that the feature evolved independently in the two groups. This is supported by the absence of the feature in the close aetosaur relative, *Revueltosaurus* (PEFO 34561).

The resolved position of *Revueltosaurus* as the sister taxon of Aetosauria also prevents a close relationship between aetosaurs and crocodylomorphs. First, *Revueltosaurus* is supported as the sister taxon of aetosaurs by 10 unambiguous and eight ambiguous synapomorphies, seven of which are found only in *Revueltosaurus* and aetosaurs (within Pseudosuchia). *Revueltosaurus* bears many plesiomorphic pectoral, pelvic, and hind limb characters absent both in paracrocodylomorphs and crocodylomorphs. Characters pertaining to the palatine and the perliymphatic foramen could not be scored in *Revueltosaurus*.

In summary, aetosaurs are not found as the sister taxon of Crocodylomorpha. Some of the features that Gower (2002) and Gower and Walker (2002) hypothesized the two clades shared are valid, but are outweighed by other characters, are not able to be scored in most taxa and therefore ambiguous, are not present in the close aetosaur relative *Revueltosaurus*, or have a larger distribution within Suchia.

Basal Crocodylomorpha

Crocodylomorpha is one of the best-supported clades in this analysis; 19 unambiguous synapomorphies and potentially 20 more ambiguous synapomorphies support this clade. My strategy for incorporating crocodylomorphs was twofold; I include most basal crocodylomorph taxa even though my sampling of the clade is not complete (*Pseudhesperosuchus, Junggarsuchus, Saltoposuchus* are not included), and I use an outgroup that has been tested in a larger context among basal archosaurs. All taxa that were found as crocodylomorphs in previous numerical analyses are also found to be unambiguous crocodylomorphs here.

Previous numerical analyses of basal crocodylomorphs found either a monophyletic Sphenosuchia (Sereno and Wild, 1992; Wu and Chatterjee, 1993; Clark et al., 2000) containing forms such as *Sphenosuchus*, *Hesperosuchus agilis*, *Dibothrosuchus*, and *Terrestrisuchus* exclusive of crocodyliforms, or a nearly paraphyletic "Sphenosuchia" whereby some forms were more closely related to crocodyliforms than to other "sphenosuchians" (Benton and Clark, 1988; Parrish, 1992; Clark et al., 2004). However, the monophyly versus paraphyly of Sphenosuchia somewhat represents two extremes as suggested by the studies of Clark and Sues (2002) and Clark et al. (2004), which found some "sphenosuchians" closer to crocodyliforms than other "sphenosuchians," but the relationships of the basalmost crocodylomorphs rested in a large polytomy.

My results suggest that "Sphenosuchia" represents a grade of crocodylomorphs leading to Crocodyliformes. A minimum of 14 additional steps is required to force the monophyly of taxa that have been considered "Sphenosuchia." However, it is clear that taxa such as *Kayentasuchus* and *Litargosuchus* share more skull synapomorphies with crocodyliforms than either do with taxa such as *Dromicosuchus* (see results). Therefore, forcing a monophyletic group composed of those taxa and other "sphenosuchians" may not be a valid comparison. Furthermore, I ran my tree constraining the monophyly of Sphenosuchia. The resulting relationships of sphenosuchians have never before been found in any previous analysis (e.g., *Hesperosuchus agilis* + *Terrestrisuchus* as the sister taxon to *Sphenosuchus*).

The paraphyly of "Sphenosuchia" may have been the result of a more complete outgroup selection. Most previous analyses used an outgroup composed of *Postosuchus kirkpatricki* (sensu Chatterjee, 1985), the aetosaur *Stagonolepis,* which is a taxon known mostly from sandstone molds, and *Gracilisuchus*, an incompletely preserved taxon with a controversial phylogenetic position. Even though these outgroups are not the best choice as demonstrated by the results here, these were some of the best outgroups available at the time of these studies. At present, there are a variety of newly described taxa and new specimens of incomplete taxa that represent more complete outgroups to Crocodylomorpha. Here, Crocodylomorpha is placed into a larger pseudosuchian context. As described above, Rauisuchidae is found as the sister taxon to Crocodylomorpha. Therefore, some of the character states once though to unite Sphenosuchia as a monophyletic clade (e.g., teeth with swollen crowns, longitudinal frontal crests) are found in non-crocodylomorphs and thus represent plesiomorphies for Crocodylomorpha.

The support of a paraphyletic Sphenosuchia is weak (Bremer of 1–3 per node). The lowest Bremer support values surround taxa represented only by limited material (e.g., *Kayentasuchus*). However, the support obtained in this analysis is greater than that of previous analyses, the Bremer support of nearly every node in previous analyses is 1 (e.g., Parrish, 1991).

Hesperosuchus and *Hesperosuchus*-like taxa (e.g., *Dromicosuchus*, *Hesperosuchus* "*agilis*") are found as some of the basal most crocodylomorphs, which is a unique result in comparison with previous analyses. In other works, *Hesperosuchus* was found well nested within Crocodylomorpha. The more basal position of *Hesperosuchus* and *Dromicosuchus* is the direct result of the sister-taxon relationship between Crocodylomorpha and Rauisuchidae within Paracrocodylomorpha in this analysis. The absence of three character states in *Hesperosuchus agilis,* CM 29894, and *Dromicosuchus* that are present in nearly all other crocodylomorphs (an interparietal suture partially or completely absent [58-1], a straight occipital margin in dorsal view [61-1], and a deep recess on the ventral surface of the basioccipital [107-1]) indicate that these three taxa are the most basal among Crocodylomorpha.

Hesperosuchus agilis (AMNH FR 6758) and CM 29894 (a specimen referred to *Hesperosuchus agilis* by Clark et al., 2000, referred to as *Hesperosuchus* "*agilis*" throughout the text) are found in a polytomy together with *Dromicosuchus* and the rest of Crocodylomorpha. Even though CM 29894 and *Hesperosuchus agilis* (AMNH FR 6758) are found together in a polytomy, I maintain that the two specimens be separated in phylogenetic analyses because they do not share any clear autapomorphies in the preserved material, they are separated by 10–20 million years temporally, and most of the overlapping elements share character states with other suchians. Additionally, both CM 29894 and *Hesperosuchus agilis* (AMNH FR 6758) can be differentiated from *Dromicosuchus* (see terminal taxa description).

CM 73372 (*HESPEROSUCHUS "AGILIS"*)

An articulated postcranial skeleton from the *Coelophysis* Quarry from the "upper siltstone" member of the Chinle Formation was referred to *Postosuchus kirkpatricki* by Long and Murry (1995), Weinbaum (2002), Novak (2004), and Peyer et al. (2008). CM 73372 is scored as a separate terminal taxon to test this assignment. This analysis finds CM 73372 as the sister taxon to all other Crocodylomorpha and not the sister taxon to *Postosuchus kirkpatricki*. This phylogenetic position strengthens the hypothesis that Rauisuchidae and Crocodylomorpha are sister taxa within Paracrocodylomorpha. Further, it shows that the similarity of the postcrania of basal crocodylomorphs and rauisuchids. Of the 19 unambiguous synapomorphies of Crocodylomorpha, only eight are postcranial. An elongated anterior (= preacetabular) process on the ilium is the only character state unambiguously placing CM 73372 closer to crocodyliforms. CM 73372 lacks crocodylomorph characters, such as elongated distal carpals and a flat dorsal margin of the ilium. The phylogenetic position of CM 73372 is near *Hesperosuchus* "*agilis,*" which is a crocodylomorph from the same quarry. These two taxa can be differentiated based on *Hesperosuchus* "*agilis*" possessing elongated distal carpals.

The placement of CM 73372 as the basalmost crocodylomorph has important implications. CM 73372 is much larger than nearly all non-crocodyliform crocodylomorphs with the possible exception of the large-bodied taxon *Redondavenator* (Nesbitt et al., 2005) from the Redonda Formation in northern New Mexico. Though *Redondavenator* is likely a basal crocodylomorph, the phylogenetic position of this taxon has yet to be tested. The estimated body size of CM 73372 (=3–4 meters) falls easily in the range of most non-crocodylomorph paracrocodylomorphs. Given that nearly all crocodylomorphs are much smaller than that of non-crocodylomorph paracrocodylomorphs, CM 73372 may represent the last large-bodied member of Crocodylomorpha until the Early Jurassic.

Furthermore, the phylogenetic position of CM 73372 illustrates the difficulty of assigning isolated postcrania or even partial skeletons to either a rauisuchid or a basal crocodylomorph in sediments from the Upper Triassic.

Pterosaurs Lie at the Base of Avemetatarsalia

I use the two most complete basal pterosaurs known to date, *Eudimorphodon* and *Dimorphodon*, to represent Pterosauromorpha and to test the phylogenetic position of the group. The highly controversial taxon *Scleromochlus* (Padian, 1984; Sereno, 1991a; Benton, 1999) is not used in this analysis. The relationships of pterosaurs to other clades of saurians are intensely debated (see summary in Bennett, 1996). Out of a discrete phylogenetic context, pterosaurs were allied with "eosuchians" (e.g., Wild, 1978), placed as the sister taxon to all other archosauromorphs (Benton 1983, 1984, 1985), and hypothesized as avian-line archosaurs (Gauthier, 1984, 1986; Padian, 1984; Benton, 1990a). Pterosaurs were, with one exception (Peters, 2000), found as either the basalmost or one of the basalmost groups of avian-line archosaurs in all numerical analyses (Sereno, 1991a; Bennett, 1996; Benton, 1999; Irmis et al., 2007a).

The monophyly of Pterosauromorpha is supported by 14 unambiguous synapomorphies and another 12 possible ambiguous character states (see tree description for details). My analysis finds pterosaurs well nested within archosauriforms as the sister taxon to Dinosauromorpha; this is a result obtained by all recent numerical analyses. The position of pterosaurs at the base of Avemetatarsalia is well supported. Bennett (1996) showed that pterosaurs lie in the same topological position as I find in a complete analysis, but he stated that pterosaurs do not possess many of the synapomorphies of more inclusive clades (Archosauria, *Euparkeria* + Archosauria, etc.). Therefore, I present a list of characters that unambiguously support archosauriform clades and indicate whether the character is present in (basal) pterosaurs:

Archosauriformes

(1) Absence of a parietal foramen (63-1). Basal pterosaurs lack a parietal foramen.
(2) Jugal-quadratojugal contact present (70-1). Present in basal pterosaurs.
(3) Ectopterygoid forms all of the lateral edge of the lateral pterygoid flange (88-1). Not known in basal pterosaurs.
(4) Ossified laterosphenoid present (92-1). Present in pterosaurs (Bennett, 1996).
(5) Antorbital fenestra present (136-1). Present in basal pterosaurs.
(6) Lateral mandibular fenestra present (138-1). Present in *Dimorphodon* and a specimen referred to *Eudimorphodon* (BPS 1994 I 51).
(7) Presence of tooth serrations (168-1). Present in *Dimorphodon*.

Erythrosuchus + Archosauria

(1) Absence of a large anteriorly opening foramen on the anterolateral surface of the maxilla (31-0). Also absent in basal pterosaurs.
(2) Basipterygoid processes directed anteriorly or ventrally at their distal tips (93-1). Not known in basal pterosaurs.
(3) Absence of a ridge on lateral surface of inferior anterior process of the prootic ventral to the trigeminal foramen (94-1). Not known in basal pterosaurs.
(4) Verticalized parabasisphenoid (97-1). Not known in basal pterosaurs.
(5) Absence of supratemporals (145-1). Supratemporals are absent in pterosaurs (Bennett, 1996).
(6) Posteroventral portion of the dentary laterally overlaps the anteroventral portion of the angular (164-1). Present in *Dimorphodon* and a specimen referred to *Eudimorphodon* (BPS 1994 I 51).
(7) Thecodont tooth implantation (174-1). Present in basal pterosaurs.
(8) Second primordial sacral rib is not bifurcated (203-1). Not known in basal pterosaurs, but the second primordial sacral rib is not bifurcated in *Campylognathoides* (BSP 1985 I 87).
(9) Entire anterior margin of the scapula is concave (217-1). Difficult to score with confidence in the highly modified scapulae of pterosaurs.
(10) Acromion process of the scapula distinctly raised above the ventral edge of the scapula (220-1). Difficult to score with confidence in the highly modified scapulae of pterosaurs.
(11) Distinct notch between the scapula and coracoid on the anterior margin (221-0).

Difficult to score with confidence in the highly modified scapulae of pterosaurs.

(12) Tarsals 1 and 2 absent (346-1). Both tarsals are absent in all pterosaurs.

(13) Absence of an ossified astragalo-calcaneal canal (369-1). There is no ossified astragalo-calcaneal canal in basal pterosaurs.

(14) Absence of a distinct centrale (381-1). Basal pterosaurs lack a centrale.

(15) Metatarsal IV about the same length or shorter than metatarsal III (393-1). Metatarsal IV is shorter than metatarsal III in *Dimorphodon* (Padian, 1983).

Vancleavea + Archosauria

(1) Postparietal(s) absent (146-1). Postparietals are absent in pterosaurs (Bennett, 1996).

(2) Postaxial intercentra absent (177-1). Postaxial intercentra are absent in pterosaurs (Bennett, 1996).

(3) Ectepicondylar flange of the humerus absent (234-1). An ectepicondylar flange is absent in pterosaurs (Bennett, 1996).

(4) Distal condyles of the femur not projecting markedly beyond shaft (318-1). Distal condyles of the femur not projecting markedly beyond shaft in basal pterosaurs.

Crurotarsi (Phytosauria + Crocodylomorpha)

(1) Parabasisphenoid plate absent (96-2). Not known in basal pterosaurs.

(2) Semilunar depression on the lateral surface of the basal tubera of the parabasisphenoid absent (98-1). Not known in basal pterosaurs.

(3) Absence of teeth on palatal process of the pterygoid (175-1). *Eudimorphodon* is the only pterosaur reported with pterygoid teeth (Wild, 1978). The pterygoid teeth are present on the palatal process of the pterygoid.

(4) Cervical ribs short and stout (196-1). The cervical ribs are short in basal pterosaurs.

(5) Ventral articular surface of the astragalus-calcaneum concavoconvex, with concavity on calcaneum (368-1). Not known in basal pterosaurs.

(6) Ventral articular surface for distal tarsal 4 and the distal end of the tuber of the calcaneum separated by a clear gap (371-1). Not known in basal pterosaurs.

(7) Articular surfaces for fibula and distal tarsal IV on the calcaneum continuous (380-1). The articular surfaces for fibula and distal tarsal IV on the calcaneum are continuous in *Dimorphodon* (Padian, 1983; Sereno, 1991a).

Archosauria

(1) Palatal processes of the maxilla meet at the midline (32-1). Not known in basal pterosaurs.

(2) Lagenar/cochlear recess present and elongated and tubular (118-1). Not known in basal pterosaurs.

(3) External foramen for abducens nerve within prootic only (122-1). Not known in basal pterosaurs.

(4) Antorbital fossa present on the lacrimal, dorsal process of the maxilla, and the dorsolateral margin of the posterior process of the maxilla (the ventral border of the antorbital fenestra) (137-2). This character is difficult to score for any pterosaur as also observed by Bennett (1996). However, a slight fossa in *Dimorphodon* (BMNH 41212) suggests that an antorbital fossa surrounded much of the border of the antorbital fenestra.

(5) Posteroventral portion of the coracoid possesses a "swollen" tuber (225-1). Difficult to score in the highly modified coracoids of pterosaurs.

(6) Lateral tuber (= radial tuber) on the proximal portion of the ulna present (237-1). Not known in basal pterosaurs.

(7) Ratio of longest metacarpal to longest metatarsal <0.5 (245-1). The apomorphically elongated metacarpal IV in pterosaurs nullifies the scoring of this character.

(8) Anteromedial tuber of the proximal portion of the femur present (300-1). Clearly present in *Dimorphodon* (fig. 39).

(9) Tibial facet of the astragalus divided into posteromedial and anterolateral basins (366-1). Not known in basal pterosaurs.

(10) Calcaneal tuber orientation, relative to the transverse plane, between 50° and 90° posteriorly (377-2). Pterosaurs lack a tuber; therefore, this character could not be scored.

Ornithodira

(1) Distal end of neural spines of the cervical vertebrae unexpanded (191-0). The neural spines of the cervical vertebrae are unexpanded in pterosaurs.

(2) Distal expansion of neural spines of the dorsal vertebrae absent (197-0). The expansion of neural spines of the dorsal vertebrae is absent in pterosaurs.

(3) Second phalanx of manual digit II (= 2.2) longer than first phalanx (255-1). This character is present in basal pterosaurs and in dinosaurs.

(4) Trenchant unguals on manual digits I–III (257-1). Present in basal pterosaurs.
(5) Tibia longer than the femur (299-1). Present in basal pterosaurs.
(6) Distal tarsal 4 transverse width subequal to that of distal tarsal 3 (347-1). Present in basal pterosaurs.
(7) Size of articular facet for metatarsal V less than half the width of lateral surface of distal tarsal 4 (348-1). Present in basal pterosaurs.
(8) Anterior hollow of the astragalus reduced to a foramen or absent (357-1). Present in basal pterosaurs.
(9) Anteromedial corner of the astragalus acute (361-1). Clearly present in *Dimorphodon* (fig. 46).
(10) Compact metatarsus, metatarsals II–IV tightly bunched (at least half of the length) (382-1). Present in pterosaurs.
(11) Osteoderms absent (401-0). Pterosaurs lack osteoderms.
(12) Gastralia well separated (412-1). The gastralia of the holotype of *Eudimorphodon* are well separated as they are in dinosaurs. In contrast, the gastralia of most non-ornithodiran archosauriforms form an extensive, interlocking basket.

The list of unambiguous character states from Archosauriformes to Ornithodira clearly illustrates that basal pterosaurs possess most of the character states that place them at the base of avian-line archosaurs. In fact, there is little conflicting data once confirmed states, unknown states, and nonapplicable states are removed. Of the contradictory data, the absence of a feature found within Archosauriformes likely represents an apomorphy of Pterosauromorpha rather than a character that does not support Pterosauromorpha within Archosauriformes, Archosauria, or Ornithodira. Other character states once cited as support for a more basal position within Archosauromorpha may represent autapomorphies or do not neccisarily point to a more basal position in Archosauromorpha given new character distributions with the addition of more basal archosaur taxa. For example, *Eudimorphodon* bears teeth on the palatal process of the pterygoid (Wild, 1978). The absence of pterygoid teeth was once thought to represent an apomorphy for Archosauria (e.g., Sereno, 1991a; Juul, 1994). However, it is now clear that some archosaurs (e.g., the dinosaur *Eoraptor*, the suchian *Turfanosuchus*) do have pterygoid teeth. Archosaurs with pterygoid teeth have them present only on the palatal ramus of the pterygoid, the same as *Eudimorphodon*.

The character states supporting pterosaurs as members of Archosauria and Ornithodira are not restricted to character states related to locomotion as suggested by Bennett (1996). As demonstrated in the list above, the character states cover features present all over the body, not just in the hind limb. Furthermore, it is difficult to argue that the restricted number of tarsals, the size of the distal tarsals, and the shape of the proximal tarsals in pterosaurs would be convergent with those of dinosauromorphs based on function alone (Sereno 1991a). In summary, Pterosauromorpha is well supported as the sister taxon to Dinosauromorpha.

LAGERPETIDAE IS A MONOPHYLETC TAXON

Lagerpetidae (sensu Nesbitt et al., 2009b), containing *Lagerpeton*, *Dromomeron romeri*, and *Dromomeron gregorii,* is found at the base of Dinosauromorpha. This clade is robustly supported by five unambiguous synapomorphies (see tree description). Most of the autapomorphies listed by Sereno and Arcucci (1994a) for *Lagerpeton* now represent synapomorphies of Lagerpetidae or are present in elements not preserved in *D. romeri* and *D. gregorii*. Currently, the presence of a bladelike fourth trochanter is the only unambiguous character that separates *Lagerpeton* from *Dromomeron*. Currently, only the pelvic girdle, posterior presacral, sacral, and anterior caudal vertebrae, and the hind limb are known for any lagerpetid.

The existence of a clade of basal dinosauromorphs outside Dinosauria significantly changes the view of early dinosauromorph evolution. Previously, phylogenies suggested that the dinosaur precursors (e.g., *Lagerpeton*, *Marasuchus*) from the Middle Triassic Chañares Formation in Argentina were successive outgroups to Dinosauria (e.g., Sereno and Arcucci, 1994b). Each branch was represented by a single taxon, and there were no clades including multiple taxa between pterosaurs and dinosaurs. The recognition of Lagerpetidae as a clade, and a diverse Silesauridae demonstrate that basal dinosauromorphs were more diverse than previously thought and evolved into several clades that existed during the Middle and Late Triassic, partially overlapping in time and space with early dinosaurs (Irmis et al. 2007a).

LAGERPETIDAE AS THE SISTER TAXON TO ALL PTEROSAURS?: Lagerpetidae was found closer to dinosaurs than pterosaurs in the analysis presented here. However, a few peculiar features in the hind limb of lagerpetids merit discussion and suggest that they may be more closely related to pterosaurs than to dinosaurs. Specifically, the ankle of lagerpetids is more similar to that of basal pterosaurs (in particular, *Dimorphodon*) than to basal dinosauriforms and early dinosaurs. The calcaneum and astragalus are coossified, the ventral surface of the calcaneum is rounded like that of the astragalus, there is no posterior groove of the astragalus, and the calcaneum lacks any sort of calcaneal tuber in both *Dimorphodon* and lagerpetids. These four character states shared between lagerpetids and *Dimorphodon* are absent in basal dinosauriforms (e.g., *Marasuchus*, *Asilisaurus*). Basal dinosauriforms have a separate calcaneum and astragalus, the ventral surface of the calcaneum, although rounded, is different from the ventral surface of the astragalus, they have a posterior groove of the astragalus, and the calcaneum bears a small calcaneal tuber. It is possible that pterosaurs and lagerpetids share additional ankle characters or differences; however, the ankle of *Dimorphodon* is heavily ossified, thus concealing the distal end of the tibia and the proximal surface of the astragalus.

Conversely, lagerpetids share the following character states with other basal dinosauromorphs, and these are apparently absent in pterosaurs: posterolateral portion (= fossa trochanterica, = posterolateral depression, facies articularis antitrochanterica) of the femoral head ventrally descended, a straight cnemial crest, the longest metatarsal longer than 50% of tibial length, metatarsal V "hooked" proximal end absent, articular face for distal tarsal 4 subparallel to shaft axis, and metatarsal V without phalanges and tapers to a point. The resulting position of lagerpetids closer to dinosaurs than to pterosaurs in my analysis indicates the convergence of character states in the ankle that are shared between *Dimorphodon* and lagerpetids, the reversal of the character states to the plesiomorphic condition at Dinosauriformes, or a combination of both. Only new material of basal pterosaurs or lagerpetids can further test the hypothesis that lagerpetids may be more closely related to pterosaurs than to dinosaurs.

"SILESAURS" ARE MONOPHYLETIC AND SISTER TAXON OF DINOSAURIA

Dzik (2003) described the Late Triassic *Silesaurus opolensis* from nearly complete material from Poland. *Silesaurus* bears a curious mix of classical dinosaurian features (e.g., possession of a brevis fossa of the ilium, large ascending process of the astragalus), ornithischian dinosaur features (e.g., presence of a "beak," herbivorous teeth), and non-dinosaurian characters (e.g., closed acetabulum, a notch ventral to the femoral head, quadrapediality). Although Dzik (2003) only commented on the potential dinosaurian relationships in the initial publication, subsequent publications hypothesized that *Silesaurus* is a non-dinosaurian dinosauriform (Langer and Benton, 2006; Ezcurra, 2006; Nesbitt, 2007; Irmis et al., 2007a). There was also speculation that *Silesaurus* is an early member of the Ornithischia (Ferigolo and Langer, 2007; Dzik and Sulej, 2007). The potential that *Silesaurus* may represent the sister taxon of Dinosauria renewed the spark in basal dinosaur studies because *Silesaurus* is nearly complete and well preserved; *Silesaurus* can help with character optimization at the base of Dinosauria, and it can help resolve the topology of contentious taxa. For example, the phylogenetic positions of controversial taxa (e.g., *Herrerasaurus*, *Eoraptor*) are directly related to the diagnosis of Dinosauria (see Langer and Benton, 2006) and character optimizations at the base of Dinosauria. These two problems are directly related to the outgroup of Dinosauria.

Since the discovery of *Silesaurus*, other *Silesaurus*-like taxa have been identified from Triassic localities across Pangaea. These taxa include *Sacisaurus* from the Late Triassic of Brazil (Ferigolo and Langer, 2007) and the recognition that *Eucoelophysis* represents a

Silesaurus-like taxon rather than a coelophysoid theropod (Nesbitt et al., 2005b; Ezcurra, 2006; Nesbitt et al., 2007). Additionally, Nesbitt et al. (2007) hypothesized that *Pseudolagosuchus* from the Middle Triassic of Argentina and *Technosaurus* from the Late Triassic of Texas may be close relatives to *Silesaurus*.

Recently, two explicit phylogenetic analyses (Langer and Benton, 2006; Irmis et al., 2007a) found *Silesaurus* as the sister taxon to Dinosauria. To date, no numerical analysis of basal dinosaur relationships placed *Silesaurus* within Dinosauria or as an ornithischian. The numerical analyses of Irmis et al. (2007a) and Ezcurra (2006) found two different relationships between *Silesaurus*-like taxa; Ezcurra (2006) found *Eucoelophysis* and *Silesaurus* as successive sister taxa to Dinosauria, whereas Irmis et al. (2007a) found a monophyletic clade of *Silesaurus* + *Eucoelophysis* as the sister taxon of Dinosauria. Furthermore, Ezcurra (2006) included *Pseudolagosuchus* and found *Pseudolagosuchus*, *Silesaurus*, and *Eucoelophysis* as successive sister taxa to Dinosauria.

The opposing positions of Ezcurra (2006) and Irmis et al. (2007) allow testing of whether *Silesaurus*-like taxa form a monoplyletic clade or they form a grade outside Dinosauria. To test this, I include many *Silesaurus*-like taxa including *Silesaurus*, *Sacisaurus*, *Eucoelophysis*, *Asilisaurus*, *Pseudolagosuchus,* and *Lewisuchus*. Potential valid *Silesaurus*-like taxa such as *Technosaurus* and a taxon known from isolated bones from the base of the Upper Triassic Dockum Group of Texas are not included in the final analysis because their scorings are redundant with other *Silesaurus*-like taxa.

All hypothesized *Silesaurus*-like taxa are recovered as members of Dinosauriformes more closely related to Dinosauria than to *Marasuchus*. This clade (Silesauridae + Dinosauria) is supported by the following 13 unambiguous synapomorphies: anterior tympanic recess on the lateral side of the braincase present (101-1); auricular recess extends onto internal surface of epiotic/supraoccipital (133-1); atlantal articulation facet in axial intercentrum, shape concave with upturned lateral borders (178-1); crest dorsal to the supraacetabular crest/rim confluent with anterior extent of the anterior (= preacetabular) process of the ilium (265-2); pubis more than 70% or more of femoral length (278-1); extensive medial contact between the ischia, but the dorsal margins are separated (291-1); sharp ridge (= dorsolateral trochanter of some) on the dorsolateral margin of the proximal portion of the femur (307-1); straight transverse groove on the proximal surface of the femur (314-1); posterolateral flange of the distal portion of the tibia nearly contacts or contacts fibula (334-1); anterior edge of the proximal portion of the fibula tapers to a point and arched anteromedially (342-1); midshaft diameters of metatarsals I and V less than II–IV (384-1); distal articulation surface of metatarsal IV deeper than broad (391-1); and metatarsal IV length subequal to or shorter than metatarsal II (395-1). These 13 character states represent a significant increase in the knowledge of character-state transformations immediately outside Dinosauria.

In my analysis, all potential *Silesaurus*-like taxa form a monophyletic clade as the sister taxon to Dinosauria (see the description of Dinosauria for characters excluding silesaurids from Dinosauria). basalmost member of the clade is a composite taxon of *Lewisuchus*/*Pseudolagosuchus* (see discussion below). The base of the clade is well resolved and is supported by four unambiguous character states including: foramina of the hypoglossal nerve (XII) nearly aligned in a near anteroposteriorly plane (113-1); rugose ridge on the anterolateral edges of the supraoccipital (127-1); cervical centra 3–5 longer than middorsal (181-1); notch ventral to the proximal head of the femur (304-1). The next clade closer to *Silesaurus* contains the *Asilisaurus*, *Eucoelophysis*, *Sacisaurus*, and *Silesaurus*. Seven unambiguous and four ambiguous synapomorphies support this clade. The seven unambiguous synapomorphies include: anterior extent of the dentary tapers to a sharp point (155-1); dentary teeth absent in the anterior portion (166-1); maxillary and dentary crowns apicobasally short and subtriangular (173-1); sacral ribs shared between two sacral vertebrae (208-1); straight medial articular facet of the proximal portion of the femur (309-1); distal condyles of the femur divided posteriorly between ¼ and ⅓ the length of the shaft (324-1). Some of the ambiguous characters supporting this clade, such as teeth fused to the bone of attachment at the base (174-0) and foramina for entrance of cerebral branches of internal carotid artery into the braincase positioned on the ventral surface, represent characters only present in silesaurids among avian-line archosaurs. Although both *Sacisaurus* (21% characters scored) and *Eucoelophysis* (6% characters scored) are largely incomplete, a clade containing these two taxa and *Silesaurus* is supported here.

Is a monophyletic Silesauridae incompatible with the results of Ezcurra (2006)? Ezcurra (2006) hypothesized that *Eucoelophysis* is more closely related to Dinosauria than *Silesaurus*. He cited three unambiguous synapomorphies supporting *Eucoelophysis* + Dinosauria including: proximal end of the pubis with acetabular depression poorly developed or absent (214-1); pubic shaft nearly straight (217-1); and femoral trochanteric shelf absent (239-0). The first two characters are scored from the pubis of *Eucoelophysis*. Nesbitt et al. (2007) questioned the inclusion of the pubis originally assigned to *Eucoelophysis* to the holotype because the preservation is different from the rest of the holotype, the pubis was not found articulated to the other material, and there were other taxa mixed in with the holotype of *Eucoelophysis*. Therefore, the pubis originally assigned to *Eucoelophysis* cannot be shown to belong to the rest of the holotype with any confidence. The first two characters listed by Ezcurra (2006) must be scored as "?" for *Eucoelophysis*. The last character, femoral trochanteric shelf absent, is difficult to interpret because it was homoplastic in Ezcurra's (2006) analysis, and a femoral trochanteric shelf is absent in smaller specimens of *Silesaurus* (Nesbitt et al., 2007). Therefore, there were no concrete character states separating *Eucoelophysis* from *Silesaurus* in Ezcurra's (2006) analysis. When Ezcurra's (2006) character scores were modified and rerun, *Eucoelophysis* and *Silesaurus* formed a weakly supported monophyletic clade. Nevertheless *Pseudolagosuchus* is still basal to both forms when the analysis is reanalyzed using these modifications.

One of the most surprising results of this study is the inferred convergence between both *Silesaurus* and ornithischians and *Silesaurus* and theropods. A monophyletic Silesauridae results in two Middle Triassic members, *Lewisuchus*/*Pseudolagosuchus* and *Asilisaurus*, as the two basalmost members of the clade. These two taxa each have only two sacral vertebrae, a convex articulation for the fibula on the calcaneum, a calcaneal tuber, the absence of a brevis fossa, the absence of a large ascending process of the astragalus, and the absence of a deep depression on the posterior portion of the neural arches of the cervicals. Therefore, character states that *Silesaurus* was found to share with dinosaurs (e.g., presence of brevis fossa, a large ascending process of the astragalus, the absence of a calcaneal tuber) by Langer and Benton (2006), Ezcurra (2006), and Irmis et al. (2007a) are convergent between *Silesaurus* and members of the Dinosauria. Similarly, character states that appear synapomorphic with theropods (e.g., deep depression on the posterior portion of the neural arches of the cervicals, "four" sacral vertebrae) are also interpreted as convergent because they are not found in the taxa basal to *Silesaurus* and basal toTheropoda.

Ferigolo and Langer (2007) and Dzik and Sulej (2007) hypothesized a close relationship between *Silesaurus* and ornithischians and cited potential synapomorphies between the two taxa. Here, the placement of *Silesaurus* as more closely related to ornithischians that to any other taxon requires an addition of a minimum of 11 steps to the tree. Furthermore, nearly all of the classic dinosaur synapomorphies (e.g., open acetabulum, see below) become homoplasies among the three major dinosaur lineages. However, all the characters cited that do not occur in a variety of dinosauriforms (e.g., increasing the number of sacral vertebrae) are restricted to the dentition and mandible characters. The acquisition of ornithischian-like dentition and a "beak" evolved by the Middle Triassic (e.g., *Asilisaurus kongwe*), and these character states were retained through much of the Triassic. However, the basalmost taxon in Silesauridae, *Lewisuchus*/*Pseudolagosuchus*, lacks a tapering, toothless anterior end of the dentary and bears typical carnivorous teeth (recurved posteriorly, mediolaterally compressed). The position of *Lewisuchus/Pseudolagosuchus* suggests that the ornithischian-like dentition of *Silesaurus* and other silesaurids is convergent with that of some ornithischians. Furthermore, the dentition of *Silesaurus* is much more like that of taxa such as *Lesothosaurus* in general form (e.g., no extensive shearing surface). This is at odds with the type of teeth in the hypothesized basalmost ornithischians, *Pisanosaurus* and *Heterodontosaurus* (Butler et al., 2008b). Ferigolo and Langer (2007) suggested that the tapering anterior portion of the dentary in *Silesaurus* and *Sacisaurus* was homologous to the predentary of ornithischians. Even if *Silesaurus* and *Sacisaurus* are scored as having a predentary, the position of silesaurids does not change. Furthermore, an anteriorly tapering dentary also occurs in a number of archosauromorphs suggested to be herbivorous such as the aetosaur *Longosuchus* and most rhynchosaurs such as *Hyperodapedon*. Finally, many recent papers (Parker et al., 2005; Butler et al., 2006; Nesbitt et al., 2007; Irmis et al., 2007b; Flynn et al., 2010) have shown the many dangers of primarily using teeth to assign specimens to various clades, as evidenced by the large number of clades in the Triassic that have herbivorous teeth.

LEWISUCHUS AND *PSEUDOLAGOSUCHUS*: *Lewisuchus*, represented by a skull, an anterior portion of a skeleton, and a tibia (Romer, 1972d), and *Pseudolagosuchus*, represented by a few vertebrae, a pelvic girdle and much of a hind limb, are both from nodules from the Chañares Formation. Although *Lewisuchus* has been mostly ignored since Romer's initial description, *Pseudolagosuchus* has been important to character optimizations at the base of Dinosauria (Novas, 1996; Ezcurra, 2006). Arcucci (1997, 1998, 2005) argued that *Lewisuchus* and *Pseudolagosuchus* are synonymous; Arcucci (1998) stated that the tibia and dorsal vertebrae of *Lewisuchus* are similar to those of *Pseudolagosuchus*, but failed to cite discrete character states. Hutchinson (2001a, 2001b) and Langer and Benton (2006) accepted the synonymy of the two taxa. Nesbitt et al. (2007) suggested that *Pseudolagosuchus* may be more closely related to *Silesaurus* than to other dinosauriforms based on a few potential synapomorphies, but did not discuss *Lewisuchus*.

Here, both *Lewisuchus* (31% characters scored) and *Pseudolagosuchus* (23% characters scored) are kept separate as distinct terminal taxa for the first run of the analysis. In the strict consensus tree (MPTs = 432, TL = 1292), *Pseudolagosuchus* and *Lewisuchus* are found as dinosauriforms, but they are found in a polytomy with a silesaurid clade (*Asilisaurus* + *Eucoelophysis* + *Sacisaurus* + *Silesaurus*) and Dinosauria (fig. 57). *Lewisuchus* was found as a silesaurid in two MPTs, whereas *Pseudolagosuchus* is found with *Lewisuchus* in a polytomy at the base of Silesauridae. In a subsequent run, *Lewisuchus* and *Pseudolagosuchus* are combined into one terminal taxon (54% characters scored). The resultant consensus tree (fig. 52) resolves a *Lewisuchus/Pseudolagosuchus* taxon as the basalmost member of Silesauridae.

WHAT CHARACTER STATES SUPPORT *LEWISUCHUS* AND *PSEUDOLAGOSUCHUS* WITHIN SILESAURIDAE? *Pseudolagosuchus* shares only one unambiguous synapomorphy with other silesaurids (a notch ventral to the proximal head of the femur [304-1]) and one ambiguous synapomorphy (straight transverse groove on the proximal surface of the femur [314-1]). However, *Lewisuchus* shares three unambiguous synapomorphies with other silesaurids including: exits of the hypoglossal nerve (XII) nearly aligned in a near anteroposteriorly directed plane (113-1), rugose ridge on the anterolateral edges of the supraoccipital (127-1), and cervical centra 3–5 longer than middorsal (181-1).

This phylogenetic analysis places both taxa in the same topological position, and both *Pseudolagosuchus* and *Lewisuchus* share synapomorphies with other silesaurids independently of each other. Moreover, the four unambiguous synapomorphies that are shared between *Lewisuchus/Pseudolagosuchus* and other silesaurids have a CI of 1, demonstrating that the character shared by *Lewisuchus/Pseudolagosuchus* and other silesaurids are unique among basal archosaurs. Currently, the two taxa cannot be formally synonymized at present because they do not share any autapomorphies. The two taxa overlap in only one element, the tibia. In

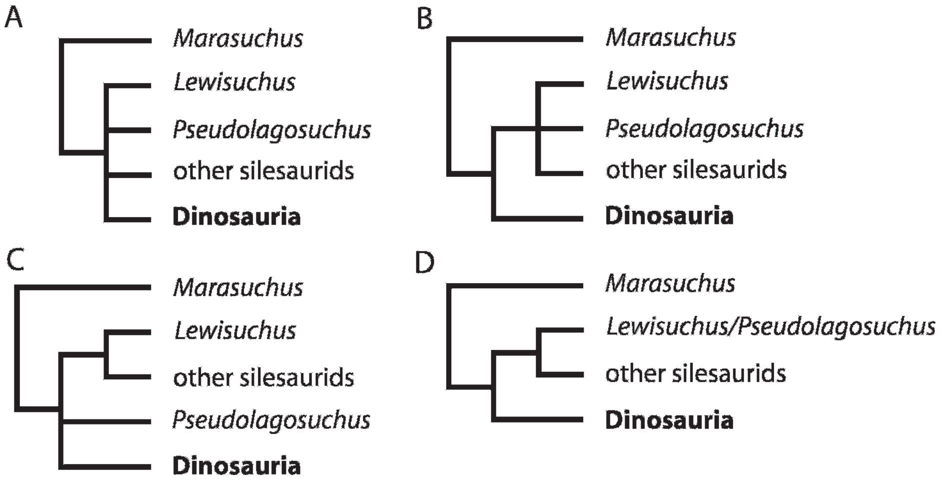

Fig. 57. The possible pylogenetic positions of *Lewisuchus* and *Pseudolagosuchus* when both taxa are kept as separate terminal taxa (A–C) compared to the result when *Lewisuchus* and *Pseudolagosuchus* are combined in a single terminal taxon (D).

retrospect, the tibia of *Lewisuchus* (UNLR 01; Romer, 1972d: fig. 8, incorrectly identified as the femur) bears a strong cnemial crest like that of other dinosauriforms, specifically *Pseudolagosuchus*. A discrete cnemial crest does not unambiguously indicate that *Pseudolagosuchus* and *Lewisuchus* are synonymous, though it does indicate that both taxa are dinosauriforms. If they are synonymized, *Lewisuchus* (Romer, 1972d) will have priority over *Pseudolagosuchus* (Arcucci, 1987).

Silesauridae conclusions. Silesaurids are a clade of potentially herbivorous dinosauriforms that were present from the Anisian to at least the middle of the Norian. Currently, the stratigraphically oldest member of the avian-line archosaurs is *Asilisaurus kongwe* from the Manda Beds (Nesbitt et al., 2010). As indicated by the sister-group relationship between silesaurids and dinosaurs, it is clear that the lineage leading to Dinosauria must have been present by the Anisian (fig. 58B).

Dinosaurs Are Monophyletic

The monoplyly of Dinosauria is well supported in accordance with nearly all previous numerical phylogenetic analyses (Gauthier, 1986; Benton and Clark, 1988; Juul, 1994; Benton, 1999; 2004; Langer and Benton, 2006; Irmis et al., 2007a). I tested the monophyly of Dinosauria in the broadest context yet constructed and including most "thecodonts" as proposed by various authors arguing for a diphyletic or polyphyletic origination of the three major lineages of Dinosauria (e.g., theropods evolved from pseudosuchians, whereas sauropodomorphs evolved from proterosuchians [Thulborn, 1975]). Dinosauria is diagnosed by 12 unambiguous synapomorphies, many of which were found previously (see below). As a consequence, the placement of silesaurids, especially *Silesaurus*, is well supported outside Dinosauria. The following paragraphs describe the unambiguous and ambiguous synapomorphies for Dinosauria in a comparative context with previous results.

Unambiguous synapomorphies found here and previously: supratemporal fossa present anterior to the supratemporal fenestra (144-1) (Gauthier, 1986; Novas, 1996; Sereno, 1999); epipophyses present in postaxial anterior cervical vertebrae (186-0) (Novas, 1996; Langer and Benton, 2006); apex of deltopectoral crest situated at a point corresponding to more than 30% down the length of the humerus (230-1) (Bakker and Galton, 1974; Novas, 1996; Sereno, 1999; Fraser et al., 2002; Langer and Benton, 2006; Ezcurra, 2006; Irmis et al., 2007a); radius shorter than 80% of humerus length (241-1) (Irmis et al., 2007a); fourth trochanter a sharp flange (316-

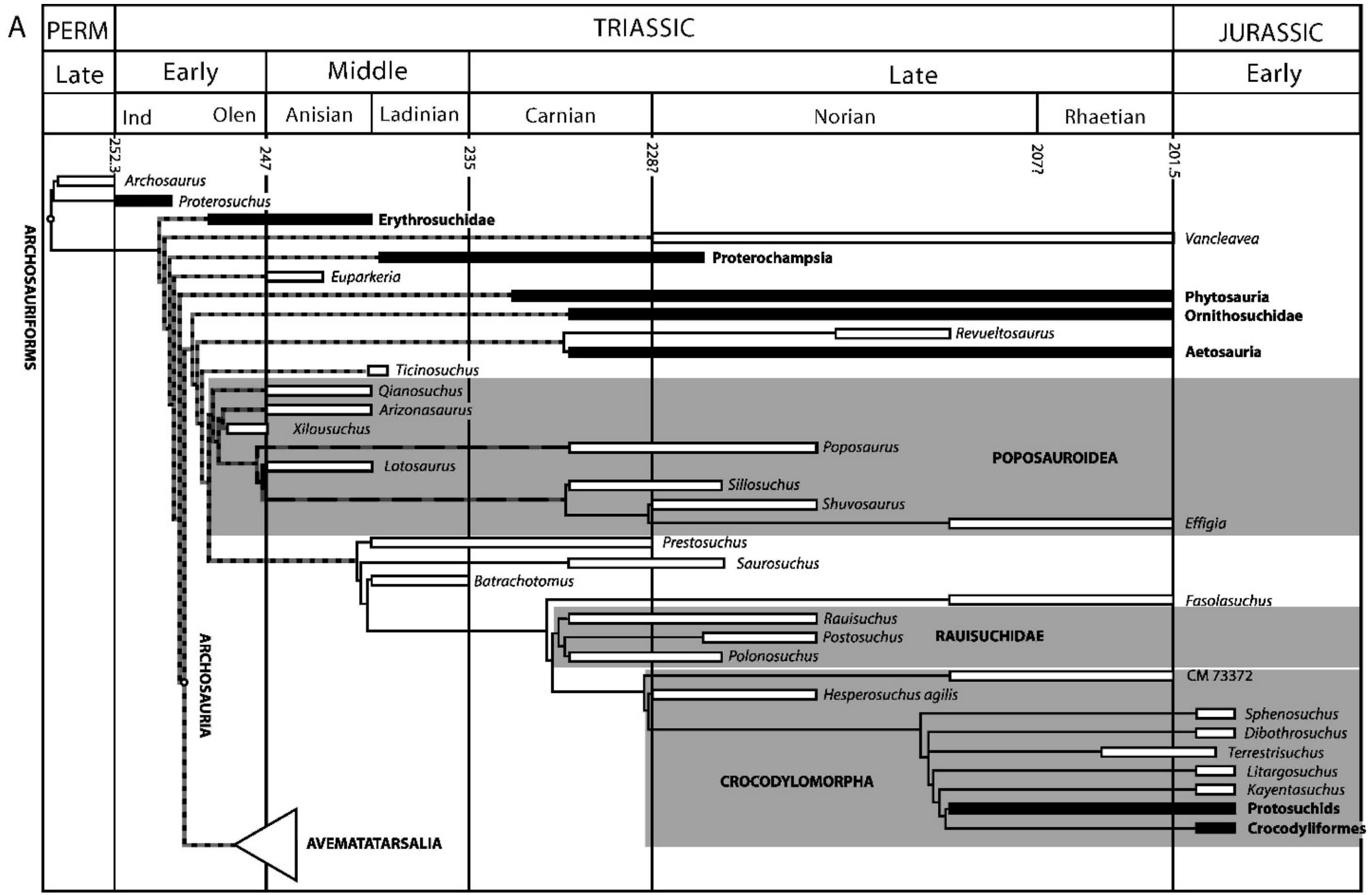

Fig. 58. **A,** time-calibrated phylogeny of archosauriforms based on the relationships found in the phylogeny presented in figure 51. Timescale based on Gradstein et al. (2004) with the recent modifications of Muttoni et al. (2004, 2009), Mundil et al. (2004, 2010), Furin et al. (2006), and Schaltegger et al. (2008). The black bars represent ranges of clades whereas white boxes represent the possible range of taxa. Short dashed line = lineages that diverged by the end of the Early Triassic. Long dashed line = lineages that diverged by the end of the Anisian. Abbreviations: PERM = Permian; Ind = Induan; Olen = Olenekian.

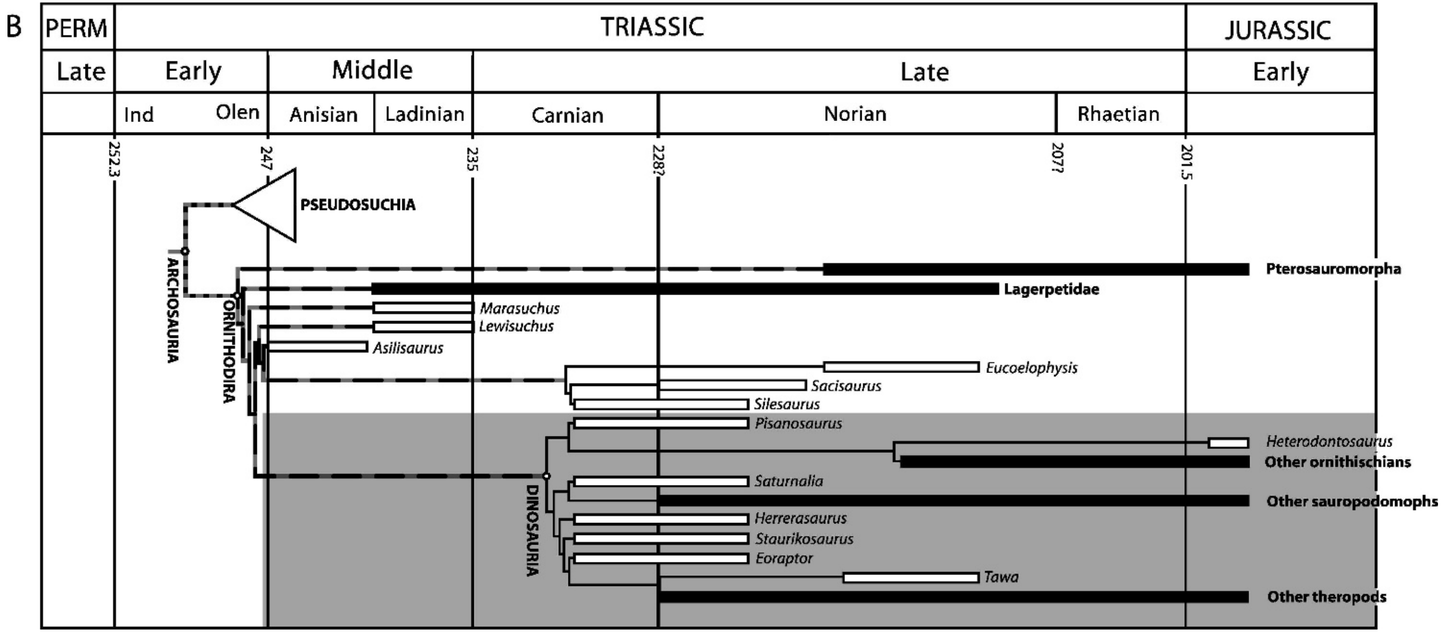

Fig. 58. (Continued) **B,** time-calibrated phylogeny of avemetatarsalians based on the relationships found in the phylogeny presented in figure 52.

1) (similar to a character cited by Bakker and Galton, 1974); fourth trochanter asymmetrical, with distal margin forming a steeper angle to the shaft (317-1) (found in ACCTRAN in Langer and Benton, 2006; Ezcurra, 2006); proximal articular facet for fibula of the astragalus and calcaneum occupies less than 0.3 of the transverse width of the element (362-1) (Langer and Benton, 2006).

Unambiguous synapomorphies found here for the first time are: exocciptials do not meet along the midline on the floor of the endocranial cavity (115-1); proximal articular surfaces of the ischium with the ilium and the pubis separated by a large concave surface (297-2); cnemial crest arcs anterolaterally (328-2); distinct proximodistally oriented ridge present on the posterior face of the distal end of the tibia (336-1).

Potential synapomorphies found here and by others include: ventral margin of the acetabulum of the ilium (273-2) (Bakker and Galton, 1974; Gauthier, 1986; Novas, 1996; Fraser et al., 2002; Langer and Benton, 2006; Ezcurra, 2006; Irmis et al., 2007a); concave articular surface for the fibula of the calcaneum (378-2) (Novas, 1989, 1996); postfrontal absent (44-1) (Benton 1984; Novas, 1996; Sereno, 1999; Fraser et al., 2002; Langer and Benton, 2006); posttemporal opening absent or less than half the diameter of the foramen magnum (141-1) (Novas, 1996; Sereno, 1999; Langer and Benton, 2006; Irmis et al., 2007a); three or two phalanges on manual digit IV (258-2) (Novas, 1996; Sereno, 1999; Fraser et al., 2002); posterior process of the jugal is split by the anterior process of the quadratojugal (71-3) (Sereno and Novas, 1994).

Potential synapomorphies found here only include: three premaxillary teeth (6-0); premaxillary narial fossa expanded in the anteroventral corner of the naris (9-1); concave emargination ventral to the proximal head of the femur (304-2); calcaneal tuber absent (373-1); interclavicle absent (214-1); proximal articular surface of the humerus separated by a gap from the deltopectoral crest (233-1).

Many character states were cited as dinosaur synapomorphies in previous phylogenetic studies that are not found here. The character states did not optimize at Dinosauria in my analysis for three reasons: the addition of silesaurids, some of the cited states were divided into two or more characters, or, in rare cases, the characters were not used. The recent addition of silesaurids into a phylogenetic analysis (e.g., Irmis et al., 2007a) pulled some of the character states outside Dinosauria. Specifically, the following character states do not optimize at Dinosauria because either silesaurids have the same state or the optimization is ambiguous because of new sampling of silesaurids: large anterior trochanter (Bakker and Galton, 1974; Gauthier, 1986; Novas, 1996; Fraser et al., 2002); metatarsals II and IV subequal in length (Sereno, 1991a); reduced ischiadic medioventral lamina (Novas, 1992, 1996); reduced pubis/ischium contact (Fraser et al., 2002); reduction of the tuberocity that laterally bounds the ligament of the femoral head (Novas, 1996; Sereno, 1999); cnemial crest present on tibia (Sereno, 1999); astragalar ascending process present (Sereno, 1999); ectopterygoid dorsal to transverse flange of the pterygoid (Sereno and Novas, 1994; Novas, 1996; Sereno, 1999); pedal digit V shorter than metatarsal I (foot tridactyl in typical dinosaur condition) (Gauthier, 1986; Fraser et al., 2002); quadrate head exposed in lateral view (Sereno and Novas, 1992; Novas, 1996; Sereno, 1999); distal tarsal 4 proximally flat (Novas, 1996; Sereno, 1999; Ezcurra, 2006); posteroventrally oriented glenoid (Bakker and Galton, 1974; Fraser et al., 2002). Most of the previously hypothesized synapomorphies for Dinosauria fit into this category.

Character states that I view as either too simplistic or representing several changes are divided into two or more characters. These include reduced manual digits IV and V (Gauthier and Padian, 1985; Gauthier, 1986; Fraser et al., 2002), inturned femoral head/offset femoral head (Bakker and Galton, 1974; Gauthier, 1986; Fraser et al., 2002; Ezcurra, 2006; Irmis et al., 2007a), mesotarsal ankle (Bakker and Galton, 1974; Gauthier, 1986; Fraser et al., 2002), at least three sacral vertebrae (Novas, 1996; Sereno, 1999; Fraser et al., 2002; Ezcurra, 2006), and the presence of a brevis fossa (Novas, 1996; Sereno, 1999; Fraser et al., 2002). For example, the absolute number of sacral vertebrae is not used. Instead, I split the number of sacral vertebrae into three characters: the presence or absence of a dorsosacral, the presence or absence of a caudosacral, and the presence or absence of an insertion.

Finally, the following characters are not used in this analysis: astragalus with a straight caudal margin (Langer and Benton, 2006); elongate vomers reaching posteriorly at least to the level of the antorbital fenestra (Gauthier, 1986; Fraser et al., 2002); scapula at least three times longer than wide at the base (Gauthier, 1986); ossified, paired sternal plates present (Sereno, 1999).

The previous paragraphs demonstrate that most of the synapomorphies that were proposed for Dinosauria in both a nonphylogenetic and a phylogenetic context are found once again in this comprehensive analysis. Furthermore, as I increased the number of basal members of Dinosauria as well as the number of successive sister taxa, the same characters states optimize at Dinosauria. Remarkably, this is true even though the placement of taxa within Dinosauria remains variable. For example, the findings of Butler et al. (2008b), which placed *Heterodontosaurus* as one of the basalmost ornithischians, had little effect on the optimization of character states at Dinosauria. Furthermore, the same is true for the position of *Herrerasaurus*, either as a saurischian outside Eusaurischia or as a theropod. These observations indicate stabilization of the diagnosis of Dinosauria.

Consequently, synapomorphies at Dinosauria are informative for incorporating fragmentary dinosaur specimens or isolated bones into a phylogeny. For example, Nesbitt et al. (2007), incorporated dozens of fragmentary (potential) dinosaur specimens from the Triassic of the western United States. The incorporation of the more fragmentary dinosaurian fossils led to a better understanding of diversity, distribution, and abundance of early dinosaurs in North America.

MAJOR LINEAGES OF DINOSAURIA: Ornithischia consists of taxa (*Pisanosaurus*, *Eocursor*, *Heterodontosaurus*, *Lesothosaurus*, and *Scuttelosaurus*) that were found as ornithischians in all previous numerical phylogenetic analyses. Ornithischians form a monophyletic clade well supported by 14 unambiguous and seven potential synapomorphies (Bremer = 5). The relationships of these taxa are unresolved, but this analysis is not designed to resolve these relationships. In the most complete analysis, Butler et al. (2008b) found *Pisanosaurus* as the basalmost member of the lineage, as found in other analyses. However, Butler et al. (2008b) found a basal position for *Heterodontosaurus*, which differed from other analyses but was suggested by some authors (Bakker and Galton, 1974). The Triassic record of ornithischians remains poorly represented (Irmis et al., 2007b; Butler et al., 2007, 2008b), but new finds are rapidly filling in the gaps in the early evolution of Ornithischia (Butler et al., 2007, 2008a).

As previously found, Saurischia consists of sauropodomorphs and theropods. Seventeen unambiguous and seven ambiguous synapomorphies support this clade. Contrary to recent findings of Langer and Benton (2006), Ezcurra (2006), and Irmis et al. (2007a), no non-eusaurischian saurischians are found here; *Herrerasaurus*, *Eoraptor*, and *Staurikosaurus* were found within Theropoda (see below). The relationships found for Sauropodomorpha, with *Saturnalia* as the basalmost taxon, reproduce the results of more comprehensive phylogenetic analyses of sauropodomorph relationships (e.g., Yates, 2003; Upchurch et al., 2007). Sauropodomorpha is well supported by six unambiguous and seven potential synapomorphies.

HERRERASAURUS, *STAURIKOSAURUS*, AND *EORAPTOR* ARE THEROPODS: The phylogenetic positions of Herrerasauridae and *Eoraptor* remain the most controversial of basal Dinosauria. Surprisingly, both taxa are known from essentially complete skeletons, a rarity among any Triassic dinosaur. The phylogenetic position of both *Eoraptor* and Herrerasauridae potentially determines the diagnoses and character optimizations at Eusaurischia, Sauropodomorpha, and Theropoda. The systematic position of Herrerasauridae (*Herrerasaurus* + *Staurikosaurus*) was variously considered as the sister taxon to Dinosauria (Gauthier, 1986; Brinkman and Sues, 1987; Novas, 1989, 1992; Benton, 1990a; Fraser et al., 2002), as non-eusaurischian saurischian (Langer, 2004; Langer and Benton, 2006; Ezcurra, 2006; Irmis et al., 2007; Smith et al., 2007; Yates, 2007), or within Theropoda (Novas, 1996; Sereno, 1999, 2007). Similarly, *Eoraptor* was found as either a non-eusaurischian saurischian (Langer, 2004; Langer and Benton, 2006; Yates, 2007) or as a basal theropod (Sereno et al., 1993; Sereno, 1999; Ezcurra, 2006).

Both members of the Herrerasauridae, *Staurikosaurus* and *Herrerasaurus*, and *Eoraptor* are incorporated in the analysis with three basal sauropodomorphs and the well-known neotheropods *Coelophysis bauri*, *Dilophosaurus*, *Allosaurus*, and *Velociraptor*. Although sampling is far from complete in both Sauropodomorpha and Theropoda, the selected taxa are chosen because they were found to be basal in all phylogenetic analyses of basal Dinosauria (e.g., Rauhut, 2003; Langer and Benton, 2006; Yates, 2007).

Herrerasaurus, *Staurikosaurus*, and *Eoraptor* fall into Theropoda when *Tawa* is also in the analysis. Furthermore, a monophyletic Herrerasauridae is not recovered; *Staurikosaurus* is more closely related to neotheropods than to *Herrerasaurus*. Theropoda is generally well supported (Bremer = 4) by eight unambiguous and five potential synapomorphies. However, many of the unambiguous synapomorphies found in this analysis are found in the manus (metacarpals proximal ends abut one another without overlapping [246-1]; extensor pits on the proximodorsal portion of metacarpals I–III deep and asymmetrical [250-1]). Langer and Benton (2006) argued that these character states are predatory features and should be viewed as convergences. Furthermore, two synapomorphies of the manus, metacarpal proximal ends abut one another without overlapping and extensor pits on the proximodorsal portion of metacarpals I–III deep and asymmetrical, are also clearly present in *Heterodontosaurus*. Other synapomorphies of Theropoda (mediolaterally thin pubic boot [284-1], distal caudal vertebrae elongated more than a quarter of the adjacent centrum [211-1], lateral [fibular] condyle of the proximal portion of the tibia level with the medial condyle at its posterior border [331-1], and humerus length shorter than 0.6 of the length of the femur [231-1]) have high CI values and seem to only occur in *Herrerasaurus*, *Staurikosaurus*, *Eoraptor*, *Tawa*, and neotheropods. Another potential synapomorphy, bone wall thickness at or near midshaft of the femur, thickness/diameter >0.2, <0.3 (323-1), seems to support Theropoda with the current constitution.

Most of the characters used by Langer and Benton (2006) to exclude *Herrerasaurus* and *Eoraptor* from Eusaurischia are included in this analysis. Langer and Benton (2006) found five unambiguous synapomorphies supporting Eusaurischia. The results obtained here suggest that these five character states are convergent within basal Sauropodomorpha and Neotheropoda.

The relationships of basal ornithischians are unresolved here, and thus, the optimizations of character states at Dinosauria and Eusaurschia may be affected. To test for the possibility that the unresolved relationships of ornithischians are influencing the position of *Herrerasaurus* and similar forms, the ornithischian relationships were constrained to those found by Butler et al. (2008b) and Irmis (2008). The in-group composition of Theropoda did not change; however, the support for this clade dropped (Bremer of 4 vs. 1).

The removal of *Tawa* reduces Saurischia into a large polytomy containing *Herrerasaurus*, *Staurikosaurus*, Sauropodomorpha, and *Eoraptor* + Neotheropoda. These results suggest that *Tawa* bears a suite of morphological features preserved in neotheropods and *Herrerasaurus*-like taxa. A more complete understanding of the transformation of in-group members and character optimizations will follow with a more thorough investigation of the anatomy of *Tawa*. For example, Nesbitt et al., (2009c) included more neotheropod taxa and found a similar relationship between *Tawa* and other neotheropods.

Tawa + Neotheropoda form a robust clade supported by seven unambiguous synapomorphies. Neotheropod is the most well-supported node. It is supported by 16 unambiguous synapomorphies, many of which only occur only in neotheropods. As previously found (e.g., Rauhut, 2003; Yates, 2005; Smith et al., 2007), *Dilophosaurus* is more closely related to Aves than to *Coelophysis bauri*.

THE EARLY RECORD OF ARCHOSAURIFORMS

By definition, the most basal archosauriforms are the proterosuchians, a group known from Russia, South Africa, and China (Gower and Sennikov, 1997). Unexpectedly, proterosuchians appear in the fossil record before any other clade of archosauriform. The oldest recorded archosauriform, *Archosaurus rossicus* Tatarinov, 1960, derives from the uppermost Permian Vyazniki locality in Russia (~253–252 Ma). This locality produced typical members of the Permian assemblage such as pareisaurs (*Obirkovia*) and anthracosaurs (chroniosuchians) (Sennikov and Golubev, 2006). The increased number of teeth (7–9) and a downturned anterior portion of the premaxilla of *Archosaurus* clearly unites the form with *Proterosuchus*. In fact, *Archosaurus* was added to the phylogenetic analysis and was found well supported as the sister taxon to *Proterosuchus*. *Proterosuchus fergusi* from South Africa is the next taxon to appear in the fossil record. Detailed stratigraphic sections and intense sampling at the Permian-Triassic boundary in South Africa placed the first occurrence of *Proterosuchus* seven meters above the Permian-Triassic boundary (Smith and Botha, 2005; Botha and Smith, 2006). The proximity of the first appearance of *Proterosuchus* essentially at the Permian-Triassic boundary calibrates the phylogeny of basal archosauriforms.

Non-archosaurian archosauriforms such as *Fugusuchus*, *Proterosuchus*, NM QR 3570 (Modesto and Botha-Brink, 2008), and *Vjushkovia*/*Garjainia* seemed to have been the only members of the Archosauriformes present in the Early Triassic. However, the occurrence of *Xilousuchus* in the late Early Triassic of China and *Asilisaurus kongwe* from the Anisian of Africa implies that most major archosaur lineages were present by the late Early Triassic and the Anisian (fig. 58A–B). The phylogenetic position and age of *Xilousuchus* also indicates that the lineages of the non-archosaurian archosauriforms *Vancleavea*, Proterochampsia, *Euparkeria*, and Phytosauria were also present in the Early Triassic even though the earliest members of these lineages appear either in the Middle or Late Triassic.

Quality of the Early Archosaur Fossil Record

The archosaur fossil record is generally considered well sampled in the Triassic (Muller and Reisz, 2005). This is clear from the extensive collections of vertebrates from the Triassic of the western United States, Argentina, Brazil, and Europe (e.g., Rogers et al., 1993, 2001; Jenkins et al., 1994; Long and Murry, 1995; Shishkin et al., 2000; Langer, 2005a, 2005b; Schoch et al., 2010). However, the phylogeny presented in this paper suggests that much of the early diversification of Archosauria occurred in the Early Triassic and the Anisian. Furthermore, *Xilousuchus* is the only member of the Archosauria that is clearly present in the Early Triassic. The only other potential archosaur from the Early Triassic is *Vytshegdosuchus* Sennikov, 1988 (possibly a paracrocodylomorph). *Xilousuchus* and other sail-backed poposauroids are the first members of Archosauria to appear in the fossil record. Poposauroids, well nested within Suchia, forces the major lineages of archosaurs (Avemetatarsalia, Aetosauria, Ornithosuchidae, primitive members of Paracrocodylomorpha) back into the Early Triassic. As a result, the ghost lineages of many of these clades are increased relative to previous hypotheses of archosaur relationships (Sereno, 1991a; Gower and Sennikov, 2000; Nesbitt, 2003). Specifically, major lineages of archosaurs have long ghost lineages (Ornithosuchidae $>$ 13 my; Aetosauria $>$ 13 my; Avemetatarsalia $>$ 3 my; Paracrocodylomorpha $>$ 5 my) given the long duration between the implied origination date and the first appearance of a member of that clade (fig. 58A–B). By the Middle Triassic, crown archosaurs are present in nearly all terrestrial Middle Triassic rock formations (personal obs.) and even a few marine formations (e.g., *Ticinosuchus*, *Qianosuchus*). By the Late Triassic, all major archosaur lineages are present and sampled in nearly all Late Triassic deposits around the world.

How do the relationships of Archosauriformes in the Triassic stand up to measures of stratigraphic fit? To test this question, I applied three commonly used stratigraphic fit methods, Spearman rank correlation (SRC; Norell and Novacek, 1992), Manhattan

TABLE 1
Taxa and Ages Used for Measuring Stratigraphic Fit

Taxon	Age
Mesosuchus browni	Anisian
Prolacerta broomi	Early Triassic
Proterosuchus fergusi	Early Triassic
Erythrosuchus africanus	Anisian
Vancleavea campi	Early Norian
Chanaresuchus bonapartei	Ladinian
Tropidosuchus romeri	Ladinian
Euparkeria capensis	Anisian
Parasuchus hislopi	Carnian
Smilosuchus gregorii	Early Norian
Pseudopalatus pristinus	Middle Norian
Ornithosuchus longidens	Late Carnian–Early Norian
Riojasuchus tenuisceps	Late Norian
Revueltosaurus callenderi	Middle Norian
Stagonolepis robertsoni	late Carnian–Early Norian
Aetosaurus ferratus	Mid to Late Norian
Longosuchus meadei	Late Carnian–Early Norian
Ticinosuchus ferox	Anisian
Qianosuchus mixtus	Anisian
Xilousuchus sapingensis	late Early Triassic
Arizonasaurus babbitti	Anisian
Poposaurus gracilis holotype	Late Carnian–Early Norian
Lotosaurus adentus	Anisian
Sillosuchus longicervix	Late Carnian
Effigia okeeffeae	Late Norian
Shuvosaurus inexpectatus	Early–mid-Norian
Combined Prestosuchus	Ladinian
Saurosuchus galilei	Late Carnian
Batrachotomus kuperferzellensis	Ladinian
Fasolasuchus tenax	Late Norian
Rauisuchus triradentes	Late Carnian–Early Norian
Polonosuchus silesiacus	Late Carnian–Early Norian
Postosuchus kirkpatricki	Early Norian to mid-Norian
CM 73372	Late Norian
Dromicosuchus grallator	Mid to Late Norian
Dibothrosuchus elaphros	Early Jurassic
Terrestrisuchus gracilis	Late Norian
Sphenosuchus acutus	Early Jurassic
Litargosuchus leptorhynchus	Early Jurassic
Kayentasuchus walkeri	Early Jurassic
Crocodyliformes	Mid to Late Norian
Lagerpeton chanarensis	Ladinian
Dromomeron gregorii	Late Carnian–Early Norian
Dromomeron romeri	Middle Norian
Marasuchus lilloensis	Ladinian
Eudimorphodon ranzii	Middle Norian
Dimorphodon macronyx	Early Jurassic
Lewisuchus/Pseudolagosuchus	Ladinian
Silesaurus opolensis	Late Carnian–Early Norian
Pisanosaurus mertii	Early Norian
Asilisaurus kongwe	Anisian
Eucoelophysis baldwini	Middle Norian
Sacisaurus agudoensis	Early Norian to mid-Norian

TABLE 1
(Continued)

Taxon	Age
Staurikosaurus pricei	Late Carnian–Early Norian
Eoraptor lunensis	Late Carnian
Saturnalia tupiniquim	Late Carnian–Early Norian
Plateosaurus engelhardti	Middle Norian
Efraasia minor	Middle Norian
Tawa hallae	Middle Norian
Coelophysis bauri	Late Norian
Herrerasaurus	Late Carnian

stratigraphic measure* (MSM*; Siddell, 1998; Pol and Norell, 2001, 2006; Boyd et al., 2010), and Gap Excess Ration (GER; Wills, 1999; Pol and Norell, 2006; Wills et al., 2008; Boyd et al., 2010).

The oldest occurrence of each taxon was used for all three measures. However, absolute dating in the terrestrial Triassic is nearly nonexistent (Irmis and Mundil, 2008) and correlations of rock units across basins and even continents remains tenuous. As a result, most taxa are either reported as a range (e.g., Anisian) or confined to a certain portion of the Stage (e.g., late Carnian). Therefore, a range for each taxon is given in the description of each terminal taxon. MSM* and GER (modified) take stratigraphic uncertainty into account (Pol and Norell, 2006; Boyd et al., 2010) and give a range of values. For the purposes of this test, a pruned phylogenetic analysis was used based on the more complete phylogenetic presented above. Each taxon was binned into one of 12 bins (see table 1). Bins were based on the geological timescale of Gradstein et al. (2004) and modifications of the Triassic timescale by Muttoni et al. (2004), Furin et al. (2006), and Schaltegger et al. (2008). Uncertainty in age boundaries (e.g., Anisian = 245 ± 1.5 Ma) allowed overlap in age bins. Taxa from the same bonebed (e.g., *Hesperosuchus* "*agilis*" and *Effigia* are both from the *Coelophysis* Quarry) were forced to be equal and taxa stratigraphically older were forced to be older than taxa stratigraphically younger in the same stratigraphic sequence (Pol and Norell, 2006). One thousand replicates were preformed for each measure for MSM* and GER. For SRC, the cladogram was transformed into a pectinate phylogram. Non-archosaurian archosauriforms, avian-line archosaurs, and pseudosuchians were examined separately.

Only the SRC value for pseudosuchians (= 0.81) is significant (P = 0.002) among basal archosauriform clades (fig. 59). This is not surprising given the extensive record of pseudosuchians throughout the Triassic in comparison to that of avian-line archosaurs through Dinosauria and Archosauriformes to Archosauria. Appearance of archosaurs before most of the diversity of non-archosaurian archosauriforms and a low number of nodes between Archosauriformes and Archosauria are two possible factors that resulted in a low SRC (= 0.31) value and a nonsignificant P value (= 0.517) for non-archosaurian archosauriforms (fig. 59). Furthermore, the avian-line archosaurs also had a low SRC (= 0.49) and a nonsignificant P value (= 0.132). This is possibly the result of having a derived member of the clade, *Asilisaurus kongwe*, appearing in the fossil before all other avian-line archosaurs.

The MSM* score range (0.08–0.13) was very low in comparison with the GER score range (0.50–0.69). The low range of the MSM* suggests that the phylogeny has a poor fit with the stratigraphic record, although these data are derived from a large phylogenetic tree. All three measures indicate that the early fossil record of archosauriforms is poor during the Triassic.

Additionally, these results are not surprising given the paucity of terrestrial Early Triassic deposits around the world. Recognition of a gap in the archosauriform record during the Early Triassic is important because it directs future collection efforts to the Early Triassic to find additional archosauri-

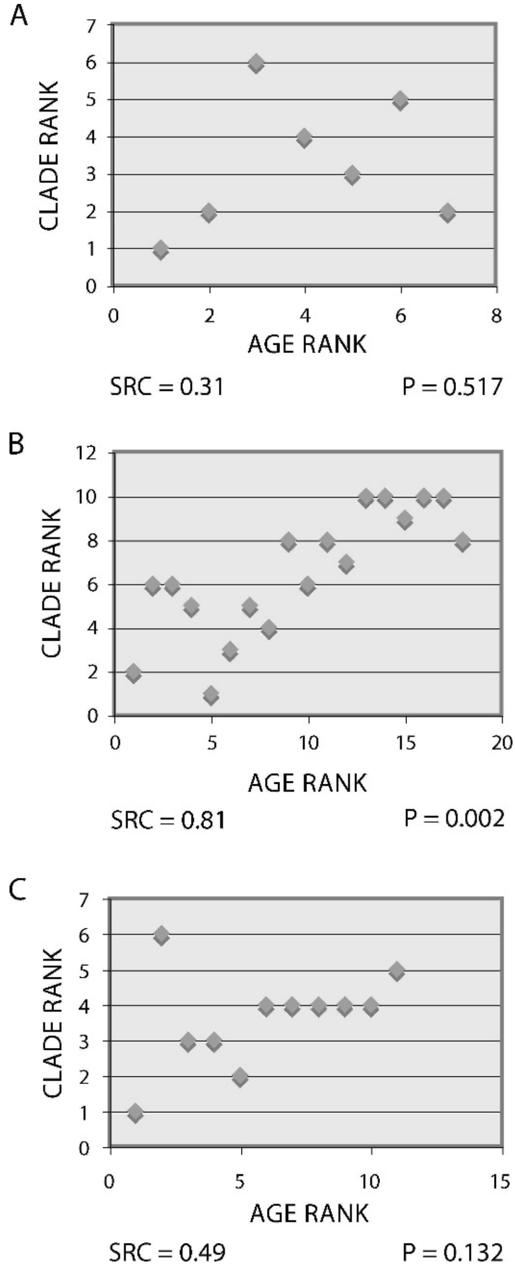

Fig. 59. Relationship between age rank and clade rank for the pectinate components of non-archosaurian archosauriforms (A), pseudosuchians (B), and avian-line archosaurs (C) used in this analysis. SRC values calculated in PAST (Hammer et al., 2001).

forms and the oldest members of Archosauria. Much of what we know about Early Triassic archosauriforms derives from South Africa (Rubidge, 2005) and Russia (Shishkin et al., 2000; Tverdokhlebov et al., 2002) and small isolated localities in Poland (Czatkowice Quarry; Borsuk-Bialynicka et al., 1999) and China (Heshanggou Formation; Rubidge, 2005). Although the Early Triassic outcrops in South Africa are extensive, only two non-archosaurian archosauriforms are known to date (*Proterosuchus* and NM QR 3570). Other areas that have an Early Triassic terrestrial record such as India (Panchet and Denwa formations), Antarctica (lower Fremouw Formation), Australia (Kockatea, Blina, Knocklofty, Archadia, and Terrigal formations), South America (Sanga do Cabral Formation), Pakistan (Mitti Member of the Mianwali Formation), Greenland (Wordy Creek Formation) and North America (Moenkopi Formation) all have the potential for producing archosauriforms or even early members of Archosauria.

Poor support for the basal lineages in Pseudosuchia (see above) may be the direct result of the absence of a good fossil record in early archosaurs. It is possible that early representatives of these lineages cannot been identified easily because of the long ghost lineages major lineages for of archosaurs in combination with rapid character evolution (Nesbitt, 2009) and high homoplasy. For example, aetosaurs appear in the ?Carnian (*Stagonolepis*) in an easily identifiable bauplan, but their lineage extends to the late Early Triassic given the calibrated phylogeny. To date, a basal member of that Aetosauria has not been identified prior to the Late Triassic. However, *Turfanosuchus*, which was variously considered a "rauisuchian" (Parrish, 1993) or a non-archosaurian archosauriform (Wu and Russell, 2001), may be a close relative of Aetosauria as demonstrated in some of my MPTs (see fig. 54).

Calibrating the Crocodylian-Avian Split

Because crocodylians and avians are each others' closest living relatives, a divergence estimate for these two clades is necessary to estimate molecular evolutionary rates. That said, a number of molecular studies attempted to estimate the crocodylian-avian split. Most recently, molecular workers estimated a crocodylian-avian split of 257.9 Ma (279–238 Ma, 95% confidence) using mitogenomic data (Pereira and Baker, 2006), whereas Hugall et al. (2007) estimated a crocodylian-avian split of 190 Ma using Rag-1. Most molecular workers used an estimate between 240–255 Ma (e.g., Janke and Arnason, 1997; Janke et al., 2005).

Beginning with Benton (1990b), many archosaur workers provided a minimum divergence estimate for crocodylians and avians along with their hypothesized phylogeny. Although Benton (1990b) provided an estimate in the Anisian (240 Ma), he used *Stagonosuchus*, a fragmentary "rauisuchian" taxon that has yet to be tested in a phylogeny. The time-calibrated phylogeny of Sereno (1991a) indicated a minimum divergence time at the Anisian-Ladinian boundary (~240 Ma). Gower and Sennikov (2000) further modified the results of Sereno (1991a) by incorporating possible fragmentary suchians from the Early Triassic of Russia. Nevertheless, these fossils have yet to be described or placed into a robust phylogenetic framework. In a preliminary phylogenetic analysis, Nesbitt (2003) showed that *Arizonasaurus*, a pseudosuchian from the Anisian of North America, represented the oldest known member of Archosauria at the time of publication. Unfortunately, a more refined date for *Arizonasaurus* cannot be given beyond 245–237 Ma, the span of the Anisian (Gradstein et al., 2004).

Muller and Reisz (2005) stated that archosaurs have a well-sampled fossil record during the Triassic. However, the results present in my time-calibrated phylogeny suggest that a minimum of five nodes were present by the end of Early Triassic. In concert with an estimate from pseudosuchians, the presence of a member of the Silesauridae, the sister taxon to Dinosauria, in the Anisian indicates that avian-line archosaurs diverged by the end of the Anisian. Therefore, a date greater than 245 Ma should be used to calibrate molecular divergence estimates.

Distribution of the Earliest Archosaurs

A full analysis of the biogeography of basal archosauriforms is beyond the scope of this work. However, I focus on the biogeography of the early archosaurs. The presence of the poposauroid *Xilousuchus* in the Early Triassic and the silesaurid *Asilisaurus kongwe* suggests that many of the major lineages of archosaurs were present by the end of the Anisian. Even though the ghost lineages of many major archosaur clades are present by the end of the Early Triassic, the first members of those clades (e.g., Aetosauria, Ornithosuchidae) do not appear in the fossil record until the Late Triassic. Therefore, they have no bearing on the early biogeographical history of Archosauria as a whole.

How are the earliest members of the Archosauria distributed? Unfortunately, most early archosaur fossils are known only from isolated elements and only a few from partial skeletons (e.g., *Xilousuchus*, *Arizonasaurus*, *Lotosaurus*, *Qianosuchus*, *Stagonosuchus*) that can be incorporated into a phylogeny. The comprehensive phylogenetic analysis allows more fragmentary or even isolated bones to be placed in a biogeographic context. The ankle of archosauriforms has been critical to the understanding of relationships (Brinkman, 1981; Chatterjee, 1982; Cruickshank and Benton, 1985; Sereno and Arcucci, 1990; Sereno, 1991a; Parrish, 1993). My extensive phylogenetic analysis presented here allows isolated proximal tarsals to be placed in a phylogenetic analysis. Four calcanea (fig. 60) from the Anisian of China (IVPP unnumbered; fig. 60A), two different taxa from the Anisian Moenkopi Formation of North America (MSM 4673 and MSM 4672; fig. 60B–C), and the Anisian Manda Beds of Tanzania (NMT RB39; fig. 60D) were placed into a phylogenetic analysis. Each specimen was found as belonging to Suchia when each one was added independently. Similarly, the holotpye of *Vytshegdosuchus* (an ilium, PIN 3361/134) was placed in the phylogenetic analysis and it was found as a paracrodylomorph in a large polytomy of other paracrodylomorph taxa. The data from partial skeletons and the isolated elements give a much more complete picture of the distribution of basal suchians by the end of

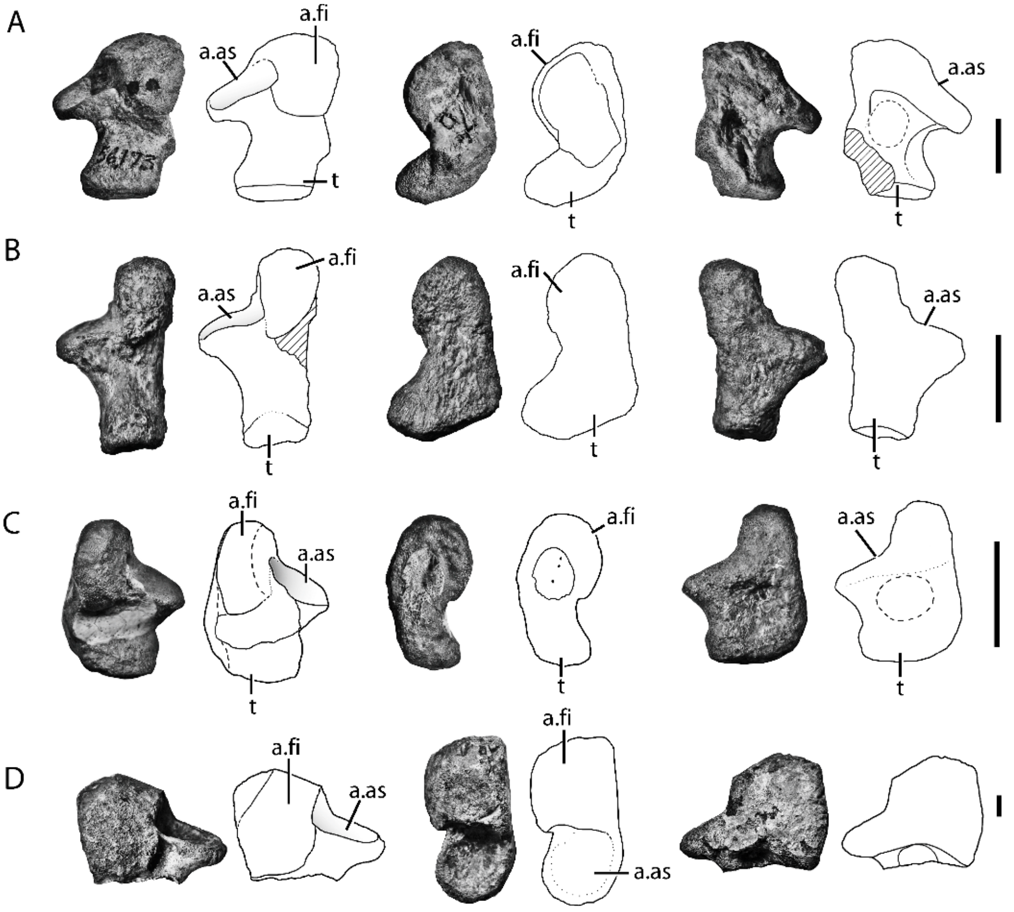

Fig. 60. Calcanea of Anisian suchians. **A,** Right calcaneum of a suchian (IVPP unnumbered; Young, 1964: fig. 60A) from the Upper Ehrmaying (= Ermaying) Formation of China in proximal (left), lateral (middle), and ventral (right) views. **B,** Right calcaneum of a suchian (MSM 4673) from the Moenkopi Formation of western North America in proximal (left), lateral (middle), and ventral (right) views. **C,** Left calcaneum of an additional suchian (MSM 4672) from the Moenkopi Formation of western North America in proximal (left), lateral (middle), and ventral (right) views. **D,** Partial left calcaneum of a suchian (NMT RB39) from the Manda Beds of southeastern Africa in proximal (left), anterior (middle), and ventral (right) views. Anatomical abbreviations in the appendix. Scale bars = 1 cm.

the Anisian (fig. 61). More specifically, nearly all of the first archosaurs to appear in the fossil record belong to Poposauroidea. By the end of the Anisian, poposauroids were present from Africa to the northeastern corner of Asia.

A near cosmopolitan distribution of genus-level taxa (e.g., *Lystrosaurus*, *Proterosuchus*) in the earliest Triassic was common but was soon absent by the end of the Early Triassic through the Middle Triassic (Sahney and Benton, 2008). Poposauroids appear to show the opposite pattern.

PROSPECTUS

This work intended to provide a framework for future studies in archosaur paleobiology. It provides a rigorously defined terminal taxon, detailed character descriptions incorporating a wide range of basal archosaur morphologies, and a thorough

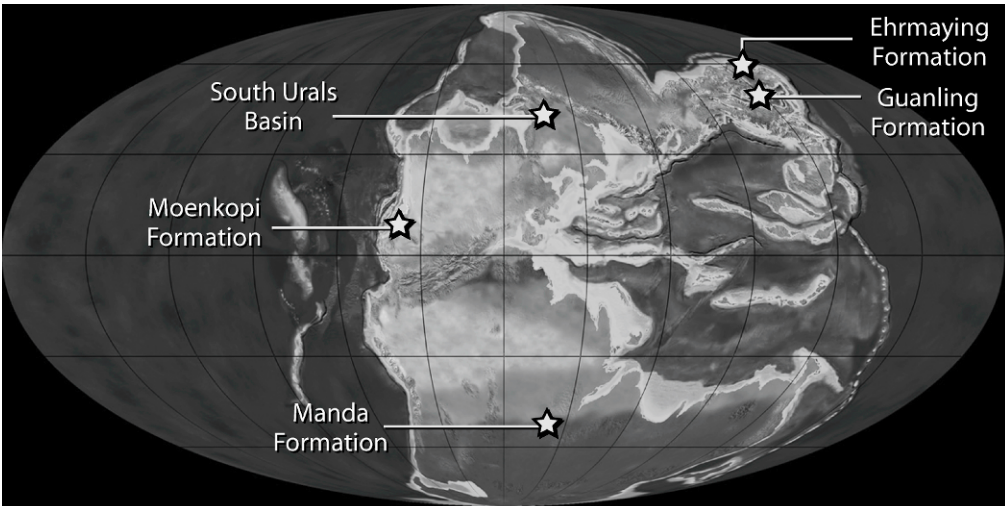

Fig. 61. The distribution of Anisian suchians illustrating that the clade was distributed throughout Pangaea early in the evolution of Archosauria. Multiple suchian taxa are present in the Moenkopi Formation and the Manda Beds. Palaeogeographic globe after http://jan.ucc.nau.edu/~rcb7/globaltext2.html.

discussion of the results. It is hoped that this work will provide a model for incorporating new specimens and characters into an even larger phylogenetic analysis. Additionally, this analysis is the first to provide a framework in which fragmentary or even isolated elements from anytime in the Triassic could be placed into a testable phylogenetic hypothesis. Results of incorporating more fragmentary specimens will result in a better understanding of paleoecology, biogeography, biostratigraphy, and assemblage evolution of Triassic vertebrate assemblages.

This analysis is far from the "last word" on basal archosaur relationships and, I hope, this work will encourage other basal archosauriform workers to continue to work on the relationships within the clade. For example, part of this analysis have been used and expanded to examine the relationships of silesaurids (Nesbitt et al., 2010) and early theropods (Nesbitt et al., 2009c).

Detailed osteology of basal archosauriforms are welcomed. I urge archosaur workers to be explicit when assigning specimens to previously known taxa. Poor criteria for assigning specimens to taxa has led to much confusion over the past 20 years. Suprageneric taxa should not be used in any case. Further discussion and illustration of each phylogenetic character and its states are needed, especially discussions of population variation, ontogentic variation, and scoring strategies. Also, I encourage basal archosaur workers to record where the specimen is from and cite an authority on temporal correlation (biostratigraphical or absolute dates) when discussing the age of each fossil.

Even though this analysis provides the largest, most comprehensive phylogeny of basal archosaurs to date, there is a plethora of work to follow. The weakest supported portion of the tree includes two areas within Pseudosuchia, the bases of Suchia and Paracrocodylomorpha. Additionally, I advocate that basal archosaur workers examining the relationships of smaller clades (e.g., aetosaurs, phytosaurs, crocodylomorphs) use a nonhypothetical outgroup and experiment with different taxa as the outgroup.

The phylogenetic hypothesis found here predicts the origin and early diversification of major lineages of Archosauria occurred in the late Early Triassic and the early portion of the Middle Triassic. New fieldwork in the first half of the Triassic is required to fill in some of the longer ghost lineages of Phytosauria, Ornithosuchidae, and possibly even Dinosauria. Discovery of early members of the Pseudosuchia have the potential to resolve the base of the Suchia and Paracrocodylomorpha.

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APPENDIX 1

INSTITUTION LIST

AMNH, American Museum of Natural History, New York, New York, U.S.A; **AZA**, **ALM** Refer to locality designations for specimens of *Arganasuchus*. Specimens stored at MNHN; **BES**, Museum Cicico di Storia Naturale, Milano, Italy; **BSP**, Bayerische Staatssammlung für Paläontologie und historische Geologie, München, Germany; **BMNH**, Natural History Museum, London, England; **BP**, Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa; **BPS**, Bayerische Staatssammlung für Paläontologie und historische Geologie, München, Germany; **CM**, Carnegie Museum of Natural History, Pittsburg, Pennsylvania, U.S.A.; **CUP**, Fujen Catholic University of Peking collection stored at FMNH; **DINO,** Dinosaur National Monument, Utah-Colorado, U.S.A.; **EM**, Elgin Museum, Elgin, United Kingdom; **FMNH**, Field Museum of Natural History, Chicago, Illinois, U.S.A.; **GPIT**, Institut und Museum für Geologie und Paläontologie, Universität Tübingen, Germany; **GR**, Ruth Hall Museum of Paleontology at Ghost Ranch, New Mexico, U.S.A.; **GZG**, Geowissenschaftliches Zentrum der Universität Göttingen, Göttingen, Germany; **IGM**, Mongolian Institute of Geology, Ulaan Bataar, Mongolia; **ISI**, Indian Statistical Institute, Kolkata, India; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **MACN**, Museo Argentinas Ciencias Naturales, Buenos Aires, Argentina; **MB,** Museum für Naturkunde der Humboldt Universität, Berlin, Germany; **MCN**, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; **MCP**, Museu de Ciêncian e Tecnologia PUCS, Porto Alegre, Brazil; **MCSNB**, Museo Civico di Scienze Naturali di Bergamo, Italy; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.; **MCZD**, University of Aberdeen Zoology Department, Aberdeen, United Kingdom; **MFSN**, Museo Friulano di Storia Naturale, Udine, Italy; **MNA**, Museum of Northern Arizona, Flagstaff, Arizona, U.S.A.; **MNHN**, Museum National d'Histoire Naturelle, Paris, France; **MSM**, Arizona Museum of Natural History, Mesa, Arizona, U.S.A. (formerly Mesa Southwest Museum); **NMT,** National Museum of Tanzania, Dar es Salaam, Tanzania; **NMMNH**, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, U.S.A.; **NM QR**, National Museum, Bloemfontein, South Africa; **NMS**, National Museums of Scotland (formerly Royal Scottish Museum, RSM), Edinburgh, United Kingdom; **PEFO**, Petrified Forest National Park, Arizona, U.S.A.; **PIN**, Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; **PIZ**, Paläontologisches Institut und Museum der Universität, Zürch; **PVL**, Istituto Miguel Lillo, Tucuman, Argentina; **PVSJ**, Division of Paleontology of the Museo de Ciencias Naturales de la Universidad Nacional de San Juan, Argentina; **RC**, Rubidge collection, Wellwood, Graaff-Reinet, South Africa; **SAM**, South African Museum, Cape Town, South Africa; **SMNS**, Staatliches Museum fur Naturkunde, Stuttgart, Germany; **TM**, Transvaal Museum, Pretoria, South Africa; **TMM**, Vertebrate Paleontology Laboratory, Texas Natural Science Center, Austin, Texas, U.S.A.; **TTU**, Texas Tech University Museum, Lubbock, Texas, U.S.A.; **UCMP**, University of California Museum of Paleontology, Berkeley, California, U.S.A.; **UFRGS**, Institute of Geosciences, Federal University of Rio Grande de Sul, Porte Alegre, Brazil; **UMMP**, University of Michigan Museum of Paleontology, Ann Arbor, Michigan, U.S.A.; **UMZC**, Museum of Zoology, Cambridge University, Cambridge, England; **UNC**, University of North Carolina, Chapel Hill, North Carolina, U.S.A.; **UNLR**, Museo de Paleontologia, Universidad Nacional de La Rioja, LA Rioja, Argentina; **U of Mo**, University of Missouri, Columbia, Missouri, U.S.A.; **USNM**, National Museum of Natural History, Washington, D.C., U.S.A.; **UUVP**, University of Utah, Vertebrate Paleontology Collections, Utah, U.S.A.; **UW**, Wyoming State Museum, University of Wyoming, Laramie, Wyoming, U.S.A.; **WARMS**, Warwickshire Museum, Warwick, United Kingdom; **YPM**, Yale Peabody Museum, New Haven, Connecticut, U.S.A.; **ZPAL**, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

APPENDIX 2

ABBREVIATION LIST

3rd	third distal tarsal
4th	fourth distal tarsal
a.	articulates with
ab	anterior bar
ac	acetabulum
acr	acromian process
afo	antorbital fossa
ah	anterior hollow
al	alveolus
an	angular
ap	ascending process
amt	anteromedial tuber
anp	anterior process
aof	antorbital fenestra
ar	articular

as	astragalus
ax	axis
bf	bone fragments
bpt	basipterygoid processes
bt	basitubera
c	crest
ca	calcaneum
ce	centrale
cf	attachment site of the caudifemoralis
ch	internal choana
cl	clavicle
cn	cnemial crest
cor	coracoid
cp	cultriform process of the parabasisphenoid
ctf	crista tibiofibularis
d	dentary
dp	deltopectoral crest
drop	descending process of the opisthotic
dv	dorsal vertebrae
en	external naris
eo	exoccipital
f	frontal
fi	fibula
fl	flange
fo	fossa
fov	fenestra ovalis
for	foramen
g	groove
gl	glenoid
ic	internal carotid
id	interdental plates
if	attachment for the iliofibularis
il	ilium
inc	interclavicle
ip	ischial peduncle
is	ischium
j	jugal
k	keel
l.	left
la	lacrimal
laf	lacrimal foramen
lr	lateral ridge
ls	laterosphenoid
lt	lateral tuber
ltf	lower temporal fenestra
met	metotic foramen
mf	mandibular fenestra
mp	medial process of the articular
mr	medial ridge
mt V	metatarsal V
mx	maxilla
n	nasal
nc	neural canal
ns	neural spine
o	orbit
oc	occipital condyle
op	opisthotic
pa	parietal
pal	palpebral
pb	parabasisphenoid
pc	posterior condyles
pd	predentary
pf	prefrontal
pfo	perilymphatic foramen
pg	posterior groove
pmt	posteromedial tuber
pmx	premaxilla
pn	pneumatic cavities
po	postorbital
pof	postfrontal
poz	postzygapophysis
pp	paroccipital process
pr	prootic
pre	prearticular
pu	pubis
pup	pubic peduncle
pt	pterygoid
ptf	posttemporal fenestra
qj	quadratojugal
qu	quadrate
r	ridge
r.	right
ra	radius
rad	radiale
ro	“roller”
sac	supraacetabular crest
sc	scapula
sf	surangular foramen
sm	“septomaxilla”
sp	splenial
sq	squamosal
sr	sacral rib
st	stapes
su	surangular
t	tooth
ta	tabular
ti	tibia
tu	tuber
u	ulna
ul	ulnare
utf	upper temporal fenestra
vsm	middle cerebral vein
V	cranial nerve V (trigeminal)
VI	cranial nerve VI (abducens)
VII	cranial nerve VII (facial)
XII	cranial nerve XII (hypoglossal)

APPENDIX 3

TAXON SCORES

The complete list of characters and scores are available on Morphobank (O'Leary and Kuaufman, 2007; at http://www.morphobank.org/).

	10 . 20 . 30 . 40 . 50 .
Mesosuchus browni	?1000?0000000?1000000?0000?00?100000?00000000?0000
Prolacerta broomi	0000020000?00?0000000?0000000?100000?0000000000000
Archosaurus rossicus	????03010???
Proterosuchus fergusi	000003010000000000000?0000200010000000000000000000
Erythrosuchus africanus	0100020000020000000000000000000000000000?000000000
Vancleavea campi	1100020000100?100000000000?00?000000???0?00100000?
Chanaresuchus bonapartei	10000200000001000000000000000000000000000001001100
Tropidosuchus romeri	10??0?000000000000000?0000?0000?0000001??001001100
Euparkeria capensis	0100000000?000000000000000100010000000000000000100
Parasuchus hislopi	??0003000100011000100000002000000000000000?000010100
Smilosuchus gregorii	??000300010001100010000000200000000000000000010100
Pseudopalatus pristinus	??000300010001100010000000200000000000000000010100
Gracilisuchus stipanicicorum	01000000000000000000000000100000?00001000000000100
Turfanosuchus dabanensis	00030200000000000000000000200000?00001000?000000100
Ornithosuchus longidens	??000001000010000000000000000?001100?0000?000000100
Riojasuchus tenuisceps	00000001000010000000000000000110110000000000000100
Revueltosaurus callenderi	00030200000300110000000100120100100000000010000100
Stagonolepis robertsoni	00000210000?00110000000111201001000??0?10000100100
Aetosaurus ferratus	0000011000000011?0000?011020100?000?100??00010010?
Longosuchus meadei	??001?????0?001?0000000110201000?000000010000??01?0
Ticinosuchus ferox	?????????????000?000000?0000010??????0?0???0??????
Qianosuchus mixtus	10001300000101000001000110100001000000000?000000100
Xilousuchus sapingensis	?00012000000?0000000100011000000 1??0??0????????????
Arizonasaurus babbitti	???01???0?0??00000010001100000001?00??????000?00100
Poposaurus gracilis holotype	??
Poposaurus gracilis Yale	?????200??0?0???00??00????????????????????????????
Lotosaurus adentus	?00004?0000200?0?1001?00110000100000000000000000000
Sillosuchus longicervix	??
Effigia okeeffeae	100014?000?200?0?1001??111000000000000000011???000
Shuvosaurus inexpectatus	100014?000?20????1?0????????????0?0??000?011000100
Prestosuchus chiniquensis	?????????????????0?????????????1??????????????????
UFRGS 156=T	0100010000000000?0000?000010110?0?000000?00000010?
UFRGS 0152=T	??0???????0??0?0?0000?0000101101000?0?????0?00010?
Combined *Prestosuchus*	0100010000000000?0000?000010110100000000?00000010?
Saurosuchus galilei	0100010000?00000000000?000100101000000000101000100
Batrachotomus kuperferzellensis	??0001001001000100000001100001010110100?0110000110
Fasolasuchus tenax	01000100000101??000001000010010 1?10?1?????????????
Rauisuchus triradentes	010?01000?010????????????????????11?????0??????110
Polonosuchus silesiacus	01000100000100?00000010002101101011010 0?????10011?
Postosuchus kirkpatricki	01000100000100100000010002101101011010 0?011010?110
Postosuchus alisonae	??????????????????????????????????1?????????????1?
CM 73372	??
Hesperosuchus agilis	???????0?0????1?00?0000??0????02??0??????111???1??
Dromicosuchus grallator	00010200001101100000000000100 10?0100001??111100110
Hesperosuchus "agilis"	00010200001101100000000000100102010000 11?111100110
Dibothrosuchus elaphros	?0010200001?01100000000 0?0000002010000111111???110
Terrestrisuchus gracilis	?????????????1100000000?00000002???000????11100111
Sphenosuchus acutus	?1010?00001?011000000000001 0??020100?0110111100110
Litargosuchus leptorhynchus	00010100001?011000000?00?000010?0000001??011???111
Kayentasuchus walkeri	?10101000011011000000??000100102??0??01????????111

APPENDIX 3

(Continued)

	10 . 20 . 30 . 40 . 50 .
Orthosuchus stormbergi	00020100001?01?0100000000010??020?00?011?011100111
Alligator mississippiensis	0?02020000000?10000?010000?0??020000???11011100110
Protosuchus haughtoni	000201000011001000000?000010010?00000011?011100111
Protosuchus richardsoni	000201000011001000000??000100102000000111011100111
Eudimorphodon ranzii	10?0?100000?00?000000?011000000?0?0??0??????0?????
Dimorphodon macronyx	10??1200000000??00000?011000000??????00?????0??10?
Lagerpeton chanarensis	??
Dromomeron gregorii	??
Dromomeron romeri	??
Marasuchus lilloensis	??
Asilisaurus kongwe	??
Eucoelophysis baldwini	??
Sacisaurus agudoensis	?????????????010?0?0??000000000???????????????????
Lewisuchus admixtus	?????????????01000?00?0?0000?00?????????????0001?0
Pseudolagosuchus majori	??
Lewisuchus/Pseudolagosuchus	?????????????01000?00?0?0000?00?????????????0001?0
Eocursor parvus	??
Silesaurus opolensis	??000200000000010?0000?0000000001??000?0??00?00010?
Pisanosaurus mertii	??????????????1?00??0?1??0????????????????????????
Heterodontosaurus tucki	01000000101001100000011000000001000000001011000100
Lesothosaurus dianosticus	01000300000001100000001000000001000000000?011000100
Scutellosaurus lawleri	??????????????1??0??0?1??00???0??????????00????10?
Herrerasaurus ischigualastensis	01000100100100000000?0000000000?0000010000?1000100
Staurikosaurus pricei	??
Eoraptor lunensis	010001001012000000000?000100000??001111000?100010?
Saturnalia tupiniquim	?????????????????0??0????????????????11???????????
Plateosaurus engelhardti	10101200100100100000000010100001000111100001000100
Efraasia minor	?01011001001001000000000?0000001?00??110?001???10?
Tawa hallae	10000000101?00000000010?00000001000??1100001000100
Coelophysis bauri	10101100101?0000?0000?010100000 10?010110000100010?
Dilophosaurus wetherelli	10101100?01?0000?00001??000100010?0??110???100010?
Allosaurus fragilis	101012001001010?00000100102100010011111000010001 00
Velociraptor mongoliensis	101011001000010100000?0000010001?001111?000100010

	60 . 70 . 80 . 90 . 100 .
Mesosuchus browni	000000010000000000??0?000000000000000000?0000010000
Prolacerta broomi	00000000000000000??0?000000000000000000?0000000000
Archosaurus rossicus	??
Proterosuchus fergusi	000000000000100000?13000000000000000001000100000000
Erythrosuchus africanus	00000000000010000011010000000000000001000111001000
Vancleavea campi	00000?00000010?000?10000000100000????????1????????
Chanaresuchus bonapartei	00001000000010000001000010000000000001 0?0?11011000
Tropidosuchus romeri	0000100000001000000?1000010000000000?001??????011?00
Euparkeria capensis	000000000000100000A10000200000000000001000111011000
Parasuchus hislopi	000?00000000100000010000001000000000001??0111121100
Smilosuchus gregorii	00000000000010000001000000100000000001??011?121100
Pseudopalatus pristinus	00000000000010000001010000100000000000?0?0111121100
Gracilisuchus stipanicicorum	00000000000010011001110020010000 00?001????1?221101
Turfanosuchus dabanensis	0001000000?0100000110000100000000 0??0?0???11021101
Ornithosuchus longidens	000?00000001100000010000000000000001001000?????????
Riojasuchus tenuisceps	00000000000110000001000000000000001001 0?011?221101

APPENDIX 3
(Continued)

	60 . 70 . 80 . 90 . 100 .
Revueltosaurus callenderi	00010000000010011011200020000000000000010?0111221101
Stagonolepis robertsoni	00010000001110011??1?001?0000001000001?101??221101
Aetosaurus ferratus	0001000??011110110112000200010?100000???????221?01
Longosuchus meadei	??01??0000?11???1?1????12000?00??0?00?0001?1221101
Ticinosuchus ferox	??
Qianosuchus mixtus	000000000000?0000011000020000000000000??10???02??01
Xilousuchus sapingensis	??11001101
Arizonasaurus babbitti	?00000000000100000?100002000000000?0010???11001101
Poposaurus gracilis holotype	??
Poposaurus gracilis Yale	??
Lotosaurus adentus	00000100000010000011000120000000?????0??111021111
Sillosuchus longicervix	??
Effigia okeeffeae	0000010020?01?0010????000000?01100?0010?0101221101
Shuvosaurus inexpectatus	0000010020?0100010??00000000?01100?0010??101221101
Prestosuchus chiniquensis	??
UFRGS 156=T	11000?000?00100000?100000000?00000?00?0??1??221101
UFRGS 0152=T	1?00000????0???0?0???0001000000000?0010??111221101
Combined *Prestosuchus*	110000000?00100000?10000?000000000?0010??111221101
Saurosuchus galilei	11000?000000100000011??0020000000000000100 0111221101
Batrachotomus kuperferzellensis	1?0000001000101000?100002000000000000001100111221101
Fasolasuchus tenax	??
Rauisuchus triradentes	1200000?????????00?1??003?01?????0?0011???????????
Polonosuchus silesiacus	0200001??????0?100?111003?010000 10???1111???????0?
Postosuchus kirkpatricki	02000010100010110011110030010000 10?0011??111221101
Postosuchus alisonae	???1??????
CM 73372	??
Hesperosuchus agilis	???0????1???????????????210110000????????????????1
Dromicosuchus grallator	00001?00100010?1001111002?0110000?????????????????
Hesperosuchus “agilis”	?0001?00100010010011110002?01100000?00111?1????????
Dibothrosuchus elaphros	00001?0120101??1?01??????1011000000001??1111221101
Terrestrisuchus gracilis	0000????20?01??1001111000??1100000?00??0??????????
Sphenosuchus acutus	00001?012010100100111110210110000000011111111221101
Litargosuchus leptorhynchus	??001??1010?1?0?001111102?01?0?0?0?0??????????1???
Kayentasuchus walkeri	10101?0?011?1????01??????101?????????????011????????
Orthosuchus stormbergi	00101??1011011?10??11100110110000000011?01???21?10
Alligator mississippiensis	?010??01011011010??11100010111100000 01???1?1221110
Protosuchus haughtoni	??101?0101101?01001111102??111000000?1??????221?10
Protosuchus richardsoni	?0101?0101101101001?11?02101110000000011001??221110
Eudimorphodon ranzii	?????????????00?0001000?0?0??0010?????????????????
Dimorphodon macronyx	?0???0?????????0000001??000??????0??????????????????
Lagerpeton chanarensis	??
Dromomeron gregorii	??
Dromomeron romeri	??
Marasuchus lilloensis	??01221100
Asilisaurus kongwe	??????????????????????????0?00000?????????????????
Eucoelophysis baldwini	??
Sacisaurus agudoensis	??
Lewisuchus admixtus	??000????????0001??1??000000?00001?011????01221100
Pseudolagosuchus majori	??
Lewisuchus/Pseudolagosuchus	??000????????0001??1??000000?00001?011????01221100
Eocursor parvus	????????00001?????????????????????????????0?221100
Silesaurus opolensis	0000?1000?00100000?1100020000?0001???10???01021100

APPENDIX 3
(Continued)

	60 . 70 . 80 . 90 . 100 .
Pisanosaurus mertii	`??????????????????????????????????????????????????`
Heterodontosaurus tucki	`00000000200010000001300010000000001?011???101221100`
Lesothosaurus dianosticus	`0000000A00001000000130000000100001001?000101221100`
Scutellosaurus lawleri	`??0????12???1?????????????0000???0?0?????0???????????`
Herrerasaurus ischigualastensis	`00000000000010000001300010000000001??1??0?10?22?101`
Staurikosaurus pricei	`??????????????????????????????????????????????????`
Eoraptor lunensis	`00000?0?0??010000011300010000000001?01?????0??21?01`
Saturnalia tupiniquim	`?????1????????????????????????????????????????????`
Plateosaurus engelhardti	`00000100000010000001300100000000000010011000101221100`
Efraasia minor	`0000?10???0??????00????1?00000000?????????01221100`
Tawa hallae	`000000000???100001?130000000?00001??110??101221101`
Coelophysis bauri	`000001000?001000011130001000??00010011000101221101`
Dilophosaurus wetherelli	`0000000??????0?0011?300000000?000?0????00?01221101`
Allosaurus fragilis	`00000000000010000011300000000000000010111000101221101`
Velociraptor mongoliensis	`0000010000?0100000013100000000000001011100010122110?`
	110 . 120 . 130 . 140 . 150 .
Mesosuchus browni	`000000000000000???000?00010?0?0??000?000?000000???`
Prolacerta broomi	`000000000000000000000?00000??00??000?0000000010??1`
Archosaurus rossicus	`??????????????????????????????????????????????????`
Proterosuchus fergusi	`00000000000000000?00000001000000?00101001100000??1`
Erythrosuchus africanus	`00000000000000000000010000000000000111000100100??0`
Vancleavea campi	`???0?00000???00??0???????10??????00??00100??110??1`
Chanaresuchus bonapartei	`000000000000000000000??0??0???00000111010000110??0`
Tropidosuchus romeri	`?0?0?00000??0?0?????0?????0??????0011101?000110??0`
Euparkeria capensis	`00000000000000000000001001000000000111000000100??0`
Parasuchus hislopi	`000000000000000????000?00?????0??0011111?000110??1`
Smilosuchus gregorii	`0001?0000000000???000??0?10???0??00111210000110??1`
Pseudopalatus pristinus	`00010000000000000000001001000000000111210000110??1`
Gracilisuchus stipanicicorum	`0010??0000?????????????0??0??????00121000000110??0`
Turfanosuchus dabanensis	`0000000?0000020????001100?00?00??0012100?000110??0`
Ornithosuchus longidens	`??????0000????????????????0??????00121000200110??0`
Riojasuchus tenuisceps	`0000?000000??00?????0??0??0??????00121000200110??0`
Revueltosaurus callenderi	`0000000000?00200??0002100??????0?0012100?00011???0`
Stagonolepis robertsoni	`000000?0001002?011000??00??01020?0012100001011???0`
Aetosaurus ferratus	`?000?00000??????????0??0?1???????00121000010111000`
Longosuchus meadei	`0000000000100200?10002100?00?02000012100001011???0`
Ticinosuchus ferox	`?????????????????????????????????001210???0?????0?`
Qianosuchus mixtus	`?00???000??????????????0?????????0012100?000110??0`
Xilousuchus sapingensis	`00000000?000000001?001100?00000?00?12100??????????`
Arizonasaurus babbitti	`000000000000000011000110 0?00000100012100?000?1????`
Poposaurus gracilis holotype	`??????????????????????????????????????????????????`
Poposaurus gracilis Yale	`??????????????????????????????????????0???????????`
Lotosaurus adentus	`000000000000000????001100?00000??00121001000110???`
Sillosuchus longicervix	`??????????????????????????????????????????????????`
Effigia okeeffeae	`0010000?0?????101100 0??00??0??0?00012100?000110??0`
Shuvosaurus inexpectatus	`00100000010000101100 0??00100??0000012100?000110???`
Prestosuchus chiniquensis	`??????????????????????????????????0??1????????????`
UFRGS 156=T	`0000?00100000?0?????0??0??0??????0?12100?100110??0`
UFRGS 0152=T	`000000010000020???0001100000?00??00121000?0?11???0`
Combined *Prestosuchus*	`000000010000020???0001100000?00??00121000100110??0`

APPENDIX 3
(Continued)

	110 . 120 . 130 . 140 . 150 .
Saurosuchus galilei	00000100000002001??00?100100?00????12?000100111110
Batrachotomus kuperferzellensis	0000010100000?00110001100100001110012100110111??00
Fasolasuchus tenax	??????????????????????????????????012?00??????????
Rauisuchus triradentes	????????0????????????????????????????100??0???????
Polonosuchus silesiacus	???????????????????????????????????12?00?10???111?
Postosuchus kirkpatricki	0??01101001002001100 1??01??0???1?00121001101111110
Postosuchus alisonae	????1??1?0??????1???????1?0?????1?????????????111?
CM 73372	??
Hesperosuchus agilis	???01?01?0??0111?????????????????0012??0??01??????
Dromicosuchus grallator	???????100???????????????????????0012100?00111??00
Hesperosuchus "agilis"	???0?1?100????1??1??1??????????????12100?001111100
Dibothrosuchus elaphros	??10111100110111?1?11211010111???0?12100100111???0
Terrestrisuchus gracilis	?????11??0??0?1?????????0?0??????001210??00111????
Sphenosuchus acutus	???011110011011111111211010111111??12100100111???0
Litargosuchus leptorhynchus	???????110???????????????10??????00121001000111?00
Kayentasuchus walkeri	????1???1??????11???????0?0?????1?0121001?0?11???0
Orthosuchus stormbergi	???0?11110???11?????2?????0??????00121001000111100
Alligator mississippiensis	?0?0110000110111111122 1?00011101?000?1011001111?00
Protosuchus haughtoni	?0?0?11110????1?????2?????0??????0?121001000111100
Protosuchus richardsoni	?0?01111101101111?1?2???0001??1??00121001000111100
Eudimorphodon ranzii	?????????????????????????????????101?000?00?110??0
Dimorphodon macronyx	?????????????????????????????????1012100?200??0??0
Lagerpeton chanarensis	??
Dromomeron gregorii	??
Dromomeron romeri	??
Marasuchus lilloensis	0000000??01?01000???0??00?00????0?????????????????
Asilisaurus kongwe	?????????????????????????????????0????????????????
Eucoelophysis baldwini	??
Sacisaurus agudoensis	???????????????????????????????????121????????????
Lewisuchus admixtus	1000000001??110????00?10??10??0??0?12??0?00?1?????
Pseudolagosuchus majori	??
Lewisuchus/Pseudolagosuchus	1000000001??110????00?10??10??0??0?12??0?00?1?????
Eocursor parvus	1000?0?????????????????0??0??????????1????0??1????
Silesaurus opolensis	10000000?0101100010001100?100000100121?0?000110??0
Pisanosaurus mertii	?????????????????????????????????0???1????????????
Heterodontosaurus tucki	1110000000100110??000??00?0???0??00121001001111100
Lesothosaurus dianosticus	1000000000?00?10???00??00100?00??00121001001111100
Scutellosaurus lawleri	?????0????????1??????????????????0?12?????????????
Herrerasaurus ischigualastensis	1000?0000000??1????00??0?100?????00121001001110??0
Staurikosaurus pricei	?????????????????????????????????????1????????????
Eoraptor lunensis	?000???0?0??????????0????????????0012100?001110??0
Saturnalia tupiniquim	??????0????????????????0??????????1???????????????
Plateosaurus engelhardti	1000000000000110010001100?00?020?01121001?01110??0
Efraasia minor	1000000000000110???00?100100?0???0112100?001?????0
Tawa hallae	?000000000000?1?1?0001100100000010012100?001110??0
Coelophysis bauri	10100000?0100110??000?10??00?000?00121?01001110??0
Dilophosaurus wetherelli	10000000?11001100?0?01100?00102??00121?01101??0??0
Allosaurus fragilis	100000000110011????00??00000??2??00121001101110??0
Velociraptor mongoliensis	10000001011?01111???0??0A?00?????00121001001110??0

APPENDIX 3
(Continued)

	160 . 170 . 180 . 190 . 200 .
Mesosuchus browni	00000000000??000001??0?0010??00?000100000?00000000
Prolacerta broomi	00000?00000?000000000000000000101100000000000001000
Archosaurus rossicus	??
Proterosuchus fergusi	00?000000000000001000000000000?00000000000000001000
Erythrosuchus africanus	00000000000001000100000111000?00?00000000?00010000
Vancleavea campi	0?0000?0?00??1001100000 1??1???00?001?00?000?0?0000
Chanaresuchus bonapartei	00000000000001000100000101100000000000000000000000
Tropidosuchus romeri	0??00??0??00?1?001000?010110001000000000000??00000
Euparkeria capensis	00000000100001000100000101000000000000000100000 1000
Parasuchus hislopi	00?00?00?100?1?0110000011 11?0000?0000000100001 1000
Smilosuchus gregorii	00?00000110001001 10000?1111??00?0000000100001?000
Pseudopalatus pristinus	00?000001100?10011 0000?1111000000000000000100001 1000
Gracilisuchus stipanicicorum	0??00000?0000100010000011110000?0000000?1000?1?000
Turfanosuchus dabanensis	0??000?0?000?10001000001011?????????00001?000?1??0
Ornithosuchus longidens	0?000000?1000?00010000011 11??????0??0001100???1010
Riojasuchus tenuisceps	0?000000110001000100000111100000000000000111000?1010
Revueltosaurus callenderi	00000000100001001200 00?1111000000000 10000200001 1010
Stagonolepis robertsoni	00?21101?000?101000010?1111???????0?0000100011 1010
Aetosaurus ferratus	0??21??1?000?10101001 0?1111?????????????????????0
Longosuchus meadei	?0021101000001010000 10?11110?00000??00001000??1010
Ticinosuchus ferox	0??00?????00????01000001??1???0?0000?000?0?0111000
Qianosuchus mixtus	0??00??0??0001?001?00?01111?0?1?1000000000?010000?
Xilousuchus sapingensis	00000110100 0??0001000001??1000?0100100000001 10????
Arizonasaurus babbitti	000001101000?10001000001111000 10?000000000 1110010?
Poposaurus gracilis holotype	???1???0?
Poposaurus gracilis Yale	????????????????010?0001??1??????0???00?0010100001
Lotosaurus adentus	0??0110110000102???????????100000000?00000?11?0101
Sillosuchus longicervix	?????????????????????????????1???10?0???110000 0??0001
Effigia okeeffeae	00?01001000 11102?????????111???00?01?0?1100?01?0011
Shuvosaurus inexpectatus	0000100100011??2?????????11100000000000 11100????00?1
Prestosuchus chiniquensis	00?00????00??10001?00001??1????0?0?00000?00??????0
UFRGS 156=T	0?000010??00010001000001111000000000000000?0001?100?
UFRGS 0152=T	0000001010000??0?1000001111?????????????????01?1000
Combined *Prestosuchus*	0000001010000100010000011110000000000000?0001?1000
Saurosuchus galilei	0??0?????????????00??000011110000000000000020001?1000
Batrachotomus kuperferzellensis	0000011010000100010000011110000000000000002000111000
Fasolasuchus tenax	000001 1?1???0??001000001??1?00000000000000 10001?100?
Rauisuchus triradentes	?????1?010??0?0??10000?11110?100?0010000?0001?000?
Polonosuchus silesiacus	0012011?1??????00100000 111001?0?000?000??????????
Postosuchus kirkpatricki	0002011010000100010000011 11???????????000?1?01?0000
Postosuchus alisonae	?????11?1???????010?0001??10010000 0?00002100 11000?
CM 73372	?????????????????????????????1???0??0??0000?000?10000
Hesperosuchus agilis	00020??????????00100 0001??10000000000000001?00?1??0?
Dromicosuchus grallator	000?02101?0001000100 0001??1????????0??000000??10000
Hesperosuchus "agilis"	00?20210??00?10001000001 1110?00000??0000?00??1?0??
Dibothrosuchus elaphros	0??002?0?0000100010000011110000000000000001000 01??0?
Terrestrisuchus gracilis	000002?0?00001?001000001111??00?000000000000?10000
Sphenosuchus acutus	000202101 0000?000100 0001111?000???000000??00?1????
Litargosuchus leptorhynchus	0????2?0?0?0?10?0?000?01?11???00?0000000000 0?1000?
Kayentasuchus walkeri	00101????1?0???00??000?1??????????????????????????
Orthosuchus stormbergi	00?202?0?000?1000?0010?11110?0000000000 0?000?10010
Alligator mississippiensis	001000000000001000000 10?11110000000000 00?1100010010

APPENDIX 3
(Continued)

	160 . 170 . 180 . 190 . 200 .
Protosuchus haughtoni	0??002101102?10?01000?011110?10?000??00000???1001?
Protosuchus richardsoni	0??002101102?1000??00001111??10000000000?0?0?10010
Eudimorphodon ranzii	0?000000?00?0?001?0000?1011???1???00000000???100?0
Dimorphodon macronyx	0??00??0??0??1?01?0000?1??1???1?1??????000???1000?
Lagerpeton chanarensis	???0
Dromomeron gregorii	??
Dromomeron romeri	??
Marasuchus lilloensis	??????????????????????????10100?0000000000000?0000
Asilisaurus kongwe	000110000???0??1010?1?10??11?010100000000000100000
Eucoelophysis baldwini	??
Sacisaurus agudoensis	0?101??????????102001110??1???????????????????????
Lewisuchus admixtus	01000??????????00100000?1111101?1?0000000000?0000?
Pseudolagosuchus majori	???0
Lewisuchus/Pseudolagosuchus	01000??????????00100000?1111101?1?0000000000?00000
Eocursor parvus	?100?001??1001?0?2011?11??1???????0?0001????0??010
Silesaurus opolensis	01121001000001010100101011111010000000000000100000
Pisanosaurus mertii	??000001?012??00?2111111??1????0?0???0000??????0??
Heterodontosaurus tucki	1?0B00010012010B121001111111000000010000000000?2011
Lesothosaurus dianosticus	110000010012010002011011111??0000001000000???0?001?
Scutellosaurus lawleri	110B0???????????02011011??10??00?00??0?0000?0??000
Herrerasaurus ischigualastensis	0??00000?00001?001000001111100?01001100100001?2000
Staurikosaurus pricei	00000?00?000?1?001000001??1???????01?00??0????0000
Eoraptor lunensis	00?00000????0??001?00?01011???0??001?0??0000?02000
Saturnalia tupiniquim	???0???????????002001001??1??????0??100000?01?0000
Plateosaurus engelhardti	01010001100001100201100111111000100110000000100000
Efraasia minor	000000?1?000?1?002001001??11??10?001100?0?00100000
Tawa hallae	00000000?000?1?001000001??111011111111010000100000
Coelophysis bauri	00?00000?00001?00100000111111011111111000000100001
Dilophosaurus wetherelli	0000001000?0011001000001111100011111120000001000000
Allosaurus fragilis	00000010000001100100000111110010101112000000100000
Velociraptor mongoliensis	00000000?000011001000001111???????????????0010?001
	210 . 220 . 230 . 240 . 250 .
Mesosuchus browni	0000000000000000000010?000000????0??0000?0000000?0
Prolacerta broomi	0000000000000000000010?000000000000000000000000000
Archosaurus rossicus	??
Proterosuchus fergusi	000000000000000?000010?000000??0?0?00000?000000??0
Erythrosuchus africanus	001000000000???0100100?0000001?0001001?00??0?00??0
Vancleavea campi	???000000000???010010?????0??0000100000000000???0
Chanaresuchus bonapartei	0010000000?0???0100100?000000000010000000?????????
Tropidosuchus romeri	00100000000?0??0100100?0000000000100??????????????
Euparkeria capensis	0010000000000010100000?00000000001000000000000??0
Parasuchus hislopi	001000000??00010001000?001000000000000000?00000??0
Smilosuchus gregorii	0010000001000010100000?001000000000000000?????????
Pseudopalatus pristinus	001000000??00010100000?00100000000000000???000???0
Gracilisuchus stipanicicorum	0010000000?0????1?????????????????????????????????
Turfanosuchus dabanensis	001000000?????????1??????????00000001?????????????
Ornithosuchus longidens	0?10?0?0?1?000101001010010000000??00???0?0?0100???
Riojasuchus tenuisceps	00?010010???????100101011?00000001001100?0001000?0
Revueltosaurus callenderi	001000000000?0101001010010000000000011011000?0???0
Stagonolepis robertsoni	0010000000??001?1011???0100000000000?????00010???0

APPENDIX 3
(Continued)

	210 . 220 . 230 . 240 . 250 .
Aetosaurus ferratus	?0100000???000101?010100100000000000011011000?00??0
Longosuchus meadei	00?000000??0???01011?10010000000000011011000100000
Ticinosuchus ferox	0??0000001000??010???100?00??0000?0011??0000100??0
Qianosuchus mixtus	01??0010?10?001010010????0??00000?00??????????????
Xilousuchus sapingensis	??
Arizonasaurus babbitti	111000100???00??1001?10010000?????????????????????
Poposaurus gracilis holotype	??1???1?0???
Poposaurus gracilis Yale	1110111?00110??0?00??1001?000010000011000000100??0
Lotosaurus adentus	?11?0010???0???0100000?0101000000000110?0?00100??0
Sillosuchus longicervix	111011110???????0????10000100??????1??????????????
Effigia okeeffeae	11111011?0110??0000??10000110??0?101?1?00000100??0
Shuvosaurus inexpectatus	11111011??11???0??0??1000?1100000101110???????????
Prestosuchus chiniquensis	??10?000????001?1?11010010001??00?????????????????
UFRGS 156=T	??
UFRGS 0152=T	00?0000001?????010?????0100??0000?00??????????????
Combined *Prestosuchus*	0010000001??0010101101001000100?0?00??????????????
Saurosuchus galilei	?01000000???
Batrachotomus kuperferzellensis	01100010010000?01011?1001?000000000011110?????????
Fasolasuchus tenax	????????????????????????????????????1110??????????
Rauisuchus triradentes	?0??000?010?????101?????1?1?0?????????????????????
Polonosuchus silesiacus	?????????1??
Postosuchus kirkpatricki	001000000??0???01001110?101000010000111?0?00100??0
Postosuchus alisonae	??????????0?0???1???1101101000?100001111?00?100000
CM 73372	??100000?1??????1?????????????0?????0?????000100?0
Hesperosuchus agilis	?0??000?0??0???010011111101000011100111101?0?00??0
Dromicosuchus grallator	?01000000?00201010011111101000011100011?0100100?10
Hesperosuchus "agilis"	????????????20101001?????????0?1?10011110100?00?10
Dibothrosuchus elaphros	????????????????10011111101000?1010011110110?00?10
Terrestrisuchus gracilis	00100000010020111001111110100001010011110100100?10
Sphenosuchus acutus	????????????201010011111101000?1?100??????????????
Litargosuchus leptorhynchus	?????????0002??11001?120101000010100?1?101?0??????
Kayentasuchus walkeri	??
Orthosuchus stormbergi	?0100000???02??01001112010000001010011110110?10??0
Alligator mississippiensis	00100000010020101011012010000000110010111100100??0
Protosuchus haughtoni	????????????????????1???????????????????????????1?
Protosuchus richardsoni	?0100000???0?011000111201000000?010011111110100???
Eudimorphodon ranzii	0??????0?0100010??????1?1?0??0001100?0?00001??????
Dimorphodon macronyx	?????????010???0??????101?0??0001100?????001?0???0
Lagerpeton chanarensis	001000000???
Dromomeron gregorii	??
Dromomeron romeri	??
Marasuchus lilloensis	001000000000???01?0????0??1??000?1001???0?????????
Asilisaurus kongwe	00?00001000?????1?01?1001?100000?100??00??????????
Eucoelophysis baldwini	??
Sacisaurus agudoensis	????????????????1?01?????0100?????????????????????
Lewisuchus admixtus	????????????????11010100101000?00??0??????????????
Pseudolagosuchus majori	001000000???
Lewisuchus/*Pseudolagosuchus*	001000000???????11010100101000?00??0??????????????
Eocursor parvus	?0?01?1?0??????01101??????1??1?0?1001?????????????
Silesaurus opolensis	00?000110000???01101010010100000010010?00??0?00??0
Pisanosaurus mertii	??
Heterodontosaurus tucki	?0?011100001?1?01101?0?0101?0100110010001000110001
Lesothosaurus dianosticus	?0??111?0??1???011010?????1??100?10000?0100010???0

APPENDIX 3
(Continued)

	210 . 220 . 230 . 240 . 250 .
Scutellosaurus lawleri	???0???00?00?1??1?0??0?00?00000011001000?????????0
Herrerasaurus ischigualastensis	001000001011?1??1?01??????1??110110010000000112011
Staurikosaurus pricei	00100?00101???????????????????????????????????????
Eoraptor lunensis	0010?000?0?1?1?01001?0??10100110110010001000111??1
Saturnalia tupiniquim	00?000001001???01001000?01010010001101??01??0??????
Plateosaurus engelhardti	00100100100001?0100100?010100100111010001000101010
Efraasia minor	001000001001?1?01001?0?01010010011101000100010?010
Tawa hallae	0010?000?011?1?01101??????1??11011001000000011200?
Coelophysis bauri	00?01110101111?01101?0?010100110110010001000112111
Dilophosaurus wetherelli	00?011101??1?1?11101?1001010011001001000010?0112??1
Allosaurus fragilis	00101111111111?00101010010100110110010001000112111
Velociraptor mongoliensis	0011111110?111?00101?11010100100110010000000012111

	260 . 270 . 280 . 290 . 300 .
Mesosuchus browni	0????00?0000?00??0?00000000000000??00000000000000?
Prolacerta broomi	000000000000?00??0?00000000000000??00000000000000?
Archosaurus rossicus	??
Proterosuchus fergusi	00?0?0??0000?00??0?00000000000000??00000000000000?
Erythrosuchus africanus	1??0????0?00?00??1010000000000000??000000000000000
Vancleavea campi	0??0?0??010??00??0?00000000?000????00???0000000?00
Chanaresuchus bonapartei	?????????????00??100000000000000??000000000000000
Tropidosuchus romeri	?????????????00??1?00000000000000??000000?00000000
Euparkeria capensis	10?0?00?0100?00??100000000000000??000000000000000
Parasuchus hislopi	0????00?0?00?00??10?000?000000000??00?000000000000
Smilosuchus gregorii	?????????????00??100000000000000??000000000000000
Pseudopalatus pristinus	0000?0???100?00??100000000000000??000000000000000
Gracilisuchus stipanicicorum	?????????????00??1000000000100010??00000010000000?
Turfanosuchus dabanensis	?????????????00??1000000000000??0??0??00????????01
Ornithosuchus longidens	0??0???????0?00??1000000000100010??00?0001000000?1
Riojasuchus tenuisceps	0??0????0?0??00??10000000001000?0??0?000????000?01
Revueltosaurus callenderi	00????0??????00???000000000000000??000000000000001
Stagonolepis robertsoni	1000000?0100?00??101000000000000???00?0000000000?1
Aetosaurus ferratus	0000????0100?0A??10?000000000000???00?00000000001
Longosuchus meadei	000000?00100?00??1010000000000000??00?000?00000001
Ticinosuchus ferox	00?0?00?0100?????10?0?0?000000?00??0??0?101100?101
Qianosuchus mixtus	?????????????010?10?00200000000010001100100100010?
Xilousuchus sapingensis	??
Arizonasaurus babbitti	?????????????01001010020000?00011100211010110001?1
Poposaurus gracilis holotype	?????????????11111??0120000?????????????1011?????1
Poposaurus gracilis Yale	000000020100?1111110012?00010001110021101011000?01
Lotosaurus adentus	000000000100?11101?0002?01?????????01???2?10000?0?
Sillosuchus longicervix	?????????????11111?00121?101000111002?102?1?000??1
Effigia okeeffeae	0?00?0???????111112000210?10?0001111021212010000??3
Shuvosaurus inexpectatus	?????????????1111120002101010001111021212010000?03
Prestosuchus chiniquensis	?????????????0?????10000000?00??100?1???10110?0?01
UFRGS 156=T	??
UFRGS 0152=T	?????????????00??101000000010001100010101011020101
Combined *Prestosuchus*	?????????????00??101000000010001100010101011020101
Saurosuchus galilei	?????????????01001010000000010000?10001000101100 0??1
Batrachotomus kuperferzellensis	?????????????010010100000001000110001000100100 00101
Fasolasuchus tenax	????????????????????????????001????010?01???000?01

APPENDIX 3
(Continued)

	260 . 270 . 280 . 290 . 300 .
Rauisuchus triradentes	?????????????010010?0000000?00????????????????????
Polonosuchus silesiacus	??
Postosuchus kirkpatricki	0????0??0100?01001?10000000?????????1???1011000?01
Postosuchus alisonae	000?000?0100????????????????????100???????????????
CM 73372	0??0????0????010011?002?000100?11000??10101000?101
Hesperosuchus agilis	?????????????010?111?001100?00??100???10????????01
Dromicosuchus grallator	?????????????010?1110000100?00?????01???????????01
Hesperosuchus “agilis”	0000000?0100???????????????1001?10001010????????01
Dibothrosuchus elaphros	0000?0??0100?00??1100021100???????????????????????
Terrestrisuchus gracilis	0??0000?0100?010?1100021100100110??010001000002001
Sphenosuchus acutus	??
Litargosuchus leptorhynchus	?????????????????11?????????????????????0?00????1?
Kayentasuchus walkeri	?????????????0?????0??21?????????????????????????1
Orthosuchus stormbergi	0000000?0100?010?1100020100000?10??01??00000002001
Alligator mississippiensis	00?000020100??0????00021000000?00??01???0000002101
Protosuchus haughtoni	??
Protosuchus richardsoni	0?0000??0100?010?1100021100000?10??010?00000002001
Eudimorphodon ranzii	0000101101?1?00??11???0?00?000000??00??00??000001?
Dimorphodon macronyx	0000??1101?1?00??11?000100?000?00??00??0???0000011
Lagerpeton chanarensis	?????????????00??1000000000000000??000000000000011
Dromomeron gregorii	??11
Dromomeron romeri	??11
Marasuchus lilloensis	?????????????00??1000001000000010??110000000001111
Asilisaurus kongwe	?????????????02??1000010000?00??0??110?01001001??1
Eucoelophysis baldwini	??????????????????????10?????????????????????????1
Sacisaurus agudoensis	?????????????02????010?00001000?0??1???0?0???????1
Lewisuchus admixtus	??
Pseudolagosuchus majori	?????????????02????0?0100001000?0???1010??????1?11
Lewisuchus/Pseudolagosuchus	?????????????02????0?0100001000?0???1010??????1?11
Eocursor parvus	?????????????02??1101020000?110????01??0100?002?11
Silesaurus opolensis	?????????????02??1001010000100010??110101000001101
Pisanosaurus mertii	???????????????????0????????000???????????????2???
Heterodontosaurus tucki	0000111201000?2??1100021000111010??01??0100000211?
Lesothosaurus dianosticus	00?0?0??0100002??1101021000111010??01??01000002111
Scutellosaurus lawleri	?????????????02??110102?1001110?????1??00??????111
Herrerasaurus ischigualastensis	001110130110102??100002100010001110110101020002101
Staurikosaurus pricei	?????????????02??1000021000100?1110110101?1?00?11?
Eoraptor lunensis	0011110??110102??100112?001100011???1000101000?11?
Saturnalia tupiniquim	?????????????02??100101100010001100110001021002101
Plateosaurus engelhardti	111111120100?02??100002100010001100110001021002101
Efraasia minor	11?1?11?0100?02??1000021000100010??110001021002101
Tawa hallae	001110120110102??1001120001100??110?1010??1???2?12
Coelophysis bauri	001111130?10112??110212111110001110 11?101011102112
Dilophosaurus wetherelli	0011?1120?10112??11021210111000?110?10101011112102
Allosaurus fragilis	1011111?1???102??1102021011100?1101110201011112102
Velociraptor mongoliensis	0000111?1???102??11020210111100111011?200001002102

	310 . 320 . 330 . 340 . 350 .
Mesosuchus browni	??00000000000?0??000000000000000000000??10001000??
Prolacerta broomi	??00000000000?0??000000000000000000000??100010000?
Archosaurus rossicus	??
Proterosuchus fergusi	??00000000000?0??000000000000000000000?01000000000

APPENDIX 3
(Continued)

	310 320 330 340 350
Erythrosuchus africanus	10000000000001 0??000000000000000000000001000110000
Vancleavea campi	10000000000000???100?00000000000000000??1000110???
Chanaresuchus bonapartei	1000100000000110010000000000000000000100101011000?
Tropidosuchus romeri	10001000000000100100000?00000000000000100101011000?
Euparkeria capensis	1000100000000010010000000000000000000000000?0010000
Parasuchus hislopi	1000?0000000001001 0?00?0?00000??0000001000100100??
Smilosuchus gregorii	100000000000001001000000000000?00000001100100?????
Pseudopalatus pristinus	10000000000000100100000000000000000000110010010000
Gracilisuchus stipanicicorum	1000?0000000001001?000?00000???000001000???0010000
Turfanosuchus dabanensis	10001000000000100100000?000000100000?010001???????
Ornithosuchus longidens	1000?00100000110010?00?0?0?0?1000000??1????0??????
Riojasuchus tenuisceps	10001001000000100101 00?0000001?00000101100100100 00
Revueltosaurus callenderi	10001000000000100100000000000001000000100000 1001?000
Stagonolepis robertsoni	1000?0000000001001 0?00?00000????0000??11001001????
Aetosaurus ferratus	10001000000000100100?0?00000?10?000010???0??0?????
Longosuchus meadei	10001000000000100100000000000001000000101100?0010?00
Ticinosuchus ferox	1??0?0??00??0?1001?????0???00?0?0000?000??100100??
Qianosuchus mixtus	?000?00000000?1001?????000?00???0??0??00??00110???
Xilousuchus sapingensis	??
Arizonasaurus babbitti	000010000000011001100010 0?0???????????????????????
Poposaurus gracilis holotype	0000?00000000?1001????????????????????????????????
Poposaurus gracilis Yale	0000100000000110 01??0010000001?00000?0001010?10010
Lotosaurus adentus	??00?000000001100111???0000001?000?0??0000101?????
Sillosuchus longicervix	0??0??00?00?0?1001??0??0??????????????????????????
Effigia okeeffeae	0100??00000011???1110110000001?0100010001010110010
Shuvosaurus inexpectatus	01001000000011 12?1110110000001?0000010001010110010
Prestosuchus chiniquensis	10001000000001100100000000000?00000010110010010000
UFRGS 156=T	??
UFRGS 0152=T	1000100000000110 0100?000000001000000?01100100?????
Combined *Prestosuchus*	10001000000001100100000000000010000001011 0010010000
Saurosuchus galilei	?0001000000?0110010100?000000?000000101100?0010000
Batrachotomus kuperferzellensis	00001000000001100111000000000 10000001001001001????
Fasolasuchus tenax	0000?00000010010011100?0000???????????0100110??010
Rauisuchus triradentes	???????????????????????????0????0000?00??01???????
Polonosuchus silesiacus	??
Postosuchus kirkpatricki	0000100000 0?00100111 00?0000001000000100110110?????
Postosuchus alisonae	???????????????????????????0?10?000010011011010010
CM 73372	0?00?000000100???1????00???0010000001001101101?010
Hesperosuchus agilis	0000100000010010 01??1??00?000100000010??1011010010
Dromicosuchus grallator	000010000011001001110 0?000000100000010001 0110?????
Hesperosuchus "agilis"	000010000001 00???111??00???0???000?01?001011010010
Dibothrosuchus elaphros	??
Terrestrisuchus gracilis	000010100001001001010010000001000000100010?1110010
Sphenosuchus acutus	???????????????????????????00100000010????????????
Litargosuchus leptorhynchus	?????????????????1??1??0?0?00?????????001???11?0??
Kayentasuchus walkeri	0?001?11000110100???1?????????????????????????????
Orthosuchus stormbergi	00000000000100100101 10?000000100000010???0?1110010
Alligator mississippiensis	000010?00011001001011000000001000000100010111A0010
Protosuchus haughtoni	??
Protosuchus richardsoni	0?001000000100100111100000000100?0001000101111?010
Eudimorphodon ranzii	???????0?00????2?1??0??0?0??????0????????????11?00
Dimorphodon macronyx	0000?000000000???1010020000000?00?000?00??1??11100
Lagerpeton chanarensis	110011000100?011010100?0010100?0000000001010111100

APPENDIX 3

(Continued)

	310 . 320 . 330 . 340 . 350 .
Dromomeron gregorii	11001?01010010100101011011110000000000????????????
Dromomeron romeri	11001100010010?2?101?1101111000000000000101???????
Marasuchus lilloensis	0000100100101010010?00?000010000000001001010011100
Asilisaurus kongwe	000110111010111001010?1100010000010001??1110??????
Eucoelophysis baldwini	2001??11100001???1????1100010?100?????????????????
Sacisaurus agudoensis	0011101110000110010????100010010110001????????????
Lewisuchus admixtus	??
Pseudolagosuchus majori	00011?110010111?01010??000010000010001001?10??????
Lewisuchus/Pseudolagosuchus	00011?110010111?01010??000010000010001001?10??????
Eocursor parvus	0002101200001111110100?000020000?20101001?101?????
Silesaurus opolensis	2011101110A001100101?0110001001011000100111011?10?
Pisanosaurus mertii	?????????????????1010??0000?00000100010011101?????
Heterodontosaurus tucki	0??????20?0?1011110100?0000200001101??00110?111100
Lesothosaurus dianosticus	000210120000101111?1000000020000020101??111??1????
Scutellosaurus lawleri	000?1?120000?0111101?0000002000002010?001?1011????
Herrerasaurus ischigualastensis	0102102100101011110101?000020010010101001110111101
Staurikosaurus pricei	000210110010111111010??0000200100100010011101?????
Eoraptor lunensis	?0??1?110?00????110?0???000C0010?10001001?10111101
Saturnalia tupiniquim	00021021001011111101?1?000020000111010011101111101
Plateosaurus engelhardti	00021021000011111101010000020000011101001110111101
Efraasia minor	00021021000011111101010000020000011101001110111101
Tawa hallae	00022011000012110101011000020011010001001110111101
Coelophysis bauri	00021021001012110101?11000021011111101001110111100
Dilophosaurus wetherelli	00021?12000012110101?110?0021011121101001110111100
Allosaurus fragilis	00022002000010110101011000021011121101001110111100
Velociraptor mongoliensis	010220?200001011010101100002101?12110?001?00?111??

	360 . 370 . 380 . 390 . 400 .
Mesosuchus browni	0??00000?0000000??0000000000?00000000000?0000?0000
Prolacerta broomi	????0000?0000000??0000000000?0000000000000000?1000
Archosaurus rossicus	??
Proterosuchus fergusi	00000000?0000000??0000000000?0000000000000000?1000
Erythrosuchus africanus	0?000000?000?0?0001000000000?010000?000000101?000?
Vancleavea campi	????0000?0001000001000000000?01000000?0?00????00??
Chanaresuchus bonapartei	???00000?00000100010000000?0?010000001000011000020
Tropidosuchus romeri	??000000?0001010001000000010?0100000010000110?0020
Euparkeria capensis	00000000?1000010001000000110?0100000000000100?0000
Parasuchus hislopi	0??00000??000010?110?0010111?11000000000001000?001
Smilosuchus gregorii	??000000?1000010011010010111?1100001????00????00?2
Pseudopalatus pristinus	01000000?1000010011?10010111?1100001000000100?0002
Gracilisuchus stipanicicorum	0??00000?1000011011011010221?1100000000000100?0100
Turfanosuchus dabanensis	???????0?????????1101101?221?1????????????????????
Ornithosuchus longidens	?????0?????????1?21010010120???000?????????????1?2
Riojasuchus tenuisceps	00100000?1000011021010010120?1100000000000100?0102
Revueltosaurus callenderi	00100000?10000110110110102210110?000000?00??0?00??
Stagonolepis robertsoni	????00????????11???0?1????????10?00000?0??10?0000?
Aetosaurus ferratus	?????????????????????1?1?2?1????????????????0????2
Longosuchus meadei	???00000?1000111011021010221?1100000000000010??0002
Ticinosuchus ferox	???000?0?1000011?11011010221?110000?000000100????2
Qianosuchus mixtus	?????000??00??1??11011010221?110000?00?000101?0002
Xilousuchus sapingensis	???2

APPENDIX 3
(Continued)

	360 . 370 . 380 . 390 . 400 .
Arizonasaurus babbitti	??
Poposaurus gracilis holotype	??
Poposaurus gracilis Yale	01?00001?10001110110110111121?11000000?00?0101000A1
Lotosaurus adentus	???00000?100001??11011010121?11000000000?0101?1001
Sillosuchus longicervix	??
Effigia okeeffeae	0110000??10000110110 11?1?121?110000000011 0101?00?1
Shuvosaurus inexpectatus	01100001?10000110110110101 21?1100000000110101?00?1
Prestosuchus chiniquensis	00?0000??1000011?11021010221?1100000000000101?10?2
UFRGS 156=T	??
UFRGS 0152=T	???????0?????????11021010221?1?000000000??????100?
Combined *Prestosuchus*	00?00000?1000011?11021010221?1100000000000101?1002
Saurosuchus galilei	0??00001?100001??1102101?121?110?000000000101?1002
Batrachotomus kuperferzellensis	?????0?1???????1?110?1010221?1?0000000??00????10?2
Fasolasuchus tenax	01110001?1000111111021011121?11???????????????????
Rauisuchus triradentes	?????00???0?0?1?1110??????????1???????????????????
Polonosuchus silesiacus	??
Postosuchus kirkpatricki	???10001?1000111111021011121?1100000000110101?10?0
Postosuchus alisonae	01110001?1000111111021011121?110000000010010101010
CM 73372	01110001?1000111111021011121?110000000011010?01010
Hesperosuchus agilis	??1?0001???????1?1?0?10???21?110?000?00??0?0??002?
Dromicosuchus grallator	????00?1???????1?1102101 1?21?1?1?000??????????????
Hesperosuchus "agilis"	01110001?1000111111021011121?11000000001?0101?00??
Dibothrosuchus elaphros	??
Terrestrisuchus gracilis	01110001?1000111111021011121?111000010?10010110110
Sphenosuchus acutus	???????????????1???????????????100??????0???1?????
Litargosuchus leptorhynchus	??????????????1??1?0??0??121?1?1??000?????????012?
Kayentasuchus walkeri	??
Orthosuchus stormbergi	???10001?1000?111110210111 21?11??00???0??0????002?
Alligator mississippiensis	01110001?1000111111011011111?110100000010011110020
Protosuchus haughtoni	??
Protosuchus richardsoni	0?010001?1000111111021011121?111000000010010110020
Eudimorphodon ranzii	?????01???1???1???11?01??????111?00010?1?010101000
Dimorphodon macronyx	0?0??01???101?1???11??1??????111000010?01?10??1?00
Lagerpeton chanarensis	0?1?1010011010110?11?01????20111100000000000000120
Dromomeron gregorii	????1??????????10?????????????????????????????????
Dromomeron romeri	????1010011010110?1??01????2?1????????????????????
Marasuchus lilloensis	001?0110011000110?101000012001111000000000100?012?
Asilisaurus kongwe	????0110011000100?10100001?00111????????1?10?????1
Eucoelophysis baldwini	??
Sacisaurus agudoensis	??
Lewisuchus admixtus	??
Pseudolagosuchus majori	????0110011000100?10?00001?0011???????????????????
Lewisuchus/Pseudolagosuchus	????0110011000100?10?00001?0011???????????????????
Eocursor parvus	?????1?????????????????????????11?????00??????????
Silesaurus opolensis	????0110011010100?10?01????20111110??0001010100121
Pisanosaurus mertii	????0110??111?1?0?10?01????211111?????0?1?10??????
Heterodontosaurus tucki	0?0??110??1?1?1???11?01??????111110000?0101010?120
Lesothosaurus dianosticus	??0?01100?11101?0?10?01????211111100000010101????0
Scutellosaurus lawleri	????01100111101?0?1??01????211?10????????????????0
Herrerasaurus ischigualastensis	1?0?0110111110 1?0?10?01????201111100000011101?0110
Staurikosaurus pricei	??
Eoraptor lunensis	10???1?0???1?01?0?10?0?????2?11111000000 1?1010?1?0
Saturnalia tupiniquim	100?0110111110 1?0?10?01????201111100000011101001?0

APPENDIX 3
(Continued)

	360 . 370 . 380 . 390 . 400 .
Plateosaurus engelhardti	100?01101111101?0?10?01????20111010000001110100110
Efraasia minor	1?0?0110??111?1?0?10?01????20111010000001110100110
Tawa hallae	100?01101?11101?0?10?01????21111110000001010 1?0120
Coelophysis bauri	100?01100111101?0?11?01????2111111100010 10??10012?
Dilophosaurus wetherelli	100?01100111101?0?10?01????21111111000101 01?100120
Allosaurus fragilis	1?0?02100?11101?0?10?01????21111011000001010100120
Velociraptor mongoliensis	????0210??111?1?0?11?01?????11110110000010101 00120

	410 .
Mesosuchus browni	0??????????0
Prolacerta broomi	0??????????0
Archosaurus rossicus	????????????
Proterosuchus fergusi	0??????????0
Erythrosuchus africanus	0???????????
Vancleavea campi	1?1?10001 1?2
Chanaresuchus bonapartei	100?0?0001??
Tropidosuchus romeri	100?0??000??
Euparkeria capensis	110100000000
Parasuchus hislopi	1100?00000?0
Smilosuchus gregorii	1100??0000?0
Pseudopalatus pristinus	110010000010
Gracilisuchus stipanicicorum	11100000011?
Turfanosuchus dabanensis	1110??00?1??
Ornithosuchus longidens	110000100010
Riojasuchus tenuisceps	11000020001?
Revueltosaurus callenderi	11001?211012
Stagonolepis robertsoni	11001121101?
Aetosaurus ferratus	1?0011211012
Longosuchus meadei	110011211012
Ticinosuchus ferox	111000000100
Qianosuchus mixtus	111?00000100
Xilousuchus sapingensis	????????????
Arizonasaurus babbitti	0???????????
Poposaurus gracilis holotype	????????????
Poposaurus gracilis Yale	0???????0??0
Lotosaurus adentus	0???????????
Sillosuchus longicervix	0???????????
Effigia okeeffeae	0??????????0
Shuvosaurus inexpectatus	0???????????
Prestosuchus chiniquensis	???????????0
UFRGS 156=T	1110?000?10?
UFRGS 0152=T	11?0?000?1??
Combined *Prestosuchus*	1110?000?100
Saurosuchus galilei	1110?000010?
Batrachotomus kuperferzellensis	1111?010?010
Fasolasuchus tenax	1??1?0??????
Rauisuchus triradentes	1111?011001?
Polonosuchus silesiacus	111??0?0????
Postosuchus kirkpatricki	1111?01000??
Postosuchus alisonae	1111?0100010
CM 73372	111100?000?0

APPENDIX 3
(Continued)

	410 .
Hesperosuchus agilis	1111?010?010
Dromicosuchus grallator	111100100010
Hesperosuchus "agilis"	111100100010
Dibothrosuchus elaphros	???1????????
Terrestrisuchus gracilis	11??00100010
Sphenosuchus acutus	1????0?????0
Litargosuchus leptorhynchus	1?1?000?001?
Kayentasuchus walkeri	??1?????????
Orthosuchus stormbergi	1110?021?01?
Alligator mississippiensis	110011A?1011
Protosuchus haughtoni	1110?021101?
Protosuchus richardsoni	111010211010
Eudimorphodon ranzii	0??????????1
Dimorphodon macronyx	0???????????
Lagerpeton chanarensis	0???????????
Dromomeron gregorii	????????????
Dromomeron romeri	0???????????
Marasuchus lilloensis	0???????????
Asilisaurus kongwe	0???????????
Eucoelophysis baldwini	????????????
Sacisaurus agudoensis	????????????
Lewisuchus admixtus	0???????????
Pseudolagosuchus majori	0???????????
Lewisuchus/Pseudolagosuchus	0???????????
Eocursor parvus	0???????????
Silesaurus opolensis	0???????????
Pisanosaurus mertii	0???????????
Heterodontosaurus tucki	0??????????2
Lesothosaurus dianosticus	0???????????
Scutellosaurus lawleri	1?????000???
Herrerasaurus ischigualastensis	0???????????
Staurikosaurus pricei	0???????????
Eoraptor lunensis	0??????????1
Saturnalia tupiniquim	0???????????
Plateosaurus engelhardti	0???????????
Efraasia minor	0??????????1
Tawa hallae	0??????????1
Coelophysis bauri	0??????0????
Dilophosaurus wetherelli	0??????????1
Allosaurus fragilis	0??????????1
Velociraptor mongoliensis	0??????????1