# The osteology of *Pulanesaura eocollum*: implications for the inclusivity of Sauropoda (Dinosauria)

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We present the complete osteology of the putative basal sauropod *Pulanesaura eocollum*. Current phylogenetic hypotheses suggest that *Pulanesaura* is the sister taxon of *Vulcanodon* + other sauropods, a position supported primarily by derived features of its axial skeleton and forelimb. A question of nontrivial importance is therefore the relative position of *Pulanesaura* with respect to current higher taxonomic groupings within Sauropodomorpha. The most recently proposed cladistic definition of Sauropoda (the most inclusive clade not including *Melanorosaurus*) places *Pulanesaura* as an unambiguous sauropod, whereas another commonly cited definition (the least inclusive clade containing *Vulcanodon* and *Saltasaurus*) suggests it is the most proximate sauropod outgroup. In addition to the issues pertaining to the validity of *Melanorosaurus*, we highlight a suite of features that can be shown to unambiguously and exclusively co-occur at the base of Sauropoda *sensu* the latter definition, arguing in favour of its continued use. As a corollary to this interpretation, we suggest that, instead of being simple diagnostic artefacts, (complex) apomorphies remain valid signifiers of notable phylogenetic loci whose contribution to our current classificatory schemes remains underexploited.

 $ADDITIONAL\ KEYWORDS:\ Jurassic-osteology-phylogenetic\ nomenclature-Sauropoda-Sauropodom or pha.$ 

### INTRODUCTION

The evolutionary relationships of sauropodomorph dinosaurs immediately basal to Sauropoda have been explored in great depth in recent years (e.g. Yates, 2003a, 2004, 2007a; Yates & Kitching, 2003; Pol & Powell, 2007; Upchurch, Barrett & Galton, 2007a; Pol, Garrido & Cerda, 2011; Otero & Pol, 2013; McPhee et al., 2014, 2015b). Perhaps the most noteworthy aspect of this work has been the substitution of a fully inclusive, mutually monophyletic 'Prosauropoda' and Sauropoda for a pectinate grade of stem-sauropodomorphs forming successively distal taxa to Sauropoda (see Peyre de Fabrègues, Allain & Barriel, 2015 for a recent review). However, elucidating the precise membership content of non-sauropodan Sauropodomorpha/ Sauropodiformes has been complicated not only by differing opinions on the node-or-stem based definition of both Sauropodiformes and Sauropoda but also by a lack of consensus as to what exactly constitutes a 'true' sauropod.

Whereas the possible ecological dynamics anteceding the origins of the sauropod *bauplan* has been a topic of focused discussion recently (McPhee et al., 2015a), most recent cladistic definitions have tended to demarcate the sauropod 'node' with reference to the vaguely defined acquisition of quadrupedality (e.g. Yates, 2007b; Yates et al., 2010; Otero & Pol, 2013). However, it is generally appreciated that most non-sauropodan sauropodomorphs were at least facultative quadrupeds (Remes, 2008), whereas most larger-bodied 'near-sauropod' taxa (e.g. Antetonitrus) probably exercised a mixedsuite of quadrupedal and bipedal behaviours depending on the specific locomotory and/or feeding context (McPhee *et al.*, 2014, 2015a). This confusion is further exacerbated by a paucity of associated post-crania (i.e. completely preserved appendicular skeletons) in taxa bordering the sauropodomorph-sauropod transition, as

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well as a general tendency within the literature to overstate the phylogenetic relevance of robusticity and/or graviportalism along the sauropodomorph stem leading to Sauropoda (e.g. Ezcurra & Apaldetti, 2012; McPhee *et al.*, 2014; see also McPhee & Choiniere, 2016).

Here we present the complete anatomy of the recently named *Pulanesaura eocollum* (McPhee *et al.*, 2015a). Effectively straddling the basal sauropodomorph-sauropod transition, this taxon provides empirical insight into both the anatomy of the earliest sauropods and the underlying processes potentially driving the development of the derived sauropod *bauplan*. *Pulanesaura* therefore has direct bearing on current controversies regarding the morphological and/ or functional criteria employed when determining the inclusivity of Sauropoda. This latter point provides the primary topic of discussion following the description.

#### INSTITUTIONAL ABBREVIATIONS

BP, Evolutionary Studies Institute, Johannesburg, South Africa (formerly Bernard Price Institute); NMQR, National Museum, Bloemfontein, South Africa; PULR, Museo de Ciencias Naturales, Universidad Nacional de La Rioja, La Rioja, Argentina; PVL, Paleontología de Vertebrados, Instituto 'Miguel Lillo', San Miguel de Tucumán, Argentina; SAM-PK, Iziko-South African Museum, Cape Town, South Africa.

## SYSTEMATIC PALAEONTOLOGY

The material described herein is from a multiindividual (at least two) bone bed from the Early Jurassic upper Elliot Formation of South Africa. Full quarry details are provided in McPhee *et al.* (2015a). Furthermore, although the diagnosis and associated specimen information given in the original study is not modified here, it should be noted that the correct catalogue number for the holotypic anterior dorsal vertebra is BP/1/6982, and not BP/1/6882.

#### DESCRIPTION

Reference sources for the primary comparative taxa mentioned in the description are given in Table 1.

#### Dentition

At least two isolated teeth (BP/1/6204, 6207) have been recovered from the *Pulanesaura* quarry (Fig. 1). BP/1/6204 is figured in detail in McPhee *et al.* (2015a: fig. 2).

Both teeth are represented by crowns only, with BP/1/6204 displaying a clean break at what appears to be the root-crown juncture. It is clear from the

preserved morphology that the base of the crown would have been separated from the root via a marked constriction.

Both teeth are essentially symmetrical in labial view, with mesial and distal margins that are convex with respect to the apicobasal axis, although this convexity could only be said to be pronounced in BP/1/6204 (with the mesial margin displaying slightly more basal convexity than the distal). Whereas a sub-lanceolate tooth morphology, like that observed in *Pulanesaura*, characterizes a number of basal sauropodomorphs (e.g. Thecodontosaurus; Plateosaurus), the mesial and distal convexity of BP/1/6204 nonetheless suggests the incipient development of the spatulate (sensu Upchurch, Barrett & Dodson, 2004) morphology that is developed further in basal sauropods (e.g. Spinophorosaurus; Shunosaurus). In contrast, a great number of basal sauropodomorphs display comparatively slender, elongate teeth [e.g. Massospondylus; Anchisaurus; Yunnanosaurus (Galton & Upchurch, 2004; Barrett & Upchurch, 2007)].

The denticles of both teeth are notably small and restricted to the apical third of the crown. The reduction of denticles (in terms of either size or topographic distribution) has a complex distribution throughout Sauropodomorpha (being present in, e.g., *Massospondylus*; *Yunnanosaurus*; *Melanorosaurus*; *Leonerasaurus*; Neosauropoda) suggesting that this feature, taken independent of other morphological data, presents only limited phylogenetic information (see also Barrett, 1999). Generally speaking, however, the restriction of denticles to the apical part of the crown tends to characterize basal sauropods (Barrett & Upchurch, 2007; Barrett *et al.*, 2007).

BP/1/6204 is lingually recurved with an apicobasally convex labial surface and concave lingual surface in which the apex of the crown is positioned above the base of the lingual surface (McPhee et al., 2015a: fig. 2; c.f. Tazoudasaurus). Whereas both teeth are 'D' shaped in cross-section with transversely convex labial sides, BP/1/6207 lacks the lingual recurvature of the former, being apicobasally straight along both labial and lingual surfaces. Furthermore, while both teeth lack the marked concavity of the lingual surface typical of Eusauropoda (Upchurch et al., 2004), the mesial and distal edges of the crown in BP/1/6207 are present as raised, continuous ridges that bracket the lingual surface along its apicobasal length (Fig. 1). Whereas some heterogeneity within the teeth of Pulanesaura is therefore presumed, both teeth share the putatively derived feature of pronounced longitudinal ridges (= 'fluting') running the apicobasal length of the crown. Present on both the labial (especially in the case of BP/1/6204) and lingual surfaces, these ridges are especially pronounced on the latter, where they radiate symmetrically from the mesiodistal midline. Similar sculpturing

Table 1.	Source	of	comparative	data	used	in	this	stud	ly
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Taxon	Source(s)
Aardonyx celestae	Various elements catalogued BP/1/5379-6893
Adeopapposaurus mognai	Martinez, 2009
Anchisaurus polyzelus	YPM 1883; Galton, 1976
Antetonitrus ingenipes	BP/1/4952a,b,c; McPhee et al., 2014
Blikanasaurus cromptoni	SAM-PK 403
Coloradisaurus brevis	PVL 5904 (field no. 6); Apaldetti et al., 2012
Eucnemesaurus spp.	Yates, 2007b; BP/1/6234
Isanosaurus attavipachi	Buffetaut et al., 2000
Jingshanosaurus xinwaensis	Zhang & Yang, 1994
Kotasaurus yamanpalliensis	Yadagiri, 2001
Lamplughsaura dharmaramensis	Kutty <i>et al.</i> , 2007
Leonerasaurus taquetrensis	Pol et al., 2011
Lessemsaurus sauropoides	PVL 4822; Pol & Powell, 2007
Lufengosaurus huenei	IVPP V15; Young, 1941
Massospondylus carinatus	BP/1/4377, 4693, 4924, 4934, 4998, 5000, 5241
Melanorosaurus readi	Yates, 2007a; NMQR 1551, 3314
Mussaurus patagonicus	Otero & Pol, 2013
Plateosauravus cullingworthi	SAM-PK 3341–3356, 3602–3603, 3607–3609
Plateosaurus engelhardti	Huene, 1926; Yates, 2003b
Riojasaurus incertus	PVL 3808; Bonaparte, 1971
Sanpasaurus yaoi	McPhee et al., 2016
Shunosaurus	Zhang, 1988
Spinophorosaurus	Remes et al., 2009
Tazoudasaurus naimi	Allain & Aquesbi, 2008
Vulcanodon karibaensis	Cooper, 1984

has been reported in a specimen of *Melanorosaurus* (BP/1/5334 Yates, 2007a), an isolated tooth from the lower Lufeng Formation [cf. Eusauropoda (Barrett, 1999), *Tazoudasaurus* and Eusauropoda (Upchurch *et al.*, 2004; Barrett & Upchurch, 2007)].

Dispersed among these ridges, within the apical half of the crown, are a series of ultra-fine, vertically oriented enamel wrinkles (McPhee et al., 2015a: fig. 2; Fig. 1). Although Yates (2004, 2007a) reported the presence of enamel wrinkling in the basal sauropodomorphs Anchisaurus and Melanorosaurus [see also Leonerasaurus: Pol et al. (2011)], the condition in these taxa is either ambiguous or incipient, with wrinkling in the teeth of Anchisaurus indiscernible with the naked eye (B.W.M., pers. observ.). Well-developed enamel wrinkling is therefore only observed in Pulanesaura, Chinshakiangosaurus (Upchurch et al., 2007b), the isolated lower Lufeng Formation tooth (Barrett, 1999) and Tazoudasaurus basal to Eusauropoda [see also Spinophorosaurus (Remes et al., 2009) and Amygdalodon (Carballido & Pol, 2010)]. Although enamel wrinkling has been reported in Lamplughsaura (Kutty et al., 2007) and Gongxianosaurus ['longitudinal striations' (He et al., 1998)], the nature and extent of this wrinkling has yet to be demonstrated.

None of the teeth recovered from the *Pulanesaura* quarry display strong evidence of occlusal wear-patterns.

#### Cervical vertebra

A single, nearly complete middle cervical vertebra (BP/1/6199) is preserved (Fig. 2). The anterior end of the centrum (primarily of the right lateral side) has been eroded away, and it is also possible that the element may have experienced slight diagenetic compression along its sagittal axis. This element was interpreted as a C3 by Yates, Wedel & Bonnan (2012), a referral that is followed here, although the anteroposteriorly short neural spine suggests it may have come from closer to the middle of the cervical series.

As mentioned by Yates *et al.* (2012), the centrum is completely solid and acamerate, without any signs of incipient pneumatization. The posterior articular facet is sub-circular in general outline, with a deeply concave articular face. The extent of this concavity (assuming that it is natural) is greater than in the isolated middle/posterior cervical centrum of *Antetonitrus* (BP/1/4952), while potentially also possessing a sharper rim. This morphology is suggestive of a pronounced ball-and-socket arrangement that



**Figure 1.** Isolated tooth (BP/1/6207) in (A) labial, (B) lingual and (C) mesial/distal views. Abbreviation: mr, marginal ridge. Scale bar = 1 cm.



**Figure 2.** Anterior-middle cervical vertebra (BP/1/6199) in (A) dorsal, (B) ventral, (C) right lateral, (D) anterior and (E) posterior views. Abbreviations: ep, epipophysis; ns, neural spine; poz, postzygapophysis; prz, prezygapophysis; vk, ventral keel. Scale bar = 5 cm.

may have been more developed than the plesiomorphic intercentral cartilaginous discs presumed for non-sauropodan sauropodomorphs. Unfortunately, the unpreserved anterior end of the centrum means that it cannot be confirmed if *Pulanesaura* displayed the derived sauropodan condition of opisthicoelous cervical vertebra seen in, for example, *Isanosaurus* and *Tazoudasaurus*. The ventral surface of the centrum is mediolaterally thin in ventral view and concave in side view. The beginnings of an anterior ventral keel can be discerned just prior to the sagittal midline (as in other sauropodomorph taxa, e.g., *Massospondylus; Antetonitrus; Isanosaurus*). Although the anteroposterior extent of this keel is unknown due to the missing anterior end of the centrum, it is unlikely based on preserved morphology that it would have been as continuously developed as in the cervical centra of massospondylids such as *Massospondylus* (BP/1/5241) and *Adeoppaposaurus* (Martinez, 2009).

The parapophyses are located slightly posterodorsally relative to the anteroventral corner of the centrum, whereas the diapophyses are located directly at the neurocentral suture c. 2.5 cm posterodorsal to the parapophyses. As in *Aardonyx*, the diapophyses are preserved as low tubercles and not borne on pendant flanges as in most sauropodomorph taxa (Yates *et al.*, 2010) (although the latter morphology is likely to have been more developed in more posterior cervical vertebrae).

The postzygapophyses are dorsally elevated with respect to the prezygapophyses, approaching an angle of about 20° (when the anterior margin of the neural spine is positioned vertically) relative to the coronal plane [note that this is incorrectly given as the 'sagittal' plane by McPhee et al. (2015a)]. Similarly oblique postzygapophyseal facets are observed in the cervical vertebrae of sauropod taxa such as Tazoudasaurus (Allain & Aquesbi, 2008: fig. 9), Patagosaurus (Rauhut et al., 2011), Shunosaurus and possibly Kotasaurus (Yadagiri, 2001: fig. 4). A similar morphology appears to have been present in the anterior-to-middle cervical vertebrae of both Leonerasaurus (see Pol et al., 2011: fig. 5) and Lamplughsaura (Kutty et al., 2007: figs 9, 10). In contrast, most non-sauropodan sauropodomorphs tend to display anterior-to-middle postzygapophyses that are only negligibly offset relative to the coronal plane (McPhee et al., 2015a: fig. 4). In Pulanesaura, this morphology produces a postzygapophyseal articular facet that is appreciably more dorsoventrally expansive than in the prezygapophyses, with the ventral component of this expansion interpreted here as the incipient formation of the centropostzygapophyseallamina (Wilson, 1999).

The articular facets of both prezygapophyses and postzygapophyses are offset about 30° from the horizontal. Although the anterior margin of the centrum is incomplete, it is obvious that the prezygapophyses would have extended well beyond it. The epipophyses are well-developed ridges that terminate well short of the posterior margin of the postzygapophyses, as in the majority of all basal sauropodomorphs with the possible exception of *Pantydraco* and *Plateosaurus* (Yates, 2003a, b; *contra* Apaldetti, Pol & Yates, 2012). The presence of well-developed epipophyses is consistent with vertebrae from the anterior half of the cervical series (B.W.M., pers. observ.). As in most non-sauropodan sauropodomorphs, *Pulanesaura* is distinguished by a complete absence of diapophyseal laminae (*sensu* Wilson, 1999) in at least the mid-cervical vertebrae.

Measured from the neurocentral suture to the top of the neural spine, the neural arch is c. 1.4 times the dorsoventral height of the posterior face of the centrum. This metric (in which the neural arch is higher than the posterior centrum) is a derived feature for Sauropodomorpha, being observed previously only in *Lessemsaurus* + Sauropoda (although there appear to be no associated cervical neural arches and centra in the *Lessemsaurus* PVL 4822 assemblage).

The neural spine is comparatively tall for any early sauropodomorph anterior/mid-cervical, with its maximum dorsoventral height (measured as the height of the spine from the dorsal tip of the prespinal fossa to the dorsal edge of the anterior margin of the spine) being 0.98 times its anteroposterior length (measured as the maximum length of the dorsal margin of the neural spine). This is taller than the neural spine of a similarly positioned (based on general proportions and the development of the epipophyses) cervical neural arch in Aardonyx (0.78: BP/1/6615), as well as being significantly taller than the plesiomorphic condition of, for example, Massospondylus (0.33: BP/1/5241) [it is possible that *Lamplughsaura* preserves similarly proportioned cervical neural spines (Kutty et al., 2007: fig. 10)]. Nonetheless, the cervical neural spine of Pulanesaura differs from that of basal sauropods (e.g. Tazoudasaurus; Spinophorosaurus) in lacking the pronounced spinozygapophyseal laminae that connect both the prezygapophyses and postzygapophyses to the top of the neural spine via well-developed, dorsoventrally sloping sheets. The dorsal margin of the neural spine is not ornamented by any laterally oriented swellings of bone, differing from the condition in a number of basal sauropodomorphs (e.g. Massospondylus; Aardonyx) (although this morphology is often more pronounced towards the end of the cervical series).

#### Dorsal vertebrae

There are five dorsal neural arches, representing each region of the dorsal axial column with the exception of the posterior-most dorsal vertebrae (Figs 3–5). There are no dorsal centra well enough preserved to yield adequate description. The following description will provide a brief overview of the relevant morphological features of the dorsal vertebrae, before detailing the anatomy of specific regions of the preserved dorsal series. Serial position of the vertebrae was determined with respect to the relative anteroposterior length of



**Figure 3.** Anterior dorsal vertebrae. A–D, BP/1/6982 (holotype) in (A) anterior, (B) posterior, (C) right lateral and (D) left lateral views. E–G, BP/1/6984 in (E) anterior, (F) right lateral and (G) left lateral views. Abbreviations: aidf, anterior infradiapophyseal fossa; dp, diapophysis; hyp, hyposphene; ns, neural spine; pcdl: posterior centrodiapophyseal lamina; poz, postzygapophysis; prdl, prezygodiapophyseal lamina; prz, prezygapophysis. Scale bars = 5 cm.

the neural spines and/or arches, the presence/absence of the prezygodiapohpyseal laminae (PRDL) and the position of the parapophyses; the combination of which provides a relatively robust indication of serial position in early sauropodomorphs. Terminology for vertebral laminae follows Wilson (1999).

The dorsal neural arches of *Pulanesaura* provide a good example of the transitional condition between basal Sauropodomorpha and the more derived morphology of Sauropoda. This is seen primarily in the increased relative height (vs. anteroposterior length) of the neural spines – a development that is especially marked in the anterior-most elements (see, e.g., *Plateosaurus* cf. *Tazoudasaurus*). As the dorsal series progresses posteriorly, the neural spines increase in length along the sagittal axis, changing from a distinctly anteroposteriorly compressed morphology in the anterior-most elements to the more typical basal condition of mediolaterally compressed, anteroposteriorly

elongate neural spines from the mid-dorsals onwards. This suggests that the anterior-most dorsal vertebrae adopted the sauropod-like anteroposterior constriction of the neural spine prior to the middle/posterior dorsal vertebrae in sauropodomorph evolution.

Spinal laminae are restricted to the sheet-like spinopostzygapophyseal laminae (SPOL; especially prevalent in the mid-dorsals onwards) that form large, buttressing structures between the postzygapophyses and the posterior margins of the neural spine. Incipient spinoprezygapophyseal laminae (SPRL) can be observed on the anterior margin of the neural spines in the anterior-most dorsals, although these are significantly less developed than the SPOL.

The assortment of diapophyseal laminae in *Pulanesaura* is consistent with other saurischian dinosaurs. These consist of the anteriorly oriented PRDL that join the diapophyses to the prezygapophyses, the anteroventrally oriented paradiapophyseal – or



**Figure 4.** Middle dorsal vertebrae. A–C, BP/1/6183 in (A) anterior, (B) posterior and (C) right lateral views. D–F, BP/1/6770 in (D) anterior, (E) posterior and (F) left lateral views. Abbreviations: dp, diapophysis; hyp, hyposphene; ns, neural spine; pcdl, posterior centrodiapophyseal lamina; podl, postzygodiapophyseal lamian; poz, postzygapophysis; pp, parapohysis; ppdl, paradiapophyseal lamina; prdl, prezygodiapophyseal lamina; prdr, prezygodiapophyseal ridge; prz, prezygapophysis; spol, spinopostzygapophyseal lamina. Scale bars = 5 cm.



**Figure 5.** Posterior dorsal vertebra (BP/1/6183a) in (A) anterior, (B) posterior and (C) left lateral views. Abbreviations: pcdl, posterior centrodiapophyseal lamina; psf, pneumatic subfossa; spol, spinopostzygapophyseal lamina. Scale bar = 5 cm.

anterior centrodiapophyseal – laminae (PPDL/ACDL) that link the diapophyses with the parapophyses (when the latter has risen to the level of the neural arch), the posteroventrally directed posterior centrodiapophyseal laminae (PCDL) linking the diapophyses with the posteroventral corner of the pedicles and the posteriorly oriented postzygadiapophyseal laminae (PODL) joining the diapophyses with the postzygapophyses.

As in all known sauropodomorphs basal to *Tazoudasaurus*, the PRDL appears to have been absent (or highly reduced) from around the mid-dorsal vertebrae onwards, leading to the concomitant disappearance of the anterior infradiapophyseal fossa (*sensu* Yates *et al.*, 2012). However, BP/1/6770 (a posterior mid-dorsal neural arch) preserves a low but distinct ridge extending from the diapophyses to the base of the prezygapophyses. This ridge is interpreted as homologous to the PRDL, and represents a possible apomorphic feature of *Pulanesaura*, although it is likely that the PRDL reduces in a graded fashion throughout the dorsal series of most basal sauropodomorphs [e.g. *Massospondylus*: BP/1/4934; *Mussaurus* (Otero & Pol, 2013)].

The hyposphenes in all *Pulanesaura* vertebrae are well-developed equilateral triangles that are over half the dorsoventral height of the neural canals they apically frame - a similar proportion to that seen in other Elliot Formation taxa such as Aardonyx (BP/1/6566) and Antetonitrus (BP/1/4952a). However, the hyposphenes of Pulanesaura can be distinguished from both of these taxa insofar as the ventral surface is relatively flat and featureless while the posterior surface is only minimally concave with respect to the lateral walls of the hyposphene. In contrast, the hyposphenes in Antetonitrus display a low, median ridge along the length of the ventral surface, whereas the posterior surfaces of the hyposphenes in *Aardonyx* are deeply excavated, being bound by the posteriorly projecting lateral walls of the hyposphene. As in all derived 'nearsauropod' taxa, the neural canals in the dorsal neural arches of Pulanesaura are high and slot shaped, differing from the sub-circular morphology observed in more basal sauropodomorph taxa [e.g. Eucnemesaurus (BP/1/6107)].

Towards the rear of the dorsal series (although the posterior-most elements are not preserved), the dorsal neural arches are proportionately anteroposteriorly shortened, consistent with the morphology of other large-bodied sauropodiforms (e.g. *Aardonyx*; *Antetonitrus*; *Tazoudasaurus*).

#### Anterior dorsal vertebrae

There are two anterior dorsal neural arches. BP/1/6982 [designated the holotype of *Pulanesaura* (McPhee *et al.*, 2015a)] is the anterior-most of the two and

is probably from the cervicodorsal transition (possibly D1). It is missing the dorsal half of the neural spine, left diapophysis and the two anterior pedicles (Fig. 3A–D). BP/1/6984, possibly a D3, is much more poorly preserved than BP/1/6982 and, although it preserves most of the neural spine, is missing the right prezygapophysis and most of the posterior aspects of the neural arch (Fig. 3E–G). General equivalence in size suggests that both of these elements belonged to the same individual.

The neural spines of the anterior dorsal vertebrae represent one of the more apomorphic features of Pulanesaura. Unlike the majority of non-sauropodan sauropodomorphs (e.g. *Plateosaurus*; *Aardonyx*) for which the anterior-most dorsal series is known, the neural spines of Pulanesaura are markedly dorsoventrally elongate relative to their anteroposterior length. Although the posterior margin of the neural spine in BP/1/6984 is eroded, extrapolating from the basally complete neural spine of BP/1/6982 yields a dorsoventral height by anteroposterior length of c. 3.15. As the tip of the neural spine is poorly preserved in BP/1/6984 with no obvious terminal surface, it is possible that this metric may have been even greater in life. In comparison, the neural spines of the anterior dorsal vertebrae of the penecontemporaneous Aardonyx (BP/1/6642) present a dorsoventral height/anteroposterior length ratio of 1.18, with a similar measurement observed in Massospondylus (1.14: BP/1/5241). In terms of general morphology and orientation, the anterior dorsal neural spines of *Pulanesaura* appear similar to figured representations of the dorsal vertebrae of Kotasaurus (Yadagiri, 2001: fig. 4), in which a distinct anteriorly directed bowing can be observed along the anterior margin of the neural spine.

The prezygapophyses of BP/1/6982 are massive, sheet-like structures set at a sharp angle of  $c. 45-50^{\circ}$ from the horizontal. Although a number of sauropodiform taxa present vertebrae from the cervicodorsal transition in which the prezygapophyses are enlarged with respect to the rest of the dorsal series (e.g. Aardonyx: BP/1/6591), this tendency appears to have been developed to an exaggerated extent in Pulanesaura. In contrast, the articular facets of the prezygapophyses of BP/1/6984 are appreciably less expansive and are only negligibly offset with respect to the horizontal. Of three infradiapophyseal fossa in BP/1/6992 both the anterior and posterior fossa are considerably deeper than the central infradiapophyseal fossa, the former being conical in shape with sharply tapered medial terminations that extend well beneath the central arm of the diapophyses. In BP/1/6984, only the anterior infradiapophyseal fossae are preserved, being anteroposteriorly broader and less deeply excavated than in BP/1/6982. In both elements, the diapophyses are raised above the horizontal

and, while this appears more strongly developed in BP/1/6984, it is clear that BP/1/6982 has experienced some taphonomic distortion, with each of its diapopheses preserved at incongruent angles. Only BP/1/6982 preserves postzygapophyses, which are medially separated by a very deep and mediolaterally narrow postspinal fossa. They are set at a similar angle to the prezygapophyses.

# Mid-dorsal vertebrae

There are two mid-dorsal vertebrae present in the *Pulanesaura* assemblage. One (BP/1/6183) is from the anterior-middle dorsal transition, possibly a D4–D5 (Fig. 4A–C), while the other (BP/1/6770) is clearly from the latter end of the mid-dorsal series (Fig. 4D–F). Both are almost entirely complete, although some sections of the prezygapophyses of BP/1/6770 are missing.

The proportions of the neural spines, while being more anteroposteriorly elongate than in anterior dorsal elements, closely resemble those of Antetonitrus ingenipes in being of appreciable relative height. In BP/1/6770, the dorsoventral height of the neural spine is 1.64 times the anteroposterior width of the base. This metric is essentially equivalent to that of a posterior mid-dorsal from the Antetonitrus holotype (BP/1/4952: 1.60). Nonetheless, in anteroposterior view, the lateral margins of neural spines of Pulanesaura are sub-parallel throughout their length, lacking the transverse dorsal expansion of the spine seen in the mid-dorsals of Antetonitrus and Lessemsaurus. SPRLs are only moderately developed in the mid-dorsal vertebrae, framing a deep, slit-shaped prespinal fossa; however, the SPOLs are more developed than in any comparable Elliot taxon, with the greatest depth of the post-spinal fossa (the recess between the postzygapophyses) being over one third of the anteroposterior length of the base of the neural spine. The SPOLs are also more finely constructed and less mediolaterally separated than the same processes in Antetonitrus.

As mentioned above, the PRDL is present as a low ridge in the more posterior mid-dorsal vertebra (BP/1/6770), as is plesiomorphic for Sauropodomorpha; however, the anterior mid-dorsal vertebra (BP/1/6183) still displays a pronounced, sub-horizontally oriented PRDL that connects to the anteroposterior elongate, platform-shaped prezygapophyses. As the parapophyses already occupy a relatively high position on the neural arch by this point of the dorsal series (being clearly completely raised above the neurocentral suture), it is possible that this represents a transitional shift towards the retention of the PRDLs throughout the dorsal series in later sauropods.

In contrast to a mid-dorsal from the *Antetonitrus* holotype, there is no evidence of invasive pneumaticity in any of the *Pulanesaura* mid-dorsal vertebrae. However, a series of fine, vertically oriented striations can be observed within the posterior infradiapophyseal fossa of BP/1/6770, suggesting that this fossa nonetheless housed a non-invasive homolog of the pulmonary air-sac system, even if diverticula were not present at this point of the axial skeleton.

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# Posterior dorsal neural arch

A single posterior dorsal neural arch (BP/1/6183) is present, although it is likely to have occupied a more anterior than posterior position within the last few dorsal vertebrae, possibly representing a D10–D12 (Fig. 5). This element is not dramatically different in morphology to that of BP/1/6183, the primary difference being the subtle anteroposterior shortening of the arch and the slight transverse widening of the dorsal summit of the neural spine - as are typical of posterior dorsal vertebrae in derived sauropodiform dinosaurs (e.g. Aardonyx; Antetonitrus). The most notable feature of this element is the small, mediolaterally narrow subfossae located within the anterior margins of the posterior infradiapophyseal fossae. These subfossae (and the pneumatic nature of their origin) have previously been discussed in detail by Yates et al. (2012).

# Caudal vertebrae

Three caudal vertebrae are present. Of the two anterior caudal vertebrae, BP/1/6646 is clearly from the anterior-most part of the tail, whereas BP/1/6201 is interpreted as an anterior mid-caudal. BP/1/7741 is probably from a position somewhere within the middle caudal series.

In describing the morphology of the anterior caudal vertebrae, the anterior-most element (BP/1/6646) will be discussed in detail first, followed by a brief description of the relevant features of BP/1/6201.

The anterior-most caudal vertebra (BP/1/6646) is preserved almost entirely complete, missing only a portion of the posteroventral margin of the centrum, the anterior portion of the left prezygopophysis, and the lateral terminations of the transverse processes (Fig. 6A–D). The bi-concave centrum is highly anteroposteriorly compressed, with the dorsoventral height of the posterior face 1.90 times the anteroposterior length of the centrum. This compares with a metric of 1.43 in an anterior caudal vertebra of Antetonitrus (BP/1/4952) and 1.58 in the same element of Aardonvx (although neither elements are probably from the anterior-most part of the caudal series). It is also higher than the putative 'vulcanodontid' anterior caudal vertebra (BP/1/6105) that was collected from an adjacent locality of the Heelbo location (Yates, Hancox & Rubidge, 2004), which displays a height/length ratio of 1.67. In the original Pulanesura description (McPhee



**Figure 6.** Anterior caudal vertebrae. A–D, BP/1/6646 in (A) anterior, (B) posterior, (C) left lateral and (D) right lateral views. E–H, BP/1/6201 in (E) anterior, (F) posterior, (G) right lateral and (H) dorsal views. Abbreviations: hyp, hyposphene; ns, neural spine; poz, postzygapophysis; prdl, prezygodiapophyseal lamina; prz, prezygapophysis; tp, transverse processes. Scale bars = 5 cm.

et al., 2015a), it was stated that the proportions of the anterior caudal vertebra were therefore most similar to Tazoudasaurus (Allain & Aquesbi, 2008: To1-100) outside of Eusauropoda. However, the anterior caudal vertebrae of the referred Melanorosaurus specimen NMQR 1551 are similarly anteroposteriorly compressed, being roughly twice as high as long (Galton, Van Heerden & Yates, 2005). Unfortunately, the [possibly 'arthritic' (Raath, 1972: 11)] anterior-most caudal vertebrae are poorly preserved in *Vulcanodon* (Raath, 1972; Cooper, 1984). However, available information suggests that the anterior-most elements (from c2 onwards) were only moderately higher than long (Raath, 1972: Plate III; Cooper, 1984), suggesting a reversal to proportionately longer caudal centra in that taxon [although the possibility that the preserved tail elements of Vulcanodon are from a more posterior section than given in Raath (1972) cannot be discounted].

The ventral surface of BP/1/6646 is transversely convex and anteroposteriorly concave. In contrast, specimens of *Melanorosaurus* (e.g. SAM-PK 3449), Vulcanodon and the Heelbo vulcanodontid (BP/1/6105: Yates et al., 2004) display a ventral sulcus along the sagittal axis of caudal centra (a variable feature for Sauropodomorpha, being present also in, e.g., Lufengosaurus). However, Pulanesaura shares with the Heelbo 'vulcanodontid' a pronounced offset between the anterior and posterior articular facets (the posterior being appreciably lower than the anterior) as well as a general equivalence in the dorsoventral and mediolateral dimensions of both articular facets (Yates et al., 2004). Aardonyx, in contrast, displays only a moderate offset between the two facets, both of which are relatively ovoid in shape (height/ width ratio of 1.34: BP/1/6753), whereas none of the subovoid (height/width ratio of 1.15) anterior caudal vertebrae preserved within the Antetonitrus holotypic assemblage (BP/1/4952) display a marked offset between the facets.

The neural arch contacts the entirety of the dorsal surface of the centrum, although the slight anterior incline of the arch produces a distinct shelf on the posterodorsal edge of the centrum that is absent on the anterodorsal surface, the latter being confluent with the anterior surface of the neural arch.

The neural spine of the anterior-most caudal vertebra in Pulanesaura marks a dramatic increase in relative height compared to the middle-posterior dorsal neural spines, with the dorsoventral height three times that of the anteroposterior height. Previously, the tallest neural spine from this area of the axial skeleton for any Elliot Formation sauropodomorph taxon was an anterior caudal/caudosacral neural arch from the Antetonitrus holotypic assemblage (BP/1/4952), which records a height/basal length ratio of 2.67. In contrast to the basal sauropods Tazoudasaurus and 'Kotasaurus', both of which display anterior caudal neural spines which are oriented almost completely vertically with dorsoventrally straight anterior and posterior margins, Pulanesaura retains the posteriorly bowed, arcuate morphology typical of most non-sauropodan sauropodomorphs [cf. NMQR 1551: Melanorosaurus (Galton et al., 2005: figs 1.5, 1.6)].

Spinal lamination in this element is restricted to finely delineated SPOLs that run from the postzygapophyses to over halfway the dorsal height of the neural spine. This condition is similar to that seen in the anterior caudal/caudosacral neural arch of *Antetonitrus*. It is possible that similarly developed SPRLs laterally framed the anterior margin of the neural spine, but poor preservation makes this difficult to confirm.

The prezygapophyseal articular facets are positioned higher dorsally than the postzygopohyseal facets, with both set at a relatively steep angle of over 45°. Although the articular facets of the postzygapophyses are comparatively smaller in area than those of the prezygapophyses, they are nonetheless more developed than the highly reduced, 'pinched' morphology evident in Tazoudasaurus (Allain & Aquesbi, 2008: 368). The prezygapophyses possess the same ossified lip of bone along their medioventral margin as in the anterior caudal/caudosacral neural arch of Antetonitrus (McPhee et al., 2014: fig. 6B). Although the dorsal margins of both transverse processes/diapophyses are not preserved, the well-preserved struts of bone that extend dorsolaterally from the prezygapophyses strongly suggest the presence of blunt yet well-defined PRDLs that would have connected the prezygapophyses to the dorsal margin of the transverse processes. This is the first time that diapophyseal laminae have been inferred in the caudal vertebrae of any Elliot Formation sauropodomorph taxon and possibly represent the incipient development of the laminar condition seen in the anterior caudal vertebrae of more derived sauropod taxa like Tazoudasaurus.

The transverse processes of the anterior-most caudal vertebra are anteroposteriorly narrow, dorsoventrally high and mediolaterally restricted. Although no

obvious cortical bone is preserved at the tips of either transverse process, agreement in the morphology of both processes suggests they were laterally abbreviated, tapering to a sharp termination some several centimetres lateral to the arch itself. In contrast, even the anterior-most caudal vertebrae of most non-sauropodan sauropodomorphs [e.g. Plateosaurus (Huene, 1926)] possess wing-like transverse processes that are laterally flaring and dorsoventrally shallow. It is possible that the lateral restriction of the transverse process in *Pulanesaura* represents either (1) the tapered point of articulation with a narrow sacral or caudal rib that was not subsequently preserved (thus possibly rendering this element a caudosacral) or (2) a response to the space-claiming, expanded sacral rib of the element intermediately anterior to it. Unfortunately, it is difficult to confirm either hypothesis given the material at hand. The marked dorsoventral orientation of the transverse rib, which subsequently crosses the neurocentral suture to terminate ventrally well within the upper half of the centrum, recalls the condition of derived sauropods (e.g. Mamenchisaurus: Ouyang & Ye, 2002; Diplodocus: Hatcher, 1901) and was proposed as a possible synapomorphy of Pulanesaura + Sauropoda by McPhee et al. (2015a). However, the caudal rib of the only anterior caudal vertebra figured for Tazoudasaurus (Allain & Aquesbi, 2008: fig. 16) displays the typical (= plesiomorphic) dorsoventrally shallow condition (see also Haplocanthosaurus: Hatcher, 1903). This suggests that the morphology in *Pulanesaura* is possibly exaggerated due to the preservational/anatomical conditions discussed above, and thus remains only a tentative apomorphy of the genus for now.

Ventral to the postzygapophyses a small yet welldeveloped hyposphene is present. A hyposphene on the neural arches of anterior caudal vertebrae is a derived feature for Sauropodomorpha, being present in specimens of *Melanorosaurus* (SAM-PK 3449), the Heelbo 'vulcanodontid' (BP/1/6105), *Antetonitrus* and Sauropoda (Upchurch, 1998; Yates *et al.*, 2004). The neural canal is sub-circular in shape, being slightly higher than wide. This differs from most nonsauropodan sauropodomorph taxa (e.g. *Aardonyx*; *Antetonitrus*) that range from having essentially circular neural canals in the anterior caudal vertebrae to neural canals that are slightly wider than high.

A large, caudal vertebra from the posterior end of the anterior series is also preserved (BP/1/6201) (Fig. 6E–H). This element is complete with the exception of the dorsal two thirds of the neural spine and the left postzygapophysis, while the ventral margins of the anterior and posterior articular facets of the centrum are poorly preserved. Generally speaking, this vertebra is unremarkable for Sauropodomorpha, documenting the serial lengthening of the centrum relative to its height (height/length ratio = 1.34). It is clear from the preserved morphology that the neural spine displayed the straight, posterodorsally inclined morphology typical of caudal vertebrae. A distinct winnowing of the anterior margin of the neural spine suggests the presence of a keel that probably extended from the dorsal apex of the prespinal fossa to at least halfway up the dorsoventral height of the neural spine. This inference is supported by the presence of a similar process in the anterior-to-middle caudal vertebrae of, for example, *Antetonitrus* and *Eucnemesaurus* (BP/1/6234) as well as a partial mid-caudal vertebra from the same quarry (see below).

The small prespinal fossa is dorsoventrally elongate, being both higher and deeper than mediolaterally wide. This fossa is bracketed from below by a thick shelf of bone that also serves as the dorsal roof of the neural canal.

The transverse processes are mediolaterally extensive, wing-like structures that, as in all sauropodomorphs, slope posterolaterally from their origin at the neurocentral juncture. However, these processes are interesting in that both rise from their bases in a similarly gradual fashion and terminate (although the lateral-most tips are not preserved in either) with a distinct dorsal offset from the horizontal. Although taphonomic processes cannot be ruled out, the dorsally elevated transverse processes of BP/1/6201 possibly distinguishes *Pulanesaura* from most other forms that tend to display more horizontally oriented transverse processes (e.g. *Antetonitrus; Aardonyx;* c.f. *Adeopapposaurus*).

#### Middle caudal vertebra

The middle caudal series is represented by a single, small- to medium-sized vertebra that is missing most of the neural spine, both sets of zygapophyses, and the terminal ends of both transverse processes (BP/1/7741) (Fig. 7A–C). The height of the anterior face of the centrum is 1.16 times its transverse width. This is intermediate between a similarly serially located midcaudal vertebra of *Aardonyx* (1.04: BP/1/6754) and a mid-caudal vertebra referred to *Eucnemesaurus fortis* (1.30: BP/1/6220). A distinct chevron facet is observable on the ventral edge of the posterior articular facet, although it does not appear to have been as well developed as in the ventrally extensive facet in *E. fortis* (BP/1/6220; Yates, 2007b).

As mentioned above, the preserved section of the base of the anterior margin of the neural spine displays a well-defined keel. In contrast to BP/1/6201, the transverse processes of BP/1/7741 appear to have been confluent with the horizontal plane. However, this element shares with the former transverse processes that appear to have tapered to a relatively sharp lateral

termination, as opposed to the more anteroposteriorly rounded condition observed in other sauropodomorph taxa [e.g. *Eucnemesaurus*; *Adeopapposaurus*; *Aardonyx* (BP/1/6754)].

#### Chevron

The one well-preserved chevron (BP/1/6205) is typical for basal sauropodomorphs, displaying much the same proportions as mid-tail chevrons described for, for example, *Antetonitrus* (Fig. 7D, E). The proximal end is transversely expanded relative to the rest of the chevron in anterior view, whereas the element expands slightly ventrally in lateral view. The proximal articular surface is too poorly preserved to determine whether it was a single planar facet or divided longitudinally into two facets as in some chevrons associated with the *Antetonitrus* holotypic assemblage. A raised, median ridge extends for some length of the anterior surface of the shaft, being located mainly within the proximal half of the element.

#### Forelimb and pectoral girdle

The forelimb and pectoral girdle of *Pulanesaura* are represented by a left clavicle, a poorly preserved right humerus, a left ulna and an isolated right metacarpal IV.

#### Clavicle

A single left clavicle is preserved (Fig. 8). Unfortunately, the absence of an associated right clavicle means that it cannot be determined if the clavicles contacted medially in a bracing, furcula-like fashion [as has been suggested for a specimen of *Massospondylus* (BP/1/5241: Yates & Vasconcelos, 2005)] or simply lay along the anterodorsal margin of the acromial region of the scapulocoracoid. The rugose, possibly articular surface of the medial end of the clavicle, offers some evidence that the clavicular pair were arranged in an anteriorly offset, semi-fused manner and that the pectoral girdle in derived sauropodiforms/basal sauropods was therefore relatively immobile (see Yates & Vasconcelos, 2005). However, this cannot be confirmed given the available evidence.

The clavicle is spatula shaped, with a tapered medial end and an expanded, dorsoventrally flattened lateral end. The element is broadly triangular in cross-section, with the apex of the triangle directed dorsally. The ventral surface of the expanded lateral end is heavily striated, suggesting strong ligamentous attachments with the acromial region of the scapula. The clavicle is moderately bow shaped in dorsal view, with the lateral end directed posteriorly with respect to the medial end.



**Figure 7.** A–C, middle caudal vertebra (BP/1/7741) in (A) anterior, (B) posterior and (C) right lateral views. D, E, chevron (BP/1/6205) in (D) anterior and (E) lateral views. Abbreviations: ak, anterior keel; mr, median ridge; tp, transverse process. Scale bars = 5 cm.

Figured representations of clavicles in basal sauropods [e.g. *Shunosaurus* (Zhang, 1988); *Omeisaurus* (He, Kui & Cai, 1988)] suggest that the clavicles in these forms may have been comparatively thinner and possibly straighter, while specimens of *Omeisaurus* may have displayed a more sharply expanded, lanceolate distal end of the clavicle (Dong, Zhou & Zhang, 1983). However, the level of available information pertaining to the morphology of the clavicle in other, phylogenetically relevant sauropodiforms precludes a full comparative assessment of the clavicle in *Pulanesaura*.

# Humerus

The single right humerus (BP/1/6193) is very poorly preserved, especially in regards to the proximal end (Fig. 9). Both the humeral head and most of the

deltopectoral crest are absent, while only the left condyle of the distal end is preserved in its entirety. While this unfortunately limits the degree of functional and phylogenetic information that can be drawn from this important appendicular bone, the observable morphology is nonetheless suggestive. Overall, the preserved portion of the humerus in Pulanesaura is consistent with a sauropod-like 'columnarization' of the element. Although the absence of the proximal portions may be exaggerating the relative length of the shaft, the segment of the shaft distal to the deltopectoral projection still appears relatively elongate compared to most basal sauropodomorphs (e.g. *Massospondylus*; Antetonitrus), potentially extending to over half the preserved length of the humerus. As in the basal sauropods Tazoudasaurus and Vulcanodon, the transverse expansion of the distal condyles is not particularly



Figure 8. Left clavicle (BP/1/6752) in (A) dorsal, (B) ventral, (C) posterior and (D) anterior views. Scale bar = 5 cm.

marked, while the deep cuboid fossa observed on the anterior face of the distal humerus in all known nonsauropodan sauropodomorphs does not appear to have been present. This suggests that effective flexion of the elbow did not play a pronounced role in the locomotory/functional suite of *Pulanesaura* (see Discussion). Unfortunately, the lack of a well-preserved proximal end precludes assessment of the degree of deflection of the distal condyles relative to the humeral head [which is reduced in sauropods (Remes, 2008)], although the preserved morphology suggests that it was not particularly pronounced.

The posterior surface of the distal end (= olecranon fossa) is flat-to-shallowly concave, similar to – if slightly reduced – most non-eusauropodan sauropodomorphs.

# Ulna

The left ulna (BP/1/6210) is incompletely preserved, lacking the articular surface of the proximal end, the anterior portion of the anterior process and sections of the periosteal surface of the distal end (Fig. 10). Nonetheless, much of the relevant morphology can still be discerned.

The ulna is of the same general size (albeit of slightly more delicate build) as the large pair of ulnae preserved within the *Antetonitrus* holotypic assemblage (BP/1/4952). As the majority of the *Pulanesaura* elements tend to be slightly smaller than those of the

comparably more robust *Antetonitrus*, it is possible that this size equivalence represents a sauropod-like elongation of the antebrachial elements in *Pulanesaura*. However, in the absence of articulated remains, this possibility remains purely speculative.

The proximal surface of the ulna of Pulanesaura can be distinguished from that of Antetonitrus (McPhee et al., 2014) with respect to the morphology of both the medial and lateral processes. The lateral process of the proximal ulna in *Pulanesaura* is a thinly walled, laterally extensive process that may have been even more developed than is currently suggested by the preserved morphology. In contrast, the lateral process of Antetonitrus, while certainly more laterally extensive than the weakly developed equivalent of more basal sauropodomorphs (e.g. Plateosaurus; *Massospondylus*), is only moderately more developed than the medial process, while being also anteroposteriorly stouter than the same process in Pulanesaura. As a result, the radial fossa of *Pulanesaura* is appreciably deeper mediolaterally than the same process in either Antetonitrus or Aardonyx. This is possibly suggestive of a more 'sauropodan' antibrachial posture in Pulanesaura (see Bonnan, 2003; Bonnan & Senter, 2007; Bonnan & Yates, 2007).

The medial process of the proximal ulna of *Pulanesaura* is distinct in being a well-defined strut of bone that rises from about the mid-height of the shaft, appearing increasingly anteroposteriorly narrow towards its apex.

This differs from the condition observed in *Antetonitrus* in which the medial process is an obtusely delineated ridge of bone that is thicker anteroposteriorly than laterally. *Aardonyx* (BP/1/5379) is interesting in possessing a medial process that is more developed than the lateral process in all linear dimensions. A right ulna located within the syntype assemblage of *Melanorosaurus* 



**Figure 9.** Right humerus (BP/1/6193) in (A) anterior, (B) posterior and (C) lateral views. Abbreviation: dpc, deltopectoral crest. Scale bar = 5 cm.

(SAM-PK 3449) also displays a sharply tapered medial process potentially similar to the non-eroded condition of Pulanesaura. However, in Pulanesaura, the angle between the medial and anterior processes is considerably more acute than in any of the above comparative taxa, ostensibly as a result of the medial-wise migration of the anterior process. Although it is tempting to view this as a mechanically regulated shift towards a more anteriorly cradled proximal radius (i.e. the sauropodan condition), it is possible that this morphology may have been augmented by taphonomic deformation. Unfortunately, the poor condition of the proximal articular surface precludes any assessment of whether the olecranon process in *Pulanesaura* was well developed as in non-sauropodan sauropodomorphs or reduced as in basal sauropod taxa such as Vulcanodon. The absence of the proximal half of the anterior process also means that it cannot be confirmed if Pulanesaura displayed the same medial deflection of the anteroproximal end of the anterior process as in Antetonitrus (McPhee et al., 2014).

Although taphonomically distorted, it is clear that the shaft was mediolaterally compressed as in other sauropodomorph taxa. The poor condition of the distal end precludes a detailed assessment of its orientation to the rest of the element, although a pronounced, proximodistally elongate radial-ligament scar can be seen on the anterolateral corner of the bone several centimetres proximal to the distal surface. The distal end of the ulna in *Pulanesaura* appears to have lacked the distinct medially directed bowing observed in the distal ulnae of specimens of *Melanorosaurus* (Bonnan & Yates, 2007 and to a lesser extent in *Antetonitrus*), although preservation again renders this observation tentative.



**Figure 10.** Left ulna (BP/1/6210) in (A) anterior, (B) posterior, (C) lateral, (D) medial and (E) proximal views. Abbreviations: ap, anterior process; lp, lateral process; mr, medial ridge; rf, radial fossa. Scale bars = 5 cm.

#### Metacarpal IV

The manus is represented by a single metacarpal that is here tentatively identified as the right metacarpal IV (Fig. 11). This interpretation is based on the triangular shape of the proximal end (the proximal end of the second metacarpal is generally sub-trapazoidal in shape in most non-eusauropodan sauropodomorphs) and the comparatively stout proportions of the shaft (the shaft of metacarpal III is proportionally elongate in most non-eusauropodan sauropodomorphs).

The triangular proximal end is broadest on the ventral margin, while the medial and lateral sides are subequal in length. Due to the slight concavity of the medial margin, the medioventral corner of the proximal edge is the most acute, although no corner displays the rounded, obtuse morphology observed on the dorsal (= dorsomedial) corner of the fourth metacarpal in basal sauropodomorph taxa such as *Mussaurus* and *Plateosaurus* (Huene, 1926; Otero & Pol, 2013). There is no evidence for an *Antetonitrus*-like tubercle on the ventrolateral corner of the shaft just below the proximal end (McPhee *et al.*, 2014), although that character is typically restricted to the second metacarpal.

Both the ventral and lateral margins are straight. Measured at its mediolaterally widest point, the proximal end is 0.68 times the total proximodistal length of the bone. This compares with a ratio of, for example, 0.39 in Mussaurus (Otero & Pol, 2013) and ~0.35 in Plateosaurus (measured from Huene, 1926: table 4, fig. 5), consistent with the semi-stout, possibly loadresisting morphology of the manus of many sauropodiform taxa [e.g. Melanorosaurus: 0.60 (NMQR 3314); see also Remes, 2008; McPhee et al., 2014]. In contrast, basal sauropod taxa such as *Tazoudasaurus* display a proportionally longer fourth metacarpal (0.55: Allain & Aquesbi, 2008: table 4), a reversal (with respect to current phylogenetic hypotheses) that possibly represents a functional intermediary to the semi-tubular colonnade of Neosauropoda.

The shaft tapers mediolaterally towards the distal end and is triangular in cross-section, consistent with the morphology of the proximal end. The distal articular ginglymus is not divided into clearly differentiated condyles, although the ventrolateral corner of the distal end extends laterally as a well-defined protuberance of bone. A similar morphology is observed in the



**Figure 11.** Right metacarpal IV (BP/1/6191) in (A) dorsal, (B) ventral, (C) medial, (D) lateral and (E) proximal views. Scale bar = 2 cm.

distal end of the fourth metacarpal of other sauropodomorph taxa (e.g. *Plateosaurus*; *Mussaurus*). The collateral ligament pits are present as weakly developed, shallow fossae.

#### Ischium

There are three ischia (BP/1/6184, 6202, 7366) present among the assemblage, all being of the same essential size-class. It is probable that BP/1/6184 and BP/1/7366, the former being of the left side and the latter of the right, pertained to the same individual. The following description will focus on the two right ischia (BP/1/6202, 7366) as they are the most complete (with the exception of the pelvic articular surfaces and the distal-most end of both ischial blades).

The ischium of *Pulanesaura* is a proximodistally long, slender element that, measured at its greatest preserved proximodistal length, is c. 2.4 times longer than the maximum preserved dorsoventral breadth of the proximal plate (Fig. 12). Although incomplete, this is similar, if not slightly longer than the same metric in a number of non-eusauropodan sauropodomorphs (e.g. Eucnemesaurus entaxonis; Massospondylus). Unfortunately, no pubis is present with which to assess if the pubic apron in Pulanesaura had undergone a sauropod-like reduction in length relative to the ischium (Upchurch et al., 2004; Remes et al., 2009). As in most non-eusauropod sauropodomorphs, the anteroventral margin of the proximal ischial plate is gently medially concave and thinly laminar, in contrast to the more mediolaterally robust dorsoventral margin. Pulanesaura does not appear to have displayed the 'notch' between the ventrodistal corner of the proximal



**Figure 12.** Right ischium (BP/1/7366) in (A) lateral, (B) dorsal and (C) medial views. Abbreviations: ac, acetabulum; de, distal expansion; ds, dorsal sulcus. Scale bar = 10 cm.

plate and the ischial shaft that has been described in specimens of *Plateosaurus* (Yates 2003b) and a referred element of *Riojasaurus* (Bonaparte, 1971). However, the general subtlety of this feature, along with its undoubted sensitivity to taphonomic alteration (the ischium tending to be at its thinnest at that point), cautions against suggestions of homology (note that the original character pertaining to this feature has been removed in the current analysis, see below). The ischial contribution to the posteroventral corner of the acetabulum is well preserved between the iliac and pubic peduncles. This surface is present laterally as a thickly rounded wall of bone that slopes proximomedially towards the more acute, finely rimmed medial wall of the acetabulum.

The dorsolateral surface of the ischial blade bears a pronounced groove that extends along the proximal third of its length. This groove is common throughout Saurischia and probably represents the proximal insertion point of the adductores femores musculature (Carrano & Hutchinson, 2002). As in the majority of non-neosauropodan sauropodomorphs, the ischial shaft is triangular in cross-section with a dorsoventrally expanded distal end. There is some disagreement in the shape of the ischial blades between BP/1/6202 and BP/1/7366, with the former being transversely thick posterodorsally and transversely thin anteroventrally, whereas the latter is broadest along the medial symphysis with the apex of the triangle directed entirely laterally. This discrepancy is interpreted here as taphonomic flattening in the case of BP/1/6202 (which can also be seen in the marked flattening of the poorly preserved distal end). Although missing its distal terminus the distal end of BP/1/7366, based on the shaft morphology, is likely to have been subtriangular in cross-section, and probably wider along its mediolateral axis than dorsoventrally. The distally expanded, subtriangular ishcium of Pulanesaura distinguishes it from more derived sauropods (e.g. Patagosaurus; Neosauropoda) that tend to display dorsoventrally flattended, blade-like ishchial shafts (Wilson & Sereno, 1998). The distal ischium of *Pulanesaura* appears to have maintained a relatively straight sagittal axis, lacking either the anteroventral or posterodorsal deflection seen in a number of basal sauropodomorph forms [e.g. Coloradisaurus; Massospondylus; E. entaxonis (McPhee et al., 2015b)].

#### Tibia

There are two tibiae present within the assemblage, a left (BP/1/6200) and a right (BP/1/6980) (Fig. 13). As both agree in size, it is possible that they are from the same individual. In this respect, the differences in the distal articular surfaces between the two [the distal end of BP/1/6980 is mediolaterally compressed with a



**Figure 13.** A–F, left tibia (BP/1/6200) in (A) anterior, (B) posterior, (C) lateral, (D) medial, (E) proximal and (F) distal views. G–L, right tibia (BP/1/6980) in (G) anterior, (H) posterior, (I) lateral, (J) medial, (K) proximal and (L) distal views. Abbreviations: cc, cnemial crest; ap, ascending process; dp, descending process. Scale bar = 10 cm.

more anteriorly positioned anterior ascending process (= astragalar articular facet)] are probably attributable to taphonomic processes.

In general morphology, the tibia of *Pulanesaura* is markedly similar to that of *Antetonitrus*, with the distinction of being generally less robust. Consistent with the morphology observed in *Antetonitrus*, *Vulcanodon* and *Tazoudasaurus*, the proximal articular surface of the tibia in *Pulanesaura* is over twice as long anterposteriorly as it is transversely wide. In BP/1/6200 (for which the proximal surface is the better preserved of the two), the anteroposterior length of the proximal surface is 2.06 times the transverse width. This compares with a metric of 1.97 for *Antetonitrus* and 2.61 for *Tazoudasaurus* (Allain & Aquesbi, 2008: table 6). In contrast, the majority of non-sauropodan sauropodomorphs (e.g. *Plateosauravus*; *Coloradisaurus*; *Lessemsaurus*) display subtriangular proximal tibiae in which the anteroposterior length is roughly 1.3–1.6 times the transverse width.

Consistent with the derived condition (for basal Sauropoda), the anteroposterior length of the proximal articular surface is approximately half the proximodistal length of the bone (see Ezcurra & Apaldetti, 2012; McPhee et al., 2014). As in Antetonitrus and more derived sauropodiformes, the proximal articular surface is relatively flat with respect to the horizontal plane, lacking the anterodorsal incline of the proximal surface seen in more basal forms (e.g. Massospondylus; Mussaurus; Blikanasaurus). Nonetheless, the cnemial crest of *Pulanesaura* retains the plesiomorphic condition for Sauropodomorpha insofar as the anterior-most projection of the crest also represents the highest proximal point of the tibia. In the basal sauropods Vulcanodon, Tazoudasaurus and Spinophorosaurus, the anteriormost projection of the cnemial crest sits roughly at the

proximodistal midpoint of the process. The cnemial crest is a stout flange of bone that is directed mainly anteriorly and slightly laterally, as in most non-eusauropodan sauropodomorphs (e.g. Melanorosaurus; Antetonitrus; *Vulcanodon*). Posterior to the cnemial crest, on the proximolateral side of the shaft, there is a slight rugose concavity [erroneously described as a 'convex' depression in McPhee et al. (2014)] that would have facilitated the various ligamentous attachments associated with the proximal fibula. Pulanesaura appears to have lacked the distinct notch ('lateral sulcus') between the cnemial crest and proximal lateral condyle observed in Antetonitrus. The lateral condyle is more proximally developed than the medial condyle, the latter of which does not appear to have been particularly prominent on either tibia. The lateral condyle is cantered slightly posterior to the anteroposterior midpoint of the proximal surface, as opposed to the relatively more anterior placement of the lateral condyle in Antetonitrus. This results in a concomitantly less expansive posterior margin of the proximal surface in Pulanesaura than in the former taxon. Furthermore, the lateral condyle does not overhang the tibial shaft to the same lateral extent as that observed in Eucnemesaurus (Yates, 2007b; McPhee et al., 2015b).

Consistent with the dimensions of the proximal surface, the midshaft is deepest along the anteroposterior axis, with the anteroposterior depth being 1.72 times the transverse width. While this falls considerably short of the highly compressed tibial midshaft of *Tazoudasaurus* [2.75: To1-380; 1.91: To1-76 (Allain & Aquesbi, 2008: table 6)], it is nonetheless greater than the same metric in *Antetonitrus* (1.43) and greater still than the sub-circular morphology observed in most non-sauropodan sauropodomorphs.

The distal end is mediolaterally expanded with respect to the shaft, although not to the extent observed

in Tazoudasaurus. The morphology of the distal tibia is similar to that of Antetonitrus in being roughly subtriangular with an anterolaterally directed anterior ascending process. This differs from the condition of most non-sauropodan sauropodomorphs in which the distal articular surface is transversely rectangular in shape with a more laterally positioned anterior ascending process. Although incomplete in BP/1/6200 and moderately distorted in BP/1/6980, it is clear that the posterior descending process did not extend as far laterally as the anterior ascending process (rendering the latter visible in posterior view). This feature, once hypothesized as a synapomorphy of Sauropoda (e.g. Yates, 2004), is now known to have a wider distribution among Sauropodomorpha (e.g. E. entaxonis; Mussaurus; Aardonyx). The distal surface of the shaft medial to the anterior ascending process in gently concave.

# First pedal ungual

The pes of *Pulanesaura* is currently represented by two first pedal unguals. BP/1/6186 is tentatively assigned to the left foot (Fig. 14A–D), while BP/1/6983 (which preserves only the proximal articular portion) is potentially from the right side of the same individual (Fig. 14E, F). BP/1/6186, in being essentially complete, will form the focus of the following description.

Pedal ungual I in *Pulanesaura* is a mediolaterally compressed, ventrally recurved element that bears greater morphological similarity to the first pedal ungual of the basal sauropods *Vulcanodon* and *Tazoudasaurus* than it does to the dorsoventrally squat first pedal unguals of derived non-sauropod sauropodiform taxa such as *Antetonitrus* and *Blikanasaurus*.

The concave proximal articular surface is high and ovoid with sub-parallel sides. This surface is divided



**Figure 14.** First pedal unguals. A–D, BP/1/6186 in (A) medial, (B) lateral, (C) proximal and (D) dorsal views. E, F, BP/1/6983 in (E) lateral and (F) proximal views. Scale bar = 2 cm.

into two distinct articular facets, with the lateral facet being larger and more distally receded than the medial. Separating these two facets is a sharp, longitudinal ridge that runs from the overhanging, proximodorsal lip to the moderately developed flexor tubercle. As in Vulcanodon, the base of this tubercle is ventrally convex (in proximal view), contrasting with the ventrally flat proximal surface of a number of non-sauropodan sauropodomorphs [e.g. Massospondylus (BP/1/4377); Mussaurus; Aardonyx]. Both the proximodorsal lip and the flexor tubercle extend proximally to an equal degree, differing from Aardonyx and Antetonitrus in which the proximodorsal lip clearly exceeds the flexor tubercle in proximal extent. Measured at its widest mediolateral point, the proximal articular surface is 0.58 times its dorsoventral height. This value is lower than in any other currently recognized Elliot taxon (i.e. Aardonyx: 0.71; Blikanasaurus: 0.84; Antetonitrus: 0.94) with the possible exception of Massospondylus, which retains the plesiomorphic condition of also having a relatively mediolaterally compressed first pedal ungual (albeit with a flat proximal base).

As in most sauropodomorphs, the medioventral edge of the shaft forms a sharper angle than the lateroventral, while the medial surface is flat-to-shallowly concave compared to the convex lateral surface. The degree of ventral curvature along the sagittal axis is less marked than in most basal sauropodomorph taxa (e.g. Plateosaurus; Massospondylus; Mussaurus), and more similar to the broadly arched morphology observed in derived sauropodiform taxa [e.g. Antetonitrus; Vulcanodon; Omeisaurus (He et al., 1988)]. Nutrient grooves are visible on both the medial and the ventral surfaces of the ungual, extending from the proximoventral corner of the shaft in concert with the general curvature of the element. Interestingly, the groove on the medial surface follows a much more ventral course than the lateral groove, which appears to rise to just shy of the dorsal margin of the shaft of the ungual. The tip is bluntly pointed in the manner typical of derived sauropodiforms.

#### DISCUSSION

#### PHYLOGENETIC ANALYSES AND THE INTERRELATIONSHIPS OF *PULANESAURA*

The phylogenetic relationships of *Pulanesaura* were explored in-depth in McPhee *et al.* (2015a). However, for the purposes of the current discussion, the analysis was repeated with the following modifications to the character-by-taxon matrix used in the previous study: the newly described *Xingxiulong* (Wang, You & Wang, 2017) from the Early Jurassic of China (Lufeng Formation) was included; *Sarahsaurus* was reincluded (see McPhee *et al.*, 2014) with modified scorings based on Marsh (2013) and personal observation of both the holotype and paratype by K. J. Chapelle (pers. comm.); Melanorosaurus was treated as two separate OTUs (NMQR 3314 and NMQR 1551) as per McPhee et al. (2017); and scorings for Riojasaurus were restricted to information available within the holotype [PVL 3808 (Bonaparte, 1971); B.W.M., pers. observ.]. The latter decision is justified on the grounds that previous scorings for *Riojasaurus*, particularly those pertaining to the cranial anatomy, were heavily augmented via the referred specimen PULR 56 (Bonaparte & Pumares, 1995). However, this specimen differs from the holotype in the following respects: transverse width of the distal condules of the humerus 0.44 times the total length of the bone in PVL 3808 vs. 0.32 in PULR 56; tibia:femur ratio 0.85 in PVL 3808 vs. 0.67 in PULR 56; and pubes shorter than tibiae in PVL 3808 vs. the opposite condition in PULR 56 [see also comments by Bonaparte (1999) regarding differences in the proportions of the dorsal vertebrae between the two specimens]. This suggests PULR 56 is not referable to Riojasaurus qua PVL 3808.

Finally, an additional character (ch. 134) has been added to the matrix, based on the observations in McPhee *et al.* (2015a: fig. 4): orientation of the anteriorto-middle cervical postzygapophyses: planar (minimally offset) with respect to the prezygapophyses [0]; dorsally raised roughly 20° relative to the coronal plane [1]; and dorsally raised at least 30° or more relative to the coronal plane [2] (ordered). A state was also added to the characters pertaining to the length:height ratio of the anterior-most caudal centra (185) and the depth of the radial fossa of the ulna (ch. 218) in order to attempt to homologize the greater degree of variation present in those structures (see matrix in supplementary material).

The resulting strict consensus tree [18 most parsimonious trees; 1292 steps; consistency index: 0.334; retention index: 0.699; recovered via a heuristic search of 1000 replicates of Wagner trees followed by TBR branch swapping with ten trees saved per replication in TNT 1.5 (Goloboff & Catalano, 2016)] is roughly congruent with previously published topologies (e.g. Apaldetti et al., 2012; Otero & Pol, 2013; McPhee et al., 2015b). A notable exception is the sauropodiform (sensu McPhee et al., 2014) position for the holotype of Riojasaurus (PVL 3808) (Fig. 15). However, we stress the provisional nature of this result, with major revisions to this matrix planned for a more in-depth treatment of basal sauropodomorph phylogenetics in the future. Nonetheless, the position of *Pulanesaura* within this topology appears relatively robust and is supported by the same (both unambiguous and ambiguous) characters enumerated in McPhee et al. (2015a). The additional character outlined above (scored '1' in Pulanesaura) also provides tentative support for a close relationship to Sauropoda; however, the unknown morphology of the cervical series in taxa immediately peripheral to Pulanesaura [e.g. Gongxianosaurus (now potentially lost for good: Xing *et al.*, 2017) and *Vulcanodon*] means that the polarity of this character remains ambiguous for the time being. In the original analysis, it was suggested that these features supported a sauropodan affinity for *Pulanesaura*, an interpretation given further rationale based on hypothesized palaeoecological links between this taxon and Sauropoda (McPhee *et al.*, 2015a). However, a sauropodan relationship for *Pulanesaura* is only reflected within one of the currently cited definitions of Sauropoda (see below), whereas an alternative definition places *Pulanesaura* as sister to Sauropoda

(Fig. 15). Here we suggest that the latter definition currently represents the more cogent reflection of our understanding of the basal divergence of Sauropoda and argue for its continued use, a position justified with respect to the following discussion.

#### SAUROPODA: DEFINITION AND DIAGNOSIS

Although both the defining attributes and suborderlevel classification of Sauropoda have a long history (Marsh, 1878; see reviews in Upchurch *et al.*, 2004;



**Figure 15.** Abbreviated (beginning at the basal-most node for Sauropodomorpha) strict consensus tree of the current analysis. Modified from McPhee *et al.* (2015a) with the additions/alterations mentioned in the text. Circles indicate the relative proportions of the first metatarsal: maximum proximal breadth 0.4 times or less its proximodistal length (open); maximum proximal breadth between 0.4 and 0.7 times its proximodistal length (half-open); maximum proximal breadth greater than 0.7 times its proximodistal length (closed). Dashed lines represent Sauropoda *sensu* the most inclusive clade not including *Melanorosaurus*' (NMQR 1551 and 3314); grey square represents Sauropoda *sensu* the least inclusive clade containing *Vulcanodon* and *Saltasaurus* (preferred definition).

Wilson, 2005a; Wilson & Curry Rogers, 2012), most recent definitions of the group follow (reflexively or otherwise) phylogenetic nomenclatural conventions (e.g. de Queiroz & Gauthier, 1990, 1994; Sereno, 1999a, 2005; Cantino & de Queiroz, 2010) whereby the boundary relationships of higher taxa are set via the naming of deliberately allocated taxonomic specifiers - either internally (for node-based groupings) or internallyexternally (for stem-based groupings) - within a cladistical framework. Wilson & Sereno (1998; see also Sereno, 1999b) proposed the first popularly cited (stembased) phylogenetic definition of Sauropoda as all taxa more closely related to Saltasaurus than Plateosaurus, a definition that assumed the mutual monophyly of 'Prosauropoda' and Sauropoda (e.g. Benton et al., 2000; Galton & Upchurch, 2004). However, subsequent taxonomic revision, progressive refinement and expansion of cladistic data matrices, and additional fossil sampling over the intervening years has resulted in the consensus that 'prosauropods' are paraphyletic with respect to Sauropoda (Yates, 2003a, 2007a; Upchurch et al., 2007a; Pol et al., 2011; although see Peyre de Fabrègues, Allain & Barriel, 2015). Recognizing that 'prosauropod' paraphyly expanded the constituency of Sauropoda to include a number of forms never traditionally regarded as sauropods (e.g. Massospondylus), Yates (2007a, b) introduced a modified stem-based definition intended to restrict Sauropoda to a more apical grouping within the expanding sauropodomorph stem: the most inclusive clade containing Saltasaurus but not Melanorosaurus.

The primary rationale behind this definition was that it represented the 'clade of specialised gigantic quadrupeds that form the traditional Sauropoda' (Yates, 2007b: 12) and hence was consistent with Marsh's (1878) initial diagnosis of the group (see Wilson, 2005a). This interpretation was further parsed into specific appendicular modifications associated with the adoption of a columnar limb stance and graviportal locomotory style by Yates et al. (2010; see below). Although we have no issue with the underlying motivations behind this definition, we locate two specific problems with it: (1) the validity of *Melanorosaurs* is currently in serious doubt (McPhee et al., 2015b, 2017) and (2) the sauropodan affinity of several taxa hypothesized to be more derived than *Melanorosaurus* (e.g. Antetonitrus) has been questioned on the grounds of both discrete character information and inferred locomotory specializations (Carrano, 2005; Wilson, 2005b; McPhee et al., 2014, 2015a). For this reason, some workers have recently opted for the older, more conservative nodebased definition of Sauropoda introduced by Salgado, Coria & Calvo (1997): the least inclusive clade containing Vulcanodon and Eusauropoda (or Saltasaurus in more recent variants) (Langer et al., 2010; McPhee et al., 2014; Peyre de Fabrègues et al., 2015).

Although relatively fragmentary (i.e. information from both the cranium and pre-sacral axial series is missing entirely), and known primarily from a single monographic treatment published over 30 years ago (Cooper, 1984), the Pliensbachian–Toarcian age (Yates et al., 2004) Vulcanodon nonetheless shares with all later sauropods an unambiguous suite of features associated with the adoption of a fully columnar forelimb posture and the attendant shift to an obligately quadrupedal gait (Upchurch, 1998; Wilson & Sereno, 1998; Wilson, 2002; Upchurch et al., 2004; see below). Nonetheless, several of these features have been ascribed to taxa located at nodes basal to Vulcanodon (see, e.g., Yates & Kitching, 2003; Pol & Powell, 2007; Yates, 2007b; Otero & Pol, 2013; McPhee et al., 2014). As columnar-limbed graviportalism (excluding for now the accessory requirement of gigantic size) appears to represent an uncontroversial defining criterion of Sauropoda, there remains the possibility that Sauropoda thusly understood is potentially more inclusive than implied by the current node-based (sensu Salgado et al., 1997) definition. Discussion of the characters most germane to the recent formulation of sauropod ingroup hypotheses is given below and follows primarily those features given explicit mention in Yates et al. (2010).

# Elongation of the forelimb relative to the hindlimb (humerus:femur ratio > 0.8)

The humerus-to-femur length ratio is variable throughout Sauropodomorpha, ranging from ~0.60 in 'typical' 'prosauropod' genera like *Plateosaurus* (Rauhut et al., 2011) and Lufengosaurus (IVPP V15) to closer to ~0.77 in putative sauropodiform taxa such as Riojasaurus (PVL 3808) and 'Melanorosaurus' (NMQR 3314) (a similar metric is also observed in the possibly more basal *Plateosauravus*). Although this metric becomes fixed towards the larger end of the range within Sauropoda [estimated value of ~0.65 in *Vulcanodon* (Cooper, 1984)], it very rarely exceeds 0.8 and is potentially as low as 0.6 in the basal eusauropod Shunosaurus (Rauhut et al., 2011: table 8.1; see McPhee et al., 2014: fig. 25). This cautions against overemphasis of this specific humeral metric, especially when treated independent of character data that potentially has a closer functional and/or homologous link with the suite of forelimb novelties currently optimizing at the base of Sauropoda s.s. (e.g. loss of the cuboid fossa; concomitant reduction the deltopectoral crest and medial tuberosity of the humerus; reduction in the transverse width of the distal condyles relative to humeral length: Table 2). Nonetheless, as the relative elongation of the antebrachium and a concomitant shortening of the epipodium appear to

Feature/morpheme	Character representation (not comprehensive)	Notes/distribution
Glenoid		
Anteroventral rotation thereof	No explicit homology hypothesis	Occurs in all known sauropods, although is inade- quately preserved in all early branching sauro- pods ( <i>Isanosaurus</i> , <i>Vulcanodon</i> , <i>Tazoudasaurus</i> ). See Remes (2008) for further discussion.
Humerus Elengation relative to	Couthing 1086. Upshursh at al. 2007.	The humanic formur ratio (and/or forelimb)
femur	Yates, 2007a	hindlimb) is generally held to increase at the base of Sauropoda. However, this is less straight- forward than generally appreciated. See text for details.
Medial tuberosity (proximomedial corner of humeral head) reduced	No explicit homology hypothesis	Reduced in 'near sauropods' like Antetonitrus and Lessemsaurus. Condition unknown in Pulanesaura and Vulcanodon. Highly reduced- to-absent in Tazoudasaurus, Kotasaurus and all later sauropods.
Reduction of deltopectoral crest	Wilson & Sereno, 1998; Sereno, 1999b; Wilson, 2002; Upchurch <i>et al.</i> , 2007; Yates, 2007a	The deltopectoral crest is a complex structure in Sauropodomorpha, displaying a range of condi- tions of uncertain homology and interdepend- ence: Although the sigmoid curvature is lost in several taxa basal to Sauropoda (e.g. Antetonitrus, Leonerasaurus), strong reduction of the struc- ture appears to be exclusive to Sauropoda s.s. Restricted to the proximal half of the humerus in all sauropods, this condition is also observed in some non-sauropod taxa (e.g. Plateosauravus and Adeoppaposaurus) and the 'near-sauropod' Leonerasaurus. Very poorly preserved in key basal taxa like Vulcanodon and Pulanesaura.
Transverse narrowing of distal condyles	Yates & Kitching, 2003; Upchurch <i>et al.</i> , 2007; Yates, 2007a	A humerus with distal condyles transversely expanded 0.33 times or more the total length of the bone was previously considered synapomor- phic for the traditional 'Prosauropoda'. Although all sauropods display a ratio that falls below this value, the same also applies for some non- sauropod taxa (e.g. <i>Plateosaurus</i> ; NMQR 3314: ' <i>Melanorosaurus</i> '). The condition in <i>Vulcanodon</i> and <i>Pulanesaura</i> is ambiguous
Loss of the cuboid fossa (inter-condylar fossa)	Ibid.	Potentially reduced in <i>Pulanesaura</i> and <i>Lamplughsaura</i> . Absent in all known sauropods, although the condition in <i>Kotasaurus</i> is uncertain.
Antebrachium		
Elongation of radius and ulna	Yates & Kitching, 2003; Galton & Upchurch, 2004; Upchurch <i>et al.</i> , 2007; Yates, 2007a	A radius/ulna that is ~0.6 the length of the humerus is plesiomorphic for Sauropodomorpha (e.g. <i>Riojasaurus</i> , <i>Antetonitrus</i> ). Although <i>Vulcanodon</i> and <i>Kotasaurus</i> have been recon- structed with ratios of ~0.9, <i>Tazoudasaurus</i> and <i>Mamenchisaurus</i> display values closer to 0.7.

Table 2. Features/sub-characters of greatest relevance to the parasagittal forelimb 'complex'

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Feature/morpheme	Character representation (not comprehensive)	Notes/distribution
		Inter-element ratios aside, the maximum proxi- mal breadth of the sauropod ulna is ~0.3 times its overall length ( <i>Kotasaurus</i> , <i>Sanpasaurus</i> ), vs. ~0.4 in non-sauropodan taxa (e.g. <i>Massospondylus</i> , <i>Aardonyx</i> ).
Deep radial fossa (proximal ulna)	Wilson & Sereno, 1998; Yates & Kitching, 2003; Upchurch <i>et al.</i> , 2007; Yates, 2007a	Shallowly developed in a number of basal sauropo- diform taxa (see text), possibly more developed in <i>Pulanesaura</i> . A deep fossa is currently present only in <i>Vulcanodon</i> and more derived sauropods.
Loss of olecranon pro- cess of ulna	Upchurch, 1998; Wilson & Sereno, 1998; Yates, 2007a	Condition unknown in <i>Pulanesaura</i> . Characterizes all sauropods (although secondarily reacquired in some titanosaurs).
Manus Shortening of the manus	Sereno <i>et al.</i> , 1993; Yates & Kitching, 2003; Upchurch <i>et al.</i> , 2007; Yates, 2007a	Ambiguous, generally phrased as the length of the entire hand compared to the humerus + radius. A major issue is the lack of explicit measurement criteria (e.g. is it taken from whichever digit is longest, and must both phalanges and distal carpals be considered?). Although the rarity of complete hands further limits the usefulness of this character, the evolution of the sauropodo- morph manus is generally considered to entail the stepwise shortening of the structure relative to the rest of the limb, undoubtedly related to general phalangeal reduction. See also below.
Elongation of the first metacarpal	Sereno, 1999b; Yates & Kitching, 2003; Upchurch <i>et al.</i> , 2007; Yates, 2007a	Of uncertain relation to the above, this feature has a complex distribution within early sauropodo- morphs. Primitive sauropodomorphs display a proximal breadth/total length ratio of roughly 0.6–0.8 (e.g. <i>Plateosaurus</i> ). In 'near-sauropod' taxa like <i>Antetonitrus</i> and <i>Lessemsaurus</i> , the first met- acarpal is extremely stout, being wider proximally than long. However, <i>Tazoudasaurus</i> displays a ratio that falls within the plesiomorphic range, suggesting an early sauropod 'reversal'. The frag- mentary surviving information for the manus of <i>Vulcanodon</i> also suggests that overall lengthen- ing of the metacarpus occurred early in sauropod evolution (see Remes, 2008: fig. 8-8).

#### Table 2. Continued

Sauropoda follows the preferred definition herein. See Table 1 for taxon references.

characterize the sauropodomorph-sauropod transition (McPhee *et al.*, 2014), it is plausible that a general increase in the relative length of the forelimb to the hindlimb represents a legitimate synapomorphy of the latter (Wilson, 2005a: table 1.2). However, the absence of well-preserved, associated appendicular skeletons in a number of key taxa (e.g. *Pulanesaura*, *Tazoudasaurus*) obscures a better understanding of this transition (also cf. the plesiomorphically elongate epipodium of *Lamplughsaura*).

# Development of a large lateral process (i.e. radial fossa) on the proximal end of the ulna

Several recent studies have stressed the phylogenetic and functional significance of the radial fossa of the ulna (i.e. the deep recess on the anterolateral corner of the proximal ulna formed of the forking anterior and lateral processes; Wilson & Sereno, 1998; Bonnan, 2003; Yates & Kitching, 2003; Bonnan & Yates, 2007). Whereas this feature would have been of clear utility in bracing the radius of a large, columnar-limbed

quadruped, the condition observed in all 'prosauropods' is measurably less pronounced than the characteristic tri-radiate morphology of eusauropods (McPhee et al., 2014: fig. 26). Although modestly developed in some 'near-sauropod' taxa (e.g. Aardonyx; Antetonitrus), the radial fossa is generally no more than a shallow depression in the majority of taxa basal to Pulanesaura (McPhee et al., 2015a). Whereas this may simply represent the incipient stages of the derived condition, a shallow radial fossa is also observed in some taxa for whom a habitually bipedal posture has been inferred [e.g. Aardonyx (Yates et al., 2010); Mussaurus; see Otero & Pol (2013) for further discussion]. It is possible, therefore, that the apomorphic manifestation of this feature is conditional upon the development of other forelimb novelties that are generally considered as robust indicators of a more parasagittal stance (i.e. reduced lateral flexion of the elbow, loss of the olecranon process; relative elongation of the radius/ulna; see Remes, 2008; Table 2). In this respect, the incipient presence of a shallow radial fossa in some 'nearsauropods' provides tentative evidence for a grade of facultative-habitual quadrupedality in an animal for which the forelimb architecture remained largely plesiomorphic.

# Increase in the number of sacral vertebrae from three to at least four

A long-standing synapomorphy of Sauropoda (Upchurch, 1998; Wilson & Sereno, 1998; Wilson, 2002), the presence of four sacral vertebrae is now known to characterize several taxa occupying disparate positions within the basal sauropodomorph stem (Pol *et al.*, 2011; Wang *et al.*, 2017). This condition is also highly variable in both arrangement (i.e. the additional sacral vertebra can be co-opted from either the dorsal or caudal series) and appearance [*Melanorosaurus* (NMQR 1551) cf. *Leonerasaurus*]. More work and additional fossil sampling is required to establish the polarity of putative homologies and better understand key transformations throughout the evolution of the sauropodomorph sacrum.

# Straightening of the femoral shaft; midshaft eccentricity; migration of the trochanters

The sauropodomorph femur presents a suite of features that reflect the progressive shift towards a more graviportal locomotory style, a process that appears to have begun early in the evolution of the group (Rauhut *et al.*, 2011). Each of these changes has a relatively wellunderstood functional correlate: (1) loss of the sigmoid curvature of the shaft = a more columnar limb stance; (2) anteroposterior compression ('eccentricity') of the shaft = the accommodation of increased mediolateral loading at larger sizes and/or wider gauges; (3) distal migration the main femoral trochanters = a slower gait typified by longer lever arms of the pelvic musculature whereby force is increased at the expense of velocity [see Carrano (1999, 2005) for further discussion]. Yates *et al.* (2010) correctly pointed out that although none of these changes alone provides prima facie evidence of a quadrupedal locomotory habit, they are generally associated with the increase in both body size and gut capacity characteristic of quadrupedal herbivores.

It is likely due to the apparently stepwise nature of these changes that the femur has, in the past, tended to be treated as phylogenetic shorthand for assessing a taxon's closeness to, or inclusion within, Sauropoda (e.g. Yates & Kitching, 2003; Yates et al., 2010; McPhee et al., 2014: fig. 27). However, the very fact that these changes are repeatedly observed in association with size increase in most other (non-ornithopod) dinosaurian herbivores (see Carrano, 2000, 2001, 2005) cautions against a priori assumptions of homology when framing character hypotheses predicated on femoral morphology. Given that progressive size increase appears to have characterized most sauropodomorph lineages from the mid-Norian onwards, some morphological convergence is to be expected. [N.B. An unrelated, yet similar, concern applies to taphonomic deformation of the long bone architecture, with the curvature and eccentricity of the femoral shaft particularly sensitive to distortion/exaggeration by diagenetic processes (Moser, 2003: 178; McPhee et al., 2014; cf. McPhee et al., 2015b; Peyre de Fabrègues & Allain, 2016).]

Concerns regarding the potential artificiality of the linear femoral progression inferred for the basal sauropodomorph-sauropod transition are best illustrated via an exploration of the femoral morphology of the large-bodied South African taxon Antetonitrus and more derived sauropods. In the femora of derived sauropod taxa (e.g. *Diplodocus*, *Brachiosaurus*), the highly reduced-to-absent lesser trochanter is located on the proximolateral corner, whereas the similarly reduced fourth trochanter is positioned upon the medial surface of the midshaft of the femur (Wilson, 2005). Although in Antetonitrus the same trochanters are located in a similar topographical position, there are important morphological differences. These pertain primarily to the fourth trochanter, which in Antetonitrus remains massive and plesiomorphic, suggesting a heightened functionality of the major femoral retractors/adductors compared to more derived eusauropod taxa [see McPhee et al. (2014) and McPhee & Choiniere (2016) for further discussion]. Furthermore, contra to previous assessments, the evolution of this process does not appear to represent a simple progression from a position upon the posterior surface of the proximal half of the femur towards a more distal position (midshaft or

within distal half) on the medial surface. Although both Vulcanodon (Cooper, 1984) and Tazoudasaurus (Allain & Aquesbi, 2008) appear to possess the 'derived' condition, the closely related (*sensu* all recent analyses) Isanosaurus displays a femur in which the fourth trochanter is located well within the proximal half of the shaft (Buffetaut et al., 2000). Moreover, the fourth trochanter of the Middle Jurassic taxa Spinophorosaurus and *Shunosaurus*, while relatively distally placed, is located entirely upon the posterior surface of the femur (Zhang, 1988: fig. 53; Remes et al., 2009: fig. 4h). These examples suggest an unappreciated degree of femoral variation presaging the evolution of the derived eusauropodan *bauplan*, reflecting either differential locomotory requirements or incongruent anatomical responses to similar mechanical controls.

#### Entaxony of the pes

Lastly, particular focus has been given in recent years to changes in the proportional architecture of the sauropodomorph pes (Coombs, 1975; Yates & Kitching, 2003; Carrano, 2005; Yates et al., 2010; McPhee et al., 2015b). In basal dinosaurs, the major weight-bearing axis is directed along the central digit of the foot, with the third metatarsal the most developed element of the metatarsus: the 'mesaxonic' condition [e.g. Herrerasaurus (Novas, 1994)]. In contrast, the weight-bearing axis of the pes in eusauropods has shifted medially, with the first metatarsal being the most robust element: the 'entaxonic' condition. The latter condition probably reflects the lateral displacement of the pes in wider-bodied taxa (thus increasing the mechanical load of the inner sections) and/or the anterolateral rotation of the foot, as evidenced by most sauropod trackways (Bonnan, 2005).

Yates (Yates & Kitching, 2003; Yates et al., 2010; see also McPhee et al., 2014) pointed out that the first metatarsal of sauropodiform taxa like Antetonitrus and Aardonyx was volumetrically enlarged compared to that of more basal taxa. This was interpreted as evidence of a shift towards a more sauropodan form of locomoting, drawing a tentative link between these earliest Jurassic taxa and later eusauropods. That early sauropods like Vulcanodon (Cooper, 1984) and Tazoudasaurus (Allain & Aquesbi, 2008) retained comparatively elongate first metatarsals was explained away as an evolutionary 'reversal' (Yates et al., 2010: 793). However, entaxony s.s. is a twofold process that, in addition to involving enlargement of the first metatarsal, requires a concomitant reduction in the relative size of the median elements of the pes. Here we demonstrate that this pattern is not as straightforward as the simple, linear enlargement of the first metatarsal with the synchronous reduction of the third metatarsal.

Examination of Figure 15 (which highlights the distribution of the multi-state character 'relative proportions of the first metatarsal') suggests that a marked increase in the transverse width (i.e. in robusticity) of the first metatarsal occurs on at least one (although potentially more) occasion prior to the emergence of Sauropoda sensu Salgado et al. (1997). This occurs on the sauropodiform stem near to Sauropoda in which several taxa (Antetonitrus; Blikanasaurus; Aardonyx; Jingshanosaurus) display a first metatarsal that has become markedly stout, that is, its maximum proximal breadth is subequal to its proximodistal length [N.B. Lessemsaurus is not scored for this character as the first metatarsal figured in Pol & Powell (2007: fig. 12) is actually a third metatarsal (B.W.M., pers. observ.).] Nonetheless, in all of these taxa, the third metatarsal remains the longest element of the pes by an appreciable margin (with the third metatarsal being 1.73 times the length of metatarsal I in Antetonitrus and 1.6 in Blikanasaurus). In contrast, whereas the basal-most 'true' sauropods (i.e. Vulcanodon and Tazoudasaurus) display first metatarsals that are proportionally unchanged from the generalized condition of, for example, Eucnemesaurus, this element is nonetheless 'enlarged' relative to the third metatarsal, the latter being reduced in length compared to the rest of the metatarsus in *Vulcanodon* (mt III/mt I = 1.48; Cooper, 1984). This relationship is maintained in basal eusauropod taxa such as Shunosaurus (Zhang, 1988: fig. 55; Bonnan, 2005); however, the first metatarsal of Eusauropoda recalls that of the non-sauropodan sauropodiform taxa above in being the proportionally widest element of the metatarsus.

The above suggests the occurrence of at least two discrete, unrelated pedal strategies within taxa bordering the basal sauropodiform-sauropod transition: (1) in several genera of derived non-sauropodan sauropodiform, the first metatarsal adopted a robust morphology independent of major proportional alterations of the rest of the pes; (2) in contrast, the general proportional morphology of the first metatarsal of the earliest sauropods (i.e. Vulcanodon; Tazoudasaurus) remained relatively unchanged, while the rest of the pes underwent something of an 'homogenization' in which some digits shortened (i.e. the third) while others became relatively longer (i.e. the fifth). This latter strategy can probably be termed entaxony in the explicit, unequivocal sense. Although the postulation of evolutionary/causal explanations for the convergent development of a eusauropod-like first metatarsal in, for example, *Blikanasaurus* and *Antetonitrus* is likely to remain largely speculative, one plausible hypothesis [viz. the scenario favoured by McPhee et al. (2014, 2015a) and McPhee & Choiniere (2016)] suggests it may have been a response to the additional stresses applied to the inner pes during phases of (wider gauged) bipedal locomotion. In this respect, the retention of a proportionately elongate third metatarsal in non-sauropodan sauropodiforms possibly reflects the structural maintenance of a sub-digitigrade foot posture, which in turn contributed to the stride length necessary for efficient bipedal locomotion (Patel, 2009). Nonetheless, corroboration/falsification of this hypothesis awaits the application of more nuanced biomechanical analyses.

#### PULANESAURA AND THE MEANING OF SAUROPODA

The relevance of the morphologies outlined above to the possible grouping relations of *Pulanesaura* is unfortunately obscured by the non-preservation in the latter of many of the structures in question. Although specific features of the humerus and ulna of *Pulanesaura* were proposed in McPhee *et al.* (2015a) as presenting a shift towards a more sauropod-like form of forelimb parasagittalism, their disassociation and poor manner of preservation severely limits their contribution to our understanding of that particular transition. For these reasons, *Vulcanodon* continues to represent perhaps the best exemplar of the basal-most sauropod condition, an interpretation reflected in the retention of the node-based definition of Salgado *et al.* (1997, see above) preferred here.

If the above discussion has emphasized anything it is that, with respect to available information (e.g. there is currently a near-total absence of cranial information known for early sauropods), it is apomorphies of the forelimb that provide the most cogent approximation of the traditional conception of sauropods as 'columnar-limbed quadrupeds'. This condition is represented by an integrated suite of modifications that clearly reflect a shift towards parasagittalism of the structure [see Remes (2008), McPhee et al. (2015a) and above; this transition was also potentially correlated with an increase in the relative elongation of the metacarpus, as suggested by surviving information on the fragmentary manus of Vulcanodon (Raath, 1972; Remes, 2008)]. Moreover, in contrast to the hindlimb modifications discussed above, which are potentially more sensitive to size increase and hence susceptible to misleading convergences, the derived sauropodan forelimb configuration appears to have evolved only once - at the base of what can historically be considered Sauropoda (Salgado et al., 1997; Wilson & Sereno, 1998; Sereno, 1999b). (N.B. Although these features were undoubtedly acquired in a stepwise fashion as part of a multi-taxic transformation series, current phylogenetic hypotheses nonetheless suggest that the ultimate distillation of the complex occurred relatively rapidly.)

The tendency for specific sets of features (i.e. complex apomorphies) to regularly optimize at or around a

specific phylogenetic locus is intriguing, and is potentially emblematic of interesting evolutionary events that mark a genuine departure from the historical dynamics that had held sway prior [e.g. adaptive radiations, vicariant cladism (Assis & de Carvalho, 2010)]. This has already been discussed in more general terms with respect to sauropod evolution, with Barrett & Upchurch (2007: 105) suggesting that the initial radiation of Sauropoda is consistent with a 'correlated progression' model of evolution whereby the development of one character(s) facilitates the elaboration/origin of another within a positive feedback loop of mutual fitness (e.g. herbivory favours increasing stomach capacity favours increasing size favours quadrupedality favours a columnar forelimb stance favours further specializations of the feeding apparatus; see also McPhee et al., 2015a). This idea is also mirrored in recent 'cascade' theories pertaining to the origins sauropod giganticism (Sander et al., 2011; Sander, 2013) [see Button, Barrett & Rayfield (2017) for a recent synthesis of these two concepts].

As a further conceptual consideration, it is worth asking if, in certain instances, the morphological tokens of such events should be reflected in the codification/classification of the resultant clade? The relevance of apomorphies to our classificatory schemes has a long and rather fraught history, with the primary criticism being the perceived lability - and potential homoplastic expression – of character data compared to that of taxon-based specifiers (see discussion in, e.g., Benton, 2000; Nixon & Carpenter, 2000; Langer, 2001; Lee, 2001; Sereno, 2005; Bertrand & Härlin, 2008). Nonetheless, the mutability of most cladistic topologies renders the choice of 'node-fixing' object a relatively arbitrary one (Härlin, 1998; Bertrand & Härlin, 2008). In this sense, the repeated tendency for a subset of characters to concentrate upon a particular point of phylospace suggests that the 'stability' criterion (Cantino & de Queiroz, 2010) is fulfilled no more or less successfully via apomorphies than is the case with a particularly 'dependable' taxonomic specifier (Franz, 2005). A potential corollary of incorporating character information (when it is warranted, e.g., in pectinate grades) into classificatory considerations is the closer epistemic link between character observations (homology hypotheses) and the manner in which those observations are co-opted into phylogenetic reconstructions. This suggestion has been addressed (although not always explicitly) in the recent literature on natural kinds (homeostatic property cluster natural kinds sensu Boyd, 1991, 1999). The explanatory strength of this line of theorizing, it is argued, extends from treating properties not as traditional essences, but as integrated clusters that co-occur with better than chance probability (projectability), thus contributing to scientific induction and generalization

(Griffiths, 1999; Keller, Boyd & Wheeler, 2003; Rieppel, 2005, 2006, 2008; Rieppel & Kearney, 2007; Assis & Brigandt, 2009). The homeostatic mechanism in this sense refers to the causal processes that maintain the boundary and integrity of the kind and, although generally historical (i.e. genealogical) in nature, can also include, for example, developmental, modular and/or functional influences (see Wagner & Schwenk, 2000; Wagner, 2001; Rieppel, 2005).

Although this form of character (or, more appropriately, topological) congruence could also potentially be couched in an individualist paradigm as a form of 'recurrence of concordance' [sensu Haber (2016), see that work for further discussion, cf. 'consilience of inductions' (Ruse, 1987)], it is likely that natural kinds qua similarity classes will remain of greater pragmatic (i.e. empirical) relevance to most palaeontologists given the nature of our data [although these approaches are not entirely mutually exclusive (Pleijel & Härlin, 2004; Brigandt, 2009)]. Thus, the defining features of the sauropod forelimb meet the epistemic (inductive and explanatory) requirements of an integrated locomotory complex clearly distinguishable from that of the plesiomorphic sauropodomorph condition (McPhee et al., 2015a). A more focused treatment of character information with respect to our naming practices also represents a potential compromise between positions that treat names as (often theory-free) tokens of ostensive reference (to, e.g., hypotheses: Härlin, 1998; Bertrand & Härlin, 2008; cf. Fitzhugh, 2008) and those that view names as emblemizing biologically interesting groupings accessible to scientific description, understanding and communication (Keller et al., 2003; Franz, 2005; Rieppel, 2005, 2006, 2008; Rieppel & Kearney, 2007; Assis, 2011). In summary, although these issues warrant an independent, more in-depth future treatment, it is nonetheless clear that Sauropoda has a genuine meaning formed of the intensional properties generally associated with it. Greater consideration of the properties that render organismal groupings of interest in the first place is required in order to reconcile classificatory practice with the explanatory aims (e.g. repeatability, communication) of empirical science.

#### CONCLUSION

*Pulanesaura* provides a suggestive insight into the sequence of trait acquisition at the transition from basal Sauropodomorpha to Sauropoda. Although this transition is obscured by a continued paucity of complete specimens at key points along the sauropodomorph stem, changes pertaining to anatomical regions such as the dentition, neck, forelimb and pes are slowly coming into sharper focus. However, ambiguities

stemming from the differing constituencies that result from the current node- or stem-based definitions of Sauropoda have introduced some confusion regarding the condition of specific synapomorphies. In particular, the potentially overly permissive stem-based definition has tended to view as synapomorphic certain hindlimb features that are probably more homoplastic than previously appreciated. The (node-based) definition preferred here is argued with reference to an unambiguous subset of forelimb specializations that stand as a cogent proxy for traditional conceptions of what a sauropod 'is'. In this respect, focused consideration of the character information most germane to phylogenetic hypotheses suggests that anatomical data continue to have a classificatory role to play beyond reflexive a posteriori diagnosis.

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