

The appendicular skeleton of *Neuquensaurus*, a Late Cretaceous saltosaurine sauropod from Patagonia, Argentina

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Otero, A. 2010. The appendicular skeleton of *Neuquensaurus*, a Late Cretaceous saltosaurine sauropod from Patagonia, Argentina. *Acta Palaeontologica Polonica* 55 (3): 399–426.

Neuquensaurus, from the Late Cretaceous of Argentina and one of the first dinosaurs described from Patagonia, is one of the most derived sauropod dinosaurs, and its proportions and size place it among the smallest sauropods ever known. In this context, *Neuquensaurus* is central to understanding late stages of sauropod evolution. This contribution offers a full description of the appendicular skeleton of *Neuquensaurus*. The anatomical analysis reveals that the appendicular skeleton of *Neuquensaurus* exhibits unique characteristics only shared with closely related saltosaurine titanosaurs; for example, the laterally directed preacetabular lobe of the ilium, the prominent fibular lateral tuberosity, and the presence of an intermuscular line on the femoral shaft, which is proposed here as a synapomorphy of Saltosaurinae. *Neuquensaurus* also displays many reversals to primitive character states, such as the presence of a prominent olecranon process of the ulna, a trochanteric shelf, a lesser trochanter and an ischial tuberosity. Additional characters that allow its evaluation in a phylogenetic context are here provided. Among them are the extremely deflected femoral shaft, the elliptical femoral cross-section, and the anterolaterally oriented cnemial crest.

Key words: Sauropoda, Saltosaurinae, *Neuquensaurus australis*, *Neuquensaurus robustus*, appendicular anatomy, sauropod evolution, Patagonia, Argentina.

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Received 19 August 2009, accepted 28 April 2010, available online 29 April 2010.

Introduction

Neuquensaurus (= “*Titanosaurus*”) *australis* (Lydekker, 1893) (Fig. 1) is one of the better preserved sauropods from the Upper Cretaceous of Patagonia. It represents, together with *Neuquensaurus robustus* (Huene, 1929), *Saltasaurus lorica-tus* Bonaparte and Powell, 1980, *Rocasaurus muniozi* Salgado and Azpilicueta, 2000, and *Bonattitan reigi* Martinelli and Forasiepi, 2004, a member of Saltosaurinae Powell, 1992 (= Saltosaurini Salgado and Bonaparte, 2007). *Neuquensaurus* is a small sauropod (femoral length 0.75 m) characterized by features in the axial (e.g., posterior caudal centra dorsoventrally flattened) and appendicular skeleton (e.g., fibular lateral tuberosity strong developed), that separate it as a distinctive taxon within Titanosauria (Wilson 2002). The most significant morphological features in the anatomy of *Neuquensaurus* are present in the appendicular skeleton (Huene 1929; Wilson and Carrano 1999; Wilson 2002; Powell 2003; Salgado et al. 2005; Otero and Vizcaíno 2008), which departs from the typical sauropod limb pattern. Because of its young geological age and anatomical peculiarities, *Neuquensaurus* figures prominently in discussion of the late stages of sauropod evolution (Wilson and Carrano 1999; Wilson 2005; Salgado et al. 2005).

“*Titanosaurus*” *australis* was erected and first described by Lydekker (1893) based on a series of associated caudal vertebrae and some elements of the limbs recovered from Neuquén Province, Patagonia, mostly belonging to the same individual (Lydekker 1893: 4). As noted by Wilson and Upchurch (2003: 139), Lydekker does not specify how many individuals those elements belongs to, and the fragments of the girdles and limbs were not associated with the type caudal vertebrae (Wilson and Upchurch 2003: 139). Huene (1929) later referred to “*Laplata-saurus*” *araukanicus* Huene, 1929 some elements previously assigned to “*T*”. *australis* by Lydekker and made an extensive description of that material, with the inclusion of numerous elements (mostly belonging to several adult and sub-adult individuals) collected in the early 20th century in the course of fieldwork carried out by the Museo de La Plata, Argentina. The collected bones were discovered intermixed; hence Huene couldn’t determine single individuals: “The separation (of the bones) pitifully had to be made by examination; therefore, errors are not excluded” (Huene 1929: 23, translated from the Spanish). Huene made a classification of the limb bones housed at the Museo de La Plata and assigned to the genus *Titanosaurus*, according to their peculiar shape and relative proportions, recognizing two Patagonian taxa: “*Titanosaurus*” *australis*

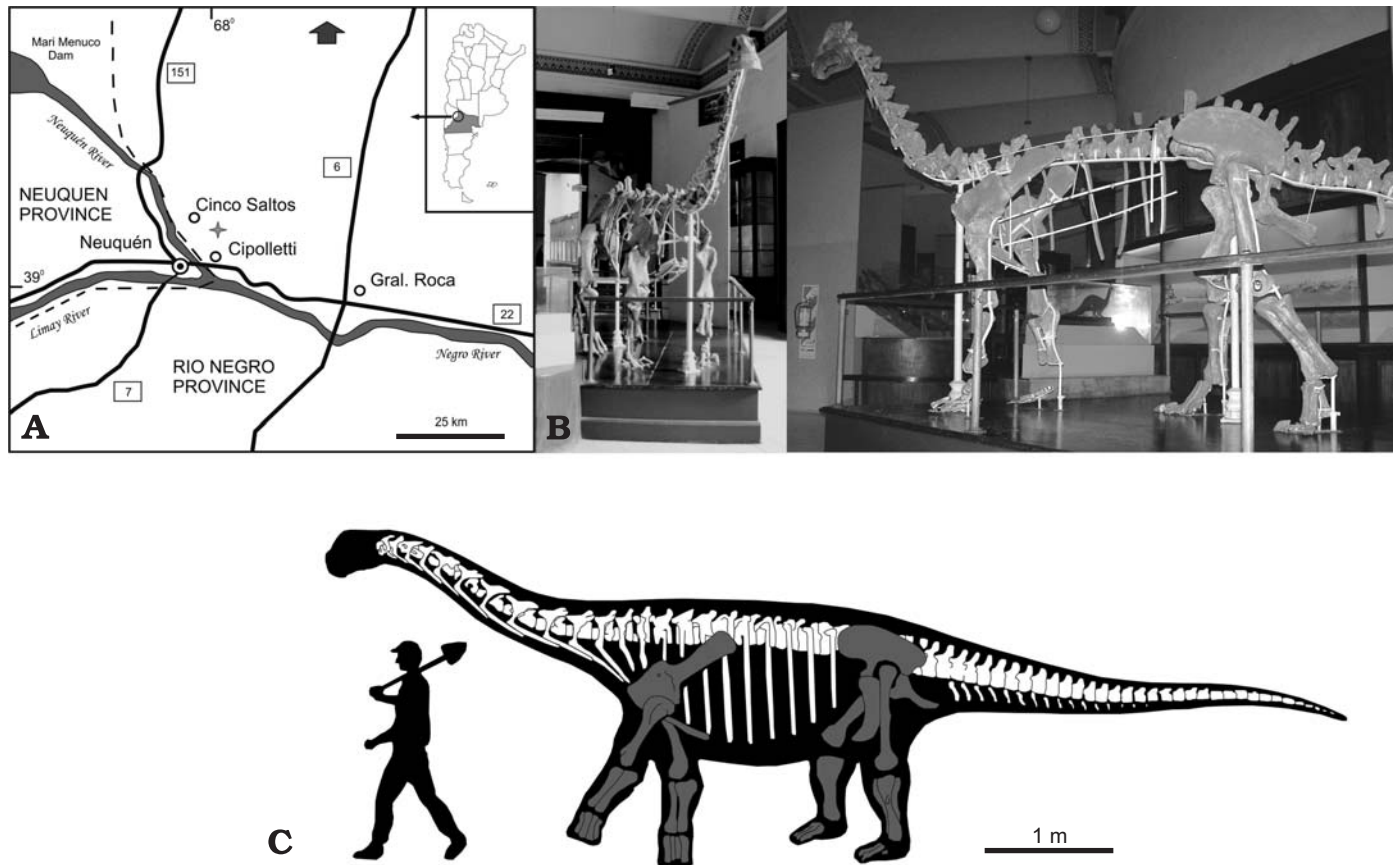


Fig. 1. The saltasaurine sauropod *Neuquensaurus australis*, from the Anacleto Formation (Upper Cretaceous), Patagonia, Argentina. **A.** Site map showing the Cinco Saltos area where specimens of *Neuquensaurus* have been recovered. **B.** Restoration of the skeleton mounted at the Museo de La Plata, Argentina. **C.** Skeletal reconstruction and body shape of *Neuquensaurus* showing preserved appendicular elements in dashed zones; adapted from *Opisthocoelicaudia* silhouette in Wilson and Sereno (1998).

and “*Titanosaurus*” *robustus* Huene, 1929. Huene (1929) classified the long bones of “*Titanosaurus*” *australis* and “*T.*” *robustus* “...without determining or differentiating the vertebral material of each species ... Huene (1929) used the name of “*Titanosaurus*” *australis* in an arbitrary way to identify the form possessing slender limb bones and creating for the remainder the species “*T.*” *robustus*, without taking into account the fact that the type material of the species “*T.*” *australis* ... consists of a series of caudal vertebrae” (Powell 2003: 43). Though Huene’s descriptions were detailed and helpful, they were not extensively comparative with other sauropods yet known. Those taxa received scant attention for some 50 years, until Bonaparte and Gasparini (1978) re-studied limb bones referred by Huene (1929) to “*T.*” *robustus* (i.e., left femur, left ulna, right ulna, and left radius). They specified lectotype for those materials, indicating that they may correspond to the same individual (Bonaparte and Gasparini 1978: 397). Powell (2003, adapted from his dissertation written in 1986) also revised the specimens of *Titanosaurus* and reconsidered the anatomy and validity of both species of the genus. He observed that the Indian type species of the genus *Titanosaurus* (*Titanosaurus indicus* Lydekker, 1877) more closely resembles “*Laplatasaurus*” *araukanicus* than “*T.*” *australis*. Accordingly, the latter was included in a

new genus, thus erecting *Neuquensaurus australis* as a new taxonomic entity with a modified diagnosis (Powell 2003), while *N. robustus* was regarded as a nomen dubium (Powell 2003; Wilson and Upchurch 2003). Subsequently, McIntosh (1990) tentatively referred “*T.*” *australis* and “*T.*” *robustus* to the genus *Saltasaurus*, arguing that the differences between those taxa noted by Bonaparte and Powell (1980) are not of taxonomic importance (McIntosh 1990: 395). Powell (1992) and later Wilson and Upchurch (2003) did not recognize genus-level differences between those species. Salgado et al. (2005) recently described a new specimen of *N. australis*, adding to information on axial and appendicular elements known for the species, and provided a revised diagnosis. Additionally, Salgado et al. (2005) include in their description of the new specimen other elements that were found associated with the latter and they “...provisionally interpreted [them] as belonging to the same genus” (Salgado et al. 2005: 625). Moreover, other newly discovered material potentially belonging to *Neuquensaurus* remain undescribed and are included in the present analysis.

The present study is focused on the appendicular anatomy of *Neuquensaurus*. Bearing in mind its disarticulated condition (which has made a detailed study of its osteology difficult), the new discoveries of the last years, and unpub-

lished new materials, as well as the similarity with *Neuquensaurus robustus*, a re-assessment and comparative description of all available appendicular material of *Neuquensaurus australis* and *N. robustus* is given here.

Institutional abbreviations.—MACN, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina; MCS, Museo de Cinco Saltos, Cinco Saltos, Argentina; MPEF, Museo Paleontológico “Egidio Feruglio”, Trelew, Argentina; MLP-Av, Museo de La Plata, Rancho de Ávila Collection, La Plata, Argentina; MLP-CS, Museo de La Plata, Cinco Saltos Collection, La Plata, Argentina; MLP-Ly, Museo de La Plata, Lydekker’s Collection, La Plata, Argentina; MPCA-CS, Museo Provincial “Carlos Ameghino”, Cinco Saltos Collection, Cipolletti, Argentina; PVL, Collection of Vertebrate Paleontology of Instituto “Miguel Lillo”, Tucumán, Argentina.

Other abbreviations.—M., muscle; Mm., muscles.

Systematic paleontology

Dinosauria Owen, 1842

Saurischia Seeley, 1887–1888

Sauropodomorpha Huene, 1932

Sauropoda Marsh, 1878

Titanosauria Bonaparte and Coria, 1993

Saltosauridae Bonaparte and Powell, 1980

Saltosaurinae Powell, 1992

(= Saltosaurini Salgado and Bonaparte, 2007)

Genus *Neuquensaurus* Powell, 1992

Type species: Titanosaurus australis Lydekker, 1893.

Neuquensaurus australis (Lydekker, 1893)

Holotype: MLP-Ly 1/2/3/4/5/6, caudal vertebrae.

Neuquensaurus robustus (Huene, 1929) nomen dubium

Lectotype: Left ulna (MLP-CS 1094), right ulna (MLP-CS 1095), left radius (MLP-CS 1171), left femur (MLP-CS 1480) (Bonaparte and Gasparini 1978).

Remarks.—All currently materials referred to the appendicular skeleton of *N. australis* mentioned by Lydekker (1893), Huene (1929), Powell (2003), and Salgado et al. (2005) are listed in Appendix 1, as well as those specimens referred by Huene (1929) and Powell (2003) to *N. robustus*. The new specimens not yet published are also included in Appendix 1. In some cases, the original remains are presumed to be missing, so interpretations were based on illustrations in Huene (1929). In the worst cases, neither material nor drawings were available at all (see Appendix 1 for details).

Stratigraphic and geographic range.—(Fig. 1A) The holotype and limb elements of “*Titanosaurus*” *australis* studied

by Lydekker (1893) come from Neuquén. Unfortunately, Lydekker did not give a more precise location of the bones nor the specific stratigraphic position. The materials of “*T. australis*” and “*T. robustus*” studied by Huene (1929) come from General Roca and Cinco Saltos (“Gobernación de Río Negro”, currently Río Negro Province), from strata belonging to the “Dinosaurier schichten” (Keidel 1917). Those “Dinosaur beds” where *Neuquensaurus*’ remains were found correspond to the Anacleto Formation (“Senonense inferior”, Huene 1929: 11). The specimen of *N. australis* and associated elements cited by Salgado et al. (2005) were recovered from Cinco Saltos, Río Negro Province (top of Anacleto Formation, early Campanian) (Salgado et al. 2005).

Description

It is remarkable that a complete analysis including the axial skeleton of both *Neuquensaurus australis* and *Neuquensaurus robustus* is needed to assess the definitive assignment of all the elements to the former valid taxon and to elucidate the taxonomic status of the latter. Such study is, of course, out of the scope of this contribution. I will focus the descriptions primarily on the multiple associated hind limb elements that Huene (1929) referred to “*Titanosaurus*” *australis*. Elements previously referred to “*Titanosaurus*” *robustus* will be described in each section devoted to the respective element only if there is a reason to believe that they probably represent *N. australis*. Where they differ in morphology from *N. australis*, each will appear at the end of the corresponding section, with some comments. Any elements for which referral to *N. australis* is dubious will be treated in a separate descriptive section as cf. *Neuquensaurus*.

The phylogenetic relationships of Titanosauria remains obscure, in part, because the fragmentary nature of most genera. To avoid nomenclatural ambiguities, I will follow the phylogenetic definitions for Titanosauria as follows:

Titanosauria Bonaparte and Coria, 1993: *Andesaurus delgadoi* Clavo and Bonaparte, 1991, *Saltosaurus loricatus* Bonaparte and Powell, 1980, their most recent common ancestor, and all descendants.

Saltosauridae Bonaparte and Powell, 1980: *Opisthocoelecaudia skarzynskii* Borsuk-Białynicka, 1977, *Saltosaurus loricatus* Bonaparte and Powell, 1980, their most recent common ancestor, and all descendants.

Saltosaurinae Powell, 1992 (= Saltosaurini Salgado and Bonaparte, 2005): *Neuquensaurus australis* (Lydekker, 1893), *Saltosaurus loricatus* Bonaparte and Powell, 1980, their most recent common ancestor, and all descendants.

Pectoral girdle

Huene (1929) mentioned the existence of thirteen bones of the pectoral girdle of *Neuquensaurus*. However, of those, eleven are present today in the collections of the Museo de La Plata (Appendix 1). There is also a left coracoid fused to a

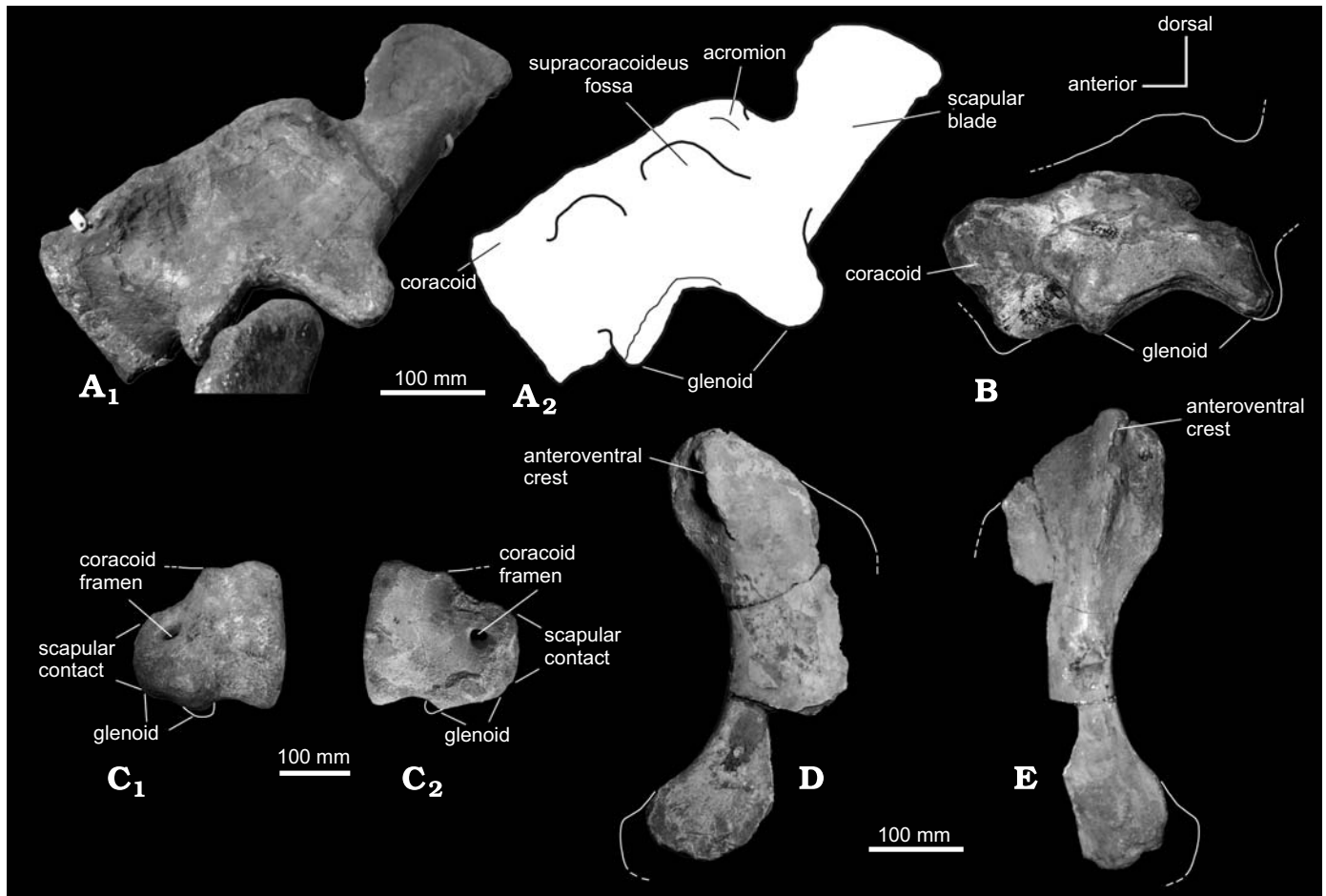


Fig. 2. The saltasaurine sauropod *Neuquensaurus australis*, from the Anacleto Formation (Upper Cretaceous), Patagonia, Argentina. Pectoral girdle. A. Left scapulocoracoid (MLP-CS 1096) in lateral view; photograph (A₁) and explanatory drawing (A₂). B. Fragment of left scapulocoracoid (MLP-CS 1298) in lateral view. C. Right coracoid (MLP-Ly 14) in lateral (C₁) and medial (C₂) view. D. Right sternal plate (MLP-CS 1295) in ventral view. E. Left sternal plate (MLP-CS 1104) in ventral view.

fragment of scapula (MLP-CS 1298) that was previously described as a fragment of ilium (Huene 1929; Powell 2003) and is re-described herein.

Scapula (Fig. 2A, B).—The description of the scapula is mainly based on MLP-CS 1096 (Fig. 2A) because it is the better-preserved specimen. The scapula and coracoid are co-ossified, as in *Opisthocoelicaudia* (Borsuk-Białynicka 1977). The scapula consists of two well-defined portions, a wide proximal part and a narrow distal, elongated scapular blade. The whole structure has a sigmoid shape in dorsal view and is medially curved. The ventral margin of the scapular blade is straight while the dorsal edge is sigmoid, with its proximal portion narrower than the distal one, which is expanded as in *Saltasaurus*. The dorsal margin of the proximal portion of the scapula is rugose, at the site where the anterior portion of the *M. levator scapulae* originated. The acromion is medially curved and laterally concave, as in *Saltasaurus*. The contact between the latter and the scapular blade is U-shaped. The scapular blade has a longitudinal ridge on its lateral surface (Huene 1929; Salgado et al. 2005). The proximal portion of the scapula is in contact with the coracoid,

forming a nearly 90° angle glenoid fossa, resulting in a sub-triangular shape of the fossa. The glenoid is thick and faces ventrolaterally. The glenoid lip of the scapula presumably faced anteroventrally. There is a depression on the proximolateral surface of the scapula, also seen in *Saltasaurus*, which is interpreted as the supracoracoideal fossa, origin site of the *M. deltoideus scapularis* (*M. scapulohumeralis anterior sensu* Borsuk-Białynicka 1977). There are also a fragment of right scapula (MLP-CS 1129) and a fragment of left scapula (MLP-CS 1301) that may belong to *N. australis*. The former was referred by Huene (1929: 36) to probably pertain to the same individual as MLP-CS 1096, which is likely. Both specimens have the same proportions and general outline, and also present a flat, rugose muscular scar posterior to the acromion. On the other hand, the also fragmentary specimen MLP-CS 1301 has the general outline and the medially-curved scapular blade of MLP-CS 1096. As pointed out by Huene (1929), it is highly probable that MLP-CS 1301 belongs to a juvenile specimen of *N. australis*.

The general aspect of the scapula of *N. australis* resembles that of other Titanosauria, such as *Saltasaurus*, *Opistho-*

coelicaudia (Borsuk-Białynicka 1977), *Lirainosaurus* (Sanz et al. 1999), and *Alamosaurus* (Gilmore 1922). However, the scapula of the Patagonian specimen differs from these titanosaurs in having a glenoid lip that ends in a right angle.

Coracoid (Fig. 2A–C).—There are three preserved coracoids (MLP-CS 1096, MLP-CS 1298, and MLP-Ly 14). Two of them (MLP-CS 1096 and MLP-CS 1298) are co-ossified with the respective scapula. The coracoid corresponds in size to the proximal portion of the scapula. It is stout and firmly fused to the scapula along its posterior surface although the suture is not evident. The ventral margin of the element contacts the anterior margin in a nearly 90° angle, giving the coracoid a quadrangular outline, resembling that of *Saltasaurus* (Wilson 2002; Powell 2003). The glenoid (ventral) portion is notably rugose and thick, particularly the infraglenoid lip. The medial surface is flat, while the lateral surface presents a concavity, origin site of *M. supracoracoideus*. There is a slight ridge anterior to the concavity, perpendicular to the dorsal margin, which Huene (1929: 37) referred to as the attachment site of pectoral musculature. It may actually correspond to the *M. coracobrachialis*. In MLP-CS 1096 and MLP-CS 1298 the coracoid foramen is not evident, although there is a slender non-perforated hole close to the margin of the scapular contact.

The general quadrangular outline of the coracoid is similar to that of other saltosaurines (i.e., *Saltasaurus*) and several Titanosauria (e.g., *Lirainosaurus*, Sanz et al. 1999), but differs from others (e.g., *Opisthocoelicaudia*, Borsuk-Białynicka 1977; *Rapetosaurus*, Curry Rogers and Forster 2001; Curry Rogers 2009; and *Isisaurus*, Jain and Bandyopadhyay 1997) in which the outline is roughly oval. The lateral ridge present in MLP-CS 1096 is also present in *Saltasaurus* (PVL 4017-92, Powell 2003: 35).

Sternal plates (Fig. 2D, E).—There are two sternal plates mentioned by Huene (1929) as belonging to *Neuquensaurus australis* (MLP-CS 1104 and MLP-CS 1260). The general outline of the sternal plate is crescentic as in other Titanosauria (Salgado et al. 1997; Wilson 2002; Curry Rogers 2005), with lateral margins strongly concave. The anterior portion is robust and becomes thinner towards its lateral and posterior borders. The anteroventral region has a stout crest which runs anteroposteriorly, and was the origin site of *M. pectoralis* (Huene 1929; Borsuk-Białynicka 1977). The crest is ventrolaterally oriented. The dorsal surface is almost flat. The right sternal MLP-CS 1104 and the left sternal MLP-CS 1260 are very similar in size and general proportions, so that they are symmetrically equal. As pointed out by Huene (1929: 36), it is very probable that pertain to a single individual.

Crescentic sternal plates are also present in *Rapetosaurus* (Curry Rogers 2009); *Alamosaurus* (Lucas and Hunt 1989), *Opisthocoelicaudia* (Borsuk-Białynicka 1977) and *Saltasaurus* (Powell 2003). Nonetheless, the most interesting features of the sternal plates present in *N. australis* are their large size and the presence of the large anteroventral ridge. A similar ridge is present in *Saltasaurus* (Powell 2003: pl. 39b), al-

though it is much less developed than in the Patagonian specimens.

There is also a right sternal plate (MLP-CS 1295) referred by Huene (1929) and Powell (2003) as a left sternal of *N. robustus*. I consider these as belonging to *N. australis* due to their close resemblance, general outline, and the presence of the well developed anteroventral crest (contra Huene 1929: 36).

Forelimb

Several elements of the forelimb are represented, including well preserved right and left humeri, ulnae and radii; however many others elements described by Huene (1929) are missing.

Humerus (Fig. 3).—Nine humeri are preserved in total. The humerus is a robust bone, as in other Titanosauria (robustness index, RI = 0.305–0.339, Appendix 2A), but more slender than that of *Opisthocoelicaudia* (RI = 0.37, Wilson and Upchurch 2003). The proximal and distal portions are expanded, particularly the former, reaching in some cases (e.g., MLP-CS 1050) 50% of the total length of the bone. The proximal portion is slightly medially oriented with respect to the distal end, as in *Saltasaurus* (Powell 2003). It is mediolaterally expanded and anteriorly concave. The humeral head is rounded and well developed. The lateral margin of the diaphysis is also concave. The proximal surface has its greater robustness in the central part, corresponding to the humeral head, being more slender on its lateral and medial margins. The dorsal edge of the proximal end is straight and forms a 90° angle with the lateral margin, as in *Saltasaurus* and *Opisthocoelicaudia* (Borsuk-Białynicka 1977: fig. 7B). The most notable features of the proximal portion are the above-mentioned mediolateral expansion and the robust deltopectoral crest, which runs down the lateral edge of the anterior face of the proximal half of the bone: this is longitudinally oriented, and slightly medially twisted. This structure has a rugose surface, which was the site for the attachment of the abductor musculature (i.e., *M. pectoralis*, *M. dorsalis* scapulae, and *M. deltoideus* scapularis). There is a deep surface on the anteroproximal portion of the humerus, medial to the deltopectoral crest, which is interpreted as the site of insertion of the *M. coracobrachialis* (“coracobraquial breve” sensu Huene 1929; see also Powell 2003). The posterior surface has a tuberosity placed posteroventrally to the deltopectoral crest. This structure is also seen in *Opisthocoelicaudia* (Borsuk-Białynicka 1977: fig. 7D) and *Saltasaurus*, although it is less developed in these taxa than in *Neuquensaurus*. This tuberosity was the site of insertion of *M. latissimus dorsi*, not the “braquial inferior” (contra Huene 1929).

The humeral shaft is mediolaterally expanded and its cross section is approximately elliptical, with its anteroposterior length 70% of the mediolateral breadth (eccentricity index, ECC index = 1.3–1.45, Appendix 2A). The posterior surface of the proximal portion of the humerus has a

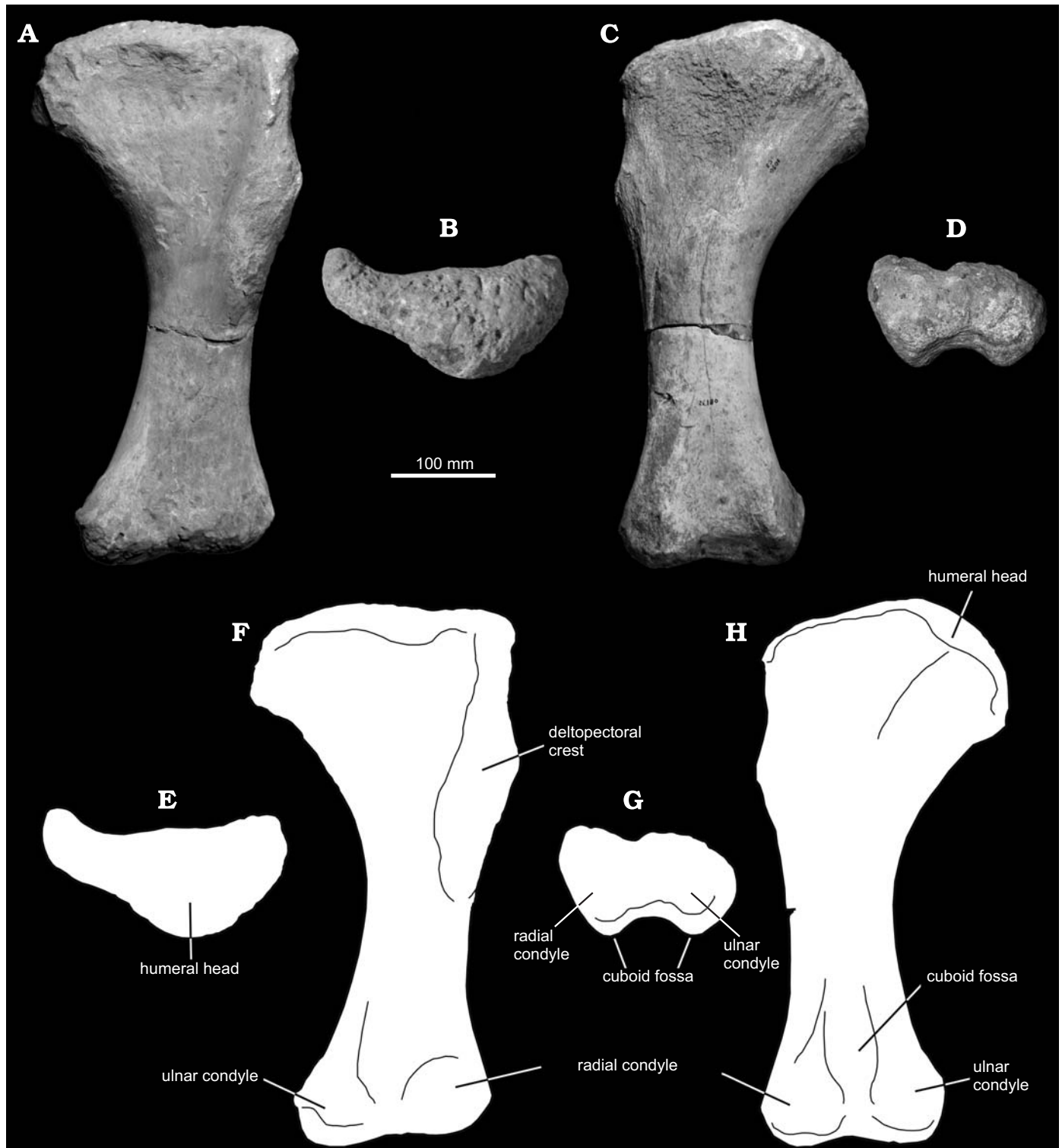


Fig. 3. The saltosaurine sauropod *Neuquensaurus australis* (Lydekker, 1893), from the Anacleto Formation (Upper Cretaceous), Patagonia, Argentina. Humerus. Left humerus (MLP-CS 1050) in anterior (A, F), proximal, anterior towards top (B, E), posterior (C, H), and distal, anterior towards top (D, G) views. Photographs (A–D) and explanatory drawings (E–H).

longitudinally oriented convex area flanked by two depressions, which correspond to the origin site of the humeral heads of *M. anconeus*. The distal end of the humerus is less expanded than the proximal one. The condyles are asymmetrical, being the lateral condyle the more robust. They

are separated by the cuboid fossa, which is well developed in saltosaurines.

A proximal portion of a right humerus (MLP-CS 1019) was referred by Huene (1929) to "*Titanosaurus*" *robustus*. As he pointed out, this bone lacks the acute angle between

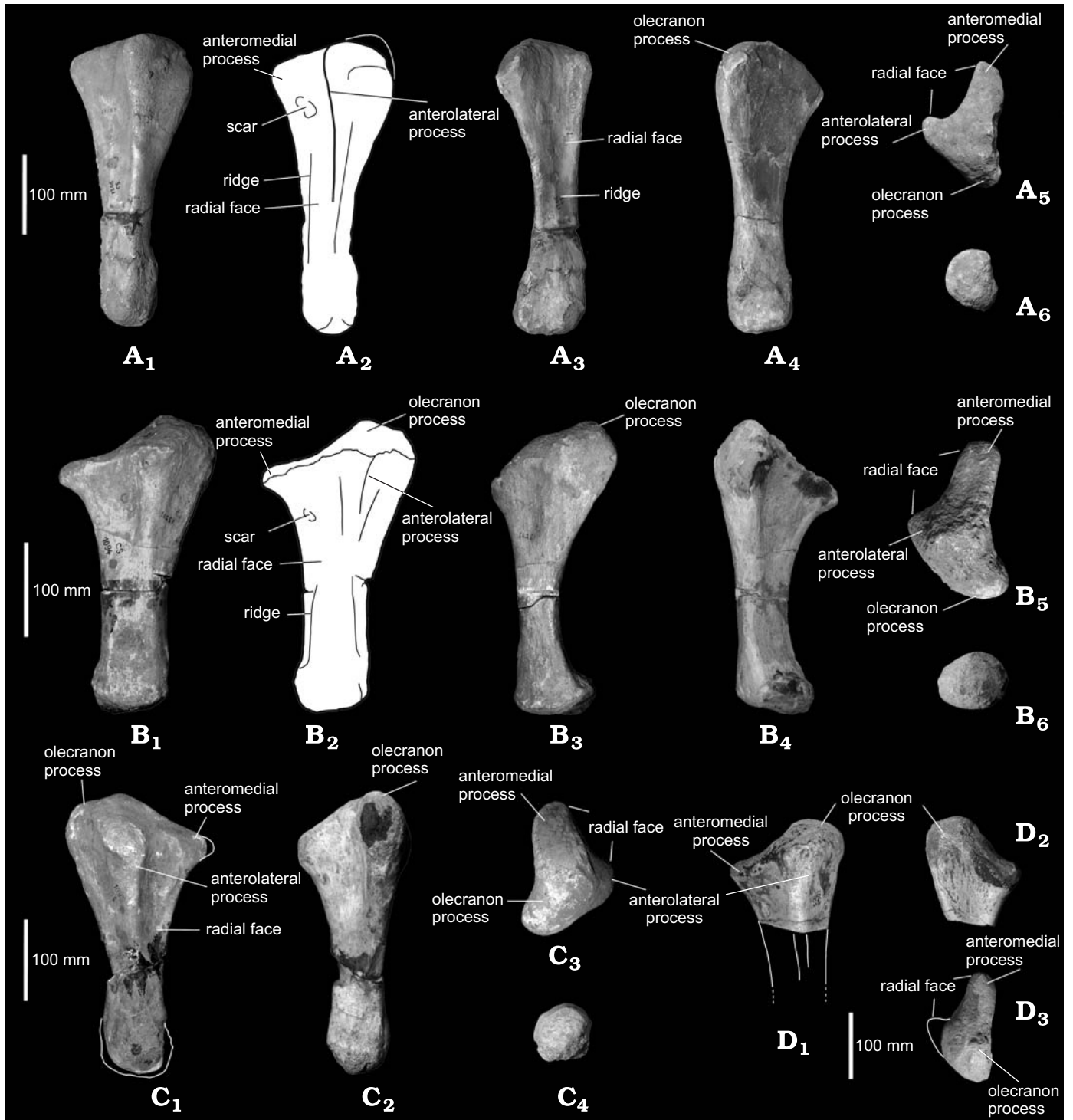


Fig. 4. The saltasaurine sauropod *Neuquensaurus*, from the Anacleto Formation (Upper Cretaceous), Patagonia, Argentina. Ulna. **A.** Left ulna of *Neuquensaurus australis* (Lydekker, 1893) (MLP-CS 1306) in lateral (A₁, A₂), anterior (A₃), posterior (A₄), proximal, anterior towards top (A₅), and distal (A₆) views; photographs (A₁, A₃–A₆) and explanatory drawing (A₂). **B.** Lectotype of *Neuquensaurus robustus* (Huene, 1929) nomen dubium (MLP-CS 1094) as specified by Bonaparte and Gasparini (1978); left ulna in lateral (B₁, B₂), posterolateral (B₃), medial (B₄), proximal, anterior towards top (B₅), and distal (B₆) views; photographs (B₁, B₃–B₆) and explanatory drawing (B₂). **C.** Lectotype of *N. robustus* nomen dubium (MLP-CS 1095) as specified by Bonaparte and Gasparini (1978); right ulna in lateral (C₁), posteromedial (C₂), proximal, anterior towards top (C₃), and distal (C₄) views. **D.** Left ulna of *N. robustus* nomen dubium (MLP-CS 2004) as proposed in this contribution, in lateral (D₁), medial (D₂), and proximal, anterior towards top (D₃) views.

the dorsal and lateral edges seen on the other humeri. However, that portion of the bone is not well preserved and shows abrasion marks as well as the periosteum damaged. In other

respects, the bone presents similar proportions and a robust and elongated deltopectoral crest of those seen in *Neuquensaurus australis*. Despite the fact that it is difficult to assess a

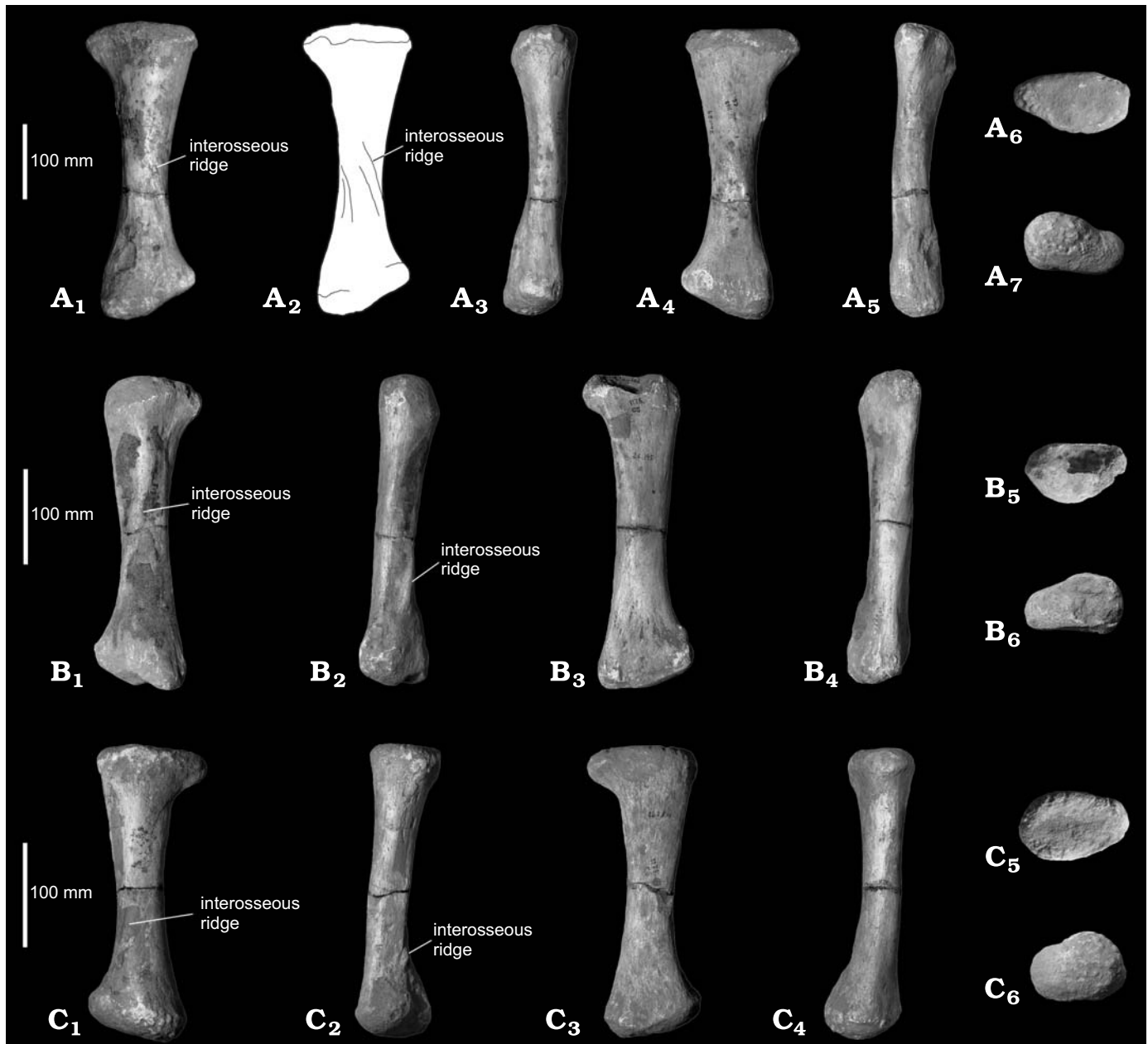


Fig. 5. The saltasaurine sauropod *Neuquensaurus*, from the Anacleto Formation (Upper Cretaceous), Patagonia, Argentina. Radius. **A.** Right radius of *Neuquensaurus australis* (Lydekker, 1893) (MLP-CS 1169) in posterior (A₁, A₂), lateral (A₃), anterior (A₄), medial (A₅), proximal, anterior towards top (A₆), and distal (A₇) views; photographs (A₁, A₃–A₇) and explanatory drawing (A₂). **B.** Left radius of *N. australis* (MLP-CS 1176) in posterior (B₁), lateral (B₂), anterior (B₃), medial (B₄), proximal, anterior towards top (B₅), and distal (B₆) views. **C.** Lectotype of *Neuquensaurus robustus* (Huene, 1929) nomen dubium (MLP-CS 1171), as specified by Bonaparte and Gasparini (1978); left radius in posterior (C₁), lateral (C₂), anterior (C₃), medial (C₄), proximal, anterior towards top (C₅), and distal (C₆) views.

definitively taxonomic identity to that bone, I find no reason to consider MLP-CS 1019 as different from *N. australis*.

The most notable features of *Neuquensaurus* humeri are their robustness and the mediolateral development of the proximal portion, as well as the almost right angle between the dorsal and lateral margins of the proximal portion, also seen in other Titanosauria, such as *Saltasaurus* (PVL 4017-92, Powell 1992), *Opisthocoelicaudia* (Borsuk-Białynicka 1977), *Alamosaurus* (Lucas and Hunt 1989), and *Magyarosaurus* (McIntosh 1990: fig. 16.10).

There is also a left humerus (MLP-Ly 25) that Lydekker (1893: pl. 4: 2) assigned to *Microcoelus patagonicus* Lydekker, 1893. Huene (1929) described that bone together with those of “*Titanosaurus*” *australis* due to their close resemblance. Also, Powell (2003: 45) regarded *Microcoelus patagonicus* as a nomen dubium because of the lack of diagnostic features. I agree with Huene (1929) in the fact that the humerus referred by Lydekker to *M. patagonicus* must be considered as belonging to *Neuquensaurus australis* because of their similar size and proportions, the well developed and

distally expanded deltopectoral crest, and the almost right angle between the lateral and dorsal margin.

Ulna (Fig. 4).—Ten ulnae were mentioned by Huene (1929), although only eight of those can be located, one of those of dubious affinities. The proximal portion of the ulna is wide and is formed by three structures. Two conspicuous ridges anteromedially and anterolaterally directed, respectively, frame the olecranon on both sides: the anterolateral (AL), and the anteromedial (AM) processes (Bonnar 2003: 607). The third structure is the olecranon process, which is placed posterolaterally and was the insertion site of the tendons of *M. anconeus*. It is a well defined structure, although it does not protrude above the articular surface. Those three elements (the olecranon plus the two processes) define a tri-radiate proximal cross-section. The radial (anterior) and medial surfaces are concave. There is a longitudinal ridge on the radial surface that corresponded to the origin site of *M. pronator quadratus* (Huene 1929; Meers 2003). There are also two left ulnae (MLP-CS 1053 and MLP-CS 2004) which Huene (1929: 39) and Powell (2003: 39) both referred to *N. australis*. However, those bones does not resemble the slender appearance of the ulna of *N. australis*, but have the stout look and extremely developed ulnae of *N. robustus* (MLP-CS 1094 and MLP-CS 1095), which constitute part of the lectotype designed by Bonaparte and Gasparini (1978). The olecranon process of MLP-CS 1053 (Huene 1929: pl. 11: 2), MLP-CS 2004, MLP-CS 1094, and MLP-CS 1095 are strongly developed, projecting above the proximal articulation (contra Curry Rogers 2005: 85). I consider MLP-CS 1053 and MLP-CS 2004 as belonging to *N. robustus*.

A well defined but not projecting olecranon process is also present in other Titanosauria, such as *Rapetosaurus* (Curry Rogers 2009: fig. 37) and *Magyarosaurus* (McIntosh 1990: fig. 16.11 L). An olecranon process that project above the articular surface, as seen in *N. robustus*, is also present in the camarasaurid *Janenschia* (Upchurch 1995: fig. 14 B) and in the titanosaurs *Saltasaurus* (PVL 4017-74), *Opisthocoelicaudia* (Borsuk-Białynicka 1977: fig. 8A) and *Malawisaurus* (Gomani 2005: 22).

Radius (Fig. 5).—Five radii of *Neuquensaurus* are preserved. There are two additional radii with dubious affinities. The radius is a rather bent bone. Its proximal end is more expanded than the distal one; it is roughly oval in proximal view and its dorsal margin is straight, with rugosities on the proximal and distal ends. The proximal portion is medially expanded. The anti-ulnar (anterior) face is straight, while the ulnar (posterior) face is convex. On the latter there is a furrow flanked by two ridges oriented obliquely from the anteromedial to the posterolateral side of the diaphysis (“interosseous ridge”, Curry Rogers 2009). The medial ridge could correspond to the insertion site of the *M. pronator teres* (see also Huene 1929; Borsuk-Białynicka 1977). The distal surface of the bone is elliptical and its distal margin is oriented obliquely with respect to the long axis of the diaphysis, from the ventromedial to the dorsolateral side.

A well developed interosseous ridge is also observed in *Saltasaurus* (PVL 4017-92, contra Curry Rogers 2005: 87), *Aelosaurus* (Salgado and Coria 1993: fig. 6), *Opisthocoelicaudia* (Borsuk-Białynicka 1977), and *Rapetosaurus* (Curry Rogers 2009).

Huene (1929) referred to “*Titanosaurus*” *australis* several radii (MLP-CS 1176, MLP-CS 1172, MLP-CS 1169, and MLP-CS 1175), which differ from MLP-CS 1167 and MLP-CS 1174. The formers are more robust (see Appendix 2C), have the proximal and distal ends more expanded and the interosseous ridge more developed. In this sense, those materials close resembles the lectotype of *N. robustus* (MLP-CS 1171). I consider MLP-CS 1172, MLP-CS 1175, and MLP-CS 1169 as belonging to *N. robustus*. On the other hand, MLP-CS 1176 is longer than the lectotype of *N. robustus* and has less expanded proximal and distal ends: hence, its assignation to *N. australis* is probably correct.

Carpus and manus (Fig. 6).—The only carpal (MLP-CS 1234) tentatively assigned to “*T.* *australis*” by Huene (1929: pl. 12: 1) is missing. The overall shape is rounded although its proximal surface is almost pyramidal. No other anatomical details can be gleaned from Huene’s drawing.

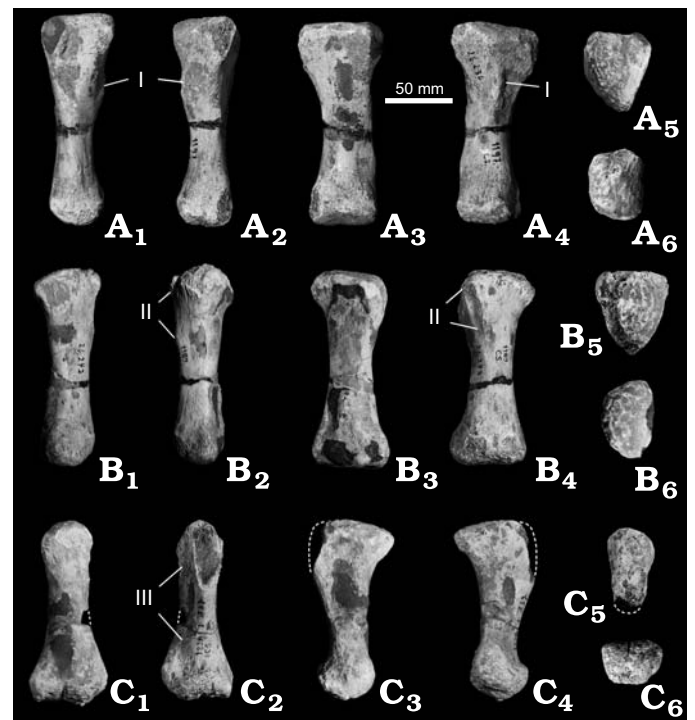


Fig. 6. The saltasaurine sauropod *Neuquensaurus robustus* (Huene, 1929) nomen dubium, from the Anacleto Formation (Upper Cretaceous), Patagonia, Argentina. Metacarpals. **A.** Right metacarpal II (MLP-CS 1197) in anterior (A₁), posterior (A₂), lateral (A₃), medial (A₄), proximal, anterior towards top (A₅), and distal, anterior towards top (A₆) views. **B.** Right metacarpal III (MLP-CS 1189) in anterior (B₁), posterior (B₂), lateral (B₃), medial (B₄), proximal, anterior towards top (B₅), and distal, anterior towards top (B₆) views. **C.** Right metacarpal IV (MLP-CS 1238) in anterior (C₁), posterior (C₂), lateral (C₃), medial (C₄), proximal, anterior towards top (C₅), and distal, anterior towards top (C₆) views.

There are three metacarpals (MLP-CS 1197, MLP-CS 1189, and MLP-CS 1238, Fig. 6) that were erroneously assigned by Huene (1929) as metatarsals of “*Titanosaurus*” *robustus* (Powell 2003). Metacarpal II (MLP-CS 1197, Fig. 2A) is columnar, with expanded ends. The proximal portion is rugose and has a triangular outline, with the apex on the palmar side. The medial side of the triangle is convex and articulated with the concave surface of metacarpal I (Apesteguía 2005). On the proximomedial side there is a short, longitudinal ridge facing downward, which is the articulation area for metacarpal I. The lateral and anteroproximal sides of the bone are flat. However, there is a longitudinal ridge that extends from the middle of the shaft to the distal portion, close to the distal end. The distal part of metacarpal II is quadrangular in outline and bears rugosities.

Metacarpal III (MLP-CS 1189, Fig. 2B) is similar to metacarpal II in general outline. Its proximal portion has a triangular shape, with slight convex sides. The diaphysis is columnar with a triangular cross-section, while the distal end is quadrangular in cross section. Rugosities are present on the proximal and distal portions and the anterior side of the shaft is flat. The lateral side has a ridge flanked by rugosities.

Metacarpal IV (MLP-CS 1238, Fig. 2C) has a characteristic subrectangular cross-section in proximal view (Apesteguía 2005). The lateral and medial sides are concave for articulation with metacarpals V and III, respectively. The anterior surface is almost flat and the palmar side is broader proximally. On the lateral and medial sides of the proximal

end there are two ridges flanking both sides that probably correspond to attachment sites for tendons (Huene 1929).

Some pedal phalanges (MLP-CS 1202, 1204, 1206, 1222, 1223, 1224) were erroneously drawn as belonging to the manus by Huene (1929; pl. 12: 13–15) and will be described accordingly below.

As in other neosauropods (e.g., *Diplodocus*, *Camarasaurus*, *Brachiosaurus*, *Rapetosaurus*, *Opishocoelicaudia*), the proximal end of metacarpals II and III form triangular wedges in proximal views. Metacarpal IV of *Neuquensaurus* shares with other titanosaurs the presence of a subrectangular proximal end with concave sides for articulation with metacarpals III and V (Apesteguía 2005).

Pelvic girdle

Several ilia, ischia and pubes were previously described (Lydekker 1893; Huene 1929; Powell 2003; Salgado et al. 2005). Eleven incomplete ilia of *Neuquensaurus australis* and materials referred to *Neuquensaurus robustus* were described by Lydekker (1893) and Huene (1929); seven of those could be located in the MLP collection (MLP-CS 1056, MLP-CS 1057, MLP-CS 1258, MLP-CS 1259, MLP-CS 2008, MLP-Ly 17, and MLP-Av 2069). Salgado et al. (2005) assigned to *N. australis* an almost complete pair of ilia (MCS-5/16) fused to the sacrum, and a fragment of ischium (MCS-5/24). There is also a fragment of ischium that probably pertains to the genus that has not previously been described (MPCA-CS 001) and is described here for the first time.

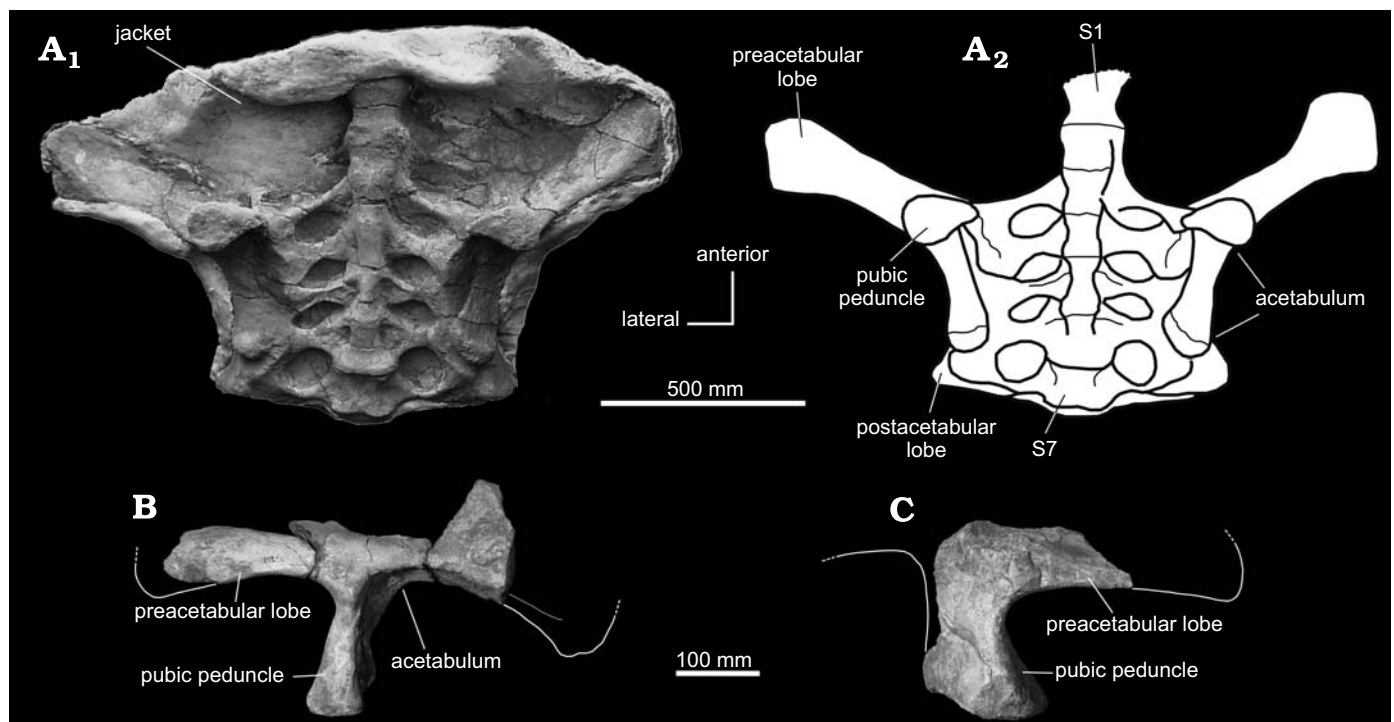


Fig. 7. The saltasaurine sauropod *Neuquensaurus australis* (Lydekker, 1893), from the Anacleto Formation (Upper Cretaceous), Patagonia, Argentina. Sacrum and ilium. A. Sacrum with both ilia (MCS-5/16) in ventral view; photograph (A₁) and explanatory drawing (A₂). B. Left ilium (MLP-Av 2069) in lateral view. C. Right ilium (MLP-Ly 17) in lateral view. Note that MCS-5/16 (A₁) is still into the plaster jacket.

Ilium (Fig. 7).—The description of the ilium is based on the original material described by Lydekker (1893) (MLP-Ly 17), a fragment of left ilium described by Huene (1929) (MLP-Av 2069) as belonging to “*Titanosaurus*” *robustus*, which I consider more probably that of *N. australis*, and those elements described by Salgado et al. (2005) (MCS-5/16). The ilium has both expanded preacetabular and postacetabular portions. The preacetabular lobe of MCS-5/16 (Fig. 7A) is subhorizontally oriented and projects laterally, as in others titanosaurs (Borsuk-Białynicka 1977; Salgado et al. 1997, 2005; Jain and Bandyopadhyay 1997; Upchurch 1998). The whole iliac blade has a “twisted” configuration, so that the outside surface of the preacetabular lobe faces upward, whereas the outside surface of the postacetabular lobe faces downward (Salgado et al. 2005). The pubic peduncle is transversely expanded and anteroventrally directed, and its ventral (distal) surface has a triangular shape, with one of the vertices pointing inwards. The ischiadic peduncle is poorly developed, as in other sauropods (Wilson 2002). The shape of the preacetabular lobe is semicircular and it faces anterodorsally when the ilium is oriented with the ischial and pubic peduncles in the same plane (Salgado et al. 1997). The fragment of left ilium described by Huene (1929) (MLP-Av 2069) as belonging to “*T. robustus*”, I consider more closely similar to that of *N. australis* because of its general proportions, the mediolateral development of the pubic peduncle and the same angle between the preacetabular lobe and the pubic peduncle.

An anteroventrally directed pubic peduncle is also reported in *Opisthocoelicaudia* (Borsuk-Białynicka 1977: fig. 12). The most noteworthy feature of the ilium of *Neuquensaurus* is the lateral projection of the preacetabular lobe with respect to the long axis of the ilium (Salgado et al. 2005). This condition is related to the great development of the hind limb extensor musculature (Otero and Vizcaíno 2008). This condition is also present in other saltasaurines, such as *Saltasaurus* (PVL 4017-92) and *Rocasaurus* (MPCA-Pv 46), and non-titanosaur sauropods, such as *Camarasaurus* (Osborn and Mook 1921: figs. 49, 87).

Ischium (Fig. 8).—The description of the ischium is based on MCS-5/24 and a hitherto undescribed, well preserved but incomplete right ischium (MPCA-CS 001). Additionally, Huene (1929: 40, pl. 14: 3) mentioned the existence of a fragment of a left ischium (MLP-CS 1261) that resembles MCS-5/24. The ischium is, as in other titanosaurs (see Salgado et al. 1997: fig. 5), a short bone with a relatively broad blade. This could be related to the development of the site of origin of the adductor musculature (Otero and Vizcaíno 2008). MCS-5/24 is slender, more so than MPCA-CS 001. The latter is a robust bone, showing thickened articular surfaces. The iliac peduncle is well developed and stout, and is separated from the main body of the ischium (Curry Rogers 2005: character 332), as in *Saltasaurus* and *Rocasaurus*. The pubic peduncle, only preserved in MPCA-CS 001, is extensive, as in other titanosaurs. In MPCA-CS 001 there is a protuberance on the lateral surface

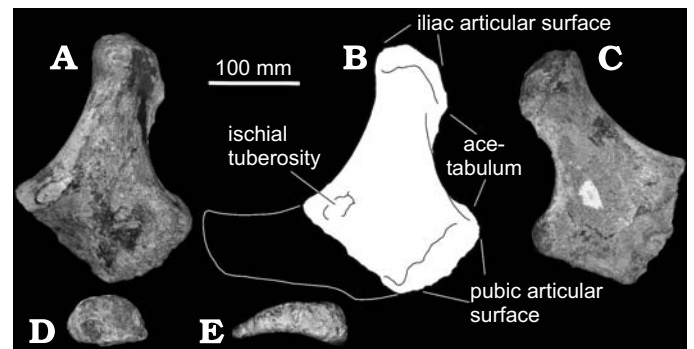


Fig. 8. The saltasaurine sauropod *Neuquensaurus australis* (Lydekker, 1893), from the Anacleto Formation (Upper Cretaceous), Patagonia, Argentina. Ischium. Right ischium (MPCA-CS 001) in lateral (A, B) and medial (C) views; photograph (A, C) and explanatory drawing (B). Iliac articular surface, lateral towards top (D). Pubic articular surface, lateral towards top (E).

of the posterior margin, over the line of the pubic contact, also reported in MLP-CS 1261 (Huene 1929: 41). This is the ischial tuberosity, an elongated process with rugosities over the surface, which was the site of origin of the *M. flexor tibialis internus 3* (Borsuk-Białynicka 1977; Hutchinson 2001a, 2002). The posterior margin is similar to that of *Saltasaurus*, and differs from *Rocasaurus* in being less concave.

The assignment of MPCA-CS 001 to *Neuquensaurus australis* is mainly based on the presence of the ischial tuberosity, which is mentioned by Huene (1929: 41). This tuberosity can not be seen in MCS-5/24 because the ischial blade is damaged. The ischial tuberosity is also reported in other Titanosauria, such as *Opisthocoelicaudia* (Borsuk-Białynicka 1977), *Rapetosaurus* (Curry Rogers 2009), *Rocasaurus* (MPCS-Pv 46), and *Saltasaurus* (PVL 4017-99).

The ischium of *Neuquensaurus* has a similar morphology to that of other Titanosauria (e.g., *Saltasaurus*, *Rocasaurus*, *Aelosaurus*, *Isisaurus*, *Alamosaurus*) in which the whole structure has a semilunate shape with a distally expanded blade.

Pubis (Fig. 9).—Five incomplete pubes of *Neuquensaurus* are preserved. Only MLP-CS 1102 has a relatively well-preserved shaft. The pubis is an expanded bone with thick proximal and distal margins. The proximal end is wider than the entire shaft, while the distal end is as wide as the shaft. There is a longitudinal crest on the ventral surface of the bone, close to the lateral margin (“ventral crest”, Powell 2003: fig. 43: 1b). The presence of the longitudinal crest determinates two parallel areas, which were the sites of origin of the *M. puboischiofemoralis externus 1* and 2 (Borsuk-Białynicka 1977; Otero and Vizcaíno 2008). The dorsal surface of the pubis is flat. The obturator foramen is only partially preserved in MLP-CS 1102 and is placed near the puboischial contact. The posteromedial margin of the pubic blade is becomes thinner close to the contralateral pubis.

The crest on the ventral surface of the pubis is also present in other titanosaurs such as *Saltasaurus* (PVL 4017-95), *Isisaurus* (Jain and Bandyopadhyay 1997: fig. 24B), *Opistho-*

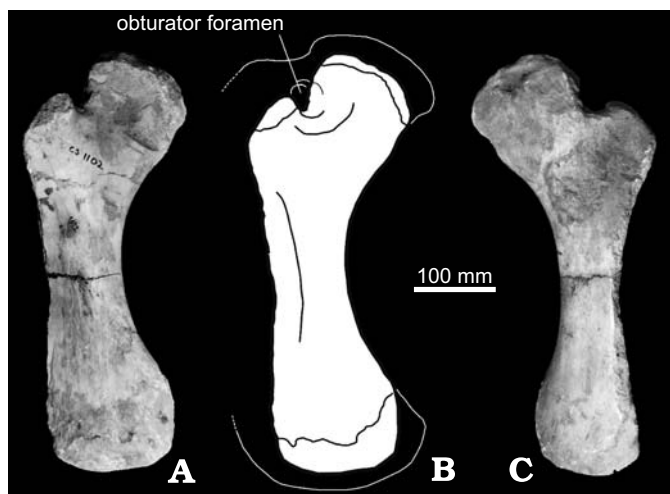


Fig. 9. The saltasaurine sauropod *Neuquensaurus australis* (Lydekker, 1893), from the Anacleto Formation (Upper Cretaceous), Patagonia, Argentina. Pubis. Right pubis (MLP-CS 1102) in anterolateral (A, B) and medial (C) views; photograph (A, C) and explanatory drawing (B).

coelicaudia (Borsuk-Białynicka 1977: fig. 12) and *Aeolosaurus* (Salgado and Coria 1993: fig. 8), although it is more weakly developed than in *N. australis*.

Hindlimb

Femur (Fig. 10).—Eleven femora of *Neuquensaurus* are preserved. The femur is a large, mediolaterally expanded bone, as in other titanosaurs (mediolateral/anteroposterior breadth more than 1.35, Appendix 2D). The femoral head is prominent, robust and positioned dorsomedial to the greater trochanter, as in *Rocasaurus* and *Saltasaurus*. In MCS-5/27 and MCS-5/28, which was referred by Salgado et al. (2005) to *N. australis*, and MLP-CS 1480 (lectotype of *N. robustus*), the femoral shaft is straighter at its medial than at its lateral margin, becoming more sudden at the beginning of the femoral head. The greater trochanter is present and placed laterally to the femoral head, although positioned at a lower level. In better-preserved materials (e.g., MCS-9), superficial rugosities can be observed over the surface of the greater trochanter. Distal to the greater trochanter, on the posterolateral surface of the proximal portion of the femora, there is a sigmoidal ridge that is here interpreted as the remainder trochanteric shelf (Fig. 10A₃, A₄), site of insertion the extensor *M. ischiotrochantericus* (Otero and Vizcaíno 2008). This structure was maintained throughout archosaurian evolution, being present both in ornithischians and saurischians (Novas 1996; Hutchinson 2001b, see Discussion). A lateral bulge, very well developed in MCS-9, is present on the lateral surface of the shaft, distal to the greater trochanter, as in other Titanosauriformes (Salgado et al. 1997; Wilson and Sereno 1998). The curved outline of the lateral bulge determines the medial deflection of the proximal third of the shaft (Salgado et al. 1997; Wilson and Sereno 1998; Wilson 2002; Curry Rogers 2005; but see Discussion). The fourth trochanter, restricted to the posterlateral surface of the shaft, is

low and rugose and is the site of insertion of the caudofemoral musculature.

There is a *linea intermuscularis cranialis* on the anterior surface of the shaft (Fig. 10A₁, A₂) as in other Archosauriformes (Hutchinson 2001b). This is a structure related to the distribution of the femoral extensor muscles of the leg (e.g., *M. femorotibialis*, Otero and Vizcaíno 2008). The *linea intermuscularis cranialis* (“*arista longitudinalis*” sensu Huene 1929: 42) is a dorsoventrally elongated crest along the midline of the anterior surface of the shaft. It begins at the level of the lateral bulge, extending to the intercondylar zone. A similar structure is also seen in *Saltasaurus* (PVL 4017-83, “long rugosity” sensu Powell 2003), *Rocasaurus* (MPCS-Pv 46), and *Bonatitan* (MACN-RN 821). The *linea intermuscularis cranialis* has its origin at the base of the greater trochanter, extending distally on to the posterior surface of the femur. That structure is particularly well developed in MCS-9. The distal condyles are prominent, with the fibular condyle more developed than the tibial one. As mentioned by Wilson and Carrano (1999), the distal portion of the femur has the condylar surface forming a dorsomedial angle with respect to the major axis of the femur. It determines a dorsomedial inclination or “beveled condition” of the femoral shaft when in articulation with the tibia, producing a “wide-gauge” gait, typical of titanosaurs.

The femur of *Neuquensaurus* resembles that of *Saltasaurus* and *Rocasaurus* in its general robustness, the prominent femoral head, and the extreme mediolateral development of the diaphysis. It differs from the much more slender femur of *Bonatitan* (Appendix 2D). The femora of *Neuquensaurus*, *Saltasaurus*, *Rocasaurus*, and *Bonatitan* share the presence of the intermuscular line and prominent trochanteric shelf (Otero 2009). The femur of *Neuquensaurus* differs from that of other titanosaurs (e.g., *Lirainosaurus*, Sanz et al. 1999; *Rapetosaurus*, Curry Rogers 2005, 2009) in having the femoral head oriented medially, rather than dorsomedially, when the distal condyles are aligned to the horizontal plane (Wilson and Carrano 1999).

The element MLP-CS 1480, which is part of the lectotype of *N. robustus* specified by Bonaparte and Gasparini (1978), has no substantial differences respect the femora referred by Huene (1929) and Salgado et al. (2005) to *N. australis* and are not here deemed of taxonomic differences. I consider those elements as belonging to the same taxon (see Discussion).

Tibia (Figs. 11, 12).—There are four complete tibiae, two right and three left. There are also two incomplete tibiae (MLP CS 1303, MLP CS 1093) and one complete tibia (MLP CS 1123) mentioned by Huene (1929) that is now missing. One of the complete tibiae assigned to *N. australis* (MCS-5/25, Salgado et al. 2005) is articulated with the fibula (Fig. 12). The tibia is a relatively short and robust bone (Appendix 2E) as in *Saltasaurus* (PVL 4017-84), with well developed proximal and distal ends. The tibial diaphysis is elongated anteroposteriorly and flattened mediolaterally. The proximal articular face is oval-shaped and the cnemial crest is well-developed, robust and anterolaterally oriented. The distal artic-

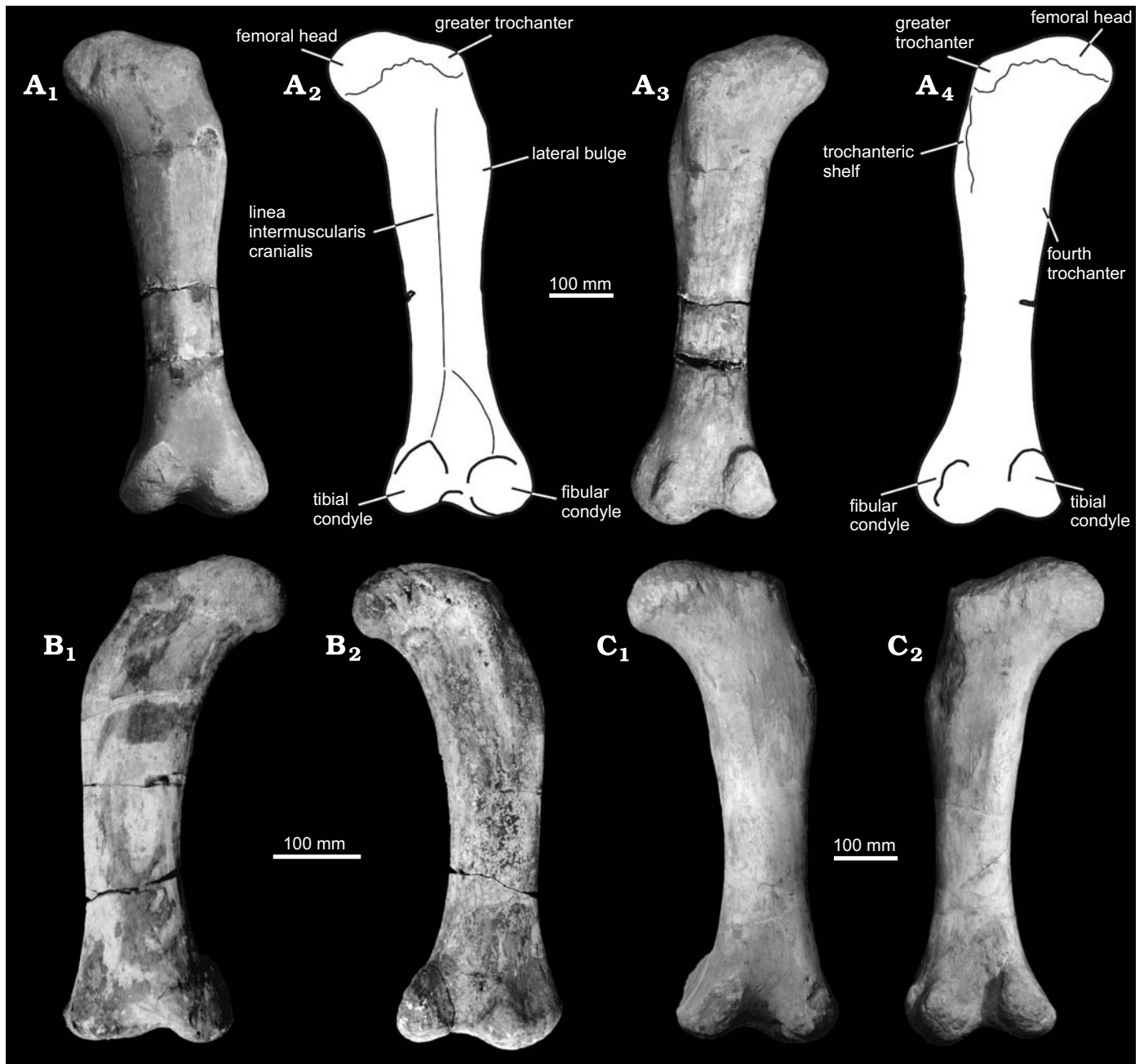


Fig. 10. The saltosaurine sauropod *Neuquensaurus*, from the Anacleto Formation (Upper Cretaceous), Patagonia, Argentina. Femur. **A.** Left femur of *Neuquensaurus australis* (Lydekker, 1893) (MLP-CS 1118) in anterior (A₁, A₂) and posterior (A₃, A₄) views; photographs (A₁, A₃) and explanatory drawings (A₂, A₄). **B.** Right femur of *Neuquensaurus robustus* (Huene, 1929) nomen dubium (MCS-9) as proposed in this contribution in anterior (B₁) and posterior (B₂) views. **C.** Lectotype of *N. robustus* nomen dubium (MLP-CS 1488) as specified by Bonaparte and Gasparini (1978); left femur in anterior (C₁) and posterior (C₂) views.

ular surface is heart-shaped. There is a concavity on the inner face of the cnemial crest in which the fibula articulates. The dorsal edge of the crest has a rugose area, which was the site of insertion for the common tendon of the extensor musculature (e.g., Mm. ilirotibiales, Mm. femorotibiales, Otero and Vizcaíno 2008). The area behind the crest has a proximodistally elongate concavity that follows the length of the crest (see also Salgado et al. 2005). There is no significant difference between MLP-CS 1264 (referred to *N. robustus*, Fig.

11A) and the tibiae of *N. australis* (MCS-5/25, Fig. 11B) (see Appendix 1).

The tibiae of *Neuquensaurus* as well as those of *Saltasaurus* differ from other Titanosauria (*Malawisaurus*, Gomani 2005; *Rapetosaurus*, Curry Rogers 2009) in their general robustness and the great development of the cnemial crest.

Fibula (Figs. 12, 13).—There are five well-preserved fibulae. One of them (MCS-5/26, Fig. 12) is articulated with the

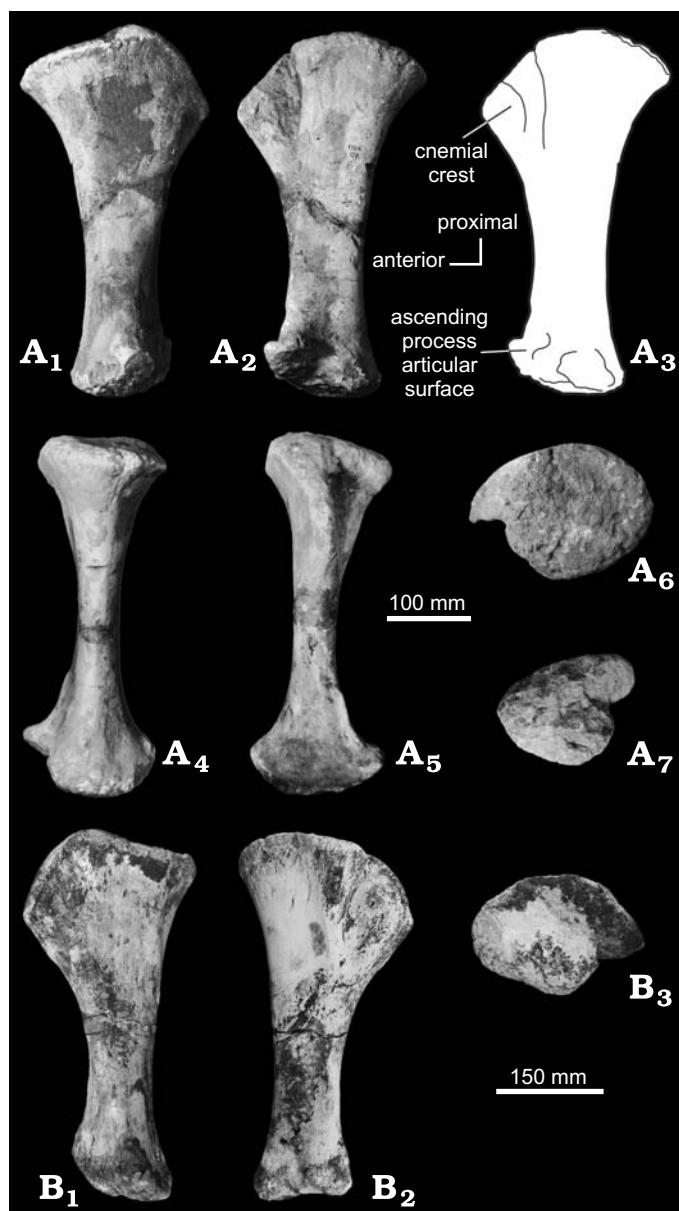


Fig. 11. The saltasaurine sauropod *Neuquensaurus robustus* (Huene, 1929) nomen dubium, from the Anacleto Formation (Upper Cretaceous), Patagonia, Argentina. Tibia. **A.** Left tibia (MLP-CS 1264) in medial (A₁), lateral (A₂, A₃), posterior (A₄), anterior (A₅), proximal, medial towards top (A₆), and distal, medial towards top (A₇) views; photographs (A₁, A₂, A₄–A₇) and explanatory drawing (A₃). **B.** Right tibia (MCS-6) in medial (B₁), lateral (B₂), and proximal, medial towards top (B₃) views.

tibia (see above description). It is a slender, mediolaterally-compressed bone (Appendix 2F). The fibulae have a slightly sigmoid shaft. The proximal portion is anteroposteriorly elongated and the distal articular face is oval-shaped. The most notable feature of the bone is the lateral tuberosity, on the proximolateral surface of the bone. This structure, a characteristic feature of Eusauropoda (Wilson and Sereno 1998), is extremely well developed in *Neuquensaurus* (Powell 2003). With an oval-shaped geometry, it originates on the anteroproximal portion of the shaft and runs

posterodistally toward the distal portion. This tuberosity was the site of insertion of the *M. iliofibularis* (Otero and Vizcaíno 2008), not the *M. flexor digitorum longus* (contra Borsuk-Białynicka 1977).

Tarsus and pes (Figs. 12, 14).—There is a right astragalus fused to the tibia (MCS-5/29, Fig. 12G, N), hence the proximal surface is not available for description. The astragalus is transversely narrower than the distal tibial surface (Salgado et al. 2005). Nonetheless, caution is warranted when comparing the proportions of those structures because the distal articular surfaces of *Neuquensaurus* tibiae are broadly expanded (Curry Rogers 2005: character 343), and thus give the appearance that the astragalus is relatively narrow. The mediolateral width of the astragalus is 75% the anteroposterior length. Proximally, the astragalus is pyramidal, whereas ventrally it is almost flat. The posterior fossa is not divided by a vertical crest. The other astragalus (MLP-CS 1216, Huene 1929: pl. 17: 1) is similar in proportions and shape to MCS-5/29. The calcaneum (MLP-CS 1233, Huene 1929: pl. 17: 2) is rounded in proximal view and sub-triangular in anterior view.

Two first metatarsals, assigned to *N. robustus* (MLP-CS 1179 and MLP-CS 1185), are known. Metatarsal I is short and stout, with expanded proximal and distal ends, with the former more so than the latter. Its general outline is sub-rectangular, and its medial and lateral margins are concave. The distal articular surface is oriented obliquely with respect to the long axis. The element MLP-CS 1179 is considerably bigger than MLP-CS 1185; hence the latter is presumed to belong to a juvenile individual. Both materials were referred by Huene (1929) as “left” metatarsals; however they correspond to the right side. The first metatarsal of *N. australis* drawn by Huene (1929: pl. 17: 3), now missing and presumed lost, is similar to those assigned to *N. robustus*, although the former is more slender.

Metatarsal II (MLP-CS 1183) was originally described by Huene (1929) as a first metatarsal. It is re-described herein as a left metatarsal II. It is quite longer and gracile than metatarsal I. The diaphysis is transversely compressed, as seen in other titanosaurs (González Riga et al. 2008; Curry Rogers 2009). As in metatarsal I, the distal articular end has two defined condyles. The lateral one faces quite downwards.

There are two metatarsal III (MLP-CS 1191 and MCS-10). Its proximal end has an asymmetrical drop-shape, while the distal end has a symmetrical sub-rectangular shape. Huene (1929: 44) mentioned the existence of other two metatarsal IIIs; however, no materials or drawings could be found.

Metatarsal IV (MLP-CS 1193) has been described by Huene (1929) as the second metatarsal. It is longer than metatarsals I and II. Its proximal end is flat, has a sub-rectangular cross-section, and bears two notches at both medial and lateral sides for articulation with metatarsals II and IV, respectively. The proximal end is expanded and oriented perpendicularly with respect to the distal end. Metatarsal IV is the longest, with a sub-oval cross-section. The flat proxi-

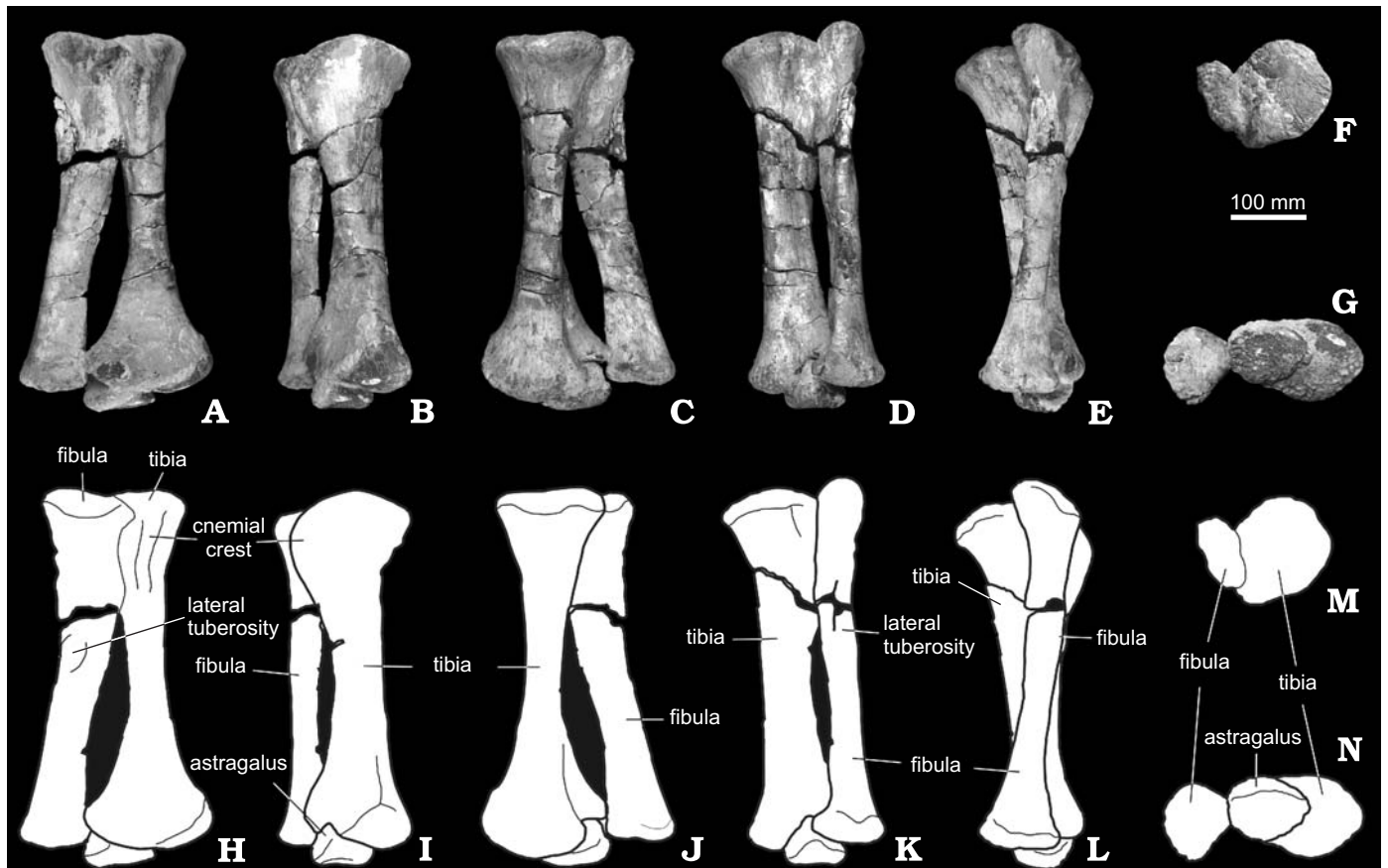


Fig. 12. The saltasaurine sauropod *Neuquensaurus australis* (Lydekker, 1893), from the Anacleto Formation (Upper Cretaceous), Patagonia, Argentina. Tibia, fibula, and astragalus. A–N. Articulated right tibia (MCS-5/25), right fibula (MCS-5/26) and right astragalus (MCS-5/29) in anterior (A, H), anteromedial (B, I), posterior (C, J), posterolateral (D, K), lateral (E, L), proximal (F, M, posterior towards top) and distal (G, N, anterior towards top) views; photographs (A–G) and explanatory drawings (H–N).

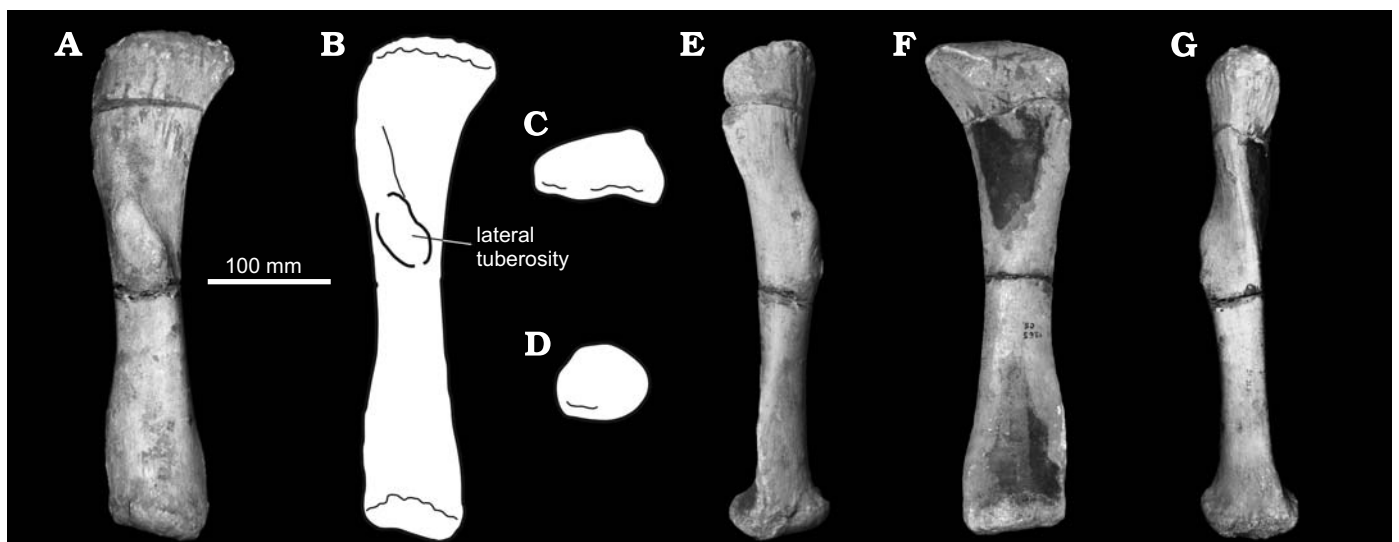


Fig. 13. The saltasaurine sauropod *Neuquensaurus robustus* (Huene, 1929) nomen dubium, from the Anacleto Formation (Upper Cretaceous), Patagonia, Argentina. Fibula. Right fibula (MLP-CS 1265) in lateral (A, B), proximal, medial towards top (C), distal (D), posterior (E), medial (F), and anterior (G) views; photographs (A, E–G) and explanatory drawings (B–D).

mal end is sub-triangular, while the distal end is rectangular. The anterior surface is flat.

Metatarsal V (MLP-CS 1180) has a “paddle-like” shape (“axe-like”, sensu Huene 1929; see also Bonnan 2005), with

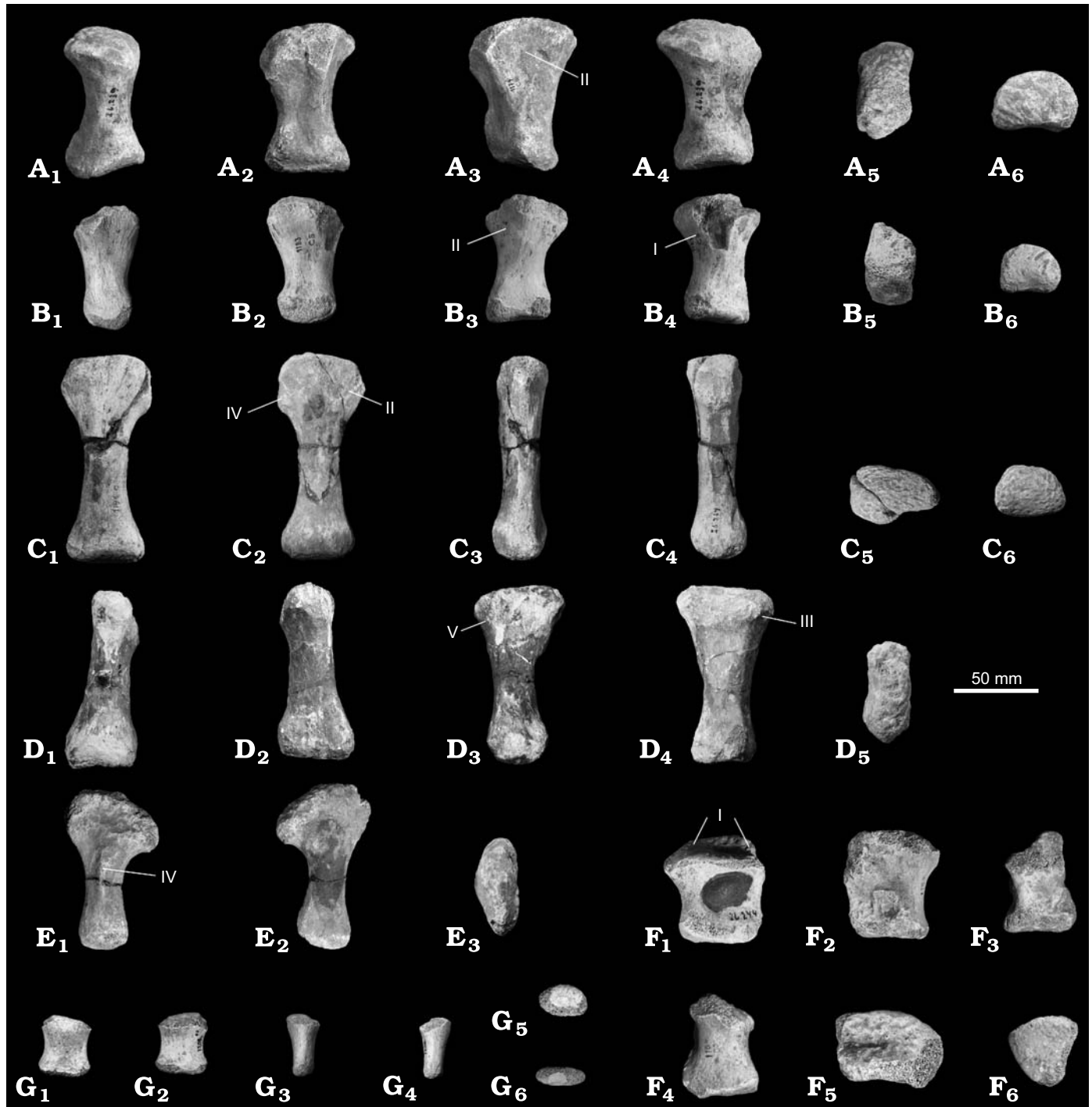


Fig. 14. The saltasauroine sauropod *Neuquensaurus*, from the Anacleto Formation (Upper Cretaceous), Patagonia, Argentina. Metatarsals. **A.** Right metatarsal I of *Neuquensaurus robustus* (Huene, 1929) nomen dubium (MLP-CS 1179) in anterior (A₁), posterior (A₂), lateral (A₃), medial (A₄), proximal, anterior towards top (A₅), and distal, anterior towards top (A₆) views. **B.** Left metatarsal II of *N. robustus* nomen dubium (MLP-CS 1183) in anterior (B₁), posterior (B₂), lateral (B₃), medial (B₄), proximal, anterior towards top (B₅), and distal, anterior towards top (B₆) views. **C.** Left? metatarsal III of *Neuquensaurus australis* (Lydekker, 1893) (MLP-CS 1191) in anterior (C₁), posterior (C₂), medial (C₃), lateral (C₄), proximal, anterior towards top (C₅), and distal, anterior towards top (C₆) views. **D.** Right? metatarsal IV? of *N. australis* (MLP-CS 1193) in anterior (D₁), posterior (D₂), lateral (D₃), medial (D₄), proximal, anterior towards top (D₅). **E.** Left metatarsal V of *N. australis* (MLP-CS 1180) in medial (E₁), lateral (E₂), and proximal, anterior towards top (E₃). **F.** Pedal phalanx in anterior (F₁), posterior (F₂), lateral (F₃), medial (F₄), proximal, anterior towards top (F₅), and distal, anterior towards top (F₆) views. **G.** Pedal phalanx in anterior (G₁), posterior (G₂), lateral? (G₃), medial? (G₄), proximal, anterior towards top (G₅), and distal, anterior towards top (G₆) views.

the proximal end characteristically expanded dorsoventrally and a narrower distal end (McIntosh 1990). The proximal

portion is rugose, the lateral surface is convex, and the medial surface also bears rugosities and has a longitudinal ridge.

There is a left metatarsal V (MLP-CS 1182), referred by Huene (1929) to “*Titanosaurus*” *robustus*, which is stouter than MLP-CS 1180 (the proximal major breadth/shaft length ratio of MLP-CS 1182 is 2.8, and the same ratio in MLP-CS 1180 is 5.3).

There are two preserved pedal phalanges. One of them (MLP-CS 1206) was previously incorrectly assigned to the manus (Huene 1929; see above). MLP-CS 1206 is very short, longitudinally compressed and mediolaterally expanded. The other phalanx (MLP-CS 1184) corresponds to the first digit. It is a short and robust bone with a slight depression on its proximal end, which articulates with the metatarsal I. The distal end is triangular.

Metatarsals I, II and V of *Neuquensaurus* are the smallest and robust. Metatarsal I is the stoutest of the pes and resembles that of other neosauropods, such as *Apatosaurus* (Bonnan 2005), *Rapetosaurus* (Curry Rogers 2009), and *Opisthocoelicaudia* (Borsuk-Białynicka 1979). Metatarsals III and IV are the largest and are most gracile, as in other sauropods (McIntosh 1990), and are very similar to those of *Rapetosaurus* (Curry Rogers 2009). The “paddle-like” condition of metatarsal V of *Neuquensaurus* is shared with other sauropods (Bonnan 2005).

cf. *Neuquensaurus*

Two additional fragments of scapulae (MLP-CS 1296 and MLP-CS 1292) were mentioned by Huene (1929) as belonging to “*Titanosaurus*” *australis*. However, those elements do not resemble MLP-CS 1096 and MLP-CS 1129 at all. One of those (MLP-CS 1292) is a small scapular blade, but much more gracile than MLP-CS 1301. The other element (MLP-CS 1296) is a scapular blade that lacks the distal portion. Due to its bigger size and fragmentary condition it is difficult to refer MLP-CS 1296 to *Neuquensaurus australis*. The specimen MCS-7 was found associated with other remains assigned to *N. australis* (Salgado et al. 2005). As Salgado et al. (2005: 630) pointed out, “it is smaller than the associated bones and lack the characteristic species features” (e.g., strongly sigmoid dorsal ridge). Also, MCS-7 has a straight scapular blade while MLP-CS 1096 has a medially curved blade. As Salgado et al. (2005) commented, there is no evidence besides the topographical association supporting referral of MCS-7 to *Neuquensaurus*.

The fragments of left (MLP-CS 1167) and right (MLP-CS 1174) radii assigned by Huene (1929) and Powell (2003) to *N. australis* do not resemble those referred to *N. australis* nor to the lectotype of *N. robustus*. Actually, the formers are less robust, do not have a well developed interosseous ridge, and its distal ends are less expanded. It is probably that MLP-CS 1167 and MLP-CS 1174 were wrong assigned by those authors and actually pertain to a different genus from *Neuquensaurus* (e.g., Titanosauria indet.)

Huene (1929) assigned with doubt distal portions of metacarpal II (MLP-CS 1186), metacarpal III (MLP-CS 2003), and metacarpal IV (MLP-CS 1187) to “*T.*” *australis*;

however, they are much larger than the remaining metacarpals assigned to the genus and thus their assignment is tentative (see also Powell 2003).

There are three fragmentary ilia (MLP-CS 1056, MLP-CS 1057, and MLP-CS 1258) that Huene (1929) referred to “*T.*” *australis*. Unfortunately those elements only preserve the pubic peduncle and part of the preacetabular lobe; hence their assignment to a single species is vague. They do not resemble the original material described by Lydekker (1893) or that described by Salgado et al. (2005). The main differences lie on the mediolateral development of the pubic peduncle, which is more mediolaterally expanded in MLP-Ly 17 and MCS-5/16. Besides, the angle between the pubic peduncle and the preacetabular lobe is approximately 80° in MLP-Ly 17 and MCS-5/16 and nearly 60° in MLP-CS 1056, MLP-CS 1057, and MLP-CS 1258. Therefore, I consider the latter elements as cf. *Neuquensaurus*.

Huene (1929) and Powell (2003) mention the existence of a fragment of left pubis (MLP-CS 1263) as belonging to *N. australis*. This bone is highly damaged and has nothing in common with the elements referred to *N. australis*.

Discussion and comparisons

Phylogenetically relevant characters

The most significant morphological features in the anatomy of *Neuquensaurus* are present in the appendicular skeleton (Huene 1929; Wilson and Carrano 1999; Wilson 2002; Powell 2003; Otero and Vizcaíno 2008). As for other members of Saltosaurinae (e.g., *Rocasaurus* and *Saltasaurus*), the morphology of the appendicular skeleton of *Neuquensaurus* differs from the typical sauropod limb pattern. The major anatomical changes of the appendicular skeleton of *Neuquensaurus*, as well as its most phylogenetically informative characters, are discussed below (Fig. 15).

Olecranon.—The ulnae of sauropod outgroups possess a primitively well-developed olecranon process (Young 1941; Cooper 1981). This structure is reduced in *Vulcanodon* and basal sauropods (Cooper 1984; Wilson and Sereno 1998; Wilson 2002). The reduction of that process within Sauropoda enabled the alignment of the elbow joint, resulting in a typical columnar limb, which accommodated the extreme loadings achieved in large-bodied sauropod (Wilson and Sereno 1998; Wilson 2005). There are intermediate states of development of the olecranon process in some sauropods such as *Apatosaurus* (“posterior process” sensu Wilhite 2003: fig. 2.16B), with the process becoming particularly prominent within Titanosauria (Wilson and Sereno 1998; Wilson 2002; Powell 2003). The presence of a well-developed olecranon process is a characteristic reversal feature of *Neuquensaurus* and other members of Titanosauria (i.e., *Saltasaurus*, Wilson 2002: character 167). *Janenschia*, a camarasaurid sauropod (sensu Bonaparte et al. 2000) also displays a well defined olecranon process that pro-

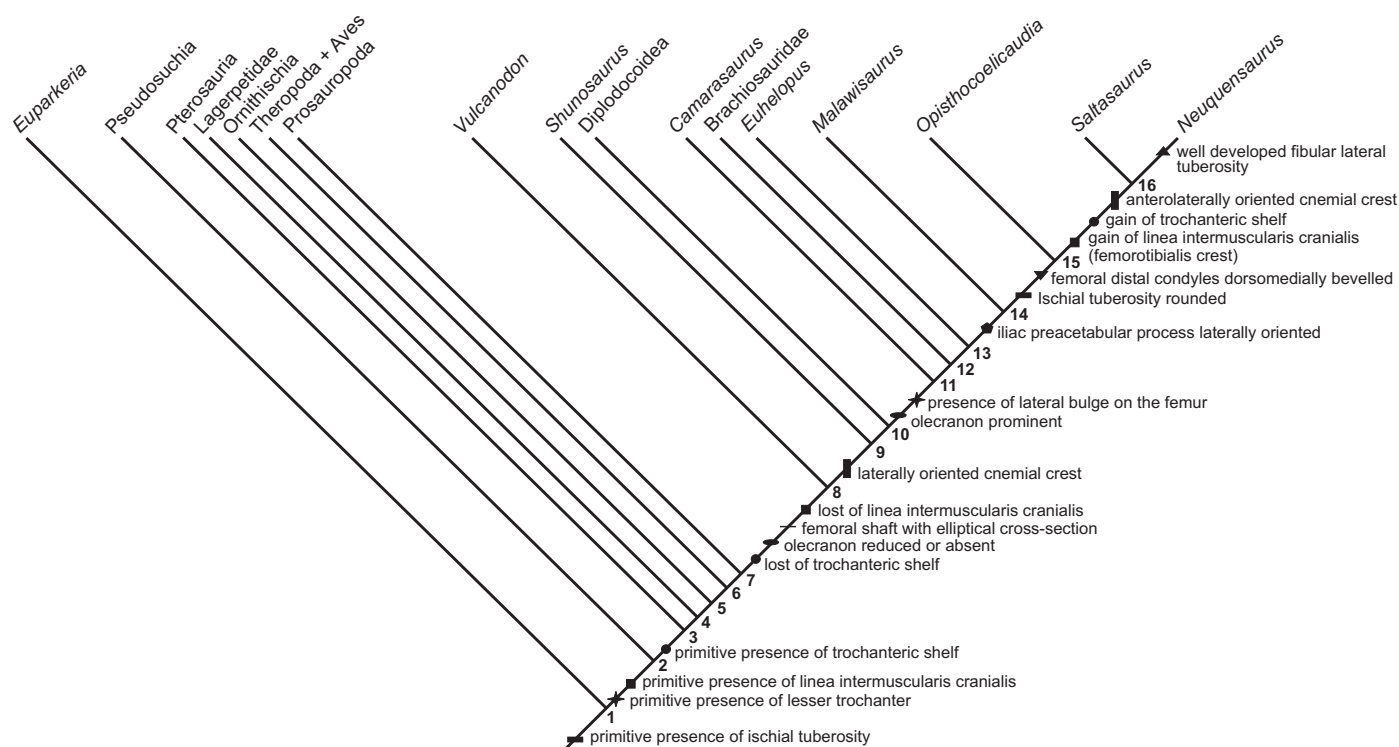


Fig. 15. Phylogenetic relationships of Archosauriformes, showing main hypotheses of sauropod evolution (adapted from Wilson 2002; Nesbitt et al. 2009; Taylor 2009). Symbols indicate appendicular character evolution according to the interpretation given in the present paper. The numbers indicate cladogram nodes as follows: 1, Archosauriformes; 2, Archosauria; 3, Ornithodira; 4, Dinosauromorpha; 5, Dinosauria; 6, Saurischia; 7, Sauropodomorpha; 8, Sauropoda; 9, Eusauropoda; 10, Neosauropoda; 11, Macronaria; 12, Titanosauriformes; 13, Somphospondyli; 14, Titanosauria; 15, Saltasauridae; 16, Saltasaurinae.

jects above the articular surface of the ulna (Upchurch 1995: fig. 14B), indicating that this is not an exclusive feature of titanosaurs, but that it is more broadly distributed among macronarians.

As Apesteguía (2004) pointed out, the olecranon process, coupled with others features, has been hypothesized as an important functional element in the nesting behavior of Saltasaurinae.

Iliac blade.—The “twisted” configuration in the ilium of *Neuquensaurus* is the most significant pelvic innovation present in Saltasaurinae (Salgado et al. 2005). As a result, the pre- and postacetabular lobes are oriented outward. As in sauropod outgroups (i.e., prosauropods, theropods) and also ornithischians, *Neuquensaurus* has a preacetabular lobe of the ilium that is equal to or less than iliac length (Wilson and Sereno 1998: character 82). However, in *Neuquensaurus* as well as in other saltasaurine titanosaurs (i.e., *Saltasaurus*, *Rocasaurus*), this configuration is achieved not by a separation of entire iliac blades, but by a lateral divergence of the preacetabular lobes. This is a derived feature (Wilson 2002: character 187) that was proposed to be related to the attachment for the iliopsoas complex (as in the extinct therizinosaurid theropods and the extant xenarthrans; Apesteguía 2004). The lateral divergence of the preacetabular lobes, thus produce an alignment between the femoral protractor lines of action and the direction of travel (Wilson 2005), increasing

the anteroposterior component of the line of action of leg extensor muscles (Otero and Vizcaíno 2008).

Ischial tuberosity.—The ischial tuberosity is an ancestral feature present in basal Reptilia (Hutchinson 2001a). In sauropodomorphs it is a rounded scar on the proximolateral surface of the ischium and, in crocodylians, it is the site of insertion of *M. flexor tibialis internus* 3 (Hutchinson 2001a, 2002; Otero et al. in press). In Neornithes, the ischial tuberosity shifts toward the proximodorsal process of the ischium, representing another character state for the same feature, and maintaining the muscular correlate (Hutchinson 2001a, 2002). The presence of a rounded ischial tuberosity in basal sauropods such as *Patagosaurus* (Hutchinson 2001a), as well as in terminal forms like *Neuquensaurus* and other titanosaurs (e.g., *Opisthocoelicaudia*, Borsuk-Białynicka 1977: fig. 12; *Rapetosaurus*, Curry Rogers 2009: fig. 41A), represents a primitive archosaurian character state that has been maintained throughout archosaurian evolution with occasional re-appearance within Sauropoda.

Trochanteric shelf.—The trochanteric shelf is a sigmoid crest on the lateral surface of the proximal end of the femur. It is present in basal Dinosauromorpha (e.g., *Lagerpeton*, Hutchinson 2001b; *Dromomeron*, Nesbitt et al. 2009) and was maintained throughout dinosaurian evolution with different character states, assuming many specialized forms

(Novas 1992, 1996; Hutchinson 2001b). As in *Dromomeron* (Nesbitt et al. 2009: fig. 2B), the trochanteric shelf of *Neuquensaurus* is situated on the posterolateral surface of the proximal femur. Within Dinosauria, it is not clear what muscle attachment(s) the trochanteric shelf corresponds to (Hutchinson 2001b). In Neornithes (Hutchinson and Gatesy 2000; Hutchinson 2001b, 2002) the proximal portion of the shelf is related to the insertion of the M. iliofemoralis externus (IFE, the cranial portion of the primitive M. iliofemoralis of basal Reptilia). Other interpretations (Novas 1996) emphasize its relationship with Mm. iliotrochanterici and M. ischiotrochantericus (= M. ischiofemoralis of birds) within Dinosauria. The trochanteric shelf is present as a small mound in basal sauropodomorphs (Hutchinson 2001b); however, some prosauropods (e.g., *Coloradisaurus brevis* Bonaparte, 1978, PVL 5904 and specimens from “El Tranquilo”, probably *Mussaurus patagonicus* Bonaparte and Vince, 1979) display this feature as a sigmoidal structure. There is no mention of a trochanteric shelf-like structure among Sauropoda except in *Saltasaurus* (“elongated rugosity”, Powell 2003) and in specimen MCS-9 of *Neuquensaurus australis* (Lydekker, 1983) (Otero and Vizcaíno 2008). In addition to that material, a remainder of the trochanteric shelf is also present in MLP-CS 1118 and also in MLP-CS 1480, the latter referred to *Neuquensaurus robustus* by Huene (1929). Following Novas (1996), the remainder trochanteric shelf of sauropods is the insertion site of M. ischiotrochantericus (Otero and Vizcaíno 2008).

Femur deflected medially and the identity of the “lateral bulge”.—The medially deflected condition of titanosaurian femora was first noted by Huene (1929: 42) in his description of “*T. australis*”. The deflected femur, with its associated lateral bulge, is a synapomorphy of Titanosauriformes (Salgado et al. 1997; Upchurch 1998; Wilson and Sereno 1998; Wilson 2002). Saltasaurines exhibit an extreme condition of femoral deflection because of the asymmetry of femoral distal condyles, which yield a mediolateral inclination (Wilson and Carrano 1999). The great development of the lateral bulge increases the deflection of the proximolateral margin of the femur. However, the homology of the “bulge” remains obscure. The lateral bulge was first observed by Huene (1929: 41) and named by McIntosh (“sharp deflection”, 1990: 370), who interpreted it as a vestige or homolog of the lesser trochanter (see also, Bonnan 2004; Carrano 2005). The lesser trochanter of sauropodomorphs has been characterized as a small spine (Hutchinson 2001b: character 7). On the contrary, according to Wilson (2002: character 197), the lesser trochanter is a primitive character within Sauropoda, only present in *Vulcanodon*, whereas Titanosauriformes display a well-developed bump or bulge that reaches the greater trochanter. Fusion of the lesser and greater trochanter is present in juvenile neornithines (Hutchinson 2001b); hence, the condition present in Titanosauriformes, in which both trochanters reach one to another, likely represents a convergence with the condition seen in modern birds and their close relatives.

Linea intermuscularis cranialis.—This structure represents an ancestral condition for archosaurs (Hutchinson 2001b). It is absent in non-saltasaurine sauropods, although it is well developed in *Neuquensaurus*, as well as *Saltasaurus* (PVL 4017-83, “long rugosity”, Powell 2003), *Rocasaurus* (MPCA-PV 46) and *Bonatitan* (MACN-RN 821). Although the linea intermuscularis cranialis present in saltasaurine sauropods is not actually a “line”, but a crest, the topological placement is identical to the linea intermuscularis cranialis present in other archosaurs (Hutchinson 2001b), and also seems to be the structure that forms the boundary between both heads of Mm. femorotibiales (Otero and Vizcaíno 2008). I propose to term this structure femorotibialis crest, and regard it as a different character state of the linea intermuscularis cranialis. This structure therefore represents a derived character within Archosauria and most likely represent a synapomorphy of Saltasaurinae.

Femoral distal condyles.—Primitively, basal sauropods have straight-shafted femora. The “beveled” condition of the titanosaurian femora was noted by Wilson and Carrano (1999). Wilson (2002: character 201) proposed it as a synapomorphy of Saltasauridae, in which the distal condyles are not perpendicular to the long axis of the femur, but beveled dorsomedially relative to the femoral shaft. *Neuquensaurus* also displays this asymmetry in the distal femoral condyles, showing an increase in the size of the fibular condyle: this result in a particularly marked “beveled” condition (Salgado et al. 2005; Otero and Vizcaíno 2008: fig. 5.6). This means that the condyles were held level in life and that the long axis of the femur was therefore inclined dorsomedially rather than being vertical.

Femoral midshaft.—Prosauropods and theropods exhibit suboval midshaft femoral cross-sections, with a ratio between the mediolateral width and anteroposterior diameter of 0.93 in the prosauropod *Coloradisaurus brevis* Bonaparte, 1978 (PVL 5904) and 1.09 in the theropod *Condorraptor currumili* Rauhut, 2005 (MPEF-PV-1690). Nearly all sauropods display at least, some degree of eccentricity of the femoral shaft, except the diplodocoid *Amphicoelias*, which have an almost circular femoral cross-section (Osborn and Mook 1921: fig. 125). The highest values of femoral eccentricity are present within saltasaurines (*N. robustus* = 1.58; *Saltasaurus* = 1.65, see Appendix 3); however, *Brachiosaurus altithorax* Riggs, 1903 and *Giraffatitan brancai* (Janensch, 1914) reported high values too (ECC almost 2.0, Taylor 2009). Although Titanosauria is characterized by an extremely femoral eccentricity (Wilson and Carrano 1999), several non-titanosaur sauropod also exhibit an even more marked disparity between these two femoral diameters (e.g., *Amargasaurus*, Appendix 3). Hence, the change from the round femoral section of prosauropods to the elliptical cross-section of most sauropods seems to be gradual along a continuum.

The anteroposteriorly compressed femoral shaft in sauropods is a character usually associated with large body size (Wilson and Sereno 1998; Wilson and Carrano 1999; Otero and Vizcaíno 2008). Limb bones of large animals like sauropods have to support a mediolateral couple force generated

by their own weight (Wilson and Carrano 1999; Carrano 2001). In the particular case of *Neuquensaurus* and other derived titanosaurs, there is an extra factor of bone bending stress, related to the standing pose which is typically wider during locomotion (Wilson and Carrano 1999; Otero and Vizcaíno 2008). This helps to explain the relationship between the geometry of the titanosaur femoral morphology and the support of mediolateral bending by achieving an extreme eccentric cross-section.

Fibular lateral tuberosity.—The fibular lateral tuberosity has been a matter of discussion because its homology is not resolved. This structure is present in Eusauropoda (Wilson and Sereno 1998; Wilson 2002) as an elliptical bump on the lateral side of the proximal fibula, being extremely well developed in *Neuquensaurus*. Huene (1929) interpreted it as the insertion site of *M. peroneus*, while Borsuk-Białynicka (1977) and Wilson and Sereno (1998) suggested it to be the origin site for *M. flexor digitorum longus*. Nevertheless, it seems that the lateral trochanter of the fibula was the insertion site for the *M. iliofibularis*, a flexor muscle that is present in the same topographical position on the fibular shaft of both living crocodiles (Otero et al. in press) and Neornithes and was recently inferred to be present in *Neuquensaurus australis* (Otero and Vizcaíno 2008).

Cnemial crest.—The cnemial crest is present and is quite distinctive among sauropods. In Eusauropoda it projects laterally as a thin plate (Wilson and Sereno 1998; Wilson 2002). In *Neuquensaurus* and other saltosaurine sauropods (e.g., *Saltasaurus*, PVL 4017-84) it is well developed, robust and anterolaterally oriented. An anteriorly projecting cnemial crest is present in *Vulcanodon* (Cooper 1984, Wilson 2002) and sauropod outgroups (Cooper 1981; Galton 1990; Wilson 2002). Thus, the state in *Neuquensaurus* and its closest relatives is an intermediate character state for the cnemial crest. Although the functional significance of that structure remains obscure (Wilson and Sereno 1998), the anterolateral projection and the robustness of the saltosaurine cnemial crest could be related to the shift of the insertion site of the leg extensor *Mm. femorotibiales*, *M. ambiens* and *Mm. iliotibiales* (Otero and Vizcaíno 2008).

N. australis vs. *N. robustus*: comparisons

Many of the multiple specimens described by Lydekker (1893) and Huene (1929) seem to pertain to a single individual; others, to a single genus and even species. However, several elements described by those authors as “*Titanosaurus*” *robustus* probably belong to the type species, “*Titanosaurus*” *australis*, and vice versa. On the other hand, the status of others cannot really be determined: they may belong to the type species, or they may represent another species or even genus.

There are several elements originally described and referred to “*T. robustus*” which actually I consider here as belonging to *Neuquensaurus australis*. The right sternal plate MLP-CS 1295 was erroneously described by Huene (1929)

as “left” and belonging to “*T. robustus*” because the anteroventral crest is a little bit shorter than in *N. australis* and the lateral border is more concave (Huene 1929: 36). However, that element has damaged its periosteum and the blade is not complete. On the other hand, the general outline and relative proportions are similar to the sternals referred to *N. australis* (MLP-CS 1260 and MLP-CS 1104). Hence, the differences between MLP-CS 1295, MLP-CS 1260, and MLP-CS 1104 are not here deemed of taxonomic importance. A similar situation occurs with the right humerus MLP-CS 1019, in which “the proximal end ... has an oblique orientation respect the proximal and laterals axis” (Huene 1929: 49, translated from the Spanish). Nonetheless, the aspect of MLP-CS 1019 is altered by its broken proximolateral end. Out of this, the proportions and the deltopectoral crest, which is well preserved, are identical to those of *N. australis*. The fragment of left ilium (MLP-Av 2069) close resembles the original fragment of right ilium (MLP-Ly 17) of “*T. australis*” described by Lydekker (1893), despite that the former was referred by Huene (1929) as belonging to “*T. robustus*”.

Likewise, many elements originally referred to “*T. australis*” by Huene (1929) closely resembles the lectotype of “*T. robustus*” specified by Bonaparte and Gasparini (1978). The fragment of left ulna MLP-CS 2004 was originally referred by Huene (1929) to “*T. australis*”, but differs considerably from the other ulnae assigned to the species. Actually, MLP-CS 2004 has the olecranon process projecting above the proximal end articulation and is as robust as the ulnae included in the lectotype of *N. robustus*. A similar situation occurs with the radius. The elements MLP-CS 1169, MLP-CS 1172, and MLP-CS 1175, referred by Huene (1929) to “*T. australis*”, show no taxonomic differences with the lectotype of “*T. robustus*” MLP-CS 1171 and have the same proportions.

The condition of the femur, tibia and fibula deserves a special consideration because there are two real morphotypes of those bones and no type material to compare them. Among the specimen described by Salgado et al. (2005) and its associated elements there are two clearly morphs: one gracile and one robust. The gracile elements were found associated in such a way that they may be assumed with confidence to pertain to a single individual (Salgado et al. 2005). Such elements include the left and right femur (MCS-5/27 and MCS-5/28, respectively), and the right tibia (MCS-5/25) and fibula (MCS-5/26). Those elements differ from MCS-9 (right femur) and MCS-6 (right tibia) despite the fact that all of them were found in the same area. The latter bones are more robust than the former although they are similar in length. Actually, MCS-9 more resembles the lectotype of *N. robustus* (MLP-CS 1480) and both have similar robustness indices (see Appendix 2D). Likewise, MCS-6 is similar to MLP-CS 1264, which is referred to the latter species. Therefore, I propose here to consider MCS-9 and MCS-6 as belonging to *N. robustus*. The right fibula described by Salgado et al. 2005 (MCS-5/26) is slender than MLP-CS 1264, referred by Huene (1929) to “*T. robustus*” and have the lateral trochanter less developed. Its assignation to a different species seems to be correct.

Finally, several elements referred by Huene (1929) to either “*T. australis*” or “*T. robustus*” seems to pertain to a different species or even genus due to their differences and/or their fragmentary condition. That is the case of the scapulae MLP-CS 1296, MLP-CS 1292, and MCS-7; the fragments of left (MLP-CS 1167) and right (MLP-CS 1174) radii; distal portions of metacarpal II (MLP-CS 1186), metacarpal III (MLP-CS 2003), and metacarpal IV (MLP-CS 1187); three fragmentary ilia (MLP-CS 1056, MLP-CS 1057, and MLP-CS 1258); and a fragment of left pubis (MLP-CS 1263). Such elements are tentatively considered here as cf. *Neuquensaurus*.

Saltosaurinae, a well defined South American clade of dwarf (?) sauropods

Despite the taxonomic goings and comings of the systematic names, it is clear that there was a well defined group of sauropods of small-to-medium size, which inhabited southern South America, and can be differentiated from titanosaurs from the rest of the world by particular features. Such a clade, the Saltosaurinae, is clearly endemic to South America. The four species of saltosaurines: *Neuquensaurus australis* (Lydekker, 1983), *Rocasaurus muniozi* Salgado and Azpilicueta, 2000, *Saltasaurus loricatus* Bonaparte and Powell, 1980, and *Bonatitan reigi* Martinelli and Forasiepi, 2004 have been reported in Neuquén, Río Negro, and Salta provinces. It is noteworthy that saltosaurines are absent farther south than 42°S, although this may be due to the presence of the North Patagonian massif as a geographic barrier (Salgado 2000). The saltosaurines are exclusively forms of the Uppermost Cretaceous (Campanian–Maastrichtian), hence radiation of the group seems to have occurred during a short period of time.

One of the most interesting features of saltosaurines is body size. Saltosaurines have been reported as the smallest sauropods known, only comparable to dicraeosaurine diplocoids (Salgado 1999, 2000) and the titanosaurid *Magyarosaurus* (Jianu and Weishampel 1999). In the case of saltosaurines and *Magyarosaurus* the mechanism hypothesized as responsible for their small size is heterochrony (Jianu and Weishampel 1999; Salgado 2000), which is defined as the change in the timing of ontogenetic events (McKinney 1986). As McNamara (1982: 130) pointed out, “changes in ontogenetic sequences though time occur by contraction, extension, or a shift in timing of rates of morphological development”. In the specific case of size reduction through successive ontogenies, the heterochronic process involved is paedomorphosis, which include neoteny (reduction in rate of development), progenesis (precocious sexual maturation reduces the period of juvenile allometric growth), and post-displacement (retardation in onset of growth of particular organs) (McNamara 1982; McKinney 1986). Following McKinney and McNamara (1991) and Salgado (2000) the advantage of the progenesis is that it advances reproductive capability, assuming that this characteristic is positively influenced by natural selection. On the contrary, if the selected character was the small size, both mechanisms neoteny and

progenesis, could be equally plausible. In the latter case, saltosaurine sauropods could evolve as a result of predation pressure (or lack thereof). That is, if juveniles and adults of saltosaurines ancestors lived in different environments and if the predation pressures were high in the adults environments, then the selection would favored those forms that tended to delay the time of maturation or stopping the development. This is explained in that, usually, large predators avoid small prey because the energy expenditure does not compensate the earnings (McKinney and McNamara 1991).

Conclusions

The appendicular skeleton of *Neuquensaurus* displays many derived character states within Sauropoda, such as the outwardly oriented preacetabular lobe of the ilium, a medially deflected femur, beveled femoral distal condyles, an eccentric femoral midshaft, and a well developed fibular lateral tuberosity. Most of these features characterize Saltosauridae (Wilson 2002; Curry Rogers 2005). The presence of a prominent olecranon, a trochanteric shelf, a lesser trochanter, and an ischial tuberosity represent reversals to primitive character states; while the linea intermuscularis cranialis present on the femur of *Neuquensaurus* (and also in *Saltasaurus*, *Rocasaurus*, and *Bonatitan*) represents novel character within Sauropoda that support, together with axial information, their inclusion into the monophyletic Saltosaurinae.

Acknowledgements

I would like to thank Leonardo Salgado (Universidad del Comahue, Neuquén, Argentina), Zulma Gasparini (Museo de La Plata, La Plata, Argentina), Jeff Wilson (University of Michigan, Michigan, USA), Nathan Smith (Field Museum of Natural History, Chicago, USA) and Phillip Mannion (University College, UK) for the critical reviews of the manuscript. Sebastián Apesteguía (Universidad Maimónides, Buenos Aires, Argentina), Mike Taylor (University College, UK), Richard Cifelli (University of Oklahoma, Oklahoma, USA) and two anonymous reviewers provided helpful comments on the manuscript. Ignacio Cerda (Museo de Cinco Saltos, Cinco Saltos, Argentina), Marcelo Reguero (Museo de La Plata, La Plata, Argentina), Horacio Pomi (Museo de La Plata, La Plata, Argentina), Jaime Powell (Instituto “Miguel Lillo”, Tucumán, Argentina), Juan Carlos Muñoz (Museo Provincial “Carlos Ameghino”, Cipolletti, Argentina), Eduardo Ruigomez (Museo “Egidio Feruglio”, Trelew, Argentina) and Alejandro Kramarz (Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina) are also thanked for permitting me access to the material in their care.

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Appendix 1

List of all material assigned to *Neuquensaurus australis* (Lydekker, 1893), those referred to *Neuquensaurus robustus* (Huene, 1929) nomen dubium, and elements with dubious affinities. (*) figured by Lydekker (1893); (**) figured by Lydekker (1893) and later referred to *Laplatasaurus araukanicus* by Huene (1929); (***) not figured by Lydekker (1893).

| Taxon | Material | No. collection | Remarks | Author's mention |
|--------------------------------|-----------------------|----------------|--------------------------------|--|
| <i>Neuquensaurus australis</i> | left scapulocoracoid | MLP-CS 1096 | present | Huene (1929) Powell (2003) |
| | left scapulocoracoid | MLP-CS 1298 | present | Huene (1929) |
| | right scapula | MLP-CS 1129 | present | Huene (1929) Powell (2003) |
| | left scapula | MLP-CS 1301 | present | Huene (1929) |
| | scapula | not numbered | missing? | Lydekker (1893) *** |
| | scapula | MLP-Ly 107 | missing? | Lydekker (1893) *** Powell (2003) |
| | right coracoid | MLP-Ly 14 | present | Lydekker (1893)*, Huene (1929), Powell (2003) |
| | coracoid | MLP-Ly 95 | missing? | Lydekker (1893) ***, Huene (1929), Powell (2003) |
| | right coracoid | MLP-Ly 105 | missing? | Lydekker (1893) ***, Huene (1929), Powell (2003) |
| | right sternal plate | MLP-CS 1260 | present | Huene (1929) Powell (2003) |
| | right sternal plate | MLP-CS 1295 | present | Huene (1929), Powell (2003) |
| | left sternal plate | MLP-CS 1104 | present | Huene (1929), Powell (2003) |
| | left humerus | MLP-Ly 25 | present | Lydekker (1893)* |
| | right humerus | MLP-CS 1051 | present | Huene (1929), Powell (2003) |
| | right humerus | MLP-CS 1049 | present | Huene (1929) |
| | right humerus | MLP-CS 1099 | present | Huene (1929), Powell (2003) |
| | right humerus | MLP-CS 1019 | present | Huene (1929), Powell (2003) |
| | right humerus | MLP-CS 1091 | missing? | Powell (2003) |
| | right humerus | MLP-Ly 124 | missing? | Lydekker (1893)***, Powell (2003) |
| | right humerus | not numbered | missing? | Lydekker (1893)** |
| | left humerus | MLP-CS 1050 | present | Huene (1929), Powell (2003) |
| | left humerus | MLP-CS 1100 | present | Huene (1929), Powell (2003) |
| | left humerus | MLP-CS 1479 | present | Huene (1929), Powell (2003) |
| | left humerus | MCS-8 | present | Salgado et al. (2005) |
| | left humerus | MLP-Ly 89 | missing? | Lydekker (1893)***, Powell (2003) |
| | right ulna | MLP-CS 1305 | present | Huene (1929), Powell (2003) |
| | left ulna | MLP-CS 1058 | present | Huene (1929), Powell (2003) |
| | left ulna | MLP-CS 1306 | present | Huene (1929), Powell (2003) |
| | left radius | MLP-CS 1176 | present | Huene (1929), Powell (2003) |
| | radius | MLP-CS 1173 | missing? | Huene (1929), Powell (2003) |
| | carpal | MLP-CS 1234 | missing? | Huene (1929), Powell (2003) |
| | sacrum with both ilia | MCS-5/16 | present | Salgado et al. (2005) |
| | right ilium | MLP-Ly 17 | present | Lydekker (1893)* |
| | ilium | MLP-CS 2008 | present | Huene (1929), Powell (2003) |
| | ilium | MLP-CS 1229 | missing? | Huene (1929), Powell (2003) |
| | fragmentary pelvis | not numbered | missing? | Lydekker (1893)** |
| | left ischium | MCS-5/24 | present | Salgado et al. (2005) |
| | right ischium | MPCA-CS 001 | present | present contribution |
| | left ischium | MLP-CS 1261 | present | Huene (1929) |
| | right pubis | MLP-CS 1102 | present | Huene (1929), Powell (2003) |
| right pubis | MLP-CS 1304 | present | Huene (1929), Powell (2003) | |
| right pubis | MLP-CS 1294 | present | Huene (1929), Powell (2003) | |
| right pubis | MLP-Ly 109 | missing? | Lydekker (1893), Powell (2003) | |

| Taxon | Material | No. collection | Remarks | Author's mention |
|---|-----------------------|----------------|--------------|--------------------------------|
| <i>Neuquensaurus australis</i> | right femur | MLP-CS 1107 | present | Huene (1929), Powell (2003) |
| | right femur | MLP-CS 1122 | present | Huene (1929) |
| | right femur | MLP-CS 1101 | present | Huene (1929), Powell (2003) |
| | right femur | MLP-CS 1124 | present | Huene (1929) |
| | right femur | MCS-5/28 | present | Salgado et al. (2005) |
| | right femur | not numbered | missing? | Lydekker (1893)** |
| | left femur | MLP-CS 1121 | present | Huene (1929), Powell (2003) |
| | left femur | MLP-CS 2005 | present | Huene (1929), Powell (2003) |
| | left femur | MCS-5/27 | present | Salgado et al. (2005) |
| | left femur | MLP-CS 1118 | present | Huene (1929), Powell (2003) |
| | femur | MLP-CS 1120 | missing? | Powell (2003) |
| | femur | not numbered | missing? | Lydekker (1893)*** |
| | femur | not numbered | missing? | Lydekker (1893) *** |
| | right tibia | MLP-CS 1093 | present | Huene (1929), Powell (2003) |
| | right tibia | MCS-5/25 | present | Salgado et al. (2005) |
| | left tibia | MLP-CS 1103 | present | Huene (1929), Powell (2003) |
| | left tibia | MLP-CS 1123 | present | Huene (1929), Powell (2003) |
| | left fibula | MLP-CS 1098 | present | Huene (1929), Powell (2003) |
| | left fibula | MLP-Ly 127 | present | Lydekker (1893), Powell (2003) |
| | right fibula | MCS-5/26 | present | Salgado et al. (2005) |
| | right astragalus | MCS-5/29 | present | Salgado et al. (2005) |
| | right astragalus | MLP-CS 1216 | missing? | Huene (1929), Powell (2003) |
| | right calcaneum | MLP-CS 1233 | missing? | Huene (1929) |
| | right metatarsal I | MLP-CS 1199 | missing? | Huene (1929), Powell (2003) |
| | left metatarsal II | MLP-CS 1177 | missing? | Huene (1929), Powell (2003) |
| | right metatarsal III | MCS-10 | present | Salgado et al. (2005) |
| | left? metatarsal III | MLP-CS 1191 | present | Huene (1929), Powell (2003) |
| | right metatarsal III | MLP-CS 1201 | missing? | Huene (1929), Powell (2003) |
| | left metatarsal III | MLP-CS 1178 | missing? | Huene (1929), Powell (2003) |
| | right? metatarsal IV? | MLP-CS 1193 | present | Huene (1929), Powell (2003) |
| | right metatarsal IV? | MLP-CS 1237 | present | Huene (1929), Powell (2003) |
| | right metatarsal IV | MLP-CS 1198 | missing? | Huene (1929), Powell (2003) |
| | left metatarsal IV | MLP-CS 1190 | missing? | Huene (1929), Powell (2003) |
| | left metatarsal V | MLP-CS 1180 | present | Huene (1929), Powell (2003) |
| | left metatarsal V | MLP-CS 1181 | missing? | Huene (1929), Powell (2003) |
| | phalanx | MLP-CS 1206 | present | Huene (1929) |
| pes phalanx | MLP-CS 1223 | missing? | Huene (1929) | |
| pes phalanx | MLP-CS 1222 | missing? | Huene (1929) | |
| left pes phalanx | MLP-CS 1224 | missing? | Huene (1929) | |
| ungual left pes | MLP-CS 1204 | missing? | Huene (1929) | |
| ungual left pes | MLP-CS 1202 | missing? | Huene (1929) | |
| <i>Neuquensaurus robustus</i> nomen dubium | scapula? | MLP-Av 2064 | present | Huene (1929), Powell (2003) |
| | right ulna | MLP-CS 1095 | present | Huene (1929), Powell (2003) |
| | right ulna | MLP-CS 1053 | present | Huene (1929), Powell (2003) |
| | left ulna | MLP-CS 1094 | present | Huene (1929), Powell (2003) |
| | left ulna | MLP-CS 2004 | present | Huene (1929), Powell (2003) |
| | ulna | MLP-CS 1091 | missing? | Huene (1929), Powell (2003) |
| | ulna | MLP-CS 1055 | missing? | Huene (1929) |

| Taxon | Material | No. collection | Remarks | Author's mention | |
|---|--------------------------|----------------|-------------|-----------------------------|-----------------------|
| <i>Neuquensaurus robustus</i> nomen dubium | right radius | MLP-CS 1169 | present | Huene (1929), Powell (2003) | |
| | right radius | MLP-CS 1172 | present | Huene (1929), Powell (2003) | |
| | left radius | MLP-CS 1175 | present | Huene (1929), Powell (2003) | |
| | left radius | MLP-CS 1171 | present | Huene (1929), Powell (2003) | |
| | right metacarpal II | MLP-CS 1197 | present | Huene (1929), Powell (2003) | |
| | right metacarpal III | MLP-CS 1189 | present | Huene (1929), Powell (2003) | |
| | right metacarpal IV | MLP-CS 1238 | present | Huene (1929), Powell (2003) | |
| | left ilium | MLP-Av 2069 | present | Huene (1929), Powell (2003) | |
| | left ilium | MLP-Av 2083 | missing? | Huene (1929), Powell (2003) | |
| | right ilium | MLP-Av 2068 | missing? | Huene (1929), Powell (2003) | |
| | right pubis | MLP-Av 2066 | present | Huene (1929), Powell (2003) | |
| | left femur | MLP-CS 1480 | present | Huene (1929), Powell (2003) | |
| | right femur | MCS-9 | present | Salgado et al. (2005) | |
| | right femur | MLP-CS 1125 | missing? | Huene (1929), Powell (2003) | |
| | right tibia | MLP-CS 1303 | present | Huene (1929), Powell (2003) | |
| | right tibia | MCS-6 | present | Salgado et al. (2005) | |
| | left tibia | MLP-CS 1264 | present | Huene (1929), Powell (2003) | |
| | right fibula | MLP-CS 1265 | present | Huene (1929) | |
| | right fibula | MLP-Av 2060 | present | Huene (1929) | |
| | right fibula | MLP-Av 2059 | missing? | Huene (1929) | |
| | right metatarsal I | MLP-CS 1185 | present | Huene (1929), Powell (2003) | |
| | right metatarsal I | MLP-CS 1179 | present | Huene (1929), Powell (2003) | |
| | left metatarsal II | MLP-CS 1183 | present | Huene (1929), Powell (2003) | |
| | left metatarsal II? | MLP-CS 1236 | present | Huene (1929), Powell (2003) | |
| | left metatarsal V | MLP-CS 1194 | present | Huene (1929), Powell (2003) | |
| | left metatarsal V | MLP-CS 1182 | present | Huene (1929), Powell (2003) | |
| | right metatarsal V | MLP-CS 1195 | missing? | Huene (1929), Powell (2003) | |
| | phalanx | MLP-CS 1184 | present | Huene (1929) | |
| | cf. <i>Neuquensaurus</i> | left scapula | MCS-7 | present | Salgado et al. (2005) |
| | | right scapula | MLP-CS 1292 | present | Huene (1929) |
| left scapula | | MLP-CS 1296 | present | Huene (1929) | |
| left ulna | | MLP-CS 1052 | present | Huene (1929), Powell (2003) | |
| metacarpal II | | MLP-CS 1186 | present | Huene (1929), Powell (2003) | |
| metacarpal III or IV | | MLP-CS 2003 | present | Huene (1929), Powell (2003) | |
| metacarpal IV | | MLP-CS 1187 | present | Huene (1929), Powell (2003) | |
| right ilium | | MLP-CS 1056 | present | Huene (1929), Powell (2003) | |
| right ilium | | MLP-CS 1057 | present | Huene (1929), Powell (2003) | |
| right ilium | | MLP-CS 1258 | present | Huene (1929) | |
| left ilium | | MLP-CS 1259 | present | Huene (1929) | |
| left pubis | | MLP-CS 1263 | present | Huene (1929), Powell (2003) | |
| Titanosauria indet. | right radius | MLP-CS 1167 | present | Huene (1929), Powell (2003) | |
| | left radius | MLP-CS 1174 | present | Huene (1929), Powell (2003) | |

Appendix 2

Measurements of *Neuquensaurus* in cm. RI, robustness index, was calculated as follows: RI = average of the greatest widths of the proximal end, mid-shaft and distal end of the element/length of the element (taken from Wilson and Upchurch 2003). ECC, eccentricity index, was calculated as follows: ECC = (femoral mid-shaft width/femoral antero-posterior width) (taken from Carrano 2001).

A

| Humerii | MLP-CS 1049 | MLP-CS 1050 | MLP-CS 1051 | MLP-CS 1099 | MLP-CS 1100 | MLP-CS 1479 | MLP-CS 1019 |
|-----------------------------------|-------------|-------------|-------------|-------------|-------------|-------------|---------------|
| Length | 50.5 | 48 | 50 | 55.5 | 52 | 53 | not preserved |
| Maximum proximal width | 22.2 | 21.7 | 20.7 | 23 | 22.1 | 21.4 | 24.8 |
| Maximum distal width | 17.3 | 18 | 16.7 | 19 | 19.2 | 17.5 | not preserved |
| Midshaft mediolateral diameter | 9.3 | 9.2 | 9.2 | 9.6 | 9.4 | 9.7 | 10.3 |
| Midshaft anteroposterior diameter | 6.4 | 6.4 | 6.9 | 6.6 | 6.7 | 6.8 | 7.8 |
| RI | 0.322 | 0.339 | 0.306 | 0.309 | 0.325 | 0.305 | – |
| ECC | 1.453 | 1.437 | 1.333 | 1.454 | 1.402 | 1.426 | 1.32 |

B

| Ulnae | MLP-CS 1058 | MLP-CS 1305 | MLP-CS 1306 | MLP-CS 2004 | MLP-CS 1052 | MLP-CS 1094 | MLP-CS 1095 |
|--------------------------------|-------------|-------------|-------------|---------------|-------------|-------------|-------------|
| Length | 34 | 30 | 35 | not preserved | 27 | 32 | 32 |
| Maximum proximal width | 15.2 | 8.8 | 11.7 | 14.3 | 13.5 | 14.4 | 14 |
| Maximum distal width | 7.9 | 7.8 | 6.7 | 8.1 | 7.4 | 7.6 | 7.6 |
| Midshaft mediolateral diameter | 6.5 | 5.3 | 5.8 | not preserved | 6.6 | 5.7 | 5.7 |
| RI | 0.290 | 0.243 | 0.230 | – | 0.339 | 0.288 | 0.284 |

C

| Radii | MLP-CS 1169 | MLP-CS 1175 | MLP-CS 1176 | MLP-CS 1171 |
|--------------------------------|-------------|-------------|-------------|-------------|
| Length | 29.6 | 29 | 33.7 | 28 |
| Maximum proximal width | 11.4 | 10.4 | 10 | 10.5 |
| Maximum distal width | 9.3 | 9.7 | 9.7 | 9.2 |
| Midshaft mediolateral diameter | 4.5 | 4.8 | 5.11 | 4.5 |
| RI | 0.283 | 0.286 | 0.245 | 0.288 |

D

| Femora | MLP-CS 1101 | MLP-CS 1121 | MLP-CS 1118 | MCS-9 | MLP-CS 1480 |
|-----------------------------------|-------------|-------------|-------------|-------|-------------|
| Length | 71 | 73 | 74 | 81 | 73 |
| Maximum proximal width | 22.4 | 22.4 | 21.7 | 25 | 24 |
| Maximum distal width | 24 | 21.2 | 23.1 | 27.6 | 23.3 |
| Midshaft mediolateral diameter | 12.2 | 11 | 12 | 16.7 | 12.7 |
| Midshaft anteroposterior diameter | 7.8 | 8.1 | 7.9 | 8.8 | 8 |
| RI | 0.275 | 0.249 | 0.255 | 0.285 | 0.273 |
| ECC | 1.564 | 1.358 | 1.518 | 1.897 | 1.587 |

E

| Tibiae | MLP-CS 1103 | MCS-5/25 | MCS-6 | MLP-CS 1264 |
|--------------------------------|-------------|----------|-------|-------------|
| Length | 46 | 44.5 | 45 | 41 |
| Maximum proximal width | 22.8 | 17 | 23 | 18 |
| Maximum distal width | 10.2 | 16.5 | 17 | 12.3 |
| Midshaft mediolateral diameter | 8.6 | 6.666 | 9.324 | 8.2 |
| RI | 0.301 | 0.300 | 0.365 | 0.313 |

F

| Fibulae | MLP-CS 1098 | MLP-Ly 127 | MCS-5/26 | MLP-CS 1265 |
|--------------------------------|-------------|------------|----------|-------------|
| Length | 43 | 37 | 44.5 | 40 |
| Maximum proximal width | 10.3 | 11 | 12 | 14.8 |
| Maximum distal width | 6.9 | 8.5 | 9.5 | 7.9 |
| Midshaft mediolateral diameter | 5.1 | 5 | 6 | 5.2 |
| RI | 0.172 | 0.220 | 0.205 | 0.232 |

Appendix 3

Table showing the ECC values for some prosauropods and sauropods.

| Taxon | N1 collection | ECC |
|--------------------------------|---------------|-------|
| <i>Neuquensaurus australis</i> | MLP-CS 1118 | 1.518 |
| <i>Neuquensaurus robustus</i> | MLP-CS 1480 | 1.587 |
| <i>Saltasaurus loricatus</i> | PVL 4017-83 | 1.65 |
| <i>Rocasaurus muniozi</i> | MPCA-Pv 46 | 1.333 |
| <i>Bonatitan reigii</i> | MACN-RN 82 | 1.4 |
| <i>Amargasaurus cazau</i> | MACN-N 15 | 1.5 |
| <i>Coloradisaurus brevis</i> | PVL 5904 | 0.93 |
| <i>Riojasaurus incertus</i> | MPEF-PV 1690 | 1.09 |