Zapalasaurus bonapartei, a new sauropod dinosaur from La Amarga Formation (Lower Cretaceous), northwestern Patagonia, Neuquén Province, Argentina.*

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Abstract

An incomplete skeleton from Puesto Morales (Neuquén Province, Argentina) is described as a new species of sauropod, *Zapalasaurus bonapartei*. The unit that yielded the holotype of this dinosaur is the Piedra Parada Member of the La Amarga Formation, whose age is regarded as Barremian-lower Aptian. Several characters are interpreted as autapomorphies of *Zapalasaurus bonapartei*: cervical vertebrae with a lamina uniting the prezygapophysis and the zygapophyseal portion of the postzygadiapophyseal lamina, cervical vertebrae with the diapophyseal portion of the postzygadiapophyseal lamina reduced, cervical vertebrae with poorly developed spinoprezygapophyseal laminae, mid and posterior caudal vertebrae with anteroposteriorly elongated neural spines, whose anterodorsal comers are higher than their posterodorsal ones, and caudal centrum length doubles over first 20 vertebrae. *Zapalasaurus bonapartei* is considered as the sister group of the other diplodocoids (excluding Haplocanthosaurus). Diplodocoids were abundant in the Early Cretaceous, becoming extinct by the early Late Cretaceous. The record of *Zapalasaurus bonapartei* shows that, at least in the Neuquina Basin, basal diplodocoids were more diverse than previously thought.

Keywords: Sauropoda ; Diplodocoidea ; Lower Cretaceous ; La Amarga Formation ; Piedra Parada Member ; Neuquén Province ; Argentina

1. Introduction

The record of sauropod dinosaurs from the Neuquina basin (northeast of Patagonia, Argentina) is made up of mostly titanosaurian remains, almost all of which come from the Upper Cretaceous (Powell, 2003; Salgado, 2003). The most recent sauropod remains found pertain to other groups from the lower part of the Upper Cretaceous (lower part of the Huincul Formation, in the Neuquén Province), which demonstrates that the solitary existence of titanosaurs within sauropods is the situation that comes about after the Cenomanian (Salgado and Coria, 2005).

In the last few years some important finds have permitted us to increment our knowledge about the dinosaur faunas of the Lower Cretaceous, and to also better our

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comprehension of the evolution of sauropods during this interim (Bonaparte, 1999; Salgado et al., 2004).

Presently, sauropod remains found in the Neuquina basin corresponding to the Barremian-Albian have pertained to diplodocoids (Salgado and Bonaparte, 1991; Bonaparte, 1999); Salgado et al., 2004), and less so, to titanosaurs (Leanza et al., 2004).

In this work we present a new sauropod from the Lower Cretaceous of the Neuquén Province. The holotype was excavated in 1995-1996 by a joint commission of the Museo Argentina de Ciencias Naturales "Bernardino Rivadavia," of Buenos Aires, the Museo "Prof. Dr. Juan A. Olsacher," of Zapala, Neuquén, under the direction of José F. Bonaparte. Additional material from the same specimen was removed in April 2004, in a campaign by the Museo de Geología y Paleontología of the Universidad Nacional de Comahue and the museo zapalino.

Institutional Abbreviations: Pv-MOZ, vertebrate paleontological collection of the Museo "Prof. Dr. Juan A. Olsacher," Zapala, Neuquén, Argentina.

2. Geology of the Area

The area where the fossil material came from is located near the southwest border of the Neuquina basin, above the north bank of the China Muerta stream (Fig. 1). This area has excellent outcrops of the Lower Cretaceous, analyzed in detail only recently by Leanza and Hugo (1995, 1997) and Leanza (2002). This sequence, next to marginal basin deposits, is found interdigitated with fluvial and lacustrine continental sediments; correlated with marine and littoral deposits of the Bajado del Agrio Group (Leanza and Hugo, 1999; Leanza, 2002) that outcrop in the depositional center of the basin (Fig. 2).

In accordance with the sedimentological characteristics and lithostratigraphic relationships of the levels pertaining to the holotype of *Zapalasaurus bonapartei* gen. et sp. nov. in the La Amarga Formation, below whose denomination is grouped a thick packet of continental sediments of lower Cretaceous age, between the Initial and Intermediate Miránica disconformities (Leanza and Hugo, 1995, 1997) (Fig. 2).

The first descriptions of these deposits were made by Roll (1939), who located them on top of the Intersenonian disconformity, and referred this formation to the "Strata with Dinosaurs" of the Upper Cretaceous. This scheme was followed later by Herrero Ducloux (1946) who also included an adjoining assemblage of units under the name "Groups of the Río Limay."

The model that established that these units were deposited preceding the Intersenonian disconformity arose from the studies by Pozzo (1953). The same conclusions were obtained by Parker (1964), who with the term "Group of the Amarga" placed those deposits between the Middle-Upper Barremian and the Aptian, homologous with the deposits of the Huitrín Formation, in the north and center of the basin.

The formal naming of the La Amarga Formation was made by Musacchio (1970), who established the type locality near the stream of the same name, on the northwest side of China Muerta Hill. On the basis of the presence of microfossils, Musacchio (1970, 1971a, 1971b) established that the lowest section of this unit was Barremian in age. Later workers assigned this unit to the Barremian-Aptian (Marchese, 1971), and, by its

correlation with the upper part of the Agrio Formation, to the Hauterivian-Barremian (Uliana et al., 1975; Dellapé et al., 1978).

In a recent and complete revision of the La Amarga Formation, Leanza and Hugo (1995, 1997) recognized three members, Puesto Antigual, Banados de Caichigüe, and Piedra Parada, reaching a thickness of approximately 160 m. On the basis of stratigraphic relationships, these authors assigned an age between the Late Hauterivian and Barremian (Leanza and Hugo, 1995, 1997; Leanza, 1999), finally joining the lapse of Barremian – early Aptian (Leanza, 2002; Leanza et al., 2004).

The Puesto Anitgual member is made up of the lowest deposits of this unit, represented by approximately 30 to 40 m of medium to coarse sands and fan deposits that originated in a high energy fluvial environment. Many vertebrate fossils have been collected from these strata, including dinosaurs (Salgado and Bonaparte, 1991; Bonaparte, 1996a, 1996b), crocodiles (Chiappe, 1988), pterosaurs (Montanelli, 1987), and small mammals (Bonaparte, 1986).

The Bañados Member of Caichigüe surpasses to the anterior, conforming a sequence of approximately 20 m of thickness composed of lutites, calcareous limolites, micritic limestones, and thin intercalations of sands that originated in a lacustrine or lagoon environment. These deposits contain numerous microfossils represented by non-marine charophytes and ostracodes (Musacchio, 1970, 1971a, 1971b, 1979, 1981, 1990), as well as microfloral elements assigned to Araucaracea and Podocarpacea (Volkheimer, 1978).

The Piedra Parada Member is the last unit that makes up the La Amarga Formation. Its deposits are a monotone sequence of fluvial origin composed of arenites, conglomerates, sandy fan-deposits and limolites. With thicknesses that range between 110 and 190 m, until this moment paleontological records were not accounted for proceeding from these levels.

Conforming to this lithostratigraphic scheme, the holotype of *Zapalasaurus bonapartei* comes from fan deposits of alluvial floodplain located in the upper sections of the Piedra Parada Member (Fig. 3), constituting the first fossil record from this unit.

3. Systematic Paleontology

SAURISCHIA Seeley, 1887
SAUROPODOMORPHA Huene, 1932
SAUROPODA Marsh, 1878
DIPLODOCOIDEA Upchurch, 1995

Zapalasaurus gen. nov.
Etymology: in reference to Zapala, a city of the Neuquén Province, Argentina, located some 80 km to the north of the holotype locality (Fig. 1).
Type Species: *Zapalasaurus bonapartei* sp. nov.
Diagnosis: cervical neural arches with a lamina that unites the prezygapophysis and the zygapophyseal area of the postzygadiapophyseal lamina (podl), with the form of a continuous lamina; cervical neural arches with the postzygadiapophyseal lamina reduced in its diapophyseal area; cervical neural arches with the spinoprezygapophyseal lamina (sprl) poorly developed, not reaching the full extent of the neural spine; mid- and

posterior caudal vertebrae with the neural spine anteroposteriorly enlarged, whose anterior extreme is located at a level higher than the posterior level; caudal vertebrae double in length in the first 20 vertebrae (convergent with diplodocines).

Zapalasaurus bonapartei sp. nov.
Figs. 4-8
Etymology: in homage to Dr. J. Bonaparte, who collected the holotype material, and in recognition of his professional career, and to his important work in understanding Mesozoic vertebrates.
Holotype: Pv-6127-MOZ: an anterior to mid- cervical vertebra, a fragment of a transverse process of the sacrum, 17 caudal vertebrae that possibly make up a continuous series, a left ischium, a left pubis, a fragment of an ilium, an incomplete left femur and a complete left tibia.
Horizon and locality: 39^{o} 33' 19" S; 70^{o} 09' 11" W. Puesto Morales, La Picaza, South-center of the Province of Neuquén. Piedro Parada Member of the La Amarga Formation (upper Barremian – lower Aptian, Leanza and Hugo, 1997) (Figs. 1, 2).

4. Description

4.1 Cervical vertebra (Fig. 4)

An incomplete anterior to mid- cervical vertebra has been preserved. It was found badly preserved, deformed, mostly on its left side. The vertebra seems to have been as long as it is tall. The vertebral body is opisthocoelous, which is known by its lightly concave posterior articular face. From viewing the only preserved area of the ventral face of the centrum, it can be seen that it is transversely concave. Two deep pneumatic fossae exist at each side of the centrum. Both fossae are separated medially by a thin partition of bone. Dorsally, the pneumatic fossa is closed by a lamina of bone that is lightly expanded towards the front and back. This fossa is double, as in the majority of eusauropods (Wilson, 2002, character 83), such that the lamina that unites dorsally is found divided in two segments (laminae a and b, Figure 4).

Above the neural arch there are distinct laminae of bone, as is characteristic of all eusauropods (Wilson, 2002, character 81). From the diapophysis splits the anterior centrodiapophyseal lamina (acdl), the posterior centrodiapophyseal lamina (pcdl), and the prezygadiapophyseal lamina (prdl); the latter is notably robust (Fig. 4C). From the prezygapophysis, a robust lamina is directed toward the rear that ends before the area between the postzygapophyses (that are not preserved). A similar lamina can be seen in the fifth cervical of *Camarasaurus grandis* Marsh (Wilson and Sereno, 1998: Fig 11A, B), in the last cervicals of *Amargasaurus cazaui* Salgado and Bonaparte (pers. obs.). the homology of this last lamina is difficult to establish. In *Amargasaurus cazaui*, between the eighth and eleventh cervical, the progressive development posteriorly of a lamina that originates in the proximal area of the prezygapophysis of the prezygadiapophyseal lamina (prdl), and which ends at the postzygadiapophyseal lamina (podl). The area of the postzygapophyseal lamina that remains is between the point of union with the new lamina and diapophysis (that which arrives at the diapophyseal area of the podl) returns practically vertically, forming an angle with the rest of the podl (the zygapophyseal area

of the podl), in so much that the new lamina and the zygapophyseal area of the podl form a continuous lamina. This observation on the holotype of *Amargasaurus cazaui* permits the identification, in *Zapalasaurus bonapartei*, a small vertical lamina of bone that develops from the diapophysis, like the diapophyseal segment of the podl (Fig. 4C). This segment has lost its importance, a difference that is observed from *Camarasaurus grandis* and *Amargasaurus cazaui*. As in *Amargasaurus cazaui*, in *Zapalasaurus bonapartei* the new lamina and the zygapophyseal areas of the podl are found aligned, forming one unique lamina.

In *Zapalasaurus bonapartei* there are two poorly developed laminae of bone that are interpreted as the spinoprezygapophyseal laminae (sprl), which do not reach the full extent of the spine (Fig. 4A, C). In anterior view, both centroprezygapophyseal laminae (cprl) are observed to be very robust and undivided (Fig. 4A).

The neural spine of the cervical vertebra is short and rounded distally. Two robust spinopostzygapophyseal lamina (spol) encircle the deep fossa on top of the neural canal (Fig. 4B), and there are two centropostzygapophyseal laminae (cpol) (Fig. 4B).

4.2. Sacral vertebrae

A fragment was preserved that is interpreted as a distal part of a sacral rib. The articular end is somewhat expanded and has a smooth superficial convexity that would contact the ilium. In general terms, the element is similar to the fifth sacral rib of *Haplocanthosaurus* Hatcher (Hatcher, 1903: Fig. 16e).

4.3 Caudal vertebrae (Fig. 5, picture 1)

A series of 17 caudal vertebrae are preserved (Fig. 5, picture 1). While the vertebrae were not found articulated, they are possibly a continuous series (J. Cocca, pers. comm., 2004). While this cannot be confirmed, it is suggested since no morphological jumps are observed between the vertebrae. Therefore, it is very probable that the vertebral elements found correspond to a segment within the first 20 vertebrae in the line.

All of the caudal bodies are slightly amphicoelous. Their ventral faces are concave mostly at the ends of the centrum, at least in the vertebrae on which this can be observed. In general, the anterior caudals have a short centrum, although towards vertebra 15 in the series they have practically doubled in length (see picture 1). We interpret this characteristic as an autapomorphic feature of *Zapalasaurus bonapartei*, convergently developed in the diplodocines (character 20, Wilson, 2002, character 120).

In the first caudals part of the right transverse processes are preserved, which would have projected outwards and upwards. Sadly, it is not possible to know if said processes were triangular or wing-like. In all elements which can be seen in their caudal quarter, the portion of the transverse process corresponding to the neural arch are strongly developed, and are directed outwards and upwards, as in more derived diplodocoids.

The prezygapophyses project anterodorsally in the anterior caudal vertebrae, although towards the 11^{th} and 12^{th} they are directed anteriorly.

In some of the first caudals there is a structure that can be interpreted as the base of the spinopostzygapophyseal lamina (spol), which seems to have been located laterally.

The anterior end leaves from the presence of a robust foundation, clearly observable in the caudal quarter of the vertebra.

Without a doubt, the spinoprezygapophyseal laminae (sprl) do not participate in the formation of a lateral lamina, as happens in the diplodocids, the dicraeosaurids, and in *Amazonsaurus* Carvalho, Avilla and Salgado (Carvalho et al., 2003). On the contrary, the sprls run parallel to the anterior margins of the spine until reaching its extremity.

In the caudal quarter of the series (the best preserved in the anterior caudals) a robust prezygadiapophyseal lamina (prdl) and a very incipient postzygadiapophyseal (podl) is present. Over the diapophysis is a deep concavity, as in *Amazonsaurus* and in other diplodocoids. Nevertheless, there is no indication of other diapophyseal laminae.

The neural spines seem to be short compared with other diplodocoids and, definitively, are not vertical as in the diplodocines, since they are inclined towards the rear. From the third to eighth caudal, the angle between the prezygapophysis and the neural spine is approximately 90 degrees. From caudal 8 and posterior, this angle is significantly smaller.

Towards the 10^{th}-11^{th} caudals the neural spine is shorter and extended anteroposteriorly. In this region of the tail, the anterodorsal corner of the spine is elevated in relation to the posterodorsal corner, which is also interpreted as a diagnostic character for this species.

4.4. Ischium

A left ischium is preserved. Its proximal portion is laminar and the ischiadic process thin and oval in cross section. The major axis of the ischiadic process forms an angle of 50 degrees with the proximal expansion. The iliac pedicle is incompletely preserved. The lamina, although incomplete, is slightly deep. In general, the ischium is similar to *Limaysaurus* Salgado, Garrido, Cocca and Cocca (Calvo and Salgado, 1995: Fig. 14; Salgado et al., 2004), although in that genus the ischiadic process is somewhat more planar (Calvo and Salgado, 1995: Fig. 14B).

4.5 Pubis (Figs. 6B,C,7)

An incomplete left pubis is preserved. In contrast to other diplodocoids from higher levels and assigned to *Limaysaurus sp*. by Salgado et al. (2004), the body of the pubis is laminar. The medial lamina extends over a good part of the length of the preserved part of the pubis. In *Limaysaurus*, the reduction of the laminar portion of the pubis possibly signifies a decrease or at least a modification of the insertion area for the *puboischiofemoralis externus* muscle (Borsuk-Bialynicka, 1977; Carrano and Hutchinson, 2002). In *Zapalasaurus*, in principle, said muscle would have had a normal distribution and development.

4.6 Ilium (Fig. 7)

A fragment of the left ilium was collected, corresponding to part of the acetabulum. The scarce quality of the material prohibits observation of any features of interest.

4.7 Femur (Fig. 8A, B)

Two fragments of a left femur were preserved. The distal portion is better preserved. The tibial and fibular condyles are observable, though the latter is very poorly preserved. The transverse width of the femur at the distal condyles is 30.5 cm, while the width at the diaphysis is 16.5 cm.

4.8 Tibia (Fig 8C)

A complete left tibia is preserved. The proximal and distal ends are equally expanded anteroposteriorly. The cnemial crest is not completely preserved, although apparently it occupied a relatively low position, different from the condition in *Limaysaurus tessonei* Calvo and Salgado (Calvo and Salgado, 1995: Fig. 15b). The proximal articulation is oval (the width is less than half the length), although it cannot be ruled out that this may be the result of deformation.

Discussion

The combination of characters observed in the sauropod from Puesto Morales allows the recognition of a new genus and species of sauropod: *Zapalasaurus bonapartei*. Compared with other taxa found in the area of La Picaza and La Amarga (central-south of the province of Neuquén), and those coming from stratigraphic levels of the lower Cretaceous, the sauropod from Puesto Morales exhibits notable differences. With respect to *Amargasaurus cazaui* (lower Barremian, Puesto Antigual, Amarga Formation), the new sauropod is distinguished by the low height of the cervical neural spines, and by the amphiplatyan condition of the anterior caudal vertebrae (lightly procoelous in *Amargasaurus*). Also, *Zapalasaurus* lacks the following diagnostic characters of *Limaysaurus* (Aptian, Puesto Quiroga Member of the Lohan Cura Formation): cervical neural arches with accessory laminae extended anterodorsally from the postzygadiapophyseal lamina, anterior caudal neural spines with lateral laminae swollen distally, ending in robust bone, and median part of the pubis oval in transverse section (Salgado et al., 2004).

On the other hand, *Zapalasaurus* exhibits a series of characters that are interpreted as autapomorphies: cervical neural arches with a lamina uniting the prezygapophysis and the zygapophyseal sector of the postzygadiapophyseal lamina; cervical neural arches with the postzygadiapophyseal lamina reduced in its diapophyseal sector; cervical neural arches with the spinoprezygapophyseal lamina poorly developed, not reaching the tip of the neural spine; mid- and posterior caudal vertebrae with the neural spine anteroposteriorly enlarged, whose anterior extreme is located at a level higher than the posterior extreme; caudal vertebrae doubling their length in the first twenty vertebrae (convergent with diplodocines).

With the objective of knowing the probable phylogenetic relations of *Zapalasaurus bonapartei*, an analysis of distinct diplodocoids has been performed on the basis of 37 characters (the majority of these taken directly or reformulated from Wilson, 2002), with Camarasauromorpha and *Jobaria* Sereno Beck, Dutheil, Larsson, Lyon,

Moussa, Sadleir, Sidor, Varricchio, Wilson, and Wilson as successive outgroups (Appendices 1 and 2) (Camarasauromorpha has been scored using *Camarasaurus* Cope, *Brachiosaurus* Riggs, and Titanosauria). The program Nona (Goloboff, 1999) was used and one unique tree was obtained of L = 47; C_i= 0.78; R_i = 0.87. The strength of bootstrap and Bremer indices obtained (Figure 9) show that, excepting Diplodocoidea (bootstrap index = 85) and Diplodocinae (*Barosaurus* Marsh + *Diplodocus* Marsh) (80), the other groups are poorly supported.

According to this analysis, the Diplodocoidea include *Haplocanthosaurus*, although there exist serious doubts about the relationships of this genus (Upchurch et al., 2004). The analysis shows that *Zapalasaurus* is the sister group of the diplodocoids more derived than *Haplocanthosaurus* (Fig. 9). With these it shares the character of anterior caudal vertebrae with a well-developed dorsal component to the transverse process (character 26). The remaining diplodocoids, at the same time, share a character than is not found in *Zapalasaurus*: spinoprezygapophyseal laminae (sprl) in the anterior caudal vertebrae present and laterally extended (character 24). The Flagellicaudata (Harris and Dodson, 2004) are diagnosed by: bifid presacral neural spines (character 7), centropostzygapophyseal lamina (cpol) divided in the mid- and posterior dorsal vertebrae (character 14), anterior caudal vertebrae procoelous (character 21), hemal canal closed (character 30), pubis with prominent ambiens process (character 32), distal extreme articulation of both ischia forming an angle of 50 degrees (character 34), medial thickness of the distal extreme of the ischium greater than the lateral thickness (character 35), and posterior projection of metatarsal I present (character 36).

The analysis shows that *Suuwassea* Harris and Dodson (Harris and Dodson, 2004) is a dicraeosaurid (defining the Dicraeosauridae as diplodocoids more closely related to *Dicraeosaurus* Janensch than *Diplodocus*, Upchurch et al., 2004).

The Rebbachisauridae (including *Limaysaurus*, *Nigersaurus*, *Rebbachisaurus* Lavocat and *Amazonsaurus*) is diagnosed by: absence of complementary hyposphene-hypantrum articulations in the dorsal vertebrae (character 13), posterior dorsal neural spines four times longer than the vertebral centrum (character 16), neural spines of the posterior dorsal and anterior caudal vertebrae with a petal-like aspect (character 17), and extreme distal expansion of the scapula (character 31). *Amazonsaurus* is a rebbachisaurid (contra Salgado et al., 2004). *Rayososaurus* Bonaparte has not been included in the analysis, due to the fragmentary condition of the material, although the presence of a distally expanded scapula (Bonaparte 1996b; Salgado et al., 2004) permits its relationship with the Rebbachisauridae.

6. Conclusions

Until recently, the sauropod record in the upper part of the Lower Cretaceous (Aptian-Albian) of Patagonia consisted of one unique group of diplodocoids: the rebbachisaurids, represented by two distantly related genera: *Limaysaurus* and *Rayososaurus* (Leanza et al, 2004). The record of *Agustinia* (a possible diplodocoid) and *Zapalasaurus* has suggested that the diversity of basal diplodocoids in the upper part of the Lower Cretaceous of South America is greater than was thought. Of all forms, these three last genera are poorly known, in part due to fragmentary materials, and it is hoped that new explorations uncover more complete materials.

As it seems, in the Lower Cretaceous of South America diplodocoids were at least as abundant and diverse as titanosauriformes. This situation contrasts notably with that which is found in the Lower Cretaceous of North America, in which there is no record of sauropods pertaining principally to these groups (Tidwell et al., 2001; Salgado and Bonaparte, in prep.).

In the north of Patagonia, towards the end of the Cenomanian (at least until the age corresponding to the base of the Huincul Formation), the last diplodocoids of the Rebbachisauridae went extinct, giving a place for the radiation of the eutitanosaurs (Salgado and Coria, 2005; Salgado and Bonaparte, in prep.). This faunal replacement had been occurring all over the world, and involved various groups of dinosaurs (Coria and Salgado, 2005). At least in the north of Patagonia, a lineage of basal titanosaurs with mid- and posterior amphiplatyan caudals had remained at least until the Turonian (Salgado and Bonaparte, in prep.).