Not just a pretty face: anatomical peculiarities in the postcranium of Rebbachisaurids (Sauropoda: Diplodocoidea)

Sebastián Apesteguía*a,b*, Pablo Ariel Gallinaa,b and Alejandro Haluza c

Area de Paleontología, Fundación de Historia Natural Félix de Azara, CEBBAD, Universidad Maimónides, Valentín Virasoro 732, 1405 Ciudad Autónoma de Buenos Aires, Argentina; bCONICET, de Buenos Aires, Argentina; cÁrea Laboratorio e Investigación, Museo Municipal Ernesto Bachmann, Villa El Chocón, Neuquén, Argentina

Rebbachisauridae are poorly known ‘bizarre’ sauropods with two nearly complete skeletons collected: Limaysaurus tessonei and Nigerosaurus taqueti. Whereas the latter taxon allowed the understanding of their cranial novelties, other species show some peculiarities in the postcranium. L. tessonei, Rebbachisaurus garasbae and a new form (MMCH-Pv-49) from Villa El Chocón, Patagonia, exhibit peculiar pectoral girdles and the loss of the hyposphene–hypantrum accessory articulations in their amphiplathian dorsal vertebrae. Actually, the postzygapophyses are not only devoid of hyposphenal locks but also additionally show a curved postzygapophyseal eave that allows a sliding over the corresponding structure of the anterior side of the neural arch, a curved concave and elongated platform continuous along both prezygapophyses: the prezygapophyseal shelf. As the ‘ball and socket’ opisthocoelous centra in macronarians optimised mobility, the ‘U-eaves and shelf complex’ of rebbachisaurids permitted wider movements between successive vertebrae. While in titanosaurs the increased mobility occurred related to the centrum shape, in rebbachisaurids it is related to a complex system in the neural arch. Furthermore, whereas macronarians show large centra, rebbachisaurids underwent a minimisation of the centrum. These changes in both sauropod lineages probably had an outstanding relevance in the diversity and ecological roles that sauropods experienced in Cretaceous terrestrial ecosystems.

Keywords: Rebbachisauridae; vertebral articulation; torsion movements

Introduction

The Rebbachisauridae are a monophyletic group of poorly known and quite ‘bizarre’ basal diplodocoid sauropods (Calvo and Salgado 1995; Wilson and Sereno 1998; Wilson 2002; Upchurch et al. 2004; Gallina and Apesteguía 2005; Sereno et al. 2007). They range in an intermediate size between the large diplodocoids, such as Diplodocus and Apatosaurus, and smaller forms such as dicraeosaurids.

They were first described by Nopcsa (1902) after the finding of a single dorsal vertebra recovered by the military in Neuquén Province, Argentina, during or few years after the genocide committed by the association of Chilean and Argentinian governments against the original communities of Patagonia.

Despite its good preservation quality, this material remained as Sauropoda incertae sedis until its correct assignation, with rebbachisaurid affinities, by McIntosh (1990) and Calvo and Salgado (1995). Later, some of its peculiarities prompted its taxonomic validation as the Nopcsaspondylus alarconensis species (Apesteguía 2007).

As the Nopcsa’s material was not originally named, the first member of the clade in receiving a formal name was found in rocks of the Gara Sba quarry, southwest from Kem Kem, in the territory of Ait Rebbach, Morocco, half a century later and briefly described by Lavocat (1954) as Rebbachisaurus garasbae. Although originally considered as Early Cretaceous, the finding of elasmobranchs in the Mawsonia-bearing part of the sequence permitted an assignation of the Kem Kem beds to the Cenomanian (Sereno et al. 1996; Cavin et al. 2001).

The material type was composed of several bones of the same specimen including several ribs, the right scapula, eleven fragmentary vertebrae, part of the sacrum, a humerus and part of the pelvic girdle, but because of its fragile condition it was left mostly unprepared. Due to their fragility, additional specimens were also difficult to collect and a proposed second species of Rebbachisaurus was considered as doubtful and possibly is not even a diplodocoid (R. Allain, personal communication 2009).

Again, the material housed in the Muséum National d’Histoire Naturelle de Paris did not receive extensive consideration by palaeontologists until the discovery in 1988 by José Bonaparte of an additional member of this group. The finding and description of the almost complete skeleton of the rebbachisaurid Limaysaurus tessonei (Calvo and Salgado 1995) in Cenomanian–Turonian rocks of the same region permitted the first study of a good rebbachisaurid skeleton. However, the poor preservation quality of bone surfaces in the specimen precludes any detailed study.
Additional specimens described by Salgado et al. (2004) permitted to better define the two genera and to discuss their anatomical details. New undescribed materials from Cenomanian–Coniacian beds of Chubut Province, Central Patagonia (Lamanna et al. 2001), permitted to support a more extended and homogeneous distribution of the clade in South America.

A new finding in 1991 by José Bonaparte in Aptian rocks of Neuquén, Argentina, permitted the study of *Rayososaurus agrioensis* (Bonaparte 1996), composed of a single specimen that preserved two partial femora and an incomplete, but diagnostic scapula with the peculiar hook-shaped acromial process (Gallina and Apesteguía 2005).

Despite the morphological differences and the chronological distance of around 20 million years, some authors preferred to combine the rather incomplete *Rayososaurus* with the species of *L. tessonei* in phylogenetic analyses.

The recognition of the recurrence of these forms and the importance of a clade with a southern signature led Bonaparte (1997) to coin Rebbachisauridae for a family that he already recognised as different from the remaining diplodocoids (Bonaparte 1996). This name was later used by Sereno et al. (1999), Wilson (1999), Pereda Suberbiola et al. (2001, 2003), Carvalho et al. (2003) and Harris and Dodson (2004). The formal definition was later given by Upchurch et al. (2004) and subsequently used by Salgado et al. (2004), Gallina and Apesteguía (2005), Wilson (2005) and Apesteguía (2007). This stem-based definition considers the Rebbachisauridae as the diplodocoids more closely related to *Rebbachisaurus* than to Diplodocus.

The discovery of a superbly preserved new African rebbachisaurid in the Aptian–Albian sediments of Niger by the Sereno’s team increased the importance of the clade (Sereno et al. 1999, 2007; Sereno and Wilson 2005). The material, despite still awaiting a detailed postcranial description, permitted an evaluation of the quite peculiar rebbachisaurid skull and lower jaws, demonstrating to be highly distinctive from those of any other clade, especially titanosaurs.

These, especially with the squared jaws of *Antarc-
tosaurus wichmannianus* (Huene 1929), were misunder-
stood by several authors as belonging to diplodocoids (Jacobs et al. 1993; Upchurch 1998; Wilson and Sereno 1998). The finding of new and well-preserved lower jaws of both rebbachisaurid (Sereno et al. 1999; Sereno and Wilson 2005; Sereno et al. 2007) and titanosaur (Apesteguía 2004) permitted a clear differentiation and the definitive status of titanosaurs for squared-jawed forms such as *Antarc-
tosaurus* (Huene 1929), *Bonitasaura* (Apesteguía 2004) and materials from Brazil (MPM125R), as already stated by Huene (1929), Powell (2003, written in 1986) and Salgado (2000). Furthermore, although both clades share slender crowned teeth, the detailed descriptions allowed the recognition of much more slender and partially striated crowns in rebbachisaurids (Sereno et al. 1999; Sereno and Wilson 2005; Apesteguía 2007) than in derived titanosaurs.

In the postcranium, both clades are easier to differentiate, as rebbachisaurids bear diagnostic dorsal neural arch features, such as posterior dorsal neural spine reaching four times the length of the centrum, petal-shaped posterior dorsal and anterior caudal neural spines and the absence of a hyposphene–hypantrum articular complex (shared with derived titanosaurs). Basal rebbachisaurids, such as *Histriasaurus*, lack some of these features (Apesteguía 2007; Sereno et al. 2007).

Although first considered as a southern lineage, recent findings extended the record of rebbachisaurids to the northern hemisphere. New discoveries include Lower Cretaceous materials from the Barremian of Spain (Rebbachisauridae indet. MPS-RV II; Pereda Suberbiola et al. 2003) and England (Mannion 2009). It is quite evident that although originated as a neopangean lineage, rebbachisaurids experienced a wide radiation between the Late Jurassic and Early Cretaceous. As far as the fossil record indicates, the group became restricted to southern continents towards the beginning of the Late Cretaceous, where they survived until Turonian to Coniacian times. The extinction of rebbachisaurids in South America was recognised by Salgado (2000) and later by Apesteguía (2002) and Leanza et al. (2004), which joined this event of a major extinction of carcharodontosaurid theropods.

The most important rebbachisaurid specimens lack extended descriptions of the postcranial skeletons (e.g. *Nigersaurus taqueti* and *L. tessonei*), and the remaining species are very incomplete.

Further, the poor knowledge on the basal forms of the clade, those rebbachisaurids provided with hyposphene–hypantrum complex, as *Histriasaurus boscariolli* (Dalla Vecchia 1998), and the isolated neural arch MACN PV N35 (Apesteguía 2007) as well as others that lack dorsal vertebrae, such as *Zapalasaurus* (Salgado et al. 2006), makes understanding the in-group relationships difficult. However, a recent analysis by Sereno et al. (2007) shows a quite resolved tree of the group, which includes *Histriasaurus* and *Zapalasaurus* as part of the Rebbachisauridae.

**Institutional abbreviations**

Anatomical abbreviations

cpol, centropostzygapophyal lamina; med.cpol, medial centropostzygapophysyal lamina; med.spol, medial spinopostzygapophysyal laminae; lat.cpol, lateral centropostzygapophysyal lamina; lat.spol, lateral spinopost-zygapophyal laminae; tpol, intrapostzygapophysyal lamina

Description

The most remarkable features in the postcranium of rebbachisaurids are focused in the pectoral girdle and in the dorsal and caudal vertebrae. The scapula was preserved in several species of rebbachisaurids and its traits are thus considered as diagnostic. Although the basic shape is not very different from other diplodocoids, the rebbachisaurid scapula is strongly expanded both in the proximal and distal ends. The proximal expansion or acromium forms posterodorsally a horn that was termed 'acromial hook' by Gallina and Apesteguía (2005). The distal expansion is characteristically developed in both sides in a racket-shaped semicircle (Lavocat 1954). A strong ridge runs from the glenoid to the end of the hook only in Rebbachisaurus, Limaysaurus and Rayososaurus.

Dorsal vertebrae are also characteristic in rebbachisaurids. Although the variation among the series is still waiting for a detailed description of the most complete specimens, the more characteristic features are the small centrum height with respect to the neural arch (Lavocat 1954), a neural spine reaching four times the length of the centrum in posterior dorsals and petal-shaped neural spines in posterior dorsals and anterior caudals that can end in a semicircular or a truncated straight border. Additionally, they bear large flat spaces between the prespinal lamina and the diapophysis, and the characteristic absence of a hyposphene–hypantrum articular complex, a structure present in Dicraeosauridae (Janensch 1950), Brachiosaurus altithorax (Riggs 1903) and Phuwiangosaurus sirindhornae (Martin et al. 1994). Although titanosaurans also show an important development of the med.cpol (Apesteguía 2005), laterally, the lateral centropostzygapophysyal lamina (lat.cpol) is also present.

In the crown Rebbachisauridae, such as Limaysaurus, devoid of hyposphene–hypantrum, med.cpol arise from a meeting point between the postzygapophyses and form a tall 'gothic' window that frames the neural canal. This is particularly evident in L. tessonei and also in the new specimen from El Chocón (MMCH-Pv-49). Additionally, diapophyses are highly inclined and long.

In Haplocanthosaurus, Dicraeosauridae and Histriasaurus, well-developed lateral spinopostzygapophysyal laminae (lat.spol) laterally frame the spine, reaching the lateral end of each postzygapophysis. Conversely, in MACN PV N35, Limaysaurus, Nopcsaspondylus and MMCH-Pv-49, postzygapophyses are only dorsally reached by the medial spinopostzygapophysyal laminae (med.spol), which are fused on their dorsal development to the postspinal lamina, as occurring in Apatosaurus louisae (see Gilmore 1936; Wilson 1999). However, this condition is variable along the series as seen in detail (Figure 2(D)) made on a dorsal vertebra more posterior in the sequence.

Although they are very well preserved in additional material of R. garasbæ (unpublished) and N. alarconensis (lost), the good preservation in the figured dorsal vertebra of L. tessonei (Calvo and Salgado 1995) prompts to consider it as the lamellotype (Apesteguía 2005). In the case of R. garasbæ, N. alarconensis and MMCH-Pv-49, the situation is even more complex, as an additional lamina
runs dorsally connecting the postspinal lamina with the medial end of the postzygapophyses facets. It is interesting to note that this different postspinal lamina, running only in the middle of the small triangle formed by the converging med.spol, evidences the existence of a previous postspinal lamina running under the extant. As evident in N. alarconensis and MMCH-Pv-49, where it is slightly fused and in R. garasbae, where it is completely separated and parallel, this lamina has a different origin.

In the case of Haplocanthosaurus (Hatcher 1903), a taxon very close to both the base of Diplodocoidea (Wilson 2002) and Macronaria, long med.cpol reach a very reduced rhomboidal and basally wide hyposphene that hangs from the contact of the subhorizontal postzygapophyses, as seen in Camarasaurus and Diplodocus.

In most cases, when devoid of accessory articular structures, zygapophyses develop peculiar shapes. In the case of titanosaurs, anterior caudal postzygapophyses are concave and ear-like instead of flat, with elevated borders that provide a sliding structure but also limit the movement. This kind of postzygapophyses partially resembles the cup-like postzygapophyses of some dorsal vertebrae of Brachiosaurus.

As seen in MMCH-Pv-49 from El Chocón, Nopcsasponylus and also in R. garasbae, the postzygapophyses are not interrupted by the hyposphene or any breakage in the continuity of the articular surface (Figure 2) as they are connected by the respective intraprezygapophyseal lamina and tpol, giving the curved morphology described above (Figures 2–4).

This way, they show a curved postzygapophyseal eave (Figure 3(B)) that allows a sliding over the corresponding structure in the prezygapophysis, a curved concave and elongated platform continuous along both prezygapo-
physes: the prezygapophyseal shelf (Figure 3(A)). Postzygapophyses are attached to the base of the neural spine by means of the med.spol that form a supporting triangle of laminae. The articular surface of the postzygapophyses is physically continued along well-developed postzygodiapophyseal laminae. However, the articular facets are lateromedially extended but have anteroposteriorly short surfaces. They are dorsomedially oriented in the prezygapophyses and ventrolaterally in the postzygapophyses. In the case of MMCH-Pv-49 and *R. garasbae*, the articular surfaces are extensive, where they are shorter in *Nopcsaspondylus, Limaysaurus* and the remaining outer forms.

**Discussion**

The relationship among individual elements of the axial skeleton involves the association of both osseous and soft tissues. This way, the centrum articular surfaces and the development of zygapophyses on the neural arch have a significant protagonism in the construction of the main structural constituents of the vertebrate body: the vertebral column. Moreover, the relative degree of development of the concavity and convexity of the centrum facets as well as the orientation and areal expansion of zygapophyses allow different possible movements.

Several Late Cretaceous sauropod lineages have independently lost restrictions in their dorsal vertebrae (e.g. rebbachisaurids in Diplodocoidea and derived titanosaurids in Macronaria) to which the loss of the accessory articulations, such as the hyposphene–hypaptrum complex is directly linked.

Since their first representatives, most dinosaurs show an increased control of the vertebral mobility both in the way of extra articulations and locks (Saurischia) as well as in ossified tendons over dorsal and caudal vertebrae.
(Ornithischia). In Saurischia, there are few ways of control, some of them based on the centrum articulation and others on the neural arch.

Within Neosauropoda, the centrum articulation in presacral vertebrae can be opisthocoelous (e.g. macronarians) or amphiplathyan (e.g. diplodocoids). The former model allows a highly mobile ball and socket contact between successive vertebrae, whereas the latter involves a less complex relation. Actually, the development of a ball and socket system of vertebral articulation in the dorsal vertebrae of the Macronaria shows a decisive step that contributed to the acquisition of vertebral mobility in the lineage. This is represented by the opisthocoelous dorsal of all macronarians and the addition of the procoelous caudal vertebrae of titanosaurs (with a consequent biconvex sacrum).

In the neural arch, zygapophyses link all vertebrae permitting a controlled degree of mobility related to the size and orientation of the facets. Furthermore, the movement control was improved in some groups after the acquisition of accessory articulation elements (i.e. hypospene–hypantrum complex; Apesteguía 2005). Additionally, whereas basal macronarians (i.e. Camarasaurus) bear wide postzygapophyses and large hypsophenes and basal titanosauriforms (i.e. Brachiosaurus) bear reduced and centred zygapophyses that prevent lateral movements, basal titanosaur show both plesiomorphic and rhomboidal hypsophenes (e.g. Andesaurus) or only a system of strengthened med.cpol that partially replaces the hypsophenes (Bonaparte and Coria 1993; Apesteguía 2005). In titanosaurs, the loss of the hypospene–hypantrum complex occurred in derived Upper Cretaceous forms, providing them a higher vertebral mobility. New evidence shows that forms with such characteristics were already present since at least in Barremian times (Apesteguía 2007). As titanosaurs show quite separated postzygapophyses, the main movement and pivot centre is located around the large opisthocoelous centrum.

Concerning the mobile capabilities of the centrum itself, the ball and socket system of articulation acquired by macronarians allows a great mobility of vertebrae around the longitudinal centrum axis, whose articulation line follows the original location of the notochorda. However, although highly permissive, this system is limited to a wide movement within the centrum articular sphere. On the other hand, amphiplathyan centrum articulation is less specific. Although it does not provide a sliding concave–convex articular surface, it does not restrict mobility to the specific area of centrum overlap, and additional excursions of the vertebral centra are thus permitted. However, this is restricted by structures in the neural arch.

In basal macronarians, both the opisthocoelous centra and wide or bifid hypsophenes controlled the movements of the column.

Figure 3. MMCH-Pv-49, scheme of the dorsal vertebra in (A) anterior and (B) posterior views, showing a schematic representation of the articular surfaces of the neural arch.

Figure 4. Schematic representation of the rebbachisaurid vertebral series showing the system in which successive vertebrae fit.
In rebbachisaurids, the wide but permissive amphiplathyrian system plus the ‘U-eave and shelf complex’ permitted an increased flexibility between successive vertebrae along the axial skeleton (Figure 4).

Hence in this sketch, vertebral morphology in rebbachisaurid sauropods shows novelties in both structural and biomechanical aspects.

The particular construction of zygapophyseal articulation allowed these dinosaurs to develop torsion movements instead of flexion ones. This situation is in agreement with the amphiplathyrian condition of the centrum that allows wide possible movements over the articular plane as well as the absence of accessory articulation elements as the hyposphene-hypantrum complex.

Considering that rebbachisaurids underwent a substantial minimisation of the vertebral centrum, the main pivot and articular structure of the vertebra has moved from ventral to dorsal in the vertebra. Examining the maximum possible torsion movements (Figure 5), the vertebral centrum moves substantially, but much less than the neural spines do, as the pivot point is only a few centimetres over the neural canal. Minor torsion movements along successive vertebrae will permit the flexible neural cord to be out of alignment, avoiding cord strangling.

An amphiplathyian contact between vertebrae allows a widely distributed capability of torsion in the vertebral column, permitting a wide variety of postures in both resting and movement situations.

Under the model of articulation presented here for rebbachisaurids, the pivot point is located higher than in their relatives. This way, the vertebral column is capable of tolerating the small torsion mobility along the column without major structural stress. In mammals, a system with amphiplathyian vertebrae that allows vertebral torsion explains how horses lie down laterally over the ground to rest, with the scapular and pelvic girdles in straight angle with respect to the neck and head and rise up rapidly. It probably allowed rebbachisaurids similar capabilities.

A movement of torsion also has an important influence in locomotion, particularly in vertebrates that do not run regularly, whereas the flexion is the main attribute of the vertebral column in runners. Accordingly, living ungulates such as giraffes and camels present an amble walk that comprises the use of both legs on one side alternately with both on the other (Janis et al. 2002). This gait mode needs mobility of vertebral segment between both girdles, in particular those including torsion efforts. Although based on the trackways, there is no evidence of amble walk in sauropods; this condition would have been physically possible in rebbachisaurids taking into account its peculiar vertebral anatomy. As additional data, the referred mammals are basically homopodous, as are derived titanosaurians, shown by the Latest Cretaceous tracks from Bolivia (Apesteguía et al. 2007) in contrast to basal titanosauriforms and all diplodocoid sauropods, which were clearly heteropodous. In this context, highly heteropodous tracks discovered in the early Late Cretaceous rocks from northern Patagonia that also provided the remains of Limaysaurus and Cathartesaura are tentatively referred to rebbachisaurids (Figure 6).

**Convergent but different**

The recent research on titanosaurians and diplodocoids demonstrated several convergent issues (Salgado and Calvo 1997; Wilson 2002), although some are plesiomorphic for the clade. In the skull, some of them have elongated ‘horse-like’ skulls; curved occipital plane and condyle; squared symphysis (especially in rebbachisaurids); narrow-crowned, cylindrical teeth restricted to the anterior part of the snout; comb-like dentition (Coria and Chiappe 2001) and nostrils retracted to the top of the head. The postcranial also shows vertebrae with single neural spines, complex vacuities and the already described loss of the hyposphene-hypantrum complex and perhaps a long whip-tail. This set of convergences is quite remarkable in two non-closely related sauropod lineages that only share their existence during the Cretaceous.

This way, both Late Cretaceous titanosaurians and rebbachisaurids acquired a reduction in restrictions in the dorsal vertebrae allowing greater flexibility or movement of the column (Wilson and Carrano 1999; Gallina and Apesteguía 2005). In the case of saltasaurines, the sum of

Figure 5. MMCH-Pv-49, line drawing of the dorsal vertebra in posterior views showing the maximum movement possibilities based on the ‘U-eave and shelf’ articulation.
the opisthocoelian articulation mobility to the already present light camellate bony structure, loss of accessory articulations, a skeleton with articulations vastly replaced by cartilage and other calcified tissues, and wide and flared anterior blades of the ilium that allowed muscular insertions and viscerae sustainment allowed the group to enjoy a higher mobility and a greater column flexibility (Wilson and Carrano 1999; Powell 2003). This could have also helped them to gain a faster distribution over the abrupt lands that appeared with the early steps of the Andes rise. However, while in opisthocoelous titanosaurs the increased mobility occurred relating to the centrum shape, in amphiplathyan rebbachisaurids this responded as a complex system in the neural arch. Furthermore, where macronarians show large centra and separated zygapophyses, rebbachisaurids underwent a minimisation of the centrum, perhaps comparable to the small centra of stegosaurian vertebrae, and a joining of zygapophyses, changing the larger articular structure between vertebrae from ventral to dorsal with respect to the neural canal, a feature unique in Saurischia.

Conclusions

Upper Cretaceous sauropods experienced new ways of life acquiring more flexible vertebral columns along different paths. There were only two lineages of Upper Cretaceous sauropods: rebbachisaurid diplodocoids and titanosaurian macronarians. Whereas the latter are represented by dozens of species, the diversity, biogeography and ecological importance of the Rebbachisauridae in early Upper Cretaceous terrestrial ecosystems are still far from understood (Gallina et al. 2002). As both lineages show these features convergently, it is possible that their success in southern continents during the early Late Cretaceous was prompted by their increased skeletal mobility and cranial novelties. However, the acquired adaptations have a different story (and timing) as derived from different phylogenetic histories and anatomical models. In titanosaurians, the main source of vertebral mobility is provided by the large and opisthocoelous vertebral centra. Conversely, in rebbachisaurids, the main pivot point is located in the lower part of the neural arch, right over the neural canal, whereas the centra underwent a minimisation in size and importance.

This change in the location of the larger articular structure between vertebrae is not minor, as it implies a change from ventral to dorsal with respect to the neural canal, a feature unique in Saurischia. A perhaps comparable minimisation of the centrum and enlargement of the dorsal articular structure is also present in the stegosaurian ornithischians.

Although highly different from the macronarian ‘ball and socket’ opisthocoelous centra, the ‘U-eave and shelf complex’ optimises the torsion between successive vertebrae, allowing rebbachisaurids a further mobility on their amphiplathyean centra.

The existence of the connection between the two sides of the anterior side of the neural arch by means of the prezygapophyseal shelf and the presence of large flat spaces between the prespinal lamina and the diapophysis creates a wide continuity in the anterior surface of the neural arch, whose possible function is beyond the scope of this work.

The presence of an articulation like the ‘U-eave and shelf complex’ represents for the first time the recognition of biomechanical abilities unexpected for this group of graviportal tetrapods. The peculiar anatomical trait described here would have allowed them to achieve a wide variety of postures in both resting and movement situations. Moreover, this valuable tool would have increased its significance in the context of a distribution in a supercontinent where wide deserts and rising mountains became common.

Rebbachisaurids were successful and widely distributed in Early Cretaceous and survived until the middle of the Upper Cretaceous in north Africa and South America,
sharing environments with other sauropods, particularly basal titanosaurians. Despite their extinction in Africa which is not well known, they became extinct in South America by the Coniacian–Santonian boundary, altogether with carcharodontosaurid theropods (Apesteguía 2002; Leanza et al. 2004) and perhaps eilenodontine rhynchocephalians, as part of the Patagonian Limayan to Early Coloradoan fauna. The stabilisation of these sauropod specialisations is better viewed taking into account several of the environmental characteristics of the Late Cretaceous. Perhaps, the most important of them are the growing angiosperm importance, the relatively low ornithischian diversity in the southern terrestrial ecosystems and the topographical changes as a result of the Upper Cretaceous continental colliding and fragmentation.

Acknowledgements
We thank Dr Jorge Calvo (CEPALB, Argentina) for allowing PAG to see L. tessonei, Dr Ronan Allain for permitting SA to see the holotype of R. garasbae and then Leonardo Salgado, Jeffrey Wilson and Heinrich Mallison for sharing their opinions on the subject.

References
Huene F. 1929. Los Saurisquios y Ornitisquios del Cretácico de Gondwana. Nuevas evidencias en la Formación El Molino (Maastrichtiano) en Cal Or de los Kem Kem de la Daoura. Comp Rend 19th Con Inter Geol 70A.
Janensch W. 1929. Die Wirbelsa¨ule der Gattung Dicraeosaurus. Z. Mu¨nchner Geowissenschaftliche Abhandlungen. Reihe 70A.
Wilson JA. 1999. [Chicago(IL )]: University of Chicago Evolution and phylogeny of sauropod dinosaurs [PhD Dissertation].