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ANATOMICAL TERMINOLOGY FOR THE SACRUM OF SAUROPOD DINOSAURS

BY

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Abstract — The sacrum represents a key anatomical element for understanding Dinosauria, beginning with the first use of the taxon name in 1842. A five-vertebra sacrum was originally considered diagnostic of dinosaurs, and variation in the number of sacral vertebrae has been used to diagnose smaller groups of dinosaurs. Despite its centrality to early definitions of Dinosauria, utility for diagnosing smaller groups, and manifest complexity in certain groups (e.g., sauropods and theropods), the sacrum has played a relatively minor role in determining phylogenetic relationships among dinosaurs. Part of this oversight may be due to the absence of nomenclature to describe the parts of the sacrum. Here I present a nomenclature for the sauropod sacrum that is designed to aid description of the complex structures involved and to facilitate development of novel character data. Although based on sauropods, it is applicable to closely related taxa, such as other sauropodomorphs and theropods.

INTRODUCTION

Owen (1842: 102-103) diagnosed the original triumvirate of Dinosauria, which he considered "gigantic Crocodile-lizards of the dry land," by "a large sacrum composed of five anchylosed vertebrae of unusual construction." Since that time, the sacrum has furnished mostly meristic characters, which have been applied at higher and lower taxonomic levels, but little of its "unusual construction" has contributed to traditional taxonomies or numerical cladistic analyses of dinosaurs. Here I provide a nomenclature for the sacrum of sauropod dinosaurs that is intended to facilitate description of the complex elements involved and foster development of new phylogenetic characters. I begin by discussing the definition of the sacrum and changing opinions on the bony elements that it comprises. I then briefly examine the contribution of sacral characters to both traditional taxonomy and cladistic analysis before presenting a nomenclature for the units, junctions, apertures, and vertebral laminae of the sacrum in sauropod dinosaurs.

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DEFINITION AND COMPONENTS OF THE SACRUM

The word 'sacrum' is derived from the Latin term *sacer*, which means holy thing or temple (Brown, 1954). 'Sacrum' is itself a translation of the Greek word *hieron*, meaning sacred or large (Oscar, 1987). Most explanations of its adoption into human anatomy have focused on these two meanings, either relating to: (1) its use in sacrificial rituals or its proximity to organs of procreation; or (2) its relatively large size (Singer, 1954). More recently, Oscar (1987) has suggested that 'sacrum' and 'hieron' draw their sacred meanings from Egyptian mythology, specifically the story of Osiris. After being killed by his brother Set, Osiris was resurrected by his sister and wife Isis. Set killed Osiris a second time and then chopped his body into pieces that were scattered throughout the Levant. Osiris was then resurrected a second time by Isis from his sacrum. In Egyptian symbology, Osiris' sacrum is represented by the *djed* column, which is an elongate, columnar structure resembling the sacrum and lumbar vertebrae of an ox (Budge, 1918; Gordon and Schwabe, 2004: fig. 6.8). The role of the *djed* in burial rituals preparing the dead for the afterlife may have contributed to the sacred origins of the term 'sacrum.'

In practical terms, vertebrate paleontologists have identified sacral vertebrae by their contact with the ilium (e.g., Romer 1956: 227). Typically, limbed amphibians have a single or a pair of sacral vertebrae, and limbed amniotes have two or more. Basal dinosaurs have two or three sacral vertebrae (e.g., Sereno et al., 1993; Langer, 2003; Ezcurra, 2010; Pol et al., 2011), and the number of sacral vertebrae in sauropods ranges from 4-7 (see below).

The processes that extend laterally to contact the ilium, which sometimes are referred to as 'transverse processes,' have been interpreted in different ways by sauropod specialists. The main argument concerns the constituency of the transverse process. Marsh (1895: 495) interpreted the transverse process as comprising only a sacral rib, contending that there are "no diapophyses on sacral vertebræ." Cope (1877a, 1877b, 1878) did not offer an opinion on the composition of the sauropod transverse process.

Like Marsh, Osborn (1899: 203) regarded the transverse process as containing a rib, but limited it to the lower portion: "The sacral ribs unite with the neck of the ilium; the diapophysial laminae unite with the plates and crests of the ilium." Janensch (1929b: 76; translated from the German) came to the same conclusion, identifying two sections of the transverse process, "an upper one that represents the diapophysis, and a lower one that represents the rib, thus forming the true sacral rib ... the true sacral ribs are fused together ventrally." Upchurch et al. (2004: 285) also regarded the transverse process as a composite structure, which they called the 'sacral plate,' made from "the sacral transverse processes (dorsally) and a genuine modified rib (ventrally)."

In his description of *Haplocanthosaurus*, Hatcher (1903) provided a third view: the sacral vertebrae lack ribs altogether. Adopting the view of Osborn (1899) that the diapophyses contact the blade of the ilium, Hatcher (1903) identified the entity others called the 'sacral rib' as the parapophysis. Thus, in the view of Hatcher (1903), the sacral transverse processes comprised the diapophysis and parapophysis, which were separated by a foramen (see below) and contacted the ilium independently. This opinion was based largely on his interpretation of the tail:

> The transverse processes of the caudals decrease rapidly in size as we proceed posteriorly and in the twelfth caudal they are reduced to a rounded knob of bone on either side of the centrum near the superior border, while just above this on the middle of the side of the neural arch there is a second prominence less pronounced, however, than that on the centrum....Of these prominences or tuberosities the superior or that one situated on the neural arch doubtless represents a rudimentary diapophysis, while the inferior or that situated on the side of the centrum may be considered as homologous with the parapophysis. It would, therefore appear as though the transverse processes in the anterior caudals were made up of the coalesced diapophyses and parapophyses (Hatcher, 1903: 18-19; emphasis in original).

Although he contended that the sacral rib was replaced by the more robust transverse process, Hatcher (1903: 20) was agnostic as to whether this was a true elimination or an incorporation of the rib into the transverse process.

The view of the composition of sacral elements advanced in this paper resembles aspects of the views of both Marsh (1895) and Hatcher (1903). Three separate osteological units can be observed in subadult sauropod specimens; no other units have been recovered in sauropod sacra. These units are the neural arch, centrum, and rib, which are present in all vertebrae except the distal tail, which lacks ribs. The mutual co-ossification of these units characterizes cervical, sacral, proximal and mid-caudal, and occasionally posterior dorsal vertebrae. Thus far there is no ontogenetic evidence that the sacral rib (or 'sacral plate') is a composite structure that includes some part of the diapophysis (e.g., Osborn, 1899; Janensch, 1929a; Upchurch et al., 2004). There is, however, anatomical evidence that it does not. As Hatcher (1903) observed, in middle and posterior caudal vertebrae, which lack ribs, there are prominences on the centrum and near the neurocentral junction that represent remnants of the diapophysis and parapophysis. Retention of rudimentary costal articulations (i.e., parapophysis, diapophysis) in vertebrae lacking ribs suggests that ribs do not include those parts. Furthermore, anterior sacral vertebrae, which are derived from dorsal vertebrae and bear ribs that resemble dorsal ribs, the main part of the rib contacts the body of the ilium and sometimes develops a second process that contacts the ilium near the acetabulum. This suggests that both acetabular and alar arms of the sacral ribs are derived entirely from the rib, not from the rib and the diapophysis. Thus, in this view only the rib contacts the ilium; neither the diapophysis nor the parapophysis has a direct connection with the ilium in any sauropod sacrum thus far described.

SACRAL CHARACTERS IN TRADITIONAL TAXONOMY

Sacral characters have played an important part in traditional taxonomies of sauropods, starting from the time that well preserved skeletons were collected from the Upper Jurassic of western North America.

Marsh (1878, 1879, 1881) considered the number of coalesced sacral vertebrae to be diagnostic of sauropod genera, in part distinguishing '*Atlantosaurus*' (4 sacral vertebrae), *Apatosaurus* (3 sacral vertebrae), '*Brontosaurus*' (5 sacral vertebrae), and '*Morosaurus*' (4 sacral vertebrae). It was soon recognized, however, that the number of coossified vertebrae also varies with the age of the individual (Osborn, 1898: 230). In addition to ontogenetic variation, Williston (1898: 173) observed intrageneric variation in the degree of fusion in the sacrum of *Camarasaurus*: "the condition of ossification varies with age, the middle three uniting earliest, the first next and the fifth last. The slight union of the fifth might, indeed, be absent in the adult with out affording generic or even specific characters." Riggs (1903: 196) demonstrated that the three adequately known North American sauropods (i.e., *Apatosaurus* [including '*Brontosaurus*'], *Diplodocus*, '*Morosaurus*') each had five sacral vertebrae: three "primary" sacral vertebrae bracketed by two "secondary" sacral vertebrae, which were modified dorsal and caudal vertebrae (see Wilson and Sereno, 1998 and Pol et al., 2011 for further discussion on the acquisition of sacral vertebrae in sauropods). By the mid-twentieth century, possession of five sacral vertebrae was

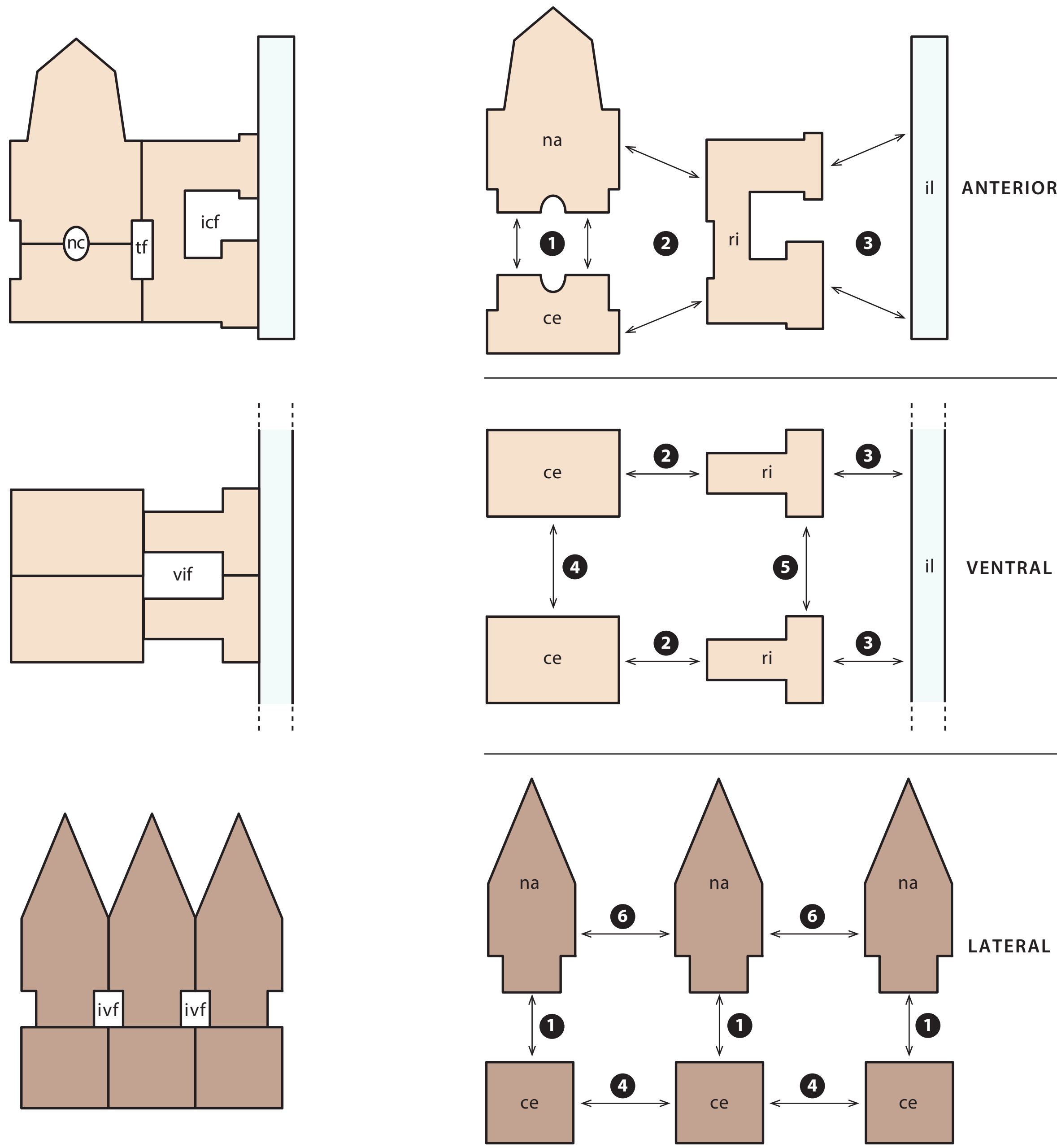

FIGURE 1 — Schematic representation of the junctions between osteological units in the sacrum and ilium. Units are assembled in the left-hand column and separated for clarity in the right-hand column. Anterior view shows junctions between osteological units within a single sacral element and to the ilium; ventral and lateral views also show junctions between sacral elements. Numbers in black circles refer to: 1, neurocentral junction; 2, costovertebral junction; 3, iliocostal junction; 4, intercentral junction; 5, intercostal junction; 6; interneural junction. Abbreviations: *ce*, centrum; *icf*, intracostal fenestra; *il*, ilium; *ivf*, intervertebral foramen; *na*, neural arch; *nc*, neural canal; *ri*, rib; *tf*, transverse foramen; *vif*, ventral intercostal foramen. The sacrum and ilium are shown assembled in Figure 2.

TABLE 1 — Sacral characters used in cladistic analyses of sauropod dinosaurs. The first use of each character is recorded; many of these characters were used multiple times in subsequent analyses (e.g., number of sacral vertebrae).

Character	State 0	States 1-n	Reference
Number of sacral vertebrae	Not specified	Four, five, or six	Upchurch 1995
Height of sacral neural spines	Not specified	Greater than two times centrum height	Upchurch 1995
Posterior trunk and sacral vertebrae	Amphiplatyan/platycoelous	Opisthocoelous	Salgado et al. 1997
Sacral centra, pneumatic fossae or very deep depressions	Absent	Present	Upchurch 1998
Ratio of sacral width to the average length of the sacral centra	Less than 2.5	Four or more	Upchurch 1998
Dorsal surface of sacral ribs	Lie below dorsal rim of ilium	Level with dorsal rim of ilium	Upchurch 1998
Sacrum, sacricostal yoke	Absent	Present	Wilson & Sereno 1998
Sacral vertebrae, number supporting acetabulum	Four or fewer	Five or more	Wilson 2002
Sacral vertebrae, ventral margin	Rounded	Ventrally concave	Curry Rogers 2005
Sacral neural spines, prespinal lamina	Anteroposteriorly expanded	Transversely expanded	Curry Rogers 2005
Sacral neural spines, postspinal lamina	Present	Absent	Curry Rogers 2005
Sacral neural spines, prespinal lamina	Single proximally	Divided proximally, arising from prezygapophyses	Curry Rogers 2005
Sacral neural spine	Meets transverse process at ≥ 90°	Meets transverse process at < 70°	Curry Rogers 2005
Sacral ribs, proximal excavation	Absent	Present	Curry Rogers 2005

widely regarded as diagnostic for sauropods (e.g., Lapparent and Lavocat, 1955; Romer, 1956), with six sacral vertebrae further characterizing titanosaurs (Huene, 1927). With the discovery of more basal sauropods, which had only 4 sacral vertebrae, a range of 4-6 sacral vertebrae was recognized for sauropods (Steel, 1970; McIntosh, 1990).

In addition to sacral count, several other sacral characteristics were employed in early sauropod taxonomies. Marsh (1877: 87), in his brief description of '*Titanosaurus montanus*,' the first Morrison sauropod (now considered a nomen dubium; McIntosh, 1990), noted that each sacral centrum was "... so deeply concave as to materially lessen its bulk ..." and each sacral centrum carried "... a very large cavity in each side, connected with the outer surface by an elongated foramen ... a pneumatic opening, designed to lessen the weight of the enormous sacral mass." He also drew attention to other sacral features, such as the enlargement of the neural canal (Marsh, 1879, 1896: pls. 23, 28) and elongation of the neural spine (Marsh, 1881). Sacral characters were not included in the traditional taxonomies of Janensch (1929a) or Bonaparte (1986, 1999).

SACRAL CHARACTERS IN CLADISTIC ANALYSES

Sacral characters typically contribute less than 2% of character data to cladistic analyses of dinosaurs (e.g., theropods, Rauhut 2003; ornithischians, Butler 2009). The sacrum is especially complex in sauropod dinosaurs, but within that clade sacral characters have played a similarly minor role in establishing interrelationships (≤ 3% total characters in three analyses, Whitlock, 2011:fig. 8; 2% in sauropodomorph analyses, Mannion and Upchurch, 2010: table 2).

The traditional characters mentioned above were all drawn upon in later cladistic treatments of sauropod dinosaurs. Table 1 lists the 14 different sacral characters used in cladistic analyses focused on sauropods. The most commonly used character is the number of sacral vertebrae, which all studies agreed increased systematically in sauropod history. Basal sauropods and immediate outgroups (e.g., *Leonerasaurus*, *Melanorosaurus*; Pol et al., 2011) are distinguished from other dinosaurs by the addition of a fourth sacral vertebra, *Patagosaurus* and more derived sauropods had five sacral vertebrae, and somphospondylans (*Euhelopus* + Titanosauria) had six (Wilson, 2002). Within Titanosauria, *Neuquensaurus* autapomorphically possesses seven sacral vertebrae (Salgado et al., 2005; D'Emic and Wilson, 2011). Other features include proportional characters (e.g., height of neural spines), pneumatic characters (e.g., presence of pleurocoels), and neural arch lamina characters (e.g., shape of prespinal lamina). Although these characters apply at higher and lower taxonomic levels, they do not cover the scope of morphological variation within sauropod sacra.

INSTITUTIONAL ABBREVIATIONS

CM — Carnegie Museum of Natural History, Pittsburgh, USA
SM — Sirindhorn Museum, Phu Kum Kao, Kalasin Province, Thailand.

ANATOMICAL NOMENCLATURE OF THE SAUROPOD SACRUM

Here I present a nomenclature for the sauropod sacrum that is designed to aid description of these complex structures and to facilitate development of novel character data (Table 2). I refer to the Nomina Anatomica Veterinaria (NAV; ICVAN, 1973) and the Nomina Anatomica Avium (NAA; Baumel and Witmer, 1993), but I have not restricted myself to those sets of terms in this work because they are neither sufficiently descriptive nor consistent for the topic. Instead, the proposed terminology includes NAA/NAV terms, traditional 'Romerian' terms (Wilson, 2006), and new terms. Although based on sauropods, this nomenclature is applicable to closely related taxa (e.g., basal sauropodomorphs, theropods).

Osteological Units
(Figs. 1-2; Table 2)

Four osteological units can be identified in the postaxial vertebrae of posthatchling sauropods: centrum, neural arch, rib, and chevron. The chevron is only present in the caudal region, where it is interposed between adjacent centra, but the other three units are present in all vertebral regions. The sacrum is composed of serial elements that usually fuse to one another and to the ilia at maturity. Often referred to as a series of 'sacral vertebrae', each serial element actually consists of a sacral vertebra (i.e., centrum, neural arch) and a pair of sacral ribs. These latter structures have also been called 'pleuropophyses' in modern reptiles because they are "precociously fused" to the vertebra (Hoffstetter and Gasc, 1969: 263) and not often recovered as isolated elements. However, sauropod ribs are often found separate from the elements to which they later fuse (e.g., *Rapetosaurus*; Curry Rogers, 2009: figs. 23-26), so it is more practical to use the term 'sacral rib' instead of 'pleuropophysis' for them.

The relatively rich sample of morphology and ontogenetic states of sauropod sacra now available has clarified the nature and contacts of the sacral ribs in sauropods, which were a source of disagreement in the past (see above). The sacral vertebrae and ribs have the same basic relationship to one another that they have in presacral vertebrae: the tuberculum and capitulum of the rib contact the diapophysis and parapophysis of the vertebra, respectively. There are, however, important differences in the position and shape of those contacts and in the shape of the rib that distinguish the sacrum from the neck and trunk.

As noted elsewhere (e.g., Wilson, 1999), in cervical vertebrae the diapophysis and parapophysis project laterally from the neural arch and centrum, respectively, but in dorsal vertebrae the parapophysis migrates onto the neural arch into a position anterior and slightly ventral to the diapophysis. In the sacrum, the parapophysis migrates back down to the centrum. Both the parapophysis and the diapophysis are flush, or nearly flush, on the vertebra and not usually separated from one another by a gap. (The exception to this generality is in the anteriormost sacral vertebrae, which resemble dorsal vertebrae in this regard, as discussed below.) Rather, the diapophysis and parapophysis typically form a vertically elongate, continuous articular surface that extends from neural arch to the ventral centrum.

The sacral rib is a near-vertically oriented, plate-like structure that is approximately 'C' shaped in anterior view. Its articular surface for the vertebra may be flat, slightly concave, or contain a sharp notch. Separate tubercula and capitula are only present in the latter two cases, most typically the anteriormost elements. The lateral, free ends of the sacral rib contact the ilium. Hatcher (1903: 35) referred informally to these as "horizontal" and "ascending" branches of the parapophysis (i.e., his interpretation of the sacral rib), but more specific designations would be more useful. The lower arm of the 'C' contacts the base of the ilium just above the acetabulum and peduncles, and I will refer to it as the 'acetabular' arm of the sacral rib (even if it does not always border the acetabulum). The upper arm of the 'C' contacts the blade of ilium near its dorsal margin, and I will refer to it as the 'alar' arm of the sacral rib.

Adjacent acetabular arms of the sacral ribs contact one another distally to form the "sacricostal yoke" (Riggs 1903:178), which is an anteroposteriorly oriented bar that contacts the base of the ilium and typically forms part of the acetabular surface in eusauropods (Wilson and Sereno, 1998), as well as in some other dinosaurs (e.g., basal sauropodomorph *Yunnanosaurus*; Lü et al., 2007). Here, I recommend Riggs' (1903) original spelling of 'sacricostal' rather than the alternative 'sacrocostal' (e.g., Upchurch et al., 2004; Lü et al., 2007; Rose, 2007; Butler et al. 2011), because it uses the appropriate combinative form 'sacri-' for a second declension neuter noun.

TABLE 2 — Proposed anatomical terms for the osteological units, junctions, and apertures of the sauropod sacroiliac complex.

	Anatomical Term	Definition
Units	Neural arch	Dorsomedian unit of vertebra
	Centrum	Ventromedian unit of vertebra
	Rib	Paramedian unit adjacent to vertebra
Junctions	Neurocentral	Intraelement junction between neural arch and centrum
	Costovertebral	Intraelement junction between rib and vertebra
	Iliocostal	Junction between rib and ilium
	Intercentral	Interelement junction between adjacent centra
	Intercostal	Interelement junction between adjacent acetabular arms of rib
	Interneural	Interelement junction between adjacent neural arches
Apertures	Neural canal	Axially oriented aperture between neural arch and centrum
	Intervertebral foramen	Transversely oriented aperture between adjacent vertebrae
	Transverse foramen	Paraxially oriented aperture between rib and vertebra
	Intracostal fenestra	Paraxially oriented aperture between rib and ilium
	Dorsal intercostal foramen	Dorsoventrally oriented aperture between adjacent ribs
	Ventral intercostal foramen	Dorsoventrally oriented aperture between adjacent ribs

Junctions between Osteological Units
(Fig. 1; Table 2)

As noted above, four osteological units can be identified in the postaxial vertebrae of posthatchling sauropods: centrum, neural arch, rib, and chevron. The neural arch, centrum, and rib contact one another at two junctions, which may remain open, sutured, or fused in different ontogenetic stages. In the cervical, sacral, and caudal regions, junctions between neural arch and centrum (i.e., neurocentral junction) and between vertebra and rib (i.e., costovertebral junction) are usually fused at maturity. In the dorsal region, in contrast, the costovertebral junction remains mobile in mature individuals.

There are six junctions in the sauropod sacroiliac complex. These include the two junctions within a single sacral element mentioned above, plus three junctions between adjacent sacral elements (i.e., intercentral junction, interneural junction; intercostal junction) and one junction between the sacrum and ilium (i.e., iliocostal junction). Intraelement junctions are present in all vertebral regions, so they should be referred to by both region and number. I propose ‘cv’, ‘d’, ‘s’ and ‘ca’ as abbreviations for the cervical, dorsal, sacral, and caudal regions, respectively. The neurocentral and costovertebral junctions of the fifth sacral vertebra are ‘neurocentral junction s5’ and ‘costovertebral junction s5,’ respectively. The latter can be modified with ‘right’ or ‘left’ as appropriate. Junctions with the ilium occur only in the sacrum by definition, and so they do not require an ‘s’ before the element number (e.g., right iliocostal junction 3). Interelement junctions can be referred to by the numbers of adjacent vertebrae. These should receive regional designations because intercentral junctions and interneural junctions occur between all vertebrae, though they usually fuse in the sacrum only (e.g., interneural junction s4/5).

Terminology for junctions also can be applied to the suture between elements (e.g., ‘costovertebral suture s4’) or to describe the coalescence between units (e.g., ‘intercentral fusion s3/4’).

The sequence and timing of fusion between the osteological units of the sacrum is a fascinating but understudied subject. In the well-represented sauropod *Camarasaurus*, the sacral neurocentral and costovertebral junctions fuse at or near the time the cervical neurocentral junctions fuse (Ikejiri, 2003; Ikejiri et al., 2005), but the order of fusion within those categories or between them and the other sacroiliac junctions is unknown. So is the variation of the sequence of fusion within Sauropoda. The neurocentral junction is not necessarily the first of the sacroiliac junctions to fuse. In one individual of the titanosauriform *Phuwiangosaurus*, for example, interneural junctions 2-5 fuse

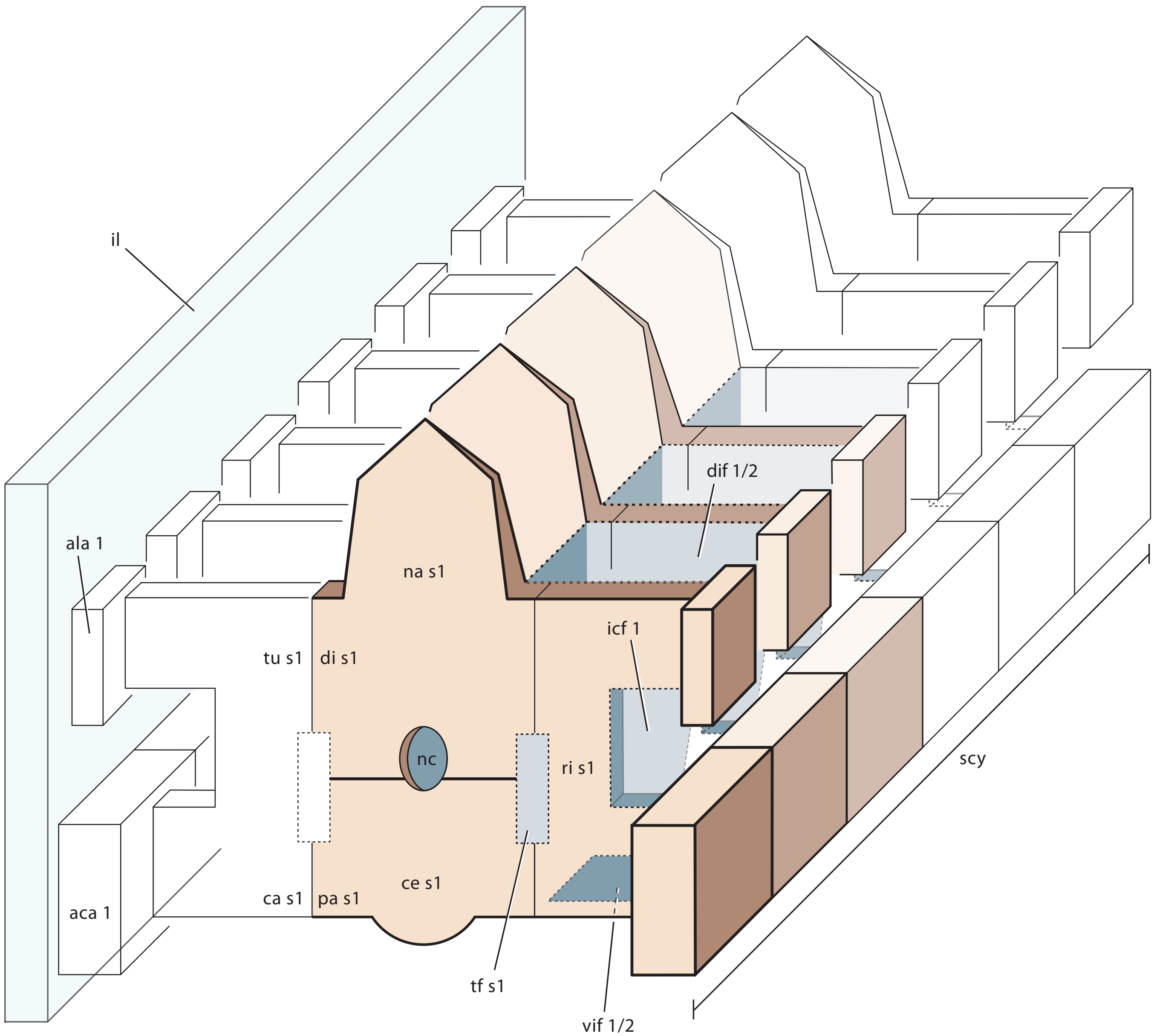

FIGURE 2 — Schematic representation of the assembled sauropod sacrum and ilium (right side only) in anterolateral view. Abbreviations: *aca*, acetabular arm of sacral rib; *ala*, alar arm of sacral rib; *ca*, capitulum; *ce*, centrum; *di*, diapophysis; *dif*, dorsal intercostal foramen; *icf*, intracostal fenestra; *il*, ilium; *na*, neural arch; *nc*, neural canal; *pa*, parapophysis; *ri*, rib; *s*, sacral; *scy*, sacricostal yoke; *tf*, transverse foramen; *tu*, tuberculum; *vif*, ventral intercostal foramen. Color scheme matches that of Figure 1.

before the neurocentral, intercentral, intercostal, costovertebral, iliosacral, and other interneural junctions (SM K11-0044, -0046, -0048, -0050; Suteethorn et al., 2009: fig. 14). A similar pattern of early interneural fusion also characterizes a specimen of *Haplocanthosaurus* (CM 879). Other sauropods may present different fusion sequences. More detailed description of the junction between sacral units and particularly their state of fusion requires multiple ontogenetic stages, which are now becoming available (e.g., *Camarasaurus*, *Diplodocus*, *Phuwiangosaurus*, *Shunosaurus*).

Apertures
(Fig. 2; Table 2)

Between and within the osteological units of the sacrum and the ilia are apertures that are oriented and located axially (i.e., neural canal), paraxially (i.e., transverse foramina; intracostal fenestrae), dorsoventrally (i.e., intercostal foramina), and transversely (i.e., intervertebral foramina).

Neural canal and Intervertebral Foramina.— As in other parts of the vertebral column, the spinal cord is nearly completely enclosed by the neural arch and centrum of adjacent vertebrae in the sacrum. The only apertures in this coosified neural canal (i.e., canalis vertebralis; Baumel and Witmer, 1993) are the intervertebral foramina that open between zygapophyses, neural arch pedicles, and centra of adjacent vertebrae. Intervertebral foramina are labeled by the vertebrae between which they open. Because they are present in all vertebral regions, specific intervertebral foramina should be referred to by both region and number. The intervertebral foramen between the first and second sacral vertebrae is referred to as ‘intervertebral foramen s1/s2’ and the one preceding it would be ‘intervertebral foramen d12/s1’ in a sauropod with 12 dorsal vertebrae. The spinal nerves, blood vessels, and occasionally air sacs of each segment pass through the intervertebral foramen. Apart from differences in size (see Giffin, 1990, 1995), there are few major differences in the structure or position of the neural canal and intervertebral foramina in presacral, sacral, and caudal vertebrae. The extensive fusion of the sacrum occasionally facilitates preservation of a natural cast of the large space enclosed by the neural canal and intervertebral foramina (e.g., Marsh, 1896: fig. 34).

Dorsal and Ventral Intercostal Foramina.— In dorsal or ventral views of the sacrum, a series of oval openings are visible between the sacral ribs on either side of the midline. These openings permit passage of the spinal nerve and other soft tissues into and out of the sacrum. These are termed ‘fenestrae intertransversariae’ in the synsacrum of birds (Baumel and Witmer, 1993), ‘foramina sacralia’ in other reptiles (Hoffstetter and Gasc, 1969), and differentiated into ‘foramina sacralia dorsalia’ and ‘foramina sacralia pelvina’ in mammals (ICVAN, 1973). In sauropods, they were referred to as ‘intervertebral fenestrae’ by Wilson and Sereno (1998: 43), a term that could be confused with the intervertebral foramina described above and that does not adequately describe the apertures, which are between pairs of ribs, not between vertebrae.

None of the above terms is entirely satisfactory nor consistently applied to sauropod sacra, in which these between-rib spaces form vertically elongate canals. In a six-vertebra sacrum, there are 10 such intercostal canals, five on each side, each of which has an upper and a lower opening. The upper opening is here termed the ‘dorsal intercostal foramen’ and is bounded by the diapophyses, tuberculum, alar arm of the sacral rib, and ilium. Individual dorsal intercostal foramina can be labeled by the vertebrae they span (e.g., ‘dorsal intercostal foramen 2/3’). The lower complement to this opening is here termed the ‘ventral intercostal foramen,’ which opens between the parapophysis, capitulum, and acetabular arm of the sacral ribs. In most sauropods, the ilium is excluded from the margin of the ventral intercostal foramina by the sacricostal yoke.

Transverse Foramen.— In addition to the dorsoventrally-oriented openings between ribs, there is a series of paraxially-aligned intracostal openings between the sacral vertebra, sacral rib, and ilium. The more medial of these is a holdover from the presacral series, in which the articular processes of the rib and the costal articulations of the vertebra form a ring of bone through which passes the vertebral artery, vein, and associated nerves. The opening formed by this bony ring is called the ‘foramen transversarium’ in mammals and birds (ICVAN, 1973; Baumel and Witmer, 1993). Here, I use the more general term ‘transverse foramen’ and reference it by the corresponding vertebral region and number (e.g., ‘transverse foramen s1’). Transverse foramina are generally present in anterior sacral vertebrae, which tend to resemble dorsal vertebrae, but they are not generally present in the posterior sacral centra, which tend to resemble caudal vertebrae.

Intracostal Fenestra.— The other paraxially-aligned intracostal openings are between the ribs and ilium. The C-shaped sacral ribs have acetabular and alar processes that attach in different places on the ilium, leaving a gap. The presence and size of these gaps vary along the sacral series, and they are usually absent in at least the last sacral vertebra. They have no analog or homolog in living tetrapods, and so I propose the term ‘intracostal fenestrae’ because they open between arms of the rib and probably did not transmit soft tissue structures (and thus qualify as fenestrae, not foramina). The opening between the fifth sacral rib and the ilium is termed ‘intracostal fenestra 5.’ Hatcher (1903: pl. 5, fig. 1) identified one such opening in the sacrum of *Haplocanthosaurus*, which he labelled ‘pf’. There was no legend for nor textual reference to this abbreviation, but ‘pf’ probably refers to ‘parapophyseal foramen,’ based on Hatcher’s (1903: 15, 19-22, 35) contention that the sacral ribs are equivalent to parapophyses. Upchurch et al. (2004: 285) also recognized the presence of an opening between the distal end of the ‘sacral plate’ and the ilium but did not name it.

NEURAL ARCH LAMINAE

Wilson (1999: 642) suggested that the vertebral laminae of the sacrum are serially homologous with those of the presacral diapophyses, despite the incorporation of the sacral rib into the transverse process of the vertebra. There are important changes that make the laminar configuration in the sacrum distinct from the presacral region. The most striking of these arises from the fusion of sacral neural arches to one another, which results in the

TABLE 3. — New character statements (sensu Sereno, 2007) based on variation in the sacra of sauropod dinosaurs.

Character	Statement
Sacricostal yoke, shape	(0) Flat horizontally (1) Beveled ventromedially
Parapophyses, position	(0) Located on a single centrum (1) Shared between two centra
Sacral rib 1, shape	(0) Undivided distally (1) Divided distally into alar and acetabular rami
Sacral rib 6, shape	(0) Undivided distally (1) Divided distally into alar and acetabular rami
Iliac crest, orientation	(0) Perpendicular to sacral axis (1) Orthogonal to sacral axis
Sacral ribs 5-6, alar arms, contact	(0) Absent (1) Present
Sacral vertebrae, timing of fusion	(0) Neurocentral fusion before interneural fusion (1) Interneural fusion before neurocentral fusion
Sacral neural spines, contact	(0) Fused (1) Connected via fused prespinal and postspinal laminae

coalescence of certain vertebral landmarks. For example, some adjacent neural spines are continuous, and the prespinal and postspinal laminae coalesce into a single median plate connecting sequential vertebrae. The prezygapophyses and postzygapophyses also lose their independence in adjacent sacral vertebrae. As a consequence, laminae associated with those landmarks can traverse the zygapophyses and continue onto the adjacent vertebra. Sets of laminae sharing a zygapophyseal component can join to create an uninterrupted lamina. Examples of this include the prezygodiapophyseal and spinopostzygapophyseal laminae, as well as the prezygodiapophyseal, spinopostzygapophyseal, and postzygodiapophyseal laminae. These combined laminae can be referred to by their original names and their serial position, joined by a plus sign to indicate their coalescence and referred to in the singular (e.g., 'postzygodiapophyseal s2 + spinopostzygapophyseal lamina s2 + prezygodiapophyseal s3'; 'postspinal s3 + prespinal s4 lamina').

CONCLUSIONS

The sacrum of dinosaurs, and in particular sauropod dinosaurs, is complex in form and composed of a variable number of vertebrae. The number of vertebrae in the sacrum has contributed to reconstructing the phylogenetic relationships of Sauropoda, but the complexity of form has received less attention. The sauropod sacrum represents a potentially valuable source of character data (Table 3). Characters of interest phylogenetically include the sequence of fusion of the six sacroiliac junctions, the presence/absence, shape, and bordering elements of the sacroiliac apertures, and the pattern of lamination in sacral neural arches. Most are available for study in existing specimens. Fusion sequence, however, requires ontogenetic series to be fully resolved, which are extraordinarily rare. Partial series are now available for some sauropods, which allow partial sequences to be reconstructed. Anatomical terms for the sacrum proposed here will facilitate recovery of phylogenetic character data from the sacroiliac complex.

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LITERATURE CITED

BAUMEL, J. J., and L. M. WITMER. 1993. Osteologia. In J. J. Baumel (ed.). Handbook of Avian Anatomy: Nomina Anatomica Avium. Second Edition. Nuttall Ornithological Club, Cambridge, Massachusetts, 45-132.

BONAPARTE, J. F. 1986. The early radiation and phylogenetic relationships of sauropod dinosaurs, based on vertebral anatomy. In K. Padian (ed.), The Beginning of the Age of Dinosaurs, Cambridge University Press, Cambridge and New York, 247-258.

———. 1999. Evolución de las vértebras presacras en Sauropodomorpha. Ameghiniana, 36: 115-187.

BROWN, R. W. 1956. Composition of Scientific Words. Smithsonian Institution Press, Washington, D. C., 882 pp.

BUDGE, E. A. W. 1911. Osiris and the Egyptian Resurrection. Philip Lee Warner, London, 442 pp.

BUTLER, R. J., P. UPCHURCH, and D. B. NORMAN. 2008. The phylogeny of the ornithischian dinosaurs. Journal of Systematic Palaeontology, 6: 1-40.

BUTLER, R. J., JIN, L., CHEN, J. and GODEFROIT, P. 2011. The postcranial osteology and phylogenetic position of the small ornithischian dinosaur *Changchunsaurus parvus* from the Quantou Formation (Cretaceous: Aptian-Cenomanian) of Jilin Province, north-eastern China. Palaeontology, 54: 667-683.

COPE, E. D. 1877a. On a gigantic saurian from the Dakota epoch of Colorado. Paleontological Bulletin, 25: 5-10.

———. 1877b. On the Vertebrata of the Dakota Epoch of Colorado. Proceedings of the American Philosophical Society, 17: 233-247.

———. 1878. On the saurians recently discovered in the Dakota Beds of Colorado. The American Naturalist, 12: 72-85.

CURRY ROGERS, K. 2005. Titanosauria. In K. A. Curry Rogers and J. A. Wilson (eds.). The Sauropods: Evolution and Paleobiology, University of California Press, Berkeley, 50-103.

———. 2009. The postcranial osteology of *Rapetosaurus krausei* (Sauropoda: Titanosauria) from the Late Cretaceous of Madagascar. Journal of Vertebrate Paleontology, 29: 1046-1086.

D'EMIC, M. D., and J. A. WILSON. 2011. New remains attributable to the holotype of the sauropod dinosaur *Neuquensaurus australis*, with implications for saltasaurine systematics. Acta Palaeontologica Polonica, 56: 61-73.

EZCURRA, M. D. 2010. A new early dinosaur (Saurischia: Sauropodomorpha) from the Late Triassic of Argentina: a reassessment of dinosaur origin and phylogeny. Journal of Systematic Palaeontology, 8: 371-425.

GIFFIN, E. B. 1990. Gross spinal anatomy and limb use in living and fossil reptiles. Paleobiology, 16: 448-458.

———. 1995. Postcranial paleoneurology of the Diapsida. Journal of Zoology, London, 235: 389-410.

GORDON, A. H., and C. W. SCHWABE. 2004. The Quick and the Dead: Biomedical Theory in Ancient Egypt. Egyptological Memoirs, 4: 1-236.

HATCHER, J. B. 1903. Osteology of *Haplocanthosaurus*, with description of a new species, and remarks on the probable habits of the Sauropoda and the age and origin of the *Atlantosaurus* beds. Memoirs of the Carnegie Museum, 2: 1-75.

HOFFSTETTER, R., and J.-P. GASC. 1969. Vertebrae and ribs of modern reptiles. In C. Gans, A. d'A. Bellairs, and T. S. Parsons (eds.), Biology of the Reptilia, Volume 1. Morphology A, Academic Press, London and New York, 201-310.

HUENE, F. 1927. Short review of the present knowledge of the Sauropoda. Memoirs of the Queensland Museum, 9: 121-126.

INTERNATIONAL COMMITTEE ON VETERINARY ANATOMICAL NOMENCLATURE. 1973. Nomina Anatomica Veterinaria, 2nd edition. Published by the International Committee on Veterinary Anatomical Nomenclature under the financial responsibility of the World Association of Veterinary Anatomists, Vienna, Austria, 218 pp.

IKEJIRI, T. 2003. Sequence of closure of neurocentral sutures in *Camarasaurus* (Sauropoda) and implications for phylogeny in Reptilia. Journal of Vertebrate Paleontology, 23: 65A.

IKEJIRI, T., TIDWELL, V. and D. L. TREXLER. 2005. New adult specimens of *Camarasaurus lentus* highlight variation ontogenetic variation within the species. In V. Tidwell and K. Carpenter (eds.). Thunder-Lizards: The Sauropodomorph Dinosaurs. Indiana University Press, Bloomington, 154-186.

JANENSCH, W. 1929a. Material und Formengehalt der Sauropoden in der Ausbeute der Tendaguru Expedition. Palaeontographica (Supplement 7), 2: 1-34.

———. 1929b. Die Wirbelsäule der Gattung *Dicraeosaurus*. Palaeontographica (Supplement 7), 3: 37-133.

LANGER, M. C. 2003. The pelvic and hind limb anatomy of the stem-sauropodomorph *Saturnalia tupiniquim* (Late Triassic, Brazil) PaleoBios, 23: 1-30.

LAPPARENT, A. F. de, and R. LAVOCAT. 1955. Dinosauriens. In J. Piveteau (ed.), Traité de Paléontologie, V, Masson, Paris, 784-962.

LÜ, J., T. LI, S. ZHONG, Y. AZUMA, M. FUJITA, Z. DONG, and Q. JI. 2007. New yunnanosaurid dinosaur (Dinosauria, Prosauropoda) from the Middle Jurassic Zhanghe Formation of Yuanmou, Yunnan Province of China. Memoir of the Fukui Prefectural Dinosaur Museum, 6: 1-15.

MANNION, P. D., and P. UPCHURCH. 2010. Completeness metrics and the quality of the sauropodomorph fossil record through geological and historical time. Paleobiology, 36: 283-302.

MARSH, O. C. 1877. Notice of a new gigantic dinosaur. American Journal of Science (Series 3), 14: 87-88.

———. 1878. Principal characters of American Jurassic dinosaurs. Pt. I. American Journal of Science (Series 3), 16: 411-416.

———. 1879. Principal characters of American Jurassic dinosaurs. Pt. II. American Journal of Science (Series 3), 17: 86-92.

———. 1881. Principal characters of American Jurassic dinosaurs. Part V. American Journal of Science (Series 3), 21: 417-423.

———. 1895. On the affinities and classification of the dinosaurian reptiles. American Journal of Science (Series 3), 50: 483-498.

———. 1896. Dinosaurs of North America. Annual Report of the US Geological Survey 1894-1895, 16: 133-244.

MCINTOSH, J. S. 1990. Sauropoda. In D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), The Dinosauria, University of California Press, Berkeley, 345-401.

OSBORN, H. F. 1898. Additional characters of the great herbivorous dinosaur *Camarasaurus*. Bulletin of the American Museum of Natural History, 10: 219-233.

———. 1899. A skeleton of *Diplodocus*. Memoirs of the American Museum of Natural History, 1: 191-214.

OWEN, R. 1842. Report on British fossil reptiles. Pt. II. Report of the British Association for the Advancement of Science, 1841: 60-204.

———. 1859. On the orders of fossil and recent Reptilia, and their distribution in time. Report of the British Association for the Advancement of Science, 1859:153-166.

POL, D., A. GARRIDO, and I. A. CERDA. 2011. A new sauropodomorph dinosaur from the Early Jurassic of Patagonia and the origin and evolution of the sauropod-type sacrum. PLoS ONE, 6: e14572. doi:10.1371/journal.pone.0014572.

RAUHUT, O. W. M. 2003. The interrelationships and evolution of basal theropod dinosaurs. Special Papers in Palaeontology, 69: 1-215.

ROMER, A. S. 1956. Osteology of the Reptiles. University of Chicago Press, Chicago, Illinois, 772 pp.

ROSE, P. J. 2007. A new titanosauriform sauropod (Dinosauria: Saurischia) from the Early Cretaceous of Texas and its phylogenetic relationships. Palaeontologia Electronica, 10: 1-65.

RIGGS, E. S. 1903. Structure and relationships of opisthocœlian dinosaurs. Part I. *Apatosaurus* Marsh. Field Columbian Museum, Geological Series, 2: 165-196.

SALGADO, L., S. APESTEGUÍA, and S. HEREDIA. 2005. A new specimen of *Neuquensaurus australis*, a Late Cretaceous saltasaurine titanosaur from north Patagonia. Journal of Vertebrate Paleontology, 25: 623-634.

SALGADO, L., R. A. CORIA, and J. O. CALVO. 1997. Evolution of titanosaurid sauropods. I: Phylogenetic analysis based on the postcranial evidence. Ameghiniana: 34: 3-32.

SERENO, P. C. 2007. Logical basis for morphological characters in phylogenetics. Cladistics, 23: 565-587.

SERENO, P. C., C. A. FORSTER, R. R. ROGERS, and A. M. MONETTA. 1993. Primitive dinosaur skeleton from Argentina and the early evolution of Dinosauria. Nature, 361: 64-66.

STEEL, R. 1970. Saurischia. Handbüch der Paläoherpetologie, 13: 1-88.

SUGAR, O. 1987. How the sacrum got its name. JAMA, 257: 2061-2063.

SUTEETHORN, S., J. LE LOEUFF, E. BUFFETAUT, V. SUTEETHORN, C. TAUBMOOK, and C. CHONGLAKMANI. 2009. A new skeleton of *Phuwiangosaurus sirindhornae* (Dinosauria, Sauropoda) from NE Thailand. In E. Buffetaut, G. Cuny, J. Le Loeuff, and V. Suteethorn (eds.). Late Palaeozoic and Mesozoic Ecosystems in SE Asia. Geological Society of London Special Publication, 315: 189-215.

UPCHURCH, P. 1995. Evolutionary history of sauropod dinosaurs. Philosophical Transactions of the Royal Society of London, B, 349: 365-390.

———. 1998. The phylogenetic relationships of sauropod dinosaurs. Zoological Journal of the Linnean Society, 124: 43-103.

UPCHURCH, P., P. M. BARRETT, and P. DODSON. 2004. Sauropoda. In D. B. Weishampel, P. Dodson, and H. Osmólska (eds.). The Dinosauria, 2nd Edition. University of California Press, Berkeley, 259-324.

WHITLOCK, J. A. 2011. A phylogenetic analysis of Diplodocoidea (Saurischia: Sauropoda). Zoological Journal of the Linnean Society, 161: 872-915.

WILLISTON, S. L. 1898. The sacrum of *Morosaurus*. Kansas University Quarterly, 7: 173-175.

WILSON, J. A. 1999. A nomenclature for vertebral laminae in sauropods and other saurischian dinosaurs. Journal of Vertebrate Paleontology, 19: 639-653.

———. 2002. Sauropod dinosaur phylogeny: critique and cladistic analysis. Zoological Journal of the Linnean Society, 136: 217-276.

———. 2006. Anatomical nomenclature of fossil vertebrates: standardized terms or lingua franca? Journal of Vertebrate Paleontology, 26: 511-518.

WILSON, J. A., and P. C. SERENO. 1998. Early evolution and higher-level phylogeny of sauropod dinosaurs. Society of Vertebrate Paleontology Memoir, 5: 1-68.

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