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## **The higher-level phylogeny of Archosauria (Tetrapoda: Diapsida)**

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**SYNOPSIS** Crown group Archosauria, which includes birds, dinosaurs, crocodylomorphs, and several extinct Mesozoic groups, is a primary division of the vertebrate tree of life. However, the higher-level phylogenetic relationships within Archosauria are poorly resolved and controversial, despite years of study. The phylogeny of crocodile-line archosaurs (Crurotarsi) is particularly contentious, and has been plagued by problematic taxon and character sampling. Recent discoveries and renewed focus on archosaur anatomy enable the compilation of a new dataset, which assimilates and standardises character data pertinent to higher-level archosaur phylogeny, and is scored across the largest group of taxa yet analysed. This dataset includes 47 new characters (25% of total) and eight taxa that have yet to be included in an analysis, and total taxonomic sampling is more than twice that of any previous study. This analysis produces a well-resolved phylogeny, which recovers mostly traditional relationships within Avemetatarsalia, places Phytosauria as a basal crurotarsan clade, finds a close relationship between Aetosauria and Crocodylomorpha, and recovers a monophyletic Rauisuchia comprised of two major subclades. Support values are low, suggesting rampant homoplasy and missing data within Archosauria, but the phylogeny is highly congruent with stratigraphy. Comparison with alternative analyses identifies numerous scoring differences, but indicates that character sampling is the main source of incongruence. The phylogeny implies major missing lineages in the Early Triassic and may support a Carnian-Norian extinction event.

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## INTRODUCTION

The archosaurs (“ruling reptiles”, Cope 1869) are a speciose and diverse group that includes birds, dinosaurs, and crocodylomorphs, as well as a range of extinct taxa restricted to the Mesozoic (Fig. 1). The clade Archosauria represents one of the fundamental divisions of vertebrate phylogeny, and has been a successful and at times dominant group ever since its origination in the Late Permian or Early Triassic. Palaeontologists have long recognised numerous archosaur subgroups, including the flying pterosaurs, the long-snouted phytosaurs, and the armoured aetosaurs, as well as the extant crocodylians and birds (and their dinosaur precursors). However, many aspects of the higher-level phylogeny of Archosauria have proved elusive, which is frustrating for several reasons. Most notably, lack of a clear phylogenetic framework hampers understanding of character evolution patterns on the line to two diverse and successful extant clades (birds and crocodylians), prevents a more rigorous analysis of terrestrial biogeographic patterns during the heyday of Pangaea, and frustrates attempts to understand the end-Triassic extinction and the establishment of “modern” ecosystems.

Poor understanding of the higher-level phylogeny of Archosauria does not indicate a lack of effort. Since the widespread inception of cladistics in vertebrate palaeontology in the mid 1980s, numerous studies have examined the large-scale phylogeny of Archosauria (Gauthier 1986; Benton & Clark 1988; Sereno & Arcucci 1990; Sereno 1991a; Juul 1994; Bennett 1996; Benton 1999, 2004; Irmis *et al.* 2007a). These studies largely agree that crown-group Archosauria is divided into two large clades: a group consisting of birds and their close relatives (Avemetatarsalia) and a group consisting of crocodylomorphs and their close relatives (Crurotarsi). Both of these main lines of archosaur evolution have been the subject of further study, which has largely resolved relationships in Avemetatarsalia (Sereno & Arcucci 1993, 1994; Novas 1996; Ezcurra 2006; Langer & Benton 2006; Irmis *et al.* 2007a) but continues to disagree on nearly every aspect of crurotarsan interrelationships (Parrish 1993; Benton & Walker 2002; Gower 2002; Nesbitt 2003, 2007; Nesbitt & Norell 2006; Weinbaum & Hungerbühler 2007). Perhaps most problematic, there is no clear consensus on which

crurotarsan clade is most basal and which taxa are most closely related to crocodylomorphs.

Although numerous studies have been published, many are preliminary, limited, or unsatisfactory. Most recovered phylogenies are poorly supported on the whole, with crurotarsan ingroup relationships especially prone to mediocre support values (Gower & Wilkinson 1996). More fundamentally, many analyses are characterised by limited or problematic taxon and character sampling (see below). First, although several archosaur subgroups have been recognised and characterised by synapomorphies their monophyly has not been explicitly tested in a global analysis. Furthermore, many taxa, especially a range of enigmatic crurotarsans called “rauisuchians,” are often excluded from analyses, and the choice and construction of characters often masks true morphological variability. In light of these issues, previous authors (e.g. Gower 1999; Nesbitt 2005, 2007) have called for restraint in studies of archosaur phylogeny, even going so far as stating that no higher-level analyses should be carried out until the anatomy of basal archosaurs is better described and understood.

We believe that the time has come to revisit higher-level archosaur phylogeny in a more complete, detailed, and rigorous light. The past several years have witnessed the discovery of numerous new basal archosaurs (e.g. Gower 1999; Dzik 2003; Sen 2005; Sulej 2005; Li *et al.* 2006; Nesbitt & Norell 2006; Ferigolo & Langer 2007; Jalil & Peyer 2007; Irmis *et al.* 2007a), the discovery of important new material of previously-known taxa (e.g. Alcober 2000; Nesbitt 2003, 2005; Parker *et al.* 2005; Weinbaum & Hungerbühler 2007), and the reinterpretation and redescription of taxa (e.g. Benton 1999; Benton & Walker 2002; Gebauer 2004; Ezcurra 2006; Nesbitt 2007). This wealth of new anatomical information has yet to be assimilated into a single analysis. Such an analysis is becoming increasingly necessary, as description and interpretation of new archosaur material is often facilitated by a phylogenetic framework, while quantitative studies of macroevolution, biogeography and extinction demand it.

Here we present a new higher-level analysis of crown-group archosaur phylogeny that integrates data from previous analyses, new anatomical information revealed by new discoveries and reinterpretation of taxa, and new characters gleaned from personal observation of specimens. Included are 47 new characters (25% of the total) and eight taxa

that have yet to be included in an analysis, and overall taxonomic sampling is more than double that of any previous study. The result is the largest and most expansive dataset yet applied to archosaur phylogeny, which we use to assess aspects of archosaur history. Additionally, we compare our dataset to previous studies, evaluate the degree of overlap using quantitative metrics, and attempt to pinpoint important sources of disagreement.

#### INSTITUTIONAL ABBREVIATIONS

**AMNH**, American Museum of Natural History, New York, USA; **BMNH**, The Natural History Museum, London, England; **BSPG**, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Germany; **IVPP**, Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing, China; **LH**, Long Hao Institute for Stratigraphic Paleontology, Hohhot, China; **MLP**, Museo de La Plata Museum, Argentina; **MCN**, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; **MNA**, Museum of Northern Arizona, Flagstaff, Arizona, USA; **MNHN**, Museum National d’Histoire Naturelle, Paris, France; **NMS**, National Museums of Scotland, Edinburgh, Scotland; **PIMUZ**, Paläontologisches Institut und Museum der Universität, Zurich, Switzerland; **PULR**, Museo de Ciencias Naturales Universidad Nacional de La Rioja, La Rioja, Argentina; **PVL**, Fundación Miguel Lillo, Universidad Nacional de Tucumán, San Miguel de Tucumán, Argentina; **PVSJ**, Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan, Argentina; **SAM**, South African Museum, Cape Town, South Africa; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart, Germany; **TMM**, Texas Memorial Museum, Austin, Texas, USA; **TTUP**, Texas Tech University Museum, Lubbock, Texas, USA; **UCMP**, University of California Museum of Paleontology, Berkeley, USA; **UFRGS**, Federal University of Rio Grande do Sul, Porto Alegre, Brazil; **UMMP**, University of Michigan Museum of Paleontology, Ann Arbor, Michigan, USA; **WARMS**, Warwickshire Museum, Warwick, England; **YPM**, Yale University Peabody Museum of Natural History, New Haven, USA; **ZPAL**, Institute of Paleobiology of the Polish Academy of Sciences, Warsaw, Poland.

## PREVIOUS ANALYSES OF ARCHOSAUR PHYLOGENY

Over 20 published analyses have considered the higher-level phylogeny of Archosauria or its two main clades, Avemetatarsalia and Crurotarsi. These analyses often differ substantially, especially concerning crurotarsan ingroup relationships (Fig. 2). The main areas of agreement and disagreement are highlighted below, along with a discussion of the problematic aspects of many previous studies.

### **Archosauria**

A monophyletic Archosauria, consisting of birds, crocodylomorphs, and other taxa (e.g., dinosaurs) to the exclusion of other reptile clades such as squamates and sphenodontians, is routinely recovered in morphological phylogenetic analyses (e.g., Benton & Clark 1988; Gauthier 1986; Juul 1994; Benton 1999, 2004). Numerous characters reviewed in these analyses support archosaur monophyly. Molecular phylogenies, which can only address the relationships of extant taxa, also consistently place birds and crocodylomorphs as sister taxa. However, some molecular phylogenies have placed turtles within the archosaur clade, usually as the sister taxon to crocodylomorphs (e.g., Hedges & Poling 1999; Cao *et al.* 2000). This relationship has yet to be corroborated by morphological data (see review in Harris *et al.* 2007), and combined morphological and molecular analyses have yet to be published. As this debate awaits resolution, we do not include turtles in our morphological analysis (see below).

### **Avemetatarsalia**

The bird line of crown-group Archosauria, Avemetatarsalia, includes birds, dinosaurs, pterosaurs, the enigmatic taxon *Scleromochlus*, and a range of “dinosauromorphs” that are closely related to dinosaurs. Relationships within this clade are well understood on the whole: studies generally agree that dinosaurs are a monophyletic group, pterosaurs are closely related to dinosaurs, and several dinosauromorphs are the closest relatives to dinosaurs (Novas 1989, 1992, 1996; Sereno



& Novas 1992; Sereno *et al.* 1993; Sereno & Arcucci 1993, 1994; Sereno 1999; Ezcurra 2006; Langer & Benton 2006; Irmis *et al.* 2007a).

Current disagreement focuses on the relative relationships of dinosaur precursors and the position of *Scleromochlus*. It is largely agreed that the dinosauromorphs *Lagerpeton*, *Marasuchus*, and *Pseudolagosuchus* form successive outgroups to Dinosauria (Sereno & Arcucci 1993, 1994; Novas 1996; Benton 1999, 2004). However, the relationships of several newly-discovered dinosauromorphs (e.g. *Dromomeron*: Irmis *et al.* 2007a; *Eucoelophysis*: Sullivan & Lucas, 1999 Ezcurra, 2006 Nesbitt *et al.*, 2007; *Sacisaurus*: Ferigolo & Langer 2007; *Silesaurus*: Dzik 2003) have only been addressed in a few studies (Ezcurra 2006; Langer & Benton 2006; Irmis *et al.* 2007a). It is possible that some of these taxa fall out in a successive array of dinosauromorphs leading to dinosaurs, form their own monophyletic dinosauromorph group, or are true dinosaurs, all of which need to be adequately tested in a higher-level analysis. The small and puzzling *Scleromochlus* from the Late Triassic of Scotland was long thought to be a crurotarsan, but phylogenetic analyses invariably place it among Avemetatarsalia (see review in Benton 1999). However, analyses disagree on whether *Scleromochlus* is the sister group to Pterosauria (Sereno 1991a; Novas 1996) or a basal avemetatarsalian that is sister to Pterosauria + Dinosauroomorpha (Benton 1999, 2004).

## **Crurotarsi**

The crocodile line of crown-group Archosauria, Crurotarsi, includes crocodylomorphs (crocodilians and their close extinct relatives), along with several distinctive clades restricted to the Triassic, including phytosaurs, aetosaurs, and ornithosuchids. Additionally, Crurotarsi includes a range of enigmatic, mostly predatory forms commonly referred to as “rauisuchians,” which may or may not constitute one or several monophyletic groups, as well as a handful of singleton taxa (e.g. *Gracilisuchus*, *Qianosuchus*, *Revueltosaurus*). In general, the higher-level relationships of Crurotarsi are poorly understood, and there is no clear consensus on even the major divisions of the clade. We discuss the differing placements of each major group individually below.

*Phytosauria*. Phytosaurs (also known as Parasuchia) are a group of semiaquatic and long-snouted Late Triassic taxa that superficially resemble gharials. They are diagnosed by numerous synapomorphies (Ballew 1989; Sereno 1991a; Long & Murry 1995; Hungerbühler 2002), and are often recovered as the most basal group of crurotarsans (Gauthier 1986; Benton & Clark 1988; Sereno 1991a; Benton 1999; Nesbitt 2007). However, not all analyses agree on this placement: phytosaurs are often recovered in an unresolved basal polytomy with other taxa (Sereno & Arcucci 1990; Juul 1994; Bennett 1996; Benton 2004; Gower & Nesbitt 2006), and Parrish (1993) found this group to be the sister taxon to all crurotarsans other than ornithosuchids, which were recovered as most basal in his study. Notably, however, no study has recovered phytosaurs as particularly closely related to crocodylomorphs, aetosaurs, any “rauisuchians,” or any of the singleton taxa. Thus, consensus generally places phytosaurs as basal crurotarsans, possibly the basal-most group.

*Aetosauria*. Aetosaurs (also known as Stagonolepididae) are a group of quadrupedal, armoured herbivores (and possibly omnivores) known globally from the Late Triassic. They are diagnosed by numerous synapomorphies (Parrish 1994; Long & Murry 1995; Heckert *et al.* 1996; Heckert & Lucas 1999, 2000; Harris *et al.* 2003; Parker 2007). Many studies advocate a position more derived than phytosaurs, but less derived than crocodylomorphs and “rauisuchians” (Gauthier 1986; Benton 1999; Benton & Walker 2002; Nesbitt 2003, 2007). However, other studies find Aetosauria in a basal polytomy with phytosaurs and other taxa (Benton 2004), as the sister group to various “rauisuchians” (Benton & Clark 1988; Juul 1994), as the sister group to crocodylomorphs + some “rauisuchians” (Parrish 1993), or as the sister group to Crocodylomorpha (Gower 2002; Gower & Walker 2002; Gower & Nesbitt 2006).

*Ornithosuchidae*. Ornithosuchids are a bizarre clade comprising a handful of genera (*Ornithosuchus*, *Riojasuchus*, *Venaticosuchus*) that superficially resemble bird-line archosaurs. They were originally regarded as members of Avemetatarsalia (Gauthier 1986; Benton & Clark 1988), but more recent studies agree that they are crurotarsans, based on several shared ankle characters (Sereno & Arcucci 1990; Sereno 1991a; Benton

1999, 2004). However, the position of ornithosuchids among Crurotarsi remains unresolved: they are sometimes placed as the sister taxon to various “rauisuchians” and closely related to Crocodylomorpha (Juul 1994; Benton 1999; Benton & Walker 2002; Nesbitt 2007), found to be the basal-most crutotarsan group (Parrish 1993), or placed in an unresolved basal polytomy with phytosaurs and other groups (Sereno & Arcucci 1990).

*Crocodylomorpha*. This ingroup clade encompasses extant crocodylians and their immediate fossil relatives, including sphenosuchids (e.g. *Hesperosuchus*, *Sphenosuchus*, *Terrestriisuchus*) and protosuchids (e.g. *Protosuchus*) (see Clark *et al.* 2000, 2004; Sues *et al.* 2003). Recent studies (Olsen *et al.* 2000; Benton & Walker 2002) identify *Erpetosuchus* from the Late Triassic of Scotland and North America as the sister taxon to Crocodylomorpha, which has not been contradicted by any other analysis. Identifying the sister taxon and other close relatives of *Erpetosuchus* + Crocodylomorpha is of considerable importance and the subject of intense debate. Most studies recover *Postosuchus* from the Late Triassic of Texas and/or other “rauisuchians” as close relatives to crocodylomorphs (Gauthier 1986; Benton & Clark 1988; Parrish 1993; Juul 1994; Benton 1999, 2004 Olsen *et al.* 2000; Benton & Walker 2002; Nesbitt 2003, 2007). Furthermore, some of these studies indicate that *Gracilisuchus* from the Middle Triassic of Argentina and/or ornithosuchids are also more closely related to crocodylomorphs than are phytosaurs and aetosaurs. However, some authors have argued for a sister-group relationship between Crocodylomorpha and Aetosauria, based largely on braincase characters (Gower 2002; Gower & Nesbitt 2006).

*Singleton Taxa*. The singleton taxa *Gracilisuchus*, *Qianosuchus*, and *Revueltosaurus* do not clearly belong to any of the unique crurotarsan ingroup clades. *Qianosuchus*, from the Middle Triassic of China, has only been included in a single analysis, a modified version of Benton’s (2004) matrix, which recovers this semi-aquatic taxon in a large basal polytomy with numerous other taxa (Li *et al.* 2006). *Revueltosaurus*, from the Late Triassic of North America, was long considered one of the oldest ornithischian dinosaurs (Hunt 1989), but recent discoveries clearly demonstrate that it is a crurotarsan (Parker *et*

*al.* 2005). However, this taxon has yet to be included in a higher-level analysis of Crurotarsi or Archosauria. Finally, *Gracilisuchus* has been included in several studies, which either place it as one of the most basal crurotarsans (Benton & Clark 1988), a close relative of crocodylomorphs and some “rauisuchians” (Parrish 1993; Juul 1994; Olsen *et al.* 2000; Benton & Walker 2002), or within a basal polytomy with several other taxa (Benton 2004).

“*Rauisuchians*”. The most problematic issue in crurotarsan phylogeny involves a range of Middle-Late Triassic taxa commonly referred to as “rauisuchians.” This nebulous assemblage includes taxa of diverse body forms, including large-bodied quadrupedal predators (*Postosuchus*, *Prestosuchus*, *Saurosuchus*), sail-backed taxa (*Arizonasaurus*, *Ctenosauriscus*), and superficially dinosaur-like cursors (*Effigia*, *Poposaurus*, *Shuvosaurus*). There is little consensus on whether all “rauisuchians” constitute a monophyletic group or which assemblages of “rauisuchian” taxa comprise monophyletic subgroups (Gower 2000). Regardless, “rauisuchians” are sometimes assumed to be monophyletic for the sake of cladistic analyses (Gauthier 1986), or are commonly represented by one or two exemplar taxa, usually *Postosuchus* and Prestosuchidae (*Prestosuchus* and *Saurosuchus*) (Juul 1994; Benton 1999). Some cladistic analyses have included a larger sample of “rauisuchians” (Benton & Clark 1988; Parrish 1993; Benton & Walker 2002; Gower 2002; Nesbitt 2003, 2007; Benton 2004; Weinbaum & Hungerbühler 2007), but none of these studies includes even a majority of currently-known “rauisuchian” taxa. The most comprehensive analyses to date are those of Parrish (1993), Nesbitt (2007), and Weinbaum & Hungerbühler (2007). Parrish (1993) analyses eight “rauisuchian” taxa and argues for a polyphyletic *Rauisuchia* comprising three separate monophyletic groups. Weinbaum & Hungerbühler (2007) also include eight “rauisuchians” and recover a paraphyletic *Rauisuchia*, with a monophyletic clade of *Poposaurus*-like forms and a paraphyletic array of *Postosuchus*-like forms that are close outgroups to Crocodylomorpha. In contrast, Nesbitt (2007) analyses seven “rauisuchians” and finds support for a monophyletic *Rauisuchia* that is the sister taxon to Ornithosuchidae. Other studies with more limited taxon sampling indicate that “rauisuchians” are monophyletic (Benton 1999; Nesbitt 2003), that some “rauisuchians”

are closely related to aetosaurs (Jülich 1994) or ornithosuchids (Benton & Walker 2002), and that some “rauisuchians,” most notably *Postosuchus*, are close relatives of, perhaps even sister taxon to, Crocodylomorpha (Benton & Clark 1988; Parrish 1993; Jülich 1994; Olsen *et al.* 2000).

In this paper we use the term “rauisuchians” in quotation marks to refer to the entire assemblage of taxa that have long been considered members of this group, but which may not form a monophyletic clade. We use the capitalized taxon name *Rauisuchia* to refer specifically to a monophyletic clade comprised of *all* “rauisuchian” taxa. This distinction is necessary because only some analyses find a monophyletic *Rauisuchia*, and many authors still use the term “rauisuchians” to refer to these animals in a paraphyletic sense.

### **Comments on Previous Analyses**

Traditional notions of archosaur phylogeny were often based on reference to adaptive or locomotor grades (Huene 1922; Romer 1972d; Charig 1976; see review in Sereno 1991a), and the flurry of cladistic analyses over the past two decades has succeeded in moulding archosaur systematics into a more rigorous and explicit discipline. However, many of these analyses are unsatisfactory and problematic.

First, most analyses are characterised by limited or problematic taxon sampling. Most importantly, “rauisuchian” taxa are often ignored, incompletely sampled, or conveniently assumed to form one or a few monophyletic groups, even though there is evidence to the contrary (Gower 2000). In fact, no published analysis has provided a rigorous and convincing test of “rauisuchian” monophyly and relationships. This is a critical issue that bears on basal archosaur phylogeny as a whole. From a theoretical standpoint, increased taxon sampling is widely held to increase phylogenetic accuracy (Graybeal 1998). From a more practical standpoint, it is possible and even probable that various “rauisuchian” taxa are close relatives or sister taxa to some of the monophyletic crurotarsan ingroups (phyosaurs, aetosaurs, ornithosuchids, crocodylomorphs).

Other problems with taxonomic sampling are evident. Archosauria includes a range of unique and speciose ingroup taxa that must be adequately represented in higher-level studies. Numerous strategies for representing suprageneric terminals have been

discussed in the literature (Yeates 1995; Bininda-Emonds *et al.* 1998; Prendini 2001), and archosaur systematists have generally either chosen single basal exemplar species (Parrish 1993; Benton & Walker 2002; Nesbitt 2003) or scored composite terminals for assumed ancestral states (Gauthier 1986; Benton & Walker 1988; Sereno 1991a; Juul 1994; Bennett 1996; Benton 1999, 2004; Nesbitt 2007). However, simulations show that the use of single exemplars is prone to error (Wiens 1998), and while explicit and quantitative ancestral state reconstruction is generally accepted, none of the analyses have clearly presented their data, methods, and assumptions. Finally, older phylogenetic analyses often scored *Postosuchus* on the basis of a chimaeric assemblage of fossils (Chatterjee 1985; Long & Murry 1995), and some analyses of crurotarsan phylogeny have used phytosaurs and aetosaurs as outgroups, even though there is no consensus on whether these taxa are basal members of the group.

Second, most analyses are also hampered by problematic character sampling. Several analyses are specific to either the bird or crocodile line. As a result, characters long thought to be pertinent to one line may be neglected in studies of the other line, although sometimes they are also variable and thus phylogenetically informative in both lines. In the same vein, the construction of many characters sometimes masks true morphological diversity. The vast majority of previously-used characters are binary, but many are better expressed as three- or four-state characters that take into account additional variation. Often recognition of these additional states is a result of more complete taxon sampling, demonstrating an intimate association between poor taxon and character sampling that can plague higher-level archosaur analyses.

Finally, one problem not so readily apparent is that no previous higher-level analysis has adequately tested the monophyly of long-recognised archosaur subgroups. Instead, these groups are represented by exemplars or composite terminals, which implicitly assume monophyly. Although monophyly is highly likely for distinctive groups such as Pterosauria, Phytosauria, and Aetosauria, no study has scored a range of taxa in each group and tested these assumptions in a global analysis.

## NEW CLADISTIC ANALYSIS

A new phylogenetic analysis of the higher-level relationships of crown group Archosauria is presented here. “Crown group Archosauria” is equivalent to Avesuchia (Benton 1999) and excludes taxa such as erythrosuchids, proterochampsids, proterosuchids, and *Euparkeria*, which fall out of the crown group as defined by the most recent common ancestor of the extant birds and crocodylomorphs. Our analysis includes 187 characters scored for 52 ingroup taxa and three outgroups, making it the largest and most complete analysis of archosaur phylogeny yet undertaken. Details of taxon selection, outgroups, and character choice are presented below, and the character list (Appendix 1) and data matrix (Appendix 2) are appended to the end of the paper.

The characters used in this phylogenetic analysis were included in a larger database of skeletal features meant to quantify the overall anatomy and morphospace occupation of basal archosaurs (Brusatte *et al.* 2008a, b). However, those studies were macroevolutionary analyses and not systematic works, and they did not provide a parsimony analysis or discuss the interrelationships of archosaur clades. Furthermore, the character data relevant to basal archosaurs has been updated and revised for the current study, which includes the input of two authors (JBD and MCL) who were not involved in the macroevolution studies.

## **Materials and Methods**

*Ingroup selection.* Fifty-two ingroup generic taxa were selected, including 20 total exemplars representing the seven archosaur subgroups (Tables 2, 3). The 32 non-exemplar terminals include every unequivocal and substantially complete crown-group archosaur that does not clearly belong to one of the seven suprageneric subgroups. Among these generic terminals are several taxa (e.g. *Dromomeron*, *Eucoelophysis*, *Lewisuchus*, *Sacisaurus*) that are highly incomplete, but are nonetheless included because they may preserve phylogenetically-useful information (Kearney & Clark 2002) and do not fulfill Wilkinson’s (1995) criteria for safe taxonomic reduction. Excluded terminals include taxa that do not clearly belong to crown-group Archosauria (e.g. *Doswellia*: Weems 1980; *Turfanosuchus*: Wu & Russell 2001), taxa whose holotype material is undiagnostic or lost (e.g. *Heptasuchus*: Dawley *et al.* 1979; Wroblewski, 1997), taxa that are possibly chimaeric (e.g. *Agnostiphys*: Fraser *et al.* 2002; Langer 2004), taxa that have

not been properly named and described (e.g. Charig's Middle Triassic Tanzanian material: Gower 2000), and taxa based on single elements or extremely fragmentary specimens (e.g. *Dongusuchus*, *Energosuchus*, *Jaikosuchus*, *Tsylmosuchus*, *Vjushkovisaurus*, *Vytshegdosuchus*: Gower & Sennikov 2000; *Ctenosauriscus*, *Hypselorhachis*: Nesbitt 2005; *Sikannisuchus*: Nicholls, Brinkman & Wu 1998; *Fenhosuchus*: Young 1964; *Procerosuchus*, *Hoplitosuchus*: Huene 1942; *Luperosuchus*: Romer 1971a).

The 20 exemplar genera were chosen to represent the seven suprageneric archosaur subgroups (Table 3). We have chosen to represent each archosaur ingroup taxon with three exemplar genera (two in the case of Ornithosuchidae, which includes only two well-known taxa), as three is the minimum number needed to simultaneously test monophyly adequately (Donoghue & Smith 2001) and resolve ingroup polymorphism (if no missing data). Additional exemplars for each group would provide a more stringent test of monophyly, but were not included because: 1) doing so would increase worker-hours and computational time, 2) the monophyly of these groups has never been seriously doubted, and 3) the main goal of this study is to analyse higher-level archosaur phylogeny. The sets of three genera were selected with the dual goal of accurately representing the ancestral condition of the taxon, which is critical for placing the taxon in the higher-level analysis, and representing divergent morphology, which is important for a stricter test of monophyly. Additionally, we selected genera whose anatomy is well known (thus reducing uncertain scores), which are well described in the literature, and which were easily available for personal examination in museum collections.

Pterosauria was included, even though some authors argue that this subgroup does not belong to crown-group Archosauria (Bennett 1996; Peters 2000). We follow the majority view that pterosaurs are crown archosaurs (e.g. Gauthier 1986; Benton & Clark 1988; Sereno 1991a; Benton 1999, 2004; Hone & Benton 2007; Hone 2007), but remain open to the possibility that they may fall elsewhere, which can only be adequately tested by a larger-scale analysis of diapsid phylogeny.



*Outgroup selection.* Three outgroups were chosen: *Erythrosuchus*, *Euparkeria*, and Proterochampsidae, which previous studies have indicated are the three closest outgroups to crown-group Archosauria (Sereno & Arcucci 1990; Sereno 1991a; Benton 1999, 2004). Proterochampsidae was scored almost completely on *Chanaresuchus*, one of the best-known members of the clade (Romer, 1971c). However, as proterochampsids occupy an important position as the closest outgroup to crown-group Archosauria, we referred to other taxa (*Gualosuchus*: Romer, 1971c; *Proterochampsa*: Sill, 1967; *Tropidosuchus*: Arcucci, 1990) to score characters that could not be observed in *Chanaresuchus* due to missing data.

*Character choice.* The taxa were scored for 187 characters (Appendix 1), 47 of which are new to this study (reviewed below). Other characters were culled from the literature, and every published character informative for higher-level archosaur phylogeny was considered. Some characters were dismissed if they: (1) were poorly defined or could not be sufficiently quantified, (2) exhibited overlapping variation that cannot be separated in ingroup and outgroup taxa, (3) were redundant with other characters, or (4) were only informative for archosaurs because of scoring mistakes (see Table 4 for shared data with other studies). Most of the included characters are binary (154, 82%), but 29 are divided into three states (16%) and four exhibit four states (2%). Ten of the characters (numbers 36, 37, 48, 88, 102, 113, 123, 126, 138, 162) are ordered and the rest are unordered. Characters were ordered if they form a presumed evolutionary sequence, and most involve a clear intermediate state between discrete end-member conditions of element length, fusion, or number. Characters were selected from all regions of the skeleton, and include 76 (41%) cranial characters, 21 (11%) axial characters, and 90 (48%) appendicular characters. Most of these (128, 68%) concern the shape, length, or location of elements, while 52 (28%) are presence-absence characters. Three characters (1%) relate to bone fusion and two characters each (1%) refer to bone texture and the number of elements.

Characters were selected with the primary goal of elucidating the higher-level relationships of crown-group Archosauria. Thus, synapomorphies of Archosauria itself and of the seven suprageneric ingroup taxa were not included, nor were characters only

pertinent to the ingroup phylogeny of these taxa. However, it is possible that increased taxon sampling may reveal a wider distribution for characters once thought to be synapomorphies of the various suprageneric ingroups. Therefore, proposed synapomorphies of these groups were reviewed and critically assessed, and all characters showing clear variability in other archosaur taxa were included. Lists of synapomorphies considered for each ingroup include: Aetosauria (Parrish 1994; Heckert & Lucas 1999; Parker 2007), Crocodylomorpha (Clark *et al.* 2000, 2004; Sues *et al.* 2003), Ornithischia (Sereno 1999; Langer & Benton 2006), Ornithosuchidae (Sereno 1991a), Phytosauria (Sereno 1991a), Pterosauria (Sereno 1991a), and Saurischia (Sereno 1999; Langer & Benton 2006).

Characters are listed in a standardised format (Appendix 1), with consistent use of anatomical terms and measurements (based on Sereno 2007b). Also listed are the original authorship of each character (the first author to include the character in a numerical phylogenetic analysis) and all successive authors who used or modified the character. Because many characters are modified, we include all previous usage that we consider to represent the spirit of the character as worded and coded here. A more complete description of each character is not provided, as many have been discussed and defined in the literature previously.

*New characters.* The 47 new characters include 26 cranial characters (55%), four axial characters (9%), and 17 appendicular characters (36%). Of these characters, 24 were previously listed and discussed in the literature (Gower 1999; Nesbitt 2005, 2007; Langer & Benton 2006), but have yet to be included in a quantitative analysis. The other 23 characters are entirely new to this study, and were gleaned from examination of specimens and published figures and descriptions. The majority of these new characters are pertinent to the interrelationships of “rauisuchians,” and several are synapomorphies of various “rauisuchian” subgroups. Characters new to this study are illustrated (Figs. 3, 4) and described in Supplementary Appendix S1.

*Analytical Protocols.* We subjected our dataset to a parsimony analysis, and used a heuristic search (tree bisection and reconnection, with 10,000 random addition sequence

replicates) in PAUP\*v.4.0b10 (Swofford, 2000) to find the most parsimonious trees. Clade robustness was assessed with bootstrap (10,000 replicates, fast addition sequence) and Bremer support (decay) indices (Fig. 5), both being used as problems have been identified with each method (Kitching *et al.* 1998). Bremer supports were calculated by searching in PAUP\* for the shortest trees not compatible with the node in question. Because of the size of the dataset only a single heuristic search replicate was run for each node, meaning that many Bremer support values may be overestimates. However, several additional partial heuristic searches were run for each node to check that the Bremer values were approximately correct. The additional cost needed to assume alternative topologies found in previous studies was determined by constraining relationships in PAUP\*.

Three empirical tests were conducted to examine the effect of potential taxonomic and character sampling biases. First, as some authors argue that pterosaurs do not belong to crown-group Archosauria, the three pterosaur exemplars were removed and the analysis rerun to determine what influence pterosaurs may have on the phylogenetic relationships of other taxa. Second, traditionally some of the strongest character support for higher-level archosaur relationships involved the ankle joint (Sereno 1991a). This has led some authors to suggest that an over abundance of ankle characters, many of which may be correlated, may bias the results of phylogenetic analysis (see review in Dyke 1998). Thus, we removed all characters concerning the astragalus and calcaneum (numbers 158-174) and reran the analysis. Third, there is uncertainty whether a skull referred to *Prestosuchus* by Barberena (1978) represents the same taxon as material originally described by von Huene (1942). As reviewed by Gower (2000), this situation is complicated by von Huene's (1942) failure to designate holotype specimens. Although Krebs (1976) subsequently erected lectotype and paralectotype specimens it is possible that this material is chimaeric. Pending a detailed revision of *Prestosuchus* taxonomy, which is currently in progress by one of us (JBD), we scored this taxon based on both von Huene's specimens (BPSG AS XXV 1-45) and the referred skull (Appendix 3). However, we also ran a subsequent analysis in which von Huene's material and the referred skull were treated as separate terminals (the former includes all postcranial scores for

*Prestosuchus* plus scores for cranial characters 12, 14, 16-17, 71-73; the latter includes all cranial scores and no postcranial scores).

We analyzed the congruence between our phylogeny and the known fossil record of taxa using the Gap Excess Ratio (GER: Wills 1999), which is well suited for analyzing a largely extinct group of terrestrial vertebrates known almost entirely from point occurrences in the fossil record. This metric compares the missing gaps implied by a phylogenetic hypothesis to the minimum and maximum gaps possible for that set of taxa. We used the software Ghosts 2.4 (Wills 1999) to run this analysis on our strict consensus phylogeny, with polytomies resolved in a “worst case” scenario and the absolute ages of the first occurrence of terminal taxa based on the timescale of Gradstein *et al.* (2004), which we use for consistency despite recent arguments that the Triassic timescale may need extensive revision (Furin *et al.* 2006; Irmis & Mundil 2008).

## Results

The parsimony analysis recovered 70 most parsimonious trees (MPTs), each with a length of 747 steps, a consistency index (CI) of 0.31, and a retention index (RI) of 0.68.

The strict consensus of the most parsimonious trees is well resolved (Fig. 5). Avemetatarsalia and Crurotarsi are recovered as monophyletic clades, and each of the ingroup clades represented by exemplars is found to be monophyletic. Within Avemetatarsalia, *Scleromochlus* is the sister taxon to Pterosauria, and together these taxa comprise the sister group to Dinosauromorpha. Within Dinosauromorpha, *Lagerpeton* and *Dromomeron* are sister taxa, followed successively by *Marasuchus*, *Pseudolagosuchus*, a clade of dinosauromorphs centered on *Silesaurus*, and Dinosauria. This “*Silesaurus*” clade, which is the immediate sister taxon to Dinosauria, includes *Lewisuchus* as its most basal taxon and a polytomy of *Silesaurus*, *Sacisaurus*, and *Eucoelophysis*. Dinosauria is comprised of Saurischia and Ornithischia.

Relationships within Crurotarsi are almost completely resolved, with the exception of one area of the tree. Phytosauria is recovered as the most basal crurotarsan clade. Taxa traditionally regarded as “rauisuchians” comprise a single, monophyletic group, which is sister taxon to a clade comprised of Ornithosuchidae and the problematic taxon *Revueltosaurus*. The rauisuchian clade is divided into two major subclades. The

first includes taxa often referred to as “rauisuchids” and “prestosuchids,” including *Batrachotomus*, *Postosuchus*, *Prestosuchus*, *Rauisuchus*, *Saurosuchus*, and *Teratosaurus*. Within this clade are sister-group pairs of *Batrachotomus* + *Prestosuchus* and *Postosuchus* + *Teratosaurus*, and all relationships are completely resolved. The second rauiisuchian subclade includes taxa often referred to as “poposaurids,” “ctenosauriscids,” “shuvosaurids,” and “chatterjeeids,” including *Arizonasaurus*, *Effigia*, *Poposaurus*, and *Shuvosaurus*. Resolution is poor within this clade, but *Yarasuchus* and *Qianosuchus* are recovered as basal taxa and a sister-taxon grouping of *Effigia* and *Shuvosaurus* is found. The large clade comprising rauiisuchians and ornithosuchids is the sister taxon to a clade uniting aetosaurs and crocodylomorphs. Aetosauria, *Gracilisuchus* and *Erpetosuchus* are placed as successive outgroups to Crocodylomorpha.

A list of synapomorphies, as optimised under accelerated (ACCTRAN) and delayed (DELTRAN) transformation assumptions, is presented in Supplementary Appendix S2.

*Tree support measures.* Although the strict consensus tree is well resolved, support for nearly every clade is poor. Bremer support for most clades is only one or two, meaning most clades fall apart in the strict consensus of all trees one or two steps longer than the shortest tree. Exceptions include the major clades Avemetatarsalia (3), Crurotarsi (5), Dinosauromorpha (3), Poposauroida (4), as well as the sister group pairs of *Effigia* + *Shuvosaurus* (7) and *Dromomeron* + *Lagerpeton* (4). Not surprisingly, some of these clades are the only groupings to exhibit bootstrap percentages greater than 50%. Additionally, Dinosauria (68%), *Scleromochlus* + Pterosauria (64%), and the sister taxon pairs of *Postosuchus* + *Teratosaurus* (61%) and *Batrachotomus* + *Prestosuchus* (81%) also have relatively high bootstrap percentages, although their Bremer support is low. High bootstrap and Bremer support characterises most of the ingroup clades represented by exemplars, but these values must be taken as extremely conservative estimates of support since autapomorphies of the clades were not considered. Unfortunately, our study is too large to subject to Double Decay Analysis (Wilkinson *et al.*, 2000) in RadCon (Thorley & Page 2000).

*Phylogenetic Taxonomy and Clade Names.* Although the phylogeny presented here contains several interesting and novel clades, we refrain from naming any new taxa and do not present or modify explicit definitions. The state of basal archosaur taxonomy is best described as chaotic. Numerous names have been erected and defined, many of which are used by different authors to refer to vastly different subsets of taxa. Much of this confusion stems from attempts to pigeonhole taxa, especially basal crurotarsans, into discrete groups without reference to cladistic analysis (e.g. Alcober & Parrish 1997; Alcober 2000; Sen 2005; Sulej 2005). However, several authors have named new taxa based on cladistic analyses, which has saturated the literature with names that refer to poorly-supported clades that are may not be found in alternative studies (Gower & Wilkinson 1996). For instance, the term Paracrocodyliformes, given by Weinbaum & Hungerbühler (2007) to unite “rauisuchid/prestosuchid” “rauisuchians” and crocodylomorphs to the exclusion of “poposaurids,” makes little sense when applied to our topology. This clearly was not the intention of the original authors, and demonstrates how labile and unstable such names are in the current arena of archosaur systematics. Thus, we recommend that authors follow the lead of Nesbitt (2005, 2007), Jalil & Peyer (2007), and others in refusing to name and define new clades until stronger consensus is reached, especially within Crurotarsi.

We apply existing names to several clades in our cladogram (Fig. 5), such as Avemetatarsalia, Crurotarsi, Suchia, Rauisuchia, Dinosauromorpha, Dinosauriformes, and Dinosauria, each of which has been defined and is commonly used in the literature to refer to clades very similar or identical to those recovered here (e.g. Sereno 1991a, 2005; Benton 1999, 2004; Sereno *et al.* 2005). However, deciding how to label certain crurotarsan clades is more difficult, as some of these names have never been defined and have been used very differently by different authors.

We do not label several nodes, including the Aetosauria + Crocodylomorpha node, the ornithosuchid + rauisuchian node, and the cluster of enigmatic rauisuchians centred on *Ticinosuchus*. However, we do refer to the major clade of “rauisuchids,” “prestosuchids,” and the subclade centered on *Ticinosuchus* as Rauisuchoidea, a superfamily-level taxon that has not previously been used but is considered established under the ICZN Principle of Coordination. Within Rauisuchoidea we use the names

Rauisuchidae and Prestosuchidae to refer to clusters of taxa including the eponymous *Rauisuchus* and *Prestosuchus*, as defined by Sereno (2005; linked to Sereno *et al.* 2005). Both of these names have long and unstable histories in archosaur systematics, but Sereno (2005) argued that erecting stem-based definitions centred on *Rauisuchus* and *Prestosuchus* is necessary to stabilise the usage of Rauisuchidae and Prestosuchidae. We realise that Teratosauridae (Cope 1871) was named prior to the more widely used Rauisuchidae (Huene 1936), and if *Rauisuchus* and *Teratosaurus* are in the same family-level clade as advocated by the present study then the former name has priority.

We refer to the second major clade of rauisuchians (*Arizonasaurus*, *Bromsgroveia*, *Effigia*, *Lotosaurus*, *Poposaurus*, *Qianosuchus*, *Shuvosaurus*, *Sillosuchus*, *Yarasuchus*) as “Puposauroida,” following usage outlined by Weinbaum & Hungerbühler (2007). Sereno’s (2005) definition of Puposauridae refers to this clade, but we prefer Puposauroida because this group includes several subclades that have traditionally been given family-level status. One such clade is Shuvosauridae, which we use to refer to *Effigia* + *Shuvosaurus*, a clade equivalent to the Chatterjeeidae of previous authors (e.g. Long & Murry 1995). As most other relationships within Puposauroida are still unresolved we do not use additional family-level taxa such as Puposauridae or Ctenosauriscidae.

*Alternative topologies.* Specific alternative topologies are reviewed in the discussion section below, but two deserve further comment. First, enforcing all rauisuchians, crocodylomorphs, and ornithosuchids to form a monophyletic group to the exclusion of aetosaurs, as has been found in many previous studies, requires an additional four steps. Second, enforcing ornithosuchids and poposauroids to form a clade, and thus demolishing a monophyletic Rauisuchia, requires only one additional step. Despite this alteration the relationships within both poposauroid and rauisuchoid clades are essentially identical to those in the original analysis, indicating that only a small amount of character data supports a monophyletic Rauisuchia.

*Character and Taxon Alterations.* When the pterosaur exemplars are removed and the dataset reanalyzed, the revised analysis returns 1785 MPTs (710 steps, CI = 0.32, RI =

0.67), the strict consensus of which (Fig. 6A) shows nearly identical relationships within Avemetatarsalia with one exception: the dinosaurian clade Saurischia is no longer recovered. Perhaps surprisingly, relationships within Crurotarsi are severely affected by the removal of pterosaurs, as *Revueltosaurus* is now recovered as the most basal crurotarsan, followed successively by Phytosauria, an Aetosauria + Crocodylomorpha grouping, and a clade comprising rauisuchians and Ornithosuchidae. Within this latter clade is a sister grouping of poposauroids and ornithosuchids, which prevents a monophyletic Rauisuchia. Furthermore, several taxa recovered as basal rauisuchoids (*Arganasuchus*, *Fasolasuchus*, *Stagonosuchus*, *Ticinosuchus*) and basal poposauroids (*Qianosuchus*, *Yarasuchus*) in the original analysis now fall into a basal polytomy. This suggests that pterosaurs play a critical role in determining character polarity at the base of Avemetatarsalia, which has far-reaching influence on the phylogeny of Archosauria as a whole. Therefore, the question of pterosaur relationships may have broader and more problematic implications than realised.

Second, when ankle characters are removed, the analysis recovers 196 MPTs (708 steps, CI = 0.29, RI = 0.66), the strict consensus of which (Fig. 6B) still separates monophyletic Avemetatarsalia and Crurotarsi. Relationships within Avemetatarsalia are unchanged, but those within Crurotarsi are substantially less resolved. Phytosaurs, aetosaurs, crocodylomorphs (plus their immediate relatives), and a clade of rauisuchians + ornithosuchids all fall into a basal polytomy, and rauisuchians no longer form a monophyletic clade. Although these alterations may appear alarming, it must be remembered that this is a strict test that removes an entire region of the skeleton from the analysis. Overall, the persistence of the two major clades (Avemetatarsalia and Crurotarsi) and many clades within Crurotarsi suggests that, although the ankle is an important source of character data, there is enough phylogenetic signal in other regions of the skeleton to support many major clades, even considering the high levels of homoplasy in the analysis.

Third, when the type series and referred material of *Prestosuchus* are treated as separate terminals, the analysis recovers 120 MPTs with one less step (746 steps) and tree statistics (CI = 0.30, RI = 0.67) to the most parsimonious trees in the original analysis. The strict consensus topology is very similar to that of the original analysis, and there is a



polytomy between between *Batrachotomus*, von Huene's *Prestosuchus* material, and the referred *Prestosuchus* skull. Thus, it is apparent that the original material of *Prestosuchus* and the referred skull belong to very closely related taxa.

## COMPARATIVE CLADISTICS

The current study is only the latest in a long line of analyses focusing on higher-level archosaur phylogeny. As outlined above, eight major studies have analysed Archosauria as a whole, while 13 others have focused intensively on either Avemetatarsalia or Crurotarsi. Few other vertebrate groups have received this sort of attention. However, despite the wealth of studies, little consensus has emerged, especially concerning crurotarsan interrelationships. This begs the obvious question: why have over two decades of research failed to produce at least moderate agreement? To begin to answer this question we focus on exactly how and why our study disagrees with previous work. This entails critically assessing the character data, which is often overlooked at the expense of simply comparing and contrasting cladogram topologies.

### **Character Sampling**

Differences in character sampling could explain incongruence between studies. We quantify the amount of shared character data between our study and alternatives using the character similarity index (CSI: Sereno & Brusatte, in press). This index measures 1.0 in the case of total overlap (i.e. identical character lists) and decreases as the percentage of shared characters relative to pooled characters (total characters from both analyses) decreases. Only informative characters are taken into account, and thus CSI values for previous analyses of Avemetatarsalia and Crurotarsi only include characters in the current analysis relevant to the ingroup relationships of those clades.

CSI values (Table 4) demonstrate the remarkable difference between the character lists of the current analysis and earlier studies. Among studies focusing on Archosauria as a whole, the highest amount of character overlap is with the analysis of Irmis *et al.* (2007a), which shows 36% character similarity with the current analysis (CSI = 0.36). The average CSI for the eight quantitative general archosaur analyses is 0.25. This large

disparity in shared character data is largely one-sided: the current analysis includes a vast majority of characters used in previous analyses (87% of total informative characters), but the previous analyses lack numerous characters employed in the current study. Of course, this is to be expected, as our analysis is an assimilation of previous datasets and new characters that were often unknown or unavailable to previous workers.

### **Scoring Differences**

We quantify the degree to which characters shared between analyses have been scored differently using the character state similarity index (CSSI: Sereno & Brusatte, in press). This index measures 1.0 in the case of total overlap (i.e. all shared characters scored identically in all taxa common to both analyses) and decreases as the percentage of mismatched scores increases relative to total number of shared scores. Positive scoring differences which involve disagreement between affirmative scores (e.g. 0 versus 1) are counted as a single mismatch, while those disagreements that involve missing data (e.g. 1 versus ?) incur a penalty of 1/2. In cases of suprageneric taxa, we only count a scoring difference if our three exemplars all agree in exhibiting a score that is different from the representative terminal or single exemplar in the alternative study.

Scoring differences between our analysis and earlier studies are documented as CSSI values (Table 4), together with the gross number of positive and missing datum scoring differences involving generic and suprageneric taxa shared between studies. Most CSSI values are within the range of 0.90 and 1.00, and the average CSSI is 0.93. Whether these values are standard or abnormal cannot be said because similar comparisons have yet to be undertaken for other groups. The lowest CSSI value (0.69) is with the analysis of Parrish (1993), which is plagued by discrepancies between the text and data matrix (Gower & Wilkinson 1996; Gower, 2000) and has been criticised for problematic character definitions and scores (e.g. Juul 1994; Gower & Wilkinson 1996; Gower 2000). Comparatively low CSSI values are also seen with the recent analyses of Weinbaum & Hungerbühler (2007) (0.85) and Irmis *et al.* (2007a) (0.88).

The sheer number of scoring differences with alternative studies may appear alarming, but in most cases is the result of increased understanding of archosaur anatomy, discovery of new fossil material, or publication of detailed anatomical descriptions,

which results in new data that were largely unavailable to previous authors. The large number of missing datum scoring differences testifies to this fact, as most stem from our ability to fill in uncertainties (“?”) in previous studies. However, positive scoring differences reflect true disagreements between our study and alternatives. Many of these concern taxa that we have studied first hand, especially *Batrachotomus*, *Gracilisuchus*, *Lotosaurus* (which has been inaccessible to many researchers), *Postosuchus*, *Prestosuchus*, *Rauisuchus*, *Saurosuchus*, and *Ticinosuchus*, and partially reflect our ability to correct mistaken scores derived from the literature alone. In other cases, it is clear that our analysis and alternative studies advocate different interpretations of anatomical structures or character construction, and these should be examined by future workers.

### **Comparison to Alternative Studies**

To what extent do these differences in character choice and in character state scores affect the resulting trees? We compared our analysis with four previous studies (Parrish 1993; Juul 1994; Benton 2004; Nesbitt 2007), and reran these analyses using scores that we favour in all cases where there are scoring differences. Raw differences with these studies are enumerated in Table 4, and both the original and reanalyzed topologies produced by these analyses are shown in Figure 7. Note that the dataset of Nesbitt (2007) produces the same topology even when our favoured scores are included, and thus it is not figured.

The most important result of this experiment is that, despite changed scores that reflect our interpretations of the data, the modified analyses fail in nearly every case to produce unique relationships found in our analysis, namely a basal position for phytosaurs, a close relationship between aetosaurs and crocodylomorphs, and a monophyletic grouping of “rauisuchian” taxa. Thus, scoring differences are not a primary reason why earlier studies recover different relationships than those found here. Character and taxon sampling are more likely sources of incongruence. The current analysis and alternatives share a minimal amount of character data, and in essence are analyzing very different regions of character space. At the simplest level, it is noteworthy that our analysis dismisses several unequivocal synapomorphies of incongruent nodes in previous

studies, and that previous studies do not include many unequivocal synapomorphies of unique clades recovered here. The effect of taxonomic sampling is difficult to test empirically, but it is noteworthy that most previous studies include only a small sample of “rauisuchians” and employ very different strategies for representing suprageneric ingroups.

## DISCUSSION

### **Monophyly of Archosaur Ingroups**

Each of the seven suprageneric ingroup taxa represented by exemplars was found to be monophyletic. This is not unexpected, but significant, as the present analysis is the first rigorous test of the monophyly of these groups within a global analysis of archosaur phylogeny. The current analysis also provided a very conservative test of monophyly, as no ingroup synapomorphies were included. Thus, there is enough variability and phylogenetic signal in characters pertinent to the higher-level phylogeny to support the monophyly of all ingroups. As a result, we consider the monophyly of these clades to be strongly supported.

### **Higher-level phylogeny of Archosauria**

The current analysis produces a well-resolved tree, in contrast to many previous studies that recover numerous polytomies, especially within Crurotarsi. However, most clades are poorly supported, including many groupings (e.g. Avemetatarsalia, Crurotarsi, Dinosauria, Dinosauromorpha) that have been robustly supported in alternative studies and are united by several unambiguous synapomorphies in the present analysis. For instance, Avemetatarsalia (16 synapomorphies, 4 unambiguous) and Crurotarsi (14 synapomorphies, 4 unambiguous) are supported by considerable character data but exhibit low bootstrap support, and although Bremer supports appear high these are likely overestimates. Taken at face value, this suggests that archosaur phylogeny as a whole is poorly constrained and many clades may be no more than mirages. Certainly, increased taxon and character sampling in the current dataset indicate that archosaur phylogeny is characterised by high levels of homoplasy, and is perhaps much more homoplastic than

was thought. However, many of the low support values likely also result from the inclusion of many fragmentary taxa, which often lack regions of the skeleton that record important synapomorphies. Few previous analyses have included even a small subset of these fragmentary taxa, so comparing support values between our analysis and other studies may be misleading.

Here we review some of the most interesting aspects of our analysis. In the following discussion, “synapomorphies” refer to those character changes found under both ACCTTRAN and DELTRAN assumptions, and “unambiguous synapomorphies” refer to those with a CI of 1.0 (Appendix S2).

Avemotarsalia is united by 16 synapomorphies, four of which are unambiguous, making it one of the better-supported clades. This clade is also supported by a Bremer support index of three, which although perhaps an overestimate because of our search strategy does testify to the robustness of the clade. Within this group, *Scleromochlus* and Pterosauria are united as sister taxa, a relationship found in some (Sereno 1991a; Novas 1996) but not all previous analyses. Benton (1999, 2004) has argued that *Scleromochlus* is the basal-most avemetatarsalian, and thus an outgroup to a Pterosauria + Dinosauromorpha clade. The position of *Scleromochlus* in our analysis is supported by five synapomorphies, and it requires only one additional step to recover the topology found by Benton (1999, 2004). Thus, a Pterosauria + *Scleromochlus* clade must be considered tentative.

Dinosauromorpha is united by eight synapomorphies, two of which are unambiguous, and characterised by a Bremer support of three. Within this group *Lagerpeton* and *Dromomeron* are united as a basal clade, as also found by Irmis *et al.* (2007a). This clade is one of the best supported in our analysis, as it is united by seven synapomorphies (three unambiguous) and supported by a Bremer index of four. All dinosauromorphs except for *Lagerpeton* and *Dromomeron* comprise Dinosauriformes, which is supported by seven synapomorphies (one unambiguous). Ten synapomorphies for Dinosauria are found under both ACCTTRAN and DELTRAN. However, numerous additional dinosaur synapomorphies described by previous authors (e.g. Novas 1996; Sereno 1999) are included in the present analysis but are either optimised as uniting a more inclusive clade (ACCTTRAN) or a less inclusive clade within Dinosauria

(DELTRAN) because of rampant missing data in basal dinosaurs and especially close dinosaur outgroups. Thus, although Dinosauria may appear weakly supported it is potentially supported by extensive character data and has one of the more robust bootstrap percentages in the analysis.

The basic nested hierarchy within Dinosauromorpha, with *Lagerpeton* as a basal taxon followed sequentially by *Marasuchus* and Dinosauria, is recovered in every alternative analysis. The present analysis is the first to test the relationships of a full range of dinosauromorph taxa closely related to true dinosaurs. Four taxa—*Lewisuchus*, *Eucoelophysis*, *Sacisaurus*, and *Silesaurus*—comprise a clade that is the sister taxon to Dinosauria. This finding is consistent with the results of Irmis *et al.* (2007a), which place *Silesaurus* and *Eucoelophysis* in a clade that is sister to Dinosauria, but contrasts with the analysis of Ezcurra (2006), which finds *Silesaurus* and *Eucoelophysis* as successive outgroups to Dinosauria. The placement of *Lewisuchus*—which has hitherto never been included in a dinosauromorph phylogeny—as a basal member of a “*Silesaurus*” clade is interesting. *Silesaurus* and *Sacisaurus* have clearly diverged from the basal dinosauromorph body plan, as they were quadrupedal herbivores with beaks and teeth similar to those of ornithischian dinosaurs (Dzik 2003). However, *Lewisuchus* is a more traditional dinosauromorph that was undoubtedly carnivorous and likely bipedal. Therefore, the aberrant features of *Silesaurus* and *Sacisaurus* are unambiguously optimized as unique to their subclade and not as possible primitive states for Dinosauria. Furthermore, our analysis agrees with previous studies in recovering *Sacisaurus* and *Silesaurus* as non-dinosaurian dinosauromorphs. Placing these taxa within Ornithischia, as suggested by some authors (e.g. Ferigolo & Langer 2007), requires an additional 10 steps and is highly unparsimonious with our dataset.

The second major division of crown-group Archosauria, Crurotarsi, is supported by 14 synapomorphies, four of which are unambiguous, and a Bremer index of five. While likely an overestimation, this Bremer value is much higher than that of nearly every other clade in the phylogeny. A monophyletic Crurotarsi including phytosaurs, ornithosuchids, aetosaurs, crocodylomorphs, and “rauisuchians” has been found in nearly every analysis published subsequent to Sereno & Arcucci’s (1990) influential

clarification of archosaur tarsal morphology. However, ingroup relationships within Crurotarsi are a frequent topic of disagreement, as reviewed above.

We place Phytosauria as the basal-most crurotarsan clade, which is consistent with most previous studies. Parrish (1993) placed Ornithosuchidae as the basal-most crurotarsan clade, but this topology requires an additional six steps in our analysis.

Relationships within Suchia constitute some of the most novel and interesting aspects of the current analysis. First, our analysis places Aetosauria as the sister group to a *Gracilisuchus* + (*Erpetosuchus* + Crocodylomorpha) clade, a relationship supported by eight synapomorphies (two unambiguous). Previous analyses have reached little consensus on the position of Aetosauria, but the majority recover this clade as a basal lineage nested between phytosaurs and crocodylomorphs + “rauisuchians.”

Gower (2002), however, presented evidence for a close relationship between aetosaurs and crocodylomorphs based on braincase characters (see also Gower & Walker 2002; Gower & Nesbitt 2006). Our analysis is the first study taking into account data from the entire skeleton that recovers a close relationship between these clades. The two unambiguous synapomorphies of an Aetosauria + Crocodylomorpha clade in our analysis are braincase characters identified by Gower (2002): a completely ossified perilymphatic foramen (character 68) that is positioned laterally (character 69). These characters may be problematic, however, as they can only be scored as present in *Sphenosuchus* and *Stagonolepis* in the current analysis, and braincase data are missing for many crurotarsan taxa. Regardless, for our dataset an aetosaur and crocodylomorph clade is well supported relative to other suchian clades, as it takes an additional four steps to enforce a grouping of all “rauisuchians” (including ornithosuchids) and crocodylomorphs to the exclusion of aetosaurs, as is advocated by alternative analyses. It is also worth noting that there are two additional characters discussed by Gower & Walker (2002) that may support an aetosaur and crocodylomorph clade, a restricted dorsal fossa on the palatine and a ventromedial process on the prefrontal that projects into the antorbital cavity, but they were excluded here since they are difficult to score in many taxa because of missing data and insufficient published figures. A close relationship between aetosaurs and crocodylomorphs deserves further testing, and authors should no longer use aetosaurs as an outgroup in analyses of “rauisuchian” and crocodylomorph phylogeny, as this

implicitly assumes that the latter two groups form a clade exclusive of aetosaurs (e.g. Olsen *et al.* 2000; Weinbaum & Hungerbühler 2007).

Second, we recover a monophyletic Rausuchia, which unites all taxa commonly referred to as “rauisuchians” in the literature (see above). The speciose clade Rausuchia is divided into two major subclades: Popsauroidea and Rausuchoidea (e.g. Rausuchidae + Prestosuchidae). However, our evidence for a monophyletic Rausuchia must be regarded as weak, as the clade is united by only two synapomorphies, neither of which is unambiguous. Furthermore, it takes only one additional step to unite poposauroids and ornithosuchids (the sister taxon to Rausuchia) to the exclusion of rausuchoids. Previous analyses disagree on whether “rauisuchians” constitute a monophyletic clade, but these include only a fraction of taxa considered here. At present, we consider the question of “rauisuchian” monophyly to be unresolved, but the possibility of a monophyletic Rausuchia should be seriously considered (see Gower 2000; Gower & Nesbitt 2006; Weinbaum & Hungerbühler 2007).

The first major rausuchian subclade, here termed Rausuchoidea, is united by only two synapomorphies, neither of which is unequivocal. Most rausuchoid taxa possess a dorsally oriented crest on the ilium extending from above the acetabulum. A similar crest is present in many poposauroids but extends anterodorsally, and there has been much discussion in the literature questioning the homology of these features (Gower 2000; Weinbaum & Hungerbühler 2007). A dorsally oriented crest is optimised as a synapomorphy of Rausuchoidea in the present analysis but it is not unambiguous, as *Prestosuchus* possesses an anterodorsal crest (BPSG AS XXV 7) and the more basal *Stagonosuchus* possesses a very weak dorsally oriented crest (Gower 2000; Gebauer 2004). Similarly, an anterodorsal crest is optimised as an ambiguous synapomorphy of Popsauroidea. The mere presence of a crest is a synapomorphy of Rausuchia, which indicates that this structure is a homologous feature among rausuchian taxa that exhibits variation informative for lower-level relationships.

Rausuchoidea is divided into three discrete clades: a basal cluster centred on *Ticinosuchus*, Prestosuchidae and Rausuchidae. The first clade, which unites the Middle Triassic *Ticinosuchus* and *Stagonosuchus* with the Late Triassic *Arganasuchus* and *Fasolasuchus*, is united by only two synapomorphies. *Ticinosuchus* has been regarded as



a “prestosuchid” in the literature (e.g. Parrish 1993; Sen 2005), but these assignments were not based on discrete phylogenetically-defined clades. Although we do not place *Ticinosuchus* in the clade we label Prestosuchidae, it falls out very near *Prestosuchus* in the larger scheme of raiisuchian phylogeny. Thus, we consider our findings consistent with the non-cladistic referrals of previous authors.

Prestosuchidae and Raiisuchidae form a clade exclusive of the *Ticinosuchus* group. This clade is supported by four synapomorphies, most notably the unambiguous presence of a kinked postorbital ventral process (character 44). This character has long been recognised as a unique feature of some “rauisuchians,” but its phylogenetic utility has been debated (Sill 1974; Long & Murry 1995; Alcober 2000). Prestosuchidae is united by only four synapomorphies, but these include the unambiguous presence of an oblique ridge on the lateral surface of the ventral ramus of the squamosal (character 49). This character was originally identified by Gower (1999) as a potential synapomorphy of *Batrachotomus* + *Prestosuchus*, but is also present in *Saurosuchus* (PVSJ 32). Although this character has a slightly wider distribution, the sister-group relationship between *Batrachotomus* and *Prestosuchus* is robustly supported by some of the highest tree support values in the analysis, as well as 14 synapomorphies. A close relationship between these two taxa was also hinted at by Gower (1999).

Raiisuchidae is supported by only two synapomorphies, including the unambiguous deep and wedge-shaped parabasisphenoid (character 62). The raiisuchid *Postosuchus* was often used as an exemplar for a poposauroid clade in early cladistic studies, before it was realised that this taxon as originally described by Chatterjee (1985) was a chimaera of three different taxa, including *Poposaurus* and *Shuvosaurus* (Long & Murry 1995). However, more recent analyses have still considered *Postosuchus* as a poposauroid (Alcober & Parrish 1997; Alcober 2000), a relationship considered highly unlikely based on the current analysis, as it would require an additional 11 steps. Thus, the raiisuchoid affinities of *Postosuchus* are considered strong, although the closest relatives of this taxon are still somewhat uncertain. Only two synapomorphies unite *Postosuchus* + *Teratosaurus*, but one of these is the unambiguous presence of a deep pit in the posterodorsal corner of the lateral surface of the squamosal (character 50).

The second major clade of rauisuchians, here termed Puposauroidea, is united by four synapomorphies. Perhaps unexpectedly, the enigmatic Middle Triassic *Qianosuchus* is recovered as a basal poposauroid. This semi-aquatic taxon has a body plan and general morphology that differs vastly from other poposauroids—and other crurotarsans in general—but but this could reflect its divergent lifestyle and not phylogeny. Additionally, the Middle Triassic *Yarasuchus* is placed as the most basal poposauroid. This taxon was previously referred to Prestosuchidae (Sen 2005), and it only requires one additional step to assume such a position in the current analysis.

A clade of poposauroids more derived than *Yarasuchus* and *Qianosuchus* is supported by five synapomorphies and high tree support values (Bremer index=4). Relationships within this clade are unresolved, save for the robustly supported sister-group pairing of *Effigia* and *Shuvosaurus* (Shuvosauridae). This clade is supported by high tree support values (Bremer support = 7, bootstrap = 100%) and several synapomorphies (26 total, six unambiguous), as well as numerous synapomorphies that are optimised at more inclusive nodes because of missing data in other poposauroids, many of which lack cranial remains. These include two unambiguous synapomorphies. As discussed by Nesbitt (2007), shuvosaurids share many characters with avemetatarsalian taxa, especially theropod dinosaurs, and these must be interpreted as convergences in the current analysis. One remarkable convergence is bipedal posture, present in avemetatarsalians, *Effigia*, *Poposaurus*, and *Shuvosaurus*, but unknown among other crurotarsans with the possible exception of ornithosuchids and *Revueltosaurus* (see below).

Other poposauroid relationships are unresolved, leaving open the question of whether Ctenosauriscidae *sensu* Nesbitt (2005, 2007), a group that includes the high-spined *Arizonasaurus* and *Lotosaurus*, is monophyletic. However, it takes an additional 12 steps to unite *Lotosaurus* with Rauisuchidae (Parrish 1993), a relationship considered highly improbable based on our dataset.

The speciose clade Rauisuchia is sister taxon to a group of Ornithosuchidae + *Revueltosaurus*. The Ornithosuchidae + *Revueltosaurus* clade is united by three synapomorphies, including an ambiguous angled articulation between the premaxilla and maxilla (character 18), also seen in some aetosaurs (*Aetosaurus*: SMNS 5770). The

position of *Revueltosaurus* must be considered tentative, as it is based on weak character support and low tree support values. Additionally, all scores for *Revueltosaurus* were based on published descriptions of incomplete material (Hunt *et al.* 2005; Parker *et al.* 2005). *Revueltosaurus* is one of the few generic taxa in our analysis that is not clearly similar to any other taxa in overall morphology, and further study of its anatomy in light of newly discovered specimens, which have been briefly described as sharing several synapomorphies with Aetosauria, should help resolve its relationships (Parker *et al.* 2007). However, the close relationship between ornithosuchids and rauisuchians has been suggested before (e.g. Nesbitt 2007).

Finally, *Gracilisuchus* and *Erpetosuchus* are placed as sequential outgroups to Crocodylomorpha. These relationships are characterised by some of the highest tree support measures in the analysis, as well as substantial character data. The position of *Erpetosuchus* as a close crocodylomorph outgroup is consistent with previous studies (Olsen *et al.* 2000; Benton & Walker 2002), but the placement of *Gracilisuchus* is more interesting. Some analyses have recovered this taxon as a close relative of crocodylomorphs, as suggested by Brinkman (1981), but these relationships have generally been poorly supported, and alternative positions have been advocated. Importantly, the placement of *Gracilisuchus* with crocodylomorphs may also help unite Aetosauria as a close relative. Thus, *Gracilisuchus* may retain important character transformations near the base of Crocodylomorpha, and should be considered in future studies of morphological transitions and character evolution on the line to extant crocodiles.

### **Implications for Archosaur Evolution**

*Stratigraphy, Sampling, and the Archosaur Fossil Record.* Examining the congruence between a phylogenetic hypothesis and the stratigraphic ranges of taxa can be illuminating. Stratigraphic congruence analysis is useful as a general measure of tree support, particularly when, as here, traditional tree metrics (bootstrap, Bremer support) are weak. Analyzing stratigraphic congruence can also reveal information on the quality of the fossil record and potential sampling biases.

There are several metrics to quantify the congruence between a specific phylogenetic hypothesis and the fossil record, but there is debate over the potential biases and relevant uses of each (see review in Pol *et al.* 2004). We calculated the Gap Excess Ratio (Wills 1999) for our phylogeny. Our strict consensus tree is characterized by a GER of 0.437, which randomisation tests show to be stratigraphically congruent at the  $p = 0.07$  level (see Wills 1999 for details of the significance tests). Thus, although our phylogeny is poorly supported by traditional tree support values, it is consistent overall with the known stratigraphic record.

The current analysis requires several major ghost lineages and range extensions (Fig. 8), a problem that is common to all analyses, and largely reflects the undersampled Early-early Middle Triassic. Many of the longest missing lineages are near the base of the tree and are apparent in both Crurotarsi and Avemetatarsalia. The oldest unequivocal member of crown-group Archosauria is likely the early Anisian *Arizonasaurus* (Nesbitt 2005), which is roughly 243 million years old (based on the timescale of Gradstein *et al.* 2004). *Bromsgroveia*, *Qianosuchus*, *Stagonosuchus*, and *Yarasuchus* are also Anisian, but their more precise age is unresolved. Thus, a lineage extension of at least 15 million years is necessary to pull the Carnian-Norian basal crurotarsan taxon Phytosauria into the early Anisian. A slightly smaller but still substantial ghost lineage is apparent at the base of Avemetatarsalia, as the oldest unequivocal members of the group are currently a number of late Ladinian forms (*Lagerpeton*, *Lewisuchus*, *Marasuchus*, *Pseudolagosuchus*) from the Chañares Formation of Argentina. This missing lineage is at least nine million years, and potentially as long as 15 million years depending on the exact age of the Chañares Formation.

Within Crurotarsi, many basal members of Popsauroidea and Rauisuchoidea are among the oldest known taxa. However, within Rauisuchoidea, a missing lineage of 20+ million years may be needed to link the Carnian *Arganasuchus* and Norian *Fasolasuchus* with the Anisian-Ladinian *Ticinosuchus* and *Stagonosuchus*. Poor resolution within Popsauroidea hampers more precise determination of missing lineages. A long ghost lineage spanning much of the Carnian-Norian may be needed to link the shuvosaurids with other poposauroids, depending on the resolution of poposauroid interrelationships. However, this lineage is likely more apparent than real, as Nesbitt (2007) has identified

several fragmentary shuvosaurid-like specimens from a number of Norian and possibly Carnian units in the western United States. Finally, it is clear that a gap of at least 15 million years exists between Rausuchia and its sister taxon, Ornithosuchidae + *Revueltosaurus*, which is first known from the Carnian.

Substantial missing lineages are present at and around the base of Crocodylomorpha. These include a long ghost lineage at the base of the *Erpetosuchus* + Crocodylomorpha clade, whose length depends on the precise age of the Chañares taxon *Gracilisuchus*, and a substantial lineage extension for Aetosauria, which is first known from the early Carnian but must be extended at least into the Ladinian. The Aetosauria + Crocodylomorpha clade also has a long ghost lineage at its base, but again its length depends on the age of *Gracilisuchus*.

Within Avemetatarsalia a ghost lineage of approximately 13 million years is needed to bring the *Scleromochlus* + Pterosauria clade to the same stratigraphic level as its sister taxon, Dinosauromorpha. Within Dinosauromorpha there is a large, possibly 20+ million year gap, between the Chañares taxon *Lagerpeton* and its sister taxon, *Dromomeron* from the early Norian of North America. There is also a large gap between the Chañares taxon *Lewisuchus* and more derived members of the “*Silesaurus*” group, which are from the Late Carnian and Norian.

Missing lineages are especially concentrated in the Anisian and Ladinian, and many almost certainly extend into the Early Triassic. Our poor knowledge of this time is partially a result of undersampling, but the lack of unequivocal archosaur fossils in otherwise well-sampled Early Triassic units (e.g. Shubin & Sues 1991) is also telling. It may be that crown-group archosaurs radiated and diversified into major clades (Avemetatarsalia, Crurotarsi, Suchia, Rausuchoidea, Poposauroidea) in the Early Triassic, but may have been rare or geographically localised. Major ingroup clades such as Phytosauria, Ornithosuchidae, and Aetosauria also likely originated at this time, even though unambiguous fossils of these groups first appear in the Carnian. The search for transitional forms linking these clades to other archosaur groups has long been vexing, and remains a critical unresolved issue.

*Extinction and Faunal Change.* The Triassic was a critical period in earth history, as many major lineages originated and ecosystems reshuffled in the aftermath of the Permo-Triassic extinction. Major changes in faunal composition and terrestrial ecosystem structure occurred during and immediately after the Triassic, likely the result of a single end-Triassic extinction (Olsen *et al.* 1987; Hallam 1990; Olsen *et al.* 2002) or two extinction events at the end of the Carnian and Rhaetian (Benton 1986b, 1991, 1994; Simms *et al.* 1994).

Although basal archosaurs were diverse in the Middle-Late Triassic the only lineages that extended into the Jurassic were the speciose clades Crocodylomorpha, Dinosauria, and Pterosauria, each of which comprises several subgroups that originated in the Late Triassic and passed into the Jurassic (e.g. Ornithischia, Sauropodomorpha, and Theropoda within Dinosauria). The major clades Phytosauria and Aetosauria, as well as possibly Ornithosuchidae and Poposauroida, extend into the Rhaetian but not the Jurassic, apparently going extinct at or near the Triassic-Jurassic boundary. Extinctions at the Carnian-Norian boundary are less clear. Saurischia and Ornithischia are known from the late Carnian and clearly passed into the Norian. The first pterosaurs are early Norian in age, but a range extension into the Carnian is necessary to link this clade to its sister taxon *Scleromochlus*. Furthermore, at least two lineages of non-dinosaurian dinosauromorphs (those leading to *Dromomeron* and *Eucoelophysis*) extended into the Norian. A third involving *Sacisaurus* is possible, depending on the exact age of this taxon and its relationship with *Eucoelophysis* and *Silsaurus*. Within Crurotarsi, the major lineages Phytosauria, Ornithosuchidae, Aetosauria, and Crocodylomorpha are first known from the Carnian and clearly pass into the Norian. However, some poposauroid and rauisuchoid lineages from the Ladinian-Carnian apparently do not extend into the Norian. Unfortunately, poor constraint on the age of many formations at or near the Carnian-Norian boundary, especially those of the western United States (see Nesbitt 2007; Irmis & Mundil 2008), make it difficult to be sure whether some of these rauisuchian lineages extended into the Norian.

In summary, several major archosaur groups passed through the Carnian-Norian boundary, but some basal lineages apparently went extinct before the boundary. Studies of the Carnian-Norian extinction have indicated that most archosaur groups passed

through this horizon, and identified the extinction among key non-archosaurian herbivorous groups such as rhynchosaurs, dicynodonts, and chiniquodontids (Benton 1986b, 1991, 1994). However, our analysis indicates that a lineage-based approach instead of more traditional analyses based on “higher taxa” may reveal hidden support for a Carnian-Norian extinction also among archosaurs. This awaits testing with more refined statistical techniques and a larger dataset that takes into account fragmentary but diagnostic specimens that are not included in our cladistic analysis.

*Posture and Locomotion.* Numerous studies have focused on the evolution of locomotor strategies and limb posture in basal archosaurs (e.g. Charig 1972; Cruickshank 1979; Bonaparte 1984; Parrish 1986, 1987; Sereno 1991a). Traditionally, many authors argued that the erect gait of dinosaurs was a key improvement that allowed these forms to dominate terrestrial ecosystems during the Mesozoic (e.g. Charig 1972). Erect posture was often thought to have evolved sequentially from sprawling through semi-erect morphologies, and many basal archosaurs (“thecodonts”) were viewed as transitional taxa between sprawling archosaur outgroups and the fully erect dinosaurs (Charig 1972; Cruickshank 1979; Parrish 1986). Subsequent authors noted that many crurotarsans had erect postures that were different from those in dinosaurs, but notions of progressionism still pervaded discussions of postural evolution in archosaurs (e.g. Chatterjee 1982). The publication of explicit, cladistic-based archosaur phylogenies in the early 1990s indicated that erect posture may have evolved at the base of crown-group Archosauria, and that this need not have evolved through a semi-erect intermediate (Sereno 1991a; Parrish 1993).

Increased taxonomic sampling in the present phylogenetic analysis allows for a more confident discussion of postural evolution among archosaurs. Most close archosaur outgroups (e.g. proterosuchids, erythrosuchids, proterochampsids) possessed sprawling gaits. The outgroup *Euparkeria* is often described as “semi-erect,” but this postural category is difficult to define (Sereno 1991a). What is most important is that *Euparkeria* clearly did not possess the fully erect gait of many crown-group archosaurs, defined by Parrish (1987:397) as characterised by “flexion and extension of the major joints of the hind limb occur(ring) within horizontal axes that are perpendicular to the line of march of the animal.” Such a gait is seen in all crown-group archosaurs analysed in the present

study with the exception of phytosaurs, which possess a sprawling gait similar to that of archosaur outgroups. Thus, when optimised onto the current phylogeny, it is equally parsimonious to say that erect posture: 1) evolved at the base of the crown group and reversed to the primitive sprawling condition in phytosaurs; or 2) evolved independently in Avemetatarsalia and Suchia (i.e. all crurotarsans except phytosaurs) (Fig. 9).

Further study of archosaur locomotion is clearly needed. Most importantly, a consensus is lacking on the posture of many crurotarsan groups (see review in Sereno 1991a). For instance, Parrish (1993) considers prestosuchid “rauisuchians” as sprawlers, even though *Prestosuchus* and other similar taxa seem to conform to his earlier definition of erect posture (Parrish 1987). Second, intermediate postures such as “semi-erect” are poorly defined and thus often dismissed in more recent discussions of postural evolution, including here, although possible intermediates ought to be considered. Finally, more focused morphological study is needed to assess possible homologies between the erect postures of avemetatarsalians and suchians, which greatly differ in gross anatomy (e.g. open vs. closed acetabulum, vertical vs. horizontal acetabular orientation, digitigrade vs. plantigrade foot posture, mesotarsal vs. crurotarsal ankle structure).

### **Status of Archosaur Systematics and Future Directions**

The current study more than doubles character and taxon sampling relative to previous studies. This increase is primarily the result of two factors. First, we include a range of “rauisuchian” taxa, many of which were ignored in previous studies because of the assumed monophyly of this group. This, in turn, concealed numerous characters that vary among the entire array of “rauisuchians” and often among other archosaurs as well. Second, we include a large amount of new data that has come to light during a renaissance in the discovery, description, and reinterpretation of basal archosaur material over the past decade.

Although clear progress is being made in the discovery of phylogenetic data, has this translated into progress in resolving archosaur phylogeny? The answer is mixed. The broad pattern of avemetatarsalian phylogeny has been stable for over a decade. Current debate focuses mainly on the exact placement of genera such as *Scleromochlus*,



*Silesaurus*, and *Eucoelophysis* and not on the monophyly of Dinosauria or the hierarchical nesting of long-known taxa like *Lagerpeton* and *Marasuchus*. Crurotarsan phylogeny, however, has long been unstable and poorly resolved. The vast increase in character and taxon sampling in the present analysis does result in a well-resolved tree but most clades are poorly supported. Thus, our poor understanding of crurotarsan phylogeny may reflect something more fundamental. Only a very small amount of character data is relevant to the major basal divergences within Crurotarsi, and unique clades such as Phytosauria and Aetosauria are not clearly linked to other taxa by transitional fossils. This is comparable to missing the entire array of basal dinosauromorphs that link Dinosauria with Pterosauria and *Scleromochlus*, or the range of feathered theropods linking dinosaurs and birds. The absence of transitional fossils may be a simple result of undersampling, but ghost ranges indicate that such forms should be discovered in the Anisian and Ladinian, which have produced scores of “rauisuchians” and dinosauromorphs. This missing record is puzzling and deserves further study, as discovery of Early-Middle Triassic transitional forms may hold the key to finally resolving the higher-level relationships of Crurotarsi.

Other issues demand further work. While many systematists study the interrelationships of dinosaurs, fewer work on crurotarsans. Similarly, certain regions of the skeleton (especially the skull and hindlimb) are well studied, whereas other regions (most notably the axial column) have received little attention. Character sampling and scoring are major issues that must not be swept under the table in a rush to incorporate new data, a recommendation first delivered by Juul (1994). We have noted substantial disagreement in character scoring between our analysis and some previous studies, and have identified character sampling as an important source of differing results among published studies. Sereno & Brusatte (in press) have noted similar levels of disagreement among some dinosaur workers. Finally, as morphological phylogenies become more comprehensive, it will be illuminating to combine these datasets with molecular data for extant taxa, to better understand archosaur evolution and the contentious systematic relationships of turtles.

Reconstructing the higher-level phylogeny of crown-group Archosauria is not simply an end in itself, but a gateway to a deeper understanding of archosaur evolution and biology. Grand hypotheses of large-scale faunal change, biogeographic distribution,

and the evolution of important anatomical, behavioural, and physiological complexes demand a phylogenetic context. Recent macroevolutionary studies of early archosaur history (e.g., Brusatte *et al.* 2008a,b) have relied on phylogenetic data, and further studies of archosaur biogeography during the heyday of Pangea and the patterns of archosaur extinction during the Triassic and Jurassic await examination in a phylogenetic framework.

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## FIGURE LEGENDS

**Figure 1.** The skulls of several basal archosaurs, showing the diversity of cranial form within the group during the Triassic. A, *Nicrosaurus* (Phytosauria); B, *Aetosaurus* (Aetosauria); C, *Lotosaurus* (Poposauroida, “rauisuchian”); D, *Postosuchus* (Rauisuchoida, “rauisuchian”) (image reversed); E, *Riojasuchus* (Ornithosuchidae) (cast); F, *Plateosaurus* (Dinosauria: Sauropodomorpha). Scale bars for A, C-F equal 10 centimetres. Scale bar for B equals 5 cm.

**Figure 2.** A strict consensus of recent higher-level cladistic analyses of crown-group Archosauria. This is a strict consensus of the cladograms presented by previous studies, with clades shown here denoting those that are recovered in every previous study, just as a strict consensus of several most parsimonious trees from a character analysis denotes clades found in every individual MPT. Polytomies indicate areas of disagreement between previous studies. Dashed lines indicate taxa that have only appeared in a single study. Although early studies united Ornithosuchidae with Avemetatarsalia, it is placed with Crurotarsi in this tree, reflecting consensus that emerged after revision of ornithosuchid tarsal morphology (Serenó & Arcucci, 1990; Sereno, 1991a).

**Figure 3.** Illustration of cladistic characters new to this study (selected cranial characters). A, *Scleromochlus* (after Benton, 1999); B, *Herrerasaurus* (after Sereno & Novas, 1993); C, *Aetosaurus* (after Walker, 1961 and SMNS 5770); D, *Shuvosaurus* (after Rauhut, 1997); E, *Prestosuchus* (after Barberena, 1978); F, *Batrachotomus* (after Gower, 1999 and SMNS 52970, 80260). All skulls in left lateral view and scaled to same length. Numbers refer to character number in Appendix 1, and numbers in parentheses refer to character states.

**Figure 4.** Illustration of cladistic characters new to this study (selected postcranial characters). A, scapula-coracoid of *Sphenosuchus* (after Walker, 1990); B, scapula-coracoid of *Ornithosuchus* (after Walker, 1964); C, ilium of *Parasuchus* (after Chatterjee, 1978); D, ilium of *Eudimorphodon* (after Wild, 1978); E, ilium of *Arizonasaurus* (after

Nesbitt, 2005); F, pubis of *Parasuchus* (after Chatterjee, 1978); G, pubis of *Tikisuchus* (after Chatterjee & Majumdar, 1978); H, pubis of *Herrerasaurus* (after Novas, 1993). All illustrations in left lateral view, and corresponding elements scaled to same length and oriented identically for each of comparison. Numbers refer to character number in Appendix 1, and numbers in parentheses refer to character states.

**Figure 5.** A strict consensus of the 70 most parsimonious trees (747 steps, CI = 0.31, RI = 0.68) recovered by the current analysis. Numbers next to clades refer to bootstrap percentages (fast addition sequence, 10,000 replicates)/Bremer support values. Labelled nodes are those given a name (see text), but no definitions are given (circles do not necessarily represent node-based definitions). Suprageneric ingroup taxa represented by exemplars are collapsed. The analysis recovers the following topologies for the exemplars: Aetosauria: *Aetosaurus* (*Desmatosuchus*, *Stagonolepis*); Crocodylomorpha: *Protosuchus* (*Sphenosuchus*, *Terrestrisuchus*); Ornithischia: trichotomy; Phytosauria: *Parasuchus* (*Mystriosuchus*, *Rutiodon*); Pterosauria: *Dimorphodon* (*Eudimorphodon*, *Pteranodon*); Saurischia: trichotomy.

**Figure 6.** Strict consensus topologies when the current analysis is run with selected taxon and character alterations. A, Pterosauria excluded (1785 trees, 710 steps, CI = 0.32, RI = 0.67); B, all characters pertaining to the astragalus and calcaneum excluded (196 trees, 708 steps, CI = 0.29, RI = 0.66). Saurischia is shown as a single terminal in tree A (to save space), but is actually collapsed, with all saurischian genera falling into a basal polytomy with a monophyletic Ornithischia.

**Figure 7.** Comparison with alternative studies. A, Parrish (1993); B, Juul (1994); C, Benton (2004). Tree to the left is the strict consensus topology of the original analysis, including Benton's (2004) tree that was not reported in his study. Tree to the right is the strict consensus of all trees (single MPT in the case of Benton [2004]) resulting from a modified analysis in which disputed scores are changed to those favoured by the current analysis. Numbers next to nodes are bootstrap percentages/Bremer support values.

**Figure 8.** A phylogram of the strict consensus topology from the current analysis, scaled to a global chronostratigraphic timescale of the Triassic and Early Jurassic. Chronostratigraphic ranges, absolute ages, and stage-level terminology based on the timescale of Gradstein *et al.* (2004). Dotted vertical lines represent postulated extinction events at the Carnian-Norian and Triassic-Jurassic boundaries. Thick grey lines represent major ghost lineages, thick black lines represent the ranges of suprageneric archosaur ingroups (those represented by exemplars in the current study), and dotted lines represent coarse error bars on the dating of fossil taxa. All generic taxa are treated as point occurrences, with each “point” referring to the approximate stratigraphic position of the holotype or another well constrained specimen. These “points” are placed at the midpoint of the most precise stratigraphic assignment possible, based on reference to the primary literature (i.e. if the best resolution is “Carnian” then the taxon is placed at the midpoint of the Carnian). The coarse error bars then extend to cover the entire “most precise” interval (i.e. for the Carnian taxon these error bars would cover the entire Carnian). For those taxa known from multiple well-constrained specimens the error bars extend to cover the entire observed range of the taxon. Because of uncertainty in the Triassic time scale (see Furin *et al.*, 2006) this figure is only meant as an approximate diagram, not an exhaustive summary of the distribution of each taxon, which is fraught with difficulties (see Nesbitt 2007; Rayfield *et al.*, 2007). ET = Early Triassic, Rha = Rhaetian.

**Figure 9.** Postural transformation within Archosauria. Sprawling and erect posture optimised (ACCTRAN) onto a simplified version of the phylogenetic hypothesis advocated here. “Semi-erect” posture, as has been hypothesised for *Euparkeria*, is treated as sprawling pending further analysis of archosaur posture and locomotion. It is equally parsimonious to consider erect posture as having: 1) evolved at the base of crown-group Archosauria and then lost in phytosaurs; or 2) evolving independently in Avemetatarsalia and Suchia (the clade of all crurotarsans except for phytosaurs).



**Table 1.** Previous phylogenetic analyses focusing on crown-group Archosauria and its two major clades, Avemetatarsalia and Crurotarsi. Excluded from this table are non-quantitative descriptions of characters (Benton & Clark 1988) or studies that presented a datamatrix but did not analyse it quantitatively (e.g. Gauthier 1986; Novas 1989, 1992; Sereno 1999). Informative characters refer to those characters that are phylogenetically informative for crown-group archosaurian ingroup relationships. "--" refers to a value that was not reported in the original publication, which was not reanalysed for this study. Some preliminary versions of later analyses (e.g. Gower 2002 for Nesbitt & Norell 2006) are not included, nor are some analyses that recycled a previous dataset (e.g. Li *et al.* 2006).

**ARCHOSAURIA**

<b>Authors</b>	<b>Generic Suprageneric</b>		<b>Informative</b>	<b>MPTs</b>	<b>TL</b>	<b>CI</b>	<b>RI</b>
	<b>Taxa</b>	<b>Taxa</b>					
Sereno & Arcucci, 1990	0	5	23	3	39	0.90	--
Sereno, 1991a	3	4	28	1	42	0.88	--
Juul, 1994	4	9	51	3	154	0.57	--
Bennett, 1996	2	5	63	3	209	0.68	--
Benton, 1999	5	9	63	1	139	0.62	0.80
Benton, 2004	10	8	64	18	172	0.59	0.82
Nesbitt, 2007	12	7	70	1	158	0.60	0.84
Irmis <i>et al.</i> , 2007a	25	0	80	1	298	0.48	0.74

**AVEMETATARSALIA**

<b>Authors</b>	<b>Generic Suprageneric</b>		<b>Informative</b>	<b>MPTs</b>	<b>TL</b>	<b>CI</b>	<b>RI</b>
	<b>Taxa</b>	<b>Taxa</b>					
Novas, 1993	3	5	23	1	68	0.75	--
Novas, 1996	4	4	37	1	44	0.84	0.87
Ezcurra, 2006	25	1	26	1	794	0.44	0.68
Langer & Benton, 2006	7	3	6	1	203	0.61	0.56

**CRUROTARSI**

<b>Authors</b>	<b>Generic Suprageneric</b>		<b>Informative</b>	<b>MPTs</b>	<b>TL</b>	<b>CI</b>	<b>RI</b>
	<b>Taxa</b>	<b>Taxa</b>					
Parrish, 1993	18	0	32	6	70	0.64	0.83
Olsen <i>et al.</i> , 2000	7	0	14	1	44	0.80	0.76
Benton & Walker, 2002	14	0	35	112	95	0.64	0.70
Nesbitt, 2003	6	2	24	2	--	0.72	0.79
Gower & Nesbitt 2006	8	2	13	5	39	0.77	0.86
Weinbaum & Hünigerbuhler 2007	8	3	34	2	48	0.77	0.86

**CURRENT ANALYSIS**

<b>Authors</b>	<b>Generic Suprageneric</b>		<b>Informative</b>	<b>MPTs</b>	<b>TL</b>	<b>CI</b>	<b>RI</b>
	<b>Taxa</b>	<b>Taxa</b>					
Brusatte <i>et al.</i>	32	7	187	70	747	0.31	0.68

**Table 2.** A list of stand-alone generic outgroup and ingroup terminals. \* = Outgroup taxon Proterochampsidae primarily based on the genus *Chanaresuchus*. E,M,L = early,middle,late; T = Triassic.

**OUTGROUPS**

<b>Genus</b>	<b>Age</b>	<b>Location</b>	<b>Author</b>
<i>Erythrosuchus</i>	E-M Triassic	Africa (South Africa)	Broom, 1905
<i>Euparkeria</i>	Early Triassic	Africa (South Africa)	Broom, 1913
Proterochampsidae*	M-L Triassic	South America	Romer, 1971c

**AVEMETATARSALIA**

<b>Genus</b>	<b>Age</b>	<b>Location</b>	<b>Author</b>
<i>Dromomeron</i>	Norian (LT)	North America (New Mexico)	Irmis <i>et al.</i> , 2007a
<i>Eucoelophysis</i>	Norian (LT)	North America (Arizona)	Sullivan & Lucas, 1999
<i>Lagerpeton</i>	Ladinian (MT)	South America (Argentina)	Romer, 1971b
<i>Lewisuchus</i>	Ladinian (MT)	South America (Argentina)	Romer, 1972b
<i>Marasuchus</i>	Ladinian (MT)	South American (Argentina)	Romer, 1971b
<i>Pseudolagosuchus</i>	Ladinian (MT)	South America (Argentina)	Arcucci, 1987
<i>Sacisaurus</i>	Carnian-Norian	South America (Brazil)	Ferigolo & Langer, 2007
<i>Scleromochlus</i>	Carnian (LT)	Europe (Scotland)	Woodward, 1907
<i>Silesaurus</i>	Carnian (LT)	Europe (Poland)	Dzik, 2003

**CRUROTARSI**

<b>Genus</b>	<b>Age</b>	<b>Location</b>	<b>Author</b>
<i>Arganasuchus</i>	Carnian (LT)	Africa (Morocco)	Jalil & Peyer, 2007
<i>Arizonasaurus</i>	Anisian (MT)	North America (SW USA)	Welles, 1947
<i>Batrachotomus</i>	Ladinian (MT)	Europe (Germany)	Gower, 1999
<i>Bromsgroveia</i>	Anisian (MT)	Europe (England)	Galton, 1985
<i>Effigia</i>	?Rhaetian (LT)	North America (New Mexico)	Nesbitt & Norell, 2006
<i>Erpetosuchus</i>	Carnian (LT)	Europe (Scotland)	Newton, 1894
<i>Fasolasuchus</i>	Norian (LT)	South America (Argentina)	Bonaparte, 1978
<i>Gracilisuchus</i>	Anisian (MT)	South America (Argentina)	Romer, 1972a
<i>Lotosaurus</i>	Middle Triassic	Asia (China)	Zhang, 1975
<i>Poposaurus</i>	Carnian-Norian	North America (Wyoming, Texas)	Mehl, 1915
<i>Postosuchus</i>	Carnian-Norian	North America (SW USA)	Chatterjee, 1985
<i>Prestosuchus</i>	Ladinian-Carnian (LT)	South America (Brazil)	Huene, 1942
<i>Qianosuchus</i>	Anisian (MT)	Asia (China)	Li <i>et al.</i> , 2006
<i>Rauisuchus</i>	Ladinian-Carnian (LT)	South America (Brazil)	Huene, 1942
<i>Revueltosaurus</i>	Norian (LT)	North America (SW USA)	Hunt, 1989
<i>Saurosuchus</i>	Carnian (LT)	South America (Argentina)	Reig, 1959
<i>Shuvosaurus</i>	Norian (LT)	North America (Texas)	Chatterjee, 1993
<i>Sillosuchus</i>	Carnian (LT)	South America (Argentina)	Alcober & Parrish, 1997
<i>Stagonosuchus</i>	Anisian (MT)	Africa (Tanzania)	Huene, 1938
<i>Teratosaurus</i>	Carnian-Norian	Europe (Germany, Poland)	Meyer, 1861
<i>Ticinosuchus</i>	Anisian-Ladinian	Europe (Switzerland, Italy)	Krebs, 1965
<i>Tikisuchus</i>	Carnian (LT)	India	Chatterjee, 1987
<i>Yarasuchus</i>	Anisian (MT)	India	Sen, 2005

**Table 3.** A list of suprageneric ingroup terminals and the set of three exemplar taxa selected to represent each (except for Ornithosuchidae, which is represented by two taxa).

LT = Late Triassic, LK = Late Cretaceous.

<b>Suprageneric Taxon</b>	<b>Age</b>	<b>Exemplars</b>
Aetosauria	Carnian-Rhaetian (LT)	<i>Aetosaurus</i> , <i>Desmotosuchus</i> , <i>Stagonolepis</i>
Crocodylomorpha	Carnian (LT)-Extant	<i>Protosuchus</i> , <i>Terrestrisuchus</i> , <i>Sphenosuchus</i>
Ornithischia	Carnian (LT)- Maastrichtian (LK)	<i>Heterodontosaurus</i> , <i>Lesothosaurus</i> , <i>Psittacosaurus</i>
Ornithosuchidae	Carnian-Rhaetian (LT)	<i>Ornithosuchus</i> , <i>Riojasuchus</i>
Phytosauria	Carnian-Rhaetian (LT)	<i>Mystriosuchus</i> , <i>Parasuchus</i> , <i>Rutiodon</i>
Pterosauria	Norian (LT)- Maastrichtian (LK)	<i>Dimorphodon</i> , <i>Eudimorphodon</i> , <i>Pteranodon</i>
Saurischia	Carnian (LT)-Extant	<i>Coelophysis</i> , <i>Herrerasaurus</i> , <i>Plateosaurus</i>

**Table 4.** Comparison of the current analysis with alternative studies. Listed are numbers of shared taxa (both genus-level and suprageneric) between the current analysis and the alternative study in question; the number of informative characters in the alternative analysis; the number of shared characters between the current analysis and the alternative; the number of “used” characters: informative characters in the alternative analysis that were used in the current study (not always equivalent to shared characters since some shared characters were uninformative in the alternative analysis); the number of positive scoring differences (those concerning differences between affirmative scores, such as 0 and 1) and the number of missing datum scoring differences (those concerning the change to or from a missing datum, such as ? to 0) for both genus-level and suprageneric taxa; and Character Similarity (CSI) and Shared Character State (CSSI) Indices (see text). CSI values for those analyses focusing on Avemetatarsalia or Crurotarsi only are calculated using only those characters informative for each major lineage (118 and 157 characters, respectively) in the present analysis. CSSI values only measure scoring differences among taxa common to both analyses.

Analysis	Shared Generic Taxa	Shared Suprageneric Taxa	Informative Characters	Shared Characters	Used Characters	Positive Scoring Diffs. = Generic/Suprageneric	Missing Datum Scoring Diffs.=Generic/Suprageneric	Character Similarity Index (CSI)	Shared Character State Index (CSSI)
Sereno & Arcucci, 1990 (CA)	0	5	23	21 (11%)	21 (91%)	0/0	0/2	0.11	0.99
Sereno, 1991a (CA)	3	4	28	27 (15%)	26 (93%)	2/2	5/3	0.15	0.96
Juul, 1994 (CA)	4	9	51	44 (24%)	44 (86%)	21/ 20	13/16	0.23	0.90
Bennett, 1996 (CA)	2	5	63	34 (19%)	37 (59%)	3/6	12/3	0.16	0.93
Benton, 1999 (CA)	5	9	63	60 (33%)	59 (94%)	17/ 14	25/19	0.32	0.94
Benton, 2004 (CA)	10	8	64	59 (32%)	56 (88%)	34/ 8	46/19	0.31	0.93
Nesbitt, 2007 (CA)	10	7	70	66 (36%)	65 (93%)	34/ 12	65/12	0.35	0.92
Irmis <i>et al.</i> 2007a (CA)	17	0	80	70 (38%)	70 (88%)	88/ 0	101/0	0.36	0.88
Novas, 1989 (A)	3	1	8	6 (3%)	7 (88%)	0/0	0/0	0.05	1.00
Novas, 1992 (A)	3	2	8	15 (8%)	8 (100%)	2/0	0/0	0.14	0.97
Novas, 1993 (A)	3	4	23	21 (11%)	21 (91%)	2/0	4/0	0.18	0.97
Novas, 1996 (A)	4	3	37	35 (19%)	34 (92%)	1/0	16/0	0.29	0.96
Sereno, 1999 (A)	2	2	18	14 (8%)	14 (78%)	0/0	0/0	0.11	1.00
Ezcurra, 2006 (A)	10	0	26	21 (11%)	22 (85%)	5/--	2/--	0.17	0.97
Langer & Benton, 2006 (A)	2	3	6	9 (5%)	6 (100%)	1/0	0/0	0.08	0.98
Parrish, 1993 (C)	15	0	32	17 (9%)	18 (56%)	45/ --	67/--	0.10	0.69
Olsen <i>et al.</i> , 2000 (C)	6	0	14	13 (7%)	13 (93%)	2/--	5/--	0.08	0.94
Benton & Walker, 2002 (C)	13	0	35	29 (16%)	32 (91%)	17/ --	33/--	0.18	0.91
Nesbitt, 2003 (C)	5	2	24	14 (8%)	15 (63%)	2/2	6/0	0.09	0.93
Gower & Nesbitt, 2006 (C)	6	2	13	7 (4%)	7 (54%)	0/1	2/0	0.04	0.96
Weinbaum & Hungerbühler 2007 (C)	8	3	34	28 (15%)	28 (82%)	26/ 7	23/2	0.18	0.85

## APPENDIX 1: CHARACTER LIST

1. Skull, length: less than (0) or greater than (1) 50% length of presacral column. (Serenó, 1991a:33; Novas, 1996:33; Benton, 1999:1; Benton, 2004:1; Irmis, *et al.* 2007a:1)
2. Antorbital fenestra, shape: elliptical or circular (0); triangular, with elongate and narrow anterior point (1). (Benton & Clark, 1988; Benton & Walker, 2002:38; Benton, 2004:6; Weinbaum & Hungerbühler, (2007:4)
3. Orbit, anteroposterior length: less (0) or greater (1) than 25% skull length. New character, originally described by Nesbitt (2007).
4. Orbit, shape: circular or elliptical (0); tall and narrow, with maximum height more than 1.5 times maximum width (1). (Benton & Clark, 1988; Benton & Walker, 2002:39)
5. External naris, length of longest dimension: less (0) or greater (1) than longest dimension of antorbital fenestra. (Benton & Walker, 2002:37)
6. External nares, elements separating opposing nares on dorsal midline: premaxilla only (0); premaxilla and nasal (1); nasal only (2). (Benton & Walker, 2002:36)
7. Infratemporal fenestra, size: greater or equal (0) or smaller (1) than supratemporal fenestra. (Benton & Clark, 1988; Juul, 1994:31; Benton, 1999:7; Benton & Walker, 2002:41; Benton, 2004:11)
8. Infratemporal fenestra, shape: elliptical (0); triangular, with dorsal margin much shorter than ventral margin (1). (Benton & Clark, 1988; Benton & Walker, 2002:42; Weinbaum & Hungerbühler, 2007:9; Irmis *et al.*, 2007a:15)
9. Supratemporal fenestra, orientation: exposed primarily dorsally (0); exposed primarily dorsally but with a small sliver visible in lateral view (1); exposed widely laterally (2). New character, see Appendix S1 and Figure 3.
10. Supratemporal fenestra, extent of surrounding fossa: limited (0); extensive, present on squamosal, postorbital, parietal, and sometimes the frontal (1). (Weinbaum & Hungerbühler, 2007:10)
11. Skull, slit-like fenestra between premaxilla and maxilla (greatest dimension greater than three times lesser dimension): absent (0); present (1). (Benton & Clark, 1998; Parrish, 1993:23; Juul, 1994:37; Benton, 1999:2; Benton & Walker, 2002:34; Nesbitt, 2003:4; Benton 2004:2; Weinbaum & Hungerbühler, 2007:1; Irmis *et al.*, 2007a:3)

12. Premaxilla, inclination of anterior border: vertical (0); slopes posterodorsally (1).  
New character, see Appendix S1 and Figure 3.
13. Premaxilla, length of ventral margin compared to ventral margin of maxilla: shorter (0); longer, premaxilla forms elongate snout and maxilla unreduced (1); longer, maxilla reduced in size (2). New character, see Appendix S1 and Figure 3.
14. Premaxilla, subnarial process articulating with maxilla, form: absent or very short (0); elongate and finger-like (1); short and triangular (2). New character, see Appendix S1 and Figure 3.
15. Premaxilla, subnarial process articulating with maxilla, extent: terminates ventral to (0) or posterior to (1) external naris. (Langer & Benton, 2006:5; Irmis *et al.*, 2007a:4)
16. Premaxilla, dorsal process articulating with nasal to form internarial bar, length: shorter (0) or longer (1) than ventral margin of premaxilla body. (Nesbitt & Norell, 2006:75; Nesbitt, 2007:75)
17. Premaxilla, dentition: present, bearing teeth (0); absent, edentulous (1). (Nesbitt & Norell, 2006:73; Nesbitt, 2007:73)
18. Premaxilla, articulation with maxilla, form of ventral border: at same level as maxilla ventral border (0); angled relative to maxilla ventral border, forming an arch between the elements (1). New character, see Appendix S1.
19. Maxilla, anterior ramus extending anterior to ascending ramus: absent, anterior surface of maxilla smoothly convex (0); present, distinct step separating anterior portion of maxilla and ascending ramus (1). (Irmis *et al.*, 2007a:5)
20. Maxilla, anteroposterior length at the base of the ascending ramus: greater (0) or less (1) than one half dorsoventral depth of maxillary main body at the level of the anterior edge of antorbital fenestra. New character, see Appendix S1 and Figure 3.
21. Maxilla, form of antorbital fossa on lateral surface: shallowly excavated and not set apart by strong ridge (0); deeply excavated and demarcated by a strong ridge (1). (Weinbaum & Hungerbuhler, 2007:2)
22. Maxilla, length of portion of bone anterior to anterior margin of antorbital fenestra: longer (0) or shorter (1) than portion posterior to anterior margin of antorbital fenestra. (Olsen *et al.*, 2000:2; Benton & Walker, 2002:2)



23. Maxilla, articulation with opposing maxilla on palate to form secondary bony palate: absent (0); present (1). (Gauthier, 1986; Benton and Clark, 1988; Parrish, 1993:40; Olsen *et al.*, 2000:3; Benton and Walker, 2002:3)
24. Maxilla, dentition: present, bearing teeth (0); absent, edentulous (1). (Nesbitt & Norell, 2006:74; Nesbitt, 2007:74)
25. Nasal, position of anterior portion in lateral view: below or at same level as skull roof (0); elevated above skull roof, giving the skull a “roman nose” appearance (1). New character, originally described by Gower (1999).
26. Nasal, rugose lateral ridge: absent (0); present (1). (Weinbaum & Hungerbuhler, 2007:3)
27. Nasal, midline depression in dorsal view: absent (0); present (1). New character, originally described by Gower (1999).
28. Lacrimal, exposure on the skull roof: absent (0); present (1). (Weinbaum & Hungerbuhler, 2007:5)
29. Skull roof (nasal and frontals), sculpturing: present, consisting of marked grooves and ridges (0); absent, skull roof smooth (1). New character, originally described by Nesbitt (2007).
30. Prefrontal, contact with nasal, extent: broad (0); reduced to a point or excluded by frontal-lacrimal contact (1). (Serenó, 1991a:16)
31. Prefrontal, descending process forming anterodorsal rim of orbit, size: elongate, extends approximately 1/3-1/2 length of preorbital bar (0); shortened, only slightly contributes to preorbital bar (1). (Olsen *et al.*, 2000:5; Benton & Walker, 2002:5)
32. Prefrontal, posterior process underlying frontal dorsal to orbit: absent (0); present (1). (Olsen *et al.*, 2000:7; Benton & Walker, 2002:7)
33. Frontal, contribution to dorsal orbital rim: present (0); absent, excluded by a palpebral ossification (often erroneously regarded as an “enlarged prefrontal”) contacting the postfrontal/postorbital lateral to frontal (1). New character, see Appendix S1.
34. Frontal, sagittal crest along midline in dorsal view: absent (0); present (1). New character, see Appendix S1.
35. Frontal, dorsal surface, participation in supratemporal fossa: absent (0); present (1). (Novas, 1993:8; Novas, 1996:20; Sereno, 1999:2; Irmis *et al.*, 2007a:16)

36. Postfrontal: present (0); present but reduced & does not articulate with parietal (1); absent (2). (Gauthier, 1986; Benton & Clark, 1988; Sereno & Arcucci, 1990:2; Novas, 1993:10; Juul, 1994:16; Bennett, 1996:33; Novas, 1996:16; Benton, 1999:5; Sereno, 1999:1; Olsen *et al.*, 2000:8; Benton & Walker, 2002:8; Benton, 2004:9; Weinbaum & Hungerbuhler, 2007:6; Irmis *et al.*, 2007a:14). Ordered.
37. Parietals, midline suture between opposing elements: present, butt joint (0); partially obliterated (1); absent, parietals fused on midline (2). (Benton & Clark, 1988; Olsen *et al.*, 2000:15; Benton & Walker, 2002:15). Ordered.
38. Parietals, posteroventral edge, width: less (0) or greater (1) than ½ width of occiput. (Benton & Clark, 1988; Olsen *et al.*, 2000:16; Benton & Walker, 2002:16)
39. Parietals, shape of posterior margin in dorsal view: v-shaped (0); straight (1). (Olsen *et al.*, 2000:18; Benton & Walker, 2002:18)
40. Parietal, sagittal crest along midline in dorsal view: absent (0); present (1). (Olsen *et al.*, 2000:17; Benton & Walker, 2002:17)
41. Jugal, shape: triradiate (0); elongate and rod-like (1). New character, see Appendix S1 and Figure 3.
42. Jugal, participation in posterior edge of antorbital fenestra: present (0); absent, excluded by maxilla-lacrima contact (1). (Benton & Clark, 1988; Olsen *et al.*, 2000:4; Benton & Walker, 2002:4; Irmis *et al.*, 2007a:12)
43. Jugal, lateral surface, form: smooth or marked by a shallow rim delimiting the antorbital fossa (0); ornamented by a deep and rugose ridge delimiting the antorbital fossa, which is continuous with a similar ridge on the maxilla (1). (Nesbitt, 2003:20)
44. Postorbital-Jugal postorbital bar, form: straight or curved (0); stepped, with distinct anterior projection on postorbital (1). (Benton & Clark, 1988; Juul, 1994:38; Benton, 1999:6; Benton & Walker, 2002:40; Benton, 2004:10)
45. Postorbital and Squamosal, position of dorsal bar: at same level as ventral processes of bones (0); distinctly offset from ventral processes, forming overhanging brow over lateral temporal fenestra (1). (Weinbaum & Hungerbuhler, 2007:12; Irmis *et al.*, 2007a:18)
46. Squamosal, ridge along dorsal surface along edge of supratemporal fossa: absent (0); present (1). (Olsen *et al.*, 2000:12; Benton & Walker, 2002:12)

47. Squamosal, position of posterior process: at same level or dorsal to anterior process (0); below anterior process and set off by distinct step (1). New character, see Appendix S1 and Figure 3.
48. Squamosal, ventral process: present, forms posterodorsal border of lateral temporal fenestra (0); present, does not participate widely in lateral temporal fenestra (1); absent (2). (Gauthier, 1986; Benton & Clark, 1988; Sereno, 1991a:A; Parrish, 1993:24; Olsen *et al.*, 2000:11; Benton & Walker, 2002:11). Ordered.
49. Squamosal, ridge trending posteroventrally on lateral surface of ventral ramus: absent (0); present (1). New character, originally described by Gower (1999).
50. Squamosal, deep pit on the posterodorsal corner of the lateral surface: absent (0); present (1). New character, see Appendix S1 and Figure 3.
51. Squamosal ventral process and Quadratojugal dorsal process, orientation: subvertical or broadly convex anteriorly (0); distinct process on squamosal ventral process projecting into infratemporal fenestra (1); slopes anteriorly to form a triangular projection into the infratemporal fenestra comprised of both elements (2); triangular projection completely divides infratemporal fenestra into two openings (3). (Parrish, 1993:25; Olsen *et al.*, 2000:13; Benton & Walker, 2002:13,43,45; Weinbaum & Hungerbuhler, 2007:11)
52. Quadrate and quadratojugal, orientation: roughly vertical, do not reach upper margin of infratemporal fenestra (0); sloping anterodorsally at approximately 45 degrees, reach upper margin of infratemporal fenestra (1); sloping strongly posterodorsally (2). (Benton & Clark, 1988; Benton & Walker, 2002:44; Weinbaum & Hungerbuhler, 2007:8)
53. Quadrate, quadrate foramen: present (0); absent (1). (Benton & Walker, 2002:47)
54. Quadrate, distal articular surface, form of condyles: two convex condyles separated by a groove (0); one convex condyle (1). New character, originally described by Nesbitt (2007).
55. Quadrate, distal articular surface, shape: oval, with mediolateral long axis (0); square (1). New character, originally described by Nesbitt (2007).
56. Ectopterygoid, position relative to transverse flange of pterygoid: ventral (0); dorsal (1). (Novas, 1993:13; Novas, 1996:19; Benton, 1999:10; Sereno, 1999:3; Irmis *et al.*, 2007a:20)

57. Ectopterygoid, lateral process for articulation with jugal, length: anteroposteriorly shorter (0) or longer or equal to (1) medial process. New character, originally described by Nesbitt (2007).
58. Ectopterygoid, form of articulation with jugal: single-headed (0); double-headed (1). (Hungerbuhler & Weinbaum, 2007:7)
59. Braincase, size of posttemporal fenestra between parietal, supraoccipital, and exoccipital-opisthotic: large (0); reduced to small fissure or entirely closed (1). (Novas, 1993:11; Bennett, 1996:15; Novas, 1996:17; Sereno, 1999:5; Benton, 2004:11; Langer & Benton, 2006:17; Irmis *et al.*, 2007a:21)
60. Braincase, occipital condyle, shape: spherical or slightly dorsoventrally compressed (0); extremely dorsoventrally compressed, transverse width greater than twice dorsoventral height, resulting in a crescent shape (1). New character, see Appendix S1.
61. Braincase, basal tubera, orientation (with cultriform process held horizontally for reference): vertical, located ventral to occipital condyle (0); horizontal, located at same level as occipital condyle and flooring endocranial cavity (1). New character, see Appendix S1.
62. Parabasisphenoid, dorsoventral depth: short and rod-like (0); deep and wedge-shaped, with trough-like median pharyngeal recess (1). (Parrish, 1993:28,29; Juul, 1994:70; Benton, 1999:12; Gower, 2002:17; Benton, 2004:17; Weinbaum & Hungerbuhler, 2007:13)
63. Parabasisphenoid, position of foramina for cerebral branches of internal carotid artery: posterior surface (0); posterolateral surface (1); anterolateral surface (2). (Parrish, 1993:7; Gower, 2002:1; Benton, 2004:21)
64. Parabasisphenoid, position of basiptyergoid processes: ventral to basal tubera (0); at same level of basal tubera (= "horizontal parabasisphenoid") (1). (Benton, 2004:19; originally uninformative for crown group in Gower & Sennikov, 1996:7)
65. Parabasisphenoid, depth of recess: shallow (0); deep (1). (Nesbitt & Norell, 2006:76; Nesbitt, 2007:76)
66. Exoccipital-opisthotic, form of lateral surface: smooth (0); marked by subvertical crest, with hypoglossal foramina anterior to crest (1); marked by subvertical crest, with

hypoglossal foramina posterior to crest (2). (Gower, 2002:2; Weinbaum & Hungerbuhler, 2007:14)

67. Exoccipitals, contact of opposing elements along floor of endocranial cavity: present (0); absent (1). (Gower, 2002:5; originally uninformative for crown group in Gower & Sennikov, 1996:17)

68. Opisthotic, form of border of perilymphatic foramen: incompletely ossified (0); entirely ossified such that the ventral ramus of the opisthotic forms a perilymphatic loop (1). (Gower, 2002:21)

69. Opisthotic, position and orientation of perilymphatic foramen: medial position, perilymphatic duct transmitted posteromedially or posteriorly (0); lateral position, duct transmitted posterolaterally or laterally (1). (Gower, 2002:22)

70. Prootic, form of openings for trigeminal nerve and middle cerebral vein: combined into single foramen (0); partially or completely subdivided into separate foramina by a process of the prootic (1). (Gower, 2002:23)

71. Dentary, teeth: present up to anterior tip (0); absent at anterior tip but present posteriorly (1); completely absent (2). New character, see Appendix S1 and Figure 3.

72. Dentary, expansion of anterior region relative to main body: absent (0); present (1). New character, see Appendix S1 and Figure 3.

73. Dentary, length of symphysis: anteroposteriorly short (0); anteroposteriorly expanded and deep (1). (Bennett, 1996:47; Irmis *et al.*, 2007a:28)

74. Surangular, lateral ridge: present (0); absent (1). New character, originally described by Nesbitt (2007).

75. Surangular, posterior surangular foramen: absent or extremely small foramen (0); present as a large opening or fenestra (1). New character, originally described by Nesbitt (2007).

76. Articular, medial process: present (0); absent (1). New character, originally described by Gower (1999).

77. Cervical vertebrae, anterior centrum length:height ratio: less (0) or greater (1) than 2.0. (Nesbitt, 2003:17; Weinbaum & Hungerbuhler, 2007:17)

78. Cervical vertebrae, length of anterior centra: less (0) or greater (1) than length of middorsal centra. (Sereno & Arcucci, 1990:6; Sereno, 1991a:21; Juul, 1994:65; Bennett, 1996:100; Benton, 1999:16; Benton, 2004:32; Irmis *et al.*, 2007a:34)
79. Cervical vertebrae, level of anterior articular face: at same level as posterior face or slightly offset across entire column (0); anterior centra dorsally offset from posterior face, resulting in a parallelogram shape of individual anterior cervicals (1); all centra dorsally offset from posterior face, resulting in a strong S-shaped neck overall (2). (Gauthier, 1986; Benton & Clark, 1988; Sereno, 1991a:AA; Novas, 1993:1; Bennett, 1996:101; Novas, 1996:6; Benton, 1999:15; Benton, 2004:31; Irmis *et al.*, 2007a:33)
80. Cervical vertebrae, form of ventral margin in lateral view: straight or slightly concave, constriction less than 35% of centrum height at midpoint (0); strongly concave, resulting in a highly waisted centrum, constriction greater than 35% height of centrum at midpoint (1). New character, see Appendix S1.
81. Cervical vertebrae, epiphyses in postaxial anterior elements: absent (0); present (1). (Novas, 1993:9; Novas, 1996:21; Langer & Benton, 2006:33)
82. Cervical vertebrae, form of parapophyses: single structure (0); divided into separate dorsal and ventral articular surfaces (1). (Weinbaum & Hungerbuhler, 2007:18)
83. Cervical vertebrae, deep fossae (true pleurocoels or similar depressions) on the lateral surface: absent (0); present (1). (Nesbitt & Norell, 2006:79; Nesbitt, 2007:79)
84. Dorsal vertebrae, height of neural spines: less (0) or greater (1) than four times centrum height. (Nesbitt, 2003:6)
85. Dorsal vertebrae, spine tables (expanded apex) on neural spines: absent (0); present (1). (Juul, 1994:20; Bennett, 1996:57; Benton, 2004:35)
86. Dorsal vertebrae, deep fossa beneath region where posterior centroparapophyseal and paradiapophyseal laminae (or similar series of laminae) meet: absent (0); present (1). New character, originally described by Nesbitt (2007).
87. Dorsal vertebrae, hyosphene-hypantrum accessory articulations: absent (0); present (1). (Juul, 1994:66; Benton, 1999:18; Benton, 2004:36; Weinbaum & Hungerbuhler, 2007:20; Irmis *et al.*, 2007a:38)
88. Sacral vertebrae, number: two (0); three (1); four or more (2). (Gauthier, 1986; Benton & Clark, 1988; Novas, 1992:14; Juul, 1994:46; Bennett, 1996:56; Novas,

1996:24; Sereno, 1999:6; Benton, 1999:19; Nesbitt, 2003:8; Langer & Benton, 2006:42; Nesbitt & Norell, 2006:19; Nesbitt, 2007:19; Weinbaum & Hungerbuhler, 2007:22; Irmis *et al.*, 2007a:39). Ordered.

89. Sacral vertebrae, extent of fusion: absent or limited to centra (0); extensive, zygapophyses completely fused (1). New character, originally described by Nesbitt (2007).

90. Sacral vertebrae, form of centrum rims: prominent, individual sacrals well demarcated (0); reduced, individual sacrals poorly demarcated and entire structure cylindrical (1). New character, originally described by Nesbitt (2007).

91. Caudal vertebrae, midcaudal elements, accessory anterior projection on neural spine: absent (0); present (1). (Benton & Clark, 1988; Juul 1994,:34; Benton, 1999:20; Benton & Walker, 2002:48; Benton, 2004:37; Weinbaum & Hungerbuhler, 2007:21)

92. Cervical ribs, length and shape: long and slender (0); short and stout (1). (Gauthier, 1986; Benton & Clark, 1988; Juul, 1994:26; Benton, 1999:17; Benton, 2004:33; Irmis *et al.*, 2007a:37)

93. Sacral ribs, anteroposterior length: long, forming broad plate that expands laterally in dorsal view (0); short, forming a waisted projection in dorsal view (1). (Nesbitt, 2003:7; Weinbaum & Hungerbuhler, 2007:24)

94. Sacral ribs, first rib, location of articulation on ilium: midsection of iliac blade (0); anterior end of preacetabular process (=“anterior crest”) (1). (Nesbitt, 2003:15)

95. Sacral ribs, form and articulation of first rib with ilium: plate-like, contacts ilium in straight parasagittal articulation (0); distal end slightly dorsally expanded relative to shaft (1); entire rib dorsoventrally expanded and contacts ilium in C-shaped articulation (2). (Langer & Benton, 2006:44; Irmis *et al.*, 2007a:40)

96. Dorsal osteoderms: present, with a single osteoderm or osteoderm pair per vertebra (0); present, with multiple osteoderms per vertebra (1); absent (2). (Gauthier, 1986; Sereno & Arcucci, 1990:7,8; Sereno, 1991a:12,22; Parrish, 1993:5; Juul, 1994:14,15; Bennett, 1996:60,61; Benton, 1999:72; Nesbitt, 2003:1; Weinbaum & Hungerbuhler, 2007:33; Irmis, *et al.* 2007a:120)

97. Dorsal osteoderms, texture: smooth (0); sculptured (1). (Parrish, 1993:16; Benton, 1999:73; Benton & Walker, 2002:56; Benton, 2004:95; only character in Benton (1999) not used by Nesbitt & Norell (2006) and Nesbitt (2007).
98. Forelimb, length relative to hindlimb: greater than (0) or less than (1) 60%. (Gauthier, 1986; Sereno, 1991a:BB; Juul, 1994:45; Bennett, 1996:107; Novas, 1996:37; Benton, 1999:24; Benton, 2004:43; Irmis *et al.*, 2007a:45)
99. Scapula, depth of distal expansion: less (0) or greater (1) than 2.5 times narrowest region of shaft. New character, see Appendix S1 and Figure 4.
100. Scapula-coracoid, notch on dorsal margin between scapula and coracoid: absent or small (0); present and large (1). (Parrish, 1993:14; Benton, 1999:23; Benton, 2004:42; Irmis *et al.*, 2007a:43)
101. Coracoid, position of contribution to glenoid: at same level (0) or ventral (1) to scapular glenoid. New character, see Appendix S1 and Figure 4.
102. Coracoid, postglenoid process: absent (0); present and small (1); present and hypertrophied (2). (Irmis *et al.*, 2007a:44). Ordered.
103. Interclavicle: present (0); absent (1). (Gauthier, 1986; Benton & Clark, 1988; Sereno & Arcucci, 1990:9; Sereno, 1991a:23; Juul, 1994:44; Bennett, 1996:59; Benton, 1999:22; Benton, 2004:39; Irmis *et al.*, 2007a:42)
104. Clavicle: present (0); rudimentary or absent (1). (Gauthier, 1986; Sereno & Arcucci, 1990:10; Sereno, 1991a:24; Bennett, 1996:104; Benton, 1999:21; Benton & Walker, 2002:49; Benton, 2004:38; Irmis *et al.*, 2007a:41)
105. Humerus, width of proximal end: greater (0) or less (1) than twice midshaft width. New character, originally described by Nesbitt (2007).
106. Humerus, form of medial margin under inner tuberosity: confluent with shaft (0); strongly arched and angled approximately 45 degrees to shaft (1). (Sereno & Arcucci, 1990:11; Sereno, 1991a:4; Bennett, 1996:65)
107. Humerus, extent of deltopectoral crest: less than (0) or greater than (1) 35% of the length of the bone. (Gauthier, 1986; Novas, 1993:2; Juul, 1994:59; Novas, 1996:22; Benton, 1999:26; Sereno, 1999:8; Benton, 2004:45; Ezcurra, 2006:169; Langer & Benton, 2006:49; Irmis *et al.*, 2007a:47)



108. Humerus, form of deltopectoral crest: rounded (0); subrectangular, with angular corners (1). (Sereno & Arcucci, 1990:12; Sereno, 1991a:25; Novas, 1992:1; Juul, 1994:51; Bennett, 1996:108; Benton, 1999:25; Benton, 2004:44; Irmis *et al.*, 2007a:46)
109. Manual digits IV and V: elongated, 3+ and 3 phalanges, respectively (0); reduced, IV shorter than metacarpal III and with three or fewer phalanges and V with two or fewer phalanges (1). (Gauthier, 1986; Novas, 1992:8; Novas, 1993:15; Novas, 1996:23; Benton, 1999:30; Sereno, 1999:9; Benton, 2004:49; Irmis *et al.*, 2007a:58)
110. Acetabulum, antritrochanter for articulation with the femur: absent or restricted to ischium (0); present on both ilium and ischium, with an overall kidney shape (1). (Benton, 1999:35; Benton, 2004:54 Irmis *et al.*, 2007a:66; originally noted by Sereno *et al.*, 1993)
111. Ilium, ratio of blade length to depth above acetabulum: less than (0) or greater than (1) 4.5 (Benton & Clark, 1988; Weinbaum & Hungerbuhler, 2007:26).
112. Ilium, form of dorsal margin: straight or convex (0); concave and saddle-shaped (1). New character, see Appendix S1 and Figure 4.
113. Ilium, form of the ventral margin of the acetabular contribution: convex, acetabulum closed (0); straight or concave, acetabulum slightly perforate (1); straight or concave, acetabulum completely open (2). (Gauthier, 1986; Benton & Clark, 1988; Novas, 1992:9; Novas, 1993:16; Juul, 1994:60; Bennett, 1996:111; Novas, 1996:25; Benton, 1999:34; Benton & Walker, 2002:52; Nesbitt, 2003:13; Benton, 2004:53; Langer & Benton, 2006:69; Ezcurra, 2006:197; Weinbaum & Hungerbuhler, 2007:29; Irmis *et al.*, 2007a:65). Ordered.
114. Ilium, ridge extending from the dorsal margin of the acetabulum: absent (0); present and extending dorsally (1); present, extending anteriorly onto the preacetabular process (2). (Parrish, 1993:32; Juul, 1994:39; Benton, 1999:31; Nesbitt, 2003:12,14; Weinbaum & Hungerbuhler, 2007:28; Irmis *et al.*, 2007a:62)
115. Ilium, ridge extending from the dorsal margin of the acetabulum, orientation at its dorsal termination: oriented anteriorly only (0); oriented anteriorly and posteriorly (1). New character, see Appendix S1.
116. Ilium, length of preacetabular process: shorter (0) or equal or longer (1) than postacetabular process. (Nesbitt, 2007:83)

117. Ilium, form of preacetabular process: large and deep (0); small, shallow, and finger-like (1). New character, see Appendix S1 and Figure 4.
118. Ilium, preacetabular process, extent of anterior margin: terminates posterior (0) or anterior (1) to anterior margin of pubic peduncle. (Weinbaum & Hungerbuhler, 2007:27; Irmis *et al.*, 2007a:61)
119. Ilium, deep fossa on preacetabular process: absent (0); present (1). New character, originally described by Nesbitt (2007:p. 48).
120. Ilium, form of the ventral margin of the postacetabular process: unsculptured or excavated by a small furrow (0); excavated by a deep cavity (1); excavated by a brevis fossa (*sensu* Novas 1992, 1996) (2). (Gauthier, 1986; Novas, 1992:15; Novas, 1993:17; Juul, 1994:47; Novas, 1996:26; Benton, 1999:32; Sereno, 1999:10; Benton, 2004:51; Ezcurra, 2006:206; Nesbitt, 2007:32; Irmis *et al.*, 2007a:63)
121. Ilium, lamina of bone connecting preacetabular and postacetabular processes and rising dorsally above each: absent (0); present (1). New character, originally described by Nesbitt (2007).
122. Pubis, form: plate-like (0); rod-like and curved posteriorly (1); rod-like and straight (2). (Ezcurra, 2006:217)
123. Pubis, length: shorter than ischium (0); longer than ischium but shorter than three times acetabulum diameter (1); longer than three times acetabulum diameter (2). (Gauthier, 1986; Benton & Clark, 1988; Sereno, 1991a:13; Novas, 1992:6; Novas, 1993:6; Juul, 1994:32,35; Bennett, 1996:76; Novas, 1996:13; Benton, 1999:36,37; Benton & Walker, 2002:53,54; Nesbitt, 2003:18); Benton, 2004:55; Ezcurra, 2006:212; Weinbaum & Hungerbuhler, 2007:31; Irmis *et al.*, 2007a:68). Ordered.
124. Pubis, form of posterior portion of acetabular margin: continuous with anterior margin and forms articular surface for femur (0); recessed from anterior margin and forms nonarticular surface (1). (Sereno & Arcucci, 1990:13; Sereno, 1991a:14; Bennett, 1996:77; Benton, 1999:38; Benton & Walker, 2002:55; Benton, 2004:56; Irmis *et al.*, 2007a:70)
125. Pubis, ridge on the lateral surface: absent (0); present (1). New character, originally described by Nesbitt (2007).

126. Pubis, extent of medioventral lamina (obturator flange): extensive, measuring approximately entire length of bone (0); reduced, measuring approximately 50-70% length of bone (1); very reduced, measuring less than 50% length of bone (2). New character, see Appendix S1 and Figure 4. Ordered.
127. Pubis, form of distal end: unexpanded or slightly expanded (0); expanded into small pubic boot (1); expanded into large pubic boot with a posterior projection (2); expanded into large pubic boot that is greater than 1/3 length of the shaft (3). (Juul, 1994:68; Benton, 1999:39; Nesbitt, 2003:10; Weinbaum & Hungerbuhler, 2007:32; Irmis *et al.*, 2007a:72)
128. Ischium, anteroposterior length of shaft: greater or equal (0) or less than (1) length of pubis. New character, see Appendix S1.
129. Ischium, form of medioventral lamina (obturator process): well-developed, plate-like, and dorsoventrally deep (0); reduced, restricted to proximal third of bone, and dorsoventrally shallow (1). (Novas, 1992:10; Novas, 1993:18; Bennett, 1996:74 in part; Novas, 1996:27; Ezcurra, 2006:224; Irmis *et al.*, 2007a:74)
130. Ischium, form of distal end: plate-like (0); rod-like with no distal expansion (1); expanded into ischial boot (2); expanded into large ischial boot with prominent posterior projection (3). (modified from Nesbitt, 2003:9)
131. Femur, shape of head in lateral view: rounded (0); hook-shaped (1). (Irmis *et al.*, 2007a:80)
132. Femur, form of head: confluent with shaft (0); slightly offset from shaft by a ventral notch (1); distinctly offset from shaft, with an angular mesiodistal corner (2). (Benton & Clark, 1988; Novas, 1992:11; Novas, 1993:19; Juul, 1994:61; Benton, 1999:41; Benton, 2004:60; Weinbaum & Hungerbuhler, 2007:34; Irmis *et al.*, 2007a:81)
133. Femur, angle of head relative to shaft: less than 45 degrees (0); greater than 45 degrees (1). (Ezcurra, 2006:231)
134. Femur, emargination on the anterolateral side of the femoral head: absent (0); present (1). (Irmis *et al.*, 2007a:82)
135. Femur, shape of proximal articular surface: oval or wedge-shaped (0); subtriangular, due to straight anterior and posterior faces and tapering lateral corner (1). (Ezcurra, 2006:232; Irmis *et al.*, 2007a:79)

136. Femur, extent of smooth articular surface for acetabulum: restricted to the proximal portion of the head (0); extends ventrally under head (1). (Benton, 1999:42; Benton, 2004:61; Irmis *et al.*, 2007a:86; originally described by Sereno & Arcucci, 1994)
137. Femur, transverse groove on proximal articular surface: absent (0); present and shallow (1); present and deep (2). (Ezcurra, 2006:233)
138. Femur, medial margin in proximal view, tubera for femoral head ligaments: two well-defined medial tubera (0); single well-defined medial tuber (1); tubera absent, medial margin of femur gently convex (2). (Novas, 1993:20; Novas, 1996:28; Sereno, 1999:12; Ezcurra, 2006:234). Ordered.
139. Femur, form of anteromedial tuber on medial margin in proximal view: small and conical (0); large and hook-like (1). New character, originally described by Nesbitt (2007).
140. Femur, tuber on lateral margin in proximal view: present (0); absent (1). (Irmis *et al.*, 2007a:85)
141. Femur, fossa trochanterica (groove inset on posterolateral corner of proximal surface): absent or shallow (0); present and distinct (1). (Novas, 1993:3; Novas, 1996:7; Benton, 1999:43; Benton, 2004:63; Ezcurra, 2006:235; Irmis *et al.*, 2007a:83)
142. Femur, cranial (=lesser) trochanter: absent (0); present (1). (Gauthier, 1986; Benton & Clark, 1988; Novas, 1992:3; Juul, 1994:42; Bennett, 1996:80; Novas, 1996:8, 29; Benton, 1999:45; Benton, 2004:64; Ezcurra, 2006:238),
143. Femur, trochanteric shelf: absent (0); present (1). (Novas, 1992:2; Novas, 1993:33; Novas, 1996:9; Ezcurra, 2006:239)
144. Femur, greater trochanter, form of dorsal margin: rounded (0); angular, approaching 90 degrees (1). (Sereno, 1999:11; Ezcurra, 2006:237; originally described by Sereno *et al.*, 1993)
145. Femur, fourth trochanter: present (0); absent (1). (Sereno, 1991a:35; Juul, 1994:4; Bennett, 1996:81; Novas, 1996:35; Benton, 1999:44; Irmis *et al.*, 2007a:88)
146. Femur, fibular condyle, size compared to tibial condyle: smaller (0); larger (1). (Irmis *et al.*, 2007a:91)
147. Femur, groove between lateral condyle and fibular condyle: absent (0); present (1). New character, originally described by Nesbitt (2007).

148. Tibia, length: less than or equal (0) or greater (1) than length of femur. (Gauthier, 1986; Benton & Clark, 1988; Sereno & Arcucci, 1990:16; Sereno, 1991a:27; Juul, 1994:48; Bennett, 1996:113; Benton, 1999:40; Benton, 2004:59; Ezcurra, 2006:230; Irmis *et al.*, 2007a:78)
149. Tibia, cnemial crest: absent or very low (0); present and projecting anteriorly (1); present and projecting anterolaterally (2). (Gauthier, 1986; Benton & Clark, 1988; Novas, 1992:4; Novas, 1993:4; Juul, 1994:43; Bennett, 1996:82; Novas, 1996:10; Benton, 1999:46; Sereno, 1999:13; Benton, 2004:65; Ezcurra, 2006:246; Irmis *et al.*, 2007a:93)
150. Tibia, fibular crest: absent (0); present (1). New character, originally described by Nesbitt (2007).
151. Tibia, form of lateral surface of the distal end: flat (0); excavated by a groove (1). (Novas, 1992:5; Novas, 1993:5; Novas, 1996:12)
152. Tibia, median crest on posterior surface of distal end: absent (0); present (1). (Irmis *et al.*, 2007a:95)
153. Tibia, extent of posterior process for articulation with astragalus: at same level as distal anterior surface (0); projecting ventrally (1). (Novas, 1989:8; Novas, 1992:12; Juul, 1994:62; Novas, 1996:30; Benton, 1999:48; Benton, 2004:67; Ezcurra, 2006:252; Irmis *et al.*, 2007a:96),
154. Tibia, form of distal end: unexpanded and rounded (0); transversely expanded and subrectangular (1). (Gauthier, 1986; Benton, 1999:47; Benton, 2004:66; Irmis *et al.*, 2007a:94)
155. Tibia, form of posteromedial corner in distal view: smoothly rounded (0); squared off, forming a right or obtuse angle, due to presence of posterolateral flange (1). (Novas, 1993:21; Novas, 1996:11)
156. Fibula, width of distal end compared to proximal end: slightly narrower (0); equal to or greater (1); much narrower, fibula tapering distally, with distal end width less than 50% proximal end width (2). (Gauthier, 1986; Benton & Clark, 1988; Sereno & Arcucci, 1990:18; Sereno, 1991a:6; Juul, 1994:49; Bennett, 1996:84,114; Benton, 1999:49; Benton, 2004:69; Irmis *et al.*, 2007a:99)
157. Fibula, form of anterior trochanter: absent or low crest (0); large rugosity (1). (Sereno & Arcucci, 1990:17; Sereno, 1991a:5; Bennett, 1996:83; Benton, 2004:68)

158. Astragalus and calcaneum, fusion: absent (0); coossified together with other crurotarsal elements (1); coossified and other crurotarsal elements free (2). (Irmis *et al.*, 2007a:104)
159. Astragalus and calcaneum, form of articulation: flat (0); concavoconvex, with concavity on calcaneum (1); concavoconvex, with concavity on astragalus (2). (Sereno & Arcucci, 1990:22; Sereno, 1991a:19; Parrish, 1993:13; Juul, 1994:13; Bennett, 1996:88; Nesbitt, 2003:21)
160. Astragalus, anterolateral process, orientation of contact with calcaneum: ventral, astragalus overlaps calcaneum (0); lateral, astragalus abuts calcaneum (1). (Sereno, 1999:15; originally described by Sereno *et al.*, 1993)
161. Astragalus, size of ventral astragalocalcaneal articular facet: smaller (0) or equal or greater (1) than dorsal facet. (Sereno & Arcucci, 1990:23; Sereno, 1991a:11; Bennett, 1996:89; Benton, 1999:50; Benton, 2004:70)
162. Astragalus, anterior ascending process: absent (0); present but small and anterolaterally located (1); present and pyramid-shaped, anteriorly located, and articulating with a flat descending process of the tibia (2). (Gauthier, 1986; Benton & Clark, 1988; Novas, 1989:3,9; Novas, 1992:7; Novas, 1993:7,22; Bennett, 1996:117; Novas, 1996:14; Benton, 1999:52; Sereno, 1999:14; Benton, 2004:73; Ezcurra, 2006:265,268; Irmis *et al.*, 2007a:102). Ordered.
163. Astragalus, posterior ascending process: absent (0); present (1). (Irmis *et al.*, 2007a:103)
164. Astragalus, form of articular facet for tibia: simple concave structure (0); flexed (1). (Sereno & Arcucci, 1990:20; Sereno, 1991a:7; Parrish, 1993:26; Juul, 1994:28; Bennett, 1996:85; Benton, 1999:51; Benton, 2004:72; Irmis *et al.*, 2007a:100)
165. Astragalus, extent of articular facet for fibula: occupies more (0) or less (1) than 20% of the transverse width of the bone. (Langer & Benton, 2006:94)
166. Astragalus, form of anteromedial corner: squared off or rounded (0); prominent and offset, forms acute angle (1). (Novas, 1989:2; Juul, 1994:55; Novas, 1996:1; Benton, 1999:54; Benton, 2004:75; Irmis *et al.*, 2007a:105)

167. Astragalus, form of posterior margin: excavated, with concave non-articular surface (0); straight or slightly convex (1). New character, originally described by Langer & Benton (2006).
168. Astragalus, groove on posterior surface: present (0); absent (1). (Sereno & Arcucci, 1990:21; Sereno, 1991a:28; Bennett, 1996:119; Benton, 1999:53; Benton, 2004:74)
169. Calcaneum, transverse width of distal articular surface: greater than (0) or less than (1) 35% that of astragalus. (Gauthier, 1986; Novas, 1989:4; Juul, 1994:56; Bennett, 1996:116; Novas, 1996:2; Benton, 1999:56; Benton, 2004:77; Irmis *et al.*, 2007a:106)
170. Calcaneum, form of fibular facet: gently convex (0); hemicylindrical “pulley” (1); concave or flat (2). (Novas, 1989:10; Sereno & Arcucci, 1990:25; Sereno, 1991a:8; Novas, 1992:12; Parrish, 1993:3; Juul, 1994:27,63; Bennett, 1996:91; Novas, 1996:31; Benton, 1999:55,63; Benton, 2004:76,84; Ezcurra, 2006:273; Irmis *et al.*, 2007a:113)
171. Calcaneum, tuber: present and large (0); rudimentary or absent (1). (Gauthier, 1986; Novas, 1989:7; Sereno & Arcucci, 1990:27; Sereno, 1991a:29; Juul, 1994:52; Bennett, 1996:120; Benton, 1999:57; Benton, 2004:78; Irmis *et al.*, 2007a:107)
172. Calcaneum, tuber, proportions: deeper than wide (0); wider than deep (1). (Sereno & Arcucci, 1990:30; Sereno, 1991a:9; Parrish, 1993:4; Juul, 1994:29; Benton, 1999:59; Benton, 2004:80; Irmis *et al.*, 2007a:109)
173. Calcaneum, tuber, form of distal end: unexpanded (0); flared (1). (Sereno & Arcucci, 1990:28; Sereno, 1991a:10; Parrish, 1993:10; Juul, 1994:30; Benton, 1999:60; Benton, 2004:81; Irmis *et al.*, 2007a:110)
174. Calcaneum, tuber, dorsoventrally aligned median depression on distal end: absent (0); present (1). (Parrish, 1993:21; Juul, 1994:72; Benton, 1999:61; Benton, 2004:82; Irmis *et al.*, 2007a:111)
175. Distal tarsal 4, transverse width: greater (0) or subequal (1) to width of distal tarsal 3. (Sereno, 1991a:30; Juul, 1994:53; Bennett, 1996:121; Benton, 1999:64; Benton, 2004:88; Irmis *et al.*, 2007a:114)
176. Distal tarsal 4, form in proximal view: ornamented by raised ridge (0); flat or convex (1). (Novas, 1993:23; Novas, 1996:32; Ezcurra, 2006:276)

177. Distal tarsal 4, size of articular surface for metatarsal V: occupies nearly entire lateral surface (0); limited to half or less lateral surface (1). (Sereno, 1991a:EE; Novas, 1996:3; Benton, 1999:65; Benton, 2004:89; Irmis *et al.*, 2007a:115),
178. Metatarsus, form: broad weight-bearing structure, with metatarsals II-IV less than four times as long as broad (0); elongated, with metatarsals II-IV greater than four times as broad (1). (Gauthier, 1986)
179. Metatarsus, configuration: metatarsals divergent from ankle, shafts of individual elements not in close contact (0); compact, with metatarsals I-IV tightly bunched (1). (Gauthier, 1986; Benton & Clark, 1988; Sereno & Arcucci, 1990:32; Sereno, 1991a:31; Juul, 1994:50; Bennett, 1996:124; Benton, 1999:66; Benton, 2004:90; Irmis *et al.*, 2007a:117)
180. Metatarsal I, length: less than (0) or greater than (1) 85% length of metatarsal III. (Sereno, 1991a:36; Novas, 1996:36; Benton, 1999:68; Benton, 2004:92; Irmis *et al.*, 2007a:119)
181. Metatarsal I, midshaft diameter: equal to or greater (0) or less than (1) midshaft diameters of metatarsals II-IV. (Sereno, 1991a:GG; Juul, 1994:58; Novas, 1996:5; Benton, 1999:67; Benton, 2004:91; Irmis *et al.*, 2007a:117)
182. Metatarsal II, length: shorter (0) or equal to or longer (1) than metatarsal IV. New character, originally described by Langer & Benton (2006:p. 317).
183. Metatarsal III, length: less than (0) or greater than (1) 40% length of tibia. (Gauthier, 1986; Benton & Clark, 1988; Sereno & Arcucci, 1990:33; Sereno, 1991a:32; Juul, 1994:54; Bennett, 1996:125; Benton, 1999:69; Benton, 2004:93; Irmis *et al.*, 2007a:120)
184. Metatarsal IV, form of distal end: sigmoidally curved lateral to shaft (0); straight and in line with shaft (1). (Novas, 1996:15; Sereno, 1999:18; Ezcurra, 2006:282; originally described by Sereno *et al.*, 1993)
185. Metatarsal V, midshaft diameter: equal to or greater (0) or less (1) than midshaft diameter of metatarsals II-IV. (Sereno, 1991a:GG; Parrish, 1993:35; Juul, 1994:58; Novas, 1996:5; Benton, 1999:67; Benton, 2004:91; Irmis *et al.*, 2007a:118)
186. Metatarsal V, form of articular surface for distal tarsal 4: angled relative to shaft, resulting in a laterally divergent metatarsal V with a hooked proximal end (0); parallel to shaft, resulting in an unhooked metatarsal V that is parallel to or deflected behind the



remaining metatarsals (1). (Sereno, 1991a:FF; Juul, 1994:57; Novas, 1996:4; Benton, 1999:70; Benton, 2004:94; Irmis *et al.*, 2007a:123)

187. Pedal unguals, shape: mediolaterally compressed (0); dorsoventrally compressed (1).

New character, originally noted by Nesbitt (2007).

APPENDIX 2: DATA MATRIX

**OUTGROUPS**

*Erythrosuchus*

00010 00000 00021 00101 01000 00010 00000 00100 01000 0?000 00000 00000 0?00?  
000?0 01001 00000 00000 01000 0?001 ??000 00??0 011?0 0000? 00000 00000 00000  
00000 0?000 ?00?? 00000 0?00? 00001 ?0000 01000 00000 0000? 01000 0?

*Euparkeria*

00000 10010 00021 00000 01000 00110 01000 00000 00000 00000 00000 00000 00000  
00000 00?01 00000 00001 00000 00000 00000 00000 000?0 0000? 00000 00000 00000  
0000? 0?000 00010 00000 ?000? ?0000 00000 00000 00000 00000 00000 00

**PROTEROCHAMPSIDAE**

10000 00000 00000 10000 00100 00000 00000 20000 00000 00000 10000 00010 0???0  
????? 00000 00000 00000 00000 00000 10000 00000 000?0 0000? 00000 00000 00000  
0000? 0???? 00000 0?000 ??00? 00000 00000 00000 00000 ?0000 00100 00

**INGROUP EXEMPLAR TAXA**

AETOSAURIA

*Aetosaurus*

00001 21120 00010 00110 11000 00000 00000 00110 01000 00100 0000? 00?00 0?0?  
21??? 10010 ????0 0???? 0?0?0 ??0?1 01011 10000 100?1 0000? 00100 0211? 10001  
00000 00000 00000 00000 ?000? 11010 ?0010 00?01 01100 ?0000 01000 00

*Desmotosuchus*

00001 21110 00010 01000 10000 00000 00000 00110 00000 00100 20000 00000 00200  
21??1 10010 10000 00001 0?000 01001 01010 10000 100?1 0000? 00100 02110 11001  
00000 00000 00010 01000 10010 11010 00010 00001 0110? ?0000 01?00 0?

*Stagonolepis*

00001 21120 00010 00000 10000 00000 00000 00110 00000 00100 20000 00?00 00?00  
21111 10010 10000 00001 00000 01001 01010 10000 100?0 0000? 00000 02110 11001  
00000 0?000 00000 00000 1?01? 11010 ?0010 00001 01100 ?0000 01000 00

CROCODYLOMORPHA

*Protosuchus*

00000 20000 00021 00000 11100 00000 00001 22011 01001 01200 ?1100 00?10 00200  
21??1 00000 00000 00000 00000 ?100? 01011 02??0 10000 1010? 00100 02210 21003  
0000? 0???? ?0000 0?000 ?000? 0?010 ?0010 00?01 0111? ?0011 01101 00

*Sphenosuchus*

00000 20111 00021 00000 10100 01100 01011 22011 01001 11200 ?1100 00110 00200  
21111 01000 00?00 0000? ????? ?1??? 01010 02000 000?? ?????? ?????? ??????  
????? ?????? ?????? ??00 10000 ?????? ?????? ?????? ?????? ?????? 0?10? ?0

*Terrestrisuchus*

00000 10110 0????? ???00 11100 00110 01000 2?000 01001 0?200 ?1100 00100 0?????  
?1??1 01000 ?1000 00000 00000 11002 01010 120?0 00001 1010? 00100 01210 20001  
00000 00?0 00000 00100 00000 00010 10010 00001 01110 00011 01101 00

ORNITHISCHIA

*Heterodontosaurus*

00101 10001 01011 0000? 10000 00010 00001 22??1 00000 01000 00000 ???10 0??1?  
????? 01010 ?0120 10000 0?200 00??2 2?11? 00110 01111 1020? 10102 02200 20011  
0210? ?????1 ?10?0 0?120 ?0?1? 2010? ?????? ?????? 1??0 ?1110 1110? 10

*Lesothosaurus*

00101 10001 01011 0000? 11000 00010 00001 22101 00000 00000 00000 10?10 00?10  
11??0 00000 11120 10000 00200 00101 2?110 ??110 01111 1020? 10102 02200 20011  
01100 112?1 11010 01120 10111 2000? 2??1 ?????12 1???? ?010 1110? ?0

*Psittacosaurus*

0?10? 20001 00001 ?100? ??000 00010 00001 22111 0?000 00000 00?00 1??10 0?????  
????? 00010 10000 10000 ?0200 00102 2?100 00110 01110 1020? 10102 02200 20011  
0210? 1??1 ?1010 0?120 ??11? 00001 ?2001 00?02 1??0 11010 11101 10

ORNITHOSUCHIDAE

*Ornithosuchus*

00000 10101 00000 00100 11?00 00101 10000 00100 00001 00000 20000 00000 0????0  
????? 00101 10?00 00000 00100 1?001 01000 11000 100?0 0010? 00000 01210 20002  
00000 01000 01000 ?01? ?001? ?102? ?????? ??????1 01100 ?0000 0?100 00

*Riojasuchus*

01001 10100 00000 00100 11001 00101 10000 00100 00000 00000 20000 00?00 00?00  
1???? 01100 ?0000 00000 00100 ???0? 0?0?0 11??0 100?0 ?010? 00000 01210 20?0?  
0000? 0?0?? 01000 0?010 1001? 11020 ?0010 00001 01100 ?0000 10100 00

PHYTOSAURIA

*Mystriosuchus*

10000 20000 00110 00000 00000 00000 00000 00000 00000 01000 00000 00?00 00100  
00?00 01100 10000 00001 00??? ?1??? 01001 01000 10000 0000? 00100 00000 00000  
00000 00000 00000 000?? ?????? ?0?? ?????? ?????? ?????? ?????? ?????? ??

*Paleorhinus*

10000 20000 00110 00000 10000 00000 00000 00100 00000 00000 00000 00?00 00100  
00?00 01110 00000 00001 00000 ?10?0 01001 00000 10000 0100? 00000 00000 00000  
0000? 0???? ?0000 0?000 1000? 11010 ?0010 00?01 01100 ?0000 00100 00

*Rutiodon*

10000 20000 00110 00000 10000 00000 00000 00100 00000 00000 00000 00??? ?????  
????? 011?0 ?0000 00001 00000 01000 01001 01000 10000 0000? 00000 00000 00000  
0000? 0???? ?0000 0?000 ?000? ??010 10010 00001 0110? ?????? ??1?? ??

PTEROSAURIA

*Dimorphodon*

10001 000?0 00000 10010 00000 0?0?0 ??0?0 0???? 00000 ?????? ?0??? ?????? ?????  
????? 0010? ?1100 00000 0?200 00?00 2?000 00110 00000 1100? 00100 00000 00000  
00000 001?0 00001 0?101 00000 2010? ??0?? ?????? 1???1 00111 01100 00

*Eudimorphodon*

10001 00010 00000 10010 00000 0?0?0 000?0 ????? 00000 ?????? ?0??? ?????? ?????  
????? 01??? ?0100 0??00 00200 000?? 2?000 00110 00100 1100? 10100 00000 00000  
0000? 0???? 0?001 0?101 00?0? 2010? ??0?? ?????? 1???1 ?011? 01?00 00

*Pteranodon*

1000? ?000? 00?0? ?1010 00010 00010 100?0 02??0 00000 0?00? 02000 1100? ??0??  
?0??? 20100 11100 00000 00210 00000 2?000 00110 01100 1000? 10100 00000 00000  
0000? 0???? 00001 0?101 00000 2010? ??0?? ??1?? 1???1 10111 01010 10

SAURISCHIA

*Coelophysis*

00000 10001 00010 101(0,1)0 11000 00110 10001 22101 0(0,1)000 00000 00?00 10?10  
00?10 1???? 00000 ?1120 10101 11211 00002 2?100 01100 01111 0020? 00102 01200  
21011 02100 112?1 11110 01121 10111 2010? ?2001 ?11?? 1???? 11010 11101 10

*Herrerasaurus*

00000 10101 00011 00000 01000 00110 00001 20101 00000 00000 10000 10010 00210  
11??? 00001 ?1120 10001 11100 0?002 2?10? ??110 01111 0020? 10000 02200 22111  
02100 102?1 11110 00121 10111 00001 ?2001 11112 1???1 11010 11101 10

*Plateosaurus*

00001 10001 00010 10010 11001 00110 00001 22100 00000 00000 00000 10010 00210  
11??1 01000 11100 10000 11100 00002 2?110 01110 01110 0020? 00002 02200 21002  
02100 11(1,2)?1 11010 00021 10111 20001 ?2001 11112 1???1 11010 00101 10

**AVEMETATARSALIAN GENERIC TAXA**

*Dromomeron*

???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ????  
???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ???? 1001 0001?  
00000 11111 ??101 0??20 ??110 01010 21??? ????? ????? ??

*Eucoelophysis*

???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ????  
???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ?2?00 20?? 01001 ?22?1  
11010 0??1? ????? ????? ????? ????? ????? ????? ???? ??

*Lagerpeton*

???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ????  
???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ????  
001?1 00000 1?10? 01010 20200 ?1100 10112 1???1 01110 10111 10

*Lewisuchus*

???? ?0? ???? ???? ???? 11?0? ????? ????? ????? 0?000 ?0?00 001?0 ????0 00?10 ?????  
00??? ?1120 00000 0???? ?0??? 2??10 00?0 000?? ????? ????? ????? ???? 0001? ?????  
????? ?0? ???? ????? ????? ????? ????? ????? ???? ?0

*Marasuchus*

?0??? ????? 0???? ???? ?1?0? ????? ????? ????? ????? ????? ????? ???? 0021? 1????  
????? ?1120 00000 00000 0?001 2?100 00110 001?1 0100? 00000 01200 21001 00000  
10(1,2)?1 11100 0111? 10011 20000 ?1000 10110 10001 01110 10111 1?

*Pseudolagosuchus*

???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ????  
???? ???? ???? ?0?? 0???? 2???? ????? ????? ???? ???? ?1?00 20??? 00000 021?1  
11110 ?11? 10011 20001 ?2000 10?10 1000? ????? ????? ??

*Sacisaurus*

?0??? ????? 0???? ???? 1100? ????? ????? ????? ???? ???? ???? ?0??? ????? ?????  
100?? ????? ???? 0???? 0???? 2??10 ????? ????? ?100? 00000 ?2?00 2??1? 01001  
12(1,2)?1 ?1010 0??21 10111 ????? ?2??? ????? ????? ????? ????? ??

*Scleromochlus*

10100 2?010 0000? 000?0 11000 0001? ?0000 0?0?0 01000 ????0 ?2?00 ????? ????1?  
????? 01??? ????0 ???? ?20? 00?0 2?100 ?1110 000?0 ?000? ?1?0 001?? ?0001  
0000? 0???? ?00?1 ?1100 ?01? 0000? ?0?00 ???? ????1 ?0111 01110 00

*Silesaurus*

00?00 1???? 0?021 00000 01000 00?1? ?0000 ????? 0?0?? ????? ?0000 ????0 00210  
1???0 10000 11120 00000 10100 00102 2?010 01110 000?1 0100? 00002 01200 20011  
01001 122?1 11110 01021 10110 00001 ?2000 11112 1???? ?010 11101 10

**CRUROTARSAN GENERIC TAXA**

*Arganasuchus*

???? ???? ???? ?110 ?1?0? ????? ????? ????? ????? ????? ????? ????? ????  
000?? ????? ?0?? ????? ????? ????? ????? ????? ????? ????? ????? ????1? ????? 00000 00000  
01000 00000 ????? 11?? ????? ????? ????? ????? ????? ????? ??

*Arizonasaurus*

00001 10100 ????? ?11 01000 0011? ?0000 00100 0?000 00?00 ?0?00 011?0 00010  
00000 0000? 01011 01010 11111 ?112 2?1? 0000? ????? 10121 01000 01210 21012  
00000 01000 00000 00??? ?0??? ????? ????? ????? ????? ????? ????? ??

*Batrachotomus*

00011 10101 00020 ?0011 11?01 11000 00010 10101 01011 01010 ?0000 0??10 00200  
10001 01000 00000 00001 11100 0?012 ?1?11 11?00 100?0 10011 00000 02110 21002  
00000 01000 00000 ????? 00000 1101? ????? ????1 0110? ????0? ?0?00 00

*Bromsgroveia*

???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ????  
???? ???? ???? 1?111 ?112 ????? ????? ????0 1121 01011 0???? ????1? ?00?? ?????  
?000? ????? ???? ???? ???? ???? ???? ???? ???? ???? ???? ??

*Effigia*

00100 10100 01220 11010 11010 00110 00000 20110 10000 00000 ?2111 010?1 10211  
?1?0 20111 11010 00100 11211 ?11? 2?100 11?01 0???1 00120 10111 11211 23112  
12101 01011 0000? 01?01 10000 00010 10011 00001 ????0 00010 11101 01

*Erpetosuchus*

?0000 00111 00011 00000 11100 00100 0?000 22111 00001 11100 01100 00?00 ????0  
????? 00?00 ?0?00 00001 ????? ????? 01?11 110?0 000?? ????? ????? ????? ????? ?????  
????? ????? ???? ???? ???? ???? ???? ???? ???? ???? ???? ??

*Fasolasuchus*

00??0 1???? ?0010 00011 11?00 00??? ????? ????? ????? ????? ????? ????? ?????  
000?? 00000 00001 11?? ?0??? 10??? ????? ????? ????? ????? ????1? 2???? 01100 00??0  
01000 010?? ????? 11010 10010 00001 0111? ????? ????? ??

*Gracilisuchus*

00100 21121 00021 00000 11?00 00101 00000 01100 01001 10100 21100 00000 0??00  
????? 00000 ?0100 00001 00000 0100? 11001 00?0 100?0 0000? 00000 021?0 10001  
00000 0?000 00010 ?0?01 10000 00010 10010 00001 01110 ?1110 00111 00

*Lotosaurus*

00011 10010 01210 11000 11?10 00010 00010 ?0101 00000 0?000 20000 ????10 00??0  
1???? 21100 00000 10010 11110 ?1110 2?0?? ?0000 00001 00121 00010 1???? ?????  
00000 011?0 00000 01000 10000 00010 1001? 0?001 0110? ????? ????? ??

*Poposaurus*

??0?? ????? ?0?? ???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ????  
???? ?0000 01100 11211 0?111 2?11? ???0 000?0 10121 00111 02210 22012 02001  
01000 00000 0000? 1?000 ?010 10011 00001 0111? ????? ????? ??

*Postosuchus*

00010 10111 10011 00000 11000 11101 ?0100 00001 00111 01101 30?00 00100 01200  
10?0 0100? 00000 00000 11000 11001 ?010 11?0 10000 10010 00000 02210 22002  
00000 01000 00000 01000 10000 10010 10011 00001 0111? ?0000 0?100 00

*Prestosuchus*

?1011 10111 00010 00001 11?01 11000 00000 10101 01011 00010 10?00 ???10 0?0?  
?0?? 00000 0???? ?????1 11100 1?001 11?01 11000 100?0 1002? 00000 02?0 21002  
00000 01000 00000 00000 00000 11010 10010 00001 01100 00000 00100 00

*Qianosuchus*

00001 10110 00000 10111 11000 ?0?0 000?0 0???? 01000 ?00?0 20?0? ????? ?????  
???? 00?00 ?1100 ?00? ?00? 00?? 00?11 0?000 000?? 101?? 00100 010?? 10002  
0000? 0???? ????? ?0?? ?00? ?01? ?001? 0?001 0110? ?0?0 0?000 00

*Rauisuchus*

??0?? 1??1? ???10 00??? 1?00 00?? ????? 0??? 0?1?1 0?000 ????? 0??? ????? ?????  
??00 00000 00001 01000 1?001 ?1?1? 1???? ?????0 10011 00000 01?10 20?? ?????  
???? ????? ?000 ?0000 11010 10010 000?? ????? ????? ????? ??

*Revuletosaurus*

?000? ?0000 0?021 00101 11?00 00?01 10000 00?0 0?000 ?0200 ?0?? ????? ?????  
???? 00?? ?0000 ?0001 ?0?? ????? 01?? 00?0 100?0 0000? 00000 0???? ?????  
0000? 0???? ?0000 ????? ????? ?010 ?0010 00001 0110? ????? ????? ??

*Saurosuchus*

01000 10111 10011 00000 11100 00100 01000 00101 00011 00010 10000 00000 00200  
10000 000?? ?0000 00001 01000 01001 10?00 ????? ?????0 10011 00000 02?10 21002  
00000 0???? ?00?0 0?00? 1?00? 11010 10010 00001 01110 00000 01000 00

*Shuvosaurus*

00100 10100 0121? 1100? 10110 00111 00000 20110 10000 00000 22111 01011 10211  
11?0 20111 11100 0010? ??211 ?111 2?00 01??1 000?1 00120 10111 11211 23112  
12101 01011 00001 01001 10000 ?0010 10011 00001 0110? 00010 11101 01

*Sillosuchus*

???? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ?????  
???? ?1001 ?1100 1?211 0?11? 2???? ????? ?????0 1?120 ?0?10 ?1210 2101? 0000?  
0???? 000?1 0???? ????? ????? ????? ????? ????? ????? ????? ????? ??

*Stagonosuchus*

???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ????  
???? 00100 00001 01000 ??001 ????? ?0??0 100?0 1001? 00000 02010 21003 ?????  
???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ???? ??

*Teratosaurus*

?0010 20111 00010 00000 11100 101?1 101?? ????? ?1?1 01001 30000 001?? ?????  
???? 000?? ?0??? 000?? ????? ????01 ?1??? ????? ????0 10011 00000 0???? ????? ?????  
???? ????? ????? ????? ????? ????? ????? ????? ????? ????? ??

*Ticinosuchus*

0???? ????? ????? ????11 1100? ????? ????? ????? ????? ????? ????? ????? ?????  
00??? ?0100 00001 000?? 11??? 1000? 00000 0000? 1000? 00000 010?0 200?2 0000?  
0???? ????00 0?000 ?0?? 11010 ?0010 00?01 01110 ?0000 0110? 00

*Tikisuchus*

000?? ????1? 1???? ????00 11?0? ????? ?0?0 ????? 0?0?? ?10?? 20??? ????? ?120? ?0???  
01?00 0???? ????? ????? ????? ????? ????? ????? ????? ???? ?1?10 10??? ????? ?????  
???? ????? ???? ?010 ?00?? 0??01 0111? ????? ????? ??

*Yarasuchus*

0???? ????? 1??2? ????1? 01?0? ????? ????? ????? 0?0?? ????0 ?0?1? ????? ????? ?????  
???? ?1?? 00000 ?1000 0?0?1 ?101? 10?0 011?0 1000? 00000 01?10 20??? 0000?  
0???? ????00 ????00 1000? ????? ????? ????? ????? ????? ??



## APPENDIX 3: SCORING SOURCES

### OUTGROUPS

- \**Erythrosuchus*: BMNH R533, 2790-95, 3592, additional BMNH collection; scores primarily based on Gower (1996, 1997, 2003), as well as Gower & Sennikov 1996
- \**Euparkeria*: Ewer 1965; Gower & Sennikov 1996; Gower & Weber 1998
- \*Proterochampsidae: scorings primarily based on *Chanaresuchus* (MLP 1964-XI-14-12 cast skull; Romer 1971c, 1972c), but also on *Gualosuchus* (Romer 1971c), *Proterochampsia* (Sill 1967), and *Tropidosuchus* (Arcucci 1990) for those regions missing or uncertain in *Chanaresuchus*

### INGROUP GENERA:

#### **Avemotarsalia**

- \**Dromomeron*: Irmis *et al.* 2007a
- \**Eucoelophysis*: Sullivan & Lucas 1999; Ezcurra 2006; Nesbitt *et al.* 2007
- \**Lagerpeton*: PVL 4619; Romer 1971b, 1972e, Sereno & Arcucci 1990, 1993; Sereno 1991a
- \**Lewisuchus*: Romer 1972b
- \**Marasuchus*: PVL 3870, 3871, 3872, 4672; Romer 1971b, 1972e; Bonaparte 1975; Novas 1989, 1996; Sereno & Arcucci 1990, 1994; Sereno 1991a
- \**Pseudolagosuchus*: PVL 4629; Arcucci 1987; Novas 1989, 1996
- \**Sacisaurus*: MCN PV10009-10011, PV10013-10016, PV10018-10020, PV10023-10025, PV10028-10029, PV10032-10033, PV10041-10044, PV10048-10051, PV10061, PV10063, PV10075, PV10090, PV10097, PV10100; Ferigolo & Langer 2007
- \**Scleromochlus*: BMNH R3146, 3556, 3557, 3914, 4823, 4824, 5589; Benton 1999
- \**Silesaurus*: ZPal AbIII 12/6, 19/4, 361, 361/20, 361/27, 361/35, 361/39, 361/41, 362, 362/1, 363, 364/1, 364/38, 403/3, 403/4, 404/1, 404/3, 404/5, 404/7, 404/8, 404/10, 406/5, 411/1, 411/2, 411/4, 411/7, 411/9, 411/11, 411/12, 413, 415, 423/1, 432, 437/1, 452, 457, 460/1, 460/3, 461, 461/18, 461/21, 461/23, 461/24, 361/26, 837/1, 907/6, 907/8, 1216, 1218, 1228, 1271, 1272, 1884, 1885; Dzik 2003

#### **Crurotarsi**

- \**Arganasuchus*: MNHN AZA 407, 900, 901, 902, 904, 906; MNHN ALM 1-6; Jalil & Peyer 2007
- \**Arizonasaurus*: casts of referred material in SMNS collections; scores primarily based on Nesbitt 2003, 2005; Gower & Nesbitt 2006
- \**Batrachotomus*: SMNS 52970, 80283-341; Gower 1999, 2002
- \**Bromsgroveia*: WARMS G3 (holotype) and additional WARMS specimens cited in Benton & Gower (1997); Galton & Walker 1996; Benton & Gower 1997
- \**Effigia*: AMNH 30587 (holotype skull); scores primarily based on Nesbitt & Norell 2006; Nesbitt 2007
- \**Erpetosuchus*: BMNH R3139, R4807; NMS 1966.43.4A,B, 1992.31.1; Benton & Walker (2002)
- \**Fasolasuchus*: PVL 3850, 3851; Bonaparte 1981

- \**Gracilisuchus*: PULR 08; PV 4597; Romer 1972a; Brinkman 1981; Lecuona 2007
- \**Lotosaurus*: IVPP V4913, 4880, 49271, unnumbered skeleton; Zhang 1975; the pubis and ischium on the mounted skeleton (IVPP unnumbered) appear to be casts, and original material could not be located. Thus, all pubic and ischial characters are conservatively scored as uncertain, contra Nesbitt (2007).
- \**Poposaurus*: TMM 31025-12, 31025-159, 31025-177, 31025-257, 31173-53, 31173-73, 43683-1; TTUP 9243, 10526, 11203, 11441, 12138, 12556; Mehl 1915; Colbert 1961; Long & Murry 1995; Weinbaum & Hungerbühler 2007; unpublished photos of unnumbered YPM skeleton preliminary described by Joyce & Gauthier (2006). We follow Weinbaum & Hungerbühler (2007) in considering *Lythrosuchus* synonymous with *Poposaurus*.
- \**Postosuchus*: TTUP 9000, 9002; Chatterjee 1985; Long & Murry 1995; Gower 2002
- \**Prestosuchus*: BPSG AS XXV 1-4, 6-7, 10-17, 22, 24-25, 28-33, 42-43, 45, several unnumbered elements referred by von Huene (1942) to *P. chiniquensis* and *P. loricatus*. We also include scorings based on a skull referred to *Prestosuchus* by Barberena (1978), pending a revision of *Prestosuchus* taxonomy (see review in Gower 2000). Scores for the skull based on UFRGS PV 0156 T.
- \**Qianosuchus*: Li *et al.* 2006
- \**Rauisuchus*: BPSG AS XXV 60-124; von Huen, 1942; Krebs 1973
- \**Reveltosaurus*: Parker *et al.* 2005; Hunt *et al.* 2005
- \**Saurosuchus*: PVL 2062, 2198, 2557; PVSJ 32, 615; Sill 1974; Alcober 2000; Gower 2002
- \**Shuvosaurus*: TMM 31100-495, 31100-496, 31100-497, 31100-512, 31173-106, 31173-133; TTUP 3892, 9001, 9280, 9281, 9282, 10783, 10837, 10969, 11291, 11601, 11605, 11708, 11865, 12544; Chatterjee 1993; Rauhut 1997; Long & Murry 1995; Nesbitt 2007. We follow Nesbitt (2007) and others in considering *Chatterjeea* synonymous with *Shuvosaurus*.
- \**Sillosuchus*: PVSJ 85; Alcober & Parrish 1997
- \**Stagonosuchus*: Krebs 1976; Gower 1999; Gebauer 2004
- \**Teratosaurus*: We score this taxon primarily on ZPAL Ab III 563 pending revision of the genus by Brusatte *et al.* (in press). We also examined material previously referred to *Teratosaurus* (BMNH 38646; SMNS 52972); Galton 1985a; Benton 1986a; Sulej 2005
- \**Ticinosuchus*: PIMUZ T 4779, T 2471; Krebs 1963, 1965, 1976; Pinna & Arduini 1978
- \**Tikisuchus*: Chatterjee & Majumdar 1987; Gower 2002; Sulej 2005
- \**Yarasuchus*: Sen 2005

## EXEMPLAR GENERA

### **Aetosauria**

- \**Aetosaurus*: SMNS 5770, 12670, 12760, 14882, 18554; Huene 1920; Walker 1961; Schoch 2007. Because of taxonomic uncertainty we restrict scores to specimens from the Middle Stubensandstein of Germany.

\**Desmotosuchus*: MNA V9300; TMM 31100-1, 31100-213, 31100-294, 31100-312, 31172-14, 31172-24, 31173-137 40041-3; TTUP 9023, 9024, 00283, 00555, 11600; UMMP 7476; UCMP Placerias Quarry specimens (casts in SMNS collection); Long & Murry 1995; Small 2002; Parker 2008

\**Stagonolepis*: BMNH R4784, 4787, additional BMNH Elgin collection; Walker 1961; Gower & Walker 2002. Because of taxonomic uncertainty we have restricted all scores to material from the Elgin Sandstone of Scotland.

### **Crocodylomorpha**

\**Protosuchus*: Colbert & Mook 1951; Busbey & Gow 1984; Sues *et al.* 1996; Gow 2000

\**Sphenosuchus*: Walker 1990; Sereno & Wild 1992

\**Terrestriusuchus*: BMNH P. 47/21, 47/22, additional BMNH P specimens cited by Crush (1984); Crush 1984

### **Ornithischia**

\**Heterodontosaurus*: SAM-PK-K337 cast; Crompton & Charig 1962; Santa Luca 1980; Norman *et al.* 2004

\**Lesothosaurus*: BMNH R8501, R11956; BMNH RU B.15, B.17, B.23; BMNH RU C.109; Thulborn 1970, 1972; Santa Luca 1984; Sereno 1991b

\**Psittacosaurus*: LH PVI; Osborn 1923, 1924; Sereno & Chao 1988; Sereno *et al.* 1988, 2007; Sereno 1990

### **Ornithosuchidae**

\**Ornithosuchus*: BMNH R2409, 2410, 3142, 3143, 3149, 3152, 3153, 3561, 3562, 3622, 3916; Walker 1964; Sereno 1991a

\**Riojasuchus*: PVL 3827 skull cast; Bonaparte 1971; Sereno 1991a

### **Phytosauria**

\**Myrstriosuchus*: SMNS 9134, 9433, 9962, 10260, 10302, 11128, 12671, 12986, 55422, 90204, numerous unnumbered skulls and specimens; McGregor 1906; Hungerbühler & Hunt 2000; Hungerbühler 2002

\**Parasuchus*: Because of taxonomic uncertainty we restrict scores to the specimens described by Chatterjee (1978).

\**Rutiodon*: McGregor 1906; Colbert 1947; Gregory 1962; Sereno & Arcucci 1990; Sereno 1991a

### **Pterosauria**

\**Dimorphodon*: BMNH 41212, 41213, 41346, 43487, 43973; BMNH R1034, R1035; Owen 1870; Padian 1983

\**Eudimorphodon*: Because of taxonomic uncertainty we restrict scores to the holotype and specimens described by Wild (1978), which have also been reconstructed by Sereno (1991a). We have observed some material possibly referable to *Eudimorphodon* (BSP 1994 I 51) but scores are not based on these specimens.

\**Pteranodon*: Bennett 2001

### **Saurischia**

\**Coelophysis*: TTM 43418-1, 43668-1, 43692-2; Colbert 1989; Tykoski & Rowe 2004. We consider *Syntarsus* (= *Megapnosaurus*) as synonymous with *Coelophysis*.

\**Herrerasaurus*: PVSJ 53, 373, 407; PVL 2566 (original material and casts); Sereno & Novas 1992; Novas 1993; Sereno 1993; Sereno & Novas 1993; Sereno 2007a

\**Plateosaurus*: SMNS 4011, 6014-6061, 13200, 53537; scores based primarily on Galton (1984, 1985b), Moser (2003), Galton & Upchurch (2004)

#### ADDITIONAL COMPARATIVE MATERIAL

\**Ctenosauriscus*: BMNH R4976, cast of holotype

\**Hoplitosuchus*: BPSG AS XXV 52-59

\**Procerosuchus*: BPSG AS XXV 131-135, 137-139

\*Charig's African Material: "Mandasuchus" (BMNH R6792 and uncatalogued), "Hypselorhacis" (uncatalogued, field number U11/2), "Teleocrater" (BMNH R6796 and uncatalogued), "Pallisteria" (BMNH uncatalogued)

\*German aetosaur, phytosaur, and sphenosuchian crocodylomorph material in the SMNS collection; southwestern USA aetosaur and phytosaur material in the TTUP and TMM collections.

## ONLINE SUPPLEMENTARY APPENDICES

### APPENDIX S1: DESCRIPTION OF NEW CHARACTERS

Note: characters numbered according to their location in the full analysis.

9. Supratemporal fenestra oriented primarily dorsally (0), mostly dorsally but visible as a sliver in lateral view (1), or extensively laterally (2). The supratemporal fenestrae of most archosaur outgroups (e.g. *Erythrosuchus*: Gower 2003; proterochampsids: Sill 1967, Romer 1971c, Arcucci 1990) face completely dorsally, a condition also seen in basal dinosaurs (Fig. 3B; Galton 1984, 1985b; Colbert 1989; Sereno & Novas 1993), phytosaurs (Chatterjee 1978), ornithosuchids (Walker 1964; Bonaparte 1971), and many “rauisuchians” (*Arizonasaurus*: Nesbitt 2005; *Batrachotomus*: Fig. 3F, Gower 1999; *Effigia*: Nesbitt 2007; *Postosuchus*: Long & Murry 1995; *Shuvosaurus*: Chatterjee 1993). In contrast, the supratemporal fenestrae of most aetosaurs face fully laterally (Fig. 3C), a condition often held as an autapomorphy of the clade (e.g. Heckert & Lucas 1999). This state is also seen in *Gracilisuchus* (MCZ 4116, 4117; Romer 1972a; Brinkman 1981). Additionally, it is apparent that many crurotarsan taxa possess supratemporal fenestrae that are partially exposed laterally, and thus visible as a narrow sliver in lateral view (*Erpetosuchus*: Benton & Walker 2002; *Lotosaurus*: IVPP unnumbered; *Prestosuchus*: Fig. 3E, Barberena 1978; *Saurosuchus*: Alcober 2000; *Teratosaurus*: Sulej 2005; *Tikisuchus*: Chatterjee & Majumdar 1987; basal crocodylomorphs: *Terrestrisuchus*, *Sphenosuchus*, Crush, 1984 Walker 1990). In many “rauisuchian” taxa this appears to be at least partially the result of dorsolateral rotation of the squamosal. Whereas in most archosaurs (e.g. *Batrachotomus*: SMNS 80260) the

ventral ramus of the squamosal projects straight ventrally, in “rauisuchians” with a slightly laterally facing fenestra (e.g. *Rauisuchus*: BPSG AS XXV 62) the ventral ramus projects lateroventrally, and thus the primitive “lateral” surface faces partially dorsally. This rotation serves to expose the lateral margin of the fenestra in lateral view. Some pterosaurs (e.g. *Eudimorphodon*: Wild 1978), *Scleromochlus* (Fig. 3A; Benton 1999) and the crurotarsan *Qianosuchus* (Li *et al.* 2006) appear to possess fully laterally-facing supratemporal fenestrae, but we conservatively score them for the first derived state (“narrow sliver in lateral view”) here, as these specimens appear to be mediolaterally crushed (which likely results in a partially laterally facing fenestra to appear to be more fully laterally facing).

12. Anterior border of premaxilla vertical (0) or slopes posterodorsally (1). The anterior margin of the premaxilla is roughly vertical in immediate archosaur outgroups, pterosaurs, most dinosauromorphs, phytosaurs, ornithosuchids, basal crocodylomorphs, and most “rauisuchians” (Fig. 3A-C, E-F). Aetosaurs exhibit a slightly different morphology in which the anterior margin of the premaxilla is short and strongly reduced, but nevertheless the anterior margin is usually vertical or slightly inclined anterodorsally (*Aetosaurus*: Fig. 3C; SMNS 5770; *Desmotosuchus*: Small 2002). However, in *Effigia* (Nesbitt 2007), *Lotosaurus* (IVPP unnumbered), and *Shuvosaurus* (Fig. 3D; TTUP 9282; Chatterjee 1993; Rauhut 1997) the anterior margin of the premaxilla is strongly convex and slopes posteriorly, which likely relates to the presence of a cropping beak in these edentulous taxa. Not surprisingly, this condition is also seen in many ornithischian dinosaurs (e.g. *Heterodontosaurus*: Santa Luca 1980; *Lesothosaurus*: Sereno 1991b),

although a more traditional subvertical anterior border is seen in the beaked, herbivorous dinosauromorph *Silesaurus* (Dzik 2003).

13. Ventral margin of premaxilla shorter (0) or longer (1,2) than ventral margin of maxilla. Most immediate archosaur outgroups and basal archosaurs possess maxillae that are much larger than the premaxillae, and thus have a longer ventral margin (Fig. 3A-C, E-F). In contrast, some crurotarsans possess an expanded premaxilla that is longer ventrally than the maxilla. Among these taxa two general and likely non-homologous conditions are apparent. First, phytosaurs are characterised by extremely elongate premaxillae that form the majority of a greatly expanded snout. In these taxa the maxilla is still large and it appears as if the premaxillae have expanded anteriorly to form the snout. Second, the “rauisuchians” *Effigia* (Nesbitt 2007), *Lotosaurus* (IVPP unnumbered), and *Shuvosaurus* (Fig. 3D; TTUP 9282; Chatterjee 1993; Rauhut 1997) possess extremely shortened maxillae that are shorter ventrally than the premaxillae, which likely formed a beak. The premaxillae are not greatly expanded, and comparison to other crurotarsans indicates that the maxillae in these taxa are reduced. Therefore, it appears that possession of a longer premaxilla relative to the maxilla results from two different morphological transformations (expanded premaxillae and reduced maxillae, respectively), and thus this character is divided into two derived states.

14. Subnarial process of premaxilla absent or very short (0), elongate and finger-like (1), shortened and blunt (2). The premaxilla of most archosaurs is comprised of a main body and two major processes visible in lateral view, one of which floors the external naris and often contacts the maxilla (the subnarial process), and one that articulates with the nasal anterior or dorsal to the naris (the dorsal process). The subnarial

process is absent or extremely small in pterosaurs (*Dimorphodon*: BMNH 41212; *Eudimorphodon*: Wild 1978), aetosaurs (*Aetosaurus*: Fig. 3C, SMNS 5770; *Desmatosuchus*: Small 2002), ornithosuchids (*Ornithosuchus*: BMNH R2409; Walker 1964; *Riojasuchus*: Bonaparte 1971; Sereno 1991a), most phytosaurs (e.g. *Mystriosuchus*: SMNS uncatalogued, McGregor 1906, Hungerbühler 2002), *Qianosuchus* (Li *et al.* 2006), and apparently *Scleromochlus* (Fig. 3A; Benton 1999). In this analysis the states “absent” and “very small” are not separated because it is difficult to define a boundary between the two conditions, in large part because of poor preservation. It is possible that an extremely reduced process may appear as absent, especially in specimens that are poorly preserved, incompletely prepared, or incompletely figured in the literature.

Those taxa that possess a discrete subnarial process exhibit two general morphologies. First, a range of basal dinosaurs (e.g. *Herrerasaurus*: Fig. 3B, PVSJ 407, Sereno & Novas 1993; *Lesothosaurus*: BMNH RU B.23, Sereno 1991b) and “rauisuchians” (e.g. *Lotosaurus*: IVPP unnumbered; *Postosuchus*: TTUP 9000, Long & Murry 1995; *Prestosuchus*: Fig. 3E, Barberena 1978; *Rauisuchus*: BPSG AS XXV 60; *Saurosuchus*: Alcober 2000; *Shuvosaurus*: Figure 3D, Chatterjee 1993) possess subnarial processes that are elongate, often thin, and finger-like. Second, many other “rauisuchians” (e.g. *Batrachotomus*: Fig. 3F, SMNS 80260; *Effigia*: Nesbitt 2007; apparently *Yarasuchus*: Sen 2005) and basal crocodylomorphs (*Protosuchus*: Gow 2000; *Sphenosuchus*: Walker 1990) possess discrete subnarial processes that are shortened and often triangular or spade-shaped in lateral view. These two derived states do not appear to be correlated with the states of character 15, which relate to the extent of the subnarial process. Many taxa possess elongate processes that still terminate ventral to the external



naris (e.g. *Lotosaurus*, *Rauisuchus*, *Prestosuchus*), whereas some taxa have shortened processes that nonetheless extend posterior to the external naris (e.g. *Protosuchus*, *Sphenosuchus*).

18. Premaxilla-maxilla articulation level (0) or angled, forming an arch (1). The premaxilla and maxilla of most archosaurs articulate at the same level ventrally, and thus the tooth rows of both elements are smoothly continuous. Sereno (1991a:character 16) recognised that an arched diastema between the premaxilla and maxilla characterises ornithosuchids. While the diastema is a clear synapomorphy of this group, an arched or notched articulation between the premaxilla and maxilla at their ventral contact is seen in a handful of other basal archosaurs, including *Qianosuchus* (Li *et al.* 2006), *Revueltosaurus* (Parker *et al.* 2005) and the aetosaur *Aetosaurus* (SMNS 5770; Schoch 2007). In these taxa the premaxilla and maxilla meet at an angle, and the tooth row describes a broad arch in this region. This condition is also seen in some basal theropods (*Coelophysis*: Colbert 1989) and the archosaur outgroup *Erythrosuchus* (Gower 2003).

20. Ascending ramus of maxilla thick (0) or thin (1). In most basal archosaurs the ascending ramus of the maxilla is thick, with an anteroposterior length at the base that is greater than half the depth of the maxillary main body at the anterior edge of the antorbital fenestra. Note that because of the varying inclination of the ascending ramus this basal dimension is not always oriented exactly anteroposteriorly. In many of these taxa the ascending ramus is much greater than half the depth of the main body, and sometimes even thicker (e.g. *Aetosaurus*: Fig. 3C, SMNS 5770; *Ornithosuchus*: BMNH R2409; Walker 1964). However, many crurotarsans exhibit extremely thin ascending processes that are far less than half the depth of the main body, including *Qianosuchus*

(Li *et al.* 2006), *Revueltosaurus* (Parker *et al.* 2005), as well as numerous “rauisuchians” (*Arizonasaurus*: Nesbitt, 2005; *Batrachotomus*: Fig. 3F, SMNS 52970, Gower 1999; *Fasolasuchus*: Bonaparte 1981; *Prestosuchus*: Fig. 3E, Barberena 1978; *Ticinosuchus*: Krebs 1965). A thin ascending process also appears to be present in the outgroup *Erythrosuchus* (Gower 2003), but not in more proximal archosaur outgroups (*Chanaresuchus*: Romer 1971c; *Euparkeria*: Ewer 1965).

33. Frontal contributes to the dorsal orbital rim (0) or is excluded (1). Nearly all basal archosaurs and immediate archosaur outgroups possess a frontal that broadly contributes to the dorsal orbital rim, as is clearly seen in lateral and dorsal view of the skull (e.g. Alcober 2000:fig. 11). However, the “rauisuchians” *Postosuchus* (TTUP 9000; Long & Murry 1995) and *Teratosaurus* (Sulej 2005) exhibit a unique condition, in which the frontal is excluded from the orbital rim by a novel palpebral ossification, which extends posteriorly to contact the postorbital dorsal to the orbit. This ossification has previously been interpreted as a greatly enlarged prefrontal (Chatterjee 1985; Sulej 2005), but is in fact a separate ossification (S.J. Nesbitt, pers. comm.; SLB, pers. obs.). In these taxa the frontals are reduced in size and visible on the midline dorsally, but are not apparent laterally (e.g. Sulej 2005:fig. 3). *Batrachotomus* may exhibit an intermediate condition, in which an enlarged prefrontal nearly contacts the postfrontal and postorbital but allows a narrow region of the frontal to contribute to the orbital rim (Fig. 3F, SMNS 52970, 80260; Gower 1999:fig. 2). As this intermediate condition is unknown in other taxa, and a distinct palpebral is clearly absent, *Batrachotomus* is scored for the primitive state, but this character should be expanded into a three-state character if future discoveries reveal a *Batrachotomus*-like morphology in additional taxa.

34. Sagittal crests on the frontals absent (0) or present (1). The dorsal surface of the frontal of most basal archosaurs and immediate outgroups is generally flat, without any dorsal expansions. However, some crurotarsans exhibit a raised midline sagittal crest, which is low and broad in *Lotosaurus* (IVPP unnumbered) and *Saurosuchus* (Alcober 2000) and narrow, deep, and sharp in *Batrachotomus* (SMNS 80260, Gower 1999) and *Sphenosuchus* (Walker 1990). Whether these conditions are homologous is uncertain, but we score as identical all taxa possessing a dorsal midline crest pending further study of archosaur cranial anatomy. It is unlikely that this character is related to body size, judging by the large size range of the aforementioned taxa.

41. Jugal triradiate (0) or elongate (1). The jugal of most basal archosaurs and immediate outgroups is a triradiate or tetraradiate element, with an anterior ramus that contacts the maxilla (and often gives rise to a dorsal projection that articulates with the lacrimal), a posterior ramus that contacts the quadratojugal, and a dorsal ramus that articulates with the postorbital (Fig. 3A-C, E-F). Usually the jugal forms most of the ventral floor of the orbit but does not extend far anterior to this opening. Additionally, the main body of the jugal under the orbit is deep in most taxa. In contrast, the jugals of *Effigia* (AMNH 30587; Nesbitt 2007) and *Shuvosaurus* (Fig. 3D; TTUP 9280; Chatterjee 1993; Rauhut 1997) exhibit a unique morphology, in which a dorsal projection for articulation with the lacrimal is completely absent in lateral view, the dorsal ramus for articulation with the postorbital is short, the main body is shallow, and the anterior ramus extends far anterior to the orbit. Taken together, these features result in an elongate, rod-like shape of the jugal. The anterior extension of the jugal may be correlated with the reduced maxillae of these taxa (character 13), but *Lotosaurus* (IVPP unnumbered)

possesses a reduced maxilla in concert with a more traditional jugal morphology. It is also possible that the elongation of the jugal is correlated with the enlarged orbits of these taxa (character 3), but some avemetatarsalians (e.g. *Scleromochlus*: Benton 1999; basal ornithischians: BMNN RU B.23) exhibit enlarged orbits with a more traditional jugal morphology.

47. Posterior process of squamosal at same level as (0) or offset ventral to (1) anterior process. The squamosal of most archosaurs is triradiate in lateral view, with an anterior ramus that articulates with the postorbital, a ventral ramus that often contacts the quadratojugal or postorbital in some taxa, and a posterior ramus that often appears to be free-standing in lateral view but usually contacts the paroccipital process medially (Fig. 3A-E). The posterior ramus appears to be absent or extremely reduced in erythrosuchids (Parrish 1992; Gower 2003) but is present in more proximal archosaur outgroups (*Euparkeria*: Ewer 1965; proterochampsids: Sill 1964, Romer 1971c, Arcucci 1990). Within the crown group, most taxa exhibit a posterior ramus that is at the same level as the anterior ramus, or slightly offset dorsally. Note that in many taxa the squamosal is tilted posteroventrally, and although it may appear that the posterior ramus is located further ventrally, in fact the two rami are smoothly continuous and at the same level. However, in some taxa the posterior ramus is clearly offset ventrally from the anterior ramus. This is most apparent in *Batrachotomus* (Fig. 3F; SMNS 80260; Gower 1999), in which a discrete, tab-like posterior ramus is separated from the anterior ramus by a distinct step. A similar although less pronounced morphology is seen in other “rauisuchians” (*Postosuchus*: TTUP 9000, 9002, Long & Murry 1995; *Teratosaurus*: Sulej 2005; *Tikisuchus*: Sulej 2005). The condition in basal crocodylomorphs is

somewhat unclear and deserves further study. The squamosals of *Dibothrosuchus* (Wu & Chatterjee 1993), *Saltoposuchus* (Sereno & Wild 1992), and *Sphenosuchus* (Walker 1990) are tilted somewhat posteroventrally, but nonetheless exhibit a noticeable offset between the anterior and posterior rami. A similar offset is apparent in *Kayentasuchus*, *Litargosuchus* (Clark & Sues 2002), and *Protosuchus* (Gow 2000), but the enlarged and heavily modified squamosals of these taxa render homology assessment difficult. *Terrestrisuchus* is reconstructed as lacking a ventrally offset posterior process (Crush 1984:fig. 2), but the material is too fragmentary and poorly preserved to assess confidently (SLB, pers obs., NHM collection).

50. Squamosal, posterodorsal corner of the lateral surface unmarked (0) or excavated by deep pit (1). Although the squamosal is enormously variable in shape and size among basal archosaurs, in most taxa the lateral surface of the main body is unornamented and generally smooth. However, in *Postosuchus* (TTUP 9000, 9002; Chatterjee 1985:fig. 3h, 4b) and *Teratosaurus* (Sulej 2005:fig. 4g) the posterodorsal corner of the lateral surface is excavated by a deep, circular, concave pit. This pit is overhung dorsally by a rugose ridge, which forms part of a continuous lateral skull ridge that incorporates the nasal, lacrimal, prefrontal, and postorbital. However, the presence of the ridge is not invariant with the presence of this pit. Although both *Postosuchus* and *Teratosaurus* possess the ridge, several taxa (e.g. *Batrachotomus*, *Prestosuchus*, *Rauisuchus*, *Saurosuchus*) have a ridge but lack the pit, instead possessing a generally smooth lateral surface of the squamosal.

60. Occipital condyle spherical (0) or dorsoventrally compressed crescent-shaped (1). The occipital condyle of most basal archosaurs and close outgroups is essentially

spherical (e.g. *Batrachotomus*: Gower 2002:fig. 1; *Desmotosuchus*: Small 2002:fig. 5; *Erythrosuchus*: Gower 1997:fig. 2; *Herrerasaurus*: Sereno & Novas 1993:fig. 6; *Postosuchus*: Chatterjee 1985:fig. 5c). However, in *Effigia* (AMNH 30587; Nesbitt 2007:fig. 22c) and *Shuvosaurus* (TTUP 9280; Chatterjee 1993:fig. 5d, 6c) the occipital condyle is extremely dorsoventrally-compressed and crescent-shaped. A similar condition is present in some ornithischians (e.g. *Lesothosaurus*: Sereno 1991), but the condyle is not compressed to the extent seen in *Effigia* and *Shuvosaurus*, in which it approaches four times wider mediolaterally than deep dorsoventrally.

61. Basal tubera oriented vertical (0) or horizontal (1). In most basal archosaurs and close outgroups (example taxa listed for character 60 above) the basal tubera are oriented vertically, and descend as sheet-like processes ventral to the occipital condyle when the braincase is viewed in a standard orientation with the cultriform process held horizontally. However, in *Effigia* (AMNH 30587; Nesbitt 2007:fig. 22) and *Shuvosaurus* (TTUP 9280; Chatterjee 1993:fig. 5,6) the tubera are oriented horizontally. In these taxa the tubera extend anteriorly from the occipital condyle, are at the same level as the condyle in lateral view, and floor the endocranial cavity.

71. Dentary with teeth across the length of the element (0), edentulous anteriorly (1), completely edentulous (2). The dentary bears teeth in most basal archosaurs and immediate outgroups, although several derived clades (e.g. birds, ornithomimosaurian dinosaurs) lose teeth entirely. Some avemetatarsalians (e.g. some pterosaurs) as well as some crurotarsans (*Effigia*: AMNH 30587, Nesbitt 2007; *Lotosaurus*: IVPP unnumbered; *Shuvosaurus*: Fig. 3D, TTUP 9280, 9281, Chatterjee 1993) are characterised by completely edentulous dentaries, as recorded by the second derived state of this character.

The first derived state, dentary edentulous at anterior tip, characterises aetosaurs (Walker 1961; Heckert & Lucas 1999; Small 2002; Parker 2007) and the dinosauromorphs *Silesaurus* (Dzik 2003) and *Sacisaurus* (Ferigolo & Langer 2007). The lower jaw of ornithischians is edentulous anteriorly, but the toothless region is comprised of the neomorphic prementary ossification, and the dentary bears teeth up to its anterior margin. Although Ferigolo & Langer (2007) have identified a prementary in *Sacisaurus* we follow Irmis *et al.* (2007b) in questioning this identification. The potential prementary of *Sacisaurus* is a paired element present on both sides of the skull, not a single midline element as in ornithischians (Irmis *et al.* 2007b). Furthermore, it is uncertain whether the “prementary” of *Sacisaurus* is a separate element or simply an artefact of breakage. As the lower jaw of *Sacisaurus* otherwise closely resembles that of *Silesaurus*, which clearly lacks an accessory ossification, we score both taxa as possessing dentaries that are edentulous anteriorly. However, the score for *Sacisaurus* may be changed in the future if more conclusive evidence shows that a true prementary is present.

72. Anterior region of dentary unexpanded (0) or expanded (1) relative to main body. In most close archosaur outgroups the anterior region of the dentary is approximately as dorsoventrally deep as the midpoint of the main body (Fig. 3B, C). However, several archosaur taxa, including numerous avemetatarsalians and crurotarsans, are characterised by an anterior expansion of the dentary, in which this region is noticeably dorsoventrally expanded relative to the main body. In phytosaurs this expansion takes the form of a bulbous rosette, which holds an extended tooth battery at the tip of the elongated jaws (e.g. Chatterjee 1978). However, in most other taxa this expansion is more subtle, is either squared off or rounded (e.g. *Batrachotomus*: Fig. 3F,

SMNS 80260, Gower 1999; *Postosuchus*: TTUP 9000, Long & Murry 1995), and does not accommodate an enlarged tooth battery.

80. Cervical vertebrae ventral margin weakly concave (0) or highly waisted (1). In most basal archosaurs and immediate outgroups the ventral margin of individual cervicals is slightly concave in lateral view, because the articular faces extend ventrally relative to the main body of the centrum. In these taxa the “constricted region” between the ventral margin at the midpoint of the centrum and the ventral tip of the posterior articular face, measures no more than 35% of the height of the centrum as a whole, and is often much less. However, in the “rauisuchians” *Arizonasaurus* (Nesbitt 2005) and *Sillosuchus* (Alcober & Parrish 1997) the constricted region measures approximately 40% of the centrum height. This does not appear to be correlated with the extreme elongation of the cervicals in these taxa (character 77), as other taxa with elongate cervicals (*Effigia*: Nesbitt 2007; *Qianosuchus*: Li *et al.* 2006; *Shuvosaurus*: TTUP 9001, Long & Murry 1995) do not possess such highly waisted centra.

99. Scapula distal margin slightly expanded (0) or greatly expanded (1). The scapular blade of most archosaurs expands in dorsoventral depth posteriorly, but the extent of this expansion varies. Proximal outgroups exhibit a scapula with an expansion that is less than 2.5 times the minimum depth of the blade (*Chanaresuchus*: 2.3, Romer 1972c; *Erythrosuchus*: 2.4, Gower 2003; *Euparkeria*: 1.5, Ewer 1965). This condition is also seen in many ingroup taxa, including *Scleromochlus* (Benton 1999), pterosaurs (Wild 1978; Bennett 2001), some dinosauromorphs (e.g. *Marasuchus*: Sereno & Arcucci 1994), some basal dinosaurs (e.g. *Herrerasaurus*: PVSJ 53, Sereno 1993; *Coelophysis*: Colbert 1989), phytosaurs (e.g. *Parasuchus*: Chatterjee 1978; *Mystriosuchus*: SMNS



11128), ornithosuchids (*Ornithosuchus*: Fig. 4B; Walker 1964), *Gracilisuchus* (Romer 1972a), and some “rauisuchians” (*Effigia*: Nesbitt 2007; *Prestosuchus*: BPSG AS XXV 12; *Shuvosaurus*: Long & Murry 1995; *Ticinosuchus*: Krebs 1965). In contrast, many other taxa possess greatly expanded distal scapulae, in which the distal depth is greater than 2.5 times the minimal depth of the shaft, including some dinosauromorphs (*Lewisuchus*: Romer 1972b; *Sacisaurus*: Ferigolo & Langer 2007; *Silesaurus*: Dzik 2003), some basal dinosaurs (e.g. *Lesothosaurus*: BMNH RU B.17; *Plateosaurus*: SMNS 13200, 53537), aetosaurs (e.g. *Aetosaurus*: SMNS 5570; *Stagonolepis*: Walker 1964), basal crocodylomorphs (e.g. *Dromicosuchus*: Sues *et al.* 2003; *Protosuchus*: Colbert & Mook 1951; *Sphenosuchus*: Fig. 4A, Walker 1990; *Terrestrisuchus*: BMNH P collection), *Erpetosuchus* (Benton & Walker 2002), *Qianosuchus* (Li *et al.* 2006), and several “rauisuchians” (*Arizonasaurus*: Nesbitt 2005; *Batrachotomus*: SMNS 80271; *Poposaurus*: YPM uncatalogued; *Postosuchus*: Long & Murry 1995; *Rauisuchus*: BPSG AS XXV 91; *Yarasuchus*: Sen 2005).

101. Position of glenoid on coracoid level with (0) or ventral to (1) the scapular glenoid. In immediate archosaur outgroups and basal archosaurs the scapula and coracoid both contribute to the glenoid. When viewed laterally with the scapular blade held horizontal for reference, the coracoid and scapula contributions extend to approximately the same level ventrally in immediate outgroups and most ingroup taxa. In some taxa the coracoid glenoid may extend slightly further ventrally, but it is not noticeably offset from the scapular glenoid. This condition holds in taxa with both a shallowly-excavated glenoid (e.g. *Arizonasaurus*: Nesbitt 2005:fig. 27; *Euparkeria*: Ewer 1965:fig. 9; *Ticinosuchus*: Krebs 1976:fig. 11d) and a deeply concave and extensive fossa (e.g.

*Rutiodon*: McGregor 1906:pl. IX, 20-21; *Silesaurus*: Dzik 2003:fig. 9; *Sphenosuchus*: Fig. 4A, Walker 1990). On the other hand, several crurotarsans exhibit a derived state in which the coracoid contribution extends much further ventrally than the scapular contribution. Although the two regions are smoothly confluent in some of these taxa (e.g. *Parasuchus*: Chatterjee 1978:fig. 10a), in most taxa the coracoid contribution is noticeably offset and faces primarily posteriorly instead of posteroventrally (e.g. *Aetosaurus*: SMNS 5770; *Batrachotomus*: SMNS 80271; *Erpetosuchus*: Benton & Walker 2002:fig. 5c; *Mystriosuchus*: SMNS 11128, 90204; *Ornithosuchus*: Fig. 4B, Walker 1964; *Postosuchus*: Long & Murry 1995:fig. 131a; *Prestosuchus*: BPSG AS XXV 12; *Rauisuchus*: BPSG AS XXV 91; *Revueltosaurus*: Parker *et al.* 2005:fig. 3a; *Shuvosaurus*: Long & Murry 1995:fig. 164a; *Terrestrisuchus*: BMNH P collection, Crush 1984:fig. 7a; *Yarasuchus*: Sen, 2005:fig. 6a). The presence of this derived condition in taxa of a range of body sizes (*Aetosaurus*: ~50 cm body length; *Batrachotomus*: ~290 cm body length) suggests that it is not size dependent.

112. Ilium dorsal margin straight or convex (0) or saddle-shaped (1). The dorsal margin of the ilium of most basal archosaurs and immediate outgroups is shallowly convex or straight (Fig. 4C,E). However, in some dinosauiromorphs (*Lagerpeton*: Sereno & Arcucci 1993:fig. 1; *Marasuchus*: Sereno & Arcucci 1994:fig. 6) and pterosaurs (e.g. *Dimorphodon*: BMNH 41212, Padian 1983:fig. 28; *Eudimorphodon*: Fig. 4D, Wild 1978) the dorsal margin is concave and resembles a saddle in lateral view. Whether this condition is homologous between these two groups is uncertain, as the concave margin is much broader and shallower in pterosaurs and sharper and deeper in basal dinosauiromorphs. However, pending further study of basal avemetatarsalians we

conservatively choose to score a binary character here instead of creating a potentially redundant third state. A similar character was used by Ezcurra (2006:193), but was only relevant to the ingroup relationships of dinosaurs in his analysis.

114,115. The ilia of many “rauisuchians” are ornamented by a rugose swelling that arises near the dorsal margin of the acetabulum and trends dorsally or anterodorsally. This ridge-like structure varies among taxa in its strength, texture, and orientation, leading Gower (2000) to question whether it is a homologous feature throughout. Instead of *a priori* excluding characters relating to this swelling because of doubts over homology, we have attempted to incorporate the most important variable aspects of the structure into our analysis. As with any cladistic characters, these characters represent a primary hypothesis of homology that is then tested in the analysis, which we view as the most defensible method of considering ambiguous structures.

Character 114 is a three-state character that deals with the presence of the iliac swelling and its orientation (dorsal or anterodorsal). A similar character denoting the presence/absence of the swelling has been used in some previous studies and is not new to this analysis. However, previous studies have not taken into account the orientation of the swelling, which can be separated into two discrete states (dorsal or anterodorsal) and appears to be phylogenetically informative.

Character 115 refers to the morphology of the swelling at its dorsal termination. Some taxa possess a swelling that is only oriented anteriorly at its dorsal termination (*Effigia*: Nesbitt 2007; *Poposaurus*: TTUP 9243, TMM 31025-12, TMM 43683-1, Weinbaum & Hungerbühler 2007; *Shuvosaurus*: TTUP Post Quarry collection, Long & Murry, 1995 Gower, 2000; *Sillosuchus*: Alcober & Parrish 1997), whereas others have a

swelling that extends both anteriorly and posteriorly at its termination (*Arizonasaurus*: Nesbitt 2005; *Batrachotomus*: SMNS 52970; *Bromsgroveia*: WARMS G3; *Lotosaurus*: IVPP unnumbered; *Postosuchus*: TTUP 9002, Long & Murry 1995; *Rauisuchus*: BPSG AS XXV 88; *Saurosuchus*: Sill 1974; *Teratosaurus*: SMNS 52972). Importantly, these character states do not appear to be dependent on the orientation of the swelling as a whole. Although most dorsally oriented swellings expand both anteriorly and posteriorly, that of *Sillosuchus* expands only anteriorly. Furthermore, anterodorsally oriented swellings may be expanded only anteriorly (*Effigia*, *Poposaurus*, *Shuvosaurus*) or both anteriorly and posteriorly (*Bromsgroveia*, *Lotosaurus*).

We have not included any characters relating to the texture (strongly rugose, smooth, etc.) or strength (strong, weak, etc.) of the swelling, as we find these difficult to define based on our observations of specimens. Gower (2000) noted some differences in texture and strength among taxa, and further study may reveal clear variation in these features that can be explicitly formulated in a character statement. As reviewed by Gower (2000), the iliac swelling deserves further study, and we suggest that future phylogenetic analyses atomise features of the swelling into different characters as we have started to do. This will not only record variation that may be phylogenetically informative, but will also serve as a stronger test of homology than simply including a single character regarding the presence or absence of a swelling. However, we are also aware of the danger of excessive atomisation, as this may overemphasize the importance of this region. In the context of the present analysis, we feel that two characters (114, 115) best describe the most important phylogenetically informative variation without undue atomisation.

117. Iliac preacetabular process large and deep (0) or small, shallow, and finger-like (1). Although the preacetabular process of the ilium in most basal archosaurs and immediate outgroups is small and not expanded greatly anteriorly, its base is still approximately as dorsoventrally deep as the base of the postacetabular process. Additionally, in most taxa the preacetabular process and pubic peduncle are separated by a broadly concave margin and, most importantly, the dorsal surface of the preacetabular process and the blade of the ilium are smoothly continuous. This condition prevails in a wide range of taxa, including pterosaurs (e.g. *Eudimorphodon*: Fig. 4D; Wild 1978), dinosauromorphs (e.g. *Herrerasaurus*: Novas 1993; *Marasuchus*: Sereno & Arcucci 1994), phytosaurs (e.g. *Parasuchus*: Fig. 4C; Chatterjee 1978), aetosaurs (e.g. *Stagonolepis*: Walker 1961), ornithosuchids (e.g. *Ornithosuchus*: Walker 1961), crocodylomorphs (e.g. *Protosuchus*: Colbert & Mook 1951; *Terrestrisuchus*: Crush 1984), and most “rauisuchians” (e.g. *Effigia*: Nesbitt 2007; *Postosuchus*: TTUP 9002, Long & Murry 1995; *Shuvosaurus*: TTUP Post Quarry collection, Long & Murry, 1995; *Teratosaurus*: SMNS 52972, Galton 1985a; *Ticinosuchus*: Krebs, 1965). However, *Arizonasaurus* (Fig. 4E; Nesbitt, 2005) and *Bromsgroveia* (WARMS G3, Benton & Gower 1997) exhibit a unique condition in which the preacetabular process is greatly reduced, with a base that is much shallower than the base of the postacetabular process. In addition, the preacetabular process and pubic peduncle are separated by a narrow notch, and the dorsal margin of the preacetabular process is offset from the dorsal margin of the iliac blade by a distinct step. As a result, the preacetabular process of these taxa resembles a finger-like projection pointing anteriorly.

126. Medioventral lamina of pubis extensive (0), partially reduced (1), strongly reduced (2). As reviewed by Hutchinson (2001), diapsids ancestrally possessed a broad puboischiadic plate, giving the pubes and ischia a plate-like appearance in lateral view. The pubic contribution to this plate is comprised of an extensive medioventral lamina (“obturator flange” of some authors), which in lateral view extends posteroventrally from the thickened anterior shaft of the pubis. In immediate archosaur outgroups the medioventral lamina is extensive, and extends ventrally to approximately the same level as the shaft (*Erythrosuchus*: Hutchinson 2001:fig. 8, Gower 2003:fig. 33; *Euparkeria*: Ewer 1965:fig. 11, Hutchinson 2001:fig. 8; proterochampsids: Romer 1972c:fig. 2c). This condition also prevails in pterosaurs (e.g. *Dimorphodon*: BMNH 41212; *Eudimorphodon*: Wild 1978) and phytosaurs (e.g. *Mystriosuchus*: SMNS 12986; *Parasuchus*: Fig. 4F, Chatterjee 1978). In contrast, many archosaurs exhibit a reduced medioventral lamina, which is here divided into two states to record moderate (lamina measures 50-70% length of shaft) and extensive (less than 50% length of shaft) reduction. Note that this reduction is not absolute but relative, as Hutchinson (2001) has demonstrated that the medioventral lamina itself does not greatly reduce in size, but rather the pubic shaft distal to the lamina expands. Moderate reduction is seen in some dinosauromorphs (*Lagerpeton*: Sereno & Arcucci 1993), *Qianosuchus* (Li *et al.* 2006), *Tikisuchus* (Fig. 4G; Chatterjee & Majumdar 1987), and aetosaurs (e.g. *Aetosaurus*: SMNS 5770; *Stagonolepis*: Walker 1961), whereas extreme reduction characterises most dinosauromorphs (e.g. *Marasuchus*: Sereno & Arcucci 1994; *Silesaurus*: Dzik 2003; dinosaurs: Fig. 4H, Colbert 1989, Novas 1993), ornithosuchids (Walker 1964; Bonaparte 1971), crocodylomorphs (Colbert & Mook 1951; Crush 1984; Walker 1990; Hutchinson

2001), and most “rauisuchians” (e.g. Krebs 1965; Long & Murry 1995; Nesbitt 2005, 2007).

128. Thickness (anteroposterior dimension) of ischial shaft greater than or equal to (0) or less than (1) length of pubic shaft. In the vast majority of basal archosaurs and immediate archosaur outgroups the ischium is a more robust element than the pubis, and has a shaft that is anteroposteriorly longer at its midpoint than the pubic shaft. In some taxa the two shafts exhibit approximately equal length, but only in *Lagerpeton* (Sereno & Arcucci 1993), some basal dinosaurs (e.g. *Herrerasaurus*: Novas 1993), and the “rauisuchians” *Effigia* (Nesbitt 2007) and *Shuvosaurus* (TTUP 9001; Long & Murry 1995) is the pubic shaft considerably more robust than the ischial shaft.

## APPENDIX S2: SYNAPOMORPHY LIST

Note: “r” designates a reversal, underlined characters are those with a CI = 1.0

### **Crurotarsi**

ACCTRAN: 14

DELTRAN: 151

Both: 6(2),38,85,92,97,106,156,157,159,161,164,170,172,173

### **Suchia**

ACCTRAN: 1r,22,28,51(2),122,130,182

DELTRAN: 63(2)

Both: 8,95,123,124,126

### **Aetosauria + *Gracilisuchus* + *Erpetosuchus* + Crocodylomorpha**

ACCTRAN: 7,39,42,99,118

DELTRAN: 130

Both: 9(2),48,66(2),67,68,69,70,122(2)

### ***Gracilisuchus* + *Erpetosuchus* + Crocodylomorpha**

ACCTRAN: 10,14(2),23,46,95(2)

DELTRAN: 28,100

Both: 15,37,45,52,53,156r,157r,174,179,185

### ***Erpetosuchus* + Crocodylomorpha**

ACCTRAN: 7r,51r,58,91,196r,111,113,123(2),126(2),180

DELTRAN: 23,39,99

Both: 9r,36(2),37(2),40,47,102

### **Rauisuchia + Ornithosuchidae + *Revueltosaurus***

ACCTRAN: 100

DELTRAN: 28,51(2),66,122

Both: 6r,126(2),130(2),137

### **Ornithosuchidae + *Revueltosaurus***

ACCTRAN: 14r,73,76,91,123(2),149,154,182r

DELTRAN: none

Both: 18,30,31

### **Rauisuchia**

ACCTRAN: 9,11,19,86

DELTRAN: 182

Both: 87,111

### **Poposauroidea**

ACCTRAN: 5,16,20,29,57,59,64,94,156r,157r,165,179



DELTRAN: 19  
Both: 77,85r,99,106r

**Poposauroidea minus *Yarasuchus***

ACCTRAN: 11r,89,90,93,97r,98,114(2),118  
DELTRAN: 5,16  
Both: 113

**Poposauroidea minus *Yarasuchus* and *Qianosuchus***

ACCTRAN: 9r,13(2),17,127,181,185,187  
DELTRAN: 29,57,64,86,89,93,94,114(2),165  
Both: 88,96(2),119,123(2),129

***Effigia* + *Shuvosaurus***

ACCTRAN: 145  
DELTRAN: 36(2),67,90,99r,102,118,125,127(3),128,139,179,181,185,187  
Both: 3,5r,39,41,52(2),53,54,55,60,61,65,74,75,76,83,88(2),105,115r,116,120,131,132(2),  
133,135,140,150

**Rauisuchoidea**

ACCTRAN: 4,10,40,114  
DELTRAN: 14r  
Both: 96,174

***Ticinosuchus* + *Stagonosuchus* + *Araganasuchus* + *Fasolasuchus***

ACCTRAN: 97r,123r  
DELTRAN: 19  
Both: 137r,142

***Ticinosuchus* + *Stagonosuchus* + *Araganasuchus***

ACCTRAN: 147  
DELTRAN: 97r  
Both: 20

***Ticinosuchus* + *Stagonosuchus***

ACCTRAN: 86r,91  
DELTRAN: 123r  
Both: 78

**Prestosuchidae + Rauisuchidae**

ACCTRAN: 19r,23  
DELTRAN: 9,10,40,114  
Both: 44,45,101,102

**Prestosuchidae**

ACCTRAN: 2

DELTRAN: none  
Both: 49,51r,122(2),127

***Batrachotomus + Prestosuchus***

ACCTRAN: 11r,70  
DELTRAN: 4,86  
Both: 5,20,25,26,27,28r,36,42,59,88,100,151r,174r,182r

**Rauisuchidae**

ACCTRAN: 30,31,38r,58,72,91,99,123(2),147  
DELTRAN: none  
Both: 47,62

***Rauisuchus + Postosuchus + Teratosaurus***

ACCTRAN: 33,51(3)  
DELTRAN: 91,99  
Both: 43

***Postosuchus + Teratosaurus***

ACCTRAN: 85r,122(2),127(2),157r,165  
DELTRAN: 4,30,33,51(3),58  
Both: 26,50

**Avemetatarsalia**

ACCTRAN: 78,98,112,130,147,150,154,156(2),166,  
DELTRAN: none  
Both: 37(2),56,64,76,77,96(2),103,104,138,148,168,171,175,178,179,184

***Scleromochlus + Pterosauria***

ACCTRAN: 9,19,57,63r,73,111  
DELTRAN: 1,14r,  
Both: 88(2),118,145,180,182

**Dinosauromorpha**

ACCTRAN: 1r,6,10,14,15,36(2),38,40,67,79(2),108,109,140,149,169  
DELTRAN: 112,130,147,154,156(2),166  
Both: 95,122,126,162,177,181,185,186

***Lagerpeton + Dromomeron***

ACCTRAN: 94,128  
DELTRAN: none  
Both: 131,134,146,152,158(2),163,170(2)

**Dinosauriformes**

ACCTRAN: 136,143  
DELTRAN: 63(2),66,78,79(2),140,149,169

Both: 110,123(2),126(2),141,142,151,155

**Dinosauriformes minus *Marasuchus***

ACCTRAN: 93,95(2),99,120(2),129,176,178r,182,184r

DELTRAN: none

Both: 137(2),144,160,162(2)

**Dinosauriformes minus *Marasuchus* and *Pseudolagosuchus***

ACCTRAN: 122(2),143r,167

DELTRAN: 6,21,95(2),99,129,136,178r,182,184r

Both: 88,138(2),149(2),153,170(2)

***Silesaurus* + *Sacisaurus* + *Eucoelophysis* + *Lewisuchus***

ACCTRAN: 14(2),98r,108r,135,156r

DELTRAN: none

Both: 148r

***Silesaurus* + *Sacisaurus* + *Eucoelophysis***

ACCTRAN:102

DELTRAN: 135,150

Both: 71,132

**Dinosauria**

ACCTRAN: 5,176

DELTRAN: 10,14r,36(2),38,67,98,108,109,120(2),122(2),176

Both: 35,59,81,107,112r,113(2),132(2),133,137r,165

### APPENDIX S3: SCORING DIFFERENCES

A list of scoring differences between the current analysis and the analyses of Parrish (1993), Juul (1994), Benton (2004), and Nesbitt (2007). Character numbers from the original analyses are given at left, and denoted by P (Parrish 1993), J (Juul 1994), MB (Benton 2004), and N (Nesbitt 2007). Scores favoured by the current analysis are denoted by B (Brusatte *et al.*). Alternative scores are given at right. We list scoring disagreements involving taxa not included in our analysis, such as some dinosaur ingroup taxa (e.g. the exemplar theropods *Gallimimus* and *Tyrannosaurus* in Nesbitt [2007]), but these disagreements are not factored into the scoring difference counts and CSSI values in Table 4.

#### **Parrish (1993)**

- P3 *Batrachotomus* (P=?, B=1); *Rauisuchus* P=1, B=?)  
P4 *Batrachotomus* (P=?, B=1), *Rauisuchus* P=1, B=?)  
P5 *Lewisuchus* (P=1, B=0)  
P6 *Rutiodon* (P=2, B=0)  
P7 *Prestosuchus* (P=0, B=?); *Ticinosuchus* (P=0, B=?); *Saurosuchus* (P=0, B=?);  
*Lotosaurus* (P=0, B=?); *Batrachotomus* (P=?, B=1); *Fasolasuchus* (P=0, B=?);  
*Rauisuchus* (P=0, B=?); *Gracilisuchus* (P=0, B=?); *Postosuchus* (P=0, B=1)  
P10 *Marasuchus* (P=1, B=0); *Rutiodon* (P=0, B=1); *Batrachotomus* (P=?, B=1);  
*Rauisuchus* (P=1, B=?)  
P13 *Riojasuchus* (P=1, B=0); *Lotosaurus* (P=1, B=?); *Batrachotomus* (P=?, B=1)  
P14 *Ticinosuchus* (P=1, B=?); *Saurosuchus* (P=1, B=0); *Batrachotomus* (P=?, B=1);  
*Fasolasuchus* (P=1, B=?); *Postosuchus* (P=1, B=0)  
P16 *Plateosaurus* (P=0, B=?); *Ticinosuchus* (P=1, B=0); *Lewisuchus* (P=0, B=?);  
*Lotosaurus* (P=0, B=?); *Fasolasuchus* (P=1, B=0); *Rauisuchus* (P=?, B=1);  
*Gracilisuchus* (P=0, B=1); *Postosuchus* (P=0, B=?); *Alligator* (P=0, B=1)  
P19 *Marasuchus* (P=0, B=1); *Plateosaurus* (P=0, B=1); *Riojasuchus* (P=0, B=1);  
*Rutiodon* (P=0, B=1)  
P21 *Marasuchus* (P=?, B=0); *Plateosaurus* (P=0, B=?); *Prestosuchus* (P=1, B=0);  
*Lewisuchus* (P=1, B=?); *Desmotosuchus* (P=1, B=0); *Lotosaurus* (P=1, B=0);  
*Batrachotomus* (P=1, B=0); *Ticinosuchus* (P=?, B=1)  
P23 *Prestosuchus* (P=1, B=0); *Ticinosuchus* (P=1, B=?); *Lewisuchus* (P=0, B=?);  
*Lotosaurus* (P=?, B=0); *Batrachotomus* (P=?, B=0); *Fasolasuchus* (P=1, B=?);  
*Rauisuchus* (P=1, B=?); *Postosuchus* (P=?, B=1)  
P24 *Saurosuchus* (P=1, B=0); *Batrachotomus* (P=1, B=0); *Fasolasuchus* (P=1, B=?)

- P25 *Ticinosuchus* (P=0, B=?); *Lewisuchus* (P=1, B=0); *Desmatosuchus* (P=1, B=0);  
*Lotosaurus* (P=1, B=0); *Gracilisuchus* (P=1, B=0)
- P26 *Plateosaurus* (P=2, B=0); *Rutiodon* (P=0, B=1); *Prestosuchus* (P=0, B=1);  
*Ticinosuchus* (P=0, B=1); *Saurosuchus* (P=0, B=1); *Lotosaurus* (P=0?, B=1)
- P28 *Rutiodon* (P=0, B=?); *Prestosuchus* (P=0, B=?); *Ticinosuchus* (P=0, B=?);  
*Lotosaurus* (P=1, B=0); *Batrachotomus* (P=?, B=0); *Rauisuchus* (P=1, B=?);  
*Gracilisuchus* (P=1, B=?)
- P29 *Rutiodon* (P=0, B=?); *Prestosuchus* (P=0, B=?); *Lotosaurus* (P=1, B=0);  
*Batrachotomus* (P=1, B=0); *Gracilisuchus* (P=1, B=?)
- P32 *Marasuchus* (P=1, B=0); *Prestosuchus* (P=0, B=1); *Saurosuchus* (P=0, B=1);  
*Lotosaurus* (P=?, B=1); *Batrachotomus* (P=?, B=1); *Rauisuchus* (P=?, B=1);  
*Gracilisuchus* (P=1, B=0); *Alligator* (P=1, B=0)
- P35 *Riojasuchus* (P=?, B=1); *Ticinosuchus* (P=0, B=?); *Lotosaurus* (P=0, B=?);  
*Batrachotomus* (P=?, B=0); *Fasolasuchus* (P=1, B=?); *Rauisuchus* (P=0, B=?);  
*Postosuchus* (P=1, B=0); *Gracilisuchus* (P=0, B=1)
- P36 *Marasuchus* (P=1, B=0); *Prestosuchus* (P=0, B=?); *Saurosuchus* (P=0, B=1);  
*Lotosaurus* (P=0, B=?); *Fasolasuchus* (P=?, B=1); *Rauisuchus* (P=0, B=?);  
*Gracilisuchus* (P=1, B=0)
- P40 *Prestosuchus* (P=0, B=?); *Ticinosuchus* (P=?, B=1); *Saurosuchus* (P=?, B=1);  
*Lewisuchus* (P=0, B=?); *Lotosaurus* (P=0, B=?); *Rauisuchus* (P=0, B=?);  
*Gracilisuchus* (P=0, B=?)

#### Juul (1994)

- J4 *Gracilisuchus* (J=0, B=1)
- J10 Phytosauria (J=1, B=0)
- J16 Pterosauria (J=1, B=0); *Herrerasaurus* (J=1, B=?)
- J20 *Gracilisuchus* (J=?, B=1); Ornithosuchidae (J=1, B=0)
- J22 Aetosauria (J=1, B=2); Prestosuchidae (J=1, B=2)
- J26 Ornithosuchidae (J=1, B=?)
- J27 *Gracilisuchus* (J=?, B=1)
- J28 *Gracilisuchus* (J=?, B=1)
- J29 Pterosauria (J=0, B=?); *Herrerasaurus* (J=0, B=?); Ornithischia (J=0, B=?);  
Saurischia (J=0, B=?); Neotheropoda (J=0, B=?)
- J30 Pterosauria (J=0, B=?); *Herrerasaurus* (J=0, B=?); Ornithischia (J=0, B=?);  
Sauropodomorpha (J=0, B=?); Neotheropoda (J=0, B=?)
- J31 *Postosuchus* (J=1, B=0)
- J32 *Gracilisuchus* (J=?, B=1)
- J34 *Postosuchus* (J=0, B=1); Crocodylomorpha (J=?, B=1); Ornithosuchidae (J=0,  
B=1)
- J35 *Marasuchus* (J=0, B=1)
- J38 Aetosauria (J=0, B=1)
- J39 Crocodylomorpha (J=1, B=0); Ornithosuchidae (J=1, B=0); *Marasuchus* (J=1,  
B=0); *Herrerasaurus* (J=1, B=0); Ornithischia (J=1, B=0); Sauropodomorpha  
(J=1, B=0); Neotheropoda (J=1, B=0)
- J43 *Marasuchus* (J=0, B=1)
- J44 *Marasuchus* (J=?, B=1)

- J45 *Gracilisuchus* (J=1, B=0)  
 J46 *Postosuchus* (J=2, B=0)  
 J48 *Herrerasaurus* (J=0, B=1)  
 J49 *Herrerasaurus* (J=1, B=0)  
 J50 *Gracilisuchus* (J=0, B=1); *Crocodylomorpha* (J=0, B=1)  
 J53 *Postosuchus* (J=0, B=?)  
 J54 *Phytosauria* (J=0, B=1); *Gracilisuchus* (J=0, B=1); *Prestosuchidae* (J=0, B=1);  
*Postosuchus* (J=0, B=1); *Crocodylomorpha* (J=0, B=1)  
 J57 *Gracilisuchus* (J=1, B=0); *Pterosauria* (J=1, B=0)  
 J58 *Postosuchus* (J=?, B=0); *Gracilisuchus* (J=0, B=1)  
 J60 *Postosuchus* (J=1, B=0)  
 J65 *Pterosauria* (J=0, B=1); *Marasuchus* (J=0, B=1); *Herrerasaurus* (J=0, B=1)  
 J66 *Prestosuchidae* (J=?, B=1)  
 J70 *Gracilisuchus* (J=1, B=?); *Crocodylomorpha* (J=1, B=0); *Ornithosuchidae* (J=0,  
 B=?)  
 J72 *Aetosauria* (J=1, B=0); *Pterosauria* (J=0, B=?); *Marasuchus* (J=?, B=0);  
*Herrerasaurus* (J=0, B=?); *Ornithischia* (J=0, B=?); *Sauropodomorpha* (J=0,  
 B=?); *Neotheropoda* (J=0, B=?)  
 J74 *Gracilisuchus* (J=1, B=0); *Postosuchus* (J=2, B=0)

#### **Benton (2004)**

- MB1 *Lagerpeton* (MB=0, B=?); *Marasuchus* (MB=0, B=?)  
 MB2 *Prestosuchus* (MB=1, B=0); *Fasolasuchus* (MB=0, B=?)  
 MB8 *Phytosauria* (MB=1, B=0); *Gracilisuchus* (MB=1, B=0)  
 MB11 *Gracilisuchus* (MB=0, B=1); *Postosuchus* (MB=1, B=0)  
 MB12 *Phytosauria* (MB=1, B=0); *Gracilisuchus* (MB=1, B=0); *Postosuchus* (MB=2,  
 B=0)  
 MB17 *Ornithosuchidae* (MB=0, B=?); *Gracilisuchus* (MB=1, B=?); *Crocodylomorpha*  
 (MB=1, B=0)  
 MB19 *Ornithosuchidae* (MB=1, B=?); *Gracilisuchus* (MB=0, B=1); *Prestosuchus*  
 (MB=?, B=0)  
 MB31 *Prestosuchus* (MB=0, B=?)  
 MB32 *Prestosuchus* (MB=0, B=?); *Gracilisuchus* (MB=0, B=1); *Marasuchus* (MB=0,  
 B=1); *Ticinosuchus* (MB=0, B=1)  
 MB33 *Ornithosuchidae* (MB=1, B=?); *Marasuchus* (MB=0, B=?); *Herrerasaurus*  
 (MB=0, B=?); *Saurosuchus* (MB=?, B=0)  
 MB35 *Ornithosuchidae* (MB=1, B=0)  
 MB36 *Prestosuchus* (MB=0, B=1); *Saurosuchus* (MB=0, B=1); *Postosuchus* (MB=0,  
 B=1)  
 MB37 *Postosuchus* (MB=0, B=1); *Saurosuchus* (MB=?, B=0)  
 MB38 *Ticinosuchus* (MB=1, B=0); *Prestosuchus* (MB=1, B=0); *Postosuchus* (MB=1,  
 B=?); *Scleromochlus* (MB=?, B=1); *Marasuchus* (MB=?, B=1)  
 MB39 *Postosuchus* (MB=1, B=?); *Scleromochlus* (MB=?, B=1); *Marasuchus* (MB=?,  
 B=1)  
 MB42 *Ticinosuchus* (MB=1, B=?); *Postosuchus* (MB=1, B=0); *Saurosuchus* (MB=?,  
 B=0)

- MB43 *Prestosuchus* (MB=0, B=?)  
 MB51 *Prestosuchus* (MB=?, B=0); *Gracilisuchus* (MB=?, B=0)  
 MB53 *Postosuchus* (MB=1, B=0)  
 MB54 *Ticinosuchus* (MB=0, B=?)  
 MB55 *Prestosuchus* (MB=0, B=?); *Saurosuchus* (MB=0, B=?); *Gracilisuchus* (MB=?, B=0); *Marasuchus* (MB=0, B=1)  
 MB60 *Fasolasuchus* (MB=0, B=1); *Lagerpeton* (MB=1, B=0)  
 MB63 *Ticinosuchus* (MB=0, B=?); *Prestosuchus* (MB=?, B=0); *Saurosuchus* (MB=0, B=?)  
 MB64 *Ticinosuchus* (MB=0, B=?)  
 MB65 *Marasuchus* (MB=0, B=1)  
 MB66 *Scleromochlus* (MB=0, B=1); *Lagerpeton* (MB=0, B=1); *Marasuchus* (MB=0, B=1)  
 MB70 *Ticinosuchus* (MB=1, B=?)  
 MB76 *Lagerpeton* (MB=0, B=1)  
 MB78 *Scleromochlus* (MB=0, B=?)  
 MB80 *Scleromochlus* (MB=0, B=?); Pterosauria (MB=0, B=?); *Herrerasaurus* (MB=0, B=?); Theropoda (MB=0, B=?); Sauropodomorpha (MB=0, B=?); Ornithischia (MB=0, B=?)  
 MB81 *Scleromochlus* (MB=0, B=?); Pterosauria (MB=0, B=?); *Herrerasaurus* (MB=0, B=?); Theropoda (MB=0, B=?); Sauropodomorpha (MB=0, B=?); Ornithischia (MB=0, B=?)  
 MB82 Aetosauria (MB=1, B=0); *Prestosuchus* (MB=1, B=0); *Ticinosuchus* (MB=?, B=1); *Scleromochlus* (MB=0, B=?); Pterosauria (MB=0, B=?); *Herrerasaurus* (MB=0, B=?); Theropoda (MB=0, B=?); Sauropodomorpha (MB=0, B=?); Ornithischia (MB=0, B=?)  
 MB88 *Gracilisuchus* (MB=1, B=0)  
 MB89 *Postosuchus* (MB=?, B=0); *Scleromochlus* (MB=?, B=0)  
 MB90 *Gracilisuchus* (MB=0, B=1)  
 MB91 *Gracilisuchus* (MB=0, B=1)  
 MB93 Phytosauria (MB=0, B=1); Ornithosuchidae (MB=0, B=1); *Ticinosuchus* (MB=0, B=1); *Prestosuchus* (MB=0, B=1); *Gracilisuchus* (MB=0, B=1); Crocodylomorpha (MB=0, B=1)  
 MB95 *Prestosuchus* (MB=0, B=1); *Postosuchus* (MB=0, B=?); *Scleromochlus* (MB=0, B=?); Pterosauria (MB=0, B=?); *Lagerpeton* (MB=0, B=?); *Marasuchus* (MB=0, B=?); *Herrerasaurus* (MB=0, B=?); Theropoda (MB=0, B=?); Sauropodomorpha (MB=0, B=?); Ornithischia (MB=0, B=?)

### Nesbitt (2007)

- N1 *Lagerpeton* (N=0, B=?); *Marasuchus* (N=0, B=?)  
 N2 *Lotosaurus* (N=?, B=0)  
 N5 *Arizonasaurus* (N=?, B=0); *Lotosaurus* (N=0, B=?)  
 N6 *Lagerpeton* (N=0, B=?); *Arizonasaurus* (N=1, B=0); *Lotosaurus* (N=1, B=0)  
 N7 *Effigia* (N=?, B=0); *Arizonasaurus* (N=?, B=0); *Shuvosaurus* (N=?, B=0)  
 N8 *Postosuchus* (N=2, B=0)  
 N10 *Effigia* (N=?, B=0); *Arizonasaurus* (N=?, B=0); *Shuvosaurus* (N=?, B=0)

- N11 *Effigia* (N=1, B=?); *Lotosaurus* (N=0, B=1)
- N12 Phytosauria (N=1, B=0); Ornithosuchidae (N=0, B=?); Crocodylomorpha (N=1, B=0); *Effigia* (N=?, B=0); *Shuvosaurus* (N=?, B=0)
- N15 *Effigia* (N=1, B=0); *Arizonasaurus* (N=1, B=0); *Shuvosaurus* (N=?, B=0); *Sillosuchus* (N=1, B=0); *Lotosaurus* (N=1, B=0)
- N16 Aetosauria (N=1, B=0); *Effigia* (N=?, B=0); *Arizonasaurus* (N=?, B=0); *Shuvosaurus* (N=?, B=1); *Sillosuchus* (N=?, B=0); *Saurosuchus* (N=?, B=0)
- N17 Ornithosuchidae (N=0, B=?); Aetosauria (N=?, B=1); *Marasuchus* (N=0, B=?);
- N18 *Postosuchus* (N=0, B=1); *Arizonasaurus* (N=0, B=1); *Sillosuchus* (N=1, B=?)
- N20 Ornithosuchidae (N=0, B=1); *Postosuchus* (N=0, B=1); *Effigia* (N=0, B=?); *Shuvosaurus* (N=0, B=?); *Lotosaurus* (N=0, B=?)
- N21 *Postosuchus* (N=0, B=?); *Saurosuchus* (N=0, B=?)
- N22 *Postosuchus* (N=1, B=?); *Marasuchus* (N=?, B=1); *Saurosuchus* (N=0, B=?)
- N23 *Postosuchus* (N=1, B=0); *Marasuchus* (N=?, B=1); *Effigia* (N=1, B=0); *Arizonasaurus* (N=1, B=?); *Shuvosaurus* (N=1, B=0); *Saurosuchus* (N=1, B=0)
- N24 *Saurosuchus* (N=0, B=?)
- N25 *Saurosuchus* (N=0, B=?)
- N26 *Saurosuchus* (N=0, B=?)
- N30 *Lotosaurus* (N=1, B=?)
- N31 Ornithosuchidae (N=1, B=0); *Lagerpeton* (N=?, B=0); *Marasuchus* (N=1, B=0); *Gallimimus* (N=0, B=1); Sauropodomorpha (N=0, B=1); Ornithischia (N=0, B=1); *Tyrannosaurus* (N=0, B=1); *Coelophysis* (N=0, B=1)
- N34 *Postosuchus* (N=1, B=0)
- N35 *Lotosaurus* (N=0, B=1)
- N36 *Saurosuchus* (N=1, B=?)
- N37 *Marasuchus* (N=0, B=1); *Saurosuchus* (N=1, B=?); *Lotosaurus* (N=1, B=?)
- N38 *Lotosaurus* (N=1, B=?)
- N39 *Lotosaurus* (N=0, B=?)
- N40 *Shuvosaurus* (N=?, B=0)
- N41 *Lagerpeton* (N=1, B=0); *Effigia* (N=0, B=1); *Shuvosaurus* (N=0, B=1); *Sillosuchus* (N=?, B=0)
- N42 *Sillosuchus* (N=?, B=0)
- N43 *Saurosuchus* (N=0, B=?); *Sillosuchus* (N=0, B=?)
- N44 Aetosauria (N=0, B=1); *Effigia* (N=0, B=?)
- N46 *Marasuchus* (N=0, B=1)
- N47 *Lagerpeton* (N=0, B=1); *Marasuchus* (N=0, B=1)
- N48 Ornithosuchidae (N=1, B=0)
- N50 Ornithosuchidae (N=0, B=?)
- N51 Ornithosuchidae (N=?, B=1)
- N55 *Lagerpeton* (N=0, B=1)
- N59 Pterosauria (N=0, B=?); *Gallimimus* (N=0, B=?); Sauropodomorpha (N=0, B=?); Ornithischia (N=0, B=?); *Tyrannosaurus* (N=0, B=?); *Coelophysis* (N=0, B=?)
- N60 Pterosauria (N=0, B=?); *Gallimimus* (N=0, B=?); Sauropodomorpha (N=0, B=?); Ornithischia (N=0, B=?); *Tyrannosaurus* (N=0, B=?); *Coelophysis* (N=0, B=?)



- N61 Pterosauria (N=0, B=?); *Gallimimus* (N=0, B=?); Sauropodomorpha (N=0, B=?); Ornithischia (N=0, B=?); *Tyrannosaurus* (N=0, B=?); *Coelophysis* (N=0, B=?); *Saurosuchus* (N=0, B=1)
- N64 *Postosuchus* (N=0, B=?)
- N66 *Postosuchus* (N=1, B=0); Crocodylomorpha (N=0, B=1); *Lotosaurus* (N=0, B=?)
- N67 *Postosuchus* (N=1, B=0); *Lotosaurus* (N=0, B=?)
- N68 *Lotosaurus* (N=0, B=?)
- N69 Phytosauria (N=0, B=1); Ornithosuchidae (N=0, B=1); *Postosuchus* (N=0, B=1); Crocodylomorpha (N=0, B=1); *Effigia* (N=0, B=1); *Shuvosaurus* (N=0, B=1); *Lotosaurus* (N=0, B=?)
- N70 *Lotosaurus* (N=0, B=?)
- N72 *Postosuchus* (N=2, B=?); Ornithischia (N=?, B=0); *Saurosuchus* (N=3, B=2); *Sillosuchus* (N=?, B=0)
- N74 *Marasuchus* (N=?, B=0)
- N75 *Arizonasaurus* (N=0, B=?); *Lotosaurus* (N=?, B=1)
- N76 *Lotosaurus* (N=?, B=0)
- N83 *Sillosuchus* (N=1, B=?)