



An unusual new archosauriform from the Middle–Late Triassic of southern Brazil and the monophyly of Doswelliidae

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Until now the Doswelliidae was considered a monospecific family including *Doswellia kaltenbachi* from the Late Triassic of North America. The phylogenetic position of this taxon remained enigmatic until recently, when a sister-group relationship with the Proterochampsidae was suggested. In the present contribution we describe the new doswelliid species *Archeopelta arborensis* gen. et sp. nov. from the Middle–Late Triassic of Brazil. A cladistic analysis recovered *Archeopelta*, *Doswellia*, and *Tarjadia* within a monophyletic group of basal archosauriforms, the Doswelliidae. The monophyly of this family is supported by the presence of osteoderm ornamentation that is coarse, incised, and composed of regular pits and the presence of an unornamented anterior articular lamina. *Archeopelta* is more closely related to *Doswellia* than to other archosauriforms by the presence of basiptyergoid processes anterolaterally orientated, dorsal centra with a convex surface, width of the neural arch plus ribs of the first primordial sacral that are three times the length of the neural arch, and iliac blade laterally deflected, with strongly convex dorsal margin, and a length less than three times its height. The phylogenetic analysis indicates that Doswelliidae is the closest large monophyletic entity to Archosauria, which achieved a wide palaeolatitudinal distribution during the late Middle and Late Triassic time span.

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INTRODUCTION

The clade Archosauriformes includes a diverse sample of Late Permian (e.g. *Archosaurus*) and Triassic diapsids (e.g. *Proterosuchus*, *Erythrosuchus*, *Vancleavea*, *Euparkeria*), as well as the Archosauria (Gauthier *et al.*, 1989). The latter lineage was one of the main and most successful terrestrial groups of tetrapods during the Mesozoic, and includes the crown-clades Crocodylia and Aves (Gauthier, 1986). Amongst non-archosaurian Archosauriformes three main lineages have been traditionally recognized,

namely Proterosuchidae (Late Permian–Early Triassic), Erythrosuchidae (Early and Middle Triassic), and Proterochampsidae (Middle and Late Triassic) (Serenó, 1991). Since the first quantitative analyses exploring the phylogenetic relationships amongst basal Archosauriformes (Gauthier, Kluge & Rowe, 1988; Sereno, 1991; Parrish, 1992), proterosuchids have been advocated as the most basal representatives of the group, being the sister-taxon of the Erythrosuchidae and more derived archosauriforms (Serenó, 1991). In addition, erythrosuchids have been usually found basal to the Middle Triassic *Euparkeria* and the clade which encloses Proterochampsidae and Archosauria (Serenó & Arcucci, 1990; Sereno, 1991).

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

During the second part of the last century, several basal archosauriforms were reported, but the phylogenetic relationships within the group still remain equivocal. Amongst these specimens are unnamed archosauriforms from the Early Triassic of South Africa (Modesto & Botha-Brink, 2008), Argentina (Bonaparte, 1981; Ezcurra, Lecuona & Martinelli, 2009, 2010), and Brazil (Da-Rosa *et al.*, 2009), the Middle–Late Triassic *Cuyosuchus* from Argentina (Rusconi, 1951; Reig, 1961; Desojo, Arcucci & Marsicano, 2002), and the strange, heavily armoured *Vancleavea* from the Late Triassic of the USA (Long & Murry, 1995; Parker & Barton, 2008; Nesbitt *et al.*, 2009a). In addition, some forms have been allied with *Euparkeria*, informally assigned to ‘Euparkeriidae’, including *Osmolskina* (Borsuk-Bialynicka & 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 (e.g. proterosuchids, erythrosuchids, ‘euparkeriids’) is well known from the Early and Middle Triassic of Africa and Asia, and scarcer remains from North America, Europe, and Oceania (von Huene, 1960; Ewer, 1965; Wu, 1982; Thulborn, 1986; Sennikov, 1989, 1995; Parrish, 1992; Welman, 1998; Gower & Sennikov, 2000; Borsuk-Bialynicka & Evans, 2003). By contrast, the South American record of basal archosauriforms is mostly restricted to the endemic Middle and Late Triassic proterochampsids (e.g. *Chanaresuchus*, *Gualosuchus*, *Proterochampsia*, *Tropidosuchus*, *Cerritosaurus*; Price, 1946; Reig, 1959; Sill, 1967; Romer, 1971, 1972a, b; Barberena, 1982; Arcucci, 1990), with other less conspicuous forms (e.g. Bonaparte, 1981; Desojo *et al.*, 2002; Da-Rosa *et al.*, 2009; Ezcurra *et al.*, 2010). In the present contribution, the diversity of South American non-archosaurian archosauriforms is increased with the

description of a new taxon from the Middle–Late Triassic of Brazil: *Archeopelta arborensis* gen. et sp. nov. The anatomy of this animal is described and detailed comparative observations provided, and its phylogenetic relationships within basal archosauriforms are explored through a cladistic analysis. The monophyly and inclusiveness of the family Doswelliidae and implications for understanding the basal archosauriform radiation are then discussed.

GEOLOGICAL AND BIOSTRATIGRAPHICAL SETTINGS

The holotype of *Arc. arborensis* (CPEZ-239a) was found in the Sanga da Árvore outgroup (Baum Sanga *sensu* von Huene, 1935, 1938, 1942) within the Xiniquá region (São Pedro do Sul Municipality, Rio Grande do Sul State) by one of us (C. L. S.) (Fig. 1). The Sanga da Árvore outgroup belongs to the Santa Maria Sequence 1 (*sensu* Zerfass *et al.*, 2003) of the Santa Maria Supersequence [or to the lower levels of the Santa Maria Formation (*sensu* Andreis, Bossi & Montardo, 1980)], assigned to the *Dinodontosaurus* Assemblage Zone (AZ) (Fig. 2). This AZ has been biostratigraphically correlated with the fauna of the Argentinean Los Chañares Formation (Rubert & Schultz, 2004; Langer *et al.*, 2007). The age of this Argentinean sedimentary unit has been traditionally considered as Ladinian (Bonaparte, 1982, 1997; Morel, Artabe & Spalletti, 2003), but recent modifications in the Triassic timescale (Muttoni *et al.*, 2004) led us to a reconsideration of this interpretation. Stratigraphical horizons close to the base and within the Ischigualasto Formation, belonging to the same basin as the Los Chañares Formation, have been reinterpreted as late Carnian in age (*Hyperodapedon* AZ; Furin *et al.*, 2006). As a result, the underlying Los Rastros Formation must be considered as early–middle Carnian or even Ladinian in age. Thus, the Los Chañares Formation should be Ladinian or earliest Carnian in age. Accordingly, the *Dinodontosaurus* AZ of the Santa Maria 1 Sequence would be also constrained to the Ladinian–earliest Carnian time span (Fig. 2).

The name ‘Sanga da Árvore’ (= Baum Sanga) was coined by Friedrich von Huene because of the presence of a large Timbaúva tree (*Enterolobium contortisiliquum*) in the centre of the outcrop (Beltrão, 1965). This tree was later burned by lightning, but some remains of the trunk are still there. The Sanga da Árvore presents a fault that is south-west–north-east in orientation (Fig. 1), and a dicynodont specimen has been collected from the same side of the fault as *Archeopelta*. Von Huene collected specimens of *Stahleckeria potens*, *Prestosuchus chiniquensis*, and *Hoplitosuchus raui* (von Huene, 1935, 1938, 1942)

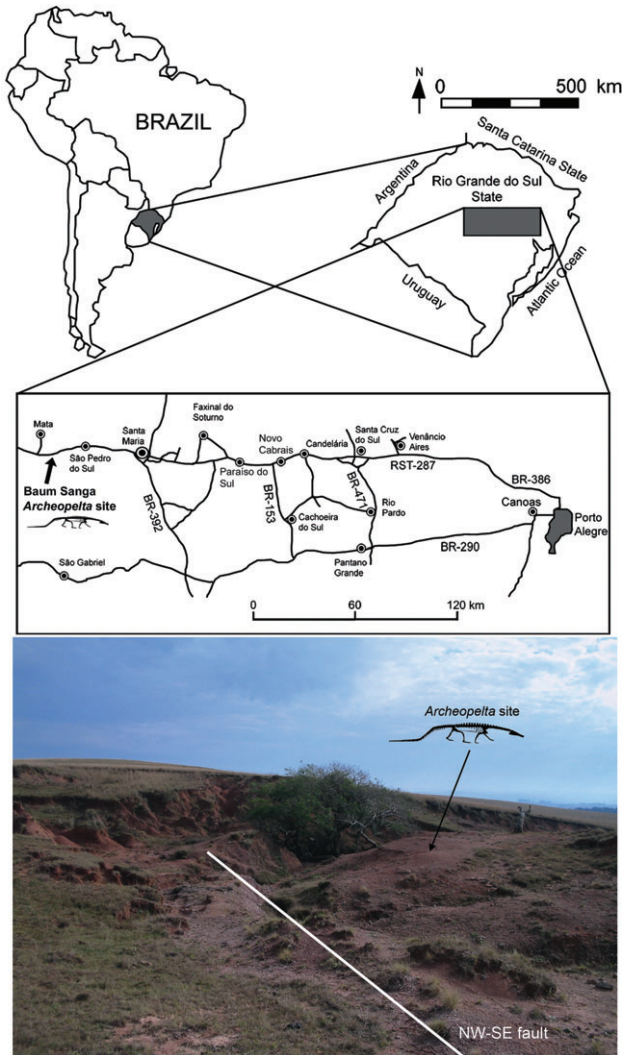


Figure 1. Map of the Brazilian region showing the location of the *Archeopelta*-bearing site (above) and photograph of the site from which *Archeopelta* was collected (below). Map modified from Reichel, Schultz & Benton Soares (2009).

from the Baum Sanga, but it is unknown from which side of the fault. In addition, the holotype of *Archeopelta* was intimately associated with cranial and postcranial remains of a medium-sized 'rauisuchian'. In fact, it was necessary to distinguish between the elements belonging to the 'rauisuchian' and that of *Archeopelta*; fortunately, size differences between the specimens helped us in this task. The 'rauisuchian' materials are around two times the size of the elements of the holotype of *Archeopelta*, for example the left femur of the 'rauisuchian' is ca. 350 mm in length and that of *Archeopelta* is 170 mm in length. Furthermore, some axial elements and a right humerus are duplicated in both specimens. Besides, the anatomy of the elements here considered

as belonging to the holotype specimen of *Archeopelta* are clearly distinct from that observed in 'rauisuchians' (see description and comparisons below). In addition, although the holotype of *Archeopelta* was found together with this 'rauisuchian' individual, no *Archeopelta*-like osteoderms were found intimately associated with the former. The size and the absence of duplicate elements suggest that all the bones considered here as belonging to the holotype of *Archeopelta* pertain to a single individual.

INSTITUTIONAL ABBREVIATIONS

BMNH, The Natural History Museum, London, UK; BSPG, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Germany; CPEZ, Coleção Municipal, São Pedro do Sul, Brazil; GPIT, Institut und Museum für Geologie und Paläontologie, Universität Tübingen, Germany; ISI, Geological Studies Unit of the Indian Statistical Institute, Calcutta, India; MACN-Pv, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Paleontología de Vertebrados, Buenos Aires, Argentina; MCP, Museo de Ciencias e Tecnología, Porto Alegre, Brazil; MCZD, Museo de Ciencias Naturales y Antropológicas de Mendoza (J. C. Moyano), Mendoza, Argentina; PIMUZ, Paläontologisches Institut und Museum der Universität Zürich; PULR, Paleontología, Universidad Nacional de La Rioja, La Rioja, Argentina; PVL, Paleontología de Vertebrados, Instituto 'Miguel Lillo', San Miguel de Tucumán, Argentina; PVSJ, División de Paleontología de Vertebrados del Museo de Ciencias Naturales y Universidad Nacional de San Juan, San Juan, Argentina; QR, National Museum, Bloemfontein, South Africa; SAM, South African Museum, South Africa; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; TTUP, Texas Tech University Museum, Lubbock, Texas, USA; UCMP, University of California Museum of Paleontology, Berkeley, CA, USA; UFRGS, Universidade Federal do Rio Grande do Sul, Porto Alegre, RS, Brazil; ZPAL, Institute of Paleobiology of the Polish Academy of Sciences in Warsaw, Poland.

SYSTEMATIC PALAEOLOGY

DIAPSIDA OSBORN, 1903

ARCHOSAUMORPHA GAUTHIER *ET AL.*, 1988

ARCHOSAURIFORMES GAUTHIER *ET AL.*, 1988

DOSWELLIIDAE WEEMS, 1980 (NEW DEFINITION)

***ARCHEOPELTA ARBORENSIS* GEN. ET SP. NOV.**

(FIGS 3–14)

Etymology: The generic name is derived from the Greek words *archo* (ancient) and *pelta* (armoured) because of the thick osteoderms that surround the

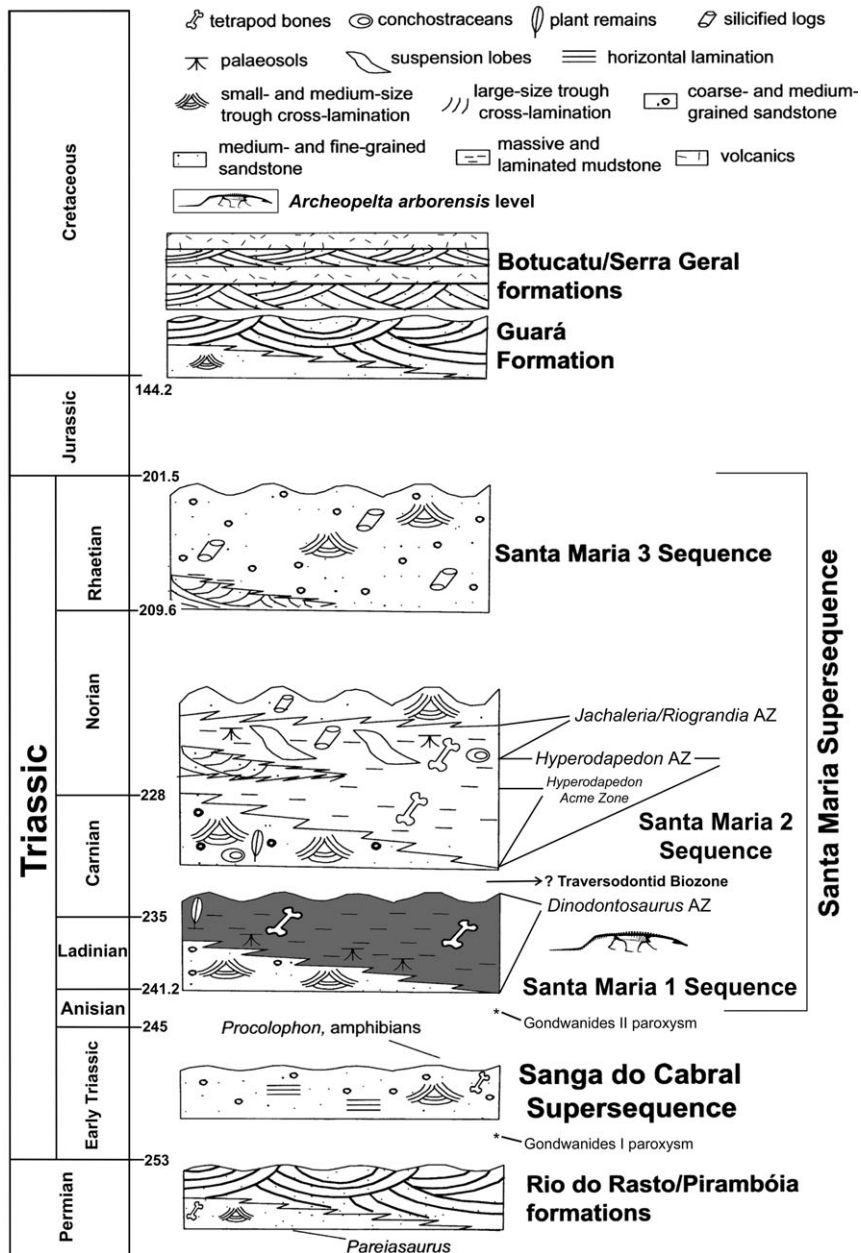


Figure 2. Chronostratigraphical column of the Santa Maria Supersequence showing the *Archeopelta*-bearing level. Modified from Zerfass *et al.* (2003) and stages boundary ages after Schoene *et al.* (2006), Schaltegger *et al.* (2008) (Triassic–Jurassic boundary), Mundil *et al.* (1996) (Anisian–Ladinian), Mundil *et al.* (2004) (Permo–Triassic boundary), and Muttoni *et al.* (2004) and Furin *et al.* (2006) for others.

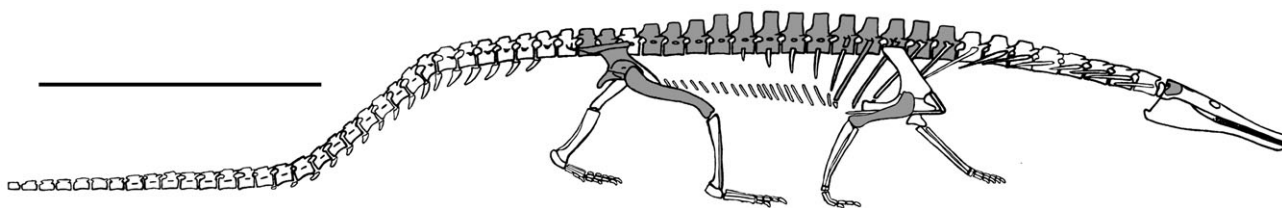


Figure 3. Preserved bones of *Archeopelta* (modified from Weems, 1980). Scale bar = 50 cm.

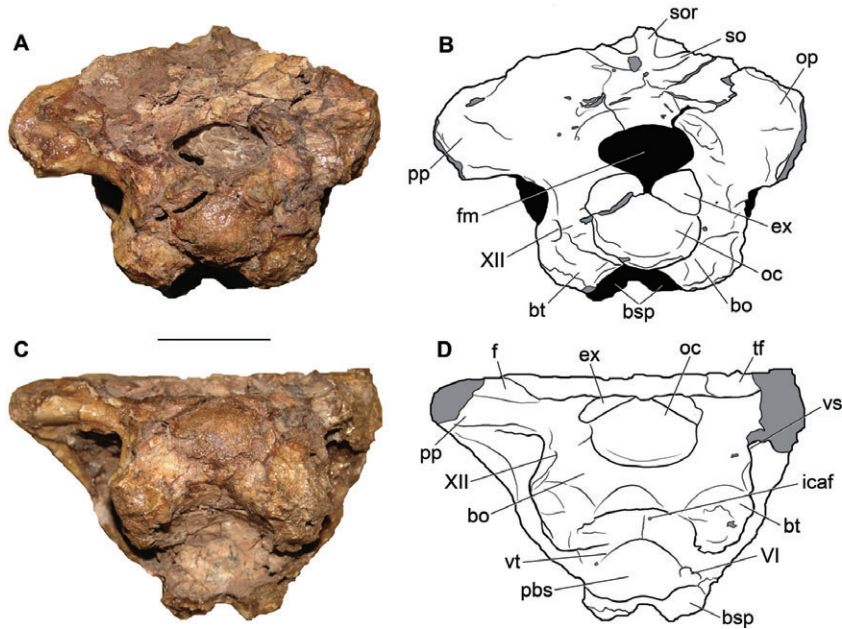


Figure 4. Basicranium of *Archeopelta* in A–B, posterior and C–D, posteroventral views. Abbreviations: VI, exit of the abducens nerve; XII, exit of the hypoglossal nerve; bo, basisphenoid; bsp, basiptyergoid process; bt, basal tuber; ex, exoccipital; f, fossa; fm, foramen magnum; icaf, internal carotid anterior foramen; oc, occipital condyle; op, opisthotic; pbs, parabasisphenoid; pp, paraoccipital process; so, supraoccipital; sor, supraoccipital ridge; tf, tympanic fossa; vs, vestibule, vt, ventrolateral crest. Scale bar: 2 cm. Black regions are for foramina/fenestra and shadows of outplane bones, and grey regions are for damaged surfaces.

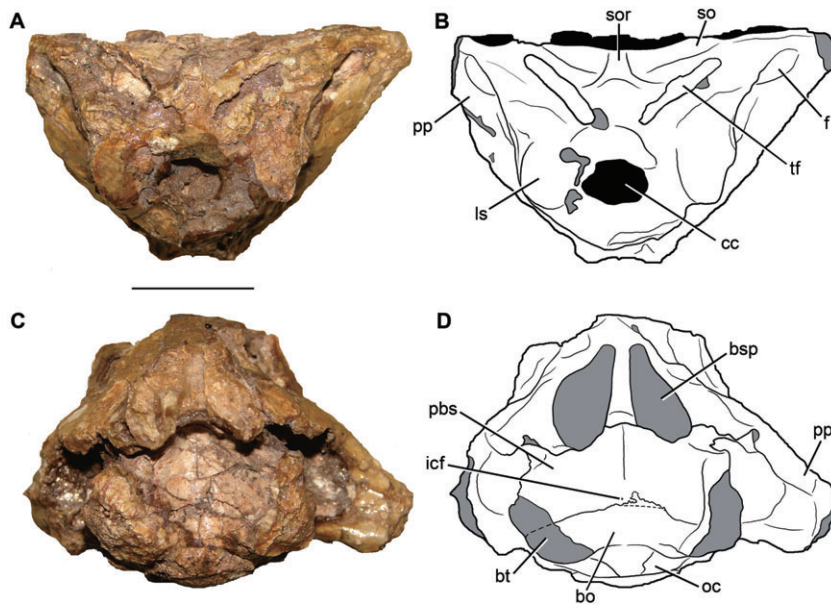


Figure 5. Basicranium of *Archeopelta* in A–B, dorsal and C–D, ventral views. Abbreviations: bo, basisphenoid; bsp, basiptyergoid process; bt, basal tuber; cc, cerebral cavity; f, fossa; icf, internal carotid foramen; ls, laterosphenoid; oc, occipital condyle; pbs, parabasisphenoid; pp, paraoccipital process; so, supraoccipital; sor, supraoccipital ridge; tf, tympanic fossa. Scale bar = 2 cm. Black regions indicate foramina/fenestra and shadows of outplane bones, and grey regions indicate damaged surfaces.

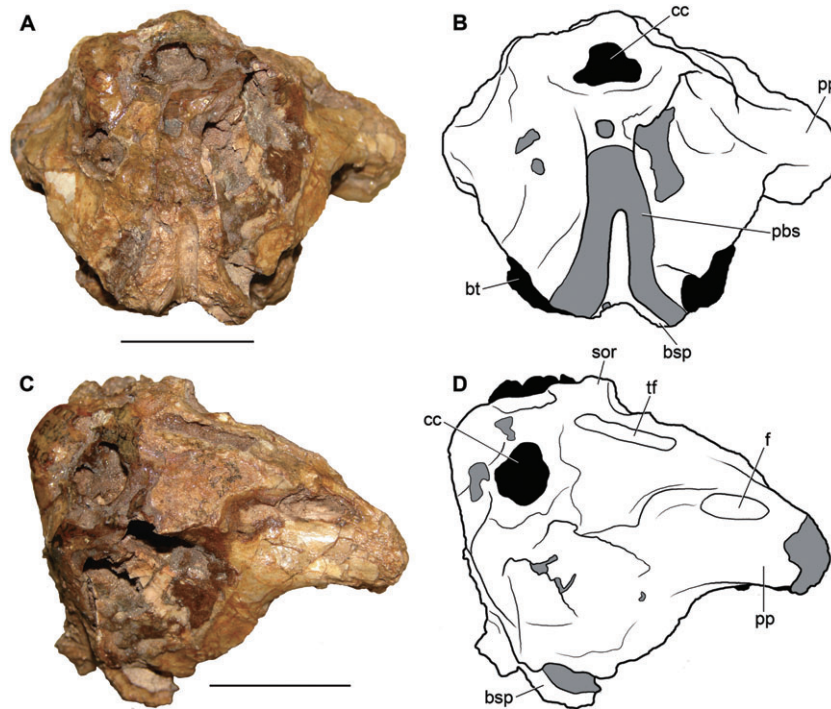


Figure 6. Basicranium of *Archeopelta* in A–B, anterior and C–D, anterodorsal views. Abbreviations: bsp, basipterygoid process; bt, basal tuber; cc, cerebral cavity; f, fossa; pbs, parabasisphenoid; pp, paraoccipital process; sor, supraoccipital ridge; tf, tympanic fossa. Scale bar = 2 cm. Black regions indicate foramina/fenestra and shadows of outplane bones, and grey regions indicate damaged surfaces.

body of the animal. The specific name is derived from the Greek word *arbore* (tree), in allusion to the Sanga da Árvore (árvore is tree in Portuguese) where the holotype specimen was found.

Holotype: CPEZ-239a: basicranium, a series of 13 dorsal vertebrae, three dorsal neural spines, two dorsal ribs, two sacral or caudal centra, ten paramedian osteoderms, three lateral osteoderms, four undetermined osteoderms, proximal end of right humerus, proximal half of right ulna, right ilium, right ischium, right femur, and proximal end of right tibia (Fig. 3).

Horizon and locality: Santa Maria 1 Sequence (*Dinodontosaurus* AZ, late Ladinian–early Carnian; late Middle–early Late Triassic; see Geological and Biostratigraphical Settings), Sanga da Árvore (Baum Sanga), Xiniquá region, São Pedro do Sul, Rio Grande do Sul State, Brazil (Figs 1, 2).

Diagnosis: *Archeopelta arborensis* is a doswelliid archosauriform distinct from other archosauriforms, including *Doswellia kaltenbachi*, by the presence of the following combination of features (autapomorphies with asterisk): basioccipital without occipital

neck separating the occipital condyle from the rest of the basicranium* (also present in *Proterosuchus*); opisthotal paraoccipital processes with large and oval fossa on their dorsomedial corner*; suture between the parabasisphenoid and basioccipital interdigitated and V-shaped in ventral view; parabasisphenoid with minute and strongly posteriorly displaced foramina for the internal carotid artery*; first primordial sacral vertebra with circular and extremely large prezygapophyses accounting for 43% of the total length of the neural arch*; and well-developed V-shaped hyposphene*. Furthermore, CPEZ-239a differs from *Tarjadia* by the presence of a vertical ridge on the dorsal surface of the supraoccipital and the absence of laterally concave dorsal vertebra centra.

New taxonomic definitions: The family Doswelliidae was coined by Weems (1980) as a monospecific entity that included *Do. kaltenbachi*, but Doswelliidae has not been phylogenetically defined previously. Accord-

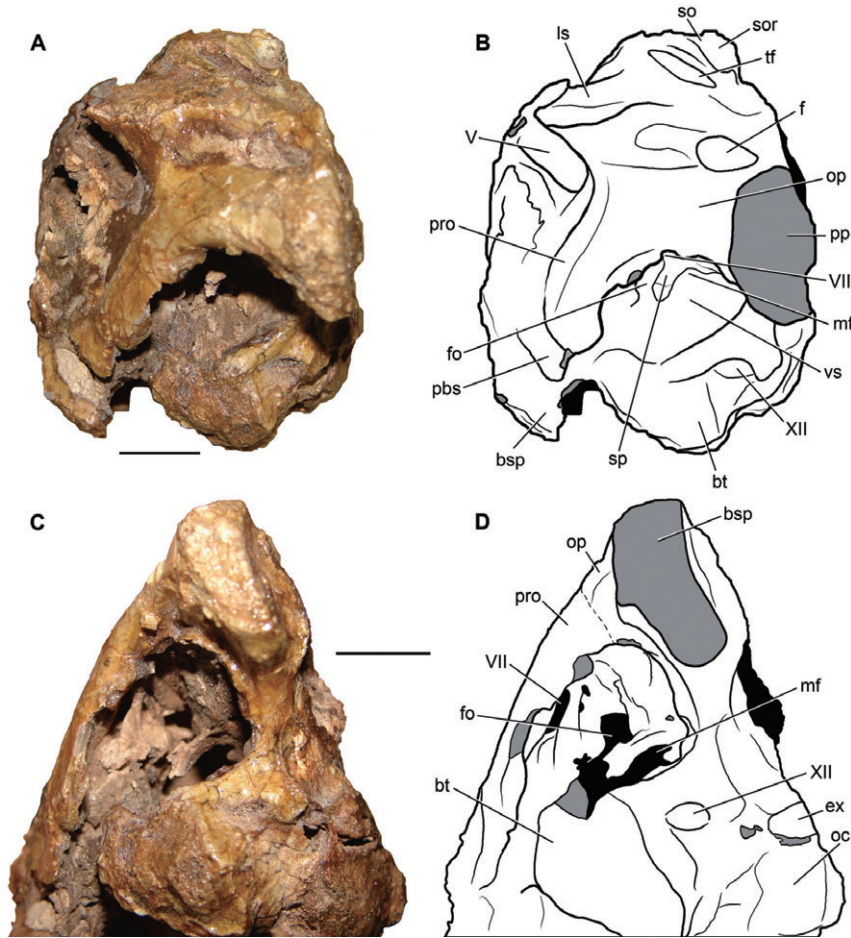


Figure 7. Basicranium of *Archeopelta* in A–B, lateral view and close up of the vestibule in C–D, lateroventral view. Abbreviations: V, exit of the trigeminal nerve; VII, exit of the facial nerve; XII, exit of the hypoglossal nerve; bsp, basipterygoid process; bt, basal tuber; ex, exoccipital; f, fossa; fo, fenestra ovalis; ls, laterosphenoid; mf, metotic foramen; oc, occipital condyle; op, opisthotic; pbs, parabasisphenoid; pp, paraoccipital process; pro, prootic; so, supraoccipital; sor, supraoccipital ridge; sp, septum; tf, typanic fossa; vs, vestibule. Scale bar = 2 cm. Black regions indicate foramina/fenestra and shadows of outplane bones, and grey regions indicate damaged surfaces.

ingly, we define here Doswelliidae as a stem-based clade that includes all archosauromorphs more closely related to *Do. kaltenbachi* Weems, 1980 than to *Proterochampsia barrionuevoi* Reig 1959, *Erythrosuchus africanus* Broom, 1905, *Caiman latirostris* Daudin, 1802, or *Passer domesticus* Linnaeus, 1758 (see synapomorphies of Doswelliidae Weems, 1980 in the Discussion). Abbreviated definition: Doswelliidae Weems, 1980 => *Doswellia kaltenbachi* Weems, 1980 ~ *Proterochampsia barrionuevoi* Reig, 1959 & *Erythrosuchus africanus* Broom, 1905 & *Caiman latirostris* Daudin, 1802 & *Passer domesticus* Linnaeus, 1758.

DESCRIPTION

Basicranium: In overall aspect, the basicranium of *Archeopelta* is proportionally dorsoventrally low (Fig. 4; Table 1), resembling the condition of

Table 1. Measurements (in millimetres) of the braincase of CPEZ-239a

Maximum height	47.6
Width along basal tubera	38.7
Height of foramen magnum	10.0
Width of foramen magnum	16.9
Height of occipital condyle	15.3
Width of occipital condyle	17.3
Length between basal tuber and basipterygoid processes	58
Width between basipterygoid processes	56*

*Incomplete.

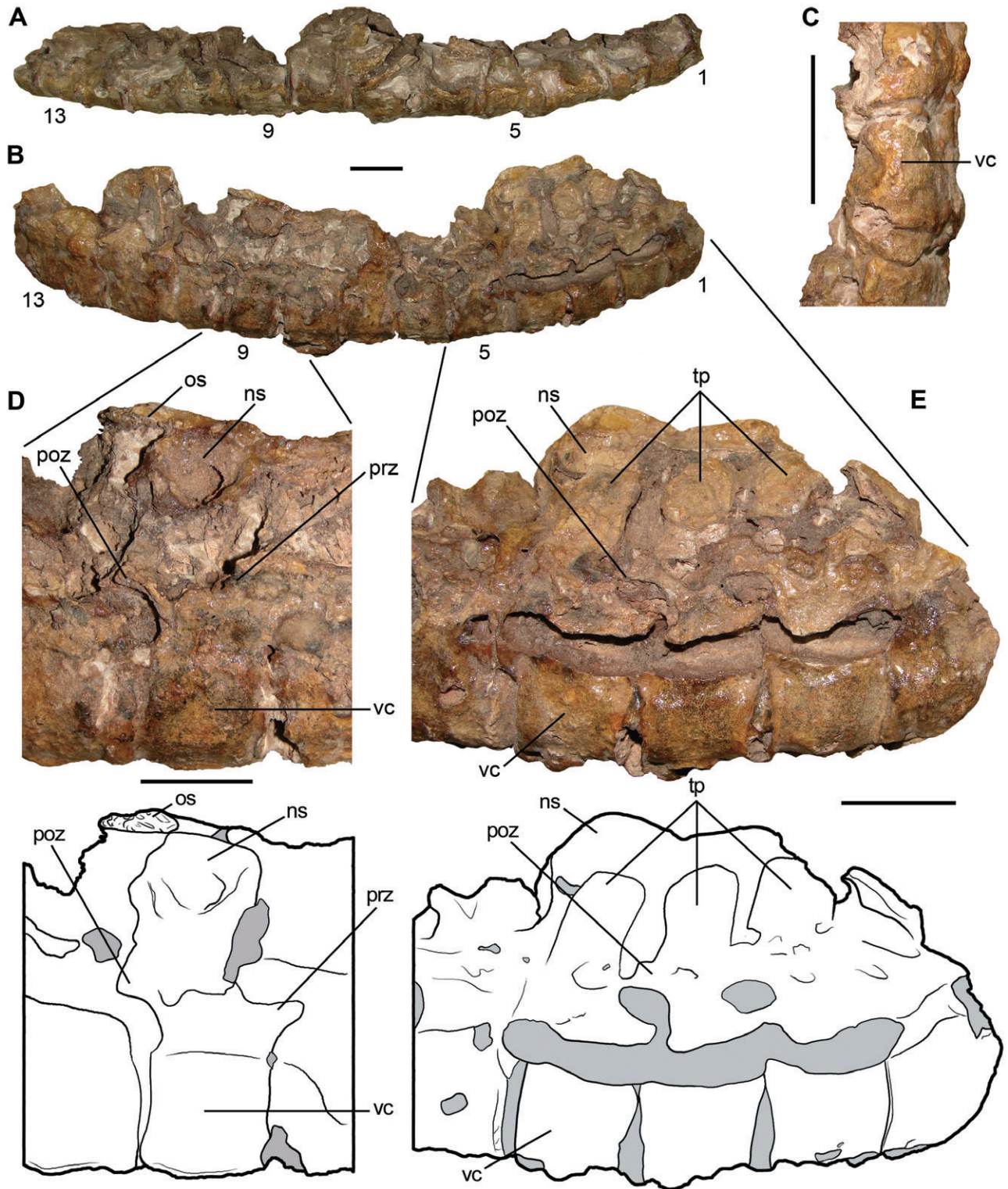


Figure 8. Dorsal vertebral series of *Archeopelta* in A, ventral and B, right lateral views, third dorsal vertebra in C, ventral view, ninth dorsal vertebra in D, right lateral view, and first to fourth dorsal vertebrae in E, right lateral view. Abbreviations: ns, neural spine; os, osteoderm; poz, postzygapophysis; prz, prezygapophysis; tp, transverse process; vc, vertebral centrum. Scale bar = 2 cm.

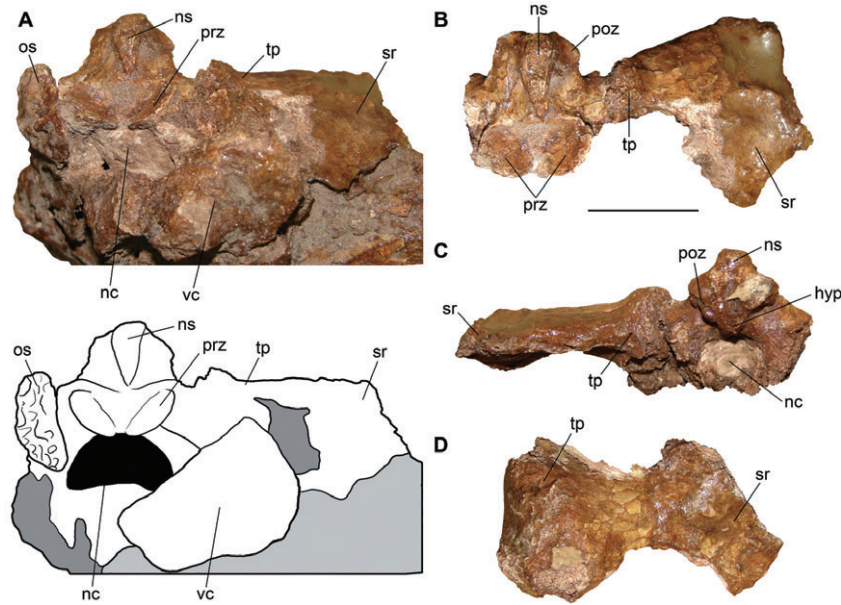


Figure 9. First primordial sacral vertebra of *Archeopelta* in A, anterior; B, dorsal; and C, posterior views; and second primordial sacral in D, dorsal view. Abbreviations: hyp, hyposphene; nc, neural canal; ns, neural spine; os, osteoderm; poz, postzygapophysis; prz, prezygapophysis; sr, sacral rib; tp, transverse process; vc, vertebral centrum. Scale bar = 2 cm.

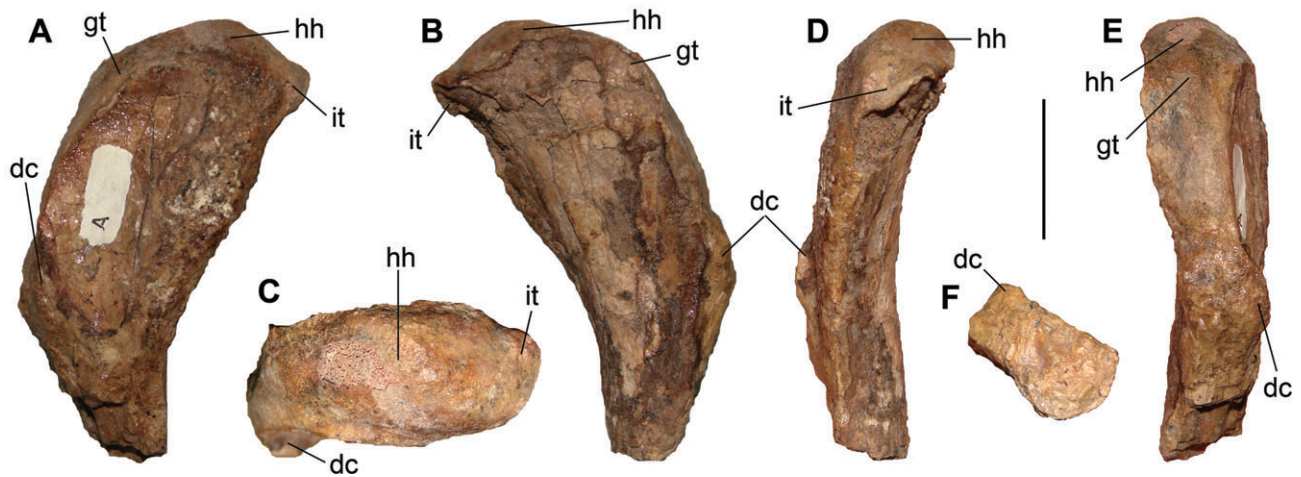


Figure 10. Proximal half of right humerus of *Archeopelta* in A, anterior; B, posterior; C, proximal; D, medial; E, lateral; and F, ventral views. Abbreviations: dc, deltopectoral crest; gt, greater tuberosity; hh, humeral head; it, internal tuberosity. Scale bar = 2 cm.

Doswellia (Weems, 1980), some proterochampsids (e.g. *Tropidosuchus*: PVL 4601; *Chanaresuchus*: PULR 07; *Proterochampsia*: Sill, 1967), and *Euparkeria* (Gower & Weber, 1998). In occipital view the foramen magnum is oval, being transversely wider than tall. The occipital condyle is poorly differentiated from the rest of the braincase because of the absence of an occipital 'neck'. This condition clearly contrasts from that of *Doswellia* (Weems, 1980: fig. 12; Dilkes & Sues, 2009: fig. 1), but resembles that of *Mesosuchus*

(Dilkes, 1998), *Proterosuchus* (QR 1484), *Euparkeria* (Gower & Sennikov, 1997), and *Marasuchus* (PVL 3872). The foramen magnum is bounded by the exoccipitals laterally, by the basioccipital ventrally, and the supraoccipital dorsally. The participation of the opisthotic into the lateral border of the foramen magnum cannot be discerned. The exoccipitals contribute to the dorsolateral corner of the occipital condyle, but they do not meet each other medially, resembling the condition in *Fugusuchus* and the

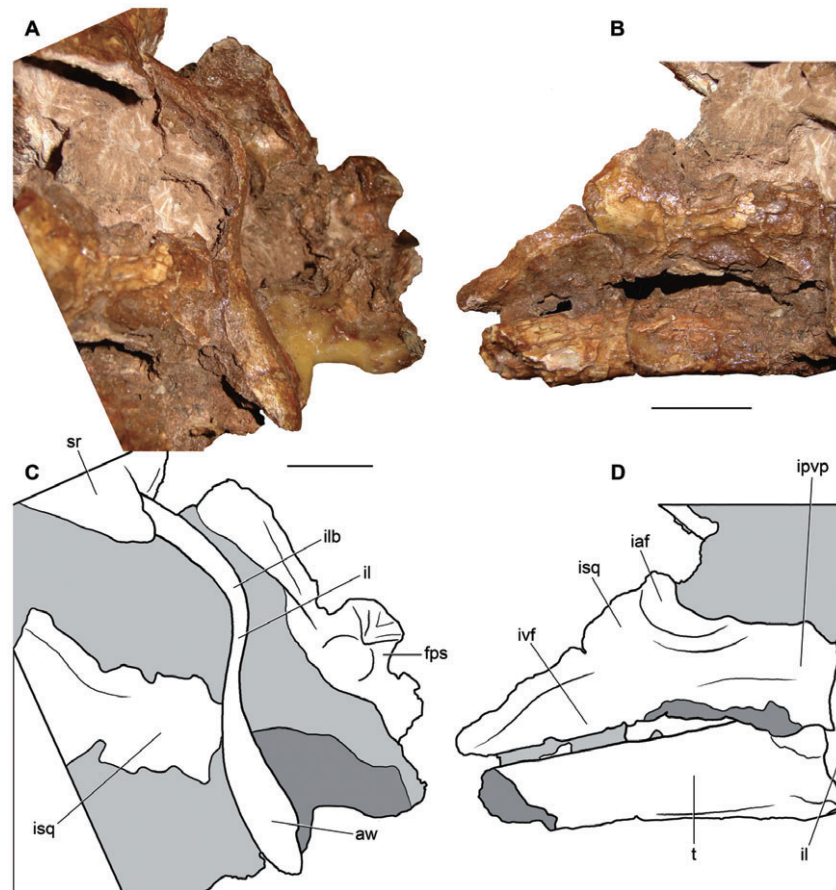


Figure 11. Pelvic girdle of *Archeopelta*. A, C, ilium in posterior view; and B, D, right ischium in lateral view. Abbreviations: aw, acetabular wall; fps, first primordial sacral; iaf, ischial acetabular facet; il, ilium; ilb, iliac blade; isq, ischium; ivf, ischial ventral flange; ipvp, ischial posteroventral process; sr, sacral rib; t, tibia. Scale bar = 2 cm. Dark grey regions indicate damaged surfaces and light grey regions indicate matrix.

erythrosuchid *Vjushkovia* (Gower & Sennikov, 1996), *Euparkeria* (Gower & Weber, 1998), *Doswellia* (Dilkes & Sues, 2009), and aetosaur crurotarsans (e.g. *Neoaetosauroides*: Desojo & Báez, 2007). By contrast, in the erythrosuchid *Erythrosuchus* (Gower, 1997) and the crurotarsan 'rauisuchians' *Saurosuchus* (Alcober, 2000) and *Arizonasaurus* (Gower & Nesbitt, 2006), the exoccipitals widely meet each other medially. The paraoccipital processes are laterally and slightly ventrally projected, but the distal end of the processes are lacking. The supraoccipital is a subtriangular bone without ornamentation. A vertical ridge is present and widens slightly dorsally, a condition absent in *Tarjadia* (Arcucci & Marsicano, 1998) but present in other basal archosauriforms (e.g. *Shansisuchus*: Young, 1964; *Euparkeria*: SAM 5867) and archosaurs (e.g. *Batrachotomus*: Gower, 2002; *Herrerasaurus*: Novas, 1993; *Silesaurus*: Dzik, 2003). The tympanic fossae are oval, deep, and large, being situated between the supraoccipital, opisthotic, and

prootic (Fig. 5). The opisthotics bear an elliptical, very deep, and large fossa on the posteromedial corner of the bone, absent in *Erythrosuchus* (Gower, 1997), *Euparkeria* (SAM 5867), *Doswellia* (Dilkes & Sues, 2009), Proterochampsidae (e.g. *Chanaresuchus*: PULR 07; *Tropidosuchus*: PVL 4601), and the crurotarsans *Stagonolepis* (Gower & Walker, 2002), *Batrachotomus* (Gower, 2002), and *Arizonasaurus* (Gower & Nesbitt, 2006). Thus, this trait is interpreted as an autapomorphy of *Archeopelta*. The suture between the prootic and the opisthotic cannot be identified. Between the exoccipital and parabasisphenoid there is a single opening for the exit of the hypoglossal nerve (XII), which is oval and situated at the base of the basal tubera. The condition of *Archeopelta* contrasts with that present in basal dinosauriforms, such as *Silesaurus* (Dzik, 2003), in which the exit of the hypoglossal nerve is represented by two foramina. The basal tubera are well separated from each other by a deep median notch, being concave, low, and wide,

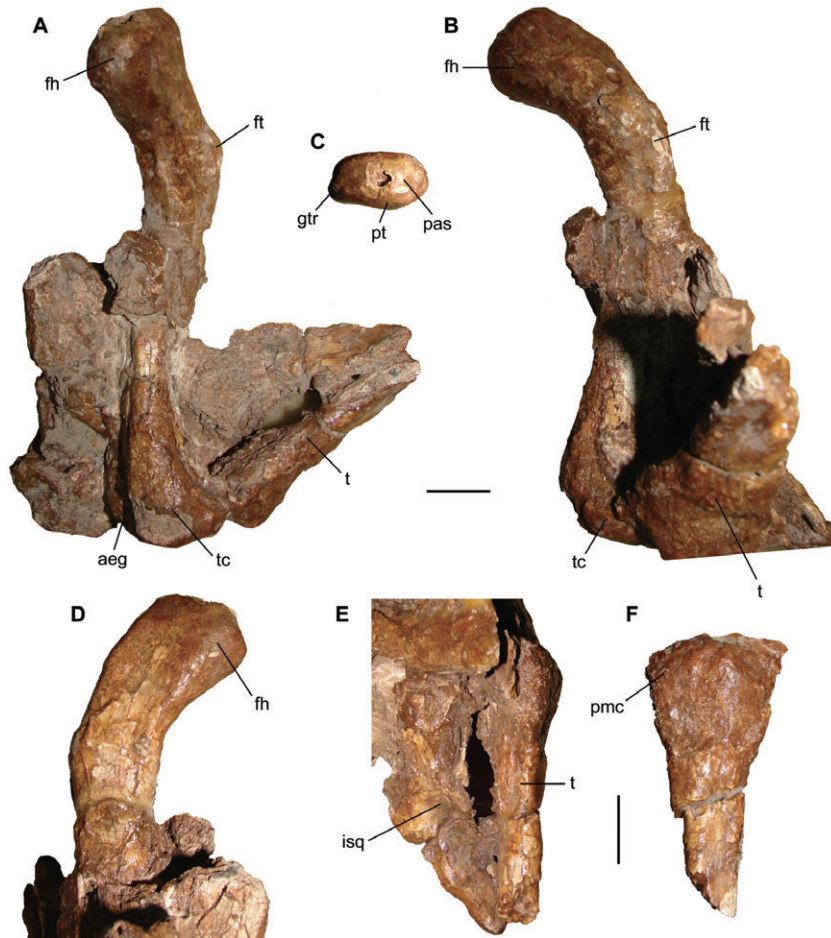


Figure 12. Hindlimb of *Archeopelta*. Right femur in A, medial; B, posterior; C, proximal; D, anterior views, and proximal end of right tibia in E, anterior views, and F, lateral views. Abbreviations: aeg, anterior extensor groove; fh, femoral head; ft, fourth trochanter; gtr, greater trochanter; isq, ischium; pas, proximal articular surface; pmc, posteromedial condyle; pt, posterior tuberosity; t, tibia; tc, tibial condyle. Scale bar = 2cm.

resembling the condition of *Euparkeria* (Gower & Weber, 1998), *Vjushkovia* (Gower & Sennikov, 1996), *Doswellia* (Dilkes & Sues, 2009), the dinosauriform *Silesaurus* (Dzik, 2003), and the crurotarsans *Neoateosauroides* (Desojo & Báez, 2007) and *Arizonasaurus* (Gower & Nesbitt, 2006). By contrast, the basal tubera of other archosauriforms, such as *Erythrosuchus* (Gower, 2002) and *Saurosuchus* (Alcober, 2000), are separated by an incipient and transversely narrow median notch. Furthermore, the basal tubera of *Archeopelta* are ventrolaterally projected and very low, as is the case in *Doswellia* (Dilkes & Sues, 2009), but contrasting with the better developed tubera of the ‘proterosuchid’ *Fugusuchus*, *Euparkeria* (Gower & Weber, 1998), and some crurotarsans including *Saurosuchus* (Alcober, 2000), *Arizonasaurus* (Gower & Nesbitt, 2006), *Xilousuchus* (Gower & Sennikov, 1996; *sensu* Nesbitt, 2009), and *Neoateosauroides* (Desojo & Báez, 2007). The suture between the parabasisphe-

noid and basioccipital is interdigitated and V-shaped in ventral view, forming a more obtuse angle than in *Doswellia* (Dilkes & Sues, 2009: fig. 1). The parabasisphenoid contributes to the anteriormost portion of the basal tubera; thus, the parabasisphenoid–basioccipital suture extends through the tubera. The parabasisphenoid is strongly anteroposteriorly compressed, contrasting with *Doswellia* (Dilkes & Sues, 2009: fig. 1), *Chanaresuchus* (PULR 07), and *Tropidosuchus* (Arcucci, 1990; PVL 4601). The ventral surface of this bone exhibits a very deep depression and only the left foramen for the exit of the internal carotid artery is preserved. It shows that these foramina are very small and situated at the posteriormost end of the parabasisphenoid, close to its suture with the basioccipital and almost at the midline of the braincase. Both traits are absent in other basal archosauriforms such as *Doswellia* (Dilkes & Sues, 2009: fig. 1), *Euparkeria* (Gower & Weber,

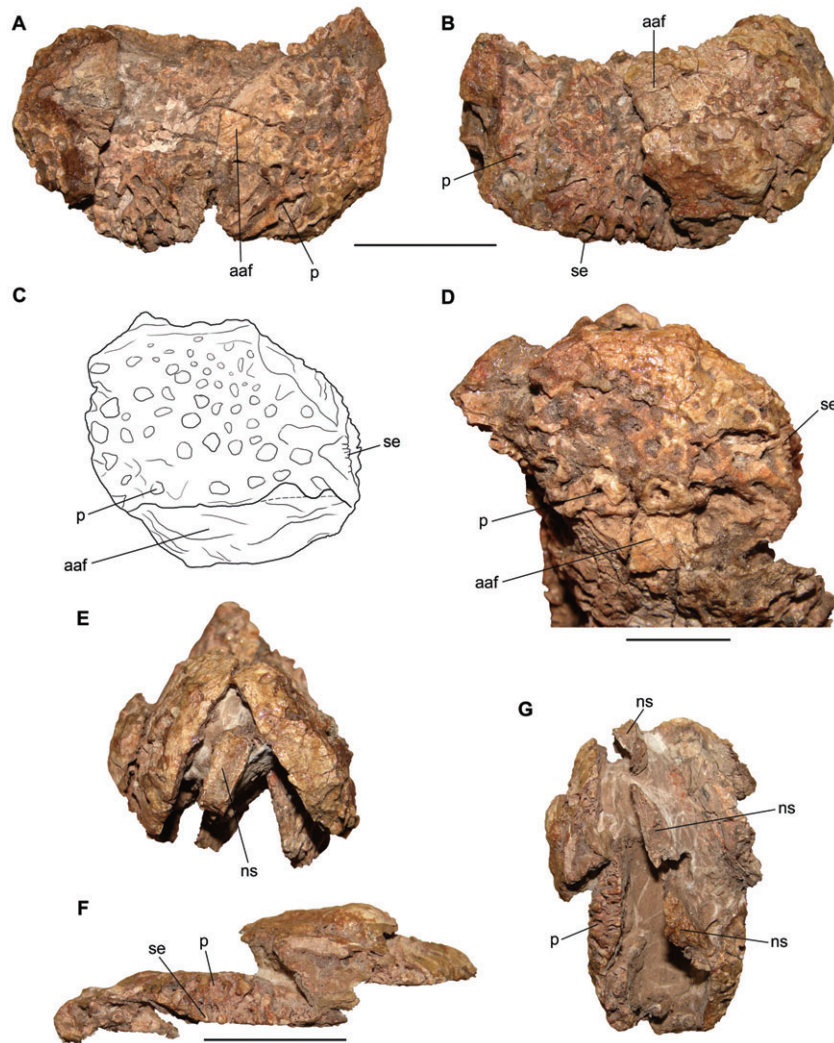


Figure 13. Paramedian osteoderms of *Archeopelta*. A, articulated left row and right row in B, dorsal and F, lateral views. Both rows in E, anterior and G, ventral views. C–D, close up of the first osteoderm of the left row in dorsal view. Abbreviations: aaf, anterior articular facet; ns, neural spine; p, pit; se, collateral serrations. Scale bar = 2 cm.

1998), *Turfanosuchus* (Wu & Russell, 2001), *Chanaresuchus* (PULR 07), *Tropidosuchus* (Arcucci, 1990; PVL 4601), the dinosauriform *Silesaurus* (Dzik, 2003), and the putative poposauroid crurotarsan *Xilousuchus* (Gower & Sennikov, 1996; *sensu* Nesbitt, 2009), in which the carotid foramina are more anteriorly situated and further from each other. By contrast, in most crurotarsans such as parasuchians (e.g. *Parasuchus*: Chatterjee, 1978), aetosaurians (e.g. *Stagonolepis*), ‘rauisuchians’ (e.g. *Batrachotomus*: Gower, 2002; *Saurosuchus*: Alcober, 2000; *Postosuchus krikpatricki*: Parrish, 1993) and crocodylomorphs (e.g. *Sphenosuchus*: Walker, 1990; *Dibothrosuchus*: Wu & Chatterjee, 1993) the foramina for the entrance of the cerebral branches of internal carotid arteries are laterally positioned. Only the

bases of the basiptyergoid processes are preserved, but they are almost vertical and situated ventral to the ventralmost level of the basal tubera, resembling the condition of *Parasuchus* (ISI R42), *Shansisuchus* (Young, 1964), *Turfanosuchus* (Wu & Russell, 2001), and *Yonghesuchus* (Wu, Liu & Li, 2001). However, in proterochampsids (e.g. *Chanaresuchus*: PULR 07; *Tropidosuchus*: PVL 4601), *Doswellia* (Wu & Russell, 2001), the basal dinosauriform *Silesaurus* (Dzik, 2003), aetosaurians (e.g. *Stagonolepis*: BMNH R4787; *Neoaetosauroides*: PVL 5298), and the ‘rauisuchians’ *Batrachotomus* (Gower, 2002), *Saurosuchus* (Alcober, 2000), and *Postosuchus krikpatricki* (Parrish, 1993) the basiptyergoid processes are lateroventrally projected. The basiptyergoid processes are closer to one another than are the basal tubera. The exits of the



Figure 14. Indeterminate bone of *Archeopelta* in several views including E, proximal view and F, cross section. Scale bar = 2 cm.

abducens nerve (VI) are located at the posterior base of the basiptyergoid processes, being posteroventrally orientated. The anterior portion of the parabasisphenoid is broken off, but in cross-section the bone is V-shaped, with a dorsal apex. The brain cavity is anteriorly bounded by the bases of the laterosphenoids and is circular in anterior view (Fig. 6). The foramen for the exit of the trigeminal nerve (V) is bounded by the prootic and by the laterosphenoid dorsomedially. Only the base of the right laterosphenoid is available.

Within the vestibule, three openings can be discerned (Fig. 7). The anteriormost opening corresponds to the foramen for the exit of the facial nerve (VII), which is separated by an oblique lamina from the metotic foramen and the fenestra ovalis. *Archeopelta* resembles *Euparkeria* (Gower & Weber, 1998), *Turfanosuchus* (Wu & Russell, 2001), and the basal dinosauriform *Silesaurus* (Dzik, 2003) in the presence of the foramen VII within the vestibule, contrasting with *Erythrosuchus* (Gower, 2002), *Prestosuchus* (UFRGS PV-152-T), and *Stagonolepis* (Gower & Walker, 2002) in which this foramen lies outside the vestibule. The metotic foramen and the fenestra ovalis are separated by an extremely thin oblique lamina, being posterodorsally to anteroventrally directed, representing the ventral ramus of the

opisthotic (*sensu* Gower, 2002). By contrast, in *Prestosuchus* (UFRGS PV-152-T) and *Batrachotomus* (Gower, 2002) the metotic foramen and the fenestra ovalis are separated by a much more sagittally developed ventral ramus of the opisthotic.

Dorsal vertebrae and ribs: An articulated series of 13 heavily damaged dorsal vertebrae is present, probably representing almost the entire dorsal region (Fig. 8; Table 2). At least four vertebrae of this series are directly associated with their overlapping paramedian osteoderms. The dorsal vertebrae are amphi-coelic and the neural arches are taller than the centra. The centra are slightly rectangular, being slightly longer than tall, resembling the condition of *Tarjadia* (Arcucci & Marsicano, 1998), *Euparkeria* (SAM 5867), *Chanaresuchus* (PVL 6244), *Turfanosuchus* (Wu, 1982), *Cuyosuchus* (MCNAM 2669), aetosaurs (e.g. *Aetosauroides*: PVL 2073), poposaurids (e.g. *Arizonasaurus*: Nesbitt, 2005; *Effigia*: Nesbitt, 2007), *Silesaurus* (Dzik, 2003), and basal dinosaurs (e.g. *Eoraptor*: PVSJ 512; *Saturnalia*: MCP 3845-PV; *Heterodontosaurus*: UCMP 129614). By contrast, the more elongated dorsal centra of *Doswellia* (Dilkes & Sues, 2009), *Marasuchus* (Serenó & Arcucci, 1994), and at least some vertebrae of *Vancleavea* (Nesbitt *et al.*, 2009a), are two times longer than tall. Con-

Table 2. Measurements (in millimetres) of the axial elements of CPEZ-239a

	'D4'	'D9'	S2
Maximum height	62.4	61.1	–
Centrum length	20.3	21.7	–
Height of the anterior surface of centrum	–	25.0	–
Height of the posterior surface of centrum	23.0	25.1	–
Height of the neural arch	41.5	36.9	26.7*
Length across zygapophyses	18.0	29.6	26.8
Length of prezygapophysis	–	–	11.0
Maximum width of the neural arch + rib	–	–	102.0

*Incomplete; 'D4/9', fourth and ninth dorsal vertebrae of the articulated series, respectively; S2, second sacral vertebra.

versely, the mid- and posterior dorsal vertebrae of erythrosuchids (e.g. *Erythrosuchus*: Gower, 2003; *Vjushkovia*: von Huene, 1960; *Shansisuchus*: Young, 1964), the basal saurischian *Herrerasaurus* (Novas, 1993), and some 'rauisuchians' (e.g. *Batrachotomus*: Gower & Schoch, 2009; *Ticinosuchus*: PIMUZ 2817; *Saurosuchus*: PVL 2198) are anteroposteriorly compressed, being almost as long as tall. The centra are subcylindrical, without a transverse constriction at mid-length. Indeed, both lateral and ventral surfaces of the dorsal centra are convex, without a ventral keel or sulcus. By contrast, in *Tarjadia* (Arcucci & Marsicano, 1998), *Erythrosuchus* (BMNH R3592), and *Cuyosuchus* (MCNAM 2669) the lateral surfaces of the dorsal vertebrae are excavated and the ventral surface is concave. In *Chanaresuchus* the dorsal centra are also transversely compressed at mid-length but the ventral surface is straight (PVL 6244). The anterior and posterior articular facets are oval, being taller than wide, contrasting with *Doswellia* in which the central articular facets are wider than tall (Weems, 1980). The diapophyses are well preserved only in the anterior dorsal vertebrae of the holotype of *Archeopelta*. They are laterally projected, being perpendicular to the longitudinal axis of the axial series. The diapophyses are thick and subrectangular in cross-section, being elongated and subrectangular in dorsal view. Such laterally extended diapophyses are also present in *Doswellia* (Dilkes & Sues, 2009), but they are proportionally shorter in *Chanaresuchus* (PVL 6244), *Erythrosuchus* (BMNH R3592), *Vancleavea* (Nesbitt *et al.*, 2009a), *Euparkeria* (SAM 5867), and *Cuyosuchus* (MCNAM 2669). Owing to the poor state of preservation of the axial elements, the presence or absence of infradiapophyseal lamina cannot be

confidently assessed. The prezygapophyses are short and anterodorsally orientated, resembling the condition of *Tarjadia* (Arcucci & Marsicano, 1998) and *Chanaresuchus* (PVL 6244). By contrast, in *Doswellia*, *Erythrosuchus* (BMNH R3592), and *Cuyosuchus* (MCNAM 2669) the prezygapophyses of the dorsal vertebrae are anteriorly projected (Dilkes & Sues, 2009). The postzygapophyses are slightly more dorsally situated than the prezygapophyses. The articular facet is circular in ventral view and slightly lateroventrally orientated. The base of the neural spine occupies most of the total length of the neural arch. The neural spines are taller than long, being subrectangular in lateral view, resembling the condition of several archosauriforms (e.g. *Chanaresuchus*: PVL 6244; *Erythrosuchus*: BMNH R3592; *Vancleavea*: Nesbitt *et al.*, 2009a). In contrast, in *Doswellia* the neural spines are considerably proportionally shorter (Weems, 1980; Dilkes & Sues, 2009). The neural spines that are preserved in articulation with the paramedian osteoderms are not T-shaped at their distal end, as is the case in *Erythrosuchus* (BMNH R3592), *Vancleavea* (Nesbitt *et al.*, 2009a), and *Chanaresuchus* (PVL 6244). In cross-section the neural spines are oval, with the anterior edge more acute than the posterior one, as also occurs in *Doswellia* (D. Dilkes, pers. comm.). In contrast, in *Chanaresuchus* the neural spines are strongly transversely compressed (PVL 6244).

A fragment of left rib shaft corresponding to the third dorsal vertebra of the available series is preserved. The element is rod-like and poorly curved, but its proximal and distal ends are lacking, preventing an assessment of whether the peculiar condition of *Doswellia* was present [see Weems, (1980) and Dilkes & Sues (2009)].

Sacral vertebrae: The neural arches of the probable second and third sacral vertebrae, following the condition seen in *Doswellia* (Weems, 1980) (the two primordial sacra), are preserved (Fig. 9). The first sacral is well preserved and only lacks its neural spine, and the second sacral only preserves the right transverse process and part of the neural canal. Two associated centra are available. However, it cannot be assessed if they pertain to a sacral or an anterior caudal vertebra. Contrasting with the available presacral vertebrae, these isolated centra are much longer than tall, with circular and planar articular facets, and showing a moderate transverse compression at mid-length.

The neural arch of the first primordial sacral is proportionally low but strongly transversely extended. In fact, the width of the neural arch plus the rib of this vertebra represents 3.8 times its length across the zygapophyses. A similar ratio is found in *Doswellia* (3.40; Weems, 1980), *Aetosauroides* (3.55;

PVL 2073), and phytosaurs (4.26; BMNH R3892), but contrasting with other archosauriforms such as *Euparkeria* (2.4; Ewer, 1965), *Tropidosuchus* (2.52; PVL 4601), and the archosaurs *Saurosuchus* (2.78; PVSJ 615), *Poposaurus* (1.32; UCMP 78719), *Gracilisuchus* (2.7; PVL 4597), *Lagerpeton* (2.73; PVL 4619), *Silesaurus* (2.35; Dzik, 2003), and *Herrerasaurus* (2.00; Novas, 1993). This morphology suggests that *Archeopelta* may possess the same condition as *Doswellia*, in which the body was transversely wide and dorsoventrally low (Weems, 1980). Interestingly, the sacral ratio observed in doswelliids is also present in the extant archosaur *Caiman yacare* (J.B.Desojo & M.D.Ezcurra, pers. observ.). In *Archeopelta* the neural canal is small in anterior view, but it is transversely wide and circular in posterior view. The transverse processes are laterally orientated and perpendicular to the longitudinal axis of the skeleton. The suture between the transverse process and the sacral ribs cannot be identified. The sacral rib is anteroposteriorly expanded at its distal end, with the anterior expansion being more prominent and subtriangular in dorsal view. The prezygapophyses are extremely large, accounting for 43% of the total length of the neural arch. The latter condition differs from the smaller prezygapophyses present in the first primordial sacral of *Doswellia* (Dilkes & Sues, 2009) and all other archosauriforms (e.g. *Cuyosuchus*: MCNAM 2669; *Erythrosuchus*: BMNH R3592; *Chanaresuchus*: PVL 6244; *Euparkeria*: SAM 5867; *Aetosauroides*: PVL 2073; *Gracilisuchus*: PVL 4597; *Leptosuchus*: UCMP 26669; *Marasuchus*: PVL 3870). The articular facets of the prezygapophyses are circular and dorso-medially orientated. By contrast, the prezygapophyses of *Doswellia* are oval in dorsal view (Dilkes & Sues, 2009). In *Archeopelta* the prezygapophyses of the first primordial sacral are separated from each other by a deep and rather narrow median notch. The postzygapophyses are short and their articular facets are lateroventrally orientated. The postzygapophyses are separated from each other by a deep vertical notch. A conspicuous V-shaped hyposphene is present and is continuous with the postzygapophyses. In contrast, a hyposphene is absent in the sacrals of *Erythrosuchus* (BMNH R3592), *Cuyosuchus* (MCNAM 2669), and *Batrachotomus* (SMNS 803242). A similar hyposphene to that of *Archeopelta* is present in the archosaur *Leptosuchus* (UCMP 26669). A pair of deep fossae is present directly ventrally to the postzygapophyses, being ventromedially bounded by the neural canal, as is the case in *Erythrosuchus* (BMNH R3592). There is a very shallow fossa lateral to the neural spine, being situated in the posterior third of the neural arch. Only the base of the neural spine is preserved. It is extended along the entire length of the neural arch that is not occupied by the prezyga-

pophyses, and is posteriorly extended at the same level as the postzygapophyses. In cross-section it is oval with a more acute anterior edge.

The neural arch of the second primordial sacral is also low, with a tall transverse process base. In anterior view, the transverse process is subtriangular and tapers towards its distal end. The sacral rib is strongly expanded anteroposteriorly in dorsal view, with a subtriangular posterior expansion. It presents a single articular facet, as occurs in *Tropidosuchus* (PVL 4601), *Erythrosuchus* (Gower, 2003), *Euparkeria* (Ewer, 1965), and basal archosaurs (e.g. *Lagerpeton*: PVL 4619; *Aetosauroides*: PVL 2073; *Saurosuchus*: PVSJ 615), but contrasting with the bifurcated second primordial sacral rib of *Prolacerta*, *Mesosuchus*, and *Proterosuchus* (Dilkes & Sues, 2009). The anterior expansion seems to have been well developed but most of it is broken off.

Humerus: The proximal end of a right humerus is preserved (Fig. 10; Table 3). Relative to the shaft, the humeral head of *Archeopelta* is proximomedially deflected, resulting in a humeral shaft that is well separated from the parasagittal mid-line of the trunk, contrasting with the usual condition found amongst basal archosauriforms (e.g. *Euparkeria*: SAM 5867; *Van cleavea*: Parker & Barton, 2008; *Erythrosuchus*: Gower, 2003). This condition agrees with the transversely wide body suggested by the axial skeleton of *Archeopelta* and comparisons with *Doswellia*. In proximal view, the humeral head is biconvex, with a better developed anterior margin. The anterior and posterior margins of the proximal articular surface are well delimited and differentiated from the shaft. The internal tubercle of the proximal end of the humerus is prominent and subtriangular in anterior view. The lateral surface of the proximal end of the bone, above the deltopectoral crest, is not preserved.

Table 3. Measurements (in millimetres) of the humerus and indetermined element of CPEZ-239a

Humerus	
Length	63.6*
Length deltopectoral crest	25.5*
Width of the humeral head	30.4
Depth of the humeral head	14.8
Indetermined element	
Length	87.8*
Width of the proximal end	26.5
Depth of the proximal end	18.2
Width of the shaft close to mid-length	15.7
Depth of the shaft close to mid-length	9.4

*Incomplete.

The anterior surface, below the proximal articular region, is concave, whereas the posterior one is convex. Below the internal tubercle, a low and rounded tuberosity is present on the lateral edge of the bone, a trait absent in other archosauriforms such as *Chanaresuchus* (PVL 6244), *Vancleavea* (Parker & Barton, 2008), *Erythrosuchus* (BMNH R3592), *Euparkeria* (SAM 5867), *Myrstriosuchus* (SMNS 10260), *Aetosauroides* (PVL 2073), and *Marasuchus* (PVL 3871), *Dimorphodon* (BMNH R41212-13), and *Herrerasaurus* (Serenó, 1993). The deltopectoral crest rises well below the proximal articular surface of the humeral head, and it is anteriorly orientated and situated on the anteromedial margin of the shaft. In lateral view, this crest is very low and trapezoidal, contrasting with the better developed crests exhibited by *Erythrosuchus* (BMNH R3592), *Euparkeria* (SAM 5867), *Batrachotomus* (Gower & Schoch, 2009), *Aetosauroides* (PVL 2073), *Stagonosuchus* (GTP 3832), but resembling *Vancleavea* (Parker & Barton, 2008) and the proterochampsid *Chanaresuchus* (PVL 6244). Below the level of the deltopectoral crest, the humeral shaft strongly tapers distally, at least as far as preserved. In cross-section, the humeral shaft presents a subrectangular contour with its major axis situated at an angle of about 30° with regard to the main axis of the humeral head.

Ilium: A large and thin bone is preserved within the block containing axial and hindlimb elements and osteoderms; however, because it is obscured by the remaining bones its morphology is extremely difficult to assess (Fig. 11A, C; Table 4). This bone is interpreted as an ilium because of the presence of a clear iliac blade and an acetabular region. The morphology of the iliac blade is quite peculiar, with a sigmoid shape in posterior view, which results in a laterally deflected blade. A laterally deflected iliac blade is also present in *Do. kaltenbachi*, a feature considered autapomorphic for the species (Dilkes & Sues, 2009), but a sigmoid element in posterior view is lacking in this taxon (Weems, 1980: fig. 21). By contrast, in *Archeopelta* the base of the iliac blade is medially deflected in a wide angle, contrasting with the condition present in other basal archosauriforms, including *Doswellia*, in which it is vertical. Accordingly, this trait is considered as an autapomorphy of *Archeopelta*. Furthermore, above the medial curvature of the base of the iliac blade, a lateral deflection is present in *Archeopelta*. The same condition is observed in *Doswellia* (Weems, 1980), but this external deflection is much more acute than in the Brazilian taxon. In other archosauriforms, the iliac blade is almost straight in sagittal view.

The iliac blade is strongly anteroposteriorly reduced in *Archeopelta*, with a well-developed ante-

Table 4. Measurements (in millimetres) of the pelvic and hindlimb elements of CPEZ-239a

Ilium	
Maximum height	74.0
Length of iliac blade	73.1
Height of iliac blade	29.7
Length of the pubic peduncle	30.0
Width of the pubic peduncle	12.1
Depth of the pubic peduncle	23.4
Ischium	
Length	77.2
Width of the pubic peduncle	9.1
Depth of the distal end	6.9
Length of the symphysis	29.1
Femur	
Length	170
Width of the femoral head	29.6
Depth of the femoral head	18.0
Length of the fourth trochanter	24.1
Width of the distal end	44.6
Depth of the distal end	36.3
Tibia	
Length	83.1*
Width of the proximal end	39.1
Depth of the proximal end	22.9

*Incomplete.

rior process but an extremely short postacetabular one, as occurs in basal archosauromorphs (e.g. *Mesosuchus*, *Prolacerta*; Dilkes, 1998). An extremely anteroposteriorly short iliac blade is also present in *Doswellia* (Weems, 1980) and *Vancleavea* (Parker & Barton, 2008), and contrasts with the condition in other archosauriforms (e.g. *Koilamasuchus*: Ezcurra *et al.*, 2010; *Euparkeria*: Ewer, 1965; *Erythrosuchus*: Gower, 2003; *Turfanosuchus*: Wu *et al.*, 2001; *Chanaresuchus*: PVL 6244; *Aetosauroides*: PVL 2073; *Leptosuchus*: UCMP 26669; *Saurosuchus*: PVL 2198; *Poposaurus*: UCMP 25962, 25974; *Batrachotomus*: SMNS 52970; *Marasuchus*: PVL 3870; *Silesaurus*: Dzik, 2003) in which the length of the iliac blade is three times greater than its height (Ezcurra *et al.*, 2010). The dorsal margin of the preacetabular process is lower than the postacetabular process, as occurs in *Doswellia* (Dilkes & Sues, 2009). As a result, the dorsal margin of the iliac blade is strongly convex in lateral view. The lateral surface of the iliac blade is ornamented by vertical striations along its dorsal margin. The preacetabular process is not well separated from the pubic peduncle, but it is clearly present, as occurs in other archosauriforms with the exception of *Proterosuchus* (Benton, 2004) and *Vancleavea* (Parker & Barton, 2008; Nesbitt *et al.*, 2009a).

The base of the iliac blade is strongly transversely compressed. The base of the blade is very long and forms an angle less than 45° to the longitudinal axis of the bone, as occurs in archosauriforms more derived than proterosuchids (Ezcurra *et al.*, 2010). Furthermore, the pubic peduncle is transversely very wide. The ischiadic peduncle is not preserved. The acetabular wall is strongly concave laterally and fully closed, contrasting with poposaurids (e.g. *Poposaurus*: UCMP 25962, 25974; *Effigia*: Nesbitt, 2007), basal crocodylomorphs (e.g. *Dibothrosuchus*: Wu & Chatterjee, 1993; *Terrestriusuchus*: Crush, 1984), and dinosaurs (e.g. *Herrerasaurus*: Novas, 1993; *Eoraptor*: PVSJ 512; *Heterodontosaurus*: UCMP 129614), in which a perforated acetabulum is present. Most of the lateral surface of the bone is obscured by the distal half of the femur and matrix.

Ischium: A right ischium is preserved closely associated with the ilium and the right hindlimb (Fig. 11B, D; Table 4). The pubic peduncle is very long, defining the ventral margin of the acetabulum. It is dorsoventrally tall, contrasting with the lower peduncle present in *Doswellia* (Dilkes & Sues, 2009) and *Vancleavea* (Nesbitt *et al.*, 2009a), but resembling the condition of *Euparkeria* (Ewer, 1965). Conversely, the iliac peduncle is very short, as occurs in other archosauriforms (e.g. *Euparkeria*: Ewer, 1965; *Vancleavea*: Nesbitt *et al.*, 2009a). At the proximal end of the bone, the ventral surface is concave. The ischial shaft is straight and slightly deflects posteromedially, with a very thin ventral lamina. The ischial plate is dorsoventrally tall, resembling the condition of *Erythrosuchus* (Gower, 2003), *Lagerpeton* (Serenó & Arcucci, 1993), *Tropidosuchus* (PVL 4601), *Vancleavea* (Nesbitt *et al.*, 2009a), and *Parasuchus* (Chatterjee, 1978). The major axis of the ischial shaft is oblique, with its ventral margin medially orientated. At the distal end of the bone, this thin lamina becomes a thick and planar articular facet for the reception of the left ischium. The distal end of the bone is subtriangular in distal view and lacks an expansion, resembling the morphology exhibited by *Tropidosuchus* (PVL 4601) and *Marasuchus* (Serenó & Arcucci, 1994). By contrast, in *Shansisuchus* (Young, 1964), *Erythrosuchus* (Gower, 2003), and *Vancleavea* (Nesbitt *et al.*, 2009a) the distal end of the ischium is rounded, whereas in *Euparkeria* (Ewer, 1965) and 'proterosuchids' (SAM C3016) the distal end is squared.

Femur: The right femur is completely preserved and is sigmoid in anterior view (Fig. 12A–D; Table 4). The femoral head is poorly defined, without a distinct femoral neck and ventral notch, contrasting with dinosaurs (Benton, 1990, 2004; Ezcurra, 2006, 2010;

Langer & Benton, 2006; Langer *et al.*, 2010; Brusatte *et al.*, 2010). The proximal articular surface of the femoral head is convex, without a longitudinal groove. In proximal view, the femoral head is oval in contour, but with a very poorly developed posterior tuber (= posterior tuberosity of Novas, 1993; Nesbitt, 2005), resembling the condition of dinosaurs (Benton, 1990; Novas, 1993; Ezcurra, 2006). The greater trochanter is poorly developed and rounded in posterior view. The fourth trochanter is prominent, low, and symmetrical in medial view, contrasting with the asymmetrical condition present in Dinosauria (Serenó, 1999; Ezcurra, 2006; Irmis *et al.*, 2007; Langer *et al.*, 2010). Nevertheless, the exact morphology of the fourth trochanter of *Archeopelta* cannot be confidently assessed because of its damaged nature. The femoral shaft has an oval cross-section at mid-length, with a transverse main axis. The distal end of the bone is strongly transversely expanded, with a transverse width representing around 150% of the transverse width of the femoral head. Such a strongly expanded distal end of the femur is absent in other known basal archosauriforms, including *Erythrosuchus* (Gower, 2003), *Turfanosuchus* (Wu & Russell, 2001), *Euparkeria* (Ewer, 1965), *Vancleavea* (Parker & Barton, 2008), *Chanaresuchus* (PVL 6244), *Tropidosuchus* (PVL 4601), *Aetosauroides* (PVL 2073), *Typothorax*, *Desmotosuchus* (Desojo & Báez, 2005), *Batrachotomus* (Gower & Schoch, 2009), *Marasuchus* (PVL 3871), *Dromomeron* (Nesbitt *et al.*, 2009b), and *Pseudolagosuchus* (PULR 053). The tibial and fibular condyles are poorly differentiated from each other at the ventral surface of the femur. Nevertheless, a wide and shallow anterior intercondylar groove separates both condyles. This groove is medially displaced from the midpoint of the distal end of the femur, as occurs in *Dromomeron* (Nesbitt *et al.*, 2009b) and *Lagerpeton* (PVL 4619). As a result, the fibular condyle is wider than the tibial condyle. In addition, the fibular condyle is more strongly anteroposteriorly developed than the tibial condyle. The anterior surface of the distal end of the femur is obscured by the proximal end of the tibia and matrix.

Tibia: The proximal end of the right tibia is preserved closely in articulation with the femur (Figs 11C, D, 12E, F; Table 4). The proximal articular surface is convex. The tibia possesses a strong anteroposterior proximal expansion. In *Archeopelta*, the posterior projection of the proximal end of the tibia is poorly developed, contrasting with the acute and better developed projection of *Chanaresuchus* (PVL 6244), *Erythrosuchus* (Gower, 2003), *Aetosauroides* (PVL 2073), *Leptosuchus* (Long & Murry, 1995), *Batrachotomus* (SMNS 52970), *Lagerpeton* (PULR 06), *Dromomeron* (Nesbitt *et al.*, 2009b), and *Silesaurus*

Table 5. Measurements (in millimetres) of the left paramedian osteoderm of the third row of the articulated series of CPEZ-239a

Length	30.7
Width	37.1
Thickness	7.7

(Dzik, 2003). Towards its mid-length the shaft tapers distally. In cross-section the shaft is oval, with an obliquely orientated major axis, as occurs in *Chanaresuchus* (PVL 6244), but not in *Aetosauroides* (PVL 2073). Some archosauriforms, such as *Erythrosuchus* (Gower, 2003), *Batrachotomus* (Gower & Schoch, 2009; SMNS 52970), and *Prestosuchus* (BSPG XXV11a), exhibit a pit situated in the posteromedial surface of the proximal half of the tibial shaft. This condition is absent in *Archeopelta* and *Chanaresuchus* (PVL 6244).

Osteoderms: At least ten paramedian, three lateral, and four undetermined osteoderms are preserved (Figs 8D, 9A, 13; Table 5). Two transverse rows of three anteroposterior columns of osteoderms are directly associated with three dorsal neural spines. Two transverse rows of paramedian osteoderms are joined to a single neural spine, as occurs in 'rauisuchians' (e.g. *Prestosuchus*: BSPG XXV7). By contrast, in *Tarjadia* (Arcucci & Marsicano, 1998), *Doswellia* (Dilkes & Sues, 2009), phytosaurs (e.g. *Leptosuchus*: Camp, 1930; *Parasuchus*: Chatterjee, 1978), and aetosaurs (e.g. *Neoaetosauroides*: PVL 3525; *Aetosauroides*: PVL 2073) a single transverse row of paramedian osteoderms are joined to a single neural spine. The osteoderms are very thick and quadrangular in outline, contrasting with the proportionally thinner dorsal osteoderms of aetosaurs (e.g. *Aetosauroides*: PVL 2073; *Desmotosuchus*: TTUP 9169; *Neoaetosauroides*: PVL 3525; *Stagonolepis*: BMNH 4789). As occurs in *Doswellia* (Weems, 1980), *Tarjadia* (Arcucci & Marsicano, 1998), some aetosaurs (e.g. *Chilenosuchus*: Casamiquela, 1980; SNGM 987/III; *Typothorax*: UCMP 126804), and the enigmatic archosauriform *Euscolosuchus* (Sues, 1992), *Archeopelta* exhibits osteoderms with a coarse reticular pattern and with deeply pitted ornamentation. Each pit exhibits the almost same size and contour, resembling *Doswellia* (Weems, 1980) and *Tarjadia* (Arcucci & Marsicano, 1998), but contrasting with *Euscolosuchus* (Sues, 1992) and aetosaurs (SNGM 987/III; UCMP 126804). No keel or blunted centre is present on the available osteoderms of *Archeopelta*, resembling the available osteoderms of *Tarjadia* (Arcucci & Marsicano, 1998), but contrasting with the dorsal eminence present in *Doswellia* (Dilkes & Sues, 2009), *Vancleavea* (Long &

Murry, 1995; Parker & Barton, 2008; Nesbitt *et al.*, 2009a), and some aetosaurs (e.g. *Chilenosuchus*: SNGM 987/III; *Typothorax*: UCMP 126804; *Stagonolepis*: BMNH 4789). The lateral margins of the osteoderms are serrated, resembling the condition of *Doswellia* (Dilkes & Sues, 2009). The dorsal osteoderms bear an unornamented anterior lamina for an overlapping articulation with the preceding osteoderm, as is the case for *Doswellia* (Weems, 1980; Dilkes & Sues, 2009), *Tarjadia* (*contra* Arcucci & Marsicano, 1998), *Revueltosaurus* (Parker *et al.*, 2005), and aetosaurs (e.g. *Chilenosuchus*: SNGM 987/III; *Desmotosuchus*: UCMP 126804). The medial and posterior borders of the osteoderms are straight, whereas the lateral and anterior ones are rounded. The ventral surface of the osteoderms is unornamented and lacks a keel. Preserved on the dorsal surface of a paramedian osteoderm is a fragmentary lateral osteoderm. The lateral osteoderm is thick and its ornamentation closely resembles that of the paramedian elements, as well as some lateral osteoderms of *Doswellia* (Dilkes & Sues, 2009).

Undetermined bone: A rod-like bone with a slightly expanded end is present, but its identification is doubtful (Fig. 14; Table 3). It does not represent the proximal half of a right ulna, because both lateral and medial surfaces of the possible proximal end are convex, the anterior process would be almost absent, and the olecranon process would be proximoposteriorly projected, with a posterior bulge at its base. All these features do not match the typical ulnar morphology present in other archosauriforms. Alternatively, this fragmentary bone could represent the distal half of a tibia. If this is the case, the distal end would be well expanded transversely and the distal articular surface for the reception of the astragalus would be divided into two distinct surfaces, one convex and the other concave. The convex surface is a result of a distally projected process. However, although we consider this bone most likely representing the distal half of a tibia, the morphology is highly unusual, and thus we consider it an undetermined element.

DISCUSSION

PHYLOGENETIC RELATIONSHIPS OF *ARCHEOPELTA* *ARBORENSIS* AND THE MONOPHYLY OF DOSWELLIIDAE

Methods: A cladistic analysis was performed in order to assess the phylogenetic relationships of *Arc. arborensis*. The data matrix was a modified version of that of Dilkes & Sues (2009). Four operational taxonomic units (*Arc. arborensis*: CPEZ-239a; *Tarjadia ruthae*:

Archosauria (*contra* Arcucci & Marsicano, 1998). Beyond the monophyly of Doswelliidae, the overall topology of the strict consensus tree resembles that of Dilkes & Sues (2009) but some differences are evident. *Chanaresuchus* was not found as the sister taxon of Doswelliidae, in contrast to the position of Proterochampsidae recovered by Dilkes & Sues (2009). Instead, *Chanaresuchus* was depicted in a more basal position, as the sister taxon of the clade including *Turfanosuchus* + Doswelliidae + more derived archosauriforms. It should be noted that the same result is obtained when Proterochampsidae (*sensu* Dilkes & Sues, 2009) is used as an OTU. As such, the monophyly of the clade including Proterochampsidae and Doswelliidae is not supported by the present analysis. Phylogenetic support (decay index) for this clade was weak in the analysis of Dilkes & Sues (2009).

The position of *Turfanosuchus* recovered by our phylogenetic analysis is equivocal, in contrast to the results of Dilkes & Sues (2009). A trichotomy was recovered that includes this taxon, Doswelliidae, and more derived archosauriforms (i.e. *Yonghesuchus* + Archosauria). This unresolved node is the result of the unstable position of *Turfanosuchus*, which is alternatively found as the sister taxon of the *Yonghesuchus* + Archosauria clade or as the most basal doswelliid. When *Turfanosuchus* is pruned and a new analysis is performed, three MPTs are obtained and *Chanaresuchus* is still found more basal than the Doswelliidae + (*Yonghesuchus* + Archosauria) node. Relationships at the base of Crurotarsi are unresolved with a polytomy amongst *Gracilisuchus*, *Qianosuchus*, Aetosauria (*Stagonolepis* + *Chilenosuchus*), and *Parasuchus*. This is result of the alternate positions adopted by *Gracilisuchus* within Crurotarsi.

Contrasting with the topology recovered by Dilkes & Sues (2009), *Euparkeria* was found as an archosauriform more derived than *Erythrosuchus*, resembling the results obtained by most previous analyses focused on basal archosauriform interrelationships (e.g. Benton, 1985, 1990, 2004; Gauthier, 1986; Benton & Clark, 1988; Sereno & Arcucci, 1990; Sereno, 1991; Parrish, 1993; Juul, 1994; Gower & Sennikov, 1996, 1997; Gower & Wilkinson, 1996; Parker & Barton, 2008; Nesbitt *et al.*, 2009a). The position of *Euparkeria* as more derived than *Erythrosuchus* is supported by the presence of an astragalus with a posterior corner of the dorsolateral margin that dorsally overlaps the calcaneum much more than the anterior portion, a calcaneal tuber relative to the transverse plane of the bone deflected at an angle of between 21 and 49° posteriorly, and the metatarsal IV midshaft diameter less than that of metatarsal III (Nesbitt *et al.*, 2009a).

Regarding the enigmatic *Vancleavea campi*, our analysis recovered it as one of the most basal known

archosauriforms, even more basal than *Erythrosuchus*. Thus, this result contrasts with that recently found by Nesbitt *et al.* (2009a), in which *Vancleavea* is more derived than *Erythrosuchus* and depicted as the sister taxon of Proterochampsidae, *Euparkeria*, and the crown Archosauria. The synapomorphies that support a more derived position for *Erythrosuchus* than *Vancleavea* are antorbital fossa present and restricted to the lacrimal and dorsal process of the maxilla (Nesbitt *et al.*, 2009a), anterior process of the jugal broad and dorsally expanded anteriorly (Gower & Sennikov, 1997), ratio of lengths between centra of mid-cervical and mid-dorsal vertebrae lower or equal than 1.0 (Dilkes & Sues, 2009), centrum of dorsal vertebrae with a lateral fossa below the neurocentral suture (Gauthier, 1986), presence of an iliac preacetabular process (Benton, 2004), pubic tubercle reduced to a rugosity (Hutchinson, 2001), ischial posteroventral process large and longer than the iliac blade (Benton, 2004), and femur with a fourth trochanter (Juul, 1994).

The inclusion of *Archeopelta* within Archosauriformes is supported by the presence of a laterosphenoid. The presence of this bone has been also reported for basal testudinatanans (e.g. *Proganochelys*, *Kayentachelys*; Gaffney, 1990; Sterli & Joyce, 2007), being suggested as a possible synapomorphy of the group including testudinatanans and archosauriforms (Bhullar & Bever, 2009). However, although the presence of a laterosphenoid seems to be more widely distributed amongst amniotans, the currently available morphological data unambiguously suggest that they are convergent acquisitions (Bhullar & Bever, 2009). Furthermore, the Brazilian form is more derived than *Proterosuchus* because of the presence of a supraoccipital with a prominent occipital peg that projects over the dorsal rim of the foramen magnum (unknown in *Vancleavea*), fused exoccipitals and opisthotics (unknown in *Vancleavea*), external foramina for passage of the abducens nerves on the anterior of a more vertical and upturned process (unknown in *Vancleavea*), ilium with a preacetabular process and dorsal margin of the pubic peduncle forming an angle of under 45° with the longitudinal axis of the bone (Fig. 16A–D), and dorsal body osteoderms. In addition, *Archeopelta* is found as more derived than *Vancleavea* because of the presence of an iliac preacetabular process, ischial posteroventral process large and longer than the iliac blade, and femur with a fourth trochanter. *Archeopelta* exhibits the following synapomorphy of the clade that comprises *Chanaresuchus* and more crownwards taxa: neural arches of mid-dorsals without or a shallow excavation (Dilkes, 1998). *Archeopelta* is more derived than the proterochampsid *Chanaresuchus* because of the absence of a parabasisphenoid with a semilunar

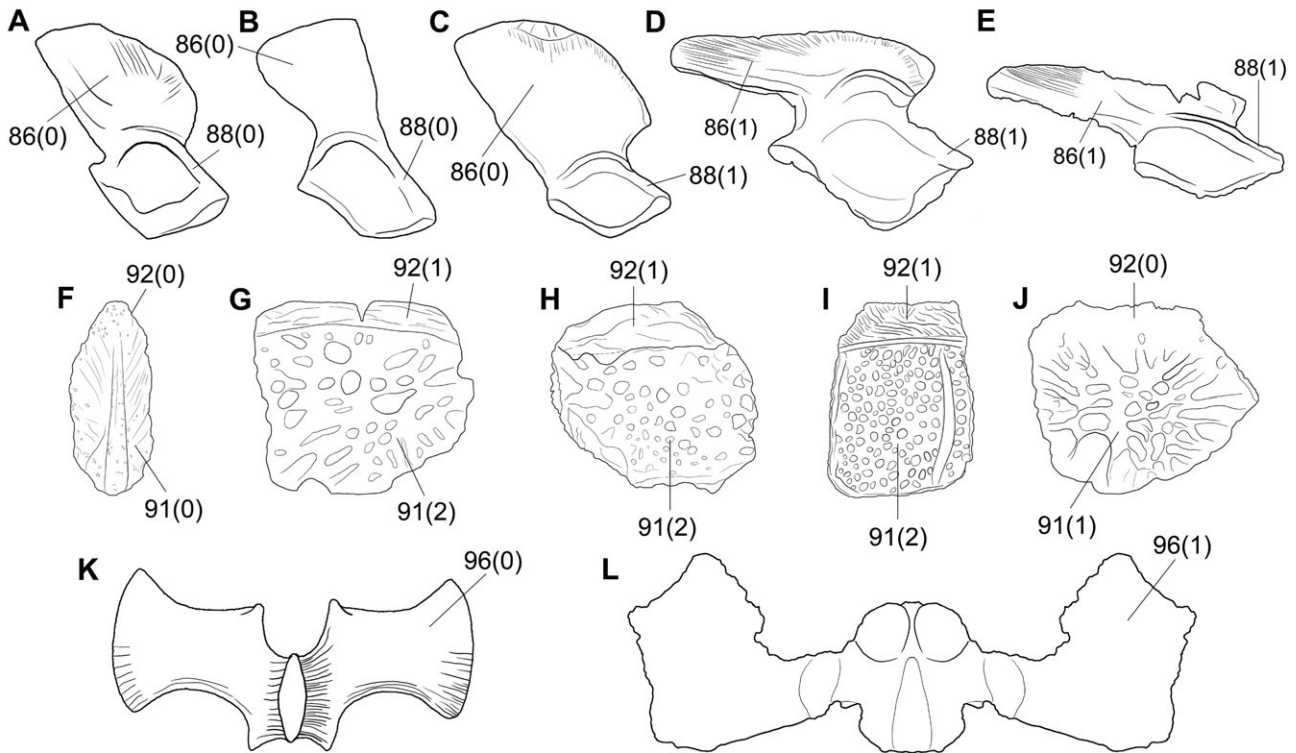


Figure 16. Character states of some new features added to the data matrix. Several ilia in lateral view: A, *Mesosuchus* (after Dilkes, 1998); B, *Vancalevea* (after Nesbitt *et al.*, 2009a), C, *Doswellia* (modified from Weems, 1980); D, *Erythrosuchus* (after BMNH R3592); E, *Chanaresuchus* (after PVL 6244). Several paramedian osteoderms in dorsal view: F, *Euparkeria* (after SAM 5867); G, *Tarjadia* (after Arcucci & Marsicano, 1998); H, *Archeopelta* (after CPEZ-239a); I, *Doswellia* (modified from Dilkes & Sues, 2009); and J, *Parasuchia* (after SMNS 12593). Primordial sacral vertebrae of K, *Euparkeria* (modified from Ewer, 1965) and L, *Archeopelta* (after CPEZ-239a) in dorsal view. Not to the same scale.

ventral depression (Gower & Sennikov, 1996). By contrast, *Archeopelta* is found as more basal than *Yonghesuchus* and archosaurs because of the posterior position of foramina for the cerebral branches of the internal carotid arteries leading to the pituitary fossa on the parabasisphenoid.

The monophyly of Doswelliidae (including *Tarjadia*, *Archeopelta*, and *Doswellia*) is supported by the two synapomorphies that are discussed below:

1. Osteoderm ornamentation coarse, incised, and composed of central regular pits of equal size and contour (Fig. 16E–I). As discussed above, the osteoderm ornamentation of *Archeopelta* is almost identical to that of *Doswellia* (Weems, 1980; Dilkes & Sues, 2009) and *Tarjadia* (Arcucci & Marsicano, 1998), consisting of coarse, incised, deep, and rather circular central pits of subequal size and arranged symmetrically on the dorsal surface of the dermal plate. It must be noted that the peripheral pits of the osteoderms of doswelliids are

groove-like and externally open, resembling the condition of some archosaurs such as parasuchians (SMNS 12593). Conversely, other basal archosauriforms exhibit an almost smooth dorsal osteoderm surface (e.g. *Chanaresuchus*: PVL 6244; *Gracilisuchus*: PULR 08) or are faintly ornamented by minute pits or/and grooves (e.g. *Erythrosuchus*: Gower, 2003, BMNH 3592; *Euparkeria*: SAM 5867; *Turfanosuchus*: Wu & Russell, 2001). Furthermore, the ornamentation pattern exhibited by parasuchians and aetosaurs also differs from that of doswelliids. In this regard, in parasuchians (e.g. Long & Murry, 1995; SMNS 12593) the ornamentation is radial and composed of irregular pits at the centre of the osteoderm and externally open marginal grooves. By contrast, in aetosaurs the patterns are more diverse, including a reticular configuration of subequal and irregular (e.g. *Chilenosuchus* SNGM 987: Desojo, 2003), a random arrangement of irregular and oval pits (e.g. *Tyothorax*; NMMNH 17344; Long & Murry, 1995: fig. 100; Lucas, Heckert & Hunt, 2002:

figs 3, 10), and radial pits and grooves (*Stagonolepis*: BMNH 4789; *Neoetosauroides*: PVL 3525; *Aetosauroides*: PVL 2073).

2. Osteoderms with anterior articular lamina (Fig. 16E–I). In the osteoderms of some archosauriforms, a structure devoid of pits, that is thinner than the rest of the dermal plate, and with a continuous and almost straight border, is observed. This structure is recognized here as an articular lamina (depending on the dorsoventral development of the structure, see Parker, 2008). By contrast, in other archosauriforms (e.g. parasuchians: SMNS 12593; *Sikannisuchus huskyi*: Nicholls, Brinkman & Wu, 1998) the dorsal surface of at least some osteoderms possesses an unornamented marginal portion, but an articular lamina cannot be discerned because it is just an unornamented extension of the dermal plate, with the same thickness as the remaining osteoderm. Accordingly, amongst archosauriforms the presence of an unornamented anterior articular lamina on the dorsal osteoderms is observed in *Archeopelta*, *Doswellia* (Weems, 1980; Long & Murry, 1995), and *Tarjadia*. Regarding the latter taxon, the available dorsal osteoderms (Arcucci & Marsicano, 1998: fig. 4) exhibit an unornamented marginal subrectangular portion with a straight border, a structure that matches with the articular lamina present in other doswelliids. By contrast, in *Euscolosuchus* (Sues, 1992), *Revueltosaurus* (Parker *et al.*, 2005), and many aetosaurs (e.g. *Stagonolepis*: BMNH 4789; *Neoetosauroides*: PVL 3525; *Aetosauroides*: PVL 2073; *Chilenosuchus*: SNGM 987; *Typhorax*: NMMNH 17344), the anterior unornamented articular projection is formed by a raised bar.

These two synapomorphies support the monophyly of Doswelliidae and, as result, the close phylogenetic relationship between *Tarjadia* and *Doswellia*. In particular, differences in the vertebral morphology (e.g. lateral fossa on the centra) and the presence of a postfrontal in *Tarjadia* are interpreted as symplesiomorphies of the group, and they do not provide support for the suggestion that *Doswellia* is not closely related to *Tarjadia* (Arcucci & Marsicano, 1998: 230).

3. Within Doswelliidae, *Doswellia* and *Archeopelta* are recovered as more derived than *Tarjadia* because of the (3) absence of dorsal vertebra centra with a lateral fossa below the neurocentral suture. Amongst Archosauriformes, the presence of blind elliptical fossae below the neurocentral suture is observed in *Euparkeria* (cast of SAM 5867), *Eythrosuchus* (BMNH 3592), *Turfanosuchus* (Wu & Russell, 2001), *Tarjadia* (Arcucci & Marsicano,

1998), and several archosaurs such as *Marasuchus* (PVL 3870), *Saurosuchus* (PVSJ 615), *Stagonolepis* (BMNH R4789a), and *Herrerasaurus* (PVL 2553). The MPTs obtained here suggest that the presence of these fossae is the symplesiomorphic condition for archosauriforms more derived than *Proterosuchus*, and in particular for Doswelliidae. Accordingly, the absence of the fossae in *Archeopelta* and *Doswellia* are interpreted as an apomorphic reversal of the node uniting these two taxa.

As a result of the incompleteness of the holotype of *Tarjadia*, several potential synapomorphies of Doswelliidae are recognized as ambiguous. However, when *Tarjadia* is excluded from the analyses the following synapomorphies of the *Doswellia* + *Archeopelta* node (and also probably of Doswelliidae) are recognized:

4. Basipterygoid processes anterolaterally orientated. In Archosauriformes the basipterygoid processes are laterally orientated, contrasting with the anterolaterally orientated processes in non-archosauriform archosauromorphs (Dilkes & Sues, 2009: character 20). Within Archosauriformes, the reversal of this condition is observed in *Archeopelta*, *Doswellia*, and some archosaurs (e.g. *Marasuchus*: PVL 3872; *Stagonolepis*: BMNH 4784). The phylogenetic analysis interpreted the presence of anterolaterally orientated basipterygoid processes as a probable apomorphy of the clade enclosing *Archeopelta* and *Doswellia*.
5. Width of the neural arch plus ribs of the first primordial sacral three times the length of the neural arch across the zygapophyses (Fig. 16J–K). This ratio is observed in *Archeopelta* and *Doswellia* (Weems, 1980), contrasting with the vast majority of Archosauriformes in which the sacral transverse processes plus its ribs are less than three times the sagittal length of the sacral neural arch.
6. Ilium with laterally deflected dorsal blade. This condition is present in *Doswellia* (Weems, 1980; Dilkes & Sues, 2009) and *Archeopelta* and is absent in all other archosauriforms. The iliac blade of some aetosaurs (Parrish, 1986; Desojo & Báez, 2005) and ‘rauisuchians’ (Bonaparte, 1982) are dorsolaterally orientated, but they differ from the doswelliid condition in that the iliac blade is not deflected from the acetabular portion.
7. Iliac dorsal margin strongly convex (Fig. 16A–D). In *Doswellia* (Dilkes & Sues, 2009) the dorsal margin of the iliac blade is strongly convex, as result of a preacetabular process that is much more ventrally positioned than the postacetabular one. This condition is also present in the non-archosauriform archosauromorphs *Mesosuchus*,

Prolacerta (Dilkes, 1998), and *Hyperodapedon huxleyi* (Chatterjee, 1974), as well as in *Archeopelta*. By contrast, in *Erythrosuchus* (Gower, 2003), *Proterosuchus* (Dilkes & Sues, 2009), *Euparkeria* (Ewer, 1965), *Chanaresuchus* (PVL 6244), *Turfanosuchus* (Wu & Russell, 2001), and archosaurs the dorsal margin of the iliac blade is gently convex, straight, or concave, and the preacetabular and postacetabular processes are situated at almost the same level. Additionally, in the bizarre archosauriform *Vancleavea* the iliac blade is subtriangular (Parker & Barton, 2008), rather than convex as is in *Archeopelta*. Here, the condition of *Archeopelta* and *Doswellia* is interpreted as a probable apomorphy of this clade, independently acquired from the condition present in several non-archosauromorph archosauriforms.

8. Maximum length of the iliac blade less than three times its maximum height (Fig. 16A–D). Contrasting with non-archosauriform archosauromorphs such as *Mesosuchus*, *Prolacerta* (Dilkes, 1998), *Hyperodapedon gordonii* (Benton, 1983), and *Hyperodapedon huxleyi* (Chatterjee, 1974), 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 three times or more longer than its maximum dorsoventral height. However, within archosauriforms, *Archeopelta*, *Doswellia*, and *Vancleavea* (Parker & Barton, 2008) are unique in presenting an anteroposteriorly reduced preacetabular process; thus the maximum length of the iliac blade accounts for less than three times its maximum height. Although this character seems to be correlated with the previous one (i.e. iliac dorsal margin strongly convex), we interpret them as independent features. We suggest that the dorsal curvature of the iliac blade is not related to the relative elongation of the postacetabular process and the overall anteroposterior development of the iliac blade. In this regard, an example is the derived rhynchosaur *Hyperodapedon* (Benton, 1983; Dilkes, 1998), in which the dorsal margin of the iliac blade is slightly convex but the maximum length of this structure is less than three times its maximum height.

In *Tarjadia* the postfrontal bone is present on the skull roof, but this element is absent in *Doswellia*. As the skull table is not preserved in *Archeopelta* the optimization of this feature within Doswelliidae is currently uncertain, but the absence of this bone may be an apomorphy of doswelliids more derived than *Tarjadia* (i.e. a synapomorphy of the *Archeopelta* + *Doswellia* clade or an autapomorphy of *Doswellia*).

Support for MPTs: In order to test the robustness of the MPTs, bootstrap and Bremer supports were performed (Fig. 15B). The bootstrap analysis was carried out with 5000 pseudoreplicates calculating absolute and GC frequencies. Bootstrap support is weak (lower than 50%) throughout much of the tree, including the Doswelliidae node, but moderately high values are observed at the base of Archosauriformes (86%) and the node containing taxa more derived than *Proterosuchus* (96%). Bremer support values are shown in Figure 15B. Decay indexes are very low (i.e. 1) along most the tree, with the exception of the node that comprises archosauriforms more derived than *Chanaresuchus* (decay index of 2). By contrast, the root of Archosauriformes and the clade that includes *Vancleavea* and more crownwards taxa exhibit high decay indexes of 8 and 6, respectively.

Searches for suboptimal trees with enforced topological constraints recovered the following results. One extra step is needed to position *Archeopelta* as the sister-taxon of *Tarjadia* or as the most basal doswelliid. This result is not unexpected, because *Tarjadia* is based on very fragmentary specimens and as a result the close affinities of *Archeopelta* and *Doswellia* are supported by a single non-ambiguous synapomorphy. Eight extra steps are necessary in order to obtain *Archeopelta* as the sister-taxon of *Chanaresuchus*, ten extra steps to obtain the Brazilian form as the sister-taxon of *Turfanosuchus*, or the Doswelliidae + more derived archosauriforms clade, or as the sister-taxon of *Yonghesuchus* + Archosauria. With regard to *Doswellia*, 11 extra steps are needed to obtain this taxon as the sister-taxon of *Chanaresuchus*, strongly contrasting with the analysis of Dilkes & Sues (2009). Furthermore, nine extra steps are necessary in order to enforce a sister-taxon relationship between *Doswellia* and *Turfanosuchus*. When the position of *Tarjadia* is constrained three extra steps are needed in order to recover it as the sister-taxon of *Chanaresuchus*, and five extra steps in order to find the Argentinean form as the sister-taxon of *Turfanosuchus*, *Yonghesuchus*, Archosauria, or the clade including Doswelliidae + more derived archosauriforms, and also to position *Tarjadia* as the most basal avemetatarsalian or the most basal crurotarsan. Three extra steps are needed in order to place *Tarjadia* as the sister-taxon of *Stagonolepis* + *Chilenosuchus* or *Parasuchus*. Furthermore, a suboptimal tree of only one extra step depicts *Chilenosuchus* as the sister-taxon of *Parasuchus*, and two extra steps are required in order to position the former as the most basal doswelliid. Finally, 15 extra steps are necessary to find *Vancleavea* outside Archosauriformes, six to be a member of Doswelliidae (as its most basal form), four to lie as more derived than *Erythrosuchus* (as it was found by Nesbitt *et al.*, 2009a), and two

extra steps to recover it as the sister-taxon of *Chanaresuchus*.

IMPLICATIONS FOR THE EARLY RADIATION OF THE ARCHOSAURIFORMES

In the present contribution we recognize a new monophyletic entity of non-archosaurian archosauriforms, comprised of *Tarjadia*, *Archeopelta*, and *Doswellia*. This monophyletic clade is added to the traditionally known lineages of basal archosauriforms, i.e. 'Proterosuchidae', Erythrosuchidae, and Proterochampsidae. Furthermore, the present phylogenetic analysis indicates that doswelliids are the closest large monophyletic entity to Archosauria. In this regard, the morphology of doswelliids is crucial in order to shed light on character optimizations of the archosaur-stem and at the base of Archosauria.

Regarding the palaeobiology of the group, there are two hypotheses concerning the mode of life of *Doswellia*. Weems (1980) proposed that *Doswellia* could be an animal of terrestrial and foraging habits, or alternatively it could be a semi-aquatic form. The latter hypothesis was stated by Weems (1980) because of the presence of pointed, conical, and recurved teeth, elongate jaws, and largely upward directed eyes, features related with aquatic and piscivorous habits. The latter could be extrapolated to *Archeopelta* because of the presence of a very similar *bauplan*. In addition, a semi-aquatic mode of life has been also suggested for members of Proterochampsidae (Sill, 1967; Romer, 1971) and *Vanleavea* (Nesbitt *et al.*, 2009a). Accordingly, if doswelliids, proterochampsids, and *Vanleavea* present an aquatic mode of life, the current phylogenetic hypothesis suggests that these habits have been independently acquired at least three times during the evolution of non-archosaur archosauriforms. Nevertheless, in order to assess more confidently the mode of life of doswelliids, more detailed analyses should be performed, such as biomechanical studies and soft tissue reconstructions (e.g. regarding the unusual pelvic girdle anatomy and orientation of the areas of muscle origin; Barrett & Rayfield, 2006).

Archeopelta comes from the Santa Maria 1 Sequence of the Santa Maria Supersequence (lower Santa Maria Formation), belonging to the *Dinodontosaurus* AZ. This AZ is biostratigraphically correlated with the fauna of the Argentinean Los Chañares Formation (Ischigualasto-Villa Unión Basin), thus chronologically constrained to the Ladinian–earliest Carnian (see above). Indeed, the Santa Maria 1 Sequence and the Los Chañares Formation share groups such as 'rauisuchians' (e.g. *Luperosuchus*, *Prestosuchus*), proterochampsids (e.g. *Chanaresu-*

chus, *Gualosuchus*, *Tropidosuchus*), cynodonts (e.g. *Massetognathus*, *Probainognathus*, *Chiniquodon*), and dicynodonts (e.g. *Dinodontosaurus*, *Stalekeria*) (Bonaparte, 1997; Marsicano, Gallego & Arcucci, 2000). As a result, *Tarjadia* and *Archeopelta* would be almost coeval taxa. By contrast, *Doswellia* comes from temporally younger beds of North America (Tecovas, Trujillo, and Cooper Canyon Formations; Long & Murry, 1995; Lucas, 1998; LeTourneau, 2003; Lehman & Chatterjee, 2005), being associated with typical Late Triassic (late Carnian and early Norian) forms, including metoposaurid temnospondyls (e.g. *Metoposaurus*, *Buttneria*), basal archosauromorphs (e.g. *Trilophosaurus*), and phytosaurian (e.g. *Paleorhinus*, *Rutiodon*, *Leptosuchus*), aetosaurian (e.g. *Longosuchus*, *Desmotosuchus haplocerus*), and 'rauisuchian' (e.g. *Postosuchus kirkpatricki*, *Poposaurus gracilis*) archosaurs (Long & Murry, 1995). In conclusion, the doswelliids were widely distributed palaeolatitudinally and temporally, present from the Middle Triassic–earliest Late Triassic of South America to the late Late Triassic of North America.

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APPENDIX 1

In the following the characters added to the data matrix of Dilkes & Sues (2009) are detailed. Characters 86–89 from Ezcurra *et al.* (2010), character 90–96 and 110–115 added here, 97–109 from Nesbitt *et al.* (2009a).

86. Maximum length of the iliac blade: less (0); more (1) than three times its maximum height. (Ezcurra *et al.*, 2010)
87. Centrum of dorsal vertebrae with a lateral fossa below the neurocentral suture: absent (0); present (1). (Gauthier, 1986)
88. Dorsal margin of the pubic peduncle forming an angle less than 45° with the longitudinal axis of the bone: absent (0); present (1). (Ezcurra *et al.*, 2010)
89. Cervical and anterior and mid-dorsal ribs with capitulum and tuberculum developed as distinct tubercles: absent (0); present (1). (Ezcurra *et al.*, 2010)
90. Thick paramedian osteoderms: absent (0); present (1). New character
91. Coarse, incised, and pitted ornamentation on osteoderms: absent (0); present and irregular pits, of different size and contour (1); present and regular pits, of equal size and contour (2). New character
92. Unornamented anterior articular lamina: absent (0); present (1). New character
93. External foramina for passage of abducens nerves: on underside of a horizontal surface (0); on the anterior of a more vertical, upturned process (1). (Gower, 2002)

94. Prominent occipital peg of supraoccipital that projects over dorsal rim of foramen magnum: absent (0); present (1). (Dilkes & Sues, 2009)
95. Ratio between the width of the neural arch + ribs of the first primordial sacral and the length of the neural arch across the zygapophyses: less than three (0); three or more (1) times.
96. Ilium with laterally deflected dorsal blade: absent (0); present (1). (Dilkes & Sues, 2009)
97. Anteromedially projecting palatal process on the anteromedial surface of the maxillae: absent (0); present (1). (Gower & Sennikov, 1997)
98. Tooth implantation: teeth fused to the bone of attachment at the base (0); free at the base of the tooth (1). (Gauthier, 1984; Benton & Clark, 1988; Benton, 1990; Bennett, 1996; Nesbitt *et al.*, 2009a)
99. Anterior process of the jugal: slender and tapering (0); broad and dorsally expanded anteriorly (1). (Gower & Sennikov, 1997)
100. Posterior end of the squamosal: does not extend posterior to the head of the quadrate (0); extends posterior to the head of the quadrate (1). (Nesbitt *et al.*, 2009a)
101. Ectopterygoid: does not form or forms some of the lateral edge of the lateral pterygoid flange (0); forms most of all the lateral edge of the lateral pterygoid flange (1). (Modified from Nesbitt *et al.*, 2009a.)
102. Posteroventral portion of the dentary: just meets the surangular (0); laterally overlaps the anteroventral portion of the surangular (1). (Nesbitt *et al.*, 2009a)
103. Entire anterior margin of the scapula: straight/convex or partially concave (0); markedly concave (1). (Gower & Sennikov, 1997)
104. Femoral condyles: prominent (0); not projecting markedly beyond the shaft (1). (Gauthier *et al.*, 1988). We consider that the distal femoral condyles are prominent when globular and well-differentiated structures from the shaft are recognized. For example, this condition is not observed in *Erythrosuchus*, *Prolacerta*, or rhynchosaurs, but present in *Vancleavea*, *Chanaresuchus*, *Archeopelta*, *Turfanosuchus*, *Euparkeria*, *Doswellia*, and archosaurs.
105. The dorsolateral margin of the astragalus: overlaps the anterior and posterior portions of the calcaneum equally (0); the posterior corner of the dorsolateral margin of the astragalus dorsally overlaps the calcaneum much more than the anterior portion (1). (Nesbitt *et al.*, 2009a)
106. Astragal posterior groove: absent (0); present (1). (Sereno, 1991)
107. Metatarsal II midshaft diameter: less than or equal to the midshaft diameter of metatarsal I (0); more than the midshaft diameter of metatarsal I (1). (Nesbitt *et al.*, 2009a)
108. Metatarsal IV: nearly the same midshaft diameter as metatarsal III (0); reduced where the midshaft diameter is less than metatarsal III (1). (Nesbitt *et al.*, 2009a)
109. Metatarsal IV: longer than metatarsal III (0); about the same length or shorter than metatarsal III (1). (Bennett, 1996; Gower & Sennikov, 1997; Nesbitt *et al.*, 2009a)
110. Posterior process of the squamosal: straight (0); ventrally curved (1). New character
111. Exposition of the lacrimal on the skull roof in dorsal view: absent (0); present (1). New character
112. Ventral process of the postorbital: ends much higher than the ventral margin of the orbit (0); ends close to or at the ventral margin of the orbit (1). New character
113. Ventral process of the squamosal: almost vertical (0); anteroventrally projected, constricting the infratemporal fenestra at mid-height (1). New character.
114. Pubic length: less (0); more (1) than two times the length of the acetabulum. New character
115. Occipital neck connecting the occipital condyle and the basioccipital body: present (0); absent (1). New character.

Characters modified from the data matrix of Dilkes & Sues (2009): 2. Antorbital fossa: absent (0); present, restricted to the lacrimal (1); present, restricted to the lacrimal and dorsal process of the maxilla (2); present on the lacrimal, dorsal process of the maxilla and the dorsal margin of the posterior process of the maxilla (the ventral border of the antorbital fenestra) (3). (Modified from Benton, 2004; Nesbitt *et al.*, 2009a.)

70. Calcaneal tuber relative to the transverse plane: lateral, angled less than 20° posteriorly (0); deflected, angled between 21 and 49° posteriorly (1); angled between 50 and 90° posteriorly (2). (Gauthier, 1984; Sereno, 1991; Parrish, 1993; Juul, 1994; Benton, 1999; Nesbitt *et al.*, 2009a)

APPENDIX 2

Character states modified from the data matrix of Dilkes & Sues (2009):

MARASUCHUS

Character 2: in *Marasuchus* the only available cranial elements corresponds to a right maxilla, preserving

the horizontal ramus and the base of the ascending process (PVL 3870), probable right squamosal and postorbital (PVL 3872), and a basicranium (PVL 3870, 3872). Accordingly, the morphology of the dorsal region of the antorbital fossa, constituted by the distal end of the ascending process of the maxilla and dorsal end of the lacrimal, is currently unknown. In this regard, the state (?) has been introduced instead of (1) in this taxon.

Character 3: in *Marasuchus* the available maxilla preserves the anterior and ventral boundaries of a well-developed internal antorbital fenestra (PVL 3870). Accordingly, this character has been codified as (1) instead of (?) in *Marasuchus*.

Character 34: in the available maxillary teeth of *Marasuchus* (PVL 3870), the crowns are distally curved. In this regard, the character state (1) has been changed instead of (?).

Character 35: the crowns of the maxillary teeth of *Marasuchus* are labiolingually compressed (PVL 3870), and as a result the character state has been codified as (1) instead of (?) for this character.

EUPARKERIA

Character 5: the external nares of *Euparkeria* are of marginal position, being widely visible in lateral view (SAM 5867), contrasting with the dorsal nares of proterochampsids, which are mostly obscured in lateral view (e.g. *Chanaresuchus*; PULR 07). Thus, the character state (0) has been introduced instead of (1) in *Euparkeria*.

Character 7: in *Euparkeria* the suture between the premaxilla and maxilla does not exhibit a notch between these elements, but the contact between the bones is almost vertical and continuous along all of its extension. Accordingly, the character state of this feature has been changed to (0) instead of (1) (see also Nesbitt *et al.*, 2009a: character 43).

Characters 45 and 46: Nesbitt *et al.* (2009a: character 25) discuss the presence of intercentra in the cervical and dorsal vertebrae of basal archosauriforms. They stated that the presence or not of intercentra could not be asserted in the axial skeleton of *Euparkeria*. Following these authors, we rescored the character states as a polymorphic (0/1) instead of (0) in the South African form.

Character 53: the second primordial sacral rib of *Euparkeria* exhibits a continuously convex lateral border in dorsal view (Ewer, 1965: fig. 8A–C), which is not bifurcated. Accordingly, this character has been codified as (1) instead of (0) in *Euparkeria*.

Character 74: following the discussion carried out by Nesbitt *et al.* (2009a) of the proportions of the calcaneal tuber shaft of *Euparkeria*, in which they

described it as broader than tall, we changed the character state to (1) instead of (0).

GRACILISUCHUS

In the following review of the character states of the data matrix of Dilkes & Sues (2009), we only used the holotype of *Gracilisuchus* (PULR 08) and its referred specimen PVL 4597. The specimen MCZ 4116 was not included in the current review because we are not confident of its assignment to *Gracilisuchus*. In this regard, the specimen MCZ 4116 differs from the holotype of *Gracilisuchus* in the presence of an obtuse angle between the anterior and posterior processes of the postorbital, strong anterior development of the iliac preacetabular process, and ilium with downturned iliac blade.

Character 10: in the holotype of *Gracilisuchus* the presence of a postfrontal cannot be confidently determined (PULR 08). Thus the character state has been rescored as (?) instead of (0) in this taxon.

Character 14: in *Gracilisuchus* (PVL 4597) the anterior process of the jugal reaches the posteroventral margin of the internal antorbital fenestra. In this regard, this character state has been modified to (0) instead of (1).

Character 16: the dorsal margin of the antorbital fossa is extended along the ascending process of the maxilla and the anterior process of the lacrimal; thus it does not reach the frontal or postorbital (PVL 4612). Accordingly, the character state has been changed to (0) instead of (1).

Character 36: in the available specimens of *Gracilisuchus* (PULR 08, PVL 4597) this character cannot be confidently assessed. Thus, this character state was modified to (?) instead of (1).

Character 41: in *Gracilisuchus* the pterygoids contact each at their posterior end, but they diverge anteriorly at a low angle, resulting in an interpterygoid median opening (PULR 08). As a result, the character state has been changed to (1) instead of (0) in *Gracilisuchus*.

Character 47: in the holotype specimen of *Gracilisuchus* the centra of the mid-cervical vertebrae are longer than that of the mid-dorsals (PULR 08; Romer, 1972a). In this regard, this character state has been changed to (1) instead of (0).

Character 52: in the holotype of *Gracilisuchus* the entire dorsal series with their respective ribs is available. In this specimen the dorsal ribs are dichocapalous (PULR 08), resulting in a rescoring of the character state as (1) instead of (?).

Character 57: the available pectoral girdle materials of *Gracilisuchus* belong to the holotype (PULR 08), and in this specimen this condition cannot be confidently assessed. Accordingly, we have modified this character state to (?) instead of (1).

Character 62: in PVL 4597 the pubic tubercle is poorly developed on the lateral surface of the proximal end of the bone. As a result, this character state has been rescored as (1) instead of (?) in *Gracilisuchus*.

Character 64: in a recent review of the hindlimb anatomy of *Gracilisuchus*, the presence of a poorly developed fourth trochanter is described (Lecuona, 2007; A. Lecuona & J.B. Desojo, unpubl. data; PVL 4597) (*contra* Romer, 1972a). Accordingly, the character state has been changed to (0) instead of (1).

Character 82: *Gracilisuchus* exhibits a nonreduced first phalanx of digit V (Lecuona, 2007; PVL 4597). In this regard, this character has been rescored as (0) instead of (1).

Character 83: the available phalanx V-1 of *Gracilisuchus* is a nonreduced element suggesting the presence of more distal phalanges (PVL 4597). In this regard, the total length of the pedal digit V cannot be determined. Thus, the character state (?) has been introduced instead of (1).

CHANARESUCHUS

Character 4: in the holotype of *Chanaresuchus* the upper tooth row presents a sharp inflexion of its alveolar margin between the premaxilla and maxilla articulation, which results in a downturned ventral premaxillary margin (PULR 07). As a result the character state (1) has been rescored as (0).

Character 8: in *Chanaresuchus* a pair of aligned foramina is present between the lacrimal and the prefrontal (PULR 07). The character state (1) has been scored instead of (?).

Character 29: in *Chanaresuchus* PULR 07 an intertuberal crest is present on the parabasisphenoid plate. The character state (0) has therefore been introduced instead of (1).

Character 30: in *Chanaresuchus* the ventral surface of the parabasisphenoid lacks a semilunar depression (PULR 07). As a result, the character state (1) has been introduced instead of (0).

Character 37: in the holotype of *Chanaresuchus* the pair of vomerines lacks teeth. Accordingly, the character state has been rescored as (1) instead of (?).

Character 54: in the available materials of *Chanaresuchus* that we were able to examine, no interclavicle is preserved (PULR 07; PVL 6244). Thus, the character state (1) has been rescored as (?).

Character 57: in PVL 6244 a large notch is present in the anterior margin of the scapulocoracoid contact. Accordingly, the character state has been rescored as (1) instead of (0).

Character 80: in PVL 6244 the metatarsal is longer than 50% of the total tibial length. As a result, the character state (1) has been introduced instead of (0).

Character 83: if digit V of *Chanaresuchus* is absent (Dilkes & Sues, 2009), this character is not applicable for this taxon. Thus, the character state (-) has been introduced instead of (1).

ERYTHROSUCHUS

Character 8: in *Erythrosuchus* a foramen is present on the suture between the lacrimal and prefrontal, indicating the posterior opening of the nasolacrimal canal (Gower, 2003; BPI 5207). Accordingly, the character state has been rescored as (1) instead of (?).

Character 15: in *Erythrosuchus* the ventral process of the squamosal laterally overhangs the proximal end of the quadrate and quadratojugal (BPI 5207). Thus, the character state (1) has been introduced instead of (0).

Character 19: Gower (2003: 23) described that the relationship between the ectopterygoid and the maxilla cannot be assessed with the currently available specimens. Accordingly, we changed the scoring of this character from (1) to (?).

Character 64: following Hutchinson (2001) and personal observations of specimens of the basal archosauriform *Erythrosuchus*, we consider that the posterolateral trochanter situated close to the midshaft of the bone is homologous with the fourth trochanter of other archosauriforms, probable zone of attachment of the M. caudofemoralis longus (Hutchinson, 2001). This hypothesis is supported by the position of this structure on the femur, which resembles that of other archosauriforms and archosaurs, as well as the presence of another trochanter closer to the femoral head, of posterior position, which seems to be the minor trochanter and insertion area of the Mm. iliofemoralis (Hutchinson, 2001). Accordingly, the insertion areas of the Mm. caudofemoralis longus and iliofemoralis seem to be distinctly separated, with one of them constituting the fourth trochanter. This interpretation contrasts with that of Nesbitt *et al.* (2009a), who stated that such a structure was absent in *Erythrosuchus*. A third position is adopted by Gower (2003) who pointed out that there is no consensus that posterolateral trochanter actually represents a homologous structure with the fourth trochanter present in other archosauriforms such as *Euparkeria* (Ewer, 1965), *Chanaresuchus* (PVL 6244), and archosaurs (e.g. *Aetosauroides*, *Marasuchus*, *Parasuchus*, *Batrachotomus*; PVL; PVL; ISI R42; SMNS). Accordingly, we have scored the character state as (1) for this character (i.e. present), as it was also codified by Dilkes & Sues (2009).

PARASUCHUS

Character 29: in ISI R42 and ISI R43 the basal tubera of the basisphenoid are connected ventrally by a

transverse and well-developed parabasisphenoid plate. In consequence, the character state (1) has been rescored as (0) in *Parasuchus*.

Character 70: in ISI R43 the calcaneal tuber is almost laterally deflected, resulting in an angle smaller than 45°. Accordingly, the character state (1) has been rescored as (0) in *Parasuchus*.

STAGONOLEPIS

Character 15: in *Stagonolepis* the state (1) has been introduced instead of (0) because the main body and ventral process of the squamosal overhang laterally the proximal end of the quadrate and the ascending ramus of the quadratojugal, respectively (Walker, 1961).

Character 19: in *Stagonolepis* the state (1) has been introduced instead of (?) because in a new species of *Stagonolepis* from Poland (Sulej, 2010) the contact between the maxilla and the ectopterygoid is evident.

Character 25: in *Stagonolepis* the state (0) has been introduced instead of (?) because in a new species of *Stagonolepis* from Poland (Sulej, 2010) the external abducens foramen (VI) is on the ventral surface of the prootic.

Character 32: in *Stagonolepis* the medial margins of the exoccipitals do not contact each other; thus the basioccipital contributes to the floor of the foramen magnum (BMNH R4784). Accordingly, the state (0) has been introduced instead of (?) in this taxon.

Character 36: in *Stagonolepis* the maxillary tooth row extends further posteriorly than the dentary tooth row, and they are not subequal (Walker, 1961). In this regard, the state (1) has been introduced instead of (0) in this taxon.

Character 49: in *Stagonolepis* the distal end of the cervical neural spines does not exhibit a terminal transversal expansion (spine table; Walker, 1961). As a result, the state (0) has been coded instead of (?) in *Stagonolepis*.

Character 50: in *Stagonolepis* the distal end of the dorsal neural spines present a transversal expansion resulting in a well-developed spine table (Walker, 1961; BMNH R4784). Accordingly, we have introduced the state (1) instead of (?) for this character in *Stagonolepis*.

Character 68: in *Stagonolepis* the astragalocalcaneal canal is present (Walker, 1961). As a result, the character state (1) has been scored instead of (?).

QIANOSUCHUS

Character 2: the character scoring of this feature has been changed from (1) to (?), because we think that the condition of this trait cannot be confidently asserted with the currently available material of this taxon.

TURFANOSUCHUS

Character 27: the partially disarticulated condition of the skull of the holotype of *Turfanosuchus* prevents us from assessing confidently the position of the occipital condyle with respect to the craniomandibular joint. As result, we prefer to rescore this character as (?) instead of (0).

Character states modified from characters of the data matrix of Nesbitt *et al.* (2009a):

Character 108 (49 of Nesbitt *et al.*, 2009a): we rescored the character states of several of the terminals used in the data matrix following personal observations of the specimens and in some cases bibliographical data. Accordingly, the plesiomorphic condition of the character (i.e. metatarsal IV with nearly the same midshaft diameter as metatarsal III) is exhibited by *Prolacerta*, *Mesosuchus*, *Proterosuchus*, *Erythrosuchus*, *Stagonolepis*, *Marasuchus*, *Qianosuchus*, and *Vancleavea*. By contrast, a metatarsal IV with a mid-shaft diameter less than that of the metatarsal III is observed in *Euparkeria*, *Chanaresuchus*, *Parasuchus*, *Gracilisuchus*, *Scleromochlus*, and *Turfanosuchus*.

EUPARKERIA

Character 106 (45 of Nesbitt *et al.*, 2009a): in *Euparkeria* the presence of a posterior groove on the astragalus has been figured by Sereno (1991), and in consequence we codified this feature as present in this South African form [i.e. character state (1) instead of (0)].

MARASUCHUS

Character 105: in *Marasuchus* the anterior corner of the dorsolateral margin of the astragalus laterally exceeds the development of the posterior corner, a condition not represented by the two character states described by this character. As the condition present in *Marasuchus* is unique amongst the taxon sample of our data matrix, we decided not to modify the character of Nesbitt *et al.* (2009a) (i.e. adding a third character state) and consider the condition of *Marasuchus* as not applicable for this character.

PARASUCHUS

Character 100 (14 of Nesbitt *et al.*, 2009a): in *Parasuchus* the anterior and posterior corners of the dorsolateral margin of the astragalus are equally laterally developed, representing the plesiomorphic condition of the character proposed by Nesbitt *et al.* (2009a). Thus, the scoring of this character has been changed accordingly.

VANCLEAVEA

Character 100 (14 of Nesbitt *et al.*, 2009a): the posterior end of the squamosal of *Vancleavea* seems to exceed the posterior level of the quadrate head. Thus, we changed the character state to (1) instead of (0). Character scorings of the data matrix:

Mesosuchus
 0000010000010?000000000?00010000000000010
 0001010000000010000000000000000000000000
 0000000-?000000000000?000001001
Prolacerta
 0000000010[01]10?000000000000000000011100
 0010111010100000000000000000000000000000
 0000000000-000000000000?000001000
Proterosuchus
 1110000010100000010100?00100001?111100001
 11100?01000000000010000000000000000000?0
 0001?00-000000001000010000000001
Euparkeria
 12111011101010000111010111011000111100011
 111[01][01]001100110001011111100111000100
 110010010111100011001111111111011010001
Doswellia
 2?????????1111?0??1000111??101110?10??01?
 000110111011011??010001?????????????????
 ?100010121?111?1111?1?????1?1100
Erythrosuchus
 121110111010111001?10111110100111111?1111
 101000000011??01011111000110000000110010
 ?101111?001?001110111000001000000
Chanaresuchus
 12100111111100111010111?1000010111110011
 1001101001111??11011101100111000000110111-
 101011100?10011111111111111000000
Parasuchus
 13112011101110101101110111010101111111110
 1001101011111111011111101111111111110010
 01110111101100?111111111011101000
Stagonolepis
 13111011101110100110110101211100101111110
 100110?011?111111011111101112111111110010
 111111011?1001111111101001011110

Gracilisuchus

1311101?1?1010101111??????101?0?111??111
 100111100111????10111111001121111111100?0
 ?101?11000?100?111?1111101001111?
Scleromochlus
 131110??0??0??0??0??0??0??0??0??0??111
 100110??0?1?1??0?1111?1110??2??000?111101-
 001??-??0?1?????0?1?011?????0
Turfanosuchus
 1311101?101??101110101011??011??111??101?
 100??111??1??????111?11??11211000???????
 ?1?1111000??0?10??111??0101111110
Yonghesuchus
 1?111?0?????1??11??1??1??????111??01?
 100?????0??????????????????????????????
 ?????????????????11?1?????????????????
Marasuchus
 ??1????????????????01101?1?011??111?????
 ??111100?11????11111111011210000?111111
 -0?111?-?100?1????11-1101?????11
Qianosuchus
 1?11101?101?110011??0?????1?11??1111?111?
 1??111?001??1??10?11111?01?12111111100??
 ?101?1??00??0?111?111??00?1?111?
Tarjadia
 ?????????0111?????????1?????????????????
 ??????1?????????????????????????????????
 ?1??1??121?0?????????????????????????
Archeopelta
 ??????????????????0011??1?011?0?????????
 ???1?1?0??1?????01?111?????????????????
 ?1?001?1211111??????1?????????????1
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