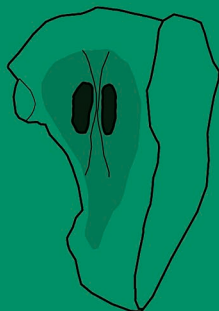


On a dicraeosaurid specimen from the Mulichinco Formation (Valanginian, Neuquén Basin) of Argentina and phylogenetic relationships of the South American dicraeosaurids (Sauropoda, Diplodocoidea)

Guillermo J. WINDHOLZ, Rodolfo A. CORIA, Flavio BELLARDINI, Mattia A. BAIANO, Diego PINO, Francisco ORTEGA & Philip J. CURRIE



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On a dicraeosaurid specimen from the Mulichinco Formation (Valanginian, Neuquén Basin) of Argentina and phylogenetic relationships of the South American dicraeosaurids (Sauropoda, Diplodocoidea)

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ABSTRACT

The osteology of *Pilmatueia faundezi* Coria, Windholz, Ortega & Currie, 2019, a dicraeosaurid sauropod from the Lower Cretaceous of Patagonia, is reassessed from the perspective of a new specimen (MLL-Pv-010) that provides additional information on the axial skeleton and the pectoral girdle. The specimen MLL-Pv-010 is composed of three articulated anterior-middle cervical vertebrae (with their respective ribs in position and an associated fourth rib), seven dorsal vertebrae with associated dorsal ribs, a distal caudal vertebra, a left scapula and the proximal end of a right scapula. The new specimen shows features, especially in the middle cervical vertebrae, that link it to *Pilmatueia faundezi*. Additionally, the specimen MLL-Pv-010 shows features previously unknown for the species, such as the morphology and orientation of the bifid neural spines of the anterior and mid-cervical vertebrae. The information obtained from the specimen MLL-Pv-010 allows us to propose an expanded diagnosis of *Pilmatueia faundezi*. Moreover, two phylogenetic analyses focusing on South American dicraeosaurids show that *Pilmatueia* Coria, Windholz, Ortega & Currie, 2019 is well nested within Dicraeosauridae Huene, 1927. One of our phylogenetic hypotheses differs from previous contributions in showing South American dicraeosaurids as a monophyletic group. However, in the second hypothesis these are not recovered as a natural group. We think that it is reasonable to recover a South American dicraeosaurid clade, and that eventually it will be best supported once more evidence is recovered.

KEY WORDS

Sauropoda,
Dicraeosauridae,
Pilmatueia faundezi,
Lower Cretaceous,
Mulichinco Formation,
new specimen.

RÉSUMÉ

Spécimen de dicraéosauridé de la Formation Mulichinco (Valanginien, Bassin de Neuquén) d'Argentine et relations phylogénétiques des dicraéosauridés sud-américains (Sauropoda, Diplodocoidea).

L'ostéologie de *Pilmatueia faundezi* Coria, Windholz, Ortega & Currie, 2019, un dicraéosauridé du Crétacé inférieur de la Patagonie, est réévaluée sur la base de l'analyse d'un nouveau spécimen (MLL-Pv-010) qui fournit des informations supplémentaires sur le squelette axial et la ceinture pectorale. Le spécimen MLL-Pv-010 est composé de trois vertèbres cervicales antérieures-médianes articulées (avec leurs côtes respectives en position et une quatrième côte associée), sept vertèbres dorsales avec les côtes dorsales associées, une vertèbre caudale distale, une omoplate gauche et l'extrémité proximale d'une omoplate droite. Le nouveau spécimen présente des caractéristiques, notamment au niveau des vertèbres cervicales moyennes, qui le relie à *Pilmatueia faundezi*. Par ailleurs, le spécimen MLL-Pv-010 présente des caractéristiques jusqu'alors inconnues pour l'espèce, telles que la morphologie et l'orientation des épines neurales bifides des vertèbres cervicales antérieures et moyennes. Les informations obtenues à partir du spécimen MLL-Pv-010 nous permettent de proposer un diagnostic élargi de *Pilmatueia faundezi*. De plus, deux analyses phylogénétiques portant sur les dicraéosauridés sud-américains montrent que *Pilmatueia* Coria, Windholz, Ortega & Currie, 2019 fait bien partie des Dicraeosauridae Huene, 1927. Une de nos hypothèses phylogénétiques diffère des contributions précédentes en montrant les dicraéosauridés sud-américains comme un groupe monophylétique. Cependant, dans la deuxième hypothèse, ils ne sont pas repris comme un groupe naturel. Nous pensons qu'il est raisonnable de considérer un clade de dicraéosauridés sud-américains, et que cette hypothèse sera mieux sous-tendue et affinée lorsque plus de données seront disponibles.

MOTS CLÉS

Sauropoda,
Dicraeosauridae,
Pilmatueia faundezi,
Crétacé inférieur,
Formation Mulichinco,
nouveau spécimen.

INTRODUCTION

Dicraeosauridae Huene, 1927 (Sauropoda, Diplodocoidea) is a clade of neosauropod dinosaurs that has been defined as all diplodocoids closer to *Dicraeosaurus* Janensch, 1914 than to *Diplodocus* Marsh, 1878 (Serenó 1998). The biochron of this clade corresponds to the Middle Jurassic - Lower Cretaceous, and its records come from Africa, Asia, North

America, and South America (Janensch 1914; Salgado & Bonaparte 1991; Upchurch 1995; Wilson 2002; Harris & Dodson 2004; Rauhut *et al.* 2005; Apesteguía 2007; Whitlock 2011; Tschopp *et al.* 2015; Gallina 2016; Xu *et al.* 2018; Coria *et al.* 2019; Gallina *et al.* 2019). Interestingly, in the Lower Cretaceous of Patagonia in Argentina, this group was a conspicuous component of the terrestrial ecosystems. Its diversity is represented so far by four species: *Amar-*

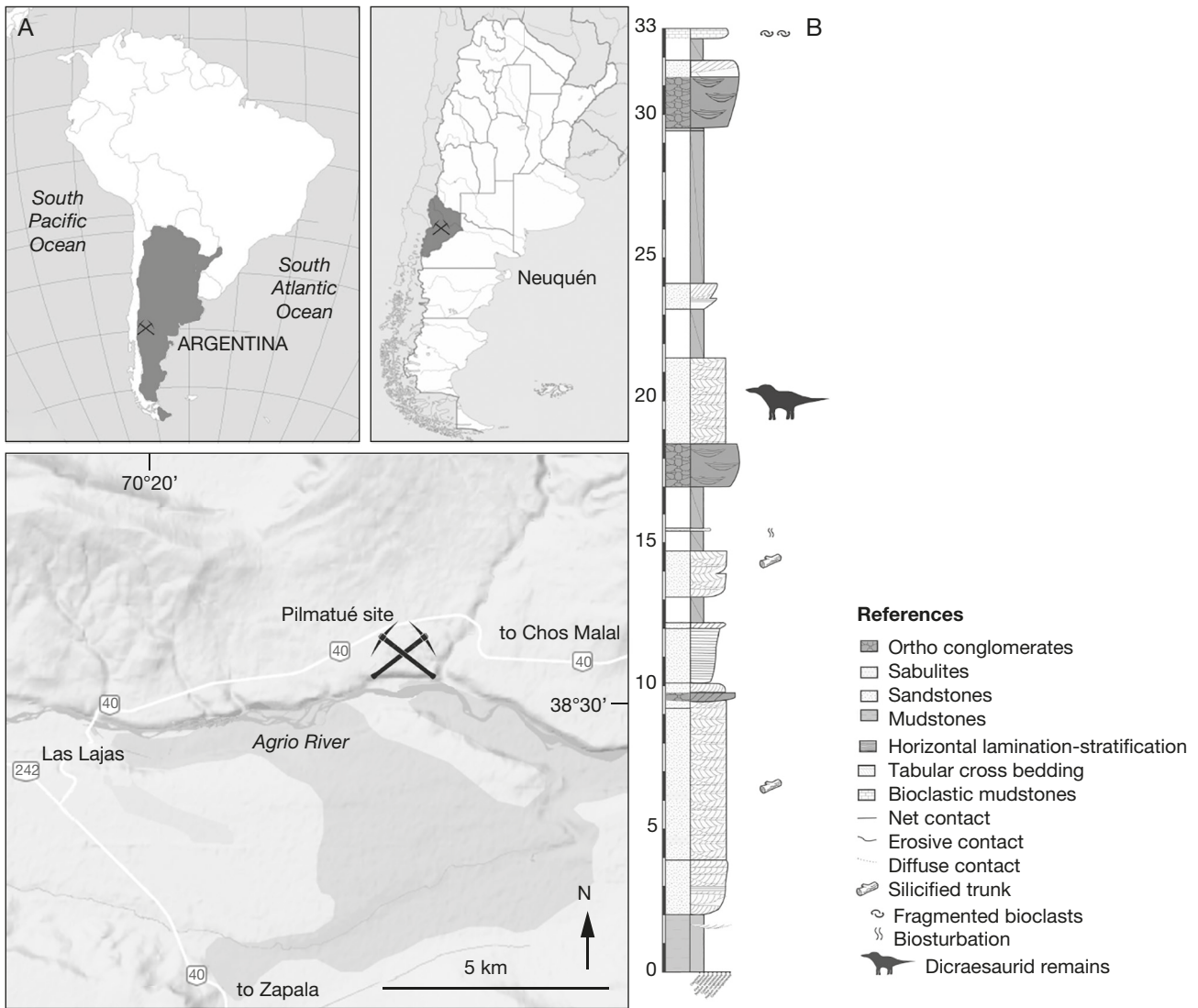


FIG. 1. — Geographical and geological provenance of *Pilmatueia faundezi* Coria, Windholz, Ortega & Currie, 2019 and the new specimen MLL-Pv-010: **A**, fossil site; **B**, stratigraphic column.

gasaurus cazau Salgado & Bonaparte, 1991; *Amargatitanis macni* Apesteguía, 2007; *Bajadasaurus pronuspimax* Gallina, Apesteguía, Canale & Haluza, 2019, and *Pilmatueia faundezi* Coria, Windholz, Ortega & Currie, 2019.

Pilmatueia faundezi (Coria *et al.* 2019) is a recently reported dicraeosaurid sauropod from the Lower Cretaceous (Valanginian) of the Neuquén Basin, Argentina. It was originally based upon a posterior dorsal vertebra (holotype), a posterior cervical vertebra (paratype), a mid-cervical vertebra, a mid-dorsal neural arch, and two mid-caudal vertebrae (referred material). A new dicraeosaurid specimen (MLL-Pv-010) collected from the same site and geological formation as the type materials of *Pilmatueia* Coria, Windholz, Ortega & Currie, 2019 is described here. The new specimen is a partially articulated trunk and includes presacral vertebrae (three articulated anterior-middle cervical vertebrae, with their respective ribs in position and an associated fourth rib, and seven dorsal vertebrae with associated dorsal ribs), a posterior caudal vertebra and both scapulae.

The new specimen MLL-Pv-010 shares with *Pilmatueia* the presence of anteriorly and posteriorly bifid ventral keels in the anterior and mid-cervical vertebrae, which is an unidentified character in other dicraeosaurids that justifies reference of the new specimen (MLL-Pv-010) to this species. Simultaneously, the cervical vertebrae of MLL-Pv-010 show features unknown to date for *Pilmatueia*, such as the morphology and orientation of the bifid neural spines. Furthermore, a distal caudal vertebra and elements from the appendicular skeleton (in this case, both scapulae) expand the anatomical knowledge of this species.

Historically, dicraeosaurid diversity consisted of a handful of taxa (Janensch 1914; Salgado & Bonaparte 1991). Recently, the number of species described has grown substantially, which has promoted the inclusion of dicraeosaurid taxa in various phylogenetic analyses (Gallina 2016; Xu *et al.* 2018; Coria *et al.* 2019; Gallina *et al.* 2019; Whitlock & Wilson Mantilla 2020). There is some agreement in previous phylogenies that show *Amargasaurus* Salgado & Bonaparte,

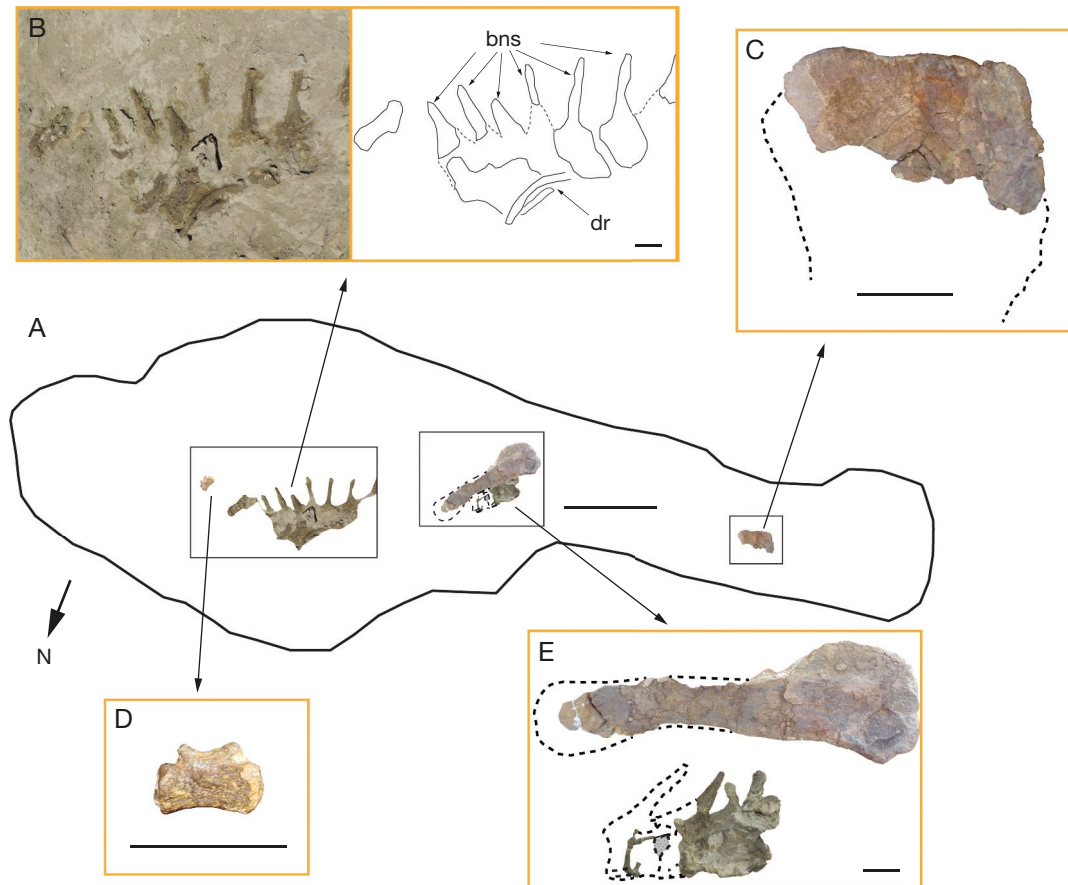


FIG. 2. — Map showing the association of the remains of MLL-Pv-010 in the field: **A**, quarry detail; **B**, dorsal vertebrae; **C**, right scapula; **D**, distal caudal vertebra; **E**, left scapula and cervical vertebrae. Abbreviations: **bns**, bifid neural spine; **dr**, dorsal ribs. Scale bars: A, 1 m; B-E, 10 cm.

TABLE 1. — Measurements (in cm) of vertebral elements of *Pilmatueia* Coria, Windholz, Ortega & Currie, 2019 (MLL-Pv-010). Abbreviations: *, preserved; –, unknown; **CaV**, caudal vertebra; **CV**, cervical vertebra.

Vertebral elements	CV 4	CV 5	CaV
Total height	30*	36*	4.5
Centrum length	14.5	–	6
Anterior centrum height	6	6	3.5
Anterior centrum width	–	–	3.5
Posterior centrum height	5.5	–	3.5
Posterior centrum width	–	–	3.5
Minimum centrum ventral width	5	–	2
Bifid neural spine height	15	15	–

1991, *Brachytrachelopan* Rauhut, Remes, Fechner, Cladera & Puerta, 2005 and *Dicraeosaurus* as a monophyletic group, with *Bajadasaurus* Gallina *et al.*, 2019 and *Pilmatueia* in a less derived position, and *Lingwulong* Xu, Upchurch, Manion, Barrett, Regalado-Fernandez, Mo, Ma & Liu, 2018 and *Suuwassea* Harris & Dodson, 2004 as the most basal forms (Gallina 2016; Xu *et al.* 2018; Gallina *et al.* 2019; Whitlock & Wilson Mantilla 2020). However, Coria *et al.* (2019) recovered *Pilmatueia* as a sister taxon to *Amargasaurus* in a more derived position, with *Brachytrachelopan*, *Dicraeosaurus*, *Dyslocosaurus* and *Suuwassea* as sister taxa. Also, *Amargatitanis* Apesteguía, 2007 is only considered in two phylogenies,

where it is recovered as a sister taxon to *Suuwassea* (Gallina 2016; Whitlock & Wilson Mantilla 2020).

Our phylogenetic hypotheses recover *Pilmatueia faundezi* well nested within Dicraeosauridae. In one of them, this taxon is recovered phylogenetically closer to *Amargatitanis* and *Bajadasaurus*, while in the other one, it is sister taxon to *Amargatitanis* and *Suuwassea*. Also, in one of our analyses the South American dicraeosaurids were recovered phylogenetically far from each other, as in previous contributions (Rauhut *et al.* 2005; Gallina 2016; Xu *et al.* 2018; Coria *et al.* 2019; Gallina *et al.* 2019; Whitlock & Wilson Mantilla 2020), whereas, in the other one these taxa cluster together in a natural group (Appendix 1).

MATERIAL AND METHODS

The identifications of the presacral vertebrae were based upon the relative positions of the parapophyses on the vertebral centra, compared with the complete presacral vertebral series of the holotype specimen of *Dicraeosaurus hansemanni* Janensch, 1914 (Janensch 1929) and personal observations on *Amargasaurus cazaui* (MACN-N 15). For the osteological description we mainly followed the nomenclature present in Romer (1956) and Upchurch *et al.* (2004a). Also, the

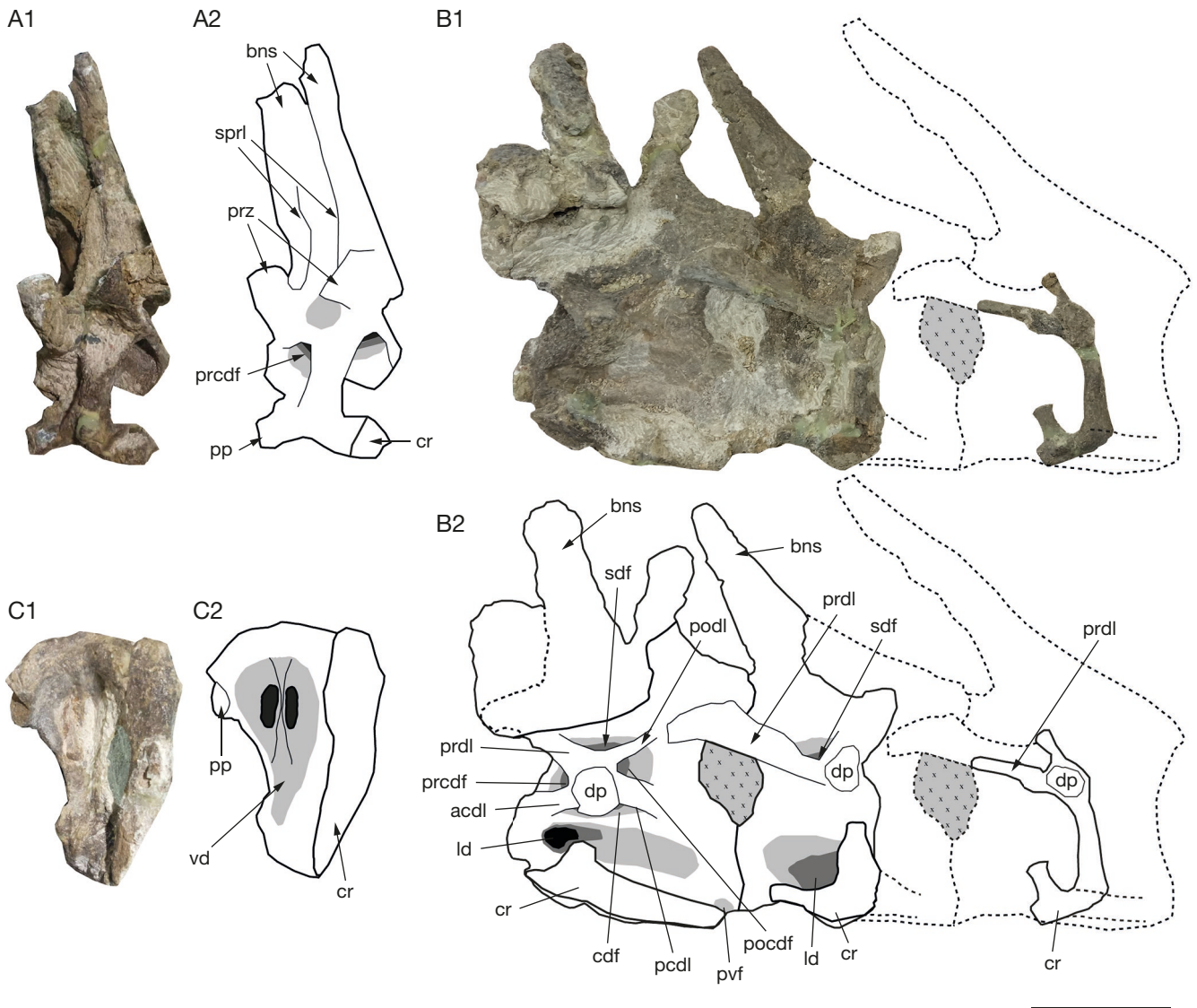


FIG. 3. — Articulated fourth, fifth and sixth cervical vertebrae of MLL-Pv-010: **A1, A2**, fourth cervical vertebra in anterior view; **B1, B2**, fourth, fifth and sixth cervical vertebrae in left lateral view; **C1, C2**, fourth cervical vertebra in ventral view. Abbreviations: **acdl**, anterior centrodiapophyseal lamina; **bns**, bifid neural spine; **cdf**, centrodiapophyseal fossa; **cr**, cervical rib; **dp**, diapophysis; **ld**, lateral depression; **pcdl**, posterior centrodiapophyseal lamina; **pcocdf**, postzygapophyseal centrodiapophyseal fossa; **podl**, postzygodiapophyseal lamina; **pp**, parapophysis; **prcdf**, prezygapophyseal centrodiapophyseal fossa; **prdl**, prezygodiapophyseal lamina; **prz**, prezygapophysis; **pvf**, posteroventral fossa; **sdf**, spinodiapophyseal fossa; **sprl**, spinoprezygapophyseal lamina; **vd**, ventral depression. Scale bar: 10 cm.

nomenclature of the vertebral laminae and fossae proposed by Wilson (1999, 2012) and Wilson *et al.* (2011) was followed.

The specimen MLL-Pv-010 was recovered approximately 100 m from the paratype and referred specimens of *Pilmatueia*, and about 1000 m from the holotype (Fig. 1). All the elements come from the same quarry, and were found at the same stratigraphic level (Fig. 2). The degree of association (some bones were articulated), the comparative sizes (Table 1), and the absence of repeated bones show that the elements described belong to a single specimen (MLL-Pv-010).

In order to explore the phylogenetic relationships of *Pilmatueia faundezi*, the new anatomical information provided by MLL-Pv-010 was scored for two phylogenetic datasets currently available for diplodocoids. In the first instance, the phylogenetic matrix is based on that of Tschopp & Mateus (2017), although several of the characters have been edited

and/or rescored. *Amargatitanis macni* (Apesteguía 2007; MACN PV N53), *Bajadasaurus pronuspinax* (Gallina *et al.* 2019; MMCh-PV 75), *Lingwulong shenqi* Xu, Upchurch, Mannion, Barrett, Regalado-Fernandez, Mo, Ma & Liu, 2018 (Xu *et al.* 2018) and *Pilmatueia faundezi* (Coria *et al.* 2019; MLL-Pv-002; 004; 005; 009; 010; 012; 015; 016; 017) were added. Finally, five new characters (characters 490, 491, 492, 493 and 494) were incorporated. Thus, the matrix now consists of 494 cranial and postcranial characters distributed among 39 OTUs (see Appendix 11). The phylogenetic analysis was carried out using TNT software, version 1.5 (Goloboff *et al.* 2008; Goloboff & Catalano 2016). The characters were equally weighted, and multistate characters are unordered. At the same time, the new specimen (MLL-Pv-010) was scored for *Pilmatueia* in the Whitlock & Wilson Mantilla (2020) matrix (see Appendix 12). This data matrix

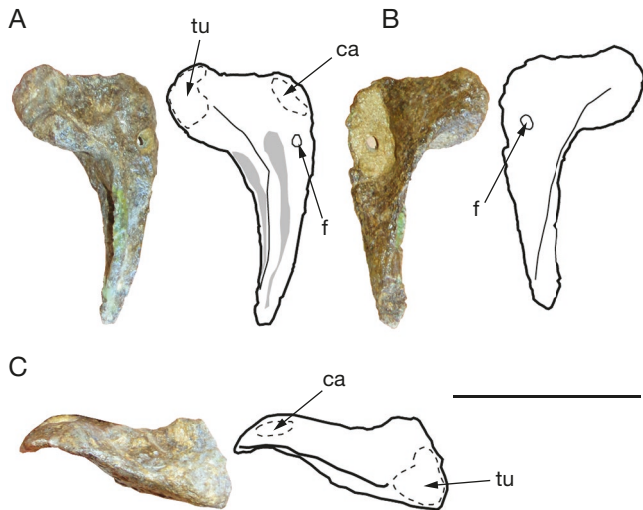


FIG. 4. — Cervical rib of MLL-Pv-010 specimen, mid-cervical rib in: **A**, medial; **B**, lateral; **C**, proximal views. Abbreviations: **ca**, capitulum; **f**, foramen; **tu**, tuberculum. Scale bar: 5 cm.

of 203 cranial and postcranial characters distributed among 35 taxa was analyzed using the same software and commands as in the previous analysis.

ABBREVIATIONS

Institutional abbreviations

MACN	Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina;
MLL	Museo Municipal de Las Lajas, Las Lajas, Neuquén Province, Argentina;
MMCH	Museo Municipal Ernesto Bachmann, Villa El Chocón, Neuquén Province, Argentina;
MOZ	Museo Provincial de Ciencias Naturales Dr. Prof. Juan A. Olsacher, Zapala, Neuquén Province, Argentina;
MPCA	Museo Provincial Carlos Ameghino, Cipolletti, Río Negro Province, Argentina;
PEF	Museo Paleontológico Egidio Feruglio, Trelew, Chubut Province, Argentina.

Other abbreviations

acdl	anterior centrodiapophyseal;
cdf	deep centrodiapophyseal fossae;
CI	consistency index;
MPTs	most parsimonious trees;
pcdl	posterior centrodiapophyseal;
podl	postzygodiapophyseal laminae;
prdl	prezygodiapophyseal laminae;
precdf	prezygapophyseal centrodiapophyseal fossae;
pocdf	postzygapophyseal centrodiapophyseal fossae;
RI	retention index;
sdf	spinodiapophyseal fossae.

SYSTEMATIC PALAEOONTOLOGY

Superorder DINOSAURIA Owen, 1842
 Order SAURISCHIA Seeley, 1887
 Suborder SAUROPODA Marsh, 1878
 Clade NEOSAUROPODA Bonaparte, 1986
 Superfamily DIPLODOCOIDEA Marsh, 1884

Clade FLAGELLICAUDATA Harris & Dodson, 2004
 Family DICRAEOSAURIDAE Huene, 1927

Pilmatueia faundezi

Coria, Windholz, Ortega & Currie, 2019

Pilmatueia faundezi Coria, Windholz, Ortega & Currie, 2019: 33.

MATERIAL TYPE. — **Holotype**. MLL-Pv-005, almost complete posterior dorsal vertebra (Coria *et al.* 2019).

Paratype. MLL-Pv-002, posterior cervical vertebra (Coria *et al.* 2019).

REFERRED SPECIMEN. — MLL-Pv-010 is an incomplete specimen consisting of three articulated anterior-middle cervical vertebrae (with their respective ribs in position and an associated fourth rib), seven dorsal vertebrae with associated dorsal ribs, a distal caudal vertebra, a left scapula and the proximal end of a right scapula.

EXPANDED DIAGNOSIS. — *Pilmatueia faundezi* is unique in having anterior and mid-cervical vertebrae with anteriorly and posteriorly forked ventral keels (new, MLL-Pv-010); cervico-dorsal vertebrae with dorsoventrally oriented ridges on the anterior surfaces of anterior centrodiapophyseal laminae; posterior dorsal vertebrae with deep fossae located posteriorly at the bases of the bifid neural spines separated by thick, low, sagittal laminae; the proximal end of the mid-cervical rib has a foramen in its medial surface (new, MLL-Pv-010); and a prominent crest on the medial surface of the scapula is close to the acromial process (new, MLL-Pv-010). Furthermore, after the phylogenetic analysis using TNT, *Pilmatueia* shows the presence of bifurcated posterior centrodiapophyseal laminae in mid-cervical vertebrae (also present in some diplodocids and *Giraffatitan*, character 194); accessory laminae in region between posterior centrodiapophyseal lamina and posterior centroparapophyseal lamina in posterior dorsal vertebrae (unknown in *Bajadasaurus*, present in *Demandasaurus* and some macronarians, character 267); and three infrahyposphenal laminae in each dorsal vertebra (also present in *Apatosaurus ajax*, character 493).

LOCALITY AND HORIZON. — The Pilmatue locality is 9 km northwest of Las Lajas, Neuquén Province, Argentina (Fig. 1) and includes extensive outcrops of the Mulichinco Formation (Stipanovic *et al.* 1968; Schwarz 2003; Schwarz *et al.* 2011). The fossil accumulation is hosted in a sandy body composed of sets of lenticular beds that conform co-sets of tabular geometry, composed of fine conglomerates to coarse-grained sandstones with tangential cross-bedding (Pino *et al.* 2021).

RESULTS

CERVICAL ELEMENTS

The new specimen (MLL-Pv-010) has three articulated anterior-middle cervical vertebrae (putatively the fourth, fifth and sixth ones) in articulation with their respective left ribs (Fig. 3). Also, another cervical rib on the left side was preserved, possibly from a subsequent cervical vertebra (cervical rib 7) (Fig. 4). The vertebrae are well preserved, although transversely crushed. The parapophyses are located in the anteroventral regions of the centra.

In anterior view, the vertebral centrum of the fourth cervical vertebra is taller than wide. The parapophyses are robust and project lateroventrally, as in the fourth cervical vertebra of *Amargasaurus* (MACN-N 15). Both the centro-prezygapophyseal and anterior centrodiapophyseal laminae frame a wide prezygapophyseal centrodiapophyseal fossa

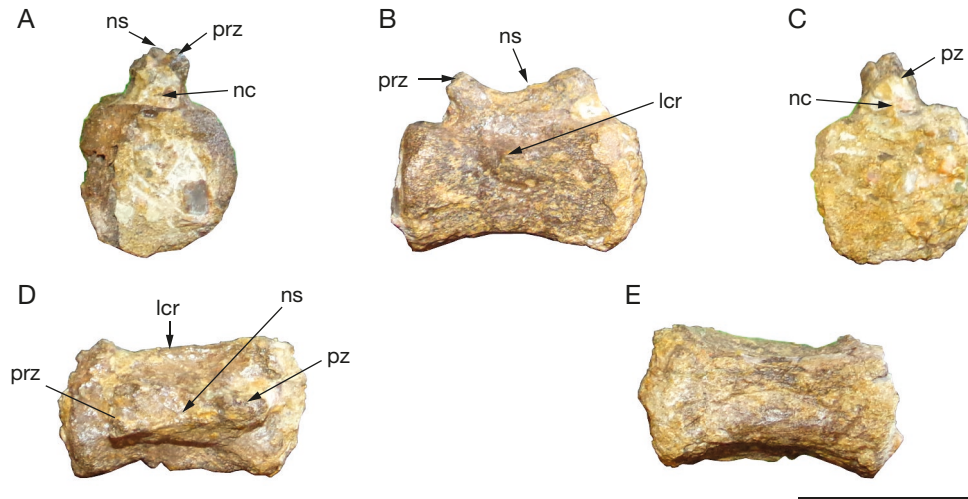


FIG. 5. — Distal caudal vertebra of MLL-Pv-010 in: **A**, anterior; **B**, lateral; **C**, posterior; **D**, dorsal; **E**, ventral views. Abbreviations: **lcr**, lateral crest; **nc**, neural canal; **ns**, neural spine; **prz**, prezygapophysis; **pz**, postzygapophysis. Scale bar: 5 cm.

that has a triangular outline. The articular surfaces of the prezygapophyses are small in comparison with those of other diplodocoid taxa, and likely diverged dorsolaterally (before being deformed) as in the mid-cervical vertebra MLL-Pv-004 of *Pilmatueia faundezi*. In other diplodocoid sauropods like *Dicraeosaurus*, *Diplodocus* and MMCH-Pv-49 (Rebbachisauridae indet.), the articular surfaces of the prezygapophyses are more developed and dorsomedially oriented (Hatcher 1901; Janensch 1929). In anterior view, the bifid neural spine is straight and projects dorsally.

In lateral view, the vertebral centra of the fourth and fifth cervical vertebrae are strongly opisthocoelous, as in the cervical vertebrae of other sauropods, such as *Amargasaurus* (MACN-N 15), *Lavocatisaurus* (MMCH-Pv 63) and *Leinkupal* Gallina, Apesteguía, Haluza & Canale, 2014 (MOZ-Pv1232; Gallina *et al.* 2014). Each is slightly longer than tall and has a wide lateral depression. In the anterior region of each lateral depression is a deep cavity, like a pleurocoel, reminiscent of those present in the cervical vertebrae of *Pilmatueia* (MLL-Pv-004) and *Amargasaurus* (MACN-N 15). The lateral depressions lack foramina, indicating absence or a low degree of pneumaticity in the middle region of the neck, as previously suggested for *Pilmatueia* (Windholz *et al.* 2019). The centrum of the fourth cervical vertebra bears a small accessory fossa posteroventral to the lateral depression, which is a feature shared with other flagellicaudatans such as *Pilmatueia* (MLL-Pv-004), *Amargasaurus* (MACN-N 15), *Australodocus* (Whitlock 2011), *Kaatedocus* Tschopp & Mateus, 2013 and *Lingwulong* (Xu *et al.* 2018).

The neural arches bear the typical configurations of laminae and fossae previously described in other sauropods, with well-developed anterior and posterior centrodiapophyseal (acdl, pcdl), prezygodiapophyseal (prdl), and postzygodiapophyseal (podl) laminae. These laminae define deep centrodiapophyseal (cdf), prezygapophyseal centrodiapophyseal (prcdf), postzygapophyseal centrodiapophyseal (pocdf) and spinodiapophyseal (sdf) fossae, all of which have triangular outlines.

The centroprezygapophyseal laminae are broad, robust and project anterodorsally, whereas the centropostzygapophyseal laminae extend dorsoventrally and are column-like.

The bifid neural spines of the fourth and fifth cervical vertebrae are at least twice as high as their respective vertebral centra, although their distal ends are missing. These structures are mediolaterally compressed and project anterodorsally, as in the anterior and middle cervical vertebrae of *Bajadasaurus* (MMCH-Pv-75), *Brachytrachelopan* (MPEF-PV 1716; Rauhut *et al.* 2005) and *Dicraeosaurus* (Janensch 1929). In contrast, the bifid neural spines of the anterior and middle cervical vertebrae in *Amargasaurus* project posterodorsally (MACN-N 15).

The ventral surfaces of the centra are poorly preserved due to weathering. However, the ventral surface of the centrum in the fourth cervical vertebra is deeply excavated by a large, anteroposteriorly long depression. In the deepest part of this depression are two small foramina, separated by an anteriorly and posteriorly bifurcated ventral keel. Ventral keels are widely distributed features within Sauropoda. Diplodocoids tend to have simple keels, as in *Kaatedocus* (Tschopp & Mateus 2013), and a posteriorly bifid keel occurs in *Dicraeosaurus* (Janensch 1929). Thus, an anteriorly and posteriorly bifurcated ventral keel is only known to occur in MLL-Pv-004 and MLL-Pv-010, both specimens referred to *Pilmatueia*.

The cervical ribs are robust and lack most of their distal shafts (Fig. 3), with the exception of one cervical rib (Fig. 4). This cervical rib is short, as in other diplodocoid sauropods such as *Amargasaurus* (MACN-N 15), *Apatosaurus* (Marsh 1877), *Dicraeosaurus* (Janensch 1929), *Diplodocus* (Hatcher 1901), *Lavocatisaurus* (MOZ-Pv1232; Canudo *et al.* 2018), *Leinkupal* (MMCH-Pv 63; Gallina *et al.* 2014), *Suuwassea* (Harris 2006) and MMCH-Pv-49 (Rebbachisauridae indet.). This cervical rib has a capitulum with a reduced articular surface, unlike other dicraeosaurid sauropods, and lacks the anterior process observed in the cervical ribs of *Amargasaurus* (MACN-N 15) and *Dicraeosaurus* (Janensch

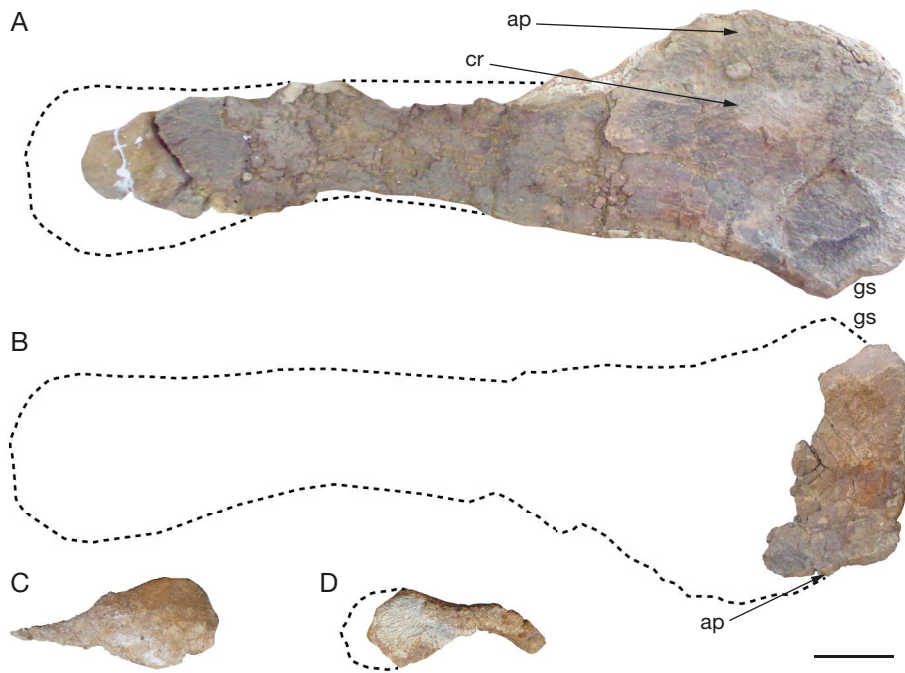


FIG. 6. — Right and left scapulae of MLL-Pv-010: **A**, left scapula in medial view; **B**, right scapula in medial view; **C**, left scapula in proximal view; **D**, right scapula in proximal view. Abbreviations: **ap**, acromial process; **cr**, crest; **gs**, glenoid surface. Scale bar: 10 cm.

1929). The entire medial surface of the rib bears a prominent longitudinal lamina. As a result, the bone has a triangular outline in cross-section. The tuberculum is robust and has a kidney-shaped articulation, whereas the articular surface of the capitulum has an elliptical outline. The proximal end of the rib has a foramen ventral to the capitulum. This is a possible nutrient foramen opening, due to the lack of external correlates that indicate a certain degree of pneumaticity in the mid-cervical vertebrae. The presence of foramina in cervical ribs is unusual in Dicraeosauridae, because *Aargasaurus* (MACN-N 15), *Brachytrachelopan* (MPEF-PV 1716) and *Dicraeosaurus* (Janensch 1929) lack them. The edges of this foramen show no indications that suggest it is a preservational artifact. On the contrary, the edges are smooth and complete. Thus, the presence of this foramen seems to be a feature that differentiates *Pilmatueia* (MLL-Pv-010) from other dicraeosaurid taxa.

DORSAL ELEMENTS

The new specimen (MLL-Pv-010) includes a sequence of seven poorly preserved dorsal vertebrae. The bifid neural spines are elongate and each has an elliptical outline in cross-section as in the dorsal vertebrae of other dicraeosaurids, such as *Pilmatueia*'s holotype specimen (MLL-Pv-005), *Aargasaurus*, (MACN-N 15), *Brachytrachelopan* (MPEF-PV 1716), *Dicraeosaurus* (Janensch 1929) and MOZ-Pv 6126 (Dicraeosauridae indet.) (Windholz *et al.* 2021). The most posterior bifid neural spines of MLL-Pv-010 are posterodorsally oriented, as in the holotype specimen of *Pilmatueia faundezi* (MLL-Pv-005) and posterior dorsal vertebrae of *Aargasaurus cazani* (MACN-N 15). MLL-Pv-010 has robust and well developed dorsal ribs comparable to those of other dicraeosaurids.

CAUDAL VERTEBRA

MLL-Pv-010 includes a well preserved distal caudal vertebra (Fig. 5). In anterior view, the centrum is as wide as high, and has a rectangular outline. The entrance to the neural canal is elliptical in outline, and is wider than tall. The neural arch is considerably lower than the centrum, and the neural spine is very small. Both prezygapophyses diverge dorsolaterally.

In lateral view, the centrum is approximately twice the length of its height. The lateral surface lacks fossae and foramina, and is concave anteroposteriorly. The dorsal sector of the centrum has a prominent crest along its entire lateral surface, as in the distal caudal vertebrae of other flagellicaudatans such as *Dicraeosaurus* (Janensch 1929) and *Diplodocus* (Hatcher 1901). The neural arch is lower and shorter than the associated centrum. The neural spine is low and anteroposteriorly long, as in the distal caudal vertebra of *Aargasaurus* (MACN-N 15).

In posterior view, the articular surface of the centrum is as wide as tall, with a subquadrangular outline. The neural canal has an elliptical outline and is transversely wider than high. Both postzygapophyses are reduced and the articular surfaces at the base of the neural spine are oriented ventrolaterally. In dorsal view, the prezygapophyses are prominent and diverge anterolaterally. The neural spine is singular and anteroposteriorly long. In ventral view, the centrum is somewhat constricted in its middle part, which makes it slightly hourglass-shaped. Its ventral surface is slightly anteroposteriorly and transversely concave as in the distal caudal vertebrae of other flagellicaudatans, such as *Aargasaurus* (MACN-N 15), *Dicraeosaurus* (Janensch 1929) and *Diplodocus* (Hatcher 1901).

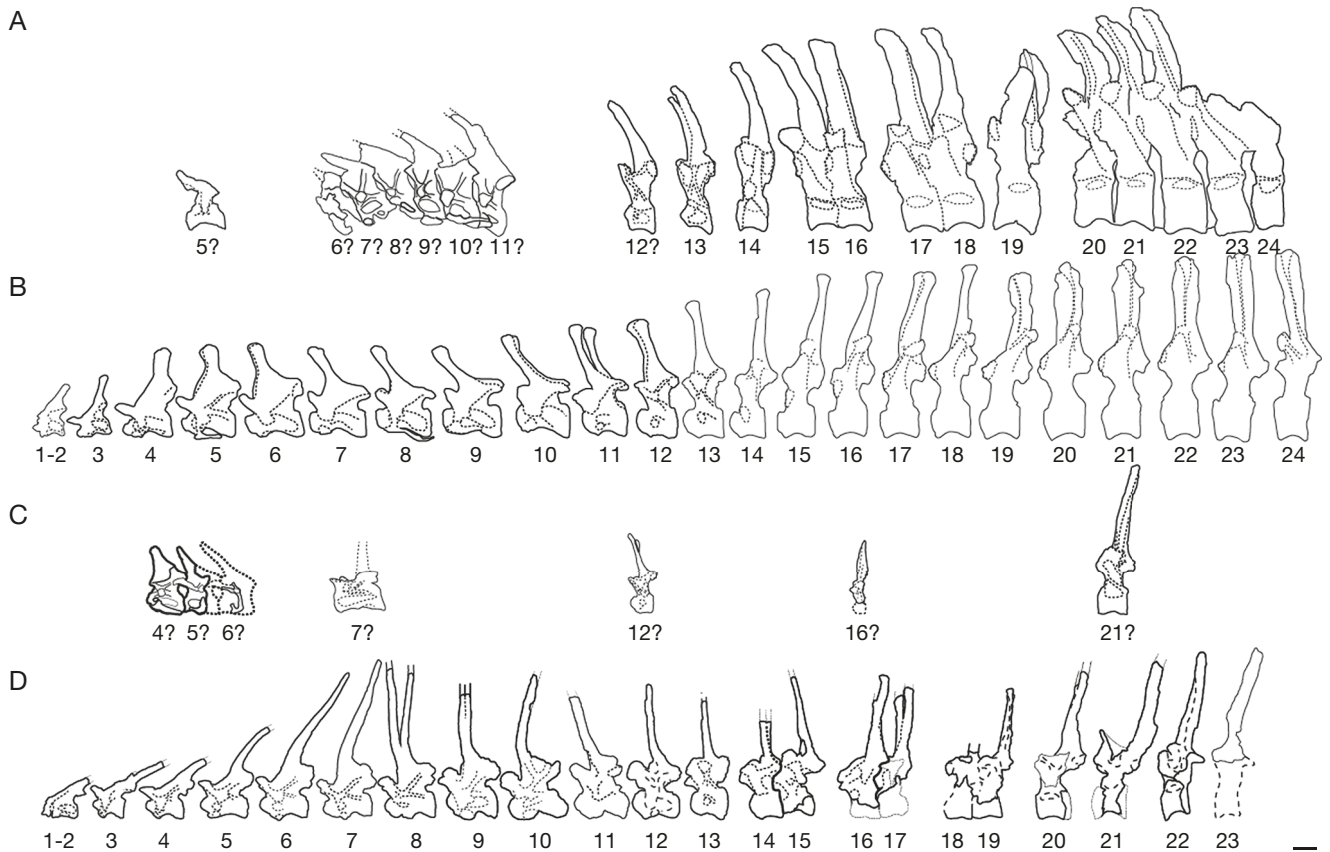


FIG. 7. — Presacral vertebrae of dicraeosaurid sauropods in left lateral view: **A**, *Brachyrachelopon* Rauhut, Remes, Fechner, Cladera & Puerta, 2005 (MPEF-PV 1716); **B**, *Dicraeosaurus* Janensch, 1914 (after Janensch 1929); **C**, *Pilmatueia* Coria, Windholz, Ortega & Currie, 2019 (MLL-Pv-002; 004; 005; 010; 014); **D**, *Amargasaurus* Salgado & Bonaparte, 1991 (MACN-N 15). Scale bar: 10 cm.

SCAPULA

MLL-Pv-010 includes right and left scapulae (Fig. 6), although both are poorly preserved. The posterior surface of the left scapula has been heavily affected by weathering, especially at the mid and distal parts of the scapular blade. The blade is distally incomplete and flat, likely due to plastic deformation. The most proximal end of the right scapula is preserved, and curves medially. The left scapula was found on top of the fourth, fifth and sixth cervical vertebrae, and was close to the right scapula. In the left scapula, the dorsal part of the posterior margin of the acromial process is slightly convex (in lateromedial view), as in other flagellicaudatans such as *Dicraeosaurus* and *Diplodocus* (Janensch 1961; Harris 2007; Tschopp *et al.* 2015) but unlike rebbachisaurids such as *Cathartesaura* (Gallina & Apesteguía 2005; MPCA-232), *Limaysaurus* (Calvo & Salgado 1995), and *Nigersaurus* (Sereno *et al.* 2007), in each of which it is concave. The acromial process is positioned proximally above the glenoid, as in the scapulae of other dicraeosaurids, such as *Amargasaurus* (MACN-N 15), *Dicraeosaurus* (Janensch 1961) and *Suuwassea* (Harris 2007); but unlike most of the non-dicraeosaurid diplodocoids where the acromial processes are nearly at the midpoints of the scapular blades (Tschopp *et al.* 2015).

In medial view, the left scapula bears a prominent, longitudinal crest, close to the acromial process. This crest is approximately as long as the acromial process and has a strongly rough texture.

This feature differentiates it from other dicraeosaurids, such as *Amargasaurus*, (MACN-N 15), *Dicraeosaurus* (Janensch 1961), *Lingwulong* (Xu *et al.* 2018), and *Suuwassea* (Harris 2007) each of which lacks a similar crest. In proximal view, the right scapula curves strongly medially, as in *Amargasaurus cazau* (MACN-N 15); however, the left scapula is flat because of post-depositional deformation.

DISCUSSION

Among sauropod dinosaurs, the presence of bifid neural spines in the presacral vertebral series evolved several times in different forms, such as *Camarasaurus* Cope, 1877, all flagellicaudatans, some mamenchisaurids, and some somphospondylians (Wilson & Sereno 1998; Whitlock 2011; Wedel & Taylor 2013; Windholz *et al.* 2021). This feature, plus the presence of a small accessory fossa posteroventral to the lateral depression of the centrum in the fourth cervical vertebra (MLL-Pv-010), are shared with other flagellicaudatans (Dicraeosauridae + Diplodocidae) (Tschopp *et al.* 2015). Furthermore, the presence of a crest along the entire lateral surface of each distal caudal centrum, and the slightly convex dorsal part of the posterior margin of the acromial process, are shared with other flagellicaudatan sauropods (Janensch 1961; Harris 2007; Tschopp *et al.* 2015).

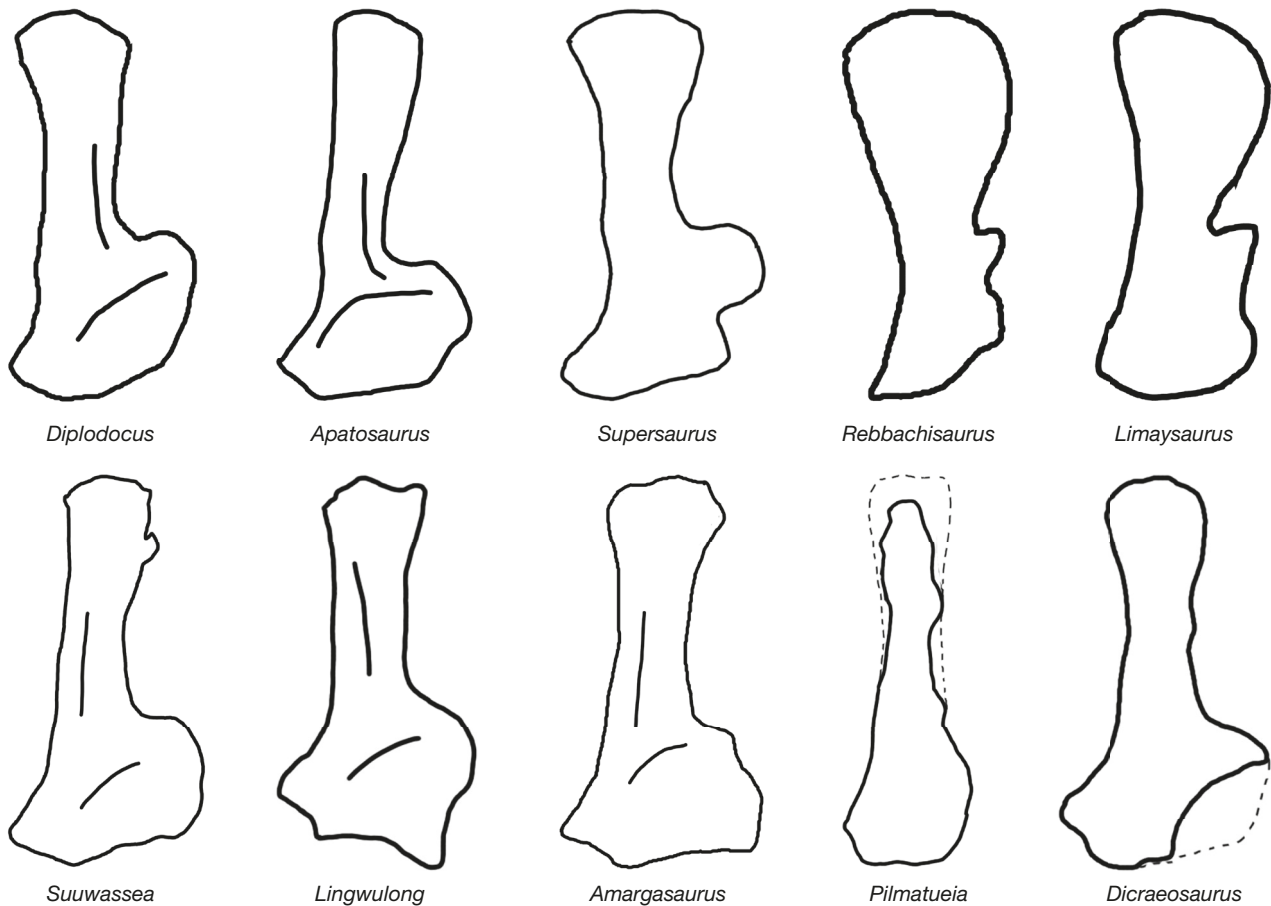


FIG. 8. — Comparison of scapular outlines of Diplodocoidea Marsh, 1884: *Amargasaurus* Salgado & Bonaparte, 1991 (MACN-N 15), *Apatosaurus* Marsh, 1877 (after Jensen 1985), *Dicraeosaurus* Janensch, 1914 (after Janensch 1961), *Diplodocus* Marsh, 1878 (after Osborn & Granger 1901), *Limaysaurus* Salgado, Garrido, Cocca & Cocca, 2004 (after Calvo & Salgado 1995), *Lingwulong* Xu, Upchurch, Mannion, Barrett, Regalado-Fernandez, Mo, Ma & Liu, 2018 (after Xu *et al.* 2018), *Pilmatueia* Coria, Windholz, Ortega & Currie, 2019 (MLL-Pv-010), *Rebbachisaurus* Lavocat, 1954 (after Wilson & Allain 2015), *Supersaurus* Jensen, 1985 (after Lovelace *et al.* 2007) and *Suuwassea* Harris & Dodson, 2004 (after Harris & Dodson 2004). Not to scale.

The new specimen (MLL-Pv-010) shares characters with other dicraeosaurids, such as extremely tall bifid neural spines in the cervical vertebrae (Fig. 7), and the position of the acromial process of the scapula proximally above the glenoid position (Fig. 8) (Janensch 1929, 1961; Harris 2007; Tschopp *et al.* 2015; MACN-N 15; MMCH-PV-75; MPEF-PV 1716). The bifid neural spines project anterodorsally, as in the anterior and middle cervical vertebrae of dicraeosaurids such as *Bajadasaurus* (MMCH-PV-75), *Brachytrachelopan* (MPEF-PV 1716) and *Dicraeosaurus* (Janensch 1929). Conversely, in *Amargasaurus* these structures project posterodorsally. In comparative terms, MLL-Pv-010 shows that the degree of development of neural spines in the anterior and mid-cervical vertebrae are low compared with other Cretaceous dicraeosaurids from Patagonia, such as *Amargasaurus* (MACN-N 15) and *Bajadasaurus* (MMCH-Pv-75).

The fact that MLL-Pv-010 comes from the same formation and geographic proximity as the holotype, paratype, and referred specimens of *Pilmatueia faundezi* prompts a detailed review. The overlapping elements are the cervical vertebrae, although they probably do not correspond exactly to the same position (MLL-Pv-010 preserved articulated fourth, fifth and sixth cervical vertebrae, while MLL-Pv-004 is a

seventh cervical vertebra and MLL-Pv-002 is a twelfth cervical vertebra) and posterior dorsal vertebrae, although these elements in MLL-Pv-010 are poorly preserved, which makes the comparisons difficult. However, MLL-Pv-010 shares with *Pilmatueia faundezi* the presence of anteriorly and posteriorly bifid ventral keels in the anterior and mid-cervical vertebrae (diagnostic character for *Pilmatueia*). Also, the posterior dorsal bifid neural spines are posterodorsally oriented both in MLL-Pv-010, as in the *Pilmatueia* holotype (MLL-Pv-005); this feature is also present in *Amargasaurus* (MACN-N 15).

This new specimen expands the diagnosis proposed by Coria *et al.* (2019) for *Pilmatueia faundezi*, adding new three autapomorphic characters (Fig. 9). The anterior and mid-cervical vertebra of *Pilmatueia* has a prominent anteriorly and posteriorly forked ventral keel. Ventral keels are widely distributed features within Sauropoda, for example diplodocoids taxa tend to have simple keels, as occurs in *Kaatedocus* (Tschopp & Mateus, 2013), or posteriorly bifid keels as occurs in *Dicraeosaurus* (Janensch 1929). An anteriorly and posteriorly bifurcated ventral keel is only known to occur in *Pilmatueia* (Fig. 9A, B). In addition, the proximal end of the mid-cervical rib has a foramen in its medial surface (Fig. 9C). The presence of cervical rib foraminae have been described

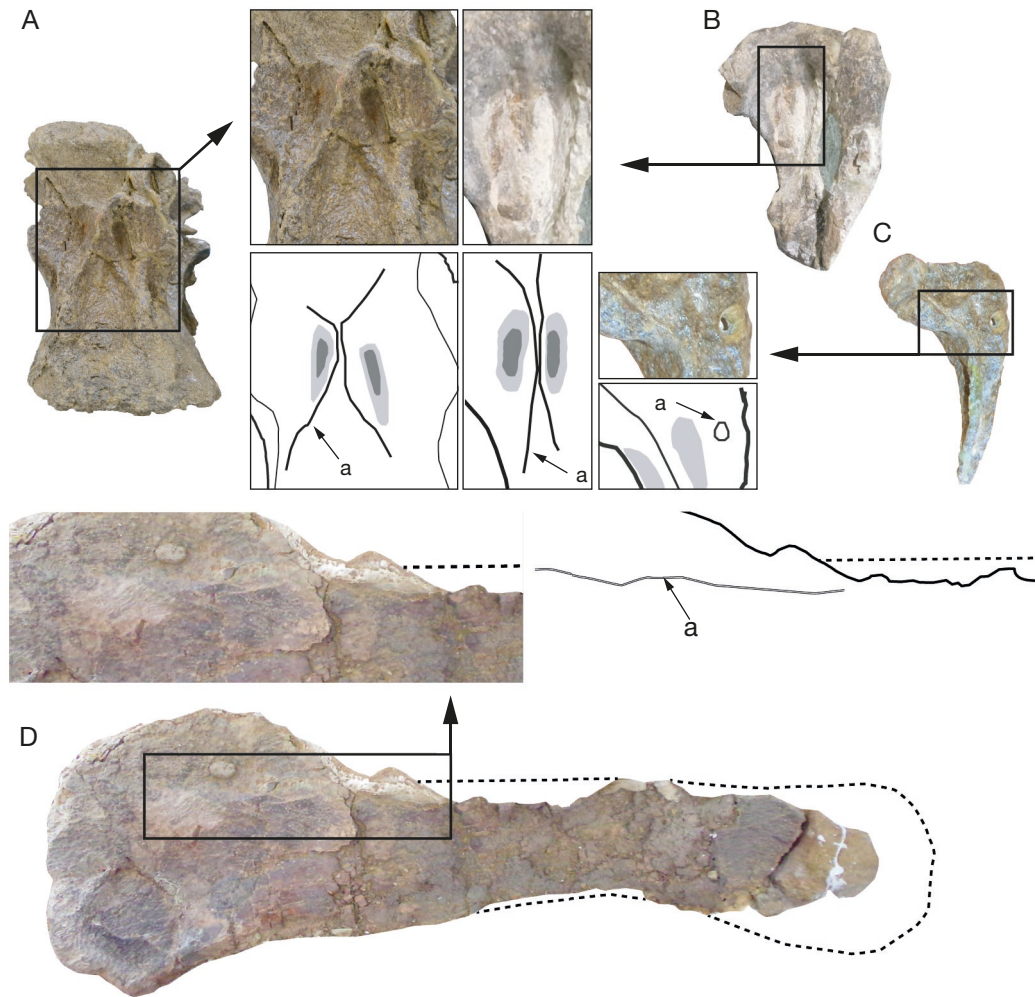


FIG. 9. — Autapomorphic characters of new specimen of *Pilmatueia* Coria, Windholz, Ortega & Currie, 2019: **A-C**, anteriorly and posteriorly forked ventral keel in: **A**, MLL-Pv-004; **B**, MLL-Pv-010; **C**, cervical rib foramina; **D**, prominent crest on scapula's medial surface, close to the acromial process. Abbreviation: **a**, automorphy. Not to scale.

for some diplodocids taxa, but, this feature is not known in the other dicraeosaurid ribs. Finally, the scapula of *Pilmatueia* (MLL-Pv-010) has a prominent crest on its medial surface close to the acromial process (Fig. 9D), which is a character that differentiates it from other dicraeosaurids.

PHYLOGENETIC IMPLICATIONS WITH TSCHOPP & MATEUS (2017) MATRIX

The analysis was run by using the Traditional Search option, starting from 1000 replicates of Wagner trees, followed by TBR branch swapping and saving 10 trees per replication. This procedure retrieved four most parsimonious trees (MPTs) of 1594 steps (consistency index (CI) = 0.345; retention index (RI) = 0.545), found in 248 of the replicates.

The strict consensus tree shows resolution in most of the groups analyzed. The internal phylogenetic relationships of Dicraeosauridae are well resolved, with the exception of a polytomy composed by *Pilmatueia faundezi*, *Amargatitanis macni* and *Bajadasaurus pronuspinax*. *Amargasaurus cazau*, *Brachyrachelopan mesai* Rauhut, Remes, Fechner, Clader & Puerta, 2005, *Dicraeosaurus hansemanni*, *Lingwulong shenqi*

and *Suuwassea emilieae* (Harris & Dodson, 2004) are a successive sequence of sister taxa (Appendix 1A). In previous contributions, South American dicraeosaurids were recovered phylogenetically far from each other (Rauhut *et al.* 2005; Gallina 2016; Xu *et al.* 2018; Coria *et al.* 2019; Gallina *et al.* 2019; Whitlock & Wilson Mantilla 2020), whereas here these taxa grouped together in a natural group (Fig. 10A). In turn, *Pilmatueia* is well-nested within Dicraeosauridae, taking two possible positions within this group, as sister taxon of *Bajadasaurus*, or as sister taxon of *Amargatitanis* and *Bajadasaurus*. *Pilmatueia* shares with *Amargatitanis* the absence of ventrolateral ridges in the anterior and mid-caudal vertebrae (character 341, unknown in *Bajadasaurus*); and shares with *Bajadasaurus* anteriorly inclined neural spines in the anterior cervical vertebrae (character 492, unknown in *Amargatitanis*).

The Cretaceous dicraeosaurid taxa (*Amargasaurus*, (*Pilmatueia*, *Amargatitanis*, *Bajadasaurus*)) are linked by sharing the absence of longitudinal flanges in the lateroventral edges on the posterior parts of the middle and posterior cervical centra (character 184, unknown in *Amargatitanis* and *Bajadasaurus*; and present in some diplodocids, rebbachisaurids,

in the macronarians *Camarasaurus* and *Isisaurus* Wilson & Upchurch, 2003, in *Haplocanthosaurus* Hatcher, 1903 and the basal sauropods *Mamenchisaurus* Young, 1954 and *Shunosaurus* Dong, Zhou & Zhang, 1983); the neural spines on the posterior cervical and anterior dorsal vertebrae are vertical (character 213, unknown in *Amargatitanis* and *Bajadasaurus*, present in the dicraeosaurid *Lingwulong*, some diplodocids, rebbachisaurids, macronarians, and *Omeisaurus* Young, 1939); the neural spines are bifid at least up to ninth dorsal vertebra (character 257, unknown in *Amargatitanis* and *Bajadasaurus*; *Brachytrachelopan* and *Dicraeosaurus* show state 1, while the basal dicraeosaurid *Lingwulong* has the plesiomorphic stage); the neural spines of the posterior dorsal vertebrae are posteriorly oriented (character 290, unknown in *Amargatitanis* and *Bajadasaurus*); and the prezygapophyses in mid-caudal vertebrae are interconnected by medial laminae that frame elliptical fossae (character 348, unknown in *Amargatitanis*, *Bajadasaurus* and *Brachytrachelopan*).

The South American dicraeosaurids (*Brachytrachelopan*, (*Amargasaurus*, (*Pilmatueia*, *Amargatitanis*, *Bajadasaurus*))) share the presence of prominent ventral keels on the midlines of the cervical centra (character 137, unknown in *Amargatitanis* and *Bajadasaurus*, present in rebbachisaurids, some apatosaurines, macronarians, and *Shunosaurus*); the summits of the bifid neural spines are cylindrical in shape in the cervical vertebrae (character 146, unknown in *Amargatitanis*, present in the diplodocids *Apatosaurus ajax* and *Galeamopus hayi*); the parapophysis is located between the anterior edge of the vertebral centrum and the prezygapophysis in the third dorsal vertebra (character 253, unknown in *Pilmatueia*, *Amargatitanis* and *Bajadasaurus*, present in *Apatosaurus louisae*, *Isisaurus* and *Shunosaurus*); the spinopostzygapophyseal laminae of the posterior dorsal vertebrae are simple (character 288, unknown in *Amargatitanis* and *Bajadasaurus*, and present in *Haplocanthosaurus* Hatcher, 1903, *Jobaria* Sereno, Beck, Dutheil, Larsson, Lyon, Moussa, Sadleir, Sidor, Varricchio, Wilson & Wilson, 1999, *Ligabuesaurus* Bonaparte, González Riga & Apesteguía, 2006, and the basal sauropods *Mamenchisaurus*, *Omeisaurus* and *Shunosaurus*).

In Gondwanan dicraeosaurids (*Dicraeosaurus* (*Brachytrachelopan* (*Amargasaurus* (*Pilmatueia*, *Amargatitanis*, *Bajadasaurus*)))) the maximum diameter of each supratemporal fenestra is less than 1.2 times the largest diameter of the foramen magnum (character 74, unknown in *Pilmatueia*, *Amargatitanis* and *Brachytrachelopan*, present in the rebbachisaurid *Limaysaurus*); the neural spines are higher than the neural arch in the mid-cervical vertebrae (character 172, unknown in *Pilmatueia* and *Amargatitanis*); the angles formed by postzygodiapophyseal and spinopostzygapophyseal laminae are straight in the mid-cervical vertebrae (character 174, unknown in *Pilmatueia*, *Amargatitanis* and *Bajadasaurus*, present in *Isisaurus*); the posterior dorsal neural spines each has a midline cleft along the dorsal surface (character 291, unknown in *Pilmatueia*, *Amargatitanis* and *Bajadasaurus*, present in some diplodocines and *Camarasaurus*); the distal transverse expansion of the ulna is less than 1.3 times the minimum width of the diaphysis (character 402, unknown in

the dicraeosaurids *Pilmatueia*, *Amargatitanis*, *Bajadasaurus* and *Brachytrachelopan*, present in some apatosaurines and *Shunosaurus*); the prefrontal length/height ratio (in lateral view) is greater than 3.0 (character 490, unknown in the dicraeosaurids *Pilmatueia*, *Amargatitanis* and *Brachytrachelopan*); the paroccipital processes are at least twice as long as wide (in dorsal view) (character 491, unknown in *Pilmatueia*, *Amargatitanis* and *Brachytrachelopan*, present in *Camarasaurus*).

Also, three ambiguous synapomorphies are shared by dicraeosaurids from Gondwana: basiptyergoid process narrowly divergent, with an angle less than 31° (character 95, unknown in the dicraeosaurids *Pilmatueia*, *Amargatitanis*, *Brachytrachelopan*, *Lingwulong* and *Suuwassee*); the basiptyergoid processes length/basal transverse diameter ratio is greater than 7.0 (character 97, unknown in the dicraeosaurids *Pilmatueia*, *Amargatitanis*, *Brachytrachelopan*, *Lingwulong* and *Suuwassee*); the area between the basiptyergoid processes and parasphenoid rostrum forms a deep slot-like cavity (character 98, unknown in the dicraeosaurids *Pilmatueia*, *Amargatitanis*, *Brachytrachelopan*, *Lingwulong* and *Suuwassee*).

Dicraeosauridae: (*Suuwassee* (*Lingwulong* (*Dicraeosaurus* (*Brachytrachelopan* (*Amargasaurus* (*Pilmatueia*, *Amargatitanis*, *Bajadasaurus*))))), share the presence of a prominent projection (ventrally directed) at the posteroventral margin of the squamosal (character 60, unknown in *Pilmatueia*, *Amargatitanis* and *Brachytrachelopan*, present in the diplodocid *Kaatedocus siberi*); distinctive sagittally arranged nuchal crest in the supraoccipital (character 77, unknown in *Pilmatueia*, *Amargatitanis* and *Brachytrachelopan*, present in the diplodocids *Galeamopus hayi* and *Kaatedocus siberi*, and *Mamenchisaurus*); a supraoccipital foramina (character 78, unknown in *Pilmatueia*, *Amargatitanis* and *Brachytrachelopan*, present in the diplodocid *Kaatedocus* and the macronarian *Giraffatitan*); subtriangular outline in the cross section of the dentary symphysis (character 108, unknown in *Pilmatueia*, *Amargasaurus*, *Amargatitanis*, *Brachytrachelopan* and *Lingwulong*); presence of a tuberosity on the labial surface of the dentary, near the symphysis (character 109, unknown in *Pilmatueia*, *Amargasaurus*, *Amargatitanis*, *Bajadasaurus*, *Brachytrachelopan* and *Lingwulong*); the width/height ratio in cervical vertebrae is less than 0.5 (character 131, unknown in *Amargatitanis*; shared with the macronarian *Camarasaurus*; *Lingwulong* has the apomorphic state); the anterolateral corner of the tooth row of the dentary, in occlusal view, is labially displaced (character 145, unknown in *Pilmatueia*, *Amargasaurus*, *Amargatitanis*, *Brachytrachelopan* and *Lingwulong*; present in the rebbachisaurid *Nigersaurus*); simple pleurocoels in the anterior cervical centra (character 161, unknown in *Amargatitanis* and *Bajadasaurus*, present in *Isisaurus* and *Jobaria*); paired fossae on the ventral surfaces of anterior cervical vertebrae (character 164, unknown in *Pilmatueia*, *Amargatitanis*, *Bajadasaurus* and *Brachytrachelopan*; present in the diplodocids *Galeamopus pabsti* and *Supersaurus vivianae*, and the eusauropods *Haplocanthosaurus* and *Jobaria*); anteriorly oriented neural spines on mid-cervical vertebrae (character 173, unknown in *Amargatitanis*; present in the diplodocids *Apatosaurus louisae* and *A. ajax*); the middle and posterior cervical vertebrae lack the lateral fossae to the

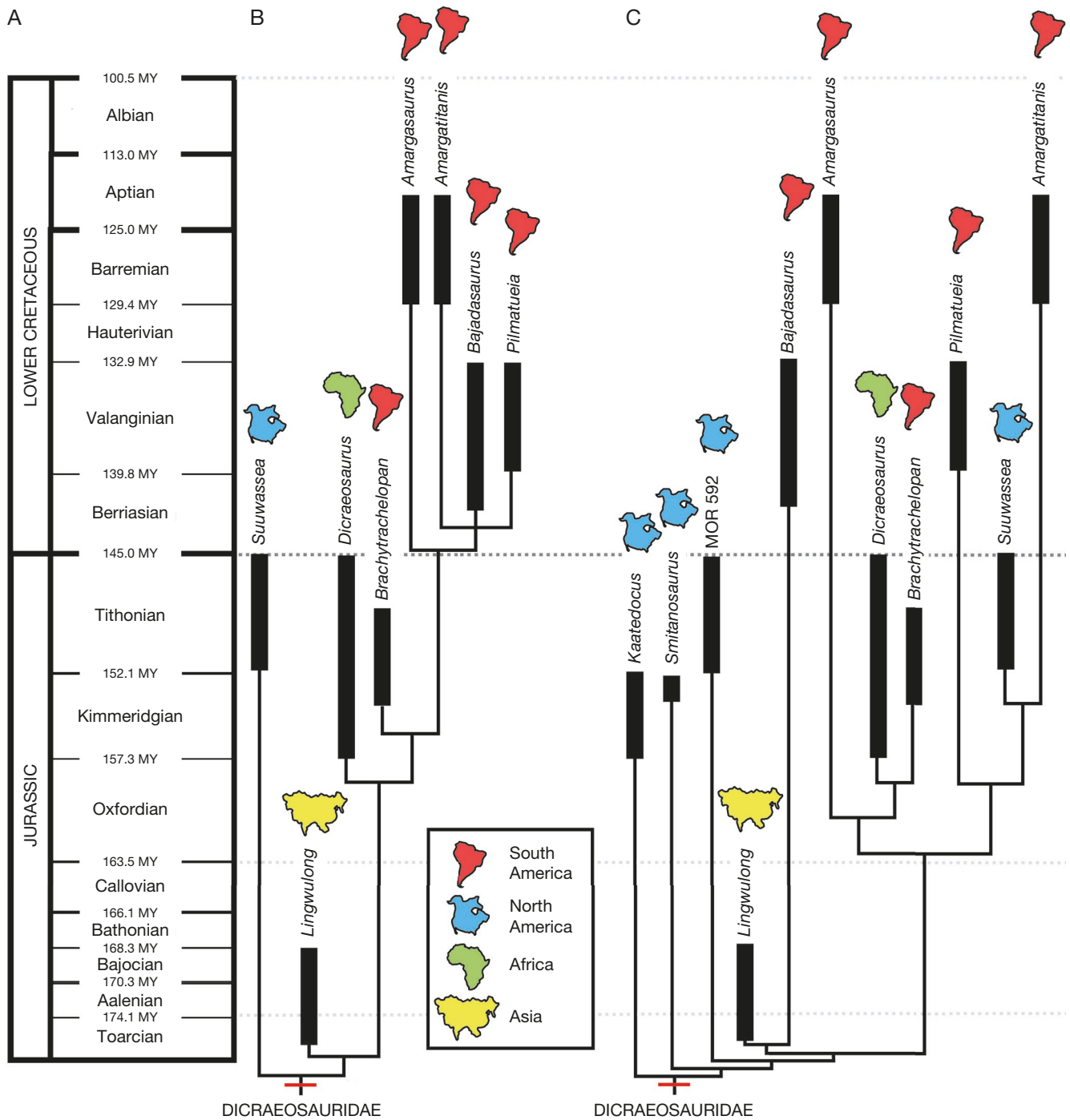


Fig. 10. — **A**, Simplified reduced consensus cladogram (calibrated phylogeny) showing the phylogenetic position of MLL-Pv-010 specimen; **B**, **C**, phylogenetic analysis with: **B**, Tschopp & Mateus (2017) matrix; **C**, Whitlock & Wilson Mantilla (2020) matrix.

prezygapophyses (character 189, unknown in *Amargatitanis*; present in some diplodocids, *Camarasaurus*, *Haplocanthosaurus* and *Omeisaurus*); parallel bifid neural spines in the posterior cervical and anterior dorsal vertebrae (character 217, unknown in *Amargatitanis*, *Bajadasaurus* and *Lingwulong*; present in the diplodocid *Kaatedocus*). A particular character shared by *Dicraeosaurus*, *Lingwulong*, and *Suuwassea* consists of a reduced contribution of the basioccipital to the dorsal side of occipital condylar neck (character 81, unknown in *Pilmateia*, *Amargatitanis* and *Brachyrachelopan*; *Amargasaurus* and *Bajadasaurus* each has the plesiomorphic state).

For almost nine decades, the Dicraeosauridae was limited to two species of *Dicraeosaurus* (Janensch 1914) from the Middle Jurassic of Africa. Near the end of the 20th century, Salgado & Bonaparte (1991) described *Amargasaurus cazau*, which expanded the distribution of the Dicraeosauridae (showing a Gondwanan distribution). This discovery also suggested that the dicraeosaurids would have reached the

Barremian (Lower Cretaceous), which to date represents the youngest record of this group. Several years later, the fossil evidence of Dicraeosauridae showed a pangeaic distribution, expanding their biochron (Harris & Dodson 2004; Xu *et al.* 2018). The oldest record is *Lingwulong shenqi*, from the Toarcian–Bajocian (Middle Jurassic) of China, which, in fact, pushed back the origin for the clade Neosauropoda (Xu *et al.* 2018). Thus, records indicate that the Dicraeosauridae originated sometime prior to the Middle Jurassic and achieved a distribution throughout Pangea. The lack of Cretaceous records in Laurasia could indicate an extinction on the continents of the northern hemisphere. In turn, the scarcity of Cretaceous records outside of South America is probably due to a preservation bias, and the only reports to date are a fragmentary dorsal vertebra from the Kirkwood Formation (Lowermost Cretaceous) of South Africa (McPhee *et al.* 2016) and postcranial fragmentary remains assigned to Dicraeosauridae indet. from the Wadi Milk Formation (Cenomanian) of Northern Sudan (Rauhut 1999). Regarding the clade composed by South American taxa, the oldest record is *Brachytrachelopan mesai* (Rauhut *et al.* 2005) from the Tithonian, suggesting a possible origin in the Upper Jurassic. The remaining records from South America come from the Lower Cretaceous and show the greatest diversity and abundance in the world for dicraeosaurids (Salgado & Bonaparte 1991; Gallina 2016; Coria *et al.* 2019; Gallina *et al.* 2019; Windholz *et al.* 2021).

PHYLOGENETIC IMPLICATIONS

WITH WHITLOCK & WILSON Mantilla (2020) MATRIX

The data matrix was analyzed with the Whitlock & Wilson Mantilla (2020) matrix using the same setting as in the previous analysis. This procedure retrieved four MPTs of 363 steps (CI = 0.614; RI = 0.798) found in 999 of the replicates. The strict consensus tree shows good resolution, except for some rebbachisaurids. The internal relations of the Dicraeosauridae family are well resolved (Appendix 1B). *Pilmatueia* is recovered as sister taxon to *Amargatitanis* and *Suuwassea*; with *Amargasaurus*, *Brachytrachelopan* and *Dicraeosaurus* as a sister group. At the same time, *Bajadasaurus* and *Lingwulong* are sister taxa in a more basal position; with MOR 592, *Smitanosaurus* and *Kaatedocus* as a successive sequence of sister taxa (Fig. 10B).

As in the phylogenetic hypothesis proposed by Whitlock & Wilson Mantilla (2020), a tendency is observed for the United States taxa to occupy the most basal positions within the Dicraeosauridae (with the exception of *Suuwassea*) suggesting a possible North American origin for this family. In this analysis, the South American dicraeosaurids are not recovered as a monophyletic group, unlike the analysis carried out previously. The different results could be explained, in principle, due to a difference in taxonomic sampling, character selection, and the presence of fragmentary and incomplete taxa. Nevertheless, we think that our first hypothesis is a better fit, because the appearance of biogeographic barriers in the Jurassic (Scotese 1991; Benedetto 2010; Ding *et al.* 2019) possibly generated vicariance phenomena between continental vertebrate faunas. Thus, it would be reasonable to recover

a South American dicraeosaurid clade that eventually may be confirmed in the future by additional evidence. Furthermore, the phylogenetic position recovered for *Suuwassea* seems to be somewhat doubtful. This conclusion, is not only due to different time range with its sister taxon *Amargatitanis*, but also because of the high number of characters that are unknown for both. Finally, *Pilmatueia* in a position close to *Bajadasaurus* would seem to be the most logical hypothesis, because these taxa come from close geographical areas and two partially synchronous geological formations (lowermost Cretaceous levels from Patagonia).

CONCLUSIONS

A new dicraeosaurid specimen MLL-Pv-010 from the Mulichinco Formation, (Valanginian, Lower Cretaceous) of Patagonia, Argentina is characterized by having extremely tall bifid neural spines in the presacral vertebrae and an acromial process of the scapula that is positioned proximally above the glenoid. Both of these features show that MLL-Pv-010 is unequivocally a dicraeosaurid sauropod, which is also supported by two phylogenetic analyses. Also, MLL-Pv-010 shares with *Pilmatueia* the presence of anteriorly and posteriorly bifid ventral keels in the cervical vertebrae, which is a character unidentified in other dicraeosaurids. Such a result allows us to refer the new specimen MLL-Pv-010 to *Pilmatueia faundezi*, which is, indeed, a more parsimonious conclusion than having a diversity of dicraeosaurids at a single locality in the same stratigraphic unit. One of our phylogenetic hypotheses differs from previous contributions in showing South American dicraeosaurids as a monophyletic group. However, in the second hypothesis these are not recovered as a natural group. We think that it is reasonable to recover a South American dicraeosaurid clade that eventually will be best supported as more evidence is collected.

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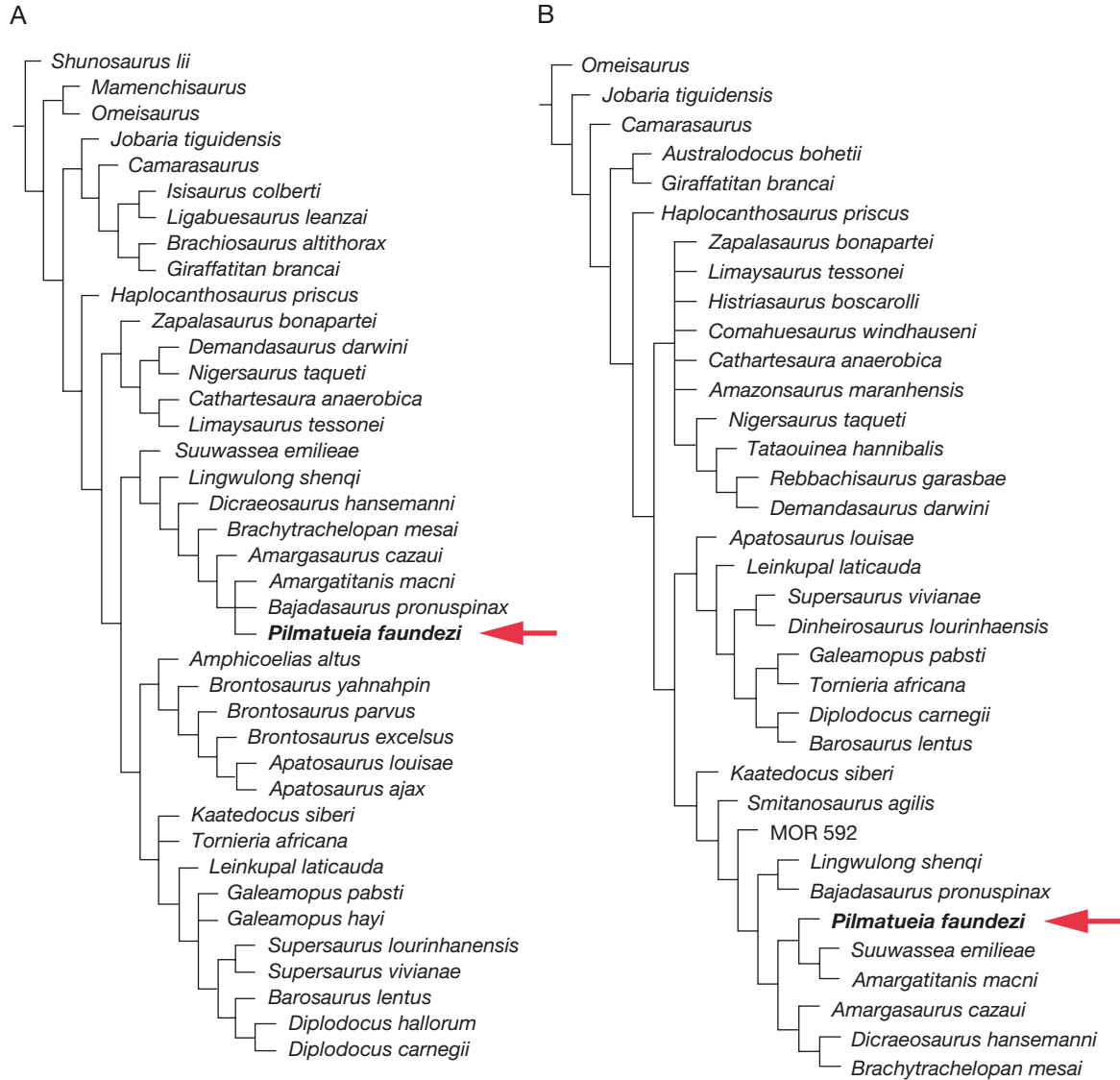
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APPENDICES

APPENDIX 1. — Cladogram showing the phylogenetic relationships of *Pilmatueia* Coria, Windholz, Ortega & Currie, 2019 in: **A**, Tschopp & Mateus (2017) matrix; **B**, Whitlock & Wilson Mantilla (2020) matrix.



APPENDIX 2. — Modified scores.

Character	Previous score (Tschopp & Mateus 2017)	New score
<i>Amargasaurus cazau</i> Salgado & Bonaparte, 1991		
23	?	1
34	0	?
40	0	?
91	?	0
92	1	0
94	?	0
133	?	1
134	?	0
135	0	1
142	0	1
143	?	0
146	0	1
159	?	0
160	?	0
173	1	2
175	1	0
176	0	?
181	?	1
183	?	0
187	1	0
188	1	0
189	1	0
190	0	?
192	?	0
199	?	0
201	?	0
207	?	1
208	?	0
209	0	1
212	?	0
225	?	0
227	?	1
228	?	0
232	?	1
241	?	0
246	?	0
254	?	0
256	?	0
261	?	1
262	1	0
263	?	1
264	?	1
294	?	0
301	?	0
305	1	?
307	?	0
314	0	1
315	1	0
316	?	0
328	1	0
329	0	?
331	0	?
339	?	0
342	?	0
345	?	0
346	1	0
349	?	0
350	0	?
352	?	0
356	?	0
357	?	0
369	?	0
371	?	1
372	?	2
374	?	0
375	?	1
377	?	0
379	?	0

APPENDIX 2. — Continuation.

Character	Previous score (Tschopp & Mateus 2017)	New score
381	?	0
382	?	1
383	?	0
384	?	1
385	?	0
402	?	0
404	?	0
405	?	0
423	?	1
446	?	0
450	?	0
453	?	0
454	?	0
455	1	0
458	?	1
459	?	0
462	?	1
463	?	1
468	?	0
471	?	0
472	?	0
473	?	0
474	?	1
475	?	1
476	?	1
<i>Brachyrachelopan mesai</i> Rauhut, Remes, Fechner, Cladera & Puerta, 2005		
131	?	0
133	0	?
135	0	1
164	0	?
172	1	2
175	1	0
177	0	1
187	?	0
191	?	0
192	?	0
195	1	0
201	?	0
204	1	0
207	0	1
216	1	?
232	?	1
241	?	0
242	?	1
246	?	1
254	?	0
278	1	0
290	0	1
291	0	1
304	?	1
420	1	?
425	?	0
<i>Dicraeosaurus</i> Janensch, 1914		
60	0	1
92	?	0
165	1	0
184	0	1
201	?	0
207	0	1
218	1	0
219	1	0
233	1	0
291	0	1
322	0	1
377	1	0
383	?	0
391	?	0
393	?	0

APPENDIX 2. — Continuation.

Character	Previous score (Tschopp & Mateus 2017)	New score
<i>Suuwassea emilieae</i> (Harris & Dodson, 2004)		
60	0	1
91	1	0
138	1	0
146	1	0
175	?	1
176	0	?
177	?	0
216	1	0
237	0	1
377	1	0
379	?	0
<i>Leinkupal laticauda</i> Gallina, Apesteguía, Haluza & Canale, 2014		
129	?	1
140	?	0
173	?	0
189	?	0
194	?	0
195	?	0
200	?	0
206	?	0
213	?	1
216	?	1
<i>Cathartesaura anaerobica</i> Gallina & Apesteguía, 2005		
134	0	?
145	0	?
170	?	0
<i>Kaatedocus siberi</i> Tschopp & Mateus, 2012		
60	0	1
90	1	0
161	0	1
<i>Galeamopus pabsti</i> Tschopp & Mateus, 2017		
260	?	0
263	1	0
<i>Giraffatitan brancai</i> (Janensch, 1914)		
266	?	0
270	0	1
444	1	0
<i>Ligabuesaurus leanzai</i> Bonaparte, González Riga & Apesteguía, 2006		
266	1	0
456	1	0
<i>Limaysaurus tessonei</i> (Calvo & Salgado, 1995)		
323	?	1
<i>Apatosaurus ajax</i> Marsh, 1877		
363	?	1

APPENDIX 3. — Modified characters.

CHARACTER 97

Basipterygoid processes, ratio of length to basal transverse diameter: < 4 (0); 4.0-7.0 (1) > 7 (2). (Modified from Tschopp & Mateus 2017). A new state was added to discriminate the highly developed basipterygoid processes of *Amargasaurus*, *Bajadasaurus* and *Dicraeosaurus*. The presence of highly developed basipterygoid processes occurs in derived forms from Dicraeosauridae, and is a character that differentiates them from the basal forms of dicraeosaurids such as *Lingwulong* (Xu *et al.* 2018) and even from other groups of sauropods, such as *Kaatedocus* (Tschopp & Mateus 2013) (Appendix 5).

CHARACTER 180

Mid- and posterior cervical vertebrae, ventral keel: single (0); bifid, connects posterolaterally to the ventrolateral edges of the centrum (1) bifid, anteriorly and posteriorly (2). (Modified from Tschopp & Mateus 2017).

CHARACTER 255

Anterior and mid-dorsal neural arch, hyposphene shape: rhomboid (0); laminar (1); triangular in shape (2). (Modified from Tschopp & Mateus 2017). A new state was added to discriminate hyposphenes with triangular outlines, present in the anterior and middle dorsal vertebrae of some dicraeosaurid sauropods. A triangular hyposphene is a character found in the dorsal vertebrae of dicraeosaurid sauropods, such as *Pilmatueia* (MLL-Pv005), *Brachyrachelopan* (MPEF-PV 1716) and *Dicraeosaurus* (Janensch 1929). This morphology is different from that present in diplodocoids such as *Apatosaurus louisae* (Gilmore 1936), whose hyposphenes have rhombic outlines (Appendix 6).

CHARACTER 257

Mid-dorsal neural spines, form: single as the bifid form (if present) does not extend past third dorsal (0); bifid form does not

extend past sixth dorsal (1); bifid neural spines at least up to the ninth dorsal (2). (Modified from Tschopp & Mateus 2017).

The apomorphic state was divided into two new states to differentiate the forms whose bifid neural spines reach the most posterior dorsal vertebrae. Within Diplodocoidea, bifid neural spines in the presacral vertebral series occur only in the flagellacaudatans (Dicraeosauridae + Diplodocidae). In diplodocids, completely bifid neural spines include the most anterior dorsal vertebrae; while in *Brachyrachelopan* (MPEF-PV 1716) and *Dicraeosaurus* (Janensch 1929) dicraeosaurids, they reach the middle dorsal vertebrae. The most derived forms of Dicraeosauridae, such as *Pilmatueia* (MLL-Pv005) and *Amargasaurus* (MACN-N 15), have completely bifid neural spines up to the most posterior dorsal vertebrae (Appendix 6).

CHARACTER 290

Posterior dorsal neural spines, orientation at its base: vertical (0); anteriorly inclined (1); posteriorly inclined (2). (Modified from Tschopp & Mateus 2017).

A new state was added to consider the posteriorly oriented neural spines in the posterior dorsal vertebrae of *Amargasaurus* (MACN-N 15) and *Pilmatueia* (MLL-Pv-005). In contrast, in *Dicraeosaurus* (Janensch 1929) the neural spines of the posterior dorsal vertebrae are vertical, whereas in *Brachyrachelopan* (MPEF-PV 1716) they are directed anterodorsally.

CHARACTER 348

Mid-caudal prezygapophyses: free (0); posteriorly interconnected by a transverse ridge, creating a triangular fossa together with the spinoprezygapophyseal laminae (1); interconnected by a transverse ridge, creating an elliptical fossa together with the spinoprezygapophyseal laminae (2). (Modified from Tschopp & Mateus 2017).

A new state was added to differentiate the elliptical outline fossa present in the mid-caudal vertebrae of *Amargasaurus* (MACN-N 15) and *Pilmatueia* (MLL-Pv-015;016). This fossa has a triangular outline in other flagellacaudatans, such as *Diplodocus longus* (Tschopp *et al.* 2015) (Appendix 7).

APPENDIX 4. — Added characters.

CHARACTER 490

Prefrontal in lateral view, length / height ratio (taken at mid-height). Short, less than or equal to 3 (0); long, greater than 3 (1). (New).

A new character was added to discriminate the short prefrontals present in *Amargasaurus*, *Bajadasaurus* and *Dicraeosaurus*; and is a character that differentiates them from other sauropods, such as *Camarasaurus*, *Galeamopus pabsti* and *Shunosaurus lii* (Zheng 1996; Chatterjee & Zheng 2002; Tschopp & Mateus 2017) (Appendix 8).

CHARACTER 491

Paraoccipital process in dorsal view. Reduced (0); well developed, at least twice as long as wide (1). (New).

A new character was added to discriminate the degree of development of the paraoccipital processes present in dicraeosaurids, which is different than in other sauropods (Appendix 9).

CHARACTER 492

Anterior cervical vertebrae, orientations of the neural spines. Vertical (0); anteriorly inclined (1); posteriorly inclined (2). (New).

A new character was added to differentiate the neural spines anterodorsally oriented, present in the anterior cervical vertebrae of *Bajadasaurus* (MACN-N 15) and *Pilmateueia*

(MLL-Pv-010). These structures are posterodorsally oriented in other dicraeosaurid sauropods.

CHARACTER 493

Mid-cervical vertebrae, median tubercle. Absent (0); present (1). (New).

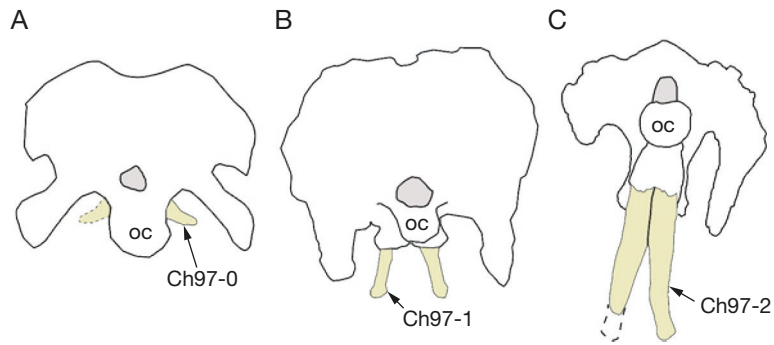
A new character was added to consider the presence of the median tubercle in the mid-cervical vertebrae of *Dicraeosaurus* (Janensch 1929) and *Pilmateueia faundezi* (MLL-Pv-004) (Appendix 10).

CHARACTER 494

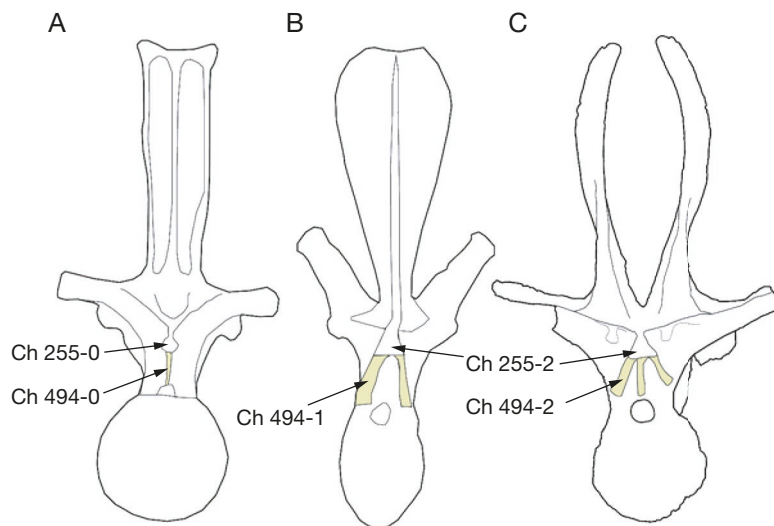
Dorsal vertebrae, infrahyposphenal laminae. Simple (ventral to the hyosphene) (0); double (ventrolaterally oriented) (1); three laminae (one ventral and two ventrolateral) (2). (New).

A new character was added to discriminate between the shapes of infrahyposphenal laminae. Three infrahyposphenal laminae occur in the dorsal vertebrae of *Pilmateueia faundezi* (MLL-Pv-005; 014) and *Apatosaurus ajax* (Marsh 1877; Upchurch *et al.* 2004). A ventrolaterally oriented pair of infrahyposphenal laminae is characteristic in the dicraeosaurids *Brachyrachelopan* (MPEF-PV 1716) and *Dicraeosaurus* (Janensch 1929); simple infrahyposphenal laminae with a sagittal arrangement are widely distributed among diplodocids, such as *Apatosaurus louisae* (Gilmore 1936) (Appendix 6).

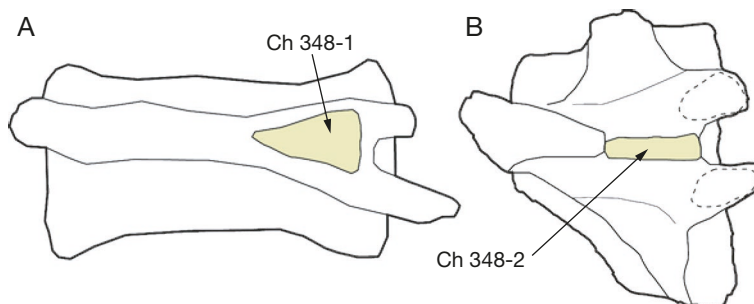
APPENDIX 5. — Sauropod skull in posterior view: **A**, *Omeisaurus* Young, 1939 (after He *et al.* 1988); **B**, *Kaatedocus* Tschopp & Mateus, 2013 (after Tschopp & Mateus 2013); **C**, *Bajadasaurus pronuspinax* Gallina, Apesteguía, Canale & Haluza, 2019 (MMCh-PV 75). Abbreviations: **Ch**, character; **oc**, occipital condyle. Image not to scale.



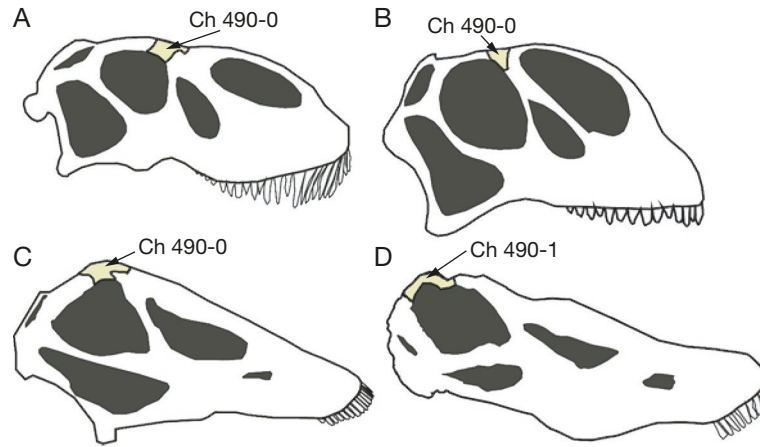
APPENDIX 6. — Flagellicaudatan posterior dorsal vertebrae (posterior views): **A**, *Apatosaurus louisae* (Holland, 1915) (after Gilmore 1936); **B**, *Dicraeosaurus hansemani* Janensch, 1914 (after Janensch 1929); **C**, *Pilmatueia faundezi* Coria, Windholz, Ortega & Currie, 2019 (MLL-Pv-005). Abbreviation: **Ch**, character. Image not to scale.



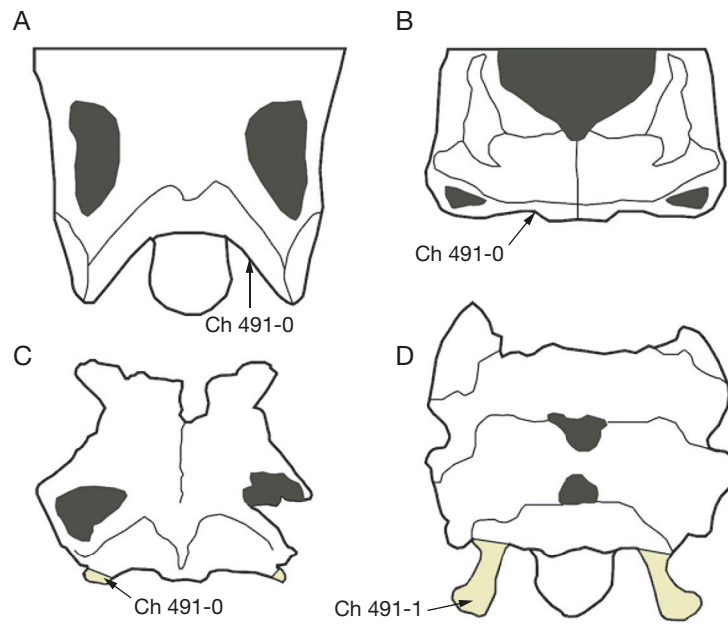
APPENDIX 7. — Flagellicaudatan mid-caudal vertebrae in dorsal view: **A**, *Diplodocus longus* Marsh, 1878 (after Tschopp *et al.* 2015); **B**, *Pilmatueia faundezi* Coria, Windholz, Ortega & Currie, 2019 (MLL-Pv-016). Abbreviation: **Ch**, character. Image not to scale.



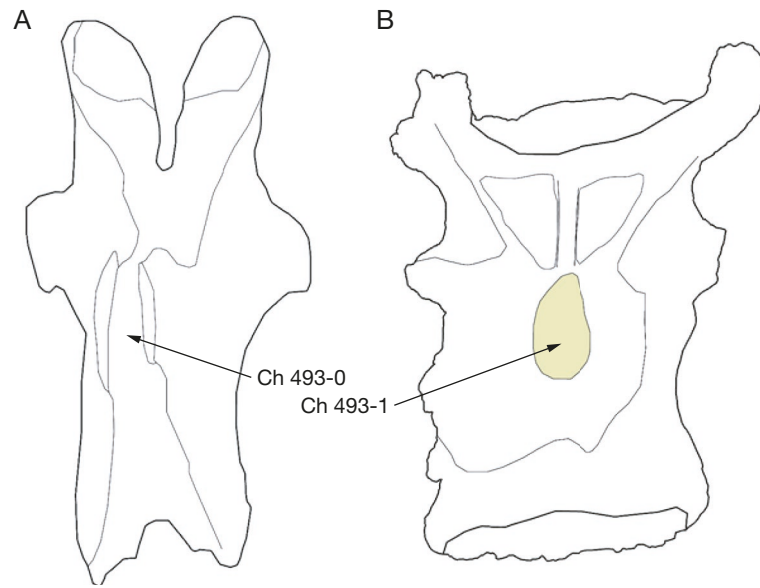
APPENDIX 8. — Sauropod skulls in right lateral view: **A**, *Shunosaurus lii* Dong, Zhou & Zhang, 1983 (after Chatterjee & Zheng 2002); **B**, *Camarasaurus* Cope, 1877 (after Zheng 1996); **C**, *Galeamopus pabsti* Tschopp & Mateus, 2017 (after Tschopp & Mateus 2017); **D**, *Amargasaurus cazau* Salgado & Bonaparte, 1991 (MACN-N 15). Abbreviation: **Ch**, character. Image not to scale.



APPENDIX 9. — Sauropod skulls in dorsal view: **A**, *Shunosaurus lii* Dong, Zhou & Zhang, 1983 (after Chatterjee & Zheng 2002); **B**, *Galeamopus pabsti* Tschopp & Mateus, 2017 (after Tschopp & Mateus, 2017); **C**, *Lingwulong shenqi* Xu, Upchurch, Mannion, Barrett, Regalado-Fernandez, Mo, Ma & Liu, 2018 (after Xu *et al.* 2018); **D**, *Dicraeosaurus hansemanni* Janensch, 1914 (after Janensch 1929). Abbreviation: **Ch**, character. Image not to scale.



APPENDIX 10. — Flagellicaudatan mid-cervical vertebrae in dorsal view: **A**, *Kaatedocus siberi* Tschopp & Mateus, 2012 (after Tschopp *et al.* 2015); **B**, *Pilmatueia faundezi* Coria, Windholz, Ortega & Currie, 2019 (MLL-Pv-004). Abbreviation: **Ch**, character. Image not to scale.



APPENDIX 11. — Data matrix in TNT format.

xread

494 39

Shunosaurus 10001000000??000?00?000000000001?00000000000000?0?0?000000?00?000000?00?00000?0?00000?00
0?0000000010000000000?00?00000000000100?00000000?0??00??0??0101??0000?000?1000??00?0000000?000?0
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Omeisaurus 10001011000??000?00?000000000010?00101000000000?0?0?0000000010?0?00?10??10?000?0000?
?01000?0??0000000000?00?00000010002?110011110?00?????????0??0010100?00?102?10011000010?100??0?000000
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Mamenchisaurus 100000110????000?00?0010000100010??0101000000000?001?0000010001000000000?010000?0?0
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Camarasaurus 1000110110000?000?00?00100001000000100110011100000?001000000001111010001000100000000
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1200001110000012100011000101211110011011101200000010100010000100010?21010110010100011000001100
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Giraffatitan 1100111100010000100000010000100000110100001110001101010000000000100100000010010001010
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????????????????0??01

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Haplocanthosaurus ???
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Appendix 11. — Continuation.

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Cathartesaura ??0?
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Zapalasaurs ??
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Appendix 11. — Continuation.

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Brontosaurus yahnahpin ???
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Tornieria ??????????????????????01?1??00?0?1?????????????????????????1111111??0011000101101001011101?1?0????0????????????
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????????????????????????????????????0?????????0?01????2111????0110????????????01[0 1]10?010?0??0?1?????????????01100100011
0010??1001?110000011111????????????00011?00??01011010111101000000010??10?011??1100????????????????????????0??

Supersaurus vivianae ???
?????1?1110011001?0??0?????????????01??1?1011[1 2]0100111[0 1]0[0 1]1101111111?000110?????010????????????0?????1????????
11000000?000?0?10?00000111001111[0 1][0 1]11001?110002011[0 1]00110001111??111010?1101?[0 1]011110?0[0
1]001101111101001010101100000101001????01001000?01120100111010000????????????????????????????000111?1020
00000101010?????????????11010101????????????????????????????1

Supersaurus lourinhanensis ???
?????????????????????1??111?00??1?????????????????????????????????????11000?1?1?1????10?1?10110?000100?011?01??00??10010?011??
??1000?000?0010??00000111101110111000101100??01111001101?111??????0?0??1????2011??1?????????????????01????????
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Leinkupal ???
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Galeamopus hayi ??????????????????????1?111?1?0010?111?0?????????????????????2?10000101001110010010110101111101?00
0010?????????????????????????1??1??1?10010111?1???????????1??10????101001001100????11111101001?001?0?0?1100011001
1?1000?00100100?1?1???0?0????001?1?00??1?1?????????????0?????????1??????????1??11??????111?012?11??1?1?1????????
??1101100?001010010?????????011101000010010002000?101?001201100101100?001000010?1010?000?1?1010?
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Galeamopus pabsti 0?1121101101111111111011101010011?1101?1001111011001111011210101?10000110001
00111002010111?1100011001?1000111011?11011110011[1 2]111011110101021011111100102211100111101111
001100000001110010110100100000111001111011?10000100100100?10110?0?0?0?00?1?10?1?110101001100010
??10?0?10110010?0100?0001??021101000?1001000?????2011
001111111101011100011?0001?01?100000??????110101?00000??1000101111101101?110101112001101101000020?

Diplodocus carnegii ???
?????1111101111[0 1]00111?0??????101201010?0011001010011000??00111001010[0 1]0110100010100[0 1]011101101
0001100100100211110001000001[0 1]00[0 1]1111012110111011111100000110111101100111111?011011110010
1114101211111101111111101001110111021100100101????40000[0 1]00010111010[0 1]0010010001[0 1]00????????
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Diplodocus hallorum ???
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