

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

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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 standardizes 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 Rausuchia 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.

Keywords: Crocodylomorpha; Crurotarsi; Dinosauria; Mesozoic; rausuchians; Triassic

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 recognized 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

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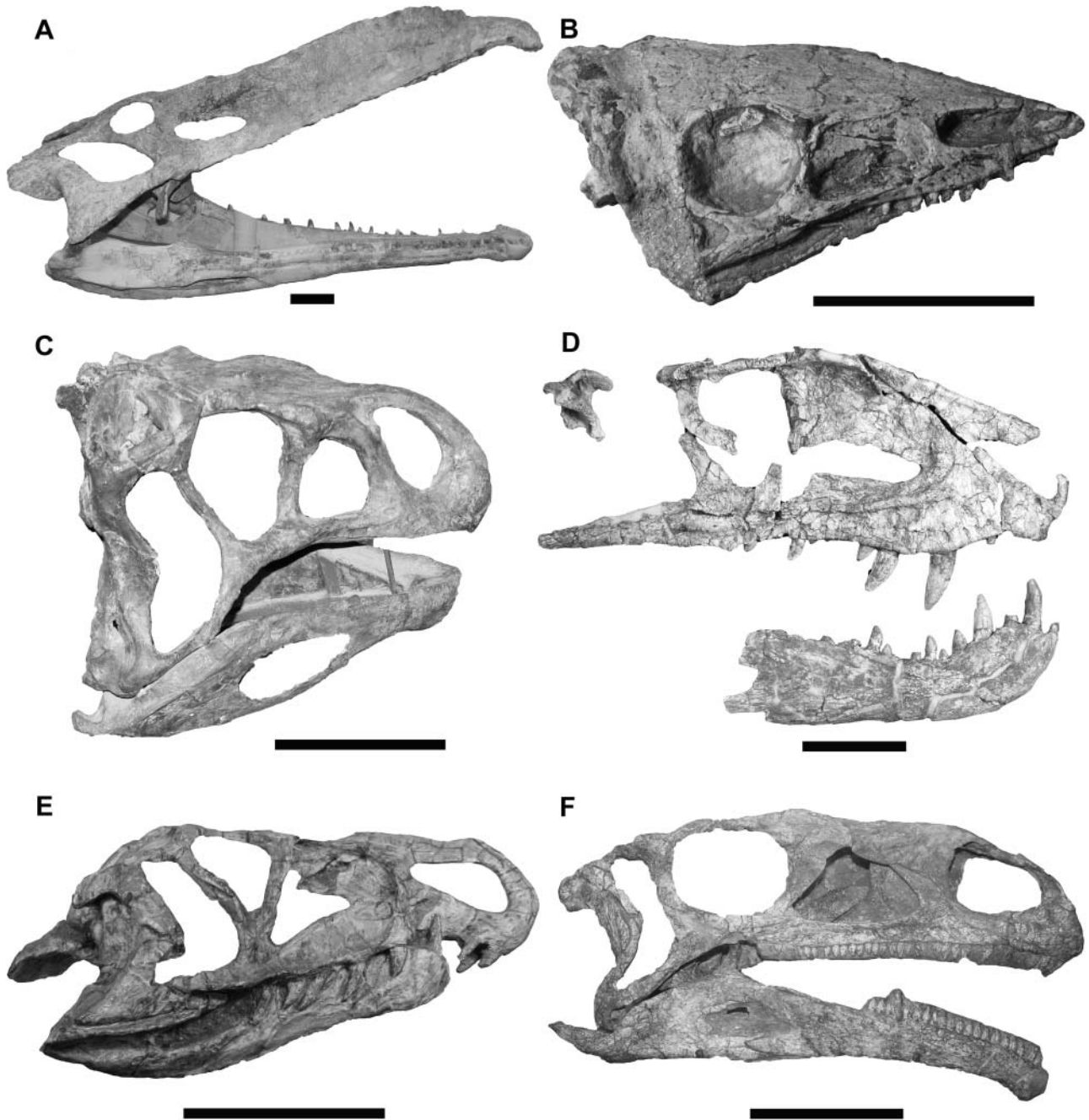


Figure 1. The skulls of several basal archosaurs, showing the diversity of cranial form within the group during the Triassic. **A**, *Nicrosaurus* (Phytosauria); **B**, *Aetosaurus* (Aetosauria); **C**, *Lotosaurus* (Popsauroida, ‘rauisuchian’); **D**, *Postosuchus* (Rauisuchoidea, ‘rauisuchian’) (image reversed); **E**, *Riojasuchus* (Ornithosuchidae) (cast); **F**, *Plateosaurus* (Dinosauria: Sauropodomorpha). Scale bars for A and C–F = 10 cm, for B = 5 cm.

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 characterized by limited or

problematic taxon and character sampling (see below). First, although several archosaur subgroups have been recognized and characterized 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 re-description 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 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, Argentina; **MCN:** Museu de Ciências Natu-

rais, 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:** Muséum 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:** Paleontología de Vertebrados, Instituto “Miguel Lillo”, San Miguel de Tucumán, Argentina; **PVSJ:** División de Paleontología de Vertebrados del Museo de Ciencias Naturales y 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:** Universidade Federal do Rio Grande do Sul, Porto Alegre, RS 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 (Table 1). 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. Gauthier 1986; Benton & Clark 1988; 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

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) and studies that presented a datamatrix but did not analyse it quantitatively (e.g. Gauthier 1986; Novas 1989, 1992; Sereno 1999). Informative characters are those 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 re-analysed 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	Generic	Suprageneric	Informative				
Authors	Taxa	Taxa	Characters	MPTs	TL	CI	RI
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	Generic	Suprageneric	Informative				
Authors	Taxa	Taxa	Characters	MPTs	TL	CI	RI
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	Generic	Suprageneric	Informative				
Authors	Taxa	Taxa	Characters	MPTs	TL	CI	RI
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 & Hungerbühler 2007	8	3	34	2	48	0.77	0.86
CURRENT ANALYSIS	Generic	Suprageneric	Informative				
Authors	Taxa	Taxa	Characters	MPTs	TL	CI	RI
Brusatte <i>et al.</i>	32	7	187	70	747	0.31	0.68

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 Upper 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 + Dinosauromorpha (Benton 1999, 2004).

Crurotarsi

The crocodile line of crown-group Archosauria, Crurotarsi, includes crocodylomorphs (crocodylians and their



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).

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 (Serenó & 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. Aetosaurus (also known as Stagonolepididae) are a group of quadrupedal, armoured herbivores (and possibly omnivores) known globally from the Upper 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 crurotarsan 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 Upper 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 Upper 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 semiaquatic taxon in a large basal polytomy with numerous other taxa (Li *et al.* 2006). *Revueltosaurus*, from the Upper 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) analysed eight 'rauisuchian' taxa and argued for a polyphyletic Rauisuchia comprising three separate monophyletic groups. Weinbaum & Hungerbühler (2007) also included eight 'rauisuchians' and recovered 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 found support for a monophyletic Rausuchia 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 (Juil 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; Juil 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 Rausuchia to refer specifically to a monophyletic clade comprised of *all* 'rauisuchian' taxa. This distinction is necessary because only some analyses find a monophyletic Rausuchia, 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 characterized 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 (phytosaur, 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 supra-generic 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 & Clark 1988; Sereno 1991a; Juil 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 chimeric 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.

Secondly, 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-recognized 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, 2008b). 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 2003) 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*, *Tsylimosuchus*, *Vjushkovisaurus*, *Vytshegdosuchus*: Gower & Sennikov 2000; *Ctenosauriscus*, *Hypselorhachis*: Nesbitt 2005; *Sikannisuchus*: Nicholls *et al.* 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 Ornithosuchiidae, 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; *Proterochampsia*: 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

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			
Genus	Age	Location	Author
<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			
Genus	Age	Location	Author
<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			
Genus	Age	Location	Author
<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 1985a
<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>	Ladinian (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 & Majumdar 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.

Suprageneric Taxon	Age	Exemplars
Aetosauria	Carnian-Rhaetian (LT)	<i>Aetosaurus</i> , <i>Desmatosuchus</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 previous studies. Listed are numbers of shared taxa (both genus-level and suprageneric) between the current analysis and the previous study; the number of informative characters in the previous analysis; the number of shared characters between the current and previous analyses; the number of 'used' characters: informative characters in the previous analysis that were used in the current study (not always equivalent to shared characters as 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 *Avematarsalia* (A) or *Crurotarsi* (C) 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 =		Character Similarity Index (CSI)	Shared Character State Index (CSSI)
							Generic/Suprageneric	Suprageneric		
Sereno & Arcucci 1990 (CA)	0	5	23	21 (11%)	21 (91%)	0/0	0/2	0/2	0.11	0.99
Sereno 1991a (CA)	3	4	28	27 (15%)	26 (93%)	2/2	5/3	5/3	0.15	0.96
Juul 1994 (CA)	4	9	51	44 (24%)	44 (86%)	21/20	13/16	13/16	0.23	0.90
Bennett 1996 (CA)	2	5	63	34 (19%)	37 (59%)	3/6	12/3	12/3	0.16	0.93
Benton 1999 (CA)	5	9	63	60 (33%)	59 (94%)	17/14	25/19	25/19	0.32	0.94
Benton 2004 (CA)	10	8	64	59 (32%)	56 (88%)	34/8	46/19	46/19	0.31	0.93
Nesbitt 2007 (CA)	10	7	70	66 (36%)	65 (93%)	34/12	65/12	65/12	0.35	0.92
Irmis <i>et al.</i> 2007a (CA)	17	0	80	70 (38%)	70 (88%)	88/0	101/0	101/0	0.36	0.88
Novas 1989 (A)	3	1	8	6 (3%)	7 (88%)	0/0	0/0	0/0	0.05	1.00
Novas 1992 (A)	3	2	8	15 (8%)	8 (100%)	2/0	0/0	0/0	0.14	0.97
Novas 1993 (A)	3	4	23	21 (11%)	21 (91%)	2/0	4/0	4/0	0.18	0.97
Novas 1996 (A)	4	3	37	35 (19%)	34 (92%)	1/0	16/0	16/0	0.29	0.96
Sereno 1999 (A)	2	2	18	14 (8%)	14 (78%)	0/0	0/0	0/0	0.11	1.00
Ezcurra 2006 (A)	10	0	26	21 (11%)	22 (85%)	5/-	2/-	2/-	0.17	0.97
Langer & Benton 2006 (A)	2	3	6	9 (5%)	6 (100%)	1/0	0/0	0/0	0.08	0.98
Parrish 1993 (C)	15	0	32	17 (9%)	18 (56%)	45/-	67/-	67/-	0.10	0.69
Olsen <i>et al.</i> 2000 (C)	6	0	14	13 (7%)	13 (93%)	2/-	5/-	5/-	0.08	0.94
Benton & Walker 2002 (C)	13	0	35	29 (16%)	32 (91%)	17/-	33/-	33/-	0.18	0.91
Nesbitt 2003 (C)	5	2	24	14 (8%)	15 (63%)	2/2	6/0	6/0	0.09	0.93
Gower & Nesbitt 2006 (C)	6	2	13	7 (4%)	7 (54%)	0/1	2/0	2/0	0.04	0.96
Weinbaum & Hungerbühler 2007 (C)	8	3	34	28 (15%)	28 (82%)	26/7	23/2	23/2	0.18	0.85

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 (Serenó 1999; Langer & Benton 2006), Ornithosuchidae (Serenó 1991a), Phytosauria (Serenó 1991a), Pterosauria (Serenó 1991a) and Saurischia (Serenó 1999; Langer & Benton 2006).

Characters are listed in a standardized format (Appendix 1), with consistent use of anatomical terms and measurements (based on Serenó 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 (Serenó 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 chimerical. Pending a detailed revision of *Prestosuchus* taxonomy, (which is currently in progress by 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 analysed 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 analysing 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

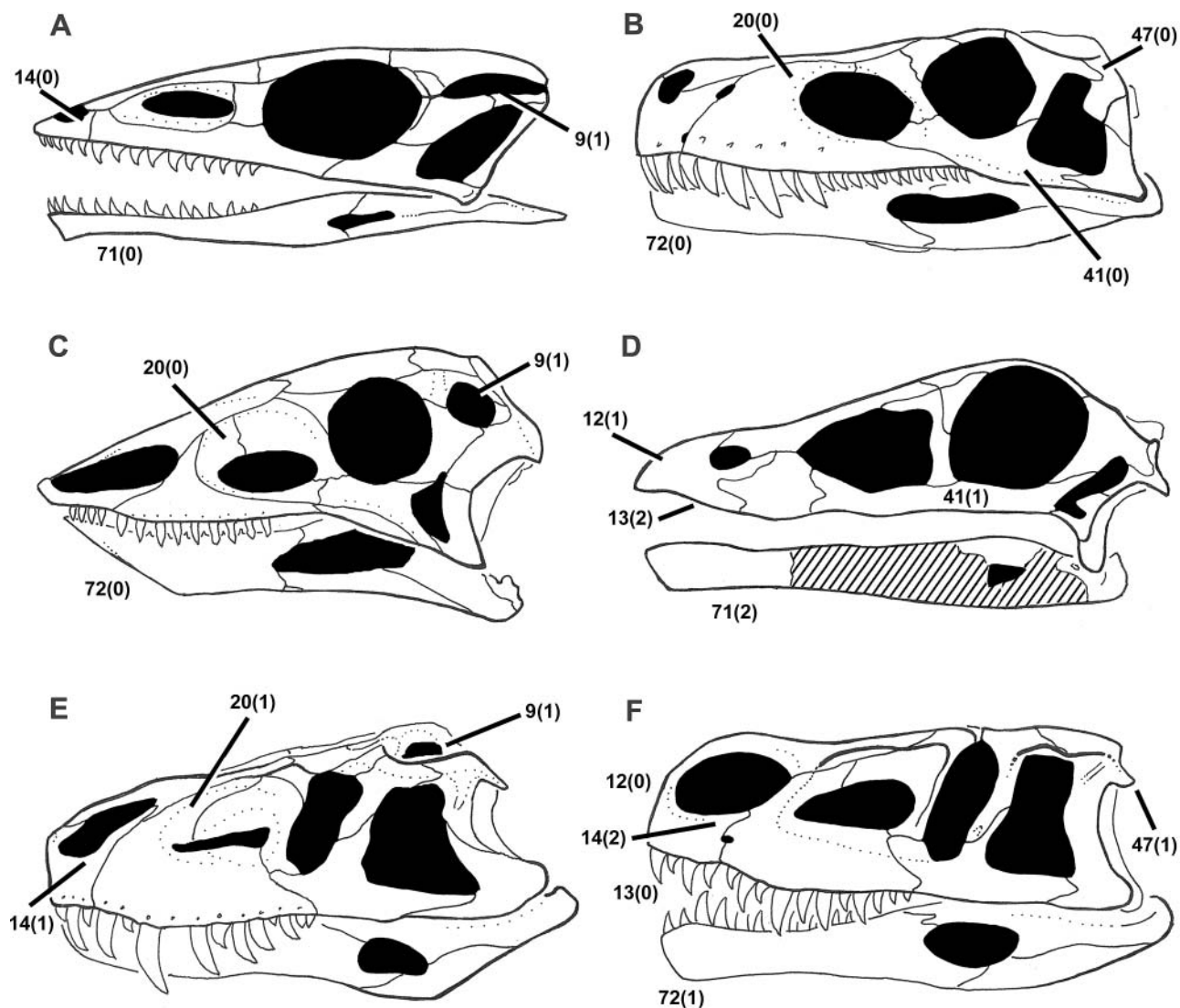


Figure 3. Illustration of cladistic characters new to this study (selected cranial characters). **A**, *Scleromochlus* (after Benton 1999); **B**, *Herrerasaurus* (after Sereno & Novas 1993); **C**, *Aetosaurus* (after Walker 1961, and SMNS 5770); **D**, *Shuvosaurus* (after Rauhut 1997); **E**, *Prestosuchus* (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.

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

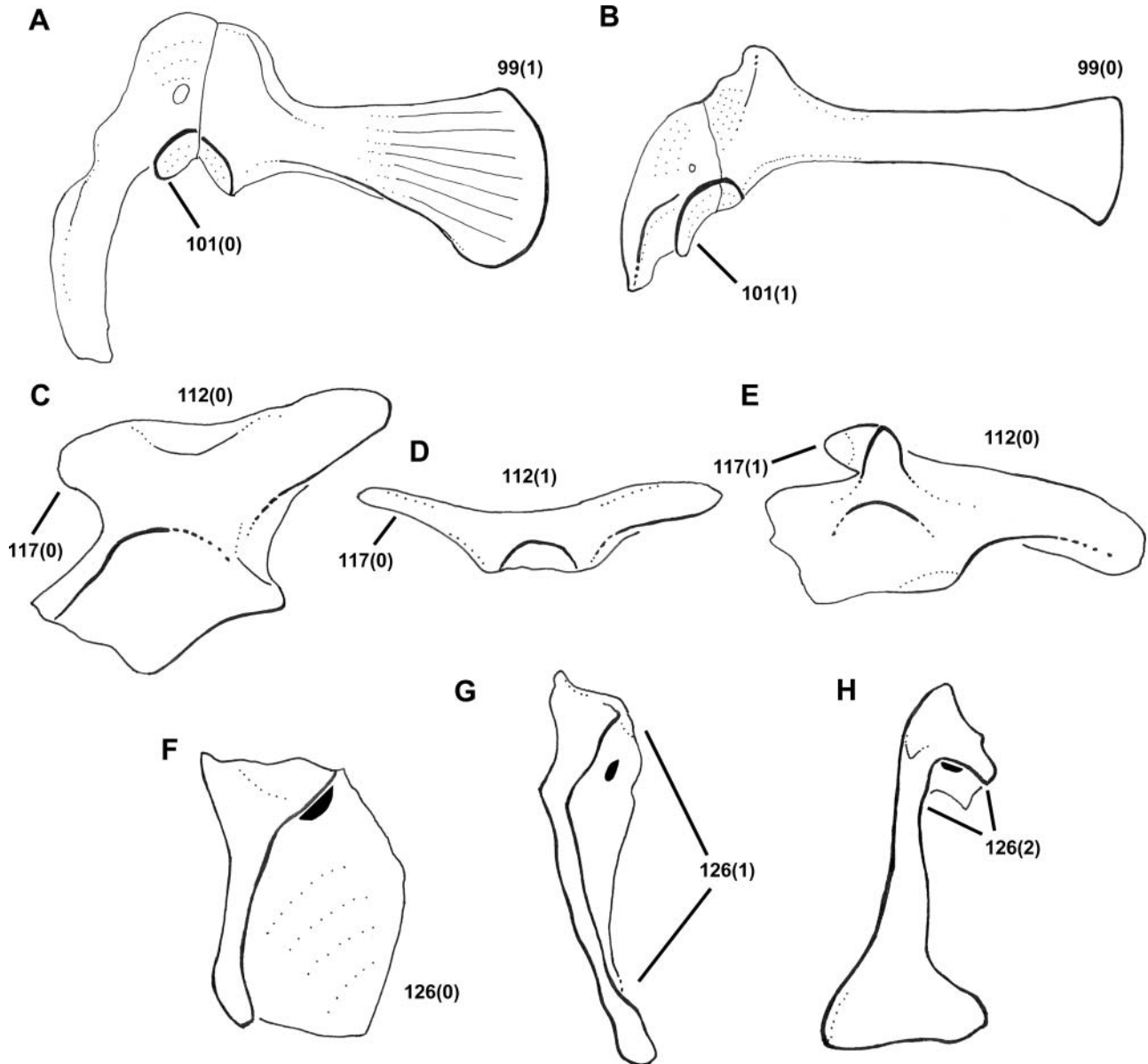


Figure 4. Illustration of cladistic characters new to this study (selected postcranial characters). **A**, scapula-coracoid of *Sphenosuchus* (after Walker 1990); **B**, scapula-coracoid of *Ornithosuchus* (after Walker 1964); **C**, ilium of *Parasuchus* (after Chatterjee 1978); **D**, ilium of *Eudimorphodon* (after Wild 1978); **E**, ilium of *Arizonasaurus* (after Nesbitt 2005); **F**, pubis of *Parasuchus* (after Chatterjee 1978); **G**, pubis of *Tikisuchus* (after Chatterjee & Majumdar 1987); **H**, pubis of *Herrerasaurus* (after Novas 1993). All illustrations in left lateral view, and corresponding elements scaled to similar length and oriented identically for ease of comparison. Numbers refer to character number in Appendix 1, and numbers in parentheses refer to character states.

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 rautsichian clade is divided into two major subclades. The first includes taxa often referred to as 'rauisuchids' and 'prestosuchids', including *Batrachotomus*, *Postosuchus*, *Prestosuchus*, *Rautsichus*, *Saurosuchus*, and *Teratosaurus*. Within this clade are sister-group pairs of *Batrachotomus* + *Prestosuchus* and *Postosuchus* + *Teratosaurus*, and

all relationships are completely resolved. The second raiusuchian 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 raiusuchians 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 characterizes 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 may not be found in alternative stud-

ies (Gower & Wilkinson 1996). For instance, the term Paracrocodyliformes, given by Weinbaum & Hungerbühler (2007) to unite ‘raiusuchid/prestosuchid’ ‘raiusuchians’ 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, Raiusuchia, 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 + raiusuchian node, and the cluster of enigmatic raiusuchians centred on *Ticinosuchus*. However, we do refer to the major clade of ‘raiusuchids’, ‘prestosuchids’, and the subclade centered on *Ticinosuchus* as Raiusuchoidea, a superfamily-level taxon that has not previously been used but is considered established under the ICZN Principle of Coordination. Within Raiusuchoidea we use the names Raiusuchidae and Prestosuchidae to refer to clusters of taxa including the eponymous *Raiusuchus* 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 *Raiusuchus* and *Prestosuchus* is necessary to stabilize the usage of Raiusuchidae and Prestosuchidae. We realize that Teratosauridae (Cope 1871) was named prior to the more widely used Raiusuchidae (Huene 1936), and if *Raiusuchus* 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 raiusuchians (*Arizonasaurus*, *Bromsgroveia*, *Effigia*, *Lotosaurus*, *Poposaurus*, *Qianosuchus*, *Shuvosaurus*, *Sillosuchus*, *Yarasuchus*) as ‘Poposauroida’, following usage outlined by Weinbaum & Hungerbühler (2007). Sereno’s (2005) definition of Poposauridae refers to this clade, but we prefer Poposauroida 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 Poposauroida

are still unresolved we do not use additional family-level taxa such as Poposauridae or Ctenosauriscidae.

Alternative topologies. Specific alternative topologies are reviewed in the discussion section below, but two deserve further comment. First, enforcing all raiusuchians, 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 Rausuchia, requires only one additional step. Despite this alteration the relationships within both poposauroid and raiusuchoid clades are essentially identical to those in the original analysis, indicating that only a small amount of character data supports a monophyletic Rausuchia.

Character and taxon alterations. When the pterosaur exemplars are removed and the dataset reanalysed, 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 raiusuchians and Ornithosuchiidae. Within this latter clade is a sister-grouping of poposauroids and ornithosuchids, which prevents a monophyletic Rausuchia. Furthermore, several taxa recovered as basal raiusuchoids (*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 realized.

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 raiusuchians + ornithosuchids all fall into a basal polytomy, and raiusuchians 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 nearly identical 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 *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 level 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) (Serenó & 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

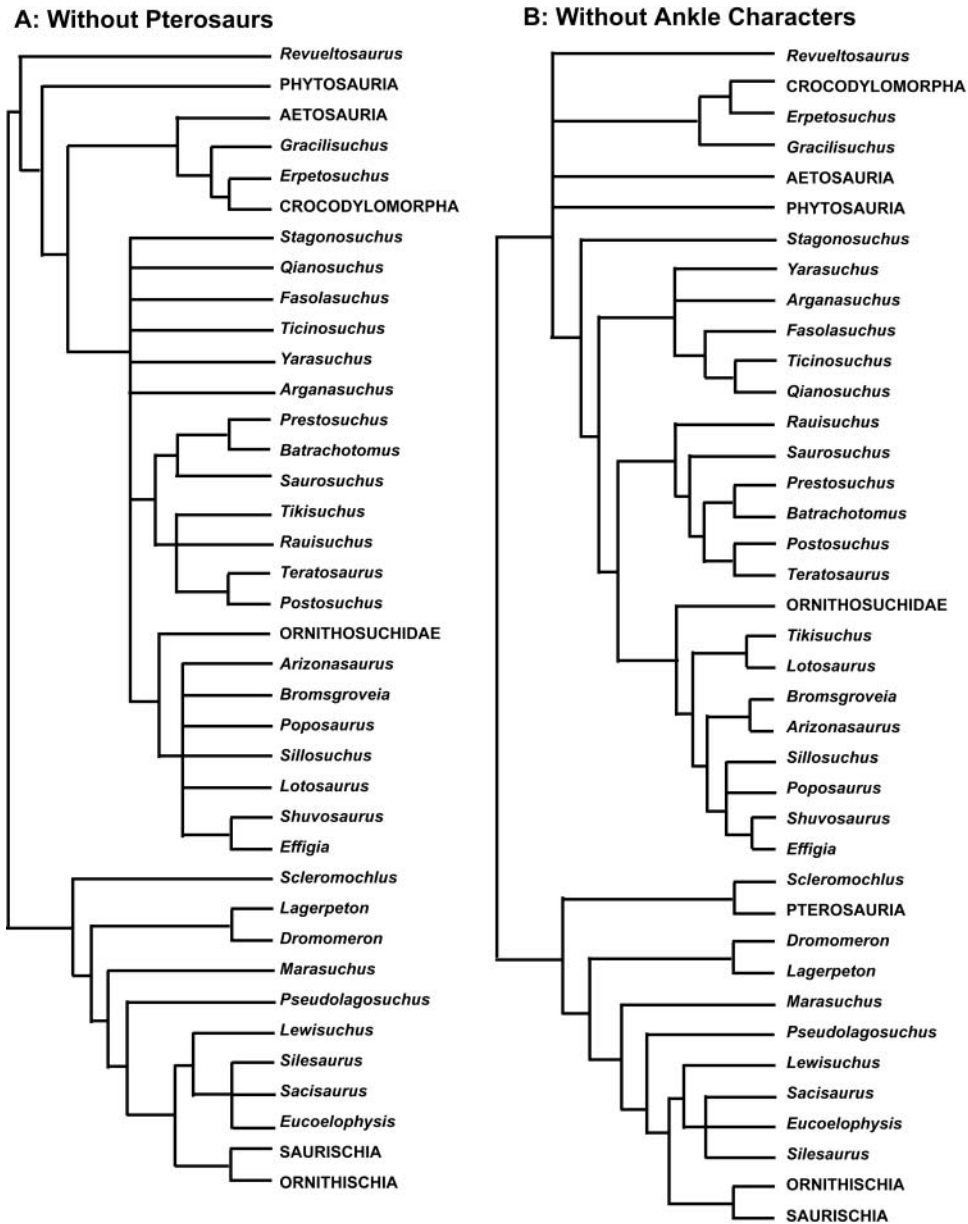


Figure 6. Strict consensus topologies when the current analysis is run with selected taxon and character alterations. **A**, Pterosauria excluded (1785 trees, 710 steps, CI = 0.32, RI = 0.67); **B**, all characters pertaining to the astragalus and calcaneum excluded (196 trees, 708 steps, CI = 0.29, 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.

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) (Serenó & 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 criticized 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) at 0.85 and Irmis *et al.* (2007a) at 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.

Comparisons with other 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 reanalysed topologies produced by these analyses are shown in Fig. 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 analysing 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 taxon 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 previous 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 supports, and

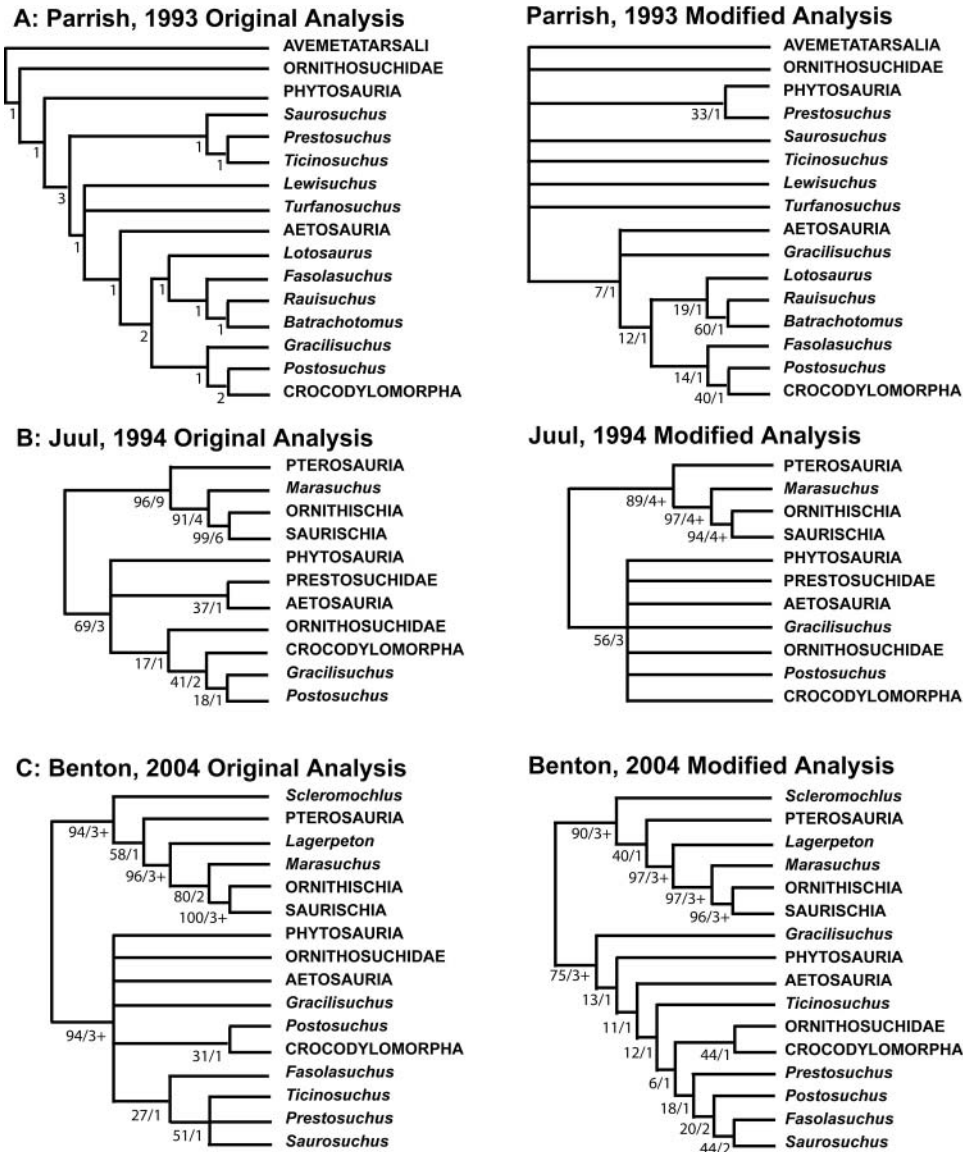


Figure 7. Comparison with previous studies. **A**, Parrish (1993); **B**, Juul (1994); **C**, Benton (2004). Tree to the left is the strict consensus topology of the original analysis, including Benton's (2004) tree that was not reported in his study. Tree to the right is the strict consensus of all 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.

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 characterized 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 compar-

ing 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 ACCTRAN and DELTRAN assumptions, and 'unambiguous synapomorphies' refer to those with a CI of 1.0 (Appendix S2).

Avemetatarsalia 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 characterized 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 ACCTAN 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 (ACCTAN) 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).

Secondly, we recover a monophyletic Rauisuchia, which unites all taxa commonly referred to as 'rauisuchians' in the literature (see above). The speciose clade Rauisuchia is divided into two major subclades: Pposauroidea and Rauisuchoidea (e.g. Rauisuchidae + Prestosuchidae). However, our evidence for a monophyletic Rauisuchia 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 Rauisuchia) to the exclusion of raiisuchoids. 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 Rauisuchia should be seriously considered (see Gower 2000; Gower & Nesbitt 2006; Weinbaum & Hungerbühler 2007).

The first major raiisuchian subclade, here termed Rauisuchoidea, is united by only two synapomorphies, neither of which is unequivocal. Most raiisuchoid 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 optimized as a synapomorphy of Rauisuchoidea 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 optimized as an ambiguous synapomorphy of Pposauroidea. The mere presence of a crest is a synapomorphy of Rauisuchia, which indicates that this structure is a homologous feature among raiisuchian taxa that exhibits variation informative for lower-level relationships.

Raiisuchoidea is divided into three discrete clades: a basal cluster centred on *Ticinosuchus*, Prestosuchidae and Rauisuchidae. 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 Rauisuchidae 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 recognized 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 realized that this taxon as originally described by Chatterjee (1985) was a chimera 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 raiisuchians, here termed Pposauroidea, 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 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 support = 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 optimized 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 Rausuchidae (Parrish 1993), a relationship considered highly improbable based on our dataset.

The speciose clade Rausuchia 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 rausuchians has been suggested before (e.g. Nesbitt 2007).

Finally, *Gracilisuchus* and *Erpetosuchus* are placed as sequential outgroups to Crocodylomorpha. These relationships are characterized by some of the highest tree support measures in the analysis, as well as substantial character data. The position of *Erpetosuchus* as a close crocodylo-

morph 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. Analysing 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 (GER) (Wills 1999) for our phylogeny. Our strict consensus tree is characterized by a GER of 0.437, which randomization 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*)



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 a 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 Rayfield *et al.* 2005; Nesbitt 2007). ET: Early Triassic, Rha: Rhaetian.

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 Pposauroidea and Rausuchoidea are among the oldest known taxa. However, within Rausuchoidea, 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 Pposauroidea 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* clade', which are from the Upper Carnian and Norian.

Missing lineages are especially concentrated in the Anisian and Ladinian, and many almost certainly extend into the Lower Triassic. Our poor knowledge of this time is partially a result of undersampling, but the lack of unequivocal archosaur fossils in otherwise well-sampled Lower 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, Pposauroidea) in the Early Triassic, but may have been rare or geographically localized. 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 Pposauroidea, 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 rausuchoid 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 rausuchian 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 ('thecondonts') 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: p. 397) as characterized 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 optimized 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) considered prestosuchid 'rauisuchians' as sprawlers, even though *Prestosuchus* and

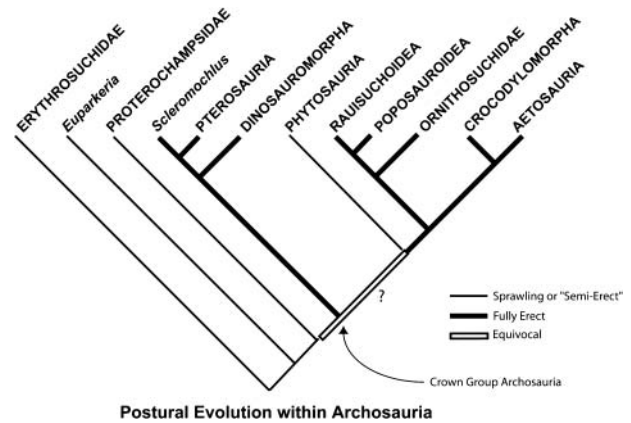


Figure 9. Postural transformation within Archosauria. Sprawling and erect posture optimised (ACCTRAN) onto a simplified version of the phylogenetic hypothesis advocated here. 'Semi-erect' posture, as has been hypothesized for *Euparkeria*, is treated as sprawling pending further analysis of archosaur 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).

other similar taxa seem to conform to his earlier definition of erect posture (Parrish 1987). In addition, 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 (2009) 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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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 Fig. 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 1988; 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 Fig. 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 Fig. 3.
 14. Premaxilla, subnarial process articulating with maxilla, form: absent or very short (0); elongate and

Appendix 1: character list

Note: numbers following year refer to character numbers in the cited reference

1. Skull, length: less than (0) or greater than (1) 50% length of presacral column. (Serenio 1991a: 33; Novas

- finger-like (1); short and triangular (2). New character, see Appendix S1 and Fig. 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 Fig. 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 & Hungerbühler 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 & 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 & Hungerbühler 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 & Hungerbühler 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). (Serenio 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 novel 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 and 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 & Hungerbühler 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 half 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 Fig. 3.

42. Jugal, participation in posterior edge of antorbital fenestra: present (0); absent, excluded by maxillalacrimal 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 & Hungerbühler 2007: 12; *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 Fig. 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 Fig. 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 & Hungerbühler 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 & Hungerbühler 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). (Hungerbühler & 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 & Hungerbühler 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 & Hungerbühler 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 Fig. 3.
72. Dentary, expansion of anterior region relative to main body: absent (0); present (1). New character, see Appendix S1 and Fig. 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 & Hungerbühler 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 & Hungerbühler 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 & Hungerbühler 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 & Hungerbühler 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 & Hungerbühler 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 & Hungerbühler 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; Irmis *et al.* 2007a: 120; Weinbaum & Hungerbühler 2007: 33)
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 Fig. 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 & Hungerbühler 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 & Hungerbühler 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; Irmis *et al.* 2007a: 62; Weinbaum & Hungerbühler 2007: 28;)
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 Fig. 4.
118. Ilium, preacetabular process, extent of anterior margin: terminates posterior (0) or anterior (1) to anterior margin of pubic peduncle. (Irmis *et al.* 2007a: 61; Weinbaum & Hungerbühler 2007: 27)
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; Irmis *et al.* 2007a: 63; Nesbitt 2007: 32)
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; Irmis *et al.* 2007a: 68; Weinbaum & Hungerbühler 2007: 31). 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 Fig. 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; Irmis *et al.* 2007a: 72; Weinbaum & Hungerbühler 2007: 32)
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; Irmis *et al.* 2007a: 81; Weinbaum & Hungerbühler 2007: 34)
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?20 011?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??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??0 10010 ?????0 0????
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00000 00000 00000 00000 ?000? 11010 ?0010 00?01
01100 ?0000 01000 00

Desmotosuchus

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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

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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??0 01010 02000 000?? ????? ????? ?????
????? ????? ????? ????? ?0000 10000 ????? ????? ?????
????? ???1? 0?10? ?0

Terrestrisuchus

00000 10110 0???? ????0 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?00 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?22 2?11? 00110 01111 1020? 10102 02200 20011
0210? ????? ?10?0 0?120 ?0?1? 2010? ????? ????? ????0
?1110 1110? 10

Lesothosaurus

00101 10001 01011 0000? 11000 00010 00001 22101
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10000 00200 00101 2?110 ??110 01111 1020? 10102
02200 20011 01100 112?1 11010 01120 10111 2000?
22??1 ???12 1???? ?0010 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

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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? ????? ?????
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?000 00200
000?? 2?000 00110 00100 1100? 10100 00000 00000
0000? 0???? 0??01 0?101 00?0? 2010? ??0?? ????? 1???1
?011? 01??0 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
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?? ?0001 ?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?? ?1001
?22?1 11010 0??1? ????? ????? ????? ????? ????? ?????
????? ??

Lagerpeton

????? ????? ????? ????? ????? ????? ????? ????? ?????
????? ????? ????? ????? ????? ????? ????? ????? ?????
??011 2???? ????? ?????0 0100? 00000 01000 10101 10010
001?1 00000 1?10? 01010 20200 ?1100 10112 1???1 01110
10111 10

Lewisuchus

????? ??0?? ????? ????0 11?0? ????? ????? ????? 0?000
?0?00 001?0 ????0 00?10 ????? 00??? ?1120 00000 0????
?0??? 2??10 00?00 000?? ????? ????? ????? ????? 0001?
????? ???1? ?0?? ????? ????? ????? ????? ????? ?????
??0?? ?0

Marasuchus

?0??? ????? 0???? ????0 ?1?0? ????? ????? ????? ?????
????? ????? ?????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

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

Sacisaurus

?0??? ????? 0???? ??000 1100? ????? ????? ????? ????0
????? ????? ?0??? ????? ????? 100?? ????? ????0 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??? ??000 ????0 ??20?
00??0 2?100 ??110 000?0 ?000? ??1?0 001?? ?0001 0000?
0???? ?00?1 ??100 ??01? 0000? ?0?00 ????0 ????? ?0111
01110 00

Silesaurus

00?00 1???? 0?021 00000 01000 00?1? ?0000 ????? 0?0??
????? ?0000 ????0 00210 1???? 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

????? ????? ????? ????10 ?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 ????0 00000 1101? ?????
????? 0110? ????0 ?0?00 00

Bromsgroveia

????? ????? ????? ????? ????? ????? ????? ????? ?????
????? ????? ????? ????? ????? ????? ????? ????? ?2111
??112 ????? ????? ????0 11121 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?000 ????? 00000 ?0100 00001
00000 0100? 11001 00??0 100?0 0000? 00000 021?0 10001
00000 0?000 00010 ??010 10000 00010 10010 00001
01110 ??110 00111 00

Lotosaurus

00011 10010 01210 11000 11?10 00010 00010 ?0101
00000 0?000 20000 ????10 00?00 1???? 21100 00000 10010
11110 ?1110 2?0?? ????0 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? ????? 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?00 000?0 0???? 01000
?00?0 20?0? ????? ????? ????? 00?00 ?1100 ????0 ?00??
00??? 00?11 0?000 000?? 101?? 00100 010?? 10002 0000?
0???? ????? ?0?? ???? ????1? ?001? 0?001 0110? ?0?00
0?000 00

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Rauisuchus

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

Revuletosaurus

?000? ?000 0?021 00101 11?00 00?01 10000 00?? 0?000
?0200 ?0?? ???? ???? ???? 00?? ?0000 ?0001 ?0??
???? 01?? 00?? 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 ???? ???? 10011 00000 02?10
21002 00000 0?? ?00?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?? 20111 11100
0010? ?2211 ?1111 2??00 01?? 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?? ???? ???? 1?120 ?0?10 ?1210 2101? 0000?
0?? 000?1 0?? ???? ???? ???? ???? ???? ????
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Staganosuchus

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

Teratosaurus

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

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

Tikisuchus

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

0?? ???? 1?? ?1? 01?0? ???? ???? ???? 0?0??
???? ?0?1? ???? ???? ???? ???? 21?? 00000 ?1000
0?0?1 ?101? 10?? 011?0 1000? 00000 01?10 20?? 0000?
0?? ?000 ?000 1000? ???? ???? ???? ???? ????
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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, 1972cc), but also on *Gualosuchus* (Romer 1971c), *Proterochampsia* (Sill 1967), and *Tropidosuchus* (Arcucci 1990) for those regions missing or uncertain in *Chanaresuchus*

Ingroup genera**Avemetatarsalia**

- **Dromomeron*: Irmis et al. 2007a
 - **Eucoelophysis*: Sullivan & Lucas 1999; Ezcurra 2006; Nesbitt et al. 2007
 - **Lagerpeton*: PVL 4619; Romer 1971b, 1972ee; Sereno & Arcucci 1990, 1993; Sereno 1991a
 - **Lewisuchus*: Romer 1972b
 - **Marasuchus*: PVL 3870, 3871, 3872, 4672; Romer 1971b, 1972ee; 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 Galton & Walker 1996; Benton & Gower (1997); 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 Huene 1942; Krebs 1973
- **Revueltosaurus*: Hunt *et al.* 2005; Parker *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.* (2009). 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
- **Tikusuchus*: Chatterjee & Majumdar 1987; Gower 2002; Sulej 2005
- **Yarasuchus*: Sen 2005

Exemplar genera

Aetosauria

- **Aetosaurus*: SMNS 5770, 12670, 12760, 14882, 18554; von 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 material; 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

- **Mystriosuchus*: 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, 1985bb), 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.