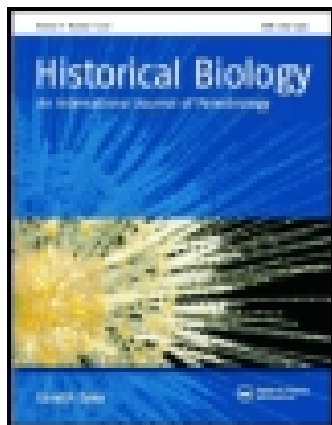


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# Morphological diversity of *Neuquensaurus* Powell, 1992 (Sauropoda; Titanosauria): insights from geometric morphometrics applied to the vertebral centrum shape

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## ABSTRACT

*Neuquensaurus* is a small-sized titanosaur from the Upper Cretaceous of Patagonia, Argentina, for which two species were recognised in the past (*Neuquensaurus australis* and *Neuquensaurus robustus*). Given that such division was only based on the relative robustness of the limb bones, the validity of the species *N. robustus* has been questioned. In this work, we studied the morphological variation of the vertebrae of this genus through geometric morphometric techniques and the description of relevant anatomical features in order to assess if there are one or more morphotypes within *Neuquensaurus*. We found two distinguishable morphotypes, one belonging to *N. australis* and other that includes specimens assigned to both *N. australis* and *N. robustus*. The occurrence of a posterior cervical vertebra with a particular anatomical feature (i.e. four spr1) could indicate the presence of another taxon than *N. australis* in the studied sample. Although the validity of the species *N. robustus* cannot be discussed on the basis of the current data, our study supports the hypothesis of at least two different morphotypes of *Neuquensaurus* (which could be related to different taxa).

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Sauropoda; *Neuquensaurus*; geometric morphometrics; axial skeleton; vertebral shape

## 1 Introduction

*Neuquensaurus* is a small-sized sauropod dinosaur from the Upper Cretaceous of Patagonia, Argentina. This genus is nested among the Saltasaurine, a high derived clade of armoured titanosaurs of South America (Powell 1992; Salgado et al. 2005; Otero 2010; D'Emic and Wilson 2011). The first-described remains, which correspond to caudal vertebral elements, were recovered from the Neuquén province, Argentina. They were studied first by Lydekker in 1893, who assigned these materials to the sauropod genus *Titanosaurus*, establishing the species *Titanosaurus australis* (Lydekker 1893) allocating those caudals to the holotype. In early twentieth century, Huene collected more materials assignable to *T. australis*, proposing a vertebral formula of 14 cervical, 10 dorsal, 6 sacral and about 45 caudal vertebrae. On the basis of the robustness of the appendicular bones, he recognised two species: *T. australis*, more gracile, and *Titanosaurus robustus* (Huene 1929), more robust. Approximately 40 years later, Bonaparte and Gasparini (1978) confirmed the Huene's statement. Later, in his revision of the taxonomic status of these species, Powell (1992) attributed the differences to sexual dimorphism or intraspecific variation and established the genus *Neuquensaurus* (Powell 1992), assigning all the materials to *N. australis* and considering *N. robustus* as *nomen dubium*. More recently, Salgado et al. (2005) reported new remains in the locality of Cinco Saltos (Río Negro province, Argentina), including both gracile and robust forms. Based on these materials, the authors argued that there were no significant differences to justify

the division into two species. Regarding the available materials of hindlimb and forelimb assigned to this species, Otero (2010) determined that they belong to this species and that it is not possible to make a separation into two valid taxa (*N. australis* and *N. robustus*). Recently, the holotype and the diagnosis of the species were expanded with an almost complete scrum (D'Emic and Wilson 2011).

Despite that both axial and appendicular bones has been referred to *N. robustus* (Huene 1929), the discussion on its validity as species has been based solely in the limb bones anatomy. The aim of this work is to reanalyse the vertebral morphology of the materials assigned to *Neuquensaurus* and determine if real anatomical differences occur. We made anatomical descriptions of relevant traits and use geometric morphometric techniques to quantify the observed morphological variation.

## 2. Materials and methods

Institutional abbreviations: MCS-Pv, Museo de Cinco Saltos, Paleovertebrate collection, Río Negro, Argentina; MLP-CS, Museo de La Plata, Cinco Saltos Collection, La Plata, Argentina; MLP-Ly, Museo de La Plata, Lydekker Collection, PVL, Instituto Miguel Lillo, Tucumán, Argentina.

Anatomical abbreviations: apcdl (accessory posterior centrodiapophyseal lamina) cpol (centropostzygapophyseal lamina); pacdf (parapophyseal centrodiapophyseal fossa); pcdl (posterior centrodiapophyseal lamina); pcpl (posterior

**Table 1.** List of materials and its estimated position in the vertebral sequence.

Assignment of vertebrae	<i>Neuquensaurus</i>	<i>S. loricatus</i>
Posterior cervical	MCS-Pv 5/17	PVL 4017–212
Posterior cervical	MLP CS 1378 (Serie 2)	PVL 4017–9
Posterior cervical	MLP CS 1374 (Serie 3)	
Posterior cervical	MLP CS 1375 (Serie 3)	
Middle dorsal	MCS-Pv 5/18	
Posterior dorsal	MCS-Pv 5/20	PVL 4017–135
Posterior dorsal	MCS-Pv 5/22	PVL 4017–136
Posterior dorsal	MLP CS 1379 (Serie 2)	PVL 4017–17
Posterior dorsal	MLP CS 1382 (Serie 2)	
Posterior dorsal	MLP CS 1383 (Serie 2)	
Posterior dorsal	MLP CS 1385 (Serie 1)	
Posterior dorsal	MLP CS 1386 (Serie 1)	
Posterior dorsal	MLP CS 1387 (Serie 1)	
Posterior dorsal	MLP 1388 (Serie 1)	
Seventh sacral	Ly 1 (Holotype)	
Seventh sacral	MLP CS 1389 (Serie 2)	
Seventh sacral	MLP CS 1390 (Serie 1)	
First caudal	Ly 2 (Holotype)	
First caudal	MCS-Pv 5/1	
First caudal	MLP CS 1391 (Serie 1)	

**Table 2.** List of materials excluded from the geometric morphometric analysis.

Assignment of vertebrae	<i>N. australis</i>	<i>N. robustus</i>
Posterior cervical		MLP CS 1376
Middle dorsal	MCS-Pv 5/19	
Posterior dorsal	MCS-Pv 5/21	
Posterior dorsal	MCS-Pv 5/23	
Posterior dorsal		MLP CS 1384

centroparapophyseal lamina); prsdf (prespinodiapophyseal fossa); spdl (spinodiapophyseal lamina); spof (spinopostzygapophyseal fossa); sprf (spinoprezygapophyseal fossa); sprl (spinoprezygapophyseal lamina); tpol (intrapostzygapophyseal lamina); tpri (intraprezygapophyseal lamina); upl (unnamed parapophyseal lamina).

### 2.1. Anatomical descriptions

We focused our analysis in anatomical features of the axial skeleton, including the presence, shape and development of neural arch laminae and fossae. We employed the nomenclature of neural laminae and fossae proposed by Wilson (1999) and Wilson et al. (2011), except for the upl, which is based in the name proposed by Salgado et al. (2005). We use the Romerian terminology (Wilson 2006) that considers the division of the vertebral body into anterior, posterior, ventral and dorsal portions (Romer 1956). The anatomical analyses of the neural arches were performed only in the cervical, sacral and caudal vertebrae, because most of the available dorsal vertebrae lack a complete neural arch.

### 2.2. Geometric morphometric analyses

In order to quantify and to analyse shape variation among vertebrae, a geometric morphometrics approach was used. We analysed the shape variation of the cervical, dorsal, sacral and caudal vertebrae of *Neuquensaurus* (Table 1); and also we analysed the shape variation of the cervical and dorsal vertebrae of *Neuquensaurus* and *Saltasaurus loricatus* simultaneously. We

ran this second analysis in order to have a point of comparison regarding the degree of variation. *S. loricatus* was chosen as the comparative species due to its phylogenetic closeness (Wilson 2002; Powell 2003; Calvo et al. 2007; Carballido and Sander 2013; Mannion et al. 2013; Salgado et al. 2014). Sacral and caudal vertebrae were not included in this second analysis because of the scarcity of comparative material of *Neuquensaurus* and the lack of seventh sacral vertebra in *S. loricatus*.

The geomorphometric analyses focused on the vertebral centrum shape variation given that the neural arches are missing in most of the material. The total sample included consisted of: 4 cervical, 3 assigned to *N. australis* and 1 assigned to *N. robustus*; 10 dorsal, 7 assigned to *N. australis* and 3 assigned to *N. robustus*; 3 sacral, 2 assigned to *N. australis* and 1 assigned to *N. robustus* and; 3 caudal vertebrae, 2 assigned to *N. australis* and 1 assigned to *N. robustus*. We also include 2 cervical vertebrae and 3 dorsal vertebrae assigned to *S. loricatus* (Table 1). To represent vertebral shape, two-dimensional coordinates of 15 landmarks and 4 semi-landmarks were captured from digital images of the left side in lateral view; when this side was missing or damaged, the reflected image of the right side was used. Coordinates were digitalised using TPSDIG 2.12 software (Rohlf 2008). To remove differences in location, orientation and scaling, we performed a Generalized Procrustes analysis (Rohlf and Slice 1990). The resulting Procrustes coordinates were analysed through principal component analyses in order to summarise and describe the major trends in shape variation and to help the visualisation of shape ordination in the constructed morphospace. Differences in the shape of vertebral centra were described by means of thin plate splines deformation grids (Bookstein 1991). These morphometric analyses were performed using TPSRELW 1.46 software (Rohlf 2008).

For this analyses, we do not included all of the vertebrae, because some of them have a degree of deformation in the centra by not allowing studying by geometric morphometric techniques, but analyse the anatomy of the neural arch. These vertebrae were pooled in other table (Table 2).

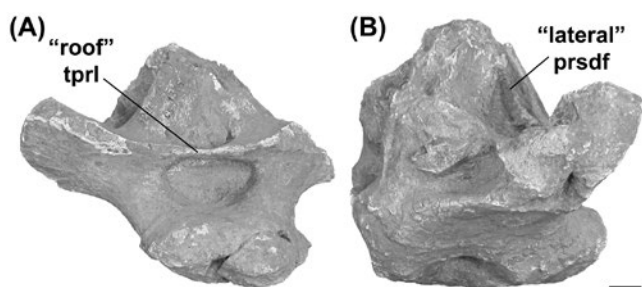
## 3. Results

### 3.1. Anatomical comparison

#### 3.1.1. Cervical vertebrae

The analyses of the cervical vertebrae determined that in some elements assigned to *N. robustus* (e.g. MLP CS-1376), the tpri continues posteriorly forming a roof over the neural canal (Figure 1(a)). Also, in the materials assigned to *N. robustus*. (e.g. MLP-CS 1376), the sprl is wide and exceeds the lateral margin of the neural canal, orienting laterally the prsdf (Figure 1(b)). By contrast, in materials assigned to *N. australis* (e.g. MLP-CS 1374), the sprl does not exceed the lateral margin of the neural canal and the prsdf is oriented anteriorly (Figure 2(a), (b)). We noted that one element assigned to *N. robustus* (MLP-CS 1378) has four parallel sprl, which split the sprf into four 'sub-fossae'. This feature is unique of this specimen in our *Neuquensaurus* sample (Figure 3).

In vertebrae assigned to *N. robustus*, the tpol is rounded and has a 'U shape', generating a shallow and wide spof. Conversely, the



**Figure 1.** Cervical vertebra assigned to *N. robustus* MLP CS 1376 showing a 'roof shaped' tprl (A) and 'lateral' prsd (B). Note: Scale bar: 2 cm.

tpol in materials assigned to *N. australis* is sharper and has a 'V shape', creating a deep and elongated spof (Figure 1(b), Figure 4(a)).

### 3.1.2. Dorsal vertebrae

The dorsal vertebrae of all *Neuquensaurus* specimens are short and rather tall. The centrum has well-developed lpf, which communicates with the internal camellate tissue. Despite that at least four dorsal vertebrae were originally assigned by Huene (1929) to *N. robustus*, MLP CS 1379 is the only element that has preserved most of its neural laminae and fossae. As observed in dorsal vertebrae assigned to *N. australis* (e.g. MCS Pv 5/22), MLP CS 1379 possesses a well-developed cpol. In MLP CS 1379, the pacdf is limited by the pcdl, the ppdl, the acpl and the dorsal margin of the vertebral centra. Two distinct laminae were observed inside the pacdf: the apcdl and an accessory lamina, which are perpendicular to the pcpl and the upl. The same pattern was observed in MCS-Pv 5/22. The only noticeable difference among these specimens relies on the presence of a second accessory lamina that is parallel to upl and pcpl, in MLP CS 1379 (Figure 5(a), (b)).

### 3.1.3. Sacral vertebrae

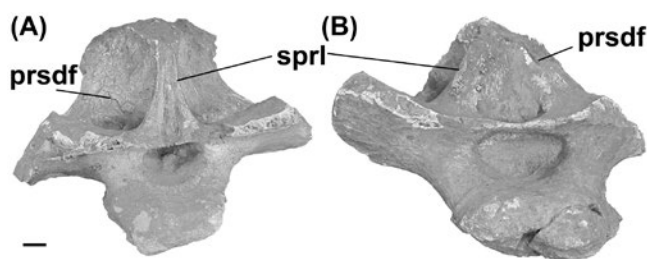
Among the seventh sacral vertebrae, the main difference was observed at the level of the spdl. This lamina is vertically oriented with respect to the transverse process in the specimen assigned to *N. robustus* (MLP CS 1389). On the other hand, its orientation is oblique (posterodorsally) in those specimens assigned to *N. australis* (Figures 6(a)–(c)).

### 3.1.4. Caudal vertebrae

No significant anatomical differences were observed in those materials assigned both to *N. australis* and *N. robustus*.

## 3.2. Analysis of shape variation of the vertebrae of *Neuquensaurus*

In the analysis of the vertebral sequence of *Neuquensaurus*, the first two RWs explained about 79.23% of the variation. The ordination of the vertebrae was congruent with the vertebral sequence. The cervical and dorsal vertebrae are located in the right upper and left upper quadrants, respectively. The sacral and caudal vertebrae located in the right lower and left lower quadrants, respectively. The cervical vertebra MLP CS 1378 is located in the right lower quadrant (point 2 in Figure 7). With respect to sacral vertebrae, MLP Ly 7 (point 17, from the holotype) and MLP CS 1390 (point 16), they are closer one to each other than



**Figure 2.** Cervical vertebrae assigned to *N. australis* MLP CS 1374 (A) and *N. robustus* MLP CS 1376 (B) showing the orientation of prsd, anterior in MLP CS 1374 and lateral in MLP CS 1376. Note: Scale bar: 2 cm.

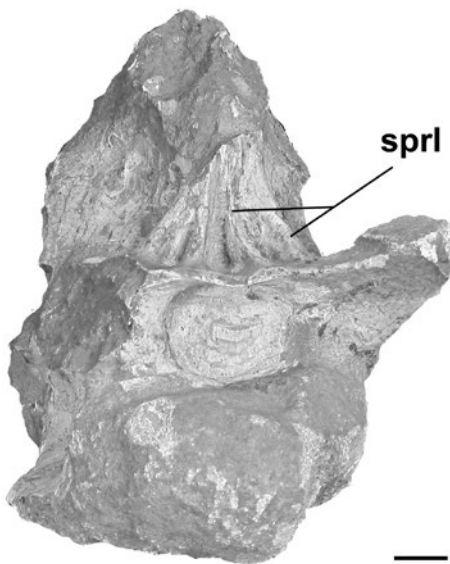
to MLP CS 1389 (point 15). The caudal vertebrae MLP CS 1392 (point 19) and MCS-Pv 5/1 (point 18) are close together, and MLP Ly 2 (holotype; point 20) was separated from the other two.

In the second analysis, which included the cervical and dorsal vertebrae of *Neuquensaurus* and *S. loricatus*, the first two RWs explained about 71.10% of the variation. The ordination of the vertebrae was congruent with the vertebral sequences in both taxa. The cervical vertebrae are located in the upper and lower right quadrants. *Neuquensaurus* showed a higher dispersion of the cervical vertebrae than *S. loricatus*. The vertebrae MCS-Pv 5/17 (point 1, *N. australis*) and PVL 4017–9 (point 5, *S. loricatus*) and MLP-1375 (point 3, *N. australis*) and PVL 4017–212 (point 4, *S. loricatus*) were grouped in clusters. The dorsal vertebrae assigned to *Neuquensaurus* are mostly in the upper left quadrant, showing higher dispersion than those of *S. loricatus*, which are located in the lower left quadrant (points 17 and 18). Among the dorsal vertebrae of *Neuquensaurus*, they are located close together, although two groups were distinguished: MLP CS 1388, MLP CS 1383 and MLP CS 1385 (points 10, 12, and 13) on one side, and MLP CS 1386 and MLP CS 1387 (points 14 and 15) on the other side (Figure 8).

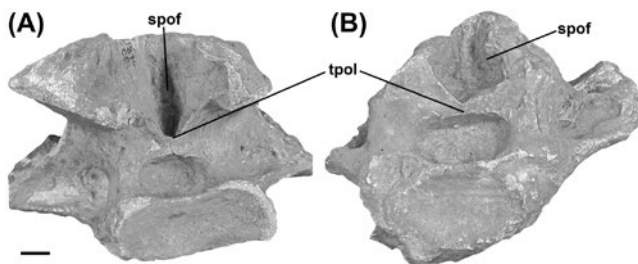
## 4. Discussion

The original differentiation between *N. australis* and *N. robustus* was made on the basis of differences in the relative proportions of the long bones (Huene 1929; Bonaparte and Gasparini 1978). This study represents the first approach based on the analyses of morphological differences between vertebrae using geometric morphometric techniques. This kind of approach allows evaluating those vertebral centra features that are not easily discernible qualitatively, such as the contours or relative position of structures. In general terms, the shape analysis of the vertebrae of the genus *Neuquensaurus* detected an overall pattern involving a clear division of the different types of vertebrae (cervical, dorsal, sacral and caudal). An exception to this pattern was observed for the material MLP CS 1378, which is actually the only cervical vertebra assigned to *N. robustus* that was included in the morphometric analysis. In this sense, this specimen was placed on the 'sacral vertebrae quadrant', which reveals a clear anatomical variation of MLP CS 1378 with regard to the other cervical vertebrae. Moreover, this vertebra, which was first assigned to *N. robustus* by Huene (1929) and later to *N. australis* by Powell (1986), possesses four sprl, a feature unique among all cervical vertebrae assigned to *Neuquensaurus*. Hence, both morphological and morphometric analyses reveal the presence of at





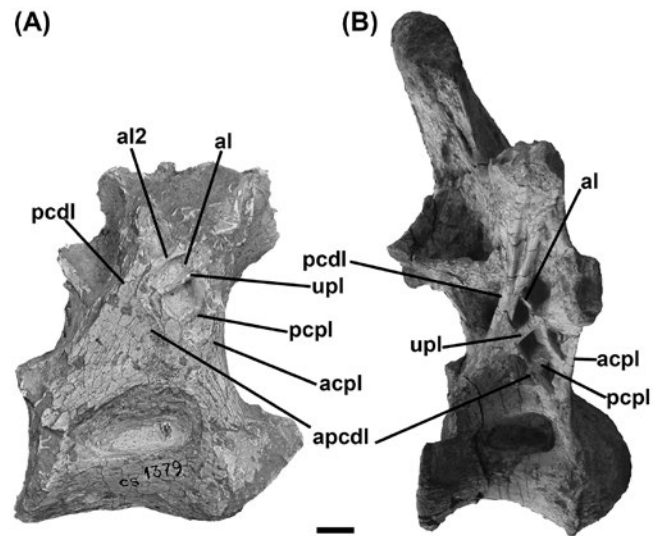
**Figure 3.** Cervical vertebra assigned to *N. robustus* MLP CS 1378 in anterior view showing four sprl and dividing sprf. Note: Scale bar: 2 cm.



**Figure 4.** Cervical vertebrae assigned to *N. australis* MLP CS 1374 (A) and to *N. robustus* MLP CS 1376 in posterior view (B) showing the differences between their tpol and spof. Note: Scale bar: 2 cm.

least two different morphotypes in the cervical vertebrae of *Neuquensaurus*.

Among the dorsal vertebrae, MCS-Pv 5/18, MCS-Pv 5/20 and MCS-Pv 5/22 (points 5, 6 and 7, respectively, in Figure 7) represented a sequence, as they were described by Salgado et al. (2005). MLP CS 1379 and MLP CS 1382 (points 8 and 10, respectively), which were previously assigned to posterior dorsal vertebrae of *N. robustus* (Huene 1929), were placed very close to the vertebra assigned that a middle dorsal to *N. australis* by Salgado et al. (2005) (point 5). This pattern suggests that the previous assignment of the position of both MLP CS 1379 and MLP CS 1382 was incorrect and these elements correspond with middle dorsal vertebrae. Specimens MLP CS 1388, MLP CS 1383, MLP CS 1385 and MLP CS 1386 (points 9, 11, 12 and 13, respectively) were placed together within the 'posterior dorsal vertebrae' quadrant (Figure 8). On the other hand, specimens MCS-Pv 5/20 and MCS-Pv 5/22 (points 6 and 7, respectively) were also recognised within this quadrant, but in a different position from the first cluster. Whereas the first cluster corresponds with the materials described by Huene (1929) and assigned to both *N. australis* and *N. robustus*, point 6 and 7 correspond with the individual of *N. australis* described by Salgado et al. (2005). The element MLP



**Figure 5.** Dorsal vertebrae assigned to *N. robustus* MLP CS 1379 (A) and *N. australis* MCS-Pv 5/22 in lateral right view (B) showing the pattern fossae and laminae. Note: Scale bar: 2 cm.

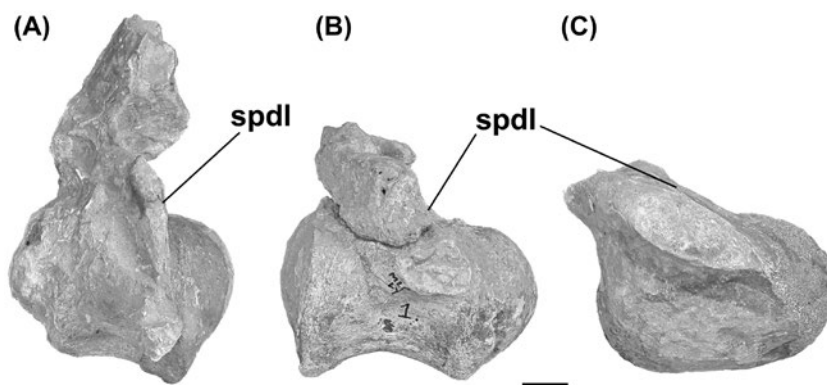
CS 1387 (point 14), despite its assignment as a posterior dorsal vertebra, is actually located far away from the other dorsal vertebrae, suggesting that this element possibly belongs to another taxon or another portion of the dorsal sequence. In synthesis, at least two (and possibly a third) different morphotypes are recognised among the dorsal vertebrae.

Regarding the sacral vertebra, MLP CS 1390 and MLP Ly 1 (both of *N. australis*) are located nearly together and share a distinctive feature related to a vertically orientated spdl. On the other hand, MLP CS 1389 (*N. robustus*, point 15) shows a posterodorsally orientated spdl. The combination of this feature plus the result of the geomorphometric analysis suggest the presence of at least two different morphotypes with regard to the sacral vertebrae anatomy of the specimens assigned to *Neuquensaurus*.

Regarding to the caudal vertebrae, although anatomical differences were detected, they do not correspond with the previous taxonomical differentiation. In this sense, MLP Ly 2 (holotype of *N. australis*; point 20 in Figure 8) is located distant from the pair formed by MCS-Pv 5/1 of *N. australis* and MLP CS 1392 of *N. robustus* (points 18 and 19, respectively). This can be explained in two ways; first, MLP Ly 2 may belong to another morphotype; second, according to D'Emic and Wilson (2011), it may be not a first caudal vertebra.

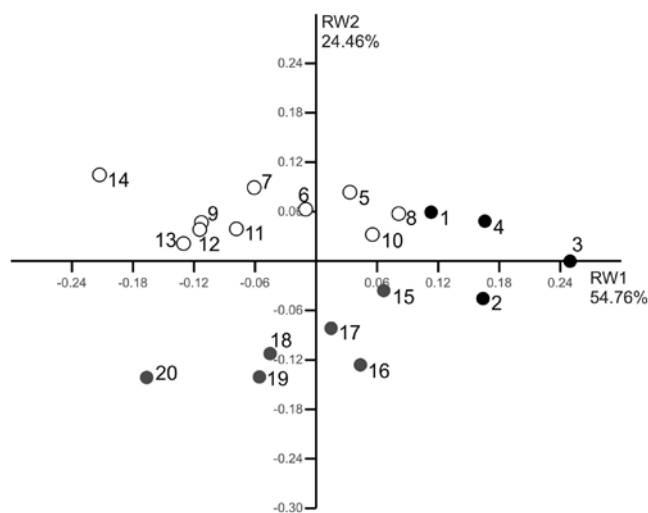
From the comparison with *S. loricatus*, the cervical vertebrae show approximately the same separation that *Neuquensaurus*. The clear separation between MLP CS 1378 (point 2) and both *Neuquensaurus* and *S. loricatus*, suggests that element belongs to other taxon, which agrees with our previous analysis.

Regarding the dorsal vertebrae, *S. loricatus* shows an organised distribution pattern, while the vertebrae assigned to *Neuquensaurus* show an irregular pattern. Again, it can be seen from this analysis that there are two distinct morphotypes within the genus *Neuquensaurus*, one corresponding to the materials collected by Huene and assigned at that time to *N. australis* and *N. robustus* and the other belonging to materials published by Salgado et al. (2005).



**Figure 6.** Seventh sacral vertebra assigned to *N. australis* MLP CS 1390 (A), MLP-Ly 1 (B) and *N. robustus* MLP CS 1389 (C) in lateral left view showing the differences at the level of spdl.

Note: Scale bar: 2 cm.

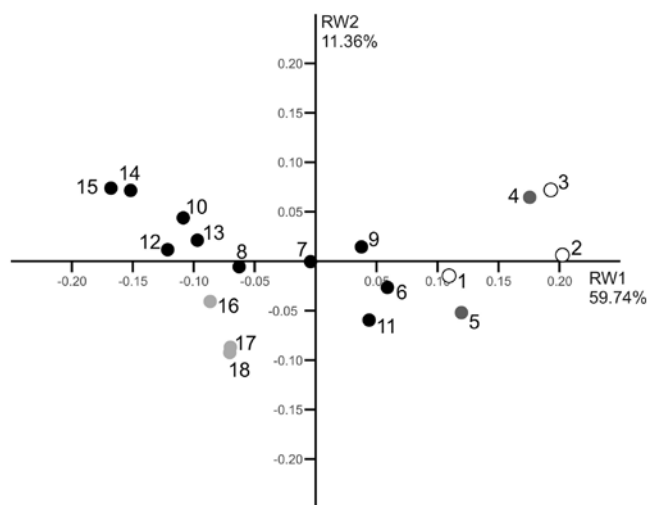


**Figure 7.** Geometric morphometric analysis of all vertebrae assigned to *Neuquensaurus*.

Notes: The black dots corresponding to cervical vertebrae, white dots corresponding to dorsal vertebrae, the light grey dots corresponding to sacral vertebrae and the dark grey dots corresponding to caudal vertebrae.

## 5. Conclusions

According to the previous studies, our morphometric analysis agrees with the existence of at least two morphotypes with regard to the axial skeleton of *Neuquensaurus*. However, our specimen assignment does not coincide exactly with the previous works. For example, on the dorsal vertebrae, one morphotype comprises the material published by Salgado et al. (2005) and the second the material collected by Huene (1929) that was assigned in part to *N. australis* and in part to *N. robustus*. Since the material described by Salgado et al. (2005) includes cervical, dorsal, sacral and caudal vertebrae and this material is overlapped with the *N. australis* holotype, we can recognise which morphotype correspond with this species (the '*N. australis* morphotype'). Because the materials included in the second morphotype comprise vertebrae assigned to both *N. australis* and *N. robustus*, which also were collected isolated, we refrain to assign the second morphotype to *N. robustus*. The occurrence of a posterior cervical vertebra with four spdl, an anatomical feature only recorded in the basal somphospondyl *Ligabuesaurus leanzai* (Bonaparte et al. 2006), indicates the presence of another taxon than *N. australis* in the studied sample. Because this vertebra was not associated with



**Figure 8.** Geometric morphometric analyses of cervical and dorsal vertebrae of *Neuquensaurus* and their comparison with cervical and dorsal vertebrae of *S. loricatus*.

Notes: The black dots corresponding to cervical vertebrae of *Neuquensaurus*, the dark grey dots corresponding to cervical vertebrae of *S. loricatus*, the white dots corresponding to dorsal vertebrae of *Neuquensaurus* and the light grey dots corresponding to dorsal vertebrae of *S. loricatus*.

elements that could be overlapped with the *N. robustus* lectotype, we cannot assign this element to this taxon. Although the validity of the species *N. robustus* cannot be discussed on the basis of the current data, our study supports the hypothesis of at least two different morphotypes in *Neuquensaurus*. Our results enhance the importance of geometric morphometric analysis in anatomical studies of sauropod dinosaurs. These kinds of studies, along with the gross anatomical descriptions, appear to be a valuable tool for discern the relative position of isolated vertebral elements and even for distinguishing between different morphotypes which could be a useful tool for systematic studies.

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## References

- Bonaparte JF, Gasparini Z. 1978. Los saurópodos de los grupos Neuquén y Chubut, y sus relaciones cronológicas [The sauropods from Neuquén and Chubut groups and their chronological relations]. *Actas VII Congreso Geológico Argentino*, Neuquén. 2:393–406.
- Bonaparte JF, González Riga BJ, Apesteguía S. 2006. *Ligabuesaurus leanzai* gen. et sp. nov. (Dinosauria, Sauropoda), a new titanosaur from the Lohan Cura Formation (Aptian, Lower Cretaceous) of Neuquén, Patagonia. *Cretaceous Res.* 27:364–376.
- Bookstein FL. 1991. Morphometric tools for landmark data: geometry and biology. New York (NY): Cambridge University Press.
- Calvo JO, González Riga B, Porfiri JD. 2007. A new titanosaur sauropod from the Late Cretaceous of Neuquén, Patagonia, Argentina. *Arq Mus Nac Rio J.* 65:485–504.
- Carballido JL, Sander PM. 2013. Postcranial axial skeleton of *Europasaurus holgeri* (Dinosauria, Sauropoda) from the Upper Jurassic of Germany: implications for sauropod ontogeny and phylogenetic relationships of basal Macronaria. *J Vertebr Paleontol.* 12(3):335–367.
- D'Emic MD, Wilson JA. 2011. New remains attributable to the holotype of the sauropod dinosaur *Neuquensaurus australis*, with implications for saltasaurine systematics. *Acta Palaeontol Pol.* 56(1):61–73.
- Huene FV. 1929. Los saurisquios y ornitisquios del Cretáceo Argentino [Saurischians and ornithischians of Argentinean Cretaceous]. *An Mus Plata.* 2:1–196.
- Lydekker R. 1893. The dinosaurs of Patagonia. *An Mus Plata.* 2:1–14.
- Mannion PD, Upchurch P, Barnes R, Mateus O. 2013. Osteology of the Late Jurassic Portuguese sauropod dinosaur *Lusotitan atalaiensis* (Macronaria) and the evolutionary history of basal titanosauriforms. *Zool J Linn Soc Lon.* 168:98–206.
- Otero A. 2010. The appendicular skeleton of *Neuquensaurus*, a Late Cretaceous saltasaurine sauropod from Patagonia, Argentina. *Acta Palaeontol Pol.* 55(3):399–426.
- Powell JE. 1986. Revisión de los titanosáuridos de América del Sur [Revision of titanosaurs of South America] [unpublished Ph.D. dissertation]. Tucumán: National University of Tucumán.
- Powell JE. 1992. Osteology of *Saltasaurus loricatus* (Sauropoda – Titanosauridae) of the Late Cretaceous of Northwestern Argentina. In: Sanz JL, Buscalioni AD, editors. *Los dinosaurios y su entorno biótico: Actas del Segundo Curso de Paleontología in Cuenca*. Instituto Juan de Valdes: Cuenca; p. 165–230.
- Powell JE. 2003. Revision of South American titanosaurid dinosaurs: palaeobiological, palaeobiogeographical, and phylogenetic aspects. *Rec Queen Victoria Mus Launceston.* 111:1–173.
- Rohlf FJ. 2008. *Tpsdig, Version 212; tpsrelw, Version 146*. Stony Brook (NY): State University of New York at Stony Brook. Available from: <http://life.bio.sunysb.edu/morph/A>
- Rohlf FJ, Slice DE. 1990. Extensions of the Procrustes method for the optimal superimposition of landmarks. *Syst Biol.* 39(1):40–59.
- Romer AS. 1956. *Osteology of the reptiles*. Chicago (IL): University of Chicago Press.
- Salgado L, Apesteguía S, Heredia S. 2005. A new specimen of *Neuquensaurus australis*, a Late Cretaceous saltasaurine titanosaur from North Patagonia. *J Vertebr Paleontol.* 25(3):623–634.
- Salgado L, Gallina PA, Paulina Carabajal A. 2014. Redescription of *Bonatitan reigi* (Sauropoda: Titanosauria), from the Campanian–Maastrichtian of the Río Negro Province (Argentina). *Hist Biol.* 27(5): 525–548.
- Wilson JA. 1999. A nomenclature for vertebral laminae in sauropods and other saurischian dinosaurs. *J Vertebr Paleontol.* 19(4):639–653.
- Wilson JA. 2002. Sauropod dinosaur phylogeny: critique and cladistics analysis. *Zool J Linn Soc Lon.* 136(2):217–276.
- Wilson JA. (2006). An overview of titanosaur evolution and phylogeny. En: *Colectivo Arqueológico-Paleontológico Salense*, editor. *Actas de las III Jornadas sobre Dinosaurios y su Entorno*. Burgos, España: Salas de los Infantes, p. 169–190.
- Wilson JA, D'Emic MD, Ikejiri T, Moacdieh EM, Whitlock JA. 2011. A nomenclature of vertebral fossae in sauropods and other saurischian dinosaurs. *Plos One.* 6(2):e17114(1–19).