Reappraisal of the Early Cretaceous sauropod dinosaur *Amargatitanis macni* (Apesteguía, 2007), from northwestern Patagonia, Argentina

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A R T I C L E   I N F O

A B S T R A C T

Amargatitanis macni Apesteguía, 2007 was described as a purported titanosaur sauropod. That referral is significant because *Amargatitanis* would represent one of the oldest known members of Titanosauria. However, this referral and even the systematic validity of the taxon were questioned. Here, all the available remains of the taxon are evaluated including a description of unpublished elements. The identity of the type material is discussed based on a first-hand examination of the specimens and evaluation of the original field notes as reliable evidence for bone association. The original holotype of *Amargatitanis* is a chimaera, as pointed out by previous authors. Herein a new, modified holotype for *Amargatitanis* is proposed. This analysis presents a revised diagnosis for *Amargatitanis macni* as a valid taxon, and description of unpublished material clarifies the anatomy of this sauropod dinosaur. The inclusion of *Amargatitanis macni* in an updated phylogenetic analysis revealed the presence of a second species of the family Dicraeosauridae in the La Amarga Formation, suggesting that, at present, there is no record of titanosaur body fossils in Patagonia prior to Cenomanian times.

1. Introduction

The record of Early Cretaceous dinosaurs from South America is scarce compared to other continents (Weishampel et al., 2004). However, several units, primarily from post-Barremian times, in Argentina and Brazil are well-documented (e.g., Leanza et al., 2004; Martill, 2007). The La Amarga Formation (Barremian), outcropping in Neuquén Province, northwestern Patagonia Argentina, is a remarkable continental unit from this period of time. In addition to saurischian and ornithischian dinosaurs, it contains a diverse vertebrate assemblage including, pterosaurs, crocodyliforms and mammals (Bonaparte, 1986, 1996; Montanelli, 1987; Chiappe, 1988; Salgado and Bonaparte, 1991; Leanza et al., 2004; Apesteguía, 2007; Pereda-Suberbiola et al., 2013).

The sauropod diversity of La Amarga was evaluated by Apesteguía (2007) on the basis of previously described diplodocoid taxa (i.e., *Amargasaurus cazaui* Salgado & Bonaparte, 1991, and *Zapalasaurus bonapartei* Salgado, Souza Carvalho & Garrido, 2006), and the description of some unstudied materials collected in 1983 and 1986 by a team leaded by José Bonaparte. Apesteguía (2007) recognized a more complex diversity than previously known,

including the already documented dicraeosaurids and basal diplodocoids, plus the addition of rebbachisaurids and titanosauriforms, which included a purported titanosaurian. This last taxon was named *Amargatitanis macni* (Apesteguía, 2007). Considering that the Early Cretaceous sauropod fauna from South America was mainly composed of diplodocoids and basal titanosauriforms (Salgado and Coria, 2005; Salgado and Bonaparte, 2007), that finding was significant because *Amargatitanis* would represent one of the oldest known members of Titanosauria. Later, this referral was questioned and briefly discussed by D'Emic (2012) and Mannion et al. (2013), who regarded the taxon as a *nomen dubium*. In this contribution, all the available remains of *Amargatitanis macni* are evaluated. The identity of the type material is modified and discussed based on first-hand examination of the specimens and evaluation of the original field notes as reliable evidence for bone association. The material published by Apesteguía (2007) is here redescribed, and supplemented with the description of unpublished elements coming from the original excavation site in order to evaluate the validity and taxonomic status of *Amargatitanis macni*. This revision includes an evaluation of the diagnostic features of *Amargatitanis* and the inclusion of this taxon in an updated sauropod phylogenetic analysis.

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2. Institutional abbreviations

CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA.

MACN, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavía', Buenos Aires, Argentina.

MB.R., Museum für Naturkunde Berlin, Germany.

MOZ, Museo Olsacher, Zapala, Neuquén, Argentina.

3. Systematic paleontology

DINOSAURIA Owen, 1842
SAUROPODA Marsh, 1878
NEOSAUROPODA Bonaparte, 1986
DIPLODOCOIDEA Marsh, 1884
FLAGELLICAUDATA Harris & Dodson, 2004
DICRAEOSAURIDAE Huene, 1927

Amargatitanis macni Apesteguía, 2007

3.1. Holotype

MACN PV N53. Two caudal vertebrae, an incomplete right ischium, a right femur, an incomplete right tibia, an incomplete right fibula, a right astragalus, and an incomplete right metatarsal I.

3.2. Comments

Apesteguía (2007) included a left scapula (MACN PV N34) and additional caudal vertebrae [MACN PV N51 (A—F)] as part of the holotype. However, there is reliable evidence (see Section 3.5.) to exclude those specimens from the holotype following article 73.1.5 of the International Code of Zoological Nomenclature. Conversely, but following the same criterion, the right ischium, the right tibia, the right fibula, and the incomplete right metatarsal I are here included among the type material.

3.3. Revised diagnosis

Amargatitanis macni can be diagnosed by the following autapomorphies (marked by an asterisk), as well as a unique combination of character states: anterior caudal prezygapophyseal centrodiapophyseal fossa deep and bearing an internal vertical lamina (*); proportionally wide proximal portion of the femur in relation to the distal end (*); fourth trochanter low, located at mid-length of the femur (shared with other flagellicaudatans); astragalus with a deep crescent-shaped posterior fossa, bearing two distant foramina (*).

3.4. Locality and horizon

The site is located 2.5 km SE from the bridge of National Route 40, crossing the La Amarga stream. The bridge is 80 km south of Zapala City, Neuquén province, Argentina. The fossil remains come from fluvial channel sands of braided rivers from the Puesto Antigual Member of the La Amarga Formation, Barremian, Lower Cretaceous (Leanza and Hugo, 1997; Apesteguía, 2007).

3.5. Comments on the site of provenance of MACN PV N53

From March 11th to 16th of 1983, Dr. José Bonaparte conducted fieldwork at the La Amarga locality. During that period, four different fossil sites (i.e., excavations) were found in an area of no more than 400 m in extent (original map in Bonaparte's field book; Apesteguía, 2007). Site number "1" included associated material recovered and listed by Bonaparte as follows: "*En total huesos logrados de este lugar: 1 fémur, 1 fíbula? incompleta, 1 tibia incompleta, 1 astragalo, 2 caudales anteriores incompletas, 2 falanges, 2 frag. de metatarsales y 1 isquión. Todo este material lleva la sigla 1.*" (the total bones recovered from this place: 1 femur, 1 incomplete fibula?, 1 incomplete tibia, 1 astragalus, 2 incomplete anterior caudal vertebrae, 2 phalanges, 2 incomplete metatarsals, and 1 ischium. All this material is labeled with the number 1). This field information coupled with anatomical and size coherence, plus the presence of a red field number "1" on the bones, housed in the collection of the 'Bernardino Rivadavía' museum as MACN PV N 53, is evidence that these bones belong to one specimen, comprising the new modified holotype specimen described here (Fig 1). Unfortunately, the phalanges and one of the metatarsals mentioned by Bonaparte were not found in the MACN collections.

The left scapula MACN PV N34 and caudal vertebrae MACN PV N51 are excluded from the holotype of *Amargatitanis macni* because they are not even mentioned in the field notes from 1983 and consequently they were not labeled with the number "1". This information suggests a different geographic provenance for the scapula and caudal vertebrae. It is possible that MACN PV N34 could correspond to the complete sauropod scapula mentioned by Bonaparte in his 1986 field notes, which describe material from another locality in the La Amarga area. The taxonomic status of these bones is beyond the scope of this contribution.

4. Description and comparisons

4.1. Vertebrae (Fig. 2, Table 1)

Two caudal vertebrae are present in the type material. One corresponds to the anteriormost part of the tail, possibly the third or fourth vertebra based on the general proportions and presence of well-developed chevron facets. The other, much smaller, vertebra probably had a more posterior position (e.g. anterior to the mid portion of the tail).

The anterior caudal preserves the centrum, the base of the neural arch, incomplete transverse processes, and the postzygapophyses with a portion of the neural spine. The centrum is short and tall in lateral aspect, and has a cylindrical perimeter clearly evident in posterior view. The anterior face is slightly concave and the posterior one is flat, as in many flagellicaudatan including the dicraeosaurids *Amargasaurus* (MACN PV N15), *Suuwassea* (Harris, 2006) and *Dicraeosaurus* (Janensch, 1929). There is no evidence of pneumatopores on the lateral walls of the centrum. Ventrally, the facets for the chevrons are located on the posterior edge, and unlike *Suuwassea* and *Dicraeosaurus* the ventral irregular foraminae are absent.

The neural arch extends dorsally two times the height of the neural canal. As in most diplodocoids and basal macronarians such *Camarasaurus* (Osborn & Mook, 1921), deep and well-developed prezygapophyseal centrodiapophyseal fosse (prcdf) are present in anterior aspect. In *Amargatitanis* this character is clearly present, visible in both anterior and lateral views, and with a thin vertical lamina inside. This condition is not present in other sauropods and is interpreted as an autapomorphy of *Amargatitanis*. Although incomplete, the transverse processes are dorsolaterally projected as in dicraeosaurids and the rebbachisaur *Demandasaurus* (Torcida et al., 2011), differing from the laterally projected transverse processes present in macronarians, and the ventrolaterally projected processes observed in derived flagellicaudatans (Gallina and Otero, 2009). Most of the vertebral laminae cannot be recognized because of the poor preservation of the neural arch; however a portion of the thick left prezygodiapophyseal lamina (prdl) is preserved. The ovoid postzygapophyses are located over a short but conspicuous hyposphenal ridge, unlike the condition present in rebbachisaurids where this ridge is absent.

Fig. 1. Evidence for grouping the holotype material of *Amargatitanis macni* (MACN PV N53). A, Original paragraph from Bonaparte's field book and registration card handwriting by José Bonaparte at MACN collection grouping material from site 1 (note that Bonaparte referred to "Pichi Picún Leufú Formation", but later was considered to be La Amarga Formation). B, Right tibia with a field number 1 in red. C, Right ischium with a field number 1 in red. D, Right astragalus with a field number 1 in red. E, Right fibula with a field number 1 in red. Not to scale.

The other caudal vertebra is represented by an incomplete centrum with a partially preserved neural arch. The centrum is slightly longer than tall, subquadrangular in anterior view. The articular facets are strongly concave, although this condition could be a result of poor preservation. The lateral walls are nearly flat, devoid of a longitudinal ridge at mid-height as present in *Dicraeosaurus* and *Suuwassea*. The neural arch is anteriorly located. Neither the zygapophyses nor the neural spine are preserved, thus an accurate position in the tail is difficult to establish.

4.2. Ischium (Fig. 3A–C, Table 2)

The right ischium is preserved. This bone was not included in the original description of *Amargatitanis macni* (Apesteguía, 2007).

Although the acetabular region is damaged, the iliac and pubic peduncles are mostly complete and oriented at a right angle to each other. Only a portion of the ischial shaft is preserved. The iliac peduncle is slightly longer than wide as in most flagellicaudatans, differing from the long and constricted peduncles present in several rebbachisaurids (Sereno et al., 2007). The pubic peduncle is as wide as its anteroposterior length. Peculiarly, the posterior border of the ischium is straight along the iliac and pubic peduncles, a condition only present in *Giraffatitan brancai* (Janensch, 1961). The proximal portion of the distal shaft is clearly oriented downward and backward at angle of an approximately 160° with respect to the iliac peduncle, differing from the lower angle present in Camarasauromorpha. This distal process has a subtriangular perimeter in cross section.
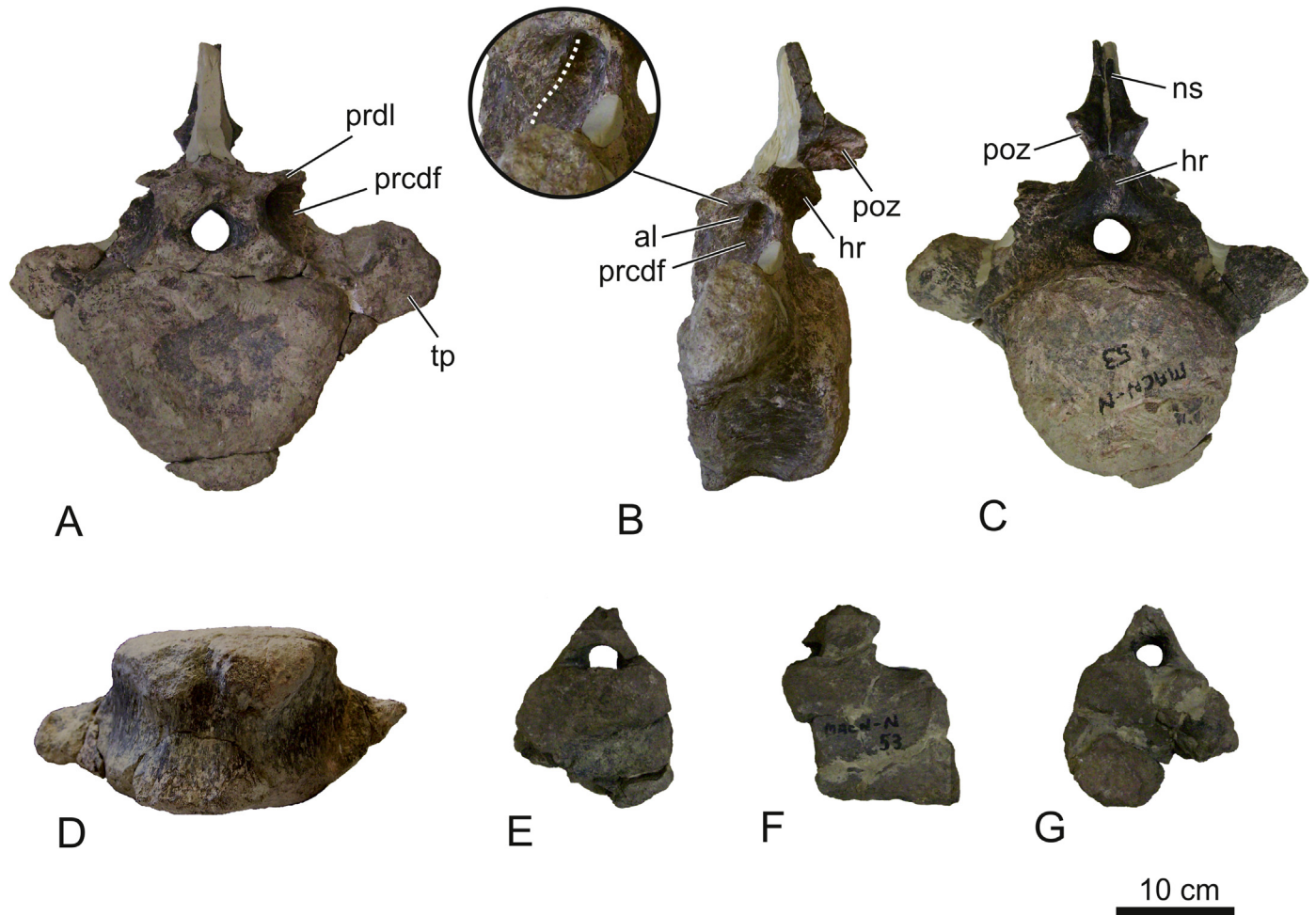
Fig. 2. Vertebral remains of *Amargatitanis macni* (MACN PV N53). Anterior caudal vertebra in: A, anterior; B, lateral, with a close-up of the prezygapophyseal centrodiapophyseal fossa and the accessory lamina inside; C, posterior; and D, ventral views. Anterior to mid caudal vertebra in: E, anterior; F, lateral; and G, posterior views. Abbreviations: al, accessory lamina; hr, hyposphenal ridge; ns, neural spine; poz, postzygapophysis; prcdf, prezygapophyseal centrodiapophyseal fossa; prdl, prezygodiapophyseal lamina; tp, transverse process.

Table 1
Measurements (cm) of axial elements of *Amargatitanis macni* (MACN PV N53).

Element	Centrum			Total height	Total width
	Length	Width	Height		
Anterior caudal	11.5	15.5	16	35*	31*
Middle caudal	14*	13	12	15.5*	13

Incomplete measurements are marked with *.

The lateral surface of the ischium is mostly flat, except for the presence of a longitudinal fossa on the posterior border. This condition is shared with other flagellicaudatans such as *Apatosaurus*, *Brontosaurus* and *Dicraeosaurus* (Tschopp et al., 2015). There is no evidence of muscle scars on the lateral surface. On the other hand, the medial surface of the ischium is concave, primarily in its middle portion on the pelvic canal. In this regard, the pubic articular facet depicts a slight curve in anterior view.

4.3. Femur (Fig. 3A–C, Table 2)

The right femur is complete except for part of the tibial condyle, which is damaged. The femur is robust, particularly its proximal portion which is transversely wide. The marked asymmetry, in terms of mediolateral width, between the proximal and distal portions of the femur (ratio: 1.2) is not present in other sauropod, and is considered here as an autapomorphy of *Amargatitanis*. The ratio present in most sauropods is close to 1.0 (e.g. *Barapasaurus*, 1.0; *Cetiosaurus*, 1.03; *Diplodocus*, 1.06; *Dicraeosaurus*, 1.01; *Camarasaurus*, 0.95; *Giraffatitan*, 1.0; *Saltasaurus*, 0.97). The massive femoral head is located higher than the greater trochanter which is partially damaged. Although the lateral border is gently curved, the proximal mid-portion of the femur is devoid of the prominent lateral bulge that characterizes titanosauriforms (Salgado et al., 1997). This condition resembles the morphology observed in other dicraeosaurid femora such as those of *Dicraeosaurus hansemanni* (MB.R. 2695) and *Amargasaurus cazaui* (MACN PV N15). The diaphysis is anteroposteriorly compressed and has a subtriangular cross section. The conspicuous fourth trochanter is located at midlength of the femur as a rounded ridge, a condition shared with other flagellicaudatans. Conversely, in rebbachisaurids the fourth trochanter is poorly developed (Mannion et al., 2012), and in derived macronarians it is located on the proximal third of the femur (Upchurch et al., 2004).

Both the tibial and fibular condyles are distally and posteriorly exposed (although the former is poorly preserved). In posterior view, the fibular condyle extends slightly beyond the level of the tibial condyle. The former is wider than the latter in ventral view.
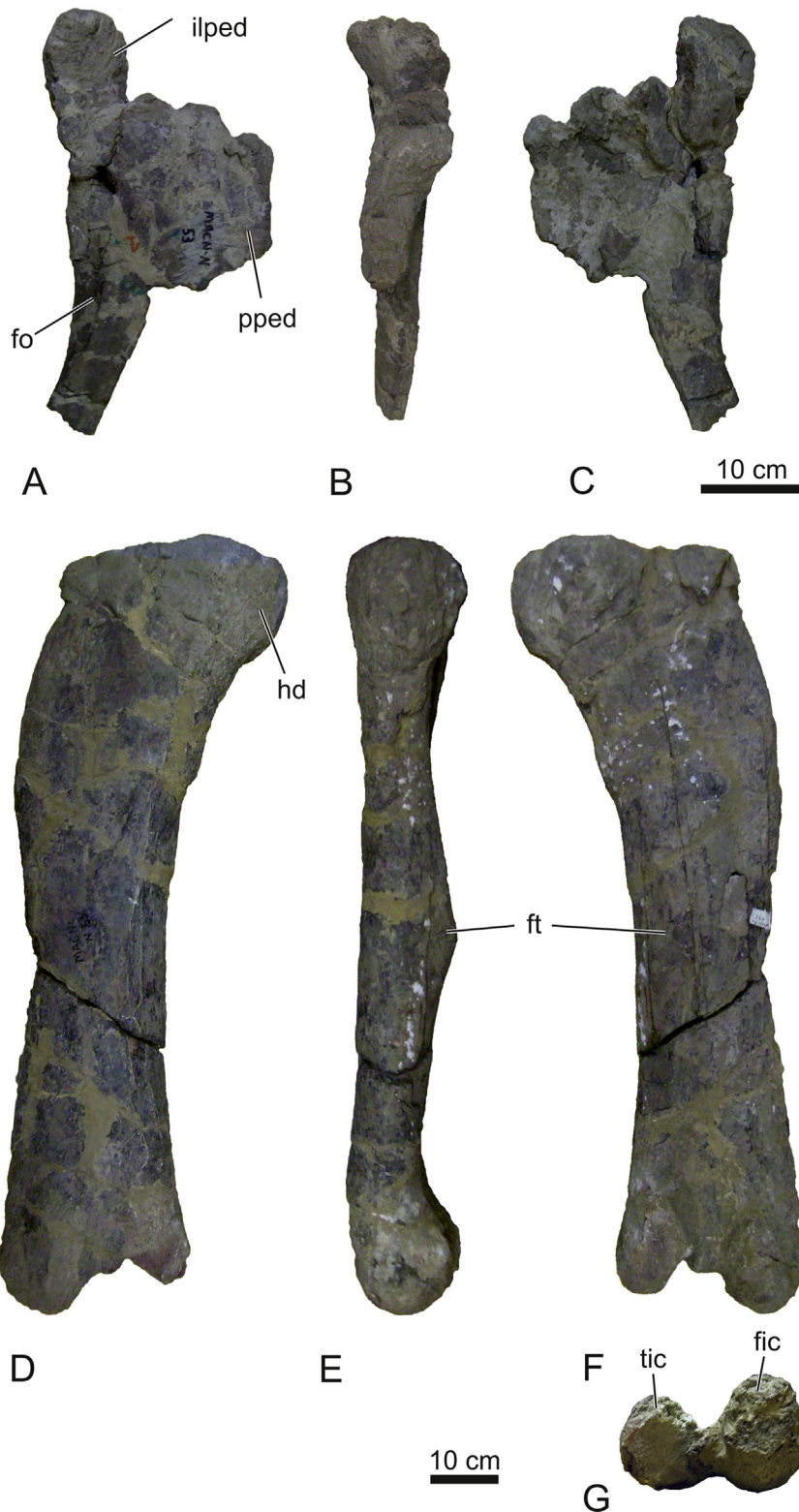
Fig. 3. Pelvic girdle and appendicular elements of *Amargatitanis macni* (MACN PV N53). Right ischium in: A, lateral; B, anterior; and C, medial views. Right femur in: D, anterior; E, medial; F, posterior; and G, distal views. Abbreviations: fic, fibular condyle; ft, fourth trochanter; fo, fossa; hd, head; ilped, iliac peduncle; pped, pubic peduncle; tic, tibial condyle.

4.4. Tibia (Fig. 4A–C, Table 2)

An incomplete right tibia is considered part of the type spec-imen. This bone was not mentioned in the original description (Apesteguía, 2007). Whereas the proximal end is mostly damaged,

the distal end is completely missing. However, the diaphysis and most of the cnemial crest are preserved and can be described. The proximal end is anteroposteriorly expanded, with a slightly concave lateral face and flat medial surface. The partially preserved cnemial crest is robust and projects more anteriorly than laterally. In lateral

Table 2
Measurements (cm) of pelvic girdle and appendicular elements of the holotype of *Amargatitanis macni* (MACN PV N53).

Element	Total length	Maximum width		
		Proximal		Distal
		Transverse	Diaphysis	Transverse
Ischium	36.5*	8	—	5.5
Femur	109	31	18.5	26
Tibia	56*	19*	11.5*	16*
Fibula	53*	—	10.5	12
Astragalus	11	12	—	16
Mtt I	7.5*	—	6	10.5

Incomplete measurements are marked with *. Dashes indicate where measurements could not be taken.

view, the crest is subtriangular and markedly low, a condition shared with *Zapalasaurus* (Pv-6127-MOZ), *Dicraeosaurus* (Janensch, 1961), and *Amargasaurus* (MACN PV N15). By contrast, the cnemial crest of most macronarians is more triangular and extends to a higher level [e.g. *Camarasaurus* (Ostrom & McIntosh, 1966), *Brachiosaurus* (Janensch, 1961), *Bonitasaura* (Gallina & Apesteguía, 2015)]. The shaft of the tibia is slightly twisted in the distal segment where it is also slightly expanded. However, this expansion is not as pronounced as the transversely expanded distal tibia present in titanosaurs (Salgado et al., 1997; Wilson, 2002).

4.5. Fibula (Fig. 4D—F, Table 2)

The right fibula is represented by a slender bone, which preserves the diaphysis and the distal portion. The bone has a triangular cross section along its entire length, with a flat surface medially and a convex face laterally. On the lateral face, a low lateral tuberosity develops at midshaft, as present in *Amargasaurus* (MACN PV N15) and *Suuwassea* (Harris, 2006). In diplodocids and most macronarians the lateral tuberosity is more conspicuous and located above the midshaft (Whitlock, 2011). The distal end is
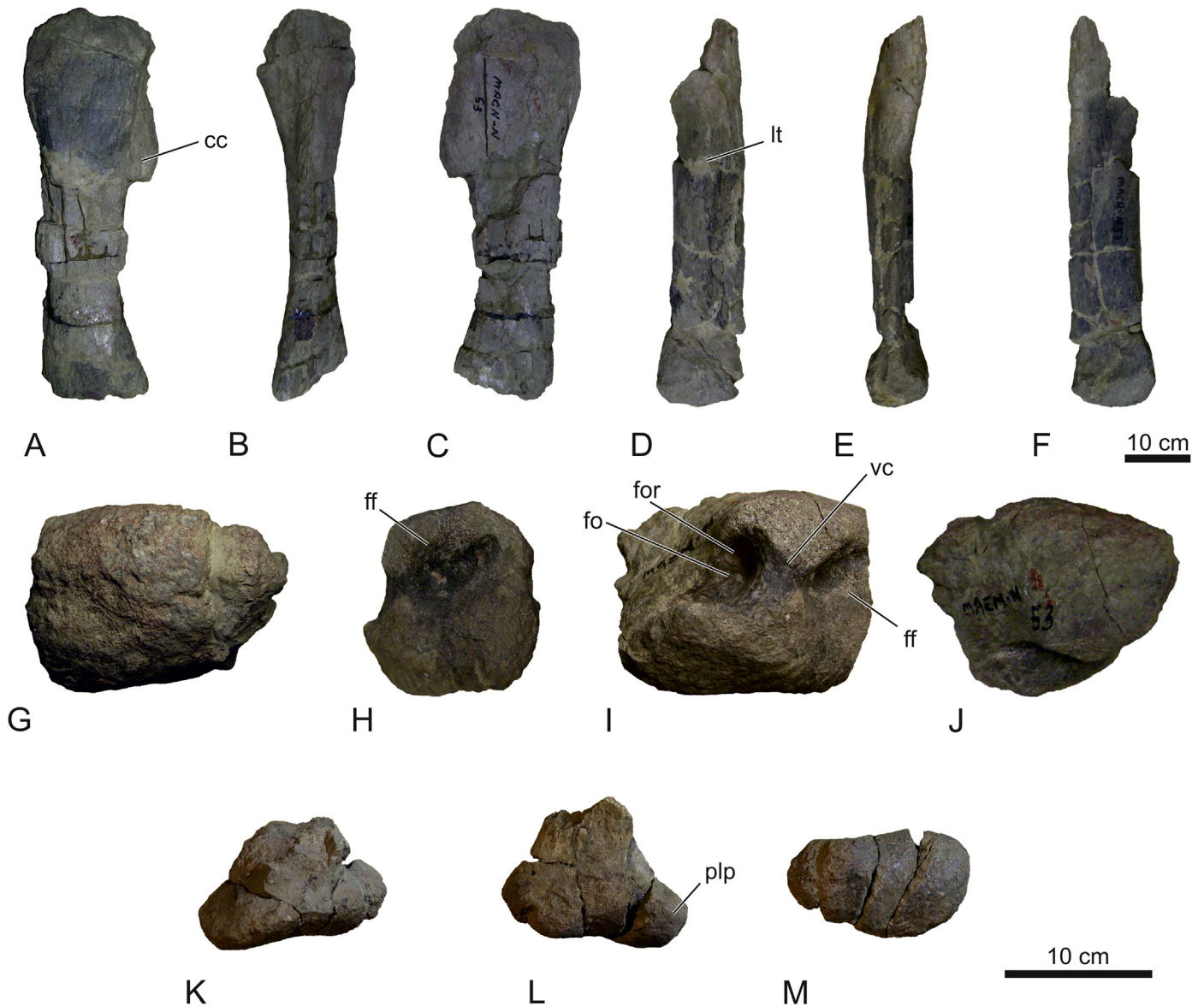

Fig. 4. Appendicular elements of *Amargatitanis macni* (MACN PV N53). Right tibia in: A, lateral; B, anterior; and C, medial views. Right fibula in: D, lateral; E, anterior; and F, medial views. Right astragalus in G, anterior; H, lateral; I, posterior; and J, proximal. Right metatarsal I in: K, anterior; L, posterior; and M, distal. Abbreviations: cc, cnemial crest; ff, fibular facet; fo, fossa; for, foramen; lt, lateral tuberosity; plp, posterolateral process; vc, vertical crest.

slightly expanded in anterior view. Distally, the articular surface for the metatarsus is rounded and has a subcircular perimeter.

4.6. Astragalus (Fig. 4G–J, Table 2)

The right astragalus is nearly complete, but lacks the anteromedial tip. As in most neosauropods, it is a massive, wedge-shaped, subtriangular bone with rugose faces (Wilson and Sereno, 1998). Its anteroposterior length is virtually equal to its proximodistal height. Proximally, the contact surface with the tibia is flat and triangular, with a low ascending process. This surface falls abruptly at an oblique angle to the posteromedial corner. In posterior view, a vertical crest is present as in other diplodocoids such as *Apatosaurus* (CM 3018) and *Dicraeosaurus* (MB.R. 2550), but differing from the condition in derived macronarians, which lack this structure (Wilson, 2002). Medial to this crest, a deep crescent-shaped posterior fossa is developed, bearing two distinct foramina inside. Although the presence of a posterior fossa with foramina is present in other neosauropods astragali (e.g. *Apatosaurus*, *Amargasaurus*, *Brachiosaurus*, *Camarasaurus*, *Bonitasaura*), the peculiar morphology and arrangement of the fossa and foramina in *Amargatitanis* are recognized as an autapomorphy of the taxon. The lateral wall of the astragalus, which contacts the fibula, is subquadrangular and has a concave surface pierced with two small foramina. As in Diplodocoidea, this fibular facet faces posterolaterally (Whitlock, 2011). Distally, the astragalus is subtriangular with a convex rugose surface for articulation with the metatarsus.

4.7. Metatarsal (Fig. 4K–M, Table 2)

The distal half of the right metatarsal I is preserved. This element has a midshaft constriction and expands distally. The rugose distal articular surface is lateromedially elongate and anteroposteriorly convex. It has an ovoid outline, differing from the constricted condition seen in *Dicraeosaurus* (MB.R. 2397) and *Apatosaurus* (CM 3018). As a result, medial and lateral condyles cannot be recognized. In posterior view, the posterolateral corner projects laterally as in most flagellicaudatans (Berman and McIntosh, 1978; Upchurch, 1998). Both, posterior and anterior faces are concave and smooth, and devoid of vascular foramina.

5. Discussion

5.1. Phylogenetic affinities

Apesteguía (2007) referred *Amargatitanis macni* to the clade Titanosauria based on several features, primarily from the scapular and femoral anatomy. D'Emic (2012) and later Mannion et al. (2013) argued the possibility that these elements could not pertain to a titanosaurian sauropod, based on the absence of diagnostic features of Titanosauria, which were originally misinterpreted due to broken areas of the scapula and the femur. This led D'Emic (2012) to regard the taxon as a *nomen dubium*. Additionally, he suggested that the remote provenance of the bones (based on personal observation of Bonaparte's field notes) included in the published holotype material argues against them pertaining to the same individual, an idea shared by Mannion et al. (2013).

In the present revision, several features observed on the modified type material revealed closer affinities to diplodocoids than macronarians, in partial agreement with the previously assessments of D'Emic (2012) and Mannion et al. (2013). The presence of a fibular facet of the astragalus facing posterolaterally (Whitlock, 2011), and the absence of a lateral bulge in the femur (Salgado et al., 1997), link *Amargatitanis* with Diplodocoidea. Additionally, the presence of a posterolateral projection on the distal condyle of

the first metatarsal (Berman and McIntosh, 1978), and anterior caudal centra with procoelous/distoplatyan articular surfaces (McIntosh, 1990), are shared with other flagellicaudatans. The position of the highest point of the femoral head laterally shifted, above the main portion of shaft (Tschopp et al., 2015), and the anterior caudal transverse processes directed dorsally (Whitlock, 2011), also support affinities with dicraeosaurids.

Amargatitanis was not previously included in a phylogenetic analysis; hence its systematic affinities were not tested in a cladistic context. In order to evaluate the hypothesis of *Amargatitanis macni* as a member of Dicraeosauridae, all the remains constituting the revised type material were included in the analyses of Carballido and Martin Sander (2014). This dataset was analyzed using TNT v.1.1 (Goloboff et al., 2008a, 2008b) with an heuristic search of 1000 replicates of Wagner trees followed by TBR (tree bisection-reconnection) branch swapping, saving 100 trees per replicate. This procedure retrieved 4 most parsimonious trees of 999 steps (CI = 0.405; RI = 0.726). A strict consensus tree recovered *Amargatitanis* as the sister taxon of *Suuwassea*, deeply nested in Dicraeosauridae. Although the node of this clade shows low support (Bremer support values and bootstrap values are shown in Fig. 5), the definition of Dicraeosauridae (stem based) includes all flagellicaudatans more closely related to *Dicraeosaurus* than to *Diplodocus*. More than five extra steps are needed to force the placement of *Amargatitanis* in another phylogenetic position, such as basal titanosaur, derived titanosauriform or even basal camarasauromorph. A Templeton test for these alternative topologies was conducted following the protocol summarized in Wilson (2002) (Table 3). The placement of *Amargatitanis* as a titanosaur or a titanosauriform can be rejected by the data with 95% confidence. Although very close to statistical significance (*P* < 0.05), the position as a basal camarasauromorph cannot be rejected. In summary, the most parsimonious placement of *Amargatitanis* is within Diplodocoidea as a dicraeosaurid, in coherence with the anatomical features and the systematic assignation hypothesized here.

6. Conclusion

The reassessment of the material assigned to *Amargatitanis macni* revealed the presence of a second species of the family Dicraeosauridae in the Barremian La Amarga Formation of Patagonia, coupled with the well-known form *Amargasaurus cazaui*. The detailed analysis of the field notes of Dr. Bonaparte, plus the recognition of field numbers present in the collected material housed in the vertebrate collection of the Buenos Aires Museum (MACN) allowed the addition of some elements and removal of others from the original holotype in order to recognize the material assemblage collected by Bonaparte from the same quarry. This analysis and the recent preparation of some bones also improved the diagnosis, thus recognizing *Amargatitanis macni* as a valid taxon. Similarly, the description of unpublished material enhanced the knowledge on the anatomy of this sauropod dinosaur.

The original assignation of *Amargatitanis* as a titanosaur (Apesteguía, 2007) has been discarded based on several points, as follow:

a) The original diagnosis and systematic referral was mainly based on the scapular anatomy, which was here excluded from the taxon in this reevaluation.
b) The purported presence of a prominent lateral bulge and distal condylar asymmetry in the femur mentioned by Apesteguía (2007) are not supported here. Instead, the lateral bulge itself is actually poorly developed, as in most sauropods outside Titanosauriformes, and the condylar asymmetry cannot be
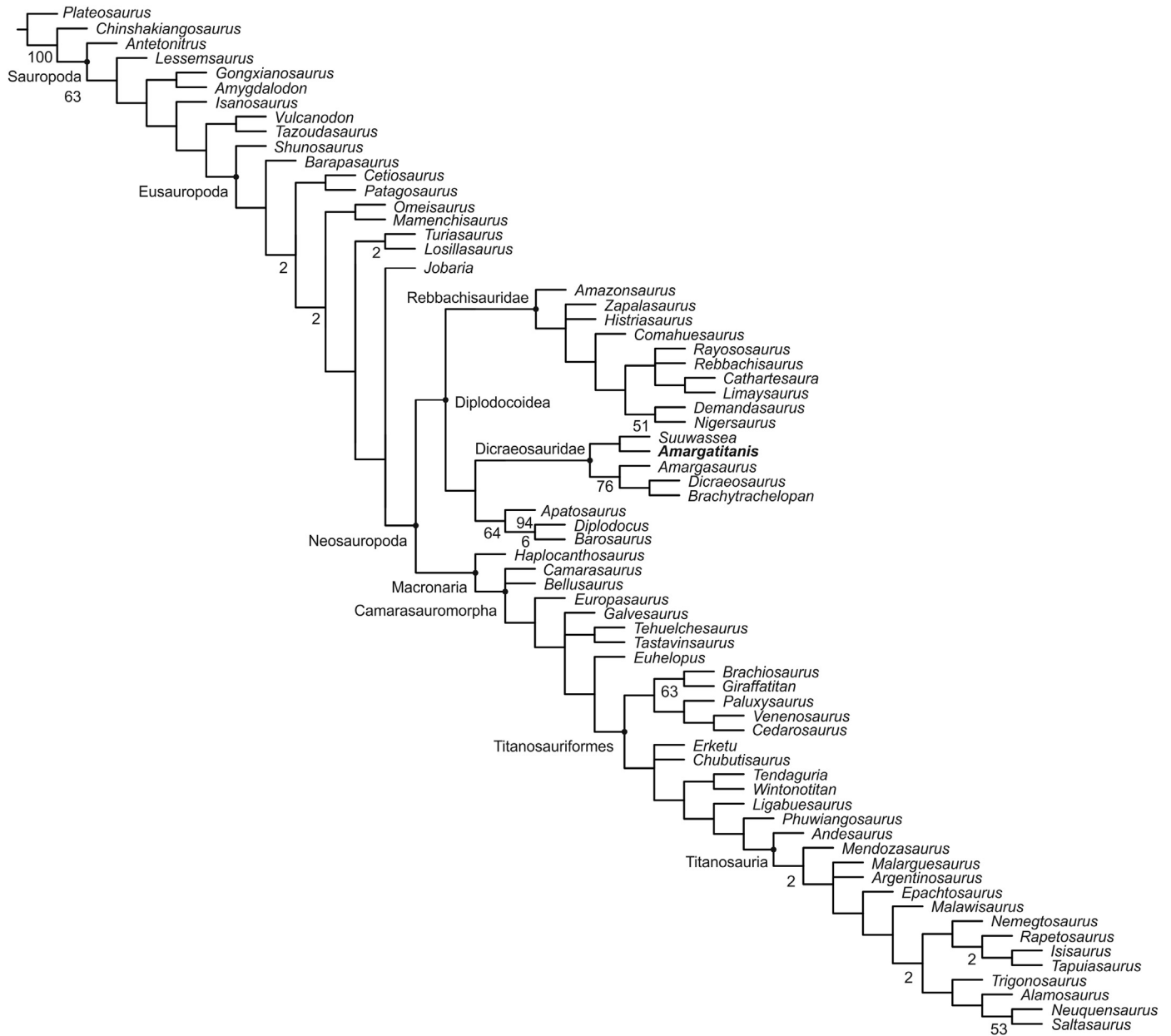
Fig. 5. Strict consensus tree showing the position of *Amargatitanis* within Diplodocoidea (based on the data set of Carballido and Martin Sander, 2014). Bremer support index higher than 1 and Bootstrap values higher than 50% are shown.

Table 3
Results of Templeton test for three alternative phylogenetic position of *Amargatitanis*.

Phylogenetic position	N	n	Tt	Significance	Comment
Basal titanosaur	7	7	0.015	$P < 0.05$	Can be rejected
Derived titanosauriform	6	6	0.03	$P < 0.05$	Can be rejected
Basal camarasauromorph	5	5	0.06	$P > 0.05$	Cannot be rejected

N: number of extra steps; n: number of deviations favoring the alternative position; Tt: Templeton test results (*P*-values).

confirmed because of the incompletely preserved distal region of the femur.

c) After the inclusion of all materials here considered as pertaining to *Amargatitanis* in an updated data matrix (see phylogenetic affinities above), the obtained results do not recover the taxon as a member of Titanosauria.

These arguments suggest that, at present, there is no record of titanosaur body fossils in Patagonia prior to Cenomanian times, from which *Andesaurus delgadoi* is known. However, the presence of teeth clearly belonging to titanosauriform broad-crowned and narrow-crowned forms in the La Amarga Formation (Apesteguía, 2007) still leaves open the possibility of discovering derived forms (i.e., titanosaurs) in the Lower Cretaceous of Patagonia.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.cretres.2016.04.002.