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NEW INFORMATION ON THE UPPER TRIASSIC ARCHOSAURIFORM *VANCLEAVEA CAMPI* BASED ON NEW MATERIAL FROM THE CHINLE FORMATION OF ARIZONA

William G. Parker and Bronson J. Barton

ABSTRACT

Two new partial skeletons from the Petrified Forest Member (Chinle Formation) of Petrified Forest National Park are referable to *Vancleavea campi* Long and Murry 1995. Although lacking good skull material, the new specimens possess postcranial elements that are either absent or poorly preserved in the holotype specimen. A phylogenetic analysis tentatively suggests that *Vancleavea campi* represents a basal archosauriform more derived than *Erythrosuchus*, *Proterosuchus*, and possibly *Euparkeria*. Comparisons with undescribed material from the Chinle Formation near St. Johns, Arizona, and Ghost Ranch, New Mexico, are needed to confirm this placement and also to determine the taxonomic validity of the genus *Vancleavea*.

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INTRODUCTION

In the early 1960s, Petrified Forest National Park naturalist Phillip Van Cleave collected the fragmentary postcranial remains of a small reptile. This specimen was originally listed by Murry and Long (1989) as a possible proterochampsid based in part on the morphology of a second specimen comprised of a right mandible and other fragmentary skull elements that had been collected by Charles Camp from the same area in 1923. Subsequently, Long and Murry (1995) recognized that the two specimens were not from the same taxon, and named two new taxa based on the material, designating the partial skull as the holotype of *Acallosuchus rectori* and the postcranial material as the holotype of *Vancleavea campi*. Long and Murry (1995) were unsure of the phylogenetic relationships of these taxa and conservatively assigned them both to Neodiapsida *incertae sedis*.

In recent years, *Vancleavea* has received more attention because of the discovery and recognition of additional material from the Late Trias-

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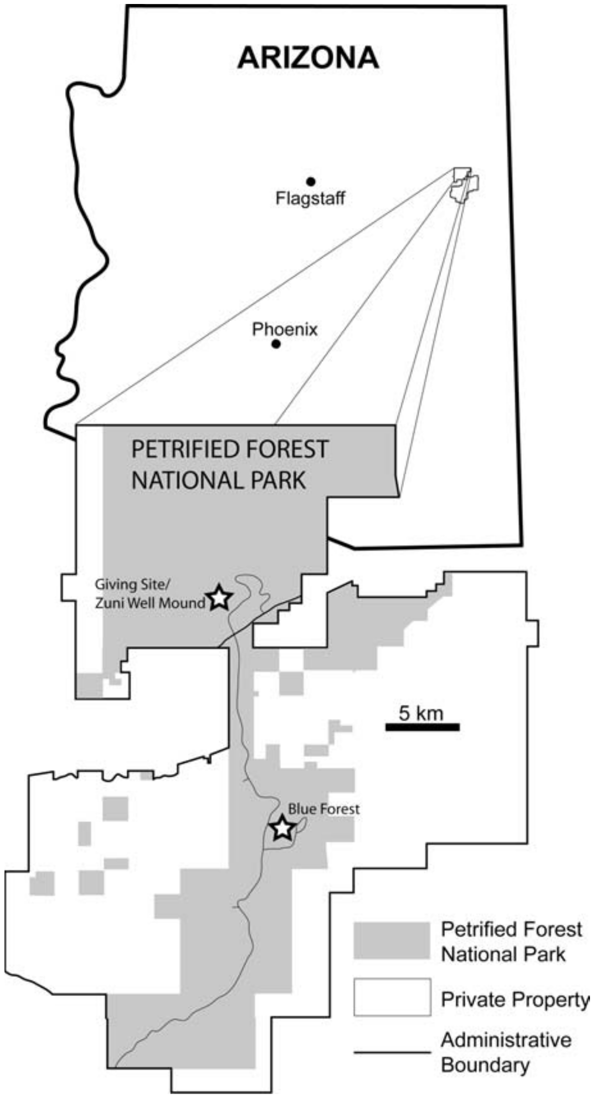

FIGURE 1. Map of Petrified Forest National Park showing the geographical locations of the main localities discussed in the text (modified from Irmis and Parker, 2005).

sic of New Mexico and Texas. In particular two articulated skeletons from the *Coelophysis* Quarry at Ghost Ranch, New Mexico, were assigned to *Vancleavea* by Hunt et al. (2002) (see also Small and Downs 2002). These skeletons are currently being described (Nesbitt et al. in review). Hunt et al. (2002) also provided an overview of all identified *Vancleavea* material and discussed the distribution of the taxon. This material includes a partial skeleton and isolated material reported by Polcyn et al. (2002) from the Chinle Formation near St. Johns, Arizona. Hunt et al. (2005) published the first photographs of the holotype of *Vancleavea campi* and provided a more detailed description and discussion of the distribution of the taxon than that provided by Long and Murry (1995) and Hunt et al. (2002). Here, we describe two new partial skeletons of *Vancleavea* from the Petrified Forest Member of the Chinle Formation in Petrified Forest National Park (PEFO) and further discuss the phylogenetic relationships of the taxon based on this new material. These specimens are referable to *Vancleavea* as they both possess the diagnostic keeled osteoderms that are characteristic of the genus (Long and Murry 1995; Hunt et al. 2002) and represent the best preserved material of *Vancleavea* from the Petrified Forest Member of the Chinle Formation. Because the type specimen of *Vancleavea campi* is fragmentary, it is desirable to supplement the original description of the taxon with other specimens from PEFO to assist other workers currently working on descriptions of material that have been tentatively referred to *Vancleavea* (e.g., the Ghost Ranch specimens).

Institutional Abbreviations. MNA, Museum of Northern Arizona, Flagstaff, USA; **PEFO**, Petrified Forest National Park, Arizona, USA; **PFV**, Petrified Forest National Park Fossil Vertebrate Locality; **SAM-PK**, South African Museum of Natural History, Cape Town, South Africa; **UCMP**; University of California Museum of Paleontology, Berkeley, USA; **USMN**; United States National Museum, Washington D.C., USA.

GEOLOGIC SETTING

The holotype specimen of *Vancleavea campi* (PEFO 2427) was collected from a geographic area in Petrified Forest National Park known as the Blue Forest (Figure 1). Although the exact discovery site for the material is uncertain, an unpublished written communication from the discoverer records its general stratigraphic provenance (Long and Murry 1995). This horizon is extremely fossiliferous and contains several productive localities that are likely sources of the holotype of *Vancleavea* (Camp 1930; Long and Murry 1995). Based on this information, Long and Murry (1995) suggested that the type material came from at or near the 'Crocodile Hill' locality (PFV 124), a site first worked by Charles Camp in 1923 (Camp 1930; Murry and Long 1989; Long and Murry 1995; Parker 2005). Another possibility is the nearby 'Dying Grounds' locality (PFV 122), which is located in the same stratigraphic horizon and represents a productive microvertebrate site (Murry and Long 1989; Long and Murry 1995; Parker 2002; Heckert 2004). Both of these localities are in a greenish-gray mudstone in the upper portion of

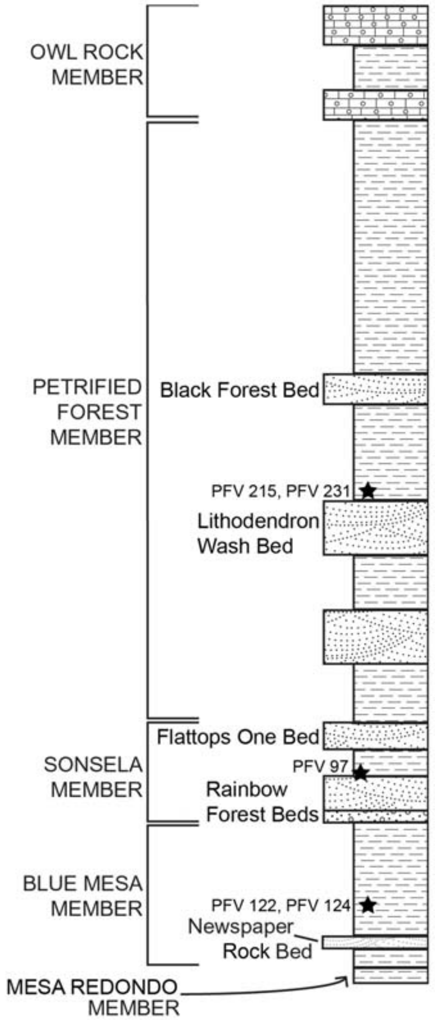

FIGURE 2. Generalized geological section of Chinle Formation exposures in Petrified Forest National Park showing the relative stratigraphic positions of the specimens (modified from Irmis and Parker, 2005).

the Blue Mesa Member of the Chinle Formation (*sensu* Woody 2006) (Unit 14 of the Blue Mesa Member [Petrified Forest Formation, Chinle Group] type section of Lucas 1993). This horizon is situated approximately 14 meters above the Newspaper Rock Bed and approximately 9 meters below the base of the overlying Sonsela Member (Figure 2; Lucas 1993; Heckert and Lucas 2002; Parker 2006; Woody 2006). Palynomorphs recovered from this horizon are considered to be latest Carnian in age (Fischer and Dunay 1984; Litwin et al. 1991), but recent recalibration of the Triassic timescale based on magnetostratigraphy and a new radiometric date from European marine sections suggest that most of the Chinle Formation, including this horizon, may be Norian in age (Muttoni et al. 2004; Furin et al. 2006).

The two skeletons described herein (PEFO 34035 and PEFO 33978) were collected from two sites in the younger Petrified Forest Member (*sensu* Woody 2006), Zuni Well Mound (PFV 215) and the Giving Site (PFV 231), respectively. Both of these sites are roughly stratigraphically equivalent and are approximately 54 meters below a prominent tuffaceous sandstone bed known as the Black Forest Bed (Ash 1992). Riggs et al. (2003) have determined a maximum age for this bed, and thus a minimum age for the quarries, of 213 +/- 1.7 based on U-Pb ages of detrital zircons. Other referred specimens from the park (listed below) are from the Blue Mesa and Sonsela Members of the Chinle Formation and were collected by researchers or park staff in the 1930s and 1980s.

SYSTEMATIC PALEONTOLOGY

DIAPSIDA Osborn 1903 *sensu* Laurin 1991

ARCHOSAURIFORMES Gauthier, Kluge, and Rowe 1988a

VANCLEAVEA Long and Murry 1995

Type Species.- *Vancleavea campi* Long and Murry, 1995, by monotypy.

Vancleavea campi Long and Murry, 1995

? 1989 "*Acallosuchus rectori*" in part; Murry and Long, p. 32.

? 1989 proterochampsid gen. et sp. nov; Murry and Long, p. 48.

v* 1995 *Vancleavea campi*; Long and Murry, p. 195, figs. 197, 198.

2002 *Vancleavea campi*; Hunt, Heckert, Lucas and Downs, p. 269, fig. 2.

2005 *Vancleavea campi*; Parker, p. 43.

v* 2005 *Vancleavea campi*; Irmis, p. 71, figs.4j, k.

v. 2005 *Vancleavea* sp.; Parker and Irmis, p. 48, figs. 3d, e.

v* 2005 *Vancleavea campi*; Hunt, Lucas and Spielmann, p. 59, figs. 2, 3, 4.

Holotype. PEFO 2427, fragmentary postcranial skeleton.

Referred Specimens from Petrified Forest National Park. PEFO 31202, left femur, from locality PFV 215 (Zuni Well Mound), Petrified Forest

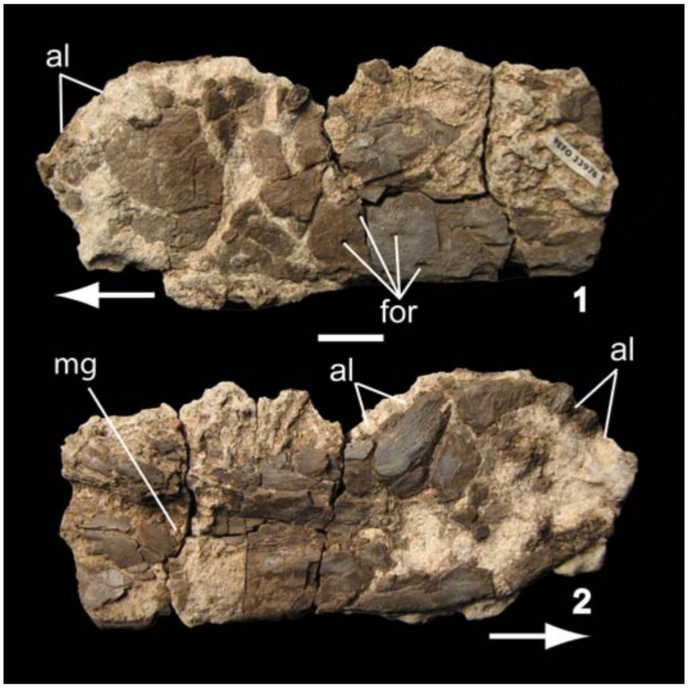

FIGURE 3. *Vancleavea campi* partial left dentary (PEFO 33978) in lateral (1) and medial (2) views. Whitish-gray areas represent matrix. Arrows point anteriorly in each view. Abbreviations: al alveoli; for, foramen; mg, meckelian groove. Scale bar is 10 mm.

Member. PEFO 33978, partial skeleton, from locality PFV 231 (The Giving Site), Petrified Forest Member. PEFO 34035, partial skeleton, from locality PFV 215 (Zuni Well Mound), Petrified Forest Member. PEFO 34224, distal end of femur, and PEFO 34231, sacral centrum, both from an unknown locality in the Blue Mesa Member. UCMP 178050, caudal vertebra, from UCMP locality V82251 (PFV 97 - Saurian Valley), Sonsela Member. Locality information for these specimens is available at Petrified Forest National Park for qualified researchers. See Hunt et al. (2002) for further referred specimens outside Petrified Forest National Park.

Revised Diagnosis. Non-archosaurian archosauriform distinguished by the following autapomorphies: 1) cervical centra with a length/width ratio of greater than 1.5; 2) mid-cervical centra with a convex posterior articular face; 3) dorsal vertebral centra with weakly developed double ventral keels; 4) caudal centra that are subrectangular in ventral view with almost no waisting and possessing extremely well-developed sharp ventral keels; 5) a carapace of numerous subrounded osteoderms, each possessing a pronounced median keel and anterior projection; and 6) ilium with a tall anteriorly directed blade that does not extend anterior to the pubic peduncle, which superficially resembles the ilium of drepanosaurs. Distinguishing synapomorphies include 1) loss of the "terminal" femoral head and ventral ridge system (*sensu* Carroll 1988) as in basal archosauromorphs and basal archosauriforms; 2) cervical vertebral diapophyses and dorsal vertebral parapophyses divided by the neurocentral suture as in *Euparkeria* and *Erythrosuchus*; and 3) presence of a prominent, medially directed femoral head as in *Euparkeria*, *Turfanosuchus*, *Doswellia*, *Chanaresuchus*, and archosaurs.

Distribution. Blue Mesa, Sonsela, and Petrified Forest Members, Chinle Formation, Arizona; Siltstone Member, Chinle Formation, New Mexico; Los Esteros Member, Santa Rosa Formation, Dockum Group, New Mexico; Bull Canyon Formation, Dockum Group, New Mexico; Redonda Formation, Dockum Group, New Mexico; and Tecovas Formation, Dockum Group, Texas (Long and Murry 1995; Hunt et al. 2002).

Age. Late Triassic, Norian (Muttoni et al. 2004; Furin et al. 2006; Irmis and Mundil 2008).

Description

Dentary. Much of the left dentary is preserved in PEFO 33978 (Figure 3). This bone is mediolaterally slender and dorsoventrally deep with a dorsally expanded anterior end. The alveoli are badly preserved but it appears that the entire length of the dentary possessed teeth with a thecodont tooth implantation. The ventrolateral surface of the anterior portion of the dentary has a pattern of thin, elongate grooves which terminate anteriorly as small foramina. The medial surface is excavated by a prominent meckelian groove (Figure 3.2). The total length of the lower jaw, based on the preserved dentary length (approximately 77 mm), is greater than the length of the femur (based on comparison with PEFO 31202, which represents an individual similar in size to PEFO 33978). At its deepest point, at the dorsal expansion of the anterior end, the dentary is 31 mm high. As figured by Wu and Russell (2001, figure 2) the anterior portion of the dentary in *Turfanosuchus dabensis* is also dorsoventrally expanded but not to the degree seen in PEFO 33978.

Vertebrae

Cervical. PEFO 33978 preserves two articulated cervical vertebrae (Figure 4.1) and two isolated centra (Figures 4.2-4.3). The mediolaterally compressed centra are elongate (L/H ratio of 2:1) and 40 mm in length. The posterior articular face is flat, whereas the anterior articular face is concave. The parapophysis is represented by an expansion along the edge of the anterolateral surface of the centrum (Figure 4.1). The ventral surface is strongly keeled (Figures 4.1-4.2). The diapophysis is divided by the neurocentral suture, between the anterior portion of the centrum and the neural arch. The neurocentral sutures appear to be articulated but open (Brochu 1996; Irmis 2007). The prezygopophyses are elongate, inclined medially approximately 45 degrees and fit into a shallow concavity at the base of the postzygopophyses of the proceeding vertebra (Figure 4.1). The postzygopophyses project posteriorly past the posterior face of the centrum and strongly overlap the neural arch of the subsequent vertebra. The neural spine is tall (25 mm) and elongate (20 mm); rectangular in lateral view (Figure 4.2). The apex of the spine is not mediolaterally expanded into a “spine-table.” The cervical vertebrae lack post-axial intercentra.

An isolated, well-preserved cervical centrum from PEFO 34035 (Figures 4.4-4.7) differs from the vertebrae described above in possessing well-developed parapophyses (Figures 4.4-4.5). The anteroventral surface of the centrum is slightly beveled (Figure 4.7) and the dorsal surface is broad, forming a shelf (the ventral portion of the diapophysis) where it meets the ventral surface of the neural arch (Figure 4.6). The lateral surfaces of the centrum are concave, and the ventral surface possesses a sharp anteroposteriorly directed keel (Figure 4.5).

Dorsal. One complete dorsal vertebra and four isolated centra are preserved in PEFO 33978. The centra are blocky, elongate (L/H ratio of 1.5:1), and platycoelus. The centra are similar size with an average length of 35 mm. The articular faces are tall and oval. The ventral surface of the centrum is broad and flat, with two very weakly developed keels that are only faintly visible (Figure 5). The dorsolateral surface of the centrum flares laterally at the neurocentral suture. The parapophysis consists of a pronounced, slightly anterolaterally projecting knob (Figures 4.8-4.9) located on the anterolateral corner of the centrum and at the base of the neural arch. The neurocentral suture divides the parapophysis with only a small percentage of the articular facet located on the neural arch (Figure 4.10). None of the neurocentral sutures in PEFO 33978 are closed.

The neural arch of the dorsal vertebra (Figures 4.11-4.12) is tall (27 mm), roughly equal to the height of the centrum. The prezygopophyses project anterodorsally just past the anterior articular face of the centrum. The articular facets of the prezygopophyses are angled about 45 degrees medially, similar to the cervical series; however, the postzygopophyses do not project as far dorsally as those of the cervical series.

The short (18 mm) transverse processes are anterolaterally expanded, project posterolaterally, and are situated posteriorly on the neural arch Figures 4.11-4.12). The articular surface (divided diapophysis) is broad. Distinct parapophyses and diapophyses in the cervical and dorsal vertebrae demonstrate that the cervical and dorsal ribs of *Vancleavea* were dolichocephalous.

Sacral. According to Long and Murry (1995) two sacral centra are preserved in the holotype (PEFO 2427); sacral centra are also known from PEFO 34035 and PEFO 34231. These centra are longer than high (L/H ratio of 1.9:1 with lengths of 30 mm and 35 mm), platycoelus, and strongly keeled ventrally (Figures 4.13-4.16). In PEFO 2427 (Figure 4.16), there is a double keel (Long and Murry 1995), whereas in the larger specimens PEFO 34035 (35 mm length; Figure 4.13) and PEFO 34231 (36 mm length) there is only a single keel. The significance of this difference cannot be unambiguously determined given the material at hand, but either the two keels merge into a single larger keel through ontogeny of the individual or sacrals one and two differ in the number of keels that they

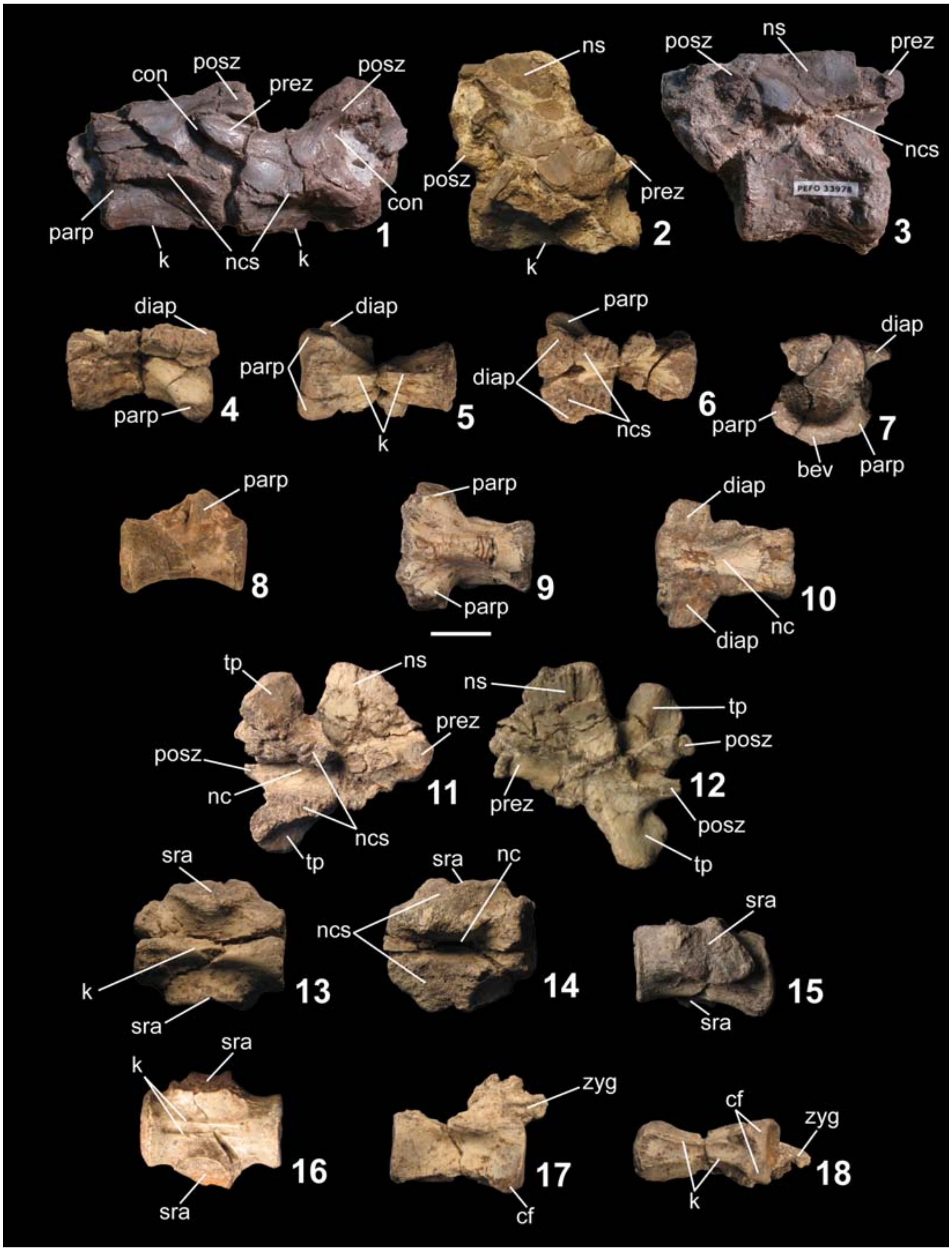

FIGURE 4. *Vancleavea campi* vertebrae. 1. (PEFO 33978) articulated postaxial cervical vertebrae in left lateral view. 2. (PEFO 33978) postaxial cervical vertebra in right lateral view. 3. (PEFO 33978) postaxial cervical vertebra in right lateral view. 4-7. (PEFO 34035) postaxial cervical centrum in lateral (4), ventral (5), dorsal (6), and anterior (7) views. 8. (PEFO 2427) dorsal centrum in lateral view. 9-10. (PEFO 34035) dorsal centrum in ventral (9) and dorsal (10) views. 11-12. (PEFO 34035) dorsal neural arch in ventral (11) and dorsal (12) views. 13-14. (PEFO 34035) sacral vertebra in ventral (13) and dorsal (14) views. 15-16. (PEFO 2427) sacral vertebra in lateral (15) and ventral (16) views. 17-18. (PEFO 34035) mid-caudal vertebra in lateral (17) and ventral (18) views. Abbreviations: bev, beveled surface; cf, chevron facet; con, concavity for prezygopophysis; diap, diapophysis; k, keel; na, neural arch; nc, neural canal; ncs, neurocentral suture; ns, neural spine; parp, parapophysis; sra, sacral rib articulation; tp, transverse process; zyg, zygopophysis. Scale bar is 10 mm.

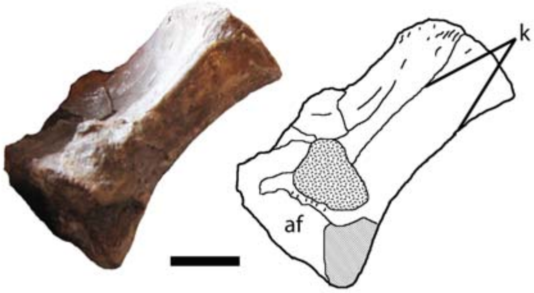

FIGURE 5. *Vancleavea campi* PEFO 33978 dorsal vertebra and interpretive drawing in ventrolateral view depicting ventral keels. Abbreviations: af, articular face; k, keel. Scale bar = 10 mm. Hatching represents broken surface. Honeycomb pattern represents matrix.

possess. Other possibilities include individual or taxonomic differences.

Raised facets for attachment of the sacral ribs cover much of the lateral side of the centrum (Figures 4.13-4.16). In one centrum (PEFO 2427) and the preserved sacral in PEFO 34035, the facet is subrounded in lateral view (Figure 4.15), whereas in PEFO 34231 and the other centrum in PEFO 2427 the facet is more anteroposteriorly elongate and particularly pronounced anteriorly. Long and Murry (1995) considered the centra with the subrounded facet from PEFO 2427 to represent the second sacral. All preserved sacral centra have open neurocentral sutures and no neural arches from this region are preserved.

It is possible that the smaller centrum, figured by Long and Murry (1995, figure k) as the first sacral, represents an anterior caudal vertebra instead and that chevrons did not occur in the anteriormost caudals, similar to other archosauriforms. Evidence for this interpretation includes a shorter centrum (30 mm length) and the lack of a broad rib attachment; however, this interpretation cannot be confirmed with the evidence at hand. Hunt et al. (2005) also considered this centrum to belong to the caudal series. Long and Murry (1995) mention a centrum in PEFO 2427 that could represent an anterior caudal because of the lack of chevron facets but did not provide a more explicit identification of the element.

Caudal. The caudal vertebrae of *Vancleavea* (Figures 4.17-4.18) are distinctive because of their box-like, rectangular shape in ventral view with almost no waisting and by the presence of two sharp ventral keels that originate at the posterior margins of the chevron facets and delineate the ventral surface of the centrum (Long and Murry 1995). All of the preserved caudal vertebrae are longer than high with oval articular faces with well-developed rims. In PEFO 2427 the presumably more anterior centra, which are anteroposteriorly shorter (average of 30 mm in length), have anteroposteriorly elongate, laterally projecting transverse processes. The more elongate (> 30 mm in length), and presumably more posteriorly situated caudal centra completely lack transverse processes.

Pectoral Girdle

Scapula. A fragment from PEFO 34035 (Fig. 6) represents the distal portion of the right scapula. Although the morphology of this fragment also appears consistent with the proximal portion of the coracoid, we interpret it as belonging to the scapula because of the lack of a noticeable coracoid foramen. A rugose articular surface for the coracoid demonstrates that the scapula and coracoid were separate elements and were not co-ossified, at least for the preserved ontogentic stage of the specimen. From the broken cross-section it appears that the scapular blade was very thin mediolaterally. A small shallow notch is present just dorsal to the glenoid.

Pelvic Girdle

Ilium. Both ilia are preserved in PEFO 34035. The left ilium is missing the posterior-most portion of the iliac blade and is diagenetically fused to the left femur; however, the right ilium is isolated and complete (Figure 7.1). The iliac blade is tall (40 mm) and separated from the acetabular by a well-defined neck. The blade apex is formed by the anterior portion of the blade. The dorsal margin slopes posteriorly toward a small posterior process. Neither the anterior or posterior portions project past the pubic or ischiadic peduncles; thus, the blade is extremely anteroposteriorly narrow. The mediodorsal surface of the iliac blade possesses elongate grooves, which originate at the neck and progress anterodorsally to the blade apex, representing attachment areas for the sacral ribs (Figure 7.2). The tall iliac blade differs greatly from those of *Erythrosuchus*, *Chanaresuchus*, *Euparkeria* (Ewer 1965, figure 11), and *Turfanosuchus* (Wu and Russell 2001, figure 9) which are low with a nearly horizontal dorsal margin and is more similar to those of non-archosauriform archosauromorphs. Particularly striking is the strong similarity of the ilium of *Vancleavea* with that of *Megalancosaurus* (Renesto 1994, figures 11-12).

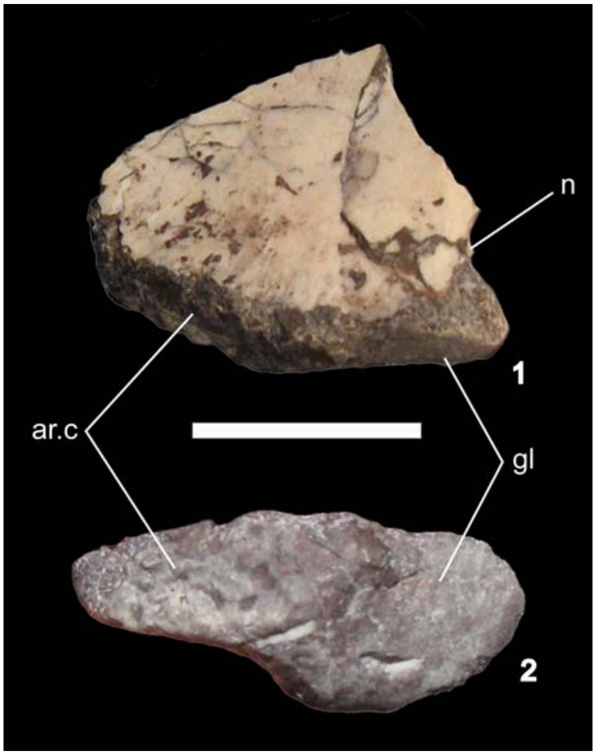

FIGURE 6. *Vancleavea campi* distal end of right scapula (PEFO 34035) in medial (1) and distal (2) views. Abbreviations: ar.c, articular surface for coracoid; gl, glenoid; n, notch. Scale bar is 10 mm.

Doswellia also has a tall, expanded iliac blade; however, it differs from *Vancleavea* in its strong lateral expansion (Weems 1980, figure 21, pl. 7).

The ilium makes up almost the entire acetabulum. A distinct supra-acetabular rim is present, and the anterior margin of the ilium is almost twice the length of the posterior margin. The pubic and ischiadic peduncles meet at an obtuse angle; both are crescentic in distal view, curving slightly laterally (Figure 7.3; Hunt et al. 2005). The pubic peduncle is mediolaterally thickened compared to the ischiadic peduncle.

Pubis. The proximal portions of both pubes are preserved in the holotype material (PEFO 2427). The pubis only contributes slightly to the acetabulum and possesses a distinct posterodorsal process (Figure 7.4). The articular surface for the ilium is mediolaterally thickened, rugose, and crescent shaped (Long and Murry 1995; Hunt et al. 2005). This surface continues posteriorly onto the posterior process and is confluent with a second rugose articular surface that is vertical and faces posteriorly to meet an anterior edge of the proximal portion of the ischium. The ventral surface of the posterior process of the pubis forms the dorsal rim of the obturator foramen. Because the ventral portion of the pubis is missing, it is not clear whether this foramen was fully enclosed by the pubis, or if it bordered the symphysis with the ischium (Long and Murry 1995). It is possible that the pubis and ischium met below this foramen, similar to basal archosauromorphs. The presence of a distinct thyroid fenestra, suggested for the Ghost Ranch specimen (Small and Downs 2002), cannot be determined from the PEFO material.

Ischium. The ischium is known from proximal portions of both ischia preserved in PEFO 2427 and the proximal portion of the left ischium in PEFO 34035. Approximately a quarter of the acetabulum is formed by the ischium, a larger contribution than that of the pubis, but much less so than that of the ilium. The acetabular portion forms a distinct ventrally flaring semicircular rim (Figure 7.4; Long and Murry 1995). The articular surface for the ilium is rugose and curves posteromedially. There is an anterior projection with a subrounded anteriorly facing articular facet for the pubis. The ventral portion is not preserved. The groove mentioned by Long and Murry (1995) and questioned by Hunt et al. (2005) is interpreted here as a scallop-shaped fracture of the bone surface.

Forelimb

Humerus. Humeri are preserved in PEFO 2427 (left, Figures 8.1-8.3), PEFO 33978 (proximal ends of the left and right, distal end of the left?, not figured), and PEFO 34035 (left, minus the distal end, Figures 8.4-8.5). The humerus has a distinct yet weakly developed deltopectoral crest as well as a distinct internal tuberosity (Figures 8.3-8.5). Because none of the elements are complete, the offset between the proximal and distal ends cannot be determined. The proximal articular surface is convex in ventral view and roughly oval in proximal view. Along this surface the humerus thickens medially, forming the medial tuberosity, which is triangular in PEFO 2427 (Figure 8.3) and PEFO 33978, but gently rounded in PEFO 34035 (Figures 8.4-8.5). The ventrolaterally directed deltopectoral crest is best preserved in PEFO 34035 and is restricted to the dorsoventral surface. The deltopectoral crest does not extend ventrally along the shaft (Figure 8.5). The overall morphology of the humerus is very similar to that of *Turfanosuchus* (Wu and Russell 2001, p. 44), where the deltopectoral crest is not well-developed and "is more appropriately regarded as a continuation of the"

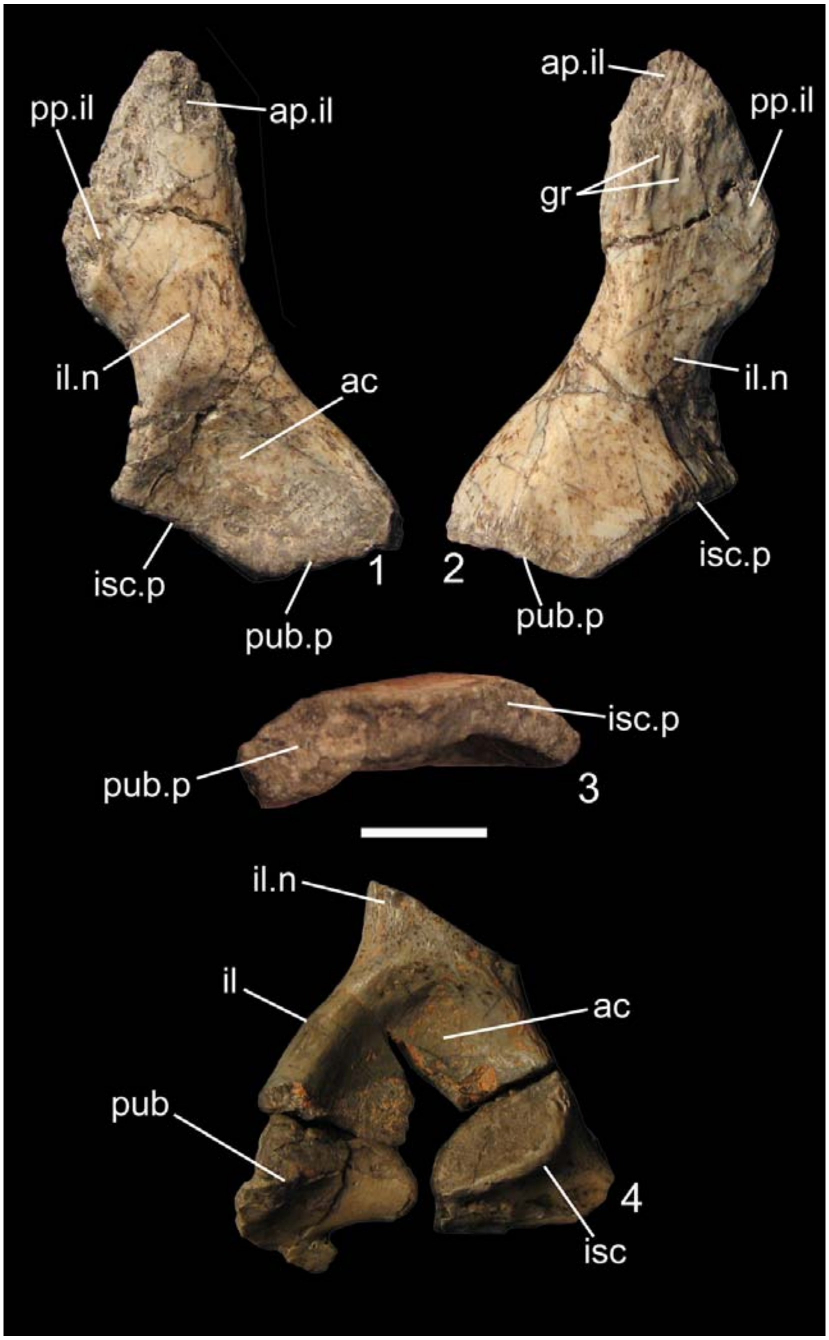

FIGURE 7. *Vancleavea campi* pelvic elements. 1-3. (PEFO 34035) right ilium in lateral (1), medial (2), and distal (3) views; 4. (PEFO 2427) right ilium, ischium, and pubis in lateral view. Abbreviations: ac, acetabulum; ap.il, anterior process of iliac blade; gr, grooves; il, ilium; il.n, iliac neck; isc, ischium; isc.p, ischiadic peduncle of ilium; pub, pubis; pub.p, pubic peduncle of ilium; pp.il, posterior process of iliac blade. Scale bars are 10 mm.

proximal head. Wu and Russell (2001) also note the presence of this humeral morphology in *Ticinosuchus* and *Euparkeria*.

The distal end of the humerus is best preserved in PEFO 2427. The ento- and ectocondyles are distinct; the entocondyle is larger than the ectocondyle (Long and Murry 1995). There is a very slight concavity between the two condyles (contra Long and Murry 1995) and the distal surface is expanded medially forming a distinct entepicondyle (Figure 8.1). No entepicondylar or ectepicondylar grooves or foramina are present. The proximal and

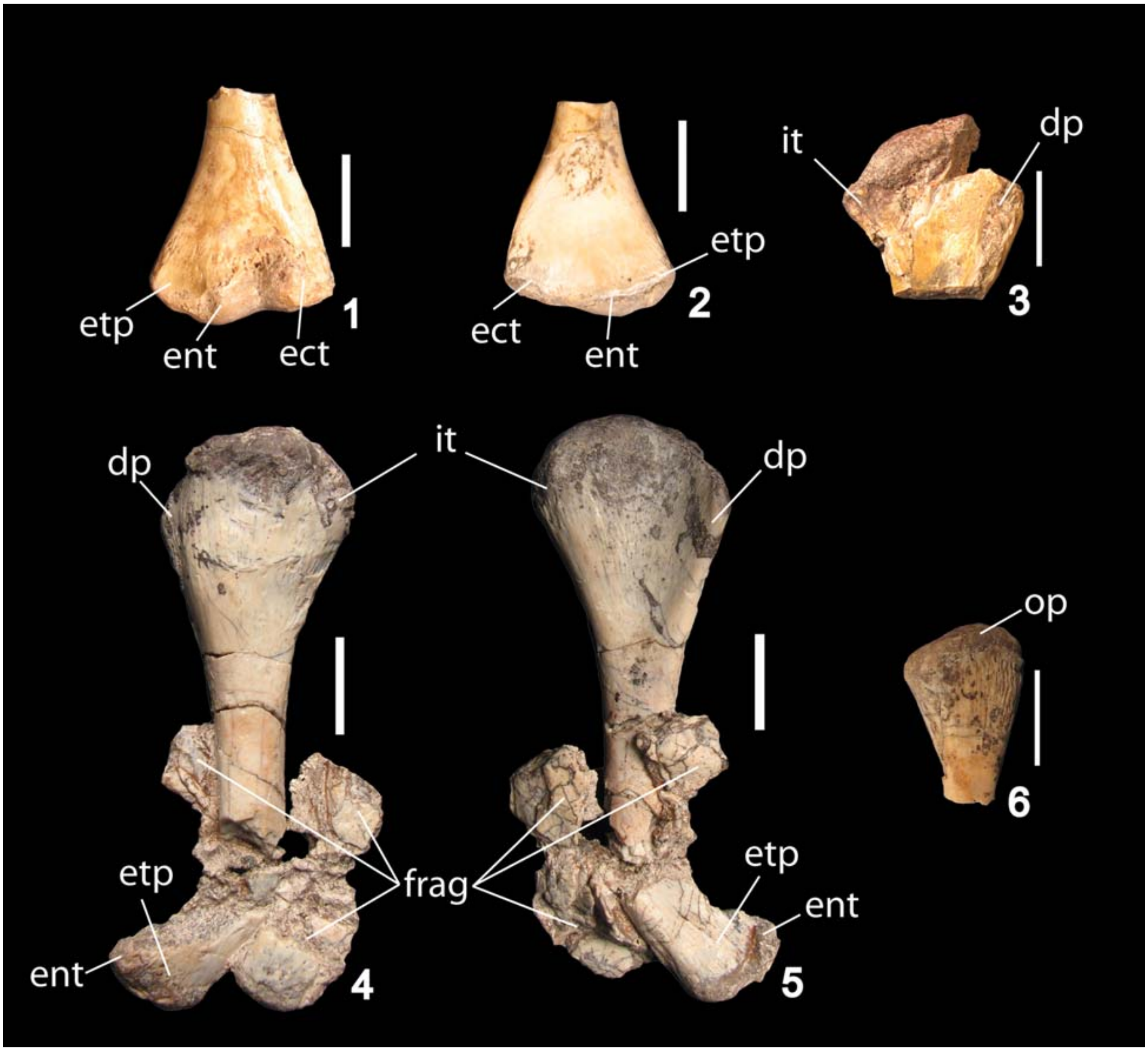

FIGURE 8. *Vancleavea campi* humeri and ulna. 1-2. (PEFO 2427) distal end of left humerus in ventral (1) and dorsal (2) views; 3. (PEFO 2427) proximal end of left humerus in ventral view; 4-5. (PEFO 34035) left humerus in dorsal (4) and ventral (5) views; 6. (PEFO 34035) proximal end of left ulna in dorsal view. Abbreviations: dp, deltopectoral crest; ect, ectocondyle; ent, entocondyle; etp, entepicondyle; frag, unidentifiable fragments; it, internal tuberosity; op, olecranon process;. Scale bars are 10 mm.

distal ends of the humerus are of equal width. The best preserved humerus (PEFO 34035) has a length of approximately 100 mm.

Ulna. The proximal end of the left ulna is present in PEFO 34035 (Figure 8.6). The proximal articular surface is gently rounded convexly, and the head is inclined slightly posteriorly. The sigmoid notch is weakly expressed. An olecranon process is present but not strongly developed.

Hind Limb

Femur. The femur is fairly derived in its morphology in comparison with that of basal archosauromorphs in that the head is slightly offset with a distinct neck and not “terminal” (*sensu* Carroll 1988). The enlarged intertrochanteric fossa and ventral ridge system found in basal amniotes, including basal archosauromorphs (Carroll 1988), are not present. The proximal articular surface is

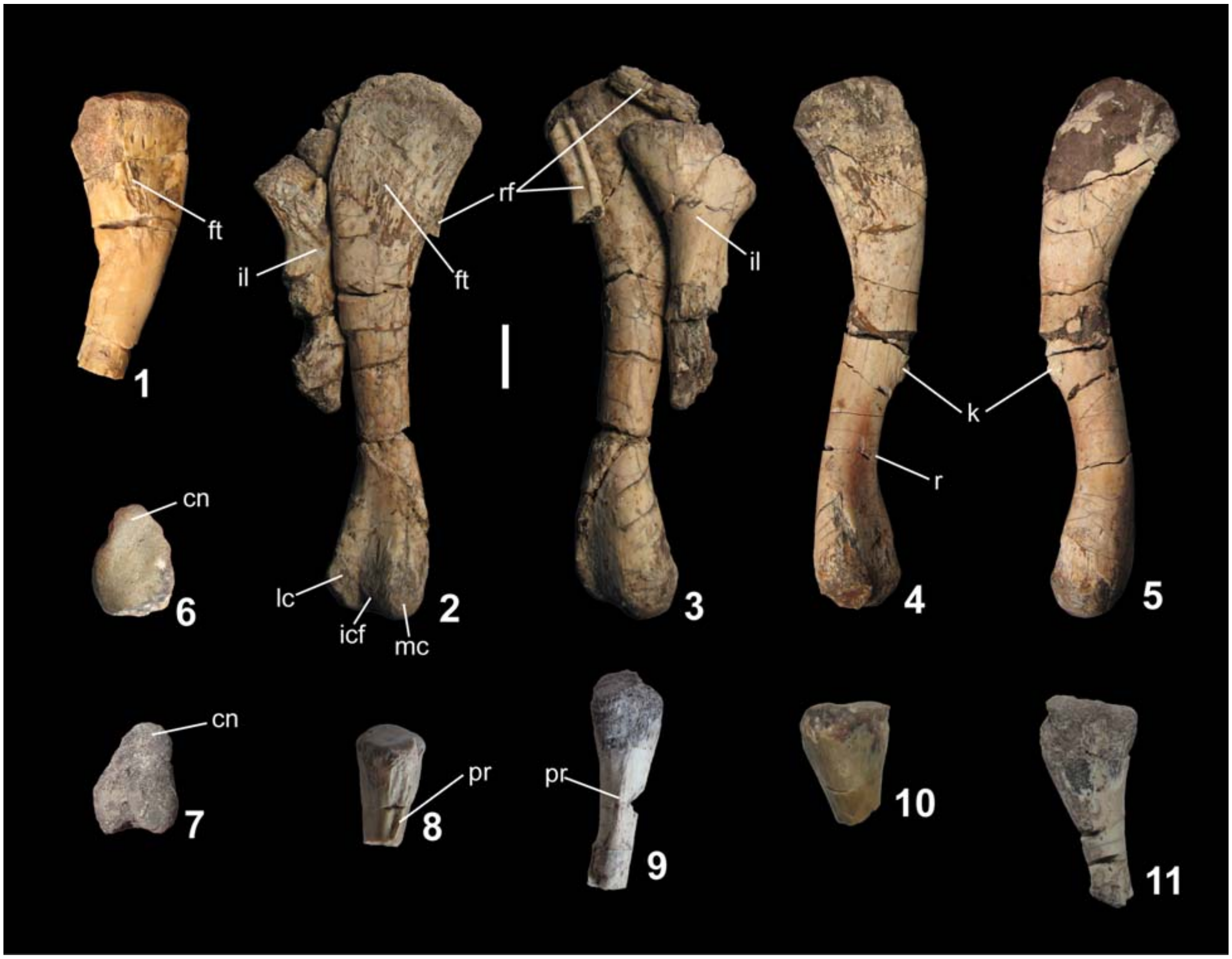

FIGURE 9. *Vancleavea campi* femora and tibiae. 1. (PEFO 2427) proximal end of right femur in posterior view; 2-3. (PEFO 34035) left femur in posterior (2) and anterior (3) views, left ilium and several rib fragments are diagenetically fused to this element; 4-5. (PEFO 34035) right femur in posterior (4) and anterior (5) views. 6. (PEFO 2427) proximal end of left tibia in proximal view. 7. (PEFO 34035) proximal end of ?right tibia in proximal view. 8. (PEFO 2427) proximal end of left tibia in anterior view. 9. (PEFO 34035) proximal end of ?right tibia in anterior view. 10. (PEFO 2427) proximal end of left tibia in medial view. 11. (PEFO 34035) proximal end of ?right tibia in medial view. Abbreviations: cn, cnemial crest; ft, fourth trochanter; icf, intercondylar fossa; il, ilium; k, kink, lc, lateral condyle; mc, medial condyle; pr, posterolateral ridge; r, ridge; rf, rib fragment. Scale bar is 10 mm.

oval in proximal view and lacks a medial tuberosity. In PEFO 2427 there is a low, elongate, rugose ridge where the head meets the shaft (Figure 9.1) which Long and Murry (1995) and Hunt et al. (2005) considered to represent the 4th trochanter; however, this ridge is not present in PEFO 34035, although it is possible that this muscle attachment surface did not ossify in this specimen. The femur of *Vancleavea* is much more similar to that of *Euparkeria* (SAM-PK-5867), *Turfanosuchus* (Wu and Russell 2001, figure 10), and *Doswellia* (USNM 186989) with its sigmidal curvature, “paddle-shaped” proximal end, and weakly developed distal condyles (Figures 9.2-9.5), than the femora of *Proterosuchus* and *Erythrosuchus*, which are straighter and expanded proximally with a prominent intertrochanteric fossa (Cruickshank 1972; Gower 2003). However, it differs from *Turfanosuchus* and pseudosuchians in lacking a distinct posterior medial tuberosity and a prominent fourth trochanter (Wu and Russell 2001, figure 10; Nesbitt 2007). On the right femur of PEFO 34035 there is a pronounced posterior ‘kink’ just ventral to midshaft (Figures 9.4-9.5) that is only weakly developed on the left femur from the same individual. A distinct ridge is present between this ‘kink’ and the medial distal condyle (Figure 9.4). There is a weakly developed intercondylar fossa between the distal condyles (Figure 9.2). The identity of the small fragment that Long and Murry (1995) took to be part of the distal end of the femur in PEFO 2427 is confirmed by the new material (see discussion in Hunt et al. 2005). Complete femora from PEFO 34035 have lengths of 128 mm.

Tibia. Proximal portions of tibiae are preserved in both PEFO 34035 and PEFO 2427 (Figure. 9.6-9.11). In proximal view the element narrows anteriorly forming a distinct, but weak, cnemial crest (Figures 9.6-9.7). The lateral margin is straight, the medial margin slightly concave. Long and Murry (1995) and Hunt et al. (2005) identified the tibial fragment from PEFO 2427 as from the right side (Figure 9.6); however, based on the lateral curvature of the anterior tip of the cnemial crest (despite the slight breakage), this element is probably from the left side. Nonetheless, both sets of authors also interpreted the element backward and thus the 'posterolateral' ridge described by those authors is actually oriented anteromedially (Figure 9.8). Furthermore, PEFO 34035 demonstrates that this ridge terminates ventrally where the proximal portion of the tibia narrows to form the main shaft (Figure 9.9).

Osteoderms. Numerous osteoderms are preserved in the Petrified Forest Member material; however, most of these are poorly preserved. The osteoderms are sub-rounded with a median keel, prominent anterior prong, and serrated margins and are best preserved in PEFO 33978 (Figures 10.1-10.2). Unfortunately, the osteoderms are poorly preserved in the holotype; however, the fragmentary keeled osteoderms ("ankylosaur" type of Long and Murry 1995) are diagnostic of the genus (Hunt et al. 2002). Long and Murry (1995) also described two additional osteoderm morphotypes, tall, triangular osteoderms, and conical osteoderms, both described as "*Stegosaurus*-like." Neither of these morphotypes can be identified in PEFO 33978 or PEFO 34035. Hunt et al. (2005) considered the conical osteoderms to belong to the diminutive aetosaur *Acaenasuchus geoffreyi*, although there is no direct evidence for this interpretation.

PHYLOGENETIC ANALYSIS

Vancleavea was placed in a matrix of 31 characters and 14 taxa to test its relationships among archosauromorphs. Included taxa (Appendix 1) are from a variety of basal archosauromorphs known from relatively complete material and included in many past phylogenetic studies (e.g., Juul 1994; Dilkes 1998; Gower and Sennikov 1997; Senter 2004). Characters were culled from several of these past studies (Appendix 2).

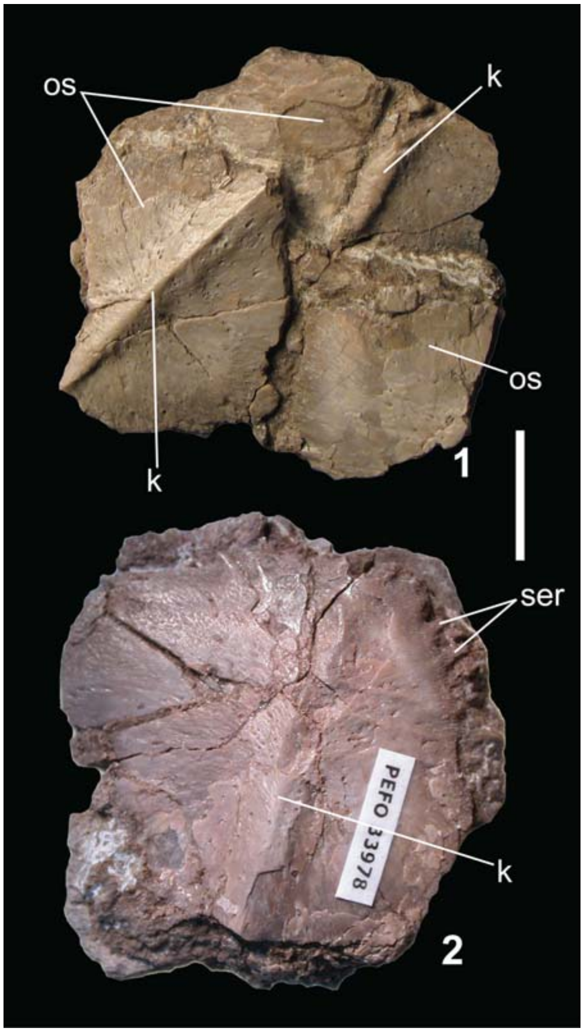

FIGURE 10. *Vancleavea campi* osteoderms. 1. (PEFO 33978) three osteoderms in dorsal view; 2. (PEFO 33978) osteoderm in dorsal view. Abreviations: k, keel; os, osteoderm; ser, serrations. Scale bar is 10 mm.

The matrix (Appendix 3) was analyzed in PAUP* version 4.0b10 for 32-bit Microsoft Windows (Swofford 2002). The characters were unordered and of equal weight. One character (number 3) was parsimony-uninformative but was retained for use in future expansion of the matrix. *Youngina capensis* Broom was set as the out-group taxon, and the tree was rooted with the out-group as paraphyletic. The default settings in PAUP* for a branch and bound search were used and resulted in 15

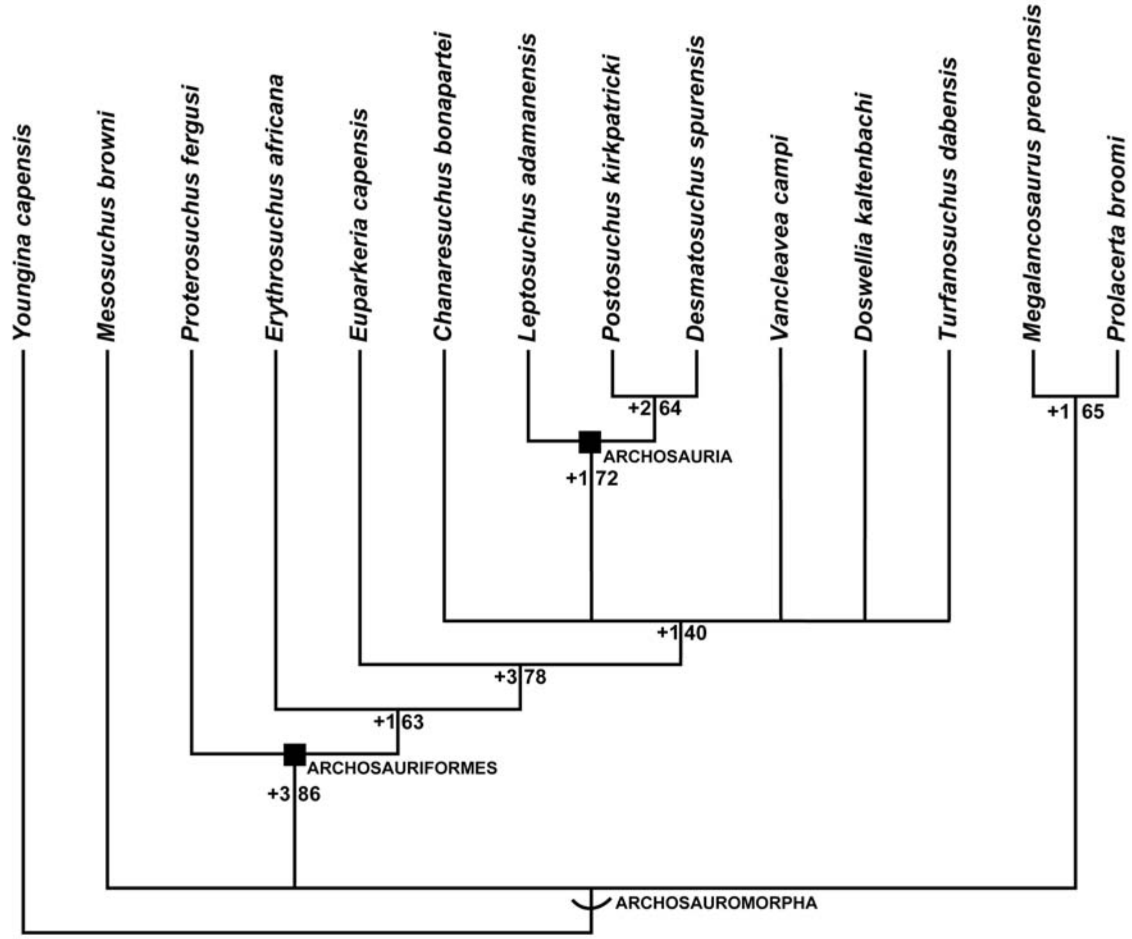

FIGURE 11. Most parsimonious tree from phylogenetic analysis of 31 characters and 14 taxa. Bootstrap values and decay indices are given for nodes.

most parsimonious trees (MPTs) with a length of 60 steps, a consistency index of .5833, a retention index of .7283, and a rescaled consistency index of .4248. Decay indices were determined using the 'keep' command in PAUP* and compiling consensus trees longer than the original consensus tree until all nodes collapsed. Bootstrap values are based on 1,000 replications.

In the strict concensus tree (Figure 11), *Vancleavea campi* nests within Archosauriformes in a polytomy with *Doswellia kaltenbachi*, *Turfanosuchus dabanensis*, *Chanaresuchus bonapartei*, and Archosauria (sensu Gauthier 1986) and is, thus according to this analysis, closer to Archosauria than is *Euparkeria capensis*. However, this idea is weakly supported (Bootstrap value of 40% for 1000 replicates), and only a single step (Tree length = 61) forms an unresolved polytomy between *Euparkeria capensis*, *Doswellia kaltenbachi*, *Turfanosuchus dabanensis*, *Vancleavea campi*, *Chanaresuchus bonapartei*, and Archosauria. Better supported is the more advanced placement of *Vancleavea campi* among basal archosauriformes as two additional steps (Tree length = 62) are necessary for *V. campi* to clade (unresolved) with *Proterosuchus fergusi* and *Erythrosuchus africana*. The clade Archosauriformes collapses at 63 steps.

Unambiguous synapomorphies supporting the inclusion of *Vancleavea campi* into Archosauriformes include the lack of post-axial intercentra, a femur with a medially inflected head, a sigmoidal femoral shaft, the lack of a distinct intertrochanteric fossa on the proximoventral surface of the femur, and the presence of osteoderms.

Long and Murry (1995), unsure of its taxonomic position, originally assigned *Vancleavea campi* to Neodiapsida *incertae sedis* but suggested that it might represent an archosauromorph, whereas Small and Downs (2002) postulated that the Ghost Ranch form possessed archosauriform affinities. The current study tentatively supports these hypotheses; however, the inclusion of skull, braincase, and tarsal characters into the matrix based on the Ghost Ranch material is needed to confirm these taxonomic affinities.

DISCUSSION

When first described, *Vancleavea* was considered an enigma because of the incomplete preservation of the holotype material; however, autapomorphic features of the skeleton allow for unambiguous referral of material to this taxon (Hunt et al. 2002; Polycyn et al. 2002; Small and Downs 2002; Parker and Irmis 2005; Hunt et al. 2005; Irmis 2005). Newly collected material from Petrified Forest National Park described here suggests that *Vancleavea* is a non-archosaur archosauriform, a finding that is further supported if the Ghost Ranch material is referable to this taxon (Small and Downs 2002; Hunt et al. 2002). Evidence provided by Small and Downs (2002) for the inclusion of *Vancleavea* within Archosauriformes include thecodont tooth implantation and an ossified laterosphenoid; however, these authors also mention the possible presence of a thyroid fenestra in the pelvis, which is a plesiomorphic character found in some basal archosauromorphs and squamates (Dilkes 1998).

Comparisons between the type material from the Blue Mesa Member of the Chinle Formation and the referred material from the Petrified Forest Member of the Chinle Formation reveal very few morphological differences. In the holotype material (PEFO 2427) the internal tuberosity of the humerus is pointed, similar to one of the Petrified Forest Member specimens (PEFO 33978), whereas in another specimen (PEFO 34035) from the Petrified Forest Member the internal tuberosity is gently rounded. The sacral centra of PEFO 2427 have double ventral keels, whereas in PEFO 34035 it is a single, broad keel. However, because of the fragmentary preservation of this material and the small sample size, these differences do not clearly represent unambiguous autapomorphies; therefore all of the referred material is assigned to the type species, *Vancleavea campi*. What remains to be determined is if any differences exist between the Ghost Ranch and Stinking Springs specimens. If one or both of these specimens show no distinct differences with the poorly preserved holotype material, but are significantly different from each other and/or the Petrified Forest Member material described here, then the holotype material must be considered non-diagnostic and *Vancleavea campi* would be a nomen dubium. This would require new taxonomic assignments for all of the referred material (Parker and Irmis 2005).

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APPENDIX 1.

Specimens and primary literature used for coding characters. Specimen numbers are given for specimens that were studied firsthand.

Chanaresuchus bonapartei (Romer 1971; Romer 1972; Sues 1976; Parrish 1993; Juul 1994).

Desmatosuchus spurensis (MNA V9300—partial skeleton; Long and Murry 1995; Parker 2008).

Doswellia kaltenbachi (Weems 1980)

Erythrosuchus africana (Gower and Sennikov 1997; Gower 2003).

Euparkeria capensis (Juul 1994; Gower and Sennikov 1997; Dilkes 1998; Senter 2004).

Leptosuchus adamanensis (UCMP 26699—skull and postcrania; PEFO 26695– postcranial skeleton; Long and Murry 1995).

Megalancosaurus preonensis (Dilkes 1998; Senter 2004).

Mesosuchus browni (Dilkes 1998; Senter 2004).

Postosuchus kirkpatricki (Long and Murry 1995; Weinbaum 2002).

Prolacerta broomi (Gow 1975; Juul 1994; Gower and Sennikov 1997; Dilkes 1998; Senter 2004).

Proterosuchus fergusi (Cruickshank 1972; Dilkes 1998; Senter 2004).

Turfanosuchus dabaensis (Wu and Russell 2001)

Vancleavea campi (PEFO 2427—postcranial skeleton; PEFO 33978—dentary and postcrania; PEFO 34035—postcranial skeleton).

Youngina capensis (Gow 1975; Dilkes 1998; Senter 2004)

APPENDIX 2.

Characters and scorings used in phylogenetic analysis.

Skull

1. Palatal teeth (pterygoid, palatine, vomer): present (0); absent (1) (Sereno 1991; Parrish 1992; Dilkes 1998; Nesbitt 2007)

2. Contact between maxilla and external naris: (0) present; (1) absent (Benton 1985; Evans 1988, Senter 2004)

3. Premaxilla: not downturned (0); downturned (1) (Gower and Sennikov 1997)

4. Antorbital fenestra: absent (0); without antorbital fossa (1); with antorbital fossa (2) (Gower and Sennikov 1997)

5. Lateral mandibular fenestra: absent (0); present (1) (Benton 1985; Gauthier et al. 1988b; Juul 1994; Dilkes 1998; Benton 2004; Senter 2004)

6. Caniniform teeth in maxilla: present (0); absent (1) (Benton 1985; Gauthier et al. 1988b; Senter 2004)

7. Ossified laterosphenoid: absent (0); present (1) (Benton and Clark 1988; Juul 1994; Dilkes 1998; Benton 2004)

8. Pineal fossa: present (0); absent (1) (Parrish 1992; Gower and Sennikov 1997)

9. Tooth implantation: non-thecodont (0); relatively “simple,” clearly thecodont (1); fully developed teeth tightly contacting alveolar bone (2) (modified from Gower and Sennikov 1997)

Pectoral Girdle

10. Anterior margin of scapula in lateral view: approximately straight/convex (0); markedly concave (1) (Gower and Sennikov 1997)

Vertebrae and ribs

11. Ratio of lengths of centra of mid-cervical and mid-dorsal vertebrae: 1.0 (0); > 1.0 and < 1.5 (1); > 1.5 (2) (Dilkes 1998)

12. Mid-cervical vertebrae neural spine: tall with approximately equal height and length (0); low, elongate (1) (modified from Dilkes 1998)

13. Mid-cervical vertebrae with mid-ventral keel: absent (0); present (1) (Chatterjee 1986)

14. Posterior face of mid-cervical centra: not convex (0); convex (1) (Senter 2004)

15. Post-axial cervical intercentra: present (0); absent (1) (Gauthier 1986; Benton and Clark 1988; Parrish 1993; Jull 1994; Dilkes 1998)

16. Spine tables (expanded apex when viewed from above) on neural spines of trunk vertebrae: absent (0); present (1) (Juul 1994; Benton 2004)

17. Hyposphene-hypantrum accessory vertebral articulations in trunk vertebrae: absent (0); present (1) (Juul 1994; Benton 2004; Nesbitt 2007)

18. Trunk ribs: most dolichocephalous (0); most holocephalous (1) (Dilkes 1998)

19. Three-headed dorsal ribs: absent (0); present (1) (Gower 2003)

Limbs

20. Entepicondylar foramen of humerus: open (0); closed (1) (Benton 1985; Gauthier et al. 1988b; Senter 2004)

21. Ectepicondylar foramen or groove of humerus: absent (0); present (1) (Dilkes 1998)

22. Pronounced olecranon process: absent (0); present (1) (Benton 1985; Evans 1988; Senter 2004)

23. Femoral head: terminal (0); inflected medially (1) (Gauthier et al. 1988)

24. Intertrochanteric fossa on proximoventral surface of femur: present (0); absent (1) (Juul 1994; Gower and Sennikov 1997; Benton 2004)

25. Femoral shaft: straight (0); sigmoidal (1) (modified from Gauthier et al. 1988b)

26. Femoral condyles: prominent (0); not projecting markedly beyond shaft (1) (Gauthier et al. 1988b)

27. Hemicylindrical calcaneal condyle: absent (0); present (1) (Sereno 1991; Juul 1994; Benton 2004; Nesbitt 2007)

Pelvis

28. Dorsal margin of ilium: posterior process only (0); large posterior process and small anterior process (1); equally developed anterior and posterior processes (2); large anterior projection (3) (Dilkes 1998)

29. Plate-like union between ischium and pubis: present (0); absent (1) (Benton and Clark 1988)

30. Number of sacral vertebrae: two (0); two plus an incipient third (1); three or more (2) (Gauthier

1986; Juul, 1994; Benton 1999; Benton 2004; Nesbitt 2007)

Osteoderms

31. Dorsal body osteoderms: absent (0); present (1); present but in median or paramedian rows over vertebral column (2) (Modified from Sereno 1991)

APPENDIX 3.

Character matrix for phylogenetic analysis

Taxon					**5**					**10**					**15**					**20**					**25**					**30**	
Youngina capensis	0	0	0	0	0	1	0	0	0	0	0	0	?	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	?
Chanaresuchus bonapartei	0	1	0	2	0	1	1	1	1	0	0	0	1	0	1	0	0	0	0	1	0	0	1	1	1	0	0	1	0	0	2
Desmatosuchus haplocerus	1	0	0	1	1	1	1	1	1	1	0	0	0	0	1	1	1	0	0	1	1	0	1	1	1	0	1	1	1	1	2
Doswellia kaltenbachi	0	?	?	?	0	?	0	1	1	?	1	0	0	0	1	1	0	0	0	?	?	?	1	1	1	?	?	1	0	1	?
Erythrosuchus africana	1	1	0	2	1	1	1	1	1	1	0	0	1	0	0	0	0	0	1	1	1	1	0	0	0	1	0	1	0	0	0
Euparkeria capensis	0	1	0	2	1	1	1	1	1	1	0	0	1	0	0	1	0	0	0	0	0	1	1	1	1	0	0	1	0	0	2
Leptosuchus adamanensis	1	1	0	1	1	1	1	1	1	1	0	0	1	0	1	1	0	0	0	1	1	0	1	1	1	0	1	1	0	0	2
Megalancosaurus preonensis	?	?	0	0	0	1	0	0	0	0	2	1	0	1	0	0	0	1	0	1	0	0	0	0	0	1	0	3	0	0	0
Mesosuchus browni	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	1	0	0	0
Postosuchus kirkpatricki	1	0	0	2	1	1	1	1	1	1	0	0	1	0	1	1	1	0	0	1	1	1	1	1	1	0	1	1	1	0	0
Prolacerta broomi	0	1	0	0	0	1	0	0	0	0	2	1	?	0	0	0	0	1	0	0	0	1	0	0	0	1	0	1	0	0	0
Proterosuchus fergusi	0	1	1	1	1	0	1	0	2	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0
Turfanosuchus dabanensis	0	1	0	2	1	1	?	1	1	?	1	0	1	0	?	1	0	0	0	1	0	?	1	1	1	1	1	1	?	0	?
Vancleavea campi	?	?	?	?	?	?	?	?	1	?	1	0	1	1	1	0	0	0	0	1	0	1	1	1	1	1	?	3	0	?	1