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A NOMENCLATURE FOR VERTEBRAL LAMINAE IN SAUROPODS AND OTHER SAURISCHIAN DINOSAURS

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ABSTRACT—The vertebrae of sauropods are characterized by numerous bony struts that connect the costovertebral and intervertebral articulations, centrum, and neural spine of the presacral, sacral, and anterior caudal vertebrae. A nomenclature for sauropod vertebral laminae is proposed that: 1) utilizes the morphological landmarks connected by the laminae (rather than their spatial orientation); and 2) provides the same name for serial homologues. This landmark-based nomenclature for vertebral laminae, which establishes the first criterion of homology (similarity), is the first step towards interpreting their phylogenetic significance.

Nineteen different neural arch laminae are identified in sauropods, although all are never present in a single vertebra. Vertebral laminae can be divided into four regional categories, with each distinct lamina abbreviated with a simple four-letter acronym: diapophyseal laminae; parapophyseal laminae; zygapophyseal laminae; and spinal laminae.

The distribution of neural arch laminae in presacral, sacral, and caudal vertebrae is evaluated to assess homology in sauropods and other saurischians. Five diapophyseal laminae and six zygapophyseal laminae characterize saurischian dinosaurs. Parapophyseal laminae and spinodiapophyseal laminae are unique to a subgroup of sauropods that includes *Barapasaurus*, *Omeisaurus*, and Neosauropoda. The presence of diapophyseal laminae in caudal vertebrae characterizes diplodocids.

Vertebral laminae probably partitioned pneumatic diverticuli on the neural arch and provided structural support for the axial column. Their basic architecture evolved in saurischians prior to the Late Triassic (Carnian), 25 million years before the first known sauropod.

INTRODUCTION

Paleontologists have marveled at the construction of sauropod vertebrae since these elements were first described more than a century ago. Describing a dorsal vertebra of *Cetiosaurus*, the first reported sauropod, Phillips (1871:255) noted that "in the angular shape of the bones, and a sort of buttressing observable in the arrangement, we seem to behold a structure of as much lightness as could be consistent with the required solidity." Seeley was so impressed by the pneumatic recesses in the vertebrae of the brachiosaurid *Ornithopsis* (Blows, 1995) that he described it as a pterosaur, observing that the presacral vertebrae were "constructed after the lightest and airiest plan . . . possessing pneumatic foramina, which are an avian and ornithosaurian [pterosaurian] peculiarity" (1870:280). The extreme structural complexity of sauropod vertebrae led others to invoke orthogenetic principles to explain their evolution. As Osborn (1899:193) remarked, "The dominating principle in construction of the [sauropod] backbone is maximum strength with minimum weight. The ingenuity of sculpture by which this is brought about, every single vertebra differing from its fellow, baffles the Lamarckian as well as the Darwinian, and tempts us to revive the old teleological explanation."

The discovery and description of abundant sauropod remains from North America and Africa during the late nineteenth and early twentieth centuries inspired a new nomenclature for vertebral laminae that allowed discussion and comparison. The earliest and most enduring system was developed a century ago by Osborn (1899) in his description of *Diplodocus*. Osborn named laminae on the basis of their planar orientation, which he believed was optimized for resisting strain. Osborn identified eight laminae subdivided into vertical, horizontal, and obliquely oriented struts. Osborn's nomenclature, the first of its kind, was adopted by his American colleagues in their descriptions of new sauropod skeletons from the Morrison Formation (Hatcher, 1901, 1903; Holland, 1906; Lull, 1919; Osborn and Mook, 1921; Gilmore, 1936).

Janensch (1929) proposed a second nomenclature for sauropod vertebral laminae. Charged with describing more than 100 tons of sauropod material collected from Tendaguru, German East Africa (present-day Tanzania; Zils et al., 1995), Janensch's nomenclature for laminae was based on vertebral landmarks (topology) rather than spatial orientation of structures. These reference points allow precise and repeatable comparisons to establish the first criterion of homology, that of similarity (Patterson, 1982). This initial test is the basis for the tests of congruence and conjunction, which provide the historical context for conjectures of homology. However perceptive, Janensch's terms were cumbersome, especially to a non-German readership, and they never wrested Osborn's terminology from its place in the descriptive literature.

The present paper has two major aims. The first is to present landmark-based anatomical terms for vertebral laminae, each associated with a four-letter abbreviation. The second is to evaluate the distribution of vertebral laminae within sauropods and their immediate outgroups to determine the appropriate hierarchical level at which they diagnose monophyletic groups.

ABBREVIATIONS

Institutional—AMNH, American Museum of Natural History, New York; **CM**, Carnegie Museum of Natural History, Pittsburgh.

Anatomical—acdl, anterior centrodiapophyseal lamina; **acpl**, anterior centroparapophyseal lamina; **cpol**, centropostzygapophyseal lamina; **cprl**, centroprezygapophyseal lamina; **di**, diapophysis; **lat. spol**, lateral spinopostzygapophyseal lamina; **med. spol**, medial spinopostzygapophyseal lamina; **nc**, neural canal; **pa**, parapophysis; **pcdl**, posterior centrodiapophyseal lamina; **pcpl**, posterior centroparapophyseal lamina; **pl**, pleurocoel; **podl**, postzygodiapophyseal lamina; **posl**, postspinal lamina; **poz**, postzygapophysis; **ppdl**, paradiapophyseal lamina; **prdl**, prezygodiapophyseal lamina; **prsl**, prespinal lamina; **prz**,

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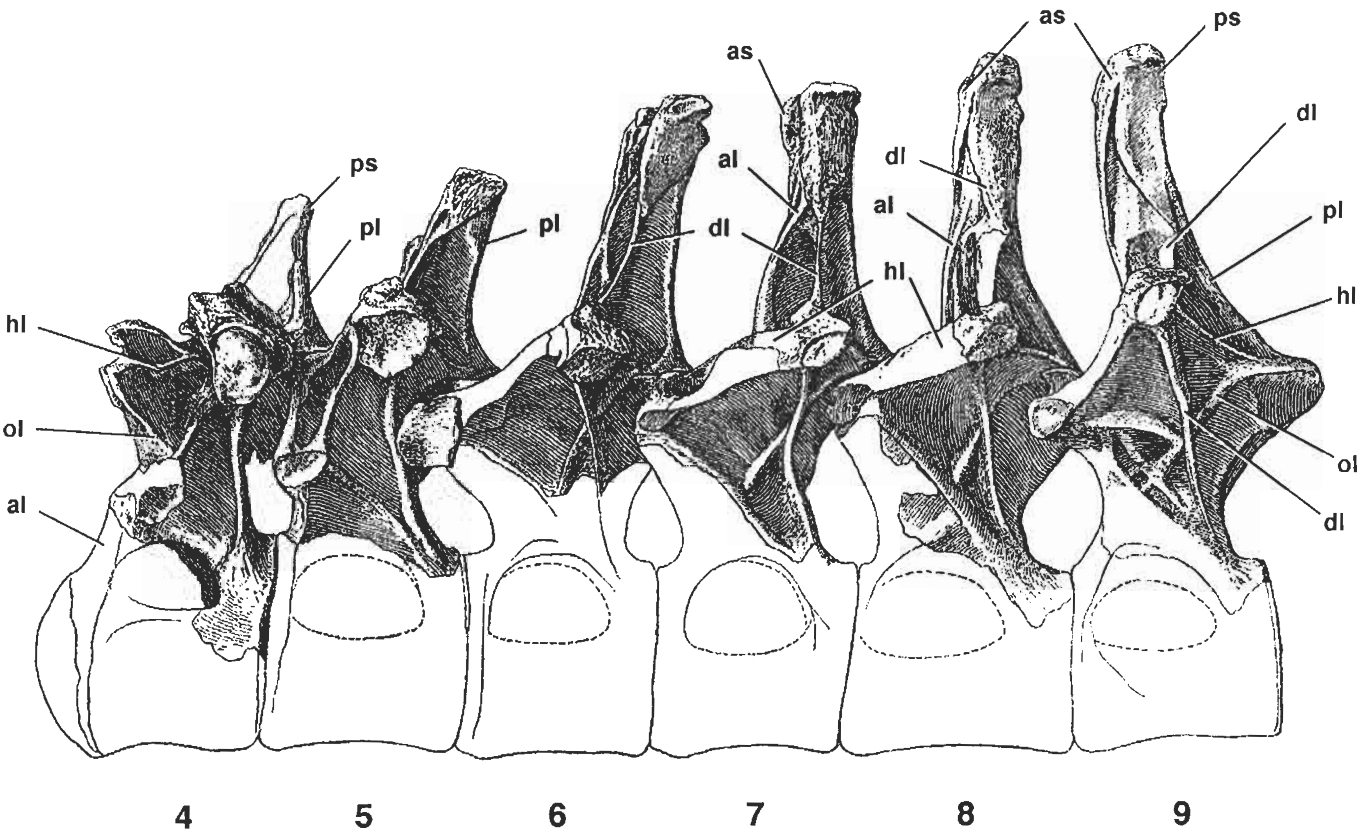

FIGURE 1. Dorsal vertebrae 4–9 of *Diplodocus* in lateral view with nomenclature and abbreviations of Osborn (1899:fig. 6). **Abbreviations: al**, anterior lamina; **as**, prespinal lamina; **dl**, diapophysial lamina; **hl**, horizontal lamina; **ol**, oblique lamina; **pl**, posterior lamina; **ps**, postspinal lamina.

prezygapophysis; **spdl**, spinodiapophyseal lamina; **sprl**, spinoprezygapophyseal lamina; **spol**, spinopostzygapophyseal lamina; **tpol**, intrapostzygapophyseal lamina; **tprl**, intraprezygapophyseal lamina.

PREVIOUS NOMENCLATURAL SYSTEMS

The nomenclature for sauropod vertebral laminae proposed by Osborn and Janensch as well as their major revisions are briefly reviewed here, as they serve as the basis of the proposed nomenclature.

Osborn (1899)

To Osborn, vertebral laminae reduced weight while "connect[ing] all the principal points of strain and stress" (1899: 195). His description of the eight posterior dorsal and four sacral vertebrae of *Diplodocus* (now considered seven dorsal and five sacral vertebrae) proceeded from this functional perspective (Fig. 1). He identified seven neural arch laminae, which he placed four main categories: vertical median, horizontal, lateral vertical, and oblique laminae (Table 1).

Vertical Median Laminae—These included the unpaired, median struts that braced the neural spine against anteroposteriorly directed strains. The two vertical median laminae are the prespinal and postspinal laminae on the anterior and posterior aspects of the neural spine, respectively.

Horizontal Laminae—These paired laminae brace the transverse processes against anteriorly and posteriorly directed strains. They pass along the length of the neural arch from the prezygapophysis through the costal capitular and tubercular facets to the postzygapophysis.

Lateral Vertical Laminae—These include three paired laminae that strengthen the neural spine against anteroposterior and mediolateral strains. They include the prezygapophysial, postzygapophysial, and diapophysial laminae that pass from the neural spine to the base of the neural arch through the prezygapophyses, postzygapophyses, and diapophyses.

Oblique Laminae—These brace the transverse processes against oblique strains. Oblique laminae project posteroventrally from the parapophyses and anteroventrally from the postzygapophyses.

Some of Osborn's terms for neural arch laminae referred to one landmark (prezygapophysial, postzygapophysial, and diapophysial laminae), whereas others were based on their orientation (horizontal, oblique) or position (prespinal, postspinal). A single landmark cannot distinguish laminae unambiguously because several laminae may emanate from a single structure. Orientation is problematic because the same lamina may change its orientation along the axial column. Hatcher (1901:16), for example, pointed out that "horizontal laminae" are only oriented as such in posterior dorsal vertebrae; their serial homologues in cervical and anterior dorsal vertebrae have an oblique orientation. The shifting orientation of vertebral laminae along the axial column has confounded their identification.

Osborn and Mook (1921)

In their monograph on *Camarasaurus* and *Amphicoelias*, Osborn and Mook nearly doubled the number of laminae named by Osborn (1899) (Table 1).

TABLE 1. Comparison of nomenclature for vertebral laminae.

Osborn 1899 (7 laminae)	Osborn and Mook 1921 (15 laminae)	Janensch 1929 (26 laminae)	Wilson 1998 (19 laminae)
diapophysial or oblique	infraprediapophysial	vorderer Centrodiapophysialleiste	anterior centrodiapophyseal
diapophysial	infrapostdiapophysial, infradiapophysial	hinterer Centrodiapophysialleiste, Centrodiapophysialleiste	centrodiapophyseal
horizontal	horizontal	Präzygodiapophysialleiste	prezygodiapophyseal
diapophysial	supradiapophysial	Supradiapophysialleiste, Lateralspinalleiste	spinodiapophyseal
horizontal	horizontal	Postzygodiapophysialleiste	postzygodiapophyseal
horizontal	horizontal	Paradiapophysialleiste	paradiapophyseal
prezygapophysial	infraprezygapophysial	Infrapräzygapophysialleiste (mediale and laterale)	centroprezygapophyseal
prezygapophysial	supraprezygapophysial	Suprapräzygapophysialleiste	spinoprezygapophyseal
horizontal	intraprezygapophysial	Intrapräzygapophysialleiste	intraprezygapophyseal
postzygapophysial	infrapostzygapophysial	Infrapostzygapophysialleiste (mediale and laterale), Infrahyposphenalleiste	centropostzygapophyseal
postzygapophysial	suprapostzygapophysial, suprahyposphenal	Suprapostzygapophysialleiste (mediale and laterale)	spinopostzygapophyseal (medial and lateral)
horizontal	intrapostzygapophysial	Intrapostzygapophysialleiste	intrapostzygapophyseal
prezygapophysial	infraprezygapophysial	vorderer Centroparapophysialleiste	anterior centroparapophyseal
oblique	oblique	hinterer Centroparapophysialleiste	posterior centroparapophyseal
horizontal	oblique	Präzygoparapophysialleiste	prezygoparapophyseal
prespinal	prespinal	Präspinalleiste	prespinal
postspinal	postspinal	Postspinalleiste	postspinal

Osborn and Mook (1921) distinguished laminae spanning the right and left prezygapophyses (intraprezygapophysial) and postzygapophyses (intrapostzygapophysial) from Osborn's (1899) other "horizontal" laminae. By their new definition, horizontal laminae included only those on the lateral aspect of the vertebrae, between the prezygapophyses, diapophyses, parapophyses, and postzygapophyses.

Whereas Osborn and Mook's treatment of "vertical median," "oblique," and "horizontal," laminae involved few changes, they further subdivided the "lateral vertical" laminae. These paired laminae were originally divided by Osborn (1899) into prezygapophysial, postzygapophysial, and diapophysial laminae. These three laminae were partitioned further by Osborn and Mook. Prezygapophysial and postzygapophysial laminae were subdivided into those rising toward the neural spine (prefixed "supra") and those descending towards the centrum (prefixed "infra"). Similarly, diapophysial laminae were factioned into "supra" diapophysial and "infra" diapophysial laminae; the latter were further separated into infra "pre" diapophysial and infra "post" diapophysial laminae in the cervical and anterior dorsal vertebrae.

Although their revised nomenclature increased the number (and length) of names applied to sauropod laminae, Osborn and Mook increased the precision of the original system by subdividing the lateral vertical laminae into eight elements. Osborn's vertical median, oblique, and horizontal laminae, however, were not refined and remained ambiguous because they designate more than one lamina.

Janensch (1929, 1950)

Janensch provided the most important revision of vertebral nomenclature; his nomenclature constitutes the basic plan endorsed and extended in this study. Janensch named laminae on the basis of their connections rather than on their spatial orientation. Terms that could apply to all vertebrae (i.e., not solely dorsal vertebrae) would link landmarks. As Janensch noted, his terms "refer to both ends of the lamina, and are thus unambiguous" (1929:46; translated from the German). Janensch recognized five categories of vertebral laminae, distinguished by their *Verlauf*, or "course." Within these five types, he specified 26 laminae: seven originating on the diapophysis, three on the parapophysis, six on the prezygapophysis, seven on the postzygapophysis, and three on the neural spine (Table 1). The nomenclature presented here represents a simplification of Janensch's terms and includes a consideration of the iterative homologies of the vertebral laminae.

DESCRIPTION OF VERTEBRAL LAMINAE

Vertebral laminae in sauropod dinosaurs can be conveniently divided into four major categories based on their connections; no distinction is made here between the "origin" and "terminus" of laminae (Table 2). The lamina connecting the diapophysis and prezygapophysis, for example, could be classified as either a diapophyseal or zygapophyseal lamina; its placement within the category of diapophyseal laminae does not reflect a sense of "origin" on the diapophysis. The distribution of 19 laminae into the four categories as defined here is somewhat arbitrary, reflecting convenience rather than "origin." The six diapophyseal laminae and three parapophyseal laminae include those radiating from the diapophysis and parapophysis to the zygapophyses, neural spine, and to the anterior and posterior aspects of the neurocentral juncture. These reflect a slight modification of Janensch's conception of the laminae emanating from these two costal articulations. Eight zygapophyseal laminae include those passing inferiorly, superiorly, and medially from the prezygapophyses and postzygapophyses. These are essentially the six prezygapophyseal and postzygapophyseal lamina identified by Osborn and Mook (1921) plus the lateral and medial sublaminae of the postzygapophyseal laminae recognized by Janensch (1929, 1950). The two spinal laminae are equivalent to the original "vertical median" laminae of Osborn (1899) and refer to the median buttresses on the anterior and posterior aspects of the neural spine.

Three views of eight cervical and dorsal vertebrae of *Apatosaurus*, an anterior caudal vertebra of *Diplodocus*, and cross-sections through dorsal neural spines of *Diplodocus* are labeled with the abbreviations corresponding to the nomenclature described herein (Figs. 2–5).

Diapophyseal Laminae (dl)

Six laminae originate on the diapophysis, the larger of the two costal articulations. A major reorganization of the size, shape, and position of the diapophyses and parapophyses occurs at the cervicodorsal transition, where the shape and function of the ribs change drastically. In the cervical series, the ribs parallel the axial column and support the neck. In mature sauropods, cervical ribs are fused to the centrum at the parapophysis

TABLE 2. Abbreviations and morphological landmarks for 19 vertebral presented in this study.

Lamina	Abbreviation	Landmark 1	Landmark 2
anterior centrodiapophyseal	acdl	diapophysis	anterior margin of neurocentral junction (lateral aspect)
posterior centrodiapophyseal	pcdl	diapophysis	posterior margin of neurocentral junction (lateral aspect)
prezygodiapophyseal	prdl	diapophysis	prezygapophysis
spinodiapophyseal	spdl	diapophysis	neural spine (lateral aspect)
postzygodiapophyseal	podl	diapophysis	postzygapophysis
paradiapophyseal	ppdl	diapophysis	parapophysis
centroprezygapophyseal	cprl	prezygapophysis	anterior margin of neurocentral junction (anterior aspect)
spinoprezygapophyseal	sprl	prezygapophysis	neural spine (anterior aspect)
intraprezygapophyseal	tprl	prezygapophysis	dorsal median margin of neural canal (anterior)
centropostzygapophyseal	cpol	postzygapophysis	posterior margin of neurocentral junction (posterior apsect)
spinopostzygapophyseal	spol	postzygapophysis	neural spine (posterior aspect)
medial spinopostzygapophyseal	med. spol	postzygapophysis	neural spine (posterior median aspect)
lateral spinopostzygapophyseal	lat. spol	postzygapophysis	neural spine (lateral aspect)
intrapostzygapophyseal	tpol	postzygapophysis	dorsal median margin of neural canal (posterior)
anterior centroparapophyseal	acpl	parapophysis	anterior margin of neurocentral junction (lateral aspect)
posterior centroparapophyseal	pcpl	parapophysis	posterior margin of neurocentral junction (lateral aspect)
prezygoparapophyseal	prpl	parapophysis	prezygapophysis
prespinal	prsl	neural spine base (anterior)	neural spine summit (anterior)
postspinal	posl	neural spine base (posterior)	neural spine summit (posterior)

and to the neural arch at the diapophysis. Dorsal ribs, in contrast, remain free and are longer and more robust than cervical ribs. Dorsal ribs project perpendicular to the axial column to connect to the sternum and support the pectoral girdle and body cavity. The cervicodorsal transition, informally referred to as the pectoral series, occurs approximately between the last three cervical and first four dorsal vertebrae. Several major changes are manifest, including reduction of centrum length, heightening of the neural spine, elongation of the diapophyses, and elevation of the parapophysis onto the neural arch. Concomitant with these changes, especially the latter, are modifications in the morphology of the diapophyseal laminae and the appearance of parapophyseal laminae. Although the length and spatial orientation of diapophyseal laminae differ between cervical and dorsal vertebrae, their connections do not.

Vertebral laminae are also present in the sacral and caudal regions of the axial column, where there are no free ribs, and hence no rib articulations (i.e., diapophysis and parapophysis). The sacral and caudal vertebrae, however, have lateral projections emanating from the centrum and/or neural arch, referred to as sacral ribs or caudal transverse processes. In adults, the sacral ribs and caudal transverse processes are firmly coossified with the centrum and neural arch, but in subadult specimens these elements are free, and the vertebrae are composed of four ossifications—two median and two paramedian elements (e.g., *Haplocanthosaurus*, Hatcher, 1903; *Camarasaurus*, Gilmore, 1925). The two median ossifications constitute the vertebral centrum and neural arch, and the two paramedian elements have uncertain serial homologies. In the sacrum, these lateral processes have been identified as either the serial homologues of the parapophyses (Hatcher, 1903) or dorsal ribs (Osborn, 1899), and in the caudal region, they have been referred to as representing fused diapophyses and parapophyses (Hatcher, 1903) or ribs (Huene, 1929:33; McIntosh et al., 1996:84).

Study of the patterns of chondrification and ossification in the axial column of extant reptiles has begun to clarify the identity of these elements. In squamates and crocodilians, the dorsal ribs, sacral ribs, and caudal transverse processes all chondrify separately from the neural arch and centrum. Later in development, sacral ribs and caudal transverse processes fuse to the vertebrae, whereas the dorsal ribs do not (Rieppel, 1993). The pattern of ossification is quite similar to the pattern of chondrification, except that in crocodilians the dorsal transverse processes originate in a separate ossification center (Rieppel, 1993). Based on these developmental patterns, Rieppel (1993) suggested that the sacral ribs and caudal transverse processes are serially homologous to the dorsal ribs. Because the ribs and their articulations on the neural arch are indistinguishable as individual elements in the sacral and caudal vertebrae of adults, it is difficult to evaluate the serial homologies of the laminae that are present in these regions. Are vertebral laminae on the transverse processes of caudal vertebrae serially homologous with those of the presacral diapophyses, parapophyses, or both? Questions like this are difficult to resolve in the absence of ontogenetic data. Nonetheless, vertebral laminae are present in the sacrum and tail, and require a descriptive nomenclature. As the diapophysis is the dominant rib articulation both in terms of the size and number of laminae it supports, it seems most conservative at this time to simply refer to sacral and caudal laminae as serially homologous with the presacral diapophyseal laminae.

Anterior Centrodiapophyseal Lamina (acdl)—The acdl projects from the diapophysis to the anterior portion of the neurocentral junction. Because the diapophysis originates on the anterior half of the neural arch, the acdl is the shortest diapophyseal lamina. The acdl is difficult to observe in lateral view of anterior cervical vertebrae because it is obscured by the pendant diapophyses, tuberculum, and other diapophyseal laminae, especially that connecting the prezygapophysis and diapophysis (Fig. 2A, B). As the diapophysis rises dorsally on the neural arch through the posterior cervical and anteriormost dorsal vertebrae, the acdl becomes longer and oriented more anteroventrally (Figs. 2D, 3A).

In the pectoral vertebrae of sauropods, the parapophysis migrates from a position ventral to the pleurocoel (last cervical vertebra) to a position adjacent to the diapophysis on the neural arch (fourth or fifth dorsal vertebra). The trajectory of the parapophysis through this transitional pectoral series intersects the path of the acdl (Fig. 3B). At this intersection, the acdl is broken into two component laminae, one linking the diapophysis and parapophysis (the paradiapophyseal lamina [ppdl]) and the other connecting the parapophysis to the anterior centrum (the anterior centroparapophyseal lamina [acpl]). The term "acdl" is not applied to these laminae, because the original connections of the acdl (Table 2) have been changed. Rather than a single lamina between the diapophysis and the anterodorsal corner of the centrum, the parapophysis has intercepted the lamina to form two composite laminae that maintain their connections even as the parapophysis moves to a position adjacent to the prezygapophysis in the posterior dorsal vertebrae. In other words, the acdl does not "reappear" in the posterior dorsal vertebrae, after the parapophyses migrates further dorsally (Fig.

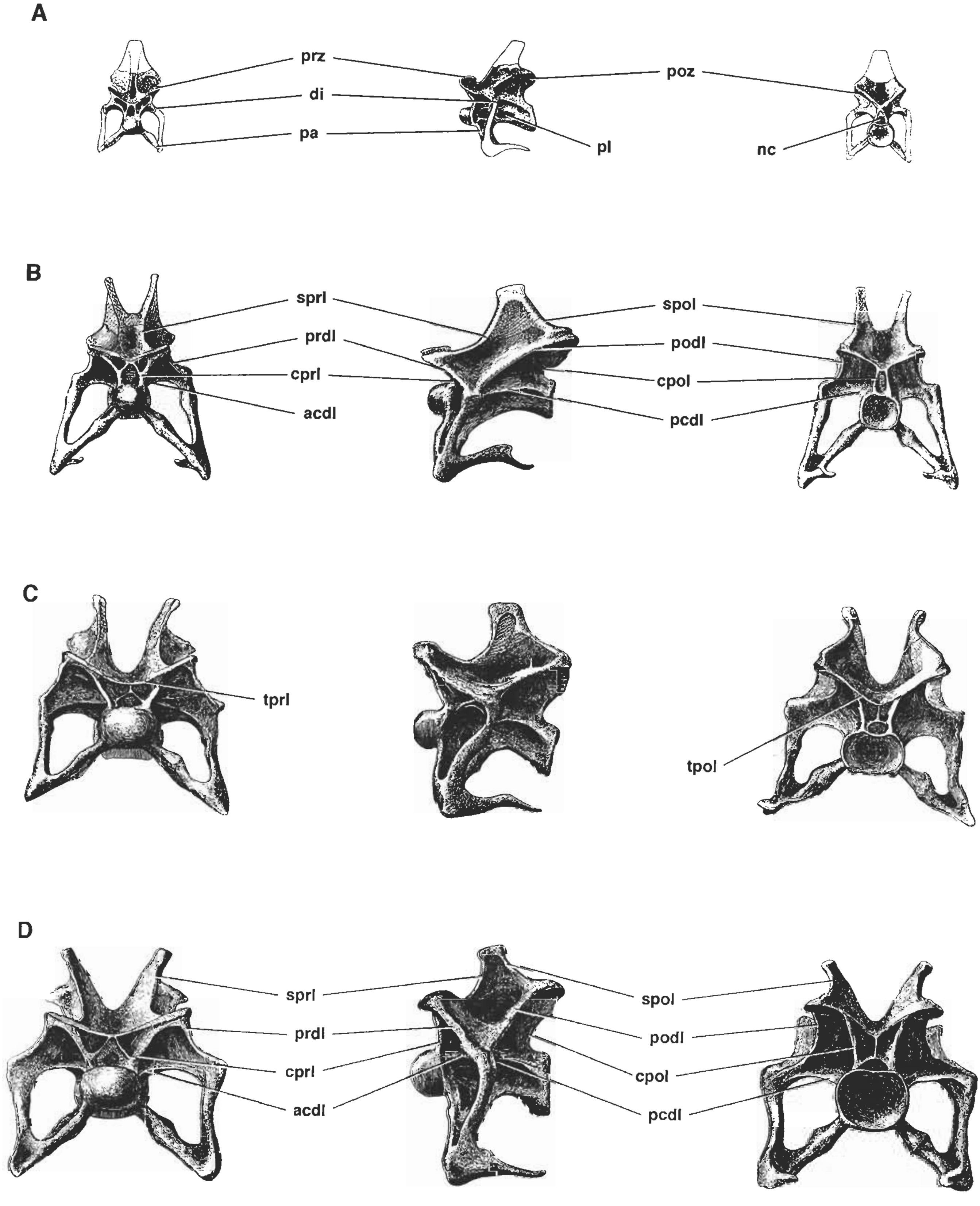

FIGURE 2. Cervical vertebrae of *Apatosaurus louisae* in anterior, left lateral, and posterior views. **A–D**, 3rd, 6th, 9th, and 12th cervical vertebrae, respectively. Modified from Gilmore (1936:pl. 24).

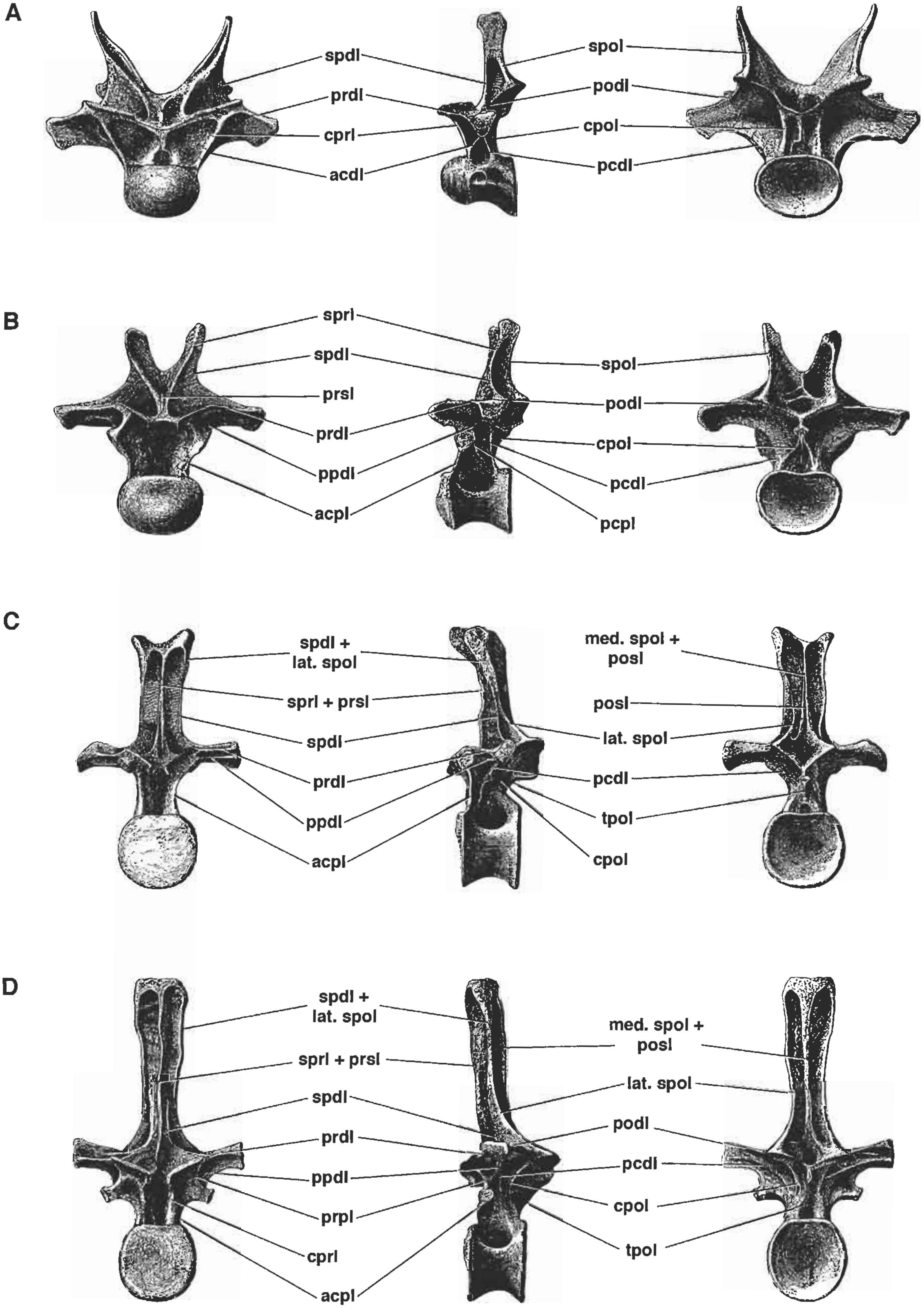

FIGURE 3. Dorsal vertebrae 1, 3, 6, and 9 of *Apatosaurus louisae* in anterior, left lateral, and posterior views. **A–D**, 1st, 3rd, 6th, and 9th dorsal vertebrae, respectively. Modified from Gilmore (1936:pl. 25).

3D). Moreover, the two laminae into which the acdl is fractioned (ppdl, acpl) do not always persist in the remainder of the dorsal vertebrae.

As in the posterior dorsal vertebrae, the acdl is difficult to identify in the sacra of most sauropods because the parapophysis and diapophysis coalesce with one another and the sacral rib to form the sacricostal yoke. A remnant of the acdl, however, may be possible to identify in anterior view (e.g., *Haplocanthosaurus*, Hatcher, 1903:pl. 5, fig. 2).

A rudimentary acdl is present in the anterior caudal vertebrae of many sauropods, especially those with well developed transverse processes, such as diplodocids. Because the transverse process is dorsoventrally deep, the acdl is a relatively short strut emanating from the base of the transverse process and projecting anteroventrally. The acdl is strongly developed in the first fifteen caudal vertebrae of *Diplodocus* (Fig. 4). Neither the acdl nor any other diapophyseal laminae are known to be present in more distal caudal vertebrae.

Posterior Centrodiapophyseal Lamina (pcdl)—The pcdl connects the diapophysis to the posterior aspect of the neurocentral junction. It is easily identifiable in the cervical region, forming an almost horizontal lamina running posteriorly at a level just superior to the dorsal margin of the pleurocentral cavities (Fig. 2B). The orientation of the pcdl becomes progressively more vertical through the dorsal vertebrae, as the diapophysis projects horizontally and the depth of the neural canal increases (Fig. 3B). Because the pcdl is never interrupted by the parapophysis, it persists further posteriorly in the dorsal series than does the acdl. For this reason, previous authors have referred to this single lamina below the diapophysis (the pcdl) as the "infradiapophysial" lamina (Osborn and Mook, 1929; Gilmore, 1936) or "Centrodiapophysialleiste" ("centrodiapophyseal lamina"; Janensch, 1929, 1950). These terms are degenerate because they can refer to more than a single lamina based on landmarks.

Like the acdl, the pcdl is partially incorporated into the sacricostal yoke, but its rudiments may be seen in posterior view of the sacrum. In the caudal vertebrae, the pcdl is retained in those genera with well developed transverse processes, but it is not usually present beyond the fifteenth caudal vertebra (Fig. 4).

Prezygodiapophyseal Lamina (prdl)—The prdl passes anteriorly from the diapophysis to the lateral aspect of the prezygapophysis. In the cervical vertebrae, the prdl is canted anterodorsally in lateral view, parallel to the spinopostzygapophyseal lamina (spol). These two laminae form the short sides of a parallelogram whose long sides are formed by the longer spinoprezygapophyseal laminae (sprl) and postzygodiapophyseal laminae (podl), and whose apices are formed by the diapophysis, prezygapophysis, postzygapophysis, and neural spine (Fig. 2B–D).

The prdl attains a horizontal orientation in lateral view by the fourth or fifth dorsal vertebra, and remains so throughout the posterior dorsal vertebrae (Fig. 3C). With the concomitant elongation of the horizontally oriented diapophyses, the long axis of the prdl is oriented transversely rather than anteroposteriorly. Although the parapophysis ascends the neural arch to the level of the prezygapophysis in the posterior dorsal vertebrae, it does not interrupt the prdl. Together, the postzygodiapophyseal lamina (podl) and the prdl form a planar structure termed the horizontal lamina by Osborn and Mook (1921), which spans the lateral portion of the neural arch from the prezygapophysis through the diapophysis to the postzygapophysis. Thus, whereas the prdl and spol maintain a parallel relationship in the cervical vertebrae, they are oriented orthogonal to one another in the middle and posterior dorsal vertebrae.

The prdl is readily distinguishable in the sacral region of most sauropods, although its connection to the prezygapophysis is obscured by the extensive fusion of the zygapophyses. For example, in *Haplocanthosaurus* the prdl, postzygodiapophyseal lamina (podl), and spinodiapophyseal laminae (spdl) form a three-way junction where they meet near the base of the neural arch of each sacral vertebra (Hatcher, 1903:fig. 15). In the anterior caudal region, the prdl forms a variably developed strut between the transverse process and prezygapophysis. As in other diapophyseal laminae, it persists through the first fifteen caudal vertebrae in diplodocids (Fig. 4).

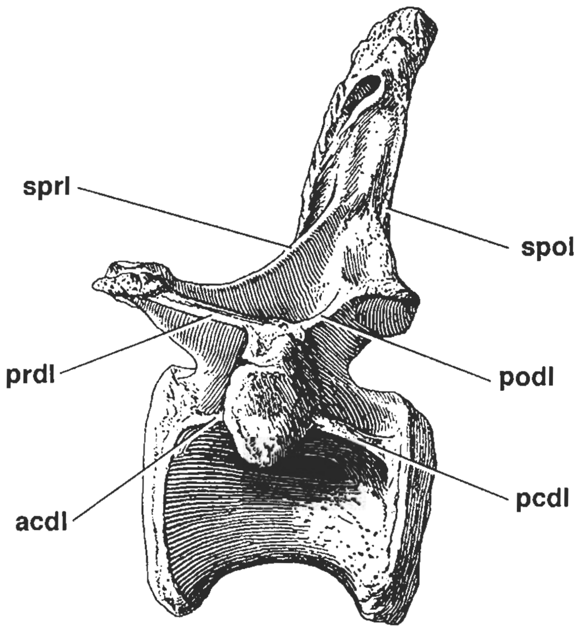

FIGURE 4. Tenth caudal vertebra of *Diplodocus* in left lateral view (from Osborn, 1899:fig. 13).

Postzygodiapophyseal Lamina (podl)—The podl forms a bony web between the diapophysis and postzygapophysis. In cervical vertebrae it is oriented posterodorsally, approximately parallel to the sprl. As mentioned above, these two laminae join the prdl and spol to form a parallelogram in lateral view. This relation persists in all the cervical vertebrae save the last two or three, which form a gradual transition series to the typical arrangement of laminae in the dorsal series (Figs. 2A–3B). Like its complementary horizontal lamina, the prdl, the podl is oriented horizontally and is longer transversely than anteroposteriorly in the posterior dorsal vertebrae.

In the sacral region, the podl is visible as a horizontal strut that meets the prdl and spdl in a three-way junction at the base of the neural spine. The podl is present in the anterior caudal neural arches of diplodocids (Fig. 4).

Spinodiapophyseal Lamina (spdl)—The spdl forms a strut from the dorsal portion of the diapophysis to the lateral aspect of the neural spine. This lamina is restricted to the dorsal and sacral vertebrae, where its broad lateral flanges are apparent in cross-section (Fig. 5; see also *Dicraeosaurus*, Janensch, 1929: pl. 5, figs. 4, 5; *Amargasaurus*, Salgado and Bonaparte, 1991: fig. 9; *Brachiosaurus*, Janensch, 1950:fig. 66). In posterior dorsal vertebrae, spdl is reinforced posteriorly by a branch of the spinopostzygapophyseal lamina (Fig. 3C, D). This lateral branch of the spol joins the spdl at about mid-spine to form a composite lateral lamina (Wilson and Sereno, 1998). This composite lamina has been referred to as the "Lateralspinalleiste" ("lateral spinal lamina") by Janensch (1929, 1950). In sacral vertebrae, the spdl forms the prominent vertical strut that courses down the neural spine to meet the conjoined podl and prdl at their midlength.

Paradiapophyseal Lamina (ppdl)—The ppdl joins the diapophysis to the parapophysis. Paradiapophyseal laminae occur only in dorsal vertebrae; the ppdl is unknown in the cervical, sacral, or caudal vertebrae of saurischian dinosaurs. As described above, the parapophysis migrates dorsally in the anterior dorsal vertebrae, bisecting the acdl to form the ppdl and acpl. In the dorsal vertebra that the parapophysis first interrupts the acdl (usually the fifth), the component ppdl and acpl are nearly coplanar (Fig. 3B). As the parapophysis assumes a position adjacent to the prezygapophysis in the succeeding dorsal vertebrae, however, these two laminae obtain a perpendicular relationship, with the ppdl oriented horizontally and the acpl oriented vertically (Fig. 3C).

As neither the parapophysis nor diapophysis are individually identifiable in sacral or caudal vertebrae, the ppdl cannot be recognized in these regions of the axial column.

Parapophyseal Laminae (pl)

Three laminae emanate from the parapophysis. Two extend anteriorly to join the parapophysis to the anterior aspect of the centrum and to the prezygapophysis; a third projects to the posterior margin of the neurocentral junction. Parapophyseal laminae are here considered to characterize only the dorsal region, where the parapophysis is both distinct and situated on the neural arch. Janensch (1929, 1950) distinguished a single parapophyseal lamina in the cervical region, the "hintere Centroparapophysialleiste" ("posterior centroparapophyseal lamina"). This structure, however, is practically indistinguishable from the ventrolateral margin of the centrum in most taxa and does not maintain a connection to the parapophysis as the latter migrates onto the neural arch in the pectoral series. Because of its indistinct morphology and lack of continuity in the dorsal region, the "hintere Centroparapophysialleiste" is not considered here as a true parapophyseal lamina.

Anterior Centroparapophyseal Lamina (acpl)—The acpl joins the parapophysis to the anterior portion of the centrum. The acpl is formed as the parapophysis rises on the neural arch and intercepts the acdl. The acpl forms the main component of the fragmented acdl; the ppdl (discussed above) forms the lesser component. With the parapophysis situated adjacent to the prezygapophysis at the anterior extreme of the neural arch, the acpl usually obtains a vertical or sub-vertical orientation, whereas the ppdl is oriented horizontally. The acpl is the most regular of all parapophyseal laminae; it is consistently present in the middle and posterior dorsal vertebrae of sauropod dinosaurs (Fig. 3B–D).

Posterior Centroparapophyseal Lamina (pcpl)—The pcpl joins the parapophysis to the posterolateral aspect of the centrum. This lamina is usually weakly developed and oriented posteroventrally. The pcpl is much less regular than either the acpl or the prezygoparapophyseal lamina (prpl), and may be present only in some dorsal vertebrae of a given sequence. In *Apatosaurus louisae*, for example, the pcpl first appears in the third dorsal vertebra (Fig. 3B), is absent from the fourth through sixth dorsal vertebrae, and reappears in the seventh dorsal vertebra (Gilmore, 1936:pl. 25). In *A. excelsus*, the pcpl is present on most posterior dorsal vertebrae (Gilmore, 1936:pl. 33). The irregularity of the pcpl may be related to the presence of the adjacent, pronounced pcdl on all dorsal vertebrae. The pcdl has a similar spatial orientation and probably a similar structural role as the pcpl.

Prezygoparapophyseal Lamina (prpl)—The prpl connects the parapophysis to the lateral aspect of the prezygapophysis. As the parapophysis rises on the neural arch at the cervicodorsal transition, it intercepts both the acdl (discussed above) and occasionally the centroprezygapophyseal lamina (cprl). As the latter is interrupted, it forms two component laminae, the vertically oriented acpl and the anterodorsally oriented prpl (Fig. 3D). Although the parapophysis interrupts the cprl in anterior and occasionally mid-dorsal vertebrae, the cprl is well developed in posterior dorsal vertebrae.

Zygapophyseal Laminae (pol, prl)

Zygapophyseal laminae are paramedian struts that brace the zygapophyses inferiorly, superiorly, and medially. Individual zygapophyseal laminae may be split into lateral and medial sublaminae in regions of the vertebral column of some sauropod genera.

Centroprezygapophyseal Lamina (cprl)—The cprl emanates from the ventrolateral aspect of the prezygapophysis and passes to the anterior portion of the centrum alongside the neural canal. This latter (inferior) connection of the cprl is coincident with that of the acdl throughout the presacral vertebrae; the inferior ends of the cprl and acdl meet at the anteriormost corner of the pedicle of the neural arch. The cprl is oriented dorsolaterally in anterior view of the cervical and anterior dorsal vertebrae (Figs. 2B–3A) and becomes vertically oriented by the posterior dorsal vertebrae, where the prezygapophyses approach each other to form the hypantrum (Fig. 3C, D). The parapophysis may interrupt the cprl at the cervicodorsal transition; in these vertebrae the cprl is replaced by its component laminae, the prpl and acpl. As mentioned above, these component laminae maintain an oblique relationship to each other. As the parapophysis reaches a position adjacent to the prezygapophysis in the posterior dorsal vertebrae, the cprl is again prominent.

The cprl is discernible in the first sacral vertebra but is more difficult to identify in succeeding sacral vertebrae, especially in those individuals with strongly coossified sacra. In the caudal series, the cprl may persist throughout the first dozen vertebrae, but is rudimentary thereafter.

Spinoprezygapophyseal Lamina (sprl)—The sprl originates on the posterior aspect of the prezygapophysis and stretches vertically along the anterior surface of the neural spine to its summit. The sprl's remain paired in most taxa; in sauropods with a single, median neural spine the sprl's merge distally, whereas in sauropods with paired or "bifid" neural spines forms they diverge distally (Figs. 2D, 3A). In the posterior dorsal vertebrae of both single and bifid-spined forms, the sprl's fuse to form a single median lamina (Fig. 3C, D). Although this median lamina has occasionally been regarded as the prespinal lamina (Salgado, Coria, and Calvo, 1997:fig. 6; discussed below), it is actually a hybrid structure comprised of the sprl and prsl.

The sprl is well developed in the sacral vertebrae of most sauropods. Because the prezygapophyses are closely apposed in this portion of the axial column, the sprl's originate close to the midline at the base of the neural spine and merge distally. The merged sprl's (together with the prsl) form a prominent median web that is distinguishable in all sacral vertebrae. The sprl is persistent in the caudal series through the first nine anterior caudal neural arches of diplodocids, where it joins the spinopostzygapophyseal lamina (spol) on the neural spine to form a composite lateral lamina. The sprl is prominent in the caudal region of dicraeosaurids (*Dicraeosaurus*, Janensch, 1929:pl. 3), where it forms a single lateral lamina (i.e., it does not meet the spol). In these anterior caudal vertebrae, the neural spine is broader transversely than anteroposteriorly. In the succeeding caudal vertebrae, however, the sprl does not form a prominent lateral lamina, and the neural spine is broader anteroposteriorly than transversely.

Intraprezygapophyseal Lamina (tprl)—The tprl's are paired laminae that project medially or ventromedially from each prezygapophysis to contact their mates at the median dorsal margin of the neural canal. In the anterior cervical vertebrae, the tprl are nearly horizontal, with a slight ventral dip above the neural canal (Fig. 2B). Passing posteriorly through the cervical series, however, the tprl's tend to have a more oblique orientation, as their lateral connection to the prezygapophyses are raised above the neural canal. In these vertebrae the trpl's connect to the dorsal margin of the neural canal via a vertical strut (Figs. 2C–3A). In anterior view, the tprl, cprl, and the lateral margin of the neural canal form a triangular space that is often deeply excavated (Fig. 2C, D).

The tprl's are elongate in the anterior dorsal region, as the prezygapophyses are broadly separated at the base of the neck. By the fourth or fifth dorsal vertebra, however, the intra-prezygapophyseal space is modified into the hypantrum of the hyposphene-hypantrum articulation, and the tprl disappears abruptly (Fig. 3B). The tprl is not identifiable in sacral vertebrae because the zygapophyses are coalesced. The tprl is present in the caudal vertebrae of *Diplodocus* (Osborn, 1899:fig. 12).

Centropostzygapophyseal Lamina (cpol)—The cpol joins the postzygapophysis to the posteriormost portion of the neurocentral junction. As with the cprl, the distal attachment of the cpol alongside the posterior portion of the neural canal coincides with that of its adjacent diapophyseal lamina, the podl. In the cervical and anterior dorsal vertebrae, the cpol's originate some distance from the midline, on the medial aspect of the postzygapophysis. In the posterior dorsal vertebrae, however, the development of the hyposphene between the postzygapophyses may bring this origin to the midline (compare Figs. 2D and 3B).

The cpol is not discernible in the sacrum of sauropod dinosaurs. In the caudal region, the cpol is reduced as the postzygapophyses approach the dorsal margin of the neural canal, disappearing after the first ten or so caudal vertebrae.

Spinopostzygapophyseal Lamina (spol)—The spol rises from the lateral margin of the postzygapophysis and passes along the posterior aspect of the neural spine. Throughout most of the axial column, the spol's are paired, although they may fuse to form a single median lamina in the posterior dorsal vertebrae (Fig. 3C, D). In the cervical region, the paired spol's are oriented dorsomedially in posterior view, and together with the cpol enclose a median "postspinous" fossa that is most pronounced in the axis (Fig. 2A, B). In lateral view, the spol maintains a parallel relationship to the prdl, forming two short sides of the parallelogram discussed above. As the neural spine becomes elongate and the neural arch anteroposteriorly abbreviate in the dorsal series, the spol attains a near vertical orientation, effectively changing its relation to the prdl by 90 degrees.

A fifth diapophyseal lamina, the spdl, appears in the mid-dorsal vertebrae of most sauropods. In the middle and posterior dorsal region of all taxa possessing the spdl, the spol splits into two rami: paired medial rami that meet at the midline of the distal neural spine, and paired lateral rami that connect to their respective spdl's to form composite lateral laminae (Fig. 4C,D). The conjoined medial rami have been referred to as the "suprahyposphenal lamina" by Osborn and Mook (1921).

The spol is persistent as a median or near median element in the sacral and anterior caudal vertebrae in most sauropods. After approximately the tenth caudal vertebra, however, the spol becomes increasingly indistinct distally until only its origin on the postzygapophysis is discernible. In diplodocids, the spol is well developed in the anterior caudal vertebrae, where with the sprl it forms a prominent, composite lateral lamina.

Intrapostzygapophyseal Lamina (tpol)—The tpol is the posterior complement of the tprl. These paired laminae originate on the medial aspect of the postzygapophyses and project medially to meet on the midline above the posterior opening of the neural canal (Figs. 2C–3A). In neural arches of the anterior cervical vertebrae, the tpol forms the ventral floor of the "postspinous" fossa described above (see spol). As in the tprl's, the tpol's may connect to the neural canal via a vertical strut (Figs. 2C–3A).

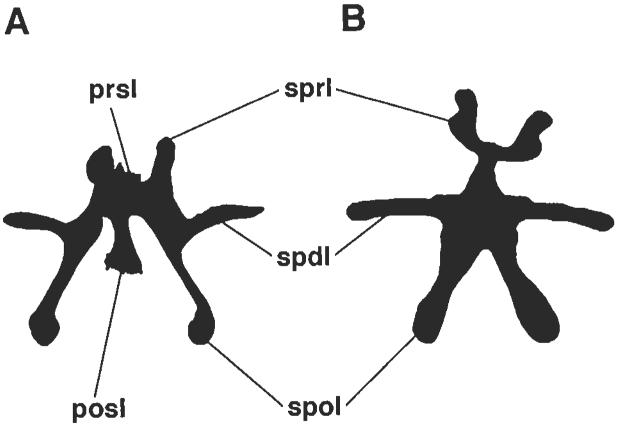

FIGURE 5. Dorsal neural spines of *Diplodocus* in transverse section. **A**, 7th dorsal vertebra; **B**, 9th dorsal vertebra. Modified from Osborn (1899:fig. 4).

Like the tprl, the tpol disappears with the first hyposphene in the fourth or fifth dorsal vertebra and is not usually present in the sacral or caudal series. In diplodocids, however, the tpol persists throughout the dorsal series as a median strut below the hyposphene (Fig. 3C,D).

Spinal Laminae (sl)

Spinal laminae are the only single, median laminae on the neural arch. Spinal laminae can be difficult to identify because of their low, roughened appearance and their proximity to the paired lamina arising from the pre- and postzygapophyses. For this reason, spinal laminae are often conflated with zygapophyseal laminae.

Prespinal Lamina (prsl)—The prsl spans the anterior aspect of the neural spine from its base to its summit. This lamina may appear as a low, roughened ridge and probably served as one of the attachments for the interspinous ligament. The prsl is most common in posterior dorsal, sacral, and caudal vertebrae, and it is present in cervical and anterior dorsal vertebrae only rarely (e.g., *Titanosaurus colberti*; Jain and Bandyopadhyay, 1997:figs. 4, 5). In taxa with single dorsal neural spines, the prsl is usually present. The prsl is not present in any deeply bifurcate neural arches, as there is no median neural spine. In these bifid-spined taxa a single, median prsl appears between the paired sprl's only in the fourth or fifth dorsal vertebra, when the median cleft in the neural spine is reduced (Fig. 3B). As the paired neural spines coalesce in the posterior dorsal vertebrae, the paired sprl are brought toward the midline and eventually incorporate the prsl into a single, composite median lamina (Fig. 3C, D; see also *Dicraeosaurus*, Janensch, 1929:pl 1). This composite median lamina persists through the sacral region.

In the caudal vertebrae, the single prsl is distinct from the paired sprl's and forms a single median lamina on the anterior aspect of the neural spine. The prsl continues posteriorly until about the fifteenth caudal vertebra, where it is reduced to a low ridge.

Postspinal Lamina (posl)—The posl is the complement to the prsl on the posterior aspect of the neural spine and probably

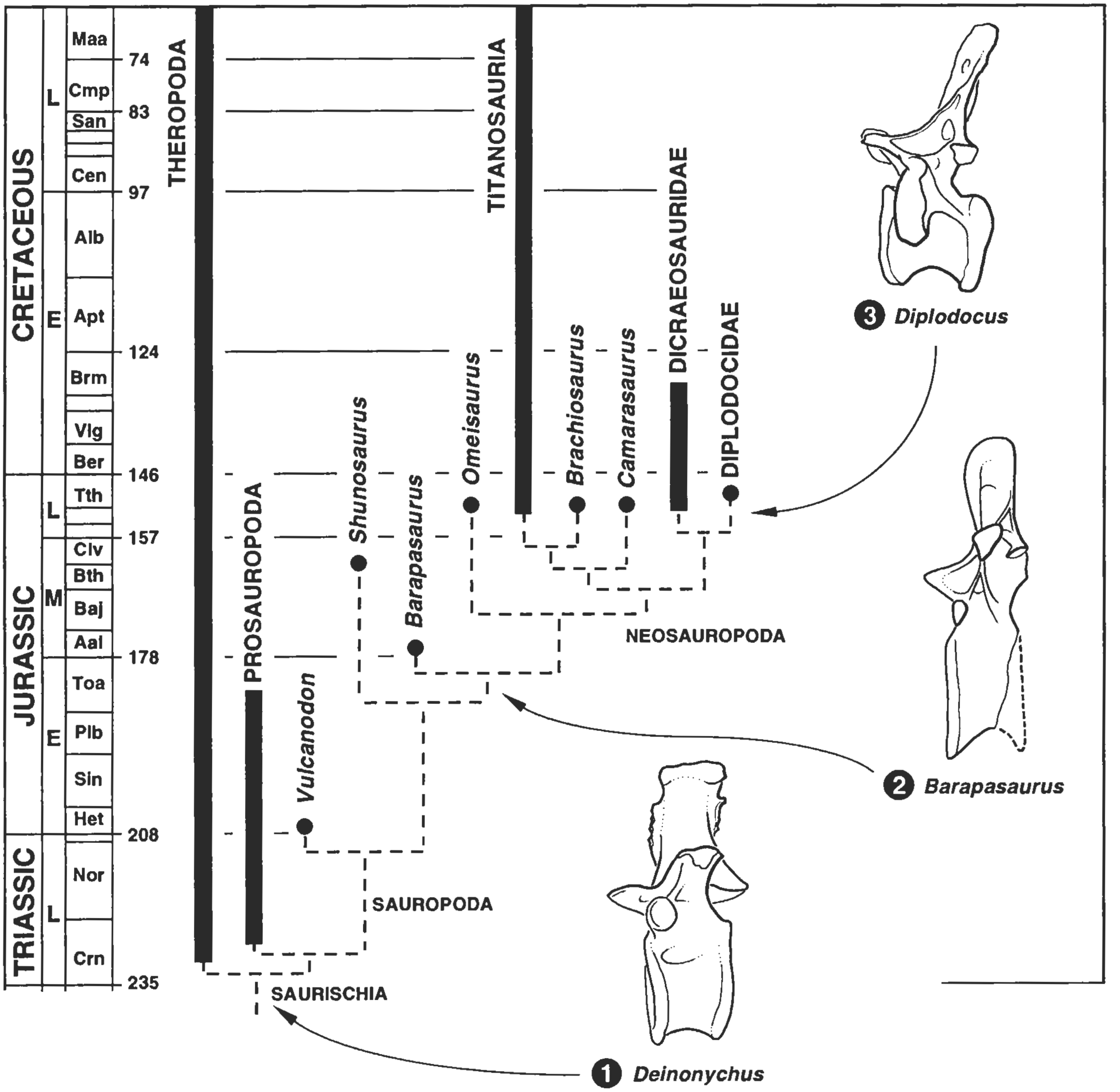

FIGURE 6. Cladogram of saurischian relationships identifying three major phases in the evolution of vertebral laminae (circled 1–3). **1**, The basic architecture of saurischian presacral neural arches includes five diapophyseal laminae (podl, prdl, pcdl, acdl) and six zygapophyseal laminae (cpol, cprl, spol, sprl, tpol, tprl). **2**, *Barapasaurus, Omeisaurus*, and Neosauropoda are characterized by the addition several vertebral laminae to the dorsal region, including two parapophyseal laminae (acpl, prpl), a diapophyseal lamina (spdl), a divided lamina (spol), and a composite lamina (spdl + lat spol). **3**, Diplodocid sauropods are characterized by diapophyseal laminae extending into the caudal region (podl, prdl, pcdl, acdl), anterior caudal vertebrae with a composite lamina (sprl + spol), presence of the tpol throughout the dorsal region, and a divided lamina in the dorsal region (cprl). Illustration of *Deinonychus* modified from Ostrom (1969:fig. 34), *Barapasaurus* modified from Jain et al. (1979:pl. 98), *Diplodocus* modified from Osborn (1899:fig. 13). Cladogram based on Gauthier (1986), Sereno et al. (1993), and Wilson and Sereno (1998); time scale from Harland et al. (1990).

served as the other attachment for the interspinous ligament. The posl is usually absent from the cervical region of most sauropods, although it is present in posterior cervical vertebrae of *Titanosaurus colberti* (Jain and Bandyopadhyay, 1997). In posterior dorsal vertebrae, the posl and medial spol coalesce to form a composite lamina. Like the prsl, the distribution of the posl within the vertebral column of bifid-spined forms is restricted to the posterior dorsal region. The posl is present in the anterior caudal vertebrae of most sauropods.

DISTRIBUTION OF VERTEBRAL LAMINAE WITHIN DINOSAURIA

The homologies of vertebral laminae were assessed by comparing the distribution of 19 laminae in the axial columns in Theropoda, Prosauropoda, and Sauropoda with a well corroborated hypothesis of their phylogenetic relationships (Fig. 6; based on Gauthier, 1986; Sereno et al., 1993; Wilson and Sereno, 1998). The basal forms *Shunosaurus* and *Barapasaurus* are used to approximate the primitive condition for Sauropoda because presacral and anterior caudal neural arches are not preserved in the basalmost sauropod, *Vulcanodon.* The analysis of the distribution of vertebral laminae was restricted to saurischians because the basal dinosauromorph *Marasuchus* and ornithischian dinosaurs are not characterized by vertebral laminae. The condition in these two outgroups to Saurischia is discussed briefly below.

The anteriormost presacral vertebrae of *Marasuchus* have low, inconspicuous diapophyses and parapophyses, and no lamination is present on the neural arch (Sereno and Arcucci, 1994: fig. 3). Only in the ninth presacral, in which the costal articular processes are more prominent, are there two low, rounded ridges present below the diapophysis (Sereno and Arcucci, 1994: fig. 3A). These rudimentary laminae are not present in posterior dorsal vertebrae (Romer, 1972:fig. 4; Sereno and Arcucci, 1994: figs. 3b, c). No laminae are present in the caudal vertebrae of *Marasuchus.* Although low ridges are present below the diapophyses of the anterior dorsal vertebra, these are not well defined and do not enclose deep fossae.

Vertebral laminae are not present in the cervical vertebrae of ornithischians, including thyreophorans (e.g., *Stegosaurus*, Ostrom and McIntosh, 1966:pls. 7–9), ornithopods (e.g., *Heterodontosaurus*, Santa Luca, 1980:fig. 5; *Iguanodon*, Norman, 1980:fig. 22; *Ouranosaurus*, Taquet, 1976:fig. 76), and marginocephalians (e.g., *Triceratops*, Hatcher et al., 1907:figs. 48–50). There is a rudimentary lamina below the blade shaped transverse process of the dorsal vertebrae of some ornithischians, but this lamina does not reach the ventral margin of the neural arch and is not as sharply defined as in saurischians (e.g., *Iguanodon*, Norman, 1980:figs. 34, 36, 39, 40; *Camptosaurus*, Galton and Powell, 1980:fig. 4; *Triceratops*, Hatcher et al., 1907:fig. pl. 40, figs. 1, 51). Moreover, dorsal vertebral laminae are not present in other ornithischians (e.g., *Stegosaurus*, Ostrom and McIntosh, 1966:pl. 14–17; *Heterodontosaurus*, Santa Luca, 1980:fig. 5; *Gasparinisaura*, Salgado et al., 1997a:fig. 2). Vertebral laminae are not present in the caudal vertebrae of ornithischians. Thus, there is not a consistent pattern of vertebral lamination among ornithischians; the most inclusive ornithischian clade is not characterized by vertebral laminae.

Some taxa outside of Dinosauria are considered to have independently acquired vertebral laminae. The poposaurids *Postosuchus* and *Sillosuchus*, for example, have well defined laminae below the diapophyses of dorsal vertebrae (Chatterjee, 1985:fig. 12; Alcober and Parrish, 1997:fig. 3G). *Sillosuchus*, moreover, has laminate caudal transverse processes (Alcober and Parrish, 1997:fig. 4D) similar to those in diplodocids.

Variation—That the vertebral laminae of sauropod dinosaurs are subject to variation was recognized long ago. Mook, for example, recognized that vertebral laminae vary during ontogeny (1917:356). In his description of *Apatosaurus*, Gilmore (1936:246–247) noted variation in the vertebral laminae of its two species, *A. louisae* and *A. excelsus*, variation along the axial column of a single individual, as well as left-right variation within a vertebra of an individual.

Recently, Curtice (1998) has suggested that laminar variation along the vertebral column as well as left-right asymmetry are potentially detrimental to phylogenetic analysis. Neither of these issues, however, is unique to vertebral laminae nor to sauropod dinosaurs. Left-right asymmetry in tooth counts and size of limb elements, for example, are well documented in both the fossil record and extant organisms. Variation along the vertebral column was described above—the migration of the parapophysis from the centrum onto the neural arch imposes changes in the position of the vertebral laminae of the dorsal vertebrae. Whether this migration occurs across the first four, five, or six dorsal vertebrae accounts for some of the variation in the exact lamination pattern among sauropod genera. Vertebral laminae are treated here as hierarchical characters: their presence in generalized regions of the skeleton may be considered diagnostic at higher taxonomic levels, whereas details of the exact vertebral level at which a given lamina appears or disappears may be diagnostic at lower taxonomic levels, such as genera or species. As an example, fur characterizes extant mammals, yet different species have greater and lesser amounts of fur covering their bodies. Presence of fur is diagnostic for a more inclusive group, whereas the variation of the distribution of fur are diagnostic of more exclusive groups.

Diapophyseal Laminae—Four principal diapophyseal laminae are present in the presacral vertebrae of all saurischian dinosaurs. These laminae project from the diapophysis to the prezygapophysis (prdl), postzygapophysis (podl), and to the anterior and posterior aspects of the neurocentral junction (acdl, pcdl) of the presacral vertebrae and occasionally in caudal vertebrae. The four principal diapophyseal laminae are well developed in the posterior cervical and dorsal neural arches of the basal theropod *Herrerasaurus.* They are also present, but weakly developed, in anterior cervical vertebrae (Sereno and Novas, 1993:figs. 11, 12; Novas, 1993:figs. 1, 2). Diapophyseal laminae are not present in the caudal region of *Herrerasaurus* (Novas, 1993:fig. 4). Prosauropods, such as *Plateosaurus* and *Lufengosaurus*, also possess strong diapophyseal laminae in the dorsal region, but these are much less conspicuous in the cervical region and absent in the caudal region (Huene, 1926:pl. 2, figs. 1, 2; Young, 1941:figs. 6, 7). The four principal diapophyseal laminae are strongly developed in the presacral vertebrae of sauropods. Three of the four principal diapophyseal laminae are present in all presacral vertebrae of sauropods, but the fourth (acdl) is replaced in the posterior dorsal vertebrae, where it is bisected by the parapophysis into constituent laminae, the ppdl and acpl. The four principal diapophyseal laminae extend into the caudal region of diplodocids. The anterior caudal vertebrae of *Diplodocus* (Fig. 4; Osborn, 1899:206; McIntosh, 1990a:389) and *Apatosaurus* (Gilmore, 1936:pl. 26), for example, have enlarged transverse processes that are braced by the podl, prdl, acdl, and pcdl. The absence of one or more of the four principal diapophyseal laminae may be diagnostic at lower taxonomic levels. *Titanosaurus colberti*, for example, lacks the prdl in the posterior dorsal region (Jain and Bandyopadhyay, 1997:fig. 9), whereas the dorsal vertebrae of *Opisthocoelicaudia* lack the podl (Salgado et al., 1997b:23, character 31).

The paradiapophyseal lamina (ppdl) and spinodiapophyseal lamina (spdl) are present only in dorsal vertebrae. As with the principal four diapophyseal laminae, the ppdl characterizes saurischian dinosaurs. In *Herrerasaurus* and *Plateosaurus*, the parapophysis rises onto the ventralmost portion of the neural arch in the dorsal vertebrae, forming the terminus of the ppdl (Novas, 1993:fig. 2; Huene, 1926:pl. 2, fig. 2). Although the ppdl appears to be present in most theropods and prosauropods, other parapophyseal laminae are not present in these forms. The ppdl is present in the dorsal region of all sauropods. In sauropods the ppdl forms a well defined strut whose length and orientation varies with the position of the parapophysis. Whereas the parapophyses of theropods and prosauropods are situated near the anterior margin of the neurocentral junction, the parapophysis of sauropods rises to a position adjacent to the prezygapophyses in posterior dorsal vertebrae. Consequently, the form of the ppdl changes from an elongate, vertically oriented strut in the anterior dorsal vertebrae to an abbreviate, horizontally oriented strut in the posterior dorsal vertebrae. Bonaparte (1986:253) noted that all Late Jurassic sauropods but *Diplodocus* lack the ppdl, although this lamina is present in, among others, *Apatosaurus* (Fig. 3), *Dicraeosaurus* (Janensch, 1929: pl. 1), and *Brachiosaurus* (Janensch, 1950:fig. 53).

The spinodiapophyseal lamina has a more restricted distribution among saurischian dinosaurs. It is not present in prosauropods or theropods, and apparently *Shunosaurus* (Zhang, 1988:figs. 30–32). The spdl is present in a subset of sauropods, and diagnoses the clade that includes *Barapasaurus, Omeisaurus*, and Neosauropoda (Wilson and Sereno, 1998:character 60). Salgado, Coria, and Calvo (1997:22, character 30) described the "accessory spino-diapophyseal laminae" as a synapomorphy for a subgroup of titanosaurs that includes *Opisthocoelicaudia, Argentinosaurus*, and an unnamed titanosaur from Peirópolis, Brazil. This lamina is well developed in the posterior dorsal vertebrae of *Opisthocoelicaudia* (Borsuk-Bialynicka, 1977:pl. 1, figs. 6, 7, pl. 3, fig. 3), the lone dorsal vertebra of *Argentinosaurus* figured in anterior view (Bonaparte and Coria, 1993:fig. 2a), and present in dorsal vertebrae 5–8 of the Peirópolis titanosaur (Powell, 1987:pl. 2, figs. 3b, 4b) but absent in the posteriormost dorsal vertebrae (Powell, 1987:pl. 2, fig. 5b). Although its distribution along the vertebral column has not yet been established, this lamina appears to be absent in all other sauropods and characterizes this titanosaur clade.

Parapophyseal Laminae—Three parapophyseal laminae are present in the dorsal vertebrae of sauropod dinosaurs, connecting the parapophysis to the anterior and posterior aspects of the neurocentral junction (acpl, pcpl) and prezygapophysis (prpl).

A lamina buttressing the parapophysis to the anterior portion of the centrum is present in the tenth dorsal vertebra of *Herrerasaurus* but not in other vertebrae (Novas, 1993:fig. 1). This structure, however, is not present in other theropods, such as *Allosaurus* and *Deinonychus* (Madsen, 1976:figs. 89–99; Ostrom, 1969:figs. 33, 34), and is not known to occur in prosauropod dinosaurs. The primitive condition for Saurischia, therefore, is to lack the acpl. The acpl is universally present in the dorsal vertebrae of sauropods, although the condition is unknown in *Vulcanodon* and *Shunosaurus*. Presence of an acpl is an ambiguous synapomorphy of *Barapasaurus, Omeisaurus*, and Neosauropoda, potentially characterizing a more inclusive sauropod subgroup.

A short buttress between the parapophysis and the prezygapophysis (prpl) is present in the dorsal vertebrae of *Barapasaurus* and all other sauropods. This parapophyseal lamina is not present in theropods or prosauropods, nor does it appear to be present in illustrations of the basal sauropod *Shunosaurus* (Zhang, 1988:figs. 31, 32).

The pcpl is the least common parapophyseal lamina. Salgado, Coria, and Calvo (1997:19, character 22) list "presence of centro-parapophyseal lamina in posterior trunk vertebrae" as a titanosaur synapomorphy. Their description of this lamina as passing posteriorly to unite with the "infradiapophyseal" lamina (i.e., the pcdl) implies that they are referring to the posterior centrodiapophyseal lamina (pcpl). In addition to being present in titanosaurs, however, the pcpl is also present in *Brachiosaurus* (Janensch, 1950:fig. 53) and *Euhelopus* (Wiman, 1929:pl. 3, fig. 4, pl. 4, fig. 2), suggesting that it characterizes a slightly more inclusive group (Titanosauriformes). Based on the cladogram in Figure 6, the appearance of the pcpl in *Diplodocus* (Osborn, 1899:fig. 7) and *Apatosaurus* (Gilmore, 1936:pls. 25, 33) is interpreted as an independent acquisition.

Zygapophyseal Laminae—A total of six laminae brace the pre- and postzygapophyses inferiorly (cprl, cpol), superiorly (sprl, spol), and medially (tprl, tpol). With the exception of the two medially oriented laminae, zygapophyseal laminae are well developed in the presacral vertebrae of saurischian dinosaurs. Hyposphene-hypantrum articulations in the dorsal vertebrae appear to preclude the development of the medially directed prezygapophyseal laminae (tprl) because these structures occupy the same location above the neural canal. Wilson and Sereno (1998:character 58) listed presence of the tprl as a synapomorphy uniting *Barapasaurus* and more derived sauropods, but this lamina clearly has a broader distribution, characterizing other saurischians such as *Allosaurus* (Madsen, 1976:pls. 12–15). The tprl and tpol represent synapomorphies of Saurischia. Unlike the tprl, however, the tpol persists in the posterior dorsal vertebrae of some suaropods. In diplodocids, the tpol descends from the hyposphene to the dorsal margin of the neural canal, and has been referred to as the "infrahyposphenalleiste" or "infrahyposphenal lamina" by Janensch (1929, 1950). Upchurch (1995:382) noted that the presence of this "vertical midline lamina . . . supporting the hyposphene" is only characteristic of *Diplodocus* and *Barosaurus* among diplodocids. It appears, however, that these conjoined medial cpol's are also present in *Apatosaurus* (Fig. 3D), suggesting that this feature is a diplodocid synapomorphy.

Spinal Laminae—Prespinal and postspinal laminae are present in several saurischians, but they do not appear to characterize Saurischia in general. The prsl and posl are present in the dorsal vertebrae of several theropods, including *Carnotaurus* (Bonaparte et al., 1990:figs. 15, 17, 19), *Allosaurus* (Madsen, 1976:figs. 14–20), *Baryonyx* (Charig and Milner, 1997:figs. 22–26), and *Deinonychus* (Ostrom, 1969:fig. 34). The basal theropods *Eoraptor* and *Herrerasaurus*, however, lack them (Novas, 1993:fig. 1; Sereno and Novas, 1993:fig. 12), suggesting that the prsl and posl are neotheropod synapomorphies. Salgado, Coria, and Calvo (1997:12) listed "presence of medial [sic] prespinal lamina in posterior trunk vertebrae" as a synapomorphy of Titanosauriformes (*Brachiosaurus* + Titanosauria). The lamina they refer to (1997:fig. 6), however, is a composite structure composed of the prsl and conjoined sprl's. This hybrid lamina is present in titanosauriforms and in diplodocoids and must be considered convergently acquired based on the evolutionary relationships of sauropod dinosaurs presented in Figure 6.

Divided and Composite Laminae—In several sauropods, individual laminae may be divided into medial and lateral sublaminae. Occasionally, these divided laminae join other laminae to form unique combinations of laminae (i.e., composite laminae). All divided laminae are zygapophyseal laminae. At least four divided and composite laminae are unique to clades within Sauropoda.

The spol is divided into medial and lateral sublaminae in the dorsal vertebrae of *Barapasaurus, Omeisaurus*, and neosauropods. The medial spol's are close to the midline and form a prominent buttress on the posterior aspect of the neural spine. The lateral spol courses anteriorly to meet the spdl midway up the neural spine to form composite lateral lamina. This feature does not appear to be present in *Shunosaurus* (Zhang, 1988: figs. 31, 32), is unknown in *Vulcanodon*, and is not present in theropods or prosauropods.

Diplodocid sauropods are characterized by one divided lamina and one composite lamina. Dorsal vertebrae of *Apatosaurus*, for example, have a divided cprl (Upchurch, 1995:381). This divided lamina does not merge with other laminae to form a composite lamina.

Anterior caudal vertebrae of diplodocoids are characterized by a pronounced lamina on the lateral aspect of the neural spine. This strut is a composite lamina formed by the conjoined sprl and spol. In *Apatosaurus* and *Diplodocus* the sprl and spol form a prominent lateral lamina in the first nine caudal vertebrae (Gilmore, 1936:pl. 26; Osborn, 1899:fig. 13). In subsequent caudal vertebrae, the sprl and spol do not contact and occupy a more median position in the neural spine. In dicraeosaurids, the sister group to diplodocids, a prominent lateral lamina is present in the first five caudal vertebrae, but this lamina is composed solely of the sprl (*Dicraeosaurus*, Janensch, 1929: pl. 3). Anterior caudal vertebrae are not known in other non-diplodocid diplodocoids (e.g., *Amargasaurus, Rebbachisaurus*). Upchurch (1995:381) noted that "complex lamination is found in the anterior caudal neural spines" of diplodocids and dicraeosaurids (i.e., Diplodocoidea). Although it does appear that diplodocoids are unique in possessing a prominent lamina on the lateral aspect of the neural spines of anterior caudal vertebrae, composition of this lamina is slightly different in each family. In diplodocids, the lateral lamina is hybrid, consisting of the sprl and the spol, whereas in dicraeosaurids it is made up entirely by the sprl. Among diplodocids, *Diplodocus* (Osborn, 1899:fig. 12) and *Barosaurus* (Lull, 1919:23, pl. 5, fig. 1) are characterized by the presence of the tprl on the neural arches of the anterior caudal vertebrae.

Upchurch (1995:371) listed "complex lamination on the anterior and middle cervical neural spines" and "prominent lamination on dorsal neural spines" as synapomorphies for all sauropods more derived than *Vulcanodon* (i.e., Eusauropoda). Although it is tempting to characterize sauropod vertebral laminae as simply more complex than those of their closest relatives, there are several factors that contribute to this notion. First, four novel laminae (spdl, acpl, prpl, spdl + lat. spol) characterize a major subgroup of sauropods (*Barapasaurus* + *Omeisaurus* + Neosauropoda). Second, sauropod vertebral laminae are much more prominent and enclose deeper fossae than those of either theropods or prosauropods. Third, vertebral laminae have a broader distribution within the axial column in sauropods. Whereas they are most pronounced in the dorsal region of theropods and prosauropods, laminae are present in the cervical region of all sauropods and in the caudal region in some (diplodocids). Thus, a combination of features contributes to the complexity of sauropod vertebral laminae: four novel laminae, pronounced laminae with deeply excavated fossae, and more extensive lamination of the vertebral column.

FUNCTIONAL SIGNIFICANCE OF VERTEBRAL LAMINAE

Vertebral laminae have been interpreted as either: 1) structural elements for resisting stress generated by the elongate neck and enormous thorax in sauropods; or 2) osseous septa of pneumatic chambers. The structural interpretation of vertebral laminae forwarded by Phillips (1871), Osborn (1899), McIntosh (1989), and others is a plausible but currently unsubstantiated argument. Laminae are interpreted as structural elements because they reduce weight and appear to be aligned along the principal axes of stress on the neural arch. To date, however, no study has evaluated the discrepancy in forces safely supported in laminate and non-laminate vertebrae.

Seeley (1870) first interpreted the complex lamination in sauropod vertebrae as evidence of axial pneumaticity (see also Romer, 1966). Britt (1993, 1997), who first examined the axial skeleton of living birds to identify osseous correlates of axial pneumaticity, listed five features for identifying pneumaticity: large foramina, fossae with crenulate texture, thin outer walls, smooth or crenulate tracks (grooves), and internal chambers (with foramina). Of these features, deep fossae and thin outer walls are present in most sauropod neural arches, whereas the presence of large foramina (coels) within fossae is pronounced in some sauropods (e.g., *Brachiosaurus*, Janensch, 1950:figs. 20–29). An additional feature that may further support the interpretation of sauropod vertebrae as pneumatic is the presence of small, circular "subfossae" within the fossae enclosed by vertebral laminae. These well defined, smooth-walled depressions are present in many sauropods and seem to be analogous to the more pronounced coels that characterize *Brachiosaurus*. Like the coels, these depressions may have housed smaller pneumatic diverticuli in life. Thus, arguments for vertebral laminae as osseous correlates of axial pneumaticity or as supportive elements seem compelling. Are either or both of these functional interpretations better supported? The sequence of acquisition of vertebral laminae among saurischians may shed light on the functional significance of these structures.

The basic pattern of vertebral lamination is present in the earliest saurischians, 25 million years before the appearance of the sauropods with long necks. The asynchronous appearance of vertebral laminae and long necks, as well as the persistence of laminae in small and relatively short-necked theropods argues against a strictly structural interpretation (Fig. 6). The origin of vertebral laminae, then, may be better explained as a correlate of axial pneumaticity in saurischians, bounding negative space filled by pneumatic diverticuli. The orientation of vertebral laminae, however, is nearly invariant across Saurischia, which suggests that they functioned as structural supports. Thus, although the principal function of vertebral laminae may have been to partition pneumatic diverticuli on the neural arch and centrum, they may have fulfilled a secondary role as supportive elements for the neck and trunk. Moreover, the increase in laminar complexity and the appearance of four novel laminae early in sauropod evolution implies an important structural role (Fig. 6). The arrangement of vertebral laminae on the neural arch may reflect stresses generated by muscle tendons (tendinous stresses) or between bones (ligamentous stresses) during development, as is often the case with trabeculae in the bone of living animals (Herring, 1993; Carter et al., 1998). Study of the internal structure of vertebral laminae in saurischians is needed.

CONCLUSIONS

Nineteen vertebral laminae are described and defined on the basis of morphological landmarks. A revised system of nomenclature, along with a corresponding set of four-letter abbreviations, provides a standard set of terms for describing vertebral laminae in saurischian dinosaurs. The distribution of vertebral laminae suggests a basic pattern of vertebral lamination in the presacral vertebrae characterized saurischian dinosaurs that included five diapophyseal laminae and six zygapophyseal laminae. This pattern was established early in dinosaur evolution, by the Late Triassic.

Although this basic lamination pattern is present in all saurischians, vertebral laminae are best developed in sauropod dinosaurs. Four additional laminae (one diapophyseal and three parapophyseal laminae), a divided lamina, and a composite lamina are present in *Barapasaurus* and all more derived sauropods. Diplodocid sauropods are characterized by a unique pattern of vertebral laminae in the caudal region as well as divided zygapophyseal laminae in the dorsal region. In general, vertebral laminae in sauropod dinosaurs appear to be fairly conservative, with most variation occurring at low taxonomic levels.

Vertebral laminae were probably osseous partitions between pneumatic cavities in the axial column of saurischian dinosaurs. Their early appearance in small, bipedal theropods 25 million years before the first known sauropod suggests that the origin of vertebral laminae was not driven by the extreme loads imposed on the axial column of large sauropods. The increased number and complexity of vertebral laminae, however, may reflect their increasing importance as structural supports in sauropod dinosaurs.

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