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Sacral anatomy of the phytosaur *Smilosuchus adamanensis*, with implications for pelvic girdle evolution among Archosauriformes

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Abstract

The sacrum – consisting of those vertebrae that articulate with the ilia – is the exclusive skeletal connection between the hindlimbs and axial skeleton in tetrapods. Therefore, the morphology of this portion of the vertebral column plays a major role in the evolution of terrestrial locomotion. Whereas most extant reptiles only possess the two plesiomorphic sacral vertebrae, additional vertebrae have been incorporated into the sacrum multiple times independently among early-diverging archosaurian (crocodylians + birds) clades. Phytosauria was a diverse, abundant, and cosmopolitan clade of archosauriforms throughout the Late Triassic, but postcrania of this clade are rarely described and few species-level taxonomic placements of phytosaurian postcranial material are available, potentially hampering knowledge of morphological disparity in the postcranial skeleton among phytosaurs. Here, we describe the sacrum of *Smilosuchus adamanensis*, a phytosaur recovered from the Upper Triassic Chinle Formation of Arizona. This sacrum consists of the two primordial sacral vertebrae, but has a vertebra incorporated from the trunk into the sacrum (= a dorsosacral) and is therefore the first Late Triassic phytosaur and one of the first non-archosaurian archosauromorphs to be described with more than two sacral vertebrae. Our interpretation of this element as a dorsosacral is justified by the lateral extent of the dorsosacral ribs, clear surfaces of articulation between the distal ends of the dorsosacral ribs and the first primordial sacral ribs, and the scar on the medial surface of each ilium for articulation with each dorsosacral rib. Additionally, we provide the first detailed description of the vertebral junction formed by two anteriorly projecting flanges on the first primordial sacral ribs and their corresponding facets on the centrum of the dorsosacral. Computed tomographic (CT) imaging reveals that the two primordial sacrals are not co-ossified and that the dorsosacral morphology of this specimen is not the result of obvious pathology. We place this incorporation of a trunk vertebra into the phytosaurian sacrum in a broader evolutionary context, with this shift in vertebral identity occurring at least seven times independently among Triassic archosauriforms, including at least three times in early crocodylian-line archosaurs and at least four times among bird-line archosaurs. Additionally, anteriorly projecting flanges of sacral ribs which articulate with the anterior-adjacent centrum have evolved several times in archosauriforms, and we interpret 'shared' sacral ribs (= a sacral rib that articulates with two adjacent sacral centra more or less equally) present in some archosaurian clades as a more extreme example of this morphology. In extant taxa the highly conserved Hox gene family plays a central role in the patterning of the axial skeleton, especially vertebral identity; therefore, the independent incorporation of a trunk vertebra into the sacrum across multiple archosauriform lineages may suggest a homologous underlying developmental mechanism for this evolutionary trend.

Key words: archosauriform; convergent evolution; phytosaur; sacrum; Triassic.

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Introduction

The sacrum, the set of vertebrae that articulate with the ilia (Mivart & Clarke, 1879), is the sole nexus between the axial skeleton and the hindlimbs, and is therefore an essential feature of the locomotion of terrestrial vertebrates. In the majority of extant non-avian reptiles the sacrum consists of two sacral vertebrae, often co-ossified with each other, with sacral ribs providing articulation of both of those vertebrae with each ilium (Hoffstetter & Gasc, 1969). However, within Archosauria (crocodylians + birds) a sacrum consisting of more than the two primordial sacral vertebrae has evolved multiple times independently, especially in Triassic forms (Juul, 1994; Novas, 1996; Rauhut, 2003; Langer & Benton, 2006; Irmis et al. 2007; Nesbitt, 2011). In taxa with three or more sacrals, the additional vertebrae can be incorporated from the trunk (= dorsosacrals) or the tail (= caudosacrals; Langer & Benton, 2006; Nesbitt, 2011), involve the insertion of a new vertebra between the two primordial sacrals (Nesbitt, 2011) or be a combination of these. Because of the morphological variability of sacra among Triassic archosaurs and other early archosauromorphs, this skeletal module possesses important morphological characters for reconstructing evolutionary relationships, with the number, origin, and co-ossification of sacral vertebrae and the morphology of the sacral ribs representing key characters in phylogenetic analyses of early archosauriforms (Gauthier, 1986; Benton, 1990; Sereno et al. 1993; Juul, 1994; Novas, 1996; Dilkes, 1998; Sereno, 1999; Rauhut, 2003; Langer, 2004; Nesbitt, 2005, 2007, 2011; Langer & Benton, 2006; Irmis et al. 2007; Smith et al. 2007; Ezcurra, 2016). Despite this, the possession of only two sacral vertebrae is the plesiomorphic archosauromorph condition, with most extinct and all extant pseudosuchians (crocodylian-line archosaurs), early dinosauromorphs, and all but two previously described non-archosaurian archosauromorphs retaining this state [e.g. Nesbitt, 2011; the exceptions being *Doswellia kaltenbachi* (Weems, 1980; Dilkes & Sues, 2009) and *Diandongosuchus fuyuanensis* (Li et al. 2012; Stocker et al. 2017)].

Phytosaurs, an abundant and cosmopolitan group of crocodile-like Triassic archosauriforms, are either the sister group to Archosauria (e.g. Nesbitt, 2011; phylogenies based on Nesbitt's 2011 matrix include Dilkes & Arcucci, 2012; Nesbitt & Butler, 2013; von Baczko et al. 2014; Nesbitt et al. 2014; Butler et al. 2014; Sookias et al. 2014) or the earliest-branching clade of pseudosuchians (e.g. Sereno & Arcucci, 1990; Benton, 1999; Brusatte et al. 2010; Ezcurra, 2016), and can therefore provide important information on morphological evolution within Archosauriformes during the origin of this clade in the Triassic. However, postcranial material for most phytosaurian species is poorly documented (e.g. McGregor, 1906; von

Huene, 1913; Camp, 1930; Chatterjee, 1978; Lucas et al. 2002; Zeigler et al. 2003; Witzmann et al. 2014) and is almost exclusively from the Late Triassic (but see Li et al. 2012 and Stocker et al. 2017 for postcrania of *Diandongosuchus*, the earliest-diverging phytosaur), creating a major limitation to interpreting the timing and order of character acquisition within this clade as well as phylogenetic relationships among early archosauriforms (e.g. Nesbitt, 2011; Ezcurra, 2016). Further, the absence of information concerning the morphology of phytosaurian sacra and pelves limits our knowledge of the evolution of a key module for terrestrial locomotion among early-diverging archosauriforms. This dearth of knowledge is partially a result of much of the known fossil record of phytosaurs being composed of isolated elements, making species- or clade-level identification of isolated postcranial elements difficult. Additionally, given this limitation, determining whether an unusual morphology is apomorphic or synapomorphic for a clade, or is the result of individual variation or pathology, is extremely difficult.

In this study, we describe a sacrum and ilium of *Smilosuchus adamanensis* from a specimen with associated cranial material recovered from the Chinle Formation in Petrified Forest National Park. This specimen possesses morphological features that are unexpected given conventional understanding of phytosaur anatomy, especially in the number of sacral vertebrae. We place this description in a comparative context of early-diverging archosauriform morphological diversity.

Institutional abbreviations

AMNH, American Museum of Natural History, New York, NY, USA; ANSP, The Academy of Natural Sciences of Drexel University, Philadelphia, PA, USA; BMNH, Natural History Museum, London, England; ISI, Indian Statistical Institute, Kolkata, India; MCCDM, Mesalands Community College's Dinosaur Museum, Tucumcari, NM, USA; MNA, Museum of Northern Arizona, Flagstaff, AZ, USA; NMT, National Museum of Tanzania, Dar es Salaam, Tanzania; PEFO, Petrified Forest National Park, AZ, USA; PVL, Instituto Miguel Lillo, Tucuman, Argentina; QG, Natural History Museum of Zimbabwe, Bulowayo, Zimbabwe; SAM, South African Museum, Cape Town, South Africa; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; TMM, Jackson School of Geosciences Vertebrate Paleontology Laboratory, University of Texas at Austin, Austin, TX, USA; TTU, Texas Tech University, Lubbock, TX, USA; UCMP, University of California Museum of Paleontology, Berkeley, CA, USA; USNM, (now NMNH), Smithsonian Institution, Washington, D.C., USA; VT, Virginia Polytechnic Institute and State University, Blacksburg, VA, USA; ZPAL, Institute of Paleobiology of the Polish Academy of Sciences, Warsaw, Poland.

Materials and methods

Provenance, taxonomic justification, and material examined

The specimen described here (PEFO 34852) was collected as associated material in 2008 and 2013 from Petrified Forest Vertebrate Locality PFV148 at the top of the Blue Mesa Member of the Chinle Formation (*sensu* Woody, 2006) in Petrified Forest National Park (PEFO). Exact locality information is protected from disclosure by the Paleontological Resources Protection Act of 2009 and is available to eligible researchers from the Division of Science and Resource Management at PEFO.

PEFO 34852 consists of a complete cranium, two presacral vertebrae, a partially disarticulated sacrum with left and right ilia, and a right femur. We focus on the sacrum and ilia here. PEFO 34852 was identified as a specimen of the non-mystriosuchinine (*sensu* Kammerer et al. 2016) leptosuchomorph phytosaur *Smilosuchus adamanensis* based on the combination of the following cranial characters using the matrix of Kammerer et al. (2016) based on the original matrix by Stocker (2010) as modified by Butler et al. (2014): an antorbital fossa is absent (3-3); a rostral crest is present but not continuous (18-1); the interorbital-nasal area is concave (21-1); there is a moderate posterior process of the squamosal (24-1); the posterior process of the squamosal is expanded in lateral view, but not rounded (25-1); the squamosal fossa extends to the posterior edge of the squamosal (30-0); the supratemporal fenestrae are partially depressed (32-1) and mostly visible in dorsal view (33-1). All characters here were found as unambiguous synapomorphies by Stocker (2010).

Computed tomography (CT)

To observe the internal structure of the sacral vertebrae of PEFO 34852, we scanned these elements with a Nikon XTH 225 ST high resolution X-ray computed tomography (CT) scanner at the Shared Materials Instrument Facility at Duke University. The elements were scanned at 225 kV, with 2000 projections (X-ray images) taken in 360 degrees of rotation. All scans were conducted with a copper filter of 1 mm thickness. We analyzed the resulting data in Mimics v. 19.0 (Materialise NV; www.materialise.com), and Mimics files of each element are available from the MorphoSource digital repository (www.morphosource.org).

Comparative description

We identify this specimen as *Smilosuchus adamanensis* based on the associated cranial material, so the majority of our comparisons are to the holotype specimen, UCMP 26699, which was originally described by Camp (1930).

General morphology

Unlike the sacra of other phytosaurs that have been described (McGregor, 1906; Camp, 1930; Lucas et al. 2002), the sacrum of PEFO 34852 consists of three sacral vertebrae which all articulate with the ilium via sacral ribs. The anteriormost vertebra we describe possesses facets on the posterior articular surface of its centrum, and the ribs of the next sacral vertebra possess anteriorly projecting flanges that articulate with these depressions. These projections and depressions have been described in the first sacral vertebra in other phytosaurs (Camp, 1930), and the surfaces for articulation with the ilia and the sacral ribs of the anteriormost sacral of PEFO 34852 are much smaller than those of the other two sacrals. Therefore, we consider the first sacral in our series to be a dorsosacral, with the second and third sacrals being primordial sacrals 1 and 2, respectively; we use this terminology for clarity in referring to these elements. All three sacral vertebrae are all well-preserved, and the right ilium is better preserved than the left ilium, with more areas of bone containing cracks or missing in the left ilium. For this reason, some iliac features described below can only be observed in the right ilium.

Dorsosacral vertebra

The centrum of the dorsosacral vertebra is anteroposteriorly longer than that of either primordial sacral 1 or 2 (51.58 mm vs. 45.74 mm and 45.50 mm, respectively), and the ventral surface is dorsally concave in lateral view, with the posterior articular surface of the centrum extending further ventrally than the anterior articular surface of the centrum (Fig. 1). There is a single, well-developed anteroposteriorly oriented midline keel on the ventral surface of the centrum. The centrum is amphicoelous, with the anterior articular surface possessing a relatively greater degree of concavity than the posterior articular surface. The roughly circular anterior centrum face is slightly mediolaterally compressed, with a rim that is anteroposteriorly thicker than that of the posterior articular surface, and which is thin and anteroposteriorly compressed relative to the edge of the anterior articular surface. The centrum possesses small (< 1 cm anterolateral length) ridges and grooves on the ventral surface oriented towards the middle of the centrum away from the edges of both the articular surfaces, and both articular surfaces possess faint, circumferential lineations visible in anterior and posterior view, respectively (Fig. 1).

The posterior articular surface is morphologically distinct from the other vertebral articular surfaces in this specimen: the left and right edges of this surface possess large posterolaterally oriented concave facets, which articulate with convex flanges extending anteriorly from primordial sacral 1 (see below). The holotype of *S. adamanensis* (UCMP 26699) possesses these same facets on the posterior articular surface of its dorsosacral vertebra (Fig. 1). The surfaces of these concave facets in PEFO 34852 are highly rugose, and both facets extend from the lateral edge of the articular surface to roughly one-third of the distance to the center of the articular surface. The medial borders of the depressions are marked by posteriorly projecting raised regions. The dorsal edge of the facets are close to the dorsalmost part of the posterior articular surface and extend ventrally on
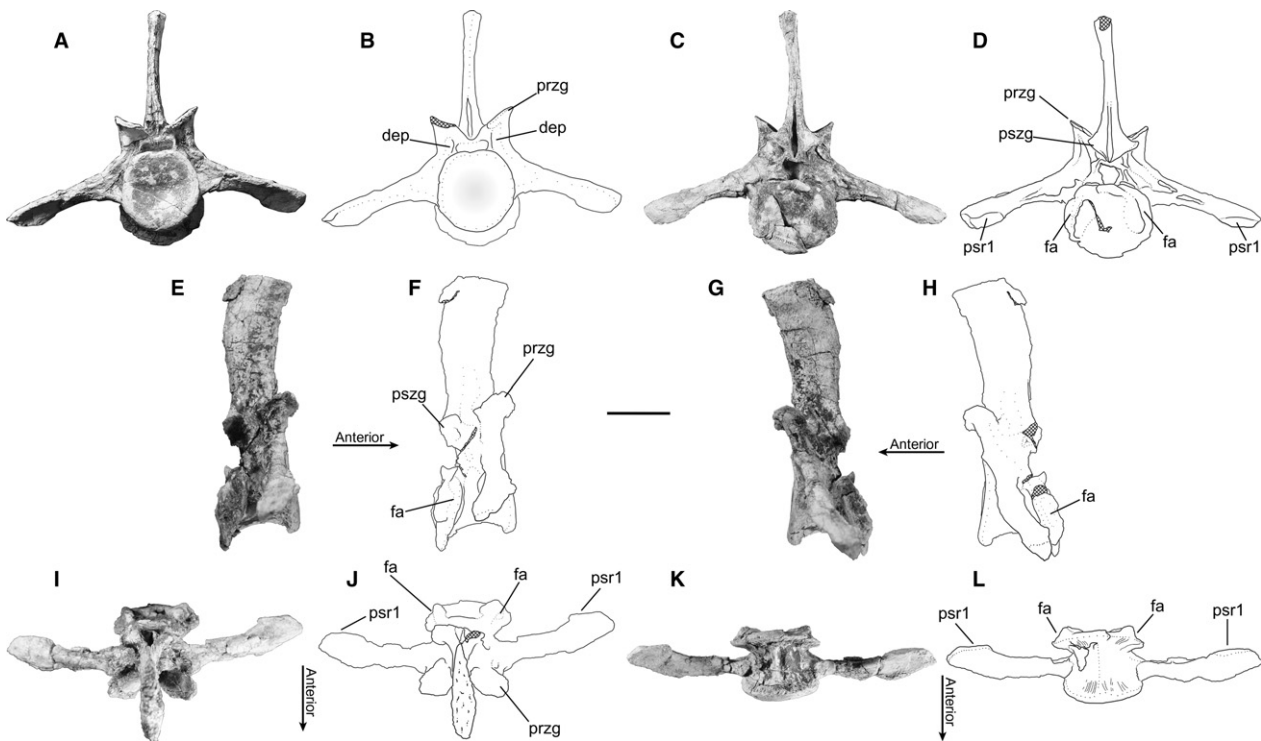
Fig. 1 The dorsosacral vertebra of *Smilosuchus adamanensis* (PEFO 34852). (A) Photograph and (B) line drawing of the dorsosacral in anterior view. (C) Photograph and (D) line drawing of the dorsosacral in posterior view. (E) Photograph and (F) line drawing of the dorsosacral in right lateral view. (G) Photograph and (H) line drawing of the dorsosacral in left lateral view. (I) Photograph and (J) line drawing of the dorsosacral in dorsal view. (K) Photograph and (L) line drawing of the dorsosacral in ventral view. Scale bar: 5 cm. dep, depression; fa, facet for articulation with a flange of primordial sacral 1; przg, prezygapophysis; psr1, surface for articulation with a sacral rib of primordial sacral 1; pszg, postzygapophysis.

either side to roughly three-fourths of the distance to the ventral edge of the centrum face. The posterior articular surface of PEFO 34852 is angled slightly anteriorly in lateral view.

The neural arch is completely fused with the centrum (*sensu* Brochu, 1996; Irmis, 2007), and the line of suture between them has been obliterated; however, because phytosaurs undergo a pattern of caudal-to-cranial neurocentral suture fusion (Irmis, 2007), this fusion does not indicate that this individual is skeletally mature. The sacral ribs are fused to both the centrum and neural arch; however, small parts of those sutures are visible and have not been completely obliterated. In contrast, the 'transverse processes' of the dorsosacral in the holotype of *S. adamanensis* (UCMP 26699) are separated from the centrum by a clear line of suture. Sacral ribs usually ossify and fuse to their respective centra postnatally and thus leave lines of suture, whereas true transverse processes fuse to centra prenatally (e.g. *Alligator mississippiensis*, Rieppel, 1993). Therefore, the clear line of suture present between the dorsosacral centrum and the sacral ribs in both PEFO 34852 and UCMP 26699 suggests that these are true sacral ribs. We therefore now refer to these structures as the sacral ribs of the dorsosacral for both specimens. The neural canal of the dorsosacral vertebra of PEFO 34852 is 3.5 times wider laterally than it is

dorsoventrally tall in anterior view (22.46 vs. 6.27 mm), but in posterior view the canal is circular. Additionally, in anterior view the neural canal is bordered laterally by short (~ 1 cm) dorsoventrally oriented laminae on each side. These laminae each extend from just dorsal to the anterior centrum face up to the prezygapophysis, joining with the prezygapophysial body just ventral to the articular surface of the prezygapophysis. A shallow depression separates each of these laminae from the laminae that connect the prezygapophyses to the sacral ribs in anterior view, and it is these depressions that accentuate the laminae that form the lateral borders of the neural canal in anterior view (Fig. 1A,B). These shallow triangular depressions expand ventrolaterally along the anterior faces of the regions of the sacral ribs closest to the centrum. These depressions are bordered dorsally and ventrally by low, proximodistally oriented ridges. In posterior view, the edge of the neural canal also consists of thin, roughly dorsoventrally oriented laminae, but because no prezygapophyses are present to create depressions, these posterior edges of the neural canal grade into the body of the neural arch. Both laminae bordering the neural canal connect to each other and to the medial portions of the postzygapophyses at the dorsal apex of the neural canal, and this connection forms a structure that is 'X'-shaped in posterior view (Fig. 1C,D). The distal edges of

both postzygapophyses are broken, the left more than the right, so that this 'X' shape is accentuated.

The sacral ribs of the dorsosacral vertebra are long, thin, and single-pronged, and our interpretation is that they articulated distally with the ilium based on the presence of a small round scar on the medial ridge of the ilium (see description of ilium below). Because the distal portions of the sacral ribs of the dorsosacral of UCMP 26699 are missing, we cannot determine whether a similar morphology is present in the holotype of *S. adamanensis*; however, the same small round scar is present on the ilium of UCMP 26699, suggesting that the sacral ribs did articulate with the ilium in the holotype of *S. adamanensis*. Although the sacral ribs of the dorsosacral vertebra generally can be described as rod-like, the distal halves are compressed anteroventrally-posterodorsally, forming a flat surface oriented at a roughly 30° angle from the horizontal in lateral view. The distalmost portions of each of these sacral ribs are slightly expanded anteroposteriorly as well, although most of the expansion is to the posterior, with the distal ends of the ribs bent slightly posteriorly. There are thin surfaces at the distalmost point of the sacral ribs that would have articulated with the ilia (Fig. 1C–D,I–L). Immediately posterior to the iliac articular surface there is a more extensive surface for articulation with the anterodistal surface of the first primordial sacral rib.

The articular surfaces of the prezygapophyses are featureless, angled roughly 45° from the horizontal in anterior view and angled medially, with a ~ 10 mm gap separating them. The prezygapophyses are each buttressed ventrally by a thick lamina that smoothly connects to the dorsal surface of the proximalmost portion of the sacral ribs of the dorsosacral, and the suture between this lamina and the rib forms a raised area. The articular surfaces of the prezygapophyses are slightly wider than these buttresses, forming thin overhangs at the dorsalmost parts of the prezygapophyses. The prezygapophyses connect with the anterior portion of the neural spine via vertically oriented tuberosities on the ventral part of the neural spine. A hollow is present at the connection of the prezygapophyses and the neural spine for articulation with the postzygapophyses of the previous presacral.

Each postzygapophysis is buttressed at its anteriormost portion by a thick, dorsoventrally oriented lamina. The postzygapophyses are oriented roughly 45° from vertical in posterior view, and they angle posteriorly in lateral view. Although the postzygapophyses are less well-preserved than the prezygapophyses, they appear to be roughly half the surface area as the prezygapophyses. The neural spine connects with the postzygapophyses via thick laminae, and the articular surfaces of the postzygapophyses are slightly wider than these buttresses, forming thin overhangs that are morphologically similar to those of the prezygapophyses. The postzygapophyses and their respective buttressing laminae on the neural spine are separated from each other

by a dorsoventrally oriented depression, which is terminated ventrally by the connection of the articular surfaces of the postzygapophyses. After reaching its deepest point anteriorly just dorsal to this area, the depression shallows dorsally and merges into the body of the neural spine.

The mediolaterally compressed neural spine of the dorsosacral is much taller dorsoventrally than the height of the centrum plus the base of the neural arch (97.54 vs. 71.26 mm). The spine becomes slightly wider anteroposteriorly towards its dorsal end, and it terminates dorsally in a slight mediolateral expansion with a rugose, flat spine table. The anterior and posterior edges of the neural spine possess cleanly broken surfaces, some of which are on areas that are not completely continuous with the rest of the neural spine. These broken surfaces may indicate that the neural spine of this dorsosacral vertebra was co-ossified with either the previous presacral or the first primordial sacral, or both, because the neural spines of primordial sacrals one and two are co-ossified (see below). However, preservation makes interpretation difficult.

Primordial sacral 1

The centrum of primordial sacral 1 is circular in anterior view, although the sacral ribs cover portions of the right and left edges of the articular surface (see below). The edge is thin and sharp, morphologically similar to that of the posterior articular surface of the dorsosacral. There are faint concentric lineations on the anterior articular surface oriented away from the edges similar to those of the dorsosacral. On the anterior half of the ventral part of the centrum, but not the posterior half, an extremely shallow anteroposteriorly oriented depression is visible, and unlike UCMP 26699, which possesses paired ventral keels along the ventral surface of the centrum; primordial sacral 1 of PEFO 34852 possesses no ventral keel (Fig. 2). The posterior articular surface is in articulation with the centrum of primordial sacral 2. Although the suture between these centra is visible along the ventral surface and has not been obliterated, the sacral ribs of primordial sacral 2 appear to be fused completely with the centrum of primordial sacral 1, and part of the ventral surfaces of the two primordial sacral vertebrae appears to potentially be co-ossified through external visual examination. However, CT scans of the articulated primordial sacral vertebrae reveal a distinct separation and clear lack of ossification between the two centra (Fig. 3). In UCMP 26699, the morphology of the articulation of these centra is more suggestive of fusion because the line of suture between these elements is nearly obliterated. The neurocentral suture of primordial sacral 1 of PEFO 34852 is completely closed, indicating fusion between the centrum and neural arch.

The neural canal is not as dorsoventrally flattened in anterior view as in the dorsosacral, but is still about twice as wide as tall (20.59 vs. 12.08 mm, respectively). Otherwise,
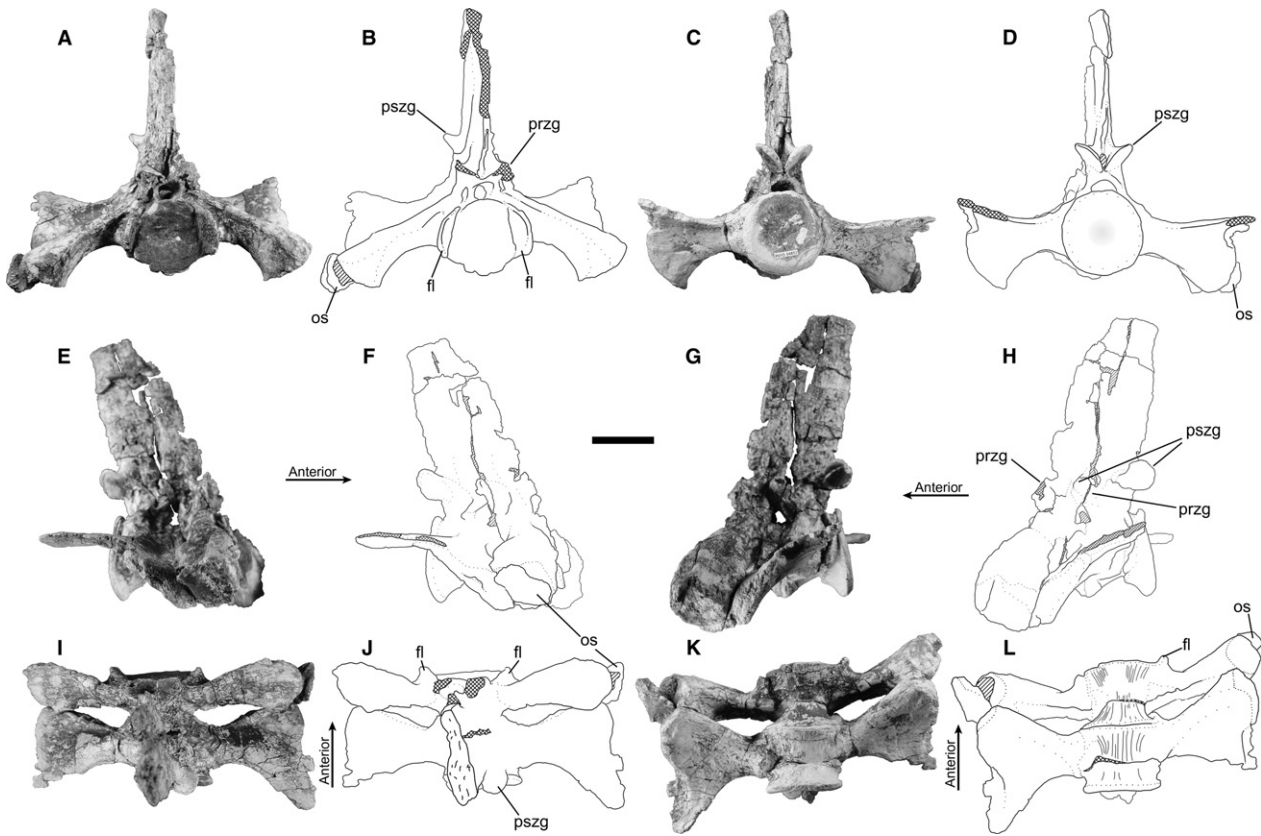
Fig. 2 Primordial sacral vertebrae 1 and 2 of *Smilosuchus adamanensis* (PEFO 34852). (A) Photograph and (B) line drawing of the primordial sacrals in anterior view. (C) Photograph and (D) line drawing of the primordial sacrals in posterior view. (E) Photograph and (F) line drawing of the primordial sacrals in right lateral view. (G) Photograph and (H) line drawing of the primordial sacrals in left lateral view. (I) Photograph and (J) line drawing of the primordial sacrals in dorsal view. (K) Photograph and (L) line drawing of the primordial sacrals in ventral view. Scale bar: 5 cm. fl, flange for articulation with a facet of the dorsosacral; os, osteoderm; przg, prezygapophysis; pszg, postzygapophysis.
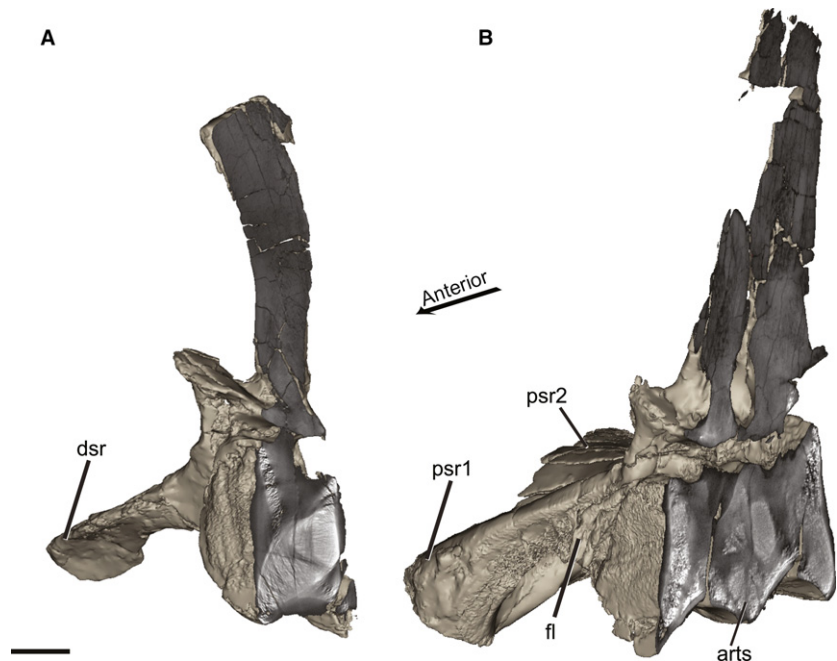

Fig. 3 Models of the (A) dorsosacral and (B) primordial sacrals from CT scan data, showing internal morphology along the sagittal plane. The dorsosacral shows no obvious internal pathologies (e.g. Witzmann et al. 2014), and the primordial sacrals are not fused to each other. Scale bar: 2 cm. arts, articular surface between primordial sacrals 1 and 2; dsr, dorsosacral rib; fl, flange on primordial sacral rib 1; psr1, primordial sacral rib 1; psr2, primordial sacral rib 2. [Colour figure can be viewed at wileyonlinelibrary.com]

the morphology of the anterior portion of the neural canal is very similar to that described for the dorsosacral, with small buttresses running from the centrum to the ventral portion of the prezygapophyses, accentuated by lateral depressions that shallow and extend ventrally along the sacral ribs.

The first primordial sacral ribs are completely fused to both the centrum and neural arch, and the anteroproximal portions of the sacral ribs form anteriorly projecting flanges that articulate with depressions in the posterior articular surface of the dorsosacral. Although the right flange is poorly preserved, the left preserves a rugose surface angled anteromedially to meet the facet of the dorsosacral with which it articulates. The dorsal edge of the flanges are close to the dorsalmost part of the centrum in anterior view and extend ventrally to roughly one-fourth of the distance to the ventralmost part of the centrum following the articulation of the sacral ribs with the centrum. These same flanges are present in both the holotypes of *Smilosuchus adamanensis* (UCMP 26699) and *'Machaeroprosopus' zunii* (UCMP 27036), but like the sacral ribs of the dorsosacral of PEFO 34852, the sacral ribs are not fully co-ossified to the centrum *sensu* Brochu (1996) because a clear line of suture is visible (Fig. 2K,L). There is a depression on the posterodorsal surface of the proximalmost part of each rib of sacral 1 of PEFO 34852. This depression forms a continuous concavity that extends across primordial sacral rib 1, the posteroventral region of the neural arch of primordial sacral 1, the anteroventral region of the neural arch of primordial sacral 2, and the anterodorsal region of the proximalmost part of the rib of primordial sacral 2. Though much more robust than the sacral ribs of the dorsosacral, the ribs of primordial sacral 1 are anteroposteriorly compressed along the middle of their shafts, but the dorsal surfaces of the ribs are dorsoventrally flattened and posteriorly elongated, such that a ridge of bone extends posteriorly and slightly ventrally along the shaft of each sacral rib (Fig. 2). Ridges project anteriorly along the dorsal regions of the ribs as well, though they are less developed with respect to the ridges extending posteriorly from the dorsal regions of the ribs. The anterior faces of the distal ends of the ribs of primordial sacral 1 possess flattened regions for articulation with the posterodistal portions of the sacral ribs of the dorsosacral. The ribs of primordial sacral 1 of UCMP 26699 possess this same morphology, adding additional evidence that the first presacral is a dorsosacral in that specimen as well. The lateral potions of the ribs of primordial sacral 1 of PEFO 34852 expand both anteroposteriorly and dorsoventrally such that the ridges projecting anteriorly and posteriorly from the dorsal surfaces of the ribs become less pronounced and more incorporated into the rib distally than they are medially. The ribs project ventrolaterally from the centrum, and the ventralmost regions of the ribs of primordial sacral 1 are more ventrally located than the ventralmost part of the centrum. These ribs are slightly anteriorly bowed in

dorsal view, and the articular surface of the rib of primordial sacral 1 is much larger than that of the rib of the dorsosacral. The long axis of the articular surface of the rib of primordial sacral 1 is anterodorsally-posteroventrally oriented in lateral aspect, and is roughly twice the length of the short axis (46.50 vs. 27.51 mm). These articular surfaces face ventrolaterally in anterior view, angled roughly 45° from the transverse plane, and are not fused with the ilium. An osteoderm is preserved on the articular surface of the right rib of primordial sacral 1 (Fig. 2A,B). The posterodistal portion of the ribs of primordial sacral 1 are articulated, but not fused, with the anterodistal portions of the ribs of primordial sacral 2 along an expanded, rugose articular surface area.

The prezygapophyses are poorly preserved and what remains are identical to those of the dorsosacral. Like those of UCMP 26699, the postzygapophyses are completely co-ossified with the prezygapophyses of primordial sacral 2, with the line of suture completely obliterated. However, the postzygapophyses of primordial sacral 1 appear to be similar to those of the dorsosacral, with the exception of less well-developed buttresses anteroventral to the postzygapophyses in primordial sacral 1 (Fig. 2). This lack of buttress development in the postzygapophyses is part of the large open space on the lateral surfaces of the proximal portion of the neural arch: a large buttress would interrupt this large, continuous depression. Although the dorsalmost and anterior surfaces of the neural spine are poorly preserved in primordial sacral 1, fusion between this neural spine and that of primordial sacral 2 is clear, especially in the dorsal half of the neural spines (Fig. 2). The maximum dorsal extent of the neural spine cannot be determined.

Primordial sacral 2

The centrum of primordial sacral 2 is extremely similar to that of primordial sacral 1. It possesses no ventral keel and is dorsally arched along its ventral surface in lateral view (Fig. 2). Thin anteroposteriorly oriented lineations cover the ventral surface of the centrum, extending from the anterior and posterior articular surfaces. The posterior articular surface of the centrum is round in posterior aspect, and the thin, circumferential laminations that are present on the articular surfaces of primordial sacral 1 and the dorsosacral are extremely faint although present here as well. The edge of the posterior articular surface is rounded in lateral view (Fig. 2C,D), and accordingly is more similar to the anterior articular surface of the dorsosacral than are any of the other articular surfaces in the sacrum. The anterior articular surface of the centrum is partially hidden through articulation with primordial sacral 1, but primordial sacral 2 is amphicoelous. The ventral edge of the posterior articular surface of primordial sacral 2 extends further posteriorly than does the dorsal edge of this articular surface. This makes the articular surface appear deflected away from a

perfect dorsoventrally straight orientation in lateral view (Fig. 2E–H). The neural arch is completely fused to the centrum.

Unlike the prezygapophyses of the dorsosacral and primordial sacral 1, primordial sacral 2 does not possess large buttresses that are continuous with the sacral ribs directly ventral to the prezygapophyses. Instead, the support for the prezygapophyses is reduced and shifted posteriorly, and the sacral rib does not appear to provide much, if any, support. This posteriorly shifted buttress borders posteriorly the large concavity on the lateral surfaces of the neural arches of primordial sacrals 1 and 2, which is also bordered dorsally by the prezygapophyses. The postzygapophyses are similar to those of the others in the sacrum, especially those of the dorsosacral, in terms of articular surface shape and orientation. However, the postzygapophyses of primordial sacral 2 are far better preserved and more complete than those of the dorsosacral. The articular surfaces of the postzygapophyses of primordial sacral 2 are smooth and oriented lateroventrally at a roughly 45° angle in posterior view, dipping slightly anteromedially in lateral view (Fig. 2C,D). Unlike the articular surfaces of the postzygapophyses of the dorsosacral vertebra, those of primordial sacral 2 do not come together at their anteromedial edges, but remain separated along their entire length. Like the dorsosacral, the neural canal of primordial sacral 2 in posterior view is circular, and the ridge that borders it is more pronounced dorsally than ventrally. The postzygapophyses are separated by a depression that is deepest anteriorly at its most ventral point and that shallows dorsally along the posterior edge of the neural spine (Fig. 2C,D).

The ribs of primordial sacral 2 are incompletely fused to their centrum, with portions of the sutural line not obliterated. Anteriorly projecting flanges similar to those on the medial portions of the ribs of primordial sacral 1 articulate and are co-ossified with the posterolateral part of the centrum of primordial sacral 1 (Fig. 2K,L). However, unlike the dorsosacral, primordial sacral 1 does not possess a space for the articulation of these flanges of the ribs of primordial sacral 2. Instead, the flanges simply cover a portion of the centrum (Fig. 2K,L). The ribs of primordial sacral 2 are anteroposteriorly wider than those of primordial sacral 1, especially in their distal three-fourths. The ribs are most robust and thickest dorsoventrally along the anterior edge, and they are dorsoventrally flattened posterior to this edge. There is a distinct ridge along the anterior face of the dorsal surface of the rib extending from near the medial end to the articulation with the rib of primordial sacral 1 (Fig. 2I,J). The sacral ribs are not only flattened but are slightly convex, with the dorsal surface of the sacral rib oriented slightly anteriorly (and the ventral surface oriented slightly posteriorly) in lateral view (Fig. 2E–H). The anterior edge of the surface for articulation with the ilium extends further ventrally than the posterior edge, and because the anterior edge is thicker than the remainder of the rib, the anterior

portion of the articular surface is thickest dorsoventrally. The articular surface shifts posteriorly from the thicker articular surface to a dorsoventrally thin ridge, and the thick region of the anterior articular surface is of equivalent anteroposterior length to the thin posterior region of the articular surface (right articular surface: 51.96 vs. 50.12 mm, respectively). This thin ridge is continuous with the dorsal surface of the sacral rib; a ventral escarpment along the distal edge of the rib forms a hollow along the distal edge of the posteroventral part of the sacral rib, and this hollow is what forms the thin ridge that makes up the posterior part of the articular surface in the sacral rib. The dorsoventrally thick region for articulation with the ilium is rugose, and the dorsoventrally thin region is too damaged to determine whether the surface is textured (Fig. 2E–H). However, the hollow ventral to the dorsoventrally thin region of the articular surface possesses small pits and mediolaterally oriented lineations. The ribs of primordial sacral 2 are not fused to the ilia.

The neural spine of primordial sacral 2 is morphologically similar to those of the dorsosacral and primordial sacral 1. The anterior edge is fully co-ossified with the neural spine of primordial sacral 1 except for the region immediately dorsal to the fused zygapophyses between primordial sacral 1 and 2 (Fig. 2E–H). The dorsal surface of the neural spine is flat, pitted and rugose, and slightly wider mediolaterally than the rest of the neural spine. The anteriormost portion of the dorsal surface of the neural spine is missing, but the spine table appears to have been wider anteriorly (Fig. 2I–J). Although less well preserved, the primordial sacral 2 of UCMP 26699 is extremely similar to that of PEFO 34852.

Ilium

The ilia of PEFO 34852 are broadly similar to other phytosaurian ilia that have been described or figured (e.g. UCMP 26699, 27036, Camp, 1930; Westphal, 1976; Lucas et al. 2002: fig 4; MCSNB 10087, Gozzi & Renesto, 2003; SMNS 52971, Nesbitt, 2011; ANSP 14688, Parker, 2013). The acetabulum is completely closed, meaning the ventral margin of the acetabulum is convex (*sensu* Nesbitt, 2011), and the ischial and pubic peduncles converge at a roughly 60° angle, with the apex formed by this convergence directly ventral to the supra-acetabular crest (Figs 4 and 5). Because there is no raised region bordering the lateral margins of the articular surfaces of the ischial and pubic peduncles except on the posteriormost region of the ischial peduncle, the depression for the articulation of the femur probably extended onto the ventrolateral surfaces of the pubis and ischium. The ilium is thick mediolaterally along the anterior border of the acetabulum dorsal to the pubic peduncle, where the supra-acetabular crest joins the ilium anteriorly, and so the anteriormost region of the pubic peduncle is thickest mediolaterally and thins posteriorly. The mediolaterally thinnest portion of the ischial peduncle is thinnest at
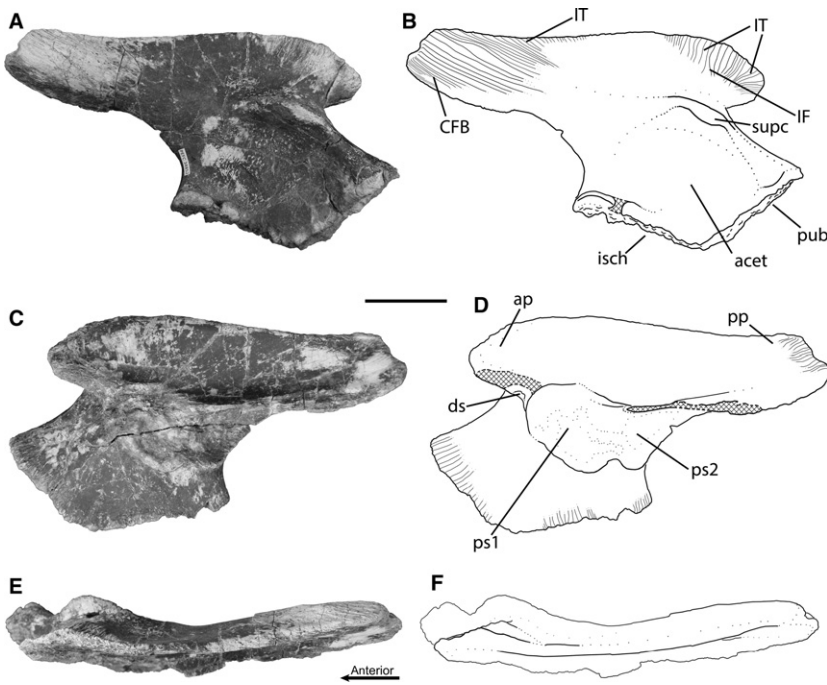
Fig. 4 Right ilium of *Smilosuchus adamanensis* (PEFO 34852). (A) Photograph and (B) line drawing of the right ilium in lateral view. (C) Photograph and (D) line drawing of the right ilium in medial view. (E) Photograph and (F) line drawing of the right ilium in dorsal view. Scale bar: 5 cm. ap, anterior process; acet, acetabulum; CFB, insertion of M. caudofemoralis brevis; ds, surface of articulation with the dorsosacral vertebra; IF, insertion of the M. iliofemoralis; isch, ischial peduncle; IT, insertion of the Mm. iliotibialis; pp, posterior process; ps1, surface of articulation with primordial sacral vertebra 1; ps2, surface of articulation with primordial sacral vertebra 2; pub, pubic crest; supc, supra-acetabular crest.
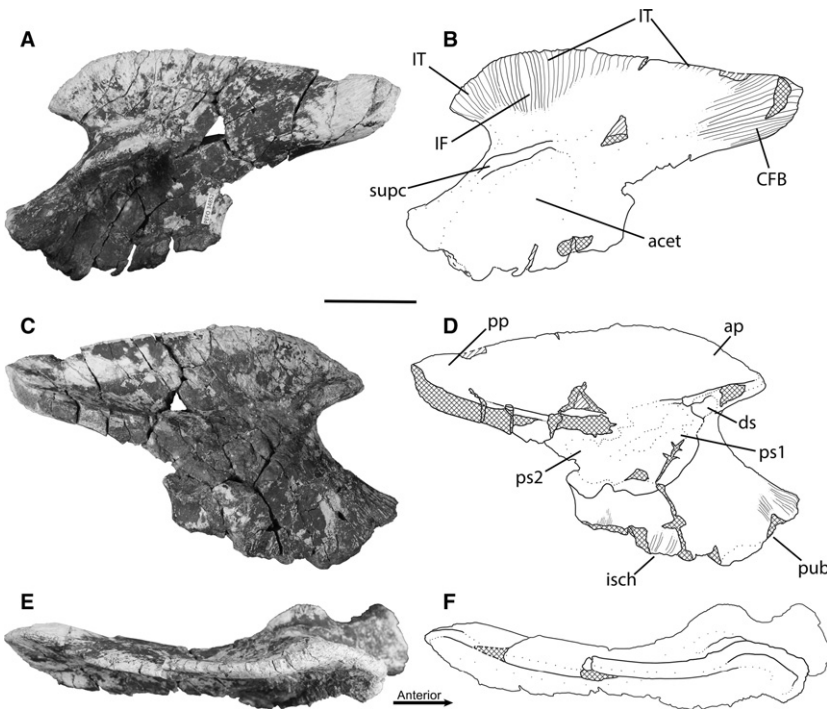

Fig. 5 Left ilium of *Smilosuchus adamanensis* (PEFO 34852). (A) Photograph and (B) line drawing of the left ilium in lateral view. (C) Photograph and (D) line drawing of the left ilium in medial view. (E) Photograph and (F) line drawing of the left ilium in dorsal view. Scale bar: 5 cm. ap, anterior process; acet, acetabulum; CFB, insertion of M. caudofemoralis brevis; ds, surface of articulation with the dorsosacral vertebra; IF, insertion of the M. iliofemoralis; isch, ischial peduncle; IT, insertion of the Mm. iliotibialis; pp, posterior process; ps1, surface of articulation with primordial sacral vertebra 1; ps2, surface of articulation with primordial sacral vertebra 2; pub, pubic crest; supc, supra-acetabular crest.

the convergence between the ischial and pubic peduncles, and thickens posteriorly, although it does not reach the mediolateral thickness of the anterior part of the pubic peduncle. The lateral surface of the acetabulum is rugose, especially the anterior three-fourths of this surface. The supra-acetabular crest projects anterolaterally from the body of the ilium, with the furthest projecting region slightly anterior of the center of the acetabulum (Figs 4 and 5). Because of this, the supra-acetabular crest extends in a posterodorsal-anteroventral orientation in lateral aspect along the anterodorsal border of the acetabulum.

There is no distinct crest dorsal to the acetabulum dividing the anterior (= preacetabular) and posterior (= postacetabular) processes (see Nesbitt, 2011 for further

discussion), but a raised region is present dorsal to the supra-acetabular crest (Figs 4 and 5). This raised region extends ventrally from the dorsal edge of the ilium to about halfway to the supra-acetabular crest on the lateral face of the ilium, and possesses a highly rugose texture with dorsoventrally oriented grooves and lineations. The anterior process does not extend further anteriorly than the pubic peduncle, whereas the posterior process effectively doubles the anteroposterior length of the ilium and extends slightly laterally, giving the ilium a slightly concave-lateral shape in dorsal view. Lineations, which we hypothesize to be muscle attachment sites, extend from the dorsal, anterodorsal, and posterodorsal edges of the ilium toward the acetabulum, especially from the posterior end of the posterior process, and the dorsal surface of the ilium is rugose (Figs 4A–B and 5A–B). We interpret the lineations on the raised region just dorsal to the supra-acetabular crest to mark the attachment site of the iliofemoralis muscle, which originates in a homologous location in *A. mississippiensis* (Hutchinson & Gatesy, 2000; Hutchinson, 2001, 2002; Tsai & Holliday, 2014). The lineations present dorsal to this raised region as well as along the dorsalmost portion of the lateral surface of the ilium we interpret to mark the attachment site of the iliotibialis muscles, following similar reconstructions of the iliac musculature of early-diverging pseudosuchians *Poposaurus gracilis* (Schachner et al. 2011) and *Prestosuchus chiniquensis* (Liparini & Schultz, 2013), which were hypothesized based on the musculature of the extant phylogenetic bracket of these taxa (i.e. crocodylians and birds). We also interpret the prominent lineations on the ventral surface of the posterior process as the origin of the caudofemoralis brevis muscle (= coccygeofemoralis brevis), again following the muscular reconstructions of early-diverging pseudosuchians by Schachner et al. (2011) and Liparini & Schultz (2013).

The anterior edge of the anterior process is angled medially roughly 90° in anterior view, forming the anterior portion of the anteroposteriorly oriented medial ridge for articulation with the sacral ribs (Figs 4C–D and 5C–D). This medial ridge extends along the ventromedial surface of the iliac crest. The medial ridge is intersected by the dorsalmost parts of the scars for the articulation with the three sacral ribs. A small scar indicating the location of the articulation for the dorsosacral sacral rib is located on this medial ridge immediately anterior to the scar for the articulation with primordial sacral rib 1 in PEFO 34852 (Figs 4C–D and 5C–D), and this feature is present in the holotype of *S. adamanensis* (UCMP 26699), although that specimen is more damaged than PEFO 34852. Unlike the scars for the primordial sacral ribs, the scar for the dorsosacral rib does not extend ventral of the medial ridge. Instead, there is a slight depression on the medial surface of the ilium just ventral to this scar. The scar for primordial sacral rib 1 is a dorsoventrally compressed ellipse with a distinct ridge along its ventral border, and with its dorsal border along the medial ridge of the

ilium for articulation with the sacrals. Because the articular surfaces of the ribs of primordial sacral 1 face ventrolaterally at a roughly 45° angle from the transverse plane, this suggests that the ilia were similarly oriented (Nesbitt, 2011). The scar for the articulation of the rib of primordial sacral 2 is deeper and more anteroposteriorly elongate, dorsally bordered by the medial ridge and ventrally by the ventral border of the posterior process. Lineations, probably attachment sites of muscles, tendons or ligaments, extend from the ischial and pubic peduncles, the dorsal edge of the ilium, and the posterior end of the posterior process towards the articular surfaces for the sacral ribs. These lineations cover the medial side of the ilium, and are especially pronounced dorsal to the medial ridge and at the medioventral sides of the peduncles. The ilia of PEFO 34852 and the holotype of *S. adamanensis* (UCMP 26699) are practically identical, though the holotype is more poorly preserved.

Discussion

Sacral morphology among phytosaurs

The axial column is poorly known for many phytosaur taxa, and in some cases, published material has since been identified as aetosaur (e.g. Mehl, 1915; Case, 1932; see listing in Stocker & Butler, 2013). All previously described phytosaurian sacra, including the holotype specimen of *Smilosuchus adamanensis* (UCMP 26699; Camp, 1930), were said to consist of two sacral vertebrae, which is the plesiomorphic state for Archosauriformes (Westphal, 1976; Gauthier, 1984; Langer & Benton, 2006; Nesbitt, 2011). This interpretation of two sacrals in all phytosaurs is carried through in phylogenetic analyses of early archosaurs and their closest relatives, which all used Late Triassic phytosaurs in their taxon sampling. Nesbitt (2011) coded all three phytosaurs incorporated in his analysis (*Parasuchus hislopi*, ISI R 43; *Smilosuchus gregorii*, USNM 18313; and *Pseudopalatus* (=*Machaeroprosopus*) *pristinus*, UCMP 34253) as possessing two sacral vertebrae, with sacral centra and zygapophyses unfused. Ezcurra (2016) also coded *P. hislopi* and *Smilosuchus* spp. as possessing two sacral vertebrae. However, the Middle Triassic *D. fuyuanensis* (ZMNH M8770; Li et al. 2012), recently identified as a non-parasuchid phytosaur more basal than *Parasuchus* (Stocker et al. 2017), was said to possess three sacral vertebrae based on sacral rib morphology of the articulated vertebrae preserved near the ilia as visible in ventral view. An additional specimen of *Diandongosuchus* currently under preparation (X.-C. Wu, pers. comm.) may provide additional information on the sacrum in this taxon for future phylogenetic analyses of Archosauriformes.

Among other early branching non-leptosuchomorph phytosaurs, a sacrum and partial pelvis attributed to *Angistorhinus grandis* (unnumbered specimen with associated

cranium in private collection; Lucas et al. 2002) possess two fused vertebrae, and both were described as lacking ventral keels with ilia fused to their respective sacral ribs (Lucas et al. 2002). Though unmentioned in that description, the anterior articular surface of the first sacral vertebra appears to possess the anteriorly projecting flanges formed by the anteroproximal portion of the sacral ribs (Lucas et al. 2002: fig 4), and these flanges were also observed in another specimen referred to *Angistorhinus,* TMM 31100-1267 (M. R. Stocker, pers. obs.). Two sacral vertebrae were also reported for *Rutiodon carolinensis* (AMNH 1), though the last presacral centrum does possess facets on its posterior articular face (McGregor, 1906: Text-fig. 21, plate VIII, fig. 16). These primordial sacral vertebrae were not fused to either each other or their respective sacral ribs (McGregor, 1906), and the primordial sacral ribs of this individual did not contact each other, unlike in PEFO 34852. The ribs for what were interpreted as primordial sacral 2 appear to possess anteriorly projecting flanges (McGregor, 1906: plate X), similar to those described in the sacral ribs of PEFO 34852; however, based on the shape of the ribs we follow von Huene (1922) in interpreting this vertebra as primordial sacral 1.

Similar to the dorsosacral of PEFO 34852, in the holotype specimen of *S. adamanensis* (UCMP 26699) and the holotype of *'M.' zunii* (UCMP 27036; Camp, 1930), the last presacral centrum possesses facets on the posterior articular face for articulation with anteriorly projecting flanges of the first sacral, as well as a midline keel along the ventral surface of the centrum (Camp, 1930). However, unlike the dorsosacral of PEFO 34852, the transverse processes of that vertebra were not interpreted to have articulated with the ilium in those specimens, but the distal ends of the transverse processes were described as flattened (Camp, 1930). We interpret the first vertebra of the sacrum of PEFO 34852 as a dorsosacral because it possesses these facets on the posterior articular face of the centrum, as well as a median keel along its ventral side. Like PEFO 34852, the first sacral ribs of *S. adamanensis* (UCMP 26699) and *'M.' zunii* (UCMP 27036) possess flanges that slightly overlap the articular face of the centrum and project anteriorly, articulating with the facets of the last presacral vertebra, and the morphology of primordial sacral ribs 1 and 2 in these taxa is similar to that of PEFO 34852. Therefore, we interpret the holotype specimens of *S. adamanensis* and *'M.' zunii* to have also possessed a dorsosacral vertebra. Some variation does exist in terms of the degree and location of co-ossification between elements. Unlike PEFO 34852, in which the pre- and postzygapophyses of the primordial sacral vertebrae are fully co-ossified to each other but the centra unfused to each other, the articulations between the primordial sacral vertebrae of the holotypes of *S. adamanensis* (UCMP 26699) and *'M.' zunii* (UCMP 27036) are the opposite, with the pre- and postzygapophyses articulating normally and the centra entirely fused. Additionally, an individual identified as *Machaeroprosopus* from eastern Arizona (USNM 15860) possesses similar morphology to PEFO 34852. One vertebral element, either the last presacral or the dorsosacral, of this individual possesses deep facets on the posterior articular surface of the centrum similar to the dorsosacral of PEFO 34852. The right sacral rib is the only rib preserved, and the lateral expansion and clear surface for articulation with the distal anterior surface of the first primordial sacral (Fig. 6B) suggest that this element is a dorsosacral, and was articulated with the ilium in life position. Additionally, the medial surface of the right ilium of USNM 15860 possesses a scar that we interpret as the articulation with the dorsosacral (Fig. 6E). The sutures between the sacral ribs and centrum, as well as the neurocentral suture, are fused and like the dorsosacral of PEFO 34852, the dorsosacral of USNM 15860 possesses a ventral keel. The proximal portions of the sacral 1 ribs of *Nicrosaurus* also project forward as flanges to articulate with the centrum of the preceding trunk vertebra (Fig. 6A; von Huene, 1922: figs 10, 12, 13; von Meyer, 1861: fig. 13, pl. 38).

Among the most derived phytosaurs, three right sacral ribs (MCCDM 1743-1, 1743-2) and a right ilium (MCCDM 1742) from the San Jon Creek Member of the Redonda Formation in east-central New Mexico, found in close association with a skull of *Redondasaurus* cf. *gregorii*, provide information on the sacrum anatomy in a mystriosuchinine phytosaur. This sacrum of *Redondasaurus* encompasses a dorsosacral vertebra and the primordial sacral vertebrae 1 and 2, and the sacral ribs of these are broadly similar to those described for *S. adamanensis* above (Fig. 7A–B). Similarly, an anterolaterally directed extension of the centrum articulation of primordial rib 1 indicates that at least this rib articulated with the centrum of the dorsosacral. However, the distal posterior flange of the dorsosacral rib is fused with the anterior flange of the primordial sacral 1 without a discernible suture.

When articulated with the ilium (Fig. 7C), the dorsoventrally expanded lateral rims of the primordial sacral ribs 1 and 2 fit in corresponding facets on the body of the ilium at the level of the central one-third and posterior one-third of the acetabulum, respectively. The thin, ventrally deflected posterior flange of primordial sacral rib 2 most likely articulated with a medially projecting ridge along the ventral side of the postacetabular process of the ilium, but a contact cannot be demonstrated because the distal rim of the rib MCCDM 1743-2 is eroded. In contrast to the weak articulation in *Smilosuchus*, the unexpanded distal rim of the dorsosacral rib in *Redondasaurus* slots into a broad groove that extends all along the medial side of the preacetabular process of the ilium. Another individual of *Redondasaurus* sp. from the Cooper Canyon Formation of Texas also possesses a dorsosacral added to the sacrum (Chavez, 2010).

Some reports of sacral ossification in phytosaurs are atypical anatomy and the result of pathology. The last presacral
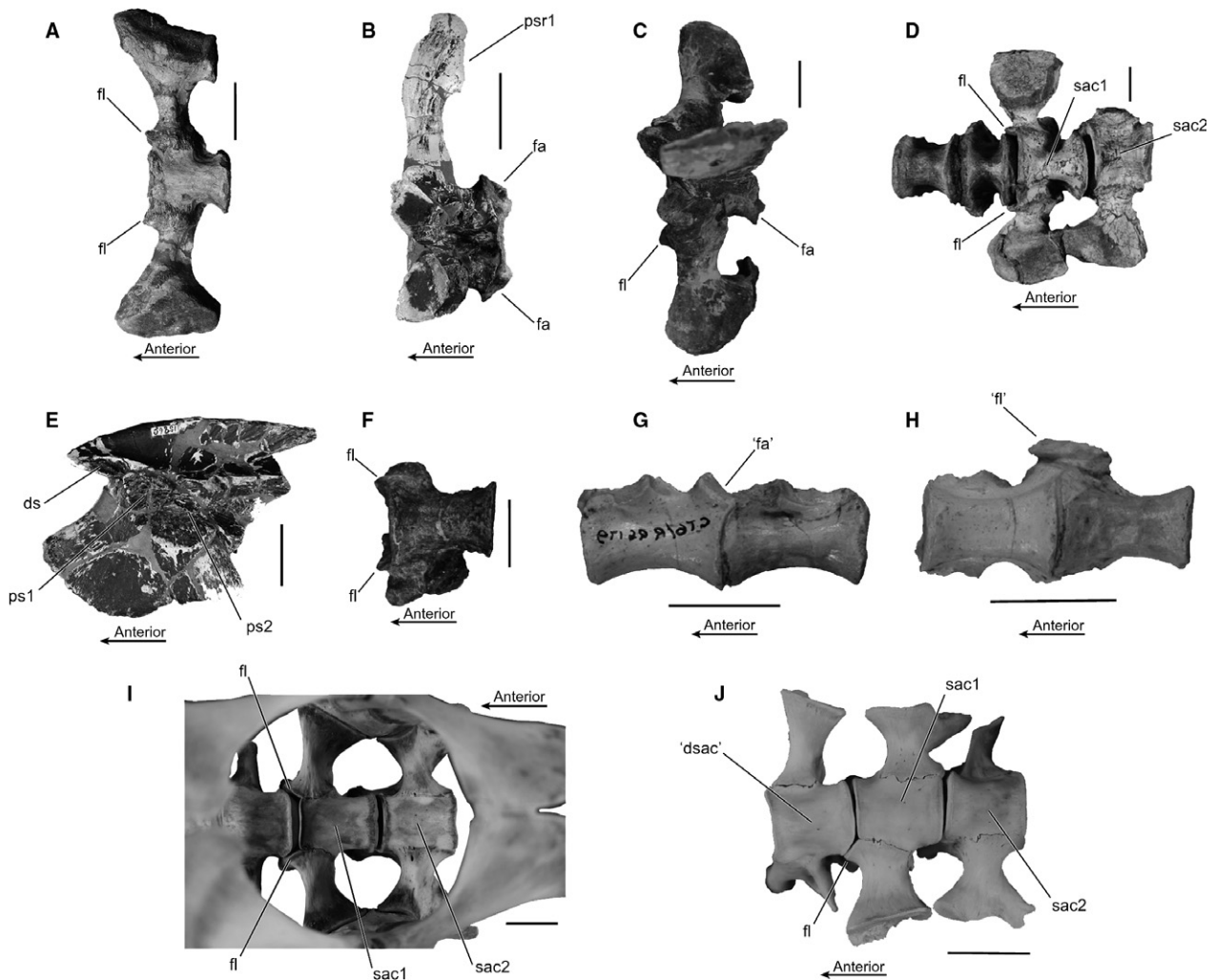
Fig. 6 Convergent structures in archosauriform sacra and pelves. (A) Sacral 1 of the phytosaur *Nicrosaurus* sp. (SMNS 5719) in ventral view. (B) Dorsosacral of the phytosaur *Machaeroprosopus* sp. (USNM 15860) in dorsal view. (C) Sacral 1 of the non-mystriosuchinine leptosuchomorph phytosaur *'Machaeroprosopus' zunii* (UCMP 27036) in dorsal view. (D) Sacrum and two trunk vertebrae of the suchian *Nundasuchus songeaensis* (NMT RB48) in ventral view. (E) Right ilium of the phytosaur *Machaeroprosopus* sp. (USNM 15860) in medial view. (F) Sacral 1 of the silesaurid *Asilisaurus kongwe* (NMT RB124) in ventral view. (G) Two sacral vertebrae of the theropod *Megapnosaurus rhodesiensis* (QG 179) in right lateral view, reversed for consistent orientation. (H) Two sacral vertebrae of the theropod *Megapnosaurus rhodesiensis* (QG 179) in ventral view; image reversed for consistent orientation. (I) Sacrum and one trunk vertebra of the crocodylian *Alligator mississippiensis* (VT Comparative Anatomy Collection) in ventral view; pubes and ischia are in foreground. (J) Anomalous sacrum of the crocodylian *Alligator mississippiensis* (VT Comparative Anatomy Collection) in ventral view, in which the posteriormost trunk vertebra articulates with the left ilium but not the right, and primordial sacral 2 articulates with the right ilium but not the left. All scale bars are 2 cm. ds, articulation surface for dorsosacral; 'dsac', 'dorsosacral' formed from anomaly; fa, facet on centrum for articulation with anteriorly projecting flange on the posterior-adjacent sacral rib; 'fa', feature similar to facet on centrum, but formed from articulation with 'shared' sacral ribs; fl, anteriorly projecting flange on sacral ribs that articulates with the centrum of the anterior-adjacent vertebra; 'fl', feature similar to flange on sacral ribs, formed by a 'shared' sacral rib; ps1, articulation surface for primordial sacral 1; ps2, articulation surface for primordial sacral 2; sac1, sacral vertebra 1; sac2, sacral vertebra 2.

and first primordial sacral of a specimen of *'Angistorhinopsis ruetimeyeri'* with spondyloarthropathy show fusion to such a high degree that the contact between these two elements was obliterated, though no fusion is present between the first and second primordial sacrals (Witzmann et al. 2014). It is clear from the CT scan of PEFO 34852 that the two primordial sacrals of this specimen are unfused (Fig. 3), and that the faceted morphology of the dorsosacral

is not the result of a pathological fusion similar to that reported by Witzmann et al. (2014).

In summary, the sacrum of phytosaurs is poorly described in the literature, and what has been described suggests that most phytosaurs possess only two sacral vertebrae. However, whether co-ossification between sacrals is common in phytosaurs is equivocal. Therefore, the sacrum of PEFO 34852 documents that members of Phytosauria possess a
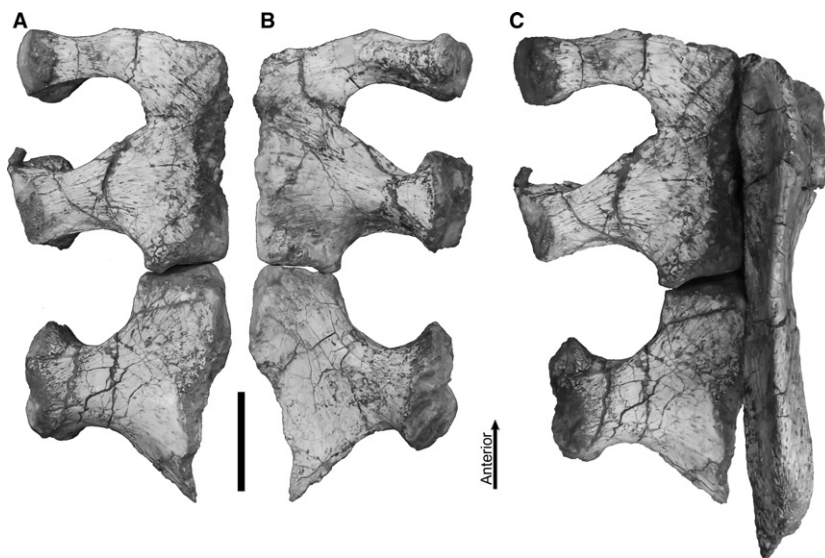
Fig. 7 Right dorsosacral rib and sacral rib 1 (MCCDM 1743-1) and right sacral rib 2 (MCCDM 1743-2) of *Redondasaurus* cf. *gregorii* in (A) dorsal view, (B) ventral view, and (C) articulated with right ilium MCCDM 1742. Scale bar: 5 cm.

greater range of morphological variation in sacra than previously supposed (Fig. 8). In addition to primordial sacral vertebrae 1 and 2, the sacrum of PEFO 34852 also consists of a dorsosacral, which is different from how all other phytosaurs have been previously described in the literature. Additionally, although the neural spines and zygapophyses of primordial sacrals 1 and 2 are fused, the centra of these vertebrae are either unfused (and merely closely associated) or only partially fused; with different phytosaurian taxa possessing differing degrees of fusion for all three of these sacral sites, these characters may possess a higher degree of variation across Phytosauria than previously realized (Figs 6 and 7). Lack of fusion in different elements may also be suggestive of the skeletal immaturity of the specimens in question (e.g. Brochu, 1996; Irmis, 2007; Griffin & Nesbitt, 2016), with fusion in one region (e.g. the zygapophyses) and not another (e.g. the centra) reflecting differential ontogenetic timing in the attainment of the 'mature' morph of these character states.

Sacral morphology across Archosauriformes

Because the possession of only the two primordial sacrals is the ancestral condition for both Archosauriformes and Archosauria, this condition is widespread among early-diverging archosauriforms. *Euparkeria capensis*, the sister taxon to Crurotarsi (Phytosauria + Archosauria, following Nesbitt, 2011), possesses only two sacral vertebrae (SAM 6048, 6049), with the first sacral rib situated anteriorly on the centrum of primordial sacral 1 with respect to the second sacral rib, which is situated centrally on the centrum of primordial sacral 2. As in PEFO 34852, the sutures between the sacral ribs and the centra are clearly visible, with the distal ends of the sacral ribs expanded laterally, the second sacral rib more expanded than the first (Ewer, 1965). The non-archosaurian archosauriform *Doswellia kaltenbachi*,

however, also incorporates a dorsosacral into the sacrum (Weems, 1980; Dilkes & Sues, 2009). The second and third sacral ribs are shifted anteriorly, so that they are 'shared' between the first and second, and second and third sacral vertebrae, respectively (Dilkes & Sues, 2009), and the depression on the posterior portion of the dorsosacral for articulation with the first primordial sacral rib is similar to the facets on the dorsosacral of *S. adamanensis*. Additionally, Nesbitt (2011) scored the ornithosuchid *Riojasuchus tenuisceps*, the sacrum of which consists of three vertebrae (Bonaparte, 1972; von Baczko & Ezcurra, 2013), as possessing a dorsosacral. Although its close relative *Ornithosuchus longidens* has also been interpreted as possessing three sacral vertebrae, with a facet on the posterior end of the dorsosacral centrum for articulation with the sacral rib of primordial sacral 1 (Walker, 1964), whether the sacrum incorporates a dorsosacral is ambiguous, and this character was scored as missing data by Nesbitt (2011).

Revueltosaurus callenderi (PEFO 34561, 34569, 36876), the sister taxon to the pseudosuchian clade Aetosauria, possesses only two sacral vertebrae as indicated by articulation scars on the medial surface of the ilium. As in phytosaurs, the second sacral rib of *Revueltosaurus* is thin dorsoventrally, elongated anteroposteriorly, and airfoil-shaped in lateral view. Among aetosaurs, the number of sacral vertebrae may be variable. Most described aetosaurs possess only two unfused sacral vertebrae (Mehl, 1915; Case, 1929, 1932; Walker, 1964; Lucas et al. 2002; Desojo & Báez, 2005; Parker, 2008); however, the sacrum of *Desmatosuchus spurensis* has been variously interpreted as possessing two primordial sacrals and a dorsosacral (Small, 1985; Nesbitt, 2011), or, conversely, only two primordial sacrals, with the last presacral vertebra fully co-ossified to the sacrum but lacking articulation with the ilium (Parker, 2008). Here, we follow Small (1985) and Nesbitt (2011) in considering the first sacral of *Desmatosuchus spurensis* a trunk vertebra that has been
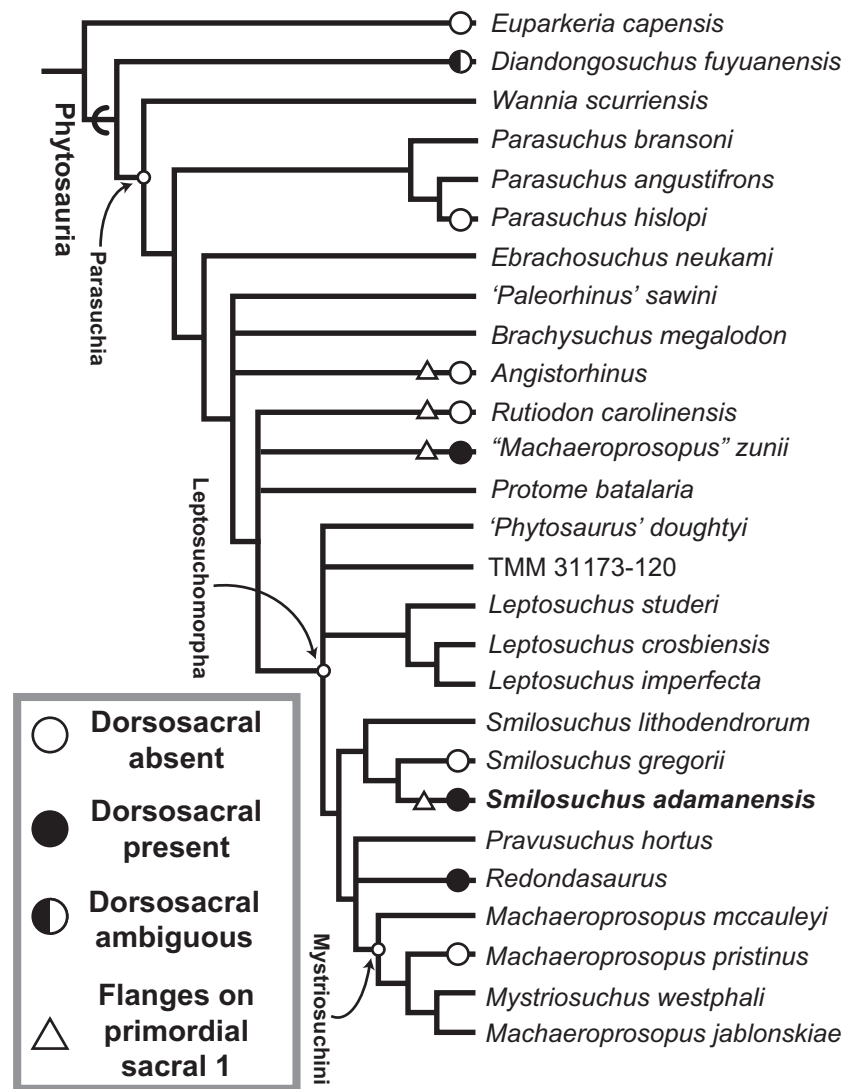
Fig. 8 Cladogram of phytosaurs showing distribution of sacral characters. Note that character states are mapped to terminal taxa, and no homology, homoplasy, or apomorphies are hypothesized here. Relationships based on Kammerer et al. (2016) and Stocker et al. (2017). *Redondasaurus* was not included in these analyses, but Hungerbühler (2002) and Stocker & Butler (2013) consider this taxon to belong to Mystriosuchini (= Pseudopalatinae), and we placed the *Redondosaurus* specimen (MCCDM 1742, 1743-1 and -2) accordingly.

incorporated into the sacrum (= a dorsosacral). This condition of a fused dorsosacral is also present in the aetosaurs *Longosuchus* (TMM 31185-40, 31100-236), *Lucasuchus* (TMM 31100-313), and TTU P-9172, identified as *Desmatosuchus* sp. (Elder, 1978; Long & Murry, 1995; Parker, 2007).

The early-diverging suchian *Nundasuchus songeaensis* (NMT RB48) was interpreted by Nesbitt et al. (2014) to possess only two sacral vertebrae, given the morphological similarity and identical relative size between the sacral vertebrae and ribs of this specimen and other early-diverging archosauriforms. However, with the absence of ilia and the first caudal vertebra in NMT RB48, a caudosacral could conceivably have been incorporated into the sacrum, although there is currently no evidence for any more than two sacrals in this taxon (Nesbitt et al. 2014). As in *S. adamanensis* and the other phytosaurs previously discussed, the bases of the first sacral ribs of *Nundasuchus* extend forward as flanges to articulate with the centrum of the last presacral vertebra (Fig. 6D; Nesbitt et al. 2014: fig.

4), although the facets present on the dorsosacral of PEFO 34852 for articulation with these flanges are absent in this taxon. Most early-diverging suchians do not incorporate a presacral into the sacrum. However, several poposauroid taxa possess dorsosacrals, including *Poposaurus gracilis* (TMM 436831-1), *Shuvosaurus inexpectatus* (TTU-P 9001), *Effigia okeeffeae* (AMNH FR 30587), and *Sillosuchus longicervix* (PVL 85; Nesbitt, 2007, 2011). These four taxa, as well as the ornithosuchid *Riojasuchus*, possess sacral ribs that are 'shared' by sacral vertebrae; that is, instead of each sacral rib articulating nearly entirely with a single sacral vertebra, the sacral ribs in these taxa articulate with two adjacent sacral vertebrae with roughly equal surface areas (Nesbitt, 2011). Given that many taxa that possess more than the plesiomorphic number of sacral vertebrae also 'share' sacral ribs (Nesbitt, 2011), these two features may be functionally associated, with the shared ribs acting as buttresses across the longer sacrum, although some taxa with three sacral vertebrae do not share sacral ribs (*Batrachotomus*,

Desmatosuchus, *Arizonasaurus*; Nesbitt, 2011). Although all extant pseudosuchians (crocodylians) retain two sacral vertebrae, the first sacral ribs of both *A. mississippiensis* (Fig. 6I,J; specimens stored in VT comparative collection) and *Alligator sinensis* (Cong et al. 1998) possess anteriorly projecting flanges morphologically similar to those of phytosaurs. The corresponding facets on the next centrum are absent in *A. mississippiensis* and *A. sinensis*, but because the last dorsal vertebra of these taxa is procoelous, well-developed facets may not be necessary for articulation.

Among bird-line archosaurs, the addition of a dorsosacral into the sacrum is common and evolved independently several times. All pterosaurian taxa for which sacra are available possess at least three, and typically four, sacral vertebrae, one of which is usually a dorsosacral (Hyder et al. 2014). Although three-dimensionally preserved pterosaurian sacra are rare, they do not appear to possess the flange-facet structure between sacral vertebrae present in many other archosaurs, nor do they appear to share sacral ribs between centra (e.g. *Anhanguera santanae*, AMNH FARB 22555, Wellnhofer, 1991). Silesaurids, a clade of non-dinosaurian dinosauriforms, are not known to incorporate a trunk vertebra into the sacrum; however, the early-diverging silesaurid *Asilisaurus kongwe* possesses anteriorly projecting flanges on the ribs of its first sacral vertebra (Fig. 6F; Nesbitt et al. 2010), similar to what we have described in PEFO 34852. In the more-derived silesaurid *Silesaurus opolensis*, which possesses three sacral vertebrae, sacral ribs are shifted such that they are shared between sacral vertebrae (Dzik, 2003; Dzik & Sulej, 2007; Nesbitt, 2011). Although two primordial sacrals is the plesiomorphic dinosaurian condition (e.g. Nesbitt, 2011), vertebrae are independently added to the sacra of some sauropodomorphs (e.g. *Saturnalia*, *Massospondylus*), but are added via insertions or as caudosacrals (see Galton, 1976; Langer, 2003; Yates, 2003; Langer & Benton, 2006; Nesbitt, 2011 for discussions of the early evolution of the sauropodomorph sacrum). However, dorsosacrals are incorporated into the sacrum in early ornithischians (*Lesothosaurus*, Sereno, 1991; *Heterodontosaurus*, SAM-PK-1332; *Eocursor*, Nesbitt, 2011), and the incorporation of a trunk vertebra into the sacrum is a synapomorphy for Neotheropoda (Nesbitt, 2011; Sues et al. 2011). The sharing of sacral ribs between vertebrae is present in more derived theropods (e.g. *Allosaurus*, *Velociraptor*, Nesbitt, 2011), but is also present in the early neotheropods *Coelophysis bauri* (C. T. Griffin, pers. obs.) and *Megapnosaurus rhodesiensis*. In the latter taxon, in specimens of skeletally immature individuals lacking fusion between sacral vertebrae or between sacral vertebrae and ribs, the surfaces of articulation on the centra for the sacral ribs are more clearly visible (e.g. QG 179; Fig. 6G,H). In these specimens, the posterior portion of the more anterior centra possesses well-developed facets on the posterodorsal portion of the posterior articular surface in lateral view. These facets are continuous with the facets on the more posterior centra, and together they form the surface of articulation with the sacral ribs. These facets are similar to the analogous facets on the posterior face of the dorsosacral of PEFO 34852, although they are more dorsally located on the *Megapnosaurus* centra.

Given that *Euparkeria* and most other early archosauriforms lack both a dorsosacral and the anteriorly projecting flange of the first sacral rib, and that analogous structures have evolved independently multiple times within crown-group archosaurs (Fig. 9; Table 1), Phytosauria is one of the earliest-diverging archosauromorph clades to have evolved a sacrum consisting of more than two sacral vertebrae, as well as the buttressing flange structure and corresponding facets. These flanges, with the sacral ribs extending slightly to articulate with the next anterior centrum, may represent an intermediate morphology between the plesiomorphic state, consisting of each sacral vertebra articulating with only one sacral rib, and a derived state of sacral vertebrae fully sharing sacral ribs. This does not imply that the sharing of sacral ribs evolved in phytosaurs as well, but simply that the full sharing of sacral ribs between vertebrae is a more well-developed form of the analogous flange-facet structure of *S. adamanensis*, other phytosaurs, and some archosaurs, with the flange representing an incompletely shared sacral rib.

Developmental mechanisms and implications

The multiple independent acquisitions of a structure among closely related taxa, in this case, the addition of a dorsosacral among Triassic archosauriforms, may suggest that a homologous underlying mechanism is responsible for this evolutionary trend. With respect to the incorporation of a trunk vertebra into the sacrum, or any other changes in vertebral formulae, changes in Hox gene expression (a highly conserved family of developmental regulatory genes) may be essential (Gaunt, 1994; Burke et al. 1995). It has been shown that Hox genes play a central role in the patterning of the axial skeleton, and particularly in determining vertebral identities, with changes in timing and expression levels of Hox genes during development resulting in shifts in the numbers and identities of vertebrae (Casaca et al. 2014). Most relevant to this discussion, the gene *Hoxd11* has been experimentally shown to play a major role in determining the trunk-sacral boundary in mouse models, with changes in expression timing causing anterior (Gérard et al. 1996, 1997; Boulet & Capecchi, 2002) or posterior (Davis & Capecchi, 1994; Zákány et al. 1996, 1997) shifts in the sacrum, the former of which involves the conversion of a trunk vertebra into a sacral vertebra. Given that Hox genes are highly conserved across Vertebrata, in particular with *Hoxd11* and associated regulatory gene homologues in the mouse and chick (a living archosauriform) being extensively conserved between these taxa (Gérard et al. 1997), this developmental gene as well as
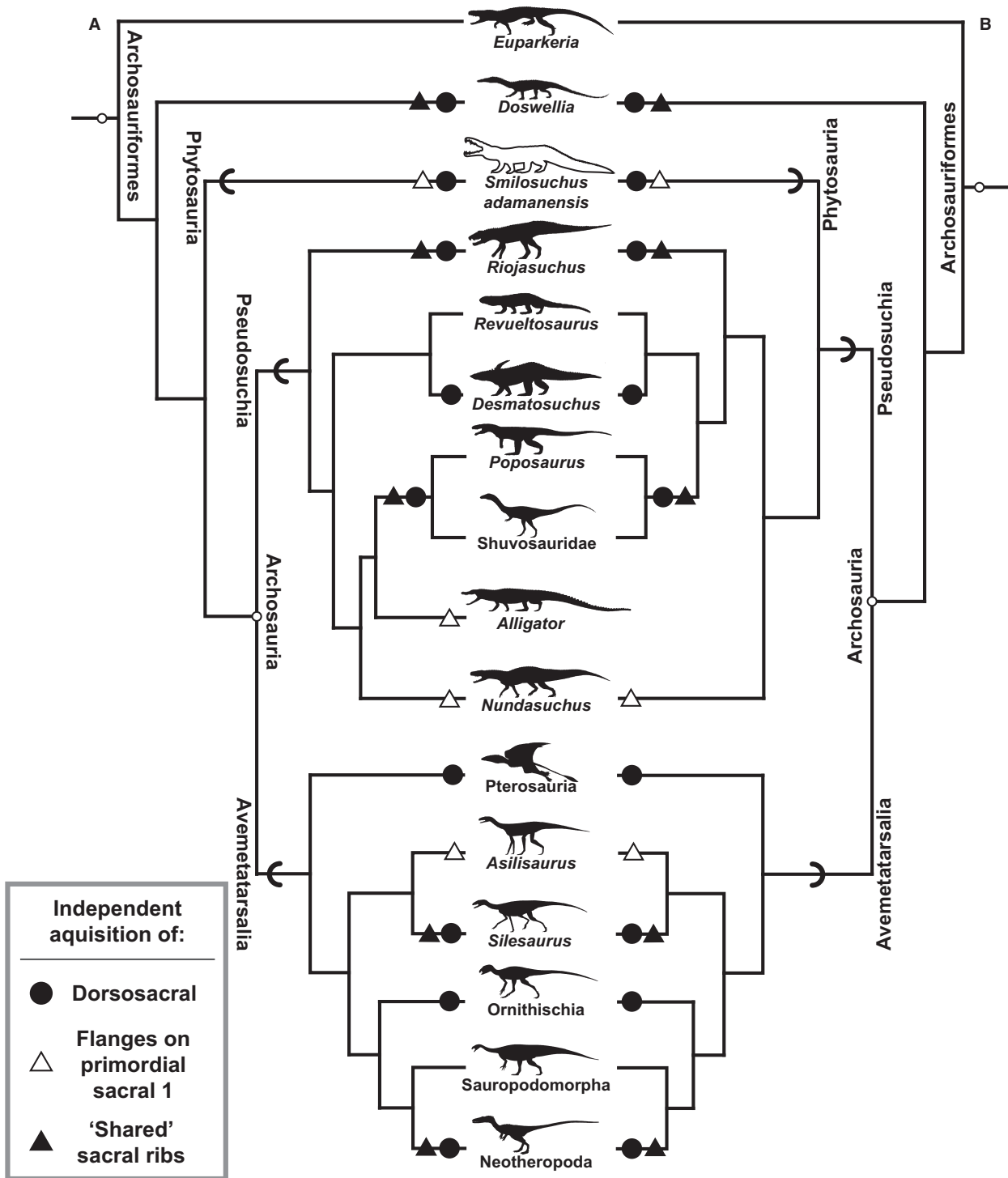
Fig. 9 Distribution of convergent sacral characters among early-diverging archosauriforms and *Alligator*. Note that most extant groups, and later-diverging extinct groups, are not included. Relationships based on (A) Nesbitt (2011) and Nesbitt et al. (2014), and (B) Ezcurra (2016). Nesbitt (2011) and Nesbitt et al. (2014) did not include *Doswellia*, but did include other proterochampsians. Ezcurra (2016) did not sample avian-line archosaurs as heavily as did Nesbitt (2011), so some of the relationships among this clade in (B) are taken from Nesbitt (2011), although the relationships recovered by these two analyses are congruent in the taxa that overlap.

related genes may have played a crucial role in the multiple independent acquisition of dorsosacrals among Triassic archosauriforms.

Because the regulation of at least some of the Hox genes that control sacral development can be altered (with subsequent phenotypic alterations of the sacrum) without

Table 1 Summary of the distribution of several convergent features of archosauriform sacra, focusing on early-diverging taxa. We interpret shared sacral ribs as a more extreme expression of the anteriorly projecting flanges on the first primordial sacral ribs.

Taxon	Phylogenetic position	Specimen/citation	Dorsosacral	Anterior flanges on first primordial sacral ribs	'Shared' sacral ribs
Doswellia kaltenbachi	Early-diverging archosauiform	NMNH 244214	Present	N/A	Present
Diandongosuchus fuyuanensis	Phytosaur	ZMNH M8770	?Absent	?	Absent
Smilosuchus adamanensis	Phytosaur	PEFO 34852, UCMP 26699	Present	Present	Absent
Riojasuchus tenuisceps	Ornithosuchid	PVL 3827	Present	N/A	Present
Ornithosuchus longidens	Ornithosuchid	BMNH 3816, 2410	?Present	Present	Absent
Desmatosuchus spurensis	Aetosaur	MNA V9300	Present	Absent	Absent
Longosuchus meadei	Aetosaur	TMM 31185-40, 31100-236	Present	Absent	Absent
Lucasuchus hunti	Aetosaur	TMM 31100-313	Present	Absent	Absent
Nundasuchus songeaensis	Early-diverging suchian	NMT RB48	Absent	Present	Absent
Poposaurus gracilis	Poposauroid	TMM 436831-1	Present	N/A	Present
Shuvosaurus inexpectatus	Shuvosaurid poposauroid	TTU-P 9001	Present	N/A	Present
Effigia okeeffea	Shuvosaurid poposauroid	AMNH FR 30587	Present	N/A	Present
Sillosuchus longicervix	Shuvosaurid poposauroid	PVL 85	Present	N/A	Present
Alligator mississippiensis	Crocodylian	VT comparative collection, unnumbered specimens	Absent	Present	Absent
Alligator sinensis	Crocodylian	Cong et al. (1998)	Absent	Present	Absent
Pterosauria	Avemetatarsalian	AMNH FARB 22555	Present	?Absent	?Absent
Asilisaurus kongwe	Silesaurid dinosauriform	NMT RB124	Absent	Present	Absent
Silesaurus opolensis	Silesaurid dinosauriform	ZPAL Ab III/404/3	Present	N/A	Present
Lesothosaurus diagnosticus	Ornithischian dinosaur	BMNH R11002	Present	?	?
Eocursor parvus	Ornithischian dinosaur	SAM-PK-K8025	Present	?Absent	?Absent
Heterodontosaurus tucki	Ornithischian dinosaur	SAM-PK-1332	Present	?	?
Neotheropoda	Saurischian dinosaurs	Nesbitt (2011)	Present	N/A	Present

deleterious effect to other regions these same genes control (e.g. *Hoxd11* and the forelimb and urogenital region, Zákány et al. 1997), this system may be highly 'evolvable', with low intrinsic constraints on change and a high level of achievable nonlethal variation. Supporting this, intraspecific sacral variations are robust with respect to the fitness of the organism, with many variations commonly appearing in natural settings and imparting no apparent, immediate deleterious effects among amphibians (Kovalenko & Danilevskaya, 1994; Kovalenko & Kruzhkova, 1996; Kovalenko & Kruzhkova, 2013a,b; Kovalenko & Kruzhkova, 2013c; Pugener & Maglia, 2009), lizards (El-Toubi, 1947; Holder, 1960; Hoffstetter & Gasc, 1969; Malashichev, 2000), and crocodylians (Reinhardt, 1874; Fig. 6J). Evolvability involves the ability of a system to generate heritable variations (Kirschner & Gerhart, 1998), and the archosauriform sacrum probably could achieve a large amount of nondeleterious intraspecific variation from relatively minor modifications to developmental processes. However, the developmental processes in question (Hox gene regulation) would conceivably only result in additions, subtractions, or insertions of sacral vertebrae (with the possible exception of producing asymmetrical sacra), thereby limiting the total amount of variation possible in a population or species to the number of vertebrae in a sacrum. With a limited number of easily achievable variations upon which natural selection could act, this would therefore be an excellent system to produce the large amount of convergent evolution such as that present among the sacra of early-diverging archosauriforms.

Conclusion

The sacrum of *Smilosuchus adamanensis* (PEFO 34852) is composed of two adjacent primordial sacral vertebrae as well as a dorsosacral vertebra that has been incorporated from the trunk. The junction between the first primordial sacral vertebra and the dorsosacral vertebra is supported by an articulation between anteriorly projecting flanges of the primordial sacral ribs and corresponding facets on the posterior end of the dorsosacral centrum. CT imaging reveals that the primordial sacral vertebrae are unfused to each other, and that the dorsosacral centrum does not possess an obvious pathology. This is the first published description of a phytosaurian sacrum possessing more than two sacral vertebrae, and the addition of a dorsosacral evolved at least eight times independently among Triassic archosauriform lineages. The flange-facet articulation is also present in the sacra of other archosaurs, and we interpret 'shared' sacral ribs (in which a sacral rib articulates

with two sacral vertebrae) as an expansion of these sacral rib flanges. Hox genes are key controllers of vertebral identity during development, and changes in the timing of expression of *Hoxd11* in particular have been shown to affect the identities of the sacral vertebrae in extant taxa. Therefore, the multiple independent acquisitions of dorsosacral vertebrae during the Triassic radiation of archosauriforms may be the expression of similar changes occurring in underlying, homologous developmental mechanisms.

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Author contributions

C.T.G.: Designed and conducted research, wrote paper, assembled figures. C.M.S: Conducted research, wrote paper, assembled figures. W.G.P.: Conducted research, wrote paper. A.H.: Wrote paper, conducted research, assembled figure. M.R.S.: Designed research, conducted research, wrote paper.

References

von Baczko MB, Ezcurra MD (2013) Ornithosuchidae: a group of Triassic archosaurs with a unique ankle joint. In: *Anatomy, Phylogeny, and Palaeobiology of Early Archosaurs and Their Kin* (eds Nesbitt SJ, Desojo JB, Irmis RB), pp. 187–202. London: Geological Society.

von Baczko MB, Desojo JB, Pol D (2014) Anatomy and phylogenetic position of *Venaticosuchus rusconii* Bonaparte, 1970 (Archosauria, Pseudosuchia), from the Ischigualasto Formation (Late Triassic), La Rioja, Argentina. *J Vertebr Paleontol* **34**, 1342–1356.

Benton MJ (1990) Origin and interrelationships of dinosaurs. In: *The Dinosauria*. (eds Weishampel DB, Dobson P, Osmolska H), pp. 11–30. Berkeley: University of California Press.

Benton MJ (1999) *Scleromochlus taylori* and the origin of dinosaurs and pterosaurs. *Philos Trans R Soc Lond B Biol Sci* **354**, 1423–1446.

Bonaparte JF (1972) Los tetrápodos del sector superior del a Formación Los Colorados, La Rioja, Argentina. (Triásico Superior) I Parte. *Opera Lilloana* **22**, 1–183.

Boulet AM, Capecchi MR (2002) Duplication of the *Hoxd11* gene causes alterations in the axial and appendicular skeleton of the mouse. *Dev Biol* **249**, 96–107.

Brochu CA (1996) Closure of neurocentral sutures during crocodilian ontogeny: implications for maturity assessment in fossil archosaurs. *J Vertebr Paleontol* **16**, 49–62.

Brusatte SL, Benton MJ, Desojo JB, et al. (2010) The higher-level phylogeny of Archosauria (Tetrapoda: Diapsida). *J Syst Paleontol* **8**, 3–47.

Burke AC, Nelson CE, Morgan BA, et al. (1995) Hox genes and the evolution of vertebrate axial morphology. *Development* **121**, 333–346.

Butler RJ, Sullivan C, Ezcurra MD, et al. (2014) New clade of enigmatic early archosaurs yields insights into early pseudosuchian phylogeny and the biogeography of the archosaur radiation. *BMC Evol Biol* **14**, 128.

Camp CL (1930) A study of the phytosaurs with description of new material from western North America. *Mem Univ Calif* **10**, 1–174.

Casaca A, Santos AC, Mallo M (2014) Controlling Hox gene expression and activity to build the vertebrate axial skeleton. *Dev Dyn* **243**, 24–36.

Case EC (1929) Description of the skull of a new form of phytosaur with notes on the characters of described North American phytosaurs. *Mem Univ Mich Mus*, University of Michigan **2**, 1–56.

Case EC (1932) A perfectly preserved segment of the armor of a phytosaur, with associated vertebrae. *Contrib Mus Paleontol*, University of Michigan **4**, 57–80.

Chatterjee S (1978) A primitive parasuchid (phytosaur) reptile from the Upper Triassic Maleri Formation of India. *Palaeontology* **21**, 83–127.

Chavez C (2010) *A new phytosaur (Archosauria: Pseudosuchia) from the Late Triassic Dockum Group of Texas)*, pp. 77. Lubbock: Texas Tech University.

Cong L-Y, Hou L-H, Wu X-C, et al. (1998) *The Gross Anatomy of Alligator sinensis Fauvel*. Beijing: Academia Sinica.

Davis AP, Capecchi MR (1994) Axial homeosis and appendicular skeleton defects in mice with a targeted disruption of *hoxd-11*. *Development* **120**, 2187–2198.

Desojo JB, Báez AM (2005) El esqueleto postcraneano de *Neoaetosauroides* (Archosauria: Aetosauria) del Triásico Superior del centro-oeste de Argentina. *Ameghiniana* **42**, 115–126.

Dilkes DW (1998) The early Triassic rhynchosaur *Mesosuchus browni* and the interrelationships of basal archosauromorph reptiles. *Philos Trans R Soc Lond B Biol Sci* **353**, 501–541.

Dilkes D, Arcucci A (2012) *Proterochampsa barrionuevoi* (Archosauriformes: Proterochampsia) from the Late Triassic (Carnian) of Argentina and a phylogenetic analysis of Proterochampsia. *Palaeontology* **55**, 853–885.

Dilkes D, Sues H-D (2009) Redescription and phylogenetic relationships of *Doswellia kaltenbachi* (Diapsida: Archosauriformes) from the Upper Triassic of Virginia. *J Vertebr Paleontol* **29**, 58–79.

Dzik J (2003) A beaked herbivorous archosaur with dinosaur affinities from the early Late Triassic of Poland. *J Vertebr Paleontol* **23**, 556–574.

Dzik J, Sulej T (2007) A review of the early Late Triassic Krasiejów biota from Silesia, Poland. *Palaeontol Pol* **64**, 3–27.

Elder RL (1978) *Paleontology and Paleoecology of the Dockum Group, Upper Triassic, Howard County, Texas)*. Austin: University of Texas, Austin.

El-Toubi MR (1947) Sacral ribs of Lacertilia. *Nature* **159**, 342.

Ewer RF (1965) The anatomy of the thecodont reptile *Euparkeria capensis* Broom. *Philos Trans R Soc Lond B Biol Sci* **248**, 379–435.

Ezcurra MD (2016) The phylogenetic relationships of basal archosauromorphs, with an emphasis on the systematics of proterosuchian archosauriforms. *PeerJ* **4**, e1778.

Galton PW (1976) Prosauropod dinosaurs (Reptilia: Saurischia) of North America. *Postilla* **169**, 1–98.

Gaunt SJ (1994) Conservation in the Hox code during morphological evolution. *Int J Dev Biol* **38**, 549–552.

Gauthier JA (1984) *A Cladistic Analysis of the Higher Systematic Categories of the Diapsida)*, pp. 564. Berkeley: University of California, Berkeley.

Gauthier JA (1986) Saurischian monophyly and the origin of birds. *Mem Calif Acad Sci* **8**, 1–55.

Gérard M, Chen JY, Gronemeyer H, et al. (1996) In vivo targeted mutagenesis of a regulatory element required for positioning the *Hoxd-11* and *Hoxd-10* expression boundaries. *Genes Dev* **10**, 2326–2334.

Gérard M, Zákány J, Duboule D (1997) Interspecies exchange of a *Hoxd* enhancer *in vivo* induces premature transcription and anterior shift of the sacrum. *Dev Biol* **190**, 32–40.

Gozzi E, Renesto S (2003) A complete specimen of *Mystriosuchus* (Reptilia, Phytosauria) from the Norian (Late Triassic) of Lombardy (Northern Italy). *Riv Ital Paleontol Stratigr* **109**, 475–498.

Griffin CT, Nesbitt SJ (2016) Anomalously high variation in postnatal development is ancestral for dinosaurs but lost in birds. *Proc Natl Acad Sci U S A* **113**, 14757–14762.

Hoffstetter R, Gasc J-P (1969) Vertebrae and ribs of modern reptiles. In: *Biology of the Reptilia*. (eds Gans C, Bellairs A d'A, Parsons TS), pp. 201–310, London: Academic Press.

Holder LA (1960) The comparative morphology of the axial skeleton in the Australian Gekkonidae. *Zool J Linn Soc* **44**, 300–335.

von Huene F (1913) A new phytosaur from the Palisades near New York. *Bull Am Mus Nat Hist* **32**, 275–283.

von Huene F (1922) Neue Beiträge zur Kenntnis der Parasuchier. *Jahrbuch Preuss Geol Landesanstalt* **42**, 59–160.

Hungerbühler A (2002) The Late Triassic phytosaur *Mystriosuchus westphali*, with a revision of the genus. *Palaeontology* **45**, 377–418.

Hutchinson JR (2001) The evolution of femoral osteology and soft tissues on the line to extant birds (Neornithes). *Zool J Linn Soc* **131**, 169–197.

Hutchinson JR (2002) The evolution of hindlimb tendons and muscles on the line to crown-group birds. *Comp Biochem Physiol A* **133**, 1051–1086.

Hutchinson JR, Gatesy SM (2000) Adductors, abductors, and the evolution of archosaur locomotion. *Paleobiology* **26**, 734–751.

Hyder ES, Witton MP, Martill DM (2014) Evolution of the pterosaur pelvis. *Acta Palaeontol Pol* **59**, 109–124.

Irmis RB (2007) Axial skeleton ontogeny in the Parasuchia (Archosauria: Pseudosuchia) and its implications for ontogenetic determination in archosaurs. *J Vertebr Paleontol* **27**, 350–361.

Irmis RB, Parker WG, Nesbitt SJ, et al. (2007) Early ornithischian dinosaurs: the Triassic record. *Hist Biol* **19**, 3–22.

Juul L (1994) The phylogeny of basal archosaurs. *Palaeontol Afr* **31**, 1–38.

Kammerer CF, Butler RJ, Bandyopadhyay S, et al. (2016) Relationships of the Indian phytosaur *Parasuchus hislopi* Lydekker, 1885. *Pap Palaeontol* **2**, 1–23.

Kirschner M, Gerhart J (1998) Evolvability. *Proc Natl Acad Sci U S A* **95**, 8420–8427.

Kovalenko EE, Danilevskaya SE (1994) On unique forms of anomalous sacral structure in tailless amphibians. *Russ J Herpetol* **1**, 30–36.

Kovalenko EE, Kruzhkova YI (1996) Certain pelvic and sacral anomalies in Anura. *Russ J Herpetol* **3**, 172–177.

Kovalenko EE, Kruzhkova YI (2013a) Individual variation in the development of the common toad, *Bufo bufo* (Anura, Bufonidae): 2. Diagnostic characters of the axial skeleton. *Russ J Dev Biol* **44**, 180–193.

Kovalenko EE, Kruzhkova YI (2013b) Individual variation in the development of the common toad, *Bufo bufo* (Anura, Bufonidae): 3. Limitations of individual variation and their causes. *Russ J Dev Biol* **44**, 194–205.

Kovalenko EE, Kruzhkova YI (2013c) Individual variation in the development of the common toad, *Bufo bufo* (Anura, Bufonidae): 1. Timing of development and anomalies of external structure. *Russ J Dev Biol* **44**, 173–179.

Langer MC (2003) The pelvic and hind limb anatomy of the stem-sauropodomorph *Saturnalia tupiniquim* (Late Triassic, Brazil). *PaleoBios* **23**, 1–30.

Langer MC (2004) Basal saurischians. In: *The Dinosauria*. 2nd edn. (eds Weishampel DB, Dobson P, Osmolska H), pp. 25–46. Berkeley: University of California Press.

Langer MC, Benton MJ (2006) Early dinosaurs: a phylogenetic study. *J Syst Paleontol* **4**, 309–358.

Li C, Wu X-C, Zhao L-J, et al. (2012) A new archosaur (Diapsida, Archosauriformes) from the marine Triassic of China. *J Vertebr Paleontol* **32**, 1064–1081.

Liparini A, Schultz CL (2013) A reconstruction of the thigh musculature of the extinct pseudosuchian *Prestosuchus chiniquensis* from the *Dinodontosaurus* Assemblage Zone (Middle Triassic Epoch), Santa Maria 1 Sequence, southern Brazil. In: *Anatomy, Phylogeny, and Palaeobiology of Early Archosaurs and Their Kin*. (eds Nesbitt SJ, Desojo JB, Irmis RB), pp. 441–468. London: Geological Society.

Long RA, Murry PA (1995) Late Triassic (Carnian and Norian) tetrapods from the southwestern United States. *N M Mus Nat Hist Sci Bull* **4**, 1–254.

Lucas SG, Heckert AB, Kahle R (2002) Postcranial anatomy of *Angistorhinus*, a Late Triassic phytosaur from west Texas. *N M Mus Nat Hist Sci Bull* **21**, 157–164.

Malashichev YB (2000) Sacrum and pelvic girdle development in Lacertidae. *Russ J Herpetol* **8**, 1–16.

McGregor JH (1906) The Phytosauria, with especial reference to *Mystriosuchus* and *Rhytidodon*. *Mem Am Mus Nat Hist* **9**, 27–100.

Mehl MG (1915) New reptiles from the Trias of Arizona and New Mexico. *Science* **41**, 735.

von Meyer H (1861) Reptilien aus dem Stubensandstein des oberen Keupers. *Palaeontographica* **7**, 253–346.

Mivart SG, Clarke R (1879) XX. On the sacral plexus and sacral vertebræ of Lizards and other Vertebrata. *Trans Linn Soc Lond 2nd Series Zool* **1**, 513–532.

Nesbitt SJ (2005) A new archosaur from the upper Moenkopi Formation (Middle Triassic) of Arizona and its implications for rauisuchian phylogeny and diversification. *Neues Jahrbuch Geol Paläontol Monat* **2005**, 332–346.

Nesbitt SJ (2007) The anatomy of *Effigia okeeffeae* (Archosauria, Suchia), theropod-like convergence, and the distribution of related taxa. *Bull Am Mus Nat Hist* **302**, 1–84.

Nesbitt SJ (2011) The early evolution of archosaurs: relationships and the origin of major clades. *Bull Am Mus Nat Hist* **352**, 1–292.

Nesbitt SJ, Butler RJ (2013) Redescription of the archosaur *Parringtonia gracilis* from the Middle Triassic Manda beds of Tanzania, and the antiquity of Erpetosuchidae. *Geol Mag* **150**, 225–238.

Nesbitt SJ, Sidor CA, Irmis RB, et al. (2010) Ecologically distinct dinosaurian sister group shows early diversification of Ornithodira. *Nature* **464**, 95–98.

Nesbitt SJ, Sidor CA, Angielczyk KD, et al. (2014) A new archosaur from the Manda beds (Anisian, Middle Triassic) of southern Tanzania and its implications for character state optimizations at Archosauria and Pseudosuchia. *J Vertebr Paleontol* **34**, 1357–1382.

Novas FE (1996) Dinosaur monophyly. *J Vertebr Paleontol* **16**, 723–741.

Parker WG (2007) Reassessment of the aetosaur 'Desmatosuchus' chamaensis with a reanalysis of the phylogeny of the Aetosauria (Archosauria: Pseudosuchia). *J Syst Paleontol* **5**, 41–68.

Parker WG (2008) Description of new material of the aetosaur *Desmatosuchus spurensis* (Archosauria: Suchia) from the Chinle Formation of Arizona and a revision of the genus *Desmatosuchus*. *PaleoBios* **28**, 1–40.

Parker WG (2013) Redescription and taxonomic status of specimens of *Episcoposaurus* and *Typothorax*, the earliest known aetosaurs (Archosauria: Suchia) from the Upper Triassic of western North America, and the problem of proxy 'holotypes'. *Earth Environ Sci Trans R Soc Edinb* **103**, 313–338.

Pugener LA, Maglia AM (2009) Skeletal morphogenesis of the vertebral column of the miniature hylid frog *Acris crepitans*, with comments on anomalies. *J Morphol* **270**, 52–69.

Rauhut OWM (2003) The interrelationships and evolution of basal theropod dinosaurs. *Spec Pap Palaeontol* **69**, 1–213.

Reinhardt J (1874) Sur les anomalies des vertebras sacrées chez les crocodilians. *J Zool* **3**, 308–312.

Rieppel O (1993) Studies on skeleton formation in reptiles. V. Patterns of ossification in the skeleton of *Alligator mississippiensis* Daudin (Reptilia, Crocodylia). *Zool J Linn Soc* **109**, 301–325.

Schachner ER, Manning PL, Dodson P (2011) Pelvic and hindlimb myology of the basal archosaur *Poposaurus gracilis* (Archosauria: Poposauroidea). *J Morphol* **272**, 1464–1491.

Sereno PC (1991) *Lesothosaurus*, 'fabrosaurids', and the early evolution of Ornithischia. *J Vertebr Paleontol* **11**, 168–197.

Sereno PC (1999) The evolution of dinosaurs. *Science* **284**, 2137.

Sereno PC, Arcucci A (1990) The monophyly of crurotarsal archosaurs and the origin of bird and crocodile ankle joints. *Neues Jahrbuch Geol Paläontol Abh* **180**, 21–52.

Sereno PC, Forster CA, Rogers RR, et al. (1993) Primitive dinosaur skeleton from Argentina and the early evolution of Dinosauria. *Nature* **361**, 64–66.

Small BJ (1985) *The Triassic Thecodontian Reptile Desmatosuchus*: *Osteology and Relationships*). Lubbock: Texas Tech University.

Smith ND, Makovicky PJ, Hammer WR, et al. (2007) Osteology of *Cryolophosaurus ellioti* (Dinosauria: Theropoda) from the Early Jurassic of Antarctica and implications for early theropod evolution. *Zool J Linn Soc* **151**, 377–421.

Sookias RB, Sullivan C, Liu J, et al. (2014) Systematics of putative euparkeriids (Diapsida: Archosauriformes) from the Triassic of China. *PeerJ* **2**, e658.

Stocker MR (2010) A new taxon of phytosaur (Archosauria: Pseudosuchia) from the Late Triassic (Norian) Sonsela Member (Chinle Formation) in Arizona, and a critical reevaluation of *Leptosuchus* Case, 1922. *Palaeontology* **53**, 997–1022.

Stocker MR, Butler RJ (2013) Phytosauria. In: *Anatomy, Phylogeny, and Palaeobiology of Early Archosaurs and Their Kin*. (eds Nesbitt SJ, Desojo JB, Irmis RB), pp. 91–117. London: Geological Society.

Stocker MR, Zhao L-J, Nesbitt SJ, et al. (2017) A short-snouted, Middle Triassic phytosaur and its implications for the morphological evolution and biogeography of Phytosauria. *Sci Rep* **7**, 46028.

Sues H-D, Nesbitt SJ, Berman DS, et al. (2011) A late-surviving basal theropod dinosaur from the latest Triassic of North America. *Proc R Soc Lond B Biol Sci* **278**, 3459–3464.

Tsai HP, Holliday CM (2014) Articular soft tissue anatomy of the archosaur hip joint: structural homology and functional implications. *J Morphol* **276**, 601–630.

Walker AD (1964) Triassic reptiles from the Elgin area: *Ornithosuchus* and the origin of carnosaurs. *Philos Trans R Soc Lond B Biol Sci* **248**, 53–134.

Weems RE (1980) An unusual newly discovered archosaur from the Upper Triassic of Virginia, U.S.A. *Trans Am Philos Soc* **70**, 1–53.

Wellnhofer P (1991) Weitere Pterosaurierfunde aus der Santana-Formation (Apt) der Chapada do Araripe, Brasilien. *Palaeontographica* **A215**, 43–101.

Westphal F (1976) Phytosauria. In: *Encyclopedia of Palaeoherpetology, 13, Thecodontia*. (ed. Kuhn O), pp. 99–120. Stuttgart: Gustav Fischer Verlag.

Witzmann F, Schwarz-Wings D, Hampe O, et al. (2014) Evidence of spondyloarthropathy in the spine of a phytosaur (Reptilia: Archosauriformes) from the Late Triassic of Halberstadt, Germany. *PLoS One* **9**, e85511.

Woody DT (2006) Revised stratigraphy of the lower Chinle Formation (Upper Triassic) of Petrified Forest National Park, Arizona. *Mus North Ariz Bull* **62**, 17–45.

Yates AM (2003) A new species of the primitive dinosaur *Thecodontosaurus* (Saurischia: Sauropodomorpha) and its implications for the systematics of early dinosaurs. *Syst Palaeontol* **1**, 1–42.

Zákány J, Gérard M, Favier B, et al. (1996) Functional equivalence and rescue among group 11 *Hox* gene products in vertebral patterning. *Dev Biol* **176**, 325–328.

Zákány J, Gérard M, Favier B, et al. (1997) Deletion of a *HoxD* enhancer induces transcriptional heterochrony leading to transposition of the sacrum. *EMBO J* **16**, 4393–4402.

Zeigler KE, Heckert AB, Lucas SG (2003) An illustrated atlas of the phytosaur (Archosauria: Parasuchidae) postcrania from the Upper Triassic Snyder quarry (Petrified Forest Formation, Chinle Group). *N M Mus Nat Hist Sci Bull* **24**, 89–104.