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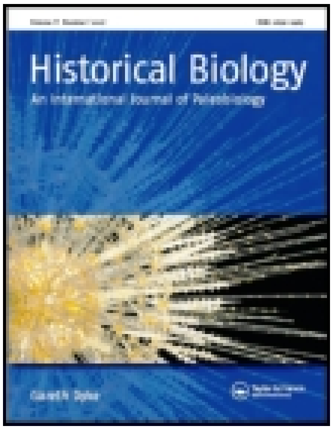

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Shape variation in presacral vertebrae of saltasaurine titanosaurs (Dinosauria, Sauropoda)

V.L. Zurriaguz[ab] & A. Álvarez[bc]

[a] Fundación de Historia Natural Félix de Azara, CEBBAD, Universidad Maimónides, Hidalgo 775, Buenos Aires C1405BCK, Argentina

[b] CONICET, Buenos Aires Argentina

[c] División Mastozoología, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Av. Ángel Gallardo 470, Buenos Aires C1405DJR, Argentina

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Shape variation in presacral vertebrae of saltasaurine titanosaurs (Dinosauria, Sauropoda)

V.L. Zurriaguz[a,b]* and A. Álvarez[b,c]

[a]*Fundación de Historia Natural Félix de Azara, CEBBAD, Universidad Maimónides, Hidalgo 775, Buenos Aires C1405BCK, Argentina;* [b]*CONICET, Buenos Aires, Argentina;* [c]*División Mastozoología, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Av. Ángel Gallardo 470, Buenos Aires C1405DJR, Argentina*

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Titanosaurs were small- to giant-sized sauropods, highly derived and highly pneumatic. Using morphometric analyses, we studied differences in shape of the presacral vertebral centra in some of these sauropods, especially in saltasaurines, and compared asymmetry patterns in lateral pneumatic foramina (LPF) between these titanosaurs and avian and non-avian theropods. Geometric morphometric analyses showed that the cervical centra tend to be elongated and dorsoventrally short, with an elliptical LPF located in the middle of the centrum; dorsal centra tend to be short and higher than the cervical centra, with the LPF slightly displaced to the anterior region. Shape variation can be described as a result of the ordering of the vertebrae within both the cervical and dorsal sequences, and therefore these methods can be applied to predict the position of isolated vertebrae. A persistent pattern of asymmetry among LPF was observed when length–height indexes were plotted. The right LPF are usually larger than those on the left side in the cervical vertebrae (except in *Saltasaurus loricatus*) but variable in the dorsal vertebrae. We propose an explanation of this asymmetry based on the asymmetric arrangement of viscera and late development of the respiratory (and air sacs) system.

Keywords: asymmetry; geometric morphometrics; pneumaticity; presacral vertebrae; Titanosauria

1. Introduction

Sauropoda is a clade of long-necked dinosaurs that inhabited all continents (Upchurch et al. 2004). Within this group lies the Titanosauria that were especially abundant in Gondwana (Powell 1992). Titanosaurs included small-sized sauropods (e.g. *Saltasaurus loricatus* Bonaparte and Powell, 1980; *Rocasaurus muniozi* Salgado and Azpilicueta, 2000) and giant-sized sauropods (e.g. *Argentinosaurus huinculensis* Bonaparte and Coria, 1993; *Futalongkosaurus dukei* Calvo, Porfiri, González Riga and Kellner, 2007). They presented relatively short limb bones; 13 cervical vertebrae, generally short and wide; 10 opisthocoelous dorsal vertebrae; 6 or 7 (in *Neuquensaurus australis*) coossified sacral vertebrae, the seventh being biconvex (at least in *Neuquensaurus*; D'Emic and Wilson 2011) and a shortened tail (Wilson 2002). A monophyletic group of titanosaurs is represented by the South American Saltasaurini (Salgado and Bonaparte 2007) which were sauropods of reduced size, highly derived (Wilson 2002) and highly pneumatic (Cerda et al. 2012).

As occurs in extant birds, titanosaurs (especially saltasaurines) exhibit osteological features in the vertebral spine related to the pneumatisation of bones which, in turn, can be associated with the development of the pulmonary diverticular system (Wedel 2009). Ontogenetically, airs sacs are formed first, diverticula grow out from the air sacs later and skeletal pneumatisation occurs last (Müller 1907; Bremer 1940 in Wedel 2003b). Anatomically, cervical and dorsal vertebrae show lateral pneumatic foramina (LPF), which are located in both lateral sides of the vertebral centra. These foramina are invaded by the lungs in dorsal vertebra of extant birds, and the same was postulated for all remaining saurischians (O'Connor 2006; Benson et al. 2011). In several dinosaurs, as can be seen in many birds, an obvious pattern of asymmetry becomes evident when vertebral LPF are observed. However, this feature has been frequently overlooked and has not been discussed extensively.

Since the diverticular system is not fossilisable, the study of pneumaticity in sauropods has to be carried out mainly using osteological information. Previous studies on these topics remain largely qualitative, focusing on the description of vertebral laminae, fossae and cavities (Wilson 1999, 2012; Wedel 2003a, 2003b, 2006, 2009; Wilson et al. 2011). To our knowledge, there have not been previous attempts of quantitative analyses of vertebral morphology in sauropods, and even less in saltasaurines. Here, we present a geometric morphometric analysis of shape variation of presacral vertebrae of three titanosaur species, two of them representatives of the South American Saltasaurini. In addition, we use a quantitative approach to assess the patterns of asymmetry of LPF in saltasaurines, making comparisons with that observed in avian and non-avian theropods.

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*Corresponding author. Email: vzurriaguz@gmail.com

2. Materials and methods

2.1 *Data-sets*

Three data-sets were used in this work. The first one includes geometric morphometric data from vertebral centra of three titanosaur species: *N. australis* (Powell 1992), *S. loricatus* (Bonaparte and Powell 1980) and *Bonitasaura salgadoi* (Apesteguía 2004). The second includes geometric morphometric data from vertebral LPF of the same species and the third includes an index based on two linear measurements from the vertebral LPF of the same three species, plus the non-avian theropod *Carnotaurus sastrei* (Bonaparte et al. 1990) and two extant avian species, *Cygnus melanocoryphus* and *Chauna torquata*. The analysed materials are housed in ornithological and paleontological Argentinean Collections (a detailed list of material is given in Appendix).

2.2 *Institutional abbreviations*

MCS, Museo de Cinco Saltos, Río Negro, Argentina; MPCA-Pv, Museo de Cipolletti ‘Carlos Ameghino’, Collection of Vertebrate Paleontology, Río Negro, Argentina; MLP-CS, Museo de La Plata, Cinco Saltos Collection, La Plata, Argentina; MLP-Ly, Museo de La Plata, Lydekker Collection; MLP-PV, Museo de La Plata, Anexus to the Ornithological Collection; PVL, Instituto Miguel Lillo, Collection of Vertebrate Paleontology, Tucumán, Argentina; MACN-OR, Museo Argentino de Ciencias Naturales, Ornithological Collection, Buenos Aires, Argentina; MACN PV, Museo Argentino de Ciencias Naturales, National Vertebrate Paleontological Collection.

2.3 *Shape variation of vertebral centra*

Variation in the vertebral centrum shape for both cervical and dorsal vertebrae was analysed using geometric morphometric techniques. Neural arches are missing in most of the material; as such they were not included in the analyses. The total sample consisted of two cervical and four dorsal vertebrae belonging to *N. australis*; five cervical and dorsal vertebrae of *S. loricatus* and two cervical and three dorsal vertebrae of *B. salgadoi* (Table 1). Two-dimensional coordinates of 11 landmarks + 4 semi-landmarks were captured from digital images of the left side in lateral view (Figure 1); when this side was missing or damaged, the reflected image of the right side was used. The *x* and *y* coordinates were digitalised using TPSDIG 2.12 software (Rohlf 2008). To remove differences in location, orientation and scaling (i.e. non-shape variation), we performed a generalised Procrustes analysis (Rohlf and Slice 1990). The resulting Procrustes-shaped coordinates were analysed through principal component analyses. Principal components [i.e. relative warps (RWs)] summarise and describe the major trends in shape variation and facilitate the visualisation of shape ordination in a low-dimensional morphospace. Differences in the shape of vertebral centra among studied titanosaurs were described by means of thin plate splines deformation grids (Bookstein 1991). Morphometric analyses were performed using TPSRELW 1.46 software (Rohlf 2008).

Table 1. Numbers assigned to vertebrae considered in vertebral centra shape analyses.

	Cervical vertebrae	Dorsal vertebrae
B. salgadoi	1 and 2	1–3
N. australis	3 and 4	4–7
S. loricatus	5–10	8–12

Note: These numbers do not reflect anatomical positions.

2.4 *Asymmetry of vertebral pleurocoels*

With the goal of analysing the asymmetry of LPF, we carried out two separate analyses. First, we built an index that represents the ratio between the height and length of each LPF of each cervical and dorsal vertebra (Table 2). These indices were calculated for *Neuquensaurus*, *Saltasaurus* and *Bonitasaura*. In addition, we estimated this index in two extant avian theropods, *Cygnus melanocoryphus* and

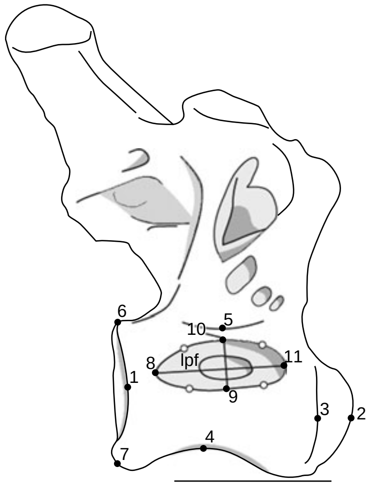

Figure 1. Diagram of landmarks (black circles) and semi-landmarks (white circles) used to represent vertebral and LPF shape. Centrum landmarks: 1: posterior end of centrum, 2: anterior end of centrum including the condyle, 3: midpoint of the anterior end of centrum excluding the condyle, 4: maximum curvature of ventral border of vertebral centrum, 5: maximum curvature of dorsal border of vertebral centrum, 6: dorsal end of cotyle, 7: ventral end of cotyle. LPF landmarks: 8: posterior end of LPF, 9: ventral-most point on ventral side, 10: dorsal-most point on dorsal side, 11: anterior end of LPF. Lines between landmarks 9, 10 and 8, 11 indicate height and length measures of LPF, respectively. LPF, lateral pneumatic foramen. Scale bar: 10 cm.

Table 2. Number of cervical and dorsal vertebrae included in LPF asymmetry plots.

	Cervical vertebrae	Dorsal vertebrae
Chauna torquata	17	7
Cygnus melanocoryphus	19	–
Carnotaurus sastrei	10	10
N. australis	2	6
S. loricatus	8	8

Note: *Cygnus melanocoryphus* lacks LPF in dorsal vertebrae.

Chauna torquata, and in the non-avian theropod, *Carnotaurus sastrei* (Bonaparte et al. 1990). We plotted separately the indexes of right and left LPF of the cervical and the dorsal vertebral series in order to assess the presence of asymmetry and its progression along the vertebral series. *Cygnus melanocoryphus* was excluded from the analysis of the dorsal vertebrae because LPF are absent in these vertebrae. The analysis of the progression of asymmetry was carried out only for *N. australis* from MCS because it presents a sequence of four dorsal vertebrae and for *S. loricatus* because it has a relatively complete sequence of cervical and dorsal vertebrae. The order assigned to each dinosaur vertebra was based on the height of the diapophyses and parapophyses, inclination of the neural spine and centrum lengths. Our expectation was that the presence of asymmetry should lead to the decoupling of the curves corresponding to the right and left LPF of each series. LPF indexes were plotted using Palaeontological Statistics (Hammer et al. 2001).

Second, we assessed the shape variation between right and left LPF, separately for the cervical and dorsal vertebrae of the studied titanosaur species. The total sample was represented by the LPF of two cervical and four dorsal vertebrae of *N. australis*, four cervical and five dorsal vertebrae of *S. loricatus* and two cervical and three dorsal vertebrae of *B. salgadoi* (Tables 3 and 4). The contour of LPF was represented by 4 landmarks + 4 semi-landmarks (Figure 1). For each data-set (i.e. LPF of cervical and dorsal vertebrae, separately), we constructed a morphospace (with the same procedure that was explained for the analysis of vertebral centra shape variation) that included right and left LPF. We examined the relative position and assessed the shape differences of each LPF couple corresponding to a given vertebra. Our expectation was that the presence of asymmetry should lead to the segregation within the morphospace of right and left LPF of the same vertebra.

Table 3. Numbers assigned to cervical LPF included in asymmetry analyses.

	Left LPF	Right LPF
B. salgadoi	1	9
	2	10
N. australis	3	11
	4	12
S. loricatus	5	13
	6	14
	7	15
	8	16

Note: Both columns indicate the couple of LPF of each vertebra.

Table 4. Numbers assigned to dorsal LPF included in asymmetry analyses.

	Right LPF	Left LPF
B. salgadoi	1	13
	2	14
	3	15
N. australis	4	16
	5	17
	6	18
	7	19
S. loricatus	8	20
	9	21
	10	22
	11	23
	12	24

Note: Both columns indicate the couple of LPF of each vertebra.

3. Results

3.1 Shape variation of vertebral centra

In the analysis of shape variation of cervical centra, the first two RWs explained about 71.88% of the variation (Figure 2). The ordination of the studied species is congruent with the phylogenetic pattern (Gallina and Apesteguía 2011); *B. salgadoi* is located on positive values of the second axis, whereas *S. loricatus* and *N. australis* are almost together on negative values of the same axis.

The consensus configuration for cervical vertebrae (Figure 2) is elongated and dorsoventrally short, with an elliptical LPF located in the central part of the lateral face of the centra and taking up a third of the vertebrae. The cervical vertebrae of the taxa situated at positive values of RW1 are elongated and low in comparison with the consensus, and present a small LPF anteriorly located that occupies less than a third of the vertebral centrum. Towards negative values of RW1, cervical centra are shorter and deeper with respect to the consensus and present a large LPF that occupies about two-thirds of the centrum. At positive values of RW2, the cervical centra have about the same elongation but are lower than the consensus; also, these present an elliptical and very elongated LPF that occupies more than two-thirds of the vertebral centra. At negative values, centra are shorter and higher, with a small and rhomboidal LPF placed at the middle of their lateral faces.

In the analysis of shape variation of dorsal centra, the first two RWs explained 59.97% of the variation (Figure 3).

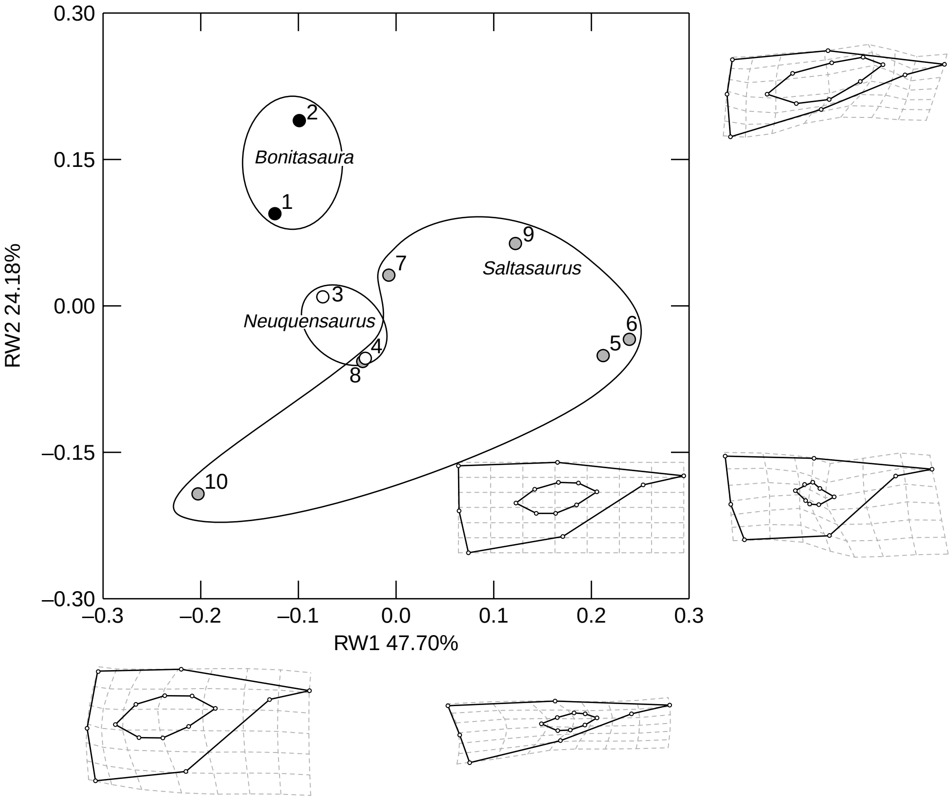

Figure 2. Ordination of the centra of cervical vertebrae of *B. salgadoi* (black dots), *N. australis* (white dots) and *S. loricatus* (grey dots). The consensus shape is depicted inside the ordination graph.

This analysis held a similar pattern of ordination to that observed for the cervical vertebrae; two of the three centra of *B. salgadoi* were located far from the other taxa, whereas *S. loricatus* and *N. australis* are situated close to each other, although not as close as in the analysis of the cervical centra.

The consensus configuration of the dorsal centra is high and anteroposteriorly short, unlike the cervical vertebrae, and presents a semi-circular LPF that occupies two-thirds of the centrum, is slightly shifted to the anterior part of the centrum and is placed close to its dorsal margin (Figure 3). Taxa located at positive values of RW1 share dorsal centra with the same height (although more elongated than the consensus), and with an elliptical LPF that is located in the central portion and occupies more than two-thirds of the centrum. At negative values, the vertebral centra are higher and shorter than the consensus, and present a sub-triangular LPF that is displaced towards the anterodorsal portion of the centrum. Taxa located at positive values of RW2 exhibit the same relative height and length as the consensus, and present a LPF with a shape defined between elliptical and triangular, which occupies two-thirds of the centrum and it is anteriorly located. Taxa located at negative values of RW2 have approximately the same proportions as the consensus, and exhibit a semicircular LPF that occupies two-thirds of the vertebral centrum and that is slightly anteriorly displaced in relation to the consensus.

3.2 Pleurocoel asymmetry

3.2.1 Indexes

The plots of height–length indexes for the three analysed theropods (one non-avian theropod, *Carnotaurus sastrei*, and two birds, *Cygnus melanocoryphus* and *Chauna torquata*) are shown in Figures 4 and 5. These taxa present a pattern of asymmetry of the LPF in the cervical vertebrae. In *Carnotaurus sastrei* and *Cygnus melanocoryphus*, the right LPF are larger than those on the left side, in both middle and the last cervical vertebrae. In *Chauna torquata*, the right LPF are larger only in the first and the last cervical vertebrae. Regarding the analysis of dorsal vertebrae, *Chauna torquata* and *Carnotaurus sastrei* showed a variable pattern.

For titanosaurs, we plotted the sequence of cervical vertebrae of *S. loricatus* (Figure 4(d)). The LPF on the left side are larger than those on the right side, except in the first vertebra where this pattern is inverted. The dorsal vertebrae of *N. australis* and *S. loricatus* showed a variable pattern (Figure 5(c), (d)).

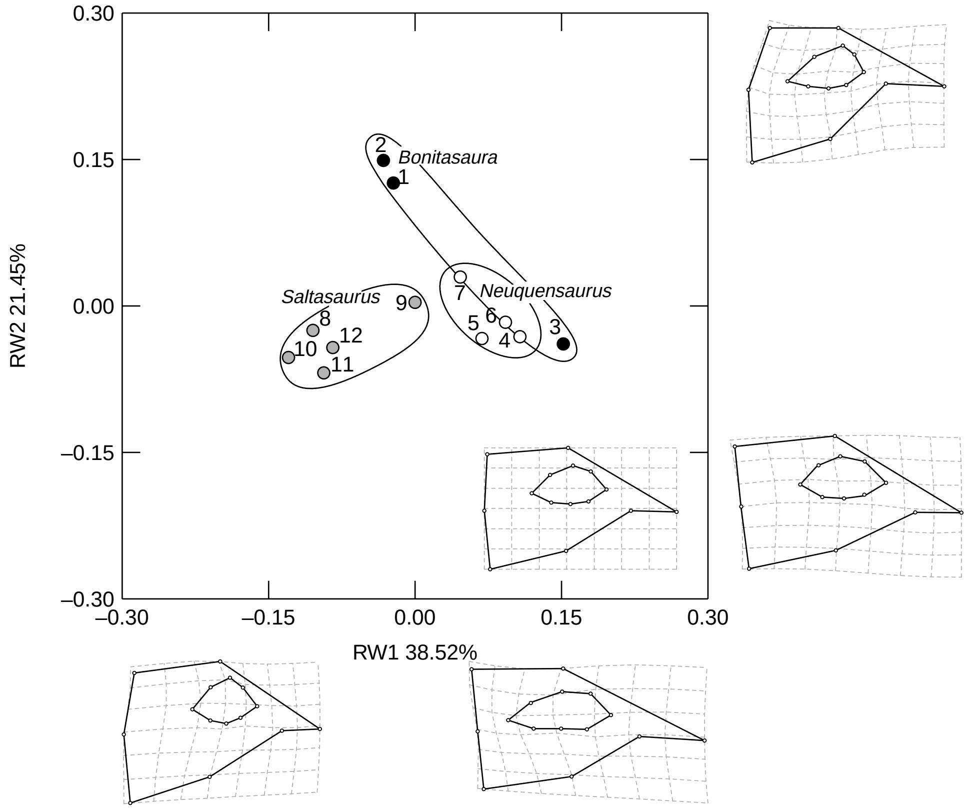

Figure 3. Ordination of the centra of dorsal vertebrae of *B. salgadoi* (black dots), *N. australis* (white dots) and *S. loricatus* (grey dots). The consensus shape is depicted inside the ordination graph.

Analysed individually, the only cervical vertebra of *N. australis* MCS-5, considered as the last cervical vertebra by Salgado et al. (2005), has the right LPF larger than the left one. The same occurs with the two last cervical vertebrae of *N. australis* of MLP. In *B. salgadoi*, the axis and the last cervical vertebra show differences in LPF size, with the left LPF larger in the axis, whereas the right one is larger in the last cervical vertebra. Regarding the dorsal vertebrae of *B. salgadoi*, the third dorsal vertebra has a larger right LPF, whereas the opposite occurs in the sixth and tenth dorsal vertebrae.

3.2.2 *Geometric morphometrics*

Regarding the geometric morphometric analysis of cervical LPF, the first two RWs explain 61.35% of the variation (Figure 6). The cervical LPF of the analysed vertebrae (axis and 13th) of *B. salgadoi* are located relatively close together. For both *N. australis* and *S. loricatus*, LPF are located separately, except those of the axis of the latter species. These results are congruent with the indexes obtained for cervical LPF indexes.

Cervical LPF of *B. salgadoi* are elliptical and elongated. Cervical LPF of *N. australis* are elliptical and elongated, but show asymmetry mainly regarding their height and, to a lesser degree, their length (Figure 6). On the other hand, cervical LPF of *S. loricatus* are elongated and high, and they are not as so elliptical as in *N. australis*; some asymmetries regarding height and secondarily length could be especially observed in the posterior cervical vertebrae, but not in the axis (Figure 6).

The ordination of LPF of dorsal vertebrae is depicted in Figure 7. The first two axes explain 70% of the total variation. LPF of *B. salgadoi* are located separately from each other. The same occurred in *N. australis*, except for the eighth dorsal vertebra (6 and 18 in Figure 7), whose LPF are close together in the morphospace. For *S. loricatus*, LPF are located separately, except those of the two last vertebrae (11 and 23, 12 and 24 in Figure 7).

Contrary to that observed in the cervical vertebrae, *B. salgadoi* showed marked bilateral asymmetry of its LPF. The right LPF is elongated, elliptical and not so high, whereas the one on the left side is rounded and higher. In the case of *N. australis*, the middle and posterior dorsal vertebrae (4 and 16, 8 and 18 in Figure 7) exhibit LPF that are rounded to elliptical. In *S. loricatus*, the right LPF in the two vertebrae (Figure 7) are rounded, whereas the left LPF are nearly elliptical and elongated.

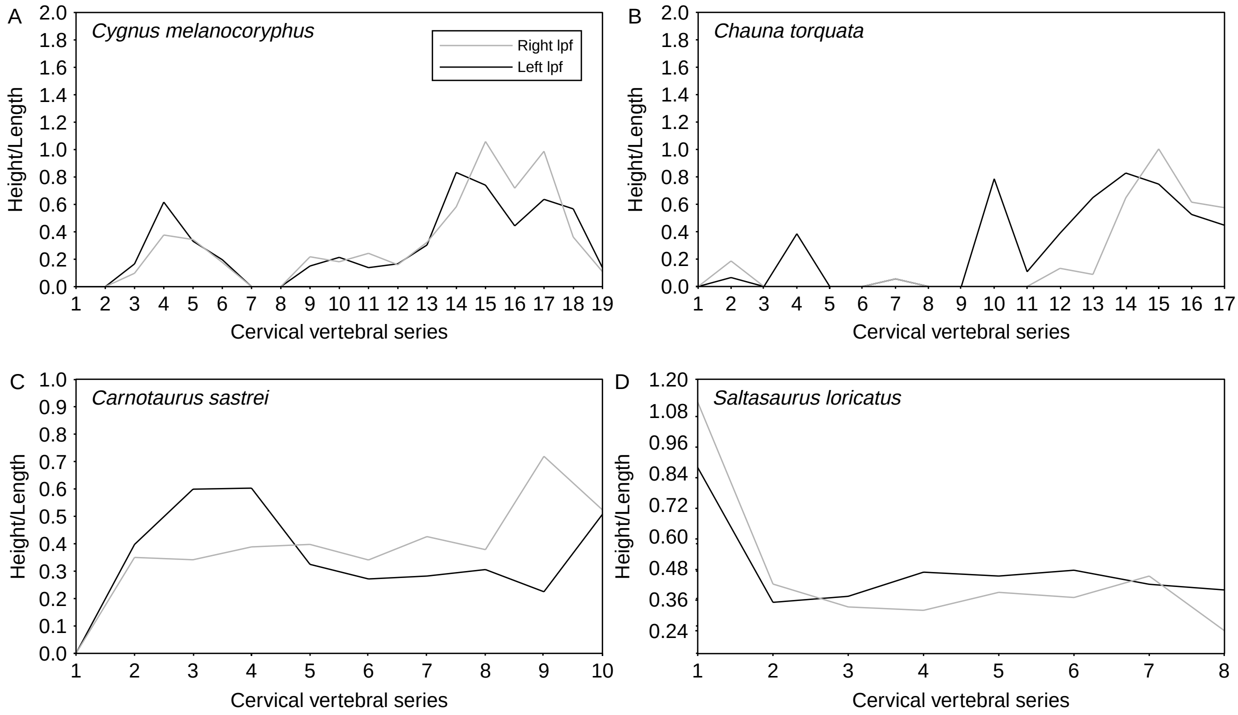

Figure 4. Height–length indexes plots for cervical LPF of *Cygnus melanocoryphus* (A), *Chauna torquata* (B), *Carnotaurus sastrei* (C) and *S. loricatus* (D). When LPF are lacking, indexes values were considered as zero.

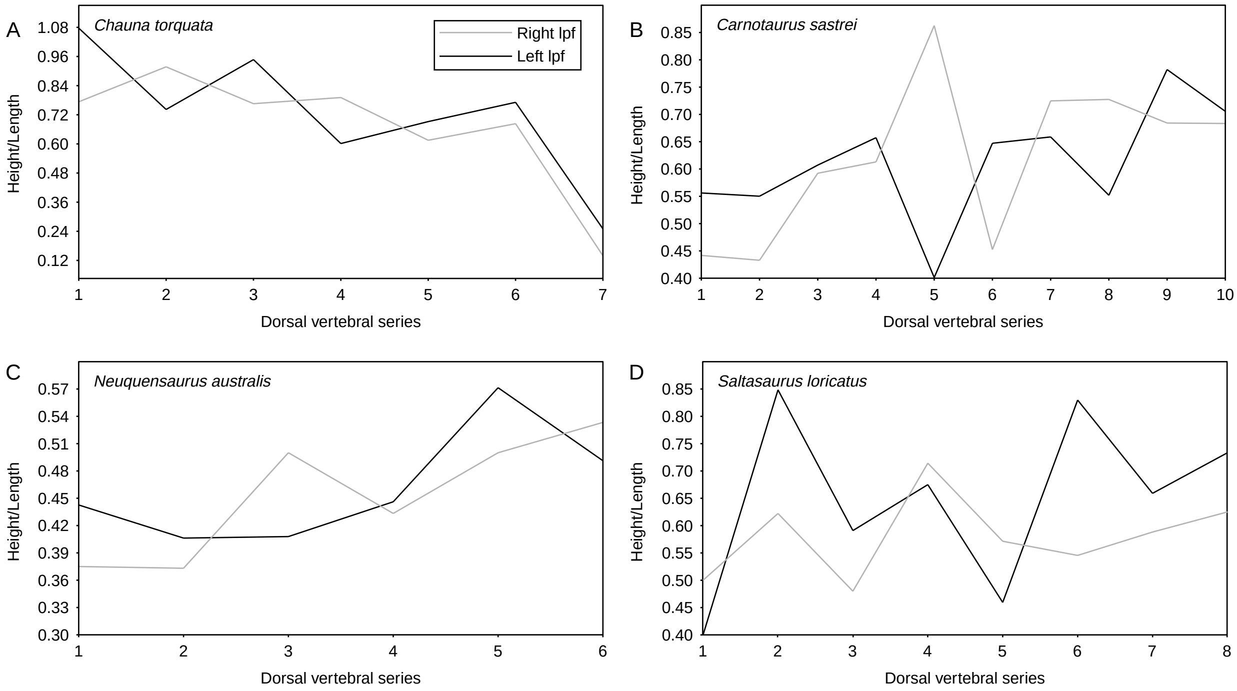

Figure 5. Height–length indexes plot for dorsal LPF of *Chauna torquata* (A), *Carnotaurus sastrei* (B), *N. australis* (C) and *S. loricatus* (D).

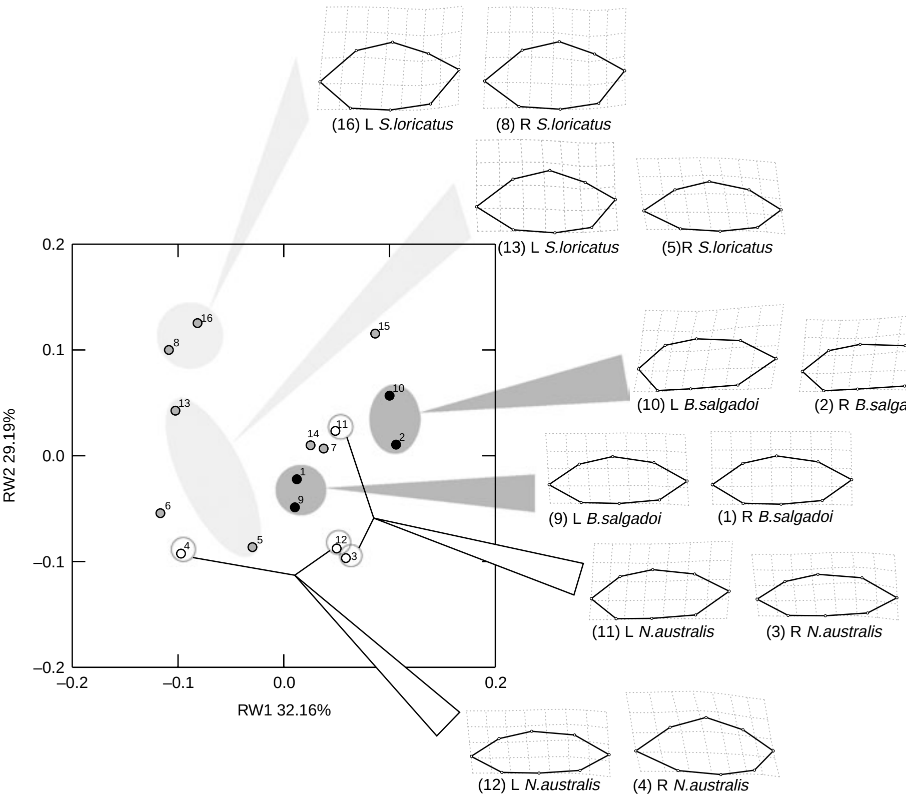

Figure 6. Ordination of right (R) and left (L) LPF couples of cervical vertebrae of *B. salgadoi* (black dots), *N. australis* (white dots) and *S. loricatus* (grey dots).

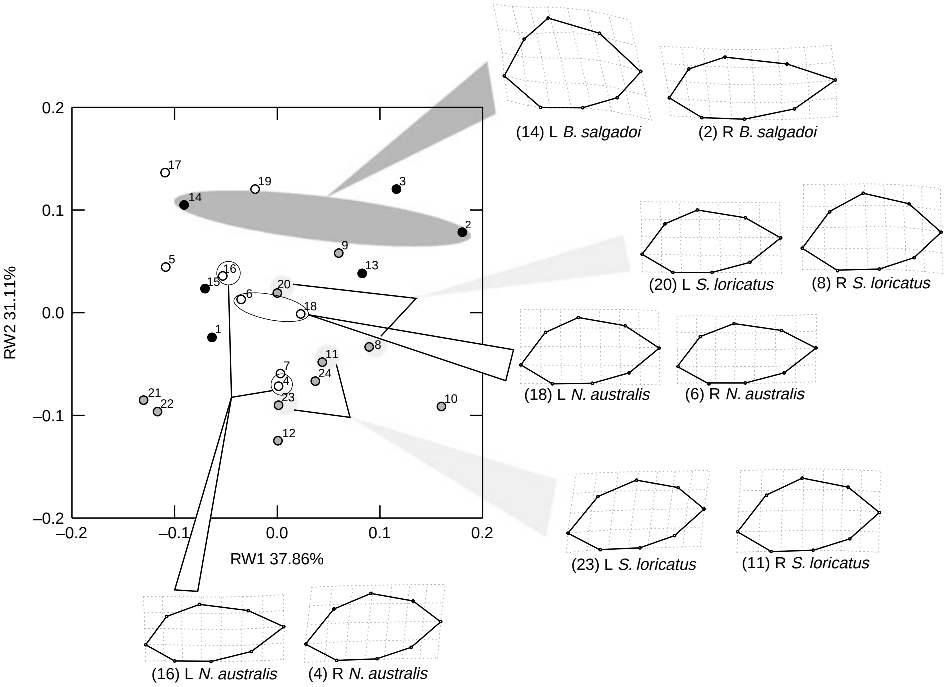

Figure 7. Ordination of right (R) and left (L) LPF couples of dorsal vertebrae of *B. salgadoi* (black dots), *N. australis* (white dots) and *S. loricatus* (grey dots).

4. Discussion

4.1 Shape variation of vertebral centra

Our results, based on geometric morphometrical techniques, show that the cervical centra of titanosaurs tend to be elongated and low, with an elliptical LPF located in the middle of the vertebral centrum. In contrast, dorsal centra tend to be anteroposteriorly short and higher than the cervical centra, with the LPF slightly displaced to the anterior region of the vertebra. These patterns are consistent with previous descriptions of vertebral morphology of titanosaurs (Bonaparte and Powell 1980; Powell 1986; Salgado et al. 2005).

Overall, shape variation can be described as an outcome of the ordering of the vertebrae within both the cervical and dorsal sequences. Among these series, extreme-positioned vertebrae show very different shape, as was the case of cervical vertebrae of *B. salgadoi* (axis and 13th vertebra; 1 and 2 in Figure 2). In the same way, vertebrae closely located within the sequence may present a similar shape, such as cervical vertebrae of *N. australis* (3 and 4 in Figure 2) and dorsal vertebrae of *S. loricatus* (8, 10, 11 and 12 in Figure 3). Based on these results, geometric morphometric techniques may be considered as a potential tool to predict the position of a vertebra within a vertebral series. As an example, an element that was considered as a middle cervical vertebra of *S. loricatus* (7 in Figure 2) was positioned closer to posterior vertebrae, suggesting that it could be a middle-to-posterior vertebra. This potential should be verified with the analysis of morphological variation in complete vertebral series and including more taxa.

In both cases (cervical and dorsal vertebrae), it is clear that the separation between the three taxa, especially among the dorsal vertebrae, corresponds to the phylogenetic pattern; *N. australis* and *S. loricatus* were located close to each other, rather than with *B. salgadoi*. The taxa formed by *S. loricatus* and *N. australis* are considered as saltasaurine group (Wilson 2002; Salgado and Bonaparte 2007; Gallina and Apesteguía 2011), whereas the latter taxon lies within Titanosauria, but without a close relationship with saltasaurines. At the same time, although the sample is small, there is an obvious grouping of vertebral elements associated with their position in the vertebral sequence. This result suggests that the application of geometric morphometric techniques may be useful not only for describing in a detailed manner the shape of vertebrae, but also for estimating their position.

4.2 Pleurocoel asymmetry

The overall observed pattern is a persistent asymmetry among LPF. In this study, it generally occurs that the right LPF are larger than those on the left side in cervical vertebrae, but variable in dorsal vertebrae. On the contrary, in most of the cervical vertebrae of *S. loricatus*, the left LPF are larger than those on the right.

A possible explanation of the asymmetry patterns observed resides in the development of pneumatic diverticula, which are epithelial tubes that extend into the lungs or air sacs. Air sacs and pneumatic diverticula are present in birds, and recently, they have been shown to exist also in non-avian dinosaurs (Wedel 2003a, 2003b, 2009; O'Connor 2006). These diverticula can be present amidst the viscera, between muscles and beneath the skin (King 1966; Duncker 1971 in Wedel 2009). Also, they can invade the bones of the postcranial skeleton, which happens in saurischians (Wedel 2003a, 2003b; O'Connor 2006; Wedel 2009). The pattern of asymmetry observed in the analysed vertebrae could be caused by a differential arrival of the diverticula on both sides of the vertebrae. This is supported by the fact that the viscera have an asymmetrical distribution into the body and, if the diverticula pass between organs that are not the same on each side of the body, their arrival to each vertebra or groups of vertebrae will be different. Embryologically, this can be supported by the late development of the respiratory system, including air sac systems in avian and non-avian saurischians. After the development of the heart, liver and kidneys, the lungs begin to develop. As the final step occurring at birth, the pneumatic diverticula make their way through the viscera to enter into the vertebrae (Duncker 1978).

The persistence of a pattern of asymmetry in the cervical vertebrae, with right LPF larger than the left one, could be related to the fact that the heart would have been located on the left side of the neck at the level of the last cervical vertebrae. Thus, the single cervical air sac that supplies air to the neck would have encountered the obstacle that represents the heart. In contrast, there is not a fixed pattern among dorsal vertebrae, as there are various organs placed at this level and the backbone receives input from different air sacs.

5. Conclusions

Geometric morphometric techniques have been previously applied to the study of several aspects of the biology of dinosaurs, such as cranial and long bone shape variation (Bonnan 2004), and ichnologic studies on trackways (e.g. Rodrigues and Santos 2003). However, quantification of vertebral shape variation among sauropods has remained unexplored. The results presented here support the potential of these techniques as a tool to study morphological variation among vertebral series and their ability to predict the position of a vertebra within a series.

In addition, we quantified and analysed the patterns of asymmetry between vertebral LPF, and established an ontogenetic hypothesis regarding the cause of such observed asymmetric patterns. More detailed studies carried out on more complete vertebral series should enable the development of a more accurate picture of patterns in asymmetry. Once achieved, we will be able to fully test the hypotheses proposed herein.

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Appendix

Fossil species: *Carnotaurus sastrei*, MACN-PV CH894; *N. australis*, MCS 5; MLP-CS 3; *S. loricatus*, PVL 4017; *B. salgadoi*, MPCA-Pv 460. Avian extant species: *Chauna torquata*, MACN 68-627, 7239, 1929; MLP 89, 806; Ornitología 5 (S. Apesteguía, personal collection); FCEN, A-353. *Cygnus melanocoryphus*, MACN 68-755, 68-033; MLP, 688; FCEN, A-367.