



## NEW INFORMATION ON A JUVENILE SAUROPOD SPECIMEN FROM THE MORRISON FORMATION AND THE REASSESSMENT OF ITS SYSTEMATIC POSITION

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**Abstract:** Morphological changes in the ontogeny of sauropods are poorly known, making difficult to establish the systematic affinities of very young individuals. New information on an almost complete juvenile sauropod (SMA 0009) with an estimated total length of about 2 m is here presented. The specimen was described as a diplodocid owing to the presence of some putative synapomorphies of this group. However, recent further preparation revealed the absence of diplodocid characters and the presence of macronarian derived characters. To test the affinities of this specimen, a phylogenetic analysis was conducted. The strict consensus tree recovers the specimen as a basal titanosauriform, in an unresolved relation with *Brachiosaurus* and *Giraffatitan*. Nevertheless, a brachiosaurid assignment is here suggested in base of the widely accepted monophyly of this group (only recovered when SMA 0009 is placed within this group). Although the existence of a new taxon cannot be completely ruled out, the combination of derived and plesiomorphic characters in the specimen suggests its assignment to *Brachiosaurus*. Sixteen extra steps are needed to place this speci-

men within Diplodocidae. The high cost to place this specimen within this group is owing to the fact that several diplodocid characters are absent in SMA 0009, such as the absence of divided centroprezygapophyseal lamina in cervical vertebrae, procoelous anterior caudal centra, composed lateral lamina in anterior caudal vertebrae, elongated middle caudal vertebrae, short cervical ribs and caudolateral projection of distal condyle of metatarsal I. Finally, the systematic position reveals few major ontogenetic transformations. These affect the pneumatic structures (e.g. change from simple pleurocoels in the cervical vertebrae to complex pleurocoels and the development of lateral excavations in the dorsal vertebrae) but also include unrecorded transformations of the neural spine (e.g. the development of the spinodiapophyseal lamina, the widening of the neural spines in the dorsal vertebrae) and allometric growth in some limb bones.

**Key words:** Sauropoda, Neosauropoda, Titanosauriformes, Brachiosauridae, *Brachiosaurus*, ontogeny, early juvenile sauropod.

SAUROPOD dinosaurs have been recovered in all landmasses excluding Antarctica (e.g. Upchurch *et al.* 2004; Mannion and Upchurch 2010a, b), being one of the most abundant land vertebrate remains from the Late Jurassic to the Late Cretaceous. Nevertheless, juvenile specimens are rarely found, and usually only isolated bones are discovered (e.g. Carpenter and McIntosh 1994; Foster 2005). Among nonadult sauropods most remains are represented by late juvenile to subadult specimens with relatively large bones, which can be easily compared with adult forms to assess its systematic assignment (e.g. Foster 2005; Ikejiri *et al.* 2005; Tidwell and Wilhite 2005). Well-preserved early juvenile sauropods are extremely rare obscuring our

understanding of the early ontogenetic changes in sauropods. This lack of knowledge also makes difficult to establish a systematic assignment to remains of early juvenile sauropods, especially for isolated bones, where only few characters could be observed.

An almost complete postcranial skeleton of a juvenile sauropod (SMA 0009), with an estimated total length of about 2 m (Schwarz *et al.* 2007), was recently discovered in the Howe Stephens Quarry of the Morrison Formation (Upper Jurassic, Wyoming). The material here described was found close to the original Howe Quarry, where Barnum Brown extracted a large number of dinosaur bones for the American Museum of Natural History (Fig. 1).

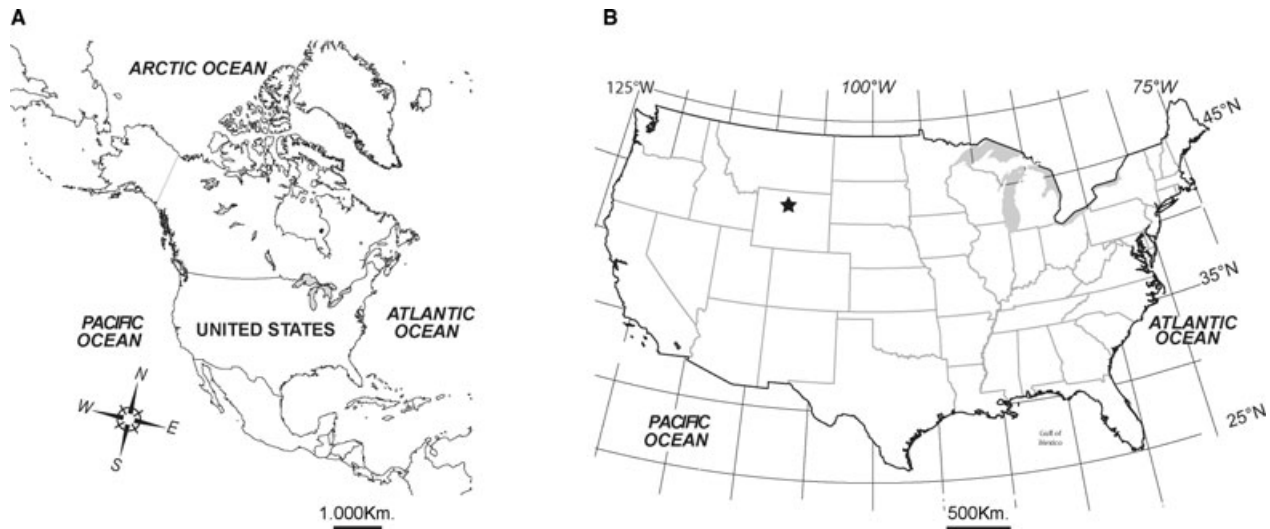


FIG. 1. Location map. A, North America. B, United States showing the exact location of the Howe Stephens Quarry (black star).

This juvenile sauropod was described by Schwarz *et al.* (2007), and identified as a diplodocid sauropod, as some putative synapomorphies of this group are observed on it. The juvenile status of this specimen was established based on bone histology (see also Klein and Sander 2008). However, recent further preparation and re-examination of the specimen revealed a number of nondiplodocid characters, as well as the absence of many synapomorphies of this group. These characters could not be properly observed previously, and thus not described by Schwarz *et al.* (2007). Additionally, most of the diplodocid synapomorphies detected on SMA 0009 are convergently present in some basal camarasauromorphs (e.g. *Camarasaurus*, *Giraffatitan*, *Brachiosaurus*). Therefore, the new observations prompted a revision of the anatomy and taxonomic assignment of the specimen SMA 0009. Here we provide a complete description of the new information, comparing this specimen with both diplodocoid and macronarian adult sauropods, especially with those from the Morrison Formation.

*Institutional abbreviations.* DFMMh/FV, Dinosaurier-Freilichtmuseum MÜNCHENHAGEN/Verein zur Förderung der Niedersächsischen Paläontologie (e.V.), MÜNCHENHAGEN; FMNH, Field Museum of Natural History, Chicago; SMA, Sauriermuseum Aathal, Switzerland.

*Anatomic abbreviations.* ACDL, anterior centrodiapophyseal lamina; ACPL, anterior centroparapophyseal lamina; CPOL, centropostzygapophyseal lamina; CPRL, centroprezygapophyseal lamina; PCDL, posterior centrodiapophyseal lamina; PCPL, posterior centroparapophyseal lamina; PODL, postzygodiapophyseal lamina; PDDL, paradiapophyseal lamina; PRDL, prezygodiapophyseal lamina; SPDL, spinodiapophyseal lamina; SPOL, spinopostzygapophyseal lamina; SPRL, spinoprezygapophyseal lamina; TPRL, intraprezygapophyseal lamina.

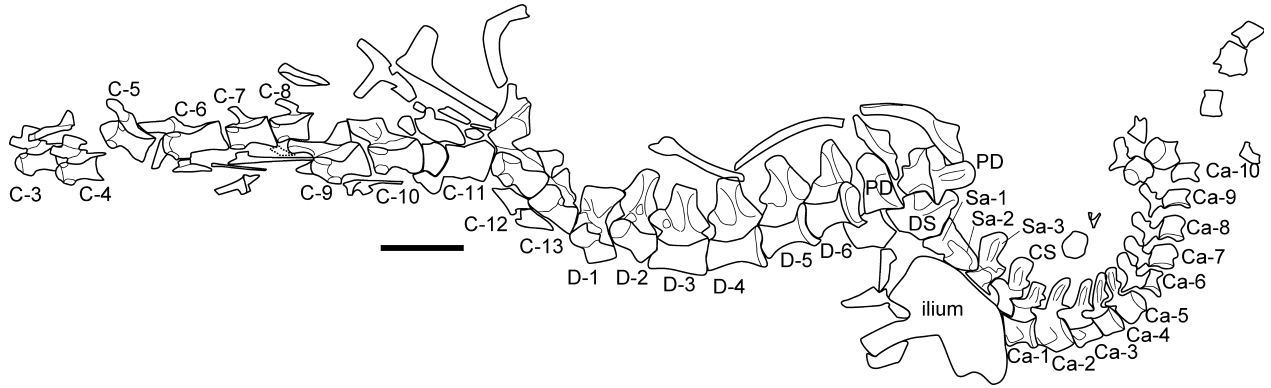
## DESCRIPTION AND COMPARISONS

*Remarks.* Most of the new information is derived from the axial skeleton but different sections of the girdles and limbs have been well prepared to ascertain the state of the different characters used in the data matrix (see Phylogenetic analysis). The description presented here is mainly based on the new information and the reinterpretations made on some elements, further description was provided by Schwarz *et al.* (2007).

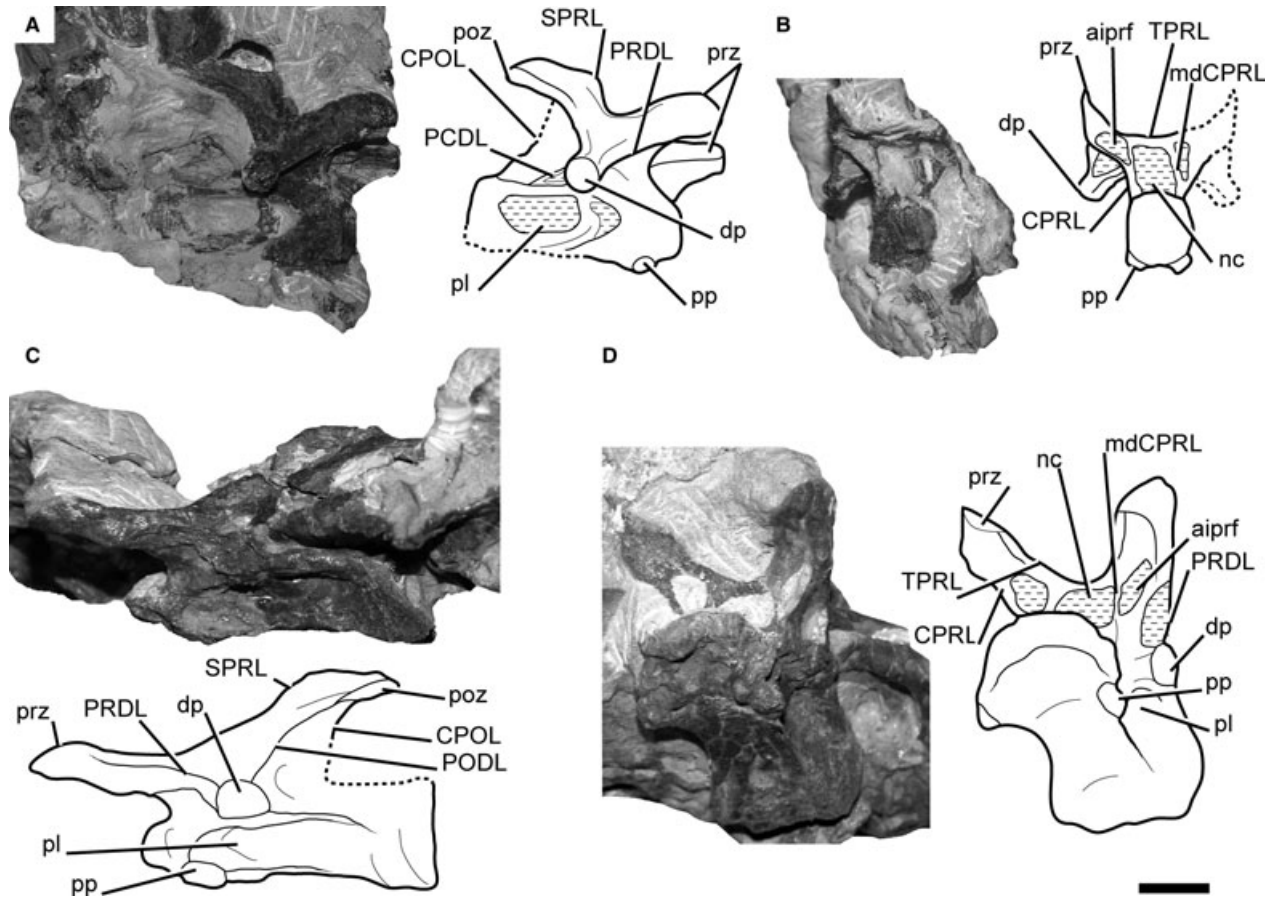
### *Comments on the position of the vertebrae*

The new information allows us to re-identify the position of the axial elements, especially in the cervico-dorsal and dorso-sacral transitions (Fig. 2). A rock-block, containing the first three preserved cervical vertebrae (as were figured by Schwarz *et al.* 2007, fig. 4B), was removed revealing the presence of one additional cervical vertebra underneath the Cep-1, as identified by Schwarz *et al.* (2007; Fig. 3). The preserved cervical vertebrae of SMA 0009 are here identified as C-3 to C-13, based on the number of cervical vertebrae (= 13) in *Giraffatitan* (Wilson and Sereno 1998; Figs 2 and 3).

The centrum previously identified as the second dorsal vertebra (Schwarz *et al.* 2007, fig. 4B) has the parapophysis still ventrolaterally positioned. This position of the parapophysis indicates a more anterior position, and we interpret this element as the last cervical centrum rather than the second dorsal centrum (C-13; Fig. 2). The following vertebra is laterally damaged, but the presence of a horizontal TPRL (Figs 2 and 4) indicates its anterior position among the dorsal vertebrae (Wilson, 1999). This element is here identified as the first dorsal vertebra (D-1; Fig. 2). Additionally, the two subsequent dorsal vertebrae (D-2 and D-3; Fig. 2) have their parapophyses on the centrum but very closely located to the neural arch (Fig. 4).



**FIG. 2.** SMA 0009, overview of the axial skeleton (modified from Schwarz *et al.* 2007), showing the vertebrae position as were identified here. Abbreviations: C, cervical vertebra; Ca, caudal vertebra; CS, caudosacral vertebra; D, dorsal vertebra; DS, dorso sacral vertebra; PD, posterior dorsal vertebra; Sa, sacral vertebra. Scale bar represents 10 cm.



**FIG. 3.** SMA 0009, cervical vertebrae. A, the anteriormost preserved cervical vertebra in lateral view. B, the anteriormost preserved cervical vertebra in anterior view. C, the third preserved cervical vertebra in lateral view. D, the third preserved cervical vertebra in anteroventral view. Abbreviations: nc, neural canal; CPOL, centropostzygapophyseal lamina; CPRL, centroprezygapophyseal lamina; dp, diapophysis; iprf, infraprezygapophyseal fossa; mdCPRL, medial division of the centroprezygapophyseal lamina; PCDL, posterior centrodiaepophyseal lamina; PCPL, posterior centroparapophyseal lamina; pl, pleurocoel; PODL, postzygodiaepophyseal lamina; poz, postzygapophysis; pp, parapophysis; PRDL, prezygodiaepophyseal lamina; prz, prezygapophysis; SPRL, spinoprezygapophyseal lamina; TPRL, intraprezygapophyseal lamina. Scale bar represents 30 mm.

The parapophysis of D-4 is almost completely positioned on the neural arch but maintains a ventral connection to the centrum. This position of the parapophysis is commonly observed in the fourth dorsal vertebra of other sauropods (e.g. *Haplocanthosaurus*, *Camarasaurus*, *Diplodocus*), supporting the current identification of the last cervical and first dorsal vertebrae. Hence, a total number of eleven cervical vertebrae are preserved in SMA 0009, and the total number of dorsal vertebrae of SMA 0009 still has to be determined. The first six dorsal vertebrae are articulated with the last ten cervical vertebrae. The subsequent dorsal vertebra is not articulated with D-6 but the centrum is perpendicular to it (Fig. 2), therefore its position along dorsal series cannot be surely determined. Because of its proximity to the dorsosacral vertebra (Figs 2 and 5) and their similar morphology, this vertebra is referred as a posterior dorsal vertebra (Figs 2 and 5).

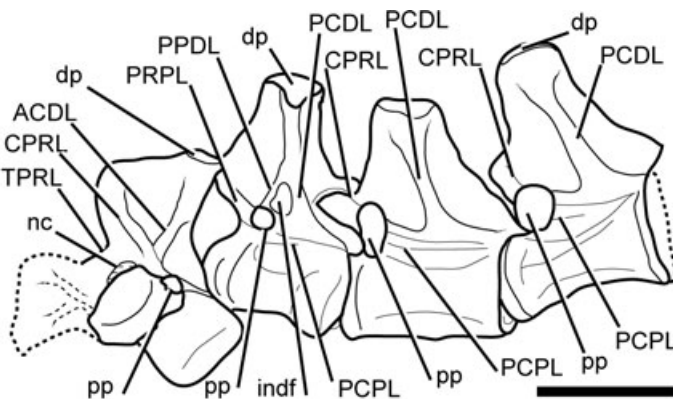
Two more vertebrae are underneath D-6 and the posterior dorsal vertebra. These elements were identified by Schwarz *et al.* (2007) as the first two sacral vertebrae, but their lateral preparation revealed the absence of sacral ribs, or sacral rib articulations on them (Fig. 5). While one of these elements is badly preserved and its identification is difficult, the other element is well preserved and does not greatly differ from the posterior dorsal vertebra. This vertebra is articulated with the first sacral vertebra (as identified here), and in the current ontogenetic status of SMA 0009, it must be strictly considered as the last dorsal element. Nevertheless, this vertebra is here referred as a dorsosacral vertebra (Figs 2 and 5), as it is very likely that this element would have been incorporated into the sacrum in a later ontogenetic stage. The dorsosacral vertebra is more similar to the last dorsal vertebra than to the other sacral vertebrae, as is also observed in other sauropods (e.g. *Camarasaurus*, *Tastavinsaurus*, *Tehuelchesaurus*; Osborn and Mook 1921; Canudo *et al.* 2008; Carballido *et al.* 2011b).

The number of vertebrae that are forming part of the sacrum in SMA 0009 is not clear, but five vertebrae in the adult form can be expected, as this is the number of vertebrae that forms the sacrum of neosauropods, being derived titanosaurs the only

exception (e.g. Salgado *et al.* 1997; Wilson and Sereno 1998; Upchurch *et al.* 2004). Two sacral vertebrae are clearly exposed (Sa-1 and Sa-3). A third sacral vertebra is not well exposed but can be clearly identified (Sa-2). The first sacral vertebra (Sa-1) shows a wider and zipper-like diapophysis, which is interpreted as the articulation with the sacral rib (Fig. 5). The Sa-2 has the transverse process deformed and posteromedially displaced, which is visible in its anterior view (Fig. 5). Two laminae, the SPDL and the PRDL, can be identified on it (Fig. 5). The interpretation of this element as the Sa-2 is also supported by the distance between Sa-1 and Sa-3. The transverse process of the third sacral vertebra (Sa-3) shows a long and curved zipper-like articulation for the sacral rib (Fig. 5). The subsequent vertebra is articulated with Sa-3 and it was not connected to the ilium. This vertebra may be later incorporated to the sacrum as a caudosacral vertebra (Figs 2 and 5), probably before the incorporation of the dorsosacral vertebra, as was suggested for other neosauropods (e.g. *Diplodocus*, *Camarasaurus*; see Wilson and Sereno 1998). Therefore, the sacrum of SMA 0009 was composed only of three sacral vertebrae as in basal sauropodomorphs and as it is expected for an early juvenile sauropod (Wilson and Sereno 1998).

#### Axial skeleton

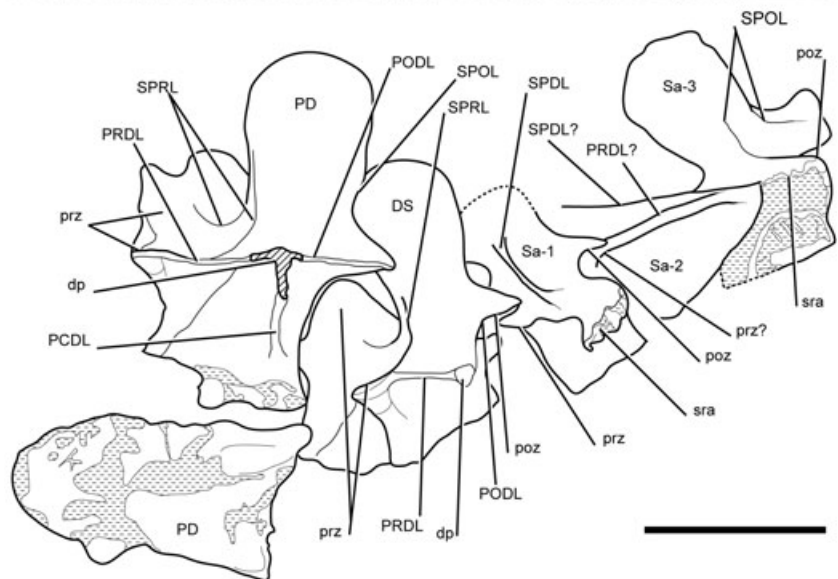
**Cervical vertebrae.** The concave ventral side of the cervical vertebrae is not excavated, and a reduced medial keel is present in C-6, but seems to be absent or greatly reduced in the other cervical centra (Fig. 3D). In ventral view, the cervical vertebrae are more similar to the slightly concave cervical centra of *Camarasaurus* (Upchurch 1995; McIntosh *et al.* 1996) than to the deeply excavated cervical centra of *Giraffatitan brancai* (Janensch 1950) or diplodocids (e.g. *Apatosaurus*, *Barosaurus*; Gilmore 1936; McIntosh 2005). Cervical vertebrae with transversally concave ventral surface were recovered by Upchurch (1998) and Upchurch *et al.* (2004) as a synapomorphic character of flagellicaudatan diplodocoids, convergently acquired in *Giraffatitan*.



**FIG. 4.** SMA 0009, lateral view of the first four dorsal vertebrae, showing the horizontal TPRL of the first dorsal vertebra, and the parapophysis displacement through the dorsal vertebrae. Abbreviations: ACDL, anterior centrodiapophyseal lamina; CPRL, centroprezygapophyseal lamina; dp, diapophysis; indf, infradiapophyseal fossa; nc, neural canal; PCDL, posterior centrodiapophyseal lamina; PCPL, posterior centroparapophyseal lamina; pp, parapophysis; PPDL, paradiapophyseal lamina; PRPL, prezygaparapophyseal lamina; prz, prezygapophysis; TPRL, intraprezygapophyseal lamina. Scale bar represents 30 mm.



**FIG. 5.** SMA 0009, posteriormost dorsal vertebrae and sacral vertebrae. Abbreviations: dp, diapophysis; DS, dorsal vertebra; PCDL, posterior centrodiapophyseal lamina; PD, posterior dorsal vertebra; PODL, postzygodiapophyseal lamina; poz, postzygapophysis; PRDL, prezygodiapophyseal lamina; prz, prezygapophysis; Sa, sacral vertebra; SPDL, spinodiapophyseal lamina; SPOL, spinopostzygapophyseal lamina; SPRL, spinoprezygapophyseal lamina; sra, sacral rib articulation. Scale bar represents 10 mm.



The lateral surface of C-3 bears a deep pleurocoel that is well delimited anteriorly, dorsally and ventrally, but becomes progressively shallower posteriorly (Fig. 3A). The division of the pleurocoel is well visible on the lateral side of the new element (C-3; Fig. 3A). A similar shape of the pleurocoel is present in the subsequent seven cervical vertebrae (C-4 to C-10), but the excavations decrease progressively in depth in posterior cervical vertebrae. Thus, the posterior cervical vertebrae have a shallow fossa, which disappears in the first dorsal vertebrae (Fig. 4). The pleurocoels, even those of more anterior cervical vertebrae, are not as complex as those of *Giraffitan brancai* (Janensch 1950) or diplodocids (e.g. *Diplodocus*, *Apatosaurus*, *Barosaurus*; Hatcher 1901; Gilmore 1936; McIntosh 2005). In these taxa the pleurocoels are divided by several bony septa, giving to them a complex structure. Among diplodocids, *Barosaurus* has the simplest pleurocoels (Lovelace *et al.* 2007), but even in this taxon these are

not as simple as in SMA 0009. The parapophysis of SMA 0009 is dorsally excavated, but lacks the septum that separates this excavation from the lateral fossa of the centrum, as in *Haplocanthosaurus* (Upchurch 1995; Upchurch *et al.* 2004; Harris 2006).

The cervical vertebrae C-3 to C-6 have a triangular and well delimited anterior infraprezygapophyseal fossa which is on both sides of the vertebrae (Fig. 3A, D). A well-developed medial division of the CPRL (mdCPRL) is present (Fig. 3A, D), and connects dorsally with the TPRL. The paired infraprezygapophysial fossae are lateroventrally bounded by the CPRL, medially by the mdCPRL and dorsally by the TPRL. It must be noted that this division of the CPRL is not homologous to the divided infraprezygapophyseal lamina of Upchurch (1995) nor the divided CPRL of Wilson (2002), which dorsally contacts the prezygapophysis and was considered a synapomorphic character of diplodocids (Wilson 2002). In contrast to the divided CPRL, the

mdCPRL (as is observed in SMA 0009) is a widespread feature in the group formed by *Omeisaurus* and more derived sauropods, being only absent in some neosauropod taxa (Harris 2006). Therefore, none of the prepared cervical vertebrae of SMA 0009 present the divided CPRL but show a medial division of the CPRL, a more widespread lamina in sauropods, which is also present in *Giraffatitan*.

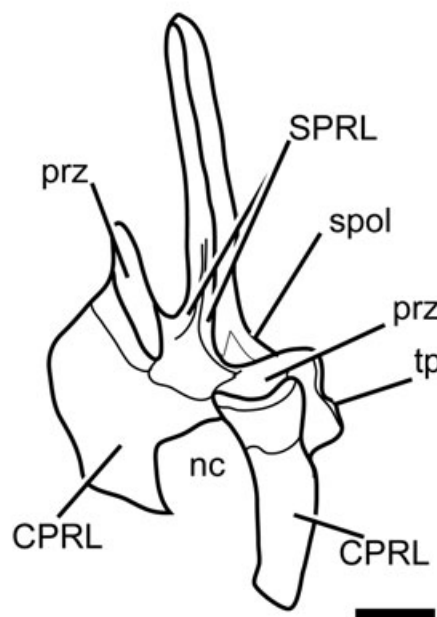
The fully prepared cervical neural spines, which correspond to C-3 until C-6, are single and without any sign of bifurcation (Fig. 3B, C). Among diplodocids, *Barosaurus* is the taxon in which the bifurcation of the neural spine occurs more posteriorly in the cervical series. In *Barosaurus*, the first bifid cervical vertebra is the ninth (McIntosh 2005). If SMA 009 had 16 cervical vertebrae, as in *Barosaurus* (McIntosh 2005) the C-6 should be the ninth cervical vertebrae. Therefore, the absence of bifurcation in C-6 differs from *Barosaurus* or any other valid diplodocid adult taxon (see Harris 2006, table 1). If, to compare with *Camarasaurus*, the total number of cervical vertebrae of SMA 0009 is assuming as 12, the neural spine of the C-6 should be compared with the seventh cervical element of this taxon. In *Camarasaurus*, the fifth cervical vertebra shows a shallow notch (Osborn and Mook 1921), whereas in the seventh cervical vertebra the neural spine is completely divided. Therefore, the absence of bifid neural spines in SMA 0009 indicates either a late appearance of this character or a difference with both diplodocid sauropods and *Camarasaurus*. As it cannot be known if the posteriormost cervical vertebrae present a bifid neural spine, this character was not scored leaving it as missing data and do not influencing the phylogenetic analysis (see below).

**Cervical ribs.** No complete cervical ribs could be observed, but the cervical rib of C-7 (Fig. 2) is the most complete exposed rib and its distal part disappears underneath C-9. This rib is articulated to the centrum and reaches the posterior articular surface

of the following cervical centrum. Therefore, the cervical ribs of SMA 0009 are at least as long as two cervical centra, probably even longer, and clearly differ from the short cervical ribs distinctive of adult diplodocoid sauropods (e.g. Wilson 2002).

**Dorsal vertebrae.** The first six dorsal centra (D-1 to D-6) are visible in lateral view and only a very shallow lateral excavation is present in D-1 and D-2 (Fig. 4). The highly developed anterior convexity, observed in the posterior dorsal centrum (Fig. 5), indicates that the opisthocoelous condition of SMA 0009 reaches the posterior dorsal vertebrae. Opisthocoelous posterior dorsal vertebrae are commonly recovered as a synapomorphic character of macronarian sauropods (e.g. Salgado *et al.* 1997; Wilson 2002). Among neosauropods, they evolved convergently in the diplodocid *Supersaurus*, in which represents an autapomorphic character (Lovelace *et al.* 2007). In *Barosaurus* and *Apatosaurus*, the last opisthocoelous dorsal vertebra is the fifth (Gilmore 1936; McIntosh 2005). In *Haplocanthosaurus*, a well-developed convexity in the anterior articular surface of the centrum can be observed as far back as the sixth dorsal vertebra (Hatcher 1903). Therefore, the opisthocoelous condition of SMA 0009 resembles the state present in macronarian sauropods or in *Supersaurus*, but lacks the ventral keel observed in the later taxon (Lovelace *et al.* 2007).

The laminae and fossae of the neural arches of the dorsal vertebrae are heavily reduced, especially in more posterior vertebrae (Figs 4 and 5). The ACDL is only present in D-1 (Fig. 4). In this vertebra, the ACDL contacts ventrally the CPRL, which is a stout and completely undivided lamina exposed in the D-1, D-3 and D-4 (Fig. 4). The same shape is observed in the posterior dorsal neural arches, in where the CPRL is a single lamina, which is not dorsally divided (Fig. 6). The ACDL extends from the anterior margin of the centrum up to the ventral side of the transverse process and contacts the PCDL below the diapophysis (Fig. 4). In D-2, the parapophysis takes a more dorsal position



**FIG. 6.** SMA 0009, posterior dorsal vertebra (PD of figure 5) in anterior view, showing its lateromedial compressed neural spine, and the absence of spinodiapophyseal lamina. Abbreviations: CPRL, centroprezygapophyseal lamina; prz, prezygapophysis; SPOL, spinopostzygapophyseal lamina; SPRL, spinoprezygapophyseal lamina; tp, transverse process. Scale bar represents 10 mm.

and the PCDL becomes substituted by the PDDL (Fig. 4). The PDDL, well developed in the second dorsal vertebra, is virtually absent in the following dorsal vertebrae (Fig. 4). The ACPL is not present in the D-2, owing to the relatively low position of the parapophysis. These morphological changes in the position of the parapophysis and its related laminae corroborate the identification of this vertebra as the first dorsal vertebra, as the same changes are observed through the first four dorsal vertebrae of other sauropods (e.g. *Diplodocus*, *Haplocanthosaurus*, *Camarasaurus*; Hatcher 1901, 1903; Osborn and Mook 1921). In D-1, the infradiapophyseal fossa is only shallowly excavated and surrounded by the ACDL and the PCDL. Another more anterior fossa, the lateral infraprezygapophyseal fossa, is observed in the first dorsal vertebra and is surrounded by the CPRL (anteriorly), the PRDL (dorsally) and the ACDL (posteriorly). In D-2, the infradiapophyseal fossa, although much reduced, is also present, but the ACDL is replaced by the PDDL, which forms the posterior margin of this fossa. In more posterior dorsal vertebrae, the PDDL is virtually absent and these two fossae are shallow and not well delimited. The PCDL is present and well developed in all the dorsal vertebrae in which the neural arches are visible. When the parapophysis is connected to the neural arch (in D-2), another lamina emerges, the PCPL (Fig. 4). This lamina is present at least until D-6 and is not observed in the posterior dorsal vertebra or in any of the following axial elements. The PCPL is very weakly developed and visible as a product of the shallow excavation present below this lamina and above the dorsal centrum. The presence of this lamina was recovered by Wilson (2002) as an unambiguous character of Diplodocidae, and thus its presence in SMA 0009 was regarded as one of the characters which allow its inclusion in diplodocids (Schwarz *et al.* 2007). Nevertheless, this lamina is convergently acquired in some taxa (i.e. *Jobaria*, *Rebbachisaurus*, *Brachiosaurus*, *Euhelopus*, *Saltasaurus* and *Opisthocoelecaudia*). In fact, this lamina was recovered as an ambiguous synapomorphy of *Jobaria* and more derived sauropods (Wilson 2002, data matrix). In the better preserved middle and posterior dorsal vertebrae of *Brachiosaurus* this lamina can be identified (FMNH P 25107; contra Taylor 2009), whereas in *Giraffatitan* its presence seems to be variable in the dorsal series (Taylor 2009).

Only two dorsal neural spines can be observed and both are exposed in lateral view. These neural spines pertain to the posterior dorsal vertebra and the dorsosacral vertebra. The posterior dorsal neural spine is also visible in anterolateral view (Fig. 6). The neural spines of these vertebrae are extremely simple, resembling the condition of nonsauropod sauropodomorphs (e.g. *Plateosaurus*; Galton 2000), in which the spine is anteroposteriorly longer than wide (Figs 5 and 6). Among sauropods, this kind of neural spine is only present in *Jobaria*, *Galvesaurus*, *Euhelopus* and *Tehuelchesaurus* (Sereno *et al.* 1999; Barco *et al.* 2005; Barco 2009; Wilson and Upchurch, 2009; Carballido *et al.* 2011b), and was not described for any sauropod from the Morrison Formation. An interesting difference of the neural spine of SMA 0009, when compared to those sauropods with lateromedial narrow dorsal neural spines, is the complete absence of the SPDL in this specimen. The presence of the SPDL was regarded as a synapomorphic character of *Barapasaurus* and more derived sauropods (Wilson 2002). Nevertheless, its presence in *Isanosau-*

*rus* and *Tazoudasaurus* indicates a more widespread character, being recovered as a synapomorphy of *Isanosaurus* and more derived sauropods, only missing in the basal sauropod *Shunosaurus* (Allain and Aquesbi 2008) and *Cetiosaurus oxoniensis* (Upchurch and Martin 2002).

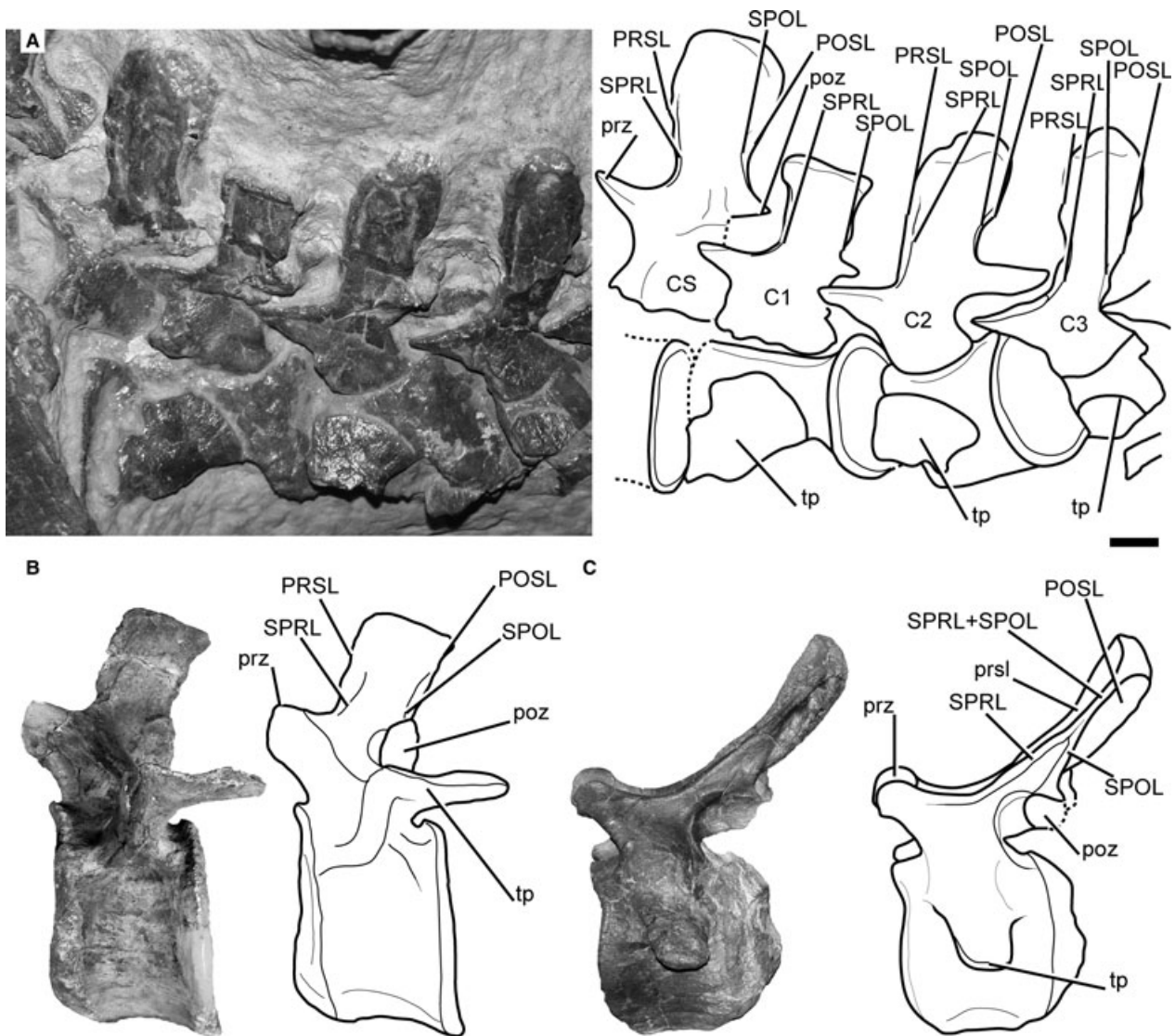
*Sacral vertebrae.* The sacral vertebrae are only slightly exposed in lateral view, and few observations can be made about their neural arches (Fig. 5). As noted above, only three vertebrae were probably connected to the ilium at the time when the animal died. Nevertheless, five sacral vertebra are expected for an adult neosauropod (e.g. Wilson and Sereno 1998; Wilson 2002; Upchurch *et al.* 2004). For this reason, it is likely that two additional vertebrae could have been incorporated to the sacrum in a later ontogenetic stage. Assuming the model proposed by Wilson and Sereno (1998), which is based on *Camarasaurus*, *Diplodocus* and *Apatosaurus*, the first vertebra to be incorporated would be the last dorsal (here described as the dorsosacral), followed by the first caudal (here described as the caudosacral).

The first sacral vertebra, as it has been identified here, has a relatively large and wrinkled tip of the transverse process, identified as a sacral rib articulation (Fig. 5). We identified this scar as a sign that this vertebra was, at least to some degree, connected with the ilium. This first sacral vertebra shows a well-visible SPDL, while the neural spine seems to be flat as in dorsal vertebrae (Fig. 5). The SPDL seems to slightly converge with the SPOL, and these two laminae seem contact each other, as in the third sacral vertebra (Fig. 5). Although no complete sacral centrum can be observed, the neural spines are definitively short, being no longer than twice the length of the centrum. The presence of higher sacral neural spines was recovered as an ambiguous synapomorphy of diplodocoids (e.g. Wilson 2002; Upchurch *et al.* 2004). This character was recovered as ambiguous owing to the absence of information in rebbachisaurids, and not as product of a character conflict in diplodocoids, which have high sacral neural spines. Hence, the shorter neural spines of SMA 0009 clearly differ from the condition of the sacral neural spines of diplodocoids, being thus similar to that of nondiplodocoid sauropods.

*Caudal vertebrae.* Several diplodocid characters of the caudal vertebrae are absent in SMA 0009. The platycoelous anterior caudal vertebrae (slightly hollowed at each end *sensu* Romer 1956; Fig. 7) are distinctive from the procoelous condition of the anterior caudal vertebrae of adult diplodocids (e.g. Wilson 2002; Upchurch *et al.* 2004; Harris 2006) or the weakly procoelous condition of the anterior caudal vertebrae of nondiplodocid adult flagellicaudatans (Harris 2006).

Another important difference between this specimen and flagellicaudatan sauropods is the absence of dorsoventrally high caudal transverse processes in SMA 0009 (the 'wing-like' process of Wilson 2002). The transverse processes of the first caudal vertebra of SMA 0009, and to a lesser degree the second caudal vertebra, are anterodorsally oriented from the posterior half of the centrum, in which are almost entirely placed (Fig. 7). This orientation of the transverse processes resembles that of *Brachiosaurus* and *Giraffatitan* (Riggs 1903, pl 75; Janensch 1950, pl. 3), being different from the more vertical or slightly posterodorsally





**FIG. 7.** A, SMA 0009, lateral view of the caudosacral vertebra (CS) and the three anteriormost caudal vertebrae (C1–C3). B, *Giraffatitan brancai* anterior caudal vertebra (MB.R. 2921.1) in lateral view. C, Diplodocid anterior caudal vertebra (SMA 0003) in lateral view. Abbreviations: POSL, postspinal lamina; poz, postzygapophysis; PRSL, prespinal lamina; prz, prezygapophysis; SPOL, spinopostzygapophyseal lamina; SPRL, spinoprezygapophyseal lamina; tp, transverse process. Scale bar of A represents 10 mm, B and C not in scale.

oriented transverse process of *Camarasaurus* (Osborn and Mook 1921, pl. 77) and diplodocids (e.g. *Apatosaurus*, *Diplodocus*; Gilmore 1936, pl. 26; Osborn 1899, pl. 25). Therefore, the transverse processes of the anterior caudal vertebrae are simple structures as were described recently for *Brachiosaurus* and thus differing from the most complex structure of diplodocoids (Gallina and Otero 2009).

Anteriorly placed neural arches, as are present in SMA 0009, were regarded as a synapomorphic character of titanosauriform sauropods (Upchurch 1995; Upchurch *et al.* 2004). Therefore, the caudal vertebrae of SMA 0009 differ from the centrally placed neural arches of nontitanosauriform neosauropods, which maintain almost the same distance from the anterior and posterior ends.

The caudal neural spines of SMA 0009 are relatively simple and lack several diplodocid characters. As in *Jobaria* and more derived sauropods (Wilson 2002), the prespinal and postspinal laminae are present in this specimen. A short and weakly developed lamina extends from the prezygapophysis up to the neural spine. This lamina, the SPRL, is commonly regarded as absent in nondiplodocid sauropods (e.g. Wilson 2002, character 121; Harris 2006, character 174). Nevertheless, the SPRL is present as a strongly reduced lamina, at least in macronarian sauropods (e.g. *Camarasaurus*, *Brachiosaurus*, *Giraffatitan*, *Andesaurus*, *Saltasaurus*). In these taxa, a thin lamina extends from the dorsomedial edge of the prezygapophysis up towards the neural spine. Indeed, although it is weakly developed, the SPRL is present in these taxa, as well as in SMA 0009. The SPRL vanishes quickly



over the anterolateral border of the PRSL, without reaching the dorsoventral mid-point of the neural spine (Fig. 7A, B). Therefore, the SPRL is present in SMA 0009, but differs from the well-developed SPRL present in flagellicaudatan diplodocoids. In this group, the SPRL is distinctively developed, running from the prezygapophysis up to the dorsal margin of the neural spine and extends over its lateral margin (Fig. 7C).

Like the SPRL, the SPOL of SMA 0009 is weakly developed and merges laterally with the POSL. These two weakly developed laminae run almost parallel to each other, disappearing dorsally in the neural spine far from each other and without any kind of contact (Fig. 7A, B). Contrary to that, these laminae contact each other in diplodocid sauropods (Wilson 2002; Upchurch *et al.* 2004). In this group of sauropods, a composite lamina (SPOL + SPRL) runs up to the dorsal end of the neural spine onto the lateral side of it, being a well-visible lateral lamina (Fig. 7C). Therefore, the amphicoelous condition of the anterior caudal vertebrae, the anteriorly positioned neural arches in the middle and posterior caudal vertebrae, the absence of a well-developed lateral SPRL and therefore the lack of the composite lateral lamina distinguish SMA 0009 from diplodocid sauropods, especially from diplodocids.

#### Limbs and girdles

As most of the new information comes from the axial skeleton, only a few comments on some of the nonaxial elements will be included here.

**Scapula.** The shape of the scapula was used by Schwarz *et al.* (2007) as one of the diplodocid characters present in SMA 0009. In this specimen the scapular blade does not present a distal expansion, which is present and well developed in *Camarasaurus* and *Brachiosaurus*. Instead of this, the edges of the scapular blade slightly diverge towards the distal part but without the expansion present on the acromion side, resembling the scapular blade of diplodocids. Nevertheless, the tuberosity present in the acromion side of the scapula is not observed in any other known sauropod and could represent an early stage in the expansion of the scapular blade. This expansion is completely absent in the bone, but probably had been present as a cartilaginous structure owing to the young age of the specimen.

**Humerus.** The humerus of SMA 0009 is not as gracile as in *Brachiosaurus* or *Giraffatitan* but either as robust as those of diplodocids. The robustness index (*sensu* Wilson and Upchurch, 2003) is about 0.29 (Table 1). This value is similar to that of other basal camarasauromorphs (e.g. *Camarasaurus*, *Tehuelchesaurus*), being more robust than that of brachiosaurids (see Table 1). Compared with diplodocids the humerus of SMA is more robust than that of *Barosaurus*, but more slender than *Apatosaurus* (Table 1). The ratio of the humerus length to femur length of SMA 0009 is 0.86 (Table 1). This indicates a relatively longer humerus than that of diplodocids (Table 1). When compared with basal camarasauromorphs (e.g. *Camarasaurus*, *Tehuelchesaurus*), the humerus of SMA 0009 is relatively longer. Among more derived forms, the humerus is not as long as that

**TABLE 1.** Relative measurements of the humerus in basal macronarian and diplodocid sauropods.

Taxon	R. I.	H-F. R.	References
SMA 0009	0.29	0.86	Schwarz <i>et al.</i> (2007)
<i>Camarasaurus</i>	0.29	0.70–0.76	McIntosh <i>et al.</i> (1996)
<i>Tehuelchesaurus</i>	0.31	0.72	MPEF-PV 1125
<i>Brachiosaurus</i>	0.22	1	Riggs (1904) and Wilson and Upchurch (2003)
<i>Chubutisaurus</i>	0.24	0.86	Carballido <i>et al.</i> (2011a)
<i>Cedarosaurus</i>	0.21	0.99	Tidwell <i>et al.</i> (1999)
<i>Apatosaurus</i>	0.35	0.62–0.65	Gilmore (1936) and Schwarz <i>et al.</i> (2007)
<i>Barosaurus</i>	0.23	0.72	McIntosh (2005)

R. I. = average of the greatest widths of the proximal end, mid-shaft and distal end of the humerus/total length of the humerus (*sensu* Wilson and Upchurch 2003).

H-F. R. = Humerus to femur ratio.

of *Brachiosaurus* or *Cedarosaurus* (Table 1), but similar to basal titanosauriforms (e.g. *Chubutisaurus*; Table 1) and closer forms (Carballido *et al.* 2011a).

**Metacarpals.** The metacarpals of SMA 0009 are relatively shorter, as in diplodocids (e.g. *Apatosaurus*; Upchurch *et al.* 2004). This low ratio between the metacarpal I and the radius is similar to that of non-neosauropods, diplodocids (Harris 2006) and *Camarasaurus* (0.26; McIntosh *et al.* 1996), but differs greatly from the higher ratio observed in *Giraffatitan* (0.51; Apesteguía 2005).

**Ilium.** The ilium of SMA 0009 is dorsally flattened instead of being bent as in diplodocids, thus being more similar to *Brachiosaurus* in which the ilium is forming a more rectangular shape, and the pubic peduncle is elongated and gracile as in brachiosaurids (Taylor 2009).

**Femur.** The femur of SMA 0009 does not have the lateral bulge but the shaft is medially straight in the proximal half of the femur. The presence of this bulge was recovered as a titanosauriform synapomorphy (e.g. Salgado *et al.* 1997, character 16; Wilson 2002, character 199). This bulge is absent in *Brachiosaurus altithorax* but present in *Giraffatitan brancai* (Taylor 2009). This character seems to have evolved early in macronarian evolution, as it is present in *Tehuelchesaurus* and other basal nontitanosauriform camarasauromorphs (Carballido *et al.* 2011b). The absence of this bulge was considered as a reversal to the plesiomorphic condition in *Brachiosaurus altithorax* (Taylor 2009). Its absence in SMA 0009 suggests a relationship with either camarasauromorphs less derived than *Tehuelchesaurus* (e.g. *Camarasaurus*), or with *Brachiosaurus altithorax*. The femur of SMA 0009 is strongly anteroposteriorly compressed, with its anteroposterior length less than the half of the mediolateral width. The presence of strongly anteroposteriorly compressed femora was regarded as a saltosaurid synapomorphy (Wilson 2002), but its presence in several titanosauriforms (e.g. *Phuwiangosaurus*, *Paluxysaurus*,

*Giraffatitan brancai*, *Brachiosaurus altithorax*; Martin *et al.* 1999; Rose 2007; Taylor 2009) indicates that this condition is present in a more inclusive group (Carballido *et al.* 2011a). The presence of this character in SMA 0009 indicates a closer relationship with this group.

## SYSTEMATIC AFFINITIES OF SMA 0009

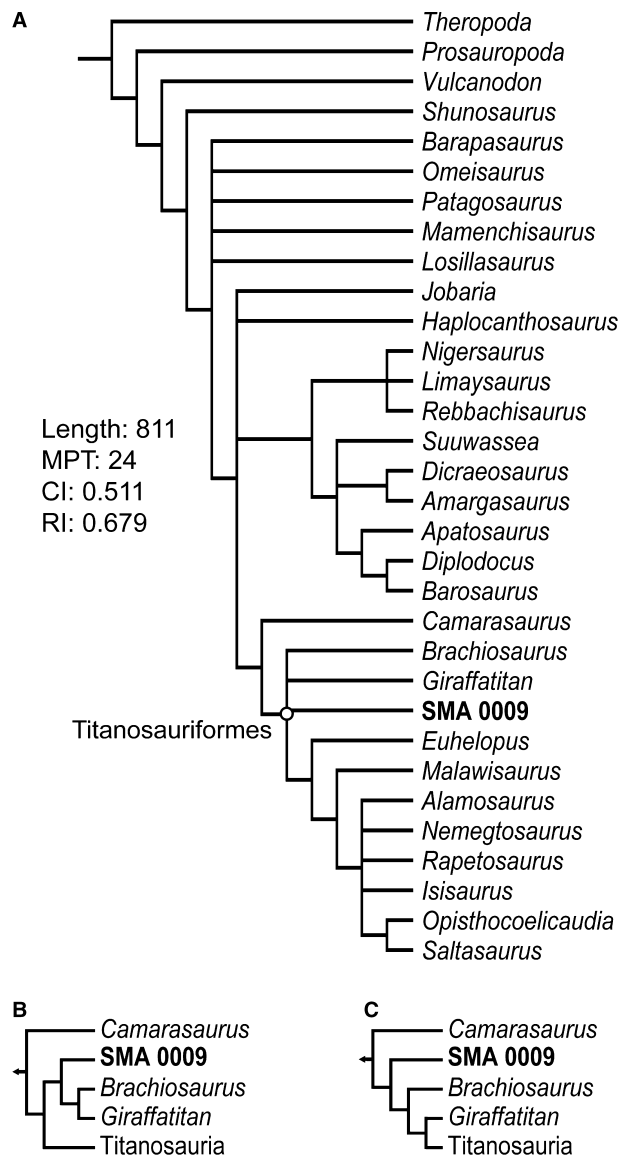
The preparation of SMA 0009 yielded new anatomical information which sheds doubt on the previous systematic assignment of this specimen. As noted by Schwarz *et al.* (2007), many of the skeletal characters are likely to have undergone ontogenetic changes, therefore giving an ontogenetic bias respect to its mature osteological signal. The amount of these morphological changes and most affected regions are far from being known in sauropods in particular and dinosaurs in general. Part of this lack of knowledge is related to the few existing early juvenile sauropod remains, given that most studies are based on late juvenile to subadult specimens mainly known from isolated bones (e.g. Carpenter and McIntosh 1994; Foster 2005; Ikejiri *et al.* 2005). Many of these changes may be predicted, but only with a robust systematic assignment and by comparisons with related adult taxa. The systematic position of the specimen SMA 0009 must be evaluated taking all the morphological characters into account and comparing them with adult forms. Thus, a phylogenetic analysis was conducted to evaluate the systematic signal presented by SMA 0009 and its most probable position among sauropod dinosaurs.

### Phylogenetic analysis

The systematic position of SMA 0009 and its phylogenetic relationships were tested through a cladistic analysis using the data matrix of Harris (2006), which was modified by Taylor (2009) to split '*Brachiosaurus*' in *Giraffatitan brancai* and *Brachiosaurus altithorax*. The information of *Brachiosaurus* was modified for characters 141 and 149 (see Appendix S1). Three new characters, referred by Taylor (2009) as apomorphies of brachiosaurids and *Brachiosaurus*, were added (see Appendix S2). The coding for SMA 0009 is provided in Appendix S3. The lack of knowledge about how the skeleton changed through ontogeny, especially in its early stages, makes it impossible to decide which character could be discarded or scored as ambiguities. Therefore, all characters of SMA 0009 were scored as they are present and observed.

An equally weighted parsimonious analysis was conducted using TNT v.1.1 (Goloboff *et al.* 2008a, b). The heuristic tree search was performed starting from 1000 replicates of Wagner trees (with random addition

sequence of taxa) followed by branch swapping (TBR) and saving ten trees per replicate. This procedure retrieved 24 most parsimonious trees of 811 steps each (CI: 0.511; RI: 0.679), found in the 95 per cent of the replicates. These trees were submitted to a final round of TBR that failed to find additional optimal trees. The strict consensus obtained does not show any difference to that of Harris (2006) and Taylor (2009), except for the relationships within Brachiosauridae and the inclusion of SMA 0009. In the strict consensus the specimen SMA 0009 is placed as a basal titanosauriform, in a polytomy with *Brachiosaurus*, *Giraffatitan* and Somphospondyli (Fig. 8A). Two different



**FIG. 8.** Results of the phylogenetic analysis. A, the strict consensus tree and the relationships of SMA 0009 with basal titanosauriforms. B–C, two possible resolutions for the polytomy obtained at the base of titanosauriforms.

resolutions are possible for this polytomy. In the first one the monophyly of Brachiosauridae is recovered (Fig. 8B), as was recently suggested by Taylor (2009) and is widely accepted (e.g. Wilson 2002; Upchurch *et al.* 2004; Ksepka and Norell 2010). In this resolution, SMA 0009 is placed as the most basal brachiosaurid. The second possible resolution (Fig. 8C) places SMA 0009, *Brachiosaurus* and *Giraffatitan* as successive sister taxa of Somphospondyli, depicting a paraphyletic Brachiosauridae.

Because the specimen is a very young sauropod an ontogenetic bias is expectable, obscuring the real phylogenetic signal of the adult forms. No extra evidence is available to prefer one of these two hypotheses, as both are equally parsimonious. Nevertheless, the first resolution (Fig. 8B) is the one which fits best to the current knowledge and the generally accepted sister group relationship of *Brachiosaurus* and *Giraffatitan*. While we are open to the possible paraphyly of these taxa, we do not believe that the information provided by this specimen can be used to reject or question the validity of this grouping. Therefore, the following discussion is based in the topology in which Brachiosauridae is recovered (Fig. 8B). This position clearly differs from the previously proposed one, in which the specimen had been suggested to be a diplodocid.

To test and compare the current phylogenetic position of SMA 0009 with the one proposed previously, a constrained parsimony analysis was conducted. In this analysis, SMA 0009 was forced to be a diplodocid sauropod followed by an identical heuristic tree search like the one described above. As a result, four most parsimonious trees of 827 steps were obtained, resulting in a considerably suboptimal topology, which requires 16 extra steps. If SMA 0009 is forced to be a flagellicaudatan sauropod, 12 extra steps are required, also resulting in a markedly suboptimal topology. To test if these topologies provide a strong worse explanation of the character data, a Templeton test was conducted following the protocol summarized in Wilson (2002). The results of the test indicate that both constrained topologies can be rejected by the data with 95 per cent of confidence ( $p < 0.05$ ), either if SMA 0009 is placed among diplodocids ( $p = 0.0005$ ) or within the more inclusive group of flagellicaudatan ( $p = 0.0026$ ). Therefore, when SMA 0009 is compared with adult sauropods, the present dataset clearly rejects its placement within flagellicaudatan, as is a less parsimonious hypothesis. The exclusion of SMA 0009 from diplodocids is supported by the absence of several characters in the specimen, as was described above (e.g. procoelous anterior caudal vertebrae; well-developed and lateral SPRL which contacts the SPOL forming a composed lateral lamina).

The closer affinities of SMA 0009 with brachiosaurid sauropods suggest either an assignment of this specimen to *Brachiosaurus altithorax*, or the presence of a new

taxon closely related to this group. The latter hypothesis cannot be completely ruled out, but as the specimen comes from the Morrison Formation (one of the most intensively worked units and with a well sauropod fauna), this hypothesis is provisionally discarded. Recently, Taylor (2009) provides a complete re-evaluation of *Brachiosaurus* and *Giraffatitan* presenting an updated diagnosis for these taxa and for Brachiosauridae.

As was noted in the description, several of the brachiosaurid characters are present in SMA 0009 (e.g. undivided CPRL in dorsal vertebrae; anteroposteriorly compressed femora; elongated and compressed pubic peduncle of the pubis). SMA 0009 solely lost the relatively long humerus characteristic of this group. Nevertheless, the ratio of the humerus length divided the femur length of SMA 0009 (0.80) is not as higher as in brachiosaurids (0.9 or higher) but is slightly higher than the ratio of *Camarasaurus* (0.76; McIntosh *et al.*, 1996).

SMA 0009 can be assigned to *Brachiosaurus* (Fig. 9) by the presence of most of the characters diagnosing this taxon (Taylor 2009; e.g. presence of a distinct tubercle in the postacetabular region of the ilium, which is present in SMA 0009 as a coarse crest; absence of POSL; vertically oriented dorsal neural spines; ilium with a subtle notch between the ischiadic peduncle and the postacetabular lobe of the ilium; straight lateral margin of the femur shaft). There are solely few characters in the diagnosis of *Brachiosaurus* which are not observed in SMA 0009. These mainly are related with different morphologies in the laminae pattern of the dorsal neural spines (e.g. SPDL-SPOL contact; mediolateral expanded and laterally triangular neural spine), being these the greatest differences of SMA 0009 with *Brachiosaurus*. These differences are interpreted as product of the ontogenetic status of SMA 0009 and are discussed below.

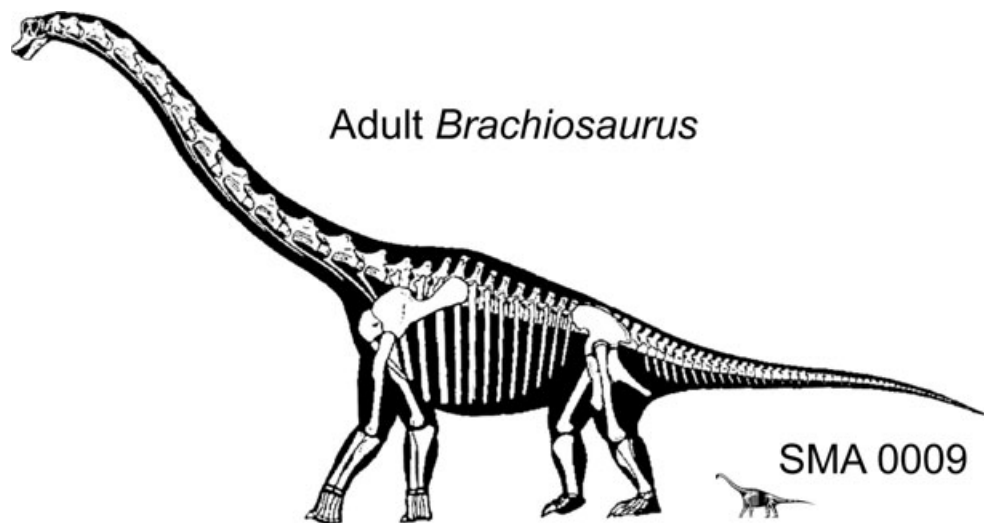
## ONTOGENETIC CHANGES IN BASAL TITANOSAURIFORMS

Into the current systematic assignment of SMA 0009, as either a baby *Brachiosaurus* specimen or a closer related form, some of the major transformations that the individual would undergo during its ontogeny can be predicted. The major morphological transformations (i.e. differences with adult brachiosaurids) are discussed below, as they can bring some light about the ontogenetic changes of, at least, basal titanosauriform sauropods.

### *Development of pneumatic structures*

As it was previously noted, the cervical pleurocoels of SMA 0009 are divided, but at the same time are extremely





**FIG. 9.** Reconstruction of *Brachiosaurus altithorax* adult skeleton, and the specimen SMA 0009, showing the size difference between them. Restorations were modified from that of *Brachiosaurus* in Wilson and Sereno (1998).

simple when compared with *Camarasaurus*, brachiosaurids and nondicraeosaurid diplodocoids. Another important pneumatic character absent in SMA 0009 is the total absence of pleurocoels in dorsal centra. The absence of pneumatic structures in SMA 0009 is regarded as product of the early ontogenetic state of the specimen and was extensively discussed by Schwarz *et al.* (2007).

#### *Morphology of the dorsal neural spine*

Two characters related to the development of the neural spine of dorsal vertebrae are the most striking features of SMA 0009. As it was noted in the description, the neural spine of the posterior dorsal vertebra (Figs 4 and 5) and the neural spine of the dorsosacral vertebra (Fig. 5) are extremely lateromedial compressed, being eight times anteroposteriorly longer than lateromedially wide (Harris 2006, character 154). This is an unusual character for a eusauropod, as the presence of wider neural spines was recently recovered as a synapomorphy of Gravisauria (Allain and Aquesbi 2008). Among neosauropods, slender neural spines were only reported for *Jobaria*, *Tehuelchesaurus*, *Galvesaurus* and *Euhelopus*, all of them adult specimens, as the size and morphology reveals. Thus, the shape of the neural spine of SMA 0009 is a very uncommon character among neosauropods and was not described for any taxa from the Morrison Formation. The SPDL of the dorsal neural spine of SMA 0009 is completely missing, as is evident in the posterior dorsal vertebra and dorsosacral neural spine (Figs 5 and 6). As previously noted, the presence of this lamina was recently suggested as a synapomorphic character of *Isanosaurus* and more derived sauropods, with only one reversion to

the plesiomorphic condition in *Shunosaurus* (Allain and Aquesbi 2008) and *Cetiosaurus* (Upchurch and Martin 2002).

The absence of SPDL in SMA 0009 can be interpreted in two different ways; either as one of the strongest autapomorphies of a new sauropod taxon from the Late Jurassic, or just as a morphological ontogenetic change. The first explanation cannot be rejected, as it is also valid for all the other autapomorphic characters recovered in the analysis. However, there are no neural spine elements from the Morrison Formation which present this characteristic. Additionally, the second explanation can be more extensively discussed and some evidence to its favour can be observed. The origin of the SPDL is not certain and recently Salgado and Powell (2010) interpreted the origin of this lamina in two different ways, recognizing two different laminae, posterior and an anterior SPDL. The first one is present in some titanosaurs and is originated as a splitting of the PODL. The second one has a more anterior origin, close to the SPRL, and would be present in diplodocoids and some titanosaurs. The specimen described here does not show any incipient SPDL in its dorsal neural spines, nor does it show them close to the SPRL or to the PODL (Fig. 5). The basal sauropod *Tazoudasaurus*, from the Early Jurassic of Morocco, presents a reduced SPDL in anterior dorsal vertebrae of the adult specimens, but this lamina is missing in the preserved neural arch of the small juvenile specimen (Allain and Aquesbi 2008). Additionally, the SPDL is only weakly developed in an isolated and very small juvenile neural arch of the basal camarasauromorph *Europasaurus holgeri* (DFMMh/FV 243), whereas this lamina is well developed in the middle dorsal vertebrae of adults (Sander *et al.* 2006). The lack of further hatchling and early juvenile

sauropod remains makes it impossible to do additional comparisons.

Whereas the SPDL is not present in SMA 0009, this lamina seems to be present in later ontogenetic stages of nonadult sauropods (e.g. Foster 2005; Lehman and Coulson 2002). Therefore, the available evidence seems to show that the SPDL first appears in early ontogenetic stages but this lamina is not present at the time of birth, as it is absent in SMA 0009, and the juvenile *Tazoudasaurus*. Although it is not known yet which of these two characters (the wide neural spine or the SPDL) appears first through the ontogeny of sauropods, some preliminary ideas can be made. The presence of SPDL in the lateromedially compressed neural spines of some sauropod (e.g. *Tehuelchesaurus*, *Galvesaurus*) could indicate that the origin of the SPDL precedes the widening of the neural spine. This is also supported by the fact that this lamina and the SPOLE are forming the wide lateral margin of the neural spine of most eusauropods, and the presence of this lamina in the mediolaterally compressed sacral neural spines of SMA 0009. If this is the case, the compressed neural spine which is present in some taxa (i.e. *Jobaria*, *Tehuelchesaurus*, *Galvesaurus* and *Euhelopus*) could indicate retention of the juvenile condition in these forms.

#### *Changes in proportions*

Although an extensive discussion on the changes in bones proportion lies outside the scope of this contribution, few major changes respect to the current systematic position of the specimen are here mentioned.

*Cervical vertebrae elongation.* As was noted by Schwarz *et al.* (2007), the cervical vertebrae of SMA 0009 are extremely short when they are compared with dorsal vertebrae. This was interpreted as a strong positive allometric growth in the neck, but a negative allometric growth in dorsal vertebrae (Schwarz *et al.* 2007), as was noted by Ikejiri (2004) for *Camarasaurus*. Based on the systematic position proposed here for SMA 0009 we suggest that this allometric growth might have occurred also, at least, in basal titanosauriform sauropods. Additionally, basal titanosauriforms show relatively longer cervical vertebrae with elongations indexes (= EI *sensu* Upchurch 1998) greater than 4 (e.g. Wilson 2002; Harris 2006). The elongations indexes of middle cervical vertebrae of SMA 0009 are around 1.8, whereas the middle cervical vertebrae of *Giraffatitan* have an elongation index of around 4.5. Although no cervical vertebrae were described for *Brachiosaurus*, the referred unpublished cervical vertebrae are indistinguishable from those of *Giraffatitan* (Taylor 2009). This suggests a strong positive allometric growth in the anteroposterior length of cervical vertebrae respect

to its dorsoventral height in brachiosauridae and possible basal titanosauriforms.

*Elongation of the humerus.* As was noted, the humerus of SMA 0009 is more robust than that of titanosauriform sauropods. Isometric growth patterns in sauropod limb bones were recently proposed (Bonnar 2004; Kilbourne and Makovicky 2010). These results are mainly based in some basal sauropodomorphs and within neosauropod, diplodocids and *Camarasaurus*. Within the current systematic position of SMA 0009, the high robustness index observed in the humerus of the specimen and its comparison with *Brachiosaurus* indicates an allometric growth. Therefore, and contrary to diplodocoids and basal macronarian sauropods, the slender humerus observed in brachiosaurids and closer related forms (e.g. *Cedarosaurus*) seems to be the product of an allometric growth of this bone, at least during early ontogenetic stages.

As was noted in the description, the ratio of the humerus length to femur length of SMA 0009 is similar to that observed in basal titanosauriform sauropods, but not as high as in brachiosaurid sauropods. Therefore, a positive allometric growth of the humerus respect to the femur seems to be the responsible of the longer humerus present in brachiosaurid sauropods. Nevertheless, the relatively longer humerus of this specimen may indicate either that this bone was relatively long at birth or that the allometric growth starts early in the ontogeny.

*Elongation of metacarpals.* The longest metacarpal of SMA 0009 is relatively shorter when compared with the length of the radius (0.33; Schwarz *et al.* 2007). This ratio is the lowest for a neosauropod, as values between 0.35 and 0.45 are widespread observed in the group formed by *Omeisaurus* and more derived sauropods. Even, higher values are present in titanosauriform sauropods (Harris 2006, character 248). Therefore, this might indicate a positive allometric growth in the metacarpals length with respect to radius length.

## CONCLUSIONS

The new information presented here proves that the juvenile specimen SMA 0009 must be excluded from diplodocids. New osteological evidence and re-evaluation of the present characters show that this specimen is instead an ontogenetically young juvenile brachiosaurid sauropod, probably belonging to *Brachiosaurus altithorax*. However, the possibility that the specimen represents a new brachiosaurid taxon or a taxon closely related to brachiosaurids cannot be completely ruled out. Nevertheless, if this is the case, similar general osteology can be expected for such form and therefore not drastically affecting some

of the general conclusions made here about the ontogenetic changes. Such ontogenetically influenced characters mainly include expectable changes of the pneumatic characters at the vertebrae and changes in the overall proportions, but also not previously recorded changes which affect the development of the neural spine.

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*Editor.* Marcello Ruta

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** List of modifications in *Brachiosaurus* to Taylor (2009) data set.

**Appendix S2.** List of characters added to Taylor (2009) data set.

**Appendix S3.** Codification of SMA 0009.

**Appendix S4.** Codification of the new characters added here.

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