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ASSIGNATION OF THE VERTEBRA CPP 494 TO *TRIGONOSAURUS PRICEI* CAMPOS *ET AL.*, 2005 (SAUROPODA: TITANOSAURIFORMES) FROM THE LATE CRETACEOUS OF BRAZIL, WITH COMMENTS ON THE LAMINAR VARIATION AMONG LITHOSTROTIAN TITANOSAURS

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Abstract.- A revision of material corresponding to a posterior dorsal vertebra of a titanosaurian sauropod dinosaur, CPP 494, is made. It comes from the Serra da Galga Member, Marília Formation, near the locality of Peirópolis, Minas Gerais Estate, Brazil. This material was originally described in 2006, as belonging to an undetermined titanosaur, but distinguishable from known species on the basis of characters related to the laminar configuration and the development of the dorsal portion of the diapophysis. A detailed comparison of the material leads to reconsider these supposed differences as variations in the dorsal axial sequences, thus allowing assigning the vertebra CPP 494 to *Trigonosaurus pricei* Campos *et al.*, 2005, which is stratigraphically and geographically close. The issue of taxonomic differentiation based on axial characters described from isolated elements, without considering the sequential variation, is briefly discussed.

Key words: Trigonosaurus pricei*, dorsal vertebra, sequential variation.*

Resumen.- Se realiza una revisión de material correspondiente a una vértebra dorsal posterior de dinosaurio saurópodo titanosaurio, CPP 494. El mismo procede del Miembro Sierra da Galga, Formación Marília, de las cercanías de la localidad de Peirópolis, Estado de Minas Gerais, Brasil. Este material fue originalmente descrito en 2006, como correspondiente a un titanosaurio indeterminado, pero distinguible de las especies conocidas por una serie de características relacionadas a la conformación laminar y al desarrollo de la cara dorsal de las diapófisis. Una comparación detallada del material lleva a reconsiderar estas supuestas diferencias como variaciones existentes dentro de las secuencias axiales dorsales, permitiendo de este modo asignar la vértebra CPP 494 a *Trigonosaurus pricei* Campos *et al.*, 2005, el cual es muy próximo tanto geográfica como estratigráficamente. Se discute brevemente la problemática de la diferenciación taxonómica basada en caracteres axiales descritos a partir de elementos aislados, sin considerarse la variación secuencial.

Palabras clave: Trigonosaurus pricei*, vértebra dorsal, variación secuencial.*

As usual in derived sauropod dinosaurs, the lithostrotian titanosaurs display complex neural arches with multiple laminae and fossae in the dorsal vertebrae (Salgado *et al.*, 2006; Salgado & Powell, 2010). Variation in the configuration of the laminar neural arch is commonly used in the determination of specific taxa or used as synapomorphies of more inclusive clades (McIntosh, 1990; Salgado *et al.*, 1997; Bonaparte, 1999; Wilson, 2002; Upchurch *et al.*, 2004; Curry Rogers, 2005; Carballido *et al.*, 2011a; D'Emic, 2012; Mannion *et al.*, 2013), but the implications of the sequential variation are poorly analyzed for many taxa and can lead to errors in systematics (see discussion in Wilson, 2012).

In the present work, we discuss the taxonomic significance of the laminar complex of a dorsal vertebra (CPP 494) from the Late Cretaceous of Brazil, previously described by Santucci & Bertini (2006). Here we focus the comparison with the stratigraphically and geographically close titanosaurs *Trigonosaurus pricei* Campos *et al.* (2005) and *Uberabatitan riberoi* Salgado & Carvalho (2008). Additionally, the variation of the laminar complex in both articulated and incompletely known dorsal sequences, and the validity of characters associated with them, are discussed for lithostrotian titanosaurs.

Institutional Abbreviations

Argentina

MAU: Museo Argentino Urquiza, Rincón de Los Sauces, Neuquén

MCS: Museo Municipal de Cinco Saltos, Cinco Saltos, Río Negro

MPCA: Museo Provincial Carlos Ameghino, Cipolletti, Río Negro.

MUCPv: Museo de la Universidad Nacional del Comahue, Neuquén, Neuquén.

UNPSJB: Universidad Nacional de la Patagonia San Juan Bosco, Comodoro Rivadavia, Chubut.

Brazil

CPP: Centro de Pesquisas Paleontológicas Llewelyn Ivor Price, Peirópolis, Minas Gerais.

MCT: Museu de Ciências da Terra, Departamento Nacional de Produção Mineral, Rio de Janeiro.

Anatomical Abbreviations

acdl: anterior centrodiapophyseal lamina.
apcdl: accessory posterior centrodiapophyseal lamina.
aprl: accessory prespinal lamina.
aspdl: anterior spinodiapophyseal lamina.
pcpl: posterior centroparapophyseal lamina.
podl: postzygodiapophyseal lamina.
prl: prespinal lamina.
pspdl: posterior spinodiapophyseal lamina.
spdl: spinodiapophyseal lamina.
sprl: spinoprezygapophyseal lamina.

BACKGROUND

The lithostrotian sauropod *Trigonosaurus pricei* was named by Campos *et al.* (2005) and, to this date, is one of the most complete titanosaur taxon found in Brazil. The partial skeleton that constitutes the holotype (MCT 1488-R) and the associated paratype (MCT 1719-R) was previously known as DGM "series B" in the literature (Powell, 1987, 2003; Campos & Kellner, 1999). It comprises an articulated axial sequence from the posterior cervicals to the last dorsal, an articulated sacrum with ilium and several anterior and middle caudals.

Prior to the erection of the genus and species, this titanosaur has been commonly utilized in cladistic analysis (Salgado *et al.*, 1997; Sanz *et al.*, 1999, Powell, 2003; Curry Rogers, 2005). Shortly after, two posterior dorsal vertebrae, CPP 491 (a centrum) and 494 (a complete vertebra) were described by Santucci & Bertini (2006) as an unnamed, large titanosaur. They distinguished it from any previously described advanced titanosaur based on the absence of ventral widening or bifurcation of the posterior centrodiapophyseal laminae (*pcdl*). Additional differences were reported between the CCP material and *Trigonosaurus pricei*, including the existence of postzygaodiapophyseal laminae (*podl*), and the presence of a large area for muscular attachment on the dorsal portion of the diapophyses.

Lately, a new titanosaur was erected by Salgado & Carvalho (2008), *Uberabatitan riberoi*, represented by three specimens, and includes axial and appendicular material, thereby allowing comparison with many of the other South American titanosaurs. Salgado & Carvalho (2008) considered that CPP 491 and 494 probably belong to *Uberabatitan* or to a closely related form, as they mentioned a few similarities (alongside several differences) between them, but no formal association was proposed.

All the material previously mentioned was recovered in nearby sites north of the Peirópolis locality, Minas Gerais State, southeastern Brazil, and corresponding to different levels of the Serra da Galga Member, Marília Formation, upper unit of the Bauru Group, Late Cretaceous.

Despite the abundance of lithostrotian sauropods in the South American fossil record (Mannion & Otero, 2012), individuals preserving the complete dorsal axial sequence are rare, and only a few known taxa provide substantial information about the sequential variation in the configuration of the neural arches. Among South American forms, besides the *Trigonosaurus pricei* holotype, only three specimens preserve the complete dorsal axial sequence: *Overosaurus paradasorum* (MAU-Pv-CO-439; Coria *et al.*, 2013), *Futalognkosaurus dukei* (MUCPv 323, Calvo *et al.*, 2008a), and an undescribed species from the Late Cretaceous of Neuquén province (MAU-PV-AC-01, Calvo *et al.* 1997).

The last two specimens are actually not available for comparisons, since their dorsal axial sequences remain unpublished or briefly described. Partial dorsal axial sequences are also known for *Epachthosaurus sciuttoi* (UNPSJB-PV 920; Martínez *et al.*, 2004), *Neuquensaurus australis* (MCS-5; Salgado *et al.*, 2005), and *Bonitasaura salgadoi* (MPCA-460; Gallina 2011).

Some other taxa preserve multiple dorsal elements, such as *Argentinosaurus huinculensis*, but the correct position of the vertebrae in the sequence is problematic (Novas & Ezcurra, 2006), restricting their comparative value. Other taxa are represented by multiple specimens that were recovered mixed in the same quarry, obscuring the assignation to particular individuals, such as in *Saltasaurus loricatus* or *Muyelensaurus pecheni* (Powell, 1992; Calvo *et al.*, 2008b).

Here we follow Wilson (1999) and Salgado & Powell (2010) regarding the anatomical nomenclature of the laminae present in the titanosaurian dorsal vertebrae.

RESULTS AND DISCUSSION

Comparison between the holotype of *Trigonosaurus pricei* and CPP 494

The overall general shape and disposition of the centrum and neural arch in CPP 494 is similar to the most posterior dorsals of MCT 1488-R. Particular resemblance is displayed with the *T. pricei* tenth dorsal, since both have the same relative position of the diapophyses and parapophyses, the neural spine and the several laminae of the neural arch (Fig. 1).

Santucci & Bertini (2006) differenciated CPP 494 from *Trigonosaurus pricei* based on the presence of postzygodiapophyseal lamina (*podl*), centrodiapophyseal laminae not widened ventrally, and the presence of a large area for muscular attachment on the dorsal portion of the diapophysis in CPP 494.

Regarding the first character, although this lamina is absent in most of the dorsal vertebrae of MCC 1488-R, in the tenth vertebra a prominent lamina connecting the diapophysis with the postzygapophysis was identified, described and figured as the podl in Campos *et al.* (2005). In fact, the existence of an incipient podl in the two posteriormost dorsal vertebrae is even included in the original diagnosis of *Trigonosaurus pricei*. Salgado *et al.* (2006) reinterpreted it as an accessory unnamed lamina, but more recently Salgado & Powell (2010) objected to this interpretation and considered it as a true podl. Here we agree in interpreting this lamina as a podl. Regardless of the identity of this lamina in *Trigonosaurus*, it is evident that the same structure is present in CPP 494, displaying the same position, direction and length.

In relation to the second character, the absence in CPP 494 of "widening or bifurcation" of the posterior centrodiapophyseal laminae, supposedly opposite to the condition of *Andesaurus* and more derived titanosaurs as proposed by Salgado *et al.* (1997), is rejected because the same character state is found in the last two dorsal vertebrae of *Trigonosaurus pricei* (see below). This character can be better stated as the presence of an accessory posterior centrodiapophyseal lamina (*apcdl*) reaching the dorsocranial region of centrum, as proposed by Salgado *et al*. (2005), or a modified anterior centrodiapophyseal lamina (*acdl*) (i.e. Wilson & Upchurch, 2009).

Since in the caudalmost dorsal vertebrae the *pcpl* expand their posterior length to reach close to the caudodorsal area of the centrum, the

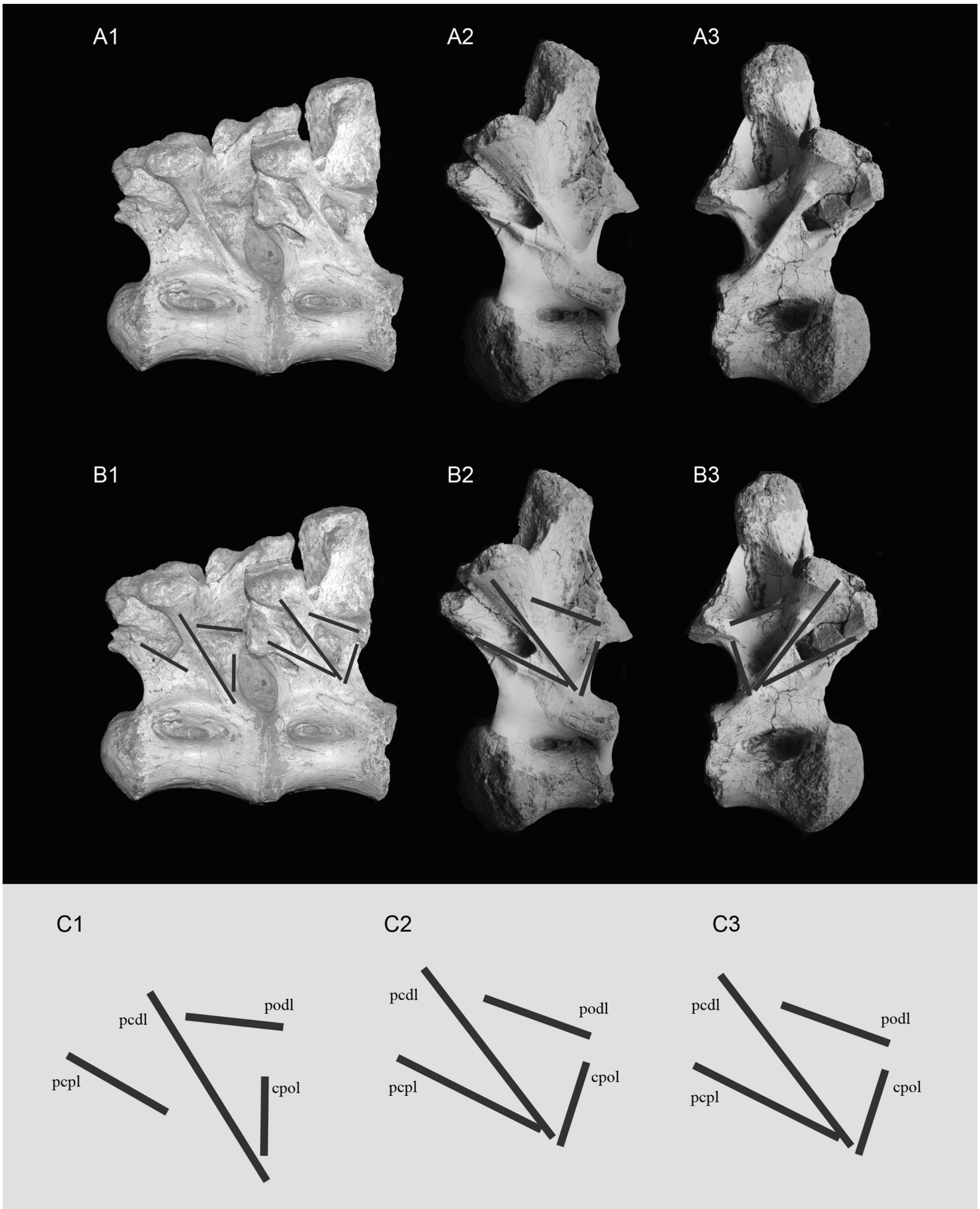

Figure 1. A. *Trigonosaurus pricei* posteriormost dorsal vertebrae. A1, ninth and tenth elements of MCT 1488-R in left lateral view; A2, tenth element of CPP 494 in left lateral view; A3, the same in right lateral view. B. Development of the principal lateral laminae discussed in the text. C. Comparison among the distribution of the laminae in: C1, ninth of MCT 1488-R; C2, tenth of MCT 1488-R; C3, tenth of CPP 494.

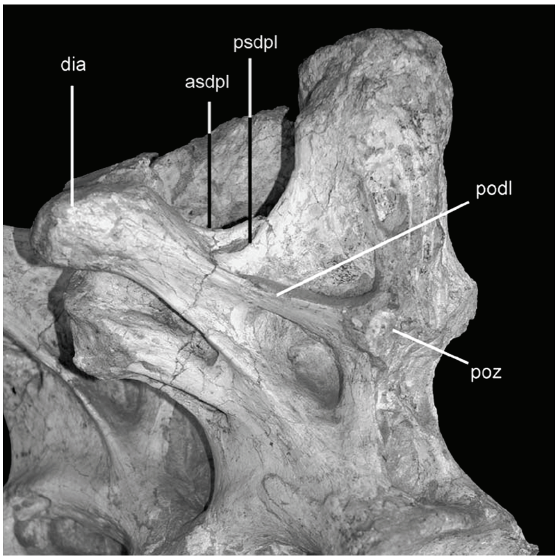

Figure 2. *Trigonosaurus pricei* holotype MCT 1488-R, tenth dorsal vertebra in left posterolateral view. Based on Campos *et al.* (2005). **Abbreviations**: *aspdl*: anterior spinodiapophyseal lamina; *pspdl*: posterior spinodiapophyseal lamina.

apcdl (or *acdl*) is restricted to a higher area of the neural arch as in *Overosaurus* and *Rapetosaurus*, or laking, as in *Trigonosaurus*, *Neuquensaurus*, *Saltasaurus* and *Muyelensaurus* (Coria *et al*., 2013; Curry Rogers, 2009; Salgado *et al.*, 2005; Powell, 1992; Juárez Valieri, pers. obs.). The assumption of the presence of this character as synapomorphic of Titanosauria has to be dismissed, since it is present in more basal somphospondylians and even basal macronarians (Carballido *et al.*, 2011b; Mannion *et al.*, 2013) and reviewed in their precise definition, restricting their validity to anterior to middle dorsal vertebrae.

Then, the absence of the *apcdl* in CPP 494 is considered here as evidence of its caudal position among dorsals. In fact, the morphology, length, and placement of the centrodiapophyseal laminae are the same between the tenth dorsal vertebra of MCC 1488-R and CPP 494.

Finally, the third character proposed as differentiating MCC 1488-R and CPP 494, pertaining to the presence of a large area for muscular attachment on the dorsal portion of the diapophysis, is also present in the ninth and tenth dorsal of *Trigonosaurus*, which are clearly visible in dorsal view (Powell 2003, pl. 15, fig. 5). In fact, this feature characterizes most somphospondylians (Sanz *et al.*, 1999; D'Emic, 2012).

The existence of an anterior spinodiapophyseal lamina (*aspdl*) (or a displaced postzygodiapophyseal lamina (*podl*) *sensu* Salgado *et al.* 2006) was reported on the right side of the neural arch of CPP 494. It was interpreted as an abnormality by Santucci and Bertini (2006, p. 355). Salgado and Carvalho (2008) interpreted this as equivalent to their *podl+spdl* (here *aspdl+pspdl*), that is present in *Uberabatitan riberoi* and *Trigonosaurus pricei*. In the holotype of *Trigonosaurus pricei* the *aspdl+pspdl* complex is prominent from the fifth to the eight dorsal vertebrae as reported by previous authors, although here we note the presence of the two lamina in the tenth dorsal vertebra too (Fig. 2). Thus, if CPP 494 is considered homologous to the tenth dorsal of MCC 1488-R and belonging to the same taxon, the existence of the *aspdl+pspdl* complex in the left face should be considered as result of individual variation.

This assumption is supported by the morphology of the right side of the neural arch of CPP 494, which is agrees with the morphology present in the *Trigonosaurus pricei* holotype. Other reports of lithostrotian titanosaurs with asymmetrical configuration of the laminar complex in dorsal vertebrae were given for *Pitekunsaurus macayai* (Filippi & Garrido, 2008), undescribed titanosaur material from Marília (Santucci & Bertini, 2006), and is also present in other species such as *Muyelensaurus pecheni* (Fig. 3), *Rinconsaurus caudamirus* and *Bonitasaura salgadoi* (MAU-PV-9 and MPCA-460; Juárez Valieri, pers. obs.; Gallina 2011).

A striking feature of CPP 494 is the presence of two paired laminae, parallel to the pres-

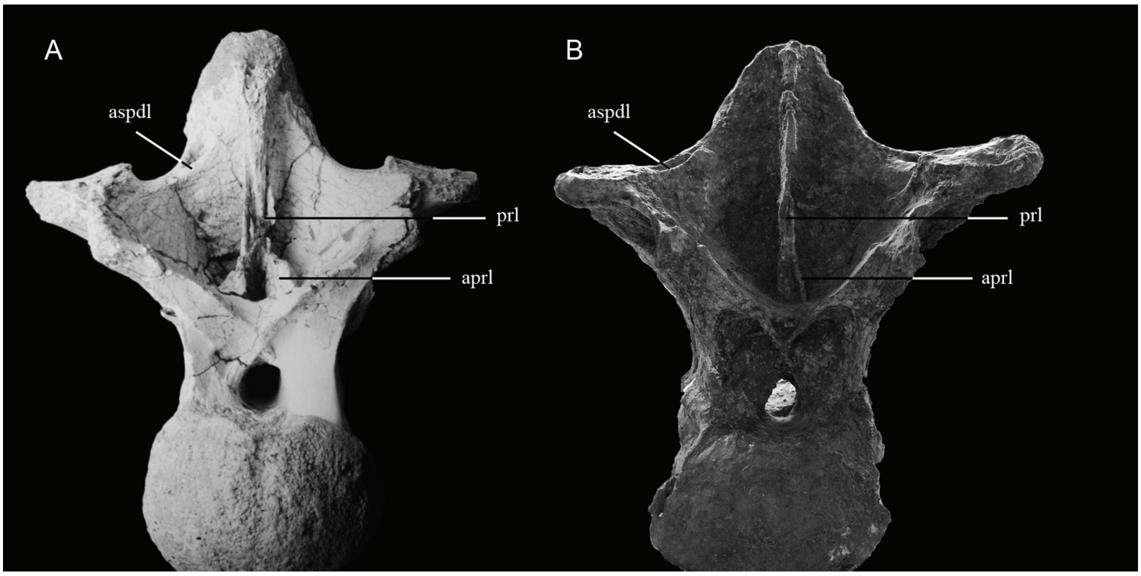

Figure 3. A. Posterior dorsal vertebra of *Trigonosaurus pricei*, CPP 494 in anterior view. B. Posterior dorsal vertebra of *Muyelensaurus pecheni*, MAU-PV-412 in anterior view. Not to the same scale. **Abbreviations**: *aprl*: accessory prespinal lamina; *aspdl*: anterior spinodiapophyseal lamina; *prl*: prespinal lamina.

pinal lamina (*prl*). Santucci & Bertini (2006) considered these as "accessory prespinal lamina". Salgado & Carvalho (2008) suggested that these elements could be homologous with the spinoprezygapophyseal laminae. The *sprl* is commonly recorded in the cranialmost dorsal vertebrae of lithostrotians, and has been reported in the mid-dorsal elements of *Uberabatitan riberoi*.

Personal observation of the *Muyelensaurus pecheni* material, housed in the MAU collection, allows us to describe a posterior dorsal vertebra (MAU-PV-412), possibly the ninth or tenth element based on the laminar composition and relative position of the neural spine, diapophysis and parapophysis, displaying the two laminae parallel to the *prl* (Fig. 2). As noted in Calvo *et al.* (2008b), some of the posterior dorsal vertebrae of *Muyelensaurus* display two short laminae that join at the base of the prl, displaying a triradiate structure, which are treated as accessory laminae. These short laminae are here interpreted as homologous to the condition present in CPP 494, and considered as accessory prespinal laminae (*aprl*) as in Santucci & Bertini (2006), since it is not possible to confirm their homology with the true sprl.

The presence of the *aprl* in the tenth dorsal vertebra of *Trigonosaurus* holotype cannot be determined as it is in contact with the precedent element. It is clear that these accessory elements are present in CPP 494, MAU-PV-412, and the larger *Uberabatitan* specimens, all being putatively adults individuals, so they maybe can be considered as structures of additional support to the ligaments which develop in mature ontogenetic stages.

CONCLUSION

The presence, orientation and shape of the laminae and fossae displayed in the neural arch, and the shape of the centrum and pleurocoel of the dorsal vertebra CPP 494, is concordant with the last dorsal of *Trigonosaurus pricei*, and thus CPP 494 is assigned to this taxon. The presence of an additional, larger specimen of *Trigonosaurus pricei* is not unexpected, as it was recovered in a locality very near from that of the holotype and belongs to the same levels of the Marilia Formation.

Based on the strong changes in the configuration of the neural arch along the dorsal sequences observed in more complete titanosaurian taxa, the necessity of review of several characters currently used in cladistic analysis of lithostrotian or even titanosaurian sauropods is evident. Lastly, extreme caution is suggested in the codification of axial characters for taxa where complete sequences are unknown.

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