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

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Rebbachisauridae are poorly known 'bizarre' sauropods with two nearly complete skeletons collected: *Limaysaurus tessonei* and *Nigersaurus 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 amphyplathian 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 Aït 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.

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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 *Antarctosaurus wichmannianus* (Huene 1929), were misunderstood 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 *Antarctosaurus* (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

MACN, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; MDE-D, Museum of Esperaza, France. MMCH, Museo Municipal Ernesto Bachmann, Villa El Chocón, Neuquén, Argentina. MNHN, Muséum Nacional d'Histoire Naturelle, Paris, France; MPM, Museu de Paleontología de Marília, Sao Paulo, Brazil.

Anatomical abbreviations

cpol, centropostzygapophyseal lamina; med.cpol, medial centropostzygapophyseal lamina; med.spol, medial spinopostzygapophyseal laminae; lat.cpol, lateral centropostzygapophyseal lamina; lat.spol, lateral spinopost-zygapophyseal laminae; tpol, intrapostzygapophyseal 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 1929) and lost in all rebbachisaurids (Bonaparte 1999; Salgado et al. 2004; Gallina and Apesteguía 2005) or only in their derived forms (as deduced from Sereno et al. 2007).

Although extremely tall neural spines and reduced, but pneumatised vertebral centra, are characteristic of rebbachisaurid (Lavocat 1954; Gallina and Apesteguía 2005), the South American specimens bear a moderately developed neural spine, as represented in the vertebrae of *L. tessonei* (Figure 1(F)) and *N. alarconensis* (Figure 1(G)). Lavocat (1954) also remarked the large size of both pleurocoels barely separated by a thin median wall. It is interesting to note that *Rebbachisaurus* is a true giant among rebbachisaurids. Whereas South American forms have dorsal vertebrae that barely reach 50 cm in height, known specimens from *R. garasbae* demonstrate dorsal vertebrae reaching 150 cm in height (MNHN 1958, 1980, 1986–1989, 1998–1999 and MDE-D-300).

Only two sauropod lineages show the loss of hyposphene–hypantrum complex: derived titanosaurs and rebbachisaurids. Both lineages arose towards the end of the Jurassic and the beginning of the Cretaceous and survived until the Late Cretaceous. Hyposphene–hypantrum complexes are present in basal sauropods and they were probably crucial in granting a large body size by stabilising the vertebral column. The loss of this structure is very rare and Bonaparte (1999) characterised its 'Rebbachisaurid' type of dorsal vertebra by the absence of a hyposphene.

The laminary complex related to the development of the hyposphene in basal rebbachisaurids is based in the medial centropostzygapophyseal laminae (med.cpol; mcpol *sensu* Apesteguía 2005) and their interference in the origin of the hyposphene, visible as a vertical strut included by Wilson (1999) in the intrapostzygapophyseal lamina (tpol). In the case of *Histriasaurus boscarollii* (Dalla Vecchia 1998) and MACN PV N35, where the hyposphene is developed (Figure 1), med.cpol arise from the end of the pendant structure and no other laminae are present, in a similar way to that occurred in *Camarasaurus grandis* (Osborn and Mook 1921), and the first dorsals of the titanosauriforms *Brachiosaurus brancai* (Janensch 1950), *Brachiosaurus altithorax* (Riggs 1903) and *Phuwiangosaurus sirindhornae* (Martin et al. 1994). Although titanosaurs also show an important development of the med.cpol (Apesteguía 2005), laterally, the lateral centropostzygapophyseal 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*, *Dicraeosaurus* and *Histriasaurus*, well-developed lateral spinopostzygapophyseal 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 spinopostzygapophyseal 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. garasbae* (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. garasbae*, *N. alarconensis* and MMCH-Pv-49, the situation is even more complex, as an additional lamina

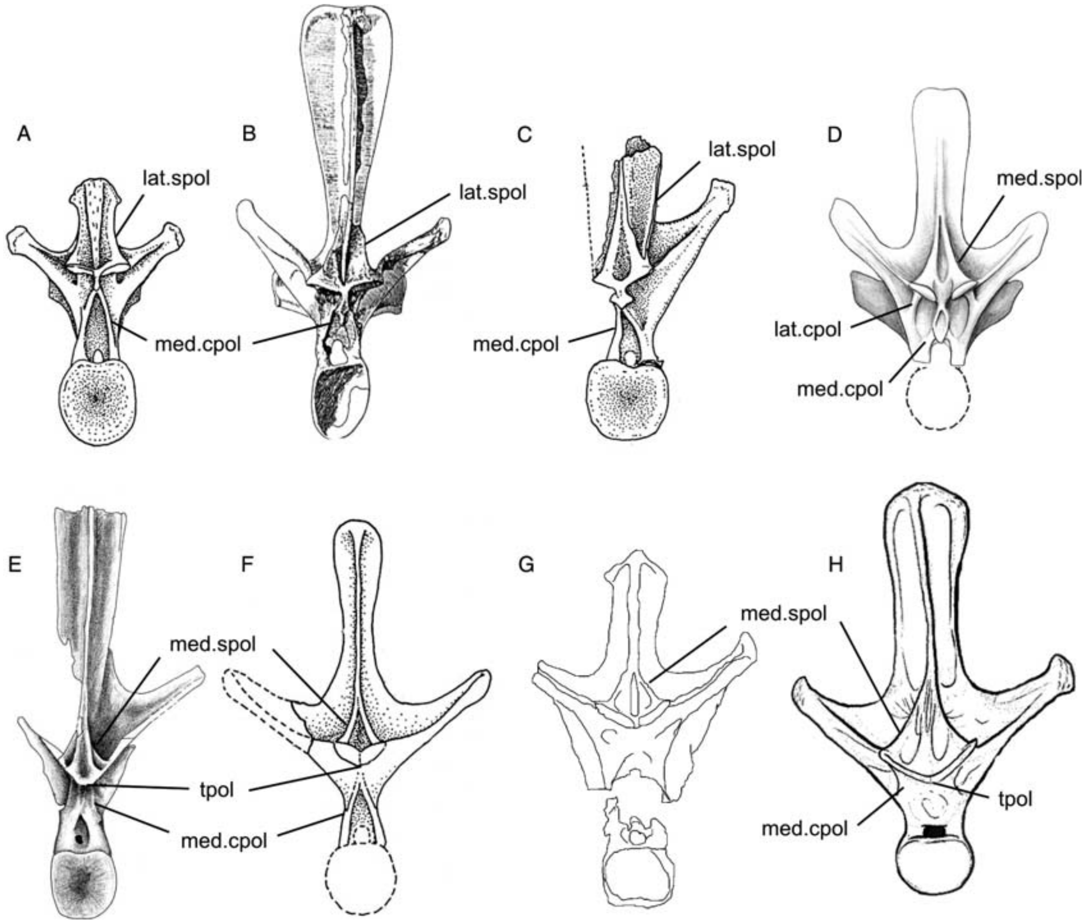

Figure 1. Sauropod dorsal vertebrae in posterior view. (A) Haplocanthosaurus priscus 13th dorsal vertebra (modified from Dalla Vecchia 1998); (B) Dicraeosaurus sattleri posterior dorsal (from Janensch 1929); (C) *H. boscarollii* (modified from Dalla Vecchia 1998); (D) MACN PV N35, basal rebbachisauroid from Patagonia (from Apesteguía 2007); (E) *R. garasbae* (modified from Bonaparte 1999); (F) *L. tessonei* (from Dalla Vecchia 1998); (G) *N. alarconensis* (from Apesteguía 2007) and (H) MMCH-Pv-49. Not to scale. Abbreviations: cpol, centropostzygapophyseal lamina; med.cpol, medial centropostzygapophyseal lamina; med.spol, medial spinopostzygapophyseal laminae; lat.cpol, lateral centropostzygapophyseal lamina; lat.spol, lateral spinopostzygapophyseal laminae; tpol, intrapostzygapophyseal 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-

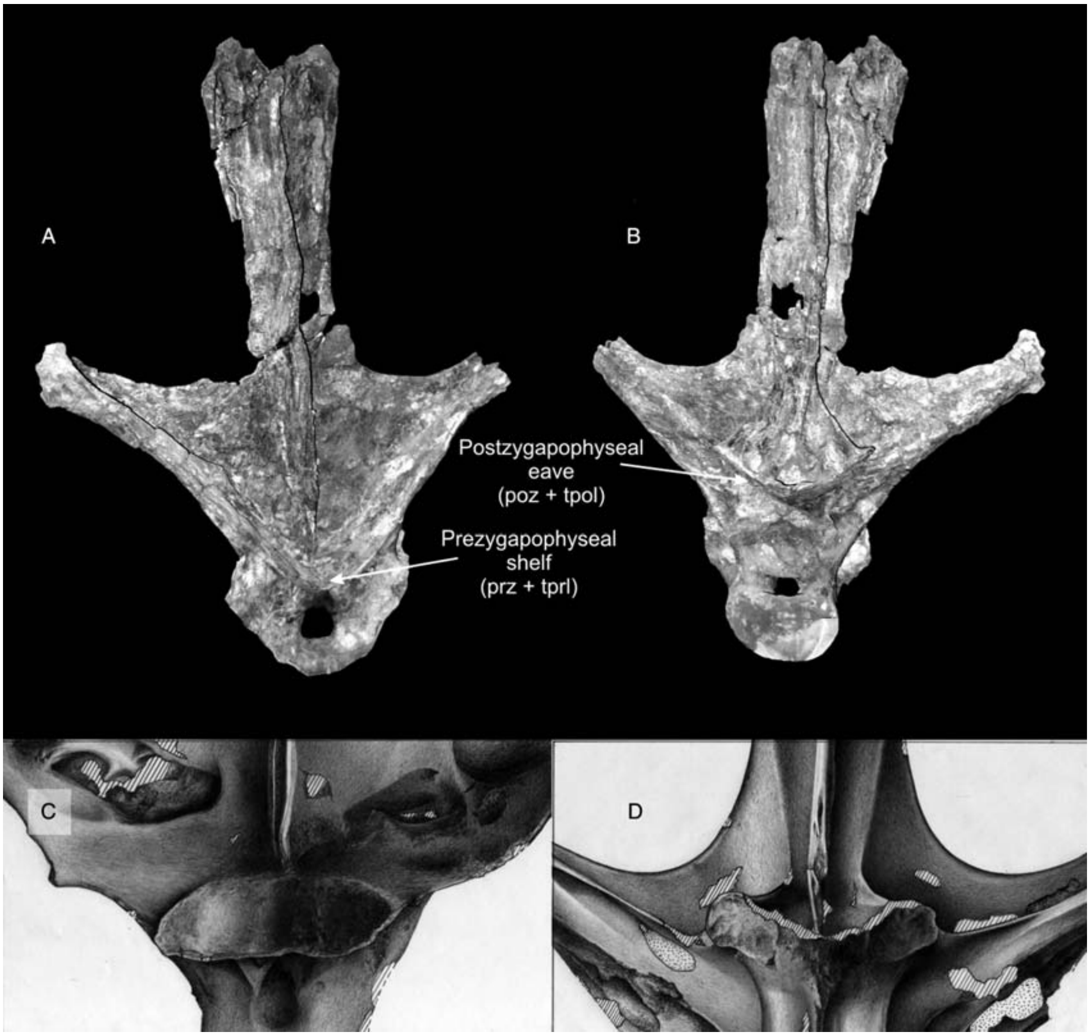

Figure 2. MMCH-Pv-49 dorsal vertebra in (A) anterior and (B) posterior views, showing the articular surfaces of the neural arch. ‘U-eave and shelf complex’ in (C) anterodorsal and (D) posteroventral views. Not to scale.

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 titanosaurs in Macronaria) to which the loss of the accessory articulations, such as the hyposphene–hypantrum 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

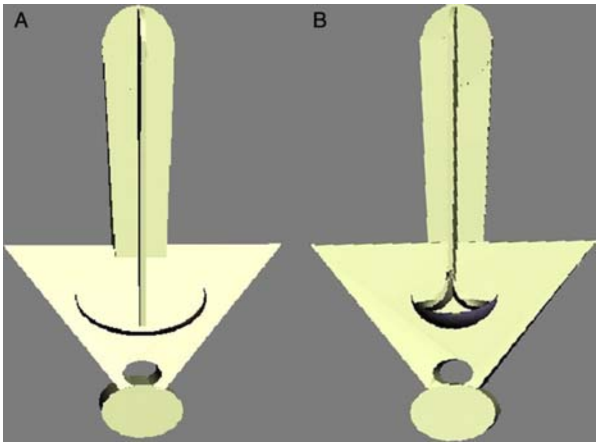

Figure 3. MMCH-Pv-49, scheme of the dorsal vertebra in (A) anterior and (B) posterior views, showing a schematic representation of the articular surfaces of the neural arch.

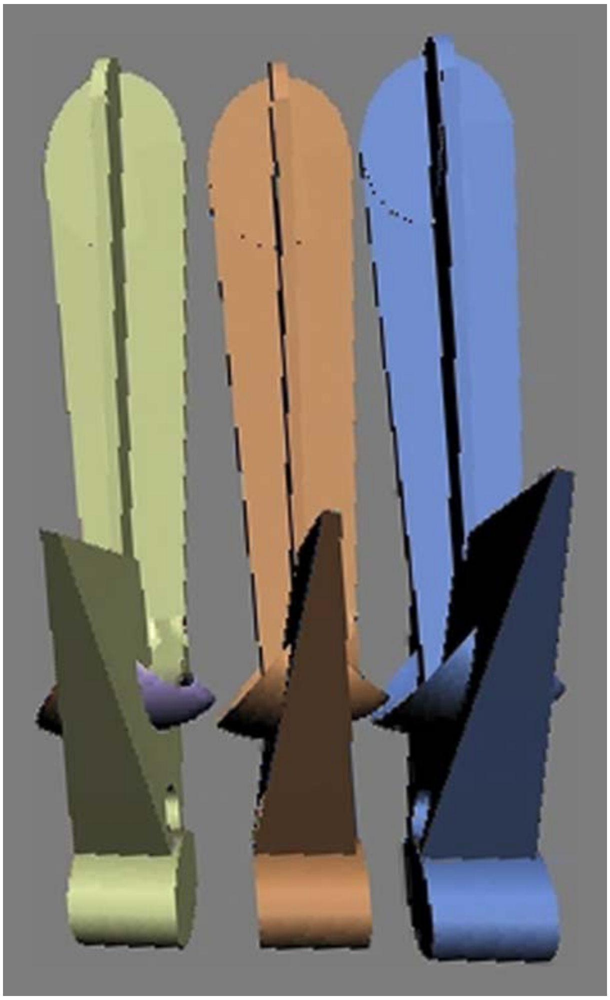

Figure 4. Schematic representation of the rebbachisaurid vertebral series showing the system in which successive vertebrae fit.

(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. hyposphene–hypantrum complex; Apesteguía 2005). Additionally, whereas basal macronarians (i.e. *Camarasaurus*) bear wide postzygapophyses and large hyposphenes and basal titanosauriforms (i.e. *Brachiosaurus*) bear reduced and centred zygapophyses that prevent lateral movements, basal titanosaurs show both plesiomorphic and rhomboidal hyposphenes (e.g. *Andesaurus*) or only a system of strengthened med.cpol that partially replaces the hyposphenes (Bonaparte and Coria 1993; Apesteguía 2005). In titanosaurs, the loss of the hyposphene–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 hyposphenes controlled the movements of the column.

In rebbachisaurids, the wide but permissive amphiplathyan 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 amphiplathyan 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 amphiplathyan 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.

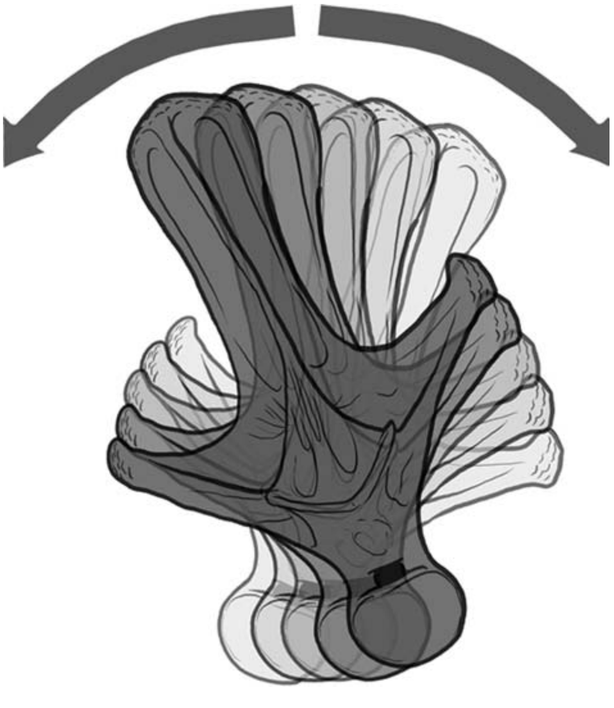

Figure 5. MMCH-Pv-49, line drawing of the dorsal vertebra in posterior views showing the maximum movement possibilities based on the 'U-eave and shelf' articulation.

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 amphiplathyan 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 titanosaurs, 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 titanosaurs 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 postcranium 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 titanosaurs 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 6. Well-preserved sauropod footprint found in 2000 by Sebastián Apesteguía in Cenomanian–Turonian rocks of the Candeleros Formation in northern Patagonia. Considering its high heteropody in contrast to the homopodous titanosaurian trackways, and the abundance of rebbachisaurids in the same area, it probably belongs to these sauropods. Scale bar: 10 cm.

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 titanosaurs, 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 amphiplathyan 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 titanosaurs. 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.

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References

Apesteguía S. 2002. Successional structure in continental tetrapod faunas from Argentina along the Cretaceous. In: Boletim do 6° Simpósio sobre o Cretáceo do Brasil–2° Simposio sobre el Cretácico de América del Sur. p. 135–141.

Apesteguía S. 2004. Bonitasaura salgadoi: A beaked sauropod in the Late Cretaceous of Gondwana. Naturwissenschaften. 91:493–497.

Apesteguía S. 2005. Thunder-Lizards: the Sauropodomorph Dinosaurs. In: Tidwell V, Carpenter K, editors. Evolution of the hyposphene–hypantrum complex within Sauropoda, Chap. 12. Bloomington & Indianapolis: Indiana University Press. p. 248–267.

Apesteguía S. 2007. The sauropod diversity of the La Amarga Formation (Barremian), Neuquén (Argentina). Gond Res. 12(4):533–546.

Apesteguía S, De Valais S, Meyer CA. 2007. Asignación unívoca de grandes huellas cuadrúpedas a saurópodos titanosaurios en la Formación El Molino (Maastrichtiano) en Cal Orck'o (Bolivia). In: Actas V Reunión Argentina de Icnología y III Reunión de Icnología del Mercosur, Ushuaia. p. 46.

Bonaparte JF. 1996. Contributions of southern South America to Vertebrate Paleontology. In: Pfeil F, Arratia G, editors. Münchner Geowissenschaftliche Abhandlungen. Reihe A. Geologie und Paläontologie 30. Cretaceous Tetrapods of Argentina. p. 73–130.

Bonaparte JF. 1997. *Rayososaurus agrioensis* Bonaparte 1995. Ameghiniana. 34:116.

Bonaparte JF. 1999. Evolución de las vértebras presacras en Sauropodomorpha. Ameghiniana. 36:115–187.

Bonaparte JF, Coria RA. 1993. Un nuevo y gigantesco sauropodo titanosaurio de la Formacion Rio Limay (Albiano-Cenomaniano) de le Provincia del Neuquén, Argentina. Ameghiniana. 30:271–282.

Calvo JO, Salgado L. 1995. *Rebbachisaurus tessonei* sp. nov. a new Sauropoda from the Albian-Cenomanian of Argentina; new evidence on the origin of Diplodocidae. Gaia. 11:13–33.

Carvalho IS, dos Santos Avilla L, Salgado L. 2003. Amazonsaurus maranhensis gen. et sp. nov. (Sauropoda, Diplodocoidea) from the Lower Cretaceous (Aptian-Albian) of Brazil. Cret Res. 24:697–713.

Cavin L, Boudad L, Duffaud S, Kabiri L, Le Loeuff J, Rouget I, Tong H. 2001. L'évolution paléoenvironnementale des faunes de poissons du Crétacé supérieur du bassin du Tafilalt et des régions avoisinantes (Sud-Est du Maroc): implications paléobiogéographiques. C R Acad Sci Paris. 333:677–683.

Coria RA, Chiappe LM. 2001. Tooth replacement in a sauropod maxilla from the Upper Cretaceous of Patagonia, Argentina. Ameghiniana. 38:463–466.

Dalla Vecchia FM. 1998. Remains of Sauropoda (Reptilia, Saurischia) in the Lower Cretaceous (Upper Hauterivian/0-Lower Barremian) Limestones of SW Istria (Croatia). Geol Croat. 51(2):105–134.

Gallina PA, Apesteguía S. 2005. *Cathartesaura anaerobica* gen. et sp. nov., a new rebbachisaurid (Dinosauria, Sauropoda) from the Huincul Formation (Upper Cretaceous), Río Negro, Argentina. Rev Mus Arg Cs Nat, n.s. 7:153–166.

Gallina PA, Apesteguía S, Novas FE. 2002. Un elefante bajo la alfombra? Los Rebbachisauridae (Sauropoda, Diplodocimorpha) del Cretácico de Gondwana. Nuevas evidencias en "La Buitrera" (Fm. Candeleros), provincia de Río Negro. Ameghiniana. 39(Suppl):10R.

Gilmore CW. 1936. Osteology of Apatosaurus with special reference to specimens in the Carnegie Museum. Mem. Carneg. Mus. 11:175–300.

Harris JD, Dodson P. 2004. A new diplodocoid sauropod dinosaur from the Upper Jurassic Morrison Formation of Montana, USA. Acta Pal Pol. 49(2):197–210.

Hatcher JB. 1903. Osteology of *Haplocanthosaurus*, with description of a new species, and remarks on the probable habits of the Sauropoda and the age and origin of the Atlantosaurus Beds. Mem Carneg Mus. 2:1–72.

Huene F. 1929. Los Saurisquios y Ornitisquios del Cretácico Argentino. An Mus La Plata. 3:1–196.

Jacobs LL, Winkler DA, Downs WR, Gomani EM. 1993. New material of an Early Cretaceous titanosaurid sauropod dinosaur from Malawi. Palaeontology. 36(3):523–534.

Janensch W. 1929. Die Wirbelsäule der Gattung Dicraeosaurus. Palaeontographica. 2(1):37–133.

Janensch W. 1950. Die Wirbelsäule von *Brachiosaurus brancai*. Palaeontographica. 3(2):27–93.

Janis CM, Theodor JM, Boisvert B. 2002. Locomotor evolution in camels revisited: a quantitative analysis of pedal anatomy and the acquisition of the pacing gait. J Vert Paleo. 22: 110–121.

Lamanna MC, Martinez RD, Luna M, Casal G, Dodson P, Smith J. 2001. Sauropod faunal transition through the Cretaceous Chubut group of Central Patagonia. J Vert Paleo. 21(Abst): 70A.

Lavocat R. 1954. Sur les Dinosauriens du continental intercalaire des Kem Kem de la Daoura. Comp Rend 19th Con Inter Geol 1952. 3:65–68.

Leanza HA, Apesteguía S, Novas FE, de la Fuente MS. 2004. Cretaceous terrestrial beds from the Neuquén Basin

(Argentina) and their tetrapod assemblages. Cret Res. 25: 61–87.

Mannion PD. 2009. A rebbachisaurid sauropod from the Lower Cretaceous of the Isle of Wight, England. Cret Res. 30(3): 521–526.

Martin V, Buffetaut E, Suttethorn V. 1994. A new genus of sauropod dinosaur from the Sao Khua Formation (Late Jurassic to Early Cretaceous) of northwestern Thailand. Comp Rend Acad Sci Paris. 319:1085–1092.

McIntosh JS. 1990. The Dinosauria. In: Weishampel DB, Dodson P, Osmólska H, editors. Sauropoda. Berkeley: Universiy of California Press. p. 345–401.

Nopcsa F. 1902. Notizen über die Cretacischen Dinosaurier. Pt. 3. Wirbel eines sudamerikanischen Sauropoden. Sitzber Berliner Akademie der Wesenschaften, Bd.. 3:108–114.

Osborn HF, Mook C. 1921. *Camarasaurus, Amphicoelias*, and other sauropods of Cope. Mem Am Mus Nat Hist. 3: 247–387.

Pereda Suberbiola X, Torcida Fernandez Baldor F, Meijide Calvo M, Fuentes Vidarte C, Izquierdo LA, Montero D, Pérez G. 2001. Un saurópodo rebaquisáurido (Dinosauria, Diplodocoidea) en el Cretácico inferior de Burgos, España. II Jorn Inter Paleont Dinos y su entorno. Resúmenes: 25–27.

Pereda Suberbiola X, Torcida F, Izquierdo LA, Huerta P, Montero D, Perez G. 2003. First rebbachisaurid dinosaur (Sauropoda, Diplodocoidea) from the Early Cretaceous of Spain: palaeobiogeographical implications. Bull Soc Géol France. 174(5):471–479.

Powell JE. 2003. Revision of South American Titanosaurid dinosaururs: palaeobiological, palaeobiogeographical and phylogenetic aspects. Rec Queen Vict Mus. 111:1–173.

Riggs ES. 1903. *Brachiosaurus altithorax*, the largest known dinosaur. Am J Sci. 15:299–306.

Salgado L. 2000. [La Plata, Buenos Aires]: Universidad Nacional de La Plata Evolución y Paleobiología de los saurópodos Titanosauridae [PhD dissertation].

Salgado L, Calvo JO. 1997. Evolution of titanosaurid sauropods II: the cranial evidence. Ameghiniana. 34:33–47.

Salgado L, Garrido A, Cocca SE, Cocca JR. 2004. Lower Cretaceous Rebbachisaurid sauropods from Aguada del león (Lohan Cura Formation), Neuquén province, Northwestern Patagonia, Argentina. J Vert Paleo. 24:903–912.

Salgado L, Carvalho IS, Garrido A. 2006. *Zapalasaurus bonapartei*, un nuevo dinosaurio saurópodo de La Formación La Amarga (Cretácico Inferior), noroeste de Patagonia, Provincia de Neuquén, Argentina. Geobios. 39:695–707.

Sereno PC, Wilson JA. 2005. The sauropods: evolution and paleobiology. In: Curry Rogers KA, Wilson JA, editors. A sauropod tooth battery: structure and evolution. Berkeley: University of California Press. p. 157–177.

Sereno PC, Dutheil DB, Iarochene M, Larsson HCE, Lyon GH, Magwene PM, Sidor CA, Varricchio DJ, Wilson JA. 1996. Predatory dinosaurs from the Sahara and Late Cretaceous faunal differentiation. Science. 272:986–991.

Sereno PC, Beck AL, Dutheil DB, Larsson HCE, Lyon GH, Moussa B, Sadleir RW, Sidor CA, Varricchio DJ, Wilson GP, Wilson JA. 1999. Cretaceous Sauropods from the Sahara and the uneven rate of skeletal evolution among dinosaurs. Science. 286:1342–1347.

Sereno PC, Wilson JA, Witmer LM, Whitlock JA, Maga A, Oumarou I, Rowe TA. 2007. Structural extremes in a cretaceous dinosaur. PLoS ONE. 2(11):e1230, doi: 10.1371/journal.pone.0001230.

Upchurch P. 1998. The phylogenetic relationships of sauropod dinosaurs. Zool J Linn Soc. 124:43–103.

Upchurch P, Barret PM, Dodson P. 2004. The Dinosauria. In: Weishampel DB, Dodson P, Osmólska H, editors. Sauropoda. 2nd ed.. Berkeley: University of California Press. p. 259–322.

Wilson JA. 1999. [Chicago(IL)]: University of Chicago Evolution and phylogeny of sauropod dinosaurs [PhD Dissertation].

Wilson JA. 2002. Sauropod dinosaur phylogeny: critique and cladistic analysis. Zool J Linn Soc. 136:217–276.

Wilson JA. 2005. The sauropods: evolution and paleobiology. In: Curry Rogers KA, Wilson JA, editors. Overview of Sauropod phylogeny and evolution. Berkeley: University of California Press. p. 15–49.

Wilson JA, Carrano MT. 1999. Titanosaurs and the origin of "wide-gauge" trackways: a biomechanical and systematic perspective on sauropod locomotion. Paleobiology. 25(2):252–267.

Wilson JA, Sereno PC. 1998. Early evolution and higher-level phylogeny of sauropod dinosaurs. Soc Vert Paleo. Memoir. 5:1–68.