A NEW TITANOSAURIFORM SAUROPOD (DINOSAURIA: SAURISCHIA) FROM THE EARLY CRETACEOUS OF CENTRAL TEXAS AND ITS PHYLOGENETIC RELATIONSHIPS

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ABSTRACT

A collection of primitive titanosauriform sauropods from the Jones Ranch locality, Early Cretaceous Twin Mountains Formation (~112 Ma), central Texas, represents one of the richest accumulations of sauropod bones in North America. Autapomorphic characters of the taxon include cranial and mid-caudal neural arches with distinct intra-prezygapophyseal laminae (tprl), accessory vertebral laminae on cranial dorsal neural arches, and dorsal neural spines that lack a postspinal lamina.

Non-vertebral skeletal elements referred to the genus *Pleurocoelus* from the Arundel Formation of Maryland and Virginia possess some diagnostic morphological characteristics and can be compared with the Jones Ranch sauropod. The latter differs from *Pleurocoelus* in the shape of the caudoventral margin of the maxilla, the shape of the distal scapular blade, and the shape of the proximal condyle of the tibia. The Jones Ranch sauropod is also morphologically distinct from all other sauropods described and named from the Early Cretaceous of North America.

Cladistic analysis places this sauropod within Titanosauriformes. The Texas sauropod does not possess synapomorphies of Somphospondyli, and derived characters that have been used to define the Titanosauria are also absent, affirming its placement as a basal titanosauriform. The new taxon from Texas is known from more material than any other North American Early Cretaceous sauropod. Description of the taxon increases the diversity of sauropods in North America during the Early Cretaceous and provides more complete, associated material that can be compared to new discoveries from this time period.

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INTRODUCTION

Sauropod fossils from the Jones Ranch locality, north-central Texas are intriguing because these remains are found within 25 km of numerous sauropod tracks and trackways (e.g., Shuler 1937, Langston 1974, Farlow 1987). Sauropod ichnofossils have been well documented in North America, but associations between skeletal remains and trace fossils have not been reported. Moreover, the Jones Ranch locality represents one of the richest known accumulations of Early Cretaceous sauropod remains in North America.

North American sauropods were most diverse during the Late Jurassic period (Hunt et al. 1994, Maxwell and Cifelli 2000). Sauropod discoveries in North America from Cretaceous strata, however, are sparse, with the exception of ichnofossils (Weishampel et al. 2004). There is no record of Cretaceous sauropods in North America prior to the Barremian, but they are known from the Barremian or Aptian through the Albian and possibly into the Cenomanian (Kirkland et al. 1998, Maxwell and Cifelli 2000). Sauropods then disappear from the North American record until the Maastrichtian (Lucas and Hunt 1989). Furthermore, much of what is known of Early Cretaceous sauropods is based on fragmentary and unassociated elements, making detailed comparisons difficult. Consequently, the taxonomy and systematics of Early Cretaceous sauropods from North America are problematic, which has serious implications for biogeographic studies. Correlating among different Early Cretaceous faunas is made difficult by the lack of precise ages for sauropod-bearing strata of that interval in North America (Jacobs and Winkler 1998).

Until the late twentieth century, most Early Cretaceous North American sauropod material was referred to *Pleurocoelus* or *Astrodon*. The topotypic material for two species of *Pleurocoelus* and the only species of *Astrodon* is from the Lower Cretaceous Arundel Formation of Maryland. *Astrodon johnstoni* was the first sauropod described from North America and was named based upon isolated teeth (Leidy 1865). Marsh (1888) later described two species of the taxon *Pleurocoelus*, *P. nanus* and *P. altus*, on the basis of isolated, fragmentary, and mostly juvenile remains. The type material for *P. nanus* consists of four vertebrae, comprising a cervical, dorsal, sacral, and a caudal. Isolated sauropod bones from the Arundel Formation were referred to *Pleurocoelus* largely based on proximity of the localities and the size of the bones. Langston (1974) and Gallup (1989) previously referred sauropod specimens from the Lower Cretaceous of Texas to *Pleurocoelus*.

Nearly all of the vertebrae known from the Arundel sauropod lack neural arches, and evidence suggests that neurocentral fusion was absent, indicating they are from juvenile individuals. Consequently, the Arundel vertebrae lack diagnostic features and are not easily distinguishable from those of other sauropods, particularly taxa for which juvenile vertebrae are not known. Serial morphological variability in sauropod vertebral columns makes direct comparisons of vertebrae from different positions difficult.

Isometric growth has been documented in the appendicular skeleton of some sauropods (Carpenter and McIntosh 1994, Wilhite 1999, 2005, Tidwell and Wilhite 2005). According to Wilhite (1999), with few exceptions, during ontogeny sauropod limb breadth measurements grow at a constant rate of approximately one-third the rate of limb length. Thus, limb proportions and morphology change little between juveniles and adults of the same taxon, and there is good potential that well-preserved, isolated sauropod appendicular elements can be confidently identified to family or genus level (Wilhite 2005). Unlike the type specimens of *Pleurocoelus*, the juvenile appendicular elements, referred to the latter taxon, can be differentiated from several other sauropod genera based on their morphology and limb proportions (personal observations; Appendices 1, 2).

Ostrom (1970) described sauropod remains from the Cloverly Formation of Wyoming and Montana. Until the last decade, the Cloverly sauropod and the Arundel taxon remained the only Early Cretaceous sauropods in North America known from more than a few isolated skeletal elements. In recent years, however, a number of sauropod discoveries from the Early Cretaceous of North America have emerged, with new specimens described from Utah and Oklahoma (Tidwell et al. 1999, Tidwell et al. 2001, Wedel et al. 2000a).

In this study, a large sample of sauropod bones from an Early Cretaceous locality in central Texas is described. The Texas sauropod is demonstrated to be different from other Early Cretaceous sauropods. A new genus is created to include this distinctive species. Finally, a cladistic analysis is performed to investigate the phylogenetic position of this new taxon and the significance of this taxon to the diversity and geographic distribution of Early Cretaceous North American sauropods is discussed.

Institutional Abbreviations

DMNH, Denver Museum of Science and Nature, Denver; **FMNH**, Field Museum of Natural History, Chicago; **FWMSH**, Fort Worth Museum of Science and History, Fort Worth; **OMNH**, Oklahoma Museum of Natural History, University of Oklahoma, Norman; **SMU**, Department of Geological Sciences, Southern Methodist University, Dallas; **TMM**, Texas Memorial Museum, Austin; **USNM**, National Museum of Natural History, Washington D.C.; **YPM**, Yale Peabody Museum, Yale University, New Haven.

Anatomical Abbreviations

acdl, anterior centrodiapophyseal lamina; **acpl**, anterior centroparapophyseal lamina; **cpol**, centropostzygapophyseal lamina; **cprl**, centroprezygapophyseal lamina; **EI**, elongation index; **hyp**, hyposphene; **nc**, neural canal; **ns**, neural spine; **pcdl**, posterior centrodiapophyseal lamina; **pcpl**, posterior centroparapophyseal lamina; **podl**, postzygodiapophyseal lamina; **posl**, postspinal lamina; **ppdl**, paradiapophyseal lamina; **pl**, pleurocoel; **prdl**, prezygodiapophyseal lamina; **prpl**, prezygoparapophyseal lamina; **prsl**, prespinal lamina; **spdl**, spinodiapophyseal lamina; **sprl**, spinoprezygapophyseal lamina; **spol**, spinopostzygapophyseal lamina; **tpol**, intrapostzygapophyseal lamina; **tprl**, intraprezygapophyseal lamina.

Other Abbreviations

JP, Jeffrey Pittman (specimen field number).

Previous Work

Langston (1974) referred a series of 21 caudal vertebrae, fragmentary remains of some cervical and dorsal vertebrae, a chevron, dorsal ribs, and a distal scapula of a sauropod from Wise County, Texas (SMU 61732), to the genus *Pleurocoelus*. Langston (1974) also noted that the same species (TMM 40435) was found in the Glen Rose Formation of Blanco County, Texas. Langston (1974, p.86) identified the Wise County specimen as *Pleurocoelus* based on the morphology of the caudal vertebrae, claiming that, "the elevated, forwardly-placed neural arch atop a slender, spool-shaped, amphiplatyan centrum is characteristic." However, distal caudals of the Late Jurassic sauropod *Brachiosaurus* also fit this description (Janensch 1950).

Salgado et al. (1995) argued that, considering the available evidence, SMU 61732 from Wise County, Texas, could not be attributed to the same genus as any of the Arundel specimens. In their discussion of sauropods from Utah, Tidwell et al. (1999) reached the conclusion that SMU 61732 is distinctly different from *Pleurocoelus*. Gomani et al. (1999) compared SMU 61732 and sauropod bones from Jones Ranch, Texas, to *Brachiosaurus*, *Euhelopus*, and *Malawisaurus*, all titanosauriform taxa whose phylogenetic positions are reasonably well established. They determined that the Texas sauropod fossils share only two derived characters with titanosaurians, while the other 10 characters they analyzed were either plesiomorphic for titanosauriforms or were synapomorphies for the Texas sauropod and *Brachiosaurus*. Gomani et al. (1999) assumed SMU 61732 and the Jones Ranch material belonged to the same species but provided no supporting evidence.

An isolated, articulated hindfoot was found north of the Wise County locality that produced SMU 61732 and described as *Pleurocoelus* sp. Gallup 1989. According to Gallup (1989), the morphology of the foot is consistent with sauropod trackways and footprints found in Texas Lower Cretaceous rocks. The abundant sauropod footprints preserved in the Glen Rose Formation, given the ichnogenus *Brontopodus* Farlow et al. 1989, were attributed to *Pleurocoelus* sp. (Langston 1974, Gallup 1989).

Study Area

The sauropod material in this study comes from the W.W. Jones Ranch, SMU Locality 282, Hood County, Texas (Figure 1). A group of students from the University of Texas at Austin discovered the site in the mid-1980s. Jeffrey G. Pittman worked the quarry for three field seasons beginning in 1985, discontinuing work in 1987. In 1993 researchers from Southern Methodist University, the Fort Worth Museum of Science and History, and Tarleton State University re-opened the quarry and have worked the site ever since.

Winkler et al. (2000) provided a description of the quarry, including certain aspects of the taphonomy, bone distribution, and depositional environment. The bone-bed occurs in the Twin Mountains Formation of the Trinity Group. At Jones Ranch the Trinity Group comprises the Twin Mountains, Glen Rose, and Paluxy formations, from bottom to top. The Twin Mountains and Paluxy formations are terrestrially derived, whereas the Glen Rose Formation is a shallow marine limestone that represents a significant marine transgression. The conformable contact between the Twin Mountains Formation and the Glen Rose limestone lies approximately 10

Figure 1. Map of Texas showing the location of the W.W. Jones Ranch, SMU locality 282.
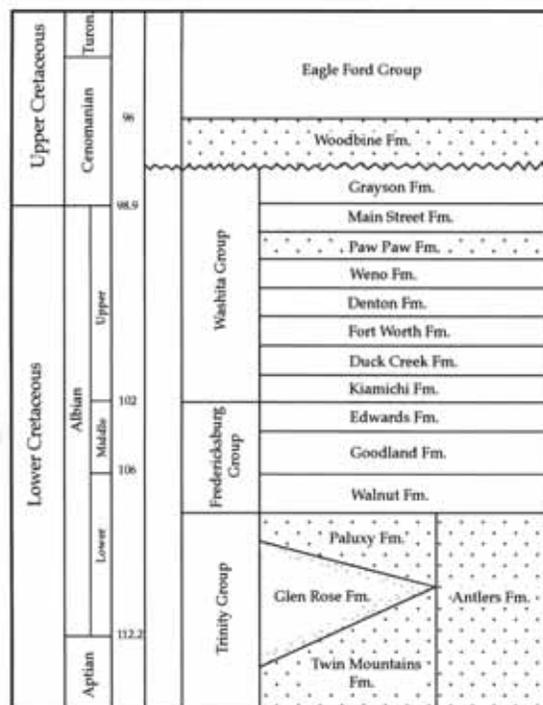

Figure 2. Stratigraphic column for the Cretaceous of central Texas. Modified from Jacobs and Winkler (1998).

m above the sauropod-producing layers at Jones Ranch (Winkler et al. 2000). Biostratigraphic correlations using ammonites suggest that the base of the Glen Rose Formation in central Texas is no older than the Aptian-Albian boundary (Young 1974). The proximity of the Jones Ranch locality to the base of the Glen Rose Formation suggests an age near this boundary, or approximately 112 Ma (sensu Gradstein et al. 1995; Figure 2).

The depositional environment at the Jones Ranch quarry is fluvial. Here the Twin Mountains Formation consists of loosely consolidated channel sands and muds with pockets of hard, calcite-cemented sandstone concretions that are typically fossiliferous. All of the bones from Jones Ranch were found within an area of 400 square meters. The majority of the large sauropod bones from the quarry were found closely associated or articulated with other elements from the skeleton. Only three bones were found with no other bone within a 1 m radius (Figure 3). The quarry has so far produced representative elements of at least four individual sauropods (minimum number of individuals based on the number of preserved femora) all comparatively similar in size. Approximately 90% of the quarry assemblage has been removed from the field and preparation of collected specimens is close to two-thirds complete. All of the sauropod bones from the quarry can be attributed to the
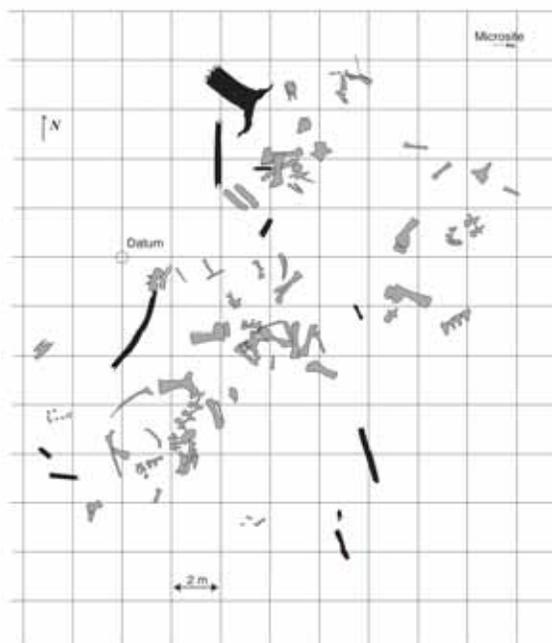

Figure 3. Quarry map of Jones Ranch, SMU Locality 282 (FWMSH 93B-10). Elements shaded in black represent petrified logs. Elements in gray are sauropod bones collected jointly by Southern Methodist University, the Fort Worth Museum of Science and History, and Tarleton State University from the period 1993-1999. Modified from Winkler and Rose (2006).

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same species based on their close association and because duplicate elements do not show appreciable variation in size, proportion, or morphology beyond what can be expected from individual variation.

SYSTEMATIC PALEONTOLOGY

Order SAURISCHIA Seeley 1887

Suborder SAUROPODOMORPHA von Huene 1932
Infraorder SAUROPODA Marsh 1878
TITANOSAURIFORMES Salgado, Calvo, and Coria 1997
Family ?BRACHIOSAURIDAE Riggs 1904
PALUXYSAURUS, gen. nov.

Etymology. The genus refers to the nearby town of Paluxy, Texas, and the Paluxy River, which flows through this region.

Type and Only Known Species. *Paluxysaurus jonesi*, sp. nov.

Diagnosis. As for the species.

PALUXYSAURUS JONESI, sp. nov.

Etymology. The species is named in honor of William R. (Bill) Jones, who for nearly two decades has graciously allowed the excavation of these important fossils on his land.

Holotype. FWMSH 93B-10-18, an associated left maxilla and nasal and teeth.

Referred Specimens. Associated partial skeletons and isolated bones from at least four different individuals from a single locality that includes: isolated teeth (FWMSH 93B-10-5, FWMSH 93B-10-6, FWMSH 93B-10-33, FWMSH 93B-10-40, FWMSH 93B-10-49, FWMSH 93B-10-50), a series of seven cervical vertebrae (FWMSH 93B-10-[28-32]) and two isolated cervical vertebrae and cervical rib fragments (FWMSH 93B-10-8, FWMSH 93B-10-19); 13 dorsal vertebrae (FWMSH 93B-10-9, FWMSH 93B-10-11, FWMSH 93B-10-13, FWMSH 93B-10-27, FWMSH 93B-10-48, TMM 42488); more than 30 caudal vertebrae (FWMSH 93B-10-12, FWMSH 93B-10-14, FWMSH 93B-10-17, FWMSH 93B-10-21, FWMSH 93B-10-37, FWMSH 93B-10-38, FWMSH 93B-10-[41-44], TMM 42488); four chevrons (FWMSH 93B-10-4, TMM 42488); several dorsal rib fragments (FWMSH 93B-10-13, FWMSH 93B-10-20, FWMSH 93B-10-23); one fused scapulocoracoid (TMM 42488); one scapula (FWMSH 93B-10-24); two coracoids (FWMSH 93B-10-34, FWMSH 93B-10-39); one sternal plate (FWMSH 93B-10-24); four humeri (FWMSH 93B-10-2, FWMSH 93B-10-7, TMM 42488); one ulna (FWMSH 93B-10-7); two radii (FWMSH 93B-10-7, FWMSH 93B-10-36); eight metacarpals (FWMSH 93B-10-1, FWMSH 93B-10-10, FWMSH 93B-10-22, FWMSH 93B-10-36, FWMSH 93B-10-47); two ilia (FWMSH 93B-10-27); five pubes (FWMSH 93B-10-27, FWMSH 93B-10-35, FWMSH 93B-10-51, TMM 42488); five ischia (FWMSH 93B-10-27, FWMSH 93B-10-35, FWMSH 93B-10-51, TMM 42488); six femora (FWMSH 93B-10-3, FWMSH 93B-10-7, FWMSH 93B-10-25, FWMSH 93B-10-27, TMM 42488); four tibiae (FWMSH 93B-10-15, FWMSH 93B-10-45, FWMSH 93B-10-46, TMM 42488); two fibulae (FWMSH 93B-10-15, FWMSH 93B-10-25); and three metatarsals (FWMSH 93B-10-16, FWMSH 93B-10-26). A number of other elements were provisionally identified in the field but have not yet been prepared.

Diagnosis. *Paluxysaurus jonesi* can be diagnosed based on the following characteristics exhibited by the holotype and referred specimens: broad nasal process of the maxilla; strong lateral curvature of the premaxillary process of the nasal; differs from *Brachiosaurus brancai* in having a shorter, non-arching premaxillary process of the nasal and a more pronounced lacrimal process of the maxilla; differs from *Pleurocoelus* sp. in the shape of the caudoventral margin of the maxilla, the shape of the distal scapular blade, and the shape of the proximal condyle of the tibia; differs from *Euhelopus zdanskyi* in that the nasal process of the maxilla rises from the middle of the bone; distinguished from *Brachiosaurus brancai* by a distinct intrapostzygapophyseal lamina (tpol) on cervical neural arches; deep postspinal fossa on caudal saurface of cervical neural arches; accessory laminae on dorsal neural arches; dorsal vertebrae that lack a postspinal lamina; mid-caudal centra articular faces angle cranially; cranial and mid-caudal neural arches with intraprezygapophyseal laminae (tprl) that form, with the spinoprezygapophyseal laminae (sprl), a prespinal fossa above the neural canal; transversely expanded cranial and mid-caudal neural spines; distal scapular blade broadly expanded on both acromial and glenoid sides; craniocaudally compressed femoral shaft. It also retains the following plesiomorphies: dorsal neural spines tapering, not flaring, distally; a long pubis relative to the length of the pubioischial articular surface; tibial proximal condyle expanded craniocaudally.

Locality and Age. W.W. Jones Ranch, SMU Locality 282 (FWMSH 93B-10), Hood County, Texas, south-southwest of the town of Tolar. The bone-bed occurs in the Twin Mountains Formation of the Trinity Group and is of late Aptian or earliest Albian age (see above).

DESCRIPTION

Skull

Maxilla. The nearly complete left maxilla and nasal of *P. jonesi* belong to the same individual. The body of the maxilla is relatively short rostrocaudally compared to *Diplodocus*, *Nemegtosaurus*, and *Brachiosaurus* and more robust than the maxilla of *Camarasaurus* (see Upchurch et al. 2004, figure 13.2). A broad, steeply sloping nasal, or ascending, process projects caudodorsally from the mid-region of the maxilla body and presents a long articular surface for the lacrimal (Figure 4). The nasal process is nearly twice the width of the same feature in any other sauropod. Rostral and ventral to the base of the nasal process is a long and broad premaxillary process. The maxilla forms a significant portion of the border of the external naris. The position of the external naris is comparable to that of *Camarasaurus* and *Brachiosaurus*. A prominent, triangular lacrimal process projects dorsally from the caudal end of the maxilla. One complete tooth is preserved in the tooth row, along with fragments of at least four others. Two additional fragmentary teeth were found in close proximity to the skull bones. In contrast to the condition in diplodocids, teeth are not restricted to the rostral portion of the maxilla. The maxilla is estimated to have held nine or 10 teeth.

Nasal. The premaxillary process of the nasal is minimally arched, indicating a relatively horizontal dorsal surface of the skull for *P. jonesi* (Figure 5.1). The premaxillary process is also narrow transversely and has a relatively strong lateral curvature at its distal (rostral) end (Figure 5.2). The lateral, or lacrimal, process of the nasal curves gently ventrally and rostrally but is broken at its distal end. Measurements for the maxilla and nasal are provided in Table 1.

Teeth. In addition to the teeth preserved within and in association with the maxilla, several other isolated sauropod teeth have been recovered from Jones Ranch (Figure 6). Teeth of *P. jonesi* are *Camarasaurus*-like, though less spatulate, and differ from the cylindrical teeth of diplodocoids and most titanosaurians. The crown apices are angled lingually. Tooth crowns have sharp mesial and dis-
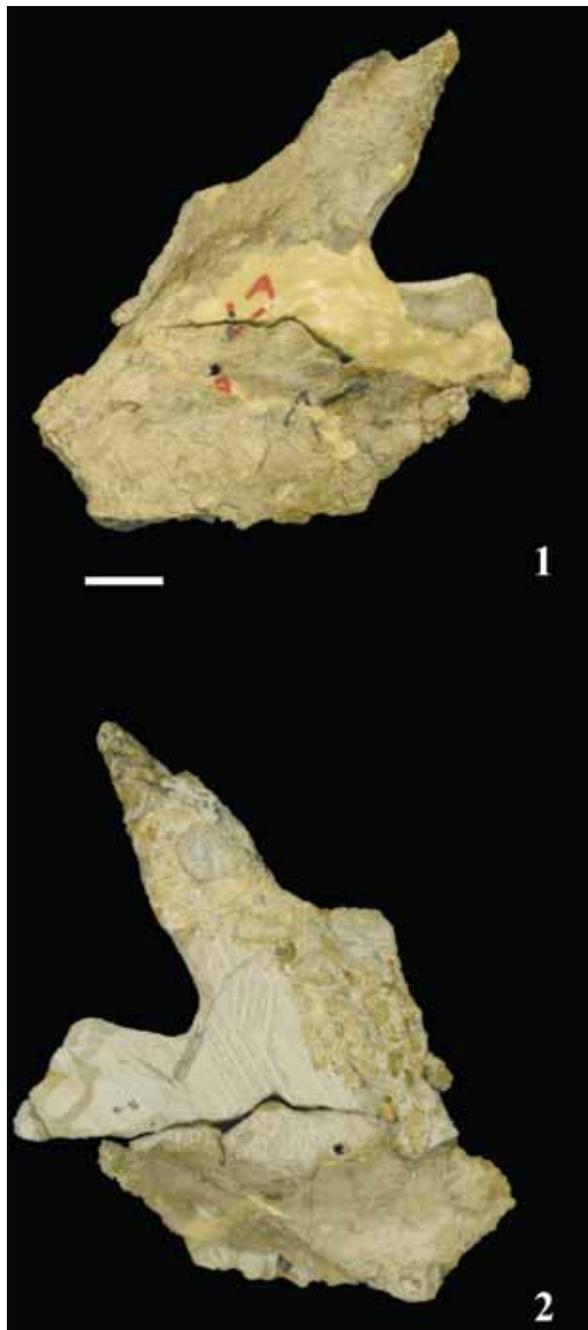
Figure 4. Left maxilla (FWMSH 93B-10-18) of *Paluxysaurus jonesi* in lateral (1) and medial (2) views. Scale bars are approximately 5 cm.

tal margins that lack denticles. Enamel exhibits a wrinkled texture at the base of the crown but is smoother apically. Teeth possess an oblique lingual surface that is angled mesiolingually. However, tooth crowns do not overlap in the jaw. Overlap of tooth crowns is a synapomorphy for most eusauropods (Wilson 2002), but is lost in *Paluxysaurus*, diplodocoids, *Brachiosaurus*, and

Figure 5. Left nasal (FWMSH 93B-10-18) of *P. jonesi* in dorsal (1) and lateral (2) views. Scale bar is 5 cm.

Table 1. Measurements of skull bones of *Paluxysaurus jonesi* (in mm).

Measurement	Specimen FWMSH 93B-10-18
Maxilla	
Greatest length	246+
Greatest height	330
Greatest transverse breadth	59
Length of tooth row	137+
Nasal	
Greatest Length	194
Transverse breadth	145+
Length of premaxillary process	45+
Length of lateral process	112+
	+ = incomplete

titanosaurians. The labial surface is strongly convex and there is also a narrow region of raised enamel on the lingual surface with shallow depressions on each side. Teeth of *P. jonesi* generally exhibit V-shaped wear facets, which is in contrast to the high-angled wear facets observed in diplodocoids and titanosaurians. Tooth wear patterns, however, are somewhat variable depending on tooth position and degree of wear.

Axial Skeleton

All of the vertebrae found at Jones Ranch appear to pertain to adult individuals, as neural arches (where preserved) are completely fused to their centra. Presacral vertebrae of *P. jonesi* are strongly opisthocoelous, lack bifid neural spines, and exhibit an extensive network of vertebral laminae. Herein, I refer to these laminae using the nomenclature of Wilson (1999).

Cervical Vertebrae. Portions of at least nine cervical vertebrae have been recovered from the Jones Ranch quarry thus far, four of which are almost complete. Bone associations in the quarry suggest that all but two of these cervical vertebrae, FWMSH 93B-10-8 and FWMSH 93B-10-19, pertain to a single individual. Cervical vertebrae FWMSH 93B-10-32, FWMSH 93B-10-28, FWMSH 93B-10-19, FWMSH 93B-10-29, and FWMSH 93B-10-30 most likely represent vertebrae C3-C9 of the cervical column, based on comparison of the centrum length ratio between the third and fourth cervical vertebrae with that of *Brachiosaurus brancai*,

the position and height of neural spines, and position relative to one another in the quarry. Most of the Jones Ranch cervical vertebrae have experienced some deformation related to crushing. All of the cervical vertebrae have long centra, as exhibited by high length-to-caudal height ratios, expressed as an elongation index [EI] (sensu Wilson and Sereno 1998; Wedel et al. 2000b; contra Upchurch [1998], who uses length/caudal centrum width to represent the EI). EI values for Jones Ranch cervical vertebrae range from 4.7 in C3 to 7.3 in C4 of the same individual (Table 2).

The height-to-width ratio of cervical centra is slightly less than 1.0 in cranial cervical vertebrae but decreases caudally. Cervical centra are characterized by long, relatively shallow lateral depressions that are perforated by small, well-defined pleurocoels (typically two in number), separated from each other by laminae of bone (Figure 7). The larger, more superficial lateral depressions do not have well-defined margins and occupy more than 80 percent of the centrum length in some vertebrae. Posterior to the parapophyses, the ventrolateral margins of the cervical centra consist of long (and in some cases very thin) pseudo-laminae that in *Brachiosaurus brancai* have been interpreted as posterior centroparapophyseal laminae (Janensch 1929, 1950). Wilson (1999) argues that the morphology of this feature is inconsistent with the definition of a true parapophyseal lamina, because the landmarks bridged by the thin bone in these cervical vertebrae are not the same as in the dorsal series.
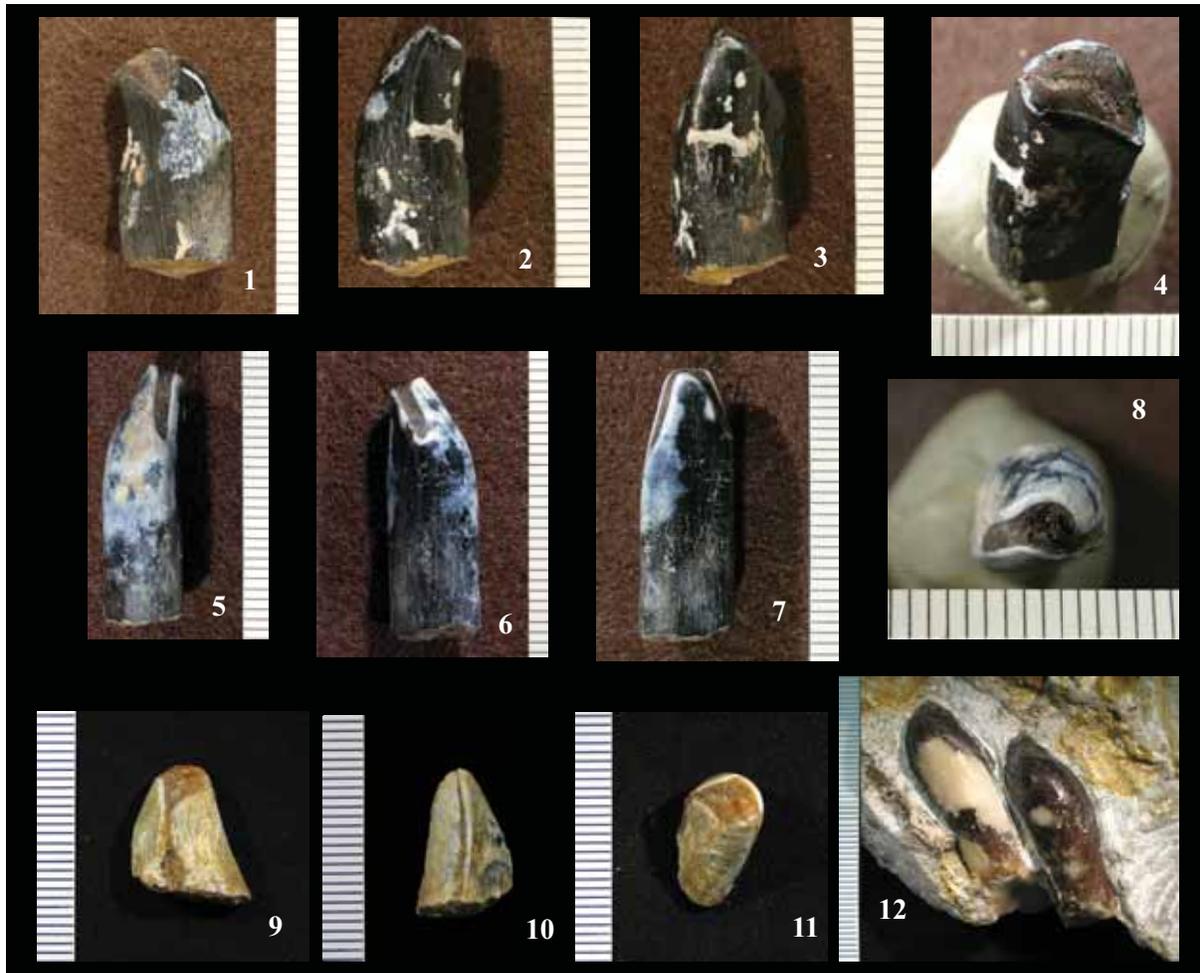
Figure 6. A-K, isolated sauropod teeth from Jones Ranch. A-D, FWMSH 93B-10-49 in distal (1), mesial (2), lingual (3), and occlusal (4) views; E-H, FWMSH 93B-10-50 in distal (5), mesial (6), lingual (7), and occlusal (8) views; I-K, FWMSH 93B-10-33 in distal (9), mesial (10), and occlusal (11) views. 12, teeth from the holotype of *P. jonesi* (FWMSH 93B-10-18) in labial view. Scales are in millimeters.

Neural arches span nearly the entire length of the centrum in the cervical series. The neural arch is tall in mid-cervical vertebrae. Prezygapophyses extend beyond the cranial condyle of the centrum. Postzygapophyses are weakly developed and are positioned cranial to the caudal margin of the centrum. Diapophyses are lightly built in cranial cervical vertebrae but become more expansive in the middle and caudal cervical vertebrae. Only cervical vertebrae six (FWMSH 93B-10-28) and eight (FWMSH 93B-10-29) preserve most of the neural spine (Figures 8, 9.1). The spine on C6 is low. In C8 the spine is missing the caudal one-third approximately, but it is tall and broad. Thus, a noticeable increase in neural spine height occurs between vertebral positions six and eight in the cervical series. A similar transition in cervical neural spine height has been documented in *Brachio-saurus brancai* and *Sauroposeidon proteles* (Wedel et al. 2000a).

Long, paired spinoprezygapophyseal laminae (sprl) (already defined) originate on the dorsal surface of the prezygapophyses and terminate near the craniodorsal margin of the neural spine (Figure 9). The sprl increases in length and becomes more prominent along the column as the neural spine migrates caudally and increases in height. In addition to broad centroprezygapophyseal laminae (cprl), the prezygapophyses are linked by paired intraprezygapophyseal laminae (tprl)(already defined). The tprl's meet medially where they are joined by a vertical lamina that divides ventrally and connects to the top of the centrum, outlining the neural canal. This accessory lamina creates two bilaterally symmetrical fossae just above the neural canal (Figure 8.2). A similar arrangement of

Table 2. Measurements of cervical vertebrae of *Paluxysaurus jonesi* (in mm).

Measurement	FWMSH 93B-10-32	FWMSH 93B-10-32	FWMSH 93B-10-28	FWMSH 93B-10-29	FWMSH 93B-10-30	FWMSH 93B-10-8
	Specimen					
Centrum length	446	661	655	553+[740e]	493+[830e]	672+[730e]
Cranial centrum height	71	84	114	--	--	70
Cranial centrum width	--	105	133	--	--	77
Caudal centrum height	94e	90e	136	--	--	114e
Caudal centrum width	110	111	103+	220	--	123
Overall vertebral height	230+	200+	330	289+	262+	295
Greatest width of arch	160e	200e	190	450e	480e	147+
Prezygapophysis height	85	95	130	--	196	107
Postzygapophysis height	105	110	130	135+	--	145
Elongation index	47.0	73	48	--	--	64

Notes. e = estimate, + = incomplete, -- = could not measure.

laminae and fossae can be seen in some cervical vertebrae of *Brachiosaurus brancai*. The spinopostzygapophyseal lamina (spol) is paired, connecting the postzygapophyses to the caudal aspect of the neural spine. Intrapostzygapophyseal laminae (tpol) (already defined) traverse between the medial surface of the postzygapophyses and the midline of vertebrae where they meet above the neural canal. The tpol's and spol's outline a deep fossa behind the neural spine. A median strut runs between the tpol and the base of the neurocentral junction. Two fossae on either side of this lamina, in conjunction with the neural canal, form a tri-radiate pattern, similar to that on the cranial surface of the vertebrae (Figure 8.3). These fossae are bounded laterally by short centropostzygapophyseal laminae (cpol).

In contrast to most somphospondylians, the diapophyseal laminae are reasonably well developed in cervical vertebrae of *Paluxysaurus jonesi*. Four laminae stem from the diapophyses. The posterior centrodiapophyseal (pcdl) and postzygodiapophyseal (podl) laminae branch at a shallow angle away from the diapophysis caudoventrally and caudodorsally, respectively. A dorsoventrally wide, long, and shallow depression opens caudal to the diapophysis between the pcdl and podl. The acdl is a thin strut of bone projecting cranioventrally, terminating near the neurocentral junction. The prezygodiapophyseal lamina (prdl) is not prominent in cranial cervical vertebrae, but in succeeding vertebrae, as the diapophysis migrates caudally and the transverse processes increase in breadth, the prdl expands and forms broad, flat

Figure 7. Articulated third and fourth cervical vertebrae (FWMSH 93B-10-32) of *P. jonesi* in lateral view. Scale bar is 10 cm.
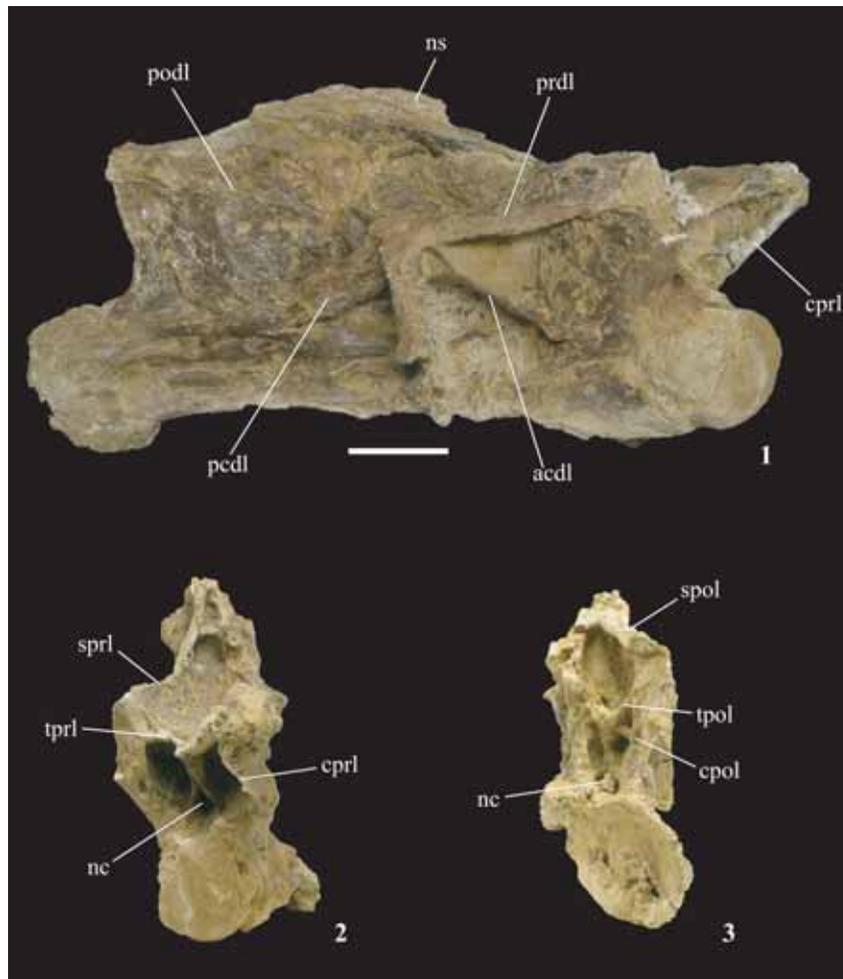
Figure 8. Sixth cervical (FWMSH 93B-10-28) of *P. jonesi* in right lateral (1), cranial (2), and caudal (3) views. See text for anatomical abbreviations. Scale bar is 10 cm.

wing-like extensions that connect the prezygapophysis to the diapophysis (Figure 9).

Differences in morphology among cervical vertebrae from Jones Ranch can be explained by individual variation, serial variation along the cervical column, taphonomic influences, or a combination of these factors. Variability in calculated elongation indices within a single individual has been documented in other sauropod taxa (e.g., Wedel et al. 2000a). Therefore, the large difference in EI values between cervical vertebrae from Jones Ranch can be expected. The specimen FWMSH 93B-10-8, a cranial cervical vertebra, probably C5, was found isolated in the quarry. The vertebra is missing the prezygapophysis, diapophysis, and parapophysis from the left side and the cranial condyle of the centrum (Figure 10). General similarities, as suggested by Wedel (2003), in the form of this vertebra with cervicals of an unnamed titanosaurian from Brazil described by Powell

(1987) may be due to preservation. Other cervicals from Jones Ranch do not closely resemble the vertebrae of the Brazilian taxon.

Cervical Ribs. Cervical ribs run subparallel to the length of the vertebral centrum, angled slightly ventrally. The ribs are long; in cranial cervical vertebrae, the ribs overlap with at least two succeeding vertebrae. Cervical ribs are dorsoventrally flattened proximally, becoming more rod-shaped along their length distally (Figure 11). The tuberculum is broad at its base and narrows dorsally where it meets the diapophysis. In cranial cervicals the diapophysis and tuberculum fuse along a nearly vertical line, but with caudal migration of the diapophysis along the cervical column, they are offset from one another in caudal cervicals, and the tuberculum angles strongly caudodorsally. Capituli are either not well preserved or displaced by post-depositional deformation in most cervical vertebrae,
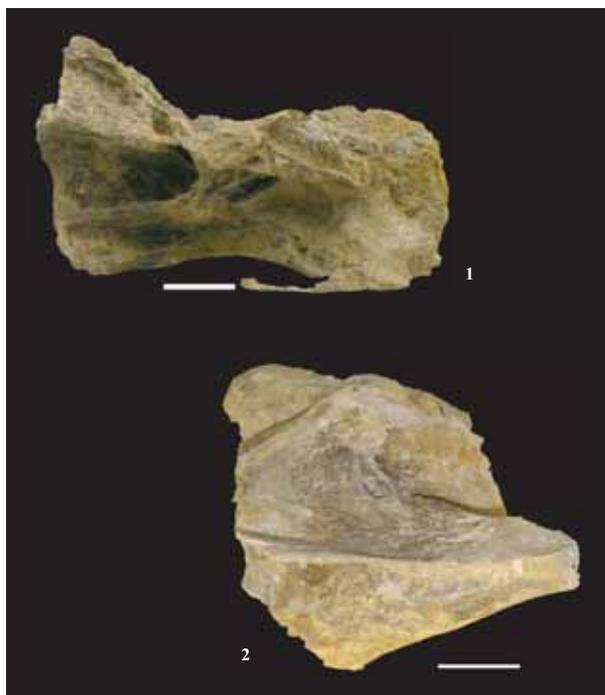
Figure 9. 1, Eighth cervical (FWMSH 93B-10-29) of *P. jonesi* in lateral view. 2, Ninth cervical (FWMSH 93B-10-30) of *P. jonesi* in dorsal view. Cranial is to the right in both figures. Scale bars are 10 cm.

therefore making description of its orientation and morphology difficult.

Dorsal Vertebrae. A total of 14 dorsal vertebrae are known from Jones Ranch. Five dorsal vertebrae have been completely prepared, including two nearly complete, articulated cranial dorsal vertebrae, FWMSH 93B-10-13, which were partially described by Gomani et al. (1999). The remaining three dorsal vertebrae were found in different parts
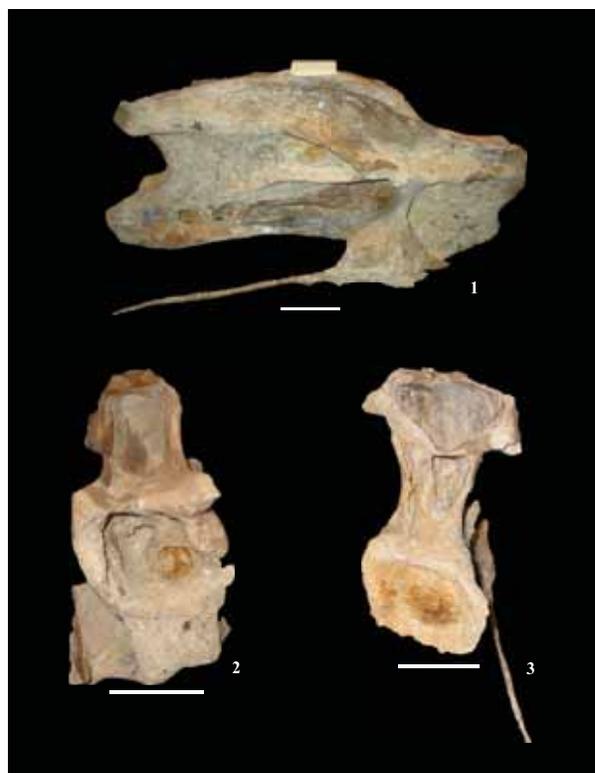
Figure 10. Fifth? cervical vertebra (FWMSH 93B-10-8) from Jones Ranch in right lateral (1), cranial (2), and caudal (3) views. Scale bars are 10 cm.

of the quarry and represent different positions within the dorsal series, most likely from more than one individual. In addition, a series of the last six vertebrae of the presacral column preserved in articulation with dorsal ribs, a complete pelvis, and a portion of the hindlimb of a single individual have been partially prepared. However, only the cranial

Figure 11. Cranial cervical vertebra rib fragments of *P. jonesi* (FWMSH 93B-10-32). Scale bar is 10 cm.

Table 3. Measurements of dorsal vertebrae of *Paluxysaurus jonesi* (in mm). See Table 2 for symbol notations. (Continued next page.)

Measurement	Specimen					
	FWMSH 93B-10-9	FWMSH 93B-10-11	FWMSH 93B-10-13	FWMSH 93B-10-13	FWMSH 93B-10-27	FWMSH 93B-10-27
Centrum length (condyle to cotyle)	--	217	270	--	204	195
Cranial centrum height	--	163	200	--	--	--
Cranial centrum width	--	248	--	159	206	--
Caudal centrum height	--	185	210	160e	175	230
Caudal centrum width	--	272	165+	193	238	273
Overall vertebral height	--	507+	654+	699+	565+	550+
Vertebral greatest width	867	629	530e	520e	520e	--
Prezygapophysis height	--	258	358	--	--	--
Postzygapophysis height	--	177	160	165	155	~140
Interprezygapophyseal distance	185	200	102	--	--	--
Diapophysis height from top of centrum	--	159	164	190	240+	--
Craniocaudal breadth of neural spine	--	50	102	102	56	--
Transverse breadth of neural spine	--	102	88	82	66	--
Centrum length without cranial ball	--	164	196	190	183	--

most vertebra in this series is informative, as the caudal five are less exposed and are extensively weathered. Measurable lengths of preserved limb elements from the quarry suggest that all sauropods individuals were comparable in size. Therefore, whereas representing different individuals, dorsal vertebrae from different regions of the presacral series are described based on the assumption that they are directly comparable.

The height-to-width ratio of dorsal vertebral centra is less than 1.0, except for the last dorsal centrum, which is approximately circular (Table 3). The ventral surfaces of the caudal half of the first dorsal centrum and some caudal dorsal vertebrae are strongly bevelled caudoventrally (Figure 12). The cranial articular ball is prominent in cranial and caudal dorsal vertebrae and the caudal articular surface of the centrum is strongly concave in all dorsals. Lateral pleurocoels in the dorsal vertebrae possess a distinct dorsal border. There is slight variation in the shape of pleurocoels, from clearly oval in the first dorsal vertebra to more eye-shaped in the third and more caudal dorsal vertebrae. Pleurocoels are elongated in dorsal vertebrae three and four, possessing sharply defined fossae occupying more than two-thirds of the centrum with the pneumatocoel at the cranial end. Pleurocoels become craniocaudally compressed near the end

of the dorsal series and are positioned cranially on the centrum.

In dorsal vertebrae of *P. jonesi* the parapophysis consists of a short, curved protrusion of bone that is convex on the cranial surface and, at least in caudal dorsal vertebrae, concave caudally. In the first dorsal vertebra the parapophysis is positioned about midway up the centrum, just cranial to the pleurocoel. Parapophyses migrate dorsally passing caudally along the dorsal series. The parapophyses migrate from the centrum to the neural arch between dorsal vertebrae three and four. In one caudal dorsal vertebra from Jones Ranch, TMM 42488 JP 1.2, the parapophysis occurs dorsal to the prezygapophysis but remains below the level of the diapophysis (Figure 13). This has not been documented in any other sauropod. Only *Haplocanthosaurus priscus* and *Brachiosaurus brancai* approach this condition. In other taxa the parapophysis is level with or ventral to the prezygapophysis in caudal dorsal vertebrae. Other caudal dorsal vertebrae from Jones Ranch do not offer sufficient preservation to assess the pervasiveness of this morphology.

Transverse processes of cranial dorsal vertebrae are robust, expanded dorsoventrally as well as craniocaudally. They are less expanded in caudal dorsal vertebrae. Diapophyses are horizontal in cranial dorsal vertebrae but begin to incline dor-

Table 3. (continued).

| Measurement	FWMSH 93B-10-27	FWMSH 93B-10-27	FWMSH 93B-10-27	TMM 42488 JP 1.1	TMM 42488 JP 1.2	TMM 42488 JP 1.31
				Specimen		
Centrum length (condyle to cotyle)	260e	280e	220e	--	196	--
Cranial centrum height	--	--	--	--	201	--
Cranial centrum width	--	--	--	--	246	--
Caudal centrum height	--	--	--	266	225	210e
Caudal centrum width	--	--	--	265	296	--
Overall vertebral height	--	--	--	593+	543+	664+
Vertebral greatest width	--	--	--	370e	400	880e
Prezygapophysis height	--	--	--	--	103	--
Postzygapophysis height	--	--	--	82	113	--
Interprezygapophyseal distance	--	--	--	--	29	--
Diapophysis height from top of centrum	--	--	--	293	268	278
Craniocaudal breadth of neural spine	--	--	--	--	40	--
Transverse breadth of neural spine	--	--	--	104	100	--
Centrum length without cranial ball	--	--	--	140	125	--
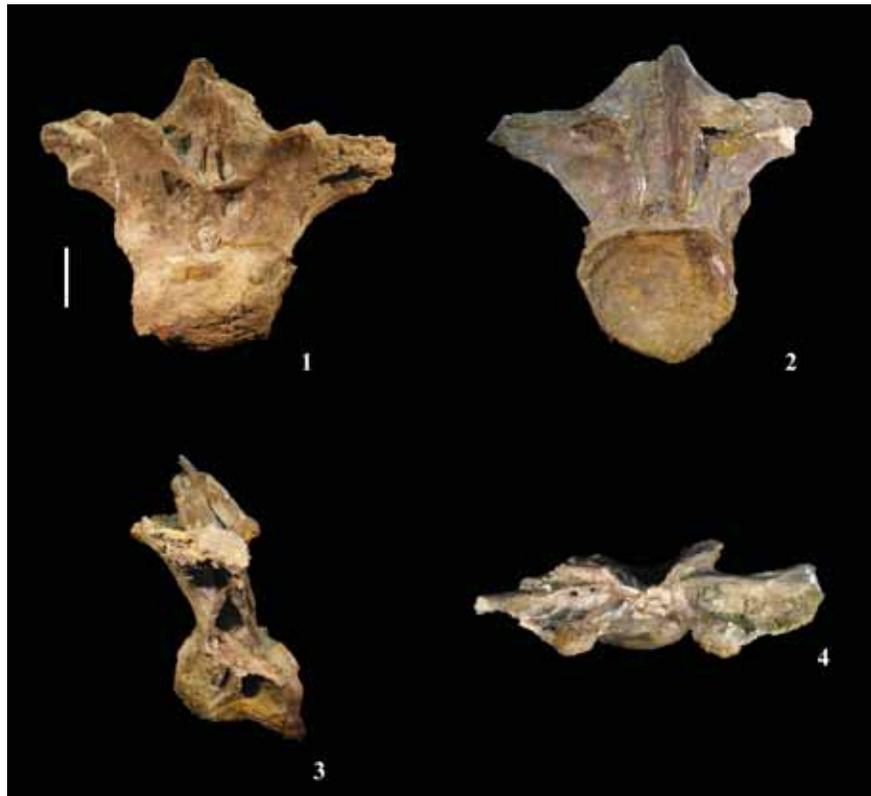
Figure 12. First dorsal vertebra (FWMSH 93B-10-11) of *P. jonesi* in cranial (1), caudal (2), left lateral (3), and dorsal (4) views. Scale bar is 10 cm.

Figure 13. Caudal dorsal vertebra of *P. jonesi* (TMM 42488 JP 1.2) in cranial (1) and right lateral (2) views. Scale bar is 10 cm.

sally in the middle of the series and become more strongly angled in caudal dorsal vertebrae, where they form approximately a 30° angle with the neural spine.

Neural spines are vertical in cranial dorsal vertebrae but are directed slightly caudally in caudal dorsal vertebrae. This upright orientation is the primitive condition exhibited by all sauropods except somphospondylians. In somphospondylians, dorsal neural spines are strongly angled caudally. In *P. jonesi* dorsal neural spines are broadly expanded transversely at their base and taper distally. Neural spines do not appear to flare at their distal ends as they do in *Brachiosaurus*; however, the terminal end of the neural spine is not completely preserved in any of the dorsal vertebrae from Jones Ranch. If dorsal neural spines did flare in *P. jonesi*, it was very minor.

Neural spines have a slightly greater craniocaudal breadth in dorsal vertebrae three and four, due to greater development of the prespinal lamina. There is no evidence of a hyposphene in the first dorsal vertebra. However, a strongly developed hyposphene is present on the caudal surface of the fourth dorsal vertebra. The hyposphene is much reduced on mid-dorsal neural arches, but the condition is presently unknown in caudal dorsal

vertebrae. As in the cervical vertebrae, the cranial face of the neural arch in cranial dorsal vertebrae is excavated by symmetrical fossae that occur above the neural canal and below the prezygapophyses.

The neural arches of the dorsal vertebrae of *P. jonesi* are supported by a greater number of vertebral laminae than those in the cervical vertebrae. Prominent tprl's connect the prezygapophyses in the first dorsal vertebra. A shorter, more horizontal tprl can be seen in dorsal vertebra three, but the lamina is not clearly developed in more caudal dorsal vertebrae. A short, but distinct horizontal connection can be recognized between the postzygapophyses in dorsal vertebra four but is absent in the first dorsal vertebra and in the caudal dorsal vertebral region. The cprl is broad and less sharply defined than other laminae throughout the dorsal series. In cranial dorsal vertebrae the cpol's form broad, parallel vertical columns on either side of the neural canal. In the fourth dorsal vertebra the cpol connects the base of the hyposphene to the caudal aspect of the neurocentral junction, and thus never actually contacts the postzygapophyses (Figure 14). With reduction of the hyposphene in caudal dorsal vertebrae, the cpol is also reduced or disappears completely. Mid-dorsal neural arches possess a small, shallow depression on the caudal
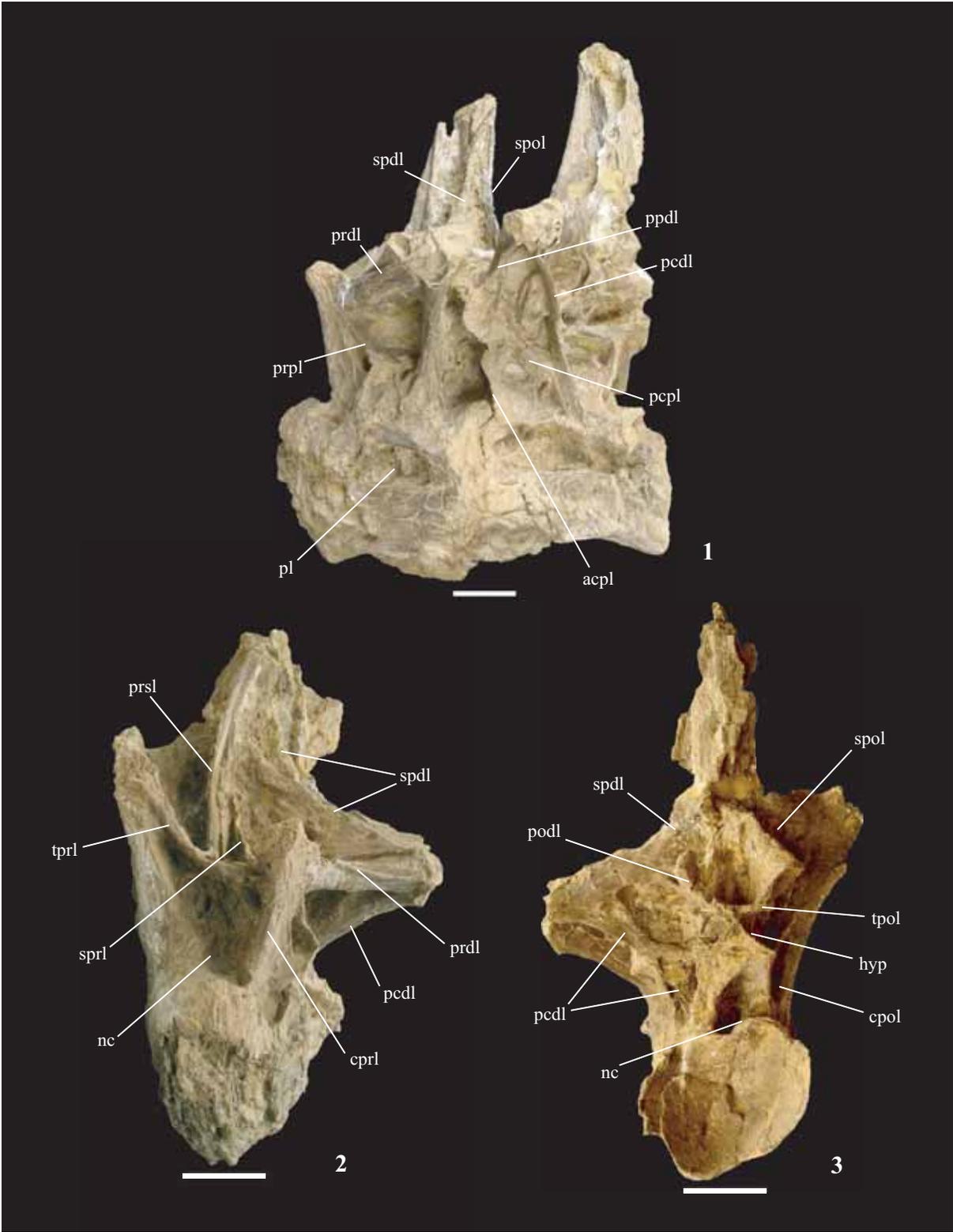
Figure 14. Articulated third and fourth dorsal vertebrae (FWMSH 93B-10-13) of *P. jonesi* in left lateral (1), cranial (2), and caudal (3) views. Scale bars are 10 cm.

surface, lateral to the hyposphene on each side of the vertebra.

Several laminae support the diapophysis and parapophysis on the neural arches of the dorsal vertebrae. The first dorsal vertebra has prominent cranial and caudal centrodiapophyseal laminae. The acdl meets the cprl at the craniodorsal margin of the centrum, forming deep infraprezygapophyseal and infradiapophyseal fossae craniodorsal and caudoventral to the acdl, respectively. No second dorsal vertebra has been recognized. In the third dorsal vertebra, the acdl is absent. A pcdl is present at this position in the dorsal series, and a single, large fossa is formed on the lateral aspect of the neural arch. In the fourth dorsal vertebra, the parapophysis has migrated dorsally onto the neural arch, just cranial and ventral to the diapophysis. In this case the parapophysis bisects what was the acdl in the first dorsal vertebra and is supported above and below by thin paradiapophyseal (ppdl) and anterior centroparapophyseal (acpl) laminae, respectively. The acpl appears in the mid- and caudal dorsal vertebrae of all sauropods except *Shunosaurus* (Wilson 2002). It is slightly longer than the ppdl in the fourth dorsal vertebra of *P. jonesi* and is oriented almost vertically. In more caudal dorsal vertebrae the ppdl is longer than the acpl. The pcdl is less expansive in mid- and caudal dorsal vertebrae as it is in cranial dorsal vertebrae. A posterior centroparapophyseal lamina (pcpl) first appears in the fourth dorsal vertebra and persists into caudal dorsal vertebrae. The presence of this lamina is a derived character shared by most neosauropods plus *Jobaria* but has been lost several times in the evolutionary history of sauropods. In dorsal vertebra four the pcpl connects the caudoventral aspect of the parapophysis to the cranial surface of the pcdl near its junction with the top of the centrum. The pcpl essentially divides the large infradiapophyseal fossa in half. Consequently, caudal to the parapophysis, the infradiapophyseal fossa is long and narrow. Below the parapophysis the acpl, pcpl, and dorsal margin of the centrum define the borders of a deep, roughly triangular infraparapophyseal fossa. The acpl and pcpl are less well developed and occur higher on the neural arch in caudal dorsal vertebrae. The conspicuous fossae that occur on the lateral surface of the neural arch in cranial and middle dorsal vertebrae also exhibit a dramatic reduction in the last dorsal vertebrae.

In dorsal vertebra three and more caudal vertebrae a short prezygoparapophyseal lamina (prpl) connects the parapophysis to the lateral surface of the prezygapophysis. The podl is short in cranial dorsal vertebrae, terminating proximally on the transverse process. In middle and caudal dorsal vertebrae the podl extends farther onto the caudal surface of the transverse process. A prespinal lamina (prsl) is particularly well developed in the third and fourth dorsal vertebrae as a thin plate of bone spanning the entire length of the neural spine. The prsl is rudimentary in the first dorsal and in caudal dorsal vertebrae and does not extend to the distal end of the spine. A weak postspinal lamina (posl) is visible in dorsal vertebra one, but there is no evidence of a posl in the other dorsal vertebrae where the caudal aspect of the neural spine is observable. In cranial dorsal vertebrae the sprl terminates near the base of the neural spine. In caudal dorsal vertebrae the sprl ends high up on the craniolateral aspect of the neural spine (Figure 14.1). In all dorsal vertebrae the spol originates on the lateral surface of the postzygapophyses and projects dorsomedially on both sides toward the midline of the neural arch forming a broad, V-shaped concave surface behind the neural spine. Only in mid-dorsal vertebrae of *P. jonesi* is the spol divided. A divided spol is a derived character that is lost in titanosaurians and is unknown in *Euhelopus*, the most basal somphospondylian, but is present in all other eusauropods, excluding *Shunosaurus*.

All *P. jonesi* dorsal vertebrae have expanded spinodiapophyseal laminae (spdl), which are responsible for producing a webbed appearance in the space between the neural spine and the diapophysis. In caudal dorsal vertebrae the spol is expanded equal to or more than the spdl and therefore also results in a broadly expanded region at the base of the neural spine. The spdl parallels the spol proximally on mid-dorsal neural arches. It is not clear whether the two laminae meet distally on the spine. Dorsal vertebrae possess a narrow but deep fossa on the caudal half of the lateral aspect of the neural spine that is bounded by the spdl, spol, and podl. One mid-dorsal vertebra, FWMSH 93B-10-27, exhibits a short accessory lamina that extends cranioventrally from the postzygapophysis and connects to the caudal aspect of the pcdl. In FWMSH 93B-10-27 this lamina defines the dorsal margin of a large, triangular fossa. In dorsal vertebra four (FWMSH 93B-10-13), there is an accessory horizontal lamina connecting the hyposphene to the middle of the pcdl, which serves as the dorsal border to the infrapostzygapophyseal fossa below, bounded by the pcdl and cpol cranially and caudally, respectively. The accessory postzygodiapophyseal lamina observed in FWMSH 93B-10-27 occurs above the fossa in FWMSH
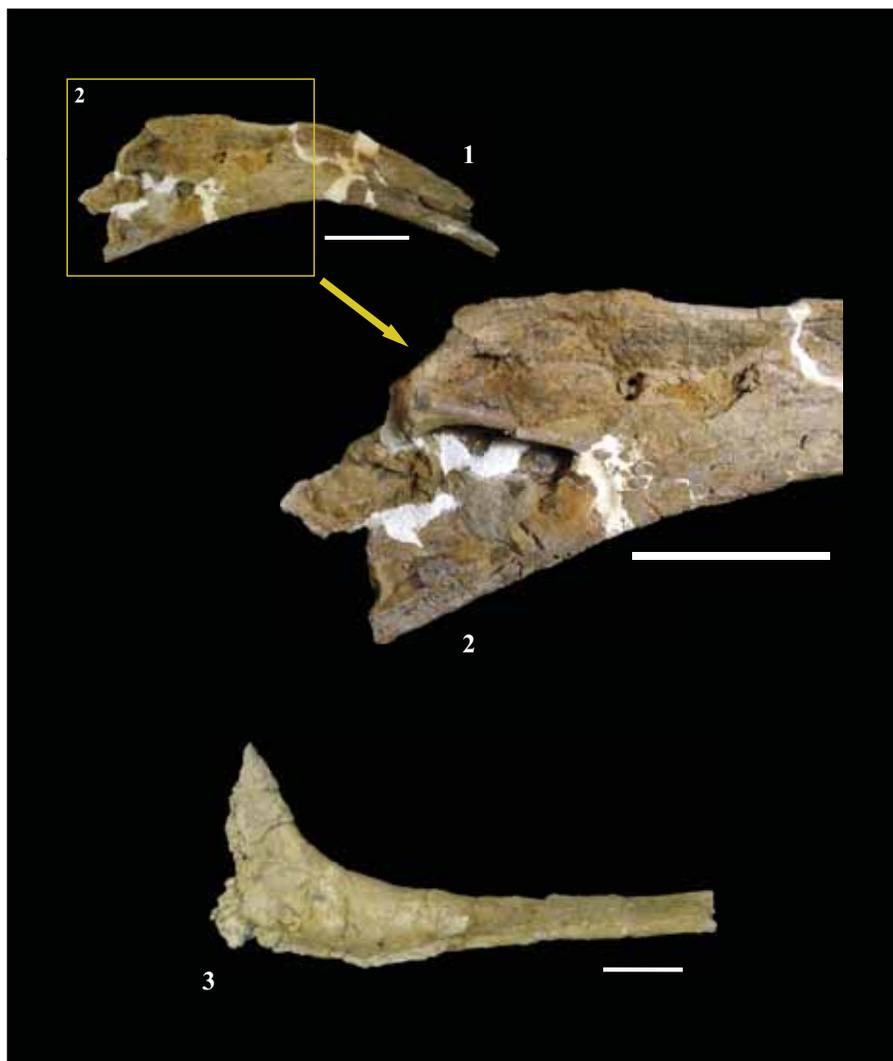
Figure 15. Dorsal ribs of *P. jonesi*. 1, FWMSH 93B-10-13 in caudal view; 2, close-up of the proximal end of FWMSH 93B-10-13 showing pneumatic cavities; 3, FWMSH 93B-10-23 in caudal view. Scale bars are 10 cm.

93B-10-13. An isolated centrum of a dorsal vertebra (FWMSH 93B-10-48) that has lost most of its exterior bone to erosion reveals a network of thin laminae of bone forming a honeycomb-like pattern. This picture of the internal pneumatic structure of presacral vertebrae in the Jones Ranch sauropod differs from the conclusions reached by Gomani et al. (1999) and Wedel (2003).

Dorsal Ribs. Dorsal ribs are broad, plank-like bones (Figure 15). Rib heads are somewhat triangular-shaped to almost L-shaped, with the capitulum oriented almost perpendicular to the proximal rib shaft. The capitulum is considerably longer than the tuberculum and narrows to a point at its distal end. The proximal third of the dorsal ribs has a convex caudal surface and concave cranial sur-

face. The proximal portion of a dorsal rib from Jones Ranch (FWMSH 93B-10-13) is rotated about the axis of the shaft distal to the proximal end (Figure 15.1). This twisting of the shaft is absent in FWMSH 93B-10-23 (Figure 15.2), which presumably represents a more cranial rib of *P. jonesi*. Some dorsal ribs exhibit pneumatic cavities on their proximal ends. Two distinct pneumatic cavities are preserved in FWMSH 93B-10-13. The smaller of the two excavates the tuberculum, and the larger is centrally located on the rib head and opens toward the rib shaft (Figure 15.2). However, the cavity itself does not seem to extend into the shaft of the rib.

Sacral Vertebrae. A nearly complete sacrum (FWMSH 93B-10-27) is known for *P. jonesi* but is

Table 4. Measurements of caudal vertebrae of *Paluxysaurus jonesi* (in mm). See Table 2 for symbol notations.

Specimen	Centrum length	Cranial centrum height	Cranial centrum width	Caudal centrum height	Caudal centrum width	Total height of vertebra
Cranial caudals						
FWMSH 93B-10-14-1	97	182	194	165	208	303+
FWMSH 93B-10-14-2	106	150	170	129	134	310
Middle caudals						
FWMSH 93B-10-21-1	137	--	--	--	180e	--
FWMSH 93B-10-21-2	131	112	168	--	--	280e
FWMSH 93B-10-21-4	128	117	144	125	144	256
FWMSH 93B-10-12-1	98	141	181	119	168	254
FWMSH 93B-10-12-2	103	111	164	100	158	217
Distal caudals						
FWMSH 93B-10-43	103	97	80	90	90	--
FWMSH 93B-10-41	109	79	88	69	81	142
FWMSH 93B-10-44	107	78	88	68	84	120+
FWMSH 93B-10-37	114	80	78	81	72	--
FWMSH 93B-10-17-1	100	--	--	68	75	134
FWMSH 93B-10-17-2	102	--	--	--	--	--
FWMSH 93B-10-17-5	89	62	51	--	--	121
FWMSH 93B-10-17-6	88	--	--	53	38	108
FWMSH 93B-10-17-7	86	54	38	46	37	91
FWMSH 93B-10-17-8	90	--	--	50	35	76
FWMSH 93B-10-38	83	58	59	50	48	--
FWMSH 93B-10-42	71	44	38	27	24	51

still undergoing preparation from a massive concretion. Only the ventral surface of the sacrum has been prepared. Four sacral vertebrae are preserved (S2-S5). A dorsosacral vertebra would have contributed a fifth vertebra (S1) to the sacral series but the centrum is missing, and all that is preserved are the transverse processes, which articulate with the ilia at the cranial end of the sacrum. The absence of a sixth sacral vertebra distinguishes *P. jonesi* from more derived somphospondylian sauropods. The centrum of the second sacral vertebra (S2) is partially exposed in three dimensions. It is small and appears compressed dorsoventrally. Relatively large sacral foramina occur between the transverse processes, or sacral ribs, of the vertebrae. Transverse processes are narrow craniocaudally at mid-length but expand distally and fuse to form the sacrocostal yoke. A more complete description of the sacrum awaits further preparation of the specimen.

Caudal Vertebrae. More than 37 caudal vertebrae have been collected from Jones Ranch. This number includes two associated series: five mid-caudal vertebrae (FWMSH 93B-10-21) and eight articulated distal caudals (FWMSH 93B-10-17). Pleurocoels are absent from the lateral surfaces of the centra, and the lateral depressions that are seen in caudal centra of some sauropod taxa have not been observed in *P. jonesi* except in one proximal centrum. All caudal vertebrae of *P. jonesi* are amphiplatyan. Centrum height is less than centrum width in proximal and mid-caudal vertebrae (Table 4). Distal caudal centra are spool-shaped and are typically slightly taller than they are wide. Some mid-caudal centra are rhombus-shaped in lateral view, with the articular surfaces angled craniodorsally (Figure 16.1). Chevron facets are weakly

Figure 16. Cranial and mid-caudal vertebrae of *P. jonesi* in left lateral (1), cranial (2), and caudal (3) views. Scale bar is 10 cm.

developed on the ventral surface of most caudal centra. A clearly defined hyposphene cannot be recognized in any caudal vertebra.

Transverse processes, or caudal ribs, are short and span the neurocentral junction in the first few caudal vertebrae. The processes are triangular in shape and curve slightly in the caudal direction. Transverse processes increase in length in mid-caudals and occur high on the centrum but do not extend onto the neural arch. In mid-caudal vertebrae transverse processes are dorsoventrally com-

pressed and broad craniocaudally at their origin, tapering laterally with a stronger caudal curvature. The neural arch is positioned cranially on the centrum of caudal vertebrae. Neural spines are short in proximal and mid-caudal vertebrae and are slightly caudally inclined (Figure 16.1). Proximal and mid-caudal neural spines flare laterally at the distal end (Figures 16.2 and 16.3).

Prezygapophyses are short and expanded dorsoventrally in the proximal most caudal vertebra, but extend well beyond the anterior margin of

Figure 17. Distal caudal vertebrae of *P. jonesi* in left lateral view. Scale bar is 10 cm.

Figure 18. Distal caudal vertebra of *P. jonesi* (FWMSH 93B-10-41) in lateral (1), cranial (2), and caudal (3) views. Scale bar is 10 cm.

Table 5. Measurements of chevrons of *Paluxysaurus jonesi* (in mm). See Table 2 for symbol notations.

Measurement	Specimen		
	FWMSH 93B-10-4	FWMSH 93B-10-4	TMM 42488 JP 1.43
Chevron length	143	157	293
Transverse breadth at distal end	--	--	23
Craniocaudal breadth at distal end	--	--	45
Depth of haemal canal	--	--	100

the centrum to articulate with the preceding vertebra in other caudals (Figures 16 and 17). Prezygapophyses are nearly horizontal in the majority of caudal vertebrae, but are angled craniodorsally in mid-caudals. Postzygapophyses are short throughout the caudal series.

Distinct spinoprezygapophyseal and spinopostzygapophyseal laminae are visible in proximal and mid-caudal vertebrae. Mid-caudal neural arches possess an intraprezygapophyseal lamina (tprl), which together with the sprl on each side of the arch encloses a prespinal fossa above the neural canal (Figure 16.2). Weakly developed prezygodiapophyseal laminae connect the transverse processes to the prezygapophyses in some mid-

Figure 19. Caudal chevrons of *P. jonesi* (FWMSH 93B-10-4) in cranial (1), lateral (2), and caudal (3) views. Scale bars are 10 cm.

caudal vertebrae, but are not visible in proximal caudals. Weak pre- and post-spinal laminae are preserved on the distal half of proximal and mid-caudal neural spines. Some proximal to mid-caudal vertebrae have lost the posl. None of the aforementioned laminae persist in distal caudals (Figure 18), and no other laminae present in the presacral series can be traced into the caudal region.

Chevrons. Three chevrons and fragments of at least three others were recovered from the Jones Ranch quarry (Table 5). Chevrons are Y-shaped in craniocaudal view but the rami are weakly forked proximally resulting in a narrow haemal canal. Chevrons are not forked in lateral view, which is a feature common to all titanosauriforms (Wilson and Sereno 1998). Shaft length of chevrons is greater than the length of the haemal canal. Chevron facets migrate to a more medial position passing caudally along the tail, and the haemal canal gradually becomes more restricted and shallower. In caudal chevrons the haemal canal becomes closed (Figure 19). Shafts are broader craniocaudally than transversely. Cranial chevrons broaden distally into the shape of a paddle. Caudal chevrons, on the other hand, taper distally. The shafts of chevrons have a slight caudal curvature. Chevron articular surfaces are round and angled medially.

Appendicular Skeleton

Pectoral Girdle

Scapula. Two almost complete scapulae were available for study, although according to the field notes of J. Pittman and D. Winkler, several other scapulae or scapulocoracoids have been collected from Jones Ranch but await preparation. The scapula of *P. jonesi* exhibits a strong medial concavity. The scapular blade is convex on the lateral surface and is roughly D-shaped in cross-section. The blade thins and flattens distally and is moderately to strongly expanded at the distal end on both the caudoventral (glenoid) and craniodorsal (acromial) margins, but to a greater degree along the latter (Figure 20). The scapular blade is concave along the acromial edge, but the degree of this cur-
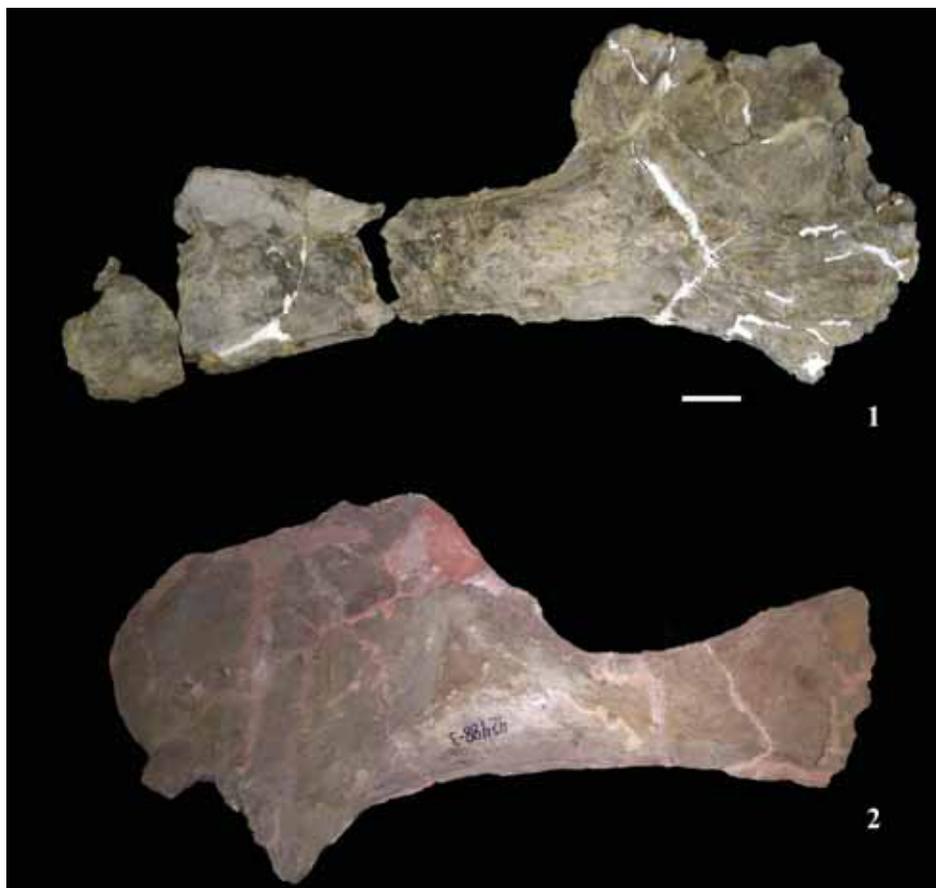

Figure 20. Scapulae of *P. jonesi* from Jones Ranch. 1, (FWMSH 93B-10-24) right scapula in lateral view; 2, (TMM 42488) left scapulocoracoid in lateral view (reversed). Scale bar is 10 cm.
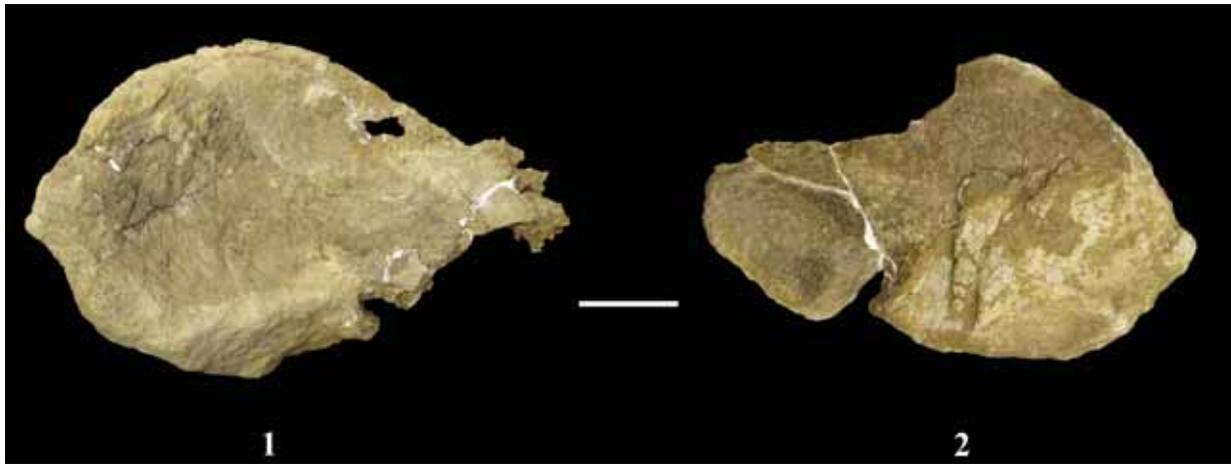
Figure 21. Coracoids of *P. jonesi* from Jones Ranch. 1, (FWMSH 93B-10-39) right coracoid in medial view; 2, (FWMSH 93B-10-34) in lateral view. Scale bar is 10 cm.

vature varies among individuals. The opposite margin is straight. The long axis of the scapular blade is oriented perpendicular to the coracoid articular surface. The coracoid articular surface of the scapula is longer than the glenoid surface. The scapular glenoid curves caudally and is slightly bevelled laterally. The acromion process is relatively short in *P. jonesi* scapulae and protrudes from the base of the shaft at a slightly acute angle. The supraspinous fossa occupying the area of the acromial notch, caudodorsal to the acromion process, is variable but generally weakly developed. The infraspinous fossa is broad and shallow.

Coracoid. Two right coracoids were found in close proximity to a right scapula and sternal plate (FWMSH 93B-10-24). A third coracoid is preserved

Table 6. Measurements of the pectoral girdle of *Paluxysaurus jonesi* (in mm). See Table 2 for symbol notations.

Measurement	Specimen		
SCAPULA	**FWMSH 93B-10-24**	**TMM 42488**	
Side	right	left	
Length	1432	1210+	
Greatest distal (superior) breadth	450e	400	
Greatest breadth (acromion to glenoid)	683	689	
Minimum breadth of shaft (dorsoventral)	213	203	
Length of coracoid articulation	319	--	
CORACOID	**FWMSH 93B-10-34**	**FWMSH 93B-10-39**	**TMM 42488**
Side	right	right	left
Coracoid height (proximodistal length)	357	309	329
Coracoid length (scapular articulation)	474	475	449
STERNAL PLATE	**FWMSH 93B-10-24**		
Side	--		
Sternal plate length	583		
Sternal plate width	289		

Figure 22. Sternal plate of *P. jonesi* found associated with a right scapula (FWMSH 93B-10-24). Scale bar is 10 cm.

in articulation with a left scapula (TMM 42488). The left coracoid (TMM 42488) strongly resembles the coracoid of *Camarasaurus grandis* (YPM 1901). The coracoid is rounded along its cranioventral margin, which is similar to all non-somphospondylian sauropods (Wilson 2002), and the medial surface of the bone is moderately concave (Figs. 20 and 21). Proximodistal length of the coracoid is less than the length of the scapular articulation, which is also primitive for sauropods (Wilson 2002, Table 6). The scapular articulation is straight. The glenoid end is thick and is bevelled laterally, similar to the scapula, whereas the bone thins considerably toward the cranial border. The caudal edge of the glenoid protrudes from the body of the coracoid as a distinct caudoventral process. The coracoid foramen is located near the middle of the bone very close to the margin of the scapular articulation.

Sternal Plate. The sternal plate of *P. jonesi* is a thin, flat bone and approximates a half-moon in outline (Figure 22). The medial margin is rounded, and the lateral border is straight. The sternal plate is elongated craniocaudally; its greatest length (measured from the craniodorsal margin to the caudoventral margin) is about twice that of the greatest transverse breadth (Table 6).

Forelimb

Almost every bone from the forelimb is known for *Paluxysaurus jonesi* with the exception of some manual elements. *P. jonesi* has a shorter forelimb than hindlimb, which is typical of most sauropods

except for *Brachiosaurus brancai*, *B. altithorax*, and *Cedarosaurus weiskopfae*. The forelimb bones of *P. jonesi* are slender relative to their overall length. Limb ratio measurements for *P. jonesi* and comparable values for other sauropod taxa are provided in Appendix 1.

Humerus. Of four humeri from Jones Ranch, three are nearly complete. An adult humerus of *P. jonesi* measures approximately 120-130 cm in length (Table 7). The humerus is hourglassed shaped. It is relatively gracile, and the transverse diameter at mid-shaft is slightly greater than the craniocaudal breadth (Figure 23). The proximal end of the humerus is relatively flat along the dorsal surface, with rounded lateral and medial corners, and little manifestation of a humeral head caudally, which occurs as a low, rounded bulge near the dorsomedial border. The proximal end is expanded medially, resulting in a concave medial edge of the shaft. The lateral margin exhibits minimal curvature. The deltopectoral crest is long and relatively narrow transversely.

The distal end of the humerus is expanded transversely. Distal breadth is approximately twice the minimum breadth of the shaft. On the caudal surface of the distal end, a well-defined olecranon fossa is bounded on both sides by distinct supracondylar ridges that extend from the lateral and medial epicondyles nearly to mid-shaft in some individuals. The distal articular surface is flat but with rugose texture, and in distal view the condyles angle caudolaterally.

Table 7. Measurements of the forelimb of *Paluxysaurus jonesi* (in mm). See Table 2 for symbol notations.

Measurement HUMERUS	Specimen			
	FWMSH 93B-10-2	FWMSH 93B-10-7	FWMSH 93B-10-7	TMM 42488 JP 1.21
Side	right	left	right	right
Greatest length	1245+	1294	782+ [1260e]	1200
Proximal transverse breadth	406	361	--	344
Distal transverse breadth	314	318	272.0	334
Minimum transverse breadth of shaft	162	152	159	169
Minimum craniocaudal breadth of shaft	114	105	100	91
Least circumference of shaft	451	435	434	457
Greatest width of dpc	83	87	--	98
Distance from distal end to start of dpc	--	668	629	684

ULNA	FWMSH 93B-10-7
Side	left
Greatest length	830
Proximal transverse breadth	278
Distal transverse breadth	153
Minimum shaft breadth	116
Least circumference	320

RADIUS	FWMSH 93B-10-7	FWMSH 93B-10-36
Side	left	right
Greatest length	789	473+ [790e]
Proximal transverse breadth	194	--
Distal transverse breadth	191	--
Minimum shaft breadth	85	--
Least circumference	253	--

Measurement METACARPALS	Specimen						
	FWMSH 93B-10-22 McII	FWMSH 93B-10-1 McIII	FWMSH 93B-10-10 McIV	FWMSH 93B-10-36 McI	FWMSH 93B-10-36 McII	FWMSH 93B-10-36 McIII ?	FWMSH 93B-10-36 McIV
Length	311	291+	357	321	--	375	--
Least circumference	197	167	176	179	--	159	--

Ulna. The forearm bones are slightly greater than 60% the length of the humerus (Appendix 1). One complete left ulna (FWMSH 93B-10-7) is known from the Jones Ranch assemblage. The distal end is bent proximomedially and caudally relative to the axis of the shaft as a result of taphonomic processes (Figures 24.1-24.4). The ulna is relatively slender, having a length that is over three times the greatest breadth at the proximal end (Table 7). Near mid-length the shaft is compressed craniocaudally. The distal end is considerably narrower than the proximal end and is approximately round in cross-section, but could be missing some bone on the caudomedial side (Figures 24.5 and 24.6).

Figure 23. Humeri of *P. jonesi* from Jones Ranch. 1-4, (FWMSH 93B-10-7) left humerus in three pieces in cranial (1), proximal (2), distal (3), and mid-shaft cross-sectional (4) views; 5, (TMM 42488 JP 1.21) right humerus in medial view; 6-8, (FWMSH 93B-10-7) distal half of a right humerus in cranial (6), caudal (7), and distal (8) views. Scale bar is 10 cm.

The proximal articular surface is nearly flat with a slightly elevated olecranon region. The proximal end of the ulna is approximately L-shaped with a deep radial fossa, which extends past mid-shaft of the bone, gradually shallowing and disappearing towards the distal end. A prominent caudal ridge extends from the proximal surface distally two-thirds of the length of the shaft. The craniomedial condylar process at the proximal end is longer and narrower than the craniolateral process (Figure 24.6).

Radius. A complete left radius (FWMSH 93B-10-7) of *P. jonesi* is preserved, found associated with the ulna described above (Figures 24.7-24.12). Similar to the ulna, the distal third of the radius is bent proximocaudally relative to the long axis of the shaft. The radius is somewhat shorter than the ulna (Table 7). The radius is compressed craniocaudally along the length of the shaft (Figures 24.9 and 24.10). Both ends are expanded transversely, the distal end being slightly more expanded than the proximal end. Distal breadth is close to twice the breadth at mid-shaft. The proximal end is triangular

in proximal view, and in distal view the condyle is sub-rectangular, the long axis running mediolaterally (Figures 24.11 and 24.12). A prominent ridge begins on the lateral margin of the shaft approximately one-third the length of the bone from the distal end, extends onto the caudal surface about halfway, and terminates at the caudal edge of the proximal condyle (Figure 24.8). This ridge fits into the radial fossa of the ulna.

Manus. A nearly complete set of metacarpals was found together along with a distal radius (FWMSH 93B-10-36). In addition to those, two complete, isolated metacarpals are known along with a third that is missing its distal portion. Comparisons of the isolated metacarpals with the articulated hand suggest that the third metacarpal was the longest in the forefoot (Table 7). The longest metacarpal-to-radius ratio could not be determined for a single individual. FWMSH 93B-10-10, identified as a metacarpal IV, was found near the ulna and radius described above (FWMSH 93B-10-7) and may belong to the same individual. A minimum ratio of the longest-metacarpal-to-radius-length using the

Figure 24. Left ulna and radius (FWMSH 93B-10-7) of *P. jonesi*. 1-6, ulna in cranial (1), caudal (2), medial (3), lateral (4), proximal (5), and distal (6) views; 7-12, radius in cranial (7), caudal (8), medial (9), lateral (10), proximal (11), and distal (12) views. Scale bar is 10 cm.

latter element was calculated to be 0.47 (Appendix 1). Metacarpals of *P. jonesi* are relatively long and slender compared to diplodocids. Assuming metacarpals of FWMSH 93B-10-36 are identified to the correct position in the manus, metacarpal I is shorter than metacarpal III, which is a primitive condition among sauropods (Upchurch 1998).

All of the metacarpals are expanded at their proximal end (Figure 25). Distal ends are only slightly expanded relative to the shaft. Two metacarpals exhibit a dorsolateral curvature of the distal shaft. In one other metacarpal, the shaft is contorted so that the proximal and distal ends are ori-

ented obliquely to one another. FWMSH 93B-10-22, identified as metacarpal II, has a triangular-shaped proximal condyle and a well-developed, rounded distal condyle (Figure 25.1). The proximal end is bevelled cranially and is expanded caudomedially. The proximal third of the medial surface of the bone is flat. At mid-shaft, a low ridge runs a short distance parallel to the length of the bone at the craniomedial edge. A probable metacarpal III (FWMSH 93B-10-1) is wedge-shaped in proximal view (Figure 25.2). The bone is broken at the distal end, but the preserved portion of the shaft is straight. Metacarpal IV (FWMSH 93B-10-10) is tri-

Figure 25. Dissociated metacarpals II, III, and IV of *P. jonesi* in proximal (a), dorsal (b), ventral (c), medial (d), lateral (e), and distal (f) views. 1, left Mc II (FWMSH 93B-10-22); 2, right? Mc III (FWMSH 93B-10-1); 3, left Mc IV (FWMSH 93B-10-10). Scale bar is 5 cm.

angular to L-shaped in proximal view (Figure 25.3). The distal condyle is weathered but is generally rounded in outline.

Pelvic Girdle

A large sandstone concretion (FWMSH 93B-10-27), containing a sacrum with associated pelvic girdle elements, other hindlimb bones, and dorsal vertebrae was removed from the Jones Ranch locality in 1997 and is currently being prepared in Fort Worth. The following description of the pelvic girdle is based on partially prepared elements of FWMSH 93B-10-27 plus additional material (pubes and ischia) found in the quarry.

Ilium. The cranial half of the ilium curves strongly laterally. The medial surface of the cranial half of

Table 8. Measurements of the pelvic girdle and hindlimb of *Paluxysaurus jonesi* (in mm). See Table 2 for symbol notations.

Measurement	Specimen			
ILIUM	**FWMSH 93B-10-27**			
Side	left			
Cranial (greatest) height	435			
Length	800+			
Cranial transverse breadth	850			
Distance between preacetabular processes	1424			
PUBIS	**FWMSH 93B-10-27**	**FWMSH 93B-10-35**	**FWMSH 93B-10-35**	**TMM 42488**
Side	left	left	right	right
Length	850+	966	930+	926+
Greatest breadth proximal end	--	--	--	313
Greatest breadth distal end	190	179+	248	154
Minimum craniocaudal breadth of shaft	--	158+	234	96+
ISCHIUM	**FWMSH 93B-10-27**	**FWMSH 93B-10-35**	**TMM 42488**	
Side	right	left	right	
Length	717+	479+	678+	
Proximal height	286	246+	324	
Minimum transverse breadth of shaft	58	--	55e	
Length of pubic peduncle	199	--	--	

the ilium faces cranioventrally but is not quite perpendicular to the axis of the sacrum. Its preacetabular process projects craniolaterally and is somewhat tapered. The distance separating the preacetabular processes of the ilia is significantly greater than the craniocaudal length of the ilium (Table 8). The pubic peduncle of the ilium is relatively short, and the ischial peduncle is significantly reduced, as is typical in all sauropods. Cranial to the pubic peduncle the ventral surface of the ilium is roughly straight, as opposed to concave.

Pubis. In addition to FWMSH 93B-10-27, an associated pubis and ischium (TMM 42488 JP 1.47, figures 26.1 and 26.2) were collected by J. Pittman in the early years of excavation at Jones Ranch, opposite pubes are associated with an ischium from another individual (FWMSH 93B-10-35, figure 26.3), and an articulated pubis and ischium were recently removed from the field and prepared (FWMSH 93B-10-51, figure 26.4). The pubis is a long, robust bone. The proximal end is moderately expanded craniocaudally and is thickened transversely at the iliac peduncle and acetabular surface. Development of the ambiens process is

minor. The shaft of the pubis is uniformly broad craniocaudally and the distal end is slightly expanded transversely relative to mid-shaft. The proximal one-half of the pubis is slightly laterally deflected beginning at the pubic apron, creating an S-shaped pubic symphysis similar to other eusauropods (Wilson 2002). The shaft of the pubis is long relative to the length of the puboischial articular surface, which is a primitive sauropod feature (Wilson and Sereno 1998).

Ischium. Five ischia have been collected (four prepared), with an additional specimen still in the field. Most of these are associated with other pelvic girdle elements. The ischium is a slender bone with an expanded pubic peduncle that is rectangular and forms a long articular surface for the pubis (Figures 26.2 and 26.4). The iliac peduncle is long and thickened transversely. A deep but not expansive acetabular surface is apparent cranioventral to the iliac peduncle. Distal to the pubic peduncle, the ischial blade abruptly narrows. The junction of the proximal shaft of the ischium and the pubic peduncle forms an angle of about 150 degrees, the shaft of the ischium projecting as much ventrally as cau-

Figure 26. Pelvic girdle elements of *P. jonesi*. 1, right pubis (TMM 42488 JP 1.47) in medial view; 2, right ischium (TMM 42488 JP 1.47) in lateral view (reversed); 3, left pubis (FWMSH 93B-10-35) in lateral view; 4, articulated left pubis and ischium in medial view (FWMSH 93B-10-51). Scale bar is 10 cm.

dally. In cross-section the distal shaft is thin and flat. The shaft is rotated about its long axis with respect to the proximal end so that in distal view the broader aspect of the shaft is angled ventromedially. The distal ends of opposing ischial shafts meet medially, forming a broad angle greater than 90 degrees in cross-section. The greatest length of the ischium is significantly shorter than that of the pubis (Table 8), but the length of the ischial shaft is nearly as long as the shaft of the pubis, which is plesiomorphic for this taxon. In articulation, at the ventral end of the puboischial contact, the pubis and ischium form nearly a right angle.

Hindlimb

Complete examples of upper and lower hindlimb bones are known for *P. jonesi* but few of the bones of the hindfoot have been identified. As in the forelimb, hindlimb bones are long and slender. Limb ratio measurements for the femur are compared across some sauropod taxa in Appendix 1. Similar comparisons were not made for the tibia and fibula due to the inconsistency in orientation of the tibia and direction of measurement chosen by different researchers for these bones.

Femur. The femur is the best-represented sauropod limb element from the quarry. Six complete or partial femora were available for study. Two of the better-preserved femora are depicted in Figure 27. Three additional femora were confidently identified in the field but have yet to be prepared. According to Pittman's field notes, a tenth femur was found in the late 1980s, but this bone cannot be located. The estimated minimum number of five sauropod

Figure 27. Femora of *P. jonesi*. 1-3, left femur (FWMSH 93B-10-3) in cranial (1), medial (2), and distal (3) views; 4-8, right femur (FWMSH 93B-10-25) in cranial (4), medial (5), caudal (6), proximal (7), and distal (8) views. Scale bar is 10 cm.

individuals from the quarry is based on the number of preserved femora.

At mid-shaft the transverse breadth is nearly twice the craniocaudal width in most individuals (Appendix 1). The proximal one-third of the shaft exhibits the prominent lateral bulge and medial deflection that has been interpreted as a synapomorphy of Titanosauriformes. As in other sauropods, the fourth trochanter is preserved as a broad, low ridge on the caudomedial surface of the shaft.

At the proximolateral border of the femur the greater trochanter is not prominent. The proximal surface of the femoral head is notably higher than the proximolateral border. The distal end of the femur is oriented perpendicular to the shaft and

distal condyles are well developed. In distal view the condyles trend slightly craniolaterally-caudomedially and are separated by deep intercondylar fossae on both the cranial and caudal surfaces. A lateral epicondyle also appears to be moderately developed at the distal end. Based on closely associated but not articulated humeri and femora, humero-femoral length ratios for *P. jonesi* fall between 0.85 and 0.88.

Tibia. Four tibiae have been identified. One is completely prepared (FWMSH 93B-10-15), and the other three are only partially prepared (TMM 42488, FWMSH 93B-10-45, and FWMSH 93B-10-46). FWMSH 93B-10-15 is a left tibia found with its corresponding fibula (Figures 28.1-28.6). Another

left tibia (TMM 42488) was collected prior to the involvement of SMU at Jones Ranch, and its provenance in the quarry is unknown.

The shaft of the tibia is strongly compressed craniomedially-caudolaterally and is more than twice as broad in the opposite direction, craniolaterally-caudomedially. The tibia is expanded at both ends relative to mid-shaft, but to a much lesser extent at the distal end (Table 9). The distal end is slightly wider transversely than craniocaudally, the articular surface for the ascending process extending out craniolaterally. The craniolateral margin of the shaft is concave, whereas the caudomedial aspect is straight. The proximal condyle is flat and diamond-shaped in proximal view. At the lateral margin, the proximal surface is strongly expanded, forming a broad tubercle that continues a short distance distally along the shaft as a low ridge. The proximal condylar surface, however, is more elongate fore to aft than transversely (Table 9). *Paluxysaurus jonesi* tibiae possess a pronounced cnemial crest. It is long, projecting craniolaterally, curving laterally at its distal extreme, and angling ventrally from the proximal condylar surface. A faint ridge extends the length of the shaft connecting the cnemial crest proximally with the articular surface for the ascending process at the distal end. Both the tibia and fibula of FWMSH 93B-10-15 were found near a right femur and right fibula (FWMSH 93B-10-25). On average, it is estimated that *P. jonesi* tibiae reach close to 60% of femur length (Appendix 1).

Fibula. Two fibulae from Jones Ranch are in the collections (FWMSH 93B-10-15 and FWMSH 93B-10-25). Both are heavily weathered. As noted above, FWMSH 93B-10-15 was found with a left tibia and FWMSH 93B-10-25 was associated with a right femur. The fibula is a slender bone (Figures 28.8-28.13) that is slightly longer than the tibia and close to two-thirds the length of the femur (Appendix 1). The proximal and distal ends are moderately expanded relative to mid-shaft, particularly in the craniocaudal direction, as in the tibia. Craniocaudal breadth at mid-shaft is slightly greater than the transverse breadth (Table 9). The distal end of FWMSH 93B-10-25 is expanded transversely to approximately 1.6 times the mid-shaft breadth and in FWMSH 93B-10-15 distal breadth is more than twice mid-shaft breadth. The lateral trochanter is well developed on the lateral surface approximately one-third the distance from the proximal end and is connected to the distal condyle by a low ridge. The proximal end is concave medially and convex laterally. The fibula thins at the proximocra-

nial border and has a small cranial prominence. The tibial articular surface, or tibial scar, is plainly visible. The fibula/femur length ratio is 0.67.

Pes. Only metatarsals I, II, and IV are known for *Paluxysaurus jonesi*. Excluding fragmentary metapodials that could not be assigned confidently to the fore or hindfoot, no other pedal elements, including phalanges, tarsals, astragali, or calcanei, have been discovered so far. Metatarsals I and II (FWMSH 93B-10-16) are from the right side and were found together in the quarry, while metatarsal IV (FWMSH 93B-10-26) is probably a left and was found as an isolated bone. The shorter metatarsal of FWMSH 93B-10-16 is identified here as metatarsal I but might in fact be metatarsal V. Due to uncertainty in the identification, characters in the phylogenetic analysis describing morphology of either metatarsal I or V were not scored and left as unknowns for *P. jonesi*.

Metatarsal II is longer than metatarsal I (Table 9). Both are robust bones and are particularly expanded at the proximal end (Figure 29). Proximal condyles of the first two metatarsals are compressed dorsoventrally, and the shaft of metatarsal II is also compressed. The transverse breadth of the distal end of metatarsal II is subequal to mid-shaft breadth. The distal end of metatarsal I is rotated medially with respect to the axis of the shaft. In metatarsal II, the distal end is rotated medially and bevelled proximoventrally with respect to the shaft. A well-developed proximomedial process is present on the ventral surface of metatarsals I and II. In metatarsal I this process extends onto the shaft and nearly reaches the distal end. Metatarsal IV is relatively slender compared to metatarsals I and II. The fourth metatarsal is expanded dorsoventrally at the proximal end. All three preserved metatarsals have well-developed, rounded distal condyles.

DISCUSSION

In recent years, the fossil record has seen an increase in the global diversity of sauropods from the Early Cretaceous. In North America, new forms have been described from Utah and Oklahoma. Additional undescribed material was reported from Utah (Britt and Stadtman 1996, Britt et al. 1997, 1998). Comparison of the Jones Ranch sauropod with specimens from the Early Cretaceous of North America and closely related titanosauriforms from other continents indicates that *Paluxysaurus jonesi* is morphologically distinct from previously described taxa.

Table 9. Measurements of the hindlimb of *Paluxysaurus jonesi* (in mm). See Table 2 for symbol notations.

Measurement	Specimen			
FEMUR	**FWMSH 93B-10-3**	**FWMSH 93B-10-25**	**FWMSH 93B-10-7**	**TMM 42488**
Side	left	right	right	left
Greatest length	1469	1442	1520e	1404+
Proximal transverse breadth	243+	383	--	--
Distal transverse breadth	299	359	340	--
Minimum transverse breadth	166	204	194	196
Mid-shaft craniocaudal breadth	115	109	--	103
Minimum circumference	445	509	--	513
Distance from distal end to 4th trochanter	784	810	808	--
TIBIA	**FWMSH 93B-10-15**	**FWMSH 93B-10-45**	**FWMSH 93B-10-46**	**TMM 42488**
Side	left	right	--	left
Greatest length	887	889	880	823
Proximal transverse breadth	154	--	--	100
Distal transverse breadth	181	--	--	133+
Minimum transverse breadth	90	--	--	--
Minimum circumference	331	--	--	--
Proximal craniocaudal breadth	169	--	--	129
Distal craniocaudal breadth	170	--	--	--
Mid-shaft craniocaudal breadth	100	--	--	--
FIBULA	**FWMSH 93B-10-15**	**FWMSH 93B-10-25**		
Side	left	right		
Greatest length	911	826+		
Proximal craniocaudal breadth	173	152		
Distal craniocaudal breadth	191	136		
Mid-shaft craniocaudal breadth	97e	73e		
Minimum circumference	265	235		
Proximal transverse breadth	89	82		
Distal transverse breadth	89+	132		
Minimum transverse breadth	63	73		
METATARSALS	**FWMSH 93B-10-16 Mt I**	**FWMSH 93B-10-16 Mt II**	**FWMSH 93B-10-26 Mt IV**	
Side	right	right	left?	
Length	172	190	195	
Proximal transverse breadth	158	163	47+	
Distal transverse breadth	65+	91	52+	
Minimum transverse breadth	73	85	49	
Least breadth of the shaft	43	28	47	
Least circumference	211	206	164	

Figure 28. Associated tibia and fibula of *P. jonesi*. 1-6, left tibia (FWMSH 93B-10-15) in cranial (1), caudal (2), medial (3), lateral (4), proximal (5), and distal (6) views; 7-12, left fibula (FWMSH 93B-10-15) in cranial (7), caudal (8), medial (9), lateral (10), proximal (11), and distal (12) views. Scale bar is 10 cm.

Pleurocoelus nanus Marsh 1888

Astrodon johnstoni was named from isolated teeth from the Arundel Formation of Maryland. Leidy (1865) provided a brief description of the teeth. Marsh (1888) described isolated and associated sauropod material from the Arundel sedi-ments that he referred to the taxon *Pleurocoelus nanus*, and he referred additional material of what he claimed to be a second, smaller species to *Pleurocoelus altus*. The distinction made between *Pleurocoelus nanus* and *Pleurocoelus altus* is primarily based on size (e.g., Marsh 1888, Gilmore 1921). Salgado et al. (1995) contended that *P.*

Figure 29. Metatarsals of *P. jonesi* in proximal (a), dorsal (b), ventral (c), lateral (d), medial (e), and distal (f) views. 1, right Mt I? (FWMSH 93B-10-16); 2, right Mt II (FWMSH 93B-10-16); 3, left? Mt IV (FWMSH 93B-10-26). Scale bar is 5 cm.

nanus and *P. altus* are not different size individuals of the same species, but provide no evidence to support this claim. I concur with Hatcher (1903b) and more recent authors (e.g., Carpenter and Tidwell 2005) that there is currently insufficient evidence to recognize more than one distinct species of sauropod from the Arundel Formation (contra Lull 1911 and Gilmore 1921). Hatcher (1903b) argued for synonymizing *Astrodon* and *Pleurocoe-*

lus, the former name having precedence; however, *Pleurocoelus* continues to be used to refer to the material described by Marsh (1888). Recently, Carpenter and Tidwell (2005) returned to this topic and suggested that referral of *Pleurocoelus* type and referred material to *Astrodon* by Hatcher (1903b) as first reviser gives *Astrodon* priority. Carpenter and Tidwell (2005) did not address the validity of the name *Astrodon* based only upon teeth. The

taxonomy of the Arundel sauropod material is problematic and likely will remain unresolved until additional material is found. Fragmentary sauropod remains from other regions that have been referred to *Pleurocoelus* (e.g., Lydekker 1889, 1890 and Rich et al. 1983), including specimens from Texas (Langston 1974 and Gallup 1989), may not be correctly assigned and need to be re-examined. Regardless of the name used for the Maryland taxon, *Paluxysaurus* can be differentiated from the Arundel sauropod material.

Some differences in morphology between *Paluxysaurus* and the Arundel sauropod (hereafter referred to as *Pleurocoelus* for simplicity) can be detected in the skull. Tooth crowns of *Paluxysaurus* are less compressed than in *Pleurocoelus.* The caudoventral margin of a small maxilla of *Pleurocoelus* (USNM 5667) slopes gradually caudodorsally, whereas this portion of the maxilla is more steeply angled in *Paluxysaurus*. The palatine shelf on the medial surface of the maxilla is narrower dorsoventrally and is more prominent than in *Pleurocoelus*, and the dorsal surface of the palatine shelf is broadly concave in *Paluxysaurus* while it is nearly horizontal in *Pleurocoelus*.

Few diagnostic features can be observed in the axial skeleton of *Pleurocoelus*. Nearly all of the vertebrae referred to this taxon lack neural arches so they are of limited comparative value. Presacral bone texture of *Pleurocoelus* is solid but vertebral centra are excavated by large, deep lateral pneumatic fossae. Presacral vertebrae of *Paluxysaurus jonesi* are more cavernous and more closely resemble vertebrae of *Brachiosaurus* in their internal structure. However, as noted by Wedel (2003), all known vertebrae of *Pleurocoelus* are from juvenile individuals, and it is not well understood how vertebral pneumaticity in sauropods changes with ontogeny.

The appendicular material of *Pleurocoelus*, however, is more distinctive. *Paluxysaurus jonesi* differs from *Pleurocoelus* in having an expanded distal scapular blade that is not rounded on the acromial side. Although the distal end of the *Paluxysaurus* scapula is expanded on the acromial side, it is distinctly different from a distal scapular blade referred to *Pleurocoelus* (USNM 8474) and the scapulae of *Camarasaurus* and *Brachiosaurus*, in that these taxa have a rounded expansion on the acromial side of the distal scapular blade, but the opposite edge of the blade is nearly straight. In *Paluxysaurus*, the scapula expands on both the acromial and glenoid margins.

Limb bones of *Paluxysaurus* are generally more slender than those of *Pleurocoelus* (Appendix 1). A juvenile femur of *Pleurocoelus* (USNM 5696) exhibits a lesser degree of medial deflection of the proximal end than the femora of *Paluxysaurus*, and the greater trochanter of the femur is less prominent in the Texas sauropod. The shape of the proximal condyle of a tibia referred to *Pleurocoelus* (USNM 5657) is more rounded (less craniocaudally expanded) than in *Paluxysaurus*.

Cedarosaurus weiskopfae Tidwell et al. 1999

Cedarosaurus weiskopfae is known from a partial skeleton of a single individual (DMNH 39045) from the Yellow Cat Member of the Cedar Mountain Formation in east-central Utah. Tidwell et al. (1999) considered the new taxon to be a brachiosaurid, most closely related to "*Pleurocoelus.*"

The most conspicuous differences in morphology between *Paluxysaurus jonesi* and *Cedarosaurus weiskopfae* occur in the caudal vertebral series. Caudal neural spines project craniodorsally from the neural arch in cranial to mid-caudals of *C. weiskopfae*. All caudal vertebrae of *P. jonesi* have neural spines that are inclined caudodorsally. Distal caudal centra of *P. jonesi* are shorter than in *C. weiskopfae* and are more rounded, with height-to-width ratios, on average, slightly greater than 1.0. Centra of distal caudals in *C. weiskopfae* are noticeably wider than tall, some having height-to-width ratios as low as 0.58.

Chevrons of *P. jonesi* have a relatively short haemal canal, comprising less than 40% of the overall length of the bone. A short haemal canal is a feature shared by *Brachiosaurus* and all more primitive sauropods. The only chevron preserved for *C. weiskopfae* appears to have a broader, deeper haemal canal; however the shaft of the chevron is broken and it is unclear how long this segment of the bone was.

Sternal plates of *P. jonesi* and *C. weiskopfae* are similarly shaped but in the former the bone is less broad transversely. In *C. weiskopfae*, sternal plate length is 73% greater than the transverse breadth. The sternal plate of *P. jonesi*, however, is twice as long as it wide. *Paluxysaurus jonesi* has a shorter acromion processes at the proximal end of the scapula than *C. weiskopfae*. The acromial side of the proximal end of the scapula in *C. weiskopfae* is markedly expanded in comparison to *P. jonesi*. The coracoid of *P. jonesi* is relatively longer proximodistally than *C. weiskopfae* and has a more rounded cranioventral margin.

The humerus of *C. weiskopfae* is slightly more slender than that of *P. jonesi* (Appendix 1). *Paluxysaurus jonesi* exhibits a greater humero-femoral length ratio than what is observed in more primitive sauropods, but the forelimb is distinctly shorter relative to the hindlimb compared to the condition in *C. weiskopfae* and *Brachiosaurus*. The ulna of *P. jonesi* is broader at mid-shaft than is *C. weiskopfae*, and the olecranon region is raised slightly higher above the proximal condyle in the former. The craniolateral arm of the proximal condyle of the ulna is significantly longer in *P. jonesi*, and the craniomedial arm is broader compared to *C. weiskopfae*. In *C. weiskopfae*, the proximal one-half of the preserved segment of the ulna is expanded craniomedially, resulting in a concave craniomedial margin of the shaft. The ulna of *P. jonesi* is less expanded craniomedially at the proximal end and below the proximal condyle. *Cedarosaurus weiskopfae* is primitive with respect to *P. jonesi* and other sauropods, except for *Venenosaurus dicrocei*, *Diplodocus* sp., and *Vulcanodon karibaensis*, in having a radius with a narrow, rounded distal condyle. In other sauropods the distal end of the radius is expanded transversely relative to mid-shaft and the distal condyle is more rectangular in shape (Appendices 3, 4).

The proximal end of the *C. weiskopfae* pubis is more expanded cranially relative to *P. jonesi*. The pubic peduncle of the ischium is broader in *P. jonesi*, whereas the iliac peduncle is more expanded craniocaudally in *C. weiskopfae*. In *P. jonesi*, the femur exhibits a greater degree of medial deflection along the proximal one-third of the shaft and a less prominent greater trochanter than in *C. weiskopfae*. The proximal tibia of *P. jonesi* is more expanded craniocaudally compared to *C. weiskopfae* and has a more prominent cnemial crest. Metatarsal II of *P. jonesi* differs from *C. weiskopfae* in that it possesses a strong medial process at the distal end. The shaft of metatarsal II in *C. weiskopfae* is more concave medially than in *P. jonesi*.

Venenosaurus dicrocei Tidwell et al. 2001

Venenosaurus dicrocei comes from the Poison Strip Member of the Cedar Mountain Formation in Utah, which is stratigraphically younger than the Yellow Cat Member that produced *Cedarosaurus weiskopfae*. *Venenosaurus dicrocei* is represented by a partial skeleton of a single individual (DMNH 40932). Some juvenile remains from the same locality may also be referable to this species. Tidwell et al. (2001) identified *V. dicrocei* as a titanosauriform that is intermediate in its morphology between *Brachiosaurus* and titanosaurians.

Caudal centra of *Paluxysaurus jonesi* lack the fossae present on the lateral surfaces of cranial caudal vertebrae of *V. dicrocei*. Like *Cedarosaurus weiskopfae*, mid-caudal neural spines of *V. dicrocei* are directed cranially, a condition that is unique to these two taxa.

The glenoid process of the scapula is weakly developed in *P. jonesi* compared to *V. dicrocei*, in which the glenoid process is quite long. Similar to *C. weiskopfae*, the craniolateral arm of the proximal ulnar condyle is short in *V. dicrocei* relative to *P. jonesi*. The proximal condylar arms in *V. dicrocei* are straight, robust processes. The ulna of *V. dicrocei* possesses a shallower radial groove than *P. jonesi* and *C. weiskopfae*. As in *C. weiskopfae*, *V. dicrocei* possesses a narrow, rounded distal radial condyle that is in sharp contrast to the distal radius of *P. jonesi*.

The pubis of *P. jonesi* differs from *V. dicrocei* in that the cranial edge of the pubic blade is straight, as opposed to concave in *V. dicrocei*. The ischium of *P. jonesi* exhibits a less pronounced caudal curvature than *V. dicrocei*.

Similar to *C. weiskopfae*, the shaft of metatarsal II in *V. dicrocei* has a stronger medial concavity than in *P. jonesi*. The proximomedial process on the caudal surface of metatarsal II in *P. jonesi* is positioned closer to the midline of the bone in *V. dicrocei*. Metatarsal IV of *P. jonesi* is missing a portion of the medial surface, but the bone is more robust than the fourth metatarsal of *V. dicrocei*.

Sauroposeidon proteles Wedel et al. 2000a

The type specimen of *Sauroposeidon proteles*, which consists of four articulated cervical vertebrae (OMNH 53062), is known from the Antlers Formation of southern Oklahoma. Wedel et al. (2000a, 2000b) concluded that *S. proteles* is most closely related to *Brachiosaurus brancai*. Elongation indices (EI) for cervical centra of *Paluxysaurus jonesi* overlap with the ranges for both *S. proteles* and *B. brancai*. Cervicals of *B. brancai* generally have EI values below 5.0, but reach a maximum of 5.4 (Wedel et al. 2000b). In addition, EI values for the sixth cervical vertebra in individuals of *B. brancai* vary by as much as 0.9. In *S. proteles*, EI values range from 4.6 to 6.1 (Wedel et al. 2000b). Similarly, *P. jonesi* cervical vertebrae exhibit a large range in EI values, and the centrum length-to-caudal height ratios are similar to *Malawisaurus dixeyi*, a significantly smaller taxon. Overlap in EI values among sauropod taxa of different ages and of dif-
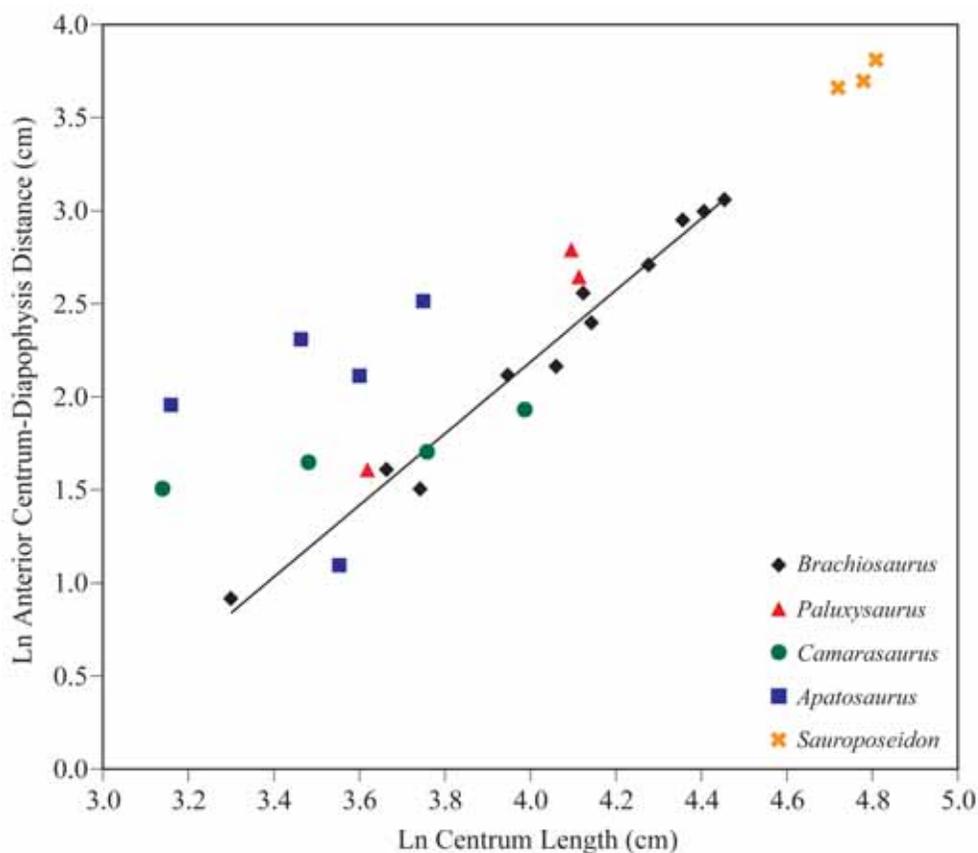
Figure 30. Plot of the measured distance from the cranial end of the cervical vertebral centrum (measured from the caudal end of the cranial ball, or condyle) to the diapophysis as a function of total centrum length (measured from the caudal end of the cranial ball to halfway up the caudal articular surface) for the cervical series 3-8. Axes have been transformed to natural logarithmic space. The regression line [Ln y = 1.925(Ln x) − 5.5126; R^2 = 0.9803] represents the curve that best fits the data for *Brachiosaurus brancai*.

ferent recent ancestry, demonstrates that length of cervical centra relative to caudal height is not necessarily a useful character for distinguishing between taxa.

Cervical vertebrae from Jones Ranch differ from *S. proteles* and *B. brancai* in having a well developed, long anterior centrodiapophyseal lamina (acdl). This lamina is short in *B. brancai* and cannot be seen in lateral view in illustrations of the cervicals provided by Janensch (1950). The acdl is completely absent from the four cervicals of *S. proteles*. Neural arches of mid-cervical vertebrae of *P. jonesi* are broader than in *S. proteles* and *B. brancai*. Mid-cervicals of *P. jonesi* have prominent, transversely expanded prezygodiapophyseal laminae (prdl) (see Figure 10.2). In both *S. proteles* and *B. brancai* transverse processes are less broad and thus the prdl is less expanded.

Wedel et al. (2000a, 2000b) cited the extreme caudal position of the diapophyses on the neural arch of *S. proteles* cervicals as a character that dis-

tinguishes it from *B. brancai* and other sauropods. However, the distance of the diapophysis from the cranial end of the centrum (minus the cranial condyle) in *S. proteles* increases with total centrum length serially along the column by the same proportion as in *B. brancai* (Figure 30). This suggests that the difference observed in the relative position of the diapophysis in cervicals of *S. proteles* and *B. brancai* may simply be a function of size of the individual. In cervical vertebrae of *P. jonesi*, *Camarasaurus*, and *Apatosaurus*, distance of the diapophysis from the cranial end of the centrum varies relative to centrum length by a different scaling factor or shows no significant relation.

SMU 61732 (*Pleurocoelus* sp. Langston 1974)

SMU 61732 consists of a series of 21 caudal vertebrae, fragments of cervical and dorsal vertebrae, a chevron, dorsal ribs, a distal scapula, and two teeth. The teeth from SMU 61732 are not well preserved. They are generally similar in size and

morphology to those from Jones Ranch, FWMSH 93B-10-33 in particular (Figures 6.9-6.11), but possess a high-angled planar wear facet as opposed to the V-shaped wear facets observed in most of the teeth from Jones Ranch. The difference in wear morphology may simply be a function of position in the tooth row. The one cervical and one dorsal vertebra from the Wise County locality both have badly crushed neural arches and reveal little about their morphology. No obvious differences can be seen from cervical and dorsal centra from Jones Ranch beyond what could be considered serial and/or individual variation in sauropod presacral vertebrae. From what is preserved of the neural arch, the cervical vertebra of SMU 61732 has prominent diapophyseal laminae as in cervicals from Jones Ranch.

Caudal centra of *Paluxysaurus jonesi* have flat articular surfaces whereas cranial caudal centra of SMU 61732 have moderately concave cranial articular surfaces and slightly convex caudal faces. A distinct hyposphene articulation is visible on the neural arch of a cranial to mid-caudal vertebra of SMU 61732. Nothing similar to this is preserved in the caudals known from Jones Ranch. Cranial and mid-caudal vertebrae of *P. jonesi* have transversely broader neural spines. Differences portrayed in the caudal vertebrae from Jones Ranch and SMU 61732 may be misleading if the vertebrae represent different positions in the tail. If that is the case, considering the amount of serial variation in sauropod caudal vertebrae, these differences seem less significant. Procoelous and amphiplatyan centra are found in the tail of *Malawisaurus dixeyi*, a basal titanosaurian sauropod from the Early Cretaceous of East Africa. In *M. dixeyi*, however, the procoelous caudals occur at the front of the tail, and caudal vertebrae from the cranial portion of the tail in *P. jonesi* (FWMSH 93B-10-14) are clearly not procoelous.

The distal end of the scapula of *P. jonesi* is slightly more expanded on the acromion side than in SMU 61732. Consequently, the acromial, or craniodorsal, margin of the scapular blade appears concave while it is straighter in the Wise County specimen. In scapulae of *Brachiosaurus brancai* significant variation exists in the amount of expansion to the acromial side of the distal blade (see Janensch 1961; plate 15, figures 1 and 2). The difference in morphology between the scapulae of *Palauxysaurus jonesi* and SMU 61732 noted here is no greater than the range of variation seen in *Brachiosaurus brancai*. The shape of the distal scapula of SMU 61732 differs from the condition in

Pleurocoelus, the genus that Langston (1974) referred this specimen to. Despite the differences noted above between *Paluxysaurus jonesi* and SMU 61732, from the currently available material, the latter cannot confidently be distinguished as a separate genus.

Cloverly Formation

Sauropod bones from the Cloverly Formation in Wyoming and Montana were described by Ostrom (1970), which he tentatively referred to the "Titanosauridae." Two dorsal vertebrae of the Cloverly sauropod (YPM 5449) figured by Ostrom (1970, plate 13f and 13g) are similar to those from Jones Ranch and may be referable to the same genus. However, noticeable differences in morphology exist between the specimens that may preclude from calling them the same species. Dorsal vertebrae of *P. jonesi* have slightly taller neural arches than the dorsals of YPM 5449 and the centrum of the first dorsal vertebra of *P. jonesi* (FWMSH 93B-10-11) has a caudoventral lip that is absent in the cranial dorsal of the Cloverly specimen. Postzygapophyses are horizontal in FWMSH 93B-10-11, whereas they are angled in the Cloverly sauropod, and the neural spine is slightly broader in the *P. jonesi* vertebra. Neural spines of caudal dorsals of the Cloverly sauropod are slightly more caudally inclined than those of the Texas sauropod. Pleurocoels on the lateral surfaces of centra of Jones Ranch dorsal vertebrae are generally eye-shaped, as opposed to the more oval cavities in the Cloverly sauropod. Apart from these minor differences, the cranial dorsal vertebra of YPM 5449 is virtually indistinguishable from FWMSH 93B-10-11.

Appendicular elements from the Cloverly Formation show fewer similarities to *P. jonesi* than do the dorsal vertebrae. The dorsal vertebrae of YPM 5449 are close to the size of dorsals of *P. jonesi*. However, an ulna associated with the same dorsal vertebrae of the Cloverly sauropod is approximately 20 cm shorter and more robust than the ulna of *P. jonesi*. Humeri of *P. jonesi* differ from an isolated, partial humerus from the Cloverly Formation (YPM 5452) in that the proximal surface is inclined medially, forming an angle greater than 90° at the proximolateral border. In the Cloverly specimen, the proximal surface is flat and forms a right angle with the lateral margin of the shaft. TMM 42488 JP 1.21 from Jones Ranch has a more horizontal proximal surface than other humeri from Jones Ranch and resembles the Cloverly humerus more than FWMSH 93B-10-2 and FWMSH 93B-

10-7. The proximomedial border of the Cloverly humerus is more expanded and pointed, and the medial edge of the shaft is more concave than in humeri of *P. jonesi*.

A right femur of the Cloverly material (YPM 5451) is missing the proximal end. The measured distance between the distal end of the femur and the fourth trochanter is greater than that in femora from Jones Ranch, suggesting that the complete length of YPM 5451 would have exceeded that known for *P. jonesi*. An isolated left tibia (YPM 5450) from the Cloverly Formation is longer and more slender than tibiae of *P. jonesi*. In the latter, tibiae are more expanded at the proximal end. Moreover, the dorsal margin of the cnemial crest occurs slightly below the proximal condyle, whereas in the Cloverly tibia the top of the cnemial crest and the proximal condyle appear to be at the same level. Teeth of *P. jonesi* are broadly similar in form to isolated teeth from the Cloverly Formation but have a tendency to be broader at mid-crown.

Euhelopus zdanskyi Wiman 1929

Maxillae of *Paluxysaurus jonesi* and *Euhelopus zdanskyi* exhibit some obvious differences in morphology. The ascending, or nasal, process in *P. jonesi* is relatively short and more than twice as broad as it is *E. zdanskyi*. The nasal process of the maxilla is angled less caudally (i.e., more vertical) in *P. jonesi*, forming a broader cranioventral margin of the antorbital fenestra. Teeth of *P. jonesi* have a more prominent longitudinal ridge on the lingual surface of the crown. Presacral vertebrae of *P. jonesi* lack the bifurcating neural spines that are present in *E. zdanskyi*, and in contrast to the Asian taxon, cranial cervical centra of *P. jonesi* are wider than they are tall (Table 2).

Phuwiangosaurus sirindhornae Martin et al. 1994

Cranial cervical vertebrae of *Paluxysaurus jonesi* are transversely narrower than those of *Phuwiangosaurus sirindhornae*. As in *Euhelopus zdanskyi*, *P. sirindhornae* has bifid caudal cervical and cranial dorsal neural spines, which is absent in *P. jonesi*. The glenoid process of the scapula is directed more ventral and the distal humerus is more transversely expanded in *P. sirindhornae*. The craniomedial process of the proximal condyle of the ulna in *P. jonesi* is roughly horizontal and level with the craniolateral arm compared to *P. sirindhornae*, in which the craniomedial arm is directed ventrally. Cranial caudal neural spines are more vertically oriented in *P. sirindhornae* and are

not transversely expanded at the distal end. Distal caudal centra of *P. jonesi* are shorter than in *P. sirindhornae*.

CLADISTIC ANALYSIS

A parsimony analysis was performed using PAUP* 4.0 beta 10 using a modified version of Wilson's (2002) character matrix. A total of 32 sauropod genera and two outgroup taxa were scored for 230 morphological characters (Appendices 3, 4). Sauropod genera containing multiple species were scored based on a combined knowledge of the morphology of all the species. Five Early Cretaceous taxa included in this analysis were not among the 27 original taxa used in Wilson's analysis. These include *Pleurocoelus*, *Paluxysaurus*, *Cedarosaurus*, and *Venenosaurus* from North America and *Phuwiangosaurus* from Asia.

Some modifications were made to Wilson's (2002) original character matrix for this analysis. The number of sacral vertebrae contributing to the acetabulum was omitted as a character from this analysis, because titanosaurians exhibit a different condition from other sauropods for this character that was not described in Wilson's (2002) character list. Therefore, new taxa added in the present analysis could not be evaluated for this state. An additional derived character state was added to describe the orientation of mid-caudal neural spines in sauropods (character 132, Appendix 3), to account for the condition observed in *Cedarosaurus* and *Venenosaurus*, changing it from a binary character to multistate.

The multistate coding Wilson (2002) used to describe the shape of the distal scapular blade cannot account for the variation in expansion of the distal scapula that exists in sauropods. Wilson introduced two derived morphological states for this character, of which one is unique to rebbachisaurids. *Camarasaurus*, *Jobaria*, and *Brachiosaurus* share the other derived state, a rounded expansion on the acromial side of the distal scapula. Applying the character state descriptions explicitly as they were originally written would require all other sauropod taxa that do not exhibit either derived state to be coded as primitive, which supposes that the distal scapular blade is not expanded on the acromial side. Clearly this is not the case for taxa such as *Paluxysaurus* and *Haplocanthasaurus*, in which the distal scapula is expanded (but not rounded) on the acromial side. The first derived character state was re-worded to reflect a more general coding of presence or

absence of an expansion on the acromial side of the distal scapula (Appendix 3).

The derived state describing distal radial breadth, approximately twice mid-shaft breadth, was found more widely distributed than among the titanosaurians, contra Wilson's (2002) original analysis. *Brachiosaurus* and *Paluxysaurus* also show the derived condition, and among titanosaurians, some possess a ratio much greater than 200% (e.g., *Alamosaurus*) and others less than 200% (e.g., *Malawisaurus*). *Malawisaurus* was coded as primitive by Wilson for this character – distal breadth slightly larger than mid-shaft breadth – but the distal transverse breadth of the radius in this taxon is at least one and one-half times the mid-shaft breadth and is perhaps as much as 80% greater. The proximal and distal ends of the radius are clearly more expanded in the titanosaurians *Opisthocoelicaudia* (Borsuk-Bialynicka 1977, text-figure 8, plate 9) and *Alamosaurus* (Gilmore 1946, figure 9) than in *Brachiosaurus* and *Paluxysaurus*. But as noted above, the radius in *Opisthocoelicaudia* and *Alamosaurus* is also broader at mid-shaft than in the latter two taxa, which results in the similar ratios. Comparing other forelimb measurement ratios confirms that the radius of *Alamosaurus* is more robust than that of *Brachiosaurus* and *Paluxysaurus* (Appendix 1), and the ratio of minimum shaft circumference to length in the radius of *Opisthocoelicaudia* as reported by Borsuk-Bialynicka (1977, p. 46) sharply contrasts from the same ratio in *Paluxysaurus* and, in fact, exceeds that reported for any other sauropod with the exception of *Saltasaurus*. *Cedarosaurus* and *Venenosaurus* would both be primitive for this character in Wilson's (2002) study. In the case of the latter two taxa this is a function of a reduction in the breadth of the distal radius. Based on these observations, a character comparing distal and mid-shaft transverse breadths of the radius was not included in the present phylogenetic analysis.

The shape of the preacetabular process of the ilium was not used as a character in this analysis, because primitive and derived states could not confidently be differentiated for some taxa. Personal observations of *Brachiosaurus* at the Field Museum in Chicago (FMNH 25107) and measurements reported in the literature indicate that the transverse breadth of the femur at mid-shaft ranges from approximately 1.6 to 2.0 times the craniocaudal width for that taxon, which suggests to me that *Brachiosaurus* deserves a different derived coding from that which it received in Wilson's (2002) analysis (character 195, Appendix 4).

The derived state of the character describing the transverse breadth of the distal fibular condyle relative to mid-shaft breadth has a homoplasious distribution in Wilson's (2002) analysis. Several taxa that were coded by Wilson as primitive for this character appear, in fact, to be closer in morphology to the derived condition (*Shunosaurus*, *Apatosaurus*, *Camarasaurus*, *Malawisaurus*, and *Opisthocoelicaudia*). *Paluxysaurus* and *Phuwiangosaurus* also appear to exhibit the derived condition. Re-scoring taxa, however, did not improve the informativeness of the character. Therefore, I regard this character as phylogenetically uninformative, and it was excluded from the final character-taxon matrix. For an explanation of all other characters and character coding strategies, see Wilson (2002) and references therein.

Results

The heuristic algorithm of PAUP* searched 28 well-documented sauropod genera, the controversial taxon *Pleurocoelus*, two recently named sauropods, and one new taxon, scored for 230 morphological characters and returned three most parsimonious cladograms (mpc). The mpc's have a length of 444 evolutionary steps, a consistency index of 0.63 and a retention index of 0.79. The relative phylogenetic positions of the 27 terminal taxa included in Wilson's (2002) original analysis are unchanged in the present analysis. The three most parsimonious cladograms differ only in the relationships among the three rebbachisaurid sauropods. In the strict consensus tree, the rebbachisaurid clade collapses to an unresolved trichotomy (Figure 31). At two steps greater than the most parsimonious cladograms (mpc + 2, 446 steps), 1382 topologies exist, and in a 50% majority rule consensus of these cladograms all clades remain stable (Figure 32). The remainder of the discussion of the results of the cladistic analysis will focus only on titanosauriform relationships and, in particular, Early Cretaceous forms from North America.

A strict consensus of cladograms one step longer than the most parsimonious ones (101 topologies) indicates a significant loss in resolution among titanosauriform clades (Figure 33). In addition to large amounts of missing data, much of the instability in relationships among titanosauriforms can be attributed to a few characters where large amounts of homoplasy exist. For instance, the character describing the shape of cranial caudal neural spines requires three independent losses or four independent acquisitions of the derived state to explain its distribution among terminal taxa. In

Figure 31. Hypothesized phylogenetic relationship between *Paluxysaurus* and other sauropods. Shown is the strict consensus cladogram resulting from an analysis involving 34 taxa and 230 morphological characters that yielded three equally most parsimonious cladograms.

addition, Wilson (2002) associated *Alamosaurus* with the derived state, transverse breadth greater than craniocaudal length, but transverse breadth of cranial caudal neural spines in this taxon is about 80% the craniocaudal length, which does not fit either the primitive (50% craniocaudal length) nor derived conditions. Repeating the PAUP analysis with the latter character excluded does not alter the topology of the three most parsimonious cladograms. Thus, the ratio of transverse breadth to craniocaudal length in cranial caudal neural spines

may be a phylogenetically uninformative character for sauropods.

Two characters in the phylogenetic analysis describe the number of presacral vertebrae in sauropods. The amount of homoplasy in the character state distributions may, in part, be a function of missing data in the character matrix as a whole. More likely it indicates that these characters are also phylogenetically uninformative; deleting these characters from the analysis has no effect on the topology of the most parsimonious cladograms.

Figure 32. 50% majority rule consensus cladogram for 1382 suboptimal reconstructions two steps longer than the most parsimonious cladograms. Numbers indicate frequencies at which branch nodes are supported among all 1382 topologies.

The new taxon from North America described here, *Paluxysaurus*, is hypothesized to be the sister taxon of *Brachiosaurus* but closely related to the three other North American Early Cretaceous sauropods included in the analysis (*Cedarosaurus*, *Venenosaurus*, and *Pleurocoelus*). *Brachiosaurus* plus the four North American Early Cretaceous taxa are all basal to Somphospondyli. The phylogenetic position of *Paluxysaurus* is not robustly supported. Only a single synapomorphy–relatively transversely broad femur at mid-shaft–supports the
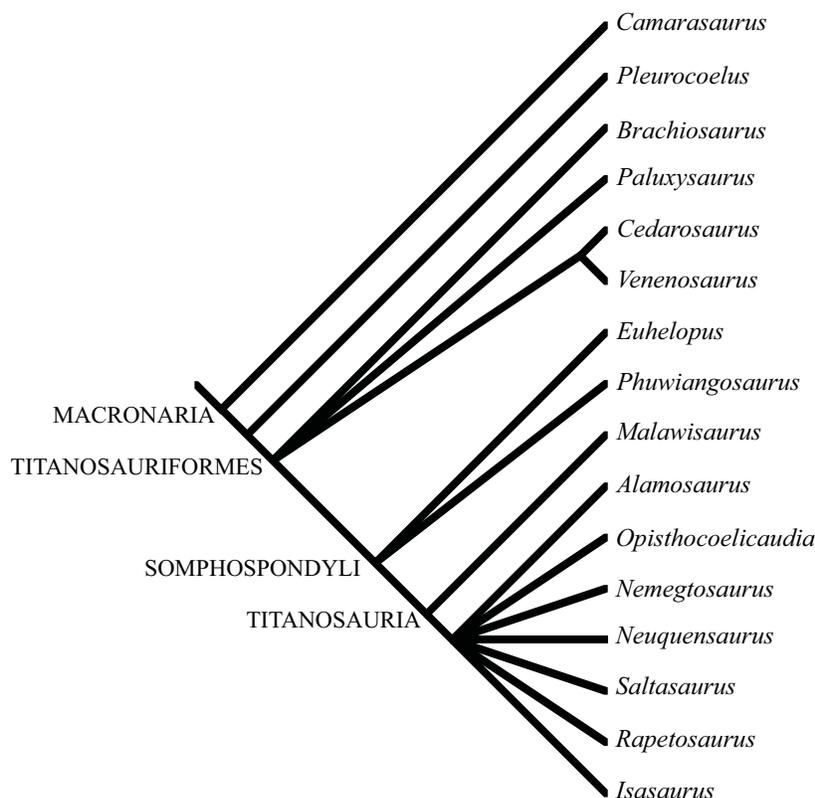
Figure 33. Strict consensus cladogram of 101 topologies one evolutionary step longer than the most parsimonious cladograms (445 steps).

sister relationship between *Paluxysaurus* and *Brachiosaurus*.

Wilson (2002) defines the group Titanosauriformes by eight derived characters shared by, "*Brachiosaurus*, *Saltasaurus*, their common ancestor, and all of its descendants" (Wilson and Sereno 1998, p. 51). *Paluxysaurus* is clearly a member of Titanosauriformes. It possesses most of the titanosauriform synapomorphies. It shares none of the derived characters that are currently used to define the groups Somphospondyli or Titanosauria. Within Titanosauriformes, *Paluxysaurus* is a basal member of the group. The Arundel sauropod also shares many of the titanosauriform synapomorphies but is here resolved as basal to both *Brachiosaurus* and *Paluxysaurus* due to primitive aspects in the morphology of the femur and the internal pneumatic structure of the presacral vertebrae.

Bootstrap Analysis

Branch support was evaluated using a non-parametric bootstrap analysis (sensu Felsenstein 1985). The 230 characters were resampled in PAUP using 10,000 heuristic search replicates, with one random sequence addition per replicate, and the maximum number of cladograms to be saved per replicate (the MAXTREES value in PAUP) limited to 500. The resulting 50% majority-rule consensus cladogram had a length of 441 steps and is depicted in Figure 34 with bootstrap support values at the branch nodes. The overall topology of the bootstrap consensus is consistent with that of the strict consensus of the three most parsimonious cladograms in Figure 31 but with loss of some resolution. *Jobaria* plus the Neosauropoda collapse to form a polytomy. In addition, within the Neosauropoda, *Haplocanthosaurus* and the Diplodocoidea are also characterized by a polytomous relationship. Among titanosauriforms the sister relationship between *Brachiosaurus* and *Paluxysaurus* breaks down, and *Isisaurus* forms a polytomy with the sister groups [*Nemegtosaurus* + *Rapetosaurus*], [*Alamosaurus* + *Opisthocoelicaudia*], and [*Neuquensaurus* + *Saltasaurus*]. Relationships among other titanosauriformes remain resolved but support values are generally low.
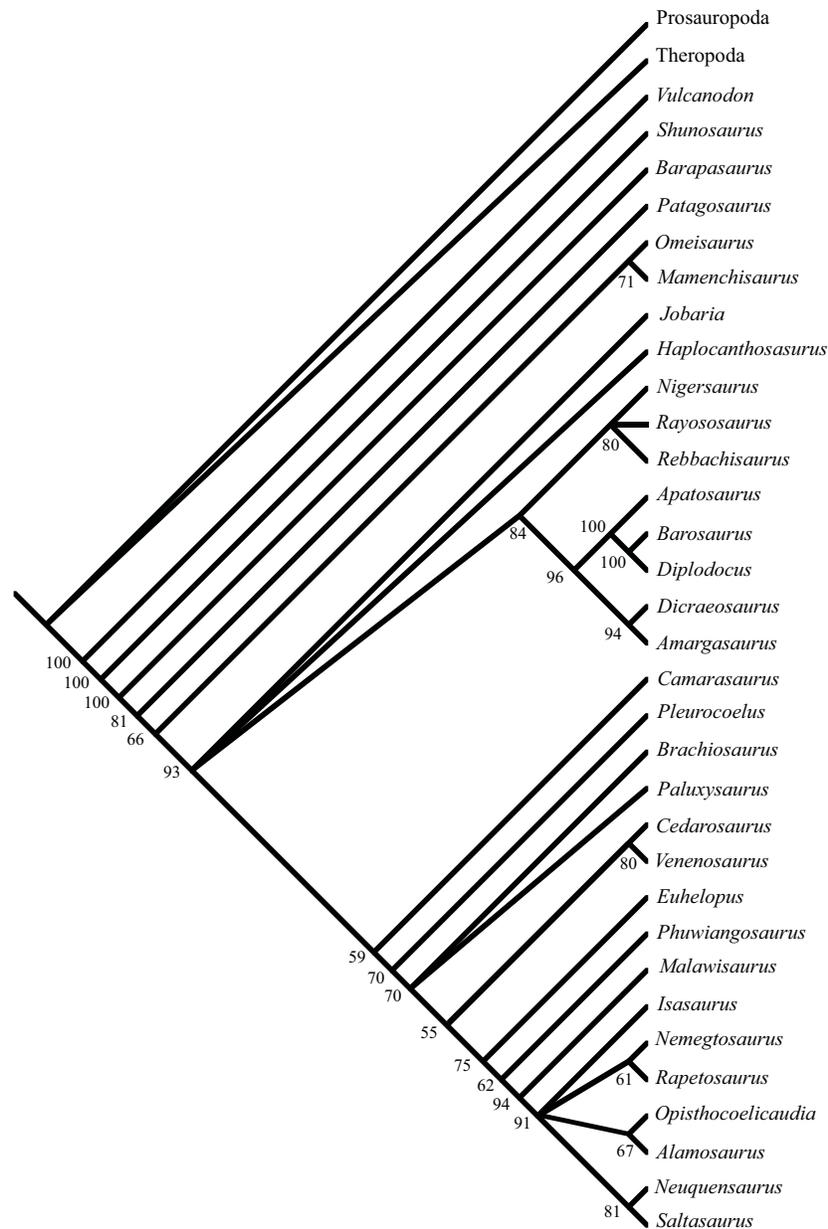
Figure 34. Bootstrap 50% majority rule consensus cladogram. Bootstrap values greater than 50% are placed at branch nodes.

CONCLUSIONS

Paluxysaurus jonesi is the most complete sauropod described from the Cretaceous of North America. *Paluxysaurus jonesi* differs from material of the Arundel sauropod in having an expanded distal scapular blade that is not rounded on the acromial side, greater medial deflection of the proximal femur, a relatively narrower distal radius compared to mid-shaft width, and a more cranio-caudally expanded proximal condyle of the tibia. The morphological differences observed between

Paluxysaurus jonesi and the Arundel sauropod are too pronounced to attribute them to ontogenetic variation. Cladistic analysis based on currently available morphological evidence suggests that *Pleurocoelus* differs from *Brachiosaurus* only in presacral vertebral bone texture and robustness of the femur. The juvenile cervical vertebrae of *Pleurocoelus* exhibit the primitive condition for presacral bone texture. Wedel (2003) claims that such vertebrae with large pneumatic fossae would develop a polycamerate internal pneumatic structure during ontogeny but not the camellate pattern

that is exhibited by *Brachiosaurus* and *Paluxysaurus*. If the latter is correct, ontogenetic variation cannot explain the different forms of vertebral pneumaticity in *Pleurocoelus* and other titanosauriforms, and it is highly unlikely that either *Brachiosaurus* or *Paluxysaurus* are adult forms of the Arundel taxon. Nevertheless, the phylogenetic position of *Pleurocoelus* is not strongly supported. If *Pleurocoelus* is a valid taxon, it is the most basal titanosauriform known, and would require redefinition of the taxon Titanosauriformes as the common ancestor of *Pleurocoelus* and the titanosaurians, and all of its descendants.

It is the opinion of the author that it has not been adequately demonstrated that the teeth of *Astrodon johnstoni* or those attributed to *Pleurocoelus* are morphologically diagnostic among titanosauriforms. Carpenter and Tidwell (2005, p. 79) note that isolated teeth cannot be referred to *Astrodon* with certainty, because "similar teeth occur in other taxa." Likewise, isolated teeth should not be referred to *Pleurocoelus*. The juvenile postcranial material that forms the type specimens of *Pleurocoelus nanus* and other material referred to that genus by Marsh (1888) cannot be compared to the teeth of *Astrodon johnstoni.* Since there is no additional associated material available for *Astrodon* for comparison, new discoveries should not be aligned with that genus. For the above reasoning, the argument to synonymize the two taxa, *Astrodon* and *Pleurocoelus*, seems unfounded. Furthermore, despite the fact that the morphology of some of the postcranial material from the Arundel Formation referred to *Pleurocoelus* by Marsh (1888), in particular appendicular skeletal elements, can be distinguished from other sauropod taxa, the grounds for referral is not morphological evidence. The type material of *Pleurocoelus* may not be diagnostic and there is no overlapping anatomy between the type and referred material of *Pleurocoelus*, making the basis for Marsh's (1888) conclusion to refer isolated bones from the Arundel Formation to that genus on size and provenance alone. Therefore, the status of either *Astrodon* or *Pleurocoelus* as valid taxonomic units is not well supported, and it is recommended that both be recognized as incertae sedis. Fragmentary sauropod remains from Texas referred to "*Pleurocoelus*" should be reassessed.

A diversity of at least four distinct sauropod taxa is now known for the Early Cretaceous of North America. A minimum of two sauropod taxa are present in Texas and Oklahoma, *Paluxysaurus jonesi* and *Sauroposeidon proteles*; and those are distinct from two taxa from Utah, *Cedarosaurus weiskopfae* and *Venenosaurus dicorcei*. Pending future discoveries from eastern and north-central North America, it remains unclear how the Arundel sauropod and the Cloverly sauropod fit into the current picture of Early Cretaceous sauropod diversity and biogeography. These taxa together have a widespread distribution across the continent, but otherwise each currently has a distribution that is relatively regionally isolated. Comparisons of the Early Cretaceous sauropod-producing vertebrate faunas in North America suggests, from currently available evidence, that the geographic ranges of the different sauropod taxa did not overlap, while other dinosaur taxa (some theropods and ornithischians) are common to the different faunas (e.g., Ostrom 1970, Jacobs and Winkler 1998). This is intriguing because the occurrences of all these taxa pre-date the completion of the Western Interior Seaway, which is generally assumed to have inhibited faunal exchange across North America in the Late Cretaceous. The distribution of sauropod taxa disagrees with the view that these large-bodied vertebrates had extensive geographic ranges. However, many of the sauropods compared in this study are only known from limited skeletal material, often from a single individual, and it may be likely that as additional sauropod material from the Early Cretaceous of North America is discovered and described, taxa will become known from multiple localities. Nevertheless, the description of the new taxon from Texas increases the diversity of sauropods in North America for the Early Cretaceous and provides more complete, associated material that can be compared to new discoveries from this time period.

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APPENDIX 1

Limb proportion measurement ratios and limb-limb length ratios compared among sauropod taxa. Breadth measurements are in the transverse direction; ranges are based on multiple species, individuals, or specimens. Symbol meaning: e = estimate; -- = no measurement; ? = questionable value. See Appendix 2 for references.

Taxon	Proximal breadth/length	Distal breadth/ length	Minimum breadth/ length	Minimum circumference/ length
Humerus				
Alamosaurus	0.42-0.43	0.33-0.35	0.17	0.47
Apatosaurus	0.46-0.50	0.33-0.39	0.18-0.20	0.50-0.55
Brachiosaurus	0.26-0.34	0.22-0.28	0.11-0.14	0.30-0.36
Camarasaurus	0.34-0.49	0.26-0.38	0.14-0.17	0.42-0.50
Cedarosaurus	0.28	0.24	0.13	0.32
Chubutisaurus	0.34e	0.26e	0.15e	--
Dicraeosaurus	0.40-0.47	0.30-0.37	0.13-0.17	--
Diplodocus	0.38e	0.29	--	0.43-0.50
Epachthosaurus	0.34	0.32	0.18	0.46
Euhelopus	0.40	0.25	0.19	--
Malawisaurus	0.36-0.39	0.29-.031	0.15-0.16	--
Paluxysaurus	0.28-0.29	0.25-0.28	0.12-0.14	0.34-0.38
Pleurocoelus	0.31	0.29	0.15	0.40
Saltasaurus	0.48-0.57	0.29-0.43	--	0.48-0.67
Shunosaurus	0.48	0.37	0.17	--

Ulna	Proximal breadth/length	Distal breadth/ length	Minimum breadth/ length	Minimum circumference/ length
Alamosaurus	0.41	0.32	0.17	--
Apatosaurus	0.44	0.23-0.25	0.17	0.47-.050
Brachiosaurus	0.34	0.17	--	--
Camarasaurus	0.35-0.40	0.17-0.23	0.11-0.14	0.35-0.39
Diplodocus	0.27?	0.18?	--	0.36?-0.40
Epachthosaurus	0.42	0.23	0.17	0.56
Malawisaurus	0.36	0.17-0.19	0.14-0.19	--
Paluxysaurus	0.33	0.18	0.14	0.39
Saltasaurus	0.51-0.56	0.24-0.28	--	0.56-0.60
Shunosaurus	0.34	0.15	0.17	--
Venenosaurus	0.35	0.16	--	0.37

Radius	Proximal breadth/length	Distal breadth/ length	Minimum breadth/ length	Minimum circumference/ length
Alamosaurus	0.36	0.33	0.15	--
Apatosaurus	0.26-0.30	0.25-0.27	0.16-0.17	0.43-0.44
Brachiosaurus	0.25	0.22	0.11	--

Appendix 1 (continued).

Camarasaurus	0.24-0.28	0.23-.025	0.11-0.15	0.33-0.38
Cedarosaurus	0.22	0.16	0.15	0.30
Dicraeosaurus	0.25	0.22	0.14	--
Diplodocus	0.20?	0.17-0.22?	0.14	0.35-0.40
Epachthosaurus	0.30	0.33?	0.15	0.45
Malawisaurus	0.23	0.17	0.10	--
Paluxysaurus	0.25	0.24	0.11	0.32
Pleurocoelus	0.21	0.26	0.11	0.35
Saltasaurus	0.32-0.46	0.14-0.34	--	0.41-0.71
Shunosaurus	0.33	0.29	0.18	--
Venenosaurus	0.22	0.21	0.11	0.34

Femur	Proximal breadth/length	Distal breadth/ length	Minimum breadth/ length	Minimum circumference/ length	Mid-shaft transverse breadth/ anteroposterior breadth
Apatosaurus	0.30-0.33	0.28-0.32	0.15-0.18	0.40-0.49	--
Brachiosaurus	0.26-0.31	0.26-.031	0.13-0.17	~0.44	1.59-2.00
Camarasaurus	0.27-0.38	0.27-0.32	0.15-0.18	0.42-0.48	1.43e
Chubutisaurus	0.29e	0.27e	0.17	--	--
Diplodocus	0.22-0.37	0.19-0.27	0.18	0.36-0.41	--
Epachthosaurus	0.31	0.28	0.21	0.50	--
Euhelopus	0.31	0.27	0.16	0.42	1.60
Haplocanthosaurus	0.28-0.33	0.22-0.31	0.16-0.18	0.41-0.45	--
Paluxysaurus	0.27	0.20-0.25	0.11-0.14	0.30-0.35	1.45-1.91
Pleurocoelus	0.29-0.30	0.27-0.29	0.14-0.15	0.40	1.34
Saltasaurus	0.30	0.31	0.19	--	1.96
Shunosaurus	0.28	0.21	0.12	--	--

Tibia	Minimum circumference/ length	Fibula	Minimum circumference/length
Apatosaurus	0.45-0.46	*Apatosaurus*	0.27-0.31
Camarasaurus	0.46	*Diplodocus*	0.22?-0.31
Diplodocus	0.35?-0.44	*Epachthosaurus*	0.30
Epachthosaurus	0.48	*Euhelopus*	0.30
Euhelopus	0.44	*Opisthocoelicaudia*	0.40
Opisthocoelicaudia	0.60	*Haplocanthosaurus*	0.36
Haplocanthosaurus	0.55	*Paluxysaurus*	0.27-0.28
Paluxysaurus	0.37	*Pleurocoelus*	0.30
Pleurocoelus	0.43		
YPM 5450	0.32		

Appendix 1 (continued).

Taxon	radius/ ulna	radius/ humerus	ulna/ humerus	humerus/ femur	tibia/fibula	tibia/femur	fibula/ femur
Alamosaurus	0.90	0.59	0.65	--	--	--	--
Andesaurus	--	--	--	0.87	--	--	--
Apatosaurus	0.93	0.73	0.78-0.79	0.63-0.64	0.93-0.96	0.61-0.63	0.64-0.65
Brachiosaurus	0.95	0.58	0.61	1.0-1.05	0.97-0.99?	0.58	0.60-0.65?
Camarasaurus	0.87-0.99	0.66-0.74	0.67-0.81	0.69?-0.89	0.92	0.63-0.64	0.68
Cedarosaurus	--	0.59	--	0.99	--	0.63?	--
Chubutisaurus	--	0.60	--	0.86	--	0.62	--
Diplodocus	0.93-0.96	0.68-0.70	0.73	0.63?-0.65	0.91-0.99	0.60-0.71	0.63-0.71
Epachthosaurus	0.89	0.59	0.66	0.80	0.96	0.64	0.67
Euhelopus	--	--	--	0.99	0.97	0.63	0.65
Haplocanthosaurus	--	--	--	--	0.95	0.52	0.55
Paluxysaurus	0.95	0.61	0.64	0.85-0.88	0.97	0.62?	0.63
Shunosaurus	1.02	0.72	0.70	0.71?	0.97	0.57	0.58
Venenosaurus	0.90	--	--	--	--	--	--

Appendix 1 (continued).

Taxon	Longest Mc/radius
Alamosaurus	0.51
Apatosaurus	0.37
Brachiosaurus	0.51
Camarasaurus	0.44-0.47
Cedarosaurus	?0.53
Chubutisaurus	0.55
Diplodocus	0.30-0.34
Epachthosaurus	0.56
Paluxysaurus	?0.45
Shunosaurus	0.35
Venenosaurus	0.52

APPENDIX 2

Limb ratios provided in Appendix 1 are based on published measurements and figures in the sources listed below. Taxa for which measurements were made by PJR are denoted by an asterisk (*).

Sauropod taxon	Reference(s)
Alamosaurus	Gilmore 1946, McIntosh 1990a, Salgado 1993
Andesaurus	Calvo and Bonaparte 1991
Apatosaurus	Riggs 1903, Gilmore 1936, McIntosh 1990b, 1995, Foster 1996
*Pleurocoelus**	Lull 1911
*Brachiosaurus**	Riggs 1904, Janensch 1961, McIntosh 1990a, 1990b
Camarasaurus	Gilmore 1925, Foster 1996, McIntosh, Miles, et al. 1996, McIntosh, Miller, et al. 1996
Cedarosaurus	Tidwell et al 1999
Chubutisaurus	del Corro 1975, Salgado 1993
Dicraeosaurus	Janensch 1961
Diplodocus	Holland 1901, Mook 1917, Gilmore 1932, McIntosh 1990a, 1990b, McIntosh and Carpenter 1998
Epachthosaurus	Salgado 1993, Martìnez et al. 2004
Euhelopus	Wiman 1929, Young 1935, McIntosh 1990a
Haplocanthosaurus	Hatcher 1903a, McIntosh and Williams 1988
*Malawisaurus**	Gomani 1999
*Paluxysaurus**	This study
Saltasaurus	Bonaparte and Powell 1980, Powell 1992, 2003
Shunosaurus	Zhang 1988
Venenosaurus	Tidwell et al. 2001

APPENDIX 3

List of morphological characters used in cladistic analysis. All characters taken directly from or modified from Wilson (2002). Character codings: (0), primitive state; (1, 2,…), derived states(s); (9), inapplicable character; (?), missing data.

1. Posterolateral processes of premaxilla and lateral processes of maxilla, shape: without midline contact (0); with midline contact, forming marked narial depression, subnarial foramen not visible laterally (1).

2. Premaxillary anterior margin, shape: without step (0); with marked step, anterior portion of skull sharply demarcated (1).

3. Maxillary border of external nares, length: short, making up much less than one-fourth narial perimeter (0); long, making up more than one-third narial perimeter (1).

4. Preantorbital fenestra: absent (0); present (1).

5. Subnarial foramen and anterior maxillary foramen, position: well distanced from one another (0); separated by narrow bony isthmus (1).

6. Antorbital fenestra, maximum diameter: much shorter than orbital maximum diameter (0); subequal to orbital maximum diameter (1).

7. Antorbital fossa: present (0); absent (1).

8. External nares, position: retracted to level of orbit (0); retracted to a position between orbits (1).

9. External nares, maximum diameter: shorter than orbital maximum diameter (0); longer than orbital maximum diameter (1).

10. Orbital ventral margin, anteroposterior length: broad, with subcircular orbital margin (0); reduced, with acute orbital margin (1).

11. Lacrimal, anterior process: present (0); absent (1).

12. Jugal-ectopterygoid contact: present (0); absent (1).

13. Jugal, contribution to antorbital fenestra: very reduced or absent (0); large, bordering approximately one-third its perimeter (1).

14. Prefontal, posterior process size: small, not projecting far posterior of frontal-nasal suture (0); elongate, approaching parietal (1).

15. Prefontal, posterior process shape: flat (0); hooked (1).

16. Postorbital, ventral process shape: transversely narrow (0); broader transversely than anteroposteriorly (1).

17. Postorbital, posterior process: present (0); absent (1).

18. Frontal contribution to supratemporal fossa: present (0); absent (1).

19. Frontals, midline contact (symphysis): sutured (0), or fused (1) in adult individuals.

20. Frontal, anteroposterior length: approximately twice (0) or less than (1) minimum transverse breadth.

21. Parietal occipital process, dorsoventral height: short, less than the diameter of the foramen magnum (0); deep, nearly twice the diameter of the foramen magnum (1).

22. Parietal, contribution to post-temporal fenestra: present (0); absent (1).

23. Postparietal foramen: absent (0); present (1).

24. Parietal, distance separating supratemporal fenestrae: less than the long axis of the supratemporal fenestra (0); twice the long axis of the supratemporal fenestra (1).

25. Supratemporal fenestra: present (0); absent (1).

26. Supratemporal fenestra, long axis orientation: anteroposterior (0); transverse (1).

27. Supratemporal fenestra, maximum diameter: much longer than (0) or subequal to (1) that of foramen magnum.

28. Supratemporal region, anteroposterior length: temporal bar longer (0) or shorter (1) anteroposteriorly than transversely.

29. Supratemporal fossa, lateral exposure: not visible laterally, obscured by temporal bar (0); visible laterally, temporal bar shifted ventrally (1).

30. Laterotemporal fenestra, anterior extension: posterior to orbit (0); ventral to orbit (1).

31. Squamosal-quadratojugal contact: present (0); absent (1).

32. Quadratojugal, anterior process length: short, anterior process shorter than dorsal

process (0); long, anterior process more than twice as long as dorsal process (1).

33. Quadrate fossa: absent (0); present (1).

34. Quadrate fossa, depth: shallow (0); deeply invaginated (1).

35. Quadrate fossa, orientation: posterior (0); posterolateral (1).

36. Palatobasal contact, shape: pterygoid with small facet for basipterygoid articulation (0); dorsomedailly oriented hook for basipterygoid articulation (1); rocker-like surface for basipterygoid articulation (2).

37. Pterygoid, transverse flange (i.e., ectopterygoid process) position: between orbit and antorbital fenestra (0); anterior to antorbital fenestra (1).

38. Pterygoid, quadrate flange size: large, palatobasal and quadrate articulations well separated (0); small, palatobasal and quadrate articulations approach (1).

39. Pterygoid, palatine ramus shape: straight, at level of dorsal margin of quadrate ramus (0); stepped, raised above level of quadrate ramus (1).

40. Palatine, lateral ramus shape: plate-shaped (long maxillary contact) (0); rod-shaped (narrow maxillary contact) (1).

41. Epipterygoid: present (0); absent (1).

42. Vomer, anterior articulation: maxilla (0); premaxilla (1).

43. Supraoccipital, height: twice (0) subequal to or less than (1) height of foramen magnum.

44. Paroccipital process, ventral nonarticular process: absent (0); present (1).

45. Crista prootica, size: rudimentary (0); expanded laterally into 'dorsoventral process' (1).

46. Basipterygoid processes, length: short, approximately twice basal diameter (0); elongate, at least four times basal diameter (1).

47. Basipterygoid processes, angle of divergence: approximately 45° (0); less than 30° (1).

48. Basal tubera, anteroposterior depth: approximately half dorsovenral height (0); sheet-like, 20% dorsoventral height (1).

49. Basal tubera, breadth: much broader than (0) or narrower than (1) occipital condyle.

50. Basioccipital depression between foramen magnum and basal tubera: absent (0); present (1).

51. Basisphenoid/basipterygoid recess: present (0); absent (1).

52. Basisphenoid-quadrate contact: absent (0); present (1).

53. Basipterygoid processes, orientation: perpendicular to skull roof (0); angled approximately 45° to skull roof (1).

54. Occipital region of skull, shape: anteroposteriorly deep, paroccipital processes oriented posterolaterally (0); flat, paroccipital processes oriented transversely (1).

55. Dentary, depth of anterior end of ramus: slightly less than that of dentary at midlength (0); 150% minimum depth (1).

56. Dentary, anteroventral margin shape: gently rounded (0); sharply projecting triangular process or 'chin' (1).

57. Dentary symphysis, orientation: angled 15° or more anteriorly to (0) or perpendicular to (1) axis of jaw ramus.

58. External mandibular fenestra: present (0); absent (1).

59. Surangular depth: less than twice maximum depth of the angular (0) more than two and one-half times maximum depth of the angular (1).

60. Surangular ridge separating adductor and articular fossae: absent (0); present (1).

61. Adductor fossa, medial wall depth: shallow (0); deep, prearticular expanded dorsoventrally (1).

62. Splenial posterior process, position: overlapping angular (0); separating anterior portions of prearticular and angular (1).

63. Splenial posterodorsal process: present, approaching margin of adductor chamber (0); absent (1).

64. Coronoid, size: extending to dorsal margin of jaw (0); reduced, not extending dorsal to splenial (1); absent (2).

65. Tooth rows, shape of anterior portions: narrowly arched, anterior portion of tooth rows V-shaped (0); broadly arched, anterior portion of tooth rows U-shaped (1); rectangular, tooth-bearing portion of jaw perpendicular to jaw rami (2).

66. Tooth rows, length: restricted anterior to orbit (0); restricted anterior to subnarial foramen (1).

67. Crown-to-crown occlusion: absent (0); present (1).

68. Occlusal pattern: interlocking, V-shaped wear facets (0); high-angled planar facets (1); low-angled planar facets (2).

69. Tooth crowns, orientation: aligned along jaw axis, crowns do not overlap (0); aligned slightly anterolingually, tooth crowns overlap (1).

70. Tooth crowns, cross-sectional shape at mid-crown: elliptical (0); D-shaped (1); cylindrical (2).

71. Enamel surface texture: smooth (0); wrinkled (1).

72. Marginal tooth denticles: present (0); absent on posterior edge (1); absent on both anterior and posterior edges (2).

73. Dentary teeth, number: greater than 20 (0); 17 or fewer (1).

74. Replacement teeth per alveolus, number: two or fewer (0); more than four (1).

75. Teeth, orientation: perpendicular to jaw margin (0); oriented anteriorly relative to jaw margin (1).

76. Teeth, longitudinal grooves on lingual aspect: absent (0); present (1).

77. Presacral vertebrae, bone texture: solid (0); spongy, with large, open internal cells, 'camellate' (1).

78. Presacral centra, pleurocoels: absent (0); present (1).

79. Atlantal intercentrum, occipital facet shape: rectangular in lateral view, length of dorsal aspect subequal to that of ventral aspect (0); expanded anteroventrally in lateral view, anteroposterior length of dorsal aspect shorter than that of ventral aspect (1).

80. Cervical vertebrae, number: 9 or fewer (0); 10 (1); 12 (2); 13 (3); 15 or greater (4).

81. Cervical neural arch lamination: well developed, with well defined laminae and coels (0); rudimentary, diapophyseal laminae only feebly developed if present (1).

82. Cervial centra, articular face morphology: amphicoelous (0); opisthocoelous (1).

83. Cervical pleurocoels, shape: simple, undivided (0); complex, divided by bony septa (1).

84. Anterior cervical centra, height:width ratio: less than 1 (0); approximately 1.25 (1).

85. Anterior cervical neural spines, shape: single (0); bifid (1).

86. Mid-cervical centra, anteroposterior length/ height of posterior face: 2.5-3.5 (0); greater than 4.0 (1).

87. Mid-cervical neural arches, height: less than that of posterior centrum face (0); greater than that of posterior centrum face (1).

88. Middle and posterior cervical neural arches, centroprezygapophyseal lamina (cprl), shape: single (0); divided (1).

89. Posterior cervical and anterior dorsal neural spines, shape: single (0); bifid (1).

90. Posterior cervical and anterior dorsal bifid neural spines, median tubercle: absent (0); present (1).

91. Dorsal vertebrae, number: 15 (0); 14 (1); 13 (2); 12 (3); 11 (4); 10 or fewer (5).

92. Dorsal neural spines, breadth: narrower (0) or much broader (1) transversely than anteroposteriorly.

93. Dorsal neural spines, length: approximately twice (0) or approximately four times (1) centrum length.

94. Anterior dorsal centra, articular face shape: amphicoelous (0); opisthocoelous (1).

95. Middle and posterior dorsal neural arches, centropostzygapophyseal lamina (cpol), shape: single (0); divided (1).

96. Middle and posterior dorsal neural arches, anterior centroparapophyseal lamina (acpl): absent (0); present (1).

97. Middle and posterior dorsal neural arches, prezygoparapophyseal lamina (prpl): absent (0); present (1).

98. Middle and posterior dorsal neural arches, posterior centroparapophyseal lamina (pcpl): absent (0); present (1).

99. Middle and posterior dorsal neural arches, spinodiapophyseal lamina (spdl): absent (0); present (1).

100. Middle and posterior dorsal neural arches, spinopostzygapophyseal lamina (spol), shape: single (0); divided (1).

101. Middle and posterior dorsal neural arches, spdl and spol contact: absent (0); present (1).

102. Middle and posterior dorsal neural spines, shape: tapering or not flaring distally (0); flared distally, with pendant, triangular lateral processes (1).

103. Middle and posterior dorsal neural arches, 'infradiapophyseal' pneumatopore between scdl and pcdl: absent (0); present (1).

104. Middle and posterior dorsal neural spines, orientation: vertical (0); posterior, neural spine summit approaches level of diapophyses (1).

105. Posterior dorsal centra, articular face shape: amphicoelous (0); opisthocoelous (1).

106. Posterior dorsal neural arches, hyposphene-hypantrum articulations: present (0); absent (1).

107. Posterior dorsal neural spines, shape: rectangular through most of length (0); 'petal' shaped, expanding transversely through 75% of its length and then tapering (1).

108. Sacral vertebrae, number: 3 or fewer (0); 4 (1); 5 (2); 6 (3).

109. Sacrum, sacricostal yoke: absent (0); present (1).

110. Sacral neural spines, length: approximately twice length of centrum (0); four times length of centrum (1).

111. Sacral ribs, dorsoventral length: low, not projecting beyond dorsal margin of ilium (0); high, extending beyond dorsal margin of ilium (1).

112. Caudal bone texture: solid (0); spongy, with large internal cells (1).

113. Caudal vertebrae, number: more than 45 (0); 35 or fewer (1).

114. Caudal transverse processes: persist through caudal 20 or more posteriorly (0); disappear by caudal 15 (1); disappear by caudal 10 (2).

115. First caudal centrum, articular face shape: flat (0), procoelous (1), opisthocoelous (2); biconvex (3).

116. First caudal neural arch, coel on lateral aspect of neural spine: absent (0); present (1).

117. Anterior caudal centra (excluding the first), articular face shape: amphiplatyan or platycoelous (0); strongly procoelous (1); opisthocoelous (2).

118. Anterior caudal centra, pleurocoels: absent (0), present (1).

119. Anterior caudal centra, length: approximately the same over the first 20 vertebrae (0); doubling over the first 20 vertebrae (1).

120. Anterior caudal neural arches, spinoprezygapophyseal lamina (sprl): absent (0); present and extending onto lateral aspect of neural spine (1).

121. Anterior caudal neural arches, sprl-spol contact: absent (0); present, forming a prominent lamina on lateral aspect of neural spine (1).

122. Anterior caudal neural arches, prespinal lamina (prsl): absent (0); present (1).

123. Anterior caudal neural arches, postspinal lamina (posl): absent (0); present (1).

124. Anterior caudal neural arches, postspinal fossa: absent (0); present (1).

125. Anterior caudal neural spines, transverse breadth: approximately 50% of anteroposterior length (0); greater than anteroposterior length (1).

126. Anterior caudal transverse processes, proximal depth: shallow, on centrum only (0); deep, extending from centrum to neural arch (1).

127. Anterior caudal transverse processes, shape: triangular, tapering distally (0); 'wing-like', not tapering distally (1).

128. Anterior caudal transverse processes, diapophyseal laminae (acdl, pcdl, prdl, podl): some absent (0); all present (1).

129. Anterior caudal transverse processes, acdl shape: single (0); divided (1).

130. Anterior and middle caudal centra, shape: cylindrical (0); quadrangular, flat ventrally and laterally (1).

131. Anterior and middle caudal centra, ventral longitudinal hollow: absent (0); present (1).

132. Middle caudal neural spines, orientation: angled posterodorsally (0), vertical (1), angled anterodorsally (2).

133. Middle and posterior caudal centra, anterior articular face shape: flat (0); procoelous (cone shaped) (1); opisthocoelous (2).

134. Posterior caudal centra, shape: cylindrical (0); dorsoventrally flattened, breadth at least twice height (1).

135. Distalmost caudal centra, articular face shape: platycoelous (0); biconvex (1).

136. Distalmost biconvex caudal centra, length-to-height ratio: less than 4 (0); greater than 5 (1).

137. Distalmost biconvex caudal centra, number: 10 or fewer (0); more than 30 (1).

138. Cervical rib, tuberculum-capitulum angle: greater than 90° (0); less than 90°, rib ventrolateral to centrum (1).

139. Cervical ribs, length: much longer than centrum, overlapping as many as three subsequent vertebrae (0); shorter than centrum, little or no overlap (1).

140. Dorsal ribs, proximal pneumatocoels: absent (0); present (1).

141. Anterior dorsal ribs, cross-sectional shape: sub-circular (0); plank-like, anteroposterior breadth more than three times mediolateral breadth (1).

142. 'Forked' chevrons with anterior and posterior projections: absent (0); present (1).

143. 'Forked' chevrons, distribution: distal tail only (0); throughout middle and posterior caudal vertebrae (1).

144. Chevrons, 'crus' bridging dorsal margin of haemel canal: present (0); absent (1).

145. Chevron haemal canal, depth: short, approximately 25% chevron length (0); long, approximately 50% chevron length (1).

146. Chevrons: persisting throughout at least 80% of tail (0); disappearing by caudal 30 (1).

147. Posterior chevrons, distal contact: fused (0); unfused (open) (1).

148. Posture: bipedal (0); columnar, obligately quadrupedal posture (1).

149. Scapular acromion process, size: narrow (0); broad, width more than 150% minimum width of blade (1).

150. Scapular blade, orientation: forming close to a 90° angle with coracoid articulation (0); forming a 45° angle with coracoid articulation (1).

151. Distal scapular blade, shape: acromial edge not expanded (0); acromial edge expanded (1); racquet-shaped (2).

152. Scapular glenoid, orientation: relatively flat or laterally facing (0); strongly bevelled medially (1).

153. Scapular blade, cross-sectional shape: flat or rectangular (0); D-shaped (1).

154. Coracoid, proximodistal length: less than length of scapular articulation (0) approximately twice length of scapular articulation (1).

155. Coracoid, anteroventral margin shape: rounded (0); rectangular (1).

156. Coracoid, infraglenoid lip: absent (0); present (1).

157. Sternal plate, shape: oval (0); crescentic (1).

158. Humeral proximolateral corner, shape: rounded (0); square (1).

159. Humeral deltopectoral attachment, development: prominent (0); reduced to a low crest or ridge (1).

160. Humeral deltopectoral crest, shape: relatively narrow throughout length (0); markedly expanded distally (1).

161. Humeral midshaft cross-section, shape: circular (0); elliptical, with long axis oriented transversely (1).

162. Humeral distal condyles, articular surface shape: restricted to distal portion of humerus (0); exposed on anterior portion of humeral shaft (1).

163. Humeral distal condyle, shape: divided (0); flat (1).

164. Ulnar proximal condyle, shape: subtriangular (0); triradiate, with deep radial fossa (1).

165. Ulnar proximal condylar processes, relative lengths: subequal (0); unequal, anteromedial arm longer (1).

166. Ulnar olecranon process, development: prominent, projecting above proximal articulation (0); rudimentary, level with proximal articulation (1).

167. Ulna, length-to-proximal breadth ratio: gracile (0); stout (1).

168. Radial distal condyle, shape: round (0); sub-rectangular, flattened posteriorly and articulating in front of ulna (1).

169. Radius, distal condyle orientation: perpendicular to long axis of shaft (0); bevelled approximately 20° proximolaterally relative to long axis of shaft (1).

170. Humerus-to-femur ratio: less than 0.60 (0); 0.60 or more (1).

171. Carpal bones, number: 3 or more (0); 2 or fewer (1).

172. Carpal bones, shape: round (0); block-shaped, with flattened proximal and distal surfaces (1).

173. Metacarpus, shape: spreading (0); bound, with subparallel shafts and articular surfaces that extend half their length (1).

174. Metacarpals, shape of proximal surface in articulation: gently curving, forming a 90° arc (0); U-shaped, subtending a 270° arc (1).

175. Longest metacarpal-to-radius ratio: close to 0.3 (0); 0.45 or more (1).

176. Metacarpal I, length: shorter than metacarpal IV (0); longer than metacarpal IV (1).

177. Metacarpal I, distal condyle shape: divided (0); undivided (1).

178. Metacarpal I distal condyle, transverse axis orientation: bevelled approximately 20° proximodistally with respect to axis of shaft (0); perpendicular to axis of shaft (1).

179. Manual digits II and III, phalangeal number: 2-3-4-3-2 or more (0); reduced, 2-2-2-2-2 or less (1); absent or unossified (1).

180. Manual phalanx I.1, shape: rectangular (0); wedge-shaped (1).

181. Manual nonungual phalanges, shape: longer proximodistally than broad transversely (0); broader transversely than long proximodistally (1).

182. Pelvis, anterior breadth: narrow, ilia longer anteroposteriorly than distance separating preacetabular processes (0); broad, distance bewteen preacetabular processes exceeds anteroposterior length of ilia (1).

183. Ilium, ischial peduncle size: large, prominent (0); low, rounded (1).

184. Iliac blade dorsal margin, shape: flat (0); semicircular (1).

185. Iliac preacetabular process, orientation: anterolateral to body axis (0); perpendicular to body axis (1).

186. Pubis, ambiens process development: small, confluent with anterior margin of pubis (0); prominent, projecting anteriorly from anterior margin of pubis (1).

187. Pubic apron, shape: flat (straight symphysis) (0); canted anteromedially (gentle S-shaped symphysis) (1).

188. Puboischial contact, length: approximately one-third total length of pubis (0); approximately one-half total length of pubis (1).

189. Ischial shaft, length: much shorter than shaft of pubis (0); equal to or longer than shaft of pubis (1).

190. Ischial shaft, shape: emarginate distal to pubic peduncle (0); no emargination distal to pubic peduncle (1).

191. Ischial distal shaft, shape: triangular, depth of ischial shaft increases medially (0); blade-like, medial and lateral depths subequal (1).

192. Ischial distal shafts, cross-sectional shape: V-shaped, forming an angle of nearly 50° with each other (0); flat, nearly coplanar (1).

193. Femoral fourth trochanter, development: prominent (0); reduced to crest or ridge (1).

194. Femoral lesser trochanter: present (0); absent (1).

195. Femoral mid-shaft, transverse diameter: subequal to anteroposterior diameter (0); 125-150% anteroposterior diameter (1); at least 185% anteroposterior diameter (2).

196. Femoral shaft, lateral margin shape: straight (0); proximal one-third deflected medially (1).

197. Femoral distal condyles, relative transverse breadth: subequal (0); tibial much broader than fibular (1).

198. Femoral distal condyles, orientation: perpendicular or slightly bevelled dorsolaterally relative to femoral shaft (0); bevelled dorsomedially approximately 10° relative to femoral shaft (1).

199. Femoral distal condyles, articular face shape: restricted to distal portion of femur (0); expanded onto anterior portion of femoral shaft (1).

200. Tibial proximal condyle, shape: narrow, long axis anteroposterior (0), expanded transversely, condyle subcircular (1).

201. Tibial cnemial crest, orientation: projecting anteriorly (0); projecting laterally (1).

202. Tibia, distal breadth: approximately 125% mid-shaft breadth (0); more than twice mid-shaft breadth (1).

203. Tibial distal posteroventral process, size: broad transversely, covering posterior fossa of astragalus (0); shortened transversely, posterior fossa of astragalus visible posteriorly (1).

204. Fibula, proximal tibial scar, development: not well-marked (0); well-marked and deepening anteriorly (1).

205. Fibula, lateral trochanter: absent (0); present (1).

206. Astragalus, shape: rectangular (0); wedge-shaped, with reduced anteromedial corner (1).

207. Astragalus, foramina at base of ascending process: present (0); absent (1).

208. Astragalus, ascending process length: limited to anterior two-thirds of astragalus (0); extending to posterior margin of astragalus (1).

209. Astragalus, posterior fossa, shape: undivided (0); divided by vertical crest (1).

210. Astragalus, transverse length: 50% more than proximodistal height (0); subequal to proximodistal height (1).

211. Calcaneum: present (0); absent or unossified (1).

212. Distal tarsals 3 and 4: present (0); absent or unossified (1).

213. Metatarsus, posture: bound (0); spreading (1).

214. Metatarsal I proximal condyle, transverse axis orientation: perpendicular to axis of shaft (0); angled ventromedially approximately 15° to axis of shaft (1).

215. Metatarsal I distal condyle, transverse axis orientation: perpendicular to axis of shaft (0); angled dorsomedially to axis of shaft (1).

216. Metatarsal I distal condyle, posterolateral projection: absent (0); present (1).

217. Metatarsal I, minimum shaft width: less than that of metatarsals II-IV (0); greater than that of metatarsals II-IV (1).

218. Metatarsal I and V proximal condyle, size: smaller than those of metatarsals II and IV (0); subequal to those of metatarsals II and IV (1).

219. Metatarsal III, length: more than 30% that of tibia (0); less than 25% that of tibia (1).

220. Metatarsals III and IV, minimum transverse shaft diameters: subequal to that of metatarsals I or II (0); less than 65% that of metatarsals I or II (1).

221. Metatarsal V, length: shorter than length of metatarsal IV (0); at least 70% length of metatarsal IV (1).

222. Pedal nonungual phalanges, shape: longer proximodistally than broad transversely (0); broader transversely than long proximodistally (1).

223. Pedal digits II-IV, penultimate phalanges, development: subequal in size to more proximal phalanges (0); rudimentary or absent (1).

224. Pedal unguals, orientation: aligned with digit axis (0); deflected lateral to digit axis (1).

225. Pedal digit I ungual, length relative to pedal digit II ungual: subequal (0); 25% larger than that of digit II (1).

226. Pedal digit I ungual, length: shorter than metatarsal I (0); longer than metatarsal I (1).

227. Pedal ungual I, shape: broader transversely than dorsoventrally (0); sickle-shaped, much deeper dorsoventrally than broad transversely (1).

228. Pedal ungual II-III, shape: broader transversely than dorsoventrally (0); sickle-shaped, much deeper dorsoventrally than broad transversely (1).

229. Pedal digit IV ungual, development: subequal in size to unguals of pedal digits II and III (0); rudimentary or absent (1).

230. Osteoderms: absent (0); present (1).

APPENDIX 4

Character-Taxon Matrix

Taxon	10	20	30	40	50
Prosauropoda	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 9 9 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0
Theropoda	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 9 9 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0
Vulcanodon	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? 0 ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?
Barapasaurus	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?
Omeisaurus	1 1 1 0 0 0 1 1 0 1	1 ? 0 0 0 ? 0 1 0 1	1 0 0 0 0 1 0 1 1 1	? 1 1 ? 0 ? 1 ? ? 1	1 1 0 0 ? 0 ? 0 ? 0
Shunosaurus	0 1 1 0 0 0 1 1 0 1	1 0 0 0 0 0 0 0 0 1	? ? 0 0 0 0 0 1 1 1	0 1 1 0 0 0 1 0 0 1	1 0 0 0 0 0 0 0 0 ?
Patagosaurus	1 ? 1 0 0 ? 1 1 ? ?	? ? ? ? ? ? 0 ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? 1 ? ? ? ? ? ? ? ?
Mamenchisaurus	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? 1 1 0 ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?
Apatosaurus	0 0 1 1 1 1 1 2 0 1	1 ? 1 1 1 ? 0 1 0 1	1 1 ? 1 0 1 0 1 1 1	1 1 1 0 0 0 2 0 ? 1	? 0 0 0 0 1 0 0 0 0
Barosaurus	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?
Brachiosaurus	1 1 1 1 0 0 1 1 1 1	1 1 0 0 0 1 0 1 0 1	1 0 0 0 0 1 0 1 1 1	1 1 1 1 0 0 1 0 1 1	1 1 0 0 0 0 0 0 0 1
Camarasaurus	1 1 1 1 0 0 1 1 1 1	1 1 0 0 0 1 0 1 0 1	1 0 0 1 0 1 0 1 1 1	0 0 1 1 0 1 1 0 1 1	1 1 0 0 0 0 0 0 0 0
Dicraeosaurus	0 0 ? 1 1 ? ? ? ? ?	0 ? ? 0 0 ? 0 1 1 1	1 1 1 1 0 1 1 1 1 1	? ? ? ? ? 1 ? 0 ? ?	1 0 0 0 1 1 1 0 1 0
Diplodocus	0 0 1 1 1 1 1 2 0 1	1 1 1 1 1 1 0 1 0 1	1 1 0 1 0 1 0 1 1 1	1 1 1 0 0 0 2 0 1 1	1 0 0 0 0 1 0 0 0 0
Haplocanthosaurus	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? 0 ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? 0 ?
Amargasaurus	? ? ? ? ? ? ? ? ? ?	1 ? ? 0 0 1 0 1 1 1	1 ? 1 1 0 1 1 1 1 ?	? ? ? ? ? ? ? ? ? ?	? ? 0 0 1 1 1 0 1 1
Euhelopus	1 1 1 0 0 ? 1 1 ? ?	1 ? ? ? ? 1 0 ? ? ?	? ? ? ? ? ? ? ? ? ?	? 1 1 0 0 ? ? 0 ? 1	1 1 ? ? ? ? ? ? ? ?
Jobaria	1 1 1 1 0 0 1 1 1 1	1 1 0 0 0 1 0 1 0 1	1 0 0 0 0 1 0 1 1 1	0 1 1 1 0 ? 1 0 ? 1	1 ? 0 0 0 ? ? 0 0 0
Malawisaurus	1 1 ? ? ? ? ? 1 ? ?	1 ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?
Nigersaurus	0 0 1 1 ? ? 1 1 0 0	? ? ? 0 0 1 1 9 0 0	1 ? ? 9 1 9 9 9 9 1	? 1 1 1 0 ? ? ? ? ?	? ? 0 0 0 1 ? 0 0 ?
Rayosaurus	? ? ? ? ? ? ? ? ? 0	1 ? ? 0 0 1 1 9 0 0	1 1 0 9 1 9 9 9 1 1	0 ? 1 1 0 ? ? 0 ? ?	? ? 1 0 0 1 0 1 0 1
Rebbachisaurus	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?
Alamosaurus	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?
Nemegtosaurus	0 1 ? 1 9 0 1 1 ? 1	0 1 0 0 0 1 0 1 0 1	0 1 0 1 0 1 0 1 0 1	0 1 1 1 1 2 1 1 1 1	1 ? 1 1 0 0 0 1 0 0
Neuquensaurus	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?
Opisthocoelicaudia	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?
Rapetosaurus	0 0 1 1 ? 1 1 1 ? 1	0 ? 0 0 0 ? 0 0 0 1	0 1 0 1 0 1 0 1 0 1	0 ? 1 1 1 2 1 1 1 ?	? ? 1 1 ? 0 1 0 0 ?
Saltasaurus	? ? ? ? ? ? ? ? ? ?	? ? ? 0 0 ? ? 1 0 1	? 0 0 1 0 1 ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? 0 1 0 0 0 1 0 1
Isisaurus	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?
Paluxysaurus	? ? 1 ? ? ? 1 1 ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?
Cedarosaurus	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?
Venenosaurus	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?
Phuwiangosaurus	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?
Astrodon	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?

Appendix 4 continued

	6 0	7 0	8 0	9 0	1 0 0
Prosauropoda	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 9 0 0	0 0 0 0 0 0 0 0 0 1	1 0 9 0 0 0 0 0 0 9	1 0 0 0 0 0 0 0 0 0
Theropoda	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 9 0 0	0 0 0 0 0 0 0 0 0 0	1 0 9 0 0 0 0 0 0 9	0 0 0 0 0 0 0 0 0 0
Vulcanodon	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? 0 ? ?	? ? 9 ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?
Barapasaurus	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? 1	? 0 ? ? ? ? 0 0 ? ?	0 1 9 ? ? 0 1 0 0 9	? 1 0 1 0 1 1 0 1 1
Omeisaurus	? 0 0 1 1 0 0 0 0 ?	1 ? ? ? 1 1 1 0 1 1	1 1 1 ? 0 0 0 1 0 4	0 1 1 1 0 1 0 ? 0 9	3 1 0 1 ? 1 1 0 1 1
Shunosaurus	0 0 0 1 1 0 0 0 0 ?	1 0 1 ? 1 1 1 0 1 1	1 2 0 ? 0 0 0 0 0 3	1 1 9 1 0 0 1 0 0 9	2 1 0 0 0 0 ? 0 0 0
Patagosaurus	? ? ? ? ? 0 ? ? ? ?	? ? ? ? 1 ? 1 0 1 1	1 ? ? ? 0 0 0 1 ? ?	0 1 1 ? 0 0 1 0 0 9	? 1 0 1 0 1 1 0 1 ?
Mamenchisaurus	? ? ? ? 1 0 0 0 0 ?	1 0 1 1 1 ? 1 ? 1 1	1 1 0 0 0 0 1 1 ? 4	0 1 ? 1 0 1 0 1 1 0	3 1 0 1 0 ? 1 ? 1 ?
Apatosaurus	0 0 1 1 ? ? ? ? ? ?	? ? ? ? 2 2 1 2 0 2	1 2 1 ? ? ? 0 1 1 4	0 1 1 0 1 0 1 1 1 1	5 1 0 1 1 1 1 1 1 1
Barosaurus	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? 0 1 ? ?	0 1 1 ? 1 1 1 ? 1 1	? 1 0 1 ? ? ? ? 1 1
Brachiosaurus	1 0 0 1 1 0 0 1 1 1	1 1 1 2 1 1 1 0 0 1	1 2 1 0 0 0 1 1 0 3	0 1 1 0 0 1 1 0 0 9	3 1 0 1 0 1 1 1 1 1
Camarasaurus	1 0 0 1 1 0 0 1 1 1	1 1 1 1 1 1 1 0 1 1	1 2 1 0 0 0 0 1 0 2	0 1 1 0 1 0 1 0 1 0	3 1 0 1 0 1 1 0 1 1
Dicraeosaurus	1 0 1 1 1 1 0 ? ? ?	? ? ? ? 2 2 1 2 0 2	1 2 1 ? 0 0 0 1 1 2	0 1 1 0 1 0 1 0 1 1	3 1 1 1 1 1 0 0 1 1
Diplodocus	1 0 1 1 1 1 0 1 0 1	1 0 1 ? 2 2 1 2 0 2	1 2 1 1 1 0 0 1 1 4	0 1 1 0 1 1 1 1 1 1	5 1 0 1 1 1 1 1 1 1
Haplocanthosaurus	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? 0 1 ? 3	0 1 1 0 0 0 1 0 0 9	2 1 0 1 0 1 1 0 1 1
Amargasaurus	? 0 1 1 ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? 0 0 1 3	0 1 9 ? 1 0 1 0 1 0	5 1 1 1 ? ? ? ? 1 ?
Euhelopus	? ? ? ? 1 0 0 1 1 ?	? ? ? ? 1 ? 1 0 1 1	1 2 1 0 1 0 1 1 ? 4	1 1 1 1 0 1 1 0 1 1	2 1 0 1 0 1 1 1 1 ?
Jobaria	? 0 0 1 0 0 0 ? ? ?	? ? ? ? 1 1 1 0 1 1	1 0 0 0 0 0 0 1 ? 3	0 1 1 0 0 0 1 0 0 9	3 1 0 1 0 1 1 1 1 1
Malawisaurus	? ? ? ? 1 0 0 ? ? ?	? ? ? ? 1 ? 1 ? ? 1	1 2 1 0 ? 0 1 1 ? ?	1 1 0 0 0 1 1 ? 0 9	? 1 0 1 0 1 ? 0 1 ?
Nigersaurus	? 0 1 1 1 0 9 1 0 0	? ? ? ? 2 2 1 1 0 2	1 2 0 1 0 1 0 1 ? ?	0 1 1 0 0 0 1 ? 0 9	? ? ? ? ? ? ? ? ? ?
Rayosaurus	1 0 1 1 ? ? ? ? ? ?	? ? ? ? ? ? 1 ? ? 2	1 2 ? ? ? 1 0 1 ? ?	0 1 1 0 0 0 1 0 0 9	? 1 ? 1 0 ? ? ? 1 1
Rebbachisaurus	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? 1 ? ?	? ? ? ? ? ? ? ? 0 9	? 1 1 ? ? 1 1 1 1 1
Alamosaurus	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? 1 1 ? ?	1 1 0 0 0 1 ? 0 9	? 1 0 1 0 1 1 0 1 0
Nemegtosaurus	0 1 0 1 1 0 1 1 1 ?	? 0 1 ? 1 1 1 ? 0 2	1 2 1 0 0 0 ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?
Neuquensaurus	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? 1 1 ? ?	0 1 0 ? 0 0 1 ? 0 9	? 1 0 1 ? ? ? ? 1 ?
Opisthocoelicaudia	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? 1 ? ?	? ? ? ? ? ? ? 0 1 0	4 1 0 1 0 1 1 1 1 0
Rapetosaurus	1 1 0 1 0 0 1 1 1 ?	? ? ? ? 1 1 1 1 0 2	1 2 1 0 0 0 1 1 ? ?	1 1 0 ? 0 1 1 ? 0 9	? 1 0 1 0 1 ? 0 1 0
Saltasaurus	? ? ? 1 ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? 1 1 ? ?	0 1 1 0 0 0 1 1 0 9	? 1 0 1 0 1 ? 1 1 0
Isisaurus	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? 1 ? ?	1 1 0 0 0 1 0 0 9	? 1 0 1 0 1 1 0 1 0
Paluxysaurus	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? 1 ? 0 1 1	1 2 ? 0 0 0 1 1 ? ?	0 1 1 ? 0 1 ? 0 0 ?	? 1 0 1 0 1 1 1 ? 1
Cedarosaurus	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? 1 ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? 0 ? ? 1 ? ?
Venenosaurus	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?
Phuwiangosaurus	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? 1 ?	? ? 1 ? ? 1 ? 1 0 1	2 ? 0 1 ? 1 1 1 ? 0
Pleurocoelus	? ? ? ? ? 0 ? ? ? ?	? ? ? ? 1 ? ? 0 ? 1	1 2 1 0 ? ? 0 1 ? ?	? ? ? 0 ? ? ? ? ? ?	? ? ? 1 ? ? ? ? ? ?

Appendix 4 continued

	1 1 0	1 2 0	1 3 0	1 4 0	1 5 0
Prosauropoda	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 9 9 0 0 0	0 0 9 0 0 0 0 0 0 0
Theropoda	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 9 9 0 0 0	0 0 9 0 0 0 0 0 1 0
Vulcanodon	? ? ? ? ? ? ? 1 ? ?	? 0 ? ? 0 ? 0 0 ? ?	? ? ? ? ? 1 0 0 0 0	1 ? ? ? ? ? ? ? ? ?	? ? ? 0 0 ? ? 1 0 ?
Barapasaurus	1 0 1 0 0 0 0 1 1 0	? 0 ? ? 0 ? 0 0 ? ?	? ? ? ? ? 1 0 0 0 0	0 0 0 0 0 9 9 ? ? ?	0 1 ? 0 0 ? 0 1 1 0
Omeisaurus	1 0 0 0 0 0 0 2 1 0	1 ? 0 1 0 0 0 0 0 0	0 0 0 0 0 1 0 0 0 0	? 0 0 0 ? ? ? 1 0 0	? 1 1 0 0 0 0 1 1 0
Shunosaurus	0 0 0 0 0 ? 0 1 0 0	0 0 0 1 0 0 0 0 0 0	0 0 0 0 0 1 0 0 0 0	? 0 0 0 9 9 0 ? 0	0 1 1 1 0 1 0 1 0 0
Patagosaurus	? 0 1 0 0 0 0 2 ? 0	? ? ? ? ? ? 0 0 ? ?	? ? ? ? ? 1 ? ? ? 0	? 0 0 0 ? ? ? 1 ? 0	0 ? ? 0 0 ? ? 1 1 0
Mamenchisaurus	1 0 ? 0 0 0 0 2 ? ?	? ? 0 1 1 0 1 0 0 0	0 0 0 0 0 1 0 0 0 0	? 0 0 0 ? ? ? 1 0 0	0 1 1 0 0 ? 0 1 ? ?
Apatosaurus	1 0 0 0 0 0 0 2 1 1	1 0 0 1 1 0 0 0 0 1	1 1 1 0 1 1 1 1 1 0	0 0 0 0 1 1 1 1 1 0	0 1 1 0 0 1 0 1 1 0
Barosaurus	1 0 0 0 0 0 0 ? ? ?	? 0 ? 1 1 0 1 1 1 1	1 1 1 0 1 1 1 1 1 1	1 1 0 0 1 1 ? ? ? ?	0 1 ? 0 0 ? 0 1 ? ?
Brachiosaurus	1 1 0 0 1 0 0 2 1 0	1 0 ? 1 0 0 0 0 0 0	0 1 1 0 0 1 0 0 0 0	0 0 0 0 ? ? ? 1 0 1	1 ? ? 1 0 ? ? 1 1 0
Camarasaurus	1 1 0 0 1 0 0 2 1 0	1 0 0 1 0 0 0 0 0 0	0 1 1 0 1 1 0 0 0 0	0 0 0 0 0 9 9 1 0 0	? 1 0 1 0 1 0 1 1 0
Dicraeosaurus	1 0 0 0 0 0 1 2 1 1	? 0 ? 1 1 0 0 0 0 1	0 1 1 0 1 1 1 0 0 0	0 0 0 0 1 1 ? 1 1 0	0 1 ? 0 0 ? ? 1 1 0
Diplodocus	1 0 0 0 0 0 0 2 1 1	1 0 0 1 1 0 1 1 1 1	1 1 1 0 1 1 1 1 1 1	1 1 0 0 1 1 1 1 1 0	0 1 1 0 0 1 0 1 1 0
Haplocanthosaurus	1 1 0 0 0 0 0 2 1 0	1 0 ? 1 0 0 0 0 0 0	0 1 1 0 0 1 0 0 0 0	0 0 0 ? ? ? ? 1 1 0	0 ? ? 1 0 ? ? 1 0 0
Amargasaurus	? 0 0 0 0 ? 1 2 ? 1	? ? ? ? 0 ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? 0 ? ? ? ? ? ? ?	0 ? ? ? ? ? ? 1 ? ?
Euhelopus	1 1 0 1 1 ? 0 3 ? 0	1 ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? 1 0 1	1 ? ? ? ? ? ? 1 1 0
Jobaria	1 1 0 0 0 0 0 2 1 0	1 0 0 1 0 0 0 0 0 0	0 1 1 0 0 1 0 0 0 0	0 0 0 0 ? ? ? 1 0 0	0 1 ? 0 0 1 0 1 1 0
Malawisaurus	1 1 0 1 1 1 0 ? ? ?	? ? ? 1 ? ? 1 0 ? 0	0 1 1 1 0 1 0 0 0 0	1 0 0 0 ? ? ? 1 0 1	? 0 9 1 1 ? ? 1 ? ?
Nigersaurus	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? 1 1 0	0 ? ? ? ? ? ? 7 1 0
Rayosaurus	1 0 0 0 0 ? 1 ? ? ?	? 0 0 1 0 0 0 0 0 0	0 1 1 0 1 1 0 0 0 0	0 0 0 0 1 1 ? 1 ? ?	? ? ? 1 ? ? ? 1 1 0
Rebbachisaurus	1 0 0 0 0 1 1 ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? 1 1 0
Alamosaurus	1 1 0 1 1 1 0 ? ? ?	? ? 1 2 3 1 1 0 0 0	0 1 1 0 1 1 0 0 0 0	1 0 1 0 ? ? ? ? ? ?	? 0 9 1 1 1 1 1 1 1
Nemegtosaurus	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?
Neuquensaurus	1 ? 0 1 1 1 0 3 1 0	? 1 ? ? 3 0 1 0 ? 0	0 1 1 ? 1 1 0 0 0 0	1 0 1 1 1 0 ? ? ? ?	? ? ? ? ? ? ? 1 1 1
Opisthocoelicaudia	1 1 0 1 1 1 0 3 1 0	? ? 1 2 2 1 2 0 0 0	0 1 1 0 1 1 0 0 0 0	1 0 2 0 1 0 0 ? ? 1	1 0 9 1 1 1 1 1 1 0
Rapetosaurus	1 1 0 1 1 1 0 3 ? ?	? ? ? ? ? ? 1 ? ? 0	? ? ? ? ? ? ? 0 0 ?	? ? 1 ? ? ? ? 1 ? ?	? ? ? ? ? ? ? 1 1 1
Saltasaurus	1 1 0 1 1 1 0 3 1 0	1 1 ? ? ? ? 1 0 ? 0	0 1 1 1 1 1 0 0 0 0	1 0 1 1 1 0 ? 1 ? ?	? ? ? 1 1 ? 0 1 1 1
Isisaurus	1 0 0 ? 1 1 0 3 1 0	? ? ? ? ? ? 1 0 ? 0	0 1 1 0 1 1 0 0 0 0	1 0 1 0 ? ? ? 1 ? ?	1 0 9 1 1 ? 0 1 0 1
Paluxysaurus	? ? 0 0 1 ? 0 2 1 ?	? 0 ? ? ? ? 0 0 0 0	0 1 1 0 1 1 0 0 0 0	0 0 0 0 0 9 9 1 0 1	1 ? ? 1 0 ? ? 1 1 0
Cedarosaurus	? ? ? ? 1 ? ? ? ? ?	? ? ? 1 ? ? 0 0 0 ?	0 ? ? ? 0 1 0 0 0 0	0 2 0 0 ? ? ? ? ? ?	1 ? ? 1 ? ? ? 1 1 0
Venenosaurus	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? 0 0 0 ?	0 ? ? ? 0 1 0 0 0 0	0 2 0 0 ? ? ? ? ? 1	1 ? ? 1 0 ? ? 1 ? 0
Phuwiangosaurus	? 0 ? 0 1 1 0 2 ? ?	? ? ? ? ? ? 0 0 ? 0	0 0 0 0 0 ? 0 0 0 1	0 ? 0 0 1 0 ? ? ? ?	? 0 ? 1 ? ? 1 ? 1 1
Astrodon	? ? ? ? 1 ? ? ? ? ?	? ? ? ? ? ? 0 0 0 ?	? ? ? ? ? ? ? ? ? 0	0 ? 0 0 ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?

Appendix 4 continued

	1 6 0	1 7 0	1 8 0	1 9 0	2 0 0
Prosauropoda	0 0 0 0 0 0 0 0 0 0	1 0 0 0 9 0 0 0 0 0	0 0 0 0 0 1 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0
Theropoda	0 0 0 0 0 0 0 0 0 0	1 1 0 0 9 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0
Vulcanodon	? ? ? ? ? ? ? ? 1 0	1 0 ? 1 1 1 0 1 0 1	? ? ? ? 0 ? ? ? ? ?	? ? 1 ? ? 0 0 0 1 0	1 0 1 0 1 0 ? ? ? 0
Barapasaurus	0 0 0 0 0 0 ? 0 1 0	1 0 1 1 1 1 0 1 0 ?	? ? ? ? ? ? ? ? ? ?	? 0 1 1 0 0 1 0 1 0	1 0 1 1 1 0 1 0 0 0
Omeisaurus	0 0 ? 0 0 0 0 0 1 0	1 0 1 1 0 1 0 1 0 1	0 1 0 0 0 0 0 0 1 1	1 ? 1 1 0 0 1 0 1 0	1 0 1 ? 1 0 0 0 ? 0
Shunosaurus	0 0 0 0 0 0 0 0 1 0	1 0 1 1 0 1 0 1 0 1	0 1 0 0 0 0 0 1 1 0	1 0 1 1 0 0 1 0 1 0	? 0 1 1 1 0 1 0 0 ?
Patagosaurus	? 0 ? 0 0 0 ? 0 1 0	1 1 1 1 1 1 0 1 0 ?	? ? ? ? ? ? ? ? ? ?	? ? 1 1 0 0 1 0 1 0	1 0 1 1 1 0 1 0 0 0
Mamenchisaurus	? ? ? ? ? ? ? 0 1 0	1 0 1 1 1 1 0 1 0 1	? ? ? ? ? ? ? ? ? ?	? ? 1 1 0 ? ? ? ? 0	1 0 1 1 1 0 1 0 0 1
Apatosaurus	0 1 1 0 0 0 0 0 1 0	1 0 1 1 0 1 0 1 0 1	1 1 1 1 0 0 0 0 1 1	1 1 1 1 0 1 1 0 1 0	0 0 1 1 1 0 1 0 0 1
Barosaurus	? ? ? ? ? ? 0 ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? 1 1 ? ? ?	? ? ? ? ? ? ? ? ? ?
Brachiosaurus	1 0 1 0 0 0 0 0 1 0	1 0 1 1 1 1 0 1 0 1	1 1 1 1 1 1 1 1 1 0	1 1 1 1 0 0 1 1 1 0	1 1 1 1 2 1 1 0 0 1
Camarasaurus	1 0 1 0 0 0 0 0 1 0	1 0 1 1 1 1 0 1 0 1	1 1 1 1 1 1 0 0 1 1	1 1 1 1 0 0 1 1 1 0	1 1 1 1 1 0 1 0 0 1
Dicraeosaurus	0 0 1 0 0 0 ? 0 1 0	1 0 1 1 1 1 0 ? ? 1	? ? ? ? ? ? ? ? ? ?	? 1 1 1 0 1 1 0 1 0	0 0 1 1 1 0 1 0 0 1
Diplodocus	0 0 1 0 0 0 0 0 1 0	1 0 1 1 1 1 0 1 0 1	? ? ? ? ? ? ? ? ? ?	? 1 1 1 0 1 1 0 1 0	0 0 1 1 1 0 1 0 1 1
Haplocanthosaurus	0 0 1 0 0 0 0 ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? 1 1 1 0 0 1 0 1 0	1 1 1 1 1 0 1 0 0 ?
Amargasaurus	0 ? 1 ? ? ? ? 0 1 0	1 0 1 1 0 1 0 ? 0 1	? ? ? ? ? ? ? ? ? ?	? ? 1 1 0 ? ? ? ? ?	? ? 1 1 1 0 ? 0 0 ?
Euhelopus	0 1 0 0 0 0 ? 1 1 0	1 0 1 ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? 1 1 1 0 0 1 0 1 0	1 1 1 1 1 1 1 0 0 1
Jobaria	1 0 1 0 0 0 0 0 1 0	1 0 1 1 1 1 0 1 0 1	0 1 1 1 0 0 0 0 1 1	1 1 1 1 0 0 1 0 1 0	1 1 1 1 1 0 1 0 0 1
Malawisaurus	? ? ? 0 0 0 1 1 1 0	1 0 1 1 0 0 0 1 0 ?	? ? 1 ? ? 1 1 1 ? ?	? ? ? ? ? ? ? ? ? 1	1 1 ? 1 1 1 ? ? ? ?
Nigersaurus	2 0 ? 0 ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?
Rayosaurus	2 0 ? 0 0 0 1 0 1 0	0 0 1 1 1 1 0 1 0 1	? ? ? ? ? ? ? ? ? ?	? ? 1 1 2 0 1 0 1 0	1 1 1 1 1 0 ? 0 0 ?
Rebbachisaurus	2 0 1 ? ? ? ? ? 1 ?	0 ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? 0	1 1 ? ? ? ? ? ? ? ?
Alamosaurus	0 1 1 1 1 ? 1 1 1 1	1 1 0 1 1 0 0 1 1 ?	9 9 1 1 1 1 1 1 2 9	9 ? ? ? ? ? ? ? 0 1	1 1 ? ? ? ? ? ? ? ?
Nemegtosaurus	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?
Neuquensaurus	0 1 0 1 1 1 1 1 1 1	1 1 0 1 1 0 1 1 1 ?	? ? ? ? ? ? ? ? ? ?	? ? 1 1 1 0 1 ? 0 1	1 1 1 1 1 1 1 1 1 1
Opisthocoelicaudia	0 1 1 1 1 1 1 1 1 1	1 1 0 1 1 0 1 1 1 1	9 9 1 1 1 1 1 1 2 9	9 1 1 1 1 0 1 1 0 1	1 1 1 1 2 1 1 1 0 1
Rapetosaurus	0 ? ? 1 0 0 1 1 1 0	1 1 0 1 ? 0 0 1 0 ?	? ? ? ? 1 ? 1 ? ? ?	? 1 1 1 0 0 1 1 0 1	1 1 1 1 0 1 1 0 1 ?
Saltasaurus	0 1 0 1 1 1 1 1 1 1	1 1 0 1 1 0 1 1 1 ?	? ? ? ? ? ? ? ? ? ?	? 1 1 1 1 0 1 1 0 1	1 1 1 1 1 1 1 1 1 1
Isisaurus	0 1 0 ? ? ? ? 1 1 0	1 1 1 1 1 0 1 ? ? ?	? ? ? ? ? ? ? ? ? ?	? 1 1 1 1 0 1 1 0 1	1 1 ? ? ? ? ? ? ? ?
Paluxysaurus	1 0 1 0 0 0 0 0 1 0	1 0 1 1 1 1 0 1 0 1	? ? 1 ? 1 ? 1 1 ? ?	? 1 1 ? 0 0 1 0 1 0	1 1 1 1 2 1 1 0 0 0
Cedarosaurus	? 0 1 0 0 0 0 0 1 0	1 0 1 1 1 1 ? 0 0 1	? ? ? ? 1 ? ? ? ? ?	? ? ? ? ? 0 1 ? ? 0	? ? ? 1 ? 1 ? 0 ? ?
Venenosaurus	0 0 ? ? ? ? ? ? ? ?	? ? ? 1 1 1 0 0 0 ?	? ? 1 1 1 ? ? ? ? ?	? ? ? ? ? 0 1 0 1 0	1 1 ? ? ? ? ? ? ? ?
Phuwiangosaurus	0 1 ? ? ? ? 1 0 1 0	? ? ? ? 1 1 0 ? 0 ?	? ? ? ? ? ? ? ? ? ?	? ? 1 1 1 ? ? 0 1 1	1 1 1 1 2 1 1 1 1 0
Astrodon	1 ? 1 ? 0 0 ? ? ? 0	? 0 1 ? 1 1 ? ? 0 ?	? ? ? ? ? 1 1 1 ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? 1 0 ? 0 0 1

Appendix 4 continued

	2 1 0	2 2 0	2 3 0
Prosauropoda	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0
Theropoda	0 0 0 0 0 0 0 0 0 0	0 0 0 0 9 9 0 0 0 0	0 0 0 0 0 0 0 0 0 0
Vulcanodon	0 0 ? 0 0 0 1 0 0 0	0 1 0 ? 1 0 0 1 0 0	1 0 0 ? 0 1 1 0 0 0
Barapasaurus	1 0 1 1 1 ? 1 ? 1 0	? ? ? 0 1 0 ? ? ? ?	? ? ? 1 ? ? 1 1 ? 0
Omeisaurus	1 0 1 1 ? 0 1 0 1 0	0 1 1 1 1 1 1 1 1 1	1 1 1 1 1 1 1 1 1 0
Shunosaurus	1 0 1 ? 1 0 1 0 ? 0	0 1 1 1 1 0 1 1 1 0	1 1 1 ? 1 1 1 1 1 0
Patagosaurus	0 0 1 ? ? ? ? ? ? ?	? ? 1 0 1 0 1 1 ? ?	? ? ? ? ? ? ? ? ? 0
Mamenchisaurus	1 0 1 ? 1 0 1 1 1 0	? 1 1 ? ? ? ? ? 1 ?	1 1 ? 1 ? ? 1 ? ? 0
Apatosaurus	1 0 1 1 1 1 1 1 1 0	1 1 1 1 1 1 1 1 1 1	? 1 1 1 1 ? 1 1 1 0
Barosaurus	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? 0
Brachiosaurus	1 0 1 1 1 1 1 1 1 0	0 1 1 1 1 0 1 1 1 ?	1 1 ? 1 ? ? 1 1 ? 0
Camarasaurus	1 0 1 1 1 1 1 1 1 0	0 1 1 1 1 0 1 1 1 1	1 1 1 1 1 1 1 1 1 0
Dicraeosaurus	1 0 1 1 1 1 1 1 1 0	? ? 1 1 1 1 1 1 ? 1	1 ? ? ? ? 1 1 ? ? 0
Diplodocus	1 0 1 ? 1 1 1 1 1 0	0 1 1 1 1 1 1 1 1 1	1 1 1 1 ? 1 1 1 1 0
Haplocanthosaurus	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? 0
Amargasaurus	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? 0
Euhelopus	1 0 1 ? 1 1 1 1 ? 0	0 ? 1 1 1 0 1 1 1 1	? 1 ? ? 1 1 1 1 ? 0
Jobaria	1 0 1 1 1 1 1 1 1 0	0 1 1 1 1 0 1 1 1 1	1 ? ? ? ? ? ? ? ? 0
Malawisaurus	? 1 1 1 1 ? ? ? ? ?	? ? 1 ? ? ? ? ? ? ?	? ? ? ? ? ? 1 ? ? 1
Nigersaurus	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?
Rayosaurus	1 0 ? ? 1 1 ? ? ? 0	? ? 1 0 0 0 1 1 1 1	? ? ? ? ? ? ? ? ? 0
Rebbachisaurus	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? 0
Alamosaurus	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? 0
Nemegtosaurus	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?
Neuquensaurus	1 1 1 ? 1 1 1 1 0 1	? ? 1 1 1 0 ? ? ? ?	? 1 ? ? ? ? ? ? ? 1
Opisthocoelicaudia	1 1 1 1 1 1 1 1 0 1	1 1 1 1 1 0 1 1 1 1	1 1 1 1 1 1 1 1 1 0
Rapetosaurus	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? 1
Saltasaurus	1 1 1 1 1 ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? 1
Isisaurus	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?
Paluxysaurus	1 0 1 1 1 ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?
Cedarosaurus	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? 1	? ? ? ? 1 ? 1 1 ? ?
Venenosaurus	? ? ? ? ? 1 1 1 1 0	? ? ? 1 1 0 1 1 ? 1	? ? ? ? ? ? ? ? ? ?
Phuwiangosaurus	1 1 ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ?
Astrodon	? 0 ? ? ? ? ? ? ? ?	? ? ? 1 ? 0 ? ? ? 1	? ? ? ? ? ? ? ? ? ?