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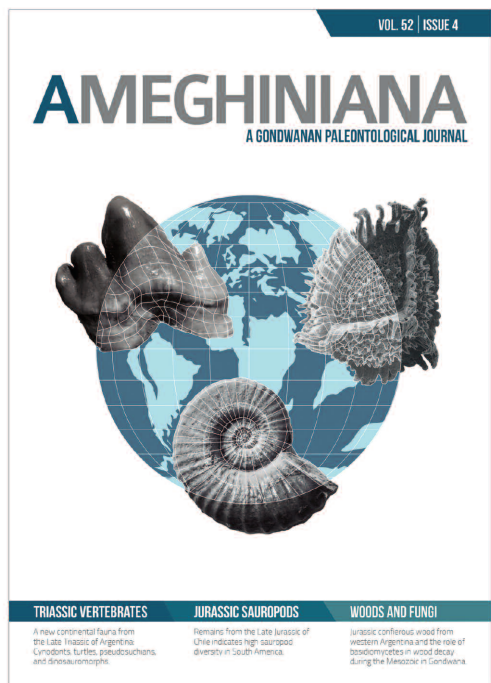
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LATE JURASSIC SAUROPODS IN CHILEAN PATAGONIA

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LATE JURASSIC SAUROPODS IN CHILEAN PATAGONIA

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Abstract. A description is provided of the first sauropod remains (*i.e.*, isolated vertebrae and appendicular bones) from the Late Jurassic of Aysén, in Chilean Patagonia (Toqui Formation, late Tithonian). Although the bones found are fragmentary, they still allow the recognition of an unsuspected sauropod diversity for this period in South America. The materials suggest the presence of at least three different sauropod lineages: an indeterminate group of sauropods, possible Titanosauriformes, and Diplodocoidea. A phylogenetic analysis of this last clade supports the placement of the remains within Diplodocinae and also provides the first unequivocal record of this clade in Late Jurassic rocks of South America. These records provide important information about the poorly known evolutionary history of sauropods in South America before the Cretaceous.

Key words. Late Jurassic. Sauropod dinosaurs. Chilean Patagonia.

Resumen. SAURÓPODOS DEL JURÁSICO SUPERIOR EN LA PATAGONIA CHILENA. Se describen los primeros restos de saurópodos (*i.e.*, vertebras aisladas y huesos apendiculares) del Jurásico Tardío de Aysén, en la Patagonia chilena (Formación Toqui, Titioniano tardío). Aunque fragmentarios, los huesos disponibles permiten el reconocimiento de una insospechada diversidad de saurópodos para ese periodo en América del Sur. Los materiales indican la presencia de, al menos, tres diferentes linajes de saurópodos: un grupo indeterminado de saurópodos, posibles Titanosauriformes y Diplodocoidea. Dentro de este último clado, un análisis filogenético ubica los restos dentro de Diplodocinae y provee el primer registro inequívoco de este clado para el Jurásico Tardío de América del Sur. Estos registros proveen información importante acerca de la pobremente conocida historia evolutiva de los saurópodos sudamericanos, previa al Cretácico.

Palabras clave. Jurásico Tardío. Dinosaurios saurópodos. Patagonia chilena.

Up to now, Late Jurassic sauropod remains from South America have only been reported from the Cañadón Calcáreo Formation (Oxfordian–Kimmeridgian; Cúneo *et al.*, 2013), exposed at different localities in Chubut Province, Argentine Patagonia. These remains include the basal camarasauromorph *Tehuelchesaurus benitezi* (from Estancia Fernández, Carballido *et al.*, 2011), brachiosaurid remains (although Mannion *et al.*, 2013, p. 150, questioned the brachiosaurid affinities of these remains) and three partial dorsal vertebrae assigned to Diplodocidae (from Estancia Mesa, Rauhut, 2006; Rauhut *et al.*, in press), and the dicraeosaurid *Brachytrachelopan mesai* (also from Estancia Mesa, Rauhut

et al., 2005). The Jurassic dinosaur record in Chile is mainly composed of tracks and trackways (Rubilar-Rogers *et al.*, 2012). However, De la Cruz *et al.* (2008) announced the discovery of the first Chilean dinosaur bones from rocks exposed in the Patagonian Central Andes of Aysén, Southern Chile. The bone-bearing unit is the Toqui Formation, dated as late Tithonian (De la Cruz and Suárez, 2006). Field trips to the fossil locality in Aysén carried out since 2009 through 2013 resulted in the discovery of new dinosaur materials, including the enigmatic theropod *Chilesaurus diegosuarezi* (Novas *et al.*, 2015) and the first bone remains of Sauropoda.

The main goal of this contribution is to describe the

isolated sauropod remains –including several caudal vertebrae, sternal plate, and appendicular bones (represented by distal ends of femur and tibia). The sauropod remains here reported provide new information on the poorly understood evolutionary history of South American sauropods before the Cretaceous.

Institutional abbreviations. **CM**, Carnegie Museum of Natural History, Pittsburgh, USA; **DFMMh/FV**, Dinosaurier-Freilichtmuseum MÜNCHENHAGEN/ Verein zur Förderung der Niedersächsischen Paläontologie (e.V.), Rehburg-Loccum, Germany; **K**, Kalasin area (material kept by the Department of Mineral Resources of Bangkok, Thailand); **MB**, Museum für Naturkunde der Humboldt-Universität zu Berlin, Berlin, Germany; **MLP**, Museo de Ciencias Naturales de La Plata, Buenos Aires, Argentina; **MMCH-Pv**, Museo Municipal “Ernesto Bachmann”, Villa El Chocón, Neuquén, Argentina; **MPCA**, Museo Provincial “Carlos Ameghino”, Cipolletti, Río Negro, Argentina; **MPZ**, Museo Paleontológico de Zaragoza, Zaragoza, Spain; **OUMNH**, Oxford University Museum of Natural History, Oxford, UK; **P.W.**, Phu Wiang area (material kept by the Department of Mineral Resources of Bangkok, Thailand); **SMA**, Sauriermuseum Aathal, Aathal, Switzerland; **SNGM**, Sernageomin, Santiago, Chile.

SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842

SAURISCHIA Seeley, 1887

SAUROPODOMORPHA Huene, 1932

SAUROPODA Marsh, 1878

Gen. et sp. indet.

Figure 1.1–3

Material. SNGM-1977, a mid or posterior dorsal vertebra, preserving the centrum and the base of the neural arch (the floor of the neural canal is not preserved).

Description. The material probably corresponds to a mid or posterior dorsal. The centrum is amphiplatyan, somewhat longer than high, and higher than wide (Tab. 1). Because of poor preservation, the posterior articular surface seems to be more nearly circular than the anterior one. In lateral view (Fig. 1.2), the anterior and posterior margins of the vertebra are straight, subparallel, and slightly inclined anteriorly (with respect to the straight line that unites the lowermost points of the anterior and posterior articular faces), whereas the ventral margin is strongly concave. At the middle of the lateral face there is a depressed area, but pleurocoels are absent. The ventral surface is flat or slightly concave transversely; in ventral view, the external margins of the centrum are strongly constricted (the lesser width is approximately 56% the greater width, Fig. 1.3, Tab. 1).

Remarks. This element resembles the dorsal vertebra of some basal eusauropods, such as the lectotype (MLP 46-VIII-21-1/2, Rauhut, 2003, fig. 1I–K) and referred specimen (MLP 36-XI-10-3/1, Rauhut, 2003, fig. 3A) of *Amygdalodon patagonicus* (Rauhut, 2003; MLP 46-VIII 21-1). In fact, the morphology of the dorsal centrum in these sauropods is similar. For instance, in *Amygdalodon* the dorsal centrum is almost as high as long, as in the Chilean material, and the width of the mid centrum is nearly 63% of the anterior width (Cabrera, 1947, p. 10; Rauhut, 2003, p. 176). Specimen SNGM-1977 also resembles the dorsal vertebrae of some dicraeosaurids, such as *Brachytrachelopan mesai*, although at least in this species the middle constriction is less notorious (the lesser width of the dorsal centra is nearly 70% of its greater width).

TABLE 1. Measurements of the vertebrae found in Aysén, in cm. Abbreviations: CL, centrum length; ACH, anterior centrum height; PCH, posterior centrum height; ACW, anterior centrum width; PCW, posterior centrum width; MCW, mid centrum width. Asterisk, estimated.

Specimen	CL	ACH	PCH	ACW	PCW	MCW
SNGM-1977	8.8	8.5	---	7.5	---	4.2
SNGM-1978	33	14.5	---	---	15*	---
SNGM-1979	22.3	18.5	16.5	17.2	16.8	9.5
SNGM-1981	10.12	9.5	9	10.6	10	---

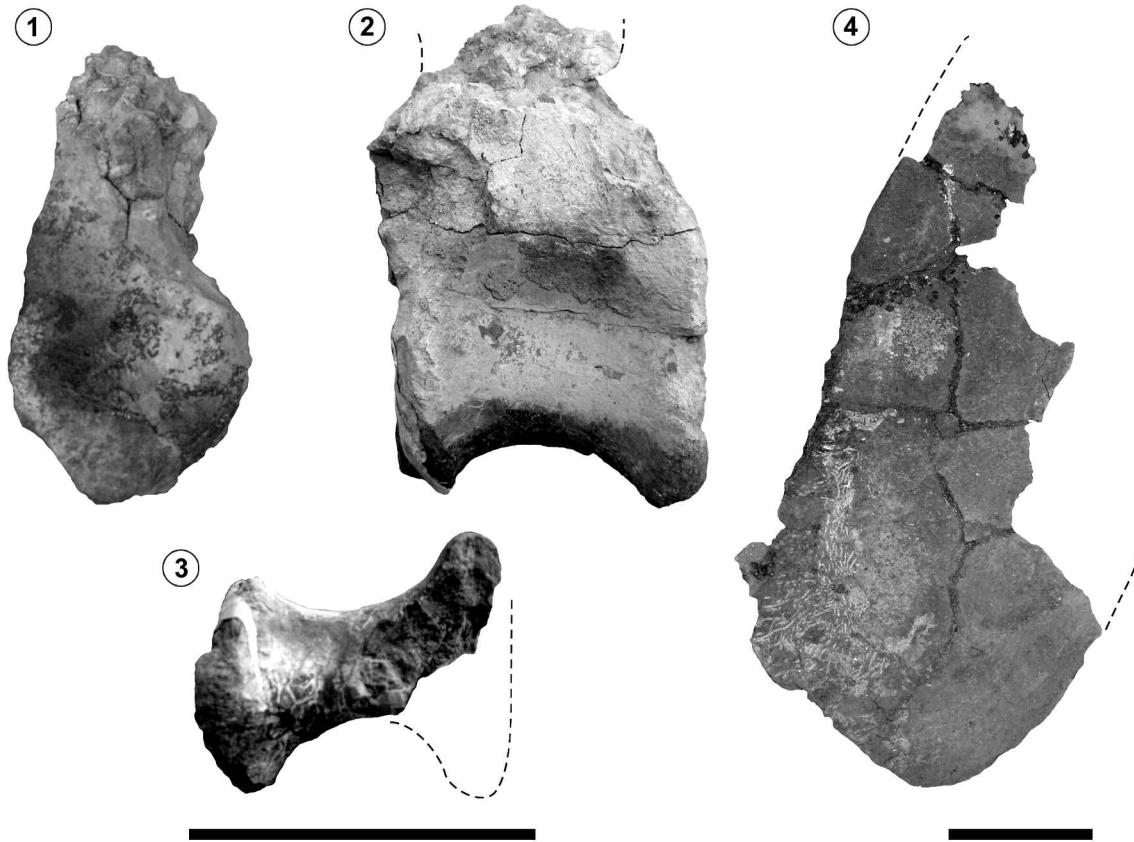


Figure 1. Sauropoda gen. *et* sp. indet., SNGM-1977, mid or posterior dorsal centrum; 1, anterior view; 2, left lateral view; 3, ventral view; 4, sternal plate. Scale bar= 10 cm.

Gen. *et* sp. indet.

Figure 2

Material. SNGM-1981 and SNGM-1982, two mid? caudal centra.

Description. SNGM-1981, the better preserved of the vertebrae, is amphiplatyan to slightly amphicoelous (the articular surfaces of SNGM-1982 are not preserved) (Fig. 2.1–3). Both articular surfaces are slightly wider than high (Tab. 1). The posterior articulation is more nearly circular than the anterior one, which is more quadrangular. In lateral view (Fig. 2.2), the lower margin of the vertebral centrum is concave, and the margins of the articular facets are subparallel.

The maximum width of SNGM-1981 is reached on the ventral quarter of the lateral face; precisely, this is attained by the presence of a longitudinal ridge on the lateral face of the centrum (Fig. 2, lr). Dorsal and ventral to this rim, the

surface of the lateral face is slightly concave (both antero-posteriorly and dorso-ventrally). The latero-dorsal surface is broader than the latero-ventral one, extending almost to the base of the neural arch. Internally, the structure of both vertebrae is apparently camellate (the condition is doubtful due to bad preservation).

Remarks. A longitudinal rim on the lateral face of the caudal centrum was reported by Salgado and García (2002) in some Late Cretaceous titanosaurs (*e.g.*, caudal vertebra 11 of *Traukutitan eocaudata* MPCV 204, caudal vertebra 10 of *Laplatasaurus araukanicus* MPCA 1501), but occurs as well in several other sauropods. For instance, a lateral ridge is also observed in at least one of the anterior caudal vertebrae of *Lusotitan atalaiensis* (Mannion *et al.*, 2013, fig. 6K). In this species, the ridge is higher than in SNGM-1981, probably because it is an anterior element. Coincidentally, in this caudal vertebra there is a conspicuous caudal rib

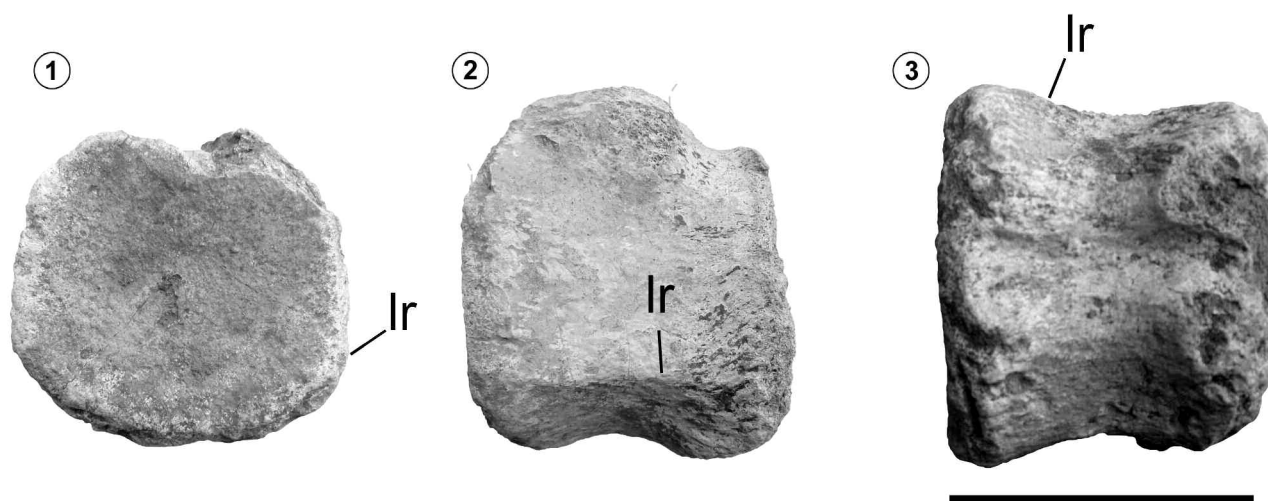


Figure 2. Sauropoda gen. et sp. indet., SNGM-1981, caudal centrum; 1, anterior view; 2, left lateral view; 3, ventral view. Abbreviation: lr, longitudinal ridge. Scale bar = 10 cm.

(Mannion *et al.*, 2013, fig. 6J–L). Furthermore, in the caudal vertebrae assigned to *Cetiosaurus* (Upchurch and Martin, 2003, fig. 3), the ridge always lies in a more dorsal position, and it is present in more posterior elements (OUMNH J1395 and OUMNH J13753). Nevertheless, we cannot claim that the Chilean vertebra belongs to a Titanosauria because we still ignore the distribution of this particular character among the Titanosauriformes. Martin *et al.* (1999, p. 66) mention a “faint longitudinal ridge” on the lateral surface of one specimen referred to *Phuwiangosaurus*. Caudal vertebra 13 of *Tastavinsaurus* (MPZ 99/9) also shows the maximum width on the basal quarter of its lateral face; although in the Chilean material the centrum is proportionally much wider than in the Spanish genus (Royo Torres, 2005, fig. 5.69). In *Janenschia* –considered by Wilson (2002) as a Titanosauria by the presence of a prominent ulnar olecranon process (his character 167), while a basal macronarian according to Carballido *et al.* (2011)– a longitudinal rim in the caudal centra has not been reported. Nevertheless, the caudal vertebra collected in Aysén is quite different to those referred to *Janenschia* by Bonaparte *et al.* (2000, text-fig. 19); its centrum is proportionally wider and, in lateral view, the ventral margin of the centrum is much less concave.

The phylogenetic analysis performed here (see Supplementary Online Information) included specimen SNGM-1981. The strict consensus tree obtained shows SNGM-1981 as part of a large polytomy involving almost all sauropods. When SNGM-1981 is pruned, the resulting consen-

sus tree shows a complete resolution. For this reason SNGM-1981 is considered as Sauropoda gen. et sp. indet.

Gen. et sp. indet.

Figure 1.4

Material. SNGM-1980, partial sternal plate.

Description. The sternal plate is poorly preserved, and it was prepared only on one of its faces. Part of the presumed internal margin of the plate is preserved. Although it is impossible to know if it was semilunate or oval in shape, it was definitively elongated. The preserved portion is deemed to be the posterior one, showing an overall similarity with the sternal plates of *Europasaurus* and *Camarasaurus* (Tschopp and Mateus, 2012, fig. 2).

Remarks. The sternal plate was found in close association with a mid-caudal vertebra (SNGM-1979) that we assign here to the Diplodocinae (see below). However, we cannot refer these two bones to a single individual and taxon, thus we prefer to refer the sternal plate to an indeterminate sauropod.

NEOSAUROPODA Bonaparte, 1986

DIPLODOCOIDEA Marsh, 1884

DIPLODOCIDAE Marsh, 1884

Gen. et sp. indet.

Figure 3

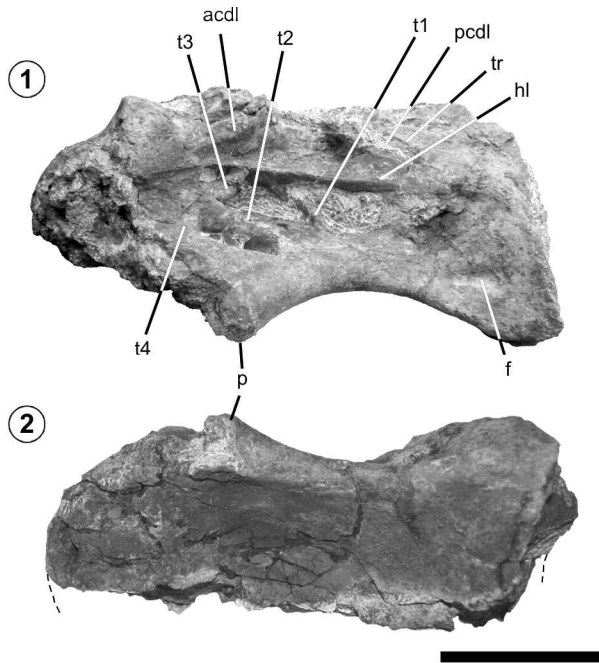


Figure 3. Diplodocidae, gen. *et* sp. indet., SNGM-1978, middle cervical centrum; 1, left lateral view; 2, ventral view. Abbreviations: **acdl**, anterior centrodiapophyseal lamina; **f**, shallow fossa; **hl**, sub-horizontal lamina; **p**, parapophysis; **pcdl**, posterior centrodiapophyseal lamina; **t1-t4**, septa; **tr**, tenuous ridge. Scale bar= 10 cm.

Material. SNGM-1978, middle? cervical centrum.

Description. The centrum belongs probably to a mid-cervical because it is relatively long and the anterior and posterior centrodiapophyseal laminae meet at an angle of nearly 120 degrees. These are not horizontal as in the anterior cervical vertebrae of other sauropods, such as *Phuwiangosaurus* (Martin *et al.*, 1999, fig. 6; P.W. 1-1), *Europasaurus* (Carballido and Sander, 2014, figs. 4C, 5B, 7B, 8D; DFMMh/FV 652.1, 291.4, 291.5, and 710) and *Kaatedocus* (Tschopp and Mateus, 2013, fig. 8; SMA 0004). In fact, that angle is as in the middle cervical vertebrae of *Europasaurus* (Carballido and Sander, 2014, fig. 9A; DFMMh/FV 838.11b), *Australodocus* (Whitlock, 2011a, fig. 2A; MB.R. 2455), *Giraffatitan brancai* (Whitlock, 2011a, fig. 2B; MB.R. 2160.25), *Barosaurus lentus* (Whitlock, 2011a, fig. 2C; CM 11984), *Diplodocus carnegii* (Whitlock, 2011a, fig. 2D; CM 84) and *Tornieria africana* (Whitlock, 2011a, fig. 2E; specimen lost). Proportionally, this centrum resembles that of cervical 8? of the diplodocine *Leinkupal laticauda*, from the Early Cretaceous of Neuquén Province, Argentina (Gallina *et al.*, 2014, fig. 1C–D; MMCH-Pv 63). The centrum length is more than twice

the maximum transverse width of its caudal surface (Tab. 1). Thus, the elongation index (EI) is nearly 2.2. Upchurch (1995, 1998) and Upchurch *et al.* (2004) interpreted that an EI greater than 4 is a synapomorphy of Diplodocinae, although high EI values also occur in some non-diplodocine taxa, such as *Euhelopus* (Wilson and Upchurch, 2009); in this sense, the material from Aysén clearly shows the plesiomorphic condition. The centrum length/ height ratio is 2.27. This index basically agrees with that of middle cervicals of *Apatosaurus*, which is considered an autapomorphic reversal by Whitlock (2011b; character 90).

The centrum is incomplete, especially on the right side (Fig. 3.2). The broken surface of this side allows the observation of internal cavities, suggesting that the whole centrum was camerate, as in non-somphospondyliian sauropods (Whitlock, 2011a). Only the base of the neural arch is preserved, including part of the floor of the neural canal and the base of the left prezygapophysis.

The centrum is strongly opisthocoelus, as in all sauropods. The lateral faces are anteroposteriorly concave and highly pneumatized. In lateral view, the lower margin of the centrum is concave, as well as its lateral margins in ventral view.

The posterior articular surface is transversely expanded, and slightly inclined anteriorly, as seen in lateral view (Fig. 3.1). The ventral face of the centrum is deeply concave, mostly at the level of the parapophyses, as also observed on cervical 15 of *Barosaurus* (Lull, 1919, pl. II, figs. 3–4; Yale Museum catalogue number 429). According to Whitlock (2011b, character 80), a ventral sulcus is typical of diplodocids, but a similar fossa is present in *Giraffatitan brancai* (MB.R. 2180.24–28, 2181.42–44, 2181.47). In *Leinkupal laticauda*, the ventral sulcus is present on cervical vertebrae 6? and 8? (Gallina *et al.*, 2014; MMCH-Pv 63). There are no posteroventral flanges projecting ventrally from the lateral surface, as typically observed in diplodocines (Tschopp and Mateus, 2013).

Only the left parapophysis is partially preserved. It faces latero-ventrally and lies within the anterior third of the centrum. The parapophysis is not excavated dorsally. The pleurocoel is somewhat anteriorly displaced, almost reaching the anterior centrum articulation.

The pleurocoel is limited dorsally by a sub-horizontal, slightly sigmoid lamina (Fig. 3.1, hl), which extends anteriorly up to the anterior articulation of the centrum. This

lamina does not correspond to the accessory posterior centrodiapophyseal lamina that Whitlock (2011a) describes for *Australodocus* and *Giraffatitan*, but to another apparently present in cervical vertebra 11 of *Leinkupal laticauda* (Gallina et al., 2014, fig. 1E; MMCH-Pv 63). The pleurocoel is divided by a series of septa, a character considered by Carballido and Sander (2014, character 115, state 3) as synapomorphic of Brachiosauridae, and independently acquired in *Demandasaurus* and diplodocids. The pleurocoel is divided by a diagonal septum (t1), which is apparently broken (Fig. 3.1). The portion of the pleurocoel that is posterior to this septum is suboval. The anterior portion, which lies above the parapophysis, is subdivided into a series of fossae. A secondary septum, represented by a robust lamina (t2), diverges from the base of the t1 (Fig. 3.1). This secondary septum is sub-horizontal, and separates two sub-fossae; a dorsal one (ventrally limited by the secondary septum [t2], posteriorly by the main septum [t1], and dorsally by the dorsal lamina [hl]), and a ventral one. Anterior to the dorsal fossa, there is a much smaller fossa, separated from the former by a third very robust septum (t3), which extends in an anteroventral-posterodorsal direction (Fig. 3.1). Finally, also the ventral fossa that is below the t2 is subdivided by a septum (Fig. 3.1, t4). The posterior subdivision of this ventral fossa is greater and much deeper than the anterior one.

At the postero-ventral corner of the lateral face of the centrum there is a small fossa or shallow concavity (Fig. 3.1, f), which is possibly reminiscent of the 'ventrolateral pneumatic fossa' of Whitlock (2011a). According to this author, this fossa occurs only in diplodocids; however, in *Diplodocus* and *Apatosaurus* its development is irregular (Whitlock, 2011a), whereas it is consistently present in *Tornieria* and *Barosaurus*. Dorsal to the horizontal lamina (Fig. 3.1, hl) there is a series of laminae including the acdl and the pcdl, which delimit a triangle within which there are two small but deep depressions (anterior and posterior). The surface posterior to the pcdl is almost flat, and with a tenuous ridge that extends parallel to the pcdl (Fig. 3.1, tr). The centro-prezygapophyseal laminae are not preserved. The floor of the neural canal has a maximum width of 35 mm.

Remarks. The phylogenetic analysis (see Supplementary Online Information) recovered SNGM 1978 as a Diplodocidae (*Diplodocus* not *Dicraeosaurus*; Taylor and Naish, 2005) by the presence of cervical pleurocoels divided in three or

more lateral excavations resulting in a complex morphology (Carballido and Sander, 2014; character 115), and by the presence of a ventral longitudinal *sulcus* (character 342, added in this study). In turn, SNGM 1978 is depicted as a basal diplodocid because it retains the plesiomorphic condition of having single and wide cavities (Carballido and Sander, 2014; character 120).

DIPLODOCINAE Marsh, 1884

Gen. et sp. indet.

Figure 4

Material. SNGM-1979, incomplete mid-posterior caudal vertebra.

Description. The position of this element in the caudal series was established based on comparisons with other diplodocids. According to its proportions, the vertebra would have had a position between caudal vertebrae 17 and 20. In *Leinkupal laticauda*, the distalmost caudal vertebra figured by Gallina et al. (2014, fig. 3D; MMCH-Pv 63) is interpreted by these authors as caudal vertebra 20. The centrum from Aysén is almost identical in proportions to this vertebra, but belongs to a much larger specimen. The caudal vertebra SNGM-1979 also resembles caudal vertebra 17 of *Barosaurus lentus* (Lull, 1919, pl. V, fig. 6; Yale Museum catalogue number 229). Nevertheless, there are minor differences compared to this species: in caudal vertebra 15 to 17 of *Barosaurus lentus* (Yale Museum catalogue number 229) the width of the anterior articulation is greater than its height (Lull, 1919), whereas in the Chilean material the anterior articular surface is more rounded.

Finally, the centrum of the caudal vertebra SNGM-1979 is also proportionally very similar to the specimen MB.R. 2956.7 [dd 357], an anterior-mid caudal referred to *Tornieria* by Remes (2006, fig. 3K–L). In the African genus, however, the transverse processes are apparently more developed, and for this reason it may correspond to a more anterior position. The centrum of SNGM-1979 is amphiplatyan and both ends of the caudal centrum are transversely expanded, although not to the extent seen in vertebra MB.R. 2956.7 [dd 357] assigned to *Tornieria* (Remes, 2006, fig. 5C), in which the centrum seems to be much more constrained at mid-length (Fig. 4.4). The minimum width of the ventral face

of SNMG-1979 is 55% the width of the anterior articulation and 60% of the posterior; whereas in the African genus these ratios are approximately 52% in both cases.

The anterior articulation is somewhat higher than the posterior one; in turn, the centrum height of the anterior articulation is 80% of the centrum length (Tab. 1). The centrum is wider ventrally. The ventral face is marked by a deep longitudinal hollow, as in diplodocines (Wilson, 2002, character 132), including *Tornieria* (Remes, 2006; but see Whitlock, 2011b).

At the postero-lateral corners of the ventral face there are the robust articular facets for the chevrons. Both facets are connected through a stout rim, which posteriorly encloses the longitudinal hollow mentioned above. Anteriorly, the ventral hollow is enclosed by another osseous rim. Unlike *Tornieria* (Remes, 2006, fig. 5C), in the Chilean material the rims that bound the ventral longitudinal groove are laterally blunt, not sharp.

On the lateral face of the centrum there is a deep pleurocoel, as in the anterior caudal vertebrae of diplodocines (Wilson, 2002; character 119), or as in the anterior caudal vertebrae of *Supersaurus* + more derived diplodocids (Whitlock, 2011b; character 134). The pleurocoel of the Chilean caudal vertebra is eye-shaped, with acute ends. The pleurocoel is located at centrum mid-length, being slightly displaced dorsally, thus occupying a similar position as the pleurocoels of the anterior-to-mid caudal vertebrae of *Tornieria* (Remes, 2006, fig. 3K–L). In the Chilean material, the length of the pleurocoel (11 cm) is almost half the centrum length (22.3 cm). In comparison, in caudal vertebra 17 of *Barosaurus* (Yale Museum catalogue number 229) the pleurocoel seems to be relatively longer than in the Chilean material (Lull, 1919).

Ventral to the pleurocoel, the lateral face of the vertebral centrum is virtually flat, as in diplodocines (Wilson, 2002, character 131). Dorsal to the pleurocoel, there is a low longitudinal protuberance, which is interpreted as the trace of the transverse process. Between the longitudinal protuberance and the base of neural arch lies a slightly concave surface.

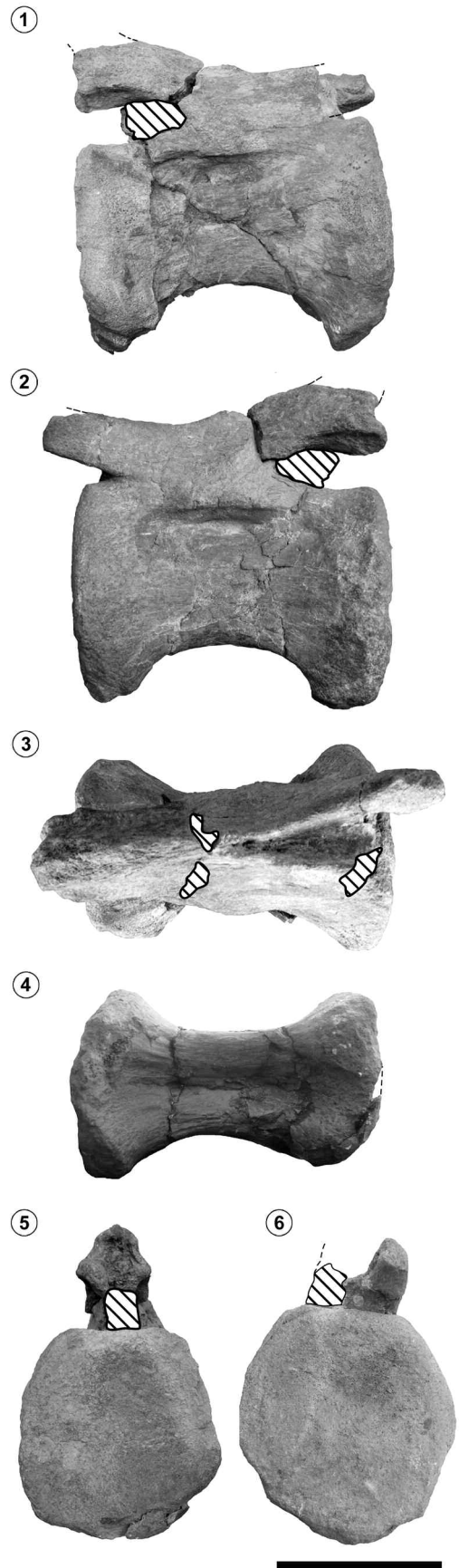


Figure 4. Diplodocinae gen. et sp. indet., SNMG-1979, mid-posterior caudal vertebra; 1, right lateral view; 2, left lateral view; 3, dorsal view; 4, ventral; 5, posterior view; 6, anterior view. Scale bar= 10 cm.

The neural arch is located at the anterior half of the centrum. The left prezygapophysis is almost complete, and relatively short, as in caudal vertebra 17 of *Barosaurus* (Yale Museum catalogue number 229). In this regard, the prezygapophyses of *Leinkupal laticauda* (Gallina et al., 2014, fig. 3D; MMCH-Pv 63) are longer and more dorsally oriented than in the Chilean caudal. The neural spine is not complete, but it was probably directed slightly posteriorly.

Remarks. The phylogenetic analysis performed (see Supplementary Online Information) unequivocally placed SNGM-1979 in the Diplodocinae (*Diplodocus* not *Apatosaurus*, Taylor and Naish, 2005) –as the sister group of *Barosaurus* + *Diplodocus*– by the presence of caudal pleurocoels (character 194); quadrangular middle caudal centra, flat ventrally and laterally (character 208), and ventral longitudinal hollow in mid caudal centra (character 209).

TITANOSAURIFORMES? Salgado, Coria and Calvo, 1997

Gen. et sp. indet.

Figure 5.1

Material. SNGM-1983, a distal end of a left femur.

Description. This bone belongs to a mid to small-sized sauropod; if the bone were proportionally similar to *Giraffatitan brancai* (Janensch, 1961; MB.R. 2694) its length would have been approximately 105 cm.

In distal view, the femur is anteroposteriorly compressed, as is typical for Titanosauriformes (Royo Torres, 2005, figs. 5.153, 5.154, 5.155) (Tab. 2). The anteromedial margin of the distal end of the femur is inclined at nearly 120° in respect to the transverse axis of the distal end, unlike in other sauropods, where such an angle is close to 90° (Janensch, 1961, abb.14–22). In this aspect, the distal end of the femur resembles that of *Phuwiangosaurus* (Martin et al., 1999, fig. 18.3; P.W. 1–16). The lateral condyle is

smaller than the medial one, as is usual in sauropods. The lateral epicondyle is developed, but much less than the lateral condyle. In *Giraffatitan brancai*, the medial condyle is narrower latero-medially, and the lateral condyle is more robust (Janensch, 1961, p. 208). Posteriorly, the intercondylar fossa is deep, as is usual among sauropodomorphs; anteriorly, there is a relatively well-developed intercondylar furrow, although not as much as in some Tendaguru sauropods, such as *Janenschia* (Wild, 1991) and *Dicraeosaurus* (Janensch, 1961, abb. 21–22). The depth of the anterior intercondylar furrow of SNGM-1983 is similar to some specimens of *Giraffatitan* (Janensch, 1961, abb. 14, st 134), in particular to the specimens MB.R. 2668 (which is the new specimen number for t6) and MB.R. 2694 (the new specimen number for st291).

Remarks. We provisionally assign specimen SNGM-1983 to Titanosauriformes because of its overall similarity to some specimens of *Giraffatitan brancai*, particularly in the depth of the intercondylar furrow and the anteroposterior compression of the femur.

Gen. et sp. indet.

Figure 5.4–6

Material. SNGM-1984, distal end of a right tibia.

Description. The anterior condyle is well developed as in most neosauropods, and sub-pentagonal in distal view (the anterior and the medial margins meet at a right angle; Fig. 5.6). The posterior condyle is also well developed; it is robust and rounded posteriorly, more than in *Apatosaurus* (Gilmore, 1936, p. 232, fig. 23D; CM 3018), *Diplodocus* (Hatcher, 1901, figs. 19, 48; CM 94), *Tornieria africana* (*Barosaurus africanus*, according to Janensch, 1961, p. 210; specimen MB.R. 2599) (Fig. 5.7), *Giraffatitan* (Fig. 5.8, St. 148), and *Phuwiangosaurus* (Fig. 5.9; K. sites 1–25).

According to Royo Torres (2005, p. 395–396), anterior

TABLE 2. Measurements of the appendicular bones found in Aysén, in cm. Abbreviations: MLWDE, mediolateral width of the distal end; APWDE, anteroposterior width of the distal end.

Specimen	MLWDE	APWDE
SNGM-1983	31	17.6
SNGM-1984	13.01	14

and posterior condyles of similar size is a character of Titanosauriformes; in contrast, in non-titanosauriform neosauropods, the anterior condyle is always larger than the

posterior one. In this regard, the Chilean material presents the condition observed in Titanosauriformes. Clearly, the antero-posterior length of the distal end of the tibia is

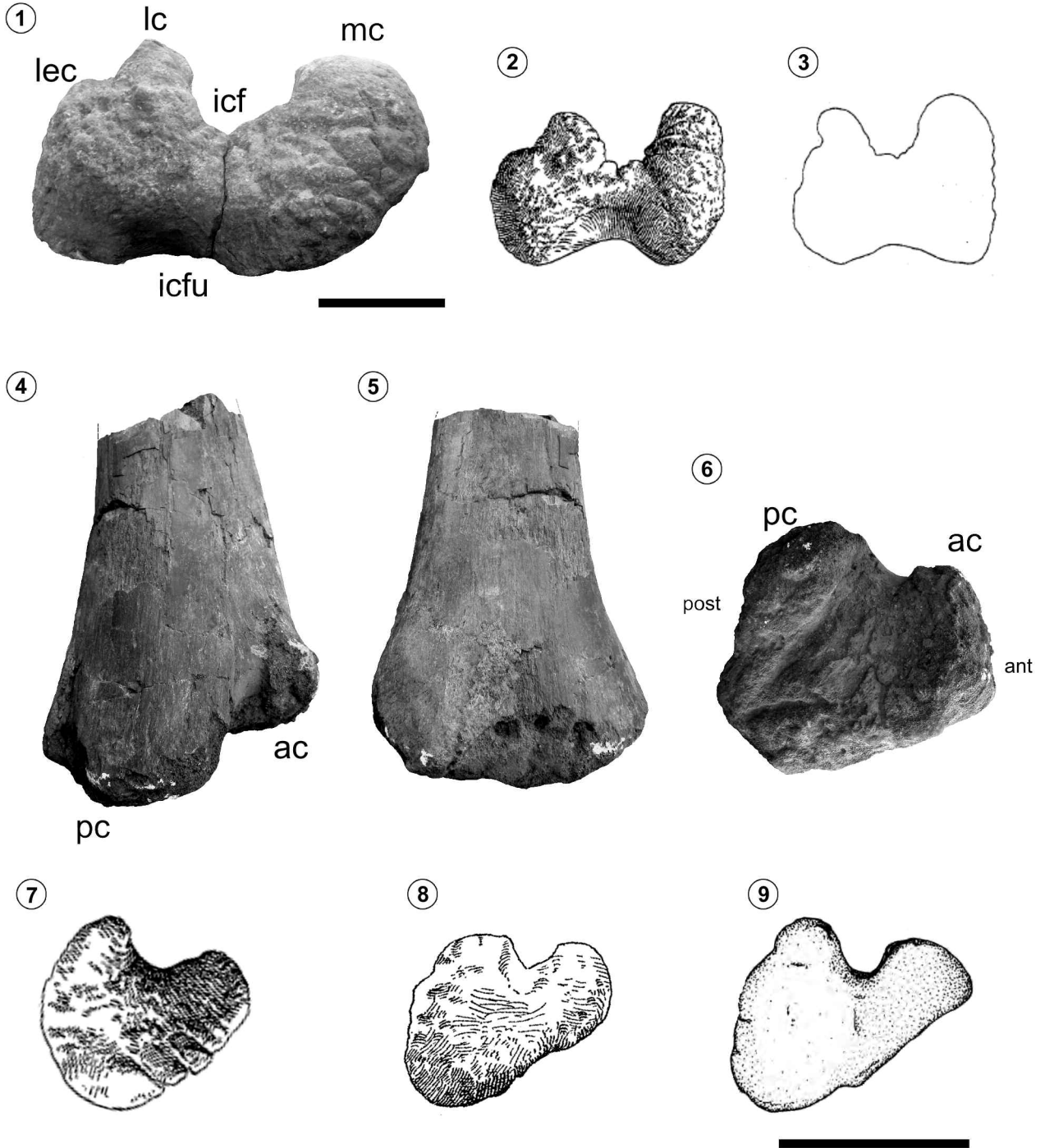


Figure 5. 1, Titanosauriformes? gen et sp. indet. distal view of a left femur SNGM-1983; 2, right femur (inverted) of *Giraffatitan brancai* (Janensch, 1961); 3, right femur (inverted) of *Tornieria robusta* (Janensch, 1961); Titanosauriformes? gen et sp. indet. distal end of a right tibia SNGM-1984 in 4, external; 5, posterior; and 6, distal views; 7, distal view of the left tibia (inverted) of Diplodocidae indet. (Remes 2009); 8, distal view of the right tibia of *Giraffatitan brancai* (Janensch 1961); 9, distal view of the left tibia of *Phuwiangosaurus* (Martin et al. 1999).

greater than its transverse width. The opposite condition (transverse width greater than antero-posterior length of the distal end), was established by Salgado *et al.* (1997) as diagnostic of their unnamed node 1 (*Chubutisaurus* + more derived titanosauriformes above node 7 in their analysis). Finally, in SNGM-1984 there is a straight postero-medial margin that is distinctly separated from the posterior and the antero-medial margins, and with which it forms a low angle (Fig. 5.6). In other sauropods (Fig. 5.8–9) the postero-medial portion of the outline of the distal surface of the tibia seems to be more rounded in distal view.

Remarks. Because the condyles of the tibia SNGM-1984 are subequal in size, it is considered to belong to a member of the Titanosauriformes (Royo Torres, 2005). Given the greater antero-posterior length of its distal end compared to its transverse width, it is probably a basal Titanosauriformes (Salgado *et al.*, 1997). The straight postero-medial edge of the tibia might be autapomorphic, because we do not know of any other titanosauriform with this feature.

DISCUSSION AND CONCLUSIONS

The materials recovered in Aysén reveal the presence of a diverse array of sauropod clades in southern South America at the end of the Jurassic. The Chilean sauropod association includes a possible basal sauropod or dicraeosaurid (represented by a dorsal centrum), one or more possible Titanosauriformes (represented by a femur and a tibia), and at least two members of Diplodocidae; one basal Diplodocidae (represented by a cervical vertebra) and a Diplodocinae (represented by a caudal vertebra). The latter would be the first evidence of this clade in the Jurassic of South America. Up to now, Gondwanan diplodocines were only known from the Upper Jurassic of Africa (Remes, 2006) and the Lower Cretaceous of Patagonia (Gallina *et al.*, 2014). The caudal vertebra SNGM-1979 collected in Aysén reveals that diplodocines were more widely distributed throughout Gondwana during the Late Jurassic. The referred African Jurassic diplodocine is *Tornieria africana*.

According to Carballido (2012), towards the Late Jurassic the three main diplodocoid lineages (rebbachisaurids, dicraeosaurids, and diplodocids) had diverged from each other and were probably widely distributed in nearly all the continents. By that time, diplodocines were already differen-

tiated within Diplodocidae, and were also widely distributed, as suggested by the caudal vertebra SNGM-1979 found in Aysén. On the other hand, Whitlock (2011b) pointed out that by the Late Jurassic diplodocids would have dispersed from North America to Europe and Africa, whereas dicraeosaurids would have dispersed from North America to South America and from there to Africa. The diplodocines recorded in Aysén show that the members of this group already lived in South America during the Late Jurassic.

Whitlock (2011a) made an interesting paleoenvironmental inference based on the relative abundance of brachiosaurids and diplodocids. According to him (Whitlock, 2011a), the faunal particularities of the Morrison Formation (scantiness of titanosauriforms and abundance of diplodocids) can be explained by its paleoecology. That unit would represent a tropical savanna of low bushes with ferns occupying the place grass does in the current ecosystems; in such an environment, podocarpaceans were limited. In turn, Tendaguru ecosystems (with relatively abundant titanosauriformes) were dominated by high conifers, Araucariaceae, Podocarpaceae and Cycadaceae; in general, ferns and brushes were scarce there. In Aysén, both groups of neosauropods occurred together (as also in the Oxfordian–Kimmeridgian Cañadón Calcáreo Formation, in Chubut, Cúneo *et al.*, 2013), although the low number of specimens hampers an accurate assessment of their relative abundance. The Toqui Formation at Aysén preserves trunks of *Podocarpoxylon* and trilete spores, indicating humid and bleak conditions (De la Cruz *et al.*, 2008). In this regard, the scanty evidence currently available suggests greater paleoecological similarities with the Tendaguru biota.

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