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NEW VERTEBRAL LAMINAE AND PATTERNS OF SERIAL VARIATION IN VERTEBRAL LAMINAE OF SAUROPOD DINOSAURS

BY

JEFFREY A. WILSON¹

Abstract — Vertebral laminae connect various projections on the neural arch (costovertebral and intervertebral articulations, neural spine) and centrum of the presacral, sacral, and anterior caudal vertebrae of sauropods and other saurischian dinosaurs. The nomenclature applied to vertebral laminae is based on the landmarks they connect. Along the vertebral series and especially through regional transitions (e.g., cervical-dorsal), the landmarks anchoring laminae vary in their relative positions. As a result, vertebral laminae change serially in shape and orientation, and some may be restricted to certain vertebral regions. Without complete vertebral series, however, understanding this variation can prove difficult and can lead to misidentification of serial variation as an interspecific or higher-level difference. Here I review recently recommended changes in laminar nomenclature and describe two patterns of serial variation bracketing laminae that have a restricted distribution in the vertebral column. I term these patterns ‘lamina capture’ and ‘lamina cutoff.’ Patterns of serial variation of vertebral laminae can be coded as cladistic characters in phylogenetic analysis.

INTRODUCTION

Vertebral laminae are bony struts that connect major projections on the neural arch and centrum of saurischians and various other tetrapods (Wilson, 1999; Gower, 2001). They provide structural support for the projections of the neural arch, and sets of laminae enclose spaces that housed air sacs in life (Britt, 1993; Wedel, 2003). Vertebral regions are defined by the nature of their ribs (e.g., thorax = ribs contact sternum; sacrum = ribs contact ilium), which means that transitions between vertebral regions are characterized by substantial changes in the position of the rib articulations and their attendant vertebral laminae. The laminae of sauropod vertebrae have long been recognized to be complex (e.g., Seeley, 1870; Phillips, 1871; Hulke, 1880). Variation in the arrangement of vertebral laminae is apparent at very fine levels, such as on right and left sides of the same vertebra (Fig. 1) or along the vertebral series of a single individual (Fig. 2), and variation is also evident at individual, specific, generic, and suprageneric levels.

The earliest nomenclature for vertebral laminae appeared at the close of the nineteenth century (Osborn, 1899). Despite the ambiguity of the terms (e.g., ‘oblique lamina,’ ‘horizontal lamina’), they were commonly employed in English-language descriptions of sauropods until late in the twentieth century, particularly those describing sauropods from the Morrison Formation of the western United States (e.g., Hatcher, 1901). Janensch (1929) proposed a far more practical, landmark-based nomenclature for vertebral laminae that never gained currency in the literature, despite partial adoption by McIntosh (1990). A century after Osborn (1899), Wilson (1999) proposed a nomenclature for laminae that, like Janensch’s, is landmark-based. Nineteen laminae, organized into four major groups (i.e., diapophyseal, parapophyseal, zygapophyseal, spinal), are specified by seven landmarks (i.e., diapophysis, parapophysis, prezygapophysis, postzygapophysis, neural spine, anterior and posterior centrum). Each lamina can be described with a four-letter acronym based on the landmarks and major groupings. For example, the lamina connecting the neural spine and

¹Museum of Paleontology and Department of Earth & Environmental Sciences, University of Michigan, 1109 Geddes Avenue, Ann Arbor, Michigan 48109-1079, U.S.A. (wilsonja@umich.edu)

postzygapophysis is the spinopostzygapophyseal lamina. Because it is classified as a postzygapophyseal lamina (-pol), its acronym is 'spol.'

Reliance on landmarks provides a topological framework within which 'primary homologues' (de Pinna, 1991) can be identified and later determined to be synapomorphy, symplesiomorphy, or homoplasy by congruence with other characters (Patterson, 1982). Within this context, identification of a particular vertebral lamina (e.g., the spinoprezygapophyseal lamina) relies only on the identification of landmarks it joins (viz., neural spine, prezygapophysis), regardless of whether we are comparing different vertebrae of a single individual (i.e., serial homologues) or equivalent vertebrae of different individuals (i.e., primary homologues). The sequence of serial variants that precede or succeed a particular lamina has no bearing on its identification, but these morphological intermediates can themselves be employed as character data (Cracraft, 2005).

In this contribution, I discuss some recently suggested changes to the nomenclature for vertebral laminae and describe two patterns of serial variants that bracket regionally-restricted laminae. I term these 'lamina capture' and 'lamina cutoff.' Some of the terms and laminae discussed in this contribution are explained in Tables 1 and 2.

INSTITUTIONAL ABBREVIATIONS

BYU	— Brigham Young University, Provo, Utah, U.S.A.
CPP	— Centro de Pesquisas Paleontológicas Lewellyn Price, Peirópolis, Brazil.
MB	— Museum für Naturkunde der Humboldt-Universität zu Berlin, Berlin, Germany.
MCT/DNPM	— Museu de Ciências da Terra, Departamento Nacional de Produção Mineral, Rio de Janeiro, Brasil.
MNHN	— Muséum Nationale d'Histoire Naturelle, Paris, France.
MNN	— Musée National du Niger, Niamey, Niger.
SM	— Sirindhorn Museum, Phu Kum Kao, Kalasin Province, Thailand.

PROPOSED MODIFICATIONS TO THE NOMENCLATURE FOR VERTEBRAL LAMINAE

Several modifications have been proposed, either implicitly or explicitly, to the nomenclatural system for vertebral laminae developed by Wilson (1999). These include descriptions of new laminae, new types of laminae, changes to terminology to comply with *Nomina Anatomica Avium* and *Nomina Anatomica Veterinaria* (NAA, NAV), and suggested reorganization of higher groupings of laminae, all of which are discussed below.

New Laminae

The terminology developed by Wilson (1999) provided enough detail to characterize most of the laminae observed in

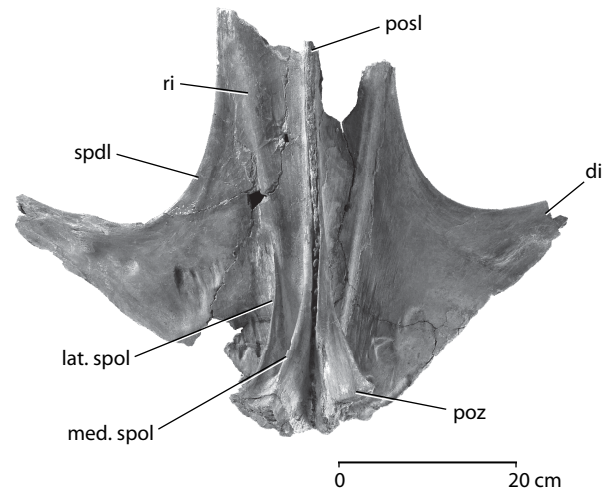


FIGURE 1 — Left-right asymmetry in vertebral laminae. Partial dorsal neural arch of *Rebbachisaurus garasbae* (MNHN-MRS 1980) in posterior view. Note the difference in arrangement of the laminae associated with the left and right postzygapophyses. Abbreviations: *di*, diapophysis; *lat. spol*, lateral spinopostzygapophyseal lamina; *med. spol*, medial spinopostzygapophyseal lamina; *posl*, postspinal lamina; *poz*, postzygapophysis; *ri*, ridge; *spdl*, spinodiapophyseal lamina.

saurischian vertebrae. However, several new laminae have been proposed since then. Some of these were given new, landmark-based names, and some simply were referred to as 'accessory laminae.'

Epipophyseal-prezygapophyseal lamina (eprl).— In saurischians that have large cervical epipophyses, there sometimes exists a prominent lamina that connects them to the prezygapophyses. Bonaparte (1996: 90) first recognized this feature in cervical vertebrae of the abelisaur *Noasaurus* and *Carnotaurus*, in which the "dorsal border of the epipophysis continues anteroposteriorly and make[s] a conical process at some distance behind the prezygapophysis. A very distinct dorsal plane is distinguished from a lateral, almost vertical plane." This feature was recognized in other theropods (Coria and Salgado, 2000; Carrano et al., 2002; O'Connor, 2007) and only later identified in sauropods (e.g., Sereno et al., 2007; Wilson and Upchurch, 2009). Bonaparte (1996) did not name this lamina, which later received different names from different authors: 'prezygo-epipophyseal lamina' ('pel,' Coria and Salgado, 2000), 'prezygoepipophyseal lamina' ('prel,' O'Connor, 2007; Ezcurra et al., 2010; Dal Sasso and Maganuco, 2011; Pol and Rauhut, 2012), 'prezygapophyseal-epipophyseal lamina' ('prezpl,' Sereno et al., 2007), and the 'epipophyseal-prezygapophyseal lamina' ('eprl,' Wilson and Upchurch, 2009; Ksepka and Norell, 2010; Whilock, 2011; Haluza et al. 2012; Mannion et al., 2012). Recently Salgado et al. (2012) described this as the 'post-prezygapophyseal lamina' ('pz-przl-1'), suggesting that the lamina connects to the postzygapophysis, not the epipophysis. In many theropods the epipophysis and postzygapophysis are positionally distinct, and their associated laminae are easily

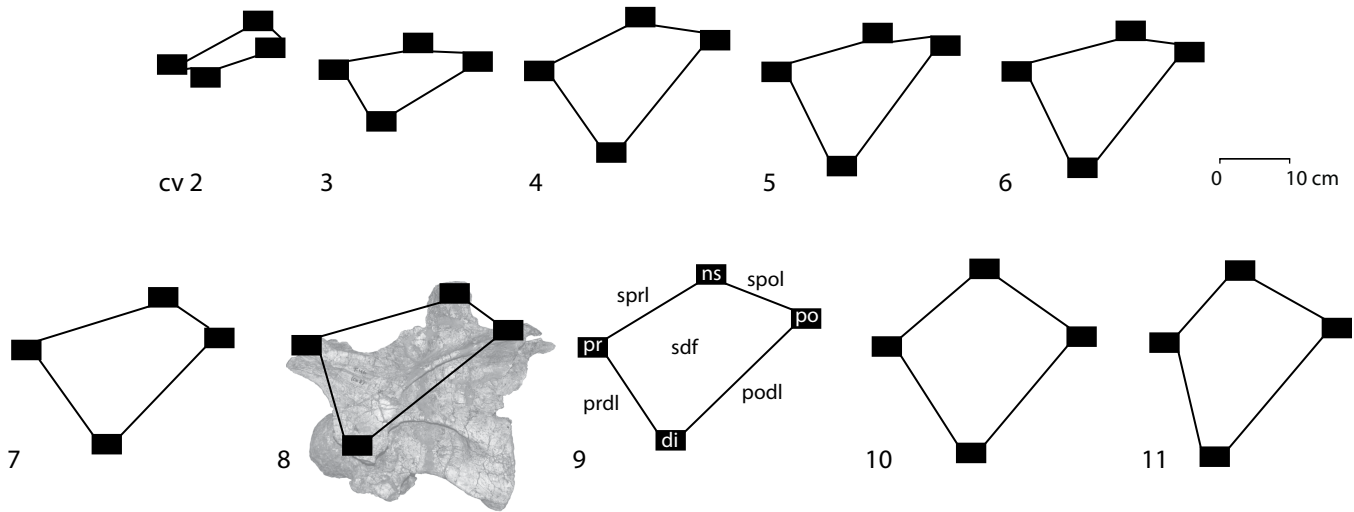


FIGURE 2 — Migration of four neural arch landmarks across an articulated series of 10 cervical vertebrae of *Jobaria tiguidensis* (Sereno et al., 1999; MNN-TIG-6), resulting in changes in orientation of vertebral laminae, as well as in the pneumatic spaces they enclose. The schematic shows four neural landmarks in left lateral view with shortest line between them indicating the position of laminae. The course of the actual laminae may be curved, as in the exemplar vertebra shown (cervical 8). Vertebrae have been aligned horizontally by the prezygapophysis. Abbreviations: *cv*, cervical vertebra; *di*, diapophysis; *ns*, neural spine; *po*, postzygapophysis; *podl*, postzygodiapophyseal lamina; *pr*, prezygapophysis; *prdl*, prezygodiapophyseal lamina; *sdf*, spinodiapophyseal fossa; *spol*, spinopostzygapophyseal lamina; *sprl*, spinoprezygapophyseal lamina.

distinguished from one another. In contrast, in sauropods those structures are much closer to one another and as a consequence, it can be difficult to distinguish between a lamina connecting to the epipophysis and one connecting to the postzygapophysis. In well preserved sauropods (e.g., *Nigersaurus*; Fig. 3), the lamina extends to the epipophysis, but in less well preserved taxa and in portions of the cervical series where the epipophysis is reduced, this is less clear. I suggest that we identify only a single lamina unless it can be demonstrated that there are two distinct laminae in sauropods, one connecting the prezygapophysis and epipophysis and another connecting the prezygapophysis and postzygapophysis.

The earliest-suggested term, ‘prezygo-epipophyseal lamina’ (‘pel’), does not fit into the nomenclatural system established by Wilson (1999), which was designed to be interpretable from either the name or the four-letter acronym. There are no epipophyseal laminae (‘el’) and there is no ‘p’ landmark. The ‘prezygo-epipophyseal lamina’ (‘prel’) and ‘prezygapophyseal-epipophyseal lamina’ (‘prepl’) are also inconsistent with that nomenclatural framework for the same reasons. Although consistency is not a requirement for anatomical terminology (see e.g., Wilson, 2006), it is a benefit. Inconsistent terminology is a disadvantage in systems designed to be interpretable forwards and backwards. In this way they are like languages, which have regular and irregular verbs. Regular verbs are much easier to conjugate than irregular verbs, whose conjugations must be memorized. Long standing in the literature might be viewed as one justification for maintaining an ‘irregular’ term, but in this case, none of the terms has achieved currency, as indicated by the references cited above. Thus there is an opportunity to use a regular term that fits

with the system, and I recommend using the term ‘epipophyseal-prezygapophyseal lamina’ (‘eprl’) for the lamina connecting the epipophysis and prezygapophysis. It requires the most minor modification of the laminar system, which is the addition of the epipophysis (‘ep’) as a landmark. The eprl is a zygapophyseal lamina, and the four-letter acronym is preserved.

Centroparapophyseal laminae in cervical vertebrae.— In their description of the holotypic cervical vertebrae of *Sauroposeidon proteles*, Wedel et al. (2000: 111) identified “centroparapophyseal laminae” that “extend from the parapophysis to the posterior end of each vertebra” and form a sharp edge along the ventrolateral margin of the centrum. This feature was highlighted in the diagnosis of that species. A similar feature is present on the ventrolateral edge of the centrum in other titanosauriforms such as *Euhelopus* (Fig. 4; Wilson and Upchurch, 2009). Apart from its variation and phylogenetic distribution, which are of interest (see D’Emic, in press), is this structure a vertebral lamina?

One of the characteristics of vertebral laminae, as discussed above, is that their orientation and shape covary serially with changes in position of their constituent landmarks (Fig. 2). Most vertebral laminae are thin plates of bone, but this is not a diagnostic feature—there are other thin plates of bone on the vertebra that are either not considered laminae or not named structures (e.g., rim of the pleurocoel, keel on ventral centrum, cotylar rim, bony strut dividing pleurocoel). They do not contact landmarks or they are ephemeral structures that do not maintain a consistent relationship to landmarks.

The parapophysis displays perhaps the most substantial positional variation in the sauropod vertebral column. Across the

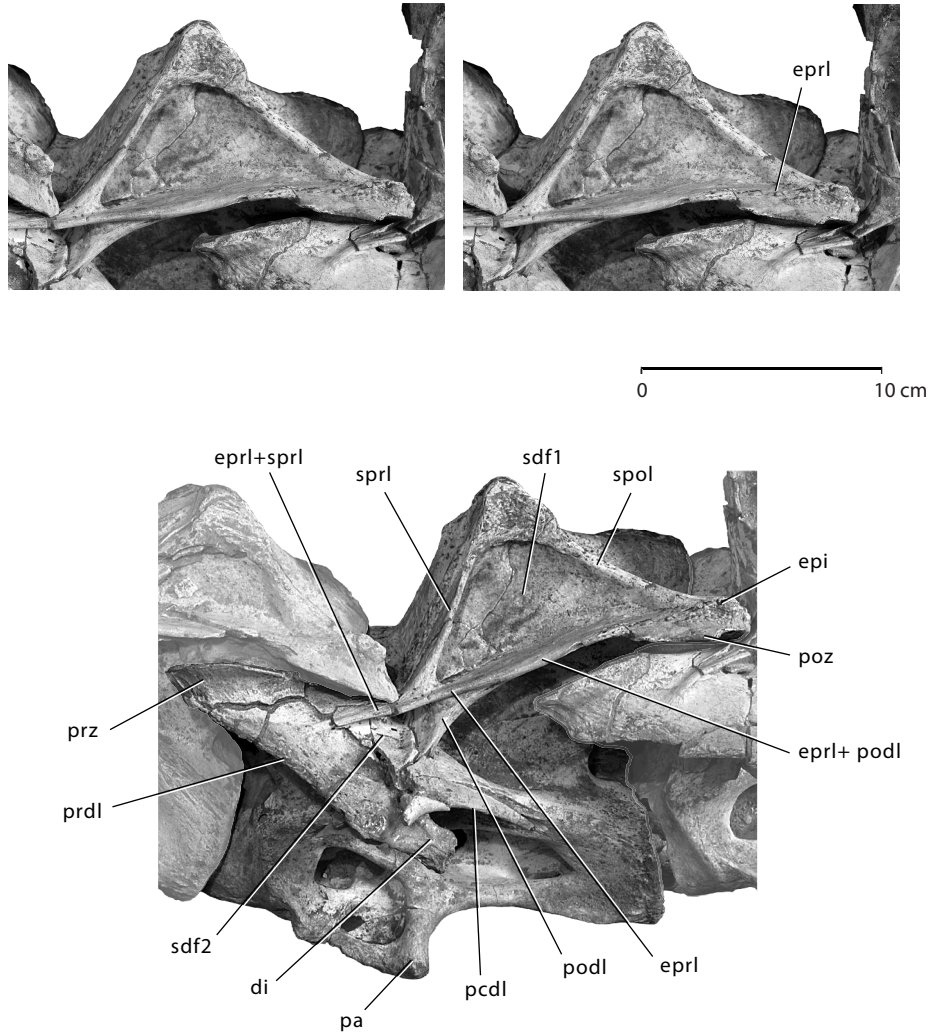


FIGURE 3 — Epipophyseal-prezygapophyseal lamina in cervical vertebrae of *Nigersaurus taqueti* (MNHN unnumbered) in left lateral view. The two partial vertebrae have been masked with a tone in the lower image. The stereopairs above show only the neural arch, in which the epipophyseal-prezygapophyseal lamina extends to the epipophysis. Abbreviations: *di*, diapophysis; *epi*, epipophysis; *epri*, epipophyseal-prezygapophyseal lamina; *pa*, parapophysis; *pcdi*, posterior centrodiapophyseal lamina; *podri*, postzygodiapophyseal lamina; *poz*, postzygapophysis; *prdi*, prezygodiapophyseal lamina; *prz*, prezygapophysis; *sdf1*, *sdf2*, spinodiapophyseal fossae 1 and 2; *spol*, spinopostzygapophyseal lamina; *spri*, spinoprezygapophyseal lamina.

span of a few cervicodorsal vertebrae, the parapophysis occupies a progressively more elevated position, starting at the ventrolateral edge of the anterior centrum and ending at a position between the diapophysis and prezygapophysis on the neural arch. Laminae that contact the parapophysis across parts of this span maintain contact with both landmarks (e.g., paradiapophyseal lamina). In contrast, the structure that Wedel et al. (2000) identified as a centroparapophyseal lamina does not migrate with the parapophysis across this transition. In sauropods that have complete presacral series (e.g., *Euhelopus*), the parapophysis does not retain a connection to the ventrolateral edge of the centrum in anterior dorsal vertebrae, in which the parapophysis is still located on the centrum. This structure is nonetheless in-

teresting because it varies within sauropods, in which it can be absent or rounded, developed as a sharp crest, or hypertrophied into a pendant flange.

Anterior and posterior spinodiapophyseal laminae (ant. spdl, post. spdl).— Divided laminae are not uncommon in sauropod dinosaurs, and occasionally they are used in diagnoses of genera or of higher-level groups. As summarized elsewhere (Wilson et al., 2011), there are numerous examples: the centroprezygapophyseal lamina is divided in diplodocoids and *Mamenchisaurus* (Wilson, 2002), the centropostzygapophyseal lamina is divided in some vertebrae of *Camarasaurus* and *Argentinosaurus* (Wilson and D’Emic, unpublished), the spinopostzygapophyseal lamina is divided in *Barapasaurus* and more derived sauropods (Wilson

and Sereno, 1998), and the posterior centrodiapophyseal lamina is divided in some vertebrae of *Saltasaurus* (Wilson and D’Emic, unpublished).

Salgado and Powell (2010) recently discussed nomenclature of vertebral laminae considering partial presacral series of several titanosaur sauropods (i.e., *Epachthosaurus*, *Barrosasaurus*, *Trigonosaurus*). They observed that the spinodiapophyseal lamina (spdl) appears to be divided in mid-dorsal vertebrae of *Epachthosaurus*, which was recognized in the description of Martínez et al. (2004), as well as in *Trigonosaurus* and *Barrosasaurus*. Although Salgado and Powell (2010: 1761) observed that in some vertebrae the spdl appears to be “a single, distally divided lamina,” in others the two rami are completely separated from one another. Salgado and Powell (2010) recognized the two rami of the spdl as distinct laminae: the anterior spinodiapophyseal lamina (‘aspdl’) and posterior spinodiapophyseal lamina (‘pspdl’). Although these have the same landmarks (i.e., diapophysis, neural spine), they attach to slightly different parts of the neural spine.

The nomenclatural issue here is whether these rami are (a) independent laminae that can be distinguished from the parent lamina (i.e., spinodiapophyseal lamina) and from each other when only one of the rami is present on a vertebra, or (b) dependent laminae that are treated as parts of a single lamina. In the former case, each independent lamina would receive its own landmark-based name. In the latter case, the rami take the name for the parent lamina (i.e., spdl) plus a positional specifier (e.g., ‘ant.’). I suggest that the two rami of the spdl discussed by Salgado and Powell (2010) are dependent laminae, because they require each other’s presence for identification. Where only one lamina is present between the diapophysis and neural spine, it must be identified as the spinodiapophyseal lamina; if two are present, then the positional distinctions allow their discrimination (i.e., ‘ant. spdl,’ ‘post. spdl’). These laminae should be treated as variants of the spinodiapophyseal lamina (Table 1) rather than as independent laminae with unique abbreviations (i.e., ‘aspdl,’ ‘pspdl’). This mirrors treatment of the spinopostzygapophyseal lamina, which in *Barapasaurus* and more derived sauropods is divided into medial and lateral rami that are called ‘med. spol’ and ‘lat. spol’ (Wilson, 1999).

Recognition of these as divided spinodiapophyseal laminae rather than independent laminae also affects the nomenclature for the fossa separating them. The fossa within the divided spinodiapophyseal lamina is the spinodiapophyseal lamina fossa (spdl-f; see Wilson et al., 2011: 7).

Spinoparapophyseal lamina.— Taylor (2009) described a spinoparapophyseal lamina in a dorsal vertebra of *Giraffatitan brancai* (for taxonomic discussion of *Brachiosaurus* and *Giraffatitan*, see also D’Emic, 2011). This new lamina was regarded by Taylor (2009: 792) as an autapomorphy “distinct from the ‘accessory spino-diapophyseal lamina’ (ASDL) of Salgado et al. (1997:22-23),” which Salgado and Powell (2010: 1762) later renamed the ‘anterior spinodiapophyseal lamina’ (see above). Identification of a spinoparapophyseal lamina in *Giraffatitan* is ambiguous because the costal processes are not preserved on the one dorsal vertebra upon which Taylor (2009) based his claim, and because other *Giraffatitan* dorsal vertebrae (and those of

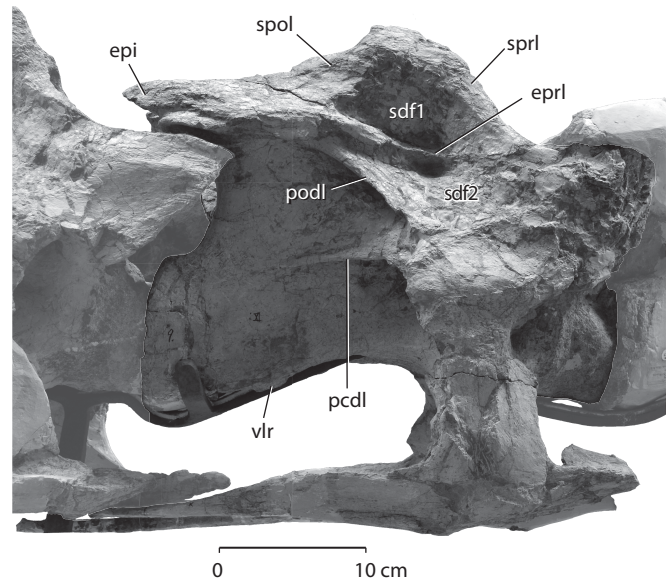


FIGURE 4—Cervical vertebra 10 of *Euhelopus zdanskyi* (PMU 233) in right lateral view. Cervical vertebra 9 and 11 have been masked with a tone. Abbreviations: *epl*, epipophysis; *epri*, epipophyseal-prezygapophyseal lamina; *pccl*, posterior centrodiapophyseal lamina; *podl*, postzygodiapophyseal lamina; *sdf1*, *sdf2*, spinodiapophyseal fossae 1 and 2; *spol*, spinopostzygapophyseal lamina; *sprl*, spinoprezygapophyseal lamina; *vlr*, ventrolateral ridge.

other titanosauriforms) suggest the lamina in question may be a serial variant of the anterior spinodiapophyseal lamina. Although not likely present in *Giraffatitan*, a spinoparapophyseal lamina (*sppl*) is present in the rebbachisaurids *Rebbachisaurus* (Wilson and Allain, in preparation) and *Nigersaurus* (pers. obs.).

Taylor (2009) identified a spinoparapophyseal lamina on a single dorsal vertebra of *Giraffatitan* (MB.R. 2181.87), which he regarded as the eighth dorsal vertebra (i.e., 20th presacral of Janensch, 1950: figs. 56, 57). In that dorsal vertebra, the transverse processes are broken near their base, and the parapophyses and diapophyses are not preserved (Fig. 5). Identification of a spinoparapophyseal lamina by Taylor (2009) was based on interpretation of the three paired laminae or lamina-like structures that lie dorsal to the ‘table’ made by the zygapophyses, diapophyses, and their interconnecting laminae. The first is a spinodiapophyseal lamina, which forms the lateral edge of the neural spine and extends between the triangular lateral process of the neural spine and the posterodorsal surface of the transverse process. The second is a transversely-oriented structure that extends between the anterodorsal surface of the transverse process and the base of the neural spine, ending abruptly at an intersection with the third structure, which is vertically oriented. In anterior view, the intersection between the second and third structures is asymmetrical: on the left side, the intersection is positioned higher than it is on the right (Fig. 5). It is the identity of these latter two structures that requires resolution.

The vertical paramedian structures closely resemble the paired spinoprezygapophyseal laminae present in more anterior

TABLE 1 — Abbreviations and morphological landmarks for 27 vertebral laminae discussed in this contribution. Laminae have been grouped by region, with the costal laminae listed first (diapophyseal laminae, *DL*; parapophyseal laminae, *PL*), followed by the zygapophyseal laminae (prezygapophyseal laminae, *PRL*; postzygapophyseal laminae, *POL*) and spinal laminae (*SL*). Modified from Wilson (1999: table 2).

	Lamina	Abbreviation	Landmarks
DL (8)	Anterior centrodiaepophyseal	acd1	Diapophysis; anterior margin of neurocentral junction (lateral aspect)
	Posterior centrodiaepophyseal	pcdl	Diapophysis; posterior margin of neurocentral junction (lateral aspect)
	Prezygodiaepophyseal	prdl	Diapophysis; prezygapophysis
	Spinodiaepophyseal	spdl	Diapophysis; neural spine
	Anterior spinodiaepophyseal	ant. spdl	Diapophysis; neural spine (anterior aspect)
	Posterior spinodiaepophyseal	post. spdl	Diapophysis; neural spine (posterior aspect)
	Postzygodiaepophyseal	podl	Diapophysis; postzygapophysis
	Paradiaepophyseal	ppdl	Diapophysis; parapophysis
PL (4)	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
	Spinoparapophyseal	sppl	Parapophysis; neural spine
PRL (6)	Centroprezygapophyseal	cp1	Prezygapophysis; anterior margin of neurocentral junction (anterior aspect)
	Medial centroprezygapophyseal	med. cp1	Prezygapophysis; dorsal median margin of neural canal (posterior)
	Lateral centroprezygapophyseal	lat. cp1	Prezygapophysis; posterior margin of neurocentral junction (lateral aspect)
	Spinoprezygapophyseal	sp1	Prezygapophysis; neural spine (anterior aspect)
	Epipophyseal-prezygapophyseal	ep1	Prezygapophysis; epipophysis
	Intraprezygapophyseal	tp1	Prezygapophysis; dorsal median margin of neural canal (anterior)
POL (7)	Centropostzygapophyseal	cpol	Postzygapophysis; posterior margin of neurocentral junction (posterior aspect)
	Medial centropostzygapophyseal	med. cpol	Postzygapophysis; dorsal median margin of neural canal (posterior)
	Lateral centropostzygapophyseal	lat. cpol	Postzygapophysis; posterior margin of neurocentral junction (lateral aspect)
	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)
SL (2)	Prespinal	prsl	Neural spine base (anterior); neural spine summit (anterior)
	Postspinal	posl	Neural spine base (posterior); neural spine summit (posterior)

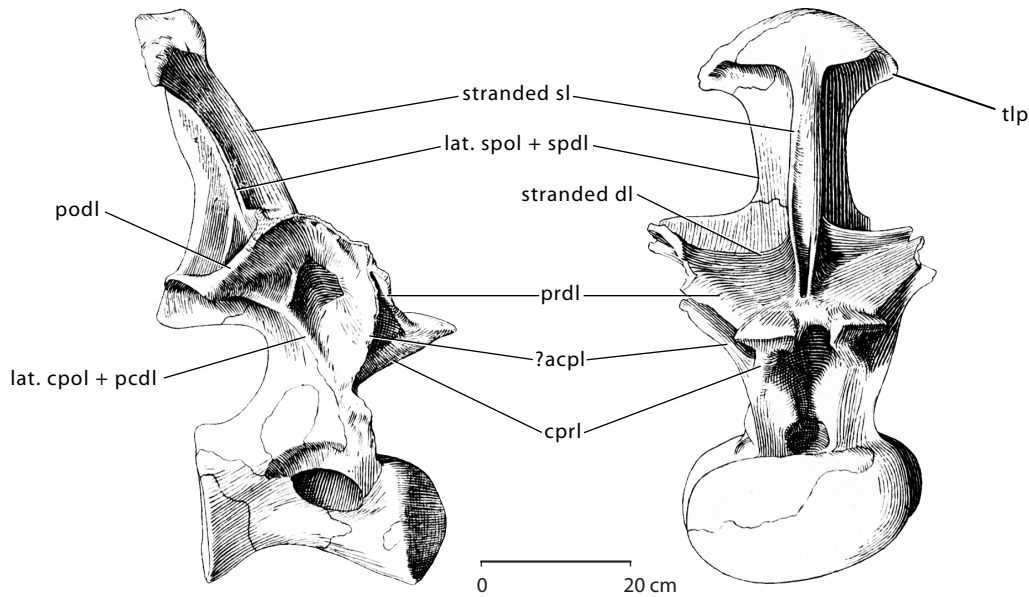


FIGURE 5 — Dorsal vertebra of *Giraffatitan brancai* (MB.R. 2181.87) in right lateral and anterior views. Modified from Janensch (1950: figs 56-57). The stranded spinal and diapophyseal laminae were identified as a spinoparapophyseal lamina by Taylor (2009), but they are here interpreted as an incipient anterior spinodiapophyseal lamina, which is present in succeeding vertebrae (Fig. 6). Identification of some of the diapophyseal and parapophyseal laminae are ambiguous because the transverse processes are not completely preserved. The scale bar was added based on proportional information in the original figure caption. Abbreviations: *acpl*, anterior centroparapophyseal lamina; *cppl*, centroprezygapophyseal lamina; *dl*, diapophyseal lamina; *lat. cpol*, lateral centropostzygapophyseal lamina; *lat. spol*, lateral spinopostzygapophyseal lamina; *pcpl*, posterior centrodiapophyseal lamina; *podl*, postzygodiapophyseal lamina; *prdl*, prezygodiapophyseal lamina; *sl*, spinal lamina; *spdl*, spinodiapophyseal lamina; *tlp*, triangular lateral process.

presacral vertebrae (e.g., Janensch, 1950: figs. 43, 51), save one important difference — their bases do not reach the prezygapophyses. Instead, they end abruptly at the base of the neural spine. I call these structures ‘stranded’ spinal laminae because they contact one landmark (i.e., the neural spine) but the other landmark is ambiguous. Stranded laminae are usually serially variants of laminae that connect to two landmarks (see Table 2). Because the transversely-oriented lamina terminates in an intersection with the ‘stranded’ spinal lamina rather than with a landmark, it too is a stranded lamina. However, because the transverse process is broken in MB.R. 2181.87, its one connection to either the diapophysis or the parapophysis cannot be unambiguously determined. Other vertebrae in the series, however, suggest that it is a stranded diapophyseal lamina. In a more posterior dorsal vertebra of the same specimen (MB.R. 2181.89), serial homologues of the stranded spinal and diapophyseal laminae form a continuous lamina that extends between the anterior neural spine and the diapophysis (Fig. 6). This lamina does not contact the parapophysis, and so it cannot be a spinoparapophyseal lamina. It is instead a second spinodiapophyseal lamina, which is positioned anterior to the other and can be referred to as the anterior spinodiapophyseal lamina.

A similar pattern of serial variation in laminae of dorsal vertebrae is present in other sauropod taxa. For example, the topotypic posterior dorsal vertebra of the titanosauriform *Phuwiangosaurus sirindhornae* has both anterior and posterior spinodi-

apophyseal laminae (Suteethorn et al., 2010: fig. 1). Although Suteethorn et al. labeled the more anterior of these the “spino-prezygapophyseal lamina” in figures, they correctly identified it as a spinodiapophyseal lamina in text, noting “the spinoprezygapophyseal lamina becomes progressively modified to act as an accessory [i.e., anterior] spinodiapophyseal lamina” (Suteethorn et al., 2010: 114). As discussed below, in *Phuwiangosaurus* the spinodiapophyseal lamina appears gradually in the dorsal series by a pattern I call ‘lamina cutoff.’ As in *Giraffatitan*, serial variants of this lamina in *Phuwiangosaurus* include one dorsal vertebra in which stranded spinal and diapophyseal laminae intersect on the anterolateral aspect of the neural spine. An undescribed neosauropod from the Early Cretaceous of Utah, North America (Britt et al., 1998) displays a similar pattern of serial variation to that observed in dorsal vertebrae of *Giraffatitan* (Figs. 5-6) and *Phuwiangosaurus*. In one vertebra, anterior and posterior spinodiapophyseal laminae are present (Fig. 7). As in other taxa, the posterior spinodiapophyseal lamina extends between the triangular lateral process of the neural spine and the posterodorsal diapophysis. The anterior spinodiapophyseal lamina extends between the anterodorsal diapophysis and the anterolateral corner of the neural spine. In the Utah taxon, as in presacral ?20 of *Giraffatitan*, right and left anterior spinodiapophyseal laminae are asymmetrical.

A spinoparapophyseal lamina can be unambiguously identified in *Rebbachisaurus garasbae* and *Nigersaurus taqueti*, reb-

TABLE 2 — Terms discussed in this contribution.

Term	Definition
Stranded lamina	A lamina that contacts only one landmark, but in adjacent vertebrae its serial homologues contact two; takes the name of the landmark to which it remains connected (e.g., ‘stranded spinal lamina’)
Segmented laminae	Stranded laminae that are oriented in a collinear fashion but extend past one another; serial variants of the stranded laminae share the same or a nearby landmark
Intersecting laminae	Vertebral laminae that intersect and pass through each other; segments on either side of intersection are collinear and maintain form
Lamina capture	Pattern of serial variation; vertebral landmarks migrate close to another and one captures the end of a lamina from the other, thereby changing the name applied to it
Lamina cutoff	Pattern of serial variation; vertebral landmarks migrate and their attendant lamina or laminae become arched in such a way that eventually a single, new lamina is formed to the exclusion of one or both original laminae

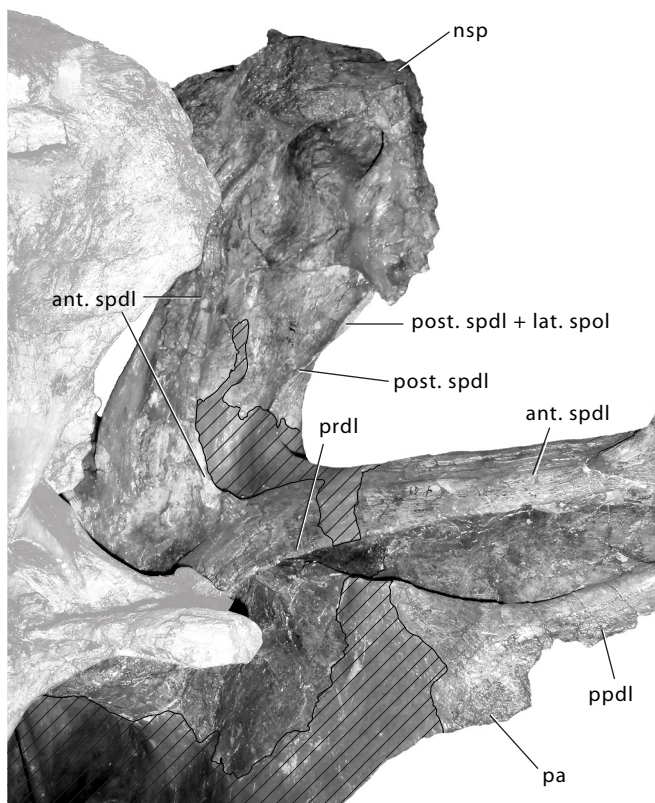


FIGURE 6 — Articulated posterior dorsal vertebrae of *Giraffatitan brancai* (MB.R. 2181.88, 89) in oblique left anterolateral view. The more anterior vertebra (MB.R. 2181.88) has been masked to highlight the more posterior (MB.R. 2181.89), which has a complete diapophysis and two spinodiapophyseal laminae. Abbreviations: *ant. spdl*, anterior spinodiapophyseal lamina; *lat. spol*, lateral spinopostzygapophyseal lamina; *nsp*, neural spine; *pa*, parapophysis; *post. spdl*, posterior spinodiapophyseal lamina; *ppdl*, paradiapophyseal lamina; *prdl*, prezygodiapophyseal lamina. Photo courtesy of M. D’Emic.

bachisaurids from the Cretaceous of northern Africa. The parapophyses and diapophyses are notably elongate and elevated on the neural arch in both. There is a prominent spinodiapophyseal lamina that is positioned between the diapophysis and neural spine, and a low, ridge-like spinoparapophyseal lamina that joins the neural spine near its base. The *sppl* is preserved in several vertebrae of the same series in each taxon.

New Types of Laminae

Two new types of laminae described here could conceivably be found anywhere in the vertebral column, but their distribution as currently known is restricted to particular regions in the column and particular portions of the vertebra. Here, I discuss the ‘segmented’ laminae described by Salgado and Carvalho (2008) and re-introduce the concept of ‘intersecting’ laminae, which was first noted, but not elaborated upon, by Osborn (1899).

‘Segmented’ laminae.— In their diagnosis of the Brazilian titanosaur species *Uberabatitan riberoi*, Salgado and Carvalho (2008: 886) listed a peculiar feature in anterior and middle cervical vertebrae, a “postzygodiapophyseal lamina (*podl*) segmented in two unconnected laminae, zygapophyseal and diapophyseal, of which the zygapophyseal segment extends rostradorsally over the diapophyseal.” This configuration of laminae is difficult to identify in photographs of cervical vertebrae, but it is best shown on the most complete cervical vertebra of *Uberabatitan* (CPP 1057 UrHo), in which two truncated laminae extend past one another near the postzygapophysis (see Salgado and Carvalho, 2008: fig. 5). Other named Brazilian titanosaurs known from adequate cervical material do not appear to share this feature (e.g., *Maxakalisaurus*, *Trigonosaurus*), but a similar configuration of laminae is present in the complete, articulated neck of the Peirópolis ‘Series A’ titanosaur, which received a preliminary description by Powell (1987, 2003) and is currently under study (Machado et al., in prep.).

My interpretation of the identity of the two ‘segmented’ laminae in *Uberabatitan* and ‘Series A’ differs in some respects from

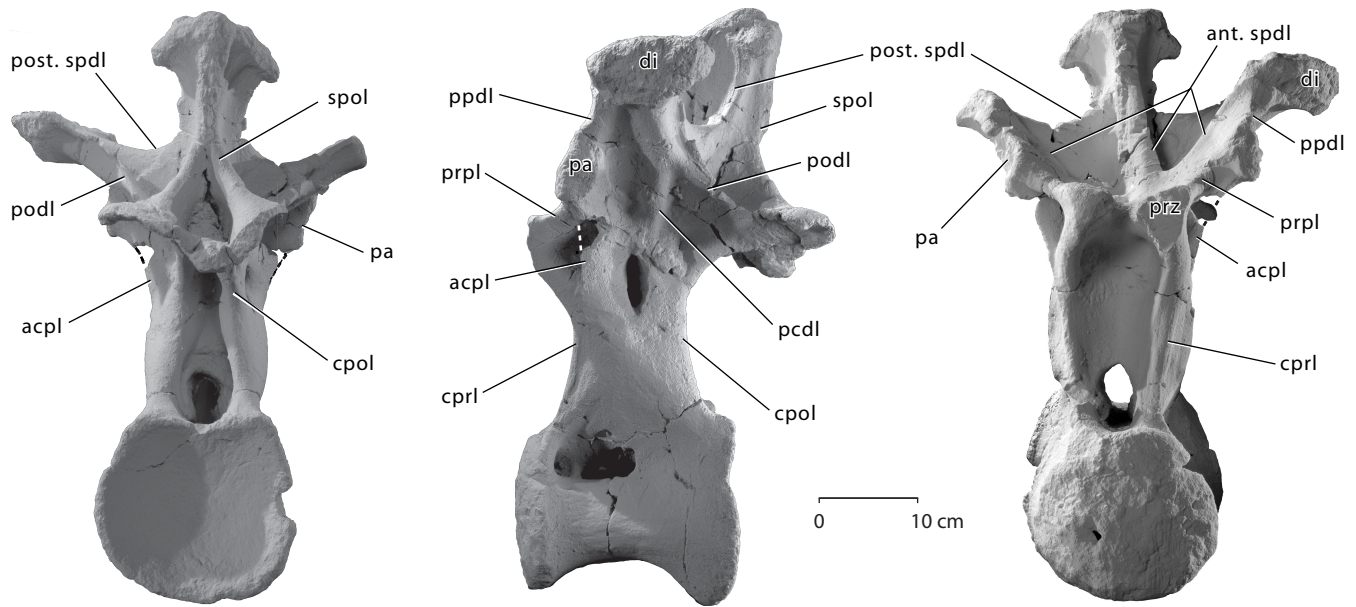


FIGURE 7 — Posterior dorsal vertebra of undescribed neosauropod from the Early Cretaceous of Utah, North America (BYU 10976; Britt et al. 1998). Note the presence of both anterior and posterior spinodiapophyseal laminae, as well as the left-right asymmetry in the former. The configuration of spinodiapophyseal laminae in this vertebra resembles that of posterior dorsal vertebrae of *Phuwiangosaurus* and *Giraffatitan* (see text). Abbreviations: *acpl*, anterior centroparapophyseal lamina; *ant. spdl*, anterior spinodiapophyseal lamina; *cpol*, centropostzygapophyseal lamina; *cprl*, centroprezygapophyseal lamina; *di*, diapophysis; *pa*, parapophysis; *pcpl*, posterior centroparapophyseal lamina; *podl*, postzygodiapophyseal lamina; *post. spdl*, posterior spinodiapophyseal lamina; *ppdl*, paradiapophyseal lamina; *prpl*, prezygaparapophyseal lamina; *prz*, prezygapophysis; *spol*, spinopostzygapophyseal lamina. Photo courtesy of B. Britt.

that of Salgado and Carvalho (2008), although I agree that the structure is of interest. The two parts of the ‘segmented’ lamina can be termed stranded laminae, because they each contact only one landmark but their serial homologues contact two (see Table 2). One of the stranded laminae contacts the diapophysis, and the other attaches near the postzygapophysis. The shorter and more ventrally-positioned stranded lamina, which contacts the diapophysis, is clearly a serial homologue of the postzygodiapophyseal lamina, as Salgado and Carvalho (2008) asserted. In the best preserved cervical vertebra of *Uberabatitan*, the longer, more dorsally-positioned of the two stranded laminae extends into the spinodiapophyseal fossa on the lateral aspect of the neural spine. The only lamina that extends into this region in sauropods is the *eprl* (Figs. 3-4; see Wilson et al., 2011). This interpretation is confirmed in the Peirópolis ‘Series A’ specimen, which has a similar configuration of laminae as in *Uberabatitan*, save that the *eprl* is more conspicuous and can be traced farther anteriorly (Fig. 8). Thus, the stranded laminae are serial variants of two different laminae, rather than variants of a single, segmented postzygodiapophyseal lamina as suggested by Salgado and Carvalho (2008). The stranded diapophyseal lamina is a serial variant of the postzygodiapophyseal lamina, as noted by Salgado and Carvalho (2008), but the other stranded lamina is a serial variant of the epipophyseal-prezygapophyseal lamina.

Given this interpretation of the anatomy, the term ‘segmented’ seems misleading. Segmentation renders a single entity into smaller subunits, or segments, which in turn can be recombined

to form the original structure. Certain laminae fit this definition. For example, the anterior centroparapophyseal lamina of the cervical region is segmented by the parapophysis into a paradiapophyseal lamina and an anterior centroparapophyseal lamina in the anterior dorsal region. In contrast, the stranded laminae in *Uberabatitan* and ‘Series A’ are not actually segments that can be recombined into a single parent lamina; they are serial variants of two distinct laminae. Despite this, retaining the original term seems the most pragmatic course of action, because this laminar configuration is thus far observed in a single named taxon, *Uberabatitan*. The nomenclatural issue can be taken up later, if this type of lamina proves to be widespread. In the meantime, I suggest describing these structures as ‘segmented,’ ‘overlapping,’ or ‘overreaching’ stranded diapophyseal and epipophyseal laminae.

So far, a functional explanation for ‘segmented’ laminae is elusive. In elongate cervical vertebrae, the *eprl* and *podl* are very similar in orientation and have landmarks that are very close to one another. They are semi-redundant, because they resist similar forces. In many sauropods with elongated necks, the semi-redundant laminae coalesce prior to reaching the landmark they share (e.g., *Nigersaurus*, Fig. 3; *Euhelopus*, Fig. 4). The ‘overlapping’ or ‘overreaching’ stranded laminae in *Uberabatitan* and ‘Series A’ may be an alternative, if rarely observed, solution.

‘Intersecting’ laminae.—In his description of a well-preserved axial skeleton of *Diplodocus*, Osborn (1899: 196) developed the

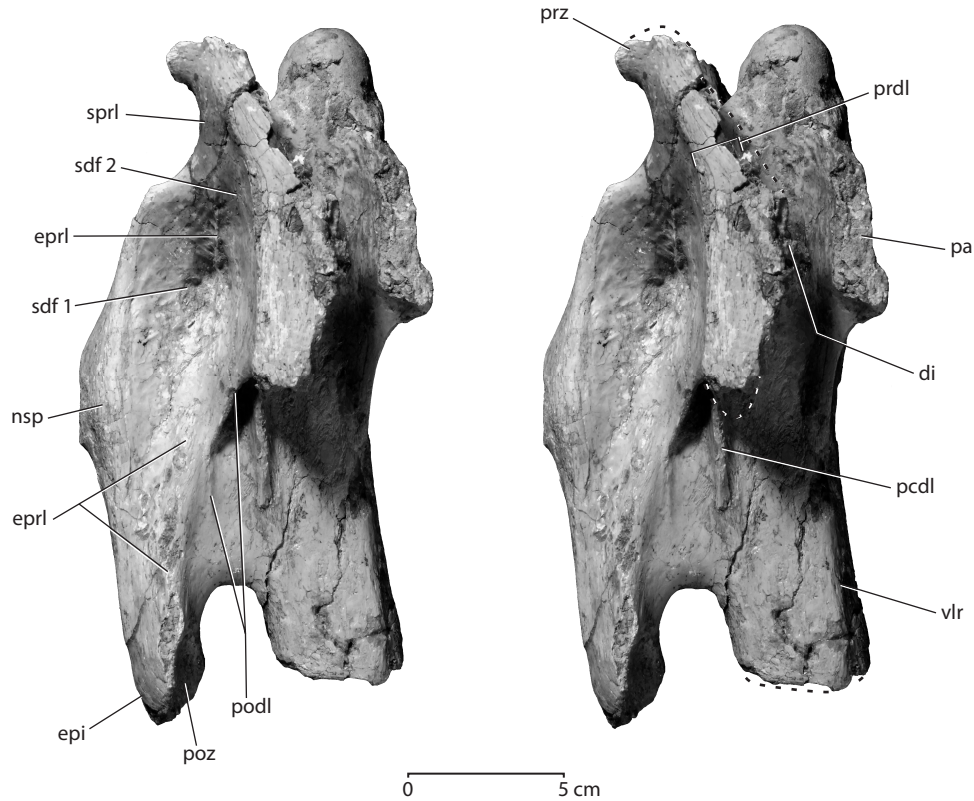


FIGURE 8 — ‘Segmented’ laminae in Peirópolis ‘Series A’ cervical vertebra 5 (MCT unnumbered). Stereopairs in right lateral (this page) and dorsal (facing page) views. A complete description of this vertebra and the vertebral series is in preparation by E. Machado (pers. comm.). Abbreviations: *di*, diapophysis; *epi*, epipophysis; *eprl*, epipophyseal-prezygapophyseal lamina; *gr*, groove; *nsp*, neural spine;

first nomenclature for vertebral laminae, including description of structures he termed “intersecting laminae,” which extended “upon sides of neural arch from prezygapophyses downwards and backwards, and from postzygapophyses downwards and forwards.” Osborn (1899: fig. 7) labeled only one such obliquely oriented lamina that intersects other laminae, located on the lower neural arch of the penultimate dorsal vertebra.

Intersecting laminae have been little discussed in the intervening century. They have appeared occasionally, but without referring to Osborn’s (1899) original paper. For example, Wilson and Upchurch (2009: fig. 20) presented an interpretation of a laminar configuration on the lower neural arch of dorsal vertebrae of *Euhelopus* that invoked intersecting diapophyseal and parapophyseal laminae.

The lectotypic posterior dorsal vertebra of *Rebbachisaurus garasbae* (Lavocat, 1954; MNHN-MRS 1958) shows evidence for intersecting laminae on the lower portion of the neural arch. *Rebbachisaurus* is characterized by thin, platy spinodiapophyseal, centrodiapophyseal, and centroparapophyseal laminae that are festooned between the neural spine and diapophysis, diapophysis and centrum, and parapophysis and centrum, respectively (Wilson and Allain, in preparation). The centrozygapophyseal laminae (viz. centroprezygapophyseal, centropostzyg-

apophyseal laminae) intersect and pass through neighboring costal laminae (i.e., anterior centroparapophyseal lamina, posterior centrodiapophyseal lamina). Together, these intersecting laminae form an approximate “M” shape on the lateral aspect of the neural arch. I identify this configuration as two pairs of intersecting laminae rather than eight smaller laminae because the lines are straight and the laminae maintain their shape on either side of the intersection: the costal laminae are larger and platy, and the zygapophyseal laminae are smaller and rounded (Fig. 9). The pattern is repeated in other, undescribed vertebrae of *Rebbachisaurus* (e.g., MNHN-MRS 1979; Wilson and Allain, in preparation).

Intersecting laminae have only been identified in dorsal vertebrae; none have been reported in cervical, sacral, or caudal vertebrae. Within dorsal vertebrae, intersecting laminae are restricted to the lower neural arch; they have not yet been identified above the zygodiapophyseal table.

Compliance with Nomina Anatomica Avium/Nomina Anatomica Veterinaria

The terminology Wilson (1999) developed for vertebral laminae used neither standardized terminology for orientation

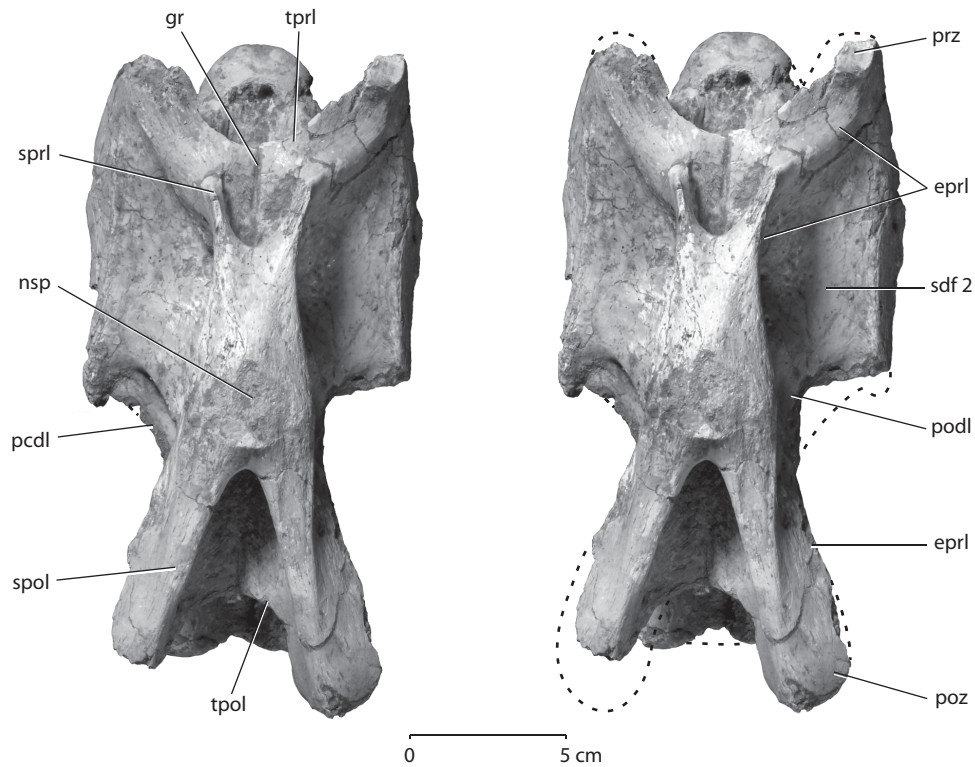


FIGURE 8 — (continued) *pa*, parapophysis; *pcdl*, posterior centrodiapophyseal lamina; *podl*, postzygodiapophyseal lamina; *poz*, postzygopophysis; *prdl*, prezygodiapophyseal lamina; *prz*, prezygapophysis; *sdf1*, *sdf2*, spinodiapophyseal fossae 1 and 2; *spol*, spinopostzygapophyseal lamina; *sprl*, spinoprezygapophyseal lamina; *tpol*, intrapostzygapophyseal lamina; *tprl*, intraprezygapophyseal lamina; *vlr*, ventrolateral ridge.

(e.g., ‘cranial,’ ‘caudal’) nor for vertebral parts that form names (e.g., ‘corporo-’ for the vertebral body). Instead, more generalized terms for orientation (e.g., ‘anterior,’ ‘posterior’) and parts (e.g., ‘centro-’) were employed. Recently it has been suggested that the terminology be modified to better agree with *Nomina Anatomica Avium/Nomina Anatomica Veterinaria* (NAA/NAV) terminology. Subsequent descriptions of saurischian axial skeletons have implemented these changes, but in slightly different ways. Upchurch et al. (2004) and O’Connor (2007) chose to modify the orientational descriptors (i.e., changed ‘anterior’ and ‘posterior’ to ‘cranial’ and ‘caudal,’ respectively), but they did not change the terms referring to vertebral parts. Harris (2006: 1092) implemented more drastic changes to the system, but even he did not make the terms fully compliant with NAA/NAV terminology:

Many of the terms created by Wilson (1999) utilize the roots ‘anterior’ and ‘posterior’ (e.g. ‘posterior centrodiapophyseal lamina’), terms that are, for logical reasons, abandoned in favour of ‘cranial’ and ‘caudal’. Constructing literal modifications of [...] Wilson’s terms to conform to Baumel et al. (1993) produces awkward, cacophonous terms (e.g. ‘lamina corporo-processus transversus’ for ‘centrodiapophyseal lamina’). Thus, the terms introduced by [...] Wilson are retained here, unchanged, though

modified such that ‘anterior’ and ‘posterior’ and the prefixes ‘pre’ and ‘post’ have been replaced with ‘cranial’ and ‘caudal’, and ‘centro-’ has been replaced with ‘corporo-’.

As I have discussed elsewhere (Wilson, 2006), one of the consequences of implementing NAA/NAV terms to fossil reptiles is that conversion of non-standardized to standardized terminology comes with a cost that may easily exceed its reward.

Here, the cost is the creation of extra sets of anatomical terms for vertebral laminae that parallel the original set of Wilson (1999). Still other sets of terms may be in the offing for researchers whose ears are tuned differently to “awkward” or “cacophonous” phrasings and are willing to adopt more or less fully compliant standardized terms. It is one thing to accept historical synonymies and terms that have long standing in the literature (e.g., *centrum*, *body*, *corpus*), but it is another thing to intentionally create synonyms, which can never completely eradicate the presence of the original terms in the literature. Intentional synonymy can lead to real confusion because users must learn to both standard and non-standard terms in order to read past and present descriptions. Perhaps this cost would be justified if the reward were great enough, but the “logical reasons” and desire “to conform with Baumel” mentioned above do not rise to this challenge. Such terminological changes for the sake of confor-

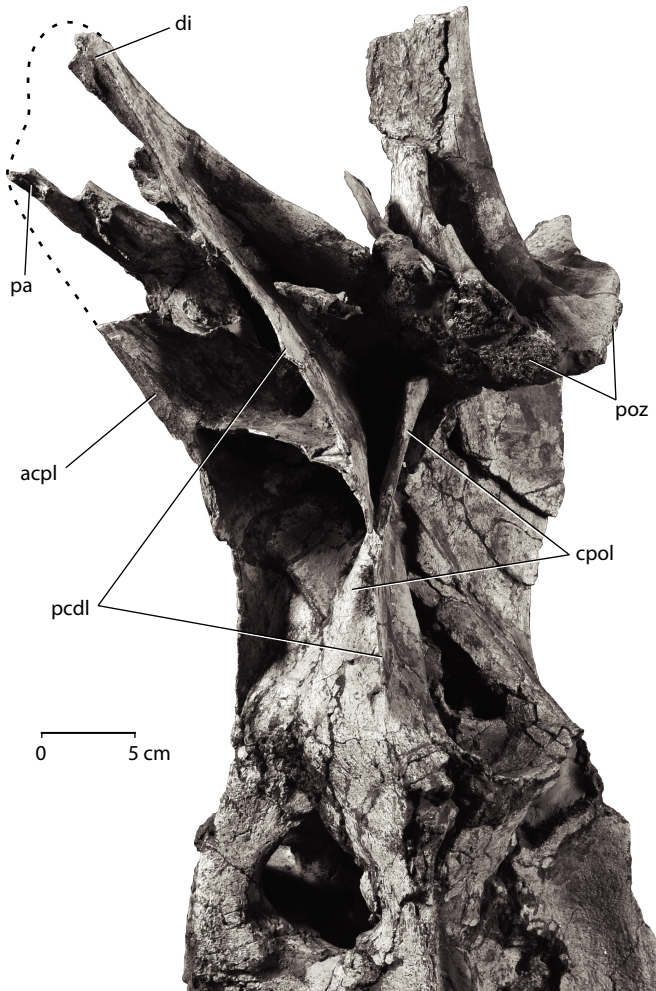


FIGURE 9 — ‘Intersecting’ laminae in a dorsal vertebra of *Rebbachisaurus garasbae* (MNHN-MRS 1958), shown in oblique left posterolateral view. Note the intersecting posterior centrodiapophyseal and centropostzygapophyseal laminae. Abbreviations: *acpl*, anterior centroparapophyseal lamina; *cpol*, centropostzygapophyseal lamina; *di*, diapophysis; *pa*, parapophysis; *pcdl*, posterior centrodiapophyseal lamina; *poz*, postzygapophysis.

mity only remove focus from the anatomical issue at hand and redirect it toward compliance, with its only concrete results being new terms to learn. This parallels similar issues in statutory law, in which focus on compliance with regulations distracts from the central issue the laws are meant to address (see Howard, 1994).

Higher-Level Groupings of Laminae

The nomenclatural system of Wilson (1999) uses two landmarks to identify each lamina. The name for each lamina, then, could conceivably be arranged two different ways (i.e., the ‘x-y’ lamina and the ‘y-x’ lamina). To avoid potential

terminological ambiguity, laminae were grouped as either diapophyseal, parapophyseal, zygapophyseal, or spinal laminae. This arrangement was admitted to be “somewhat arbitrary, reflecting convenience, rather than ‘origin’” of the lamina (Wilson, 1999: 641).

In a paper describing sauropod axial material from Spain, Barco (2005: 27-28) suggested that the higher-level groupings of Wilson (1999) might be changed to better reflect their “functional significance” (translated from the Spanish). Barco (2005) suggested that the relative proximity of landmarks to the mid-sagittal plane could be used to identify the ‘origin’ and ‘terminus’ for each lamina. Laminae, in turn, were then reorganized by their ‘origin,’ which was defined as being closest to the midline. Not surprisingly, this regrouping skewed the distribution of laminae across the categories toward midline structures: there are 7 spinal laminae, 6 “central” laminae (a new category), 5 zygapophyseal laminae, 1 parapophyseal lamina, and no diapophyseal laminae (Barco, 2005: table 3). At least two issues would need to be resolved to recommend Barco’s (2005) higher-level organization as non-arbitrary and biologically relevant. First, it must be explained why proximity to the mid-sagittal plane reflects functionality of laminae, or what this grouping of categories tells us about the function of laminae. This is especially relevant when we consider that forces are applied to the extremities of the vertebra, which are not necessarily nearer or farther from the midline. Second, why is ‘functional significance’ the best criterion for organization of laminae? One could imagine others, such as timing of ossification, appearance in phylogeny, or distance from the neutral axis, that represent competing grouping criteria. Until these issues are resolved, the original, arbitrary but unambiguous grouping of laminae is recommended.

SERIAL VARIATION IN VERTEBRAL LAMINAE: LAMINA CAPTURE AND CUTOFF

Not all laminae are present in a given vertebra or vertebral region of a single individual. For example, the epipophyseal-prezygapophyseal lamina is present only in cervical vertebrae, whereas the spinodiapophyseal lamina and parapophyseal laminae are typically restricted to dorsal vertebrae. In most cases, these laminae with restricted distribution appear at a certain point in the vertebral series, after they gradually form over the span of several vertebrae. There are different patterns of serial variation associated with the appearance of certain lamina in the vertebral column. Before describing these patterns, I briefly discriminate between primary, secondary, and serial homology to justify application of different names to serially homologous vertebral laminae.

Primary Homology, Secondary Homology, and Serial Homology

Here I follow Patterson’s (1982) restrictive definition of homology as shared similarity tested by disjunction between states and congruence with other characters (i.e., synapomorphy) and

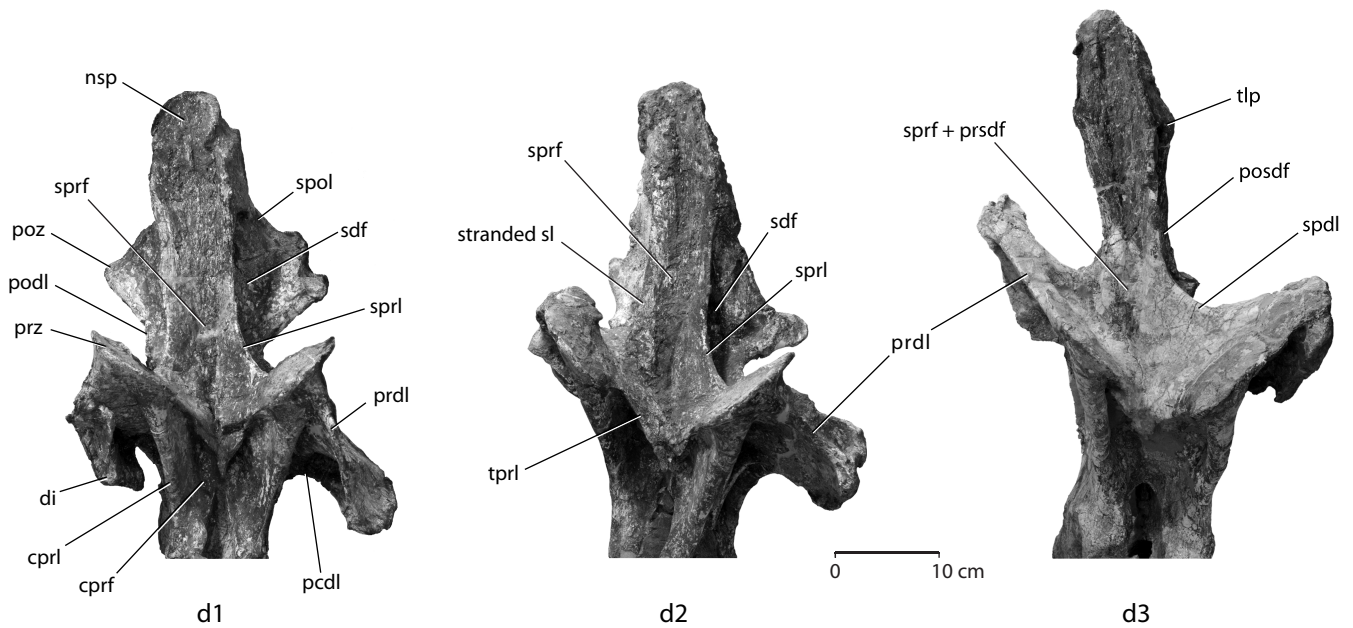


FIGURE 10 — Lamina ‘capture’ in dorsal vertebrae 1–3 of *Jobaria tiguidensis* (Serenó et al., 1999; MNN-TIG-9). Across the cervicodorsal transition, the diapophysis migrates to a position close to the prezygapophysis and captures its lamina, creating a spinodiapophyseal lamina at the expense of the spinoprezygapophyseal lamina. Abbreviations: *cprf*, centroprezygapophyseal fossa; *cprl*, centroprezygapophyseal lamina; *d*, dorsal; *di*, diapophysis; *nsp*, neural spine; *pcdl*, posterior centrodiapophyseal lamina; *podl*, postzygodopophyseal lamina; *posdf*, postzygapophyseal-spinodiapophyseal fossa; *poz*, postzygapophysis; *prdl*, prezygodiapophyseal lamina; *prsd*, prezygapophyseal-spinodiapophyseal fossa; *prz*, prezygapophysis; *sdf*, spinodiapophyseal fossa; *sl*, spinal lamina; *spd*, spinodiapophyseal lamina; *spol*, spinopostzygapophyseal lamina; *sprf*, spinoprezygapophyseal fossa; *sprl*, spinoprezygapophyseal lamina; *tlp*, triangular lateral process; *tprl*, intraprezygapophyseal lamina.

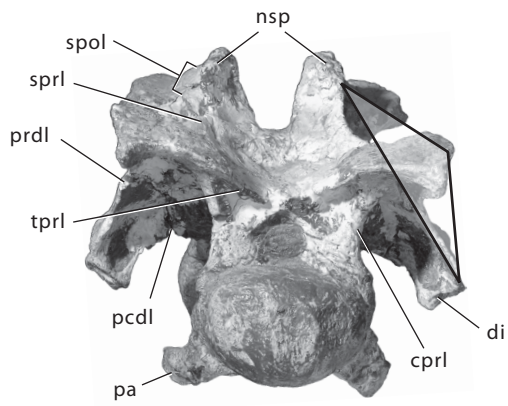
de Pinna’s (1991) distinction between ‘primary’ and ‘secondary’ homology. The latter distinguishes the initial proposition of homology based on comparative anatomy (i.e., primary homology) from the testing of that hypothesis by congruence with other characters (i.e., secondary homology). For vertebral laminae, identification and nomenclature applied to primary homologues (e.g., the spinodiapophyseal lamina) is based on landmarks and akin to scoring a character; phylogenetic analysis determines of the level at which that feature is a synapomorphy.

Serial homologues are produced as positionally and structurally similar iterations of a feature within a single organism (e.g., teeth, limbs, vertebrae, ribs). Iterates need not resemble each other; indeed, their morphological differentiation is a basic theme in evolution. Vertebrae as a whole are serially homologous, but they may contain many smaller structures that are also serially homologous (e.g., diapophyses, parapophyses, zygapophyses), each of which may vary independently. Vertebral laminae are also serial homologues that link pairs of such independently-varying serial homologues. The appearance of the spinodiapophyseal lamina in dorsal vertebrae of sauropods is preceded by a series of intermediate vertebrae that present at least two different patterns of variation, as described below. These patterns of serial variation can be evaluated in a cladistic context, an approach advocated by Cracraft (2005) and followed here (see below).

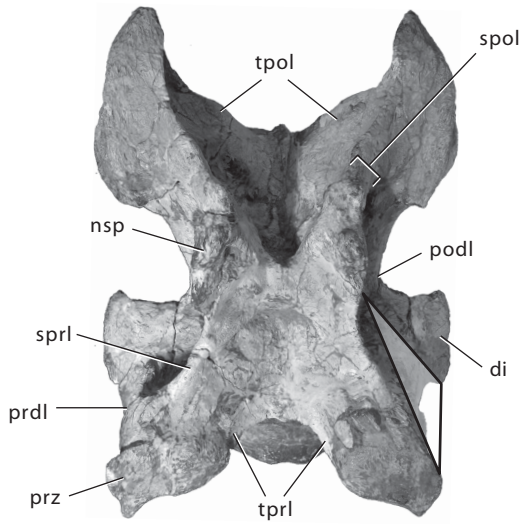
Lamina Capture

‘Lamina capture’ occurs when vertebral landmarks migrate close enough to one another that one landmark is able to ‘capture’ the end of a lamina from the other. Substitution of one of the landmarks on a lamina results, by definition, in a new name for that lamina. In lamina capture, the first appearance of the new lamina in the series is correlated with the disappearance of the other. This pattern is demonstrated by a series of vertebrae of the sauropod *Jobaria tiguidensis*, in which the diapophysis captures the spinoprezygapophyseal lamina to create a spinodiapophyseal lamina (Fig. 10).

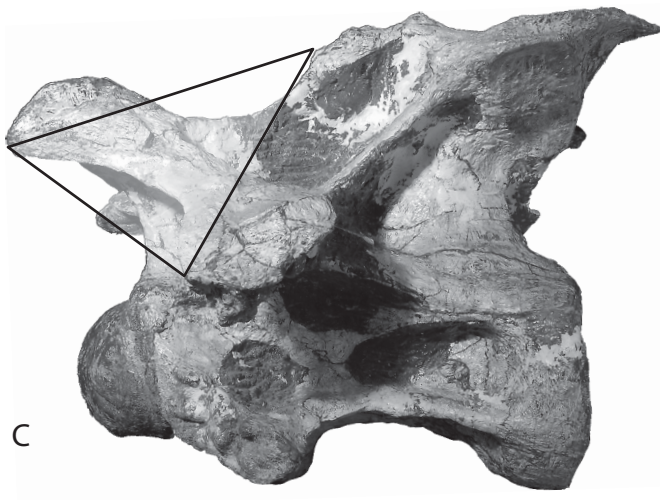
Jobaria is represented by several skeletons excavated from Tiouararén Formation deposits of Niger (Serenó et al., 1999). Skeleton MNN-TIG-9 includes a partially articulated series of 19 vertebrae starting from the axis and extending through the mid-dorsal vertebrae. Moving posteriorly along the cervical series, the neural spine and diapophysis become progressively more distanced from an imaginary line connecting the zygapophyses (Fig. 2). In most cervical vertebrae, that imaginary line forms the longer diagonal of the quadrilateral formed by the zygapophyses, neural spine, and diapophysis. However, in posteriormost cervical and dorsal vertebrae, where the neural arch is tall and narrow, the line connecting the zygapophyses forms the shorter diagonal. There is typically only one lamina



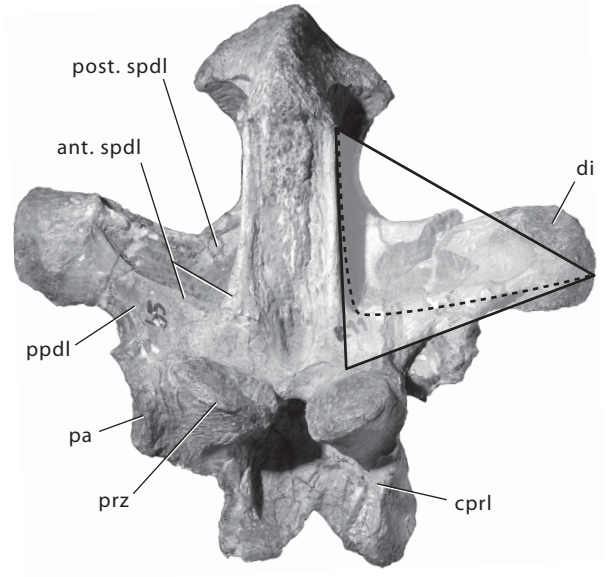
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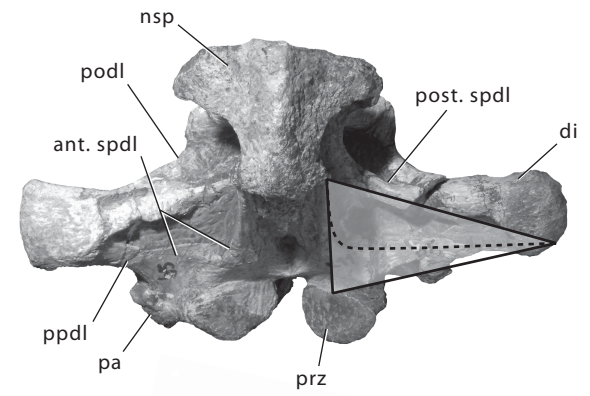
B



C



D



E



F

that spans the center of that quadrilateral on the lateral aspect of the neural arch, and it is aligned along its long diagonal. In cervical vertebrae, it is the epipophyseal-prezygapophyseal lamina; in dorsal vertebrae it is the spinodiapophyseal lamina.

In postaxial anterior cervical vertebrae of *Jobaria*, the prezygapophyses extend anteriorly beyond the condyle, but in the middle and posterior cervical vertebrae the prezygapophyses become progressively shorter until they are nearly level with the condyle in the last cervical vertebra. Across the same series of vertebrae, the diapophyses become progressively shorter and more elevated. As a result of these changes, which draw the diapophysis and prezygapophysis closer to one another, the prezygodiapophyseal lamina spanning them becomes shorter. By the first dorsal vertebra, the spinoprezygapophyseal lamina, which is now more vertically oriented, is quite close to the diapophysis (Fig. 10, left). In the second dorsal vertebra, on one side there is a stranded spinal lamina, but a normal spinoprezygapophyseal lamina is present on the opposite side of the neural arch (Fig. 10, center). In the subsequent vertebra, spinodiapophyseal laminae have replaced both the spinoprezygapophyseal lamina and the stranded spinal lamina (Fig. 10, right). The spinodiapophyseal lamina persists throughout the remainder of the dorsal series and into the sacrum, but the spinoprezygapophyseal lamina does not return. Thus, in *Jobaria*, a spinodiapophyseal lamina is formed when the diapophysis captures the end of the spinoprezygapophyseal lamina.

Salgado et al. (2006: 72-73) described a pattern of landmark migration that resembles lamina capture in the Brazilian titanosaur *Trigonosaurus*. In the cervical vertebrae of *Trigonosaurus*, the apex of the neural spine is located approximately at mid-centrum, equidistant between the prezygapophyses and postzygapophyses. In the dorsal series, the apex of the neural spine migrates posteriorly and eventually extends posteriorly beyond the cotyle in dorsal vertebra 4. This migration increases the distance between the prezygapophyses and the neural spine, and it decreases the distance between the postzygapophyses and neural spine. As a result, the spinopostzygapophyseal lamina is short, and the podl is nearly aligned with a line connecting the diapophysis and neural spine. By dorsal vertebra 5, this diapophyseal lamina has surpassed the postzygapophysis and attached to a position on the lateral margin of the neural spine, making it a spinodiapophyseal lamina. Because another spinodiapophyseal lamina is present in this and preceding vertebrae, the addition of a second necessitates discriminating between anterior and poste-

rior spinodiapophyseal laminae. The posterior spinodiapophyseal lamina, created by capture of the podl, persists in subsequent dorsal vertebrae, even when a podl is present (Salgado et al., 2006: fig. 2).

Identification of a similar pattern of lamina capture of the podl in *Bonitasaura* led Gallina (2011: 242-243) to conclude that the captured lamina connecting the neural spine and the diapophysis is the podl (not the spdl), and that the lamina connecting the diapophysis and postzygapophysis that appears in more posterior vertebrae is a new lamina “not homologous to [the] podl.” This interpretation conflates identification of primary homology, which is based on topological similarity, with serial variation. The lamina spanning the neural spine and diapophysis is the spinodiapophyseal lamina, regardless of series of intermediates in bracketing vertebrae. Both types of information are important and should be coded as character data, as discussed below, and included in a phylogenetic analysis that determines the homology of the feature in question.

Lamina Cutoff

‘Lamina cutoff’ is analogous to the formation of a cutoff across the loop of a river meander. As landmarks on the neural arch migrate along the column, the shape and orientation of laminae are affected (Fig. 2). Landmark migration can sometimes lead to serial variants in which laminae are strongly arched, rather than straight. These laminae can eventually reach a point at which their orientation is so distinct from the shortest line between major neural arch projections that a new lamina ‘cuts off’ one or more arched laminae. This pattern can characterize a pair of laminae that together form an arched or bent structure, or a single, arched lamina. The new lamina formed by lamina cutoff replaces one or both of the laminae that formed the arch.

The inferred pattern of lamina cutoff is shown in Figure 11, in which I have drawn vertices of a triangle on the anterior margin of the neural spine, diapophysis, and prezygapophyses on the left side of a cervical and dorsal vertebra of *Phuwiangosaurus sirindhornae*, a titanosauriform from the Early Cretaceous of Asia (Martin et al., 1994). As in many Asian titanosauriforms, the cervical vertebrae of *Phuwiangosaurus* are low, transversely narrow, and elongate. In cervical vertebra 5, for example, the neural spine is low, the diapophyses do not extend laterally much farther than do the zygapophyses, and the average elongation index of the centrum is 3.44 ($aEI = 2 \times \text{length}/\text{width} +$

FIGURE 11 — Lamina ‘cutoff’ in a cervical vertebra (SM K11-0017) and dorsal neural arch (SM K11-0038) of *Phuwiangosaurus sirindhornae* (Martin et al., 1994; Suteethorn et al., 2009). The posterior cervical (A, B, E) and posterior dorsal (C, D, E) vertebrae are shown in anterior (A, C), dorsal (B, D), and left lateral (E, F) views. Note the presence of two spinodiapophyseal laminae in the dorsal vertebra. The ‘L’-shaped anterior spinodiapophyseal lamina was derived from two laminae present in cervical vertebrae, the spinoprezygapophyseal and prezygodiapophyseal laminae, remnants of which form its vertical and lateral arms. The vertices of the triangles in each image link the anterior margin of the prezygapophysis, neural spine, and diapophysis on the left side of the vertebra. Dashed lines indicate the actual path of the anterior spinodiapophyseal lamina. In cervical vertebrae, the longest dimensions of the triangle are oriented anteroposteriorly and dorsoventrally; in dorsal vertebrae, they are oriented transversely and dorsoventrally. Abbreviations: *ant. spdl*, anterior spinodiapophyseal lamina; *cpdl*, centroprezygapophyseal lamina; *di*, diapophysis; *nsp*, neural spine; *pa*, parapophysis; *pcdl*, posterior centroprezygapophyseal lamina; *podl*, postzygodiapophyseal lamina; *post. spdl*, posterior spinodiapophyseal lamina; *ppdl*, paradiapophyseal lamina; *prdl*, prezygodiapophyseal lamina; *prz*, prezygapophysis; *sdf*, spinodiapophyseal fossa; *spol*, spinopostzygapophyseal lamina; *sprl*, spinoprezygapophyseal lamina; *tpol*, intrapostzygapophyseal lamina; *tprl*, intraprezygapophyseal lamina.

height; Chure et al., 2010). The triangles help to visualize the relative distances between and orientation of these landmarks, which indicate where applied forces have their greatest effect. For example, in the cervical vertebra (Fig. 11A-C), the triangle joining the prezygapophysis, diapophysis, and neural spine has a substantial anteroposterior component. Due to this position of landmarks, a force applied to the prezygapophysis would impart greater torque than would a force of equal magnitude applied to the diapophysis, because the prezygapophysis has a longer lever arm than does the diapophysis. As in other sauropod cervical vertebrae, in *Phuwiosaurus* the prezygapophysis is braced by four laminae, the spinoprezygapophyseal, centroprezygapophyseal, intraprezygapophyseal, and prezygodiapophyseal laminae, of which only one has a significant transverse component (i.e., intraprezygapophyseal).

In contrast to cervical vertebrae, dorsal vertebrae are generally taller, transversely broader, and more abbreviate anteroposteriorly in *Phuwiosaurus*, as in other sauropods. The triangle connecting the prezygapophysis, diapophysis, and neural spine is elongate dorsoventrally and transversely, but comparatively short anteroposteriorly (Fig. 11D-F). A force applied to the diapophysis causes a larger torque than does a force of equal magnitude applied to the prezygapophysis due to the difference in their lever arms. Because the dorsal vertebrae support ribs that form the thorax, ventrally directed forces are a significant portion of their loading regime. Forces applied by ribs to the diapophysis are resisted by several laminae, including the prezygodiapophyseal, paradiapophyseal, spinodiapophyseal, postzygodiapophyseal, and centrodiapophyseal. All but the spinodiapophyseal lamina are present on the cervical vertebrae. The spinodiapophyseal lamina emerges as the result of cutoff of the spinoprezygapophyseal and prezygodiapophyseal laminae, which are sharply angled relative to the shortest distance between the neural spine and diapophysis. Across the transitional cervicodorsal vertebrae, the spinoprezygapophyseal lamina gradually loses its connection to the prezygapophysis and becomes a 'stranded' spinal lamina. There also emerges a stranded diapophyseal lamina, which contacts the stranded spinal lamina in a manner similar to the *Giraffatitan* vertebra (MB.R 2181.87) discussed above. In the posterior dorsal vertebrae, the stranded diapophyseal and spinal laminae have been replaced by an 'L'-shaped anterior spinodiapophyseal lamina.

A slightly different pattern of lamina cutoff characterizes a well preserved vertebral sequence of a rebbachisaurid sauropod from Argentina (Haluzá et al., 2012), in which migration of landmarks along the series creates a highly arched spinoprezygapophyseal lamina that is eventually replaced by a spinodiapophyseal lamina in subsequent vertebrae. In cervical vertebrae of this rebbachisaurid, the neural spine is elongate and directed slightly posteriorly. In those vertebrae, the spinoprezygapophyseal lamina is gently arched, as it is in other sauropods. By the cervicodorsal transition, the neural spine is oriented anteriorly, and the spinoprezygapophyseal lamina is more tightly arched and resembles a 'J.' As the neural spine migrates farther anteriorly in subsequent vertebrae, the spinoprezygapophyseal lamina becomes more strongly arched and eventually forms a 'V'-shaped structure whose vertex is

positioned close to the diapophysis (Haluzá et al., 2012: fig. 2). By the fourth dorsal vertebra, the V-shaped spinoprezygapophyseal lamina has disappeared via lamina cutoff, replaced by a relatively straight spinodiapophyseal lamina. This spinodiapophyseal lamina persists in subsequent vertebrae. The early Late Jurassic diplodocoid *Brachytrachelopan* (Rauhut et al., 2005; Cúneo & Bowring, 2010) preserves an articulated series of cervical and dorsal vertebrae that also contain elongate, forwardly arched neural spines, but the details of the pattern of appearance of the spinodiapophyseal lamina have not yet been described.

Lamina cutoff differs from lamina capture in the relationship between the 'disappearing' and 'appearing' laminae. In lamina capture, there may be little difference in the position and orientation of the appearing and disappearing laminae, because the two landmarks at one end of the lamina are close to one another in position. In lamina cutoff, in contrast, there may be a drastic difference in the position and orientation of the appearing and disappearing laminae because the landmarks are not close to one another.

PHYLOGENETIC CONSIDERATIONS

Tracking the serial variation of landmarks along the vertebral column of a single sauropod helps identify patterns associated with laminae that have restricted distributions in the vertebral column. Given appropriate samples, we might be able to determine that the spinodiapophyseal lamina in one taxon is bracketed by vertebrae that manifest a pattern of lamina capture (e.g., *Jobaria*) or lamina cutoff (e.g., *Phuwiosaurus*). We may also discover that the spinodiapophyseal lamina is a serial variant of the spinoprezygapophyseal lamina in one taxon (e.g., *Jobaria*) and the postzygodiapophyseal lamina in the other (e.g., *Trigonosaurus*). These patterns of serial variation could represent a rich source of character data for cladistic analysis (see Cracraft, 2005).

There are several options for coding this information into characters, each of which has advantages and disadvantages (Table 3). In the composite coding option (Wilkinson, 1995), presence/absence data, variation in topological features, and variation in serial homologues are coded as separate states of a single character (Table 3, scheme 1). Composite coding avoids inapplicable data, but carries the disadvantage of mixing neomorphic data with transformational data (Serenó, 2007). For this reason, the presence of a lamina and variation in its shape and in serial iterates cannot vary independently. That is, the presence of the spinodiapophyseal lamina cannot act as a synapomorphy unless the pattern of serial variation (e.g., lamina capture, lamina cutoff) is the same. A practical concern is that the information about serial variation is much more rare than topological data in sauropods, which means that laminar characters would not carry much weight using this coding strategy.

In contrast, the reductive coding option (Wilkinson, 1995) encodes each variant as a single presence/absence character (Table 3, scheme 2). This coding scheme misrepresents the characters as independently varying, when in fact some of them are alternatives to one another. Because a lamina cannot arise

TABLE 3 — Alternative schemes for coding topological data and variation in serial homologues for vertebral laminae. 1, composite coding, wherein all information is coded as separate states of a single character; 2, reductive coding, wherein each variant is its own character; 3, recommended ‘contingent’ coding scheme, in which topological and developmental data are separated (Forey and Kitching, 2000; Sereno, 2007). Description of composite and reductive coding follows Wilkinson (1995); coding grammar follows Sereno (2007). Abbreviations: *podl*, postzygodiapophyseal lamina; *prdl*, prezygodiapophyseal lamina; *sprl*, spinoprezygapophyseal lamina.

Scheme	Character	Statement
1	Spinodiapophyseal lamina	(0) absent (1) present and arising via lamina capture of sprl (2) present and arising via lamina capture of podl (3) present and arising via lamina cutoff of sprl and prdl
2	Spinodiapophyseal lamina, arising by lamina capture of sprl	(0) absent (1) present
	Spinodiapophyseal lamina, arising by lamina capture of prdl	(0) absent (1) present
	Spinodiapophyseal lamina, arising by lamina capture of sprl	(0) absent (1) present
	Spinodiapophyseal lamina, arising by lamina cutoff of sprl and podl	(0) absent (1) present
3	Spinodiapophyseal lamina	(0) absent (1) present
	Spinodiapophyseal lamina, pattern of serial variation in preceding vertebrae	(0) lamina capture (1) lamina cutoff (9) inapplicable
	Spinodiapophyseal lamina, associated lamina	(0) sprl (1) podl (2) sprl and prdl (9) inapplicable

both by capture and by cutoff, scoring of a “1” for one character requires scoring a “0” for the other. This can result in groups can be supported by the absence of non-independently varying characters. For example, one taxon might have a *spdl* that arose as a result of lamina capture, and a second taxon might lack an *spdl* altogether. Both taxa would be scored “0” for the character coding *spdl* arising as the result of lamina cutoff, which would provide support for their monophyly despite the obvious differences in their morphology.

For practical and theoretical reasons I recommend a third approach, which has been called ‘contingent’ coding (Forey and Kitching, 2000; Sereno, 2007). Here, the neomorphic data are separated from transformational variation; the presence/absence of a lamina, identified by landmarks, is one character, and variation in its form and in the serial variation by which it ‘appears’ are separate characters. The advantage of this scheme is that it allows the laminae to be synapomorphies, but the disadvantage is that it results in inapplicable characters for those taxa that lack the lamina in question. Inapplicable characters can have undesirable consequences (Maddison, 1993), but I regard these as

less damaging than loss of synapomorphy data that results from lumping topological and serial variation characteristics into a single character in composite coding or creation of non-independently varying characters in reductive coding.

CONCLUSIONS

Vertebral laminae provide architectural support for the various vertebral projections, and in the process frame spaces that contained air sacs. The anatomical nomenclature for vertebral laminae was designed to facilitate the identification of primary, secondary, and serial homologues (Wilson, 1999). Several new laminae have been identified in the 13 years since this system was introduced. These include novel structures such as the epipophyseal-prezygapophyseal lamina (Bonaparte, 1996) and the spinoparapophyseal lamina (Taylor, 2009), as well as variants of previously-recognized structures, such as the anterior and posterior spinodiapophyseal laminae (Salgado and Powell, 2010). In addition, new types of laminae have been identified,

including ‘segmented laminae’ (Salgado and Carvalho, 2008) and ‘intersecting laminae.’

Vertebral laminae exhibit variation within vertebrae (left vs. right sides), within a vertebral region (anterior vs. posterior cervical vertebrae), and between vertebral regions (cervical vs. dorsal vertebrae), as well as at the population, species, genus, and supra-generic levels. This variation can provide useful character data for studies of saurischian evolution. This includes both presence/absence data, such as the presence of a lamina identified by topological information, as well information describing the pattern of variation in serial homologues that precede or succeed the vertebra in the column (e.g., lamina capture and lamina cutoff). Coding the topological data and variation in serial homologues into separate characters allows both the structure and the means by which it ‘appears’ in the column to act as separate synapomorphies. Emphasis on variation within vertebral laminae as character data will improve representation of axial information in saurischian datasets, which is often poorly represented, even for sauropod dinosaurs.

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Museum of Paleontology, The University of Michigan
1109 Geddes Avenue, Ann Arbor, Michigan 48109-1079
Daniel C. Fisher, Director

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