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A new basal rebbachisaurid (Sauropoda, Diplodocoidea) from the Early Cretaceous of the Neuquén Basin; evolution and biogeography of the group

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Despite that the origin of rebbachisaurids is retrieved as Late Jurassic is not until the upper Lower Cretaceous that this group can be recognised in the fossil record. The group is geographically restricted to Gondwana and Europe, and is particularly diverse in the lower Upper Cretaceous of South America. In this subcontinent, Early Cretaceous forms are solely represented by *Amazonsaurus* and *Zapalasaurus*, being the former the putative basalmost rebbachisaurid known. Here, we provide a revised description of the sauropod from the Lohan Cura Formation (Aptian–Albian) that was previously identified as *Limaysaurus* sp. The new information available (mainly based on new elements) allows us to recognise a new taxon, *Comahuesaurus windhauseni* gen. et sp. nov. The phylogenetic analysis carried out retrieved this taxon as a relatively basal form of rebbachisaurid, well separated from Limaysaurinae. In this phylogenetic context, the new taxon revealed the presence of a reduced hyposphene–hypantrum system in rebbachisaurids more derived than *Histriasaurus*, which is completely lost only in Limaysaurinae. Finally, a biogeographical scenario for rebbachisaurids is analysed through the use of a Dispersal, Extinction and Cladogenesis analysis, which retrieves a South American origin for this linage, and a fast dispersion to Africa and Europe during the Hauterivian–Barremian.

Keywords: Neosauropoda; Rebbachisauridae; hyposphene–hypantrum; biogeography

Introduction

Despite the inferred origin of the rebbachisaurid lineage in the Late Jurassic (Upchurch and Barret 2005; Sereno et al. 2007; Carballido et al. 2010; Whitlock 2011) is not until middle of the Lower Cretaceous that this group appears in the fossil record, implying a ghost lineage of some 20 million years. Early Cretaceous forms are currently known from Africa (*Nigersaurus*; Sereno et al. 1999), Europe (*Histriasaurus*, *Demandasaurus*; Apesteguía 2007; Torcida Fernández-Baldor et al. 2011) and Argentina (*Zapalasaurus*; Salgado et al. 2006). *Amazonsaurus* from Brasil (Carvalho et al. 2003) may represent a fifth rebbachisaurid taxon from the Early Cretaceous, but its phylogenetic relationships are not clear (e.g., Salgado et al. 2004; Rauhut et al. 2005; Carballido et al. 2010; Whitlock 2011; Mannion et al. 2012). *Rayososaurus* (Bonaparte 1996), initially reported as a rebbachisaurid from the Early Cretaceous of Patagonia, was recently reinterpreted as coming from the Candeleros Formation (Cenomanian, lower Upper Cretaceous; Carballido et al. 2010). In addition to *Zapalasaurus* and a fragmentary vertebra described by Apesteguía (2007), the rebbachisaurid materials reported by Salgado et al. (2004), provisionally identified as *Limaysaurus* sp., represent one of the oldest records for this group in South America. Therefore, these materials are of great importance to improve the knowledge on the early evolution and distribution of this group.

The genus *Limaysaurus* was formally defined by Salgado et al. (2004), who referred the materials collected in Villa El Chocón (from the Cenomanian Candeleros and Huincul formations; Garrido 2010), and described by Calvo and Salgado (1995) as *Rebbachisaurus tessonei*. Salgado et al. (2004) preliminary described several rebbachisaurid elements collected in the locality Cerro Aguada del León (Neuquén Province), Lohan Cura Formation (Lower Cretaceous; Figure 1), which were provisionally identified as *Limaysaurus* sp. (Salgado et al. 2004).

The assignment of the Lohan Cura form to the genus *Limaysaurus* was based on the presence of certain characters shared with *Limaysaurus tessonei* (Salgado et al. 2004). Nevertheless, these authors also noted some morphological differences that could imply a species differentiation. During the last years all the collected

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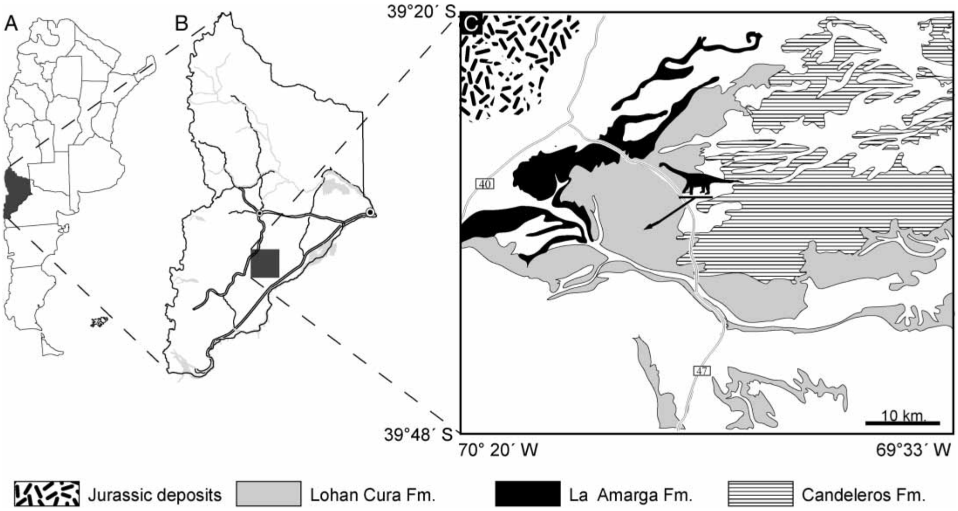

Figure 1. *Comahuesaurus windhauseni* gen. et sp. nov. locality map: (A) Argentina, (B) Neuquén province, and (C) geological map showing the type locality (modified from Leanza and Hugo 1997).

bones from Aguada del León have been fully prepared, providing new evidence that indicates a higher morphological difference with *L. tessonei*. Additionally, the knowledge on rebbachisaurids anatomy and diversity was greatly improved in the last years (e.g., Sereno et al. 2007; Mannion 2009; Apesteguía et al. 2010; Carballido et al. 2010; Mannion et al. 2011b; Whitlock 2011), making evident the necessity of study of the materials reported by Salgado et al. (2004). Here, we describe the material of the Lohan Cura Formation with the addition of new elements and revise its taxonomic and phylogenetic affinities.

Institutional abbreviations

CM, Carnegie Museum of Natural History, United States; DFMMh, Dinosaurier-Freilichtmuseum Münchehagen/Verein zur Förderung der Niedersächsischen Paläontologie (e.V.), Germany; HMN-MB, Humboldt Museum für Naturkunde, Berlin, Germany; MACN, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; MDS, Museo de Dinosaurios de Salas de los Infantes, Salas de los Infantes, Burgos, Spain; MMCH, Museo Municipal Ernesto Bachmann, Villa El Chocón, Neuquén, Argentina; MNN GAD, Musee National du Níger, Níger; MOZ, Museo Provincial de Ciencias Naturales 'Prof. Dr. Juan A. Olsacher', Zapala, Neuquén, Argentina; MUCPv, Museo de Geología y Paleontología de la Universidad Nacional del Comahue, Neuquén, Argentina.

Anatomical abbreviations

4tr, fourth trochanter; ac, acetabulum; actp, anterior caudal transverse process; amedl, anterior median lamina; alspol, accesory lateral spinopostzygapophyseal lamina; aspdl, anterior spinodiapophyseal lamina; asprl, anterior spinoprezygapophyseal lamina; clr, caudal lateral ridge; cprf, centroprezygapophyseal fossa; cprl, centroprezygapophyseal lamina; dp, diapophysis; dpc, deltopectoral crest; ec, epicondyle; fc, fibular condyle; fo, foramen; hh, humerus head; hypa, hypantrum; hypo, hyposphene; ilp, illiac pedicel; isp, ischiadic pedicel; lcpol, lateral centropostzygapophyseal lamina; lspol, lateral spinopostzygapophyseal lamina; mspol, medial spinopostzygapophyseal lamina; gtr, greater trochanter; nc, neural canal; of, obturator foramen; pcdl, posterior centrodiapophyseal lamina; pl, pleurocoel; pmedl, posterior median lamina; podl, postzygodiapophyseal lamina; posl, postspinal lamina; poz, postzygapophysis; pp, parapophysis; ppdl, paradiapophyseal lamina; prdl, prezygodiapophyseal lamina; prpl, prezygoparapophyseal lamina; prz, prezygapophysis; pspdl, posterior spinodiapophyseal lamina; psprl, posterior spinoprezygapophyseal lamina; pup, pubic pedicel; rc, radial condyle; s-cprf-d, subfossa centroprezygapophyseal dorsal; s-cprf-v, subfossa centroprezygapophyseal ventral; spdl, spinodiapophyseal lamina; spof, spinopostzygapophyseal fossa; spol, spinopostzygapophyseal lamina; sprl, spinoprezygapophyseal lamina; tc, tibial condyle; tprl, intraprezygapophyseal lamina; uc, ulnar condyle.

Systematic palaeontology

Saurischia Seeley 1887
Sauropoda Marsh 1878
Neosauropoda Bonaparte 1986a
Diplodocoidea Marsh 1884
Rebbachisauridae Bonaparte 1997
Comahuesaurus windhauseni gen. et sp. nov
Figures 2–11

Etymology

The generic name refers to the *Comahue*, the region in North Patagonia from where the new taxon was recovered. *Comahue* is a Mapuche word, which means place of abundance or perhaps 'where the water hurt' and *saurus*; *sauros* is the Greek word for lizard. The specific name honours Anselmo Windhausen for his contribution to the geological knowledge of the Neuquén basin.

Holotype

MOZ-PV 6722, posterior dorsal neural arch.

Referred material

At least three individuals are represented (Salgado et al. 2004). The bones were excavated from a single bone bed originated as a debris flow of an ephemeral river bed (Garrido and Salgado, in prep.). Anterior dorsal vertebra (MOZ-PV 6650), fragmentary dorsal centra (MOZ-PV 6645, MOZ-PV 6651, MOZ-PV 6653, MOZ-PV 6747, MOZ-PV 6751, MOZ-PV 6756), two neural arches (MOZ-PV 6652, MOZ-PV 6653), 35 caudal vertebrae (MOZ-PV 06741, MOZ-PV 06636, MOZ-PV 06634, MOZ-PV 06627, MOZ-PV 06633, MOZ-PV 06729, MOZ-PV 06638, MOZ-PV 06654, MOZ-PV 06649, MOZ-PV

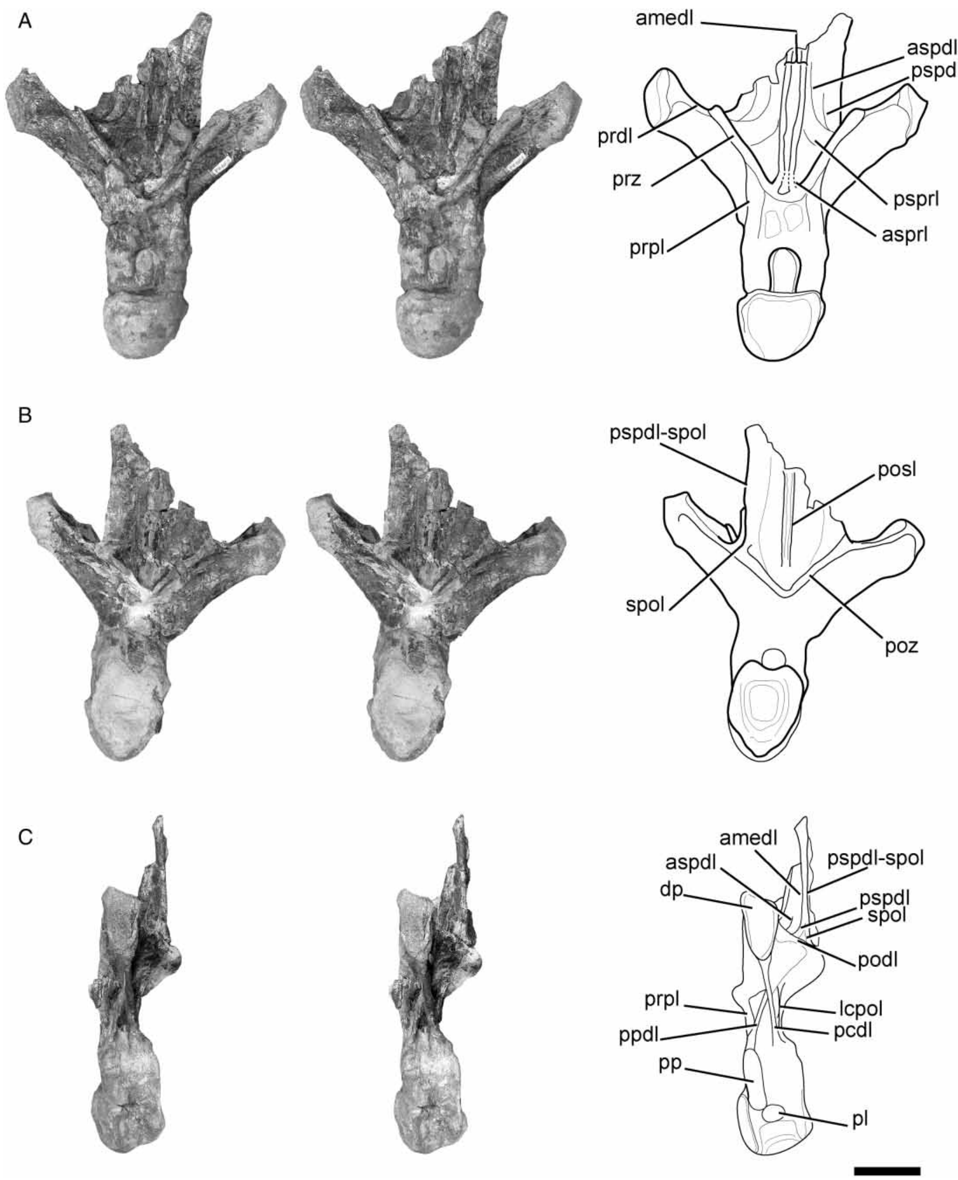

Figure 2. *Comahuesaurus windhauseni* gen. et sp. nov. anterior dorsal vertebra (MOZ-PV 6650) stereophotographs and line drawing in (A) anterior view, (B) posterior view, and (C) left lateral view. Note: Scale bar is 10 cm; see text for abbreviations.

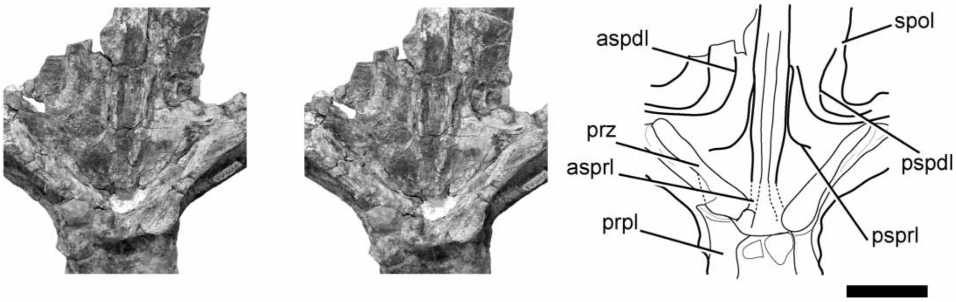

Figure 3. *Comahuesaurus windhauseni* gen. et sp. nov. detail of the anterior dorsal vertebra (MOZ-PV 6650) stereophotographs and line drawing in anterodorsal view. Note: Scale bar is 10 cm; see text for abbreviations.

06628, MOZ-PV 06646, MOZ-PV 06629, MOZ-PV 06759, MOZ-PV 06766, MOZ-PV 06632, MOZ-PV 06753, MOZ-PV 06738, MOZ-PV 06642, MOZ-PV 06639, MOZ-PV 06733, MOZ-PV 06734, MOZ-PV 06711, MOZ-PV 06641, MOZ-PV 06643, MOZ-PV 06644, MOZ-PV 06647), sternal plate (MOZ-PV 6717), one coracoid (MOZ-PV 6763), a complete right humerus (MOZ-PV 6762) and fragments of six other humeri (MOZ-PV 6664, MOZ-PV 6672, MOZ-PV 6673, MOZ-PV 6712, MOZ-PV 6714, MOZ-PV 6723), fragmentary ilium (MOZ-PV 6675), one complete pubis (MOZ-PV 6743) and seven fragments (MOZ-PV 6669a, MOZ-PV 6669b, MOZ-PV 6670, MOZ-PV 6659, MOZ-PV 6660, MOZ-PV 6667, MOZ-PV 6663), five ischia partially preserved (MOZ-PV 6676, MOZ-PV 6713, MOZ-PV 6719, MOZ-PV 6680, MOZ-PV 6658), two left femora (MOZ-PV 6728, MOZ-PV 6665), three right femora (MOZ-PV 6732, MOZ-PV 6761, MOZ-PV 6755), and four more fragmentary elements (MOZ-PV 6661, MOZ-PV 6666, MOZ-PV 6778, MOZ-PV 6721), proximal part of a tibia (MOZ-PV 6764), one left fibula partially preserved (MOZ-PV 6727).

Locality and horizon

Northern slope of Cerro Aguada del León (39°34′54.3″ S, 70°05′18.8″ W), La Picasa area, South Central Neuquén (Figure 1), Lohan Cura Formation, Puesto Quiroga Member (Leanza and Hugo 1995; Salgado et al. 2004). The age of this member is considered as Aptian–Albian (Leanza and Hugo 1997), and therefore has been correlated with the Rayoso Formation of the Bajada del Agrio Group in the central area of the basin (Leanza and Hugo 1999).

Diagnosis

C. windhauseni gen. et sp. nov. is characterised by the following characters (* indicates unique autapomorphic characters): 1*-anterior dorsal centra with strong lateral constriction, resulting in a thin ventral keel; 2*-anterior dorsal vertebrae with long prezygapophyses, which in anterior view cover around 3/4 of the transverse processes; 3*-anterior dorsal vertebrae with two spinoprezygapophyseal laminae; 4*-anterior dorsal vertebrae with two spinodiapophyseal laminae, an anterior and a posterior one; 5*-anterior median lamina formed by three different laminae, the anterior and posterior spinoprezygapophyseal laminae and the anterior spinodiapophyseal; 6*-posterior dorsal centra with the centroprezygapophyseal lamina medially divided; 7*-posterior dorsal neural arches with three spinopostzygapophyseal laminae; 8*-double contact between the posterior spinodiapophyseal lamina and the lateral spinopostzygapophyseal lamina; 9-anterior caudal vertebrae with well-developed prezygodiapophyseal fossa; 10-caudal vertebrae with short transverse process; 11-robust humerus, with a robustness index of 0.3 (*sensu* Wilson and Upchurch 2003); 12-ischium with straight shaft; 13-shaft of the ischium forming a right angle with the acetabulum; 14-iliac peduncle without a constriction or neck.

Description

Dorsal vertebrae

Salgado et al. (2004) recognised the presence of three dorsal elements, which were identified as a neural spine fragment (MOZ-PV 6722) and two posterior dorsal centra (MOZ-PV 6756 and MOZ-PV 6747). These elements were fully prepared and reveal new information that is here mentioned. Additionally, among the materials recently prepared there is an almost complete anterior dorsal vertebra (MOZ-PV 6650). Here, we provide a full description of all the dorsal elements.

Anterior dorsal vertebrae

The following description is mainly based on the most complete dorsal element (MOZ-PV 6650) and on a fragmentary centrum (MOZ-PV 6653), which provides information on the internal cavities.

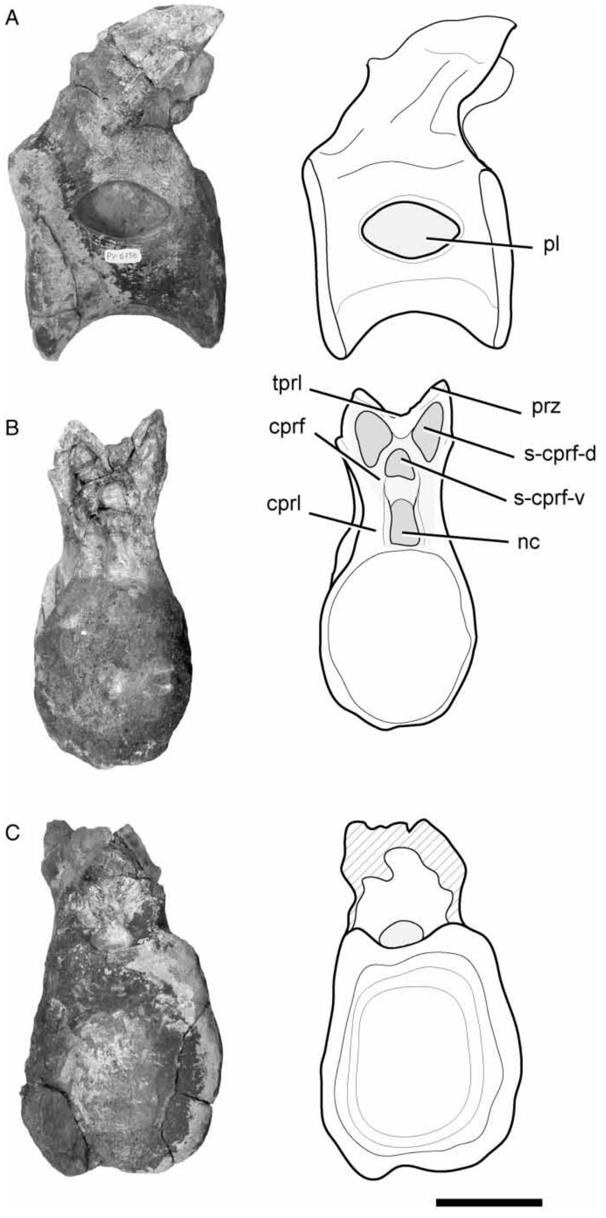

Figure 4. *Comahuesaurus windhauseni* gen. et sp. nov. posterior dorsal vertebra (MOZ-PV 6756) photographs and line drawing in (A) posterior, (B) right lateral, and (C) posterior views. Note: Scale bar is 10 cm; see text for abbreviations.

The centrum is anteroposteriorly short, being the length–height ratio (measured at posterior articular facet) less than 1 (Table 1). The anterior articular surface is slightly convex, whereas the posterior one is strongly concave, identifying the anterior dorsal centra as opisthocoelous, the generalised condition among sauropods (e.g., Salgado et al. 1997; Wilson 2002; Upchurch et al. 2004). The posterior articular surface is circular, being almost as high as wide (Table 1), and differing from the dorsoventrally compressed centra of titanosauriforms (e.g., *Ligabuesaurus*, *Saltasaurus*; Powell 1992; Bonaparte et al. 2006). Ventrally, both preserved centra have a great lateromedial compression, which starts at the ventral half of the centum, below the pleurocoels (Figure 2(C)). This constriction is not present in other rebbachisaurids, at least in which anterior dorsal vertebrae are known (i.e., *Limaysaurus*, *Nigersaurus*, MMCH-Pv-49; Haluza et al. 2012). In lateral view, the dorsal centra of *Comahuesaurus* gen. nov. are ventrally straight, whereas in *Limaysaurus* the ventral margin is strongly concave (Calvo and Salgado 1995:Fig. 8D). The pleurocoel is circular and opens internally forming two major internal air spaces, which are identified as pneumatic camerae (*sensu* Wedel 2003a, 2003b). The left and right camerae are medially divided by a narrow septum, being therefore similar in shape to those of *Nigersaurus* (Sereno et al. 2007:Fig. 3C). The same morphology can be recognised in the anterior dorsal vertebrae of other rebbachisaurids (e.g., *Demandasaurus*, *Limaysaurus*) and diplodocids (e.g., *Apatosaurus*, *Diplodocus*). Therefore, the internal pneumatization of the dorsal vertebrae seems to be only absent in dicraeosaurids among diplodocoids (e.g., *Amargasaurus*, *Dicraeosaurus*; Schwarz and Fritsch 2006).

As in other diplodocoids (e.g., Calvo and Salgado 1995; Wilson 2002), the neural arch is dorsoventrally high, being at least 3.5 times higher than the centrum. The parapophysis is ventrally positioned, located between the neural arch and the centrum (Figure 2(C)). A similar position of the parapophysis is usually present in the fourth dorsal vertebra of other sauropods (e.g., *Dicraeosaurus*, *Diplodocus*, *Camarasaurus*; Hatcher 1901:pl. 7; Osborn and Mook 1921:pl. 73; Janensch 1929:pl. 1). Therefore, the element MOZ-PV 6650 is here tentatively considered as a fourth dorsal vertebrae. The high parapophysis interrupts the centroprezygapophyseal lamina of cervical and more anterior dorsal vertebrae (Wilson 1999); therefore, the lamina that runs from the parapophysis up to the prezygapophysis is the prezygoparapophyseal lamina (Figure 2). In anterior view, the prezygoparapophyseal lamina bounds laterally two small depressions (Figure 2(A)). These are usually absent in dorsal vertebrae and are here interpreted as the reminiscence of the fossae usually observed in cervical vertebrae. Following the nomenclature of Wilson et al. (2011), these shallow fossae are identified as the centroprezygapophyseal fossae. The neural canal is bounded by a deep oval depression, similar in shape and development to that of other rebbachisaurids. Through the posterior part of the dorsal series, this fossa becomes gradually larger in rebbachisaurids (e.g., Haluza et al. 2012:Fig. 2).

The prezygapophysis is long (Figure 2 (A)) and ventrally contacts a short intraprezygapophyseal lamina. From this ventral edge, the prezygapophyses are dorsolaterally oriented at an angle of approximately 50° respect to the longitudinal axis. Up to now, rebbachisaurid anterior dorsal vertebrae were only described for *L. tessonei*

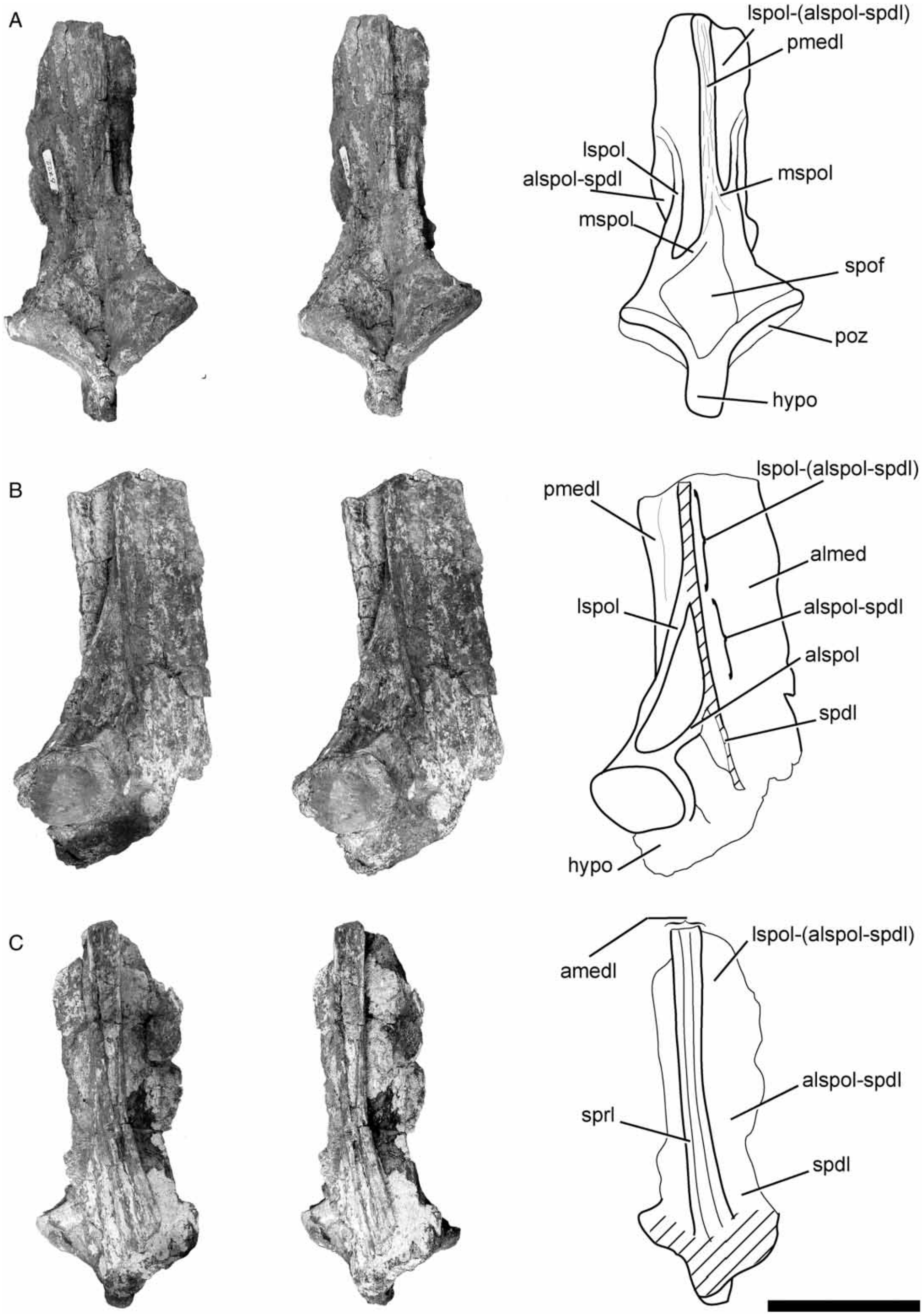

Figure 5. *Comahuesaurus windhauseni* gen. et sp. nov. posterior dorsal neural arch (MOZ-PV6722) stereophotographs and line drawing in (A) posterior, (B) right lateral, and (C) anterior views. Note: Scale bar is 10 cm; see text for abbreviations.

(Calvo and Salgado 1995), *Nigersaurus* (Sereno et al. 1999) and the rebbachisaurid MMCH-Pv-49 (Apesteguía et al. 2010; Haluza et al. 2012). In these taxa, the prezygapophyses of the anterior dorsal vertebrae are relatively short, as in other non-rebbachisaurid sauropods (e.g., *Haplocanthosaurus*, *Dicraeosaurus*, *Diplodocus*, *Europasaurus*; CM 879; HMN-MB 3677; CM 84; DFMMh/FV 894). Therefore, the long prezygapophyses of *C. windhauseni* gen. et sp. nov., which are almost twice longer than the centrum width, are regarded as a diagnostic character of this taxon.

The stout diapophysis is subcircular, with its ventral margin slightly narrower than the dorsal one (Figure 2(C)). Two laminae are ventrally running from the diapophysis: the posterior centrodiapophyseal lamina and the paradiapophyseal lamina. Whereas the posterior centro-

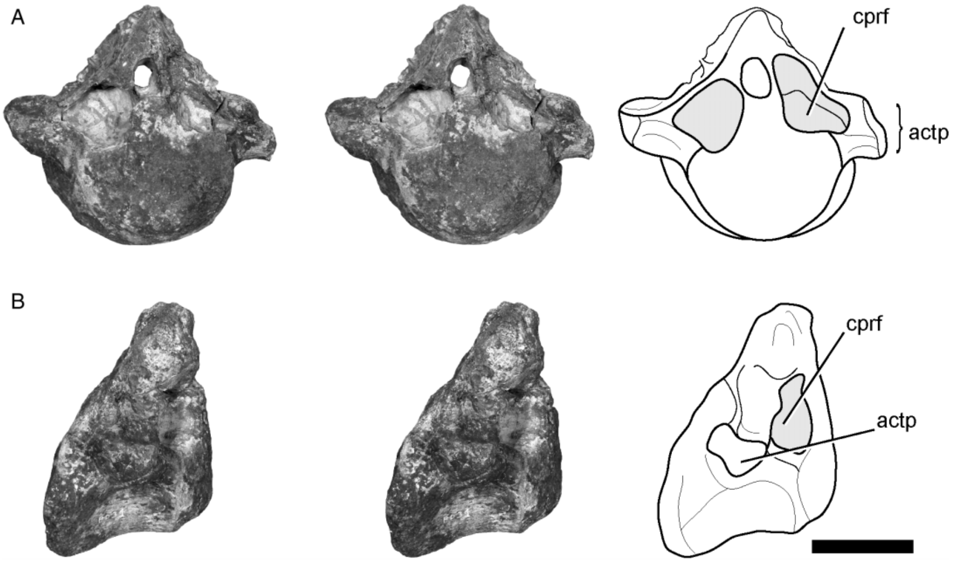

Figure 6. *Comahuesaurus windhauseni* gen. et sp. nov. first caudal vertebra (MOZ-PV 6741) in (A) anterior and (B) right lateral views. Note: Scale bar is 10 cm; see text for abbreviations.

diapophyseal lamina contacts the diapophysis, the paradiapophyseal lamina does not reach the diapophysis as it contacts, at mid-height, the posterior centrodiapophyseal lamina. Therefore, the dorsal segment of the centrodiapophyseal lamina could be considered a composite lamina. The centrodiapophyseal fossa is bounded by the posterior centrodiapophyseal lamina (posterodorsally) and the paradiapophyseal lamina (anterodorsally). Anteriorly to this fossa, the neural arch bears the prezygodiapophyseal fossa, which is posteriorly delimited by the paradiapophyseal lamina and the dorsal segment of the posterior centrodiapophyseal and paradiapophyseal laminae. A third fossa of the neural arch is present in this element that is interpreted as the postzygodiapophyseal fossa (*sensu* Wilson et al. 2011). Whereas the two later fossae are slightly developed, the postzygodiapophyseal fossa deeply penetrates the neural arch.

The postzygapophyses are also elongated, but not as much as the prezygapophyses, indicating a length reduction of the zygapophyses through the posterior dorsal vertebrae. The centropostzygapophyseal laminae are reduced, but they are well distinguishable in lateral view (Figure 2(C)). A reduction of these laminae seems to be common along the anterior dorsal vertebrae in sauropods. This morphological change is probably related with the first appearance of the medial centropostzygapophyseal lamina present in medial and posterior dorsal vertebrae (Apesteguía 2005; Apesteguía et al. 2010). Therefore, in this element, and due to its position, the centropostzygapophyseal laminae are identified as the lateral centropostzygapophyseal laminae (Figure 2 (C)). The accessory articulations, the hyposphene–hypantrum complex, cannot be recognised in this element, an absence expected for an anterior dorsal element.

The neural spine of MOZ-PV 6650 lacks its dorsal end, but, at least, the half of it is well preserved. The preserved part of the neural arch is approximately six times higher than the centrum height, measured at its posterior articular surface (Table 1), a widely distributed character among diplodocoids (e.g., Salgado et al. 2006). The neural spine is clearly higher than the distance between the centrum and the postzygapophysis, a diagnostic character of Rebbachisauridae plus Flagellicaudata (Upchurch et al. 2004). The preserved neural spine allows identifying a unique arrangement of its laminae. In *C. windhauseni* gen. et sp. nov., the neural spine is formed by six laminae, which can be all observed in anterior view except for the postspinal lamina (Figures 2(A), 3). The anterior median lamina, a hybrid structure (Wilson 1999; Salgado and Powell 2010), is formed by two lateral laminae, which bound a simple single fossa. These two laminae diverge ventrally from each other and reach the posterior edge of the prezygapophysis. Therefore, these are here interpreted as two pairs of spinoprezygapophyseal laminae (anterior and posterior). In *C. windhauseni* gen. et sp. nov., the anterior and posterior spinoprezygapophyseal laminae are forming the anterior median lamina (Figure 3). A third lamina, the anterior spinodiapophyseal lamina, forms part of the anterior median lamina. This arrangement of the anterior median lamina differs from that of all other sauropods and is interpreted as an autapomorphic character of *C. windhauseni* gen. et sp. nov. The prespinal lamina cannot be properly identified as an individualised structure, as in other rebbachisaurids with a similar arrangement of their anterior median lamina.

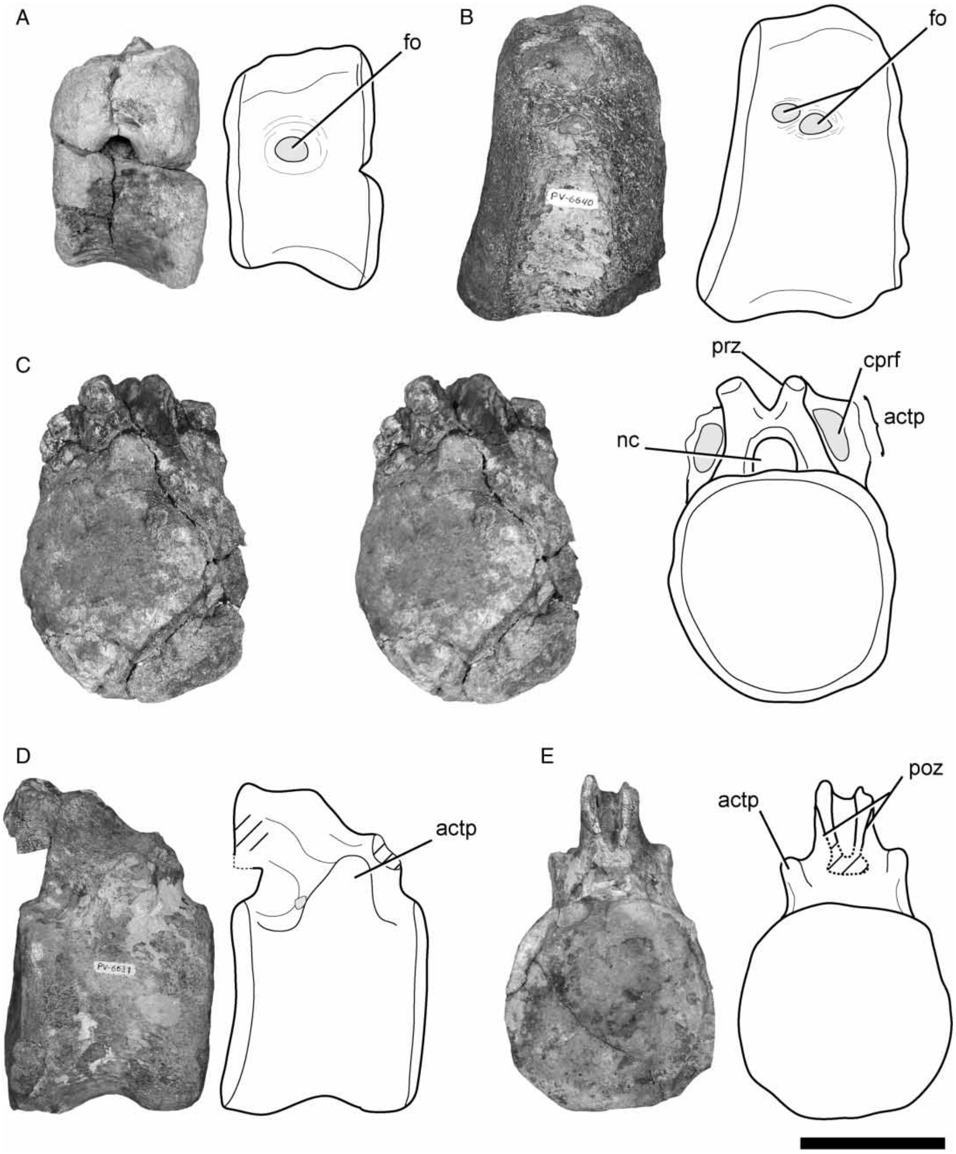

Figure 7. *Comahuesaurus windhauseni* gen. et sp. nov. anterior caudal vertebrae: (A) MOZ-PV 6637 in left lateral, (B) MOZ-PV 6640 in left lateral, and MOZ-PV 6631 in (C) anterior (stereophotographs and line drawing), (D) left lateral, and (E) posterior views. Note: Scale bar is 10 cm; see text for abbreviations.

Recently, Salgado and Powell (2010) recognised two different spinodiapophyseal laminae in titanosaurs, anterior and posterior, which are usually well differentiated on the basis of their different positions in the neural spine (Salgado and Powell 2010). In the anterior dorsal vertebra of *C. windhauseni* gen. et sp. nov., two different spinodiapophyseal lamina are recognised. These laminae closely run from each other, but are in contact with different structures of the neural spine. The anterior of these laminae (Figure 3) fix well with the anterior spinodiapophyseal lamina described by Salgado and Powell (2010) for some titanosaurs, and suggested to be the characteristic lamina of diplodocoid sauropods. The posterior spinodiapophyseal lamina is posteriorly positioned and runs up to the posterior margin of the neural spine contacting the spinopostzygapophyseal lamina (Figure 3). The simultaneous presence of an anterior and posterior spinodiapophyseal lamina in a dorsal vertebra is an unusual character solely described for some titanosaurs (see Salgado and Powell 2010). In fact, the presence of two spinodiapophyseal laminae was recognised by Salgado et al. (1997) as a synapomorphic character of the clade formed by *Opsithocoelicaudia* and *Trigonosaurs*, whereas for Upchurch et al. (2004) this represent an apomorphy of *Lirainosaurus* and more derived titanosaurs. Whereas in most titanosaurs both spinodiapophyseal laminae are ventrally linked, being *Epachthosaurus* the only exception (Salgado and Powell 2010), in *C. windhauseni* gen.

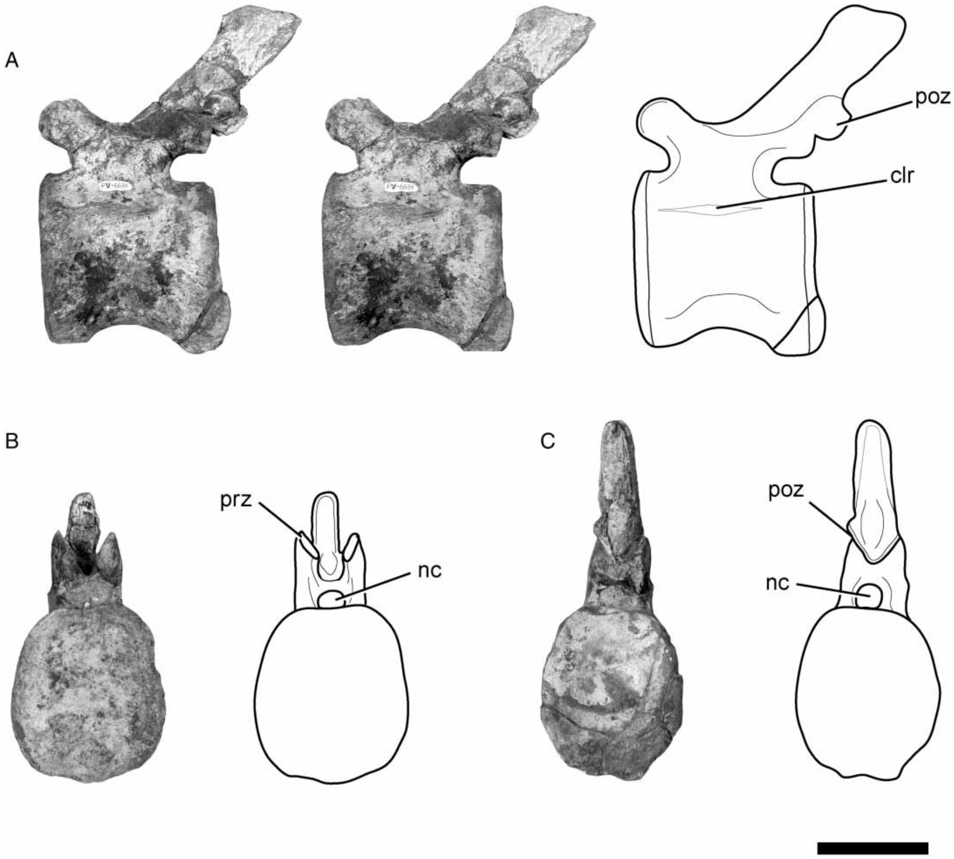

Figure 8. *Comahuesaurus windhauseni* gen. et sp. nov. middle caudal vertebrae: (A) MOZ-PV 6634 in left lateral, (B) anterior, and (C) posterior views. Note: Scale bar is 10 cm; see text for abbreviations.

et sp. nov., these two laminae run separately along the entire transverse process.

The spinopostzygapophyseal lamina contacts the posterior spinodiapophyseal lamina in a point close to its ventral origin/end, forming a lateral composed lamina (posterior spinodiapophyseal + spinopostzygapophyseal laminae; Figure 2(C)). Both spinopostzygapophyseal laminae bound a single posterior fossa, within which a single lamina can be observed. This single lamina is ventrally undivided, and therefore is interpreted as the postspinal lamina (Figure 2 (B)), which is well developed in *C. windhauseni* gen. et sp. nov.

Middle and posterior dorsal vertebrae

Middle and posterior dorsal vertebrae are represented by fragmentary elements, but provide useful information on the presacral morphology. In addition to the elements described by Salgado et al. (2004), several isolated centra and a fragmentary neural arch (MOZ-PV 6657) were recovered from the same quarry.

The isolated centrum described by Salgado et al. (2004; MOZ-PV 6756) has been recently fully prepared. This centrum preserves both prezygapophyses and its ventral laminae. The centrum is anteroposteriorly short, with a subequal total anteroposterior length and lateromedial width (Table 1). Therefore, and based on the proportions of other sauropods (e.g., *Camarasaurus*, *Diplodocus*, *Apatosaurus*), this element is interpreted as a posterior dorsal centrum, which are usually shorter than in the middle dorsals. The articular surfaces are almost subcircular, being slightly higher than wide (Table 1). The pleurocoel excavates the centrum laterally, leaving only a thin osseous septum dividing the left and right cavities. This centrum and other fragmentary centra show that the internal cavities are true pneumatic camerae (*sensu* Wedel 2003a, 2003b). The pneumatic camerae are dorsally extended, invading, at least, the ventral region of the neural arches. Therefore, the pneumatic air spaces of *C. windhauseni* gen. et sp. nov. extended from the anterior dorsal up to the posterior dorsal vertebrae.

Only a ventral fragment of the neural arch is preserved, in which both prezygapophyses can be observed. The prezygapophyses are anteriorly projected, but do not surpass the anterior condyle (Figure 4). Contrary to the condition existing in the anterior dorsal vertebrae, the

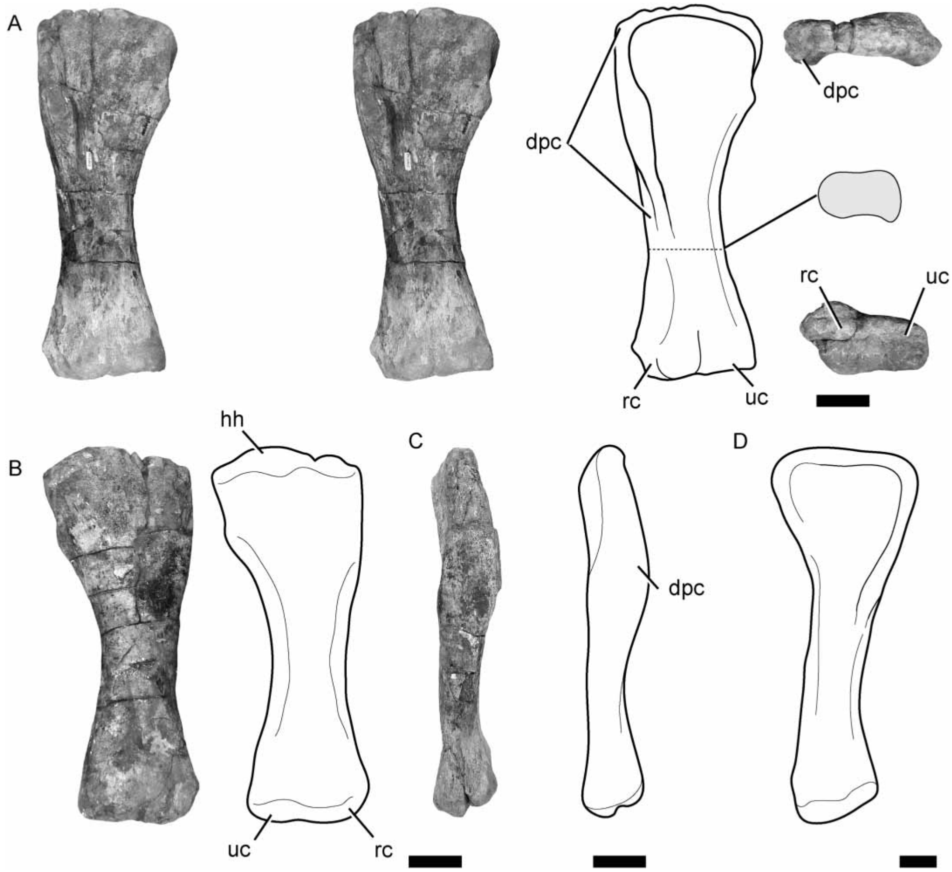

Figure 9. *Comahuesaurus windhauseni* gen. et sp. nov. right humerus (MOZ-PV 6762) in (A) anterior view (stereophotographs and line drawing) with dorsal, transverse section and distal views; (B) posterior; (C) lateral views; and (D) left humerus of *Limaysaurus tessonei* in anterior view. Note: Scale bar is 10 cm; see text for abbreviations.

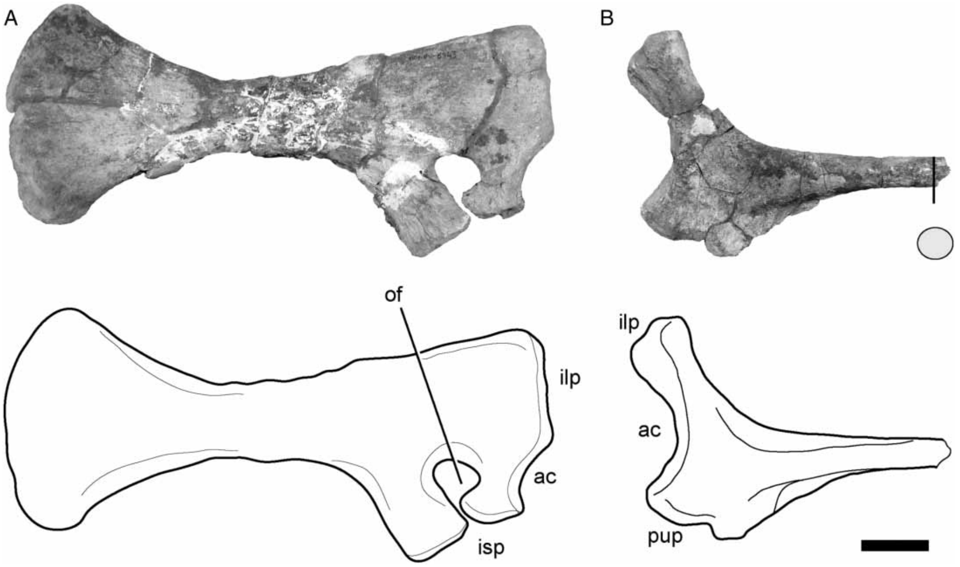

Figure 10. *Comahuesaurus windhauseni* gen. et sp. nov. pubis bones: (A) right pubis (MOZ-PV 6743) in medial view and (B) left ischium (MOZ-PV 6658) in lateral view. Note: Scale bar is 10 cm; see text for abbreviations.

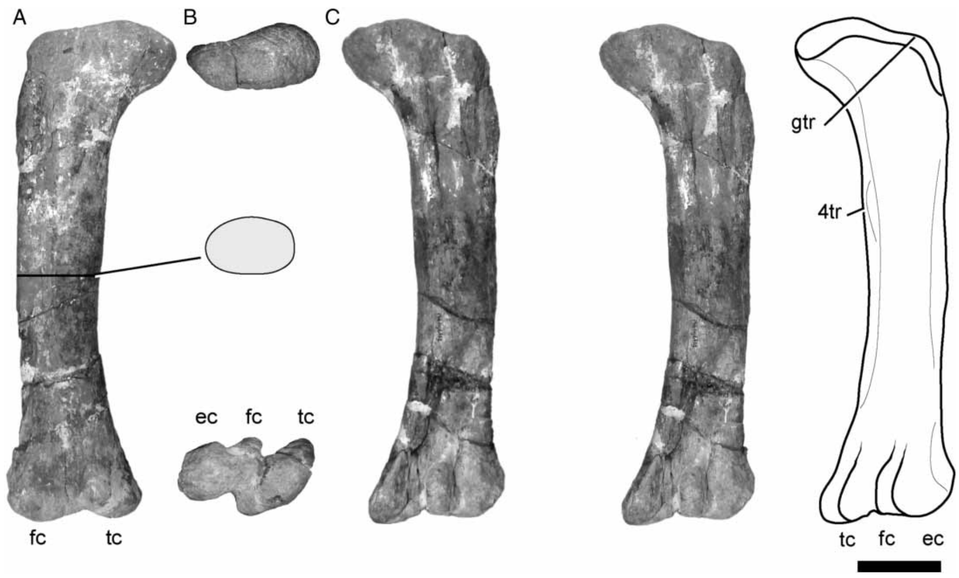

Figure 11. *Comahuesaurus windhauseni* gen. et sp. nov. right femur (MOZ-PV 6761) in (A) anterior; (B) dorsal, transverse section and distal views; and (C) posterior view (stereophotographs and line drawing). Note: Scale bar is 20 cm; see text for abbreviations.

prezygapophyses of this element have short and oval-shaped articular facets. The neural canal is lateromedially compressed and subcircular in cross-section (Figure 4). The centroprezygapophyseal fossa (*sensu* Wilson et al. 2011) is identified as the entire depression observed in anterior view, which includes a deeper and distinct subfossa located dorsally to the neural canal. This fossa is here referred as the ventral centroprezygapophyseal subfossa. An additional paired subfossa is present dorsally to it, which is here referred as the dorsal centroprezygapophyseal subfossa (Figure 4). The dorsal centroprezygapophyseal subfossae result in a middle division of the centroprezygapophyseal lamina. Whereas the presence of this division is a broadly distributed character in cervical vertebrae of sauropods, such division is generally not observed in posterior dorsal elements. Although a similar lamina was described for *Demandasaurus* (Torcida Fernández-Baldor et al. 2011), in this taxon the lamina can be identified as a divided centroprezygapophyseal lamina, as it dorsally contacts the prezygapophysis, differing thus from the condition of *C. windhauseni* gen. et sp. nov.

Table 1. Measurements (in cm) of the dorsal elements of *Comahuesaurus windhauseni* gen. et sp. nov.

Element	APL	PH	PW	Ped	TH	APL/$\bar{X}$
MOZ-Pv 6650	10.2	12.0	12.0	13.0	55.0	0.83
MOZ-Pv 6653	18.2	19.0	18.0	12.5	–	0.98
MOZ-Pv 6756	18.3	19.0	17.5	–	–	0.99

Note: APL, anteroposterior length; Ped, pedicel height, measured from the dorsal edge of the articular surface up to the intraprezygapophyseal lamina; PH, posterior height; PW, posterior width; TH, total height; $\bar{X}$, average of PS and AS.

The neural arch previously described by Salgado et al. (2004; MOZ-PV 6722) is here tentatively considered as a posterior dorsal element (from tenth to twelfth dorsal vertebra). A reexamination of this material allows us to reidentify some of its laminae, which show several unusual characters. The neural arch is composed by both postzygapophyses and an almost complete neural spine that lacks its dorsal margin. As the element was diagenetically compressed, its laminae are displaced to the left (Figure 5). The postzygapophyses are lateromedially short, similar in size to those of MOZ-PV 6756. Just below the contact of both postzygapophyses, there is a simple, rectangular-shaped process, which was identified by Salgado et al. (2004:Fig. 3A–D) as a possible fragment of the centropostzygapophyseal lamina. Nevertheless, this process is not paired (as the centropostzygapophyseal lamina is) and has its lateral margins dorsally connected with both postzygapophyses. Therefore, this process is here reinterpreted as a laminar hyposhene, slightly developed but clearly present in *C. windhauseni* gen. et sp. nov. The absence of hyposphene–hypantrum system was traditionally considered as a synapomorphic character of Rebbachisauridae (e.g., Wilson 2002; Salgado et al. 2004; Upchurch et al. 2004; Gallina and Apesteguía 2005), being only present in *Histriasaurus* (Apesteguía 2007; Whitlock 2011) and in an isolated dorsal vertebra from La Amarga Formation (Hauterivian; Apesteguía 2007). Nevertheless, a hyposphene similar to the one described here for *Comahuesaurus* gen. nov. was recently described for *Demandasaurus* (Torcida Fernández-Baldor et al. 2011).

Additionally, a similar laminar hyposphene can be recognised in some of the posteriormost dorsal vertebrae of *Nigersaurus* (MNN GAD 15-18). Therefore, although the presence of a hyposphene could be considered as an unusual character of *C. windhauseni* gen. et sp. nov., the new information on other rebbachisaurids provides some light on the evolution of the extra articulations in rebbachisaurids, which is summarised in more detail in the discussion (see below).

As in other sauropods, several laminae form the neural spine of *C. windhauseni* gen. et sp. nov. In anterior view, an anterior median lamina can be observed, which is here interpreted as being formed by the union of the left and right spinoprezygapophyseal laminae that runs dorsally close to each other but separated by a median fossa. The identification of the spinoprezygapophyseal lamina is possible due to the presence of a single median fossa and to a ventral divergence of these laminae. Therefore, the structure of the anterior surface of the neural spine is not homologous to the prespinal lamina, which is an undivided median lamina (Wilson 1999). This pattern of anterior spinal lamination resembles that of other rebbachisaurids (e.g., *Nigersaurus*, *Demandasarus*) and diplodocids (e.g., *Diplodocus*, *Apatosaurus*). In dicraeosaurids (e.g., *Dicraeosaurus*, *Brachytrachelopan*, *Amargasaurus*), the lamina on the anterior surface of the neural spine lacks a single median fossa and a ventral bifurcation, and therefore dicraeosaurids are interpreted to have a prespinal lamina (*sensu* Wilson 1999). In posterior view, the lamination pattern of *C. windhauseni* gen. et sp. nov. clearly differs from all other sauropods. Salgado et al. (2004) described two spinopostzygapophyseal laminae, but the preparation of this element allows recognising three pairs of spinopostzygapophyseal laminae. Two of them, observable in posterior view, are interpreted as the lateral and medial spinopostzygapophyseal laminae. As in other sauropods, these two laminae share a ventral segment, which contacts the postzygapophysis. Because of the deformation of this element, this segment is slightly displaced to the left side (Figure 5). The medial spinopostzygapophyseal laminae are dorsomedially directed and merge forming a single posterior median lamina (Figure 5), which can be interpreted as a fused left and right medial spinopostzygapophyseal lamina or a hybrid structure not homologable with the single postspinal lamina (*sensu* Wilson 1999). The lateral spinopostzygapophyseal lamina runs dorsolaterally from its divergence from the medial spinopostzygapophyseal lamina up to its contact with the lateral lamina. A third spinopostzygapophyseal lamina arise from the lateral surface of the postzygapophysis (Figure 5), anteriorly to the common segment of the lateral and medial spinopostzygapophyseal laminae. This third spinopostzygapophyseal lamina is considered here as an accessory spinopostzygapophyseal lamina. The accessory spinopostzygapophyseal lamina is short and contacts the spinodiapophyseal lamina at the base of the neural spine. From this base, a composed lamina runs dorsally to contact the lateral spinopostzygapophyseal lamina. Therefore, in this neural arch, there are two points of contact between the spinopostzygapophyseal lamina and the spinodiapophyseal lamina (Figure 5(B)), an unusual character not known for any other sauropod, and thus considered an autapomorphic character of *C. windhauseni* gen. et sp. nov.

Caudal vertebrae

Thirty-eight caudal elements of *C. windhauseni* gen. et sp. nov. were recovered, being most of them isolated centra previously described by Salgado et al. (2004). Nevertheless, some of the new elements here presented provide new morphological information. For descriptive purposes, the caudal vertebrae were classified in first, anterior, middle, and posterior, but the absence of articulated or associated elements prevents a more precise position in the caudal series.

First caudal vertebra

The incomplete vertebra (MOZ-PV 6741) was previously interpreted by Salgado et al. (2004) as a caudosacral vertebra or one of the anteriormost caudal elements. The general morphology of this vertebra is similar to that present in anterior caudal vertebrae of other rebbachisaurids (e.g., *Demandasaurus*, *Limaysaurus*), with an anteroposterior length/lateromedial width ratio of 0.85 (Table 2). As in the first caudal vertebra of *Demandasaurus*, the posterior articular surface is slightly concave whereas the anterior one is slightly convex (Figure 6). Therefore, this element is slightly opisthocoelous and is here interpreted as the first caudal vertebra of *C. windhauseni* gen. et sp. nov. As in most anterior caudal vertebra, there are no facets for the haemal arches. The transverse process is dorsoventrally short, very similar to that of the anterior caudal vertebrae of *Zapalasaurus* (Salgado et al. 2006; contra Whitlock 2011). Short transverse processes are common in rebbachisaurids (e.g., *Demandasaurus*, *Nigersaurus*; *L. tessonei*) being the only exception *Cathartesaura* (Gallina and Apesteguía 2005:Fig. 3B–C), an unnamed material from the Bajo Barreal Formation (Ibiricu et al. 2012), and probably *Rebbachisaurus* (Lavocat 1954; Calvo and Salgado 1995). Two deep fossae are present on the anterior surface of the vertebra, which occupy part of the centrum, neural arch and transverse process. These fossae are also present in anterior caudal vertebrae of other sauropods (Wilson et al. 2011). Among rebbachisaurids, these fossae are similar to those of *Demandasaurus* (Torcida Fernández-Baldor et al. 2011), whereas in *Zapalasaurus* they are less developed and

Table 2. Measurements (in cm) of the caudal elements of *Comahuesaurus windhauseni* gen. et sp. nov.

Element	APL	PH	PW	PS	AS	APL/$\bar{X}$
First caudal vertebra						
MOZ-PV-06741	18.5	19.0	22.0	2.8	SCx	0.90
Anterior caudal vertebrae						
MOZ-PV-06745	9.0	19.5	17.4	0.3	Fl	0.49
MOZ-PV-06637	10.0	17.0	21.0	1.6	Fl	0.53
MOZ-PV-06630	10.5	19.0	18.0	0.3	Fl	0.57
MOZ-PV-06767	12.0	19.2	20.5	0.9	Fl	0.60
MOZ-PV-06640	10.7	18.5	16.0	1.4	Fl	0.62
MOZ-PV-06648	11.0	18.0	18.0	0.3	Fl	0.61
MOZ-PV-06635	9.0	16.7	14.2	2.3	0.7	0.58
MOZ-PV-06631	14.3	15.8	16.8	1.7	1.2	0.88
MOZ-PV-06760	12.7	16.0	12.3	1.0	0.5	0.90
MOZ-PV-06636	12.7	14.5	13.0	1.7	1.0	0.92
Middle caudal vertebrae						
MOZ-PV-06634	16.6	16.4	14.0	1.8	0.4	1.09
MOZ-PV-06627	14.3	13.5	10.5	0.9	0.6	1.19
MOZ-PV-06633	16.0	13.5	12.0	1.2	0.9	1.25
MOZ-PV-06729	18.0	14.0	12.0	1.5	0.7	1.38
MOZ-PV-06638	16.8	13.0	10.0	1.5	0.7	1.46
MOZ-PV-06654	19.2	13.0	13.2	2.0	1.0	1.47
MOZ-PV-06649	18.7	13.0	11.0	1.0	0.2	1.56
MOZ-PV-06628	16.5	11.0	10.0	0.6	SCc	1.57
MOZ-PV-06646	19.8	13.5	11.0	1.1	0.2	1.62
MOZ-PV-06759	22.0	12.0	13.0	1.0	0.2	1.76
MOZ-PV-06766	19.0	11.0	9.5	1.1	0.9	1.85
MOZ-PV-06753	21.0	10.5	12.0	1.5	Fl	1.87
MOZ-PV-06738	21.5	11.5	11.5	SCc	SCc	1.87
MOZ-PV-06642	21.0	9.5	11.5	1.2		2.00
Posterior caudal vertebrae						
MOZ-PV-06639	22.5	11.5	10.5	0.7	F	2.05
MOZ-PV-06733	21.0	10.5	10.0	1.0	0.2	2.05
MOZ-PV-06711	22.0	9.5	8.0	SCc	SCc	2.51
MOZ-PV-06641	20.0	7.5	6.5	SCc	SCc	2.86

Note: APL, anteroposterior length; AS, anterior articular surface; PH, posterior height; PW, posterior width; PS, posterior articular surface; $\bar{X}$, average of PH and PW. The anterior and posterior articular surface can be Fl, flat; SCc, slightly concave; SCx, slightly convex, when concave the deep is indicated.

in *L. tessonei* are extremely well developed piercing the transverse process (Calvo and Salgado 1995). The variable degree of development of these fossae seems to vary not only phylogenetically but also positionally throughout the caudal series.

Anterior caudal vertebrae

Eleven of the 37 preserved caudals are considered anterior caudal vertebrae; a distinction mainly based on the ratio of the anteroposterior length divided by the average (width and height) of the posterior articular surface. The anterior caudal vertebrae have a ratio smaller than 1, as observed in the first 14 caudal vertebrae of other diplodocoids (e.g., *Dicraeosaurus*, *Apatosaurus*; Janensch 1929; Gilmore 1936). Excluding the first caudal vertebra, which is relatively longer than the subsequent anterior elements, the anteriormost caudal vertebrae have a ratio close to 0.5, but this measure increases along the middle of the tail (Table 2).

Seven centra were identified as the anteriormost caudal vertebrae (with a lower ratio and without haemal articular surfaces; MOZ-PV 6745, MOZ-PV 6637, MOZ-PV 6630, MOZ-PV 6635, MOZ-PV 6767, MOZ-PV 6748 and MOZ-PV 6740). These elements have a flat anterior articular surface and a slightly concave posterior articular surface, as in other rebbachisaurids (e.g., *Demandasaurus*, *L. tessonei*; Torcida Fernández-Baldor et al. 2011; MUCPv-153). The ventral surface of these centra is transversely convex, similar to the morphology observed in the first caudal vertebrae but differing from the flat–concave surface of the posteriormost anterior caudals. Most of the anteriormost elements have small lateral foramina, being particularly developed on the left side of MOZ-PV 6637 (Figure 7(A)). The lateral foramina are also present, but less developed in some of the posteriormost anterior caudal centra (e.g., MOZ-PV 6760; Salgado et al. 2004). Among rebbachisaurids, the presence of lateral foramina was recently described for the material from the Bajo Barreal Formation (Cenomanian–Turonian; Ibiricu et al. 2012), and interpreted by these authors as a presumably pneumatic fossa. Although no internal air spaces are present in the material here described, the presence of pneumaticity in anterior caudal vertebrae of, at least, some rebbachisaurids cannot be discarded. The transverse processes are dorsoventrally short, and dorsolaterally directed. The dorsal orientation of the transverse processes was recovered by Whitlock (2011:ch. 125) as a synapomorphy of the clade formed by *Amargasaurus* and *Dicraeosaurus*, and among rebbachisaurids by the Nigersaurinae + Limaysaurinae clade. Nevertheless, the absence of information in other rebbachisaurids indicates that this character may have a broader distribution.

The posteriormost anterior caudal vertebrae are relatively longer than the anteriormost elements, have articulations for the haemal arches and have less developed transverse processes. Additionally, contrary to the anteriormost caudal vertebrae, these elements are amphicoelous (with the posterior articular surface slightly more concave than the anterior one). The ventral surface of these vertebrae is slightly concave or flat. One of the recovered caudals is one of the most complete elements of this section (MOZ-PV 6631). As in other caudal vertebrae, a small foramen is observed in the centrum, which is just anteriorly to the transverse process (Figure 7(D)). These, in turn, are weakly developed and clearly directed dorsally (Figure 7(E)).

Middle caudal vertebrae

Sixteen middle caudal elements were recovered (MOZ-PV, MOZ-PV 06634, MOZ-PV 06627, MOZ-PV 06633, MOZ-PV 06729, MOZ-PV 06638, MOZ-PV 06654, MOZ-PV 06649, MOZ-PV 06628, MOZ-PV 06646, MOZ-PV 06629, MOZ-PV 06759, MOZ-PV 06766, MOZ-PV 06632, MOZ-PV 06753, MOZ-PV 06738, MOZ-PV 06642). All these elements are relatively longer than the anterior caudal vertebrae, with an elongation ratio ranging between 1 and 2 (Table 2). In other diplodocoids, this relation is observed from approximately caudal 14 up to caudal 27 (e.g., *Apatosaurus*; Gilmore 1936). All the middle caudal vertebrae lack transverse process. The anteriormost middle caudals have a low lateral crest (*longitudinal prominence*; Salgado et al. 2004). Although less developed, this crest is similar to that of other diplodocoids (e.g., *Dicraeosaurus*, *Apatosaurus*; *Diplodocus*; HMN 'skeleton m'; CM 3018; CM84, 94). Both articular surfaces are concave, with the posterior one always deeper than the anterior (around twice as deep). The ventral surface of these centra is flat–concave, as that of the middle caudal vertebrae. The neural arch is slightly displaced anteriorly, but not as much as in the caudal vertebrae of titanosaurs (Salgado et al. 1997). The prezygapophyses are short and stout and do not surpass the anterior articular surface of the centrum, differing from other rebbachisaurids (e.g., *Zapalasaurus*, *L. tessonei*, *Nigersaurus*; MOZ-PV 6127; MUCPv-153; MNN GAD 515-518).

The pedicels of the caudal vertebrae of *C. windhauseni* gen. et sp. nov. are dorsoventrally short, resulting in prezygapophyses closely positioned to the vertebral centrum, as in *L. tessonei* and *Zapalasaurus*, whereas *Cathartesaura* and *Nigersaurus* have higher pedicels, with prezygapophyses more dorsally positioned. The neural spine is anteroposteriorly long, being this distance almost twice the lateromedial width of the neural spine (Figure 8). The dorsal edge of the neural spine is straight, with the posterior edge located slightly ventrally with respect to the anterior one, as in *Zapalasaurus* (Salgado et al. 2006:Fig. 5), although not as inclined as in this taxon. The neural spine of *C. windhauseni* does not have the characteristic lateral lamina of diplodocoids (e.g., Calvo and Salgado 1995; Wilson 2002), but this is surely due to the posterior position of this element.

Posterior caudal vertebrae

Only five posterior caudal vertebrae were recovered (MOZ-PV 6639, MOZ-PV 6733, MOZ-PV 6734, MOZ-PV 6711, MOZ-PV 6641). All these elements have an elongation ratio greater than 2 (Table 2). The poor preservation of these elements prevents expanding the description given by Salgado et al. (2004).

Haemal arches

The haemal arch described by Salgado et al. (2004) is the only one preserved. This element is Y-shaped as in anterior haemal arches of other sauropods (e.g., *Camarasaurus*, *Alamosaurus*, *Apatosaurus*; Osborn and Mook 1921; Gilmore 1936, 1946). In lateral view, this element is straight and open Y-shaped (*sensu* Otero et al. 2012), differing from the curved open Y-shaped chevron of *L. tessonei*.

Humerus

A complete right humerus (MOZ-PV 6762) and six other fragmentary remains were recovered, with these fragments similar in proportions to the complete bone. The humerus was preliminary described by Salgado et al. (2004:Fig. 5B–C). This element is robust, with a robustness index (*sensu* Wilson and Upchurch 2003) of 0.30 (Table 3), differing from the more gracile humeri of other rebbachisaurids (i.e., *L. tessonei* [0.26, MUCPv-205], *Nigersaurus* [0.25; MNN GAD 12.]). Robustness indices of approximately 0.3 are commonly found in non-neosauropod sauropods (e.g., *Cetiosaurus*; Upchurch and Martin 2003) and basal macronarians (e.g., *Camarasaurus*, *Tehuelchesaurus*; Wilson and Upchurch 2003; Carballido et al. 2011b). Among flagellicaudatans, only dicraeosaurids have a robustness index of around 0.3 (e.g., *Amargasaurus*; Salgado and Bonaparte 1991), whereas in

Table 3. Principal measurements (in cm) of the girdle and limb elements of *Comahuesaurus windhauseni* gen. et sp. nov.

Element	Measurements
Right humerus (MOZ-Pv 6762)	
Total length	67.5
Proximal breadth	27.5
Mid-shaft breadth	13.0
Mid-shaft transverse length	7.5
Distal breadth	21.0
Right pubis (MOZ-Pv 6743)	
Total length	80.5
Iliac articulation length	18.5
Ischial articulation length	18.0
Mid-shaft breadth	12.5
Distal breadth	33.0
Right ischium (MOZ-Pv 6658)	
Total length preserved	43.0
Mid-shaft breadth	5.0
Left femur (MOZ-Pv 6728)	
Total length	113.0
Proximal breadth	33.0
Mid-shaft breadth	18.0
Mid-shaft transverse length	12.0
Distal breadth	29.0

diplodocids these values range from 0.23 to 0.35 (Schwarz et al. 2007). The diaphysis of the humerus is anteroposteriorly compressed (Table 3). Wilson (2002) recovered the presence of circular diaphysis as a synapomorphic character of rebbachisaurids; however, the ratio between the lateromedial width and the anteroposterior length in these diplodocoids does not greatly differ from other sauropods (Mannion et al. 2012). In *C. windhauseni* gen. et sp. nov., the humeral total length divided by the minimum diaphysis width is 5.2, whereas in *L. tessonei* and *Nigersaurus* this relation is larger than 6.5. In posterior view, the humeral head is well discernible and slightly displaced medially, but closely positioned to the lateromedial midpoint of the bone (Figure 9). From anterior view, the proximal surface of the humerus is slightly convex, as in *L. tessonei* and other rebbachisaurids, but different from the strongly convex margin of diplodocids (e.g., *Apatosaurus*; Gilmore 1936) and non-neosauropod sauropods (e.g., *Patagosaurus*, *Ferganasaurus*; Bonaparte 1986b; Alifanov and Averianov 2003). Therefore, the proximal surface of the humerus in rebbachisaurids is similar to that present in *Chubutisaurus* and more derived titanosauriforms, in which the proximal surface of the humerus forms an almost right angle with the lateral margin. The deltopectoral crest is developed and long (Figure 9), being relatively longer than in *L. tessonei*, in which the crest does not surpass the proximodistal midpoint of the humerus. The deltopectoral crest gradually decreases distally.

The distal end of the humerus is lateromedially expanded respect to the shaft, being the length of this expansion approximately 0.75 times the lateromedial length of the proximal expansion. This expansion is markedly wider than in *L. tessonei* and *Nigersaurus* (Calvo and Salgado 1995; Sereno et al. 2007). As in other non-titanosaur sauropods (e.g., Wilson 2002), the distal end is flat, and the condyles does not have a strong ventral ridge between them (Figure 9).

Pubis

Several fragments of pubes were collected, but only one right pubis is complete. As with other incomplete elements, the fragmentary pubes does not present morphological differences with the complete element. This can be only observed in medial view, because its lateral surface was exposed and eroded and is currently included in plaster. For descriptive purposes, this element was oriented with its longer axis horizontally, and consequently, its anterodorsal margin is described as dorsal, and the posteroventral as ventral (Figure 10(A)). As noted by Salgado et al. (2004), the pubis of *C. windhauseni* gen. et sp. nov. has an unusually broad distal expansion (Table 3), a character shared with *L. tessonei* (Salgado et al. 2004). The contribution of this element to the acetabulum is much reduced, being three times smaller than that corresponding to the ischium. Both pedicels are short and have a wide articulation with the ilium and ischium. The iliac and ischiatic articular surfaces are of the same length. As in *L. tessonei*, the obturator foramen of *C. windhauseni* gen. et sp. nov. is open, communicating it with the iliac articulation via a small sulcus. The obturator foramen is closed in adult sauropods, but is open in juvenile forms (Wilhite 2005). The only adult sauropod with an open foramen is *Losillasaurus* (Casanovas et al. 2001). The ambiens process of the pubis is slightly developed, a widely distributed character among non-flagellicaudatan sauropods (Whitlock 2011). The pubic shaft is long, being around five times longer than the pubo-ischiatic articulation. This ratio is similar to that of other sauropods outside Macronaria (Wilson 2002; Whitlock 2011), but larger than in other diplodocoids (e.g., *Apatosaurus*, 2.7; Diplodocus, 3.1; *Dicraeosaurus*, 3.5; Gilmore 1936; Hatcher 1901; HMN-MB 2737).

Distally, the pubis is ventrally and dorsally expanded, being the length of this expansion 2.7 times larger than the minimum ventrodorsal width of the shaft. Among rebbachisaurids, this expansion and the open obturator foramen are only present in *Comahuesaurus* gen. nov. and *Limaysaurus*, and therefore considered by Salgado et al. (2004) as synapomorphic of *Limaysaurus* (to which the new taxon here described was formerly assigned). Nevertheless, the absence of information in other rebbachisaurids prevents to know if these characters are exclusively shared by these taxa or if they are more widely distributed among rebbachisaurids.

Ischium

In addition to the proximal fragment described by Salgado et al. (2004:Fig. 5E; MOZ-PV 6713) and three other fragments (MOZ-PV 6676, MOZ-PV 6680, MOZ-PV 6716), the recently prepared elements include a right ischium, which only lack a distal fragment of its shaft (MOZ-PV 6658). For descriptive purposes, the ischium is oriented with its longest axis horizontal. Therefore, the anterodorsal margin is described as dorsal and the posteroventral as ventral (Figure 10(B)).

The pubic articular facet is wide and robust, being almost as long as the anteroposterior length of the pubic peduncle. The acetabular region is transversely narrow in its central portion and strongly expanded as it approaches the iliac and pubic articulations, as is widely distributed among rebbachisaurids, but differing from *Zapalasaurus* (Mannion et al. 2012). The iliac peduncle is long and narrow, being its length three times greater than the iliac articular facet (Figure 10(B)). This peduncle is, in lateral view, uniform, and does not have the constriction that is widely distributed among rebbachisaurids (Whitlock 2011), except for *Zapalasaurus*. The preserved shaft fragment (as well as other fragmentary ischia) is long and gracile (Table 3), as is also observed in other rebbachisaurids (e.g., *L. tessonei*, *Demandasaurus*). The ischium length is, at least, three times the anteroposterior length of the pubic pedicel, being similar to the condition in non-titanosaur sauropods. The dorsal margin of the ischiatic shaft forms an almost right angle with the acetabulum. This angle is similar to that of *Zapalasaurus* (Salgado et al. 2006), and greater than in *Demandasaurus*, *Nigersaurus* and *Limaysaurus* (70°, 60° and 60°, respectively; Pereda Suberbiola et al. 2003; Sereno et al. 2007; Calvo and Salgado 1995). The angle observed in *Comahuesaurus* gen. nov. and *Zapalasaurus* results more similar to the condition present in other non-rebbachisaurid diplodocoids (e.g., *Diplodocus*, *Apatosaurus*, *Dicraeosaurus*; Osborn 1899; Gilmore 1936; HMN-MB 1732). The ischial shaft is subcircular in cross-section (Figure 10(B)), as in *Demandasaurus* (Pereda Suberbiola et al. 2003) and *Zapalasaurus* (Salgado et al. 2006), differing from the more lateromedially compressed shaft of *L. tessonei* (Calvo and Salgado 1995). The elongated muscle scar observed in the proximal end of the ischium in *Nigersaurus* and *Demandasaurus* (Sereno et al. 2007; Whitlock 2011) is not present in *Comahuesaurus* gen. nov.

Femur

Five well-preserved and complete femora were recovered (MOZ-PV 6665; MOZ-PV 6728; MOZ-PV 6732; MOZ-PV 6755; MOZ-PV 6761), showing all of them the same morphology and general proportions. The absence of close association of the elements prevents determining the femur–humerus length ratio. The femoral head is dorsally marked by a low convexity, which can be well distinguished in posterior view (Figure 11). The lateral margin of the femur is straight, without the lateral bulge that characterises titanosauriform sauropods (Salgado et al. 1997). The posterior surface of the femur lacks the ridge between the greater trochanter and the femoral head, which is present *Demandasaurus* and *Nigersaurus* (Torcida Fernández-Baldor et al. 2011; Whitlock 2011). When the distal condyles are horizontally aligned, the femur is dorsally directed in a right angle. The femur has an elliptical cross-section at its mid-shaft, being its lateromedial width 1.5 times larger than its anteroposterior length (Table 3), a proportion widely distributed among non-titanosaur sauropods (e.g., Salgado et al. 1997). The fourth trochanter is posteriorly positioned and weakly developed, a character widely distributed among rebbachisaurids (Mannion et al. 2011c; Figure 11). The tibial and fibular condyles are well developed and restricted to the distal portion of the femur. As in other sauropods (except *Omeisaurus* and *Tehuelchesaurus*; Carballido et al. 2011b), the tibial condyle is wider than the fibular condyle (Figure 11(B)).

Discussion

Previous assignment to Limaysaurus

C. windhauseni was preliminary assigned to the genus *Limaysaurus* by Salgado et al. (2004). According to these authors, three diagnostic characters of this genus are observed in *C. windhauseni* gen. et sp. nov., which are here individually discussed.

One of the apomorphic characters proposed for *Limaysaurus* is the presence of caudal centra with its posterior articular surface more concave than the anterior one. As noted in the description, the first caudal vertebra of *Demandasaurus darwini* and *C. windhauseni* gen. et sp. nov. is slightly opisthocoelous. Although the anteriormost caudal vertebrae of *L. tessonei* were described as amphicoelous (well concave anterior and posterior articular surfaces; Calvo and Salgado 1995), the first caudal vertebra of this taxon is incomplete (pers. obs. in MUCPv-153), and therefore is impossible to know if it has the same morphology observed in *Comahuesaurus* gen. nov. and *Demandasaurus*. The first caudal vertebra is not known in other rebbachisaurids, and therefore a slightly opisthocoelous condition for this element cannot be discarded for rebbachisaurids. The anterior caudal vertebrae of rebbachisaurids, excluding the first element, are anteriorly flat or slightly excavated, and markedly concave posteriorly (*Cathartesaura*, *Nigersaurus*, *Demandasaurus L. tessonei*; Gallina and Apesteguía 2005:Fig. 3; MNN GAD 15-18; MDS-RVII 610; Salgado et al. 2004). Thus, a progressive transition from the slightly opisthocoelous first caudal vertebra up to the amphicoelous condition of middle and posterior caudal vertebrae is assumed. Therefore, based on the information of recently described taxa, this character cannot be regarded as diagnostic of *Limaysaurus* as it has a broader distribution.

As in *L. tessonei*, the pubis of *C. windhauseni* gen. et sp. nov. is distally expanded, both ventrally and dorsally. This is an unusual character among sauropods, and therefore was considered as a diagnostic character of *Limaysaurus* by Salgado et al. (2004). Nevertheless, the absence of such element in other rebbachisaurids creates an ambiguous optimisation of this character, and therefore a wider distribution cannot be discarded. Furthermore, a broader distribution is probable, given the phylogenetic results obtained, which places *C. windhauseni* gen. et sp. nov. in a basal position among rebbachisaurids (see below).

The third character proposed by Salgado et al. (2004) as synapomorphic of *Limaysaurus* is not present in *Comahuesaurus* gen. nov., as is observed in the new material here described. Whereas the ischium of *Limaysaurus* is curved, the new element here described shows that that of *Comahuesaurus* gen. nov. is straight (as in other sauropods), and therefore does not represent a shared character by these two taxa. Additionally, the angle between the shaft and the acetabulum is approximately 90° in *C. windhauseni* gen. nov. (as in *Zapalasaurus*) instead of being obtuse as in *Limaysaurus* and other rebbachisaurids.

On the basis of the new information presented here, and from the recently published rebbachisaurid materials (Sereno et al. 2007; Torcida Fernández-Baldor et al. 2011; Whitlock 2011, Haluza et al. 2012), it seems clear that the characters proposed as exclusively shared by *Comahuesaurus* gen. nov. and *Limaysaurus* either have a broader distribution within rebbachisaurids, or are not present in the new materials here described. Therefore, the assignment of the Lohan Cura rebbachisaurid to *Limaysaurus* is doubtful and need to be tested through a phylogenetic analysis.

Phylogenetic analysis

To test the phylogenetic affinities of *C. windhauseni* gen. et sp. nov., a phylogenetic analysis was performed. The data matrix used is modified from Carballido et al. (2011a), which was subsequently based on Wilson (2002) with the incorporation of previously used characters (e.g., Salgado et al. 1997; Upchurch et al. 2004; Harris 2006; González Riga et al. 2009; Whitlock 2011; Mannion et al. 2012) and 34 new ones. Additionally, several new taxa were added, ranging from basal sauropodomorphs to neosauropods. The data matrix has a broad taxon sampling with a special focus on basal neosauropods. A complete list of characters is given in Supplementary 1 and the list of taxa is given in Supplementary 2. The data matrix was edited in Mesquite V. 2.74 (Maddison and Maddison 2011), and an electronic version of the original Nexus file is available from the authors upon request. The data matrix is composed of 342 characters scored across 71 taxa. From the 49 multistate characters, 24 were analysed as ordered (12, 58, 95, 96, 102, 106, 108, 115, 116, 119, 120; 145, 152, 163, 213, 216, 232, 233, 234, 235, 252, 256, 298, 299; 301). The ordering of these characters is based on morphological similarities between the states instead of hypotheses on the evolutional sequence of character transformation.

An equally weighted parsimony analysis was carried out using TNT v.1.1 (Goloboff et al. 2008a, 2008b). A heuristic tree search was performed starting from 1000 replicates of Wagner trees (with random addition sequence of taxa) followed by TBR branch swapping (saving 10 trees per replicate). This procedure retrieved four most parsimonious trees of 998 steps (CI = 0.404; RI = 0.725), found in 185 of the replicates. The strict consensus tree of the four most parsimonious can be seen in Supplementary 3, whereas a resumed topology is shown in Figure 12.

Rebbachisaurid interrelationships

Although the data matrix was developed to test the phylogenetic position of basal neosauropods, and therefore includes multiple non-rebbachisaurid neosauropods (especially basal forms of Macronaria), we will discuss here the topology obtained in Rebbachisauridae. A complete discussion on macronarian relationships lies outside the scope of this work (see Carballido and Sander, in press.).

Rebbachisauridae. Rebbachisauridae (defined as stem) is formed by *Amazonsaurus* and more derived forms (Figure 12). The systematic position of *Amazonsaurus* has been debated and there is not a general consensus on its position. *Amazonsaurus* was initially described as a basal diplodocoid of uncertain position (Carvalho et al. 2003), and was more recently included in several phylogenetic analyses and recovered in different positions: as a basal flagellicaudatan (Salgado et al. 2004), a rebbachisaurid (Salgado et al. 2006), a limaysaurine (Carballido et al. 2010), a basal diplodocoid (Whitlock 2011), a basal rebbachisaurid (Mannion et al. 2012) and even as a macronarian (Rauhut et al. 2005). *Amazonsaurus* is here recovered as a basal form of rebbachisaurid, as in Mannion et al. (2012). With the inclusion of this taxon Rebbachisauridae is supported by two unambiguous synapomorphies: absence of hyposphenic crest in anterior caudals (character 203; reverted in *Nigersaurus* and

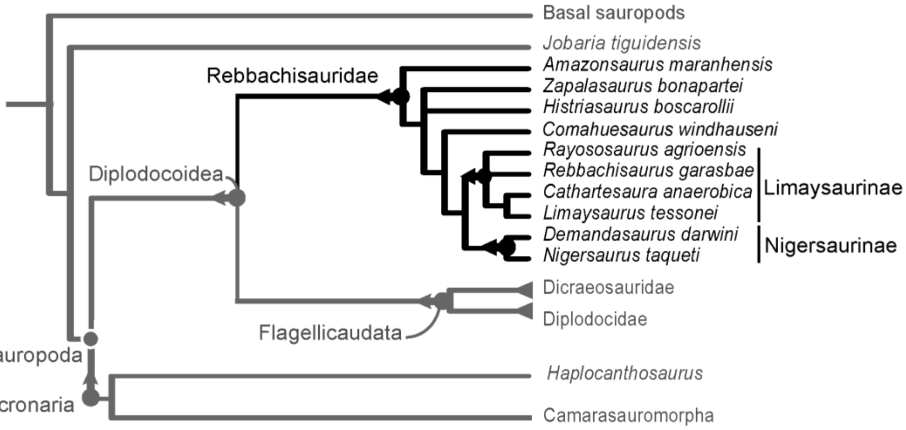

Figure 12. Resumed consensus of the fourth more parsimonious trees obtained.

convergently lost in Titanosauria); and middle caudal centra almost cylindrical, but with a flat ventral margin (character 208; with a reversal in *Demandasaurus*). It must be noted that none of these characters were used in the recent analysis of Whitlock (2011), but both were included by Mannion et al. (2012). In the present dataset only two extra steps are needed to place *Amazonsaurus* as a basal diplodocoid or a basal flagellicaudatan, whereas five extra steps are needed to place it as a basal macronarian. In addition to these unambiguous characters, 26 ambiguous synapomorphies were recovered (see Supplementary 4).

Zapalasaurus–Histriasaurus + more derived rebbachisaurids (MDR). *Zapalasaurus* and *Histriasaurus* are here recovered in an unresolved position among basal rebbachisaurids more derived than *Amazonsaurus*. Our analysis recovered a single unambiguous synapomorphy for the clade formed by *Zapalasaurus–Histriasaurus* and more derived forms: (1) transverse processes of caudal vertebrae dorsally directed (character 192). One ambiguous synapomorphy was recovered for this group (see Supplementary 4).

Zapalasaurus has also been recovered in different positions within Rebbachisauridae and outside this group. Salgado et al. (2004) recovered *Zapalasaurus* as a basal diplodocoid, whereas Sereno et al. (2007) retrieved it as part of the derived clade Limaysaurinae. More recently, Whitlock (2011) recovered *Zapalasaurus* among Nigersaurinae, the other derived clade of rebbachisaurids. More recently, Mannion et al. (2012) recovered *Zapalasaurus* outside of Nigersaurinae + Limaysaurinae in most of their trees, but occasionally found it to cluster with Nigersaurinae. In this analysis of Whitlock (2011), the nigersaurine affinities were supported by the presence of an accessory lamina in the cervical vertebrae (the epipophyseal-prezygapophyseal lamina) and a triangular lateral process in anterior and middle caudal vertebrae. Nevertheless, no lateral expansion can be confidentially identified in *Zapalasaurus*, and therefore differing *Zapalasaurus* from the nigersaurines *Nigersaurus* and *Demandasaurus*. The second character supporting this position, the epipophyseal-prezygapophyseal lamina, resembles a lamina present in other rebbachisaurids, and therefore is a widespread condition among rebbachisaurids. In the data matrix here presented three additional steps are needed to place *Zapalasaurus* as a nigersaurine or limaysaurine, resulting in a moderately less parsimonious hypothesis.

Despite the fragmentary nature of *Histriasaurus*, this taxon has traditionally been considered as a basal rebbachisaurid, a position supported by its well-developed and triangular hyposphene (Apesteguía 2007; Sereno et al. 2007).

C. windhauseni gen. et sp. nov. + MDR. As previously noted, several morphological differences suggested generic separation between *Comahuesaurus* gen. nov. and *Limaysaurus*. The inclusion of *C. windhauseni* gen. et sp. nov. in the present analysis reinforces this hypothesis, as it is recovered in a basal position among rebbachisaurids, as sister group of the derived clade formed by Limaysaurinae and Nigersaurinae, well separated from *L. tessonei* (Figure 12). If *C. windhauseni* gen. et sp. nov. is forced to be the sister taxon of *L. tessonei*, four extra steps are needed, resulting in a markedly suboptimal topology, corroborating the generic separation of the Lohan Cura rebbachisaurid and *L. tessonei*.

The clade formed by *C. windhauseni* gen. et sp. nov. and MDR is here supported by the presence of a single unambiguous synapomorphy: the reduction of the hyposphene–hypantrum system (character 152). As noted in the description, the posterior dorsal vertebrae of *C. windhauseni* gen. et sp. nov. have a laminar hyposphene similar to that of *Demandasaurus* (Torcida Fernández-Baldor et al. 2011) and *Nigersaurus* (MNN GAD 15-18). The morphology of the hyposphene is markedly different to that of *Histriasaurus* (well developed and triangular-shaped). A more detailed discussion on the evolution of this character is provided below. Two ambiguous synapomorphies were obtained (see Supplementary 4)

Limaysaurinae + Nigersaurinae. This clade is here supported by three unambiguous synapomorphies: (1) humerus relatively gracile, with a robustness index (*sensu* Wilson and Upchurch 2003) less than 0.27 (character 256; convergent in non-titanosaur titanosauriforms); (2) pubic peduncle of the ischium with a marked constriction or 'neck' (character 290); (3) angle formed by the acetabulum and the shaft of the ischium lesser than 70° (character 298). A single ambiguous synapomorphy was also recovered for this clade (Supplementary 4).

Limaysaurinae. As in the last phylogenetic analyses (Sereno et al. 2007; Whitlock 2011; Mannion et al. 2012), the present analysis recovered two derived clades of rebbachisaurids, Limaysaurinae and Nigersaurinae (*sensu* Whitlock 2011). A single unambiguous character supports Limaysaurinae: the posterior margin of the scapular acromion is closely positioned onto the mid-length of the scapula (character 238), which distinguishes *Rebbachisaurus*, *Limaysaurus* and *Rayososaurus* from *Nigersaurus* (in which the posterior margin of the acromion process is close to the glenoid and far from the mid-length of the scapula). Five ambiguous synapomorphies were recovered and mentioned in Supplementary 4.

The present analysis recovered the Moroccan taxon, *Rebbachisaurus garasbae*, as a basal form of Limaysaurinae, contrasting with previous analyses in which this sauropod was recovered as a basal rebbachisaurid (Sereno et al. 2007; Whitlock 2011; Mannion et al. 2012). Here *Rebbachisaurus* is retrieved in a polytomy of Limaysaurinae together with *Rayososaurus agrioensis*. Only one extra step is needed to place *Rebbachisaurus* as a basal rebbachisaurid, denoting the low support for the new position retrieved for this taxon.

Limaysaurus + Cathartesaura. As in recent analyses, *Limaysaurus* is recovered as the sister taxon of *Cathartesaura* (Sereno et al. 2007; Whitlock 2011; Mannion et al. 2012), a relationship supported here by one unambiguous synapomorphy: the total length of the scapular acromion is, at least, half of the scapular total length (character 239). In the analysis of Whitlock (2011), this clade is supported by an additional unambiguous apomorphy; cervical vertebrae with an accessory lamina, which is considered here as homologous with that of *Zapalasaurus*, *Nigersaurus* and *Demandasaurus*.

Nigersaurinae. As in other analyses, this clade is formed by *Demandasaurus* and *Nigersaurus*. Four characters are here recovered as unambiguous synapomorphies of this clade: (1) middle and posterior dorsal neural arches with a divided centropostzygapophyseal lamina (character 158); (2) anterior caudal vertebrae with a lateral triangular expansion (character 197); (3) ischium with a well-developed muscle scar (character 291); (4) femur with a well-delimited crest on its posterior surface, between the greater trochanter and the femoral head (character 303). Additionally, one ambiguous synapomorphy was obtained (Supplementary 4).

Evolution of hyposphene–hypantrum system in rebbachisaurids

The hyposphene–hypantrum articulation is formed by a positive structure on the posterior surface of the vertebra – the hyposphene – and a negative structure on the anterior surface of the vertebra – the hypantrum – in which the hyposphene fits (Apesteguía 2005). The presence of a hyposphene–hypantrum articulation system is a plesiomorphic character of Sauropoda, being synapomorphic of Saurischia (Apesteguía 2005). Within Neosauropoda, this accessory articulation is absent in eutitanosaurs (e.g., *Phuwiangosaurus*, *Malawisaurus*, *Neuquensaurus*), and has been traditionally considered as absent in rebbachisaurids (e.g., Calvo and Salgado 1995; Sereno et al. 2007). Apesteguía (2007) interpreted the presence of hyposphene–hypantrum system in *Histriasaurus* (Figure 13(E)) and an isolated vertebra from La Amarga Formation (MACN PV N35) as a plesiomorphic condition among rebbachisaurids. More recently, Torcida Fernández-Baldor et al. (2011) regarded the hyposphene–hypantrum of the derived rebbachisaurid *Demandasaurus* as a reversal to the plesiomorphic condition. However, whereas in *Histriasaurus* and MACN PV N35 the hyposphene–hypantrum system is well developed and triangular-shaped (as in most sauropods; e.g., *Camarasaurus*; Osborn and Mook 1921), in *Demandasaurus* it is weakly developed and laminar-shaped (Figure 13(I)). Additionally, in *Demandasaurus* this extra articulation system seems to be only developed in the posterior dorsal vertebrae, as no hypantrum is present in the middle–posterior dorsal, which solely has the hyposphene on its posterior surface. The morphology and development of the hyposphene of *Comahuesaurus* gen. nov. resemble those of *Demandasaurus*. Moreover, the posteriormost dorsal vertebrae of *Nigersaurus* also have a laminar and weakly developed hyposphene–hypantrum (MNN GAD 15-18). The different degree of development of the hyposphene–hypantrum among rebbachisaurids and the variability of this structure along the dorsal series suggest that the evolution and transformation of this character should be analysed separately in the middle and

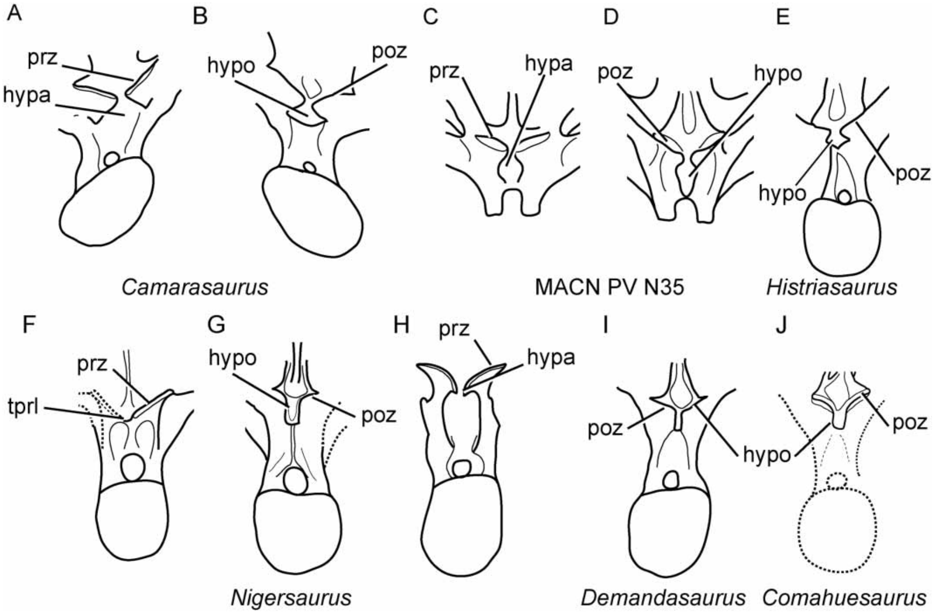

Figure 13. Dorsal vertebrae showing the different development in the hyposphene–hypantrum articulation system. Fourth dorsal vertebra of *Camarasaurus* in (A) anterior and (B) posterior views. Rebbachisaurid indet from La Amarga Formation (MACN PV N35) in (C) anterior and (D) posterior views. *Histriasaurus* in (E) posterior view. *Nigersaurus* 9th dorsal vertebra in (F) anterior and (G) posterior view and 10th dorsal in (H) anterior view. *Demandasaurus* in (I) posterior view. *Comahuesaurus windhauseni* gen. et sp. nov. in (J) posterior view.

posterior dorsal vertebrae and taking into account the degree of development of this structure (as was here translated into the characters used; chs. 151–152; Supplementary 1).

On the basis of the new information brought in this paper and in the topology recovered here, the hyposphene–hypantrum system of middle dorsal vertebrae is convergently lost in Eutitanosauria and Rebbachisauridae. However, we cannot unambiguously determine the exact node in which this change occurred in rebbachisaurids, given the lack of information for some rebbachisaurids (e.g., *Histriasaurus*, *Zapalasaurus*, *Amazonsaurus*). However, this change occurred more basally than the clade formed by Nigersaurinae + Limaysaurinae. In contrast, the posterior dorsal vertebrae of Hystriasaurus have a well-developed hyposphene, whereas this articulation is reduced and disappears completely in Limaysaurinae. Therefore, based on the evidence here presented, although a reduction in the hyposphene–hypantrum system is observed in rebbachisaurids, solely limaysaurines have completely lost this structure.

Biogeography scenario of Rebbachisauridae

The initial biogeographic information of this group was used to postulate a connection between Africa and South America during the Cenomanian (Calvo and Salgado 1995). However, the recently improved knowledge of this group resulted in a more controversial and less clear biogeographic scenario (Carballido et al. 2010; Whitlock 2011; Mannion et al. 2012). Some authors recognised two clades: one South American (Limaysaurinae) and other Afro-European (Nigersaurinae), and interpreted this pattern as resulting of vicariance (Sereno et al. 2007; Carballido et al. 2010; Whitlock 2011). Recently, Mannion et al. (2012) noted that the basal position of the South American taxa *Amazonsaurus* and *Zapalasaurus* outside of the clade Limaysaurinae indicates the absence of a clear vicariant pattern. Nevertheless, the position of *Zapalasaurus* and *Amazonsaurus* does not necessarily contradict the existence of a vicariant event.

To evaluate the biogeographic history of Rebbachisauridae on the new results obtained here (Figure 12), we reconstructed the major biogeographic events along the evolution of this clade using a Dispersal–Extinction–Cladogenesis (DEC) analysis, a method proposed by Ree et al. (2005) and recently implemented by Ree and Smith (2008). This methodology uses a maximum likelihood approach that allows incorporating the temporal information (time of origin of each node), as well as varying the relationships of the geography through the time. Given a calibrated phylogeny, this methodology infers the optimal ancestral ranges, and events of dispersions and extinctions for each node, reconstructing its ancestral condition. Because of the polytomies recovered at the base of Rebbachisauridae and Limaysaurinae, different analyses were performed (see Figure 14 for the consensus information obtained and Supplementary 5 for the complete analysis results). The calibrated topology was obtained following the methodology proposed by Norell (1992) and using the script for TNT following to Pol and Norell (2001).

As noted by other authors (e.g., Wilson 2002; Carballido et al. 2010; Whitlock 2011; Mannion et al. 2012), a long ghost lineage can be traced since the inferred origin of the rebbachisaurid lineage at least by the Late Jurassic (Kimmeridgian-Tithonian) to the oldest record of the group in the Early Cretaceous (Hauterivian–Barremian), when a diversification event is observed (Figure 14). Up to now, *Histriasaurus* is the oldest taxon (Hauterivian–Barremian age), a bias that is surely influenced by the dearth of Early Cretaceous outcrops. The DEC analysis postulates that the origin of this group was South America. The ghost lineage implies a lack of information, shedding some uncertainty on the early evolutionary history of this group. Taking into account the Late Jurassic origin for the rebbachisaurid lineage, its radiation in the Early Cretaceous probably occurred before the complete fragmentation of Gondwana (e.g., Krause et al. 2006). The DEC analysis infers a fast geographic expansion, posterior to this origin, from South America to Africa and Europe at the node leading to *Histriasaurus*, *Zapalasaurus* and MDR. While our phylogenetic analysis does not recover any African taxon at the base of Rebbachisauridae, there is a low support for the current position of *Rebbachisaurus* (only one extra step is required

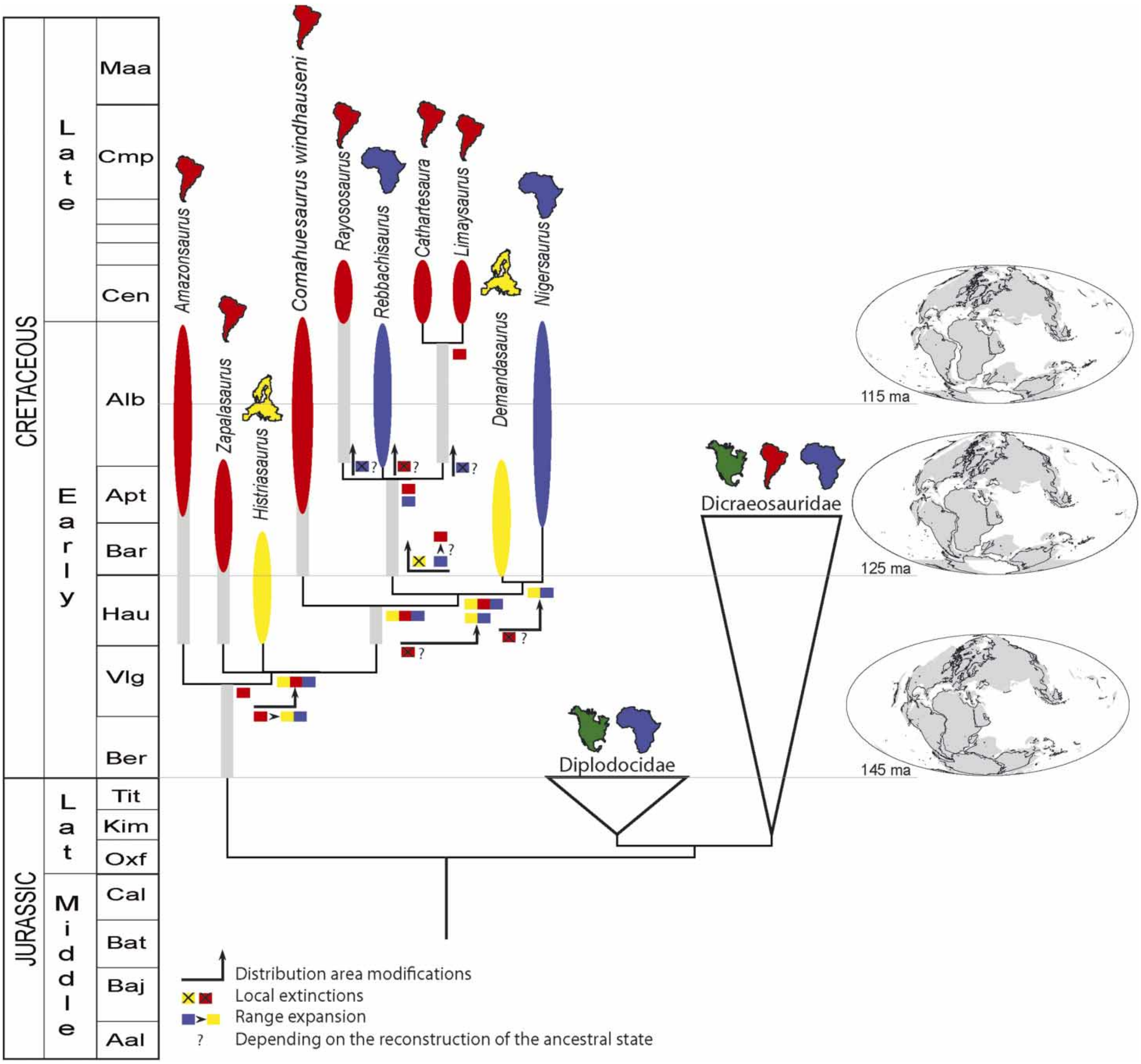

Figure 14. Phylogenetic analysis of rebbachisaurids using DEC (Ree et al. 2005; Ree and Smith 2008). Note: The results are shown in the strict consensus tree, showing the different resolutions depending on the topology used.

to place it outside Limaysaurinae), indicating that a more basal position is plausible for this taxon, as was recovered in other studies (Sereno et al. 2007; Whitlock 2011; Mannion et al. 2012). Additionally, as was recently noted by Torcida Fernández-Baldor et al. (2011), although *Histriasaurus* was here considered a European taxon, during the Hauterivian the Apulian plate was a fragment of Gondwana that split off and finally collided with the south of Europe (being today part of Italy). This migration of the Apulian plate gave origin to the Apulian route connecting Europe and Africa in the Barremian–Aptian (Torcida Fernández-Baldor et al. 2011). The close connection between South America and Africa and between Africa and Europe during the Barremian–Aptian (e.g., the Apulia route; Canudo et al. 2009) lends support to this dispersalist event and explains the presence of rebbachisaurids in the Barremian of Europe. A broad distribution of basal rebbachisaurids across these continents in the Early Cretaceous is also supported in the following nodes, although with some uncertainty, due to the lack of resolution between *Rayososaurus*, *Rebbachisaurus*, and more derived limaysaurines (Figure 14). Depending on the resolution of the clade formed by limaysaurines and nigersaurines, the former could have had an African–European distribution (when *Rebbachisaurus* is in a more basal position within Limaysaurinae), or a wider distribution, including also South America (when *Zapalasaurus* is placed basally among limaysaurines).

The upper Barremian–lower Aptian age assigned to *Demandasaurus* (Torcida Fernández-Baldor et al. 2011) pull down the time of the first diversification of rebbachisaurids in the clade formed by Nigersaurinae plus Limaysaurinae (Figure 14), resulting in a ghost lineage leading towards Limaysaurinae. This clade is recovered with a wide distribution (Figure 14), which depends on the topology used implies two scenarios: (1) an extinction in South America before the origin of Limaysaurinae + Nigersaurinae clade (and a posterior expansion of Limaysaurinae into this continent in the Aptian–Albian); or (2) a wide expansion through Europe, South America and Africa, followed by an areal extinction in South America in the early evolutionary stages of Nigersaurinae. An extinction form Europe is recovered in the early evolutionary stages of Limaysaurinae, before Albian, recovering for the clade formed by *Rebbachisaurus*, *Rayososaurus* and more derived forms an African origin (when *Rebbachisaurus* is the basalmost limaysaurine) or a South American origin (when *Rayososaurus* is the basalmost limaysaurine). Despite the Barremian origin of the Limaysaurinae lineage, it is not until the Albian that this group appears in the fossil record.

Although the general knowledge on the morphology and phylogenetic relationships of rebbachisaurids has greatly improved in the last years (Salgado et al. 2004, 2006; Sereno et al. 2007; Mannion 2009; Carballido et al. 2010; Mannion et al. 2011b; Whitlock 2011; Haluza et al. 2012, Ibiricu et al. 2012), its evolutionary history is far from being well known. Two main biases in the evolutionary history of rebbachisaurids should be taking into account. One of these issues is the lack of support in most of the nodes of this lineage (Figure 12; Whitlock 2011; Mannion et al. 2012), which is also reflected in the topological differences recovered by different authors (Figure 12; Sereno et al. 2007; Whitlock 2011; Mannion et al. 2012). The second issue to take into account is the low sauropod diversity registered in the earliest part of the Early Cretaceous (Mannion et al. 2011a), and the ghost lineage observed in rebbachisaurid evolution, through this time interval. This absence of information in the pre-Aptian ages contrasts with the rich diversity of sauropods documented in the Late Jurassic and the post-Aptian, which is surely obscuring our knowledge on the rebbachisaurids evolution. Therefore, it is hard to know how much of the great diversification inferred from the calibrated phylogeny is an artefact or a true reflect of its evolutionary history.

Conclusions

A new rebbachisaurid taxon is here described, *C. windhauseni* that improves our understanding of Early Cretaceous sauropods in general and of rebbachisaurids in particular. The detailed comparison suggested a generic separation between the materials from Aguada del Leon and *L. tessonei*. This hypothesis is reinforced by the phylogenetic analysis that recovered to the sauropod from Aguada del León in a basal position among rebbachisaurids and outside the Limaysaurinae clade. Therefore, the morphological differences with *Limaysaurus*, the phylogenetic results and the presence of several unique characters allowed us to erect a new rebbachisaurid taxon. In the base of the evidence here presented and discussed, the absence of hyposphene–hypantrum is not an apomorphic character of rebbachisaurids more derived than *Histriasaurus*. In fact, a reduction in size and number of vertebrae carriers of this structure is observed along the evolutionary history of rebbachisaurids, recovering the absence of hyposphene–hypantrum as a synapomorphic character of Limaysaurinae. The DEC analysis carried out inferred a palaeobiogeographical scenario that can be contrastable with the palaeogeographical information available. Nevertheless, both, the absence of a clear phylogentic hypothesis and the lack of information for the history of this group in the pre-Aptian Cretaceous represent a bias that should be taken into account.

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