

Original article

Redescription of *Rayososaurus agrioensis* Bonaparte (Sauropoda, Diplodocoidea), a rebbachisaurid from the early Late Cretaceous of Neuquén[☆]

*Redescription de Rayososaurus agrioensis Bonaparte (Sauropoda, Diplodocoidea),
un rebbachisauridé de la base du Crétacé supérieur de Neuquén*

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Abstract

The material belonging to the holotype of *Rayososaurus agrioensis* Bonaparte is redescribed. The great development of the acromion process, directed in a markedly posterior direction, and the ventral margin of the scapula with a strong ventrodistal expansion, interpreted as autapomorphies of the taxon, justify the validity of the species. Although the material is rather fragmentary, the racquet-shaped scapula, the distal expansion positioned at the same height as the proximal expansion, and the well-developed acromion process allow the taxon to be included within Rebbachisauridae. At the same time, the angle of less than 90° between the coracoid articulation and the scapular blade, together with the great development of the acromion process of the scapula, justify its inclusion in a clade situated as a sister group of *Cathartesaura*. On the basis of the stratigraphic calibration of the phylogenetic analysis, an important diversification event of the rebbachisaurids is deduced during the Hauterivian-Barremian. In this context, the presence of two monophyletic groups, one of which comprises African-European taxa and the other South American taxa, would place the definitive separation of South America and Africa within this time interval.

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Keywords: *Rayososaurus*; Rebbachisauridae; Patagonia; Cenomanian; Palaeobiogeography

Résumé

Le matériel appartenant à l'holotype de *Rayososaurus agrioensis* Bonaparte fait l'objet d'une redescription. Le développement prononcé du processus acromial, fortement orienté dans le sens postérieur, et la marge ventrale de la scapula avec une forte expansion ventrodistale, interprétés comme autapomorphies de ce taxon, justifient la validité de cette espèce. Bien que le matériel soit plutôt fragmentaire, la scapula en forme de raquette, l'expansion distale positionnée à la même hauteur que l'expansion proximale et le processus acromial bien développé permettent d'attribuer ce taxon au groupe des Rebbachisauridae. L'angle inférieur à 90° entre l'articulation du coracoïde et la lame scapulaire, avec le développement élevé du processus acromial de la scapula, justifie quant à lui son inclusion dans un clade situé comme groupe frère de *Cathartesaura*. À partir du calibrage stratigraphique de l'analyse phylogénétique, un phénomène important de diversification des rebbachisauridés lors de l'Hauterivien-Barrémien est déduit. En ce sens, la présence de deux groupes monophylétiques qui incluent, d'une part les taxons africains-européens, d'autre part les taxons sud-américains, situerait la séparation définitive entre l'Amérique du Sud et l'Afrique dans cet intervalle de temps.

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Mots clés : *Rayososaurus* ; Rebbachisauridae ; Patagonie ; Cénomaniens ; Paléobiogéographie

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1. Introduction

The sauropods of the Early Cretaceous include Pangaeon lineages with a broad distribution (Wilson, 2002; Upchurch et al., 2004; Harris, 2006b), but towards the end of the Early Cretaceous an incipient provincialism can be observed, as a product of the fragmentation of Gondwana (Holtz et al., 2004). In the light of the most recent phylogenies (e.g., Wilson, 2002; Upchurch et al., 2004) and a comparison of them with the fossil record, it can be deduced that the two main lineages of Neosauropoda (Diplodocoidea and Macronaria) would have emerged in the course of the Middle Jurassic, although the origin of the clades within these lineages is somewhat more controversial. One of the groups of diplodocoids of probable Pangaeon origin and of great palaeobiogeographical interest is the rebbachisaurids (Harris, 2006b; Remes, 2006). This group of sauropods is well represented in sediments of the Lower Cretaceous and the lower part of the Upper Cretaceous of South America (Calvo and Salgado, 1995; Bonaparte, 1996a; Carvalho de Souza et al., 2003; Medeiros and Schultz, 2004; Salgado et al., 2004, 2006; Gallina and Apesteguía, 2005; Apesteguía, 2007), Africa (Lavocat, 1954; Sereno et al., 1999, 2007) and Europe (Dalla Vecchia, 1998; Pereda-Suberbiola et al., 2003; Mannion, 2009). This particular distribution has led to various hypotheses being proposed concerning the origin and dispersal of the group.

The rebbachisaurids are of special importance in the identification of events of vicariance and dispersal among the great continental masses during the Early Cretaceous. Indeed, their records may prove useful for ascertaining the moment of the definitive separation of Africa and South America and the process of vicariant evolution undergone by the lineages that remained on the two continents. The presence of rebbachisaurids in Africa and South America at the end of the Early Cretaceous has been interpreted as proof of the continued existence at this time of the connection between the two continents (Calvo and Salgado, 1995). Even though the rebbachisaurids could have a Pangaeon origin in the Middle Jurassic (Wilson, 2002; Upchurch et al., 2004; Harris, 2006b), their abundance in South America and Africa has led to them being regarded as Gondwanan sauropods. In recent years there have been discoveries of rebbachisaurids in the middle part of the Lower Cretaceous of Europe, this distribution being interpreted as a result of dispersal events from Gondwana to Laurasia by means of the Apulian Route (Pereda-Suberbiola et al., 2003; Dalla Vecchia, 2005; Gheerbrant and Rage, 2006; Canudo et al., 2009). In order to be able to provide a correct explanation of these palaeobiogeographical distributions, it is indispensable to have a precise phylogenetic framework that makes it possible to interpret the relationships between the rebbachisaurids of the different continents.

Preferably, the phylogenetic framework used should sample most, if not all of the known forms of rebbachisaurids. Sereno et al. (2007) carried out a phylogenetic analysis that took into consideration most of the rebbachisaurids and included some very fragmentary ones such as *Histriasaurus* (Dalla Vecchia, 1998). Nonetheless, this analysis does not include all the South

American forms, omitting taxa such as *Amazonsaurus maranhensis* (Carvalho, Avilla and Salgado, 2003) of the Early Cretaceous of Brazil, and *Rayososaurus agrioensis* Bonaparte, 1996 of the Early Cretaceous of Neuquén (Argentina). This latter rebbachisaurid is known by material that is fragmentary but sufficiently diagnostic to be included within this clade of sauropods.

In the original description of *Rayososaurus agrioensis*, Bonaparte (1996a) noted its similarity with the taxon from Morocco *Rebbachisaurus garasbae* Lavocat, 1954. Subsequently he pointed out that the two taxa could be grouped together to form a new clade of sauropods, which he called Rebbachisauridae (Bonaparte, 1997). The autapomorphies proposed for *Rayososaurus*, the presence of a prominent acromion process (more developed than in *Rebbachisaurus*) and the semicircular separation between this process and the dorsal edge of the scapular blade, are present in other rebbachisaurids (Salgado et al., 2004; Gallina and Apesteguía, 2005; Mannion, 2009).

On the other hand, Calvo and Salgado (1995) described a sauropod from the province of Neuquén, which they also considered to be closely linked to *Rebbachisaurus garasbae*. The great similarity between these two taxa led them to regard the new sauropod from Neuquén as part of the same genus, designating it “*Rebbachisaurus*” *tessonei* Calvo and Salgado, 1995. Subsequent discoveries showed that the “synapomorphic” characters proposed for the genus were in fact plesiomorphic characters within the more inclusive group of rebbachisaurids. In the light of these new discoveries and in the absence of a correct diagnosis of *Rayososaurus agrioensis*, Wilson and Sereno (1998) decided to synonymise these two South American taxa as *Rayososaurus tessonei*. However, these two taxa lack unique characters (Salgado et al., 2004; Upchurch et al., 2004), leading Salgado et al. (2004) to propose a new genus, *Limaysaurus*, referring the material of “*Rebbachisaurus*” *tessonei* to *Limaysaurus tessonei*. For Salgado et al. (2004), the main difference between these two taxa is the presence of an acromion process directed posteriorly in *Rayososaurus agrioensis*, which is absent in *Limaysaurus tessonei* and all other known sauropods. As such, there are different interpretations of what is represented by *Rayososaurus*, and the matter calls for clarification. Finally, the stratigraphic position of *Rayososaurus* has recently been called into question (Leanza, 2003).

The objective of this paper is to describe in detail the holotype of *Rayososaurus agrioensis*, to carry out a correct diagnosis of it, to specify its most probable stratigraphic position, and to discuss its phylogenetic relations with all other known rebbachisaurids and its palaeobiogeographical implications.

2. Geographical and geological situation

The remains corresponding to the holotype of *Rayososaurus agrioensis* were recovered in 1991 in a campaign directed by Dr José Bonaparte in the area around the locality of Agrio del Medio, in the central part of the province of Neuquén

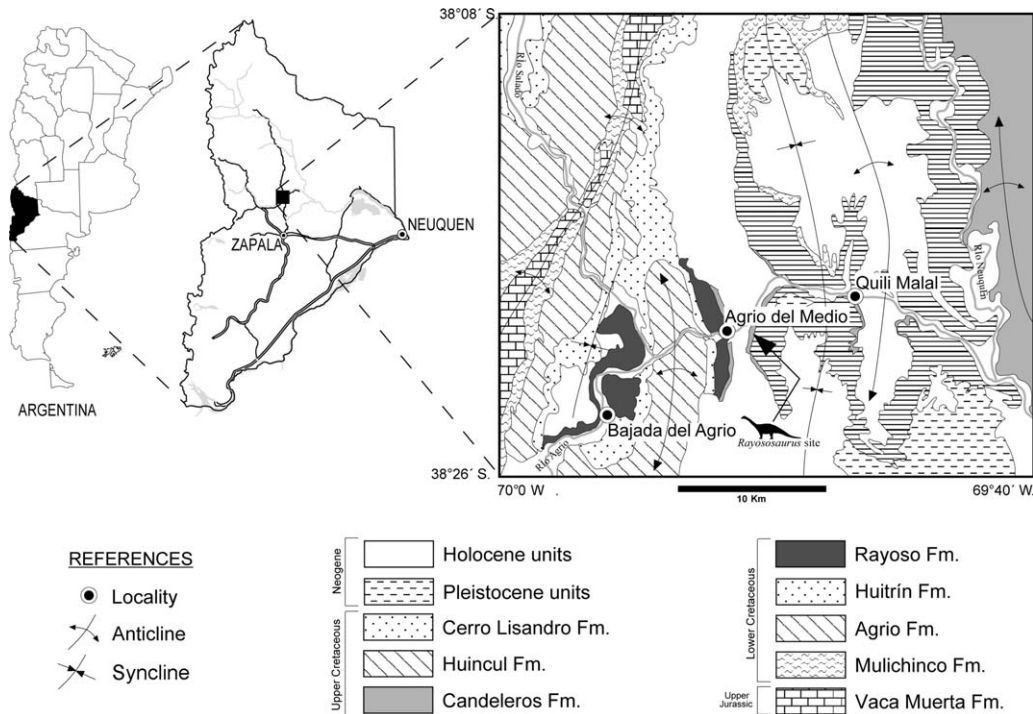


Fig. 1. Geological map of the region of Agrio del Medio, province of Neuquén, Argentine Republic.

(Patagonia, Argentina; Fig. 1). The available references regarding the location of the discovery site lack precise data with respect to the exact place where the excavation was made. According to the data provided by Bonaparte (1996a, 1996b), this was some 3 km to the south of the school in Agrio del Medio, in a level of reddish medium-grain sandstones belonging to the upper section of the Rayoso Formation.

In a stratigraphic study subsequently carried out in the region by Leanza (2003), it is suggested on the basis of the existing data that the unit of origin of *Rayosaurus* could be the Rincón Member of the Rayoso Formation (Fig. 2). However, this author also refers to the considerable margin of doubt in the matter, suggesting the possibility that the remains in question might have rolled down from higher levels. Nonetheless, given the characteristics and the state of preservation of the bones, it seems unlikely that these could have undergone any sort of dragging or retransportation at a stage after their fossilization.

Recent works of geological review carried out in 2008 and 2009 have made it possible to relocate geographically and stratigraphically the possible site where *Rayosaurus* was extracted. Detailed stratigraphic profiles have been constructed (scale 1:100), and samples taken from the outcropping units on the eastern flank of the Agrio Anticline, on the right bank of the homonymous river in the vicinity of the region of Agrio del Medio. The geological units exposed are Huitrín, Rayoso, Candeleros and Huincul Formations, distributed along a transect of approximately 3.5 km in length running from west to east (Figs. 1 and 2).

For the task of locating the excavation site, comparisons were drawn using remains of sediment removed from the femur and scapula of *Rayosaurus*, to which they were still attached.

The sediment in question is a coarse-grained to sabulitic, quartzolithic sandstone (grain size between 1.5 and 3.0 mm), poorly consolidated, with subangular to subrounded clasts, a low degree of sphericity, and moderate to poor sorting.

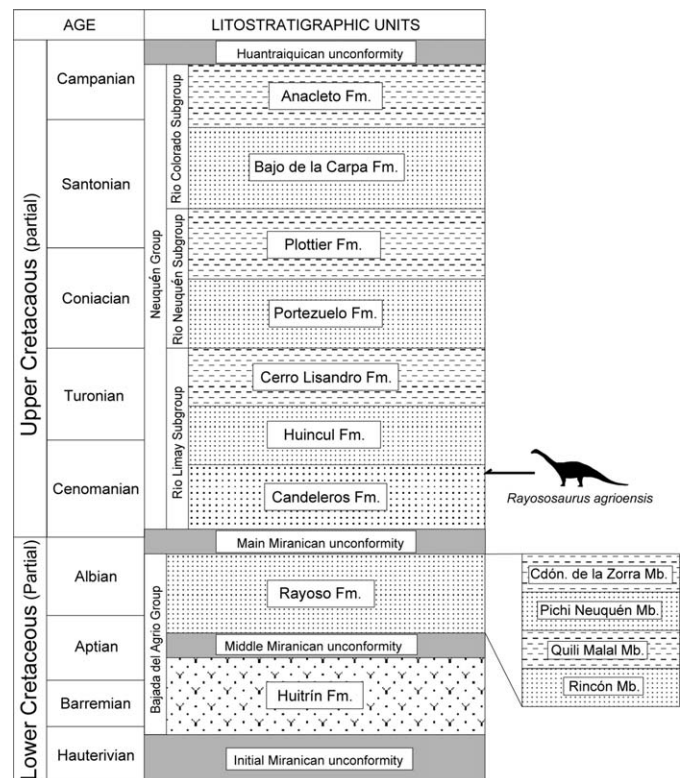


Fig. 2. Stratigraphic sketch of the “red-bed” units corresponding to the groups Bajada del Agrio and Neuquén, Cretaceous of the Neuquén Basin.

Exceptionally, lithic clasts can be observed of up to 6 mm in their main axis. The sediment displays open packing with a chaotic arrangement of its grains and a marked proportion of muddy matrix. It has a moderate reddish orange colour (10R 6/6; **Rock-Color Chart Committee, 1991**). It had not been possible to identify primary structures due possibly to the small size of the sample (less than fist-size). By means of prospection work and on the basis of the information gathered, it has been possible to locate the sector where the extraction work was carried out during the field campaign directed by Dr Bonaparte in 1991. This includes the outcroppings of the western face of the canyon situated 2.4 km east-southeast of Primary School No. 244 in Agrío del Medio (38° 21' 10" S – 69° 54' 57" W; Fig. 1).

In lithostratigraphic terms, deposits from the uppermost part of the Candeleros Formation and the base of the Huincul Formation outcrop in this sector (Río Limay Subgroup, Neuquén Group). This allows us to rule out for a start the Rayoso Formation as the possible unit of origin of the holotype of *Rayososaurus agrioensis*. Moreover, the characteristics of the clastic sediments of the Rayoso Formation differ in their compositional and textural attributes from the sample of sediment described above. The psamitic fraction that makes up the various members of this unit are composed of dominantly quartzitic sandstones that are fine to medium-grained, compact, well sorted, with grains subrounded to rounded and a high sphericity, which is evidence of good textural maturity.

In the case of the sandstones of the Huincul Formation, these differ from the sample of sediment that accompanied the *Rayososaurus* remains in two main respects: they display greater textural maturity, with a dominance of quartz grains and they lack in all cases the muddy matrix. This latter characteristic is a common attribute in the sandstones of the Candeleros Formation, endowing these deposits with their characteristic reddish colouring.

Indeed, the only deposits outcropping in the region that tally in large measure with the sediment from the original excavation site correspond to a group of levels of fluvial sandstones of the Candeleros Formation located between 10 and 15 m beneath the contact with the Huincul Formation and in the vicinity of the place where the remains were said to have come from. These levels belong to facies of coarse-grain to sabulitic sandstones, with crude stratification, arranged in thin lens-shaped bodies interpreted as deposits on the bottom of channels. On the basis of the evidence gathered, and in accordance with the timely conjecture formulated by **Leanza (2003)**, the Candeleros Formation can with a good measure of certainty be pinpointed as the unit of origin of *Rayososaurus agrioensis*, inferring for this an age within the early Cenomanian.

3. Systematic palaeontology

DINOSAURIA Owen, 1842
 SAURISCHIA Seeley, 1887
 SAUROPODOMORPHA von Huene, 1932
 SAUROPODA Marsh, 1878
 DIPLODOCOIDEA Marsh, 1884

REBBACHISAURIDAE Bonaparte, 1997

Rayososaurus Bonaparte, 1996

Rayososaurus agrioensis Bonaparte, 1996

Holotype: Museo Nacional de Ciencias Naturales “Bernardino Rivadavia” (MACN) MACN-N 41, composed of a left scapula without the distal end of the scapular blade, an almost complete right scapular blade, the distal three quarters of a left femur, and the proximal half of a left fibula. Bearing in mind that the remains come from the same site, that there is a right and a left scapula, and that the femur and the scapulae correspond to an animal of the same size, we consider that the material of the holotype of *Rayososaurus agrioensis* gathered by **Bonaparte (1996a)** belongs to a single individual.

Locality and Horizon: The remains of *Rayososaurus agrioensis* come from the locality of Agrío del Medio (38° 21' 10" S – 69° 54' 57" W), in the department of Picunches, province of Neuquén (Fig. 1). Stratigraphically, the bone-bearing level corresponds to the upper section of the Candeleros Formation (Neuquén Group, Río Limay Subgroup), with an age estimated at early Cenomanian (**Legarreta and Gulisano, 1989; Fig. 2**).

Modified Diagnosis: Sauropod characterized by the following autapomorphies: scapula which on its dorsal face presents a very well-developed acromion process directed in a markedly posterior direction; ventral margin of the scapula (evident in the right scapular blade) with a strong expansion directed ventrodorsally.

Description: Scapula (Fig. 3): In the original description of the material, **Bonaparte (1996a)** mentions the presence of a complete left scapula and the distal remains of a second, right scapula. Both materials have been located in the collections of the MACN, and, as shown by the moulds present on the right scapula, the two scapulae would have been found one on top of the other. Although the left scapula is the more complete of the two, its distal end is not preserved (Fig. 3(A)), and a plaster-cast reconstruction of it has been made. The remains of the right scapula correspond to its distal half, and almost all the scapular blade is preserved, from roughly the height where the acromion process would have been (Fig. 3(B)). Both incomplete scapulae were taken into consideration for the description of the material (Figs. 3(C–E)). Our reconstruction of the complete scapula does not differ significantly from that proposed by **Bonaparte (1996a, 1996b: fig. 31)**. For descriptive purposes, the scapula has been oriented with its longer margin in a horizontal direction, and as such its anterodorsal margin is referred to as the dorsal margin.

As noted by **Bonaparte (1996a, 1996b)**, the total length of the reconstructed scapula is calculated to be roughly 86 cm, similar in size to those of *Nigersaurus* and *Cathartesaura* (**Sereno et al., 1999; Gallina and Apesteguía, 2005**). Although the glenoid zone is poorly prepared, its articulation facet is not medially exposed as in titanosaurs (**Wilson, 2002**), but is anteroventrally exposed as commonly present out of this group. The scapula-coracoid articulation is forming an almost 35° angle with respect to the scapular blade longer margin (Figs. 3(C, D)). This angle is not as opened as in titanosaurs

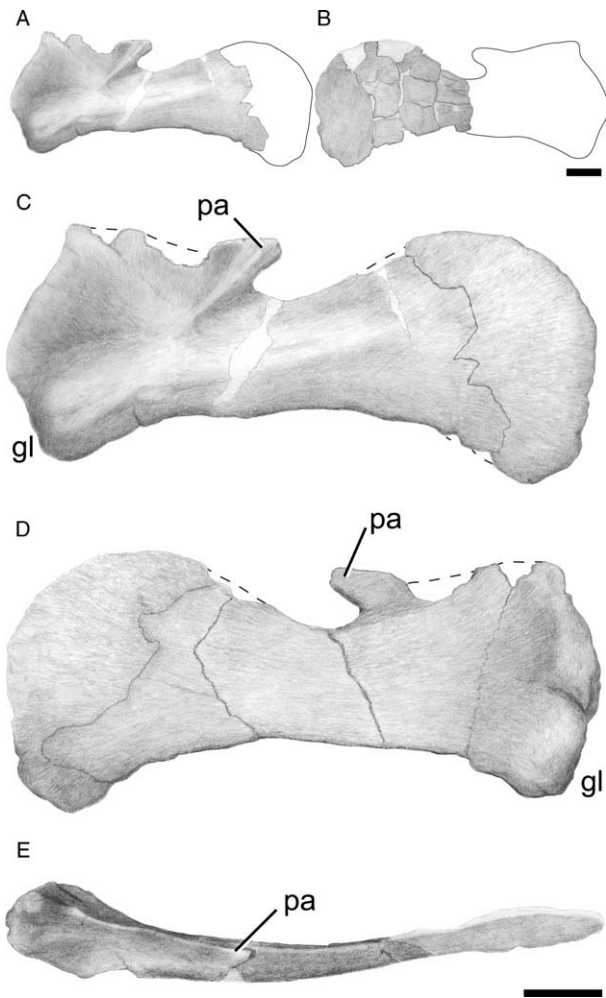


Fig. 3. Scapulae of *Rayososaurus agrioensis* as found preserved: left scapula (A) and right scapula (B), both in lateral view. Reconstruction made on the basis of the two elements in lateral view (C), medial view (D) and dorsal view (E). Scale = 10 cm. Abbreviations: pa, acromion process; gl, scapular glenoid.

(around 45°, Wilson, 2002) but is clearly higher than that of *Nigersaurus*. The most robust area of the scapula extends at an angle of approximately 20° from the scapular glenoid (where it shows its greatest thickness) to about halfway along the length of the scapula (Fig. 3(C)). About 20 cm from the glenoid, the scapula displays another widening that diverges from the aforementioned one and runs towards the posterior half of the acromion process, thus making the acromion process more robust ventrodistally (Fig. 3(C)). As a consequence of this widening, the scapula is medially flat in a dorsoventral direction and laterally convex in its proximal and middle part; it is rather flat at the distal end of the scapular blade. Thus, the scapular blade shows at its base the typical D-shape, as is observed in neosauropods (Wilson, 2002). In dorsal view (Fig. 3(E)) it is possible to make out the gentle and continuous concavity it displays in a proximodistal direction on the medial face. The distal end is dorsoventrally expanded, with a racquet-shaped scapular blade, a synapomorphy of Rebbachisauridae (Wilson, 2002; Salgado et al., 2004; Sereno et al., 2007). Contrary to what was observed by Bonaparte (1996a, 1996b), and as in *Nigersaurus*, the distal expansion is not equal to the proximal,

but is approximately 10% greater than it. The highest point of the dorsal margin of the scapular blade is at roughly the same height as the dorsal margin of the proximal end, being *Nigersaurus* the only rebbachisaurid with a distal expansion that goes beyond the height of the proximo-dorsal margin (Mannion, 2009).

The presence of a dorsal widening in the scapular blade, at the same height or somewhat higher than the dorsal margin of the proximal area, could be another synapomorphy of Rebbachisauridae (Mannion, 2009). This character is also present in *Haplocanthosaurus*, a taxon of uncertain position situated close to the base of Neosauropoda (Wilson, 2002; Upchurch et al., 2004), and in *Jobaria*, a sister group of Neosauropoda (Wilson, 2002; Sereno et al., 2007). The dorsal margin of the scapular blade runs in a roughly straight, continuous line (at an angle of about 20°) from the ventrodistal end towards the acromion process, thus forming a V-shaped angle between the acromion process and the scapular blade. *Rebbachisaurus* displays a similar angle (Lavocat, 1954: Lavocat, 1954: fig. 1), as does *Cathartesaura* (Gallina and Apesteguía, 2005: Gallina and Apesteguía, 2005: fig.4A). This angle differs from what is present in *Limaysaurus* (Calvo and

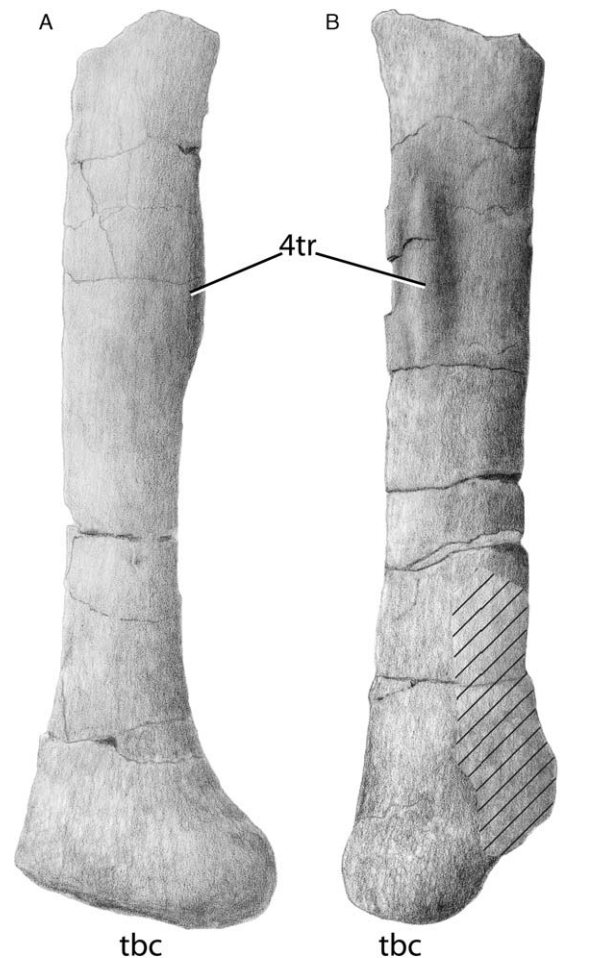


Fig. 4. Right femur of *Rayososaurus agrioensis* in posterior view (A) and in medial view (B). Scale = 10 cm. Abbreviations: 4tr, fourth trochanter, tbc, tibial condyle.

Salgado, 1995: fig. 12A) and in the rebbachisaurid of the Isle of Wight (Mannion, 2009: Fig. 2; Mannion, 2009: fig. 2). In these two taxa, the dorsal edge of the scapular blade is practically horizontal at its distal end, descending abruptly towards the acromion process and forming a U-shaped angle between this process and the scapular blade. The scapula of *Nigersaurus* (Serenó et al., 1999: Fig. 2E) seems to be in an intermediate position between these two angles. The posterior end of the acromion process has a position slightly anterior to half the total length of the scapula. The strange shape of this process in *Rayososaurus* (which is in a perfect state of preservation and shows no signs of deformation) distinguishes it from all other rebbachisaurids, and up to now is the only valid autapomorphy described for this taxon (Salgado et al., 2004). As noted previously (Bonaparte, 1996a; Salgado et al., 2004), this process is anteroposteriorly elongated and is directed posteriorly. A similar development can be observed in *Cathartesaura* (Gallina and Apesteguía, 2005: Gallina and Apesteguía, 2005: fig. 4A), although the acromion process of this taxon is directed dorsally and not posteriorly as in *Rayososaurus*. On its ventral edge the scapula of *Rayososaurus* presents a ventrally directed expansion in the shape of a point (Figs. 3(C, D)). This expansion is not present in any of the scapulae known, and as such it is considered an autapomorphic character of *Rayososaurus*.

The scapular glenoid is laterally oriented and, as in *Limaysaurus*, forms an angle of about 70° with the horizontal axis of the scapula. This condition differs from the right angle observed in *Nigersaurus*.

Femur (Fig. 4): Most of the right femur is preserved, and only the proximal end and the fibular condyle are missing (Fig. 4(A)). Proximally it presents the beginning of the expansion of the femoral head. The preserved part of the femur measures 99 cm in length, and a total length of some 125 cm has been calculated for it (Bonaparte, 1996a). As such, the femur is of a medium size, between those of smaller taxa such as Rebbachisauridae indet. of Spain (108 cm; Pereda-Suberbiola et al., 2003) and *Nigersaurus* (108 cm; Sereno et al., 1999) and longer ones such as *Cathartesaura* (141 cm; Gallina and Apesteguía, 2005) and *Limaysaurus tessonei* (138 cm; Calvo and Salgado, 1995). Even though the femur is not complete, it is evident that this element is significantly more slender than the femora of other rebbachisaurids (i.e., *Limaysaurus* sp., *L. tessonei*, *Nigersaurus*, *Cathartesaura*). The maximum total length of the femur of *Rayososaurus* would be approximately 8 times greater than the minimum lateromedial width of the diaphysis, so it would be a significantly more gracile femur than that of *Limaysaurus tessonei* or *Limaysaurus* sp. At the halfway point of the diaphysis, the lateromedial width is 150% greater than the anteroposterior width, thus showing a similar shape to that of other diplodocimorphs and differing from the titanosaurs to the extent that these possess a diaphysis that is markedly compressed anteroposteriorly (Wilson, 2002). Significantly, in *Rayososaurus* the fourth trochanter is hardly developed, as a gentle crest scarcely visible in medial view (Fig. 4(B)). The scarce development of the fourth trochanter is a character shared with other rebbachisaurids (Pereda-Suberbiola et al.,

2003; Salgado et al., 2004), differentiating them from more derived diplodocimorphs such as *Apatosaurus* or *Dicraeosaurus* (Marsh, 1877; Janensch, 1929) or from primitive macronarians such as *Camarasaurus* (Ostrom and McIntosh, 1966). As noted by Bonaparte (1996a), on the lateral margin of this trochanter a small proximo-distally expanded depression can be seen.

The tibial condyle cannot be completely described because it is not yet fully prepared. It can be seen to be well developed, both in an anteroposterior direction and lateromedially (Fig. 4).

Fibula: The fibula is in a fairly damaged condition and is rather fragmentary. The total preserved length of the left fibula is 51 cm, corresponding to two thirds of the proximal section. The maximum width of the proximal expansion measures 20 cm, and is thus double than the minimum width observed in the diaphysis (10 cm).

4. Phylogenetic analysis

Previous phylogenetic analyses that included three or more forms of rebbachisaurids failed to resolve the phylogenetic relations within this group (e.g., Wilson, 2002; Salgado et al., 2004). Recently, Sereno et al. (2007) have proposed a phylogenetic analysis in which the phylogenetic relations between most of the forms of rebbachisaurids are resolved. With a view to ascertaining the probable phylogenetic position of *Rayososaurus*, a phylogenetic analysis was carried out based on the matrix proposed by Sereno et al. (2007), with a few changes. Character 88 was modified; two characters were added; and the data from *Rayososaurus* (Bonaparte, 1996a) and *Amazonsaurus* (Carvalho de Souza et al., 2003) were incorporated (Appendix A). Despite not belonging to a formal taxon and being very fragmentary, the scapula from the Isle of Wight (Mannion, 2009) was also added to the analysis as a way to test its phylogenetic position.

The parsimony analysis was carried out using the software TNT v 1.1 (Goloboff et al., 2008a, 2008b). The search for the most parsimonious trees was performed by means of a heuristic search, starting from 1000 replications of Wagner Trees followed by TBR and saving 10 trees per replication. As a result, 20 most parsimonious trees of 155 steps were obtained, which were subject to a final round of TBR in which ten additional trees were found. The strict consensus of the results of the analysis showed an unresolved relationship in the clade formed by the South American forms and the Isle of Wight scapula. To ascertain whether this polytomy is due to a conflict of characters or is a product of different positions of some taxon, the “pruned trees” command of TNT was used. The results of this analysis revealed an uncertain position for *Amazonsaurus*, which can take a variety of positions within the clade formed by *Zapalasaurus* and more derived forms (Fig. 5). For this reason, and with a view to simplifying the discussion, this taxon has been eliminated from the analysis of all the most parsimonious trees obtained (Fig. 5). The obtained topology shows a weak support (Bremer = 1) for all the nodes except on dicraeosaurids (Bremer = 4) and *Brachytrachelopan* plus *Dicraeosaurus* (Bremer = 2).

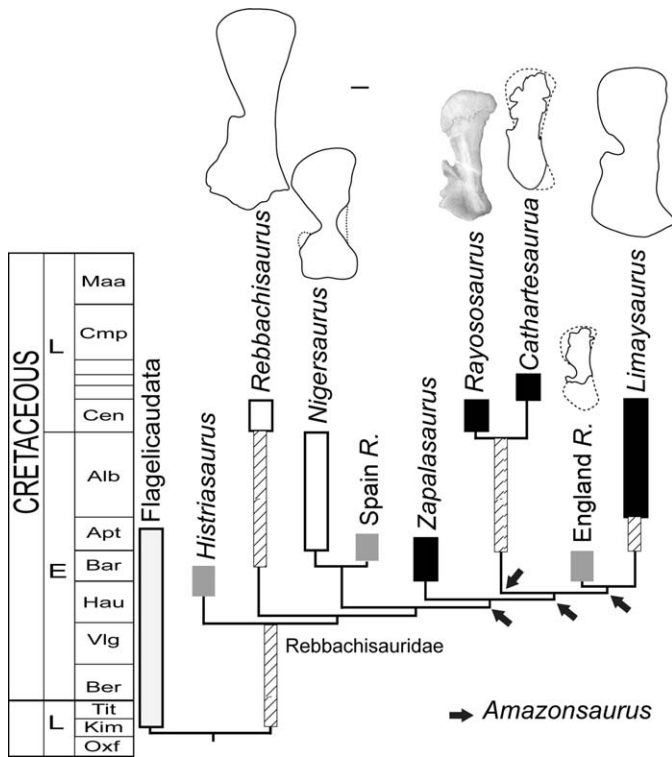


Fig. 5. Stratigraphically calibrated strict consensus of 30 MPTs (Length = 155, CI = 0.703, RI = 0.786), showing the position of *Rayososaurus* and the ghost lineages (in light grey). In white, taxa from Africa; in grey, from Europe; in black, from Patagonia. The black arrows indicate the possible positions of *Amazonsaurus*. Scale of the scapulae = 10 cm.

In general terms and once *Amazonsaurus* is excluded, the results of the analysis do not differ from those obtained by Sereno et al. (2007), where two clades are observed within Rebbachisauridae, one consisting of European-African taxa and the other consisting mostly of South American taxa (Fig. 5). *Rayososaurus* is grouped together with *Cathartesaura* because both taxa have a very well-developed acromion process (oriented dorsally in *Cathartesaura* and posteriorly in *Rayososaurus*). The scapula from the Isle of Wight was also obtained in this group, and although this element is very fragmentary some comments on its implication will be made in the next section.

5. Discussion

Despite the fragmentary state of the material, the complete redescription of *Rayososaurus agrioensis* revealed a series of unique characters that make it possible to affirm the validity of this taxon and incorporate it within one of the clades of rebbachisaurids, as a form close to *Cathartesaura*. The great development of the acromion process and its marked posterior orientation, in conjunction with the ventral expansion displayed on the ventral margin of the scapular blade, endow this scapula with a morphology that is unique among sauropods and sufficiently diagnostic to maintain the validity of the taxon. In addition to these autapomorphies, the V-shape in the dorso-

distal margin of the scapula and the gracile form of the femur make it possible to differentiate *Rayososaurus* from the holotype of *Limaysaurus tessonei*, collected in the same unit. *Nopcsaspondylus*, also from the Candeleros Formation, is only known on the basis of a neural arch and a vertebral centrum (Nopcsa, 1902; Apesteguía, 2007), making it impossible to compare with *Rayososaurus*, and only future discoveries of one or the other taxon will allow us to reaffirm the validity of these taxa.

5.1. Evolution of the scapula in Rebbachisauridae

On the basis of the results of the phylogenetic analysis (Fig. 5), a series of evolutionary observations can be made regarding the main transformations in the scapula of the rebbachisaurids. In comparison with other sauropods, the combination of the posterodorsally oriented acromion process and the expansion of the dorsal margin of the scapular blade in rebbachisaurids results in a much shorter distance between these two regions (Mannion, 2009). As a product of this shortening, two distinct morphologies can be observed within Rebbachisauridae, V-shaped and U-shaped. The V-shaped angle is recovered as an ambiguous synapomorphy of Rebbachisauridae, this being due to the absence of a scapula in *Histriasaurus* and not to a conflict of characters. This character is maintained in the more basal forms of rebbachisaurids (e.g., *Rebbachisaurus*, *Rayososaurus*, *Cathartesaura*), whereas in the more derived scapulae (those of *Limaysaurus tessonei* and from the Isle of Wight) the dorso-distal expansion extends anteriorly, resulting in the U-shape observed in these taxa. However, the position of the Isle of Wight scapula in this clade could be an artefact due to the fragmentary nature of the material rather than a genuine phylogenetic affinity with the group. In this context, the presence of an intermediate state of development between the U-shape and the V-shape in the scapula of *Nigersaurus* could indicate a certain similarity with the sauropod from the Isle of Wight, which would imply an evolutionary convergence in the acquisition of the U-shape. The presence of a posterodorsally directed acromion process together with a dorsal expansion of the scapular blade present in certain basal neosauropods (e.g., *Camarasaurus*, *Brachiosaurus*) would indicate an intermediate state between the V-shape observed in basal rebbachisaurids and the plesiomorphic state of Sauropoda where the scapular blade is practically straight or convex (Sereno et al., 2007).

The presence of a developed acromion process (C104:1) is recovered as an ambiguous synapomorphy (ambiguous due to the lack of information in *Histriasaurus*) of Rebbachisauridae, present in all the forms of this group. Over the evolutionary history of Rebbachisauridae this process comes to show increased development, being scarcely developed in *Rebbachisaurus*. The group of rebbachisaurids more derived than *Rebbachisaurus* shows an acromion process of medium development (C104:2), whereas in *Rayososaurus* and *Cathartesaura* this process is more developed than in other rebbachisaurids (C104:3).

5.2. Palaeobiogeographical implications

The greatest diversity of rebbachisaurids known worldwide comes from the Cretaceous sediments of Patagonia, specifically from various geological units of the Neuquén Basin (Salgado and Bonaparte, 2007). From this basin five taxa have been described (*Limaysaurus tessonei* [Calvo and Salgado, 1995]; *Rayososaurus agrioensis* [Bonaparte, 1996a]; *Zapalasaurus bonapartei* [Salgado et al., 2004]; *Cathartesaura anaerobica* [Gallina and Apesteguía, 2005]; *Nopcsaspondylus alarconensis* [Apesteguía, 2007]) in a time interval extending from the Hauterivian? to the Cenomanian. In addition to the diversity of Patagonia there are also remains from the northeast of Brazil, *Amazonsaurus maranhensis* (Carvalho de Souza et al., 2003) from the Itapecuru Formation (Aptian-Albian), and those of “*Rayososaurus*” sp. (Medeiros and Schultz, 2004) from the Alcântara Formation (Cenomanian; Castro et al., 2007). This latter has been classified as “*Rayososaurus*” sp. in the sense of Wilson and Sereno (1998), and as such it should be referred to *Limaysaurus* sp., although it could indeed be fragmentary remains of *Amazonsaurus*.

Apesteguía (2007) describes a neural arch and an isolated tooth from the Puesto Antigüal Member (Barremian) of the La Amarga Formation. This fragmentary material, assigned to Rebbachisauridae, represents the oldest citation of the group in South America. The remains from Puesto Antigüal are almost synchronous with those of *Histriasaurus* from the Hauterivian-Barremian of Croatia (Dalla Vecchia, 1998), which are the oldest attributed to Rebbachisauridae. The remains of *Zapalasaurus* also come from La Amarga Formation, though from more modern levels (Piedra Parada Member), dated as Barremian-Aptian (Salgado et al., 2004). Materials ascribed to *Limaysaurus* (*L. tessonei* and *L. sp.*) have been collected in slightly more modern levels: *Limaysaurus* sp. in the Lohan Cura Formation (Aptian-Albian) and *Limaysaurus tessonei* in the Candeleros Formation and the Huincul Formation (Cenomanian).

The new stratigraphic assignment of *Rayososaurus* to the base of the Candeleros Formation, together with the materials already described for this unit (Calvo and Salgado, 1995; Salgado et al., 2004; Apesteguía, 2007), testify to a significant and diverse fauna of rebbachisaurid sauropods during the Cenomanian of the Neuquén Basin, with three rebbachisaurid taxa described for the Candeleros Formation (*Rayososaurus*, *Limaysaurus* and *Nopcsaspondylus*).

The phylogenetic hypothesis proposed (Fig. 5) provides valuable information on the palaeobiogeography of the rebbachisaurids. When the phylogenetic results are compared with the fossil record, it is possible to make out an extensive ghost lineage that gives rise to the rebbachisaurids, as a result of which the origin of this lineage would need to be situated towards the end of the Late Jurassic. According to Harris (2006b), however, the origin of the three clades of Diplodocoidea is Pangaeian (Middle Jurassic), which would suggest an even greater ghost lineage. Even though, as shown in calibrated phylogenies (Wilson and Sereno, 1998; Sereno et al., 2007), the diplodocoids (defined as stem-based) might

have had their origin in the Middle Jurassic, this does not entail an equivalent age for the origin of the diplodocimorphs (defined as node-based). As such, the only two records of a diplodocoid in the Middle Jurassic (British Museum of Natural History [BMNH R.1967; Harris, 2006a, 2006b] and ‘*Cetiosaurus glymptonensis*’ [Upchurch and Martin, 2003]) could well be assigned to a non-diplodocimorph diplodocoid. Taking this latter point into account, one cannot rule out the possibility of an origin close to the Late Jurassic for the three main clades of Diplodocoidea, with the diplodocids being the only clade that would have reached North America by means of a southern continental connection (Remes, 2006). For the moment, it is not possible to ascertain a clear pattern in the origin of these three clades that might allow us to opt for one model or the other. Nonetheless, it is possible to appreciate a major diversification event in the rebbachisaurids towards the middle part of the Early Cretaceous (Hauterivian-Barremian; Fig. 5).

The initial hypothesis proposed on the basis of the presence of rebbachisaurids in South America and Africa suggested a connection between these two continents towards the end of the Cenomanian. However, leaving out of account the Isle of Wight scapula, the panorama that emerges from the new data seems to indicate that the South American rebbachisaurids show vicariant evolution with respect to the Afro-European forms. Calibrating the phylogeny obtained, it can be seen that the separation between these two groups must have taken place during the Hauterivian and Barremian, but probably not after (Fig. 5)-Thus, being this the point in time at which one would have to posit the separation of faunas between the continents of South America and Africa-Europe (connected during the Barremian-Aptian by the Apulian Route; Canudo et al., 2009). This age fits in the “Samafrica” and “Africa first” models in which Africa and South America became separated by the South Atlantic during the Early Cretaceous (140–120 Mya; Upchurch, 2008), but with the present rebbachisaurid knowledge it is impossible to take decision in any of those models (see Upchurch, 2008 for a summary of Gondwana break-up).

The presence of the England scapula (Barremian in age) in the “South America” clade could be due to three main different reasons:

- product of the fragmentary material and the little information available for this element (as was noted above);
- a range expansion event during the Barremian as product of a non-complete separation among major landmasses;
- an evidence of a non-vicariant model.

Although we incline towards the first explanation, new findings may rule out or test the model proposed above. Although the model previously discussed appears to be the best fit to the results, the lack of support at the rebbachisaurid nodes makes it difficult to make solid conclusions. Only with future discoveries enabling better understanding of the anatomy of this group and a thorough sampling of characters may provide stronger conclusions.

6. Conclusions

The redescription of the holotype of *Rayososaurus agrioensis* has made it possible to recognize two autapomorphies in its scapula, reaffirming the validity of this taxon. Initially, the type material had been ascribed to the upper levels of the Rayoso Formation (Albian; Bonaparte, 1996a) or to lower levels within the same formation, within the Rincón Member (Aptian; Leanza, 2003). However, the holotype probably comes from more recent levels belonging to the upper part of the Candeleros Formation (Cenomanian). The phylogenetic study carried out makes it possible to situate *Rayososaurus* as a rebbachisaurid related to other South American forms, above all *Cathartesaura*, also from the Cenomanian of Patagonia. The calibration of the cladogram indicates a vicariant separation between the South American and the Afro-European forms during the Hauterivian-Barremian. As such, the presence of Cenomanian rebbachisaurids in South America and Africa does not necessarily imply that there was a land connection between these two parts of Gondwana at the beginning of the Late Cretaceous.

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Appendix A

1. List of characters added and modified to the data matrix of Sereno et al. (2007)

Ch 88. Scapula, acromion process dorsal margin: convex or straight (0); with V-shaped concavity (1); with U-shaped concavity (2). Modified from Sereno et al. (2007). Ordered character.

Ch 103. The highest point of the dorsal margin of the scapular blade is: lower (0); at the same height (1); higher (2) than the dorsal margin of the proximal end. Modified from Mannion (2009). Ordered character.

Ch 104. Development of the acromion process: undeveloped (0); scarcely developed (1); very developed (2). Ordered character.

2. Codification of the taxa added

Rayososaurus: 88 (1); 89 (1); 90 (2); 91 (0); 103 (1); 104 (2)
 English Rebbachisauridae: 88 (2); 90 (2); 103 (?); 104 (1/2)
Amazonsaurus: 41 (1); 64 (1); 76 (0); 77 (0); 78 (1); 79 (1); 87 (1)

3. Codification of new and modified characters

	88	103	104
<i>Omeisaurus</i>	0	0	0
<i>Jobaria</i>	0	1	0
MACRONARIA	0	0	0
<i>Apatosaurus</i>	0	0	0
<i>Suuwassea</i>	0	0	0
<i>Diplodocus</i>	0	0	0
<i>Brachytrachelopan</i>	?	?	?
<i>Dicraeosaurus</i>	0	0	0
<i>Amargasaurus</i>	?	?	?
<i>Limaysaurus</i>	2	1	1
<i>Nigersaurus</i>	1/2	2	1
<i>Rebbachisaurus</i>	1	?	1
<i>Cathartesaura</i>	1	1	2
<i>Zapalalsaurus</i>	?	?	?
<i>Histriasaurus</i>	?	?	?
Spanish Rebbachisauridae	?	?	?

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