



The osteology and relationships of *Vancleavea campi* (Reptilia: Archosauriformes)

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Vancleavea campi Long & Murry, 1995, from the Late Triassic of western North America, represents the latest surviving non-archosaurian archosauriform known to date. We present here a detailed comparative description based on a nearly complete, articulated skeleton from the *Coelophysis* Quarry in north-central New Mexico and other fragmentary specimens. The unique combination of morphological features of *Vancleavea* is unparalleled within Reptilia; it has four unique morphologies of imbricated osteoderms covering the entire body, a short, highly ossified skull, relatively small limbs and morphological features consistent with a semi-aquatic lifestyle. *Vancleavea* is placed in a rigorous phylogenetic analysis examining the relationships of non-archosaurian archosauriforms, and is found to be more closely related to Archosauria than both *Erythrosuchus* and *Proterosuchus*, but outside of the crown group. The analysis confirms previously hypothesized relationships, which found *Euparkeria* to be the closest sister taxon of Archosauria. It is not clear whether specimens referred to *Vancleavea campi* represent a single species-level taxon or a clade of closely related taxa that lived through much of the Late Triassic of North America, given the poor fossil record of the taxon.

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INTRODUCTION

Despite a long history of studies of archosaurian reptiles, the interrelationships of their closest relatives, the non-archosaurian archosauriforms, remain poorly understood. Incomplete specimens, the absence of detailed descriptions coupled with illustrations, problematic taxonomy and geographic isolation of much of the early archosauriform material have pre-

vented more complete phylogenetic analyses from being conducted (Gower & Sennikov, 1996, 2000; Gower & Wilkinson, 1996). Only a few non-archosaurian archosauriform taxa are known from rather complete and well-described material (e.g. *Euparkeria capensis*, *Erythrosuchus africanus*, *Proterosuchus fergusi*, *Tropidosuchus romeri*), and the relationships among these are controversial (Gauthier, 1984; Sereno, 1991; Juul, 1994) or untested. In addition, fragmentary, although important, non-archosaurian archosauriform taxa, such as those from the Triassic of Russia and China, have largely been ignored (Gower & Sennikov, 1996). However, a plethora of recent descriptions of

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either new (e.g. Arcucci, 1990; Borsuk-Bialynicka & Evans, 2003) or previously known (e.g. Gower, 1996, 1997, 2003; Gower & Sennikov, 1996, 1997; Welman, 1998) non-archosaurian archosauriform taxa has allowed comparisons with other fragmentary Triassic archosauriforms.

Long & Murry (1995) named and described *Vancleavea campi* from a fragmentary, but well-preserved, partial skeleton from the Blue Mesa Member of the Chinle Formation in the Petrified Forest National Park, collected as float by Philip Vancleave, park naturalist. This taxon, described only from postcrania, has proven to be abundant, easily recognized and geographically widespread through the Late Triassic of the southwestern USA (Hunt *et al.*, 2002; Hunt, Lucas & Spielmann, 2005). Recently, *V. campi* was identified as an archosauriform (Small & Downs, 2002) based on new material that is fully described here. We focus on a complete articulated skeleton (GR 138) and an associated disarticulated specimen (GR 139) from the Ghost Ranch *Coelophysis* Quarry referred to *Vancleavea*. We also test this taxon's phylogenetic position within Archosauriformes.

INSTITUTIONAL ABBREVIATIONS

AMNH FR, American Museum of Natural History, New York, NY, USA; BMNH R, Natural History Museum, London, UK; BP, Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa; BSP, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Germany; CM, Carnegie Museum of Natural History, Pittsburg, PA, USA; GR, Ruth Hall Museum of Paleontology at Ghost Ranch, NM, USA; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA; MNA, Museum of Northern Arizona, Flagstaff, AZ, USA; NMC, National Museum, Bloemfontein, South Africa; PEFO, Petrified Forest National Park, AZ, USA; PVL, Instituto Miguel Lillo, Tucuman, Argentina; PVSJ, Division of Paleontology of the Museo de Ciencias Naturales de la Universidad Nacional de San Juan, Argentina; RC, Rubidge collection, Wellwood, Graaff-Reinet, South Africa; SAM, South African Museum, Cape Town, South Africa; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; TM, Transvaal Museum, Pretoria, South Africa; TTU-P, Texas Tech University Museum, Lubbock, TX, USA; UCMP, University of California Museum of Paleontology, Berkeley, CA, USA; UFRGS, Institute of Geosciences, Federal University of Rio Grande de Sul, Brazil; UMMP, University of Michigan Museum of Paleontology, Ann Arbor, MI, USA; UMZC, Museum of Zoology,

Cambridge University, Cambridge, UK; UNC, University of North Carolina, Chapel Hill, NC, USA; UPLR, Museo de Paleontología, Universidad Nacional de La Rioja, Argentina; USNM, National Museum of Natural History, Washington DC, USA.

ANATOMICAL ABBREVIATIONS USED IN FIGURES

a., articulates with; acr, acromion process; an, angular; ar, articular; as, astragalus; bmf, base of the mitotic foramen; bo, basioccipital; bt, basitubera; ca, calcaneum; car, carpal; cfa, *M. caudifemoralis* attachment; ctf, cristatibiofibularis; cv, cervical vertebra; d, dentary; dc, dentary caniniform tooth; di, diapophysis; do, dorsal osteoderm; dp, deltopectoral crest; epi, epiphysis; ex, exoccipital; fe, femur; fi, fibula; g, groove; gl, glenoid; h, humerus; hs, heeled scars; il, ilium; j, jugal; k, keel; l., left; lc, lateral condyle; ltf, lateral temporal fenestra; lr, lagenar recess; ls, laterosphenoid; mc, metacarpal; mec, medial condyle; mt, metatarsal; mx, maxilla; mxc, maxillary caniniform tooth; n, nasal; na, external naris; nan, non-articular notch; nc, neural canal; ncs, neurocentral suture; neo, neomorph bone; np, notochordal pit; ns, neural spine; o, orbit; oc, occipital condyle; op, opisthotic; os, osteoderms; p, parietal; pa, phalanx; par, paroccipital process of the opisthotic; pb, parabasisphenoid; pmc, premaxillary caniniform tooth; pmx, premaxilla; po, postorbital; poz, postzygapophysis; pp, parapophysis; pr, prootic; pre, prezygapophysis; prf, prefrontal; pt, pterygoid; ptf, post-temporal fenestra; qj, quadratojugal; qu, quadrate; r, ridge; r., right; ra, radius; so, supraoccipital; sp, splenial; sq, squamosal; sr, sacral rib; su, surangular; sv, sacral vertebra; sy, symphysis; t, tooth; t4, tarsal 4; ti, tibia; tu, tuber; ul, ulna; V, cranial nerve five; XII, cranial nerve twelve.

SYSTEMATIC PALAEOONTOLOGY

ARCHOSAUMORPHA HUENE, 1946 SENSU BENTON, 1985

ARCHOSAURIFORMES GAUTHIER, KLUGE, AND ROWE, 1988

VANCLEAVEA CAMPI LONG AND MURRY, 1995

Holotype: PEFO 2427, an incomplete postcranial skeleton.

Referred specimens: GR 138, GR 139. See Appendix 1.

Type horizon and locality: PFV 124, Blue Mesa Member (Early ?Norian), Chinle Formation, Petrified Forest National Park, Apache County, AZ, USA.

Revised diagnosis: *Vancleavea* differs from all basal archosauriforms in the absence of upper temporal and antorbital fenestrae and lacrimal. Autapomorphies include large caniniform, and recurved and serrated teeth in each tooth bearing bone, a well-defined depression on the lateral surface of the dentary for the maxillary caniniform tooth, the presence of a neomorph bone separating the nasals, the absence of a lacrimal, ilium lacking an anterior process and bearing a highly reduced posterior process, the exoccipitals do not participate in the formation of the occipital condyle, dorsal centra with two paramedian ventral keels and neural spines with dorsal notches at the anterior and posterior ends. In addition, *Vancleavea* has five unique osteoderm morphologies: teardrop-shaped ventral cervical region osteoderms, diamond-shaped osteoderms with midline keels on the ventral portion of the body, diamond-shaped osteoderms with a pointed anterior process on the lateral sides of the dorsal and caudal regions of the body, thin, mediolaterally compressed appendicular osteoderms, and large, vertically projecting, laterally compressed osteoderms dorsal to the neural spines of the caudal vertebrae.

Comments: Long & Murry (1995) initially classified *Vancleavea* as a neodiapsid of unknown affinities based on the fragmentary holotype. Their diagnosis of the taxon as possessing ‘primitive girdle and appendicular elements presumably indicating a sprawling grade of locomotion’ did not include specific diagnosable character states of those elements. However, Long & Murry (1995) listed the following three morphotypes of osteoderms: (1) tall, triangular (‘stegosaur-like’) plates; (2) low-keeled (‘ankylosaur-like’) plates; and (3) conical (‘stegosaur-like’) spikes. Morphotypes (1) and (2) occur in GR 138. In contrast, morphotype (3) does not occur in GR 138, and it is not clear to which element this ‘conical (‘stegosaur-like’) osteoderm’ fragment pertains (see below).

Although not listed by Long & Murry (1995), the holotype (PEFO 2427) bears the following two autapomorphies: (1) dorsal vertebrae with two paramedian keels on the dorsal centra; and (2) a femoral head without distinct neck or tubera. These two character states, combined with osteoderm morphotypes (1) and (2), clearly diagnose the holotype, and allow the referral of GR 138 to *V. campi*. GR 138 is approximately 73% the size of the holotype (proximal humerus maximum width: GR 138, ~14 mm; PEFO 2427, ~19 mm).

TAPHONOMY AND OCCURRENCE

The two skeletons of *Vancleavea* (GR 138, 139) are from the Ghost Ranch *Coelophysis* Quarry in the

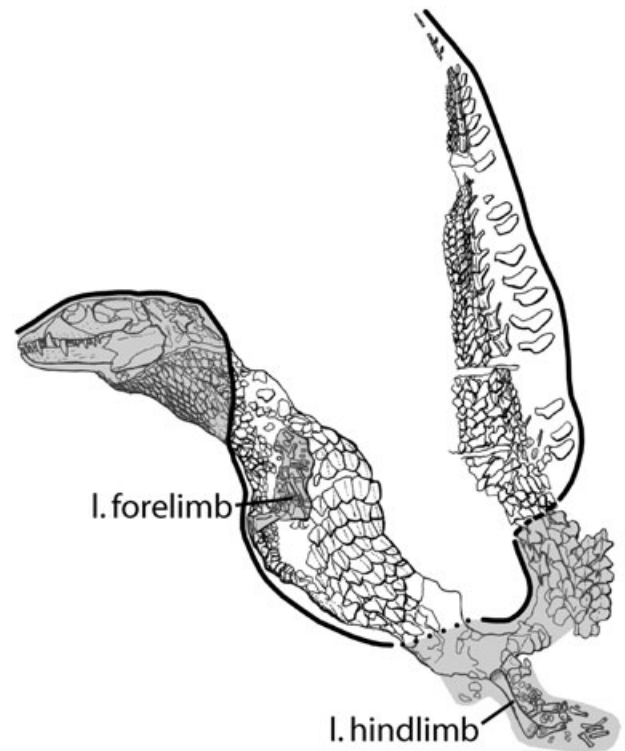


Figure 1. The crushed, twisted skeleton of *Vancleavea campi* (GR 138). The dark line traces the dorsal margin. The grey colour indicates the left side of the skeleton, and the white areas indicate the right side. The left forelimb has been flipped over from the left side to the right side.

Upper Triassic Chinle Formation of northern New Mexico. The quarry is famous for the numerous, well-preserved skeletons of the early theropod dinosaur *Coelophysis bauri*. However, together with numerous *Coelophysis*, workers have recognized an increasing diversity of vertebrates, including ‘fishes’ (Schaeffer, 1967), phytosaurs (Hunt & Lucas, 1989a, b, 1993), early crocodylomorphs (Clark, Sues & Berman, 2000), ‘rauisuchians’ (Long & Murry, 1995), *Effigia okeeffeae* (Nesbitt & Norell, 2006; Nesbitt, 2007), drepanosaurs (Harris & Downs, 2002), other small vertebrates and *Vancleavea*.

GR 138 is a nearly complete, articulated skeleton exposed laterally. The skeleton became twisted during fossilization (Fig. 1). Specifically, the head, anterior portion of the neck and pelvic region lie on the right side, exposing the left lateral side, whereas the dorsal section and tail lie on the left side, exposing the right lateral side. As a result, the ventral trunk osteoderms and tail are ‘upside down’ relative to the head and neck. In addition, the left forelimb lies on the right side of the dorsal section. The distal elements of both the fore- and hindlimbs are slightly disarticulated, as are some of the body osteoderms. However, it is not

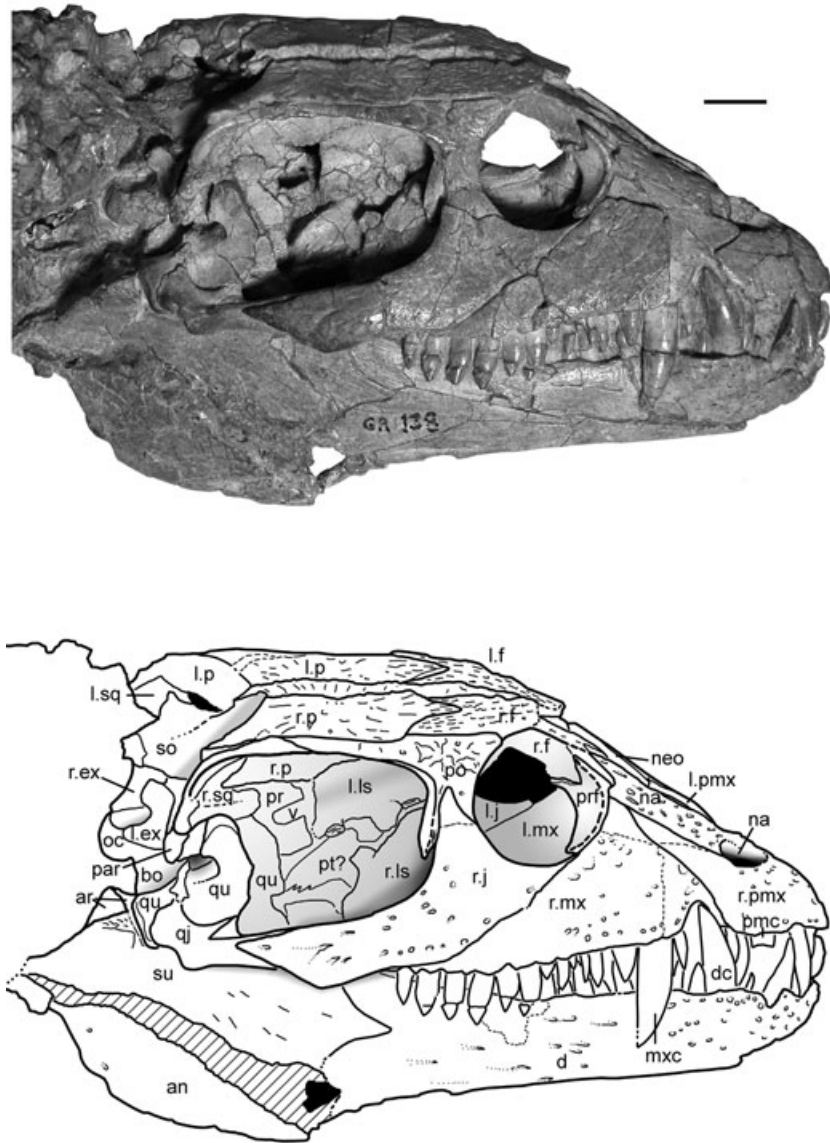


Figure 2. Right lateral view of the skull of *Vanckleavea campi* (GR 138). Scale bar, 1 cm.

clear whether the many scattered disarticulated osteoderms are from GR 138 or the completely disarticulated GR 139 located directly below GR 138 in the excavated block. The osteoderm carapace hides the pectoral girdle and many of the vertebrae and ribs in the cervical and dorsal regions.

Fine details, such as sculpturing and foramina, are visible on the surface of the exquisitely preserved GR 138. Lateral compression has deformed the skull and skeleton, as with most vertebrate remains from the *Coelophysis* Quarry (S. J. Nesbitt, pers. observ.). There is a slight displacement of some of the bones along their sutures.

PEFO 2427 was collected as float over many years by Petrified Forest National Park naturalist Philip

Vanckleave (Long & Murry, 1995). The excellent preservation allows careful comparisons among GR 138, GR 139 and PEFO 33978. PEFO 33978 was found as a mostly disarticulated skeleton in a set of carbonate concretions. The skeleton was then acid prepared to expose very fine details, especially of the osteoderms.

DESCRIPTION

SKULL

The skull (GR 138) preserves all cranial bones in articulation (Figs 2–7). However, some of the cranial bones have separated slightly along their sutures, allowing examination of the cranial element articula-

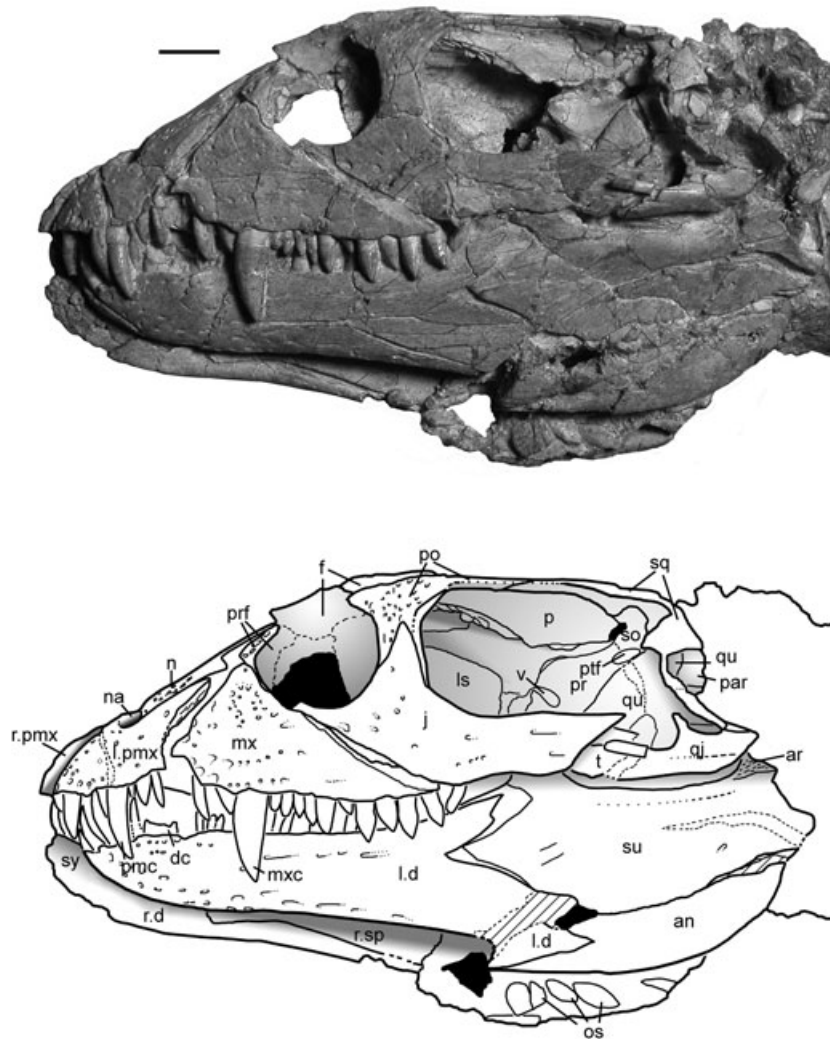


Figure 3. Left lateral view of the skull of *Vanclavea campi* (GR 138). Scale bar, 1 cm.

tions. For example, both angulars are displaced ventrally, and the left side of the skull has deflected posteriorly along the midline. Most of the braincase, palate and medial elements of the mandible are obscured by overlying bones.

The skull of *Vanclavea* (GR 138) (Figs 2, 3) lacks an antorbital and supratemporal fenestra. The lateral temporal fenestra is approximately one-third the total length of the skull (anteroposterior length, 32 mm). The nearly round orbit (diameter, 17.5 mm) lies in the anterior half of the skull. The skull table is flat with an anteroventrally sloping forehead. Originally, GR 138 was described as lacking a mandibular fenestra (Small & Downs, 2002). However, a closer inspection revealed that a small fenestra could be present. Nevertheless, whether or not a small fenestra is present, the mandibular fenestra is secondarily reduced. Here, we score the presence/

absence of the feature as unknown. A small mandibular fenestra is present in *Proterosuchus* (QR 1484; RC 96; Welman, 1998).

The secondary loss of the supratemporal fenestra (see phylogenetic hypothesis below) requires unorthodox articulations among the parietal, postorbital and squamosal. The lateral side of the parietal is usually the medial side of the supratemporal fenestra, but it now contacts the postorbital and the squamosal in an anteroposteriorly straight suture. The ventral portion of the parietal, which holds the upper temporal musculature in other taxa, now possibly holds the dorsal portion of the lower temporal musculature.

Premaxilla (Figs 2, 3, 6)

The premaxillae lie in articulation with the maxillae, but distortion of the skull has displaced the premaxillae along the midline suture. The premaxilla bears

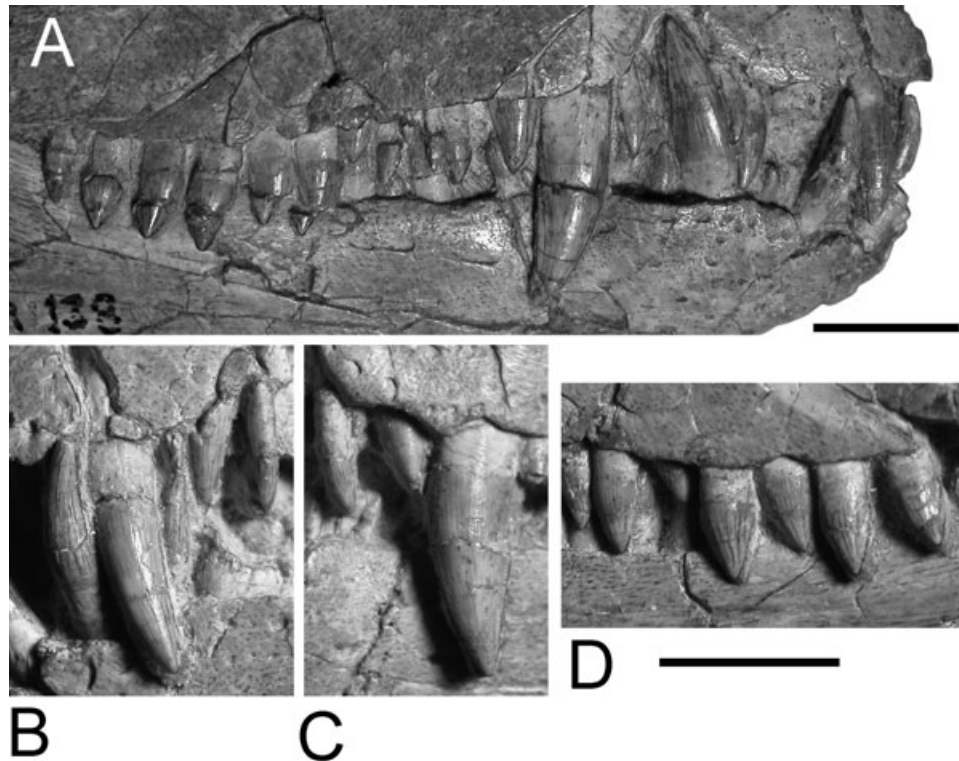


Figure 4. Dentition of *Vanclavea campi* (GR 138). The dentition from the right side of the skull (A), and close-ups of the premaxillary caniniform tooth (B), the maxillary caniniform tooth (C) and the posteriormost teeth of the maxilla (D) of the left side. Scale bars, 1 cm.

anterodorsal and posterodorsal processes. The anterodorsal process is mediolaterally thin, anteroposteriorly long and arcs posteriorly to separate the external nares and much of the nasals. The thin anterodorsal processes meet the anterior portion of the neomorph bone. Together, the anterodorsal processes form a narrow septum separating the right and left dorsally oriented external nares.

The posterodorsally projecting process is long and gradually tapers to a point. This process originates between the base of the caniniform tooth and the opening of the external naris, and it separates the anterior portion of the maxilla from the nasal. The ventral portion of the posterodorsal process has a small groove in which the dorsal portion of the maxilla attaches. The posterodorsal process is very similar to that of *Erythrosuchus* (BPI 4526; Gower, 2003) and *Shansisuchus* (IVPP specimen unnumbered; Young, 1964). Both share a similar posterodorsal angle and proportional length. However, the posterodorsal process of *Erythrosuchus* (NMC 1473) fits into a slot of the nasal, whereas the posterodorsal process of *Vanclavea* lies between the nasal and the maxilla. In comparison with *Vanclavea*, *Euparkeria* (SAM 5867) has a dorsally projecting and short pos-

terodorsal process, whereas *Proterosuchus* (BSP 514) has a posteriorly directed process.

Sculpturing is not present on the ventral portion of the body of the premaxilla, whereas small, randomly scattered nutrient foramina are present on the anterior portion of the body. The dorsal border of the body forms the lateral side of the external naris and is concave in lateral and dorsal views. The posterior border forms the anterior edge of a diastema that fits a large caniniform tooth of the dentary. The premaxillae have extensive contact along the midline and, together, they form a narrow snout that would not exceed 1.5 cm in width.

Five teeth are present in the premaxilla (Fig. 4A, B) in *Vanclavea*, whereas early archosauriforms vary in the number of premaxillary teeth: *Erythrosuchus* (BP/1/5207) has five, *Proterosuchus* (BSP 514) has seven, *Euparkeria* (SAM 5867) has three, the proterochampsid *Chanaresuchus* (UPLR 7) has at least four and *Tropidosuchus* (PVL 4601) has at least four. In *Vanclavea*, the first premaxilla tooth is the smallest, and the third tooth is a caniniform tooth comparable in size with the caniniform teeth found in the maxilla and dentary. The anteriormost teeth are round in cross-section, lack serrations and bear long roots.

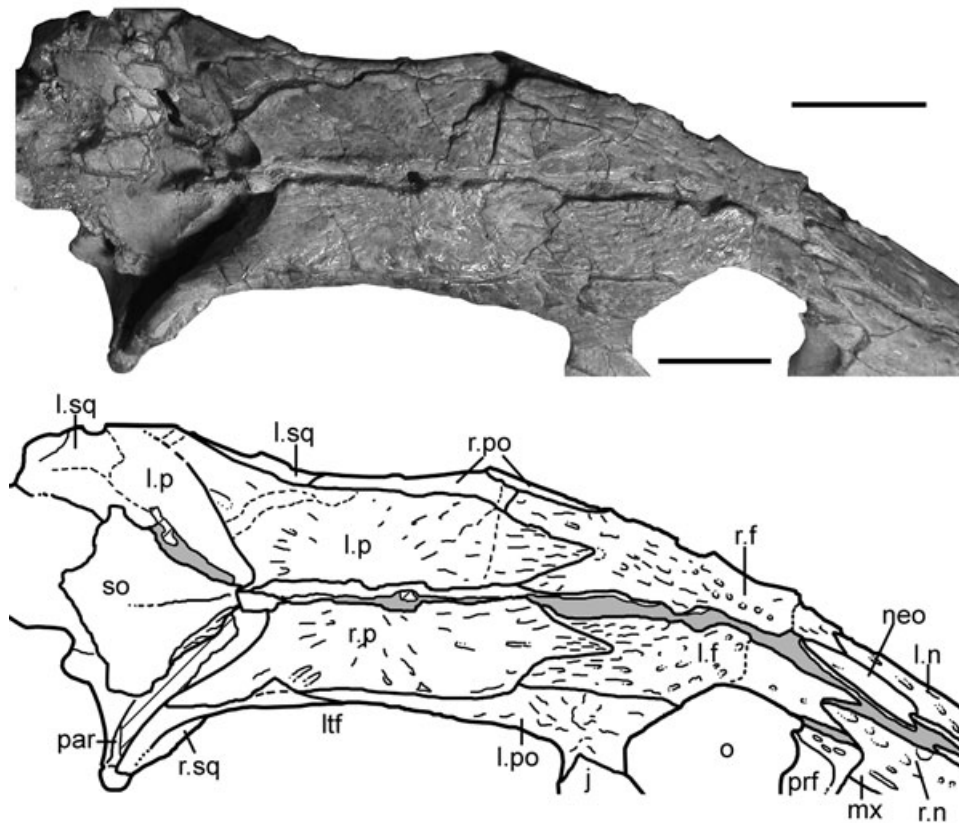


Figure 5. Dorsal view of the skull of *Vanclleavea campi* (GR 138). Scale bar, 1 cm.

Maxilla (Figs 2, 3)

The body of the maxilla is dorsoventrally tall, and the overall shape is triangular. The prefrontal and jugal exclude the maxilla from the orbit. As a consequence of the absence of an antorbital fenestra, there is no clear dorsal process similar to that seen in other archosauriforms with antorbital fenestrae. The dorsal portion fits between the prefrontal, the nasal and the posterodorsal process of the premaxilla. The anterodorsal portion is straight and slopes anteroventrally, where it meets the posterodorsal process of the premaxilla. The posterodorsal border of the body is straight, slopes posteroventrally and is slightly overlapped laterally by the jugal. The posterior extent is completely overlapped laterally by the jugal, and only the ventralmost margin and posterior teeth are visible in lateral view. Small nutrient foramina parallel the tooth row, and smaller foramina cover the maxilla.

GR 139 includes a maxilla and premaxilla articulated in ventral view. Interdental plates are clearly present. The alveoli are round. A small anteriorly directed palatal process lies on the medial side of the maxilla that articulates with the premaxilla; this is a

feature present in *Erythrosuchus* + Archosauria (see character discussion below).

A diastema for the large fourth dentary tooth lies between the anteroventral border of the maxilla and the premaxilla (Fig. 4A, B). A small amount of wear on the lateral surface of the maxilla is present where the large caniniform tooth of the dentary contacts the maxilla. Thirteen teeth are present in each maxilla. The size and shape of the teeth in the maxillae are variable along the tooth row, but consistent in both maxillae. Starting anteriorly, there is one small tooth anterior to the caniniform tooth, a large caniniform tooth, four very small bulbous teeth, six anteroposteriorly symmetrical teeth and one small tooth that make up the dentition of the maxilla. The caniniform tooth is mediolaterally compressed, posteriorly recurved at the tip and bears serrations on both the anterior and posterior edges. Replacement caniniform teeth are present in both the left and right maxillae. Strikingly, the replacement caniniform tooth is posterior to the fully erupted caniniform in the right maxilla, whereas the replacement caniniform tooth is anterior to the fully erupted caniniform in the left maxilla. The small tooth anterior to the caniniform

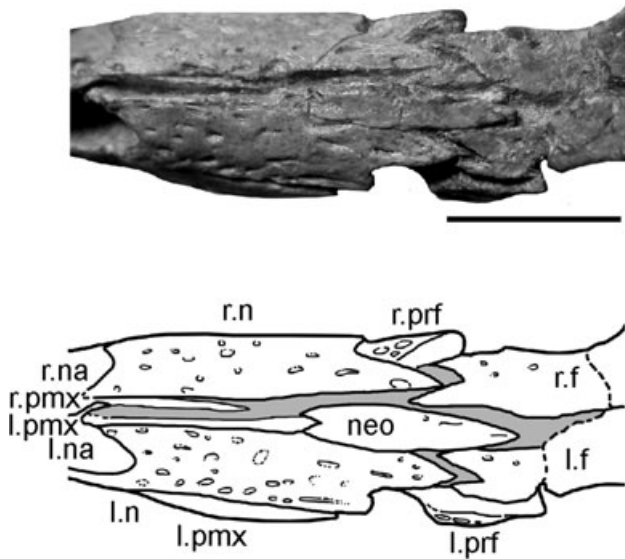


Figure 6. Anterodorsal view of the nasal region of *Vanckleavea campi* (GR 138). The anterodorsal processes of the premaxillae and the unpaired neomorphic bone prevent the nasals from contacting at the midline. Grey area indicates matrix. Scale bar, 1 cm.

tooth is rounded in cross-section and posteriorly recurved at the tip. The teeth posterior to the canini-form teeth are spade-shaped, with crowns that are slightly expanded relative to the roots. The teeth in the posterior portion of the maxilla are all approximately the same size and are larger than the group of teeth just anterior to them. These teeth are very similar to the posterior maxillary teeth of phytosaurs and could be easily mistaken for small phytosaur teeth if found isolated.

Nasal (Figs 2, 3, 5, 6)

The nasal is covered in small, randomly scattered foramina. The nasal is only exposed on the dorsal surface of the skull, and this suggests that the anterior portion of the skull in life was no more than 1 cm wide (both nasals combined) at the dorsal margin. The nasals are completely separated along the midline by a neomorphic bone posteriorly and the thin anterior premaxillary processes anteriorly; this feature is unique among known archosauriforms. A notch at the anterior edge forms the posterior border of the external naris. The external naris is rectangular, and the lateral edge is bordered anteriorly by the posterodorsal process of the premaxilla and by a small piece of the dorsal process of the maxilla posteriorly. Posteriorly, a posterior process of the nasal divides the anterior portion of the frontal into two small anterior processes. The

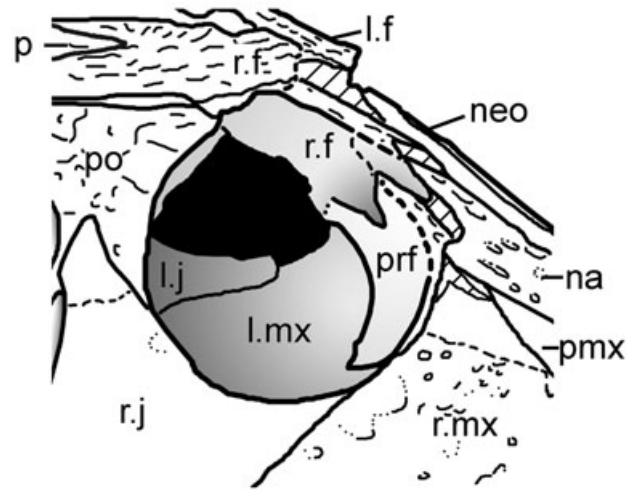
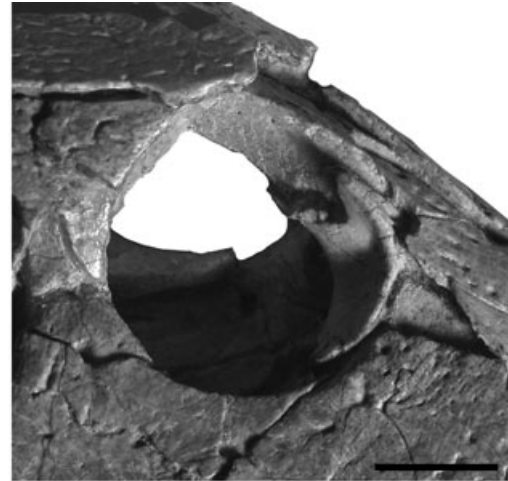


Figure 7. Close-up of the right orbital region of *Vanckleavea campi* (GR 138). A lacrimal and postfrontal are not present in the skull of *Vanckleavea*. Scale bar, 1 cm.

posterolateral edge has a small notch in the nasal that fits the dorsal expression of the prefrontal. The neomorphic bone fits into a small notch near the midline of the nasal.

Neomorphic bone (Figs 2, 5, 6)

An unpaired neomorphic bone divides the posterior portions of the nasals and divides the anterior portions of the frontals at its posterior extent. The anterior and posterior ends terminate in a point. The neomorphic element contacts the anterodorsal process of the premaxilla anteriorly.

Jugal (Figs 2, 3, 7)

Both the left and right jugals are well preserved and in near articulation. The jugal borders the ventral

and posteroventral portion of the orbit. The flat body is covered with randomly scattered foramina. The anterodorsally sloping anterior edge laterally overlaps the posterodorsal border of the maxilla. The anterodorsal portion tapers gradually and touches the posterior extent of the prefrontal. The tapering anterior portion of the jugal resembles that of archosauriforms, such as *Mesosuchus* (SAM 6536) and *Prolacerta* (BP/1/471), which lack antorbital fenestrae. The jugal has a long posterior process that is rectangular. The ventral edge slopes posterodorsally to meet the dorsal margin at the posterior extent of the element. It appears to laterally and dorsally overlap the quadratojugal, but this is not clear because of slight displacement of the bones. The lateral surface of the posterior process is slightly convex.

The well-defined dorsal process tapers to a point dorsally and fits into a slot in the postorbital. This essentially divides the ventral process of the postorbital into two smaller processes. This articulation between the two elements is unique among early archosauriforms and is an autapomorphy for *Vancleavea*.

Prefrontal (Figs 2, 3, 7)

The ossification forming the anterior portion of the orbit is here interpreted as a prefrontal and not a lacrimal. It appears that the lacrimal is not present in the skull of *Vancleavea*. The presence of a prefrontal and the absence or reduction of a lacrimal, although rare, occur in crocodyliforms that have secondarily lost the antorbital fenestra (e.g. *Mariliasuchus*; Zaher *et al.*, 2006). A lacrimal canal is not present, and the authors are unaware of any lacrimal in Archosauriformes that expands medially as much as the element in the anterior portion of the orbit.

The prefrontal is a mediolaterally thick bone that only forms a thin anterior border of the orbit. The thickened mediolateral portion bears a large orbital fossa continued from the frontals. The ventral process contacts the maxilla and the anterodorsalmost portion of the jugal. There is no clear facet for the contact between the prefrontal and the jugal.

The dorsal portion of the prefrontal is bisected by a small, anteriorly projecting process of the frontal. The more dorsal branch fits into a notch on the posterior portion of the nasal. The small dorsolateral surface has a similar texture to the nasal, with small fossae and foramina present.

Postorbital (Figs 2, 3, 5, 7)

Small foramina and short anteroposteriorly trending grooves cover the robust postorbital. Anteriorly, the postorbital contacts the frontal to form the postero-

dorsal portion of the orbit. The suture between the two elements is rather dorsoventrally thick. It is clear that there is no postfrontal separating the postorbital from the frontal. The dorsal process of the jugal bisects the ventral process of the postorbital. A slight displacement of this contact suggests that the dorsal process of the jugal sits in a distinct groove on the lateral side of the ventral process of the postorbital. The anterior portion of the divided ventral process is thin and does not continue as far ventrally as the posterior process of the ventral portion.

The thin, gently rounded posterior process overlaps the dorsal surface of the squamosal. This is unique among early archosauriforms; these taxa and most archosaurs have a tapering posterior process of the postorbital that fits into a slot of the squamosal (S. J. Nesbitt, pers. observ.). The posterior process contacts the frontal anteriorly and the parietal posteriorly. The suture between these elements is parallel to the dorsal margin of the lateral temporal fenestra.

Frontal (Figs 2, 3, 5–7)

The frontals are well preserved, separated along the midline and slightly shifted ventrally at their broken anterior ends. A posterior process of the nasal divides the anterior portion of the frontal just dorsomedial to the articulation with the prefrontal. A similar condition is found in *Shansisuchus* (IVPP V2503; Young, 1964). The posterior portion of the neomorphic bone divides the anterior portion of the left and right frontals at the midline.

The frontal forms the dorsal border of the orbit. Here, the frontal is medially waisted in dorsal view and ventrally expanded to form the inside of the orbital margin. The midline suture is dorsoventrally thick, similar to the parietals. The sculpturing, similar to that of the nasals, is rough with small grooves and a few randomly scattered foramina.

A tapering anterior process of the parietal penetrates the posterior portion of the frontal. This differs from the interdigitating and mediodorsally oriented suture in *Proterosuchus* (BSP 514), *Erythrosuchus* (BPI 5207) and proterochampsids. In *Euparkeria*, a small anterior process of the parietal invades the frontal, but it is at the midline (SAM 5867; Ewer, 1965). The lateral edges of the frontal are bordered by the postorbital for most of its length. There appears to be no distinct postfrontal, although it is difficult to see because of small cracks and slight displacements of the frontal and surrounding bones.

Parietal (Figs 2, 3, 5, 8A–C)

The parietals make up much of the skull roof and, with the frontals, create a flat skull table. Anteriorly,

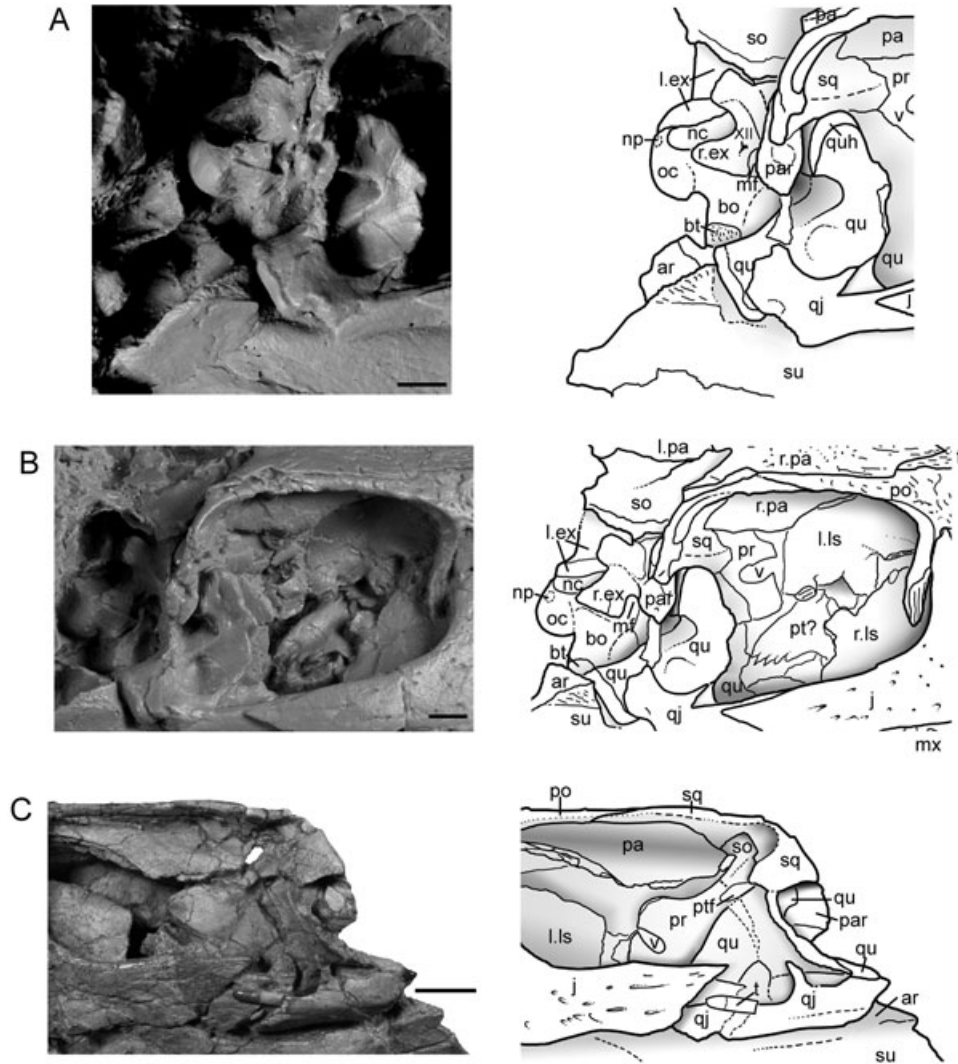


Figure 8. Close-ups of the right lateral view (A) of the braincase of *Vanckleavea campi* (GR 138), the right lower temporal region (B) and the left lower temporal region (C). Scale bar, 1 cm.

the parietal has a small tongue that fits into a slot in the frontal. The tongue reaches the postorbital bar at its anterior extent. The left and right elements are separated along the midline suture. The parietal has a pattern of radiating grooves originating from the middle and centre of the element. A small posteriorly projecting keel is present at the midline of the posterior portion of the elements. There is no separate postparietal in *Vanckleavea* as there is in *Proterosuchus* (QR 1484), *Erythrosuchus* (BP/1/5207) and *Euparkeria* (SAM 5867). The lateral side is bordered by the postorbital and the anterior part of the squamosal. The posterior margin bears a smooth fossa that continues on the supraoccipital for the temporal musculature. *Euparkeria* (SAM 5867) has a similar

shelf on the posterodorsal portion of the skull (Ewer, 1965).

A posterolateral process of the parietal tapers posteriorly dorsal to the squamosal. The posterior side of the process contacts the dorsal portion of the paroccipital process. A large post-temporal fenestra is present in *Vanckleavea* (Fig. 8C). The ventral portions of the parietals are exposed in lateral view (Figs 2, 3, 8) within the lateral temporal fenestra. The ventral process stretches from the squamosal contact to just ventromedial to the dorsal portion of the postorbital bar. The ventral margin bears two distinct facets for articulation along its length: a posterior facet for contact with the parietal and an anterior facet for contact with the laterosphenoid. A large fossa is

present along the entire length of the ventral portion of the parietal.

Squamosal (Figs 2, 3, 5, 8A–C)

The squamosal is partially preserved on the right side and more completely preserved, but distorted, on the left. The slender anterior process is dorsally overlapped by the posterior process of the postorbital where the two meet. The laterally thin body of the squamosal arcs ventrally while trending posteriorly. The posterolateral process of the parietal dorsally borders the squamosal as it arcs ventrally. The anterior side of the posterior part of the squamosal creates a smooth posterior pocket that is continuous with the large fossa on the ventral portion of the parietal. The squamosal broadens ventrally just dorsal to the articulation with the head of the quadrate and covers the head of the quadrate in lateral view. There is no posterior process posterior to the articulation of the quadrate in *Vancleavea* as well as the proterochampsids, *Euparkeria* and Archosauria (see character 14).

The articulation with the paroccipital process lies on the posteroventral corner of the body of the squamosal. It is not clear whether this contact represents real morphology, distortion or disarticulation, yet the articulation is similar on both sides. A small, anteroposteriorly thin ventral process protrudes ventrally at the anterior edge of the broad hood. This process lies on the lateral edge of the quadrate. The ventral process of the squamosal meets the dorsal process of the quadratojugal approximately halfway down the lateral temporal fenestra to create the posterior lateral temporal fenestra bar. A thin post lower temporal bar is also present in *Euparkeria* (SAM 5867) and many archosaurs.

Quadratojugal (Figs 2, 3, 8A–C)

Both quadratojugals are present, but distortion has made interpretation difficult. The quadratojugal articulates with the ventrolateral side of the quadrate. Here, the bone is anteroposteriorly flat. Anteriorly, the jugal lies on the lateral surface of the quadratojugal. The quadratojugal dorsoventrally increases in height where it meets the jugal, but details of the articulation between the two elements remain unclear. The same articulation in other archosauriforms is highly variable: in *Erythrosuchus*, the jugal fits into a slot of the quadratojugal (Gower, 2003); in *Proterosuchus*, an anterior process of the quadratojugal fits into the jugal (Cruickshank, 1972); and the jugal dorsally overlaps the quadratojugal in proterochampsids (PVL 4576, PVL 4604) and *Euparkeria* (Ewer, 1965). A posterodorsal process originates on the dorsoventral portion and is firmly attached to

the quadrate. An anterodorsal process originates in the middle of the quadratojugal body, thins dorsally, arcs anteriorly and meets the ventral process of the squamosal. The anterodorsal and posterodorsal processes are separated by a U-shaped recess on the dorsal border of the quadratojugal. The quadratojugal of *Vancleavea* differs in this respect from nearly all other archosauriforms.

Quadrate (Figs 2, 3, 8A–C)

Both quadrates are well preserved. The left quadrate is in normal articulation, whereas the right has been rotated laterally at the level of the dorsal head. The quadrate is short, measuring about two-thirds the height of the lateral temporal fenestra. The short height seems to be autapomorphic among early archosauriforms. The body of the quadrate arches anteriorly, and the anterior edge thins laterally where it contacts either the dorsal process of the quadratojugal or the thin ventral process of the squamosal. The body of the quadrate is relatively straight in *Proterosuchus*, *Erythrosuchus* (BMNH R3592; Gower, 2003), *Euparkeria* (SAM 5867; Ewer, 1965), proterochampsids such as *Chanaresuchus* (PVL 4575) and *Tropidosuchus* (PVL 4601), and Archosauria. Therefore, the strong anterior arching of the quadrate of *Vancleavea* is unique among the clade. The condyles that articulate with the articular are simply convex and measure 1 cm mediolaterally. The quadratojugal lies on the ventrolateral surface just anterior to the lateral extent of the articular condyle. There is no indication of any kind of quadrate foramen as there is in *Euparkeria* (Ewer, 1965), *Proterosuchus* (Cruickshank, 1972) and Archosauria (e.g. *Herrerasaurus*; Sereno & Novas, 1994; *Batrachotomus*; Gower, 1999). A blind pit is present on the body of the quadrate of *Vancleavea* on the lateral surface (dorsolateral when corrected for distortion) just anterior to the articulation with the quadratojugal. A similar feature was described by Gower (2003) for *Erythrosuchus* (BP/1/4680). The fossa deepens dorsally and is separated by a ridge of bone from the posterodorsal border of the quadrate in *Vancleavea*.

A deep notch lies between the dorsal border of the large fossa and the proximal quadrate head. This strong notch is not present in any other archosauriform. The proximal articular end is anteriorly directed, rounded and convex. Other bones obscure the pterygoid–quadrate articulation.

Palatal elements

Portions of the pterygoids are visible in the right lateral temporal fenestra, but no morphological details can be described. It is unclear whether *Vancleavea* had palatal teeth.

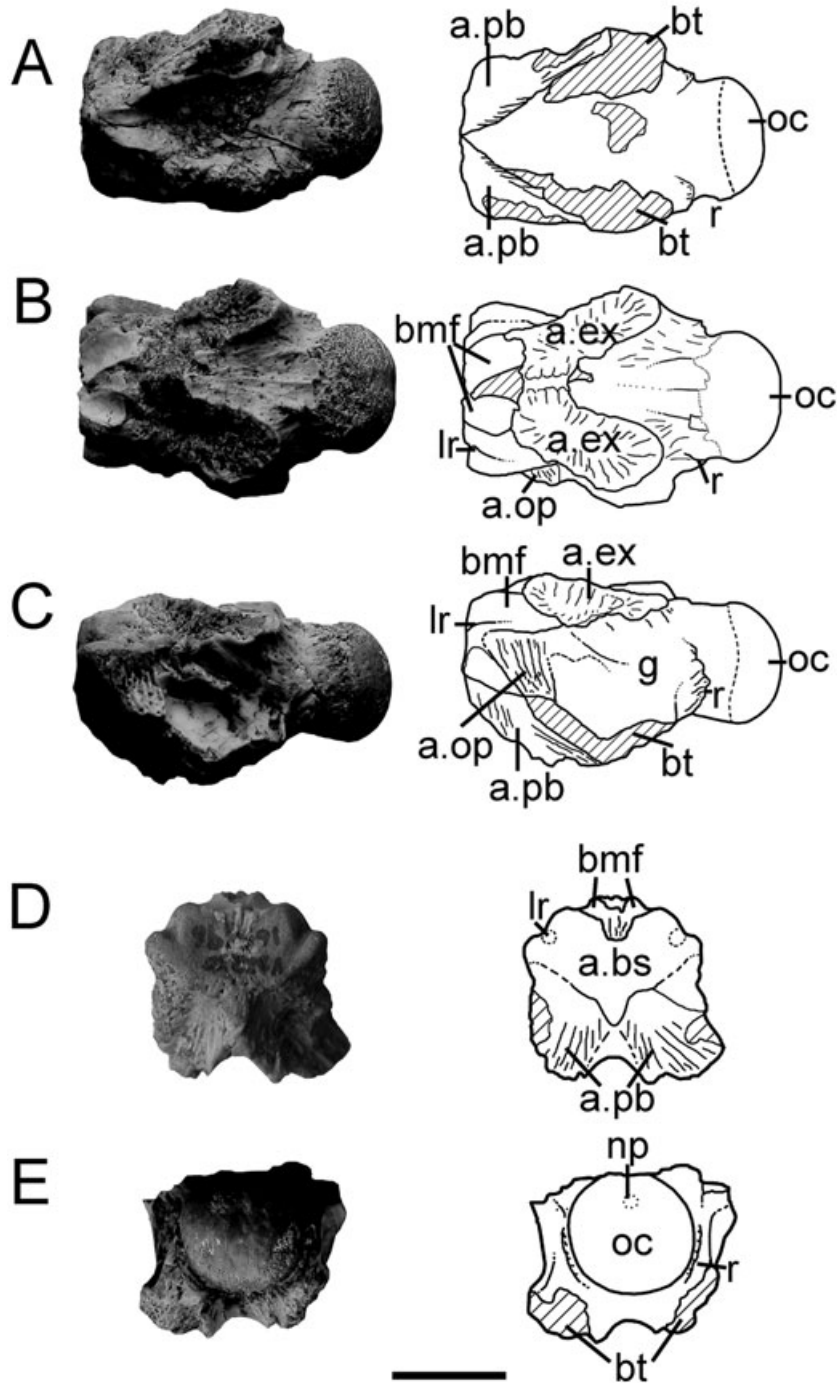


Figure 9. Nearly complete basioccipital of *Vanckleavea campi* (UCMP 165196) in ventral (A), dorsal (B), left lateral (C), anterior (D) and posterior (E) views. Scale bar, 1 cm.

Braincase (Figs 8A–C, 9)

Much of the braincase of GR 138 is covered by other elements of the posterior portion of the skull, yet parts of the lateral and posterior surfaces are visible (Fig. 8). An isolated basicranium (UCMP 165196;

Fig. 9) of a larger *Vanckleavea* (see assignment below) supplements the description.

The elongated basioccipital bears a circular occipital condyle with a circumscribing lip and a well-defined condylar neck. The elongated basioccipital is

contrasted with the rather short condition in all other archosauriforms. The distance between the occipital condyle and the trigeminal foramen in GR 138 confirms the elongation of the basioccipital observed in UCMP 165196. The exoccipitals do not participate in the formation of the occipital condyle, which is unique among archosauriforms. The exoccipitals converge anteriorly, but are still separated by a slight groove, whereas the exoccipitals diverge posteriorly to expose the floor of the basioccipital. Gower & Sennikov (1996) discussed this feature in early archosauriforms (character 17: medial margin of the exoccipitals; do not make contact = 0; make contact for a majority of their length = 1; meet anteriorly, but diverge posteriorly = 2) and assessed its usefulness in the relationships of early archosauriforms. Character state 2, exoccipitals meet anteriorly but diverge posteriorly, would be scored as present in *Van cleavea*. However, the condition in *Van cleavea* differs in the following aspects: the exoccipitals are much further apart than in any other of the taxa scored as character state 2, and the exoccipitals do not rest on the dorsal surface of the occipital condyle as they do with the other taxa scored for character state 2. Therefore, it is unclear whether the condition in *Van cleavea* is homologous to that of taxa scored for state 2 of character 17 of Gower & Sennikov (1996). UCMP 165196 indicates that the exoccipitals attach to the basioccipital in complex interdigitating sutures, not the typical flat surface found in most archosauriforms. A slit marked by a sharp ridge located ventrolateral to the articulation with the exoccipitals opens posteriorly. A fossa, lying ventral to this slit, is located on the lateral side of the basitubera. A median keel lies between the exoccipitals on the dorsal surface of the basioccipital. A foramen, possibly for cranial nerve XII, is located on the lateral side of the exoccipital in GR 138. It is not clear whether there were one or two foramina for the path of XII.

Small rugose ridges are located on the posterior face of the basioccipital just lateral to the occipital condyle. The basitubera project ventrally with a slight lateral component and project slightly more laterally than the lateral margin of the occipital condyle. The tubera are simple, mediolaterally compressed, rounded structures. A well-defined fossa is present on the ventral side of the basioccipital between the basioccipital tubera.

The lateral portion of the basioccipital preserves articulations with the parabasisphenoid and the opisthotic. The parabasisphenoid attaches to the anteroventral portion on a surface with elongated ridges and grooves. The descending process of the opisthotic articulates with a grooved surface on the dorsolateral surface at the anterior end of the articulation with the exoccipital. A smooth surface just

posterior to this articulation marks the ventral portion of the metotic foramen. A small, unfinished (not capped by compact bone) and shallow depression located anterodorsal to the articulation with the opisthotic near the articulation with the parabasisphenoid may be the lagenar recess. If so, the lagenar recess is similar to that of other non-archosaurian archosauriforms (see Gower, 2002).

The paroccipital process is short and not expanded dorsoventrally at its termination. The ventrally deflected paroccipital process bears a ridge that transects the process and leads to the dorsal portion of the foramen magnum. The sharp dorsal edge of the paroccipital process meets the supraoccipital and the parietal. It is unclear whether the opisthotic and exoccipital are fused in GR 138.

The large supraoccipital forms the dorsal portion of the posterior portion of the skull. Here, the bone is mediolaterally oriented. It is triangular in dorsal view and has a midline keel that is a continuation of the posterior projecting keel of the parietal. A keel here is typical of many archosauriforms. The broad smooth surface provided an attachment site for the upper temporal musculature. It is unclear whether any of the supraoccipital bordered the foramen magnum.

The anterior portion of the prootic is exposed on both sides of GR 138. The dorsal margin articulates with the ventral portion of the parietal, but both sides are slightly disarticulated. The trigeminal foramen is anterodorsally elongated. The small branch of the prootic ventral to the trigeminal foramen is smooth and does not bear the small ridge present in *Prolacerta* and *Proterosuchus* (Gower & Sennikov, 1996).

Both laterosphenoids are present but are disarticulated; their original position is difficult to determine. We hypothesize that the right laterosphenoid has flipped anteriorly 150° where the left element has moved anteroventrally. Despite difficulties in orienting the laterosphenoid, a few observations can be made. The left element is exposed both medially and laterally. The thick laterosphenoid is convex laterally and concave medially and has little or no notch for the anterior boundary of the trigeminal foramen. The cotylar crest, if present, is not sharp but rounded, and it is not clear whether the laterosphenoid contacts the postorbital. The anteroventral portions of the laterosphenoids articulate along the midline dorsal to the anterior opening for cranial nerve II.

The ventral portion of the parietal, the lateral surface of the prootic and the laterosphenoid together create a broad surface for the attachment of jaw muscles that span the entire length and half of the height of the lateral temporal fenestra.

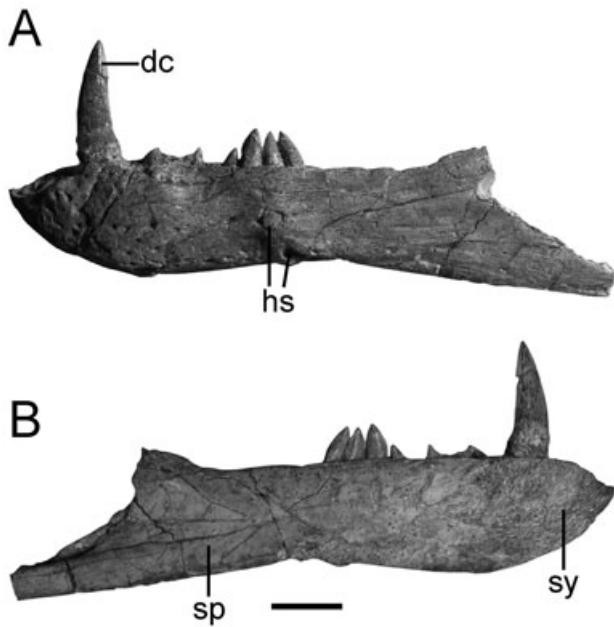


Figure 10. Left dentary and splenial of *Vancleavea campi* (GR 139) in lateral (A) and medial (B) views. The lateral side bears two heeled scars on the middle portion of the dentary. The splenial covers the medial side of the dentary. Scale bar, 1 cm.

Mandible (Figs 2, 3)

Both the right and left mandibular rami are well preserved and in articulation for GR 138. The prearticular, internal mandibular fenestra and much of the articular are covered by other elements.

Dentary (Figs 2–4, 10)

Both dentaries of GR 138 are well preserved. Additional information is provided by GR 139 (a fully three-dimensionally prepared left dentary). The robust and mediolaterally compressed element tapers to a point anteriorly (length of 6.7 cm in GR 138). A vertically oriented slot in the dentary fits the large maxillary caniniform tooth (Fig. 10) posterior to the large caniniform tooth of the dentary. The tooth margin expands laterally at the anterior end just anterior to the slot for the maxillary caniniform tooth, as with some crocodylomorphs. In addition, the dentary also slightly expands laterally posterior to the slot for the maxillary caniniform tooth.

Small nutrient foramina cover the anterior portion of the dentary on the lateral side. The small foramina decrease in frequency posteriorly until they are restricted to two parallel rows, one at the ventral edge and one at the dorsal edge. The anterior end of *Vancleavea* does not expand dorsally as with some

suchians (e.g. *Postosuchus*). A small rugose area delimits the dentary symphysis and indicates that the lower jaws were weakly held together dorsal expansions.

The tooth margin arcs posterodorsally. An anterior process of the surangular lies in a slot of the dentary and splits the posterior portion of the dentary into two parts. The dorsal portion of the dentary lies on the lateral surface of the anterior part of the surangular, and the much longer ventral portion lies on the lateral side of the angular in a groove. Both processes taper to a point posteriorly.

In dorsal view, the dentary expands laterally anterior to the slot for the maxillary caniniform tooth and just posterior to it. The tooth sockets are not well defined, and interdental plates lie between the teeth. A coronoid appears to be absent. The splenial covers much of the medial side of the dentary in both GR 138 and GR 139.

The dentary teeth are mostly covered by the maxillary teeth in GR 138, but a few are still visible in GR 139. Similar to the maxilla, the dentary contains a heterodont dentition. The anterior teeth of the dentary are very similar to the premaxillary teeth, being round in cross-section and without serrations. The fourth or fifth tooth is similar to the caniniform maxillary tooth. The large posteriorly recurved tooth fits into a gap between the maxilla and premaxilla during occlusion. Only the posterior side of the mediolaterally compressed caniniform tooth bears serrations. The teeth posterior to the caniniform tooth are most similar to the most posterior teeth in the maxilla. The dentary teeth are slightly mediolaterally compressed and are not posteriorly recurved; the apex of the tooth lies in the middle of the anteroposterior length. These teeth are poorly separated in the jaw. Furthermore, the teeth bear serrations on both the anterior and posterior edges, but lack serrations near the apex. The teeth also have slightly constricted roots at the base of the enamel.

Splenial (Fig. 10)

The splenial is thin, and only the ventral portion can be seen in right lateral view in GR 138.

Surangular (Figs 2, 3)

Both left and right surangulars are preserved in articulation with the rest of the mandible, although they are crushed. It is not clear whether a surangular foramen is present in *Vancleavea*; a surangular foramen is present in *Prolacerta* (Modesto & Sues, 2004), *Proterosuchus* (Welman, 1998), *Erythrosuchus* (Gower, 2003), *Euparkeria* (Ewer, 1965) and many crown-group archosaurs. A rounded dorsal margin stretches from the articular to the dentary. A distinct lateral ridge present in most archosauriforms (e.g.

Erythrosuchus, *Proterosuchus*) is absent in *Vancleavea*. The surangular meets the angular at its ventral margin. The anteroventral corner of the surangular is concave, indicating the possibility that a small lateral mandibular fenestra could be present. The smooth bone expands dorsally at the posterior margin to cover the articular laterally.

Angular

The ventral margin of the angular is gently rounded and forms the posteroventral margin of the mandible. The articulation with other mandible elements is discussed with those elements.

Articular (Figs 2, 3, 8)

Even though both articulars are present in GR 138, most of the morphology of the element is covered by either matrix or other elements. The articular is simple, with a large concave retroarticular process that expands posteriorly. A similar retroarticular process is present in phytosaurs (e.g. Camp, 1930). A transverse, dorsally expanded ridge separates the retroarticular process from the glenoid. The glenoid appears to be composed mostly of the transversely expanded depression.

POSTCRANIA

Vertebrae (Fig. 11)

Most of the dorsal and cervical vertebrae are covered by osteoderms in the complete skeleton, GR 138. However, vertebrae are known from the holotype (PEFO 2427), GR 139 and PEFO 33978. No intercentra are present in the cervical or caudal regions, and are possibly absent in the dorsal vertebrae, because the ventral portions of the articular faces of the centra are not bevelled as in taxa (e.g. *Proterosuchus*) with intercentra.

Cervical (Fig. 11A)

One anterior cervical is visible in lateral view in GR 138, and two articulated cervicals are present in PEFO 33978 (Fig. 11A). The centrum is rectangular in lateral view; the anterior and posterior articular facets are in the same plane. The centrum body is longer than tall. Both the anterior and posterior articular facets are square-shaped with rounded corners. The articulated cervicals of PEFO 33978 indicate that the cervical centra are slightly procoelous where the anterior articular surface is concave and the posterior articular surface is slightly convex. The centre of the posterior surface is flat, whereas the edges are rounded, thus giving the posterior articular surface a convex morphology.

Small lateral grooves surround the rims of the centrum. The middle part of the centrum is highly

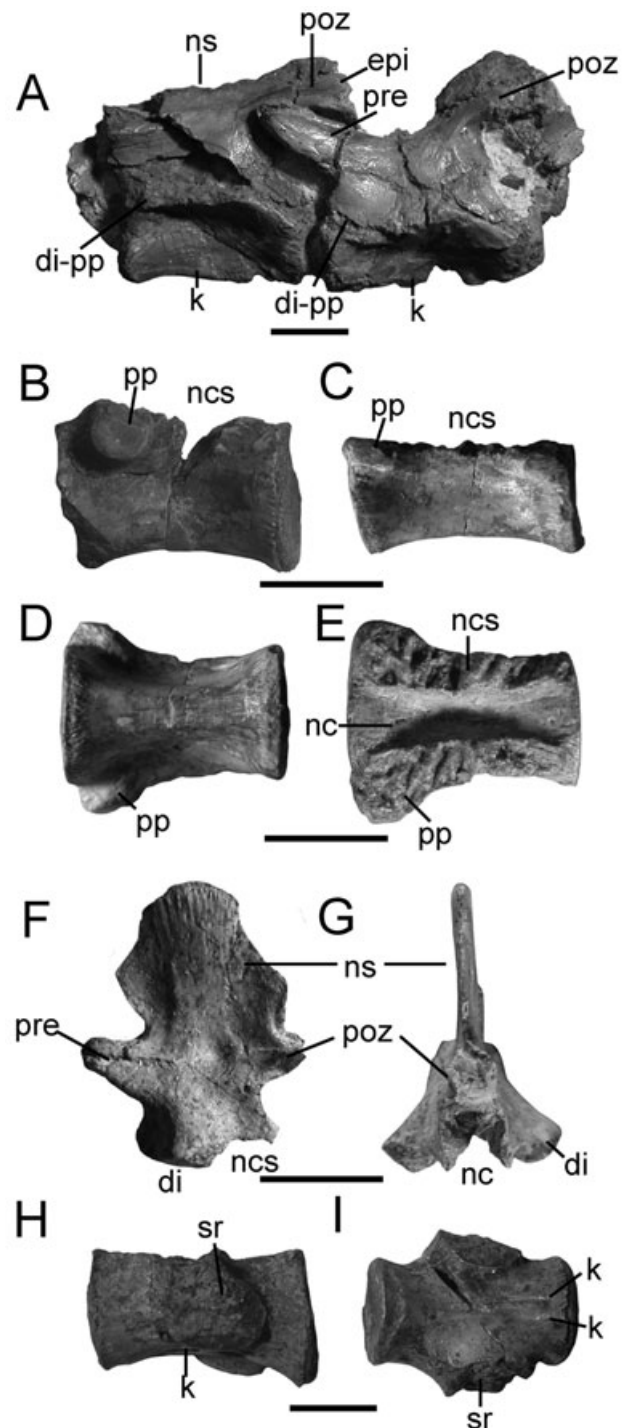


Figure 11. Vertebrae of *Vancleavea campi*. Two articulated cervical vertebrae (PEFO 33978) (A) and dorsal vertebra of the holotype (PEFO 2427) (B). Dorsal vertebra (GR 139) in left lateral (C), ventral (D) and dorsal (E) views. Neural spine of a dorsal vertebra (GR 139) in left lateral (F) and posterior (G) views. A sacral of the holotype (PEFO 2427) in left lateral (H) and ventral (I) views. Scale bars, 1 cm.

waisted in lateral view and is highly mediolaterally compressed. Furthermore, the centrum bears a strong ventral keel; the middle portion of the centrum body is only slightly mediolaterally wider than the mediolateral thickness of the keel. The ventral margin is straight, whereas other archosauriform vertebrae (e.g. *Euparkeria*, *Erythrosuchus*) have keels that are ventrally concave in lateral view.

The neurocentral suture is visible in the cervical of GR 138, but not in the articulated cervicals of PEFO 33978. Both the parapophyses and the diapophyses are poorly developed; a distinct parapophysis is not visible on any of the cervical vertebrae. The elongated prezygapophyses terminate in a rounded point anteriorly and are angled about 45° to normal. The equally elongated postzygapophyses bear small epipophyses. The presence of epipophyses has long been regarded as a dinosaurian synapomorphy (Gauthier, 1986; see references in Langer & Benton, 2006). However, epipophyses are present in a variety of archosaurs, including the pseudosuchians *Batrachotomus* (Langer & Benton, 2006) and *Revueltosaurus* (Parker *et al.*, 2005). *Vancleavea* is the first known non-archosaurian archosauriform to bear epipophyses on postaxial cervical vertebrae. The mediolaterally compressed neural spine is slightly shorter than the length of the centrum.

Dorsal (Fig. 11B–G)

The amphicoelous dorsal centra (Fig. 11B–E) have constricted lateral surfaces near the neurocentral suture. This fossa is found in nearly all archosauriforms and many basal archosaurs. The articular ends are nearly perfectly circular. The ventral margin of the dorsal vertebrae bears two paramedian ventral keels bordering a midline groove.

The parapophysis is at the extreme anterior end and adds to the expansion of the anterior portion of the centrum face. The neurocentral suture bisects the parapophysis. All specimens of dorsal vertebrae of *Vancleavea*, to our knowledge, lack a fully sutured neural arch; therefore, most centra have the neurocentral suture exposed. The neural canal is deep at the midline and laterally constricted. The neural canal shallows and expands laterally anteriorly and posteriorly. The neurocentral suture pattern on the posterior end is dominated by a prominent groove that extends from the neural canal posterolaterally to the posterior margin of the neural arch facet. The suture pattern is present at the dorsal margin of the parapophysis.

The disarticulated neural arches from GR 139 (Fig. 11F, G) have an unusual morphology in comparison with other archosauriforms. The neural spine is anteroposteriorly broad, with small radiating grooves on the dorsolateral surface. A spine

table is not present; however, the dorsal margin of the neural spine is slightly expanded with respect to the ventral portion of the neural spine. The dorsal margin is convex in lateral view. The anterior and posterior edges of the neural spine bear an expanded tab. Although there is no indication from the articulated specimens that the anterior and posterior edges of the neural spine of the adjacent vertebrae touch, they must nearly contact each other. The pre- and postzygapophyses are angled near 45°. The base of the neural spine is greatly laterally expanded, and a ventrally banked platform represents the diapophysis.

Sacral (Fig. 11H, I)

Both sacral vertebrae are known from the holotype (PEFO 2427; Fig. 11H, I), and one sacral element originally misidentified as a sacral vertebra of *Hesperosuchus* (AMNH 6758; Colbert, 1954: fig. 17G–I) actually belongs to *Vancleavea*. The sacral vertebrae have circular articular facets, a cylindrical body that is poorly waisted and a deep groove on the ventral surface flanked by two parallel ridges. The facet for the sacral ribs is greatly expanded laterally and extends over two-thirds the length of the centrum. The scar is oval-shaped and located on the last two-thirds of the centrum. Long & Murry (1995), followed by Hunt *et al.* (2002, 2005), assigned the holotype sacrals to sacral one and two. However, the two sacrals are nearly identical, and it is unclear which specimen belongs to position one and two. The sacral centra are not co-ossified in any *Vancleavea* specimens.

Caudal (Fig. 18F)

Scattered anterior caudal vertebrae and a series of mid- to posterior caudal vertebrae are articulated with the last sacral in GR 138. We estimate that 36–38 caudal vertebrae are present in the tail of *Vancleavea*. The anterior caudal vertebrae have open neurocentral sutures. From the mid-caudal vertebrae to the distal end of the tail, no suture is visible between the neural arches and the centra. The anterior caudal vertebrae have well-developed transverse processes in the anteroposterior middle portion of the centra, which become progressively shorter until they disappear posteriorly at about one-third the length of the tail. It is unclear where long posterodorsal-directed neural spines begin in the caudal series, because the anterior portion of the tail is covered by osteoderms, but by the 10th or 13th vertebra, long slender neural spines are present. The spines are posteriorly directed at 30° to normal. The neural spines continue until the end of the tail, creating a dorsoventrally deep tail. The neural spines are circular in cross-section. The centra have deep ventral

grooves bordered by well-developed parasagittal keels. Chevrons are present, mediolaterally compressed, and posteroventrally oriented.

Ribs (Fig. 14C)

A few dorsal ribs have been recovered from the disarticulated specimen (GR 139), next to the nearly complete skeleton of GR 138 (see Fig. 14C). The proximal portion of the double-headed ribs dramatically arcs laterally and medially at the distal ends. In cross-section, the robust ribs are oval. Internally, the ribs are composed of an extra thick layer of compact bone. No unambiguous cervical ribs or gastralia have been identified.

Scapula (Fig. 12)

An isolated left scapula was recovered from GR 139, whereas these elements are obscured in GR 138 by osteoderms. The tall scapula has a concave anterior and posterior margin, as with *Erythrosuchus* (Gower, 2003), *Euparkeria* (Ewer, 1965), proterochampsids and Archosauria. The glenoid is laterally expanded, and the shaft is mediolaterally thin. The dorsal end expands asymmetrically; the posterior end is larger than that of the anterior edge (sharper angle). The dorsal edge is slightly rounded and convex in lateral view. There is a small tuber on the posterior edge between the dorsal edge and the glenoid. Gower (2003) hypothesized that the similarly placed scar in *Erythrosuchus* may be the attachment for the M. subcoracoscapularis. There is a small finger-like tuber, the acromion process, on the anterior edge, which is similar to the condition in other archosaurs. Between this tuber and the glenoid, the scapula is concave. No coracoid is present in any of the *Vancleavea* specimens.

Humerus (Fig. 13)

The humerus is known from three specimens (GR 138, PEFO 2427, PEFO 33978). GR 138 preserves a left humerus in articulation with the ulna and radius. The humerus is rather simple compared with that of other archosauriforms. The proximal head is preserved and visible only in the holotype (PEFO 2427). It expands anteriorly as a small ball, and it appears that this entire proximal surface is part of the ball. The proximal end of the humerus is thick, similar to that of *Erythrosuchus* (SAM 905), rather than the thinner proximal portion of the humerus of *Euparkeria* (Ewer, 1965) and *Tropidosuchus* (PVL 4604). The deltopectoral crest is small, gently rounded and grades into the shaft well before the midshaft. The fossa medial to the crest is shallow. The shaft is well-waisted relative to the articular ends. The compact bone is thick in cross-section at midshaft as with the femur. The distal end expands anteriorly and

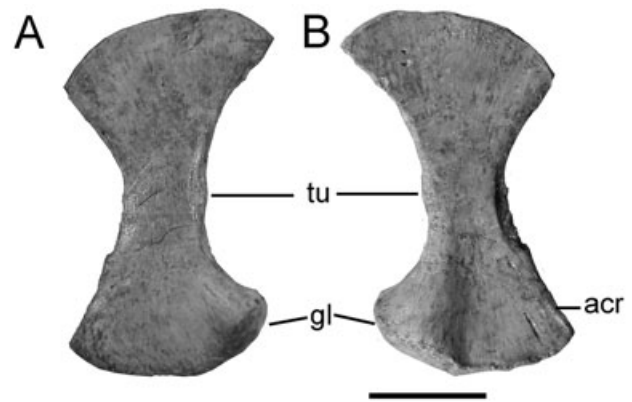


Figure 12. Left scapula of *Vancleavea campi* (GR 138) in lateral (A) and medial (B) views. Scale bar, 1 cm.

posteriorly nearly equally and is compressed dorso-laterally. The two large condyles are comparable in size. The cleft between the two condyles continues medially up the shaft on the posterior side as a small fossa. The lateral side is flat. On the anterior side, there is a sharp ridge stretching from the shaft to the distal end. There are no ectepicondylar or entepicondylar grooves.

Ulna (Fig. 13)

GR 138 includes the articulated left ulna, and an isolated right ulna (GR 139) was found among the scattered remains. The ulna has a small olecranon process and a 'c'-shaped proximal articular surface. The proximal end is mediolaterally compressed as with all non-archosaurian archosauriforms. Each side of the distal end is equally expanded mediolaterally. In addition, the distal end is convex in anterior view, similar to the distal end of the ulna of *Euparkeria* and phytosaurs. Its size compares well with the radius, which is only slightly smaller.

Radius (Fig. 13)

A left radius is present in GR 138 and as an isolated element in GR 139. The proximal articular surface is concave, and both the proximal and distal ends are slightly expanded relative to the shaft. There is a slight arc in the shaft, and the distal end is convex.

Manus (Fig. 13)

A disarticulated left manus is present in GR 138. The disarticulation of the carpals prevents unambiguous identifications; two are present. Although disarticulated, the metacarpals lie in anatomical order in posteroventral view. Metacarpal I, the most robust element, is the same length (1.10 cm) as the fifth metacarpal. The proximal end is wider than the distal

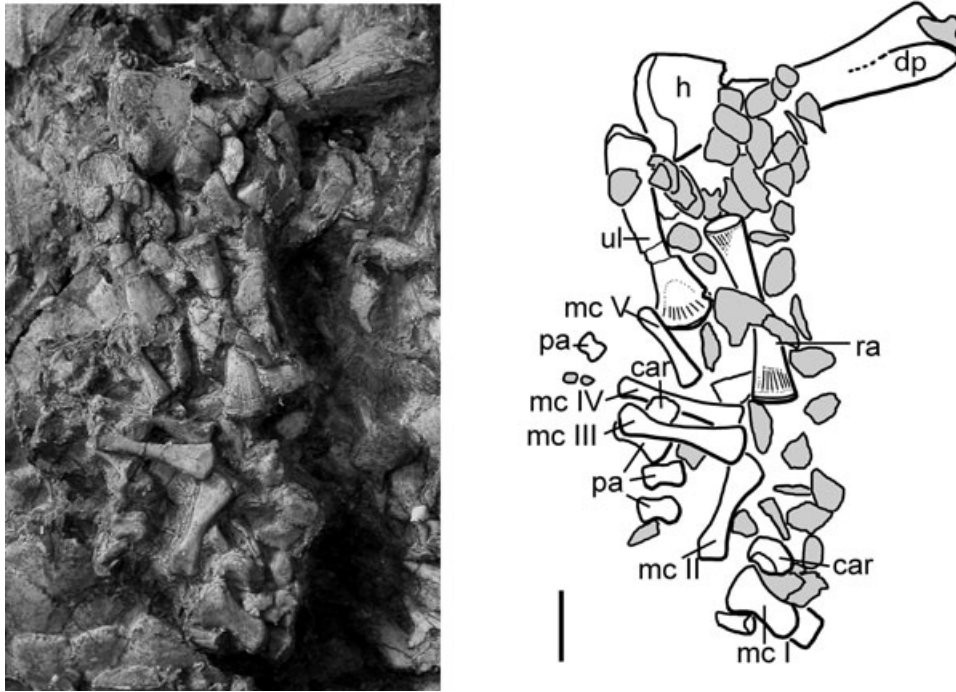


Figure 13. Left forelimb of *Vanclavea campi* (GR 138). The grey elements are appendicular osteoderms. Scale bar, 1 cm.

end. Metacarpal II is 1.44 cm long and about the same diameter as I and III at the midshaft. Metacarpal III measures 1.68 cm long, whereas metacarpal IV measures 1.68 cm long. Metacarpal V is 1.10 cm and is equally the shortest together with metacarpal I. Each metacarpal is waisted at midshaft. The articular surfaces of the metacarpals are restricted to the distal surface. It appears that there is little evidence of overlap of the proximal portions of the metacarpals, but this cannot be ruled out. Small phalanges are present and the distal ends are well rounded. There are no manual unguals known.

The manus of *Vanclavea* is about four-fifths the size of the pes [longest metacarpal III (~1.7 cm)/longest metatarsal (~2.2 cm)]. The paucity of basal archosauriform taxa with a preserved manus precludes detailed comparisons. As with *Proterosuchus* (QR 1484; Cruickshank, 1972), the metacarpals elongate from I to IV. This arrangement is also present plesiomorphically in squamates and *Trilophosaurus* (Gregory, 1945).

Ilium (Figs 14, 15)

The ilium is well preserved in GR 138, and a partial ilium is preserved in the holotype. The ilium of PEFO 2427 is approximately one-third larger than that of GR 138. The orientation of the iliac blade is unclear, but it probably was similar to that of other archosauriforms. The dorsal portion of the iliac blade is

short compared with other basal archosauriforms. The anterior process of the ilium is much reduced, but is still present. The iliac blade is foreshortened posteriorly relative to other archosauriforms. The thin dorsal margin is highly convex. The acetabulum is very shallow and shared among the ilium, pubis and ischium. The acetabular rim is poorly developed, but similar to that of *Erythrosuchus* (Gower, 2003) and *Proterosuchus* (Cruickshank, 1972). The pubic peduncle is comma-shaped in ventral view, as is the ischial peduncle. The angle between the pubic and ischial peduncles is about 135°.

Ischium (Fig. 14)

The proximal left and right ischia are preserved in PEFO 2427, and both complete elements are known from GR 139. The proximal end is the thickest and preserves the ventral portion of the acetabulum on the lateral surface. The acetabular rim is much shallower in GR 139 than in PEFO 2427. A small fossa is located ventral to the acetabular rim. The antero-proximal edge bears a dorsoventrally oriented articular surface that articulates with the pubis. The iliac articular surface is rugose and comma-shaped. The distal end thins posteriorly. The anterior margin is concave ventral to the articulation with the pubis. The dorsal margin is also concave. In articulation, the ischia form a 'V' in anterior view; the symphysis is restricted to the ventromedial surface.

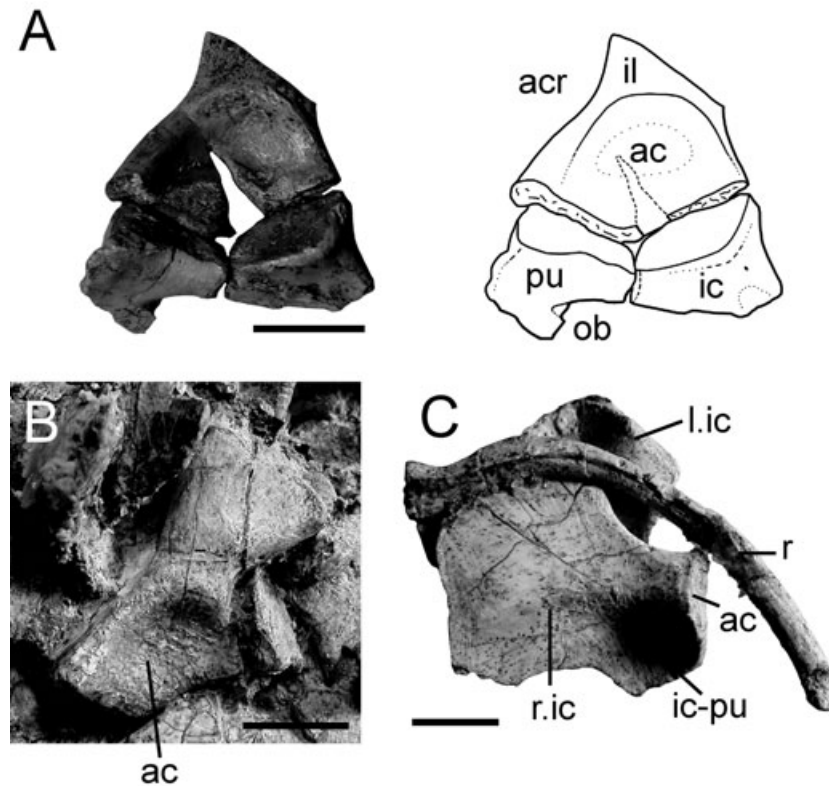


Figure 14. Pelvis of *Vanclavea campi*. The left ilium, pubis and ischium (A) of the holotype (PEFO 2427) in lateral view compared with the complete left ilium (B) in lateral view of GR 138 and the right ischium (C) in lateral view of GR 139. Scale bars, 1 cm.

Pubis (Fig. 14)

The pubis is only preserved in the holotype (PEFO 2427). The articular surface with the ilium is comma-shaped and rugose (Long & Murry, 1995; Hunt *et al.*, 2005). The lateral surface preserves the anteroventral portion of the acetabulum. The posterior portion has a small articular surface that articulates with the ischium. The medial side is convex, and it is unclear where the obturator foramen would be located (Hunt *et al.*, 2005).

Femur (Figs 15, 16)

Four femora are known: GR 138 (complete left), PEFO 2427 (right proximal portion only), PEFO 34035 (left and right) and UCMP 152662. The holotype femur (PEFO 2427) is slightly crushed mediolaterally, but also crushed with an anteroposterior component. The proximal portion of the femur has an elongate oval shape with no lateral tuber and a small anteromedial tuber. The proximal portion of the proximal edge forms a sharp corner with the posterior edge. The proximal surface is capped without finished bone, gently rounded and scalloped. The proximal head is poorly defined, being expanded but continuous with the shaft. A rugose scar is located on the proxi-

medial side. The size and degree of rugosity differ in all three specimens. The scar in *Vanclavea* is located in the position of the fourth trochanter of *Euparkeria* (Ewer, 1965) and Archosauria, but also in the same location as the internal trochanter of *Erythrosuchus* (Gower, 2003) (both attachment sites for *M. caudifemoralis*). The homology of these structures is tested below (character 36) and, based on the phylogenetic position of these taxa, it is hypothesized that they are homologous. It is not clear whether *Vanclavea* has a caudifemoralis attachment similar to that of *Euparkeria* (Ewer, 1965) and Archosauria, or that of taxa such as *Proterosuchus* (Cruickshank, 1972) and *Erythrosuchus* (Gower, 2003). However, *Vanclavea* does not have an intertrochanteric fossa, a feature usually found in taxa with an internal trochanter.

The cross-section of the femur at midshaft is circular, and the bone is very thick here. As with the clade *Euparkeria* + Archosauria, the femoral shaft is sigmoidal, and the long axis of the articular ends is twisted 45°.

The distal end is slightly rounded and separated from the shaft. The two condyles are not well developed. A cristatibiofibularis is not present, and the two

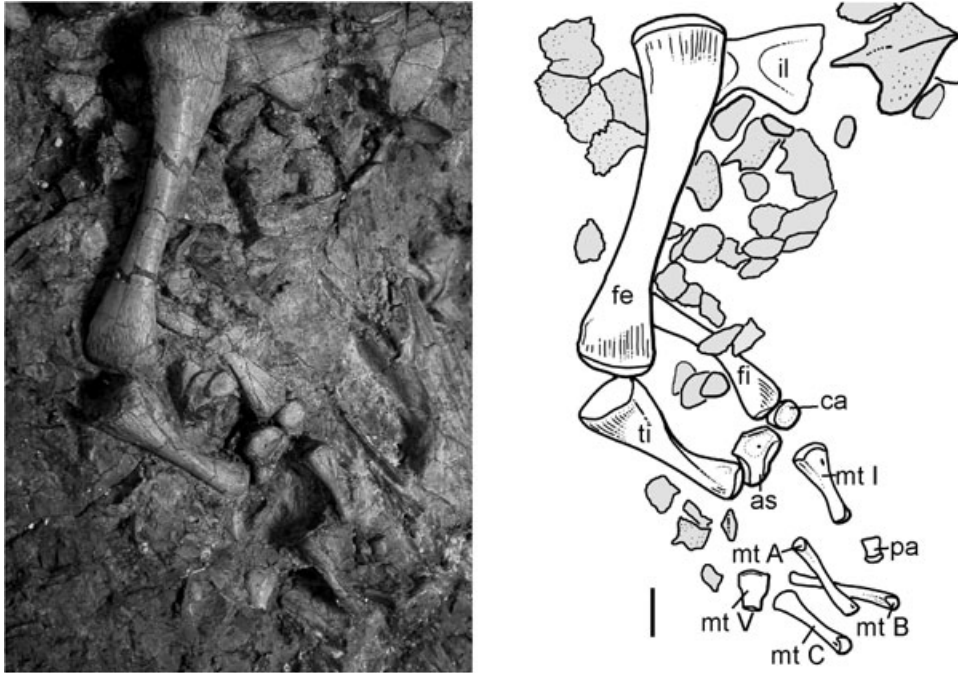


Figure 15. Left hindlimb of *Vancleavea campi* (GR 138). The hindlimb below the femur has been twisted by 180° where the lower portion of the leg is in anterior view. The metatarsals are labelled A–C and not 2–4 because they are disarticulated. Grey elements, appendicular osteoderms. Scale bar, 1 cm.

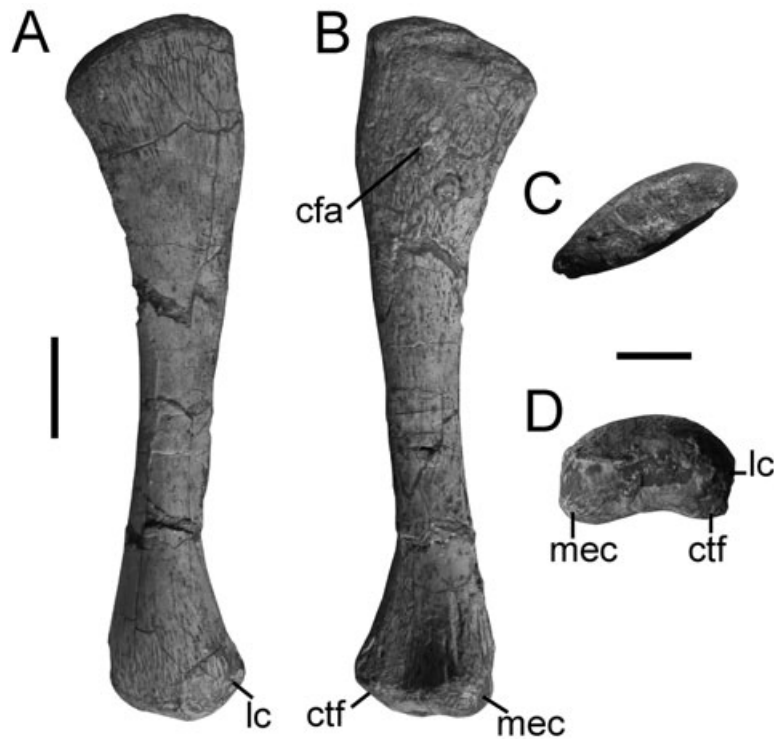


Figure 16. Left femur of *Vancleavea campi* (GR 138) in lateral (A), medial (B), proximal (C) and distal (D) views. Scale bars, 1 cm.

condyles posteriorly terminate in acute points. A concave pit separates the two condyles on the posterior/ventral side.

Tibia (Fig. 15)

A complete left tibia from GR 138 is exposed in anterior view, and a proximal portion of a left tibia (PEFO 2427) is preserved in the holotype. Long & Murry (1995) and Hunt *et al.* (2002, 2005) misinterpreted the proximal portion of the tibia as from the right side. A small, sharp ridge trends dorsoventrally on the anterior edge and represents the pinnacle of the cnemial crest. In GR 138, the cnemial crest descends two-thirds the length of the shaft. A concave depression lies just lateral to the sharp ridge. Another sharp ridge is present on the posterior edge trending dorsoventrally. The proximal surface is concave anteriorly, convex posteriorly and the edges are gently rounded (Long & Murry, 1995). In cross-sectional view at midshaft, the tibia is teardrop-shaped with a pointed anterior ridge. A slight depression on the lateral side of the anteromedial side marks the attachment of *M. puboischiotibialis*, as hypothesized for *Erythrosuchus* by Gower (2003). The distal end of the tibia is expanded, but not as much as the robust proximal portion. The distal end is convex and medially overhangs the astragalus. The shaft of the tibia is bowed medially.

Fibula (Fig. 15)

A complete left fibula is present with GR 138. This bone is mostly covered by matrix and lateral osteoderms in the block. The proximal end is expanded relative to the midshaft of the fibula, and the distal end is expanded mediolaterally to contact both the astragalus and calcaneum. The midshaft arcs laterally. The long axis of the proximal and distal ends is twisted approximately 45°. The fibula is less robust than the tibia, but is the same length. A scar for the attachment *M. iliofibularis* is not visible.

Tarsals (Fig. 15)

All of the tarsal elements were found articulated in the left hindlimb of GR 138. The left limb has rotated so that the fibula, tibia, astragalus and calcaneum are in dorsal view (Fig. 15). The calcaneum and astragalus were removed and then fully prepared. The orientation of the tarsals follows that of Gower (1996).

Astragalus (Fig. 17)

The astragalus is well preserved. The concave dorsal surface (homologous to the anterior hollow) preserves a foramen at its centre. The border of the anterior hollow lacks a distinct rim that is found in

Euparkeria (UMCZ T692), *Chanaresuchus* (MCZ 4035), *Tropidosuchus* (PVL 4601) and pseudosuchians. A similar convex surface is present on the ventral side with a larger foramen at its centre. A rounded tuber is present on the medial side of the ventral side. The rounded and broad distal surface resembles the distal roller of other archosauriforms.

In proximal view, the astragalus is divided into three surfaces: a tibial facet, a non-articular gap and a fibular facet. As the most medial facet, the tibial facet is much larger than the fibular facet. The concave articular surface stretches to nearly the ventral border. In addition, the facet opens more dorsally where the facet is more visible on the dorsal side relative to the ventral side. A small rim delineates the proximal portion of the facet. This simple tibial facet resembles that of *Prolacerta*, *Proterosuchus* (AMNH 2237) and *Shansisuchus* (IVPP field collection number 56173). In these taxa, the tibia rests on the medial side of the astragalus, and much of the medial portion of the distal end does not contact the astragalus. In contrast, the tibial facet of the astragalus occupies the entire distal end of the tibia, whereas no part of the tibia lies medial to the astragalus in *Euparkeria*, proterochampsids and Archosauria.

A concavity that is U-shaped in cross-section lies between the tibial and fibular facets. Termed the 'non-articular notch' (Sereno, 1991; Gower, 1996), this gap completely separates the tibial and fibular facets, and may be homologous to the notch present between, but not completely separating, the tibial and fibular facets in *Euparkeria*, proterochampsids and Archosauria. The non-articular notch is present in the astragalus of many non-archosauriform archosauromorphs, *Proterosuchus* and, possibly, erythrosuchians (Gower, 2003). The non-articular notch is present in the possible astragalus of *Shansisuchus* (see Gower, 1996), but absent in *Erythrosuchus* [see Gower (1996) for further discussion], and so the presence of the feature is ambiguous in erythrosuchians. Proportionally, the non-articular gap is larger in *Vancleavea* than in all other archosauriforms. Two poorly defined ridges transverse the non-articular gap on both the dorsal and ventral sides.

The fibular facet is slanted medioventrally. A rim surrounds the slightly ventrally and dorsally expanded articular facet. The facet itself is nearly flat and circular. A dorsoventrally oriented ridge separates the distal extent of the fibular facet from the flat, rectangular calcaneal articular surface. There is no notch in the astragalus on the calcaneal facet. A slightly convex calcaneal facet is also present in *Shansisuchus* and *Erythrosuchus*, but is absent in the more complex ankles of *Proterosuchus*, *Euparkeria*, proterochampsids and archosaurs.

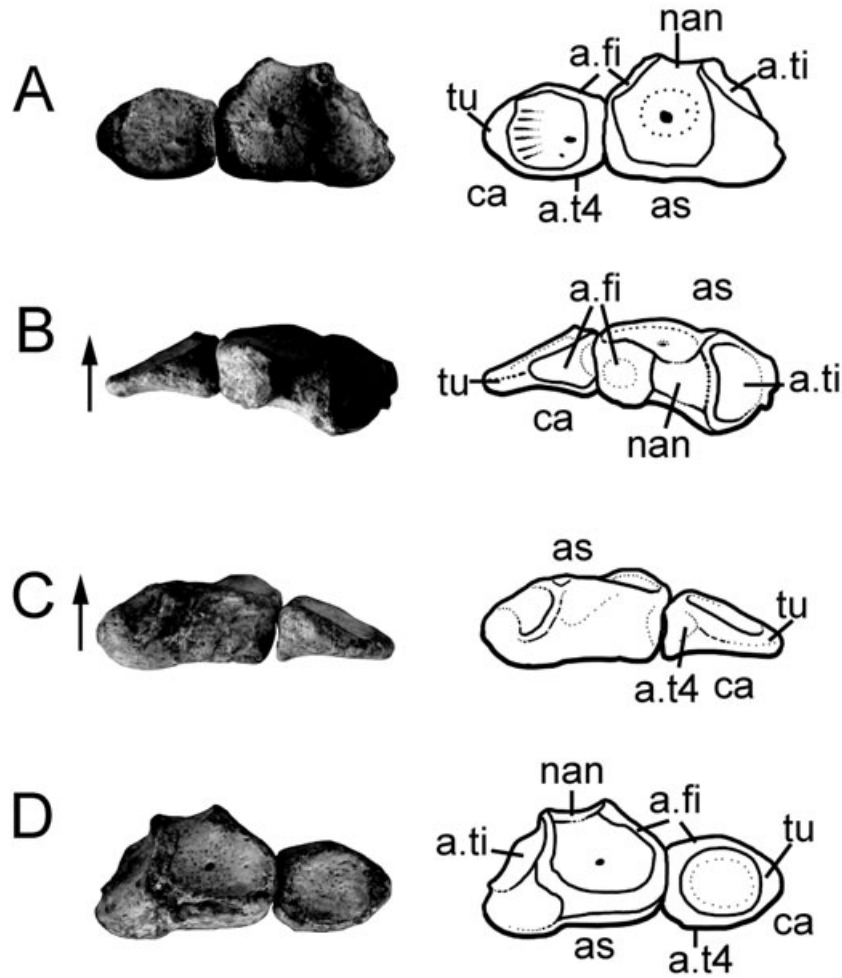


Figure 17. Left ankle of *Vanclavea campii* (GR 138) in posterior/ventral (A), dorsal/posterior (B), ventral/anterior (C) and anterior/dorsal (D) views. Arrow indicates anterior direction. Scale bar, 1 cm.

Calcaneum (Fig. 17)

The calcaneum is a small bone that is triangular in dorsal view and dorsoventrally compressed (Fig. 17). The calcaneal tuber is laterally directed with a slight ventral component (5–10° ventrally deflected). The proximal and distal surfaces converge laterally where they meet in the middle of the anteroposterior height (autapomorphy of *Vanclavea*). This creates a lateral apex that is gently rounded. The calcaneal tuber of *Vanclavea* is dorsoventrally compressed at its lateral end in contrast with those of *Tropidosuchus* (PVL 4601), *Shansisuchus* (IVPP field collection number 56173) and *Erythrosuchus* (BMNH R3592; Gower, 1996), *Euparkeria* (UMCZ T692) and pseudosuchians, in which the tuber is expanded posteriorly.

The concave dorsal and ventral surfaces have a centre that is made up of compact bone surrounded by a rim of unfinished bone. A flat and rectangular medial surface articulates with the astragalus,

similar to that described for erythrosuchians (Gower, 1996). There is no perforating canal similar to those found in *Prolacerta* (BPI 2675) and *Proterosuchus* (QR 1484, AMNH 2237). All of the medial articular face articulates with the astragalus. Here, both surfaces are nearly flat with rounded edges. The medial portion of the proximal surface articulates with the lateral portion of the distal end of the fibula. The convex articular surface is similar to that of archosauriforms. The convex distal surface extends laterally to the calcaneal tuber and articulates with tarsal 4.

Distal tarsals (Fig. 15)

Two small bones were found between the metatarsals and the astragalus and calcaneum. These are interpreted to be the third and fourth tarsals. Both are small and rounded. The larger tarsal (fourth) is one-third larger than the third tarsal. The absence of the

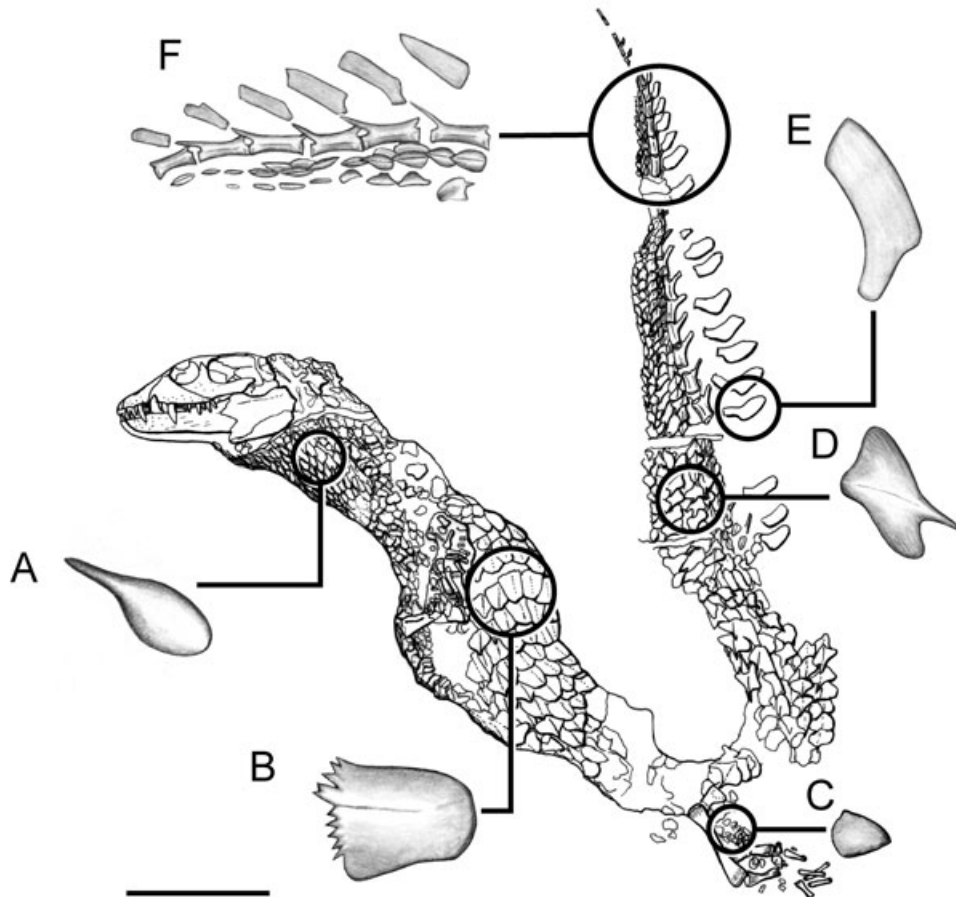


Figure 18. The articulated skeleton referred to *Vanclivea campi* (GR 138) covered in osteoderms. The enlarged drawings illustrate the five different morphologies of the osteoderms discussed in this paper: throat (A), ventral (B), appendicular (C), lateral (D) and dorsal caudal (E) osteoderms. The tail osteoderms and lateral and dorsal caudal osteoderms are highlighted (F). Scale bar, 10 cm for the skeleton. The osteoderms are not to scale.

ossification of tarsals 1 and 2 places *Vanclivea* closer to Archosauria than to *Proterosuchus* (Gower, 1996).

Metatarsals (Fig. 15)

The metatarsals have become disarticulated from the rest of the hindlimb, making the identification of each metatarsal difficult. It appears that metatarsal I (length, 1.60 cm) lies on the lateral side of the pes and near the calcaneum, whereas metatarsal V lies at the medial extent of the pes. Because the metatarsals are disarticulated, the identification of metatarsals II–VI is uncertain. For that reason, the metatarsals are assigned the following letters that correspond to Figure 15 in order to report the length: metatarsal A (length, 1.68 cm); metatarsal B (length, 2.05 cm); metatarsal C (length, 2.25 cm).

The metatarsals are well preserved and their morphology is simple. Each of the metatarsals has a very thin radius relative to the length, suggesting that

each is not supporting much weight. The articular surfaces of the metatarsals are restricted to the distal surface. The proximal articulation of the metatarsals is unclear. A single phalanx, similar to the dimensions of the manual phalanges, suggests that the toes were rather short.

Osteoderms (Fig. 18)

There are five general morphotypes of osteoderm present in the nearly articulated carapace, but some morphotypes grade into others at the boundaries between the different types.

Morphotype A – throat osteoderms (Figs 18A, 19A): Morphotype A osteoderms are throat (gular) osteoderms. They are tightly associated, slightly overlapping and stretch anterior from the pectoral girdle to the dentaries. Some morphotype A osteoderms are slightly keeled; however, most are smooth. The

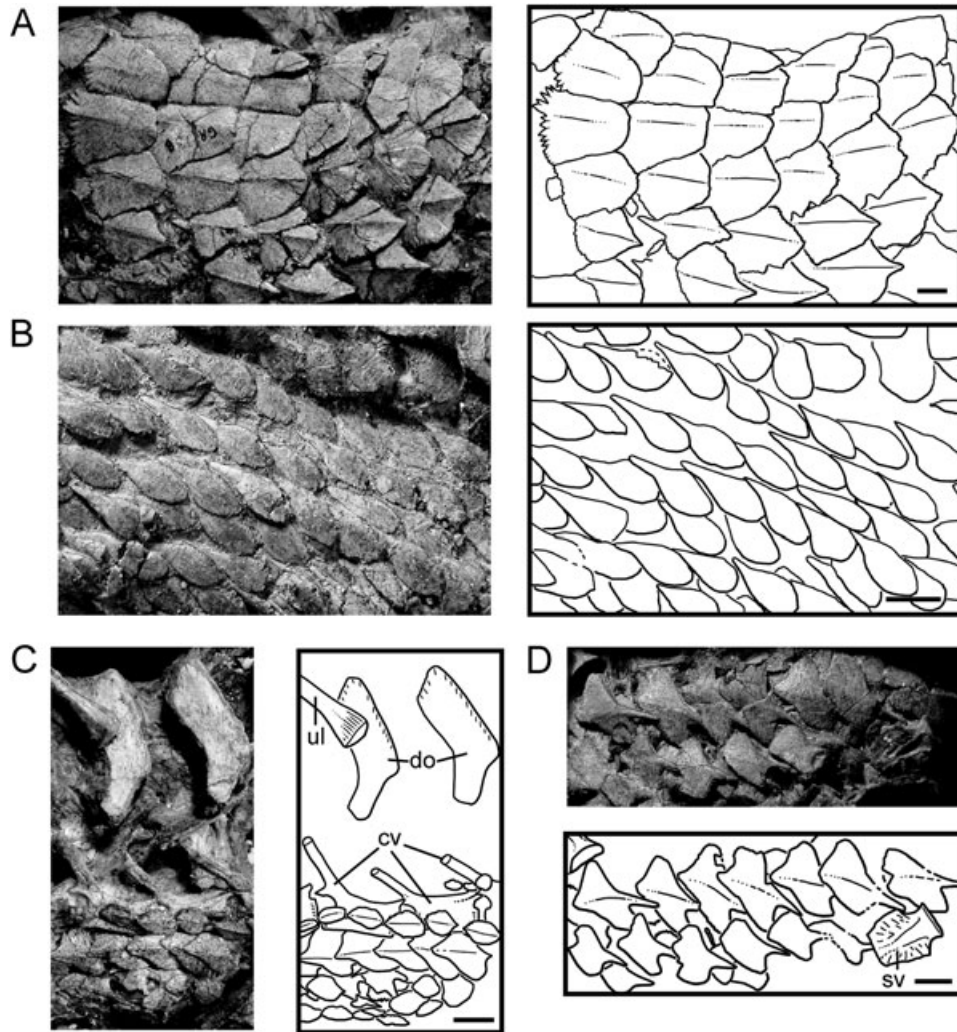


Figure 19. Osteoderms from the various regions of *Vanckleavea campi* (GR 138): ventral region (morphotype B) (A), neck region (morphotype A) (B), tail region (morphotype D) (C) and lateral side of the anterior portion of the tail (morphotype C) (D). Scale bars, 1 cm.

overall morphology is teardrop-shaped, with the point of the drop oriented anteriorly. These osteoderms grade somewhat into the morphology of the lateral osteoderms, which are slightly more expanded at their posterior margins to become more spatulate. A partial throat osteoderm is present for PEFO 33978.

Morphotype B – midline and lateral osteoderms (Figs 18D, 19C, D): The midline osteoderms are situated in one or two rows dorsal to the neural spines. It is not clear how many osteoderms lie dorsal to the neural spine of each vertebra. The midline osteoderms are similar to the lateral osteoderms in that they both have a distinct anterior process. However, the midline osteoderms are symmetrical around the

anterior process. Some of the osteoderms have a weak midline keel, and others have many small lateral processes that terminate in small points.

The lateral osteoderms are diagnostic for *Vanckleavea*. All of the lateral osteoderms have an anteroventrally directed process that terminates in a sharp point. The process originates in the middle of the dorsal and ventral edges. The main body of the osteoderm is asymmetrical, with the ventral portion shorter and anteriorly inclined, and the dorsal portion directed dorsally and much deeper than the ventral portion. The posteriormost portion of the osteoderm ends in a point. The anteroventral process articulates with the posteroventral edge of the preceding osteoderm. Some of the lateral osteoderms have an anteroventrally



Figure 20. Reconstruction of *Vanclivea campi* based on GR 138. The lateral, ventral, appendicular and neck osteoderms have been removed. The outline of the body and tail is based on the width of the osteoderms. Scale bar, 10 cm.

oriented keel that stretches from the posterior point to the anteroventral process. A row of keeled osteoderms lies just ventral to the caudal vertebrae along the length of the tail. The keel becomes more developed posteriorly. The ventral osteoderms of the tail are very similar to the lateral osteoderms.

Morphotype C – ventral osteoderms (Figs 18B, 19B): These osteoderms are the largest osteoderms present and covered the ventral portion of the animal between the pectoral and pelvic girdles. Fragments are known from the holotype, although they are extremely small. They overlap on their anterior and ventral surfaces. In general morphology, they are ‘ovate’, and there are small projections around the edges that are rounded in cross-section. These projections each terminate in a small point. The more dorsolateral of these osteoderms have a sharp keel along their midlines that trends anteroposteriorly from the anterior to the posterior edges. Small foramina are randomly present on well-preserved specimens. These osteoderms are smooth, except for the keel. They are readily recognizable and are probably diagnostic to *Vanclivea*.

Morphotype D – vertical caudal osteoderms (Figs 18E, 19C): There are approximately 30 vertically oriented osteoderms. These form a vertical fin along the midline of the dorsal margin of the tail. It is unclear how close to the pelvis these osteoderms begin, but they are not anterior to the pelvis. Each osteoderm would be connected in life to its adjacent neighbour by soft tissue dorsal to the neural spines. There is a one-to-one alignment with the caudal vertebrae. These osteoderms continue almost to the tip of the tail, with the last caudal vertebra not bearing neural spines. The anteriormost osteoderms are the largest; posteriorly they become smaller overall, as well as smaller in height. The anteriormost are posteriorly swept at the posterodorsal margin, with the base of the osteoderms expanded laterally. There is an anteroposteriorly oriented groove between the lateral expansions. The dorsal portion of each osteoderm is mediolaterally compressed. Posterior vertical osteoderms are swept posteriorly, and the lateral expansion of the base is much less pronounced. Long &

Murry (1995) describe an osteoderm of this type in the holotype (PEFO 2427). A partial specimen is preserved in PEFO 33978.

Morphotype E – lateral osteoderms covering the limbs (Figs 13, 15, 18C): Small osteoderms surround both the fore- and hindlimbs. The osteoderms are not articulated, and it is not clear whether they actually formed an unbroken protective covering around the limbs or were randomly distributed around the limbs. The osteoderms are mediolaterally compressed, and some are oval-shaped or nearly circular. They are much thinner than the body osteoderms.

‘Stegosaurus spike’

In the original description of the holotype of *V. campi*, Long & Murry (1995) described a single ‘*Stegosaurus* [-like] spike’ osteoderm. The base is all that remains of the ‘spike.’ There are no osteoderms in GR 138 that are similar. For that reason, Hunt *et al.* (2005) suspected that this element does not belong to *Vanclivea* and, instead, belongs to a fragment of a projection (= spike) from an osteoderm of the aetosaur *Acaenasuchus*. However, the projections from osteoderms of *Acaenasuchus* are angular and covered with a pattern of small pits ornamenting the surface (Long & Murry, 1995). The ‘*Stegosaurus* [-like] spike’ from PEFO 2427 lacks both of these features, and therefore does not belong to *Acaenasuchus*. Nonetheless, the holotype specimen of *Vanclivea* was collected as float over a flat surface within a very rich vertebrate fossil horizon, and thus it is not clear whether all the elements collected with the holotype of *Vanclivea* belong to this specimen.

Reconstruction

A complete reconstruction lacking all osteoderms, except the vertical caudal osteoderms, is presented in Figure 20. *Vanclivea* (GR 138) was about 1.25 m long, had proportionally short limbs and an elongated body. The length of the body and the number of vertebrae can be estimated by the length of the osteoderms (black outline) in the articulated skeleton of GR 138. The slight disarticulation in the pelvic region and the twisting and compression of the skeleton allow for an error of 5–10%. The length of the chev-

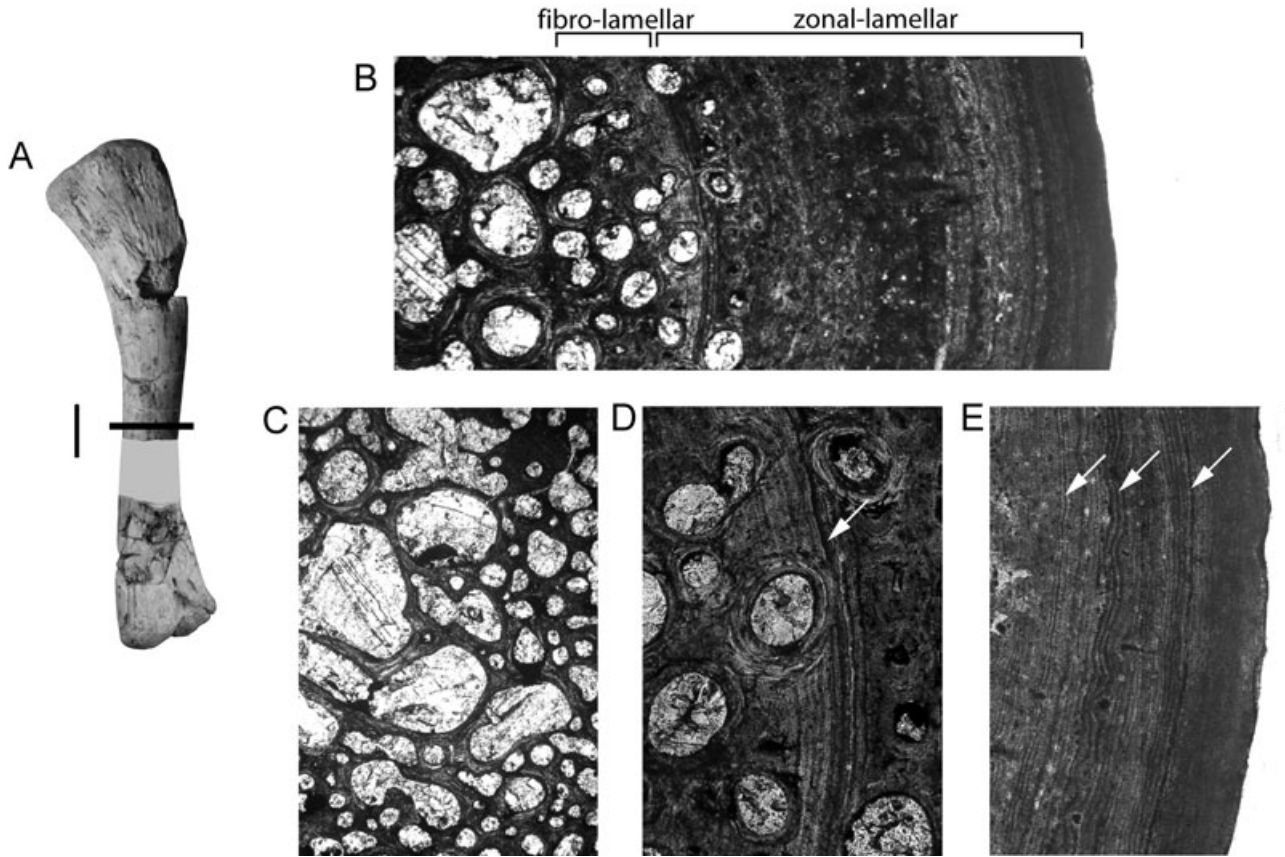


Figure 21. Femur (A) of *Vanclavea campi* (UCMP 152662) showing where the histological section was taken. A histological section of the femur was taken from the midshaft illustrating the complete section (B) and close-ups of the inner cortex (C), middle cortex (D) and outer cortex (E). Arrows indicate lines of arrested growth (LAGs). Scale bar, 1 cm.

rons is estimated on the basis of the depth of the osteoderms surrounding the tail, and the limbs are scaled to the rest of the body.

Bone histology

A large femur (UCMP 152662; Fig. 21) from the Petrified Forest Member of the Chinle Formation within the Petrified Forest National Park can be assigned to *Vanclavea* based on the following combination of characters: (1) the poor ossification of the attachment site of *M. caudifemoralis*; (2) thick cortical bone; (3) the absence of distinct proximal tubera; and (4) an arced proximal head. The specimen was sectioned near midshaft and then examined using non-polarized and polarized light microscopy.

The well-preserved bone is circular in cross-section. Cancellous tissues fill the medulla completely. Nearly all of the interstitial spaces are at least partially lined with lamellar bone (Fig. 21C). The cancellous bone is clearly formed by reabsorption of the cortical tissues and then partially infilled with one to six lamellae;

however, the number of lamellae differs across the medulla.

Lamellar zonal bone tissue comprises much of the entire radius of the femur. The most obvious line of arrested growth (LAG) lies halfway through the cortex. Four distinct LAGs (Fig. 21B, D, E) are present. The bone only bears longitudinal vascular canals, and they decrease in abundance periosteally. Only a few secondary osteons (Haversian systems) are present near the centre of the bone, and they are completely absent in the lamellar zonal bone tissues. No calcified cartilage is present in the sections studied here.

Bone histology records growth and life history strategies (Chinsamy, 1993, 1994; Reid, 1997a, b; Curry, 1999; Horner, de Ricqlés & Padian, 2000; Sander, 2000). Numerous studies have shown qualitatively, as well as more recently quantitatively, that the bone microanatomy of terrestrial and aquatic organisms differs (Nopcsa, 1923; Wall, 1983; Currey & Alexander, 1985; de Ricqlés & de Buffrénil, 2001; Laurin, Giron-

dot & Loth, 2004; Germain & Laurin, 2005; Laurin *et al.*, 2006; Krilloff *et al.*, 2008). The peculiarly thick cortex and infilling of the marrow cavity in *Vanleavea* differ from observations in other archosauriforms for which histological specimens are available [e.g. pseudosuchians (de Ricqlés, Padian & Horner, 2003), *Erythrosuchus* (de Ricqlés, 1976)]. Other archosauriforms (see de Ricqlés *et al.*, 2003, 2008) possess fibrolamellar bone tissues in the centre and throughout the cortex, tissues that the femur of *Vanleavea* lacks. The thick cortex and the lamellar infilling of the medulla of the femur of *Vanleavea* closely match those of the bones of aquatic-adapted tetrapods. de Ricqlés & de Buffrénil (2001) extensively reviewed and compared aquatic tetrapod histological sections, and found that aquatic tetrapods display histological specializations (e.g. pachyostosis). The specializations of the histology of the femur of *Vanleavea* match closely with other taxa with pachyostosis. According to de Ricqlés & de Buffrénil (2001), the pachyosteosclerotic condition combines the pachyostotic condition (thickened, finely laminated cortex) with the osteosclerotic condition (thickening of the medulla). However, the femoral radius of *Vanleavea* is not expanded (relative to other archosauriforms), when compared with the ribs and other long elements of pachyostotic taxa (e.g. *Mesosaurus*, sirenians). Furthermore, a rib of *Vanleavea* was sectioned and, although the cortex is rather thick, it does not reach the expanded dimensions of taxa with pachyostotic ribs.

Our current understanding of non-archosaurian archosauriform histology is preliminary, but new data from de Ricqlés *et al.* (2008) suggest that the close relatives of *Vanleavea* do not share the same histological specializations. For example, the medullary cavity of a rib and metatarsal of *Erythrosuchus* (Gross, 1934; de Ricqlés *et al.*, 2008), as well as that of a humerus of *Euparkeria*, is open. In addition, the sampled bones of these two taxa are more vascularized with more radial anastomoses in comparison with that of the femur of *Vanleavea*. These comparisons must be re-evaluated once the same elements of each taxon can be compared and more basal archosauriforms are sampled (e.g. proterochampsids).

The medullary cavity of the femur of *Vanleavea* contains a network of cavities partially filled by dense deposits of endosteal bone. In contrast with taxa with extensive Haversian tissues near the inner cortex (e.g. *Claudiosaurus*, *Mesoplodon*; de Ricqlés & de Buffrénil, 2001), the femur of *Vanleavea* has only a few sparsely distributed Haversian tissues. In accordance with the aquatic skeletal adaptations described below, the similarities of the compact bone tissues of the femur and ribs of *Vanleavea* with those of aquatic tetrapods support the hypothesis that *Vanleavea* had at least a semi-aquatic lifestyle.

DISCUSSION

PHYLOGENETIC RELATIONSHIPS OF *VANLEAVEA* AND BASAL ARCHOSAURIFORMES

Vanleavea possesses an interesting suite of character states never before sampled in an archosauromorph, in addition to a plethora of autapomorphic features. For example, *Vanleavea* lacks an antorbital fenestra and a supratemporal fenestra, character states generally found outside Archosauriformes, but it also possesses a variety of osteoderms, the absence of an astragalocalcaneal canal and a fully ossified laterosphenoid, character states common in archosauriforms. To test the relationships of *Vanleavea*, we placed it into a phylogenetic analysis with non-archosauriform archosauromorphs, non-archosaurian archosauriforms and members of Archosauria. *Postosuchus* and *Dromicosuchus* serve as representatives of Pseudosuchia, whereas *Herrerasaurus* and *Coelophysis* serve as representatives of Ornithodira. The character set was constructed from many previously used early archosauriform characters (Gauthier, 1984; Benton, 1985, 1990, 1999, 2004; Benton & Clark, 1988; Gauthier, Kluge & Rowe, 1988; Sereno, 1991; Parrish, 1992, 1993; Juul, 1994; Bennett, 1996; Gower & Sennikov, 1996, 1997; Dilkes, 1998; Benton *et al.*, 2000); 11 new characters were also included. Characters that were useful in resolving ingroup relationships among proterosuchians and erythrosuchians in Gower & Sennikov (1997) were excluded. *Proterosuchus fergusi* was used to represent proterosuchians, and *Erythrosuchus* was used to represent erythrosuchians, because the monophyly of both clades has not been fully tested; this is beyond the scope of this paper.

The data matrix includes 12 taxa and 50 characters. *Mesosuchus* was set as the outgroup. A heuristic search was performed with 10 000 random addition (RA) replicates using tree bisection and reconnection (TBR) branch swapping in PAUP* v4.0b10 (Swofford, 2002). Nodal support was examined using nonparametric bootstrapping, with 1000 bootstrap replicates, TBR branch swapping and 10 RA sequences. Decay indices were calculated using TreeRot v2c (Sorenson, 1999). Character state transformations were evaluated under both ACCTRAN and DELTRAN optimizations.

The phylogenetic analysis resulted in a single most parsimonious tree [Fig. 22; tree length = 67, consistency index (CI) = 0.761, retention index (RI) = 0.843]. The results generally agree with hypotheses previously obtained for basal archosauriforms (Juul, 1994; Bennett, 1996; Gower & Sennikov, 1996, 1997; Benton, 2004). *Vanleavea* is well supported as a non-archosaurian archosauriform. Although *Vanleavea* preserves a multitude of autapomorphic characters unparalleled among basal archosauriforms, the

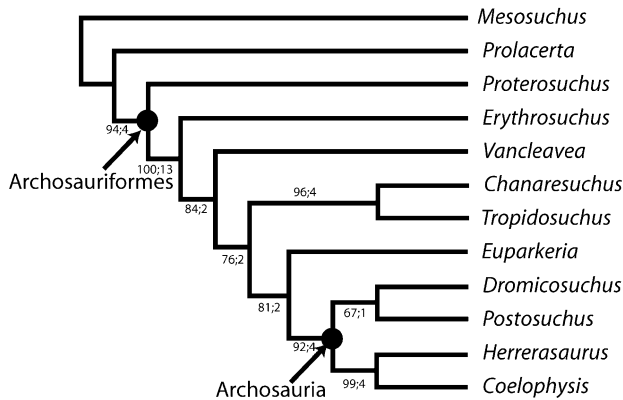


Figure 22. Archosauriform relationships with the inclusion of *Vanclleavea campi*. The unique tree [12 taxa; 50 characters; characters weighted equally; one ordered (character 5); tree length, 67; consistency index (CI), 0.761; retention index (RI), 0.843]. Support values (left, bootstrap; right) are listed at each node.

following three characters support a closer relationship to Archosauria than to *Erythrosuchus*: postaxial intercentra absent (25: 0→1); femoral distal condyles not projecting markedly beyond shaft (35: 0→1); and osteoderms present (50: 0→1). It is clear from the phylogenetic position of *Vanclleavea* that the upper temporal, antorbital and, possibly, mandibular fenestrae have been lost secondarily. Here, we obtain *Euparkeria* as the sister taxon to Archosauria. *Euparkeria* + Archosauria is supported by the following unambiguous synapomorphies: calcaneal tuber shaft proportions at the midshaft of the tuber about the same or broader than tall (43: 0→1); and the posterior corner of the dorsolateral margin of the astragalus dorsally overlaps the calcaneum much more than the anterior portion (44: 0→1).

Furthermore, we preliminarily tested the monophyly of Proterochampsidae and found that the two hypothesized members of Proterochampsidae, *Tropidosuchus* and *Chanaresuchus*, formed a monophyletic group diagnosed by the following characters: quadratojugal lateral surface with a ridge marking the posteroventral corner of the lower temporal fossa (11: 0→1); ischium about the same length or shorter than the dorsal margin of the iliac blade (29: 1→0); metatarsal II midshaft diameter more than the midshaft diameter of metatarsal I (47: 0→1); and metatarsal IV reduced where the midshaft diameter is less than metatarsal III (48: 0→1). The proterochampsids are in need of a critical taxonomic and systematic review. Although this is beyond the scope of this paper, the findings here serve as a starting point for future investigations.

This analysis also found Archosauria consisting of Pseudosuchia and Ornithodira, as hypothesized in all previous analyses of Archosauria. However, this study hypothesized a strongly supported Archosauria, whereas, in previous studies, Archosauria was only supported by two or fewer unambiguous synapomorphies. Moreover, many of the character states supporting Archosauria in previous analyses (see Juul, 1994 for comments) have been found to have a wider distribution in basal archosauriforms, are poorly defined or are not found in newly discovered basal members of the Archosauria. Here, Archosauria is supported by five unambiguous synapomorphies including: antorbital fossa 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) (5: 0→1); palatal teeth on the palatal process of the pterygoid absent (9: 0→1); entrance of the internal carotid arteries on the lateral side of the parabasisphenoid (20: 0→1); semilunar depression on the lateral surface of the basal tubera of the parabasisphenoid absent (24: 0→1); and the articular surfaces for the fibula and distal tarsal IV on calcaneum continuous (41: 0→1).

This analysis confirms the hypothesis of Small & Downs (2002) that *Vanclleavea* is an archosauriform rather than a choristodere (*contra* Downs & Davidge, 1997). Here, we find *Vanclleavea* to be a non-archosaurian archosauriform. As a stem archosaur, *Vanclleavea* is one of the geologically youngest non-archosaurian archosauriforms. Other than *Vanclleavea*, proterochampsids from South America and *Doswellia* from North America remain the only other Late Triassic non-archosaurian archosauriforms. Furthermore, *Vanclleavea* represents one of only a few Laurasian non-archosaurian archosauriforms. Others include the enigmatic *Doswellia* from the Late Triassic of Virginia (Weems, 1980; Benton & Clark, 1988) and Texas (Long & Murry, 1995) and several erythrosuchians from the Middle Triassic of Russia and China (Parrish, 1992; Gower & Sennikov, 2000). At present, it is apparent that *Vanclleavea* is the geologically youngest surviving non-archosaurian archosauriform, and that this paraphyletic group did not survive into the Jurassic.

VANCELEAVEA: SPECIES-LEVEL TAXON OR MULTIPLE TAXA?

The holotype of *Vanclleavea* (PEFO 2427) consists of a fragmentary partial skeleton collected as float. Although well preserved, many of the elements are incomplete. It is clear from comparisons between the holotype and GR 138 that both are closely related. As noted above, they both share all of the autapomorphies listed in Long & Murry (1995) and others listed

here. Furthermore, the large number of unique character states and the unique osteoderms present in the holotype allow easy recognition of the taxon from Late Triassic sediments from the western USA (Hunt *et al.*, 2002) (see Appendix 1). Hunt *et al.* (2002) demonstrated that specimens referable to *Vancleavea* are found throughout the stratigraphic sequence of Late Triassic rocks in the western USA. The time between the earliest occurrence and latest occurrence spans nearly 20 Myr, suggesting that abundant remains of *Vancleavea* may represent a clade instead of a single species.

However, separating out species-level taxa from the current specimens of *Vancleavea* is difficult at present. Many of the identifiable specimens consist solely of osteoderm or centrum fragments. Although the osteoderms are highly diagnostic for *Vancleavea*, they may be useless in identifying species-level taxa, given the large variation found in GR 138; for example, the lateral and ventral morphotypes of osteoderms grade into one another. In addition, dorsal centrum morphology varies along the vertebral column, and there is no complete dorsal series available for study.

It is exceedingly difficult to distinguish taxonomic variation from ontogenetic or individual variation, given the scant fossil record of partial or complete skeletons of *Vancleavea*. The four most complete specimens (PEFO 2427, PEFO 33978, GR 138 and GR 139), discussed in this description, lack much overlapping material. PEFO 2427, PEFO 33978 and GR 138 possess humeri, and these are used as a baseline for size comparisons among the specimens (maximum width across the proximal end: PEFO 2427, ~19 mm; PEFO 33978, ~21 mm; GR 138, ~14 mm).

There are some potential differences among the different specimens. For example, the dentaries of GR 138 and PEFO 33978 are nearly the same anteroposterior length (8 cm), whereas the maximum dorsoventral length of the dentary of PEFO 33978 (~29 mm) is nearly 2.3 times that of GR 138 (13 mm). This may represent allometric growth of the dentary in a single species-level taxon. Other differences include the size of the muscle scar for the attachment of *M. caudifemoralis*. In PEFO 2427, the muscle scar is much more distinct compared with that of GR 138, where the muscle scar is small and poorly developed. In addition, the supra-acetabular rim of the ilium is slightly more robust and sharp in PEFO 2427 than in GR 138. It is unclear whether the differences in these specimens are of systematic or ontogenetic importance when compared with the smallest specimens (GR 138 and GR 139). We conclude that the present evidence is ambiguous with regard to whether differences among the specimens are ontogenetic or taxonomic.

Therefore, we refer all of the *Vancleavea*-like specimens to *V. campi*.

MODE OF LIFE OF *VANCLEAVEA*

The unique morphology of the skeleton of *Vancleavea* greatly differs from that of its closest relatives and all other archosauriforms. Some of the unusual features of *Vancleavea* (dorsally directed naris, elongated body with short limbs, deep tail with vertical osteoderms) led Small & Downs (2002) to postulate that *Vancleavea* may have been semi-aquatic. In contrast, Hunt *et al.* (2002, 2005) drew on taphonomy and faunal associations of *Vancleavea* to infer a more terrestrial lifestyle. Here, we evaluate and discuss each hypothesis. In addition to many morphological features throughout the skeleton of GR 138, the taphonomy and sedimentology of the *Coelophysis* Quarry and other *Vancleavea* localities offer support to the hypothesis of at least a semi-aquatic palaeoecology for *Vancleavea*. The following paragraphs discuss the morphological features of *Vancleavea* that are consistent with morphological features exclusive to extinct and extant semi- or fully aquatic taxa in which behaviour and osteology can be compared.

Semi-aquatic taxa usually bear a suite of morphological characters associated with locomotion in water. Taxa that are semi-aquatic use two major methods of moving through the water: 'flipper-driven' taxa possess limbs that have been modified to be paddle-like, whereas 'tail-driven' taxa typically possess less modified limbs, but have elongated tails that form a mediolaterally compressed fin (Carroll, 1988). *Vancleavea* clearly possesses the latter, given the dorsoventrally deep tail and the absence of paddle-like appendages. The tail of *Vancleavea* is composed dorsally of long, slender, back-swept neural spines and dorsoventrally elongated osteoderms (type D, vertical caudal osteoderms). *Vancleavea* is unique in this respect; *Vancleavea* is the only taxon to create a dorsally tall tail with osteoderms. This feature has been cited previously as support for a 'sculling tail' (Small & Downs, 2002), and that view is adopted here. Dorsoventrally elongated tails are common to aquatic taxa that employ lateral undulatory locomotion (e.g. chondrichthyans, actinopterygians, ichthyosaurs, mosasaurids). The intervertebral articulations in the caudal vertebrae of *Vancleavea* would allow lateral translation, but prevent much dorsoventral translation. The tail of *Vancleavea* is similar to that of mosasaurids and marine crocodylians, such as metriorhynchids, because it is mediolaterally compressed and dorsoventrally tall, possibly possessing a fleshy fluke (see Lindgren *et al.*, 2008), although *Vancleavea* is unique in this respect. Massare (1988) categorized mosasaurids and marine crocodylians as

'axial undulatory', and found that their morphology was best suited for fast starts and lunging, traits that would indicate an ambush prey strategy. Because *Vancleavea* shares a mediolaterally compressed and dorsoventrally tall tail with mosasaurids and metriorhynchids, this could also have been a possible approach to prey acquisition for *Vancleavea*.

Small & Downs (2002) stated that reduced limb proportions also indicate that *Vancleavea* may have been semi-aquatic. Reduced limbs are often an indication that the tail provides the major propulsive movements in a taxon (Romer, 1956), and the inferred tail fin in *Vancleavea* is consistent with this idea. Although the length of the limbs, when compared with the body length, appears to be quite short in *Vancleavea* on first inspection, a close comparison of the presacral length with the hindlimb/forelimb length from a closely related taxon, *Euparkeria* (SAM 5867), indicates that the two taxa have similar ratios. In both taxa, the forelimbs are approximately one-quarter of the presacral length. In addition, the presacral length versus tail length was also comparable between the two taxa, although the tail depth is much greater in *Vancleavea*; thus, the limbs are not actually shortened when compared with those of closely related taxa. This does not preclude a semi-aquatic palaeoecology for *Vancleavea*.

The entire body of *Vancleavea* possesses flat-lying osteoderms. Hunt *et al.* (2002, 2005) argued that the heavy armour could be 'more consistent with a non-aquatic ecology', but they did not offer any support for this argument. Although many taxa with osteoderms are terrestrial, semi-aquatic taxa, such as phytosaurs, placodonts, turtles, thalattosuchians and crocodylians, retain an extensive covering of osteoderms. The highly sculptured osteoderms of phytosaurians and crocodylians, however, differ from the mostly smooth and more delicate osteoderms of *Vancleavea*.

As described above, the osteohistology of the femur of *Vancleavea* is consistent with taxa that have pachyosteosclerotic limb bones. This type of bone thickening of the limbs, where the cortex is thickened and finely laminated and the internal medullary cavity is also thickened, together with infilling of the marrow cavity, is common in aquatic-adapted tetrapods (de Ricqlés & de Buffrénil, 2001; Laurin *et al.*, 2004; Krilloff *et al.*, 2008). Alone, the histology does not indicate that *Vancleavea* was semi-aquatic. However, the histology is consistent with a semi-aquatic palaeoecology.

One of the strongest features suggesting a semi-aquatic mode of life is the presence of dorsally oriented nares (Small & Downs, 2002). Although the nares are not located at the dorsalmost extent of the skull of *Vancleavea*, the external nares are open dorsally. Nares that are directed dorsally are common to

semi-aquatic taxa, such as crocodylians and phytosaurs (Camp, 1930), which are postulated to have had a similar ecology (Hunt, 1989; Hungerbühler, 2002). Plesiosaurs and mesosaurs, other aquatic reptiles, also had dorsally oriented nares (Mazin, 2001; Modesto, 2006), and this morphology is exemplified by the condition present in whales and dolphins (Fordyce & Muizon, 2001). Reorienting the external nares to face dorsally rather than anteriorly allows the individual to stay almost totally submerged while breathing. As far as is known, dorsally directed nares are not present in any fully terrestrial taxon. Neither *Proterosuchus* (Welman, 1998) nor *Erythrosuchus* (Gower, 2003) possesses dorsally directed nares, thus indicating that the condition in *Vancleavea* is not common among basal Archosauriformes. However, dorsally directed nares have been described in proterochampsids (Romer, 1971). Given that both proterochampsids and *Vancleavea* have dorsally directed nares, it is unclear what the plesiomorphic condition (the direction of the external nares) would be for *Erythrosuchus* + Archosauria.

Despite the morphological specialities, Hunt *et al.* (2002, 2005) cited faunal associations and taphonomy as their main line of evidence for terrestriality in *Vancleavea*. However, the faunal associations observed in the death assemblage may not reflect the actual taxonomic composition of the original fauna (Brandt, 1989). *Vancleavea* specimens have been found throughout the Late Triassic deposits of western North America (see Appendix 1). The depositional environment of the *Coelophys* Quarry, the locality from which GR 138 was collected, was interpreted by Schwartz & Gillette (1994) to have been an abandoned channel in a semi-arid fluvial depositional system. This locality is renowned for its many theropods, as well as other taxa considered to be terrestrial (e.g. crocodylomorphs, drepanosaurids, 'rauisuchians'), but also preserves the remains of fishes (Schaeffer, 1967). Polcyn *et al.* (2002) also reported lungfish teeth and other fish remains from Stinking Springs, Arizona, an additional locality in which *Vancleavea* was collected. Polcyn *et al.* (2002) postulated that the sedimentology of the locality represented a stable, low-energy aquatic environment. Murry (1989), Murry & Long (1989) and Heckert (2004) also reported several aquatic taxa found with *Vancleavea* remains in the Petrified Forest National Park. In every locality that has produced *Vancleavea* specimens, the sedimentology has indicated a fluvial depositional system. This type of deposition is common to the Chinle Formation (Stewart, Poole & Wilson, 1972; Woody, 2003, 2006), which is dominated by bentonitic mudstones that are interspersed with sandstones and conglomerates representing floodplain/overbank deposits and channel facies, respectively. The large

number of postulated terrestrial vertebrates in each locality (Harris & Downs, 2002; Polcyn *et al.*, 2002) does not determine the ecology of all the vertebrates found at the locality, when clearly aquatic taxa (e.g. fishes) are present and the sediments indicate that they were deposited by water. Furthermore, a fossil assemblage may contain taxa that are usually an ephemeral aspect of the living fauna, but which have the potential to be preserved in that death assemblage at any time, thus preserving a misleading or unusual assemblage of taxa (Kidwell & Behrensmeyer, 1988). Therefore, the sedimentology of the localities in which *Vancleavea* is found is consistent with the aquatic adaptations in the skeleton of this taxon.

A re-examination of the morphological, sedimentary and taphonomic evidence provides support for a semi-aquatic mode of life for *Vancleavea*. The dorsally directed nares, mediolaterally compressed and dorsoventrally expanded tail, and pachyosteosclerotic bone histology are congruent with the morphology of other semi-aquatic taxa and, rather than supporting a terrestrial habit, the taphonomy of the *Coelophysys* Quarry provides evidence of a fluvial depositional system in which terrestrial and aquatic taxa were preserved.

CONCLUSIONS

Vancleavea campi bears great importance for the early evolution of archosauriforms for a number of reasons. *Vancleavea* is the geologically youngest early archosauriform yet described. Specimens of *Vancleavea* from the American Southwest represent one of only a few basal archosauriforms from Laurasia. Next, the taxon is represented by nearly complete material from both articulated and associated skeletons. *Vancleavea* is one of the most complete stem archosaur taxa known to which all other archosauriforms can be compared. Third, although *Vancleavea* has a unique, highly autapomorphic morphology, it occupies a morphological gap between *Erythrosuchus* and Proterochampsidae + Archosauria. *Vancleavea* is found throughout the Chinle Formation and Dockum Groups, suggesting that the taxon was very successful through much of the deposition of the Late Triassic in the American Southwest.

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APPENDIX 1: REFERRED SPECIMENS

MESA REDONDO MEMBER, CHINLE FORMATION

MNA Loc. 207C, V 3669: anterior dorsal centrum; *Placerias* Quarry, Arizona.
 MNA Loc. 207C, V 3670: dorsal centrum; *Placerias* Quarry, Arizona.
 UCMP 152646: caudal vertebra; *Placerias* Quarry (A269), Apache County, Arizona.

MONITOR BUTTE MEMBER, CHINLE FORMATION

UCM 76193 [in partim], proximal portion of a humerus (see Parrish, 1999: fig. 3a); Blue Lizard Locality, Utah.

BLUE MESA MEMBER, CHINLE FORMATION

PEFO 2427: holotype, partial postcranial skeleton; near Crocodile Hill (PFV 124), Petrified Forest National Park, Arizona.
 PEFO 4855: centrum, Dying Grounds (PFV 122), Petrified Forest National Park, Arizona.
 PEFO 34224: distal portion of a femur, locality unknown; Petrified Forest National Park, Arizona.
 PEFO 34231: sacral centrum, locality unknown; Petrified Forest National Park, Arizona.
 UCMP 152647: caudal vertebra; Crocodile Hill (PFV 124), Petrified Forest National Park, Arizona.
 UCMP 178046: dorsal centrum; Phytosaur Basin, UCMP 7040 (PFV 121), Petrified Forest National Park, Arizona.

SONSELA MEMBER, CHINLE FORMATION

UCMP 178050: caudal vertebra and fragments; Saurian Valley, UCMP V82251 (PFV 097), Petrified Forest National Park, Arizona.

PETRIFIED FOREST MEMBER, CHINLE FORMATION

GR 148: osteoderm; Canjilon Quarry, New Mexico.
 PEFO 16749: osteoderm fragments; Rap Hill (PFV 216), Petrified Forest National Park, Arizona.
 PEFO 16756: osteoderm fragments; Rap Hill (PFV 216), Petrified Forest National Park, Arizona.
 PEFO 31202: left femur; Zuni Well Mound (PFV 215), Petrified Forest National Park, Arizona.
 PEFO 33978: partial skeleton; The Giving Site (PFV 231), Petrified Forest National Park, Arizona.

PEFO 34035: partial skeleton; Zuni Well Mound (PFV 215), Petrified Forest National Park, Arizona.

PEFO 34077: vertebrae and fragments; The Giving Site (PFV 231), Petrified Forest National Park, Arizona.

PEFO 34170: caudal centrum, Dinosaur Hill (PFV 040), Petrified Forest National Park, Arizona.

PEFO 34234: caudal centrum, The Giving Site (PFV 231), Petrified Forest National Park, Arizona.

SMU 74998: disarticulated skull and skeleton; (SMU locality 253) Stinking Springs I, Arizona.

UCMP 152662: femur; Dinosaur Hill (PFV 040), Petrified Forest National Park, Arizona.

UCMP 165196: isolated basioccipital; Dinosaur Hill (PFV 040), Petrified Forest National Park, Arizona.

UCMP 165197: partial ilium; Dinosaur Hill (UCMP locality V82250) (PFV 040), Petrified Forest National Park, Arizona.

UCMP 165199: centrum; Dinosaur Hill (UCMP locality V82250) (PFV 040), Petrified Forest National Park, Arizona.

OWL ROCK MEMBER, CHINLE FORMATION

MNA V7205: femur; MNA locality 853-1, Ward Terrace, Arizona.

? ROCK POINT MEMBER, CHINLE FORMATION

SMU 27099: osteoderm; Red Rock Valley (SMU locality 118), Arizona.

SMU 27092: osteoderm; Red Rock Valley (SMU locality 118), Arizona.

'SILTSTONE MEMBER', CHINLE FORMATION

GR 138: complete skeleton; *Coelophys* Quarry, Ghost Ranch, Rio Arriba County, New Mexico.

GR 139: disarticulated skeleton; *Coelophys* Quarry, Ghost Ranch, Rio Arriba County, New Mexico.

BULL CANYON FORMATION

NMMNH P-4984: partial skeleton; locality 522, Bull Canyon, near Tucumcari, New Mexico.

NMMNH P-20852: centra; locality 5, Bull Canyon, near Tucumcari, New Mexico.

UMMP 7441: proximal portion of a humerus; Quay County, New Mexico.

REDONDA FORMATION

NMMNH P-36150: osteoderms; J. T. Gregory's Quarry 2, Apache Canyon, New Mexico.

YPM 4265: osteoderms; J. T. Gregory's Quarry 2, Apache Canyon, New Mexico.

- YPM 4268: osteoderms; J. T. Gregory's Quarry 2, Apache Canyon, New Mexico.
 YPM 4270: osteoderms; J. T. Gregory's Quarry 2, Apache Canyon, New Mexico.
 YPM 4271: osteoderms; J. T. Gregory's Quarry 2, Apache Canyon, New Mexico.
 YPM 4272: osteoderms; J. T. Gregory's Quarry 2, Apache Canyon, New Mexico.
 YPM 4273: osteoderms; J. T. Gregory's Quarry 2, Apache Canyon, New Mexico.
 YPM 4274: osteoderms; J. T. Gregory's Quarry 2, Apache Canyon, New Mexico.
 YPM 4275: osteoderms; J. T. Gregory's Quarry 2, Apache Canyon, New Mexico.
 YPM 4276: osteoderms; J. T. Gregory's Quarry 2, Apache Canyon, New Mexico.
 YPM uncatalogued (field number 1957/24): osteoderms; J. T. Gregory's Quarry 2, Apache Canyon, New Mexico.

TECOVAS FORMATION, DOCKUM GROUP

UMMP 13712: humerus; Sierrita de la Cruz Creek, Potter County, Texas.

APPENDIX 2: TERMINAL TAXA

Mesosuchus browni Watson, 1912

Age: Scathyan–Anisian.

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

Holotype: SAM 5884, partial skull and partial skeleton.

Referred to and scored material discussed below: SAM 6536, complete well-preserved skull and anterior half of the skeleton; SAM 7416, partial postcranial skeleton.

Remarks: Together with *Howesia*, *Mesosuchus* was found to be more closely related to the rhynchosaur *Hyperodapedon* than to other archosauromorphs (Dilkes, 1998). As the basalmost member of the Rhynchosauria, *Mesosuchus* preserves plesiomorphic archosauromorph character states absent in most rhynchosaurs. For example, *Hyperodapedon*, one of the most derived rhynchosaurs (Langer & Schultz, 2000), lacks palatal teeth and has a greatly expanded posterior skull table not found in *Mesosuchus* (Dilkes, 1998).

Key references: Watson, 1912; Broom, 1925; Dilkes, 1998

Prolacerta broomi Parrington, 1935

Age: Lower Triassic.

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

Holotype: UMZC 2003.40, partial skull and mandible.

Referred to and scored material discussed below: BP/1/471, complete skull; BP/1/2675, nearly complete skull with postcrania; BP/1/2676, nearly complete skeleton; UCMP 37151, skull; AMNH 9502, postcranial skeleton.

Remarks: *Prolacerta* is known from multiple well-preserved skulls and articulated postcranial skeletons. *Prolacerta* has received much attention in the literature and careful descriptions of multiple specimens are available (see key references). *Prolacerta* has had a long history of disagreement about its relationships (Modesto & Sues, 2004). Most recently, Dilkes (1998) found *Prolacerta* to be closer to Archosauria than to other 'prolacertiforms' (e.g. tanystropheids). This interpretation was originally supported by Gow (1975) and by a subsequent paper redescribing the skull (Modesto & Sues, 2004). *Prolacerta* serves as an outgroup to the Archosauriformes.

Key references: Parrington, 1935; Camp, 1945; Gow, 1975; Colbert, 1987; Evans, 1988; Gower & Sennikov, 1996; Dilkes, 1998; Modesto & Sues, 2004

Proterosuchus fergusi Broom, 1903

Age: Lower Triassic.

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

Holotype: SAM 591, partial skull.

Referred to and scored material discussed below: TM 201, incomplete skull; RC96, complete skull; BSP 514, nearly complete skull and anterior cervical vertebrae; QR 1484 (also listed as NMC 3016), complete skull and nearly complete articulated skeleton; AMNH FR 2237, fragmentary postcranial skeleton with nearly complete articulated leg; BP/1/3993, nearly complete skull with braincase.

Remarks: *Proterosuchus* is one of the most completely understood archosauriforms known from multiple complete skulls and articulated and disarticulated material from the Early Triassic of South Africa.

Much of the material is fully prepared, and many specimens have been described and illustrated. However, most of the specimens, when described, were named as new taxa. Welman & Flemming (1993) and Welman (1998) examined all of the *Proterosuchus*-like skulls from the Early Triassic of South Africa (*Proterosuchus*, *Elaphrosuchus*, *Chasmatosaurus*) and found that all of the differences cited among the taxa are either obscured by matrix or other bones, non-existent or consistent with a growth series of one taxon. Therefore, Welman (1998) attributed all known specimens of *Proterosuchus*-like skulls (*Proterosuchus*, *Elaphrosuchus*, *Chasmatosaurus*) to *Proterosuchus fergusi*. Here, we follow Welman's (1998) revision. The Chinese *Chasmatosaurus* material was not included in Welman's (1998) study and is not utilized here.

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

Erythrosuchus africanus Broom, 1905
Age: Scathyian–Anisian.

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

Holotype: SAM 905, incomplete postcranial skeleton.

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

Remarks: *Erythrosuchus* was collected from the *Cynognathus* Assemblage Zone for over 120 years, but was only recently described in sufficient detail (Gower, 1996, 1997, 2003). This large archosauriform has consistently been found as a member of Archosauriformes and has widely been used to represent all erythrosuchians, a group whose monophyly has only been examined once (Parrish, 1992). Gower (2003) concluded that all of the *Erythrosuchus*-like material from the *Cynognathus* Assemblage Zone should be assigned to the taxon *Erythrosuchus africanus*, because there is no evidence of any other erythrosuchian from the *Cynognathus* Assemblage Zone. *Erythrosuchus* is used here to represent all erythrosuchians.

Key references: Broom, 1905; Huene, 1911; Charig & Reig, 1970; Cruickshank, 1978; Gower, 1996, 1997, 2003.

Vancleavea campi Long & Murry, 1995
Age: Late Triassic (?Carnian–?Rhaetian)

Occurrence: See Appendix 1.

Holotype: PEFO 2427, an incomplete postcranial skeleton.

Referred to and scored material discussed below: GR 138, complete skeleton; GR 139, partial disarticulated skeleton.

Remarks: See text.

Key references: Long & Murry, 1995; Hunt *et al.*, 2002, 2005; Small & Downs, 2002; this paper.

Euparkeria capensis Broom, 1913
Age: Scathyian–Anisian.

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

Holotype: SAM 5867, skull and partial skeleton.

Referred to and scored material discussed below: SAM 6050, partial skull; SAM 6047b, vertebrae, femur, pelvis, pectoral girdle; SAM 6049, dorsal, sacral and caudal vertebrae, right hindlimb, and partial pelvic and pectoral girdles; SAM 6047a, skull, vertebrae and limb fragments; UMCZ T692, articulated foot with astragalus and calcaneum removed.

Remarks: *Euparkeria* has been regarded as one of the most important basal archosaurs for archosaur phylogeny, given the abundance of specimens, excellent preservation and many detailed descriptions of the anatomy. The unspecialized skeleton and skull of *Euparkeria* relative to the derived skulls of proterochampsids and the close relationship to Archosauria have made *Euparkeria* an excellent candidate for the outgroup taxon of Archosauria and Dinosauria. However, proterochampsids (Serenó, 1991; Juul, 1994; Benton, 1999) and *Euparkeria* (Benton & Clark, 1988) have both been found as the closest sister taxon to Archosauria.

Key references: Broom, 1913; Ewer, 1965; Gower & Weber, 1998; Senter, 2003.

Tropidosuchus romeri Arcucci, 1990

Age: Anisian–Ladinian.

Occurrence: Los Chañares Formation, Argentina.

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

Referred to and scored material discussed below: PVL 4602, vertebral column, hindlimbs and partial skull; PVL 4603, complete vertebral column, posterior portion of the skull, osteoderms; PVL 4604, pectoral and forelimb elements; PVL 4605, much of an articulated skeleton including skull; PVL 4606, complete skull, presacral vertebrae, pelvic girdle and hindlimb elements; PVL 4624, hindlimb elements.

Remarks: *Tropidosuchus* is one of the most complete proterochampsids, but the least described or referred. The well-preserved, articulated material includes nearly all elements, except the ulna, radius and the manus. The skull is relatively small compared with the body in comparison with the other proterochampsids from the same formation (*Chanaresuchus*, *Gualosuchus*) and from the Late Triassic period. Details of the ankle and foot derive from the articulated (right) and disarticulated (left) hindlimbs of PVL 4601.

Key reference: Arcucci, 1990.

Chanaresuchus bonapartei Romer, 1971

Age: Anisian–Ladinian.

Occurrence: Los Chañares Formation, Argentina.

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

Referred material scored and discussed below: PVL 4586, skull; PVL 4575, complete skull and nearly complete postcranial skeleton; PVL 4647, braincase and partial skull; MCZ 4035, complete skull and postcrania; MCZ 4036, skull and most of the postcranium.

Remarks: As with *Tropidosuchus*, *Chanaresuchus* is known from complete skull material and nearly the complete postcranium from the Middle Triassic Chanares Formation of Argentina. Romer (1971, 1972) described much of the cranium and postcranium from the Harvard specimens, whereas little has been described of the specimens housed in Argentinean

museums (PVL, UPLR). Few studies have mentioned these taxa since Romer's initial descriptions, and the monophyly of the proterochampsids remains largely untested. Although there is no material that overlaps in size between *Chanaresuchus* and *Tropidosuchus*, the differences in the skull and skeleton of *Tropidosuchus* from those of *Chanaresuchus*, listed by Arcucci (1990), indicate that the two taxa are unique.

Key reference: Romer, 1971, 1972; Sues, 1976; Arcucci, 1990.

Dromicosuchus grallator Sues et al., 2003

Age: Late Triassic (late Carnian or early Norian).

Occurrence: Mudstone facies of Lithofacies Association II Durham sub-basin of the Deep River basin, Newark Supergroup, USA.

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

Remarks: *Dromicosuchus* was described and named by Sues et al. (2003) from a nearly complete skeleton. *Dromicosuchus* is one of the most complete non-crocodyliform crocodylomorphs known to date and one of the very few non-crocodyliform crocodylomorphs to have a well-preserved skull and articulated postcranium. The skull and skeleton are very similar to that of the incompletely known *Hesperosuchus agilis* (Sues et al., 2003). Recently, Hunt, Spielmann & Lucas (2006) questioned the validity of *Dromicosuchus*, and suggested that it should be a subjective junior synonym of *Hesperosuchus agilis*. Hunt et al. (2006) came to this conclusion citing the absence of autapomorphies of *Dromicosuchus*. The two characters listed by Sues et al. (2003) to differentiate it from *Hesperosuchus* (the absence of the dorsoventral expansion of the anterior end of the dentary and the presence of a conical recess at the anterior end of the antorbital fossa) are valid characters, because both are absent in the holotype of *Hesperosuchus* (AMNH 6758) and the referred specimen (CM 29894) (Clark et al., 2000). The presence of a conical recess at the anterior end of the antorbital fossa is an autapomorphy; it does not occur in any other crocodylomorph or pseudosuchian with this region preserved. In addition, the proximal surface of the ulna of *Dromicosuchus* is highly convex, whereas the proximal surface of the ulna of the holotype of *Hesperosuchus* (AMNH 6758) and the referred specimen (CM 29894) is concave.

Key reference: Sues et al., 2003

Postosuchus kirkpatricki Chatterjee, 1985

Age: Late Triassic.

Occurrence: Post (= Miller) Quarry, Cooper Canyon Formation, Dockum Group.

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

Referred to and scored material discussed below: TTU-P 9002, skull and skeleton.

Remarks: Chatterjee (1985) described *Postosuchus* from an associated and partially articulated skull and a disarticulated skeleton (TTU-P 9000). Chatterjee (1985) originally assigned many small postcranial remains from the same quarry and an ilium from the Otis Chalk quarry to *Postosuchus*. Long & Murry (1995) removed the smaller postcranial remains and assigned them to a new taxon, *Chatterjeea* (= *Shuvosaurus* Nesbitt & Norell, 2006), and also removed the ilium from *Postosuchus* and named a new taxon, *Lythrosuchus*.

Key references: Chatterjee, 1985; Long & Murry, 1995; Peyer *et al.*, 2008.

Herrerasaurus ischigualastensis Reig, 1963
Age: Carnian–early Norian, Late Triassic.

Occurrence: Ischigualasto Formation, Argentina.

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

Referred material scored and discussed below: PVSJ 373, well-preserved articulated skeleton, lacking skull and most cervical and caudal vertebrae; PVSJ 407, nearly complete articulated skeleton with skull and mandible.

Remarks: *Herrerasaurus* is well studied and represented by abundant, mostly well-preserved material. *Herrerasaurus* has been found as a non-neotheropod theropod (Serenó & Novas, 1992; Sereno, 1999) in some phylogenetic analyses, but the most recent analyses place *Herrerasaurus* as a stem-saurischian (Langer & Benton, 2006; Irmis *et al.*, 2007; Yates, 2007).

Key references: Reig, 1963; Novas, 1994; Sereno, 1994; Sereno & Novas, 1994; Langer & Benton, 2006.

Coelophysis bauri Cope, 1887
Age: Norian.

Occurrence: ‘Siltstone Member’, Chinle Formation, New Mexico.

Holotype: AMNH FR 7224, complete skeleton missing the tail.

Referred material scored and discussed below: AMNH FR 7223, complete skeleton lacking the tail.

Remarks: *Coelophysis bauri* refers only to the small theropod collected from the *Coelophysis* Quarry at Ghost Ranch. Even though it has been cited as represented by hundreds of skeletons, few of the original specimens have been fully prepared, and many of the specimens have been subjected to crushing and distortion. Nonetheless, *Coelophysis* remains the most complete basal theropod available for study.

Key references: Colbert, 1989; Rauhut, 2003; Nesbitt *et al.*, 2006.

APPENDIX 3: PHYLOGENETIC CHARACTERS AND DISCUSSION

1. External naris directed: (0) – laterally; (1) – dorsally.

The external naris of non-archosauriform archosauromorphs, *Proterosuchus*, *Erythrosuchus*, *Euparkeria* and most basal members of the Archosauria opens laterally. Alternatively, the external naris of proterochampsids, *Vancleavea* and phytosaurs opens dorsally. This character has been suggested to correlate with an aquatic and semi-aquatic lifestyle (Serenó, 1991).

2. Anteromedially projecting palatal process on the anteromedial surface of the maxillae: (0) – absent; (1) – present (Gower & Sennikov, 1997).

First used as a phylogenetic character by Gower & Sennikov (1997), the palatal process of the maxilla serves to articulate with the premaxilla. Broken maxillae of specimens of *Prolacerta* (UCMP 37151), exposing the medial side, as well as complete examples (BP/1/471), indicate that no palatal process is present. No specimen of *Proterosuchus* shows a palatal process of the maxilla. The disarticulated maxilla of *Erythrosuchus* (SAM-K1098; Gower, 2003) and that of *Euparkeria* (SAM 6050; Gow, 1970) confirm the presence of a palatal process in these taxa. The maxillae of proterochampsids and archosaurs also have a palatal process.

3. Large anteriorly opening foramen on the anterolateral surface of the maxilla: (0) – present; (1) – absent.

A large anteriorly opening foramen is present on the anterolateral surface of the maxilla, just ventral to the base of the dorsal process, in *Prolacerta* (BP/1/

471; Modesto & Sues, 2004), *Proterosuchus* (RC96; Welman, 1998) and *Euparkeria* (SAM 6049), as well as non-archosauriform archosauromorphs, such as *Protorosaurus* (Modesto & Sues, 2004) and *Mesosuchus* (Dilkes, 1998). A similar opening is not present in the same position in *Erythrosuchus*, *Vancleavea*, proterochampsids and Archosauria. A similar opening between the premaxilla and the maxilla [in suchian taxa, such as *Revueltosaurus* (S. J. Nesbitt, pers. observ.) and *Batrachotomus* (Gower, 1999), and saurischian dinosaurs (Serenó & Novas, 1994) (termed the subnarial foramen)] may transmit the same vessels as the feature described above, but does not seem to be homologous (S. J. Nesbitt, unpubl. data).

4. Antorbital fenestra: (0) – absent; (1) – present (Juil, 1994; Gower & Sennikov, 1997; Dilkes, 1998).

The presence of an antorbital fenestra supports erythrosuchians + Archosauria in Benton & Clark (1988), Gauthier *et al.* (1988) and Juil (1994). With the exception of *Vancleavea*, an antorbital fenestra is present in *Proterosuchus* + Archosauria.

5. Antorbital fossa: (0) – restricted to the lacrimal; (1) – restricted to the lacrimal and dorsal process of the maxilla; (2) – present on the lacrimal, dorsal process of the maxilla and the dorsal margin of the posterior process of the maxilla (the ventral border of the antorbital fenestra). Ordered.

The antorbital fossa of *Proterosuchus* (BSP 514) is restricted to the lacrimal. *Erythrosuchus* (BP/1/5207) possesses an antorbital fossa that is restricted to the dorsal process of the maxilla and on the lacrimal. Therefore, *Erythrosuchus* is scored as state 1. The proterochampsids *Chanaresuchus* (PVL 4575) and *Tropidosuchus* (PVL 4604), *Gualosuchus* (PVL 4576) (Serenó & Arcucci, 1990) and *Proterochampsia* (MCZ 3408) have small antorbital fossae on the lacrimal and a strip of fossa on the dorsal process of the maxilla. As with proterochampsids, *Euparkeria* (SAM 5867) has a similar arrangement of the antorbital fossa. All suchians and dinosauriforms have an antorbital fossa that surrounds the antorbital fenestra (state 2).

6. Lateral mandibular fenestra: (0) – absent; (1) – present (Benton & Clark, 1988; Juil, 1994; Bennett, 1996).

A lateral mandibular fenestra is present in nearly all archosauriforms plesiomorphically, as indicated by the analyses of Juil (1994). A lateral mandibular fenestra has been reported to be small or absent in *Proterosuchus* (Charig & Reig, 1970; Cruickshank, 1972). Recently, Welman & Flemming (1993), confirmed by Juil (1994) and Welman (1998), have

shown that the well-preserved specimens of *Proterosuchus* have a small lateral mandibular fenestra. However, given the small size of the opening, the presence of this character in *Proterosuchus* deserves more discussion. The small fenestra forms at the junction of the dentary, angular and surangular in *Proterosuchus* (RC 96, TM 201; Welman, 1998). Here, the mandibular elements do not have a distinct concave region forming an edge as in *Erythrosuchus* + Archosauria. On the other hand, although there are differences, the lateral mandibular fenestra occupies the same area and is composed of the same elements in both *Proterosuchus* and other archosauriforms. The small gap may be a consequence of the slight disarticulation of the mandibular elements, but is clearly present in QR 1484 (listed as NMC 3014 in fig. 3 of Welman, 1998). Therefore, *Proterosuchus* is scored as having a lateral mandibular fenestra. The presence or absence of a lateral mandibular fenestra is difficult to determine in isolated mandibular elements of taxa near the base of Archosauriformes. It is unclear whether *Vancleavea* has a lateral mandibular fenestra. If present, it is very small, similar to that of *Proterosuchus*.

7. Tooth implantation: (0) – teeth fused to the bone of attachment at the base; (1) – free at the base of the tooth (modified from Gauthier, 1984; Benton & Clark, 1988; Benton, 1990; Bennett, 1996).

The tooth implantation of basal archosauriforms has been discussed in great detail (Romer, 1956; Hughes, 1963; Charig & Sues, 1976; Benton & Clark, 1988; Gauthier *et al.*, 1988). The terms ‘thecodont’ and ‘subthecodont’ have been confused in the literature in reference to basal archosaur dentition, and both terms have been used interchangeably to describe the same taxon and condition. Gauthier *et al.* (1988) first used the depth of the tooth sockets to code this character for basal archosauriforms. However, as explained by Juil (1994), the depth of the socket is difficult to determine and compare.

The confusion of thecodont versus subthecodont dentition may be related to different authors’ interpretations (Bennett, 1996). However, there is a clear difference between the dentition of *Prolacerta* and *Proterosuchus* and erythrosuchians + Archosauria. Here, the terms thecodont and subthecodont are abandoned. Instead, differences in how the base of each tooth attaches to the tooth-bearing element are explored. The bases of the teeth of *Prolacerta* (UCMP 37151) and *Proterosuchus* (BSP 514) are firmly attached to the tooth-bearing element by small ridges of bone that completely surround each tooth. In lateral view, the teeth have flared bases. In contrast, the bases of the teeth of erythrosuchians + Archosauria lack a bony attachment. The bases of these teeth do not have

flared bases. Furthermore, most erythrosuchians + Archosauria also have interdental plates between teeth; interdental plates are not present outside this clade within Archosauromorpha.

8. Postparietals: (0) – present; (1) – absent (modified from Juul, 1994; Bennett, 1996; Dilkes, 1998).

Postparietals are present in *Proterosuchus* (BSP 514), *Erythrosuchus* (BP/1/5207), *Shansisuchus* (Young, 1964) and *Euparkeria* (Ewer, 1965), but not in *Prolacerta* (UCMP 37151), *Mesosuchus* (Dilkes, 1998) and Archosauria. As explained by Juul (1994) the postparietals of *Proterosuchus* (BSP 514), *Erythrosuchus* (BP/1/5207), *Euparkeria* (Ewer, 1965) and *Shansisuchus* (Young, 1964) are fused into one element, whereas they remain as two elements in the much more basal diapsids *Youngina* (Romer, 1956) and *Petrolacosaurus* (Reisz, 1977). *Vancleavea* does not possess a separate postparietal.

9. Palatal teeth on palatal process of the pterygoid: (0) – present; (1) – absent (Juul, 1994; Gower & Sennikov, 1997).
10. Teeth on transverse processes of pterygoids: (0) – present; (1) – absent (Gauthier, 1984; Juul, 1994; Bennett, 1996; Gower & Sennikov, 1997).

Palatal teeth are present in a variety of archosauromorphs and even members within the archosaur crown-group (e.g. *Eoraptor*; Rauhut, 2003), including *Prolacerta* (Camp, 1945; Gow, 1975; Modesto & Sues, 2004), *Mesosuchus* (Dilkes, 1998), *Proterosuchus* (Haughton, 1924; Welman, 1998), *Euparkeria* (Ewer, 1965) and all proterochampsids (Romer, 1972; Arcucci, 1990). Palatal teeth are absent in *Erythrosuchus* and other erythrosuchians (Parrish, 1992; Gower, 2003) and most members of Archosauria, and the absence of teeth has been used to diagnose the clade (Gauthier, 1984; Benton & Clark, 1988; Gauthier *et al.*, 1988; Sereno, 1991; Juul, 1994). The presence or absence of teeth anywhere on the palate has been used as a character previously (Benton & Clark, 1988; Sereno, 1991; Juul, 1994; Benton, 1999). However, as discovered by Juul (1994), incorporating characters examining the presence/absence of palatal teeth on certain regions of the pterygoid provides additional phylogenetic information. *Prolacerta* and *Proterosuchus* both have a row of palatal teeth on the transverse processes of the pterygoids, whereas other taxa closer to Archosauria (and within) do not have palatal teeth here. Teeth on the palatal process of the pterygoid are retained by the non-archosaurian archosauromorphs *Prolacerta*, *Proterosuchus*, proterochampsids and *Euparkeria*, and the crown-group archosaurs *Turfanosuchus* (Wu & Russell, 2001) and *Eoraptor* (Rauhut, 2003).

In nearly all of the taxa with palatal teeth, it is unclear whether vomer teeth are present; in most specimens, this area is poorly preserved or covered by the dentaries. *Euparkeria* (SAM 6050) has two vomer teeth (Gow, 1970). Examination of the vomer in newly discovered specimens may provide additional character information. It is unclear whether *Vancleavea* has palatal teeth.

11. Quadratojugal lateral surface: (0) – without a ridge marking the posteroventral corner of the lateral temporal fossa; (1) – with a ridge marking the posteroventral corner of the lateral temporal fossa.

The main bodies of the quadratojugals of *Tropidosuchus* (PLV 4604) and *Chanaresuchus* (PVL 4575) have a distinct lateral temporal fossa separated by a sharp ridge. All other taxa in this analysis have a rather smooth quadratojugal.

12. Anterior process of the jugal: (0) – slender and tapering; (1) – broad and dorsally expanded anteriorly (Gower & Sennikov, 1997).

The anterior portion of the jugal in non-archosauriform archosauromorphs generally tapers anteriorly, as does the anterior portion of the jugal of *Prolacerta* (BP/1/471) and *Proterosuchus* (RC 96). *Erythrosuchus* and archosauriforms with antorbital fenestrae have an expanded anterior portion of the jugal. The lacrimal articulates on the dorsal surface of the anteriorly expanded jugal.

Gauthier (1984) used a similar character [suborbital ramus of jugal does not extend anterior to the orbit (0) or extends anterior to the orbit (1)] to support Archosauriformes. Proterosuchidae, Erythrosuchidae, Proterochampsidae and Archosauria were all scored for state 1. The character used above and Gauthier's (1984) character show the same distribution when scored correctly. *Proterosuchus* (RC 96) does not have Gauthier's state 1, so *Proterosuchus* was scored as having a slender tapering process of the jugal.

13. Supratemporals: (0) – present; (1) – absent (Gauthier, 1984; Benton, 1985, 1990; Benton & Clark, 1988; Bennett, 1996; Gower & Sennikov, 1997; Dilkes, 1998).

The supratemporal bone lies between the squamosal and the parietal on the posterior margin of the skull roof. Supratemporals are present in *Mesosuchus* (Dilkes, 1998), a number of *Prolacerta* specimens (see Modesto & Sues, 2004) and *Proterosuchus*. Supratemporals are not present in *Erythrosuchus* + Archosauria in taxa with complete skulls. As noted by Gauthier (1984) and Modesto & Sues (2004), the presence or absence of supratemporals should be based on nearly complete, articulated skull material,

because the supratemporals may be easily lost during preservation. For example, Modesto & Sues (2004) list *Prolacerta* with or without supratemporals preserved. A facet for the supratemporal on the parietal may indicate the presence of the element in incomplete specimens, but care must be taken when scoring this character.

14. Posterior end of the squamosal: (0) – does not extend posterior to the head of the quadrate; (1) – extends posterior to the head of the quadrate.

The squamosals of *Mesosuchus* (SAM 6536), *Prolacerta* (BP/1/471), *Proterosuchus* (BSP 514) and *Erythrosuchus* (BP/1/5207) terminate posteriorly just dorsal to the posterior edge of the head of the quadrate. In contrast, the squamosals of *Euparkeria* (SAM 5867), the proterochampsids *Chanaresuchus* (PVL 4586) and *Tropidosuchus* (PVL 4606), and members of crown-group Archosauria (e.g. *Arizonasaurus*, *Herrerasaurus*) have a posteriorly expanded squamosal process that terminates well posterior of the articulation with the head of the quadrate.

15. Lateral temporal fenestra: (0) – open ventrally; (1) – closed (modified from Dilkes, 1998).

The lateral temporal fenestra is open ventrally in *Mesosuchus* (SAM 6536) and *Prolacerta* (BP/1/471). In these taxa, the posterior portion of the jugal and the quadratojugal do not meet. The jugal and the quadratojugal meet to form a closed lateral temporal fenestra in all archosauriforms.

16. Parietal foramen: (0) – present; (1) – absent (Gauthier, 1984; Benton, 1985; Benton & Clark, 1988; Bennett, 1996).

The parietal foramen is present in *Mesosuchus* (Dilkes, 1998) and absent in *Proterosuchus* (see Welman, 1998) and in some specimens of *Prolacerta* (Camp, 1945; Modesto & Sues, 2004). However, in *Prolacerta*, a parietal foramen is variably present or absent according to Modesto & Sues (2004), and therefore the character is scored as polymorphic in *Prolacerta*.

17. Ectopterygoid: (0) – does not form or forms some of the lateral edge of the lateral pterygoid flange; (1) – forms all of the lateral edge of the lateral pterygoid flange.

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

18. Posteroventral portion of the dentary: (0) – just meets the surangular; (1) – laterally overlaps the anteroventral portion of the surangular.

The anteroventral portion of the surangular meets the dentary anterodorsally in *Mesosuchus* (SAM 6536), *Prolacerta* (BP/1/471) and *Proterosuchus* (RC 96). Alternatively, the posteroventral portion of the dentary laterally overlaps the anteroventral portion of the surangular in *Erythrosuchus* (BP/1/5207), *Euparkeria* (SAM 6050), in the proterochampsids *Tropidosuchus* (PVL 4601) and *Chanaresuchus* (UPLR 7) and basal members of the Archosauria.

BRAINCASE

The following braincase characters were taken from Gower & Sennikov (1996). Character descriptions can be found in Gower & Sennikov (1996). A short discussion of each character is given only when clarification is needed, new taxa are added, or characters or character states are modified in subsequent publications.

19. Ossified laterosphenoid: (0) – absent; (1) – present (Gauthier *et al.*, 1988; Benton & Clark, 1988; Parrish, 1992; Clark *et al.*, 1993; Juul, 1994; Bennett, 1996).

The laterosphenoid of archosauriforms has been well described by Clark *et al.* (1993). An ossified laterosphenoid is clearly absent in *Prolacerta* and is present in all archosauriforms. A laterosphenoid is clearly present in the proterochampsid *Chanaresuchus* (PVL 4575), which is the first confirmed presence in the any proterochampsid.

20. Foramina for entrance of cerebral branches of internal carotid artery into the braincase positioned on the surface of the parabasisphenoid: (0) – ventral; (1) – lateral (Parrish, 1993; Gower & Sennikov, 1996; Gower, 2002).

The internal carotids enter the parabasisphenoid ventrally in *Mesosuchus* (SAM 6536; Dilkes, 1998), *Prolacerta* (BP/1/2675; Evans, 1988), *Proterosuchus* (BP/1/3993; Gow, 1975), *Erythrosuchus* (BMNH R3592; Gower, 1997), *Euparkeria* (UMZC T692; Gower & Weber, 1998) and in the proterochampsids *Tropidosuchus* (PVL 4604) and *Chanaresuchus* (PVL 4647). Parrish (1993) reported that *Proterochampsia* (MCZ 3408) had both a ventral and a lateral entrance; however, all other proterochampsid specimens have the internal carotids entering from the ventral surface. Nearly all members of the Archosauria have internal carotids that enter into the parabasisphenoid laterally, with the exception of *Turfanosuchus* (Parrish, 1993; Wu & Russell, 2001), *Silesaurus* (Dzik, 2003), *Quainosuchus* (Li *et al.*, 2006) and *Ari-*

zonasaurus (Gower & Nesbitt, 2006), where the internal carotids enter ventrally.

21. Parabasisphenoid plate: (0) – present; (1) – absent (Gower & Sennikov, 1996).

The parabasisphenoid plate is an anterodorsally/posteroventrally compressed plate of bone that lies between the basitubera of the parabasisphenoid (Gower & Sennikov, 1996; Gower, 2002). This character is not present in *Mesosuchus*, but is present in *Prolacerta*, *Proterosuchus* and *Erythrosuchus* (Gower & Sennikov, 1996). In these taxa, the plate is straight. *Vancleavea* (UCMP 165196), *Tropidosuchus* (PVL 4604), *Chanaresuchus* (PVL 4647) and *Euparkeria* (SAM 5867) are scored as state 1 (following Gower & Weber, 1998). In phytosaurs, suchians and dinosauriforms, a distinct parabasisphenoid plate is not present. A low ridge may be present between the basitubera in taxa with a median pharyngeal recess; however, this ridge differs from taxa scored as state 0. Thus, these features are not considered to be homologous.

22. Ridge on lateral surface of inferior anterior prootic process below trigeminal foramen: (0) – present; (1) – absent (Gower & Sennikov, 1996).

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

23. Parabasisphenoid orientation: (0) – horizontal; (1) – more vertical (Gower & Sennikov, 1996).

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

24. Semilunar depression on the lateral surface of the basal tubera of the parabasisphenoid: (0) – present; (1) – absent (Gower & Sennikov, 1996).

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

POSTCRANIA

25. Postaxial intercentra: (0) – present; (1) – absent (Gauthier, 1984; Benton & Clark, 1988; Sereno, 1991; Parrish, 1993; Juul, 1994; Bennett, 1996).

The presence of intercentra has long been a cited character in basal archosaur phylogenies, but the distribution of intercentra within non-archosaurian archosauriforms remains controversial. Sereno (1991) listed the absence of intercentra as a synapomorphy of proterochampsids + Archosauria, because *Euparkeria* had intercentra in all presacral vertebrae. However, there are only two specimens of *Euparkeria* (SAM-PK-6047A, SAM-PK-6047B) which show preserved intercentra. In these specimens, intercentra are not found between each of the vertebrae, but sporadically throughout the presacral column (Ewer, 1965). Intercentra are apparently absent in all other specimens, although some may have been prepared away. The intercentra of SAM-PK-6047A are very small in comparison with those of *Mesosuchus* (SAM-PK-6049). Furthermore, the ventral portions of the anterior and posterior articular surfaces of the centra of *Euparkeria* are not bevelled and do not have facets for intercentra as they do in the dorsal vertebrae of *Erythrosuchus*, *Sarmatosuchus* (Gower & Sennikov, 1996) and *Proterosuchus*. The small size and apparent absence of ossification of some of the intercentra in the column of *Euparkeria* may suggest that closely related taxa that have been scored as lacking intercentra may indeed have very small intercentra. *Euparkeria* is scored as polymorphic for this character. Benton & Clark (1988) used the absence of intercentra to support the clade proterochampsids + *Euparkeria* + Archosauria (the crown-group). Intercentra are present in *Prolacerta* (Gow, 1975), *Proterosuchus* (QR 1484; Cruickshank, 1972) and *Erythrosuchus* (Gower, 2003). Intercentra are not present in *Vancleavea*.

26. Cervical centra 3–5 length: (0) – greater than height; (1) – subequal (modified from Gower & Sennikov, 1997).

The cervical vertebrae of *Prolacerta* (UCMP 37151) and *Proterosuchus* (BPS 514) have elongated anterior cervical centra that are almost twice as long as high. In contrast, the cervical vertebrae of the possible

proterosuchian *Sarmatosuchus* (Gower & Sennikov, 1997), *Erythrosuchus* (BMNH R3592; Gower, 2003), *Chanaresuchus* (PVL 4575) and *Euparkeria* (Ewer, 1965) all have anteroposteriorly short cervical centra. Early members of Archosauria have a variety of cervical lengths not considered here. The cervical centra of *Vancleavea* are longer than they are high.

27. Spine tables: (0) – absent in the cervical vertebrae; (1) – present in the cervical vertebrae (modified from Gauthier, 1984; Juul, 1994).

Spine tables are defined as a lateral expansion of the dorsal margin of the neural spines of the presacral vertebrae. The dorsal surface of the spine table is horizontally flat. Cervical spine tables are present in *Euparkeria* (SAM 6047A), *Postosuchus* (TTU-P 9002), *Hesperosuchus* (Colbert, 1954), *Riojasuchus* (PVL 3827; Bonaparte, 1971), aetosaurs (*Desmotosuchus* MNA V9300) and phytosaurs (*Pseudopalatus* UCMP 34260), but they are absent in some pseudosuchians ('Clade X' of Nesbitt, 2005; 2007). Spine tables are not present in proterochampsids, *Erythrosuchus*, *Vancleavea*, *Proterosuchus*, *Prolacerta* or *Mesosuchus*. The presence of osteoderms does not perfectly coincide with the presence of spine tables, as demonstrated by *Chanaresuchus* (PVL 4575) and other proterochampsids, which lack spine tables but possess osteoderms. Furthermore, spine tables are not present in the dorsal region of taxa with osteoderms over the entire presacral column (e.g. '*Prestosuchus*' UFRGS 156 T and *Saurosuchus* PVSJ 23). Therefore, the absence of spine tables does not determine whether or not a taxon has dorsal osteoderms.

Novas (1994) and Langer & Benton (2006) reported spine tables in *Herrerasaurus* and *Eoraptor*, respectively, in the dorsal, caudal and sacral vertebrae. These expansions are not similar to those of *Euparkeria* and *Postosuchus*. Differences in *Eoraptor* and *Herrerasaurus* include the following: the dorsal and lateral surfaces of the spine tables are rounded, the lateral sides of the expansion have longitudinal striations, and the dorsal surface is rounded and not flat as with *Euparkeria* and *Postosuchus*. Some of the 'spine tables' of the dorsal vertebrae of *Herrerasaurus* also expand anteriorly and posteriorly. A similar pattern occurs in theropods (e.g. *Tyrannosaurus rex*; Brochu, 2003) and avians (S. J. Nesbitt, pers. observ.), as well as in the suchian *Effigia* (Nesbitt, 2007). Therefore, *Herrerasaurus* is scored as absent for this character.

28. Entire anterior margin of the scapula: (0) – straight/convex or partially concave; (1) – markedly concave (modified Gower & Sennikov, 1997).

The scapulae of *Mesosuchus* (SAM-PK-6536; Dilkes, 1998), *Prolacerta* (BP/1/2675; Gow, 1975) and *Proterosuchus* (QR 1484) are wide and have a partially

concave and convex anterior margin. In contrast, the scapulae of *Erythrosuchus* (BMNH R3267a), *Vancleavea* (GR 138), *Euparkeria* (SAM-PK-5867), *Tropidosuchus* (PVL 4604), *Chanaresuchus* (PVL 4575) and Archosauria have anterior margins that are markedly concave. Gauthier (1984) described a similar character (scapula 50% taller than wide) to describe erythrosuchians + Archosauria. These two characters describe the same basic observation, and the wording of Gower & Sennikov (1997) is preferred.

29. Ischium length: (0) – same length or shorter than the dorsal margin of iliac blade; (1) – markedly longer than the dorsal margin of iliac blade (Juul, 1994).

This character measures the length of the ischium versus the length of the dorsal margin of the ilium. The dorsal margin of the ilium remains relatively the same length in archosauriforms and early members of the Archosauria, whereas the ischium is elongated relative to the dorsal margin of the ilium in taxa closer to and within Archosauria.

30. Interclavicle shape: (0) – 'T'-shaped with long lateral processes; (1) – anterolateral processes reduced or absent (modified from Gauthier, 1984; Sereno, 1991; Gower & Sennikov, 1997).

Gauthier *et al.* (1988) used a similar character to unite a less inclusive clade than that of both Sereno (1991) and Gower & Sennikov (1997). The well-preserved, articulated interclavicle of *Proterosuchus* (QR 1484) bears long tapering lateral processes. Gower & Sennikov (1997) reported that the interclavicle of one erythrosuchian, *Vjushkovia triplicostata*, has reduced lateral processes. To date, no other interclavicle is known in an erythrosuchian. As pointed out by Sereno (1991), the holotype of *Euparkeria* (SAM-PK-5867) possesses short lateral processes as with members of Archosauria. Although not completely preserved in any proterochampsid, the pectoral girdle of *Tropidosuchus* (PVL 4606) bears two thin clavicles in articulation with short processes of the fragmentary interclavicle (Arcucci, 1990).

31. Anterior process on the dorsal margin of the ilium: (0) – absent; (1) – present (Gauthier, 1984; Juul, 1994).

A small anteriorly projecting process is present dorsal to the supra-acetabular rim in *Erythrosuchus* (BMNH R3592; Gower, 2003), proterochampsids, *Euparkeria* (Ewer, 1965) and nearly all members of Archosauria plesiomorphically [see the phylogenetic trees of Gauthier (1984) and Juul (1994)]. The ilia of *Prolacerta* (Gow, 1975), *Proterosuchus* (QR 1484; Cruickshank, 1972) and non-archosauriform archosauromorphs lack an anteriorly projecting process on the dorsal margin

of the ilium. In these taxa, the anterior portion of the dorsal margin of the ilium arcs posteriorly.

32. Acetabulum: (0) – imperforate; (1) – extensively perforated (Bakker & Galton, 1974; Gauthier & Padian, 1985; Gauthier, 1986; Juul, 1994; Benton, 1999; Benton *et al.*, 2000; Fraser *et al.*, 2002; Langer & Benton, 2006).

A perforated acetabulum is only known in Dinosauria and in some crocodylomorphs.

33. Proximal head of the femur: (0) – rounded and not distinctly offset; (1) – subrectangular and distinctly offset (Gauthier, 1984; Juul, 1994; Benton, 1999).

An offset femoral head is a character used to unite members of the Dinosauria.

34. Femoral anterior (= lesser) trochanter: (0) – absent; (1) – present (Gauthier, 1986; Novas, 1992; Juul, 1994; Benton, 1999).

An anterior trochanter is present in dinosauriforms and a similar structure is present in the ornithosuchids *Riojasuchus* (PVL 3827) and *Ornithosuchus* (BMNH R2410).

35. Femoral condyles: (0) – prominent; (1) – not projecting markedly beyond the shaft (Gauthier *et al.*, 1988).

Subsequent workers have ignored this character since its formulation. Juul (1994) considered this character too subjective to score. The distal ends of the femora of *Prolacerta* (BP/1/2676), *Proterosuchus* (QR 1484) and *Erythrosuchus* (BMNH R3592), as well as rhynchosaurs and *Trilophosaurus* (Gregory, 1945), expand dorsoventrally (in sprawling orientation), whereas the femora of *Vancleavea* (GR 138), *Euparkeria* (SAM-PK-6047b), proterochampsids and Archosauria are expanded little more than the midshaft. Furthermore, the expansion of the distal ends of the femora of *Prolacerta* (BP/1/2676), *Proterosuchus* (QR 1484) and *Erythrosuchus* (BMNH R3592) is restricted to the distal end, whereas the femora of *Vancleavea*, *Euparkeria*, proterochampsids and Archosauria gradually expand, if at all.

36. Ridge of attachment of the M. caudifemoralis: (0) – blade-like with a distinct asymmetric apex located medially; (1) – ridge of attachment of the M. caudifemoralis low and without a distinct asymmetrical apex.

The transition from an internal trochanter in non-archosauriform archosauromorphs, *Proterosuchus* and erythrosuchians to the fourth trochanter of *Euparkeria*, proterochampsids and members of Archosauria has received little attention. Most phylogenetic

analyses focus on the presence/absence of the internal trochanter, as well as the presence/absence of the fourth trochanter (Benton, 1985, 2004; Gauthier, 1986; Sereno, 1991; Parrish, 1992; Juul, 1994; Senter, 2004), without testing the homology of the two structures. Parrish (1992) suggested that *Erythrosuchus* had both an internal trochanter and a fourth trochanter, but as pointed out by Gower (2003), the area Parrish suggested to be the fourth trochanter was not for the attachment of M. caudifemoralis but rather for M. iliofemoralis. Here, the observation made by Gower (2003) is followed. A detailed account of the transition between the internal trochanter and the fourth trochanter is in process (D. J. Gower, Natural History Museum, London, pers. comm.), but a short description is presented below.

The internal trochanter of squamates (Snyder, 1962) and the fourth trochanter of archosaurs both attach the M. caudifemoralis musculature and function to retract the femur. Therefore, a character that focuses on the presence/absence of the ‘internal trochanter’ and a character that focuses on the presence/absence of the ‘fourth trochanter’ prevent the two features from being homologous *a priori*. Here, the two features are considered to be homologous. This is further supported by the ambiguity of differentiating the two structures among non-archosaurian archosauromorphs, the ridge of attachment of M. caudifemoralis lies near the proximal surface of the femoral head, whereas the ridge of attachment of M. caudifemoralis lies much more distally in taxa traditionally considered to have a fourth trochanter (e.g. *Euparkeria* and Archosauria). The ridge of attachment in *Erythrosuchus*, a taxon near the transition of taxa considered to have ‘internal trochanters’ and taxa considered to have ‘fourth trochanters’, has a ridge located in a similar location to an archosaurian ‘fourth trochanter’. Therefore, the wording in the character above concentrates on the morphology of the ridge of attachment rather than the position of the ridge. Non-archosauriform archosauromorphs, *Proterosuchus* (QR 1484) and *Erythrosuchus* (BMNH R 3592) have ridges of attachment that are nearly uniformly thin (= blade-like) and have a medial (or dorsal) asymmetrical apex. In *Euparkeria* (SAM-PK-6047b) and Archosauria, the ridge of attachment is low without a distinct asymmetrical apex. The ridge of attachment of M. caudifemoralis in proterochampsids (e.g. *Chanaresuchus* PVL 4575) is expanded and sharp. However, the apex of the ridge is not asymmetrical, but symmetrical anteroposteriorly.

37. Tarsals 1 and 2: (0) – ossified; (1) – absent (Gauthier, 1984; Sereno, 1991; Gower, 1996; Benton, 2004).

Gauthier (1984) used this character to separate non-archosauriform archosauromorphs and *Proterosuchus* (tarsals 1–4 ossified) from *Euparkeria*, proterochampsids and members of the Archosauria (tarsals 3 + 4 ossified only). Sereno (1991) followed this, but restricted most of his discussion to the presence/absence of tarsal 1. Tarsals 1 and 2 are both either ossified or absent in basal archosaurs. However, Gauthier (1984) and Sereno (1991) reported that tarsal 2 is present in some fossil crocodylians and in old, mature crocodiles. Gower (1996) clarified Sereno's (1991) doubts about the presence/absence of tarsal 1 in *Erythrosuchus*; Gower (1996) conclusively showed that *Erythrosuchus* possesses only tarsals 3 and 4. *Vancleavea* only possesses tarsals 3 and 4.

38. Hemicylindrical calcaneal condyle: (0) – absent; (1) – present (Sereno, 1991; Parrish, 1993; Juul, 1994; Gower, 1996; Benton, 1999).

The hemicylindrical condyle is a feature shared by phytosaurs, ornithosuchians and suchians. A hemicylindrical condyle is located where the fibula and the calcaneum articulate and is present when this articulation is: (1) convex both anteroposteriorly and mediolaterally; and (2) mediolaterally constricted and bordered by a non-articular surface medially.

This character is not present in any specimen of *Euparkeria*. In criticisms of Sereno (1991), Parrish (1993) reported that this character was present in *Euparkeria* and unknown in proterochampsids. However, Parrish (1993) was mistaken in his interpretation of Sereno's (1991) character; the calcaneum of *Euparkeria* does have a convex articulation with the fibula, and yet this articulation does not satisfy the second criterion stated above. The articular facet of the calcaneum for the fibula is similar between *Euparkeria* and the proterochampsids *Chanaresuchus* (MCZ 4036) and *Tropidosuchus* (PVL 4601).

39. Ossified astragalo-calaneal canal: (0) – present; (1) – absent (Gauthier, 1984; Bennett, 1996; Gower & Sennikov, 1997).

This character has been largely ignored because of taxon selection for archosaur phylogenies and diapsid phylogenies; most archosaur phylogenies use *Proterosuchus* as an outgroup, whereas diapsid phylogenies use *Proterosuchus* as a terminal taxon to represent archosaurs. Gauthier (1984) demonstrated that non-archosauriform archosauromorphs and *Proterosuchus* (e.g. QR 1484) have a clear astragalo-calaneal canal between the astragalus and calcaneum in articulation, whereas *Euparkeria*, proterochampsids and Archosauria do not have a gap between the two elements. Gower (1996) explicitly showed that *Erythrosuchus*, as well as the other erythrosuchians, *Shansisuchus* and *Vjushkovia triplicostata*, lacks an

astragalo-calaneal canal. An astragalo-calaneal canal is absent in the proterochampsids *Tropidosuchus* (PVL 4601) and *Chanaresuchus* (MCZ 4035), and in *Vancleavea* (GR 138).

40. Tibial and fibular articulations of the astragalus: (0) – separated by a gap (or notch of Gower, 1996); (1) – continuous (modified from Sereno & Arcucci, 1990; Sereno, 1991; Gower, 1996).

In non-archosauriform archosauromorphs, *Proterosuchus* (QR 1484), *Shansisuchus* (IVPP field number 56173; Gower, 1996) and *Vancleavea* (GR 138), a clear, non-articular gap completely separates the articular facet of the tibia and fibula. The presence of a gap in the astragalus of *Erythrosuchus* is not clear because of the poor ossification of the astragalus. Proterochampsids and basal members of Archosauria all lack a non-articular gap. As discussed by Gower (1996), *Euparkeria* does not have a non-articular gap between the tibial and fibular facets of the astragalus, even though this was cited explicitly as a character placing *Euparkeria* outside of proterochampsids + Archosauria in Sereno (1991).

41. Articular surfaces for fibula and distal tarsal IV on calcaneum: (0) – separated by a non-articular surface; (1) – continuous (Sereno, 1991; Juul, 1994; Benton, 1999).

Sereno (1991) utilized this character to support Archosauria. This character, however, is in need of more description. In the calcaneum, a non-articular surface composed of finished, compact bone clearly separates the fibular and fourth tarsal facets in non-archosauriform archosauromorphs, *Proterosuchus*, *Erythrosuchus*, *Vancleavea*, proterochampsids and *Euparkeria*. Gower (1996) agreed with Sereno (1991) that there is a non-articular gap separating the fibular and fourth tarsal facets in *Euparkeria* (*contra* Parrish, 1993). In these taxa, the fibular facet is located directly dorsal to the fourth tarsal facet. In contrast, the fibular and the fourth tarsal articular surfaces of all basal members of the Archosauria are continuous and not separated by finished, compact bone; a thin edge of bone separates the fibular and fourth tarsal articular surfaces in Archosauria. Figure 6 of Sereno (1991) unfairly depicts the calcaneum of *Marasuchus* (labelled as *Lagosuchus*) incorrectly in the following two aspects: (1) the fibular facet is concave, not convex as depicted; and (2) the articular surfaces (shaded regions) of the fibula and fourth tarsal should be touching. The difference in the manner in which the fibula attaches to the calcaneum, either on a convex or concave surface, is explored in other phylogenetic characters (Sereno, 1991; Parrish, 1993; Juul, 1994; Benton, 1999).

42. Calcaneal tuber relative to the transverse plane: (0) – lateral, angled less than 20° posteriorly; (1) – deflected, angled between 21° and 49° posteriorly; (2) – angled between 50° and 90° posteriorly (modified from Gauthier, 1984; Sereno, 1991; Parrish, 1993; Juul, 1994; Benton, 1999).

In non-archosauriform archosauromorphs, *Proterosuchus* (AMNH FR 2237), *Erythrosuchus* (BMNH R3592) and *Vancleavea* (GR 138), the calcaneum is directed laterally with little posterior deviation (no more than 10°). In the proterochampsid *Tropidosuchus* (PVL 4601) and phytosaurs, the orientation is about 45°. The orientation of the tuber in the only known *Chanaresuchus* calcaneum (MCZ 4036) is not known. In *Euparkeria*, the extent of the posterior deflection of the tuber has been debated. Gower (1996) suggested that the tuber is nearly laterally oriented, whereas Sereno (1991) and Parrish (1993) claimed that the orientation is near 45°. Articulation of the ankle of *Euparkeria* (UMCZ T692) indicates that the tuber must have been oriented posteriorly by at least 20°; the exact range cannot be determined. The tubera of ornithosuchians and suchians project nearly perpendicular to the long axis of the astragalus (state 2).

In the above character, the posterior deflection ranges are not based on 'breaks' in the data among different taxa. Rather, the bins reflect the uncertainty of rearticulating disarticulated specimens and taphonomic disappearances prior to and after burial.

43. Calcaneal tuber shaft proportions at the midshaft of the tuber: (0) – taller than broad; (1) – about the same or broader than tall (modified from Sereno, 1991; Parrish, 1993; Juul, 1994; Benton, 1999).

Here, to make the character definition more rigorous, the shaft proportions are taken between the lateral expansion of the calcaneal tuber and the fibular facet. The tubera shafts of *Prolacerta* (BP/1/BP/1/2676), *Proterosuchus* (AMNH FR 2237), *Erythrosuchus* (BMNH R3592), *Vancleavea* (GR 138) and the proterochampsids *Tropidosuchus* (PVL 4601) and *Chanaresuchus* (MCZ 4036) are much taller than broad. The cross-sections of the tubera shafts of these taxa are anteroposteriorly compressed. In *Euparkeria*, phytosaurs, ornithosuchians and suchians, the calcaneal tubera shafts are about the same or broader than tall. The shafts of *Euparkeria* and phytosaurs are nearly round in cross-section.

44. The dorsolateral margin of the astragalus: (0) – overlaps the anterior and posterior portions of the calcaneum equally; (1) – the posterior corner of

the dorsolateral margin of the astragalus dorsally overlaps the calcaneum much more than the anterior portion.

In non-archosauriform archosauromorphs, *Proterosuchus* (AMNH FR 2237), *Erythrosuchus* (BMNH R3592), *Vancleavea* (GR 138) and the proterochampsids *Tropidosuchus* (PVL 4601) and *Chanaresuchus* (MCZ 4035), the anterior and posterior portions of the dorsolateral margin of the astragalus overlap the anterior and posterior portions of the calcaneum nearly equally. The posterior portion of the dorsolateral margin of the astragalus dorsally overlaps the calcaneum much more than that of the anterior portion in *Euparkeria* (UMCZ T692), *Dromomeron* (GR 223), *Lagerpeton* (PVL 4619), *Marasuchus* (PVL 3870), *Pseudolagosuchus* (PVL 3454), other basal dinosaurs, phytosaurs (USNM 18313) and suchians. Essentially, character state 1 is present in all basal members of Archosauria and in *Euparkeria*.

45. Astragalus posterior groove: (0) – absent; (1) – present (Sereno, 1991).

An astragalus posterior groove separates the lateral portion of the astragalus into dorsal and ventral articular surfaces. The dorsal surface articulates with the fibula dorsally and the calcaneum ventrally. The ventral surface articulates with the ventral portion of the calcaneum. The posterior groove is present in the proterochampsid *Chanaresuchus* (MCZ 4035), but not in the proterochampsid *Tropidosuchus* (PVL 4601), *Euparkeria* (UMCZ T692), phytosaurs (USNM 18313) and suchians. The groove is also present in *Pseudolagosuchus* (PVL 4529) and *Marasuchus* (PVL 3871), although Sereno (1991) suggested that a posterior groove is absent in all dinosauriforms. The groove is clearly absent in *Dromomeron* (GR 223), *Lagerpeton* (PVL 4619) and all other dinosauriforms.

46. Centrale in proximal row of tarsals: (0) – present; (1) – absent (Gauthier, 1984; Gower, 1996; Bennett, 1996; Gower & Sennikov, 1997; Benton, 2004).

A distinct centrale is present in rhynchosaurs, *Trilophosaurus* (fig. 11 of Gregory, 1945), *Prolacerta* (BP/1/2676; Gow, 1975) and *Proterosuchus* (QR 1484; see discussion in Gower, 1996). In rhynchosaurs (PVSJ 679) and *Proterosuchus* (QR 1484), the centrale (the lateralmost proximal tarsal; Gower, 1996) has partially fused with the astragalus, whereas the elements are completely separated in *Trilophosaurus* and *Prolacerta*. A partially fused or separate centrale is absent in *Erythrosuchus* (Gower, 1996), *Euparkeria*, *Vancleavea*, proterochampsids and Archosauria.

47. Metatarsal II midshaft diameter: (0) – less than or equal to the midshaft diameter of metatarsal I; (1) – more than the midshaft diameter of metatarsal I.

Metatarsal II of *Proterosuchus* (QR 1484), *Erythrosuchus* (BMNH R3592), *Euparkeria* (UMCZ T692) and members of Archosauria (e.g. *Lagerpeton*, PVL 4619; *Marasuchus*, PVL 3871; *Postosuchus*, UNC 15575; *Aetosaurus*, SMNS 5770) has a smaller or about the same midshaft diameter as metatarsal I. In contrast, metatarsal II has a much larger midshaft diameter than that of metatarsal I in *Tropidosuchus* (PVL 4601) and *Chanaresuchus* (MCZ 4035; Romer, 1972).

48. Metatarsal IV: (0) – nearly the same midshaft diameter as metatarsal III; (1) – reduced where the midshaft diameter is less than metatarsal III.

Although difficult to define, this character attempts to highlight the difference in size between metatarsal IV relative to metatarsal III of the proterochampsids *Tropidosuchus* (PVL 4601) and *Chanaresuchus* (MCZ 4035; Romer, 1972). Metatarsal IV of these taxa is greatly reduced in diameter relative to metatarsals I–III. Members of Archosauria, *Euparkeria* (UMCZ T692), *Proterosuchus* (QR 1484) and *Erythrosuchus* (BMNH R3592) have a metatarsal IV that has a midshaft diameter comparable with that of metatarsals II and III.

49. Metatarsal IV: (0) – longer than metatarsal III; (1) – about the same length or shorter than metatarsal III (modified from Bennett, 1996; Gower & Sennikov, 1997).

This classically formulated character has been used to quantify the differences in the pes of basal archosauromorphs and members of Archosauria. Originally, the formulation of this character examined the complete length (metatarsal + phalanges) of digit 4 compared with digit 3 (Gauthier, 1984; Sereno, 1991). The fourth digit of non-archosauriform archosauromorphs (e.g. rhynchosaurs, *Trilophosaurus*, *Prolacerta*) is the longest in the pes, whereas digit 3 is longer in *Euparkeria* (UMCZ T692) and all archosaurs that could be scored (Gauthier, 1984). Gower & Sennikov (1997) simplified the character by examining the length of metatarsal IV with respect to metatarsal III. Gower & Sennikov's (1997) simplification is followed here because more taxa can be scored (few taxa possess a complete pes), and there are no taxa observed by us that have a longer metatarsal III than IV, but a longer pedal digit 4 than 3 (metatarsal IV + phalanges).

Having a longer metatarsal III than metatarsal IV has a nearly uniform distribution among basal members of Archosauria, except for basal members of both the crocodylian-line and the avian-line. In these

taxa, metatarsals III and IV are subequal in length. For example, phytosaurs (*Pseudopalatus*, UCMP 34328) have metatarsals III and IV that are subequal in length. *Riojasuchus* (PVL 3827) (an ornithosuchid), two aetosaurs [*Aetosaurus* (SMNS 18554) and *Typothorax* (MCZ 1488)], a rauisuchian [*Postosuchus* (UNC 15575)] and *Alligator* all have a longer metatarsal III than metatarsal IV. Among avian-line archosaurs, pterosaurs (Wellnhofer, 1978; Wild, 1978), *Silesaurus* (ZPAL Ab III/364; Dzik, 2003) and members of Dinosauria all have metatarsal III longer than metatarsal VI. In *Lagerpeton* (PVL 4619; Sereno & Arcucci, 1994a), metatarsal VI is clearly longer than metatarsal III, whereas metatarsals IV and III are nearly the same length [metatarsal IV is reported to be shorter than metatarsal III in table 5 of Sereno & Arcucci (1994b)] in *Marasuchus*. The condition in *Lagerpeton* seems to be autapomorphic given its hypothesized phylogenetic position (e.g. Benton, 1999).

50. Osteoderms: (0) – absent; (1) – present (Gauthier, 1984; Benton & Clark, 1988; Sereno, 1991; Juul, 1994; Bennett, 1996; Dilkes, 1998; Benton, 1999).

The presence of osteoderms has been used in nearly all basal archosaur phylogenies, although the formulations of the characters have varied. Here, given the small sampling within Archosauria, just the presence/absence of osteoderms is used. Non-archosauriform archosauromorphs including *Prolacerta*, *Proterosuchus* (Thornley, 1970) and all erythrosuchians, with one possible exception, lack osteoderms. Huene (1911) and, most recently, Gower (2003), reported the presence of two osteoderms in *Erythrosuchus* (BMNH R3592). The osteoderm attached to the side of the caudal series of BMNH R3592 is poorly preserved, and few fine details can be observed. A close inspection by S.J.N. could not identify typical features (e.g. weaved bone surface, compact outer surface, small channels for blood vessels) of bony osteoderms in this specimen. The second specimen proposed to be an osteoderm of *Erythrosuchus* is well preserved, and fine features can be evaluated. The edges of the element are incomplete, exposing a spongy interior not typical of osteoderms and a cross-section of the very thin compact external surface. The thin compact outer surface differs from the typical thick, compact and laminar external surface of other osteoderms. The external surface has a pattern similar to other osteoderms, but it cannot be differentiated from other dermal skeletal elements (e.g. claw). Even if these two specimens represent osteoderms, it is clear that *Erythrosuchus* did not have many osteoderms, and certainly did not have paramedian or median osteoderms dorsal to the vertebrae; none of the presacral articulated vertebrae have associated osteoderms. Therefore, *Erythrosuchus* is coded as state 0 for this character.

APPENDIX 4: TAXON SCORINGS

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
<i>Mesosuchus</i>	0	0	0	0	–	0	0	1	0	1	0	0	0	0	0	0	0	0
<i>Prolacerta</i>	0	0	0	0	–	0	0	1	0	0	0	0	0	0	0	A	0	0
<i>Proterosuchus</i>	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1	1	0
<i>Erythrosuchus</i>	0	1	1	1	1	1	1	0	1	1	0	1	1	0	1	1	1	1
<i>Vancleavea</i>	1	1	1	0	–	?	1	1	?	?	0	0	1	0	1	1	?	1
<i>Tropidosuchus</i>	1	?	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1
<i>Chanaresuchus</i>	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1
<i>Euparkeria</i>	0	1	0	1	1	1	1	0	0	1	0	1	1	1	1	1	1	1
<i>Dromicosuchus</i>	0	?	1	1	2	1	1	1	?	?	0	1	1	1	1	1	?	1
<i>Postosuchus</i>	0	1	1	1	2	1	1	1	1	1	0	1	1	1	1	1	1	1
<i>Herrerasaurus</i>	0	1	1	1	2	1	1	1	1	1	0	1	1	1	1	1	1	1
<i>Coelophysis</i>	0	1	1	1	2	1	1	1	1	1	0	1	1	1	1	1	1	1

	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
<i>Mesosuchus</i>	0	0	1	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Prolacerta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Proterosuchus</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Erythrosuchus</i>	1	0	0	1	1	0	0	1	0	1	1	?	1	0	0	0	0	0
<i>Vancleavea</i>	1	?	?	1	?	?	1	0	0	1	1	?	1	0	0	0	1	?
<i>Tropidosuchus</i>	?	0	1	?	1	?	1	0	0	1	0	1	1	0	0	0	1	1
<i>Chanaresuchus</i>	1	0	1	1	1	0	1	1	0	1	0	?	1	0	?	0	1	1
<i>Euparkeria</i>	1	0	1	1	1	0	A	1	1	1	1	1	1	0	0	0	1	1
<i>Dromicosuchus</i>	?	?	?	?	?	?	1	0	1	1	?	?	1	0	0	0	1	1
<i>Postosuchus</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1	1
<i>Herrerasaurus</i>	1	1	1	1	1	1	1	0	0	1	1	–	1	1	1	0	1	1
<i>Coelophysis</i>	1	1	1	1	1	1	1	0	0	1	1	–	1	1	1	0	1	1

	37	38	39	40	41	42	43	44	45	46	47	48	49	50
<i>Mesosuchus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Prolacerta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Proterosuchus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Erythrosuchus</i>	1	0	1	?	0	0	0	0	?	1	0	0	1	0
<i>Vancleavea</i>	1	0	1	0	0	0	0	0	0	1	0	0	?	1
<i>Tropidosuchus</i>	1	0	1	1	0	1	0	0	1	1	1	1	1	1
<i>Chanaresuchus</i>	1	0	1	1	0	?	0	0	0	1	1	1	1	1
<i>Euparkeria</i>	1	0	1	1	0	1	1	1	0	1	0	0	1	1
<i>Dromicosuchus</i>	?	1	1	?	1	2	1	?	?	?	0	0	?	1
<i>Postosuchus</i>	1	1	1	1	1	2	1	1	0	1	0	0	1	1
<i>Herrerasaurus</i>	1	0	1	1	1	–	–	1	1	1	0	0	1	0
<i>Coelophysis</i>	1	0	1	1	1	–	–	1	1	1	0	0	1	0

A = (0/1) polymorphism.

APPENDIX 5: LIST OF THE SPECIMENS EXAMINED AND LITERATURE USED IN SCORING TAXA

Mesosuchus browni
Dilkes, 1998.

Prolacerta broomi
BP/1/2675, UCMP 37151, AMNH 9502, Camp, 1945; Gow, 1975; Evans, 1988; Dilkes, 1998; Modesto & Sues, 2004.

Proterosuchus fergusi
BSP 514, QR 1484 (unpublished photographs), Welman, 1998.

Erythrosuchus africanus

BP/1/ 5207, BMNH R3592, BMNH R3267a, Gower, 1996, 1997, 2003.

Vancleavea campi

See text.

Euparkeria capensis

SAM-PK-5867, SAM-PK-6050, SAM-PK-6049, UMCZ T692, Ewer, 1965; Gower & Weber, 1998.

Tropidosuchus romeri

PVL 4601, PVL 4602, PVL 4603, PVL 4604, PVL 4605, PVL 4606, PVL 4624.

Chanaresuchus bonapartei

UPLR 7, PVL 4586, PVL 4575, PVL 4647, MCZ 4035, MCZ 4036.

Dromicosuchus grallator

UNC 15574.

Postosuchus kirkpatricki

TTU-P 9000, TTU-P 9002.

Herrerasaurus ischigualastensis

PVL 2566, PVSJ 373, PVSJ 407.

Coelophysis bauri

AMNH FR 7224, AMNH FR 7223.