

A NEW BASAL ARCHOSAURIFORM DIAPSID FROM THE LOWER TRIASSIC OF ARGENTINA

MARTÍN D. EZCURRA,^{*1} AGUSTINA LECUONA,² and AGUSTÍN MARTINELLI³

¹Laboratorio de Anatomía Comparada y Evolución de los Vertebrados, Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia,’ Avenida Ángel Gallardo 470, 1405DJR, Buenos Aires, Argentina, martindezcurra@yahoo.com.ar;

²Museo Paleontológico Egidio Feruglio, Avenida Fontana 140, U9100GYO, Trelew, Argentina, alecuona@mef.org.ar;

³Laboratório de Geologia, FACIP, Universidade Federal de Uberlândia, Avenida José João Dib, 2545, Barrio Progresso, 38300–132, Ituiutaba, Minas Gerais, Brazil, agustin_martinelli@yahoo.com.ar

ABSTRACT—The best-known South American Early Triassic archosauriform belongs to a putative proterosuchid briefly reported by José Bonaparte in 1981, collected from the Quebrada de los Fósiles Formation (Puesto Viejo Group, Argentina). This specimen consists of well-preserved natural external molds of a partial postcranium that preserve dorsal vertebrae, osteoderms, a dorsal rib, a possible gastralium, a chevron, a humerus, an ilium, two metapodials, and an ungual. We re-describe this specimen and identify autapomorphies that allow us to recognize *Koilamasuchus gonzalezdziazi*, gen. et sp. nov. The presence of an iliac blade with a slightly convex dorsal margin and with a maximum length more than 3 times its maximum height places *Koilamasuchus* within Archosauriformes. A cladistic analysis of basal Archosauriformes positions *Koilamasuchus* more crownwards than *Proterosuchus*, *Sarmatosuchus*, *Fugusuchus*, and *Osmolskina*, as the sister taxon of the clade that includes Erythrosuchidae and Archosauria. Proterosuchidae is found to be paraphyletic. The presence of an iliac preacetabular process, a pubic peduncle that forms an angle lower than 45° to the longitudinal axis of the ilium, and dorsal body osteoderms positions *Koilamasuchus* in Archosauriformes more crownwards than proterosuchids. *Koilamasuchus* is more basal than erythrosuchids within Archosauriformes because of the presence of dorsal ribs with a poorly developed proximal end. *Koilamasuchus* importantly increases the diversity of Archosauriformes during the biotic recovery following the Permo-Triassic mass extinction.

INTRODUCTION

Archosauriformes consists of numerous stem taxa that include a Late Permian species (i.e., *Archosaurus rossicus*) and a diverse sample of Triassic forms (e.g., *Euparkeria*, *Osmolskina*, *Erythrosuchus*, *Turfanosuchus*, *Doswellia*, *Chanaresuchus*), as well as the Archosauria (sensu Gauthier et al., 1989). The latter clade was one of the most successful groups of terrestrial tetrapods during the Mesozoic, and includes the crown groups Aves and Crocodylia (Gauthier, 1986). Three main lineages of non-archosaurian archosauriforms have been traditionally recognized: Proterosuchidae (Late Permian–Early Triassic), Erythrosuchidae (Early–Middle Triassic), and Proterochampsidae (Middle–Late Triassic) (Serenó, 1991). From the first phylogenetic analyses of basal Archosauriformes (Gauthier et al., 1989; Sereno, 1991; Parrish, 1992), proterosuchids have been positioned as the most basal representatives of the group (Serenó, 1991), and erythrosuchids have usually been nested as the sister taxon of the clade that includes *Euparkeria*, Proterochampsidae, and Archosauria (Serenó and Arcucci, 1990; Sereno, 1991).

In a recent revision of the enigmatic archosauriform *Doswellia*, Dilkes and Sues (2009) performed a phylogenetic analysis that found *Euparkeria* to be more basal than *Erythrosuchus* and more derived archosauriforms, and *Doswellia* was placed outside Archosauria and as the sister taxon of Proterochampsidae (cf. Benton and Clark, 1988). As in some previous analyses (e.g., Sereno, 1991), Dilkes and Sues (2009) found Proterochampsidae to be more closely related to Archosauria than to erythrosuchids, *Euparkeria*, and proterosuchids. However, some previously enigmatic Chinese basal archosauriforms (i.e., *Turfanosuchus* and *Yonghesuchus*) were depicted as more closely related to Ar-

chosauria than to proterochampsids, *Doswellia*, and more basal forms. More recently, in the redescription of *Vancleavea*, Nesbitt et al. (2009) found this genus to be the sister taxa of Proterochampsidae plus more derived forms, and *Euparkeria* as the sister taxon of Archosauria.

During the last three decades, several basal archosauriforms have been reported, providing new information about the clade. These records include unnamed archosauriform remains from the Early Triassic of South Africa (Modesto and Botha-Brink, 2008), Argentina (Bonaparte, 1981; Ezcurra et al., 2010), and Brazil (the Bica São Tomé archosauriforms: Da-Rosa et al., 2009), and the Middle–Late Triassic *Cuyosuchus* from Argentina (Rusconi, 1951; Reig, 1961; Desojo et al., 2002). In addition, some forms have been allied with *Euparkeria*, informally grouped into “Euparkeriidae,” including *Osmolskina* (Borsuk-Białynicka and Evans, 2003), *Halazhaisuchus* (Wu, 1982), and *Dorosuchus* (Sennikov, 1989) from Middle Triassic beds of Poland, China, and Russia, respectively.

The fossil record of non-archosaurian archosauriforms (i.e., proterosuchids, erythrosuchids, ‘euparkeriids’) is well known from the Early and Middle Triassic of South Africa and Asia, in contrast to the poor record in North America, Europe, and Australasia (von Huene, 1960; Ewer, 1965; Wu, 1982; Thulborn, 1986; Sennikov, 1989, 1995; Parrish, 1992; Gower and Sennikov, 2000). In particular, the Early Triassic South American fossil record of basal archosauriforms is based on recently reported isolated remains from Brazil (Da-Rosa et al., 2009) and a putative proterosuchid from Argentina (Bonaparte, 1981; Ezcurra et al., 2010). In contrast, the South American record of basal archosauriforms is richer but mostly restricted to the endemic Middle and Late Triassic proterochampsids (e.g., *Cerritosaurus*, *Proterochampsa*, *Chanaresuchus*, *Gualosuchus*, *Tropidosuchus*; Price, 1946; Reig, 1959; Sill, 1967; Romer, 1971, 1972; Arcucci, 1990), with other less conspicuous forms (Reig, 1961; Desojo et al., 2002). Thus,

*Corresponding author.

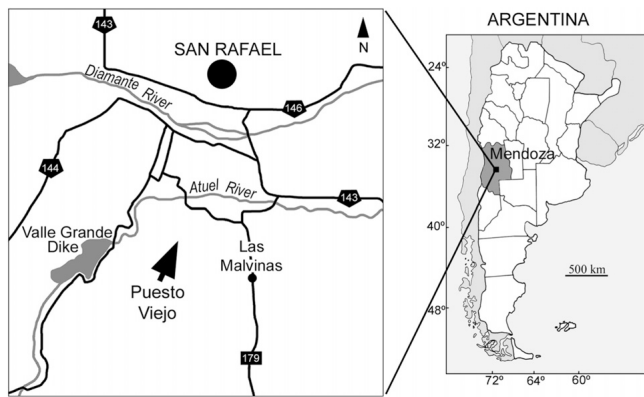


FIGURE 1. Map of the Puesto Viejo indicating the locality where *Koilamasuchus*, gen. et sp. nov., was discovered (modified from Martinelli et al., 2009).

the Early Triassic is a poorly known period for the South American early archosauriform history. As a result, and despite their scarcity, the Early Triassic archosauriform remains from this continent are very important, and the proterosuchid reported by Bonaparte (1981) is the subject of this contribution. This specimen comes from the Quebrada de los Fósiles Formation of the Puesto Viejo Group (Stipanovic et al., 2007), Mendoza Province, central-western Argentina (Fig. 1). It is based on natural external molds of a partial postcranium (Fig. 2), which Bonaparte (1981) briefly described and figured with schematic drawings. The specimen exhibits an autapomorphy and a unique combination of apomorphies that distinguish it from other known basal archosauriforms, and allow us to recognize a new genus and species. The new taxon is the most complete Early Triassic archosauriform reported from South America so far, and a better understanding of its anatomy and phylogenetic affinities will provide novel information of the early radiation of archosauriforms.

Institutional Abbreviations—**BMNH**, The Natural History Museum, London, England; **MACN-Pv**, Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia,’ Paleontología de Vertebrados, Buenos Aires, Argentina; **MCNAM**, Museo de Ciencias Naturales y Antropológicas de Mendoza (J. C. Moyano), Mendoza, Argentina; **PVL**, Paleontología de Vertebrados, Instituto ‘Miguel Lillo,’ San Miguel de Tucumán, Argentina; **SAM**, Iziko South African Museum, Cape Town, South Africa; **UCMP**, University of California Museum of Paleontology, Berkeley, California, U.S.A.; **UFMS**, Universidad Federal de Santa Maria, Santa Maria, Brazil.

Anatomical Abbreviations—**af**, articular facet; **aw**, acetabular wall; **c**, capitulum; **cg**, collateral groove; **ch**, chevron; **d**, depression; **dr**, dorsal rib; **g**, gastralia?; **h**, humerus; **hc**, hemal canal; **hh**, humeral head; **il**, ilium; **ip**, ischial peduncle; **lf**, lateral fossa; **ls**, longitudinal sulcus; **mk**, median keel; **mtc/mtf**, metacarpal/metatarsal; **ns**, neural spine; **os**, osteoderm; **p**, pit; **pop**, postacetabular process; **poz**, postzygapophysis; **pp**, pubic peduncle; **prp**, preacetabular process; **prz**, prezygapophysis; **r**, radius?; **rc**, radial condyle; **rh**, rib head; **ri**, ridge; **sp**, sigmoid proximal end; **t**, tuberosity; **tu**, tuberculum; **uc**, ulnar condyle; **un**, ungual; **vt**, vertebrate.

GEOLOGICAL AND BIOSTRATIGRAPHIC SETTINGS

The Puesto Viejo Group was originally described by González Díaz (1964, 1966, 1972) as the ‘Puesto Viejo Formation,’ which consists of a thick succession of continental sediments that can be

differentiated into lower and upper sections. That author pointed out that the lower section of the ‘Puesto Viejo Formation’ is characterized by a dominant light green-grey color, whereas the upper part comprises red sediments, which indicates two different environments (González Díaz, 1972). These lithological differences prompted González Díaz (1972) to propose the division of the ‘Puesto Viejo Formation’ into lower and upper members. The shift in the clastic contribution between the lower and upper members suggests the presence of a parallel unconformity between them (Stipanovic et al., 2007). Therefore, Stipanovic et al. (2007) considered that the lithological differences between these ‘members’ are enough to elevate the ‘Puesto Viejo Formation’ to the status of group (i.e., Puesto Viejo Group) and divide it into distinct formations. The lower and upper sections were designated the Quebrada de los Fósiles Formation and the Río Seco de la Quebrada Formation, respectively (Stipanovic et al., 2007).

The first fossils recovered from the Puesto Viejo Group consisted of sparse plant remains (Trumpy, 1940), and in 1963 González Díaz found the first vertebrate fossil, close to the Puesto Agua de los Burros, in what is now the Quebrada de los Fósiles Formation. Bonaparte (1981) described this fossil as an indeterminate proterosuchid, and it is this specimen (MACN-Pv 18119) that is subject of the present paper. Later discoveries carried out by Don Ángel Zúñiga (who was in charge of the Puesto Viejo, about 10 km from Puesto Agua de los Burros), Dr. Bonaparte, and Dr. H. Lagiglia led to the discovery and description of the first cynodont and dicynodont remains from the Puesto Viejo Group (e.g., Bonaparte, 1966a, 1966b, 1966c, 1969, 1981; Martinelli and de la Fuente, 2008; Martinelli et al., 2009).

Bonaparte (1966a, 1966b, 1967, 1981, 2000) was the first to discuss in detail the age of the Puesto Viejo Group. He regarded the Río Seco de la Quebrada Formation to be a correlative of the South African *Cynognathus* Assemblage Zone (late Olenekian–early Anisian age), due to the presence of the cynodont *Cynognathus* and the dicynodont *Kannemeyeria argentinensis*. More recently, the cynodont *Diademodon tetragonus* has been reported from the Río Seco de la Quebrada Formation (Martinelli and de la Fuente, 2008; Martinelli et al., 2009), supporting the idea that this formation is homotaxial to the *Cynognathus* Assemblage Zone (most likely to subzones B and C; Martinelli et al., 2009). Bonaparte (1981, 1982, 2000) regarded the Quebrada de los Fósiles Formation to be equivalent to the *Lystrosaurus* Assemblage Zone of Induan–early Olenekian age, based on three lines of evidence: (1) radiometric datings by Valencio et al. (1975) and Ramos (1993); (2) the correlation of the Río Seco de la Quebrada Formation to the *Cynognathus* Assemblage Zone, which implies an older age for the Quebrada de los Fósiles Formation; and (3) its fossil content (the ‘Agua de los Burros Local Fauna’ sensu Bonaparte, 1981; *Vinceria* sp., Proterosuchia indet., *Pleuromeia* sp.; Bonaparte, 1981; Zavattieri and Papú, 1993), which does not contradict a correlation with the *Lystrosaurus* Assemblage Zone.

Radiometric datings from both sedimentary units of the Puesto Viejo Group (Valencio et al., 1975; Llambías et al., 1993; Ramos, 1993) have resulted in inconclusive data (see Stipanovic et al., 2007). In addition, Zavattieri et al. (2003) described for the Quebrada de los Fósiles Formation a typical microfloristic Gondwanan Permian association together with less common Middle and Late Triassic components. The latter evidence led these authors to consider the time of deposition of the formation in the Permo-Triassic boundary, and perhaps even into the uppermost Permian. Stipanovic et al. (2007) pointed out that this interpretation is supported by the observation that no representatives of the *Dicroidium* Flora, common in Middle and Late Triassic assemblages, have been found in the whole Puesto Viejo Group. Pursuant to these observations, Stipanovic et al. (2007) assigned the Quebrada de los Fósiles Formation to the oldest Early

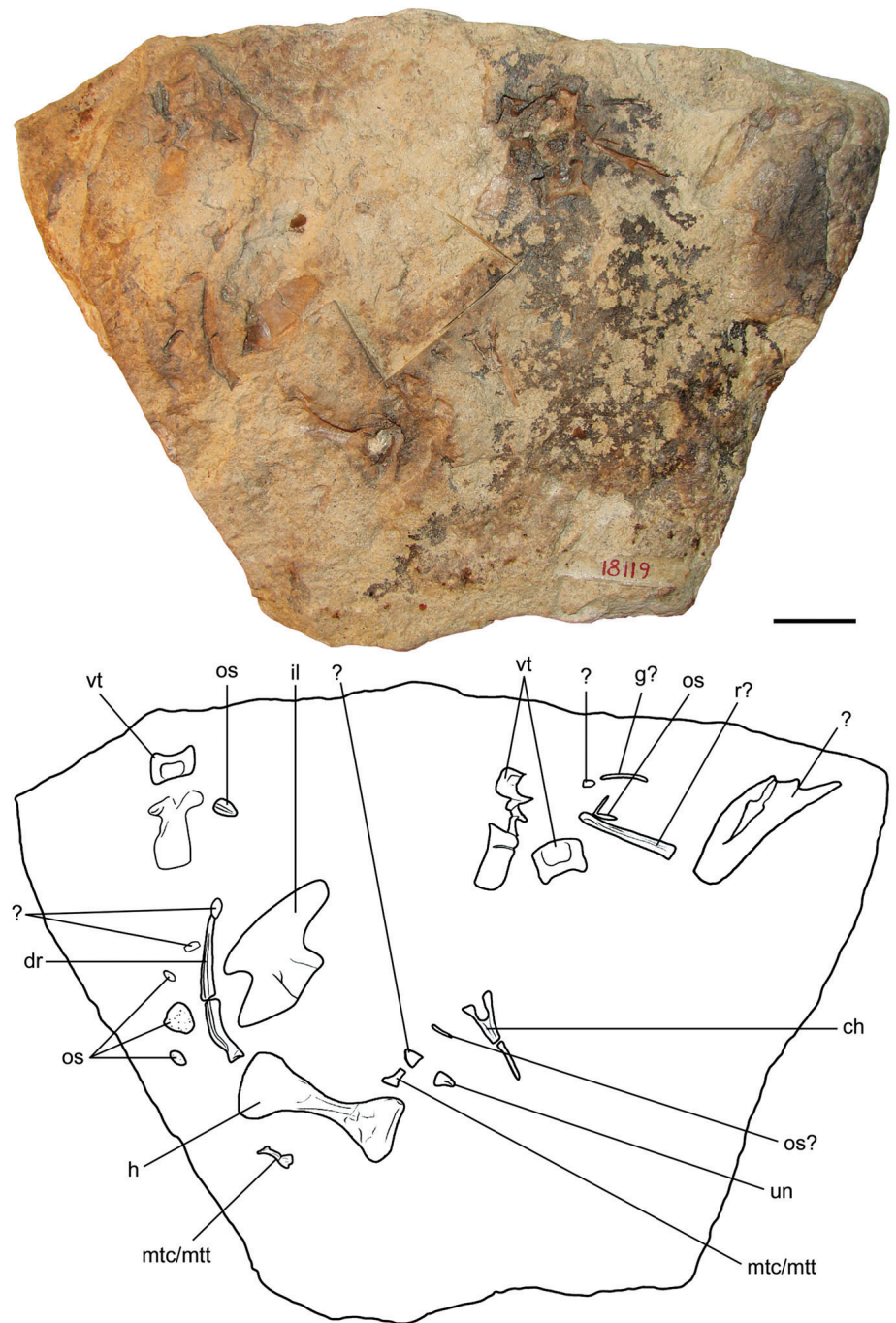


FIGURE 2. MACN-Pv 18119, block bearing the molds of the bones of *Koilamasuchus*, gen. et sp. nov., with outline drawings showing positions of the identified elements. Scale bar equals 2 cm. (Figure appears in color online.)

Triassic (Induan) or the youngest Late Permian. This inference, however, is based on negative evidence.

De Fauw (1993) studied the dicynodont remains from the Quebrada de los Fósiles Formation and referred them to *Rechnisaurus cristarhynchus*. This dicynodont species is also found in the Yerrapalli Formation of India (Roy-Chowdhury, 1970; Bandyopadhyay, 1988) and the Manda Formation of Tanzania (Cox, 1991), which are referred to the Middle Triassic (Jain and Roy-Chowdhury, 1987; Chatterjee, 1980; Cox, 1991). Accordingly, De Fauw (1993) suggested that the Agua de los Burros Local Fauna (of the Quebrada de los Fósiles Formation) is not comparable with the *Lystrosaurus* Assemblage Zone, and it would be

Anisian in age. De Fauw (1993), in fact, proposed an inversion of the Quebrada de los Fósiles and the Río Seco de la Quebrada formations, with the former younger than the latter. Bonaparte (2000) criticized the interpretation of De Fauw (1993) because it contradicts all previous geological and paleontological interpretations of the unit (González Díaz, 1966, 1972; Bonaparte, 1981; Spalletti, 1994; Zavattieri and Papú, 1993). Alternatively, Bonaparte (2000) proposed that it is more parsimonious to consider a larger biochron for *R. cristarhynchus* rather than an inversion of the sedimentary units. A recent preliminary reappraisal of the dicynodont remains from the Quebrada de los Fósiles Formation (including the purported material of *Rechnisaurus*) has

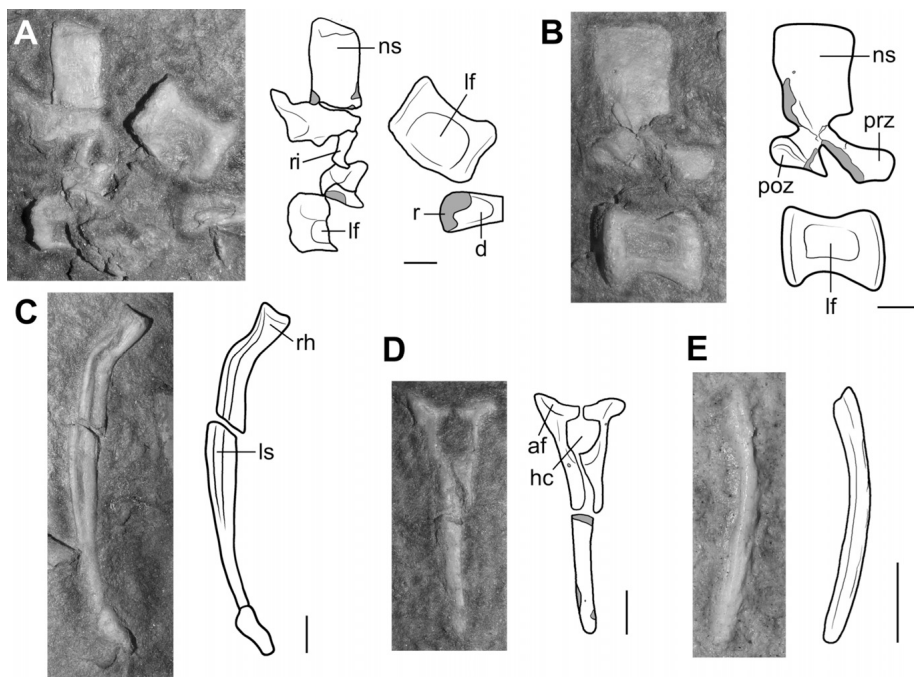


FIGURE 3. *Koilamasuchus gonzalezdiazi*, gen. et sp. nov., MACN-Pv 18119. Latex casts of the axial skeleton. **A**, fragmentary two dorsal vertebrae in lateral view; **B**, dorsal vertebra in lateral view; **C**, mid-dorsal rib in probable posterior view; **D**, chevron in anterior or posterior view; **E**, probable gastralium. Scale bars equal 5 mm.

re-assigned these materials to a new species of *Vinceria* and to an indeterminate Kannemeyeriiformes (Domnanovich and Marsicano, 2010). Based on the known biochrons of these dicynodont taxa and the current evidence, we regard the Agua de los Burros Local Fauna of the Quebrada de los Fósiles Formation to be Early Triassic in age, as regarded by most authors.

SYSTEMATIC PALEONTOLOGY

DIAPSIDA Osborn, 1903

ARCHOSAURIFORMES von Huene, 1946

ARCHOSAURIFORMES Gauthier et al., 1988

KOILAMASUCHUS GONZALEZDIAZI, gen. et sp. nov.

(Figs. 2, 3, 4B, 5, 6)

Proterosuchidae indet.: Bonaparte, 1981:285, fig. 4; Bonaparte, 1982:365.

Etymology—The generic name is derived from the Latin word *koilamas* (cavity, pocket) and the Greek word *suchus* (crocodile), in reference to the presence of lateral fossae in the dorsal vertebral centra. The specific name is in honor of Dr. Emilio F. González Díaz for his geological work in the Triassic outcrops of the Mendoza Province, especially in the Puesto Viejo Group, and discoverer of the holotype of *Koilamasuchus*.

Holotype—MACN-Pv 18119, very well preserved natural external molds of three dorsal vertebrae, at least six osteoderms, a dorsal rib, a probable gastralium, a chevron, a humerus, a probable radius, an ilium, an incomplete ungual phalanx, two metapodial fragments, and some indeterminate bone fragments (Fig. 2). All the elements are closely associated and appear to represent a single individual.

Horizon and Locality—Agua de los Burros locality, 35 km south of the city of San Rafael, Mendoza Province, Argentina (Fig. 1); Quebrada de Los Fósiles Formation, Puesto Viejo Group, Early Triassic (but see Geological and Biostratigraphic Settings).

Diagnosis—*Koilamasuchus gonzalezdiazi* is a small diapsid (total length of ca. 50 cm by comparisons with *Euparkeria*) distinguished among archosauriforms by the presence of an oblique

tuberosity on the shaft of the humerus. It is also characterized by the following combination of apomorphies: dorsal vertebral centra with a deep, well-defined, and ovoid lateral fossa; dorsal neural spines moderately tall and sub-triangular in lateral view; dorsal rib with a laterally curved proximal end and a sharp medial inflection below it, deep longitudinal sulcus on the proximal two-thirds of the shaft, and holocephalous; humerus with strongly expanded proximal and distal ends; ilium with well-developed preacetabular process; and presence of osteoderms.

DESCRIPTION

The holotype of *Koilamasuchus gonzalezdiazi* comprises well-preserved external molds of several postcranial bones, preserved in a 20-cm by 15-cm block of fine, light brown sandstone (Fig. 2). Although the preserved elements are closely associated and seem to represent a single individual, none are articulated. No ontogenetically related characters are observable in the available material (e.g., neurocentral sutures), and so the ontogenetic age of

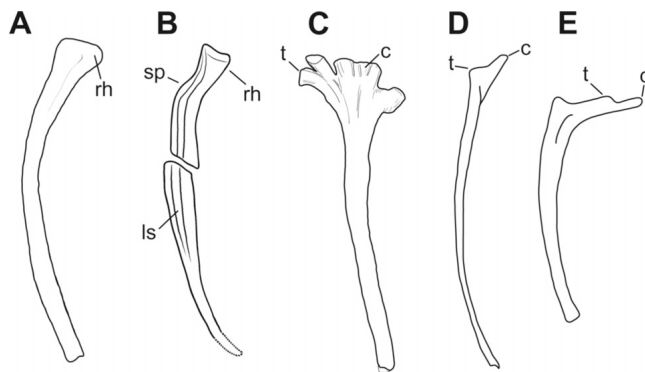


FIGURE 4. Mid-dorsal ribs of several basal archosauriforms. **A**, *Hyperodapedon gordonii*; **B**, *Koilamasuchus*, gen. et sp. nov.; **C**, *Vjushkovia triplicostata*; **D**, *Euparkeria*; **E**, *Doswellia*. Not to scale.

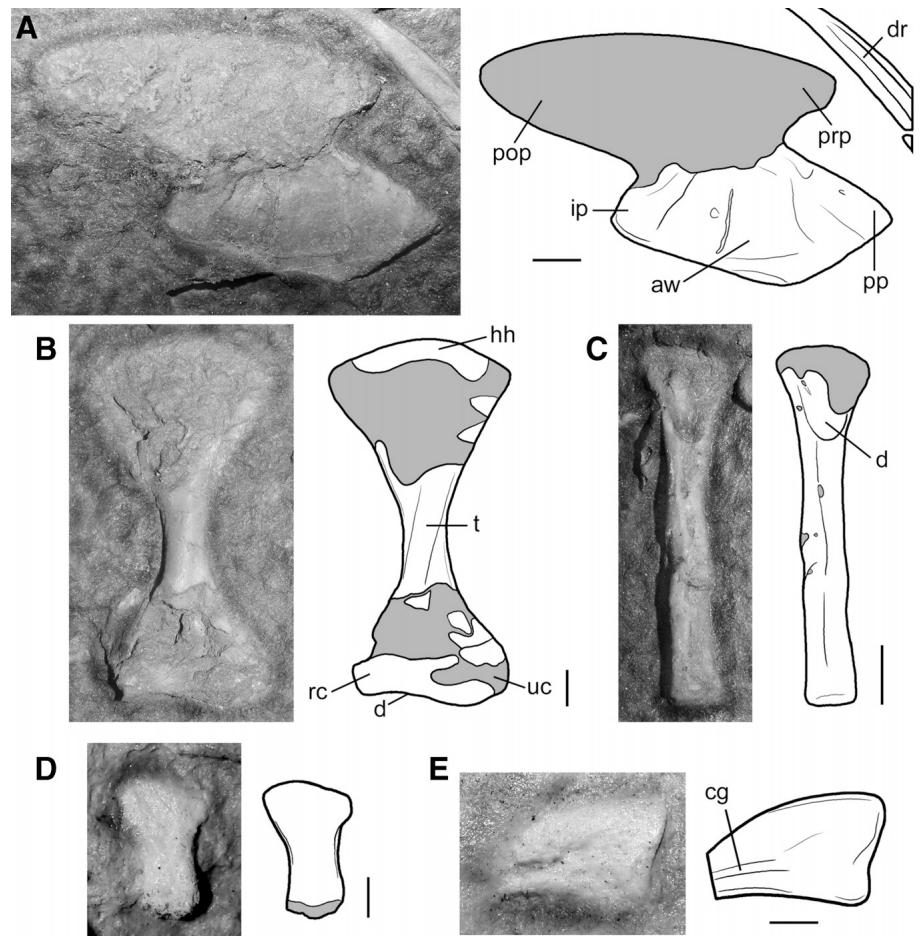


FIGURE 5. *Koilamasuchus gonzalezdiazi*, gen. et sp. nov., MACN-Pv 18119. Latex casts of appendicular skeletal elements. **A**, right ilium in medial view; **B**, humerus in probable posterior view; **C**, putative radius in probable lateral view; **D**, metacarpal or metatarsal; **E**, ungual phalanx. Scale bars equal 5 mm (**A–C**) and 2 mm (**D, E**).

the individual is unknown. The description of *Koilamasuchus* is based on the natural external molds as well as latex casts made from these bones. Measurements based on the casts are provided in Table 1.

Dorsal Vertebrae—Molds of three posterior or mid-dorsal vertebrae are available, of which two are represented by centra and neural arches and the other by an isolated centrum (Fig. 3A–B). No intercentra are preserved, but bevelling of the vertebral cen-

tra suggests their presence. The dorsal vertebrae are proportionally very tall, with a maximum height greater than 2.5 times the anteroposterior length of the centrum and a neural arch 3 times higher than the centrum. The two complete centra are almost rectangular in lateral view, being slightly longer than high (Bonaparte, 1981), contrasting with the anteroposterior short dorsal centra of erythrosuchids (e.g., *Erythrosuchus*: Gower, 2003; *Vjushkovia*: von Huene, 1960; *Shansisuchus*: Young, 1964)

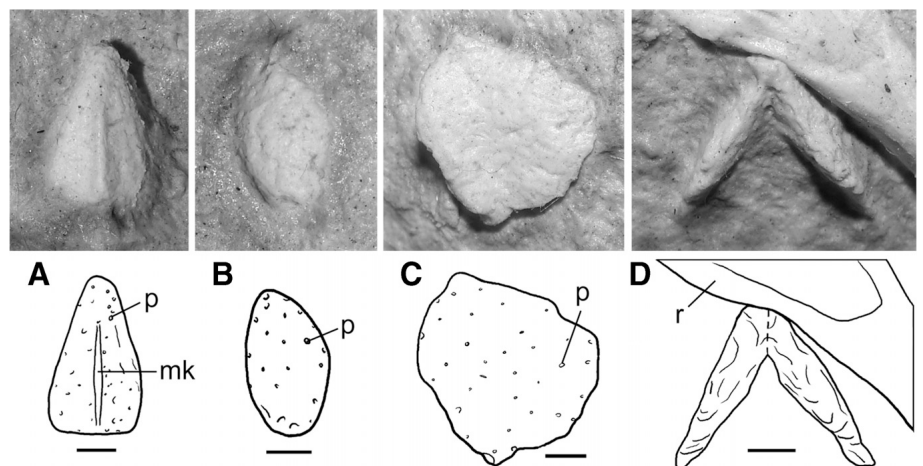


FIGURE 6. *Koilamasuchus gonzalezdiazi*, gen. et sp. nov., MACN-Pv 18119. Latex casts of the osteoderms in dorsal (**A–C**) and anterior/posterior (**D**) views. Scale bars equals 2 mm.

TABLE 1. Measurements (in mm) of selected bones of *Koilamasuchus gonzalezdiazi*, gen. et nov. sp. (MACN-Pv 18119).

Most complete dorsal vertebra	
Total height	34.8
Pre-postzygapophyseal length	16.2
Centrum length	13.5
Height of posterior articular facet	10.7
Height of neural spine	15.6
Dorsal rib	
Length	45*
Chevron	
Proximodistal height	27.6
Hemal canal height	5.7
Hemal canal width	3.7
Proximal transversal width	10.2*
Osteoderm with median keel	
Length	6.7
Width	4.6
Humerus	
Length	51.2
Width of proximal end	21.1*
Width of distal end	20.8
Minimum width of shaft	5.7
Radius?	
Length	30.3*
Ilium	
Total length	43.0
Length of iliac blade	36.3
Length of preacetabular process of iliac blade	5.9
Length of postacetabular process of iliac blade	13.4
Total height	30.5
Height of iliac blade	15.3
Height of acetabular region	14.3
Length across pubic and ischiadic peduncles	29.8

All the measurements are the maximum measurable. An asterisk (*) indicates an incomplete measurement.

and the strongly elongated ones of *Doswellia* (Dilkes and Sues, 2009), *Vancleavea* (Parker and Barton, 2008; Nesbitt et al., 2009), *Cuyosuchus* (MCNAM 2669), and the proterochampsid *Chanaresuchus* (PVL 6244). The ventral margin of the centra is concave, and the isolated centrum is symmetric in lateral view. In contrast, the other complete centrum is slightly asymmetric, with its minimum height slightly posteriorly displaced from the mid-length of the bone. This results in a more acute posteroventral margin and a more rounded anteroventral one. The centra are slightly compressed transversely at mid-length, as occurs in several archosauriforms (e.g., *Erythrosuchus*: Gower, 2003; *Chanaresuchus*: PVL 6244; *Euparkeria*: cast of SAM-PK-5867; *Cuyosuchus*: MCNAM 2669; the Bica São Tomé archosauriforms: Da-Rosa et al., 2009). The three preserved centra of *Koilamasuchus* exhibit an oval and deep lateral fossa (Bonaparte, 1981), which occupies most of the lateral surface of the centrum. This fossa may be pneumatic in nature (Britt, 1997; Gower, 2001), but no other pneumatic traits are observed in the axial skeleton. The dorsal centra of several archosauriforms are also invaded by a blind lateral fossa, including those of *Euparkeria* (cast of SAM-PK-5867), *Erythrosuchus* (BMNH R3592), *Tarjadia* (Arcucci and Marsicano, 1998), *Vancleavea* (Nesbitt et al., 2009), *Cuyosuchus* (MCNAM 2669), the Bica São Tomé archosauriforms (UFSM 11394; Da-Rosa et al., 2009), and several archosaurs (e.g., *Marasuchus*: PVL 3870; *Aetosauroides*: PVL 2073; *Arizonasaurus*: Nesbitt, 2005). In addition, the centra of the posterior cervicals and anterior dorsals of *Turfanosuchus* also exhibit a well-developed lateral fossa (Wu and Russell, 2001). In particular, the lateral fossae of the dorsal vertebrae of *Turfanosuchus* (Wu and Russell, 2001) and *Euparkeria* (cast of SAM-PK-5867) more closely resemble that of *Koilamasuchus* in being very deep, remarkably delimited, and very extensive among non-archosaur archosauriforms.

The ventral pedicles of the neural arches are not preserved, but in one of the available molds a diagonal ridge is observed (Fig. 3A). This ridge is thick, situated directly below the base of the neural spine, and slightly displaced from the mid-length of the vertebra. The ventral end is oriented towards the mid-length of the neural arch, contrasting with the anterior and posterior infradiapophyseal laminae, which are anteroventrally or posteroventrally directed, respectively. Thus, the homology of this ridge is uncertain. The diapophyses are not preserved in any of the preserved molds. The preserved prezygapophysis is moderately developed, rounded, and projects beyond the anterior articular surface of the centrum. The latter condition resembles that of other archosauriforms (e.g., *Erythrosuchus*: Gower, 2003; *Vjushkovia*: von Huene, 1960; *Euparkeria*: Ewer, 1965; *Doswellia*: Dilkes and Sues, 2009), but contrasts with the extremely short prezygapophyses of *Chanaresuchus* (PVL 6244). Furthermore, the prezygapophysis projects directly anteriorly, and so resembles the conditions in *Euparkeria* (Ewer, 1965), *Vancleavea* (Nesbitt et al., 2009), *Doswellia* (Dilkes and Sues, 2009), and the rhynchosaur *Hyperodapedon* (*H. gordonii*: Benton, 1983). In contrast, in *Tarjadia* (Arcucci and Marsicano, 1998), *Erythrosuchus* (Gower, 2003), *Tasmaniosaurus* (Thulborn, 1986), *Vjushkovia* (von Huene, 1960), and *Chanaresuchus* (PVL 6244) the prezygapophyses are anterodorsally directed. The postzygapophysis exhibits a ventrolaterally oriented articular facet, and it is short, with a distal end that extends slightly beyond the posterior level of the articular surface of the centrum. This contrasts with the postzygapophyses of *Chanaresuchus* (PVL 6244) and the Bica São Tomé archosauriforms (UFSM 11394; Da-Rosa et al., 2009), which extend farther from the posterior margin of the centrum. The main axis of the postzygapophysis is posterodorsally oriented.

The neural spines are very tall and sub-triangular in lateral view, with an anteroposteriorly deeper distal end. The neural spine represents ca. 47% of the total height of the vertebra, and thus resembles the tall neural spines of *Tasmaniosaurus* (Thulborn, 1986), *Chanaresuchus* (PVL 6244), and the Bica São Tomé archosauriforms (UFSM 11394; Da-Rosa et al., 2009), but it is not as tall as those of erythrosuchids (e.g., *Erythrosuchus*: Gower, 2003; *Vjushkovia*: von Huene, 1960; *Shansisuchus*: Young, 1964). In contrast, the dorsal neural spines are proportionally shorter in the rhynchosaur *Hyperodapedon* (*H. gordonii*: Benton, 1983), and the archosauriforms *Doswellia* (Dilkes and Sues, 2009) and *Turfanosuchus* (Wu and Russell, 2001). The dorsal neural spines of *Koilamasuchus* are vertically directed and posteriorly displaced, as in several archosauriforms (e.g., *Erythrosuchus*: Gower, 2003; *Vjushkovia*: von Huene, 1960; *Chanaresuchus*: PVL 6244; *Euparkeria*: Ewer, 1965; the Bica São Tomé archosauriforms: UFSM 11394; Da-Rosa et al., 2009). The laterally expanded distal ends of the neural spines exhibited by several archosauriforms (e.g., *Euparkeria*, *Turfanosuchus*; Ewer, 1965; Wu and Russell, 2001) is absent in *Koilamasuchus*, and so resembles the condition in *Erythrosuchus* (Gower, 2003), *Vancleavea* (Nesbitt et al., 2009), *Chanaresuchus* (PVL 6244), and the Bica São Tomé archosauriforms (UFSM 11394; Da-Rosa et al., 2009).

Dorsal Rib—The mold of a single dorsal rib, probably in posterior view, is present, but its ventral end is not preserved (Figs. 3C, 4B). The preserved portion of the dorsal rib is around 1.5 times longer than the maximum height of the ilium. Thus, the available dorsal rib of *Koilamasuchus* may be from the anterior or mid-portion of the trunk. The rib is holocephalous, resembling the condition of the anterior and mid-dorsal ribs of *Pro-lacerta* (Gow, 1975), rhynchosaurs (e.g., *Mesosuchus*, *H. gordonii*; Dilkes, 1998; Benton, 1983) (Fig. 4A), and *Proterosuchus* (Dilkes and Sues, 2009). By contrast, the anterior and mid-dorsal ribs of all other archosauriforms exhibit a distinct double-headed or triple-headed proximal end (Fig. 4C–E). The proximal peduncle of the rib of *Koilamasuchus* is incipient, contrasting with that

of most archosauriforms (e.g., *Vjushkovia*, *Euparkeria*, *Erythrosuchus*, *Doswellia*; von Huene, 1960; Ewer, 1965; Gower, 2003; Dilkes and Sues, 2009; Fig. 4), but resembles that of rhynchosaurs such as *Mesosuchus* and *H. gordonii* (Benton, 1983; Dilkes, 1998). The proximal articular surface is slightly concave. The proximal end of the dorsal rib of *Koilamasuchus* is gently laterally curved but with a strong medial inflexion below it. This morphology resembles that of *Vanclavea* (Nesbitt et al., 2009:fig. 14c), but contrasts with the condition seen in most archosauromorphs, in which the proximal end of the bone describes a continuous medial bowing (e.g., *Hyperodapedon*, *Mesosuchus*, *Euparkeria*, *Vjushkovia*, *Doswellia*). Below this inflexion, the shaft is medially bowed along its entire extension. A well-defined longitudinal sulcus is present along the entire proximal two-thirds of the preserved surface of the rib, a condition also observed in *Vanclavea* (Nesbitt et al., 2009:fig. 14c), but absent in other basal archosauriforms of which we are aware. This sulcus is very deep and faces slightly laterally at the proximal end of the bone, but along the shaft it is centered and becomes shallower distally up to merge with the bone.

Gastralium?—The mold of a very thin and slightly curved bone is present (Figs. 2, 3E). We interpret this bone as a probable fragmentary gastralium. No further details are observed.

Chevron—The mold of a single anterior chevron is preserved in a probable posterior view (Fig. 3D). The chevron represents ca. 80% of the total height of the dorsal vertebrae. The peduncles that bear the articular facets are high and well dorsolaterally projected, defining a large hemal canal. This canal is higher than wide and seems to be not fully closed proximally. The articular facets are well defined and dorsomedially oriented. The hemal spine is long, comprising more than 70% of the total length of the chevron, and tapers gently distally up to the rounded ventral tip of the bone.

Humerus—The mold of a nearly complete humerus of *Koilamasuchus* is preserved (Fig. 5B), but it could not be determined from which side it belongs. The proximal end of the bone is poorly defined and the distal end is damaged. Both proximal and distal ends are greatly expanded transversely, resembling the condition in *Hyperodapedon* (*H. gordonii*: Benton, 1983), *Vjushkovia* (von Huene, 1960), *Erythrosuchus* (Gower, 2003), *Shansisuchus*, *Wangisuchus*, *Fenhosuchus* (Young, 1964), and *Chanaresuchus* (PVL 6244). No twisting of the main axis between the proximal and distal ends is evident. The proximal end of the humerus is more expanded transversely than the distal end and exhibits a convex proximal articular surface. The deltopectoral crest is not preserved. The proximal end tapers distally and forms a strongly constricted humeral shaft. In fact, the transverse width of the proximal end is more than 3.5 times the minimum width of the shaft, which is present slightly distal to the mid-length of the bone. The strong constriction of the shaft is also emphasized by the greatly expanded distal end of the humerus. The shaft exhibits an oval cross-section, which contrasts with the anteroposteriorly depressed humeral shaft of the proterochamp-sids *Chanaresuchus* (PVL 6244) and *Tropidosuchus* (PVL 4601). Along the preserved surface of the shaft, a wide, low, and oblique ridge is present in *Koilamasuchus*, morphology absent in other archosauromorphs that we are aware (e.g., *Mesosuchus*: Dilkes, 1998; *Hyperodapedon*: Benton, 1983; *Vanclavea*: Parker and Barton, 1998; *Marasuchus*: PVL 3871; *Silesaurus*: Dzik, 2003; *Erythrosuchus*: Gower, 2003; *Vjushkovia*: von Huene, 1960; *Euparkeria*: cast of SAM-PK-5867; *Chanaresuchus*: PVL 6244; *Turfanosuchus*: Wu and Russell, 2001; *Aetosauroides*: PVL 2073), suggesting that it is an autapomorphic condition. The expansion of the distal end of the humerus of *Koilamasuchus* strongly resembles the condition in *Mesosuchus* (Dilkes, 1998), *Hyperodapedon* (*H. gordonii*: Benton, 1983), *Erythrosuchus* (Gower, 2003), *Vjushkovia* (von Huene, 1960), *Shansisuchus*, *Fenhosuchus*, *Wangisuchus* (Young, 1964), and *Chanaresuchus* (PVL

6244). In contrast, the distal end of the humerus of *Euparkeria* (cast of SAM-PK-5867) and *Turfanosuchus* (Wu and Russell, 2001) is poorly transversely expanded. Two distinct distal condyles are discernible, and they are rounded and protrude to approximately the same level distally. A wide and concave intercondylar depression is present on the distal margin of the bone separating both distal condyles. This depression is displaced from the center of the distal end; thus, one of the distal condyles is more transversely expanded than the other one. Comparisons with other archosauromorphs (e.g., *Erythrosuchus*: Gower, 2003) suggest that the broader condyle could be the ulnar condyle.

Ilium—The right ilium of *Koilamasuchus* is preserved as a mold of the medial surface of the acetabular region and a weakly defined impression of the iliac blade (Fig. 5A). The iliac blade was not described or figured by Bonaparte (1981), who may have overlooked it because of the poor preservation. The dorsal margin of the iliac blade is slightly convex, with the highest point positioned close to its mid-length, resembling that of *Erythrosuchus* (Gower, 2003). In contrast, the dorsal margin of the iliac blade is almost straight in *Osmolskina* (Borsuk-Białynicka and Evans, 2003), *Turfanosuchus* (Wu and Russell, 2001), and *Chanaresuchus* (PVL 6244), and strongly convex in *Doswellia* (Weems, 1980; Dilkes and Sues, 2009), *Howesia* (Dilkes, 1995), *Mesosuchus*, and *Prolacerta* (Gow, 1975). The preacetabular process is well developed and pointed, resembling that of the Bica São Tomé archosauriforms (UFSM 11444; Da-Rosa et al., 2009), *Turfanosuchus* (Wu and Russell, 2001), *Chanaresuchus* (PVL 6244), *Tropidosuchus* (PVL 4601), and archosaurs (e.g., *Parasuchus*: Chatterjee, 1978; *Gracilisuchus*: PVL 4597; *Marasuchus*: PVL 3871), but it is more developed than in *Erythrosuchus* (Gower, 2003), *Vjushkovia* (von Huene, 1960), and *Shansisuchus* (Young, 1964). Furthermore, in *Euparkeria* (Ewer, 1965) and *Osmolskina* (Borsuk-Białynicka and Evans, 2003) the preacetabular process is even less developed than in the above-mentioned archosauriforms, and it is absent in *Vanclavea* (Nesbitt et al., 2009). The preacetabular process of *Koilamasuchus* represents ca. 12% of the total anteroposterior length of the iliac blade and it does not project beyond the iliac pubic peduncle. The ventral margin of the preacetabular process is curved ventrally. The postacetabular process is long, representing around half of the length between the pubic and ischial embayments, and around 42% of the anteroposterior length of the iliac blade. The degree of development of the postacetabular process of *Koilamasuchus* resembles that of *Erythrosuchus* (Gower, 2003), *Vjushkovia* (von Huene, 1960), *Shansisuchus* (Young, 1964), *Euparkeria* (Ewer, 1965), and *Osmolskina* (Borsuk-Białynicka and Evans, 2003). In contrast, the length of the postacetabular processes of *Chanaresuchus* (PVL 6244) and *Turfanosuchus* (Wu and Russell, 2001) exceed the length between the pubic and ischial embayments. The posterior border of the postacetabular process is rounded and the ventral margin is straight, being posterodorsally oriented. No trace of the sutural surfaces for the sacral ribs is discernible.

The acetabulum of *Koilamasuchus* is fully closed by an acetabular wall, with a triangular ventral margin. This triangular projection is anteriorly displaced from the mid-length of the acetabulum, and thus it resembles the condition in rhynchosaurs (e.g., *Howesia*: Dilkes, 1995; *H. gordonii*: Benton, 1983), *Erythrosuchus* (Gower, 2003), *Shansisuchus* (Young, 1964), *Vonhuenia* (Ivakhnenko et al., 1997:pl. 57, fig. 3r), the Bica São Tomé archosauriforms (UFSM 11444; Da-Rosa et al., 2009), *Euparkeria* (Ewer, 1965), *Vanclavea* (Nesbitt et al., 2009), *Osmolskina* (Borsuk-Białynicka and Evans, 2003), *Turfanosuchus* (Wu and Russell, 2001), and basal dinosauromorphs (e.g., *Marasuchus*: PVL 3871; *Silesaurus*: Dzik, 2003). In contrast, in *Doswellia* (Dilkes and Sues, 2009), *Chanaresuchus* (PVL 6244), and several pseudosuchians (e.g., *Leptosuchus*: UCMP 26699; *Revueltosaurus*: Parker et al., 2005; *Batrachotomus*: Gower and Schoch, 2009; *Aetosauroides*: PVL 2073) the ventral projection is

situated at mid-length of the acetabulum or is slightly posteriorly displaced. The length between the pubic and ischial embayments represents 83% of the length of the iliac blade, a ratio greater than that observed in *Euparkeria* and *Osmolskina* (65% and 72%, respectively; Ewer, 1965; Borsuk-Bialynicka and Evans, 2003). The pubic peduncle is very elongated, representing a little more than half of the length between the pubic and ischial peduncles, and thus resembles what is seen in *Turfanosuchus* (Wu and Russell, 2001), the Bica São Tomé archosauriforms (UFSM 11444; Da-Rosa et al., 2009), *Vjushkovia* (von Huene, 1960), *Vanclavea* (Nesbitt et al., 2009), and *Doswellia* (Dilkes and Sues, 2009). The dorsal margin of the pubic peduncle is convex, contrasting with the condition seen in the Bica São Tomé archosauriforms (UFSM 11444; Da-Rosa et al., 2009), and the distal articular surface is anteroventrally oriented. The ischial peduncle is dorsoventrally reduced and is much smaller than the pubic peduncle. The distal end of the ischial peduncle is slightly posteriorly expanded, resembling *Exilisuchus* (Ivakhnenko et al., 1997:pl. 57, fig. 2a, b), *Vonhuenia* (Ivakhnenko et al., 1997:pl. 57, fig. 3r), *Vanclavea* (Parker and Barton, 1998; Nesbitt et al., 2009), and *Euparkeria* (Ewer, 1965), but contrasting with the strong posterior projection present in erythrosuchids (e.g., *Erythrosuchus*: Gower, 2003; *Vjushkovia*: von Huene, 1960; *Shansisuchus*: Young, 1964). The distal articular surface of the ischial peduncle faces slightly posteroventrally.

Ungual Phalanx—The only phalanx mold preserved of *Koilamasuchus* is the proximal half of an unguis phalanx (Figs. 2, 5E), which we could not determine whether it belongs to manus or pes. This mold is well preserved, but its distal half is poorly defined. The unguis is dorsoventrally tall and slightly curved. It has a narrow and well-defined collateral groove, which begins at mid-length of the element and becomes shallower towards the distal tip of the claw.

Metapodium—The molds of two metapodials are preserved, one represented by its proximal half (Fig. 5D) and the other by an element with damaged proximal and distal ends (Fig. 2). These elements are strongly transversely expanded at their proximal ends and, in the more complete element, the distal end is also well transversely expanded, but to a lesser degree than the proximal end. The fragmentary element exhibits an oval cross-section with a shallow median longitudinal depression. The more complete metapodial is quite gracile, being not as stout as the metapodials of *Shansisuchus* (Young, 1964), but the proportions of the bone resemble that of the central metapodials of *Mesosuchus* (Dilkes, 1998), metatarsals of *Erythrosuchus* (Gower, 1996), and metacarpals of *Euparkeria* (Ewer, 1965). Thus, we cannot determine to which autopodia they belong.

Indeterminate Limb Bone—The mold of a rod-like bone was interpreted by Bonaparte (1981) as a probable radius (Fig. 5C). Alternatively, this bone could be interpreted as a fibula, but its gracile morphology argues against such an assignment. Thus, the interpretation of Bonaparte (1981) is tentatively followed here. The putative radius is a slender bone with a slightly expanded proximal end. The preserved surface of the proximal end of the bone exhibits a large oval depression and a well-defined distal margin. This depression would have received the lateral process of the ulna. The shaft is straight and the distal end of the bone is only incidentally expanded. The latter feature casts some doubt on the present identification of the bone, because the radius of most archosauromorphs is more distally expanded (e.g., *Mesosuchus*: Dilkes, 1998; *Erythrosuchus*: Gower, 2003; *Vjushkovia*: von Huene, 1960).

Osteoderms—The molds of at least six osteoderms are observed, with a left and a right paramedian osteoderm preserved in natural articulation with each other in a sagittal aspect (Fig. 6). All of the osteoderms exhibit an axis of symmetry and numerous rounded and irregularly distributed small pits on their dorsal surfaces. None of the preserved osteoderms presents an anterior

articular facet, as is present in *Doswellia* (Dilkes and Sues, 2009), *Revueltosaurus* (Parker et al., 2005), and aetosaurs (e.g., UCMP 126804). The articulated paramedian osteoderms are dorsoventrally depressed, with some marginal rugosities at their exposed edges, and settled at an angle of ca. 60° to each other (Fig. 6E). One of the osteoderms has a well-defined sub-triangular outline in dorsal view (Fig. 6A). Its dorsal surface exhibits a longitudinal median keel (Bonaparte, 1981), of which the highest point is situated close to the posterior edge of the scute. A similar median keel is present in the paramedian osteoderms of *Euparkeria* (cast of SAM-PK-5867), *Turfanosuchus* (Wu and Russell, 2001), and *Vanclavea* (Parker and Barton, 2008). The anterior margin of the osteoderm is pointed, as occurs in *Euparkeria* (cast of SAM-PK-5867), but contrasts with *Turfanosuchus*, in which a spike-like anterior prong is continuous with the median keel (Wu and Russell, 2001). The posterior margin of the osteoderm is slightly convex, and so contrasts with the morphology in *Euparkeria* (cast of SAM-PK-5867), in which the posterior margin is strongly convex, and *Erythrosuchus* (Gower, 2003) and *Tropidosuchus* (Arcucci, 1990), in which the posterior margin is concave. The other two preserved osteoderms lack a dorsal keel. The smallest preserved osteoderms are oval in dorsal view (Fig. 6B), and the largest osteoderm also exhibits a sub-triangular contour (Fig. 6C), but it is unlike the latter two osteoderms in being as wide as long. The mold of a probable seventh osteoderm, preserved in side view, is positioned close to the chevron and the unguis. If this is an osteoderm, it is somewhat dorsoventrally thinner than the two osteoderms articulated together.

Indeterminate Fragments—Several molds of bone fragments are preserved but their identity could not be identified here. Two of these unidentified molds exhibit distinctive shapes (Fig. 2). The largest, positioned close to the putative radius, is a long, relatively wide, rectangular bone. One of its ends is not preserved, and it has a longitudinal fracture. The preserved end has a circular transverse section, resembling the condyle of a long bone, and its width is the same as that of the rest of the bone. Based on this morphology, the bone could be a pubis in anterior or posterior view, but the absence of diagnostic features precludes an accurate identification. The other unidentified element, situated over the distal end of the dorsal rib, is an elongated fragment with a median edge.

DISCUSSION AND CONCLUSIONS

Phylogenetic Analysis

A cladistic analysis was performed in order to assess the phylogenetic relationships of *Koilamasuchus gonzalezdiazi*. A data matrix was constructed combining mainly the datasets published by Gower and Sennikov (1997), Benton (2004), Dilkes and Sues (2009), and Nesbitt et al. (2009), among others. Taxa previously recognized as ‘proterosuchids,’ ‘euparkeriids,’ erythrosuchids, and other non-archosaur archosauriforms, as well as pseudosuchian and avemetatarsalian archosaurs, were included together with *Koilamasuchus*, resulting in a data matrix composed of 169 characters and 28 taxa (Appendices 1–3). The rhynchosaur *Mesosuchus* was used to root the recovered most parsimonious trees (MPTs). The data matrix was analyzed under equally weighted maximum parsimony using TNT 1.1 (Goloboff et al., 2008). A heuristic search was performed with 100 replications of Wagner trees (with random addition sequence) followed by TBR branch-swapping algorithm (holding 10 trees per replicate). Zero-length branches among any of the recovered MPTs were collapsed (i.e., ‘rule 1’ of Coddington and Scharff, 1994). Multistate characters were treated as unordered. As measures of tree support, a Bremer support and a jackknife resampling analysis, set up with 5000 pseudoreplicates and a character removal probability of 0.36, were performed.

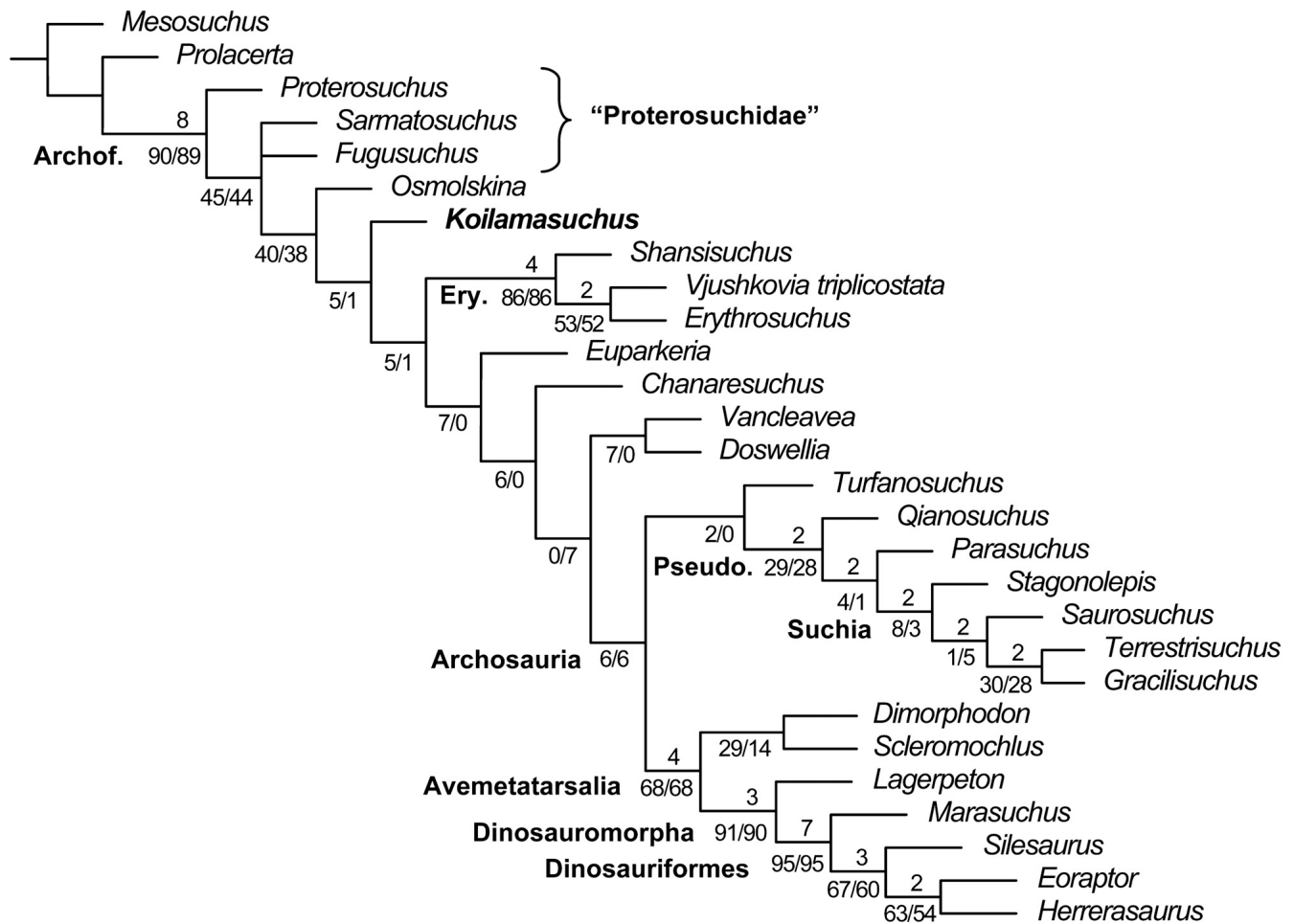


FIGURE 7. Strict consensus tree depicting the phylogenetic relationships of *Koilamasuchus gonzalezdiazi* and other basal archosauriforms, showing decay indexes higher than 1 (above) and absolute (left) and GC (right) jackknife frequencies (below) for each clade. **Abbreviations:** **Archof.**, Archosauriformes; **Ery.**, Erythrosuchidae; **Pseudo.**, Pseudosuchia.

The search recovered two MPTs of 467 steps, with a consistency index of 0.39, a retention index of 0.60, and a best score hit in 64 of the 100 replications. The MPTs identified *Koilamasuchus* as an archosauriform more crownwards than *Proterosuchus*, *Sarmatosuchus*, *Fugusuchus*, and *Osmolskina*, placing it as the sister taxon of the clade that includes Erythrosuchidae and Archosauria (Fig. 7). Accordingly, our results contrast with the proterosuchid identity suggested originally for MACN-Pv 18119 by Bonaparte (1981). Furthermore, Proterosuchidae in our analysis is a paraphyletic group, and *Osmolskina* is not a 'euparkeriid' as tentatively suggested by Borsuk-Białynicka and Evans (2003).

The inclusion of *Koilamasuchus* within Archosauriformes is supported by the presence of two synapomorphies. The first one is the presence of an iliac blade with a slightly convex dorsal margin. In rhynchosaurs (e.g., *Mesosuchus*, *Howesia*, *Hyperodapedon*) and *Prolacerta* (Dilkes, 1995, 1998) the dorsal margin of the iliac blade is strongly convex. In contrast, the dorsal margin of most archosauriforms (e.g., *Erythrosuchus*: Gower, 2003; *Vjushkovia*: von Huene, 1960; *Chanaresuchus*: PVL 6244; *Turfanosuchus*: Wu and Russell, 2001; *Leptosuchus*: UCMP 26699), including *Koilamasuchus*, is straight or slightly convex. Nevertheless, a reversal of this condition is observed in the archosauriforms *Vancleavea* and *Doswellia*, in which a strongly convex dorsal margin is present (Parker and Barton, 2008; Dilkes and

Sues, 2009). The second archosauriform synapomorphy present in *Koilamasuchus* is an iliac blade with a maximum length more than 3 times its maximum height. In Archosauriformes the postacetabular process is strongly elongated with respect to the rest of the ilium, and as a result the maximum length of the iliac blade is 3 times or more than its maximum dorsoventral height (e.g., *Vjushkovia*: 4.04 times; *Turfanosuchus*: 3.69 times; *Osmolskina*: 4.75 times; *Koilamasuchus*: 3.2 times). The latter condition contrasts with that observed in non-archosauriform archosauromorphs (e.g., *Hyperodapedon huxleyi*, *H. gordonii*, *Mesosuchus*, *Prolacerta*; Chatterjee, 1974; Benton, 1983; Dilkes, 1998) and the reversal present in *Vancleavea* (Parker and Barton, 2008), in which the iliac blade is proportionally anteroposteriorly shorter. The monophyly of Archosauriformes is quite robust, with a decay index of 8 and jackknife frequencies of 90%.

Furthermore, *Koilamasuchus* is more derived than *Proterosuchus* because of the presence of the following synapomorphies of the clade that includes the former genus and more crownward archosauriforms (e.g., *Erythrosuchus*, *Chanaresuchus*, and *Turfanosuchus*). First, contrasting with most non-archosauriform archosauromorphs (Benton, 2004; Dilkes and Sues, 2009), an ilium with a preacetabular process is observed in *Koilamasuchus* and other archosauriforms, such as *Erythrosuchus* (Gower, 2003), *Turfanosuchus* (Wu and Russell, 2001), *Euparkeria* (Ewer, 1965),

and *Chanaresuchus* (PVL 6244). The second character is the presence of an ilium with a dorsal margin of the pubic peduncle forming an angle more acute than 45° to the longitudinal axis of the bone. In rhynchosaurs (e.g., *H. gordonii*, *Howesia*, *Mesosuchus*; Benton, 1983; Dilkes, 1995, 1998), *Prolacerta* (Dilkes, 1998), and *Proterosuchus*, the pubic peduncle of the ilium is almost vertical or slightly anteroventrally oriented. In contrast, in *Koilamasuchus*, the purported 'proterosuchids' *Exilisuchus* and *Vonhuenia* (Ivakhnenko et al., 1997:pl. 57, figs. 2a, b, 3r), and other basal archosauriforms (e.g., *Euparkeria*, *Turfanosuchus*, *Erythrosuchus*, *Chanaresuchus*; Ewer, 1965; Wu and Russell, 2001; Gower, 2003; PVL 6244) the pubic peduncle is anteroventrally directed forming an angle more acute than 45° to the longitudinal axis of the ilium.

The presence of dorsal body osteoderms was traditionally considered to be a synapomorphy of the clade that includes archosauriforms more derived than erythrosuchids and 'proterosuchids' (e.g., Sereno, 1991). Nevertheless, the description of dorsal body osteoderms in *Erythrosuchus* (Gower, 2003), however, led to a reconsideration of the distribution of this character. In this regard, a recent phylogenetic analysis recovered the presence of osteoderms as a synapomorphy of the clade including all archosauriforms more derived than *Proterosuchus* (Dilkes and Sues, 2009). In our analysis, the presence of dorsal body osteoderms is found as a synapomorphy of the clade including *Osmolskina* and more crownward archosauriforms (e.g., *Koilamasuchus*, *Erythrosuchus*, *Chanaresuchus*, *Doswellia*). In contrast, more basal archosauriforms, such as rhynchosaurs (e.g., *H. gordonii*, *Howesia*, *Mesosuchus*; Benton, 1983; Dilkes, 1995, 1998), *Prolacerta* (Dilkes, 1998), and *Proterosuchus* (Sereno, 1991; Dilkes and Sues, 2009), lack dorsal body osteoderms. In addition, *Koilamasuchus* is found as more derived than *Osmolskina* due to the presence of a well-developed preacetabular process, a condition shared with more derived archosauriforms (e.g., *Erythrosuchus*, *Shansisuchus*, *Chanaresuchus*, *Turfanosuchus*). In contrast, *Proterosuchus* and non-archosauriform archosauriforms lack a preacetabular process (Dilkes and Sues, 2009), whereas *Osmolskina* exhibits poor development of this structure. *Euparkeria* also presents a poorly developed preacetabular process, but the condition is interpreted as an apomorphic reversal of the genus here.

On the other hand, *Koilamasuchus* is found to be less derived than erythrosuchids and more crownward archosauriforms (e.g., *Turfanosuchus*, *Chanaresuchus*, *Doswellia*) because of the absence of long and distinct tuberculum on the anterior and mid-dorsal ribs. The dorsal ribs of rhynchosaurs, *Prolacerta*, *Proterosuchus*, and probably *Sarmatosuchus* (Gower and Sennikov, 1997) exhibit poorly developed dorsal rib proximal ends, constituting the ancestral condition of Archosauriformes. In more derived archosauriforms (e.g., *Vjushkovia*, *Euparkeria*, *Turfanosuchus*, *Erythrosuchus*, *Doswellia*; von Huene, 1960; Ewer, 1965; Wu and Russell, 2001; Gower, 2003; Dilkes and Sues, 2009) the dorsal ribs bear long tubercular processes. In *Koilamasuchus* the preserved anterior or mid-dorsal rib is holocephalous and has a very short proximal end, closely resembling that of more basal forms, such as the rhynchosaurs *H. gordonii* and *Mesosuchus* (Benton, 1983; Dilkes, 1998) (Fig. 4).

The strict consensus of the recovered MPTs found a paraphyletic "Proterosuchidae" (contra Gower and Sennikov, 1997), with the previously recognized 'proterosuchids' *Sarmatosuchus* and *Fugusuchus* positioned more crownwards than *Proterosuchus* (synapomorphies are detailed in Appendix 4). *Osmolskina* is found as the sister taxon of the clade including *Koilamasuchus* and more crownwards archosauriforms, whereas *Euparkeria* was recovered in a more derived position, thus depicting a polyphyletic "Euparkeriidae." *Erythrosuchus*, *Shansisuchus*, and *Vjushkovia* were found within a monophyletic Erythrosuchidae (considered here to be the most inclusive clade containing *Ery-*

throsuchus africanus Broom, 1905, but not *Proterosuchus fergusi* Broom, 1903, or *Passer domesticus* Linnaeus, 1758), although *Fugusuchus* is recovered outside the group contrasting with Parrish (1992). The clade Erythrosuchidae is very well supported with a decay index of 4 and jackknife frequencies of 86%, and the following 11 synapomorphies diagnose the group: elliptical infratemporal fenestra; supraoccipital excluded from dorsal border of foramen magnum by dorsomedial midline contact between opposite exoccipitals; absence of palatine teeth; absence of teeth on palatal ramus of pterygoid; mid- and posterior dorsal centra as long as tall; mid-dorsal prezygapophyses anterodorsally oriented; posterior border of iliac ischiadic peduncle strongly posteriorly expanded; presence of pineal fossa; cervical vertebral centra as long as tall; humerus with a deltopectoral crest length more than 38% of the length of the bone; and first sacral rib plate-like, contacting ilium in a straight parasagittal articulation.

Contrasting with the phylogenetic analysis of Dilkes and Sues (2009), but in agreement with several previous authors (e.g., Gauthier, 1986; Benton and Clark, 1988; Sereno, 1991; Parker and Barton, 1998; Nesbitt et al., 2009), *Euparkeria* is positioned more crownwards than erythrosuchids, and as the sister taxon of the clade that includes *Chanaresuchus* and more derived forms. In our analysis the bizarre archosauriform *Vancleavea campi* is positioned as the sister taxon of *Doswellia*, forming a clade that is the sister taxon of Archosauria. The clade of *Vancleavea* and *Doswellia* is diagnosed by the absence of a femoral fourth trochanter, the presence of mid-dorsal neural spines situated at mid-length between the zygapophyses, and a maximum length of the iliac blade less than 3 times its maximum height. This topology is more similar to that obtained by Parker and Barton (1998) than that of Nesbitt et al. (2009), who found *Vancleavea* in a more basal position. Regarding the affinities of the Middle Triassic *Turfanosuchus*, it is recovered for the first time, in a quantitative phylogenetic analysis, as the basal-most member of Pseudosuchia. This position is supported by three unambiguous synapomorphies: the presence of a depression on descending process of postorbital, a hemicylindrical calcaneal condyle (Wu and Russell, 2001), and a pubis with a length twice than that of the acetabulum. The recovery of *Turfanosuchus* within Pseudosuchia is very interesting, because it depicts a pseudosuchian taxon that lacks the specialized crurotarsal proximal tarsals present in the other members of the group.

Searches for sub-optimal trees with enforced topological constraints recovered some interesting results. In order to obtain *Vancleavea* in the same position recovered by Nesbitt et al. (2009), i.e., directly in a more crownwards position than Erythrosuchidae, four extra steps are necessary, and a sub-optimal tree three steps longer positions *Vancleavea* as the most basal pseudosuchian or avemetatarsalian. With regards to *Koilamasuchus*, three extra steps are needed to position it as the sister taxon of Archosauriformes, but only one extra step is necessary in order to nest *Koilamasuchus* with 'proterosuchids,' erythrosuchids, *Euparkeria*, the clade of *Vancleavea* and *Doswellia*, or Pseudosuchia. These results are not unexpected due to the fragmentary condition of the holotype of *Koilamasuchus*. Thus, the general position of *Koilamasuchus* as an archosauriform is well supported, but clearly more information is needed to clarify its relationships with other members of the group.

Implications in the Early Radiation of Archosauriformes

The phylogenetic analysis performed here depicts *Koilamasuchus* as a very basal archosauriform, more derived than *Proterosuchus* and other 'proterosuchids,' but more basal than Erythrosuchidae, *Chanaresuchus*, and Archosauria. *Koilamasuchus* is one of the oldest members of Archosauriformes, together with the Late Permian *Archosaurus* and the Early Triassic *Fugusuchus*, the putative erythrosuchid *Garjainia* (Parrish, 1992),

and the probable poposauroid archosaur *Xilousuchus* (Nesbitt, 2009). *Koilamasuchus gonzalezdiazi* is currently the only valid species of Early Triassic archosauriform from South America and, together with fragmentary remains from Brazil (Da-Rosa et al., 2009), the only evidence of the group in western-most Gondwana at this time. *Koilamasuchus* does not fit with the currently known groups of basal archosauriforms (e.g., “Proterosuchidae,” Erythrosuchidae, Proterochampsidae, Doswelliidae), adding a new, small, basal archosauriform taxon that increases the diversity of the group during the biotic recovery after the Permo-Triassic mass extinction event.

ACKNOWLEDGMENTS

We thank A. Kramarz who loaned us the holotype of *Koilamasuchus* and several people who allowed us to study specimens under their care: J. Powell (PVL), S. Devinvenzi Gonzáles (MCNAM), P. Holroyd (UCMP), A. Da-Rosa (UFSM), A. Kramarz (MACN), L. Steel, S. Chapman, and P. Barrett (NHM). We thank J. Desojo (MACN) for comments and discussion of the type material of *Koilamasuchus* and other basal archosauriforms. The comments of three anonymous reviewers and editor S. Modesto improved the quality of this paper. Thanks are also extended to M. Miñana and M. Iberlucea who performed latex casts of the holotype of *Koilamasuchus*. Access to the free version of TNT 1.1 was granted by the Willi Hennig Society.

LITERATURE CITED

- Arcucci, A. 1990. Un nuevo Proterochampsidae (Reptilia-Archosauriformes) de La Fauna Local de Los Chañares (Triásico Medio), La Rioja, Argentina. *Ameghiniana* 27:365–378.
- Arcucci, A., and C. A. Marsicano. 1998. A distinctive new archosaur from the Middle Triassic (Los Chañares Formation) of Argentina. *Journal of Vertebrate Paleontology* 18:228–232.
- Bandyopadhyay, S. 1988. Vertebrate fossils from the Pranhita-Godavari valley of India with special reference to the Yerrapalli Formation. *Modern Geology* 13:107–117.
- Bennett, S. C. 1996. The phylogenetic position of the Pterosauria within the Archosauriforms. *Zoological Journal of the Linnean Society* 118:261–308.
- Benton, M. J. 1983. The Triassic reptile *Hyperodapedon* from Elgin: functional morphology and relationships. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences* 302:605–720.
- Benton, M. J. 1985. Classification and phylogeny of the diapsid reptiles. *Zoological Journal of the Linnean Society* 84:97–164.
- Benton, M. J. 1990. Origin and interrelationships of dinosaurs; pp. 11–30 in D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*. University of California Press, Berkeley, California.
- Benton, M. J. 2004. Origin and relationships of Dinosauria; pp. 7–19 in D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*, second edition. University of California Press, Berkeley, California.
- Benton, M. J., and J. M. Clark. 1988. Archosaur phylogeny and the relationships of the Crocodylia; pp. 295–338 in M. J. Benton (ed.), *The Phylogeny and Classification of the Tetrapods, Volume 1: Amphibians, Reptiles, Birds*. The Systematics Association Special Volume 35A. Clarendon Press, Oxford.
- Benton, M. J., and A. D. Walker. 2002. *Erpetosuchus*, a crocodile-like basal archosaur from the Late Triassic of Elgin, Scotland. *Biological Journal of the Linnean Society* 136:25–47.
- Bonaparte, J. F. 1966a. Sobre nuevos terapsidos triásicos hallados en el centro de la Provincia de Mendoza, (Therapsida, Dicynodontia y Cynodontia). *Acta Geológica Lilloana* 8:91–100.
- Bonaparte, J. F. 1966b. Una nueva ‘fauna’ Triásica de Argentina (Therapsida: Cynodontia-Dicynodontia). Consideraciones filogenéticas y paleobiogeográficas. *Ameghiniana* 4:243–296.
- Bonaparte, J. F. 1966c. Cronología de algunas formaciones Triásicas Argentinas basada en restos de tetrápodos. *Revista de la Asociación Geológica Argentina* 21:20–38.
- Bonaparte, J. F. 1967. New vertebrate evidence for a southern transatlantic connection during the Lower or Middle Triassic. *Palaeontology* 10:554–563.
- Bonaparte, J. F. 1969. *Cynognathus minor* n. sp. (Therapsida-Cynodontia). Nueva evidencia de vinculación faunística Afro-Sudamericana a principios del Triásico. *Gondwana Stratigraphy, I.U.G.S., Coloquio Mar del Plata 1967*:273–281.
- Bonaparte, J. F. 1981. Nota sobre una nueva fauna del Triásico Inferior del sur de Mendoza, Argentina, correspondiente a la Zona de *Lystrosaurus* (Dicynodontia-Proterosuchia). *Anales II Congreso Latinoamericano de Paleontología, Porto Alegre, 1981* 1:277–288.
- Bonaparte, J. F. 1982. Faunal replacement in the Triassic of South America. *Journal of Vertebrate Paleontology* 2:362–371.
- Bonaparte, J. F. 2000. Comentarios críticos sobre el Triásico Inferior de Puesto Viejo y Potrerillos. *Boletín de la Academia Nacional de Ciencias* 64:147–152.
- Borsuk-Białynicka, M., and S. E. Evans. 2003. A basal archosauriform from the Early Triassic of Poland. *Acta Palaeontologica Polonica* 48:649–652.
- Britt, B. B. 1997. Postcranial pneumaticity; pp. 590–593 in P. J. Currie and K. Padian (eds.), *Encyclopedia of Dinosaurs*. Academic Press, San Diego.
- Broom, R. 1903. On a new reptile (*Proterosuchus fergusi*) from the Karoo beds of Tarkastad, South Africa. *Annals of the South African Museum* 4:159–164.
- Broom, R. 1905. Notice of some new fossil reptiles from the Karoo beds of South Africa. *Records of the Albany Museum* 1:331–337.
- Chatterjee, S. 1974. A rhynchosaur from the Upper Triassic Maleri Formation of India. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences* 267:209–261.
- Chatterjee, S. 1978. A primitive parasuchid (Phytosaur) reptile from the Upper Triassic Maleri Formation of India. *Palaeontology* 21:83–127.
- Chatterjee, S. 1980. *Malerisaurus*, A new eosuchian reptile from the Late Triassic of India. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences* 291:163–200.
- Clark, J. M., H.-D. Sues, and D. S. Berman. 2000. A new specimen of *Hesperosuchus agilis* from the Upper Triassic of New Mexico and the interrelationships of basal crocodylomorph archosaurs. *Journal of Vertebrate Paleontology* 20:683–704.
- Coddington, J. A., and N. Scharff. 1994. Problems with zero-length branches. *Cladistics* 10:415–423.
- Cooper, M. R. 1984. Reassessment of *Vulcanodon karibaensis* Raath (Dinosauria: Saurischia) and the origin of Sauropoda. *Palaeontologia Africana* 25:203–231.
- Cox, C. B. 1991. The Pangaea dicynodont *Rechnisaurus* and the comparative biostratigraphy of Triassic dicynodont faunas. *Palaeontology* 34:767–784.
- Da-Rosa, A. A., G. Piñeiro, S. Dias-Da-Silva, J. C. Cisneros, F. F. Feltrin, and L. Witeck Neto. 2009. Bica São Tomé, um novo sítio fossilífero para o Triássico Inferior do sul do Brasil. *Revista Brasileira de Paleontologia* 12:67–76.
- De Fauw, S. L. 1993. The Pangean dicynodont *Rechnisaurus* from the Triassic of Argentina; pp. 101–105 in S. G. Lucas and M. Morales (eds.), *The Nonmarine Triassic*. New Mexico Museum of Natural History and Science, Bulletin 3.
- Desojo, J. B., A. Arcucci, and C. Marsicano. 2002. Reassessment of *Cuyosuchus huenei*, a Middle-Late Triassic archosauriform from the Cuyo Basin, west-central Argentina. *Upper Triassic Stratigraphy and Paleontology*. *Bulletin of the New Mexico Museum of Natural History* 21:143–148.
- Desojo, J. B., M. D. Ezcurra, and C. L. Schultz. In press. An unusual new archosauriform from the Middle–Late Triassic of southern Brazil and the monophyly of Doswelliidae. *Zoological Journal of the Linnean Society of London*.
- Dilkes, D. W. 1995. The rhynchosaur *Howesia browni* from the Lower Triassic of South Africa. *Palaeontology* 38:665–685.
- Dilkes, D. W. 1998. The Early Triassic rhynchosaur *Mesosuchus browni* and the interrelationships of basal archosauriform reptiles. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences* 353:501–541.
- Dilkes, D. W., and H.-D. Sues. 2009. Redescription and phylogenetic relationships of *Doswellia kaltenbachi* (Diapsida: Archosauriformes) from the Upper Triassic of Virginia. *Journal of Vertebrate Paleontology* 29:58–79.

- Domnanovich, N., and C. Marsicano. 2010 [dated 2009]. Los dicinodontes (Amniota: Terápsida) de Argentina: síntesis sobre el conocimiento actual del grupo. *Ameghiniana*, Resúmenes 46.
- Dzik, J. 2003. A beaked herbivorous archosaur with dinosaur affinities from the early Late Triassic of Poland. *Journal of Vertebrate Paleontology* 23:556–574.
- Ewer, R. F. 1965. The anatomy of the thecodont reptile *Euparkeria capensis* Broom. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences* 248:379–445.
- Ezcurra, M. D. 2006. A review of the systematic position of the dinosauriform archosaur *Eucoelophysis baldwini* Sullivan and Lucas, 1999 from the Upper Triassic of New Mexico, USA. *Geodiversitas* 28:649–684.
- Ezcurra, M. D., A. Lecuona, and A. Martinelli. 2010 [dated 2009]. Review of a basal archosauriform from the Early Triassic of the Puesto Viejo Group, Mendoza, Argentina. *Ameghiniana*, Resúmenes 46.
- Gauthier, J. A. 1986. Saurischian monophyly and the origin of birds. *Memoirs of the California Academy of Sciences* 8:1–55.
- Gauthier, J. A., A. G. Kluge, and T. Rowe. 1988. The early evolution of the Amniota; pp. 103–155 in M. J. Benton (ed.), *The Phylogeny and Classification of the Tetrapods, Volume 1: Amphibians, Reptiles, Birds. The Systematics Association Special Volume 35A*. Clarendon Press, Oxford.
- Gauthier, J., D. Cannatella, K. de Queiroz, A. G. Kluge, and T. Rowe. 1989. Tetrapod phylogeny; pp. 337–353 in B. Fernholm, K. Bremer, and H. Jornvall (eds.), *The Hierarchy of Life: Molecules and Morphology in Phylogenetic Analysis*. Elsevier, Amsterdam.
- Goloboff, P. A., J. S. Farris, and K. Nixon. 2008. TNT, a free program for phylogenetic analysis. *Cladistics* 24:774–786.
- González Díaz, E. F. 1964. Rasgos geológicos y evolución geomorfológica de la Hoja 27d (San Rafael) y zona occidental vecina (Provincia de Mendoza). *Revista de la Asociación Geológica Argentina* 19:151–188.
- González Díaz, E. P. 1966. Hallazgo del Infra?—Mesotriásico continental en el sur del área pedemontana mendocina. *Acta Geológica Lilloana* 7:101–134.
- González Díaz, E. P. 1972. Descripción geológica de la Hoja 27d, San Rafael, Provincia de Mendoza. *Boletín del Servicio Minero Nacional* 132:1–127.
- Gow, C. E. 1975. The morphology and relationships of *Youngina capensis* Broom and *Prolacerta broomi* Parrington. *Palaeontologia Africana* 18:89–131.
- Gower, D. J. 1996. The tarsus of erythrosuchid archosaurs, and implications for early diapsid phylogeny. *Zoological Journal of the Linnean Society* 116:347–375.
- Gower, D. J. 2001. Possible postcranial pneumaticity in the last common ancestor of birds and crocodylians: evidence from *Erythrosuchus* and other Mesozoic archosaurs. *Naturwissenschaften* 88:119–122.
- Gower, D. J. 2002. Braincase evolution in suchian archosaurs (Reptilia: Diapsida): evidence from the rauisuchian *Batrachotomus kupferzellensis*. *Zoological Journal of the Linnean Society* 136:49–76.
- Gower, D. J. 2003. Osteology of the early archosaurian reptile *Erythrosuchus africanus* Broom. *Annals of the South African Museum* 110:1–84.
- Gower, D. J., and R. R. Schoch. 2009. Postcranial anatomy of the rauisuchian archosaur *Batrachotomus kupferzellensis*. *Journal of Vertebrate Paleontology* 29:103–122.
- Gower, D. J., and A. G. Sennikov. 1996. Morphology and phylogenetic informativeness of early archosaur braincases. *Palaeontology* 39:883–906.
- Gower, D. J., and A. G. Sennikov. 1997. *Sarmatosuchus* and the early history of the Archosauria. *Journal of Vertebrate Paleontology* 17:60–73.
- Gower, D. J., and A. G. Sennikov. 2000. Early archosaurs from Russia; pp. 140–159 in M. J. Benton, M. A. Shishkin, D. M. Unwin, and E. N. Kurochkin (eds.), *The Age of Dinosaurs in Russia and Mongolia*. Cambridge University Press, Cambridge, U.K.
- Heckert, A. B., and S. G. Lucas. 1999. A new aetosaur (Reptilia: Archosauria) from the Upper Triassic of Texas and the phylogeny of aetosaurs. *Journal of Vertebrate Paleontology* 19:50–68.
- Huene, F. von. 1946. Die grossen Stämme der Tetrapoden in den geologischen Zeiten. *Biologische Zentralblatt* 65:268–275.
- Huene, F. von. 1960. Ein grosser Pseudosuchier aus der Orenburger Trias. *Palaeontographica Abteilung A* 114:105–111.
- Hutchinson, J. R. 2001. The evolution of pelvic osteology and soft tissues on the line to extant birds (Neornithes). *Zoological Journal of the Linnean Society* 131:123–168.
- Ivakhnenko, M. F., V. K. Golubev, Y. M. Gubin, I. V. Novikov, A. G. Sennikov, and A. S. Rautian. 1997. Permian and Triassic Tetrapods of Eastern Europe. *GEOS, Moscow*, 216 pp.
- Jain, S. L., and R. T. Roy-Chowdhury. 1987. Fossil vertebrates from the Pranhita-Godavari valley (India) and their stratigraphic correlation. *Gondwana Six: Stratigraphy, Sedimentology and Paleontology. Geophysical Monograph* 41:219–228.
- Juul, L. 1994. The phylogeny of basal archosaurs. *Palaeontologia Africana* 31:1–38.
- Langer, M. C., and M. J. Benton. 2006. Early dinosaurs: a phylogenetic study. *Journal of Systematic Palaeontology* 4:309–358.
- Linnaeus, C. 1758. *Systema Naturae*, tenth edition. *Holmiae, Laurentii Salvii*, 824 pp.
- Llambías, E. J., L. E. Kleiman, and J. E. Salvarredi. 1993. El magmatismo gondwánico; pp. 53–64 in V. Ramos (ed.), *Geología y Recursos Naturales de Mendoza. 12º Congreso Geológico Argentino y 2º Congreso de Exploración de Hidrocarburos (Mendoza), Relatorio Capítulo I–6*.
- Martinelli, A. G., and M. de la Fuente. 2008. Los cinodontes nomaliaformes de la Formación Puesto Viejo, San Rafael, Mendoza. *Actas Tercer Encuentro Científico ICES, Malargüe* 67–74.
- Martinelli, A. G., M. de la Fuente, and F. Abdala. 2009. *Diademodon tetragonus* Seeley, 1894 (Therapsida: Cynodontia) in the Triassic of South America and its biostratigraphic implications. *Journal of Vertebrate Paleontology* 29:852–862.
- Modesto, S., and J. Botha-Brink. 2008. Evidence of a second, large archosauriform reptile in the Lower Triassic Katberg Formation of South Africa. *Journal of Vertebrate Paleontology* 28:914–917.
- Modesto, S. P., and H.-D. Sues. 2004. The skull of the Early Triassic archosauromorph reptile *Prolacerta broomi* and its phylogenetic significance. *Zoological Journal of the Linnean Society* 140:335–351.
- Nesbitt, S. J. 2005. Osteology of the Middle Triassic pseudosuchian archosaur *Arizonasaurus babbitti*. *Historical Biology* 17:19–47.
- Nesbitt, S. J. 2009. The antiquity of Archosauria and the origin of Late Triassic archosaur assemblages. *Journal of Vertebrate Paleontology* 29(3, Supplement):155A.
- Nesbitt, S. J., Stocker, M. R., Small, B. J., and Downs, A. 2009. The osteology and relationships of *Vancleavea campi* (Reptilia: Archosauriformes). *Zoological Journal of the Linnean Society* 157:814–864.
- Novas, F. E. 1989. The tibia and tarsus in Herrerasauridae (Dinosauria, incertae sedis) and the origin and evolution of the dinosaurian tarsus. *Journal of Paleontology* 63:677–690.
- Novas, F. E. 1992. Phylogenetic relationships of basal dinosaurs, the Herrerasauridae. *Palaeontology* 63:51–62.
- Novas, F. E. 1996. Dinosaur monophyly. *Journal of Vertebrate Paleontology* 16:723–741.
- Olsen, P. E., H.-D. Sues, and M. A. Norell. 2000. First record of *Erythrosuchus* (Reptilia: Archosauria) from the Late Triassic of North America. *Journal of Vertebrate Paleontology* 20:633–636.
- Osborn, H. F. 1903. On the preliminary division of the Reptilia into two sub-classes, Synapsida and Diapsida. *Science* 17:275–276.
- Parker, W. G., and B. J. Barton. 2008. New information on the Upper Triassic archosauriform *Vancleavea campi* based on new material from the Chinle Formation of Arizona. *Palaeontologia Electronica* 11.3.14A:1–20.
- Parker, W. G., R. B. Irmis, S. J. Nesbitt, J. W. Martz, and L. S. Browne. 2005. The Late Triassic pseudosuchian *Revueltosaurus callenderi* and its implications for the diversity of early ornithischian dinosaurs. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 272:963–969.
- Parrish, J. M. 1992. Phylogeny of the Erythrosuchidae (Reptilia: Archosauriformes). *Journal of Vertebrate Paleontology* 12:93–102.
- Parrish, J. M. 1993. Phylogeny of the Crocodylotarsi, with reference to archosaurian and crurotarsan monophyly. *Journal of Vertebrate Paleontology* 13:287–308.
- Price, L. I. 1946. Sobre um novo pseudossuquiu do Triássico Superior do Rio Grande do Sul. *Boletim da Divisão de Geologia e Mineralogia* 120:1–38.
- Ramos, V. 1993. El magmatismo triásico-jurásico de intraplaca; pp. 79–86 in V. Ramos (ed.), *Relatorio Geología y Recursos Naturales de Mendoza. XII Congreso Geológico Argentino y II Congreso de Exploración de Hidrocarburos*.

- Reig, O. A. 1959. Primeros datos descriptivos sobre nuevos reptiles arcosaurios del Triásico de Ischigualasto (San Juan, Argentina). *Revista de la Asociación Geológica Argentina* 13:257–270.
- Reig, O. A. 1961. Acerca de la posición sistemática de la familia Raiusuchidae y del género *Saurosuchus* (Reptilia, Thecodontia). *Revista del Museo Municipal de Ciencias Naturales y Tradicional de La Plata* 1:73–113.
- Romer, A. S. 1971. The Chañares (Argentina) Triassic reptile fauna. XI. Two new long-snouted thecodonts, *Chanaresuchus* and *Gualosuchus*. *Breviora* 379:1–22.
- Romer, A. S. 1972. The Chañares (Argentina) Triassic reptile fauna. XII. The postcranial skeleton of the thecodont *Chanaresuchus*. *Breviora* 385:1–21.
- Roy-Chowdhury, T. 1970. Two new dicynodonts from the Triassic Yerrapalli Formation of central India. *Palaeontology* 13:132–144.
- Rusconi, C. 1951. Fósiles Cámbricos de Salagasta, Mendoza. *Anales de la Sociedad Científica Argentina* 152:255–264.
- Sennikov, A. G. 1989. A new euparkeriid (Thecodontia) from the Middle Triassic of the Southern Urals. *Palaeontological Journal* 22:66–73.
- Sennikov, A. G. 1995. Early Thecodonts of Eastern Europe. *Nauka*, Moscow, 141 pp.
- Senter, P. 2003. New information on cranial and dental features of the Triassic archosauriform reptile *Euparkeria capensis*. *Palaeontology* 46:613–621.
- Sereno, P. C. 1991. Basal archosaurs: phylogenetic relationships and functional implications. *Society of Vertebrate Paleontology Memoir* 2:1–53.
- Sereno, P. C. 1993. The pectoral girdle and forelimb of the basal theropod *Herrerasaurus ischigualastensis*. *Journal of Vertebrate Paleontology* 13:425–450.
- Sereno, P. C., and A. B. Arcucci. 1990. The monophyly of crurotarsal archosaurs and the origin of bird and crocodile ankle joints. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 180:21–52.
- Sereno, P. C., and A. B. Arcucci. 1993. Dinosaurian precursors from the Middle Triassic of Argentina: *Lagerpeton chanarensis*. *Journal of Vertebrate Paleontology* 13:385–399.
- Sereno, P. C., and F. E. Novas. 1992. The complete skull and skeleton of an early dinosaur. *Science* 258:1137–1140.
- Sill, W. D. 1967. *Proterochampsia barrionuevoi* and the early evolution of the Crocodylia. *Bulletin of the Museum of Comparative Zoology* 135:415–446.
- Spalletti, L. A. 1994. Evolución de los ambientes en el Triásico de la Sierra Pintada (Mendoza, Argentina): análisis sobre la influencia de controles intrínsecos y extrínsecos al sistema depositacional. *AAS Revista* 1:125–142.
- Stipanovic, P. N., E. F. González Díaz, and A. M. Zavattieri. 2007. Grupo Puesto Viejo nom. transl. por Formación Puesto Viejo González Díaz, 1964, 1967: nuevas interpretaciones paleontológicas, estratigráficas y cronológicas. *Ameghiniana* 44:759–761.
- Thulborn, R. A. 1986. The Australian Triassic reptile *Tasmaniosaurus triassicus* (Thecodontia: Proterosuchia). *Journal of Vertebrate Paleontology* 6:123–142.
- Trumpy, E. 1940. Probable extensión de la Cuenca Rética de Mendoza. Informe Inédito, Yacimientos Petrolíferos Fiscales, Argentina.
- Valencio, D. A., J. E. Mendia, and J. F. Vilas. 1975. Paleomagnetism and K-Ar ages of Triassic igneous rocks from the Ischigualasto-Ischichuca basin and Puesto Viejo Formation, Argentina. *Earth and Planetary Science Letters* 26:319–330.
- Weems, R. E. 1980. An unusual newly discovered archosaur from the Upper Triassic of Virginia, U.S.A. *Transactions of the American Philosophical Society* 70:1–53.
- Weinbaum, J. C., and A. Hungerbühler. 2007. A revision of *Poposaurus gracilis* (Archosauria: Suchia) based on two new specimens from the Late Triassic of the southwestern U.S.A. *Paläontologische Zeitschrift* 81:131–145.
- Wu, X. 1982. Two pseudosuchian reptiles from Shan-Gan-Ning Basin. *Vertebrata Palasiatica* 20:293–301.
- Wu, X.-C., and A. P. Russell. 2001. Redescription of *Turfanosuchus dabaniensis* (Archosauriformes) and new information on its phylogenetic relationships. *Journal of Vertebrate Paleontology* 21:40–50.
- Wu, X.-C., J. Liu, and J.-L. Li. 2001. The anatomy of the first archosauriform (Diapsida) from the terrestrial Upper Triassic of China. *Vertebrata Palasiatica* 39:251–265.
- Young, C. C. 1964. The pseudosuchians in China. *Palaeontologia Sinica* 151:1–205.
- Zavattieri, A. M., and O. H. Papú. 1993. Microfloras mesozoicas; pp. 309–316 in V. Ramos (ed.), *Geología y Recursos Naturales de Mendoza*. 12° Congreso Geológico Argentino y 2° Congreso de Exploración de Hidrocarburos (Mendoza), Relatorio Capítulo II–9.
- Zavattieri, A. M., E. Sepúlveda, E. M. Morel, and L. A. Spalletti. 2003. Límite permo-triásico para la base aflorante de la Formación Puesto Viejo, Mendoza (Argentina). *Ameghiniana* 40:17R.

Submitted November 3, 2009; accepted April 7, 2010.

APPENDIX 1. List of characters used in the phylogenetic analysis. Some characters were modified from their original sources. Abbreviations indicate the source(s) from which the characters were obtained: BC: Benton and Clark, 1988; BE85: Benton, 1985; BE90: Benton, 1990; BE04, Benton, 2004; BEN: Bennett, 1996; BW: Benton and Walker, 2002; CL: Clark et al., 2000; CO: Cooper, 1984; DE: Desojo et al., in press; DI: Dilkes, 1998; DS: Dilkes and Sues, 2009; EZ: Ezcurra, 2006; GA86: Gauthier, 1986; GA88: Gauthier et al., 1988; GO96: Gower, 1996; GO02: Gower, 2002; GS96: Gower and Sennikov, 1996; GS97: Gower and Sennikov, 1997; HL: Heckert and Lucas, 1999; HU: Hutchinson, 2001; JU: Juul, 1994; LB: Langer and Benton, 2006; MS: Modesto and Sues, 2004; NE: Nesbitt et al., 2009; NO89: Novas, 1989; NO92: Novas, 1992; NO96: Novas, 1996; OS: Olsen et al., 2000; PA92: Parrish, 1992; PA93: Parrish, 1993; SA: Sereno and Arcucci, 1993; SEN: Senter, 2003; SER91: Sereno, 1991; SER93: Sereno, 1993; SN: Sereno and Novas, 1992; WH: Weinbaum and Hungerbühler, 2007; WU: Wu et al., 2001.

- (1) Lower temporal (infratemporal) fenestra: (0) present and open ventrally; (1) present and closed ventrally; (2) absent (DI).
- (2) Antorbital fossa, depressed regions on maxilla and lacrimal forming a definite inset margin to the antorbital fenestra: (0) absent; (1) present (BE04).
- (3) Antorbital fenestra: (0) absent; (1) present (DI).
- (4) Shape of premaxilla: (0) downturned ventral margin; (1) horizontal ventral margin (DI, DS).
- (5) External nares location: (0) close to midline and near tip of rostrum; (1) marginal and near tip of rostrum; (2) close to midline and posteriorly situated (DI, DS).
- (6) Lacrimal: (0) contacts nasal, but does not reach external nares; (1) does not contact nasal or reach nares (DI, DS).
- (7) Form of suture between premaxilla and maxilla above dentigerous margin: (0) notch present in maxilla; (1) simple vertical or diagonal contact (DI, DS).
- (8) Location of nasolacrimal canal foramen/foramina: (0) in lacrimal; (1) between lacrimal and prefrontal (SEN).
- (9) Ratio of lengths of nasal and frontal: (0) equal or less than 1; (1) more than 1 (DI).
- (10) Postfrontal: (0) equivalent in size to the postorbital; (1) reduced to less than half the dimensions of the postorbital; (2) absent (BE85, GA86, BC, JU, BEN).
- (11) Parietal foramen: (0) present; (1) absent (DI).
- (12) Postparietals: (0) present and fused; (1) absent (JU, DS).
- (13) Supratemporal: (0) present; (1) absent (DI).
- (14) Anterior end of jugal: (0) enters into antorbital fenestra; (1) excluded by the contact of the maxilla and lacrimal (CL).
- (15) Squamosal overhanging quadrate and quadratojugal laterally: (0) absent; (1) present (BE04, DS).
- (16) Dorsal margin of antorbital fossa is a shelf/ridge that extends across lacrimal, prefrontal, frontal portion of orbital rim, and postorbital: (0) absent; (1) present (DS).
- (17) Depression on descending process of postorbital: (0) absent; (1) present (WU).

- (18) Quadratojugal: (0) present without an anterior process; (1) present with an anterior process that contacts jugal (DI, DS).
- (19) Contact between ectopterygoid and maxilla: (0) absent; (1) present (DI).
- (20) Orientation of basiptyergoid processes: (0) anterolateral; (1) lateral (DI, DS).
- (21) Position on basisphenoid of foramina of cerebral branches of internal carotid arteries leading to the pituitary fossa: (0) posterior/posteroventral; (1) lateral (PA93).
- (22) Exoccipitals and opisthotics: (0) discrete; (1) fused (JU).
- (23) Number of foramina for hypoglossal nerve: (0) two; (1) one (GS96).
- (24) Anteroventral process of prootic below trigeminal foramen: (0) lateral ridge present; (1) lateral ridge absent (GS96).
- (25) Position of external abducens foramen on prootic: (0) ventral surface; (1) anterior surface. (BE04).
- (26) Laterosphenoid: (0) absent; (1) present (DI).
- (27) Position of occipital condyle: (0) anterior to craniomandibular joint; (1) even with craniomandibular joint; (2) posterior to craniomandibular joint (DI, DS).
- (28) Orientation of basisphenoid: (0) horizontal; (1) more vertical (GS96).
- (29) Parabasisphenoid plate between cristae ventrolaterales: (0) intertuberal plate present; (1) absent (GS96).
- (30) Semilunar depression on parabasisphenoid: (0) present; (1) absent (GS96).
- (31) Association between paroccipital process and parietal: (0) no contact; (1) contact present immediately lateral to supraoccipital (DI, DS).
- (32) Medial margin of exoccipitals: (0) no contact; (1) contact to exclude basioccipital from floor of braincase (GS96).
- (33) Anterior and posterior edges of marginal teeth: (0) serrations absent; (1) serrations present (DI).
- (34) Curvature of mesial teeth: (0) absent; (1) present (DI).
- (35) Cross-sectional shape of mesial teeth: (0) oval; (1) laterally compressed (DI).
- (36) Posterior extent of mandibular and maxillary tooth rows: (0) subequal; (1) unequal with the maxillary tooth extending further posteriorly (BEN).
- (37) Vomerine teeth: (0) present; (1) absent (DI).
- (38) Palatine teeth: (0) present; (1) absent (DI).
- (39) Teeth on palatal ramus of pterygoid: (0) present; (1) absent (DI, DS).
- (40) Teeth on transverse flange of pterygoid: (0) single row; (1) absent (DI, DS).
- (41) Pterygoids: (0) join anteriorly; (1) remain separate (DI).
- (42) Lateral mandibular fenestra: (0) absent; (1) present (DI).
- (43) Anterior surangular foramen: (0) absent; (1) present (MS).
- (44) Posterior surangular foramen: (0) absent; (1) present (MS).
- (45) Postaxial cervical intercentra: (0) present; (1) absent (DI).
- (46) Dorsal vertebrae intercentra: (0) present; (1) absent (DI).
- (47) Ratio of lengths of centra of mid-cervical and mid-dorsal vertebrae: (0) equal or less than 1; (1) more than 1 (DI, DS).
- (48) Neural arches of mid-dorsals: (0) deep excavation; (1) no excavation or shallow excavation (DI, DS).
- (49) Distal ends of cervical neural spines: (0) no expansion; (1) expansion present in form of a flat table (DI).
- (50) Distal ends of dorsal neural spines: (0) no expansion; (1) expansion present in form of a flat table (DI, DS).
- (51) Cervical ribs: (0) sharp angle between heads and shaft such that rib lies close to cervical vertebrae; (1) gentle curvature of shaft in a posteroventral direction (DS).
- (52) Trunk ribs: (0) holocephalous; (1) dichoccephalous (modified from DI).
- (53) Second sacral rib: (0) bifurcated; (1) not bifurcated (DI, DS).
- (54) Interclavicle: (0) present with an elongate lateral processes making interclavicle T-shaped; (1) present with a reduced lateral process; (2) absent (modified from BE04). If the interclavicle is absent, characters 55 and 56 of Dilkes and Sues (2009) are not applicable.
- (55) Anterior margin of interclavicle: (0) notch present between articular facets for clavicles; (1) narrow and bluntly pointed separation between articular facets for clavicles (DI, DS).
- (56) Posterior stem of interclavicle: (0) little change in width along entire length; (1) expansion present (DI).
- (57) Scapulocoracoid notch at anterior junction of scapula and coracoid: (0) absent; (1) present. (BE04).
- (58) Scapula length: (0) less than or (1) more than twice the maximum anteroposterior width; (2) more than three times the maximum anteroposterior width (BE85, GA86). Modified from the original character sampling of Dilkes and Sues (2009).
- (59) Forelimb-hind limb length ratio: (0) more than 0.55; (1) less than 0.55 (BE04).
- (60) Dorsal margin of ilium: (0) convex with broadly rounded anterior and posterior ends; (1) straight or with only a portion slightly convex and bluntly pointed anterior and posterior ends (DI, DS).
- (61) Preacetabular process: (0) absent; (1) present but poorly developed; (2) present and well developed (modified from DI).
- (62) Pubic tubercle: (0) prominent; (1) reduced to rugosity (HU).
- (63) Ischial length: (0) less than or (1) more than twice the anteroposterior length of the acetabulum (modified from BE04).
- (64) Fourth trochanter of femur: (0) absent; (1) present (JU, DS).
- (65) Intertrochanteric fossa on ventral aspect of proximal portion of femur: (0) present; (1) absent (BE04).
- (66) Tibia-femur ratio: (0) less than 1; (1) equal to or more than 1 (BE04).
- (67) Fibular anterior trochanter (insertion site for iliofibularis muscle): (0) low rugosity; (1) robust pendent trochanter (BE04).
- (68) Astragalocalcaneal canal: (0) present; (1) absent (BEN).
- (69) Crural facets on astragalus: (0) separated by a non-articular surface; (1) continuous (SER91).
- (70) Orientation of calcaneal tuber: (0) lateral; (1) deflected more than 45° posterolaterally (SER91).
- (71) Articular surfaces for fibula and distal tarsal IV on calcaneum: (0) separated by a non-articular surface; (1) continuous (SER91).
- (72) Hemicylindrical calcaneal condyle for articulation with fibula: (0) absent; (1) present (PA93).
- (73) Astragalal tibial facet: (0) concave; (1) saddle-shaped (SER91).
- (74) Calcaneal tuber shaft proportions: (0) taller than broad; (1) broader than tall (SER91).
- (75) Calcaneal tuber distal end: (0) anteroposteriorly compressed; (1) rounded (SER91).
- (76) Ventral astragalocalcaneal articular facet: (0) small; (1) larger than dorsal articulation (SER91).
- (77) Pedal centrale: (0) present; (1) absent (BE04).
- (78) First and second distal tarsals: (0) present; (1) absent (DI, DS).

- (79) Metatarsus configuration: (0) metatarsals diverging from ankle; (1) compact metatarsus with metatarsals I–IV tightly bunched (BE04).
- (80) Metatarsal II–IV length: (0) less than; (1) equal or greater than 23% of the length of the femur plus the tibia (modified from BE04).
- (81) Ratio of lengths of pedal digits III and IV: (0) equal or less than 1; (1) more than 1 (SA).
- (82) Phalanges/phalanx on pedal digit V: (0) present; (1) absent (JU).
- (83) Ratio of lengths of pedal digits V and I: (0) more than 1; (1) less than 1 (JU).
- (84) Dorsal body osteoderms: (0) absent; (1) present in one or more rows (BEN, DS).
- (85) Dermal osteoderms on ventral side of body: (0) absent; (1) articulate and form a carapace (HL, DS).
- (86) Number of premaxillary teeth: (0) more than four; (1) four or fewer. New character.
- (87) Proportions of mid- and posterior dorsal centra: (0) almost as long as tall; (1) quite longer than tall. New character.
- (88) Centrum of dorsal vertebrae with a lateral fossa below the neurocentral suture: (0) absent; (1) present (GA86).
- (89) Orientation of mid-dorsal prezygapophyses: (0) upwards; (1) almost horizontal. New character.
- (90) Position of mid-dorsal neural spines: (0) situated at mid-length between the zygapophyses; (1) posteriorly displaced from mid-length between the zygapophyses. New character.
- (91) Height of mid-dorsal neural spines: (0) less than; (1) equal or more than the 50% of the total height of the vertebra. New character.
- (92) Cervical, anterior dorsal, and mid-dorsal ribs, proximal tubercle that bears the articular facet for articulation with the vertebrae: (0) poorly developed; (1) long and distinct. New character. This character differs from the character 52 of Dilkes and Sues (2009) because it does not refer to the holocephalic or dichcephalic condition, but to the presence of the peduncle that lodges the articular facet for the vertebrae. For example, in *Euparkeria* the most posterior ribs are holocephalous but the proximal peduncle is distinct (Ewer, 1965), and in *Doswellia* the dorsal ribs are dichcephalous, but the tubercular peduncle is only incipient (DS).
- (93) Transverse width of the distal end of the humerus: (0) less than; (1) equal or more than 2.5 times the minimum width of the shaft. New character.
- (94) Maximum length of the iliac blade: (0) less than; (1) more than 3 times its maximum height. New character.
- (95) Dorsal margin of the pubic peduncle forming an angle lower than 45° to the longitudinal axis of the bone: (0) absent; (1) present. New character.
- (96) Posterior border of the iliac ischiadic peduncle: (0) vertical or poorly posteriorly expanded; (1) strongly posteriorly expanded resulting in a tapering projection, with a posterior border settled at 45° or lower to the longitudinal axis of the ilium. New character.
- (97) Base of the posterior process of the jugal in lateral view: (0) tapering slightly; (1) semi-elliptical, with a ventral expansion (GS97).
- (98) Length of the posterior process of jugal: (0) greater than; (1) less than half of total jugal length (PA92, GS97).
- (99) Anterior process of jugal: (0) slender and tapering; (1) broad and expanded anteriorly (GS97).
- (100) Pineal fossa: (0) absent; (1) present (PA92, GS97).
- (101) Palatal processes on anteromedial surfaces of the maxillae: (0) absent; (1) present (GS97).
- (102) Tooth implantation: (0) free at the base of the tooth; (1) fused to the bone of attachment at the base (GA86, BC, BE90, BEN, GS97, NE).
- (103) Length of cervical vertebra centra: (0) greater than height; (1) subequal to height (GS97).
- (104) Anterior margin of scapula in lateral view: (0) approximately straight or convex; (1) markedly concave (GS97).
- (105) Ventral ramus of the opisthotic: (0) prominent; (1) recessed (GS96, GS97).
- (106) Crista prootica outline: (0) slightly curved; (1) sinusoidal (GS96, GS97).
- (107) Prootic midline contact on endocranial cavity floor: (0) absent; (1) present (GS96, GS97).
- (108) Basisphenoid midline exposure on endocranial cavity floor: (0) present; (1) absent (GS96, GS97).
- (109) Laterosphenoid anterodorsal channel: (0) absent; (1) present (GS96, GS97).
- (110) Parasphenoid cultriform process: (0) simple; (1) dorsoventrally constricted towards the base (PA93, JU, GS96, GS97).
- (111) ‘Pseudolagenar recess’ between ventral surface of the ventral ramus of the opisthotic and the basal tubera: (0) present; (1) absent (GS96, GS97).
- (112) Base of cultriform process of parabasisphenoid: (0) relatively short dorsoventrally; (1) tall, with the dorsal edge extending up between clinoid processes and ventral parts of cristae prootica (GS96, GS97).
- (113) Skull length: (0) less than; (1) more than 50% of length of the presacral vertebral column (SER91).
- (114) Quadrate dorsal head in lateral aspect: (0) hidden by squamosal; (1) exposed (SN, JU).
- (115) Centrum shape in presacrals 6–9 (or 10), in lateral view: (0) sub-rectangular; (1) parallelogram-shaped (GA86, SER91).
- (116) Cervical ribs: (0) slender; (1) short and stout (GA86, BC, JU).
- (117) Hyposphene-hypantrum accessory intervertebral articulations in trunk vertebrae: absent (0); (1) present (GA86, JU).
- (118) Deltopectoral crest on humerus: (0) rounded; (1) sub-rectangular (SER91, JU).
- (119) Deltopectoral crest: elongate and apex situated at a point corresponding to (0) less; or (1) more than 38% down the length of the humerus (BE90, JU).
- (120) Manual digit IV: (0) five; (1) four; (2) fewer than four phalanges (GA86, BC, SER93).
- (121) Brevis shelf on ventral surface of postacetabular part of ilium: (0) absent; (1) present (GA86, JU).
- (122) Brevis fossa with sharp margins on the ventral surface of the postacetabular process of the ilium: (0) absent; (1) present (GA86).
- (123) Acetabulum: (0) mainly laterally oriented; (1) mainly ventrally oriented (BC, JU).
- (124) Acetabulum: (0) imperforate, with a ventral acetabular wall projection anteriorly displaced from mid-length of the acetabulum; (1) imperforate, with a ventral acetabular wall projection centered at mid-length of the acetabulum; (2) perforated (modified from GA86, JU).
- (125) Acetabular antitrochanter on ilium and ischium: (0) absent; (1) present (SA).
- (126) Pubic length: (0) shorter than ischium; (1) longer than ischium but less than 3 times the width of the acetabulum; (2) more than 3 times the width of the acetabulum (SER91, JU, WH).
- (127) Pubic acetabular margin, posterior portion: (0) continuous with anterior portion; (1) recessed (SER91).

- (128) Pubic tuber in lateral aspect: (0) anteroventrally directed; (1) strongly downturned (BE85, JU).
- (129) Femoral head: (0) not distinctly offset; (1) distinctly offset (GA86, JU).
- (130) Femoral head articular surface: (0) limited extent; (1) extends under head (SA).
- (131) Fossa trochanterica on proximal face of femoral head: (0) absent; (1) present (NO96).
- (132) Femoral anterior trochanter: (0) absent; (1) present (GA86, NO92, JU).
- (133) Trochanteric shelf: (0) absent; (1) present (NO96).
- (134) Cnemial crest on tibia: (0) absent; (1) present (GA86, BC, JU).
- (135) Tibia with posterolateral flange, with receiving depression on dorsal aspect of astragalus: (0) absent; (1) present (NO92, JU).
- (136) Fibula and calcaneum shape: (0) unreduced; (1) fibula tapering and calcaneum reduced in size (GA86, JU).
- (137) Astragalar anterior ascending process: (0) absent; (1) present, occupying most of the anteroposterior depth of the astragalus; (2) present, restricted to the anterior half of the astragalar depth (GA86, NO89).
- (138) Astragalar posterior (= ventral) groove: (0) present; (1) absent (SER91, GO96).
- (139) Astragalar anteromedial corner shape: (0) obtuse; (1) acute (SER91, JU).
- (140) Calcaneal proximal articular face: (0) convex or flat; (1) concave (NO89, JU).
- (141) Calcaneal distal articular face: transverse width (0) greater; or (1) less than 35% of that of the astragalus (SER91, JU).
- (142) Calcaneal tuber: (0) prominent; (1) rudimentary or absent (GA86, SER91, JU).
- (143) Calcaneal tuber distal end, with vertical median depression: (0) absent; (1) present (PA93, JU).
- (144) Distal tarsal 4: transverse width (0) broader than; (1) subequal to distal tarsal 3 (SER91, JU).
- (145) Distal tarsal 4, size of articular facet for metatarsal V: (0) more than; (1) less than half of lateral surface of distal tarsal 4 (SER91).
- (146) Metatarsal midshaft diameters: (0) I and V subequal or greater than II–IV; (1) I and V less than II–IV (SER91, JU).
- (147) Metatarsal I length relative to length of metatarsal III: (0) 50–75%; (1) 75% or greater (modified from SER91).
- (148) Metatarsal V, hooked proximal end: (0) present; (1) absent, and articular face for distal tarsal 4 subparallel to shaft axis (SER91, JU).
- (149) Osteoderm sculpture: (0) absent; (1) present (PA93).
- (150) Shape of infratemporal fenestra: (0) elliptical or subrectangular; (1) trapezoidal, with dorsal margin much shorter than ventral margin (modified from BC, BW, WH).
- (151) Squamosal, ventral process: (0) present, forms posterodorsal border of lateral temporal fenestra; (1) present, does not participate widely in lateral temporal fenestra, or absent (modified from GA86, BC, SER91, PA93, OS, BW).
- (152) Supraoccipital: (0) excluded from dorsal border of foramen magnum by dorsomedial contact of exoccipitals; (1) contributes to border of foramen magnum (GO02).
- (153) Sacral ribs, form and articulation of first rib with ilium: (0) plate-like, contacts ilium in straight parasagittal articulation; (1) distal end slightly dorsally expanded relative to shaft; (2) entire rib dorsoventrally expanded and contacts ilium in C-shaped articulation (LB).
- (154) Pubis, form in lateral view: (0) plate-like; (1) rod-like and curved posteriorly; (2) rod-like and straight (EZ).
- (155) Width of the conjoined pubes: (0) less than; (1) greater than 75% of their length (CO).
- (156) Posterior proximal tubercle on femur: (0) well developed; (1) indistinct to absent (NO96).
- (157) Posterior end of the squamosal: (0) does not extend posterior to the head of the quadrate; (1) extends posterior to the head of the quadrate (NE).
- (158) Ectopterygoid: (0) does not form or forms some of the lateral edge of the lateral pterygoid flange; (1) forms most of all the lateral edge of the lateral pterygoid flange (NE, DE).
- (159) Posteroventral portion of the dentary: (0) touch contact with surangular; (1) laterally overlaps the anteroventral portion of the surangular (NE).
- (160) Femoral condyles: (0) prominent; (1) not projecting markedly beyond the shaft (GA88).
- (161) The dorsolateral margin of the astragalus: (0) overlaps the anterior and posterior portions of the calcaneum equally; (1) the posterior corner of the dorsolateral margin of the astragalus dorsally overlaps the calcaneum much more than the anterior portion (NE).
- (162) Metatarsal II midshaft diameter: (0) less than or equal to; (1) more than the midshaft diameter of metatarsal I (NE).
- (163) Metatarsal IV: (0) nearly the same midshaft diameter as metatarsal III; (1) reduced where the midshaft diameter is less than metatarsal III (NE).
- (164) Metatarsal IV: (0) longer than metatarsal III; (1) about the same length or shorter than metatarsal III (BEN, GS97, NE).
- (165) Posterior process of the squamosal: (0) straight; (1) ventrally curved (DE).
- (166) Exposure of the lacrimal on the skull roof in dorsal view: (0) absent; (1) present (DE).
- (167) Projection of the ventral process of the squamosal: (0) posteroventrally directed, vertical, or less than 30° from the vertical; (1) anteroventrally directed at 30° or more (modified from DE).
- (168) Occipital neck, connecting the occipital condyle and the basioccipital body: (0) present; (1) absent (DE).
- (169) Pubic length: (0) less than; (1) more than twice the length of the acetabulum (DE).

APPENDIX 2. Character states modified from the original data matrixes. Unless indicated otherwise, character numbering follows, and is modified from, Dilkes and Sues (2009).

Mesosuchus. Character 2: ‘-’ instead of ‘0’.

Prolacerta. Character 2: ‘-’ instead of ‘0’.

Chanaresuchus. Characters 4 and 29: ‘0’ instead of ‘1’. Characters 8 and 37: ‘1’ instead of ‘?’’. Characters 30, 57, 80, 113, and 148 (113 and 148 modified from characters 1 and 94 of Benton, 2004): ‘1’ instead of ‘0’. Character 54: ‘?’ instead of ‘1’. Character 83: ‘-’ instead of ‘1’.

Erythrosuchus. Character 8: ‘1’ instead of ‘?’’. Characters 10, 15, 64, and 119 (10 modified from Dilkes and Sues, 2009, following Benton, 2004; 119 modified from character 35 of Benton, 2004): ‘1’ instead of ‘0’.

Euparkeria. Characters 5, 7, 43, 53, 55, and 74: ‘1’ instead of ‘0’. Characters 45, 46, and 52: ‘0/1’ instead of ‘0’. Character 117: ‘?’ instead of ‘0’.

Gracilisuchus. Characters 10, 41, and 47: ‘1’ instead of ‘0’. Characters 14, 16, 64, and 82: ‘0’ instead of ‘1’. Characters 36, 57, and 83: ‘?’ instead of ‘1’. Characters 52 and 62: ‘1’ instead of ‘?’’. Character 121 (modified from character 51 of Benton, 2004): ‘0’ instead of ‘?’’.

Lagerpeton. Characters 134 and 140 (modified from characters 65 and 76 of Benton, 2004): ‘1’ instead of ‘0’. Character 142 (modified from character 78 of Benton, 2004): ‘?’ instead of ‘1’.

Marasuchus. Character 2: ‘?’ instead of ‘1’. Characters 3, 34, and 35: ‘1’ instead of ‘?’’. Characters 134 and 140 (modified from characters 65 and 76 of Benton, 2004): ‘1’ instead of ‘0’. Character 142 (modified from character 78 of Benton, 2004): ‘0’ instead of ‘1’.

Parasuchus. Characters 15, 29, and 70: ‘0’ instead of ‘1’.

Proterosuchus. Character 117 (modified from character 36 of Benton, 2004): ‘?’ instead of ‘0’.

Saurosuchus. Character 126 (modified from character 55 of Benton, 2004): ‘01’ instead of ‘1’.

Scleromochlus. Character 115 (modified from character 31 of Benton, 2004): ‘?’ instead of ‘0’.

Stagonolepis. Characters 15 and 36: ‘1’ instead of ‘0’. Characters 19, 50, and 68: ‘1’ instead of ‘?’’. Characters 25, 32, and 49: ‘0’ instead of ‘?’’.

Turfanosuchus. Character 27: ‘?’ instead of ‘1’. Characters 58, 104, 113, and 148 (104 modified from character 14 of Gower and Sennikov, 1997; 113 and 148 modified from characters 1 and 94 of Benton, 2004): ‘1’ instead of ‘?’’. Characters 59, 66, 67, 79, 80, 81, 82, 83, 85, 146, and 147 (146 and 147 modified, respectively, from characters 91 and 92 of Benton, 2004): ‘0’ instead of ‘?’’. Character 126 (modified from character 55 of Benton, 2004): ‘01’ instead of ‘0’.

Qianosuchus. Character 2: ‘?’ instead of ‘1’. Character 10: ‘1’ instead of ‘0’.

10?1000101	1111110111	1011101110	110001001?
000000000	000000000	00000?000	0010000110
000100000			
<i>Euparkeria</i>			
1111101111	1010000111	0101110110	0011110001
1101[01][01]0011	0[01]11100101	1111100110	
0001001100	1001011111	0101100010	10010?????1
00000?00?	000000100	000000000	000000001
0100001111	100101000		
<i>Fugusuchus</i>			
101?00??11	??00001??	0?101?0000	?1?11?????
?????0????	???????????	???????????	???????????
???????????	??????1100	????00??1	00?0???????
???????????	???????????	???????????	0???????????
?????10??			
<i>Gracilisuchus</i>			
1111101?11	1010101111	??????101?	0?111?????11
1100111100	111?????101	2111100111	1111111100
?0?1011?11	0111100010	?0010?????	1?0001000?
000002?100	0001000000	0011?00001	1?12001001
000101-?1			
<i>Herrerasaurus</i>			
1111100112	1110001100	110??10011	1011111111
0101111101	1112--?111	2111100111	10000?1111
1010010111	0101100110	?0000?????	?001101112
1002120111	1111112111	110?1101-1	0122110?11
010101101			
<i>Koilamasuchus</i>			
???????????	???????????	???????????	???????????
???????????	?0?????????	2???????????	???????????
??1?1111	001110?????	???????????	???????????
?000???????	???????????	???????????	???????????
???????????			
<i>Lagerpeton</i>			
???????????	???????????	???????????	???????????
?????1?1?0	?12--?????	211111011?	100?????1?11
01-00?1011	1?110?????	???????????	???????????
000000110	0001010111	1?011101-?	?1100?????
0000?????			
<i>Marasuchus</i>			
??1???????	???????????	1101?1?011	??11???????
????111100	?11?????111	2111110111	10000?1111
11?0??11[01]1	0?0110?????	?001?0?????	????1?010?
0001110101	1111011111	10011101-?	?1100?????
-101?????11			
<i>Osmolskina</i>			
1110??0??1	????0?0??1	0??????110	?111?????01
?1?????????	???????????	1??1???????	???????????
??10???????	??1100?????	?00?????????	??100???????
00000?????	???????????	???????????	0?????0?????
?????0?0??			
<i>Parasuchus</i>			
1111201110	1110101101	1101110101	0111111111
0100110101	1111111101	2111101110	1111111100
1001101011	1111110010	10010000??	1?10010001
0001000100	0000000000	0000000010	0100001111
000110000			

APPENDIX 3. Taxon-character data matrix used in the phylogenetic analysis.

Mesosuchus

0-00010000	010?000000	000??00010	0000000001
0000101000	0000010000	0000000000	0000000000
0000011001	0010010001	0?000?????	??00000???
0000000000	0000000000	00000000-0	0100000000
000000010			

Chanaresuchus

1110011112	1110011101	0111?10001	1011111001
1100110100	111??11101	2101100110	0000001100
11-1001001	0111100010	10010?????	0?1000000?
0001000100	0000000000	0000000101	0100001111
-11100000			

Dimorphodon

11102-1?11	??00?00??	?????2???	?0110?????
?1??111100	11?2--0201	2100?1011?	?0000?1110
01-0011111	0101??010?	?001???????	?1000?101
000[01]000110	0000010100	01010010-0	0?0000??1
0001?????			

Doswellia

2?????????2	111?0??100	0111??1011	10?10????01
?000110111	011011?????	20001?????	???????????
??10?1010	00?0100010	?00?0?????	??100010???
0001000100	0?0???????	?????????1-	-100001101
?????1?000			

Eoraptor

1110101?12	111101010?	??????20??	?1111?110
0100111100	?112--0111	2111110?1?	10000?1111
11-0011011	010110011?	?001???????	?0?1?1?112
1102120111	1101112111	110?1101-0	0?22111?11
?101011?1			

Erythrosuchus

1111101111	1011100111	0111110100	111111?111
1101000000	011??0101	2111000110	0000001100

Downloaded By: [Martinelli, Agustín G.] At: 12:54 16 September 2010

Prolacerta

0-00000010 [01]10?000000 0000000000 0001110000
 1011101010 0000000000 0000000000 0000000000
 000000?0?? ?0?0000000 01000000?0 0001000000
 0000000000 0000000000 00000000-0 0100000000
 0000000000

Proterosuchus

1010000010 1000000101 00?0010000 1?11110000
 111100?010 0000000001 0000000000 0000000000
 ?00000??11 00?1000100 01000???01 000100?00?
 0000000000 0000000000 00000000-1 0000000100
 0000000010

Qianosuchus

1?11101?11 1?110011?? 0????1?11? ?1111?111
 ?1??111?00 1??1??10?1 2111?01?11 1111111100
 ???1001?11 1??110001? 1001?????? ?0100?????
 000?001100 ?000000??? 00?-?00101 0??1001111
 ?001101?1

Sarmatosuchus

????0?0??? ?????????? 0110????100 ?1111?000
 ?????0???0? ?1?????10?? ??????????? ????0?????
 ???0001??? ???????110? ?11000???? 00??0?????
 ??????????? ??????????? ??????????-? 01????0???
 ?????0?01?

Saurosuchus

?111100011 1110010?01 1111?10011 1111?1111
 0????110111 1?1???????1 2111101111 111111110?
 ?011010001 01?1110?10 10110000?? ?0000?1???
 00100[01]1100 0000000000 0010000001 00120011?1
 00010101?

Scleromochlus

111110???? ????10???? ????20?? ?????0??11
 1100110??? 1?1??0211 21?1110?? ?0000?1111
 01?000???? ?01?0?0?? ?0?0?0???? ?1?0?00?
 000101?100 ?000000??? 0001?010-1 ?00000???1
 ?001????00

Shansisuchus

1?1110?011 1??0?01?? ?1????0??? 111110?111
 ?1????00?0 ?11??1101 210?000100 00000?1?00
 000??00?01 0111010101 11110????? ?0000?0?1?
 00000?0000 ?000000?01 ?00??010?0 0010000?10
 101100000

Silesaurus

?1111?1?1? ??????????? 01011??011 ?01111??11
 0101111000 1112--?101 2111100111 10000???10
 11-0011001 0101100?1? 100000??? ?00?00010?
 1100120100 1111112111 110??1?1-? ?11111????1
 0101????01

Stagonolepis

1111101111 1110100110 1101012111 0010111111
 0100110?01 1?11111101 2111101111 1111111100
 1011101[01]11 1111110010 100100???? 1100010002
 0011011100 0000000000 0010000011 1?12001111
 100100101

Terrestrisuchus

1111101?12 1111100101 ?1????111?? 0011111111
 11??111100 1111101101 2111110111 1111111100
 1011001001 0101100100 ?0010????? 1?1000000[12]

0002121100 0000000000 0010001001 1111001011
 000101-11

Turfanosuchus

1111101?10 1??1011101 01011??011 ??111??101
 ?100??111 ??1????101 21?1100111 11000??00
 00010011?? ?111100010 1001?????? ?01000?002
 00000[01]0100 000??00100 000??00101 0?01001?11
 ?01011101

Vancleavea

1-012-1-1? 111-0-01?? ???1?1???? 10111?????
 ?????111100 ?1?????001 0?0010?100 0000?1100
 ???110?110 ??10001000 1001?????? ?01000?000?
 00000?0?00 0000000101 000000?100 1????11?11
 000?1-10?

Vjushkovia triplicostata

1?111?1?1? ?????0?01?? 01101?0100 1??1????11
 ?1????0010 11?1111101 201?000??0 00?00?????
 ??????0?01 1111110111 1011011110 000000001?
 00000000?? ?????000???? ??????????? 001000????
 ??????0?0

APPENDIX 4. List of unambiguous synapomorphies common to all the recovered MPTs.

- Archosauriformes: 1(0→1), 3(0→1), 12(1→0), 18(0→1), 20(0→1), 26(0→1), 31(0→1), 33(0→1), 42(0→1), 45(1→0), 60(0→1), 94(0→1), 98(0→1), 150(0→1), 158(0→1).
- Sarmatosuchus* + *Fugusuchus* + Archosauria: 10(0→1), 25(0→1).
- Osmolskina* + Archosauria: 40(0→1), 84(0→1), 102(1→0).
- Koilamasuchus* + Archosauria: 61(1→2).
- Erythrosuchidae: 38(0→1), 39(0→1), 87(1→0), 89(1→0), 96(0→1), 100(0→1), 103(0→1), 119(0→1), 150(1→0), 152(1→0), 153(0→1).
- Vjushkovia* + *Erythrosuchus*: 63(0→1), 91(0→1).
- Erythrosuchidae + Archosauria: 92(0→1).
- Euparkeria* + Archosauria: 65(0→1), 98(1→0), 128(0→1), 157(0→1), 160(0→1).
- Chanaresuchus* + Archosauria: 12(0→1), 28(1→0), 30(0→1), 37(0→1), 44(1→0), 48(0→1), 124(0→1), 148(0→1).
- Vancleavea* + *Doswellia*: 64(1→0), 90(1→0), 94(1→0).
- Vancleavea* + *Doswellia* + Archosauria: 27(1→0), 138(1→0).
- Archosauria: 23(1→0), 70(0→1), 71(0→1).
- Turfanosuchus* + Crurotarsi: 17(0→1), 72(0→1), 169(0→1).
- Crurotarsi: 28(0→1), 67(0→1), 73(0→1), 74(0→1), 75(0→1).
- Parasuchus* + *Gracilisuchus*: 15(0→1), 21(0→1), 96(0→1), 116(0→1), 148(1→0).
- Stagonolepis* + *Gracilisuchus*: 17(1→0), 83(0→1), 126(0→1), 143(0→1), 153(0→1), 154(1→2), 165(1→0).
- Saurosuchus* + *Gracilisuchus*: 91(1→0), 166(0→1), 168(0→1).
- Terrestrisuchus* + *Gracilisuchus*: 41(0→1), 47(0→1), 50(1→0), 67(1→0), 96(1→0), 126(1→2), 158(1→0).
- Avemetatarsalia: 54(1→2), 57(1→0), 66(0→1), 79(0→1), 84(1→0), 93(1→0), 98(0→1), 144(0→1).
- Scleromochlus* + *Dimorphodon*: 36(1→0), 58(1→2), 113(0→1), 147(0→1), 148(1→0).
- Dinosauromorpha: 134(0→1), 139(0→1), 140(0→1), 141(0→1), 145(0→1), 146(0→1), 153(0→1).
- Dinosauriformes: 125(0→1), 126(0→1), 131(0→1), 132(0→1), 133(0→1), 137(0→1), 162(0→1), 169(0→1).
- Silesaurus* + Dinosauria: 121(0→1), 126(1→2), 135(0→1), 137(1→2), 142(0→1), 155(0→1), 156(0→1).
- Dinosauria: 119(0→1), 124(1→2), 129(0→1), 153(1→2), 154(1→2).

Downloaded By: [Martinelli, Agustin G.] At: 12:54 16 September 2010