

## EVIDENCE OF GREGARIOUSNESS IN REBBACHISAURIDS (DINOSAURIA, SAUROPODA, DIPLODOCOIDEA) FROM THE EARLY CRETACEOUS OF NEUQUÉN (RAYOSO FORMATION), PATAGONIA, ARGENTINA

LEONARDO SALGADO,<sup>\*1</sup> JOSÉ I. CANUDO,<sup>2</sup> ALBERTO C. GARRIDO,<sup>3</sup> and JOSÉ L. CARBALLIDO<sup>4</sup>

<sup>1</sup>Conicet–Inibioma, Museo de Geología y Paleontología, Universidad Nacional del Comahue, Buenos Aires 1400, 8300, Neuquén, Argentina, [salgadoleito@yahoo.com.ar](mailto:salgadoleito@yahoo.com.ar);

<sup>2</sup>Grupo *Aragosaurus*–IUCA, Paleontología, Facultad de Ciencias, C/ Pedro Cerbuna 12, Universidad de Zaragoza 50009, Zaragoza, Spain, [jicanudo@unizar.es](mailto:jicanudo@unizar.es);

<sup>3</sup>Museo Provincial de Ciencias Naturales ‘Prof. Dr. Juan Olsacher,’ Dirección Provincial de Minería, Zapala, Neuquén, Argentina, [algene@copelnet.com.ar](mailto:algene@copelnet.com.ar);

<sup>4</sup>Conicet–Museo ‘Egidio Feruglio,’ Fontana 140 9100, Trelew, Chubut, Argentina, [jcarballido@mef.org.ar](mailto:jcarballido@mef.org.ar)

**ABSTRACT**—For the first time an association of adult and juvenile rebbachisaurid sauropods is described. The material comes from the Early Cretaceous locality of Agrio del Medio (Neuquén, Argentina). The three specimens apparently formed a single group, and their death seems to have been almost simultaneous. The two juvenile specimens are represented by axial and appendicular bones. They show a close relationship with *Zapalasauros bonapartei*, which comes from a different sector of the same basin, but which is approximately the same age. The discovery at Agrio del Medio suggests that rebbachisaurid sauropods displayed gregarious behavior. The paleoenvironments in which rebbachisaurids are normally recorded implies a greater tolerance toward extremely arid environments than that shown by macronarian sauropods.

### INTRODUCTION

Gregarious behavior in dinosaurs is difficult to recognize on the basis of the fossil record. However, some evidence indicates that such social behavior was not uncommon in this group (Ostrom, 1972; Horner and Makela, 1979; Barco et al., 2006; Zhao et al., 2007; Myers and Fiorillo, 2009). This evidence has most frequently been obtained from studies of parallel dinosaur trackways (see Lockley et al., 2002). For example, Lockley (1994) proposed a herd structure for the *Brontopodus* trackways from the Late Jurassic (Morrison Formation) in Colorado, with both juvenile and adult individuals. Other evidence for gregarious behavior comes from comparisons with Recent ecosystems, bonebed assemblages, phylogenetic inferences, and skeletal morphology (Currie and Eberth, 2010).

Evidence of gregariousness deduced from sauropod fossil bones is scarce (Coria, 1994; Myers and Fiorillo, 2009) and tends to be based on the combined presence of juvenile and adult individuals at the same site. Myers and Fiorillo (2009) reviewed the evidence from Late Jurassic and Early Cretaceous sauropod sites that yielded juvenile individuals and sauropod tracks. These authors proposed the occurrence of age segregation among sauropod herds, with juvenile and adult individuals grouped in separate herds, a different conclusion from that reached by Lockley (1994). In addition, Castanera et al. (2011) recently interpreted some trackways ascribed to titanosauriform sauropods from the early Berriasian of Spain to a herd composed entirely of juvenile individuals of a similar size. There is, therefore, evidence of sauropod herds both with and without age segregation.

In 2009, a paleontological field trip was undertaken in the vicinity of the Agrio del Medio locality (Neuquén, Argentina; Fig.

1), with a view to prospecting various levels of the Rayoso Formation (Lower Cretaceous; Fig. 2). This campaign was part of a program of international cooperation between the ‘Prof. Dr. Juan A. Olsacher’ Natural Sciences Museum (Zapala, Neuquén, Argentina), the National University of Comahue (Neuquén, Argentina), and the University of Zaragoza (Spain). The initial aim was to study the sauropod *Rayososaurus*, including its stratigraphic position. After exhaustive prospecting, and a revision of the fossil material belonging to this sauropod, the conclusion was reached that the holotype of *Rayososaurus agriensis* pertained to the Candeleros Formation, not from the Rayoso Formation, and is therefore somewhat younger than initially thought (Carballido et al., 2010). In the course of this campaign, a new site was found in the Agrio del Medio locality, with the remains of one adult and at least two juvenile specimens of a rebbachisaurid sauropod. These remains undoubtedly come from the Rayoso Formation, and are thus the first dinosaur remains found in this unit. The material in question was recovered during successive field trips that took place in 2009, 2010, and 2011.

Remains of diplodocoid sauropod juveniles are rare (Whitlock et al., 2010), and those of rebbachisaurids (the group that contains the diplodocoids that are phylogenetically closer to *Rebbachisaurus garasbae* than to *Diplodocus*; Wilson in Salgado et al., 2004; Taylor and Naish, 2005; Whitlock, 2011) virtually nonexistent. There are likewise very few bone records that provide any information on the social behavior of diplodocoids (Myers and Fiorillo, 2009), and none on rebbachisaurids. This paper presents the first remains of juvenile rebbachisaurid individuals, closely associated with the skeleton of an adult specimen in situ, which, given the taphonomy of the location and the paleoenvironmental conditions inferred for the area, lead us to deduce a certain type of social conduct. The remains of the adult sauropod, which were partially articulated, will be described in a subsequent paper, once their preparation is complete.

\*Corresponding author.

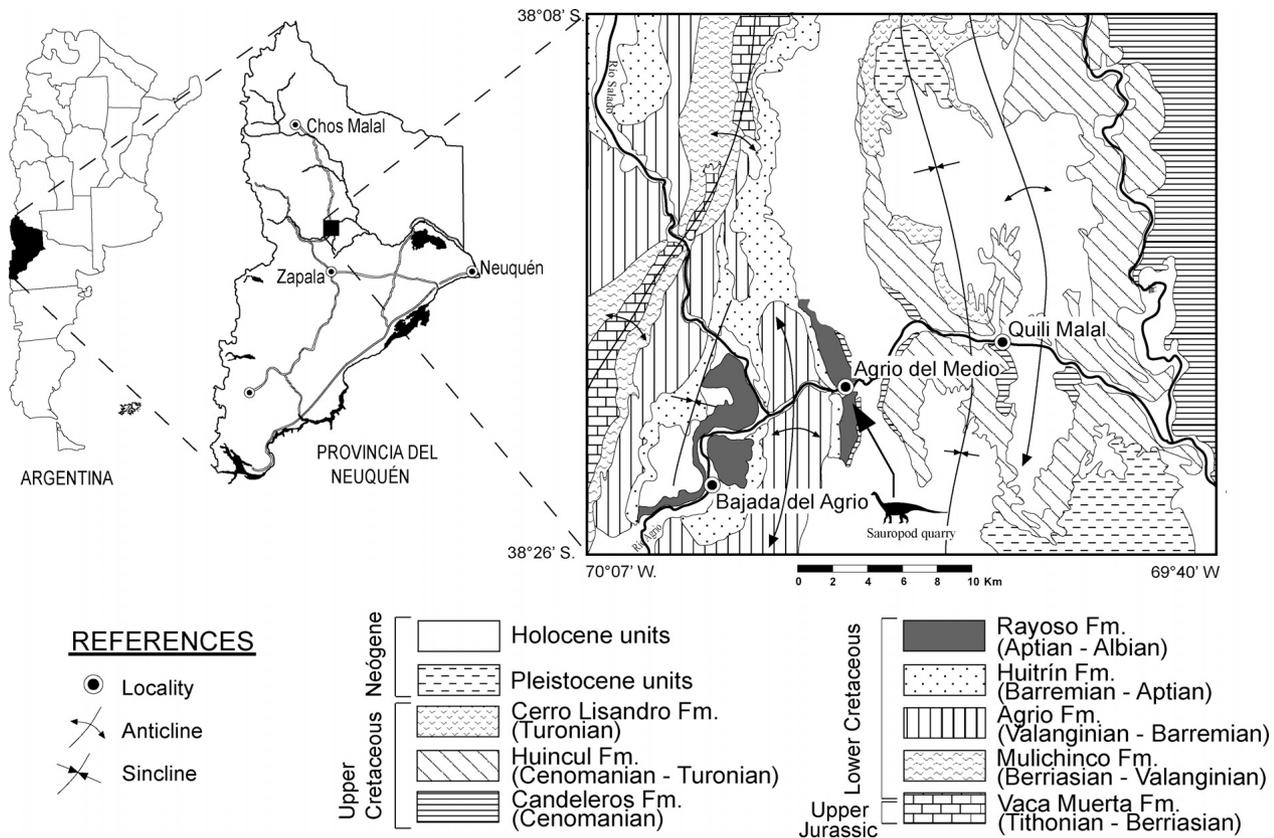


FIGURE 1. Map of location and geologic outcrops of the region where the material was collected.

## GEOGRAPHIC AND GEOLOGIC CONTEXT

The fossil remains are from the Agrio del Medio locality, situated in the central area of Neuquén Province (Patagonia, Argentina; Fig. 1). The fossiliferous layer corresponds to wacky sandstones of the Pichi Neuquén Member of the Rayoso Formation, Lower Cretaceous of the Neuquén Basin (Fig. 2). The Rayoso Formation comprises a set of clastic and evaporitic sediments composed of fine quartzitic sandstones, wacky sandstones, wackes, and mudstones, with sporadic intercalations of gypsum and thin carbonate horizons.

This unit is broadly distributed in the central and northern regions of the Neuquén Basin, being correlated towards the southern area of the basin with the fluvial deposits of the Lohan Cura Formation (Leanza and Hugo, 1995; Leanza, 2003). Its age has been ascribed by some workers to lie within the late Barremian–Aptian interval (Musacchio and Vallati, 2000; Vallati, 2006; Zavala and Ponce, 2011) and extended by other authors up to the Albian (Leanza and Hugo, 2001; Leanza, 2003).

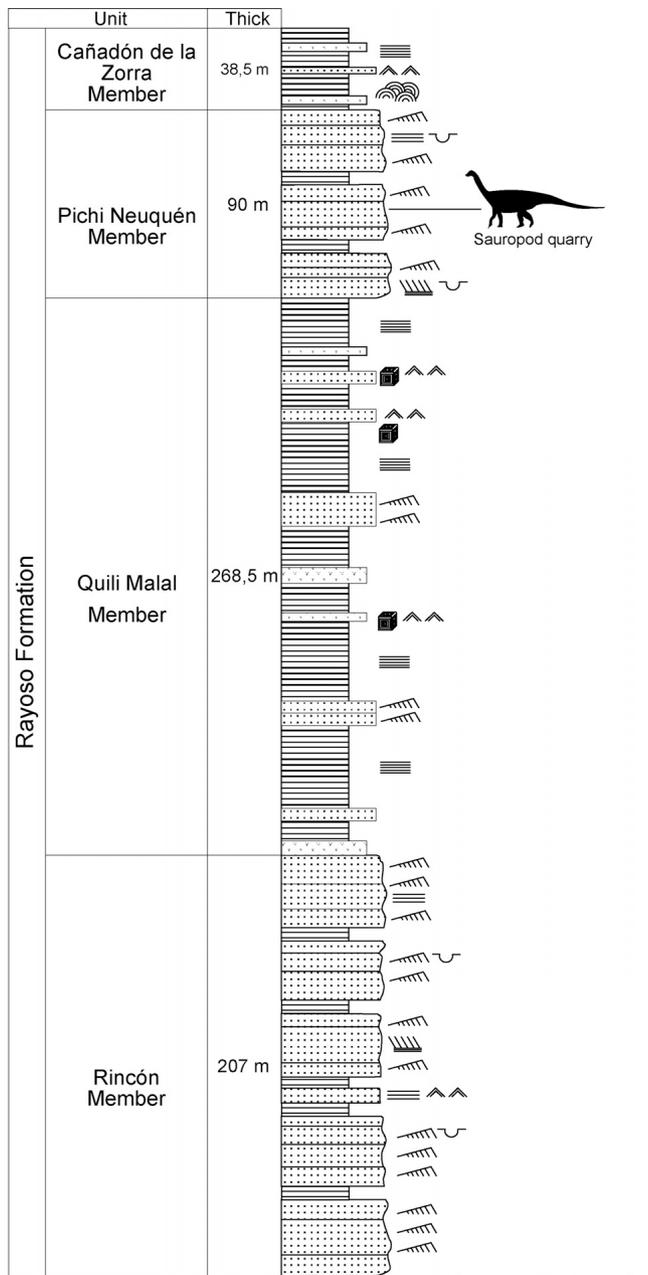
The basal limit of this unit is controversial, with diverse points of view existing on the matter (Herrero Ducloux, 1946; Gabriele, 1992; Leanza and Hugo, 2001; Zavala and Ponce, 2011). This work follows the conclusion of Leanza and Hugo (2001), according to which the basal limit of the Rayoso Formation is given by the lower contact of the Rincón Member (Fig. 2). This scheme is based on the stratigraphic and paleoenvironmental relationships between the different units (members) situated above and below the Rincón Member beds. In the region of Agrio del Medio, which corresponds to the area of the fossiliferous level, Leanza and Hugo (2001) cite an approximate thickness of 890 m for the deposits of the Rayoso Formation. Our own measurements

taken at the locality itself give a total value of 604 m for this unit (Fig. 2).

In general terms, the sediments of this unit have been associated with a continental environment, the deposition of which would have taken place in depressed or low-relief areas, with a periodic marine influence (Uliana et al., 1975; Leanza and Hugo, 2001). The dominantly pelitic and evaporitic sections of this succession (the Quili Malal and Cañadón de la Zorra members, which lie below and above the Pichi Neuquén Member, respectively; Fig. 2) have been attributed to bodies of shallow water periodically subject to sub-aerial exposure, associated with shallow lakes, marginal sabkhas, and mudflats (Uliana et al., 1975; Leanza and Hugo, 2001; Leanza, 2003). In the case of the dominantly psammitic sections (the Rincón and Pichi Neuquén members), these have been interpreted as meandering fluvial deposits developed in low-relief areas (Uliana et al., 1975; Leanza and Hugo, 2001; Leanza, 2003).

More recently, Zavala et al. (2006) interpreted the levels of the psammitic units as deposits from sandy hyperpycnal flows, developed in shallow lacustrine bodies of variable salinity. This psammitic succession (hyperpycnites) would have originated during the expansion of the lacustrine system, whereas during its contraction the pelites and evaporites that make up the rest of the sequence would have been deposited (Zavala and Ponce, 2011).

The fossiliferous level with the dinosaur remains is located in the middle part of the Pichi Neuquén Member, 44.5 m from its base. The fossil-bearing level comprises deposits of pale red color, thinly laminated fine-grained wacky sandstones, with the presence of slight bioturbation in the form of *Skolithos*-type and *Planolites*-type perforations, as well as desiccation cracks at the



## REFERENCES

- Planar cross-stratification    Symmetrical ripples    Fine-grained sandstone  
 Horizontal stratification    Bioturbation    Wacky sandstone  
 Thin lamination    Stromatolites    Gypsum  
 Climbing ripples    Pseudomorphs after hopper-faced halite

FIGURE 2. Lithostratigraphic column of the Rayoso Formation in the area of Agrio del Medio.

top. Fine, slightly muddy sandstones, characterized by the presence of climbing ripples, cover this level. Both levels exhibit tabular geometry of great continuity, providing smooth, clean contacts.

The geometry of these sedimentary bodies and the association of their internal structures suggests deposition related to unconfined flows, originated both through decantation and trac-

tion under low flow regime conditions and high sedimentation rate (Allen, 1984; Miall, 1996). According to Zavala et al. (2006), these deposits would correspond to the hyperpycnites developed by a sub-aquatic delta in a lacustrine body. However, the presence of desiccation cracks at the top of the fossiliferous level would suggest that these deposits were periodically subject to sub-aerial exposure.

Regarding the age of the Pichi Neuquén Member, there is as yet no consensus. Musacchio and Vallati (2000) place the unit within the Aptian, whereas Leanza (2003) ascribes it to the early Albian.

The bone remains make it possible to establish the presence of at least three individuals recovered from the same horizon, comprising one adult specimen and two juveniles (Fig. 3). The bones of the adult specimen showed little dispersion, with many of its cervical and caudal vertebrae articulated or semi-articulated. Though incomplete, this specimen presented few signs of transport, with the sequences of cervicals and the caudals describing a broad arc.

There are at least two juvenile individuals on the basis of two distinct size classes among the elements present. The remains of the juvenile specimens were disarticulated, yet concentrated within a limited area of less than 8 m<sup>2</sup>. Their bones were distributed in two associations (Fig. 3): one of these (association 1) was interspersed with the skeletal remains of the adult; the other (association 2) was found 5 m to the south of the first. The low dispersion of the bones, which are partially articulated or semi-articulated and associated with unconfined low-energy deposits, suggests an autochthonous concentration mode.

**Institutional Abbreviation**—MOZ-Pv, Museo Provincial de Ciencias Naturales 'Prof. Dr. Juan A. Olsacher' (Zapala, Neuquén, Argentina), Paleovetbrates Collection.

## SYSTEMATIC PALEONTOLOGY

SAURISCHIA Seeley, 1887

SAUROPODOMORPHA Huene, 1932

SAUROPODA Marsh, 1878

DIPLODOCOIDEA Upchurch, 1995

REBBACHISAUROIDAE Bonaparte, 1997

cf. *ZAPALASAUROUS* Salgado, Carvalho, and Garrido, 2006 (Figs. 4–10)

**Material**—The material consists of remains from a minimum number of two juveniles at different ontogenetic stages, associated with a partial skeleton, MOZ-Pv 1232, comprising cranial fragments, at least 32 vertebrae (six articulated cervicals, cervical ribs, one dorsal, and 25 caudals, 9 of which were articulated), a scapula and a humerus, various metapodial and autopodial bones, and various indeterminate fragments corresponding to an adult sauropod. The juvenile individual in association 1 is smaller in size than that in association 2. The remains of the larger juvenile (association 2) would indicate a size of about 50% of the size of the adult, whereas the smaller juvenile would be 20% smaller than this, with an estimated size of roughly 40% of that for the adult individual. Association 1 consists of: MOZ-Pv 1248, posterior cervical centrum; MOZ-Pv 1249, cervical neural arch; MOZ-Pv 1251, dorsal neural arch; MOZ-Pv 1252, 1253, 1254, anterior caudal centra; MOZ-Pv 1255, left radius; MOZ-Pv 1256, left ulna; MOZ-Pv 1257, right metatarsal I; MOZ-Pv 1258, metatarsal V?. Association 2 consists of: MOZ-Pv 1233, cervical centrum; MOZ-Pv 1250, cervical centrum; MOZ-Pv 1236, incomplete cervical neural arch; MOZ-Pv 1237, incomplete cervical neural arch; MOZ-Pv 1238, fragmentary neural arch; MOZ-Pv 1239, fragmentary neural arch; MOZ-Pv 1240, dorsal centrum; MOZ-Pv 1241, rib fragments; MOZ-Pv 1242, hemal arch; MOZ-Pv 1243, right ulna; MOZ-Pv 1244, left tibia; MOZ-Pv 1245, left

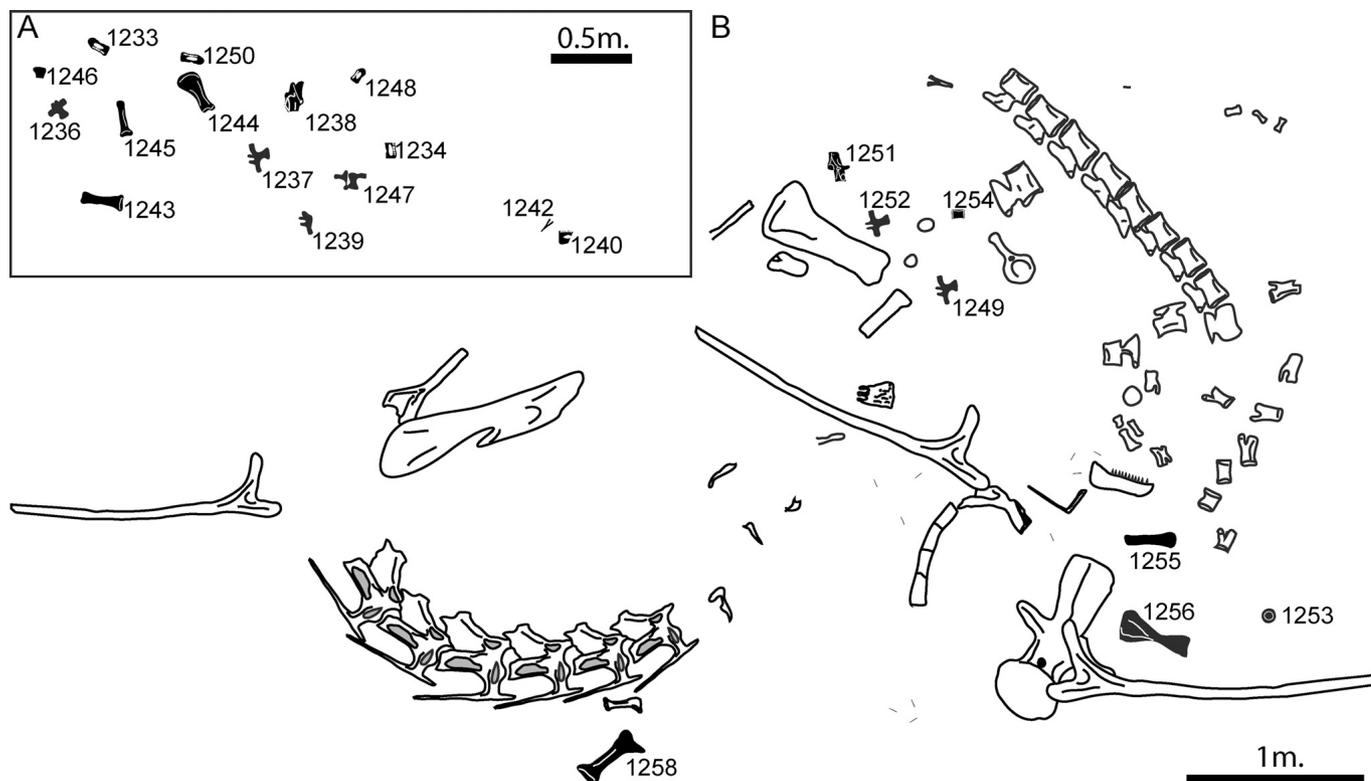


FIGURE 3. Map of the site. **A**, association 2 with remains of the smallest individual; **B**, association 1 with the remains of the adult individual and remains of the larger of the juveniles. Black in-fill designates the bones of the juvenile individuals described in this paper.

fibula; MOZ-Pv 1246, end of metatarsal; MOZ-Pv 1247, indeterminate flat fragment.

## DESCRIPTION

### Axial Skeleton

**Cervical Vertebrae**—Five fragments have been recovered from association 2. These are two vertebral centra and three fragments of very poorly preserved neural arches (Fig. 4; Table 1).

Only the probable dorsal surface of the cervical centrum MOZ-Pv 1233 is preserved (Fig. 4A). It is clearly opisthocelous and approximately twice as long as it is wide. On the right side, the pleurocoel is located on the anterior half of the centrum. Part of the pleurocentral lamina that separates the two partitions of the pleurocoel is preserved, as is the case in other rebbachisaurids (Serenio et al., 2007).

MOZ-Pv 1250 corresponds to another cervical centrum, of length and proportions similar to the previous one; only its ventral surface is preserved (Fig. 4B). As with MOZ-Pv 1233, the centrum is clearly opisthocelous and twice as long as it is wide. Short lateral projections that seem to be the parapophyses can be seen, but these are incompletely preserved. Comparing this element with MOZ-Pv 1233 suggests that the parapophyses were laminar, and that they extended along the entire ventral margin of the anterior subpleurocoel, as in most sauropods. In front of the parapophyses are some notches that would coincide with the ventral margin of the anterior subpleurocoel. There appears to be a small depressed area in the ventral surface, close to the base of the parapophysis.

MOZ-Pv 1237 (Fig. 4C) is a fragment of cervical neural arch that is deformed and incomplete. Only the left postzygapophysis, and part of the left prezygapophysis, can be identified. These are

linked by a thin lamina, similar to the condition observed in other rebbachisaurids, which was described as an accessory lamina by Calvo and Salgado (1995:fig. 8A, B) and the prezygapophyseal-epipophyseal lamina by Sereno et al. (2007:fig. 3B). Due to its contacts (pre- and postzygapophysis), this lamina is here referred as the post-prezygapophyseal lamina (Fig. 4C). The prezygapophysis (incomplete) and the postzygapophysis are 9 cm apart, a distance that corresponds approximately to the length of the above-described cervical centra that also forms part of association 2 (Table 1).

MOZ-Pv 1249 (Fig. 4D) is a cervical neural arch that is small in size and deformed. Only the neural canal and parts of the pre- and postzygapophyses are preserved. The neural spine is absent. The neural canal is 1.5 cm in width and height. The pedicles of the neural arch are short and well differentiated, although deformation has caused the right one to be wider than long, unlike the left one, which is more equidimensional. On the right side the start of an unidentified lamina can be seen. This element perhaps corresponds to an anterior or middle cervical vertebra, although, given that the inclination of the neural arch in relation to the main axis of the centrum cannot be precisely established, it is possible that the whole structure was more vertical and that this piece should be regarded as a more posterior cervical.

MOZ-Pv 1236 is an incomplete neural arch from a posterior cervical or an anterior dorsal (Fig. 4E–G). The height of the preserved portion is 9 cm. The two postzygapophyses, the neural spine, and part of the right posterior centrodiaepophyseal lamina (pcdl) are preserved. The neural spine is very low and blunt, and the postzygapophyses are very broad and high, close to the height of the neural spine, as a result of which the spinopostzygapophyseal laminae (spol) are almost horizontal. In this respect, MOZ-Pv 1236 bears a greater resemblance to *Zapalasaurus* (Salgado

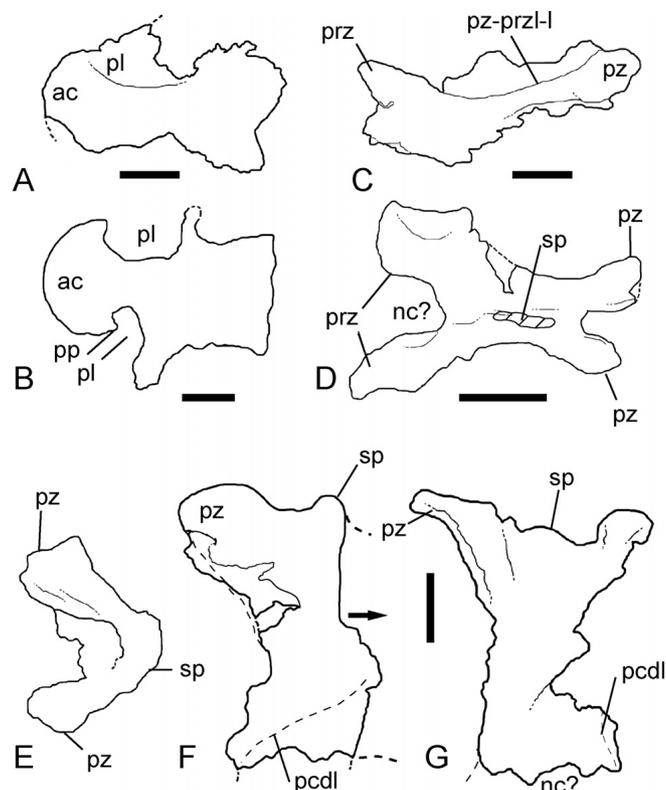


FIGURE 4. *cf. Zapalasaurus*. **A**, MOZ-Pv 1233, cervical centrum in dorsal view; **B**, MOZ-Pv 1250, cervical centrum in ventral view; **C**, MOZ-Pv 1237, cervical neural arch in left lateral view; **D**, MOZ-Pv 1249, cervical neural arch in dorsal view; **E–G**, MOZ-Pv 1236, posterior cervical neural arch in dorsal (**E**), right lateral, with a black arrow anteriorly directed (**F**), and posterior (**G**) views. **Abbreviations**: **ac**, anterior condyle; **nc**, neural canal; **pcdl**, posterior centrodiapophyseal lamina; **pl**, pleurocoel; **prz**, prezygapophysis; **pz**, postzygapophysis; **pz-przl-l**, post-prezygapophyseal lamina; **sp**, neural spine. Scale bar equals 2 cm.

et al., 2006:fig. 4) and *Nigersaurus* (Serenó et al., 2007:fig. 3) than to *Limaysaurus*, in which the cervical neural spines are very high (Calvo and Salgado, 1995:fig. 8). The postzygapophyses are not well preserved, but they seem to be oriented outwards and downwards. A deep cavity opens between the two postzygapophyses, and the separation between them would have been roughly 6 cm. If the neural spine is vertically oriented, the pcdl, which is clearly very broad, shows a very slight inclination. In anterior view, no prespinal lamina can be discerned, but just an increased robustness. In posterior view, there are no signs of the postspinal lamina (posl), although this part of the vertebra is poorly preserved.

MOZ-Pv 1248 is the posterior cervical centrum found in association 1. This element is well preserved, albeit with a slight lateral deformation (Fig. 5A–E). The centrum is opisthocoelous, and the ventral face is very convex, especially in its anterior half. A thin, short crest can be observed on the ventral surface of the centrum, which is positioned anteriorly and contacts the posterior edge of the anterior condyle (Fig. 5A). Between this crest and the parapophysis the ventral surface is gently concave. The parapophysis is projected slightly outwards. It is located at the anteroventral corner of the pleurocoel, on the posterior edge of the articular condyle. The left parapophysis, which is the better preserved, displays a triangular articular surface.

The lateral surfaces of the centrum are concave. They present large, oval pleurocoels, which are situated in the anterior part of

TABLE 1. Principal measurements (in cm) of the axial elements of *cf. Zapalasaurus*.

Element	Measurement (cm)
Cervical centrum (MOZ-Pv 1233)	
Anteroposterior length	8.8
Anterior width	5.0*
Posterior width	5.9*
Cervical centrum (MOZ-Pv 1250)	
Anteroposterior length	9.0
Anterior width	4.7
Posterior width	4.8
Cervical neural arch (MOZ-Pv 1237)	
Combined length from pre- to postzygapophysis	9.0
Cervical neural arch (MOZ-Pv 1249)	
Combined length from pre- to postzygapophysis	6.9
Separation between postzygapophyses	3.0*
Cervical neural arch (MOZ-Pv 1236)	
Separation between postzygapophyses	6.6
Cervical centrum (MOZ-Pv 1248)	
Anteroposterior length	5.3*
Anterior width	3.1
Anterior height	2.9
Posterior width	3.7
Anterior height	3.9
Dorsal centrum (MOZ-Pv 1240)	
Anteroposterior length	6.8
Anterior height	6.6
Caudal centrum (MOZ-Pv 1252)	
Anteroposterior length	2.8
Anterior width	5.0
Anterior height	4.9
Posterior width	5.2
Anterior height	4.7
Caudal centrum (MOZ-Pv 1253)	
Anteroposterior length	2.1
Anterior width	4.7
Anterior height	5.1
Posterior width	4.1*
Anterior height	4.4
Caudal centrum (MOZ-Pv 1254)	
Anteroposterior length	2.6
Posterior width	4.1
Anterior height	4.1

The asterisks indicate estimated measurements.

the centrum. The pleurocoel on the right side appears to be the better-preserved one (Fig. 5C); it is 1.3 cm long and 1 cm high. The neural pedicle is roughly 3 cm long, occupying the whole of the vertebral centrum posterior to the articular condyle (Fig. 5B). In anterior view, it can be observed that the condyle is hardly any wider than high. The posterior articulation is virtually circular (though somewhat deformed: Fig. 5E) and strongly concave, which coincides with the strong convexity of the condyle.

**Dorsal Vertebrae**—The right half of a dorsal vertebral centrum is preserved (MOZ-Pv 1240), split down its axial plane (Fig. 5F). It is not well preserved, though no signs of deformation can be seen.

The body is as long as it is high, and narrower than it is either high or long. In this respect, the vertebra MOZ-Pv 1240 is proportionately identical to MOZ-Pv 6756, which is assigned to *Limaysaurus* sp. (Salgado et al., 2004). Like this latter vertebra, the centrum of MOZ-Pv 1240 is a little higher above its posterior articulation (Table 1). It presents a deep, large, oval pleurocoel that is slightly displaced in the anterior part of the lateral side. This distinguishes it from dicraeosaurids such as *Amargasaurus*, which lack pleurocoels in their dorsal vertebrae (Salgado and Bonaparte, 1991). The pleurocoel seems to be somewhat broader than that of *Limaysaurus* sp., and in MOZ-Pv 1240 the surface of the vertebral centrum beneath the pleurocoel is thus slightly

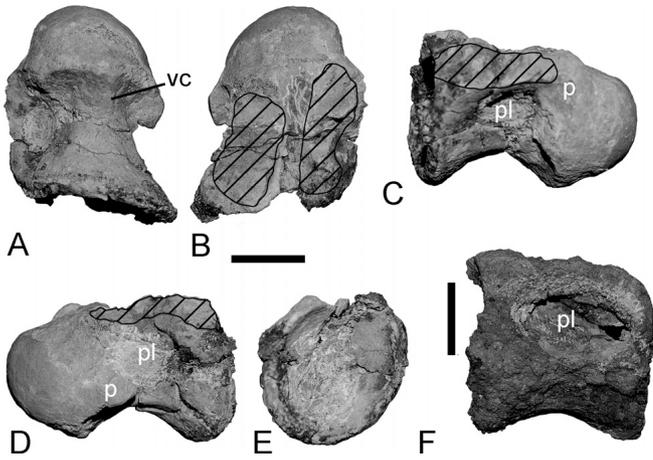


FIGURE 5. cf. *Zapalasaurus*. MOZ-Pv 1248, posterior cervical centrum in **A**, ventral; **B**, dorsal; **C**, right lateral; **D**, left lateral; and **E**, posterior views. MOZ-Pv 1240, posterior dorsal centrum in **F**, right lateral view. **Abbreviations:** p, parapophysis; pl, pleurocoel; vc, ventral crest. Scale bar equals 2 cm.

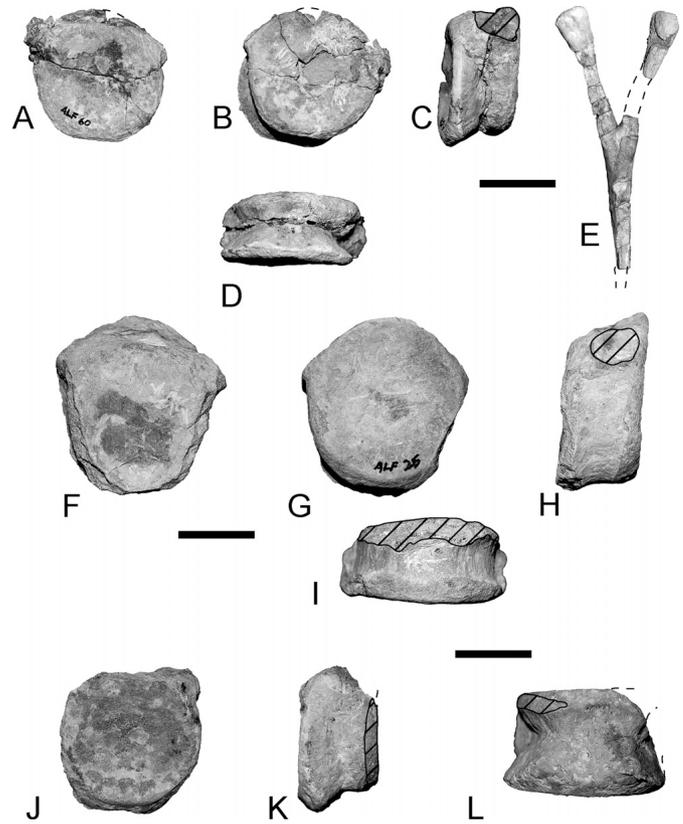


FIGURE 6. cf. *Zapalasaurus*. MOZ-Pv 1252, anterior caudal centrum in **A**, posterior **B**, anterior; **C**, lateral; and **D**, ventral views; MOZ-Pv 1242, hemal arch in **E**, posterior view. MOZ-Pv 1253, anterior caudal centrum in **F**, posterior; **G**, anterior; **H**, right lateral; and **I**, ventral views; **J–L**, MOZ-Pv 1254, anterior caudal centrum in posterior (**J**), lateral (**K**), and ventral (**L**) views. Scale bar equals 2 cm.

smaller. In both cases, however, this surface is equally convex. In both pieces, the pleurocoel extends inwardly almost as far as the axial plane of the vertebra. The pleurocoel lacks internal laminae. The posterior articular face of MOZ-Pv 1240 is somewhat concave, and the anterior one flat, as is the case in MOZ-Pv 6756.

**Caudal Vertebrae**—Three caudal centra have been recovered (MOZ-Pv 1252, 1253, 1254; Table 1), all of them belonging to association 1.

MOZ-Pv 1252 (Fig. 6A–D) is a short centrum of an anterior caudal. The anterior surface is poorly preserved, but it is likely to have been flat or slightly concave. The posterior surface is concave, as in other rebbachisaurids (Salgado et al., 2004). The lateral surfaces are also concave, as is the ventral surface, albeit only slightly. On the posterior margin of the centrum the facets for the hemapophyses can be seen; the distance between them is approximately 2 cm; this supports the presence of dorsally unbridged chevrons. On the upper part of the centrum the bases of the transverse processes can be seen.

MOZ-Pv 1253 (Fig. 6F–I) is a more posterior caudal than MOZ-Pv 1252 and presents similar characters. The facets for the hemapophyses are not well preserved, but the ventral concavity can be clearly made out. The articular surfaces are flat to slightly concave. The base of the transverse processes occupies a similar position to that in MOZ-Pv 1252. The lateral surfaces seem to be somewhat less concave than in MOZ-Pv 1252.

MOZ-Pv 1254 is a centrum from which the left anterodorsal portion is missing (Fig. 6J–L). This vertebra is lower and narrower than MOZ-Pv 1252, but it is somewhat longer. The posterior surface is concave, as in MOZ-Pv 1252. The ventral surface is also concave, and the facets for the hemapophyses are well marked on the posterior edge of the centrum. They are considerably more developed than in MOZ-Pv 1252. The base of the transverse processes is in the same position as in MOZ-Pv 1252 and 1253.

**Hemal Arch**—An almost complete anterior hemal arch is preserved (MOZ-Pv 1242) in association 2 (Fig. 6E), from which part of the right ramus and the distal end of the hemal spine are missing. MOZ-Pv 1242 is a gracile bone, and it has a hemal canal that is open and apparently long (sensu Wilson, 2002). The hemal spine is thin, and hardly any longer than wide.

**Radius**—A left radius (MOZ-Pv 1255) is preserved in association 1 (Fig. 7; Table 2). This was found very close to

an ulna from the same side (MOZ-Pv 1256; Fig. 3). MOZ-Pv 1255 is a slender bone in comparison to the radius of other diplodocoids, such as *Apatosaurus* (which, in fact, is unusually robust; Gilmore, 1936:fig. 12) and *Limaysaurus tessonei* (Calvo and Salgado, 1995:fig. 12D), although this slenderness could be due to its juvenile ontogenetic stage. The proximal end is slightly flattened, and is oval in outline. The distal end is sub-oval in outline. The anterior surface is flat in its proximal half and convex in its distal half. The ulnar surface is flat to slightly concave in its proximal half and convex in its distal half. On the ulnar surface, in the medial-most part, there is a sub-triangular area that is flat to slightly concave. The medial surface of the radius is flat, especially in its distal part, whereas the external or lateral surface is convex. The width of the distal end is slightly greater than that of the mid-shaft, as in all sauropodomorphs (Wilson, 2002).

**Ulna**—A left ulna (MOZ-Pv 1256) belonging to association 1 is preserved, as is a right ulna (MOZ-Pv 1243) belonging to association 2. The following description applies to the latter, because the former has not yet been prepared. Nevertheless, it must be noted that based on field observations both ulna present the same general shape and proportions (Table 2).

MOZ-Pv 1243 is a gracile bone, with a robustness index (sensu Wilson and Upchurch, 2003) of 0.25. The proximal end is tri-radiate, as in all sauropods (Wilson, 2002). The proximal end is transversely expanded; the medial process and above all the lateral process are very well developed. The posterior process is short (Fig. 8C), similar to that in other diplodocoids, such as



FIGURE 7. cf. *Zapalalaurus*. MOZ-Pv 1255, left radius in **A**, posterior; **B**, ulnar; **C**, proximal; **D**, distal; **E**, anterior; and **F**, medial views. Scale bar equals 5 cm.

*Apatosaurus* (Gilmore, 1936:fig. 13C). The lateral process continues as a crest extending for the whole proximal third of the ulna. The dorsal margin of the proximal end is horizontal due to the fact that the ulnar olecranon process is very low, indeed virtually non-existent, as in most sauropods (Wilson and Sereno, 1998), including diplodocoids such as *Amargasaurus* (Salgado and Bonaparte, 1991) and *Limaysaurus* (Calvo and Salgado, 1995), which distinguishes it from titanosaurs, where this process is well defined (Wilson, 2002). The distal end is anteroposteriorly expanded. In posterior view, the surface of the bone is flat in the middle part, slightly concave at the proximal end, and convex at the distal end. The radial or anterior surface (Fig. 8E) is concave at its proximal end. On this surface, at the distal end, is a longitudinal crest that separates two surfaces: an anterior surface that is slightly concave in an anteroposterior direction, and a posterior surface, also concave, that articulates with the distal end of the radius.

**Tibia**—A left tibia is preserved (MOZ-Pv 1244; Fig. 9A–E). The tibia is robust (robustness index sensu Wilson and Upchurch [2003] = 0.36) and lateromedially compressed, which gives it a laminar appearance, although this could be exaggerated by the diagenetic compression of the fossil, especially in its proximal part (Fig. 9E; Table 2). In its proportions it is similar to the holotype of *Zapalalaurus bonapartei*, which is also short (though Salgado et al. [2006:fig. 8C] reconstructed the tibia of *Zapalalaurus* with an angular cnemial crest, like that of the diplodocoids *Apatosaurus* and *Suuwasseea*).

The proximal end of the tibia is anteroposteriorly expanded, which results in a tibia that is proportionally short. The anteroposterior expansion of the tibia (including the cnemial crest) is more than 30% of the total length of the bone. The proximal outline is oval in outline, which distinguishes it from the diplodocoids, which possess a sub-circular outline (Wilson and Sereno, 1998).

TABLE 2. Principal measurements (in cm) of the limb bones of cf. *Zapalalaurus*.

Element	Measurement (cm)
Left radius (MOZ-Pv 1255)	
Total length	15.6
Proximal lateromedial expansion	4.0
Proximal anteroposterior expansion	2.2
Distal (higher) expansion	3.7
Distal (smaller) expansion	3.0
Right ulna (MOZ-Pv 1243)	
Total length	15.7
Medial process to olecranon expansion	6.4
Olecranon to lateral process expansion	5.5
Distal anteroposterior expansion	4.9
Left tibia (MOZ-Pv 1244)	
Total length	26.1
Proximal anteroposterior expansion	10.1
Anteroposterior expansion at cnemial crest height	9.8
Distal anteroposterior expansion	6.8
Distal transverse expansion	6.9
Anteroposterior mid-shaft diameter	5.1
Transverse mid-shaft diameter	1.8
Left fibula (MOZ-Pv 1245)	
Total length	27.7
Proximal expansion	9.1
Distal anteroposterior expansion	5.2
Anteroposterior mid-shaft diameter	3.6
Transverse mid-shaft diameter	1.8
Distal transverse expansion	3.8
Right metatarsal I (MOZ-Pv 1257)	
Total length	3.9
Proximal expansion	4.0
Distal expansion	3.1
Distal expansion dorsoventral width	1.6
Left metatarsal I (MOZ-Pv 1232)	
Total length	10.0
Proximal expansion	10.3*
Distal expansion	8.3
Distal expansion dorsoventral width	3.0

The asterisk indicates estimated measurement.

This morphology could have been exaggerated by lateromedial compression, though Carpenter and McIntosh (1994:268), in their study of juvenile sauropods from the Morrison Formation, described the proximal end as “oval in cross section, being wider than long,” and as such this difference could be an ontogenetic character.

The cnemial crest is well developed and projects laterally, as in most sauropods. It is situated in a relatively low position (in fact, it includes the anterior margin of the bone more than in other sauropods), as in *Limaysaurus tessonei*, *Zapalalaurus bonapartei*, and dicraeosaurids, and its outline is more rounded than that of more-derived diplodocoids such as *Apatosaurus louisae* (Gilmore, 1936:fig. 23) and *Suuwasseea emilieae* (Harris and Dodson, 2004). The tibiae of these North American sauropods both have the same cnemial crest morphology: angular and high.

The internal or medial surface of MOZ-Pv 1244 is slightly concave in its proximal part, flat in its middle part, and at its distal end it is flat anteriorly and convex posteriorly (Fig. 9D).

The distal end is as expanded transversely (6.9 cm) as anteroposteriorly (6.8 cm). The outline of the distal end is triangular, similar to other diplodocoids, such as *Dyslocosaurus* (McIntosh et al., 1992), but different from that of *Apatosaurus*, which is more sub-quadrate. The condyles are well developed, although the posterior one seems to present less development than in other sauropods such as *Apatosaurus* (Gilmore, 1936:fig. 23D). The facet for articulation with the astragalus is situated in an anterior position and is sub-triangular, as in *Dyslocosaurus* (McIntosh et al., 1992).

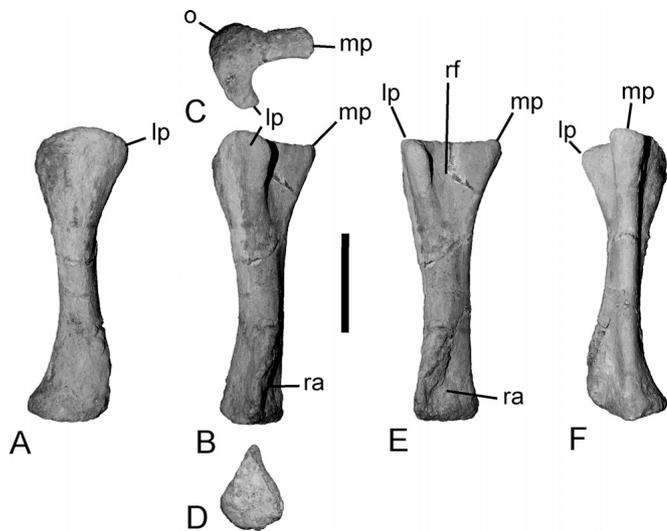


FIGURE 8. cf. *Zapalasaurus*. MOZ-Pv 1243, right ulna in **A**, lateral; **B**, anterolateral; **C**, proximal; **D**, distal; **E**, anterior; and **F**, medial views. **Abbreviations:** lp, lateral process; mp, medial process; o, olecranon; rf, radial fossa; ra, radial articulation. Scale bar equals 5 cm.

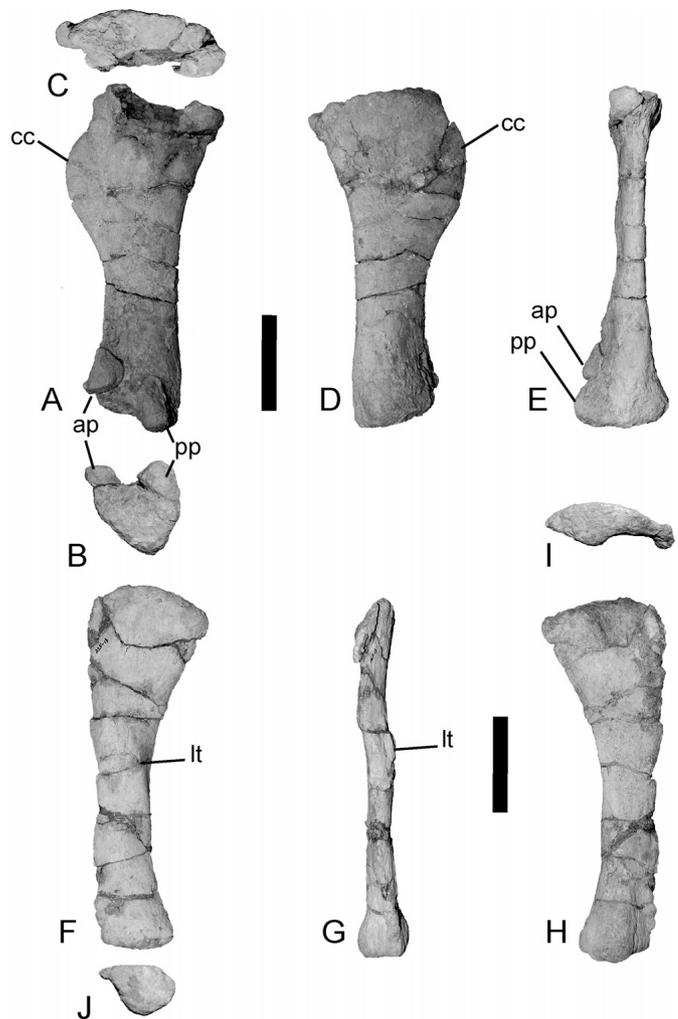


FIGURE 9. cf. *Zapalasaurus*. MOZ-Pv 1244, left tibia in **A**, lateral; **B**, distal; **C**, proximal; **D**, medial; and **E**, posterior views; MOZ-Pv 1245, left fibula in **F**, lateral; **G**, anterior; **H**, medial; **I**, distal; and **J**, proximal views. **Abbreviations:** ap, anterior process; cc, cnemial crest; lt, lateral tuberosity; pp, posterior process. Scale bar equals 7 cm.

The tibia from cf. *Zapalasaurus* and that from *Zapalasaurus bonapartei* bear a greater resemblance to the tibia from *Limaysaurus tessonei* than to those from other diplodocoids, though the cnemial crest seems to be located in a higher position in *L. tessonei* (Calvo and Salgado, 1995: fig. 15B).

**Fibula**—The left fibula preserved (MOZ-Pv 1245; Fig. 9F–J) is strongly lateromedially compressed. MOZ-Pv 1245 is hardly any longer than the tibia and is more gracile (Table 2). Its ends are slightly anteroposteriorly expanded, especially the proximal end, which is more expanded than in *Apatosaurus* (Gilmore, 1936:fig. 24). On the lateral surface the lateral tuberosity or trochanter is scarcely developed. The tuberosity is situated just within the proximal third of the bone. Immediately distal to the tuberosity is a ridge, behind which there is a flat surface. On the medial or tibial surface a protuberance can be seen proximally. This separates two concave surfaces, one anterior and the other posterior. The surface of the proximal half of the bone is flat, and the distal end is concave, behind a ridge.

**Metatarsals**—MOZ-Pv 1257 is a right metatarsal I (Mt1; Fig. 10A–F; Table 2). It is a robust, short bone, with transversely expanded ends, especially proximally, and is in proportion to that described for *Limaysaurus tessonei* (Calvo and Salgado, 1995:fig. 16D). The outline of the proximal end is sub-triangular (expanded superoplantarly), and the distal end is sub-quadrate to oval in outline. The distal articulation is twisted approximately 30° with respect to the proximal end. The distal condyles are not highly developed, as also occurs in the Mt1 of *Camarasaurus* and *Apatosaurus* (Ostrom and McIntosh, 1966). The upper surface is transversely convex in its proximal half. The plantar surface is anteroposteriorly flat and slightly concave transversely. The medial margin is more concave than the lateral one. The superolateral process is relatively well developed. It lacks the laterodistal process possessed by diplodocids (McIntosh, 1990) and some basal titanosauriforms (Upchurch, 1995; Canudo et al., 2008). MOZ-Pv 1232 is a left Mt1 (Fig. 10G, left) from the adult specimen. It is morphologically very similar to MOZ-Pv 1257, but it is broken in the area of the superolateral process. In this material the laterodistal process appears to be better developed than in the juvenile specimen.

MOZ-Pv 1258 is interpreted as a left metatarsal 4 (Fig. 10H–K). The bone has expanded ends, especially proximally. In proximal view, the articulation is slightly triangular in outline, with the longest side of this triangle corresponding to the plantar face of the metatarsal, whereas the distal articulation is sub-rectangular. The lateral surface is convex, and the medial surface is transversely concave.

A bone fragment (MOZ-Pv 1246) from association 2 resembles the end of a metapodial (Fig. 10L–N), but cannot be identified with confidence.

## DISCUSSION

The adult specimen (Fig. 3) is currently in preparation, so the observations supporting its systematic position were recorded during excavation. In spite of this, enough characters have been distinguished to enable us to identify it. The specimen can be included in Diplodocoidea on the basis of the presence of short cervical ribs (not extending beyond the posterior margin of the centrum), and non-overlapping posterior centra. It is included in the clade Rebbachisauridae + Flagellicaudata because it possesses

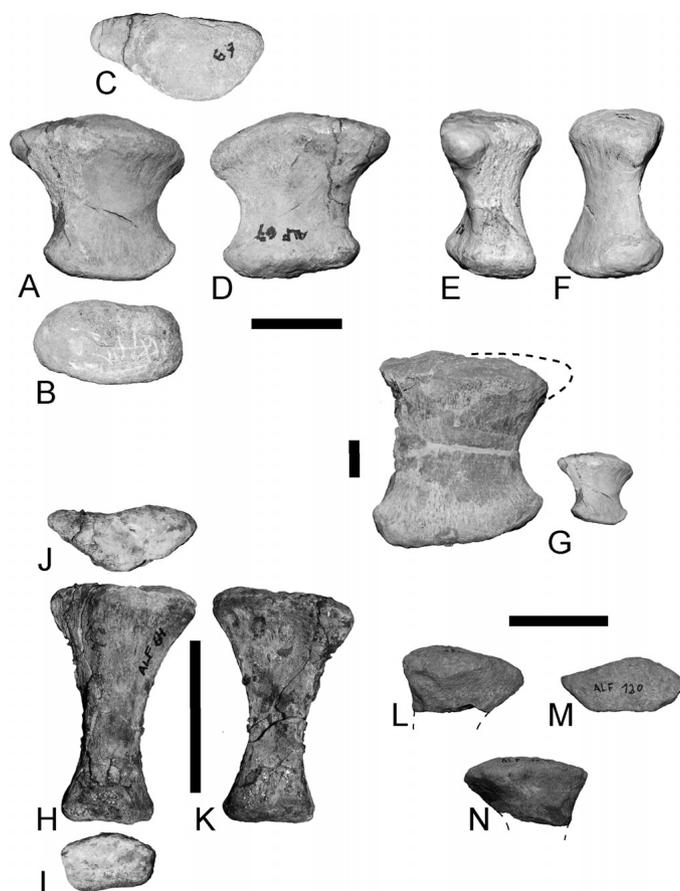


FIGURE 10. cf. *Zapalasaurus*. MOZ-Pv 1257, right metatarsal 1 in **A**, superior; **B**, distal; **C**, proximal; **D**, plantar; **E**, medial; and **F**, lateral views; **G**, comparison between metatarsal 1 of the adult specimen MOZ-Pv 1232 (left) and that of MOZ-Pv 1257, juvenile (right). MOZ-Pv 1258, left metatarsal 4 in **H**, superior; **I**, distal; **J**, proximal; and **K**, plantar views. MOZ-Pv 1246, proximal end of metapodial in **L**, plantar; **M**, proximal; and **N**, superior views. Scale bar equals 2 cm.

at least two cranial characters of the group, namely, snout shape square or blunted, and tooth rows restricted to the jaw anterior to the antorbital fenestra (Whitlock, 2011). In addition, it also possesses two postcranial characters of the group: mid-caudal vertebral centrum length at least twice height, and distal-most caudal centra at least five times longer than tall. Furthermore, it can be included in Rebbachisauridae because it possesses a post-prezygapophyseal lamina on the cervical vertebrae, which corresponds to the epipophyseal-prezygapophyseal lamina of Whitlock (2011).

The juvenile remains are more difficult to classify if taken in isolation, due to their fragmentary nature. Nonetheless, the elements that overlap between the adult and juvenile specimens are virtually identical (Fig. 10G), and their association in the same site suggests that they belong to the same taxon. The overlapping elements include cervical and caudal vertebrae, metatarsals, and hemal arches. In the juvenile material, moreover, other characters can be seen that lend weight to this proposal. Firstly, the cervical vertebral centra display a pleurocoel that is subdivided by a lamina, though this seems to be a widespread character in sauropods more derived than *Jobaria* (Whitlock, 2011). Secondly, the presence of open anterior hemal arches is a character shared with macronarians and other rebbachisaurids such as

*Limaysaurus tessonei* (Calvo and Salgado, 1995; Salgado et al., 1997). Other rebbachisaurids such as *Demandasaurus darwini* possess open hemal arches, though with the rami very close at the proximal end (Torcida Fernández-Baldor et al., 2011). In Flagellicaudata, by contrast, a reversion to the plesiomorphic state can be seen, with the presence of a transverse bridge of bone over the hemal canal (Gilmore, 1936; Upchurch, 1998; Wilson and Sereno, 1998; Whitlock, 2011).

Rebbachisauridae is a clade of basal diplodocoids present in the Early Cretaceous and early Late Cretaceous of South America, Africa, and Europe (Dalla Vecchia, 1998; Salgado et al., 2006; Sereno et al., 2007; Mannion, 2009; Whitlock, 2011; Torcida Fernández-Baldor et al., 2011). It is a complex group, whose phylogenetic relationships are in need of clarification, but which are difficult to determine due to the lack of complete specimens. Recently, the existence of two subfamilies has been proposed: Limaysaurinae (exclusively South American) and Nigersaurinae, which show a broader distribution (in South America, Europe, and Africa), with forms such as *Rebbachisaurus* and *Histriasaurus* corresponding to basal forms (Sereno et al., 2007; Whitlock, 2011; Mannion et al., in press). Taking into consideration all of the material, both adult and juvenile, the greatest morphological similarities for the new specimens within Rebbachisauridae are with *Zapalasaurus* from the La Amarga Formation of Neuquén, Argentina (Salgado et al., 2006). Although *Zapalasaurus* was initially considered as a basal diplodocoid (Salgado et al., 2006), most recent analyses have recovered this taxon in different positions within Rebbachisauridae, as a basal member of the group (Sereno et al., 2007; Carballido et al., 2010; Mannion et al., in press) or in a more-derived position as a member of Nigersaurinae (Whitlock, 2011).

None of the autapomorphies listed by Salgado et al. (2006) can be recognized in this material; however, the similarity between cf. *Zapalasaurus* from Agrio del Medio and *Zapalasaurus* is shown by the form of the tibia, with its very low cnemial crest, and the low, blunt condition of the cervical neural spines, as well as by the general morphology of the caudal vertebrae of the adult individual. For these reasons, the new material is referred to cf. *Zapalasaurus*, though this requires corroboration once the adult specimen has been prepared and a phylogenetic analysis that includes the rebbachisaurids and other basal diplodocoids has been carried out. The Aptian–Albian age ascribed to the Pichi Neuquén Member of the Rayoso Formation, the unit bearing the remains described here, is in accordance with the age of the upper part of La Amarga Formation (Piedra Parada Member), although the levels of the holotype of *Zapalasaurus bonapartei* are possibly somewhat older.

#### Probable Gregariousness in Rebbachisaurids

The Rayoso Formation is very poor in fossils, especially dinosaur skeletal remains. Indeed, the materials found at Agrio del Medio described herein are the first definitive remains from these deposits (see above). Paleoenvironmental conditions are some of the factors that could explain the scarcity of fossils in the Rayoso Formation at Agrio del Medio. Extreme aridity prevailed during the interval in which the Pichi Neuquén Member of the Rayoso Formation was deposited, which at first sight might not represent the best conditions to support a fauna of large herbivorous dinosaurs such as sauropods. However, many examples of large sauropod remains have been recovered from deposits laid down in arid environments, both in Patagonia and elsewhere. Indeed, rebbachisaurid sauropods seem to be a group that tends to be found in extremely arid paleoenvironments (Calvo and Salgado, 1995; Salgado et al., 2004), though they are also found in other environments, albeit almost always associated with other groups of sauropods. Within the Neuquén Basin, the Huincul Ridge

separated two sub-basins that persisted until the Cenomanian. To the north of the ridge, extremely arid environments were present during the Aptian, which were inhabited almost exclusively by rebbachisaurids. To the south of the ridge, equivalent deposits (Lohan Cura Formation) harbor the remains of other sauropod groups such as macronarians (Bonaparte et al., 2006). In this southern sector of the basin, when episodic conditions of aridity appear, the only sauropod remains in the record are rebbachisaurids, whereas macronarian groups disappear (Salgado et al., 2004). This may indicate that this group of diplodocoid sauropods was particularly resilient in such environments. In this regard, our results agree with those of Mannion and Upchurch (2010) who noted that rebbachisaurids might have shown different environmental preferences to other sauropods.

The remains described herein correspond to three specimens at different ontogenetic stages, forming a monotaxic bonebed. The sedimentological evidence does not suggest a catastrophic death for the specimens, nor does it indicate the existence of a trap in which sauropods of different groups were mired at different times in the same place. There is no evidence of an accumulation of transported carcasses; it is clear that the specimens are in situ, albeit partially displaced. In the case of the adult specimen, MOZ-Pv 1232, it can be said that it underwent a certain period of time exposed, given the existence of opisthotonic torsion and the degree of articulation shown by the axial skeleton. In general, the presence of a monotaxic bonebed fossil raises the possibility that the living source assemblage was gregarious. In turn, gregariousness implies that there would have been social interactions between the individuals within the group (Currie and Eberth, 2010). Extrinsic factors, such as the need to congregate at a common resource (e.g., food, water source), could offer an alternative explanation for interpreting this monotaxic bonebed. However, there is no evidence of biologic or geologic extrinsic factors for the accumulation of the bones studied. It is likely that the three specimens formed a group or were part of a larger group; it is unlikely that the three of them died at very different times in this one place. Accordingly, this site has been interpreted as representing an association of juveniles and adults that formed part of a single group and that died more or less simultaneously. One possible, though purely speculative, explanation for this is that the death of the adult triggered the death of the two juvenile individuals.

There is published evidence from the sauropod fossil record of gregarious behavior in herds composed of both juvenile and adult individuals, as well as in herds with exclusively juvenile individuals, indicating age segregation. This illustrates the scarce knowledge we have and/or the complexity of this behavior, which could vary between groups, ontogenetic stages, or trophic availabilities. In this paper we have presented evidence of the herding of juveniles with adults, which contrasts with the type of gregariousness previously proposed for diplodocids.

#### ACKNOWLEDGMENTS

This paper forms part of the project CGL2010-16447 subsidized by the Spanish Ministry of Science and Innovation, the European Regional Development Fund, the Museo Provincial de Ciencias Naturales 'Prof. Dr. Juan Olsacher,' the Dirección Provincial de Minería de la Provincia del Neuquén, and the Government of Aragón ('Grupos Consolidados'). R. Glasgow translated the text into English. The comments of reviewers P. Mannion and J. Whitlock have improved the paper.

#### LITERATURE CITED

- Allen, J. R. L. 1984. *Sedimentary Structures: Their Characteristics and Physical Basis*. Elsevier, Amsterdam, 1253 pp.
- Barco, J. L., J. I. Canudo, and J. I. Ruiz-Omeñaca. 2006. New data on *Therangospodus oncalensis* from the Berriasian Fuentesalvo track-site (Villar del Río, Soria, Spain): an example of gregarious behaviour in theropod dinosaurs. *Ichnos* 13:237–248.
- Bonaparte, J. F. 1997. *Rayososaurus agriensis* Bonaparte, 1995. *Ameghiniana* 34:116.
- Bonaparte, J. F., B. González Riga, and S. Apesteguía. 2006. *Ligabuesaurus leanzai* gen. et sp. nov. (Dinosauria, Sauropoda), a new titanosaur from the Lohan Cura Formation (Aptian, Lower Cretaceous) of Neuquén, Patagonia, Argentina. *Cretaceous Research* 27:364–376.
- Calvo, J. O., and L. Salgado. 1995. *Rebbachisaurus tessonei* sp. nov. a new Sauropoda from the Albian–Cenomanian of Argentina; new evidence on the origin of the Diplodocidae. *Gaia* 11:13–33.
- Canudo, J. I., R. Royo-Torres, and G. Cuenca-Bescós. 2008. A new sauropod: *Tastavinsaurus sanzi* gen. et sp. nov. from the Early Cretaceous (Aptian) of Spain. *Journal of Vertebrate Paleontology* 28:712–731.
- Carballido, J. L., A. C. Garrido, J. I. Canudo, and L. Salgado. 2010. Redescription of *Rayososaurus agriensis* Bonaparte (Dinosauria, Diplodocoidea), a rebbachisaurid of the early Upper Cretaceous of Neuquén. *Geobios* 43:493–502.
- Carpenter, K., and J. S. McIntosh. 1994. Upper Jurassic sauropod babies from the Morrison Formation; pp. 265–278 in K. Carpenter, K. F. Hirsch, and J. R. Horner (eds.), *Dinosaur Eggs and Babies*. Cambridge University Press, Cambridge, U.K.
- Castanera, D., J. L. Barco, I. Díaz-Martínez, F. Pérez-Lorente, and J. I. Canudo. 2011. New evidence of a herd of titanosauriform sauropods from the lower Berriasian of the Iberian Range (Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology* 310:227–237.
- Coria, R. A. 1994. On a monospecific assemblage of sauropod dinosaurs from Patagonia: implications for gregarious behavior. *Gaia* 10:209–215.
- Currie, P. J., and D. A. Eberth. 2010. On gregarious behavior in *Albertosaurus*. *Canadian Journal of Earth Sciences* 47:1277–1289.
- Dalla Vecchia, F. 1998. Remains of Sauropoda (Reptilia, Saurischia) in the Lower Cretaceous (upper Hauterivian/lower Barremian) limestones of SW Istria (Croatia). *Geologia Croatica* 51:105–134.
- Gabriele, N. A. 1992. Sales de potasio de la Formación Huitrín (Cretácico inferior), provincias de Mendoza y Neuquén. *Revista de la Asociación Geológica Argentina* 47:305–316.
- Gilmore, C. W. 1936. Osteology of *Apatosaurus* with special reference to specimens in the Carnegie Museum. *Memoirs of the Carnegie Museum* 11:175–300.
- Harris, J. D., and P. Dodson. 2004. A new diplodocoid sauropod dinosaur from the Upper Jurassic Morrison Formation of Montana, U.S.A. *Acta Palaeontologica Polonica* 49:197–210.
- Herrero Ducloux, A. 1946. Contribución al conocimiento geológico del Neuquén Extraandino. *Boletín de Informaciones Petroleras* 266:245–280.
- Horner, J. R., and R. Makela. 1979. Nest of juveniles provides evidence of family structure among dinosaurs. *Nature* 282:296–298.
- Huene, F. von. 1932. Die fossile Reptil-Ordnung Saurischia, ihre Entwicklung und Geschichte. *Monographien zur Geologie und Palaeontologie* 1:1–361.
- Leanza, H. A. 2003. Las sedimentitas huitrinianas y rayosianas (Cretácico inferior) en el ámbito central y meridional de la cuenca Neuquina, Argentina. *Servicio Geológico Minero Argentino, Serie de Contribuciones Técnicas-Geología* 2:1–31.
- Leanza, H. A., and C. A. Hugo. 1995. Revisión estratigráfica del Cretácico inferior continental en el ámbito sudoriental de la Cuenca Neuquina. *Revista de la Asociación Geológica Argentina* 50:30–32.
- Leanza, H. A., and C. A. Hugo. 2001. Hoja Geológica 3969-I Zapala. Provincia del Neuquén. *Servicio Geológico Minero Argentino, Boletín* 275:1–128.
- Lockley, M. G. 1994. Dinosaur ontogeny and population structure: interpretations and speculations based on fossil footprints; pp. 347–365 in K. Carpenter, K. F. Hirsch, and J. R. Horner (eds.), *Dinosaur Eggs and Babies*. Cambridge University Press, Cambridge, U.K.
- Lockley, M., A. S. Schulp, C. A. Meyer, G. Leonardi, and D. K. Mamani. 2002. Titanosaurid trackways from the Upper Cretaceous of Bolivia: evidence for large manus, wide-gauge locomotion and gregarious behaviour. *Cretaceous Research* 23:383–400.
- Mannion, P. D. 2009. A rebbachisaurid sauropod from the Lower Cretaceous of the Isle of Wight, England. *Cretaceous Research* 30:521–526.

- Mannion, P. D., and P. Upchurch. 2010. A quantitative analysis of environmental associations in sauropod dinosaurs. *Paleobiology* 36:253–282.
- Mannion, P. D., P. Upchurch, O. Mateus, R. Barnes, and M. E. H. Jones. In press. New information on the anatomy and systematic position of *Dinheirosaurus lourinhanensis* (Sauropoda: Diplodocoidea) from the Late Jurassic of Portugal, with a review of European diplodocoids. *Journal of Systematic Palaeontology*.
- Marsh, O. 1878. Principal characters of American Jurassic dinosaurs. Part I. *American Journal of Science, Series 3*:411–416.
- McIntosh, J. S. 1990. Sauropoda; pp. 345–390 in D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*. University of California Press, Berkeley, California.
- McIntosh, J. S., W. P. Coombs, and D. A. Russell. 1992. A new diplodocid sauropod (Dinosauria) from Wyoming, U.S.A. *Journal of Vertebrate Paleontology* 12:158–167.
- Miall, A. D. 1996. *The Geology of Fluvial Deposits: Sedimentary Facies, Basin Analysis and Petroleum Geology*. Springer-Verlag, Berlin, 582 pp.
- Musacchio, E., and P. Vallati. 2000. La regresión del Barremiano–Aptiano en Bajada del Agrio, Neuquén (Argentina); pp. 230–234 in IX Congreso Geológico Chileno, Puerto Varas, 31 July–4 August 2000, Actas 2.
- Myers, T. S., and A. R. Fiorillo. 2009. Evidence for gregarious behaviour and age segregation in sauropods. *Palaeogeography, Palaeoclimatology, Palaeoecology* 274:96–104.
- Ostrom, J. H. 1972. Were some dinosaurs gregarious? *Palaeogeography, Palaeoclimatology, Palaeoecology* 11:287–301.
- Ostrom, J. H., and J. S. McIntosh. 1966. *Marsh's Dinosauria*. The Collections from Como Bluff. Yale University Press, New Haven and London, 388 pp.
- Salgado, L., and J. F. Bonaparte. 1991. Un nuevo sauropodo Dicraeosauridae, *Amargasaurus cazau* gen. et sp. nov. de la Formación La Amarga, Neocomiano de la Provincia del Neuquén, Argentina. *Ameghiniana* 28:333–346.
- Salgado, L., R. A., Coria, and J. O. Calvo. 1997. Evolution of titanosaurid sauropods. I: Phylogenetic analysis based on the postcranial evidence. *Ameghiniana* 34:3–32.
- Salgado, L., I. de Souza Carvalho, and A. C. Garrido. 2006. *Zapalasaurus bonapartei*, un nuevo dinosaurio saurópodo de la Formación La Amarga (Cretácico Inferior), noroeste de Patagonia, Provincia de Neuquén, Argentina. *Geobios* 39:695–707.
- Salgado, L., A. Garrido, S. Cocca, and J. R. Cocca. 2004. Lower Cretaceous rebbachisaurid sauropods from Cerro Aguada del León (Lohan Cura Formation), Neuquén Province, Northwestern Patagonia, Argentina. *Journal of Vertebrate Paleontology* 24:903–912.
- Seeley, H. G. 1887. On the classification of the fossil animals commonly called Dinosauria. *Proceedings of the Royal Society of London* 43:165–171.
- Sereno, P., J. A. Wilson, L. M. Witmer, J. A. Whitlock, A. Maga, O. Ide, and T. A. Rowe. 2007. Structural extremes in a Cretaceous dinosaur. *Plos ONE* 2:e1230.
- Taylor, M. P., and D. Naish. 2005. The phylogenetic taxonomy of Diplodocoidea (Dinosauria: Sauropoda). *PaleoBios* 25:1–7.
- Torcida Fernández-Baldor, F., J. I. Canudo, P. Huerta, D. Montero, X. Pereda-Suberbiola, and L. Salgado. 2011. *Demandasaurus darwini*, a new rebbachisaurid sauropod from the Early Cretaceous of the Iberian Peninsula. *Acta Paleontologica Polonica* 56: 535–552.
- Uliana, M., D. A. Dellapé, and G. A. Pando. 1975. Distribución y génesis de las sedimentitas rayosianas (Cretácico inferior de las provincias de Neuquén y Mendoza, República Argentina); pp. 177–196 in II Congreso Iberoamericano Geología Económica, Buenos Aires, 15–19 December 1975, Actas 1.
- Upchurch, P. 1995. The evolutionary history of sauropod dinosaurs. *Philosophical Transactions of the Royal Society of London, Series B* 349:365–390.
- Upchurch, P. 1998. The phylogenetic relationships of sauropod dinosaurs. *Zoological Journal of the Linnean Society* 124:43–103.
- Vallati, P. 2006. Las primeras angiospermas en el Cretácico de la Cuenca Neuquina (centro oeste de Argentina): aspectos geológicos relacionados. *Revista Brasileira de Paleontología* 9:83–92.
- Whitlock, J. A. 2011. A phylogenetic analysis of Diplodocoidea (Saurischia: Sauropoda). *Zoological Journal of the Linnean Society* 161:872–915.
- Whitlock, J. A., J. A. Wilson, and M. C. Lamanna. 2010. Description of a nearly complete juvenile skull of *Diplodocus* (Sauropoda: Diplodocoidea) from the Late Jurassic of North America. *Journal of Vertebrate Paleontology* 30:442–457.
- Wilson, J. A. 2002. Sauropod dinosaur phylogeny: critique and cladistic analysis. *Zoological Journal of the Linnean Society* 136: 215–275.
- Wilson, J. A., and P. C. Sereno. 1998. Early evolution and higher-level phylogeny of sauropod dinosaurs. *Memoir of the Society of Vertebrate Paleontology* 5:1–68.
- Wilson, J. A., and P. Upchurch. 2003. A revision of *Titanosaurus* Lydekker (Dinosauria-Sauropoda), the first dinosaur genus with a 'Gondwanan' distribution. *Journal of Systematic Palaeontology* 1:125–160.
- Zavala, C., and J. J. Ponce. 2011. La Formación Rayoso (Cretácico Temprano) en la Cuenca Neuquina; pp. 205–222 in XVIII Congreso Geológico Argentino, Neuquén, 2–6 May 2011, Actas 1.
- Zavala, C., J. C. Ponce, M. Arcuri, D. Drittanti, H. Freije, and M. Asensio. 2006. Ancient lacustrine hyperpycnites: a depositional model from a case study in the Rayoso Formation (Cretaceous) of west-central Argentina. *Journal of Sedimentary Research* 76:41–59.
- Zhao, Q., P. M. Barrett, and D. A. Eberth. 2007. Social behaviour and mass mortality in the basal ceratopsian dinosaur *Psittacosaurus* (Early Cretaceous, People's Republic of China). *Palaeontology* 50:1023–1029.

Submitted October 20, 2011; revisions received January 17, 2012;

accepted January 19, 2012.

Handling editor: Paul Barrett.