New Remains Attributable to the Holotype of the Sauropod Dinosaur Neuquensaurus australis, with Implications for Saltasaurine Systematics

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New remains attributable to the holotype of the sauropod dinosaur *Neuquensaurus australis*, with implications for saltasaurine systematics

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The Late Cretaceous South American sauropods *Neuquensaurus australis* and *Saltasaurus loricatus* are represented by well-preserved and abundant material that has been integral to our understanding of titanosaur anatomy for decades. Although the hypodigms for these species span most of the skeleton, holotypic materials are limited to a few bones that do not overlap between the two taxa. In this contribution, we augment the holotype of *Neuquensaurus australis* with a partial sacrum that was preserved in articulation with one of the caudal vertebrae from its original description, but not recognised as such at the time. We document this field association via the presence of a broken piece of matrix on the sixth sacral vertebral centrum that has a snap-fit to matrix on the rim of the anterior condyle of the holotypic biconvex vertebra. Based on comparisons with a more complete sacrum and ilium of a referred specimen of *Neuquensaurus australis*, we interpret this biconvex vertebra to be the seventh sacral vertebra. This raises the possibility that the biconvex "first caudal" vertebra of some other titanosaurs may be part of the sacrum as well. Augmentation of the *Neuquensaurus australis* holotype to include a sacrum makes it directly comparable to the holotype of *Saltasaurus loricatus*. Morphological differences in the number, shape, and proportion of sacral vertebrae allow discrimination between *Neuquensaurus* and *Saltasaurus*, confirming their generic separation. The El Brete quarry, which preserves the holotypic sacrum and abundant referred specimens of *Saltasaurus loricatus*, also preserves a sacrum consisting of seven vertebrae that bears autapomorphies of *Neuquensaurus australis*, indicating that these two saltasaurines coexisted.

Key words: Dinosauria, Sauropoda, Titanosauria, *Neuquensaurus*, *Saltasaurus*, taxonomy, Cretaceous, South America.

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Introduction

Titanosaurs are an anatomically specialised clade of sauropod dinosaurs that predominated during the Cretaceous (Powell 2003; Curry Rogers 2005). Until recently, titanosaurs have been regarded as Gondwanan, enigmatic sauropods, due to early perceptions of their relative rareness in North America, Asia, and Europe, and the relative incompleteness of skeletal remains attributed to them (Romer 1956; McIntosh 1990). The recent proliferation of well preserved titanosaur and titanosaur-related genera on both northern and southern landmasses has led to a better understanding of their anatomy and to the recognition that they formed major components of the diversity and biomass of many Cretaceous terrestrial ecosystems (Curry Rogers 2005; Wilson 2006).

Although cladistic analyses of titanosaurs share many areas of agreement, these analyses suffer from highly disparate taxonomic content (Wilson 2006: fig. 7) and relatively incomplete taxonomic coverage. The most comprehensive analysis of Titanosauria to date was unable to resolve a stable framework for future work (Curry Rogers 2005). Thus, the potential power that titanosaurs have to address research questions in a variety of fields relevant to dinosaur palaeontology (e.g., palaeobiogeography, body size evolution, growth rates, extinction) is currently hindered by a lack of a comprehensive, resolved, and well-supported cladistic analysis of the group. Phylogenetic analyses of titanosaurs are in turn hindered by a number of concerns with alpha-taxonomy that must be resolved before including these taxa in a cladistic analysis, especially for taxa that were discovered early, such as saltasaurines. Revisions of alpha-level taxonomy have long been a part of sauropod systematics. McIntosh's detailed study of sauropods from the Morrison Formation of North America, which involved examination of quarry maps, field notes, museum collections, and original localities, led to a stable taxonomy for these taxa (Ostrom and McIntosh 1966; McIntosh and Berman 1975; Berman and McIntosh 1978; McIntosh and Williams 1988; McIntosh and Carpenter 1998; McIntosh 2005). Such revisions are ongoing, particularly within the Titanosauriformes, preparing the ground for future analyses of the group (e.g., revisions of "Titanosauridae", Salgado 2003; "*Titanosaurus*", "Titanosauridae", Wilson and Upchurch

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2003; *Phuwiangosaurus*, Suteethorn et al. 2009; *Jainosaurus*, Wilson et al. 2009; *Euhelopus*, Wilson and Upchurch 2009; *Mongolosaurus*, Mannion in press). Although revision is occurring at a slower rate than new titanosaur discoveries are being made (see taxon lists in Curry Rogers 2005; Wilson and Upchurch 2009), many of the new discoveries include or have been followed by extensive documentation of field associations (e.g., González Riga and Astini 2007; Curry Rogers 2009; Pérez et al. 2009).

As discussed below, the original holotypes of *Neuquensaurus* and *Saltasaurus* do not overlap anatomically, complicating evaluation of their validity as separate taxa. Below, we revise the holotype of the Late Cretaceous South American saltasaurine *Neuquensaurus australis* in order to evaluate its validity and referral of new materials to it. We begin by providing a review of the taxonomic history of *Neuquensaurus* and justification for augmenting the holotype, followed by a redescription of the holotypic remains. We close with a discussion of remains referred to *Neuquensaurus* and implications for the regional identity of the biconvex vertebra present in many titanosaurs.

Institutional abbreviations.—BYU, Brigham Young University Museum of Paleontology, Provo, USA; MACN, Museo Argentino de Ciencias Naturales "Bernardo Rivadavia", Buenos Aires, Argentina; MCS, Museo Cinco Saltos, Cinco Saltos, Argentina; MCT, Museu de Ciências da Terra, Departmento Nacional de Producão Mineral, de Rio de Janeiro, Brazil; MLP, Museo de La Plata, La Plata, Argentina; MPCA, Museo Provincial "Carlos Ameghino", Cipolletti, Rio Negro, Argentina; PVL, Instituto Miguel Lillo, Tucumán, Argentina.

Other abbreviations.—cpol, centropostzygapophyseal lamina; cprl, centroprezygapophyseal lamina; pcdl, posterior centrodiapophyseal lamina; posl, postspinal lamina; prsl, prespinal lamina; spol, spinopostzygapophyseal lamina; sprl, spinoprezygapophyseal lamina. (Abbreviations for vertebral laminae follow Wilson 1999).

Taxonomic history and original type series of *Neuquensaurus australis*

The British palaeontologist Richard Lydekker traveled to Argentina in 1893 to describe mammalian and reptilian fossils housed at the then newly founded Museo de La Plata. Lydekker had spent 1874–1882 describing Indian fossils and conducting fieldwork while appointed at the Geological Survey of India in Kolkata, followed by a decade in England writing a series of papers describing European fossils (Anonymous 1915). When Lydekker (1894: 4) began his work at the Museo de La Plata, he was staggered by the quantity and quality of fossil material present in the museum, remarking that "upon my arrival the reality far exceeded my most eager expectations ... I was absolutely lost in astonishment and admiration at the number and beauty of its palaeontological treasures."

Among other fossils, Lydekker (1893) described remains of sauropod dinosaurs that he attributed to new species of the genus "*Titanosaurus*", the type species of which he described from India in 1877. Lydekker's southern representative of that genus, "*Titanosaurus*" *australis*, comprised bones collected from a single locality on the right bank of the Río Neuquén near the city of Neuquén. Lydekker did not participate in the excavation, and it is unlikely that he visited the locality. It is likely that any information he had about field associations was passed to him by expedition members. No maps or quarry photographs are known to exist, and for this reason subsequent researchers have had a limited range of options to further examine or document associations.

Regarding the Museo de La Plata's collection of sauropods, Lydekker (1893: 1–2) mentioned that "By far the great majority of the bones were found at a single spot in Neuquen … mostly found in association," but he also noted that "the majority [of the bones] were picked up by the members of the expedition lying loose on the surface of the country." Later, he stated that "… the name *Titanosaurus australis* is proposed … represented by a large series of associated vertebrae from Neuquen mostly belonging to a single individual, together with the bones of the fore and hind limbs, and some fragments of the pectoral and pelvic girdles. The caudal vertebrae represented in plate I may, however, be taken as the actual types." Lydekker probably chose caudal vertebrae as the types of "*Titanosaurus*" *australis* to make them directly comparable with "*Titanosaurus indicus*", whose type series included distal caudal vertebrae (Lydekker 1877).

Lydekker (1893) separated two vertebrae from the holotypic locality as a separate species, which he called "*Titanosaurus*" *nanus* for its small size. The validity of the species "*T.*" *nanus* has not been recognised by most authors (e.g., Bonaparte and Gasparini 1978; Powell 2003; Wilson 2002; Wilson and Upchurch 2003; Upchurch et al. 2004).

German palaeontologist Friedrich von Huene visited the Museo de La Plata between 1923 and 1926 and undertook a revision of Lydekker's work. Huene was also tasked by the Museum's then-director, Luis Torres, with the description of new Patagonian dinosaur material that was collected from Río Negro Province by the museum in 1921–1922 under the direction of palaeontologist Santiago Roth and geologist Walter Schiller. Among these new materials and those Lydekker (1893) had included in "*T.*" *australis*, Huene (1929) separated some out as the new species "*Titanosaurus*" *robustus* and others as the new genus and species *Laplatasaurus araukanicus*. Huene (1929: 23, translated from the Spanish) recognised the difficulty in identifying individuals in the Cinco Saltos quarry: "The numerous bones at Cinco Saltos had been discovered in a way that does not allow determination of which bones pertain to each individual, with the exception of the few series of caudal vertebrae. Various species and various genera are completely intermixed. The separation, sadly, I had to do by examination, and in these cases errors could not be excluded...All the material had to be ordered by me in such a way that consideration of its shape, preservation, and comparison resulted in the most natural correlation possible." Huene's criteria for separating species and genera were often not transparent or testable (e.g., unspecified proportional differences).

Huene's taxonomic decisions were not commented upon for almost 50 years, until they were formalised by Bonaparte and Gasparini (1978). In their study of the sauropods of Neuquén and Chubut Provinces, Bonaparte and Gasparini (1978) designated the type caudal vertebrae listed by Lydekker (1893: pl. 1) as the holotype of "*Titanosaurus*" *australis*. Importantly, Bonaparte and Gasparini (1978) placed each taxon into a standardised stratigraphic framework. "*T.*" *australis* and "*T*". *robustus* were listed by Bonaparte and Gasparini (1978) as coming from the Río Colorado Formation (now regarded as a subgroup; Leanza et al. 2004), possibly the Bajo de la Carpa Member (now regarded as a formation; Leanza et al. 2004), as well as possibly the Allen Formation. The provenance of these materials is now regarded as the Anacleto Formation (Leanza et al. 2004; Salgado et al. 2005).

Powell (1986, 1992, 2003) provided the first exhaustive revision of South American titanosaurs, in which he re-evaluated the collection of the Museo de La Plata. In his Ph. D. thesis, Powell (1986) coined the name *Neuquensaurus* as a new genus for "*T.*" *australis* and "*T.*" *robustus*, which was first formally published in Powell (1992). Powell (2003: 40) stated that the sacrum (MLP Ly 7), as well as other caudal vertebrae (MLP Ly 66 and 48), also belong to the holotype of *Neuquensaurus australis*. The assignment of the two caudal vertebrae to the holotype of *N. australis* was established by their articulation with the holotypic caudal vertebra that preserves a fragment of the preceding neural spine (MLP Ly 5; Powell 2003), but no evidence was presented justifying inclusion of the sacrum in the holotype. In addition to these augmentations, Powell (2003: 40) suggested that two vertebrae be removed from the holotype of *N. australis*: "… MLP Ly 6 [a caudal centrum] should be discarded from the holotype, since it clearly is a caudal vertebral centrum of the same species but a different individual. MLP Ly 1 [the biconvex vertebra] should be excluded from the material corresponding to the holotype as well since its morphology clearly indicates it belongs to a titanosaurid closely related to *Titanosaurus*." As we discuss below, comparisons with the more complete Museo Cinco Saltos specimen (MCS-5) suggest that the caudal centrum (MLP Ly 6) likely pertains to the holotypic individual (see Caudal vertebrae below). The biconvex vertebra (MLP Ly 1), has a snap-fit to the sacrum (MLP Ly 7). Therefore, they belong to the same individual, which must be either included or excluded from the holotype.

McIntosh (1990) considered *Saltasaurus* and *Neuquensaurus* to be congeneric, based on his view that observed differences between them were minor. This opinion has not been followed by other authors, who typically recognise them to be distinct genera (e.g., Salgado and Azpilicueta 2000; Martinelli and Forasieppi 2004; Upchurch et al. 2004).

The most recent taxonomic review of *Neuquensaurus* came with the referral of new materials (MCS-5) to the genus by Salgado et al. (2005: 623), who stated that "The type specimen of '*Titanosaurus*' *australis* (= *Neuquensaurus australis*) was thus artificially constructed by Huene on the bas[is] of mostly isolated materials." Although Huene (1929) referred numerous remains to "*T.*" *australis*, it was Lydekker (1893) who designated the caudal vertebrae as the types, a decision formalised by Bonaparte and Gasparini (1978). The material referred to *Neuquensaurus* by Salgado et al. (2005) was referred to that genus on the basis of autapomorphies shared with both the holotype and hypodigm. Salgado et al. (2005) did not discuss Powell's (2003) modification of the holotype of *Neuquensaurus australis*, but they provided a revised diagnosis of the species, which is discussed below.

Augmentation of the holotype of *Neuquensaurus australis*

Both of the classic saltasaurine taxa, *Neuquensaurus* and *Saltasaurus*, were discovered disarticulated in bonebeds with mostly undocumented field associations (Lydekker 1893; Bonaparte et al. 1977). The hypodigms of *Neuquensaurus australis* and *Saltasaurus loricatus* consist of numerous elements that have substantial overlap postcranially. In contrast, the holotypes of each of these species are limited and do not overlap—the holotype of *Neuquensaurus* consists of six caudal vertebrae, one of which we interpret as a sacral vertebra (see below), and part of a seventh caudal vertebra (Lydekker 1893), whereas that of *Saltasaurus* is represented by a complete sacrum (Bonaparte and Powell 1980). Although *Saltasaurus* and *Neuquensaurus* are thought to represent closely related genera that define Saltasaurinae (McIntosh 1990; Salgado et al. 1997; Wilson 2002; Powell 2003; Upchurch et al. 2004; Curry Rogers 2005; Calvo et al. 2008), there is some uncertainty surrounding their taxonomy (see above). The lack of consensus regarding the distinctiveness of *Saltasaurus* and *Neuquensaurus* and uncertainty about their constituency hinders assessment of their phylogenetic relationships to other saltasaurines (e.g., *Rocasaurus*, Salgado and Azpilicueta 2000; *Bonatitan*, Martinelli and Forasiepi 2004) and referral of new specimens (e.g., MCS-5, Salgado et al. 2005).

While examining the collections of the Museo de la Plata, we attempted to articulate axial remains attributed to *Neuquensaurus* and discovered that the sacrum MLP Ly 7 and the biconvex vertebra MLP Ly 1 articulate well (i.e., their outlines are identical and the convexity of the former conforms to the concavity of the latter) and matrix remaining on each vertebra snaps together when the vertebrae are articulated (Fig. 1). This indicates that the sacrum and biconvex vertebra were articulated prior to collecting and pertain to the same individual. Based on this new information, we argue that the sacrum should be included in the holotype of *Neu-*

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quensaurus, which makes it directly comparable to the holotype of *Saltasaurus*.

The case for regarding the remaining six caudal vertebrae as belonging to the same individual as the sacrum is not as clear. Excluding the partial neural spine cemented to one of them, none of the caudal vertebrae articulate with one another. Few serially homologous anatomical features or features of preservation tie these vertebrae to one another, and we identify morphological differences between them that could be either regional or taxonomic. Fortunately, Lydekker's type series can be compared to a more complete skeleton referable to *Neuquensaurus australis* from Cinco Saltos in Río Negro Province (MCS-5; Salgado et al. 2005; see below), which includes a sacrum and 15 caudal vertebrae. Based on comparisons that we detail below, the sacrum and caudal vertebrae of the type series of *Neuquensaurus australis* can be regarded as a single individual. We could not evaluate the claim by Powell (2003: 40) that the caudal vertebrae MLP Ly 66 and 48 belong to the holotype, because they are missing from the collections of the MLP.

Systematic palaeontology

Dinosauria Owen, 1842

Sauropoda Marsh, 1878

Titanosauria Bonaparte and Coria, 1993

Saltasauridae Bonaparte and Powell, 1980

Saltasaurinae Powell, 1992

Genus *Neuquensaurus* Powell, 1992

Neuquensaurus australis (Lydekker, 1893)

Holotype: MLP Ly 1–7, an incomplete sacrum, consisting of six coosified centra and one unfused biconvex centrum, and six partial caudal vertebrae.

Type locality: Lydekker (1893: 4) mentioned only that the holotypic materials were found in near Neuquén, but Huene (1929: 4, translated from the Spanish) provided more detailed locality information: "... in the elevated right bank of the Rio Neuquén, some kilometers (2–4) from the railway bridge and in the confluence before Neuquén." Thus, the holotypic locality is near 38°58' S, 68°00' W.

Type horizon: Anacleto Formation; Santonian-Campanian (Bonaparte and Gasparini 1978; Powell 1992; Dingus et al. 2000; Leanza et al. 2004; Salgado et al. 2005).

Referred specimens.—MCS 5, a partial skeleton from Cinco Saltos (Salgado et al. 2005), which includes: MCS 5/16, sacrum and ilia; MCS 5/1–15, 15 caudal vertebrae; MCS 5/30–32, three chevrons; MCS 5/24, left ischium; MCS 5/27–28, left and right femora; MCS 5/25 right tibia; MCS 5/26, right fibula; MCS 5/29, right astragalus. MLP CS 1400, 1402, and 1407, three mid-caudal vertebrae from Cinco Saltos (part of "Series 2" of Huene [1929]). PVL 4017-18, an incomplete sacrum from El Brete. See "Other materials referred to *Neuquensaurus australis*" below for discussion of these referrals.

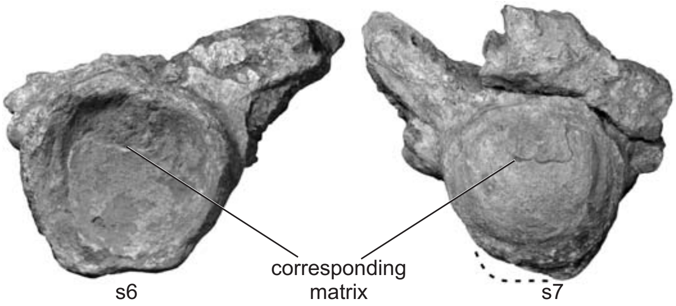

Fig. 1. Holotypic sacrum of the sauropod *Neuquensaurus australis* (Lydekker, 1893), MLP Ly 1 and 7, from the Late Cretaceous of Neuquén, Argentina. Posterior view of sixth sacral vertebra and anterior view of seventh sacral vertebra showing corresponding matrix, which snaps together when the vertebrae are articulated. The abbreviations (s6–s7) indicate sacral vertebral identity. Dashed lines indicate missing bone.

Stratigraphic and geographic range.—Referred remains come from: the same area as the holotype, Neuquén Province; Cinco Saltos, Río Negro Province (Salgado et al. 2005); and El Brete, Salta Province (Bonaparte et al. 1977; see below). Referred remains come from the same formation and the Lecho Formation (Campanian–Maastrichtian; Bonaparte and Powell 1980; see below).

Revised diagnosis.—Titanosaur sauropod with the following unique features of the holotype: length of sacral vertebral column about 1.5 times the width between the sacricostal yokes; sacral centra 4 and 5 less than half of the width of the last sacral centrum; seven sacral vertebrae (Powell 1986; Salgado et al. 2005). Referral of other remains held in the Museo Cinco Saltos (MCS-5) allows emendation of the diagnosis to include features present in other parts of the skeleton than are preserved in the holotype. Diagnostic features of the middle caudal vertebrae include: prezygapophyses with a nonarticulating anterior process, longitudinal ridge below transverse processes, podl present and elongate. Diagnostic features of the crus include: a fibula that is rotated anteromedially and translated slightly posteriorly so that the lateral trochanter is visible in anterior view (i.e., when the distal tibia is oriented transversely). Other features listed by Powell (1986) and Salgado et al. (2005) are now known to have a wider distribution within Titanosauria (see "Diagnostic features of *Neuquensaurus australis*" below).

Description

Sacrum.—Lydekker (1893: 5) briefly described a sacrum of "five vertebrae firmly anchylosed together" that he assigned to "*Titanosaurus*" *australis* (now known as *Neuquensaurus australis*, Powell 1992). We interpret this specimen (MLP Ly 7) to be composed of six coossified vertebrae that are missing their neural arches and sacral ribs. To this we add a biconvex vertebra (MLP Ly 1) that we interpret as the seventh sacral vertebra (Fig. 2).

The fused portion of the sacrum (MLP Ly 7) preserves centra and the basal portions of some neural arch laminae (e.g., the posterior centrodiapophyseal lamina [pcdl] on the

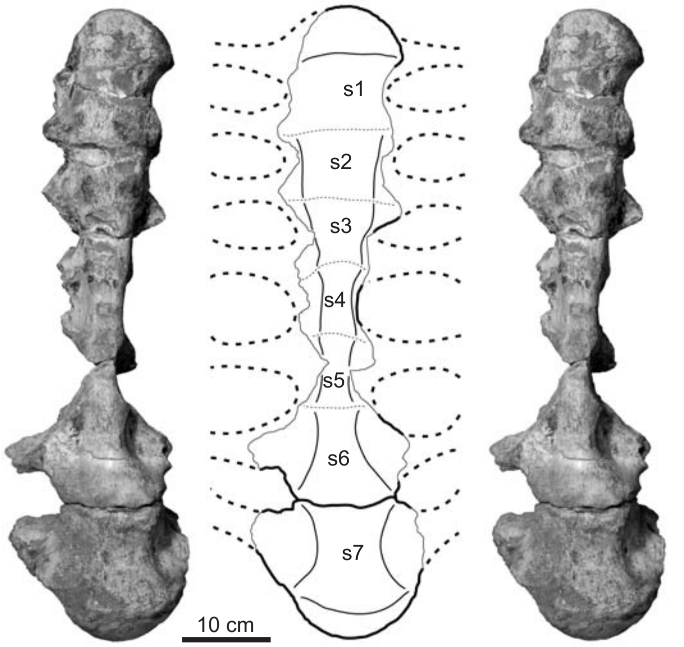

Fig. 2. Holotypic sacrum of the sauropod *Neuquensaurus australis* (Lydekker, 1893), MLP Ly 1 and 7, from the Late Cretaceous of Neuquén, Argentina. Stereophotographs and line drawings in ventral view. The abbreviations (s1–s7) indicate sacral vertebral identity. Dashed lines indicate missing bone, and dotted lines indicate intervertebral sutures.

first vertebra). We interpret this to indicate that the neurocentral junction was fully fused, and that the neural arches were broken away sometime after death. The neurocentral junctions of the sacral vertebrae close after those of the caudal vertebrae but before those of the presacral vertebrae in the non-titanosaur sauropod *Camarasaurus* (Ikejiri et al. 2005). Based on this information, we can infer that holotype of *Neuquensaurus australis* was not a young juvenile, but we do not know if it was skeletally mature.

Further evidence is required to demonstrate that these six fused vertebrae and the biconvex vertebra that articulates with them are all true sacral vertebrae. No ilia were preserved in association with the holotypic elements, so we rely on topological comparisons with the specimen MCS-5/16 of *N. australis* (see below) and other titanosaurs. In many titanosaurs, the first sacral vertebra articulates with the dorsal part of the preacetabular process of the ilium via a modified dorsal rib, and the second sacral rib articulates with a dorsoventrally elongate ridge on the ilium, which is positioned near the pubic peduncle and marks the posterior extent of the preacetabular process (e.g., *Futalognkosaurus*, MDD and JAW personal observations; MCT 1536-R, Campos and Kellner 1999). In the specimen MCS-5/16, there are six coossified centra followed by an unfused, biconvex seventh vertebra. The first sacral rib is not preserved, but the second sacral rib articulates along the iliac ridge, as mentioned above. The seventh sacral vertebra of that specimen, which is not fused to the other sacral vertebrae, bears a stout rib that contacts the ilium and forms part of the sacricostal yoke. Based on this, we identify seven sacral vertebrae in MCS-5/16 and infer that the holotype of *N. australis* also had seven sacral vertebrae.

Although Lydekker (1893) identified only five vertebrae in the fused portion of the sacrum (MLP Ly 7), we identify six. As shown in Fig. 3, the sutures between centra are clearly demarcated as raised rims of bone with striated texture. When the coalesced sacral vertebrae 1–6 are articulated with the biconvex sacral vertebra 7, the sacrum has a shallow ventral arch, as visible in lateral view (Fig. 4). The first six sacral vertebrae were also figured by Powell (2003: pl. 58: 5a, b), and since the time that it was photographed in 1986, left sacral rib 1 has been broken and lost (Fig. 2).

The sacral centra are otherwise nearly complete from the first, which is strongly convex anteriorly, to the seventh, which is strongly convex posteriorly. The vertebrae range in length from about 13 cm for the first to 7.7 cm for the third; the rest are intermediate in length. The widths of the vertebrae vary from 10.5 cm at the first inter-central suture to 4.9 cm at the suture between the sacral centra 4 and 5, to about 13 cm at the suture between the sacral centra 6 and 7 (Figs. 2, 3). The first sacral centrum is nearly 1.5 times wider than tall. The seventh sacral centrum is only slightly wider than tall and has lateral faces that are strongly angled ventrally.

Internal pneumaticity varies among the sacral vertebrae. The first, second, and third centra have small, deep, sharp-lipped foramina on the dorsal parts of their centra, but the fourth centrum only has a shallow fossa in the same location, and the fifth centrum completely lacks a fossa or foramina

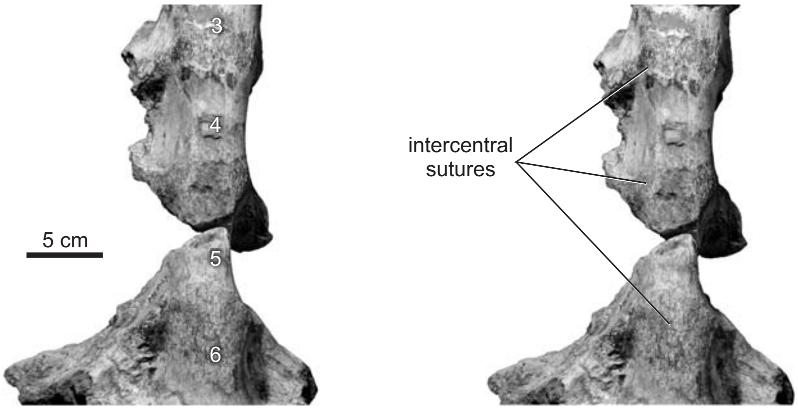

Fig. 3. Holotypic sacrum of the sauropod *Neuquensaurus australis* (Lydekker, 1893), MLP Ly 7, from the Late Cretaceous of Neuquén, Argentina. Close-up stereophotographs of sutures between sacral vertebrae 3–6 in ventral view.

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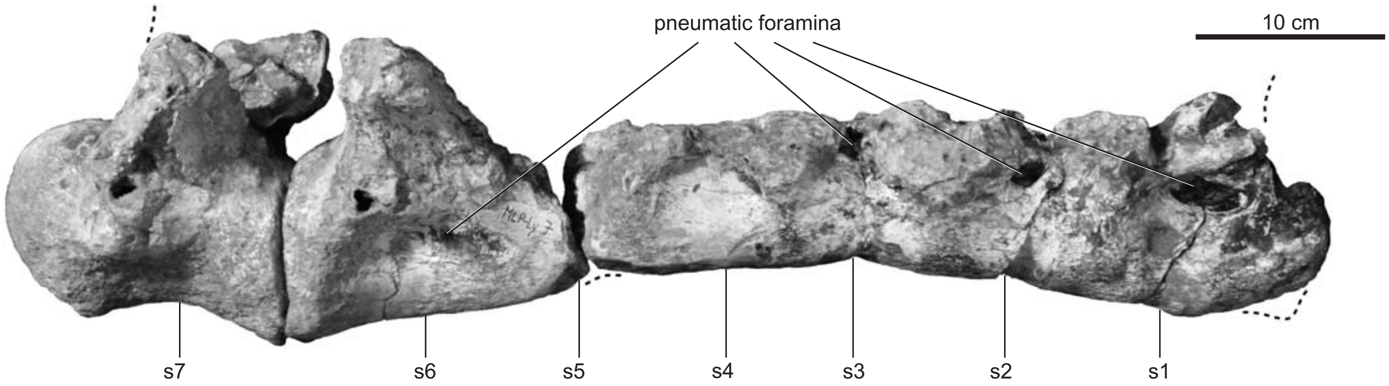

Fig. 4. Holotypic sacrum of the sauropod *Neuquensaurus australis* (Lydekker, 1893), MLP Ly 1 and 7, from the Late Cretaceous of Neuquén, Argentina in right lateral view. The abbreviations (s1–s7) indicate sacral vertebral identity. Dashed lines indicate missing bone.

(Fig. 4). Broken surfaces on the centra, proximal sacral ribs, and neural arches of the first five sacral vertebrae reveal sub-centimeter scale cells that indicate somphospondylous (= camellate) pneumaticity. The sixth sacral neural arch was also pneumatic, as visible in breaks in the bone, but it is unknown whether the centrum was pneumatic. Additional data are required to know whether the foramina piercing its side ramify into camellae.

The seventh sacral centrum (MLP Ly 1) is elongate, and the posterior condyle much more expanded than the anterior (Fig. 5). The anterior condyle is subcircular, whereas the posterior condyle is about 1.4 times wider than it is tall. A slight depression circumscribes the anterior condyle, and the posterior condyle has a slight circumferential ridge. No sutures are visible between the transverse processes, centrum, and neural arch. The ventral face of the centrum is flat and set off from the lateral face by a well-defined corner, as in the anterior caudal vertebrae of some titanosaurs (Salgado and Garcia 2002).

Caudal vertebrae.—Lydekker (1893) originally designated six elements as the type series of *N. australis*. Removing the biconvex vertebra from the caudal series leaves five elements, which we consider to represent a single individual but not an articulated series (Fig. 6). One of these elements (MLP Ly 5) actually includes parts of two different vertebrae held together by matrix, which we refer to as MLP Ly 5a (a neural spine) and MLP Ly 5b (a centrum and partial neural arch). Based on these identifications, six caudal vertebrae are represented in the type series of *N. australis*.

The first preserved caudal vertebra (MLP Ly 2; Fig. 6A) is likely the second or third in the series, based on comparisons with the referred *N. australis* material from Cinco Saltos (MCS-5). The centrum is strongly procoelous, and less elongate than the seventh sacral centrum (MLP Ly 1). The neural arch and transverse processes are largely missing, but it is clear that the transverse processes occupied the dorsal half of the centrum. The centrum is hexagonal in cross section, with lateral faces that are angled inwardly towards the weakly concave ventral face of the centrum (Fig. 6A). In lateral view, the ventral face of the centrum is weakly arched. The centrum appears to lack pneumatic foramina, but the broken neural arch reveals camellate pneumatic bone.

The second vertebra in the series (MLP Ly 3; Fig. 6B) is approximately the seventh caudal vertebra, based on comparisons with the Museo Cinco Saltos *N. australis* sacrum (MCS-5). It too is strongly procoelous and has camellate pneumaticity in its neural arch, though no camellae or pneumatic foramina are visible in its centrum. A weak ridge circumscribes the posterior condyle (Fig. 6B). The vertebra is subrectangular in proportions, with a ventrolaterally sloping face that is smaller than in the more anterior caudal vertebrae

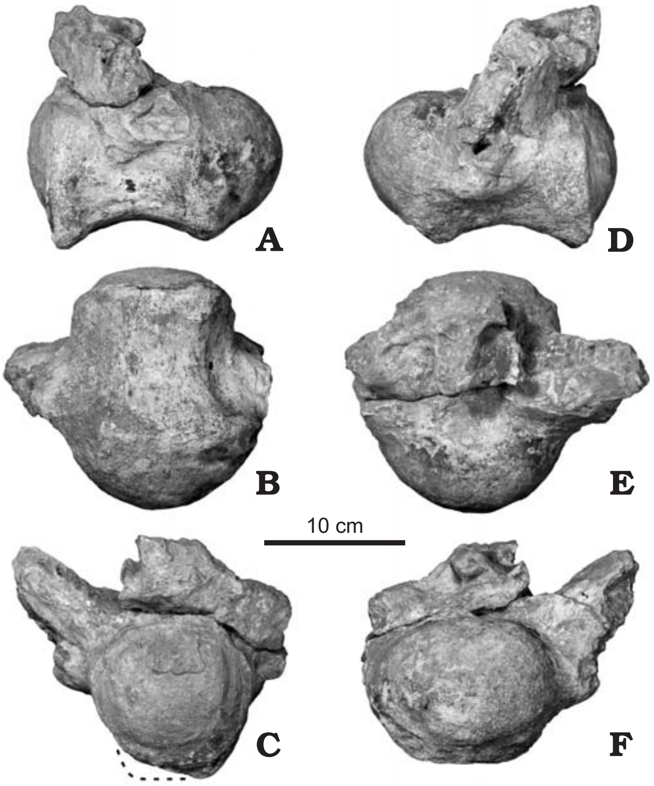

Fig. 5. Holotypic seventh sacral vertebra of the sauropod *Neuquensaurus australis* (Lydekker, 1893), MLP Ly 1, from the Late Cretaceous of Neuquén, Argentina in left lateral (**A**), ventral (**B**), anterior (**C**), right lateral (**D**), dorsal (**E**), and posterior (**F**) views.

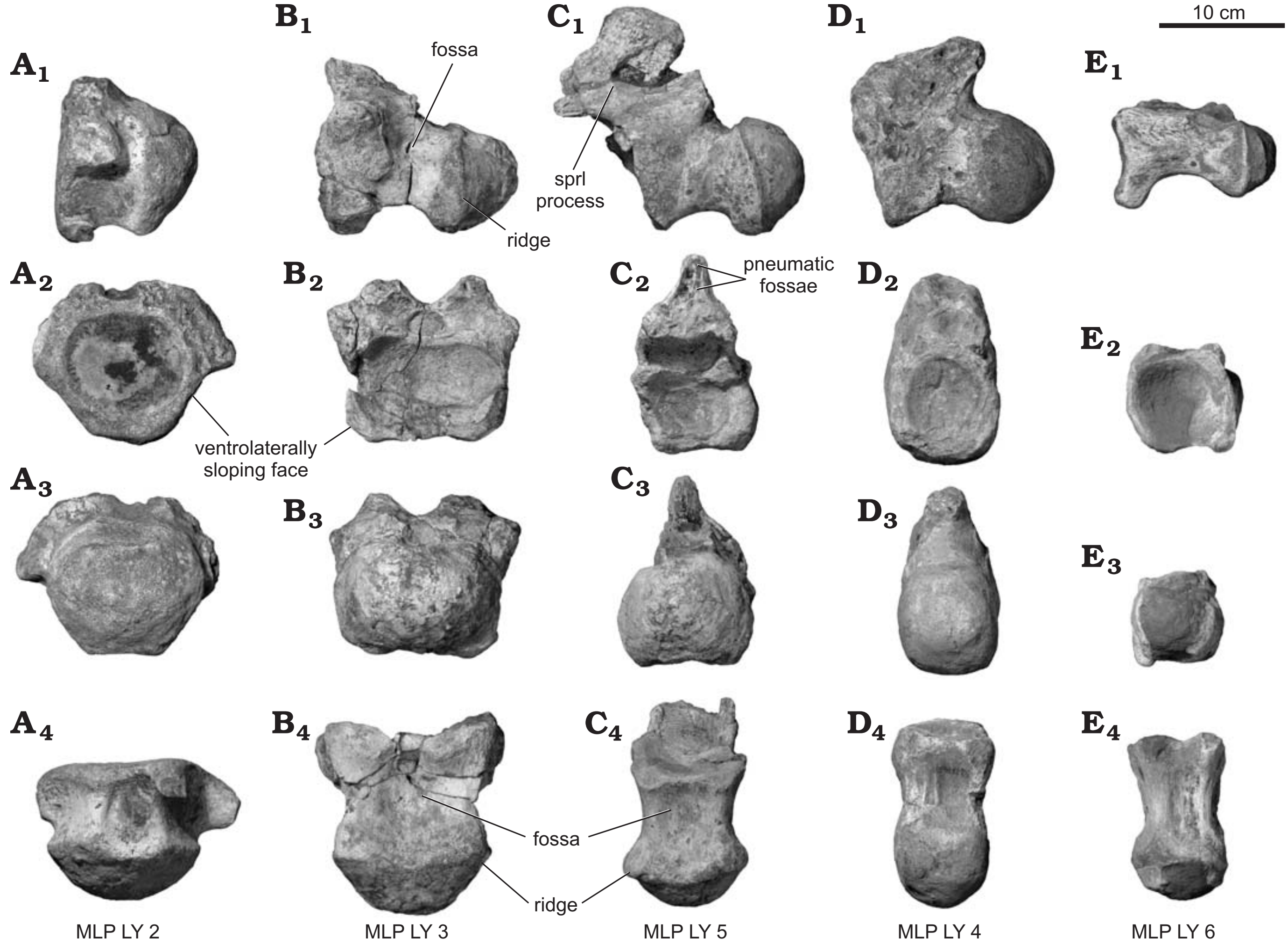

Fig. 6. Holotypic caudal vertebrae of the sauropod *Neuquensaurus australis* (Lydekker, 1893) from the Late Cretaceous of Neuquén, Argentina. **A**. MLP Ly 2, ?second or third caudal vertebra in left lateral (A_1), anterior (A_2), posterior (A_3), and ventral (A_4) views. **B**. MLP Ly 3, ?seventh caudal vertebra in left lateral (B_1), anterior (B_2), posterior (B_3), and ventral (B_4) views. **C**. MLP Ly 5a, b, parts of the ?ninth and tenth caudal vertebrae in left lateral (C_1), anterior (C_2), posterior (C_3), and ventral (C_4) views. **D**. MLP Ly 4, mid-caudal vertebra in left lateral (D_1), anterior (D_2), posterior (D_3), and ventral (D_4) views. **E**. MLP Ly 6, mid-posterior caudal vertebra in left lateral (E_1), anterior (E_2), posterior (E_3), and ventral (E_4) views. Abbreviation: sprl, spinoprezygapophyseal lamina.

(Fig. 6B). The ventral surface of MLP Ly 3 is strongly arched in lateral view, and is excavated by a fossa (Fig. 6B). The lateral face of the centrum has a horizontally-oriented ridge that extends from the transverse process to the rim of the condyle.

We interpret MLP Ly 5a and b to be the next caudal vertebrae in the series (Fig. 6C). This interpretation conflicts with the arrangement of Lydekker (1893), reflected in his numbering scheme, in which MLP Ly 4 is more anteriorly positioned than MLP Ly 5. Specifically, MLP Ly 5b has a subrectangular cross-section like MLP Ly 3, whereas MLP Ly 4 has a subcircular cross-section like MLP Ly 6. We estimate that MLP Ly 5b is approximately the tenth caudal vertebra, based on comparisons with a referred specimen of *N. australis* from Cinco Saltos (MCS-5). As mentioned above, MLP Ly 5 comprises parts of two vertebrae—the centrum and partial neural arch (MLP Ly 5b) of one vertebra cemented to the neural spine and postzygapophyses of the preceding vertebra (MLP Ly 5a). It is likely that the neural spine does not pertain to the preceding element in the preserved series (MLP Ly 3), indicating that it represents an additional vertebra. The neural spine (MLP Ly 5a), which represents approximately the ninth caudal vertebra, is posteriorly inclined as preserved and bears prespinal (prsl), postspinal (posl), spinoprezygapophyseal (sprl), and spinopostzygapophyseal (spol) laminae. The sprls diverge towards the prezygapophyses to bound a fossa that is divided by a median prsl. Between the prsl and each sprl, there are oval, sharp-lipped pneumatic openings (Fig. 6C), as in the anterior and mid-caudal vertebrae of the specimen MCS-5 and titanosaurs such as *Saltasaurus* (Powell 2003), *Bonatitan* (Martinelli and Forasiepi 2004), *Baurutitan* (Kellner et al. 2005), and *Futalognkosaurus* (Calvo et al. 2008).

The centrum of MLP Ly 5b is strongly procoelous, elongate, and roughly rectangular in anterior and posterior views. It has an arched ventral margin that is excavated by a fossa bounded by ridges and strongly developed chevron facets, but it lacks any trace of a median ridge within the fossa (Fig. 6C). The posterodorsal edges of the centrum, just in front of the posterior condyle, are pinched inwards dorsally as in MLP Ly

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3. However, there is no ridge and fossa below this surface on the ventrolateral face of the centrum. The remnants of the transverse process are present as a weak tuberosity that sits atop the anterior neurocentral junction. The neural arch preserves only the prezygapophyses, which are incomplete at their tips. In lateral view, the dorsal edge of the spinoprezygapophyseal lamina (sprl) bears a prominent process that is present in several titanosauriforms (e.g., *Alamosaurus*, Gilmore 1946; *Mendozasaurus*, González Riga 2003; *Adamantisaurus*, Santucci and Bertini 2006; *Phuwiangosaurus*, MDD and JAW personal observations).

The next preserved caudal vertebra in the series (MLP Ly 4), includes a centrum and its fused, damaged neural arch (Fig. 6D). It was positioned posterior to caudal vertebra 15, based on comparisons with the *Neuquensaurus* MCS-5. Camellate pneumaticity is visible on the broken surfaces of the neural arch and neural spine. The centrum is strongly procoelous, but lacks the ridge circumscribing the condyle present in other vertebrae. It is slightly taller than wide, in contrast to the more anterior caudal centra. The ventral surface of this vertebra is arched in lateral view and has a ventral fossa. This fossa is divided by several subtle struts longitudinally, but has no strong midline ridge. A small pneumatic foramen pierces the ventral centrum, but its profundity is unknown due to coverage by matrix.

The posteriormost-preserved vertebra of the type series is a middle to distal caudal vertebra (MLP Ly 6; Fig. 6E). As in the vertebrae anterior to it, the ventral edge is strongly arched and excavated by a subdivided fossa. The centrum is strongly procoelous and elongate, and slightly wider than tall. A circumferential ridge surrounds the condyle. Small teardrop-shaped foramina pierce the lateral wall of the centrum, and above these the raised neurocentral junction bears a longitudinally striated texture.

Discussion

Referred materials.—The distalmost caudal vertebra of the type series of *Neuquensaurus australis* (MLP Ly 6) has a particular preservational style in which the condyle is stained deep red (Fig. 6E). Although other caudal vertebrae in the Museo de La Plata collections share the morphology and identical preservation of MLP Ly 6 (e.g., MLP Ly 71), the absence of a quarry map or other information linking these to the holotype precludes regarding them as the same individual. We follow Lydekker (1893), Huene (1929), and Bonaparte and Gasparini (1978) in not regarding these other caudal vertebrae as part of the holotype.

Abundant axial, appendicular, and dermal materials in the collections of the Museo de La Plata have been referred to *Neuquensaurus*. None of these elements were found in direct association with the holotypic remains, and overlap between these referred specimens and the holotype is limited. The criteria used to assign these non-overlapping materials to *Neuquensaurus* in the past are not clear, but referral of specimens to *Neuquensaurus* must be made via materials that anatomically overlap with the holotype—the sacrum and six caudal vertebrae mentioned above—and share autapomorphies with it. A strong case can been made for referral of the specimen MCS-5 to *Neuquensaurus australis*, which overlaps with the holotypic remains and shares diagnostic features such as the presence of seven sacral vertebrae (see below).

The vertebral "series 1–4" described by Huene (1929) were considered by him to represent individuals, or mainly individuals, but there was little discussion of the criteria that led to this assessment (see above). Apart from several short articulated series of 2–6 caudal vertebrae, individuals cannot be confidently recognised among the Huene's "series". Consequently, referral to *Neuquensaurus* must be justified on a case-by-case basis using autapomorphies. We can refer three caudal vertebrae in the Museo de La Plata to *Neuquensaurus australis* (MLP CS 1400, 1402, 1407; see Diagnosis and Referred specimens above). Three other caudal vertebrae (MLP CS 1429, 1432) appear to be referable to *N. australis* based on the figures of Huene (1929: pl. 5), but the relevant parts of those vertebrae are now missing. Although other caudal vertebrae in the Museo de La Plata resemble those of *Neuquensaurus australis*, in the absence of autapomorphies and of definitive associations of individuals, we cannot confidently refer them to the taxon.

Diagnostic features.—The diagnosis for *Neuquensaurus australis* given by Powell (2003) was revised by Salgado et al. (2005: 625) to include six characters. Four of these characters can observed in the emended holotype, two in the sacrum and two in the caudal vertebrae: (i) seven sacral vertebrae; (ii) third to fifth sacral centra narrowed; (iii) mid- and posterior caudal vertebrae with parasagittal ventral ridges that bound a non-keeled ventral fossa culminating in chevron facets; (iv) lateral walls of caudal centra parallel to one another (i.e., not visible in ventral view).

The ventral narrowing of the third to fifth sacral centra was cited as an autapomorphy of *Neuquensaurus australis* by Powell (2003) and Salgado et al. (2005). This feature requires further refinement, because mid-sacral vertebrae are narrower than the first or last in several neosauropods, including *Diplodocus* (Hatcher 1901: fig. 9), *Brachiosaurus altithorax* (Riggs 1904: pl. 73: 2), an indeterminate titanosaur from Brazil (MCT 1536-R; Campos and Kellner 1999), *Trigonosaurus* (Campos and Kellner 1999: fig. 16; Campos et al. 2005: fig. 24), the topotype partial sacrum of *Alamosaurus* (PMU R 172; Mateer 1976; note this author reversed anterior and posterior on the sacrum), and *Isisaurus* (Jain and Bandyopadhyay 1997: fig. 10). In the above-listed taxa, this narrowing can be subtle (e.g., *Brachiosaurus*, *Diplodocus*) or more dramatic (e.g., *Trigonosaurus, Alamosaurus*), but in *Neuquensaurus australis*, this narrowing is autapomorphically extreme, such that the mid-sacral centra are between one-third and one-half of the widths of the first and seventh sacral centra.

All of the type series caudal vertebrae have parallel lateral walls of the centra except the anteriormost preserved centrum

(MLP Ly 2; Fig. 6), which has angled lateral faces. This condition—anterior caudal vertebrae with ventromedially sloping faces that give way to vertically-oriented lateral faces in more posterior caudal vertebrae in the series—is similar to that found in several other titanosaurs, including *Laplatasaurus araukanicus*, MUCPv-204, *Gondwanatitan*, and the referred Cinco Saltos *Neuquensaurus australis* (MCS-5; Salgado and Garcia 2002; Salgado et al. 2005). This suggests that morphology of the centrum changes along the caudal series in the holotype of *N. australis*. Likewise, the presence of parasagittal ventral ridges bounding a fossa that is not subdivided by a keel in middle and posterior caudal vertebrae is not unique to *Neuquensaurus*, but is present in other titanosaurs as well (e.g., *Alamosaurus*).

The Cinco Saltos individual (MCS-5) is much more complete than the holotype, preserving 15 complete caudal vertebrae, a sacrum and both ilia, an ischium, both femora, and an articulated tibia, fibula, and astragalus, allowing a fuller diagnosis of the taxon (Salgado et al. 2005). Based on this material, we identify three autapomorphies in the middle caudal vertebrae of *N. australis*: prezygapophyses with a nonarticulating anterior process, longitudinal ridge extending from base of transverse process, and elongate postzygodiapophyseal lamina (podl) oriented nearly parallel to the spinoprezygapophyseal lamina (sprl) and spinopostzygapophyseal lamina (spol). The fibula of *Neuquensaurus australis* is autapomorphically rotated anteromedially and translated slightly so that the lateral trochanter is visible in anterior view (e.g., Salgado et al. 2005: fig. 7H, I).

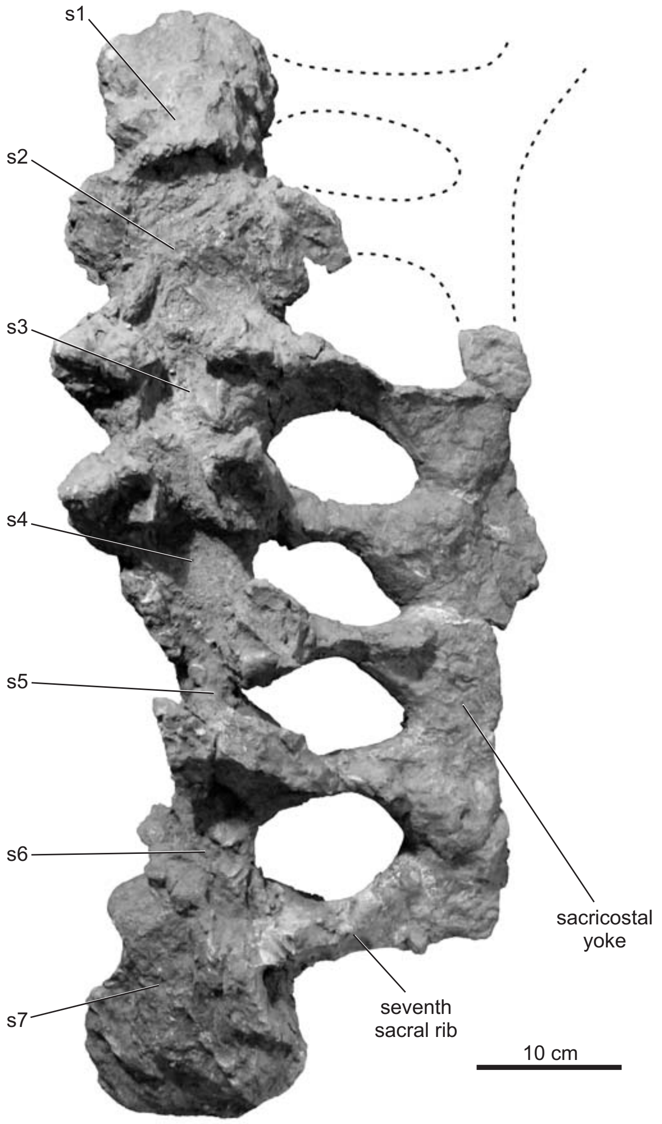

Fig. 7. Sauropod sacrum PVL 4017-18 from the *Saltasaurus loricatus* Bonaparte and Powell, 1980 quarry at El Brete, Argentina in dorsal view. Note the presence of seven sacral vertebrae. The abbreviations (s1–s7) indicate sacral vertebral identity. Dashed lines indicate missing bone.

Titanosaur sacra from the El Brete quarry, Salta, Argentina

All described remains of *Saltasaurus loricatus* (Bonaparte and Powell 1980) were collected from a single quarry in El Brete, in Salta Province, northwestern Argentina. Based on duplication of elements (femora in this case), and the presence of two unfused, small, juvenile cervical vertebrae that may or may not pertain to the same individual, the minimum number of individuals in this quarry is six (five were listed by Bonaparte et al. 1977, plus the juvenile material; MDD and JAW personal observations). A full quarry map is not available for the El Brete locality, but a partial map was given in Bonaparte et al. (1977: fig. 2) that illustrates the disarticulated nature of the specimens.

There are four titanosaur sacra from the El Brete quarry: PVL 4017-92 is the holotype of *Saltasaurus loricatus* (Bonaparte and Powell 1980); PVL 4017-93 is a similar sacrum; PVL 4017-18 is a more fragmentary, slightly longer sacrum; PVL 4017-142 is three coosified sacral centra. The holotypic sacrum of *S. loricatus* (PVL 4017-92) and the one that closely resembles it (PVL 4017-93) are subequal in size and have six coossified vertebrae that bear firmly fused contacts with the ilia. Centrum widths are subequal along both sacra, which are roughly as wide across their sacral ribs as they are long anteroposteriorly. In contrast, the slightly longer sacrum (PVL 4017-18) has seven co-ossified sacral vertebrae and unfused ilia (Powell 2003: pl. 55: 8; Figs. 7, 8). It has a length-to-width ratio of nearly 1.5 (74.2 cm long, ca. 50 cm wide). Sacral centra decrease to half their width by the fifth sacral vertebrae and then increase in size again posteriorly to reach their greatest width by seventh sacral centrum. The elongate El Brete sacrum (PVL 4017-18) matches the holotype of *Neuquensaurus australis* and the specimen MCS-5 in the number of constituent vertebrae, vertebral proportions, and sacral proportions, but it differs in that its seventh sacral centrum is fused to the remainder of the sacrum. This difference may indicate a later ontogenetic stage for the El Brete specimen, or it may be an actual taxonomic difference. The holotypic and Cinco Saltos (MCS-5) *Neuquensaurus* sacra

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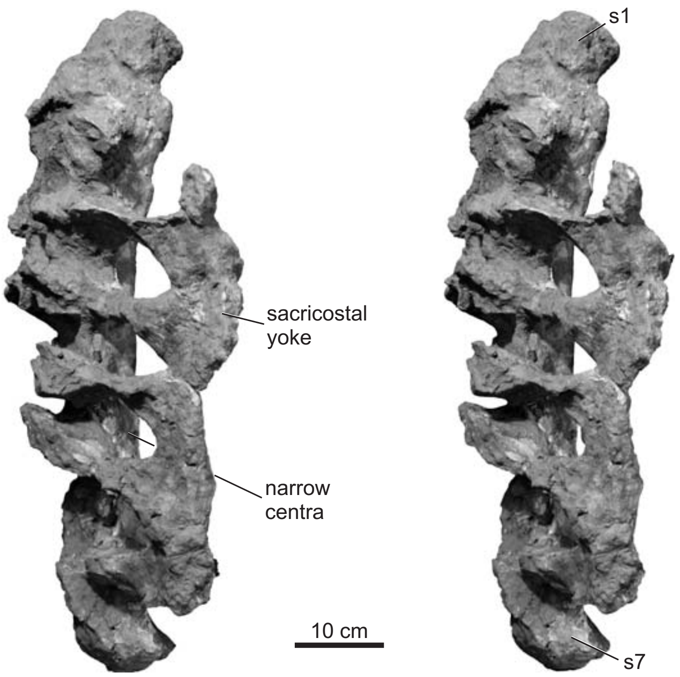

Fig. 8. Sauropod sacrum PVL 4017-18 from the *Saltasaurus loricatus* quarry at El Brete, Argentina. Stereophotographs in right lateral view, with anterior towards the top. The abbreviations s1 and s7 indicate sacral vertebral identity.

and the El Brete sacrum (PVL 4017-18) also differ in the degree of ventral curvature of both the first and last vertebrae of the sacrum (Figs. 4, 8), but we regard this variation as minor and possibly attributable to dorsoventral compression during preservation.

Differences in the number, shape, and sacral centra proportions between the elongate El Brete sacrum (PVL 4017-18) and the holotype of *Saltasaurus loricatus* (PVL 4017-19) can be interpreted in several ways. Regarding these differences as variation within the species preserves the monospecificity of the El Brete quarry (with regard to titanosaurs), but it reaches beyond our ability to defend intraspecific variation and would render homoplastic the features shared between PVL 4017-18 and *Neuquensaurus australis*. Alternatively, we could interpret these differences as indications of sexual dimorphism, which likewise would preserve the monospecificity of El Brete. However, sexual dimorphism has not been demonstrated in any titanosaur, and there does not appear to be bimodal variation in other parts of the anatomy found at El Brete. If, on the other hand, we interpret these differences as taxonomic, it suggests that a second titanosaur genus is present at El Brete. We suggest that the similarities between PVL 4017-18 and *Neuquensaurus australis* indicate that they belong to the same species: sacrum approximately 1.5 times as long anteroposteriorly as wide, seven sacral vertebrae, and sacral centra four and five narrowed to less than half the width of the first and seventh sacral centra.

Saltasaurus is typically regarded as stratigraphically younger than *Neuquensaurus* (late Campanian–Maastrichtian for the former, early to middle Campanian for the latter; Dingus et al. 2000; Powell 2003; Leanza et al. 2004), but radiometric ages for the quarry-bearing formations of either taxon do not exist (Leanza et al. 2004). Biostratigraphy in these formations is largely based on tetrapods (Leanza et al. 2004), and is therefore somewhat coarse. The presence of a sacrum attributable to *Neuquensaurus australis* in the El Brete quarry (PVL 4017-18) suggests that these two saltasaurines coexisted in the Late Cretaceous of South America, raising the possibility that some of the other materials attributed to *Saltasaurus loricatus* actually belong to *Neuquensaurus australis*, and vice versa.

Mechanism of sacral vertebral count increase in *Neuquensaurus australis*

The number of sacral vertebrae varies systematically within Sauropodomorpha. Basal sauropodomorphs (i.e., “prosauropods”) possess three sacral vertebrae, to which a fourth is added in all sauropods (Wilson and Sereno 1998). Five sacral vertebrae characterise *Patagosaurus* and more derived sauropods—one dorsal vertebra is incorporated into the sacrum in that its sacral rib touches the ilium, and it is fused to the other sacral vertebrae (Wilson 2002). Somphospondylan sauropods (e.g., *Euhelopus*, *Isisaurus*) are characterised by the addition of another dorsosacral vertebra, which both touches the ilium and is fused to the other sacral centra (Wilson 2002). In almost all titanosaurs for which a complete sacrum is known (*Epachthosaurus*, *Malawisaurus*, *Isisaurus*, *Saltasaurus*, MCT 1489-R, MLP 46-VIII-212), all centra are fused in adults and the last sacral vertebra has a posteriorly convex face. The only exceptions are *Opisthocoelicaudia* and an indeterminate titanosaur sacrum from Brazil (MCT 1536-R), in which the last sacral centrum has a concave posterior face.

Neuquensaurus australis has seven sacral vertebrae, which is autapomorphic (Salgado et al. 2005). Theoretically, this increase in sacral vertebral count may have been accomplished by incorporation of a dorsal or caudal vertebra or by duplication of an existing sacral vertebra. We rule out the hypothesis that *N. australis* incorporated a dorsal vertebra into the sacrum, because what is preserved of the first and second sacral vertebrae is morphologically and topologically identical to those in other titanosaur sacra. Moreover, the second sacral rib of *Neuquensaurus* and other titanosaurs is identical to the first sacral rib in those sauropods that have only five sacral vertebrae (e.g., *Apatosaurus*, BYU 1252). It is more likely that a seventh vertebra was added into the sacrum of *N. australis* via incorporation of a caudal vertebra by or duplication of one of the existing sacral vertebrae. How the addition of a seventh sacral vertebra evolved is informed by the sacral anatomy of outgroups to *Neuquensaurus*. However, this is complicated by the ambiguous identity of the sacro-caudal vertebrae of other titanosaurs, as discussed below.

Table 1. Biconvex sacral or anterior caudal vertebrae attributed to titanosaurs.

Taxon	Specimen number	Previous taxonomic assignment (reference)	Reference
Neuquensaurus australis	MLP Ly 1	"*Titanosaurus*" *australis* (Lydekker 1893)	Lydekker (1893: pl. 1: 1)
Neuquensaurus australis	MCS-5/16	–	Salgado et al. (2005: fig. 7A)
Alamosaurus sanjuanensis	USNM 15560; BYU 11392	–	Gilmore (1946: pl. 5: 1); MDD and JAW personal observations
Pellegrinisaurus powelli	MPCA 1500	cf. *Epachthosaurus* sp. (Powell 1986)	Salgado (1996: fig. 3)
Baurutitan britoi	MCT 1490-R	Peirópolis "series C" (Powell 1987; Campos and Kellner 1999)	Kellner et al. (2005: fig. 8)
Titanosauria indet.	MLP CS 1390	"*Titanosaurus*" *australis* (Lydekker 1893)	Huene (1929: pl. 3: 3)
Titanosauria indet.	MLP CS 1389	"*Titanosaurus*" *robustus* (Huene 1929)	Huene (1929: fig. 11)
Titanosauria indet.	MLP 52-XI-1-14	–	MDD and JAW personal observations
Titanosauria indet.	MACN 16432	*Laplatasaurus araukanicus* (Huene 1929)	Huene (1929: pl. 30: 2); Powell (2003: pl. 65: 11)
Titanosauria indet.	GSP-UM 6772	–	Malkani et al. (2001); MDD and JAW personal observations

The biconvex vertebra of titanosaurs

Two exemplars of *Neuquensaurus australis* bear biconvex vertebrae that are part of the sacrum but are unfused to other sacral centra (MLP Ly 1, MCS-5/16). In addition, two biconvex vertebrae collected from Cinco Saltos were identified by Huene (1929) as caudal vertebrae of *Neuquensaurus* (= "*Titanosaurus*") *australis* (MLP CS 1390) and *N.* (= "*T.*") *robustus* (MLP CS 1389). These vertebrae could pertain to *Neuquensaurus*, but we were unable to identify autapomorphies defending this assertion. Several other titanosaurs have biconvex vertebrae from the sacro-caudal region (Table 1): *Pellegrinisaurus* (Salgado 1996), *Baurutitan* (Kellner et al. 2005)*, Alamosaurus* (Gilmore 1946; BYU 11392, MDD and JAW personal observations), unpublished materials from the Pab Formation of Pakistan (GSP-UM 6772, MDD and JAW personal observations), an indeterminate titanosaur from Argentina (MLP 52-XI-1-14), and a vertebra that was found in the *Antarctosaurus wichmannianus* quarry (MACN 16432). Like *N. australis*, these biconvex vertebrae have posterior condyles that are much more strongly developed and dorsoventrally shorter than their anterior ones.

The biconvex vertebra in these other titanosaurs have been identified as the first caudal vertebra, but its inclusion in the sacrum in *Neuquensaurus australis* raises the possibility that some of them may actually be sacral vertebrae. In two of the three exemplars of *N. australis*, the biconvex seventh sacral centrum was not fused to the sixth sacral centrum. In one case, this vertebra was firmly incorporated into pelvis (MCS-5/16); in the holotype it was articulated to the remainder of the sacrum but that contact was nearly lost (MLP Ly 1), and in the El Brete exemplar it was fused to the preceding vertebra (Figs. 7, 8). Thus, the biconvex vertebra could be preserved as an isolated element in specimens that are incompletely fused laterally or are damaged (e.g., *Pellegrinisaurus*, *Antarctosaurus*, and the Pakistani biconvex centrum (GSP-UM 6772). Other biconvex titanosaur vertebrae can confidently be identified as caudal vertebrae, because their transverse processes resemble those of anterior caudal vertebrae in other titanosauriforms and are devoid of signs of fusion with a preceding vertebra or ilium (e.g., *Baurutitan*).

Future discoveries are needed to resolve the ambiguity over the regional identity of the less complete biconvex titanosaur vertebrae and to more fully understand the mechanism by which a seventh vertebra was incorporated into the sacrum of *Neuquensaurus australis*.

Conclusions

Saltasaurine titanosaurs are regarded as derived sauropods, but more detailed knowledge of their interrelationships has been hindered by taxonomic problems dating back to their early discovery. We have demonstrated that an incomplete sacrum in the collections of the Museo de la Plata belongs to the same individual as the holotypic caudal vertebrae of the saltasaurine *Neuquensaurus australis*, making this genus comparable to, and demonstrably distinct from, *Saltasaurus loricatus.* Autapomorphies present in the sacral and caudal vertebrae confirm referral of specimens held in the Museo Cinco Saltos and Museo La Plata to *N. australis.* A sacrum of *N. australis* is also present in the El Brete quarry, which has produced all remains of *Saltasaurus*, indicating that these genera coexisted in the Late Cretaceous of South America. *Neuquensaurus* is unique among sauropods in possessing seven sacral vertebrae, the last of which is biconvex. The biconvex vertebrae of some other titanosaurs may later be demonstrated to belong to the sacrum, rather than the caudal series, as currently presumed.

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