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A REAPPRAISAL OF THE LATE CRETACEOUS ARGENTINEAN SAUROPOD DINOSAUR *ARGYROSAURUS SUPERBUS*, WITH A DESCRIPTION OF A NEW TITANOSAUR GENUS

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ABSTRACT—*Argyrosaurus superbis* is one of the earliest-named Argentinean dinosaurs. The holotype comprises a complete forelimb, probably from the upper member of the Bajo Barreal Formation (Late Cretaceous), Chubut Province. Numerous remains have been referred to *Argyrosaurus* from Argentina and Uruguay; however, the type specimen has not been adequately diagnosed and referrals have predominantly been based upon their large size. Here we redescribe *Argyrosaurus*, demonstrating it to be a valid titanosaur genus based on five autapomorphies, as well as an unique character combination. The exact placement of *Argyrosaurus* within Titanosauria is uncertain, although the probable presence of carpal bones, otherwise unknown in titanosaurs, may indicate a basal position. None of the referred remains can be attributed to *Argyrosaurus*, and most should be regarded as indeterminate titanosauriforms. The exception to this is a partial skeleton from the lower member of the Bajo Barreal Formation (early Late Cretaceous), Chubut Province, comprising dorsal and caudal vertebrae, as well as numerous appendicular elements. This specimen is distinct from *Argyrosaurus* and can also be differentiated from other sauropods based on an unusual character combination (including plesiomorphic tarsus), plus one autapomorphy. *Elaltitan lilloi*, gen. et sp. nov., displays numerous titanosaur characters and shares several features with derived taxa such as *Neuquensaurus*, *Opisthocoelicaudia*, *Rapetosaurus*, *Saltasaurus*, and *Trigonosaurus*. *Elaltitan* can be referred to Lithostrotia; however, its precise position within this clade must await future phylogenetic analysis. The revision and description of the titanosaurs *Argyrosaurus* and *Elaltitan* provides new information on this diverse but still poorly understood clade.

INTRODUCTION

The Late Cretaceous dinosaur record of Argentina is one of the richest in the world, with titanosaur sauropods, in particular, profuse in both abundance and diversity (Salgado and Bonaparte, 2007; Novas, 2009; González Riga, 2011; Mannion and Calvo, 2011; Mannion et al., 2011). Lydekker (1893) produced the first description of Argentinean dinosaur remains, naming new species of the sauropod “*Titanosaurus*” (see Wilson and Upchurch, 2003) and erecting the binomial *Argyrosaurus superbis*. The latter consists of a partly articulated sauropod forelimb (MLP 77-V-29–1) discovered by Carlos Ameghino in 1888 in Chubut Province, southern Argentina (Fig. 1), probably from the Upper Cretaceous Bajo Barreal Formation (Lydekker, 1893; Huene, 1929a; Powell, 2003; Salgado, 2007). When originally discovered, this forelimb was apparently part of a complete skeleton; however, the specimen was subsequently collected by a Museo de La Plata commission (without the assistance of Carlos Ameghino), which managed to destroy all but the forelimb in their excavation of the skeleton (Salgado, 2007).

Comparable to the complex taxonomic history of other South American sauropods described in, or prior to, the first third of the 20th century (McIntosh, 1990; Wilson and Upchurch, 2003; Upchurch et al., 2004), numerous specimens were referred to *Argyrosaurus* from elsewhere in Argentina and Uruguay (Lydekker, 1893; Huene, 1929a, 1929b, 1931; Powell, 1986, 2003). These referrals were based primarily on their large size and robust proportions and mostly comprise isolated bones. The exception is

a partial skeleton (PVL 4628/MACN-CH 217) recovered from Chubut Province by an expedition of the Fundación Miguel Lillo and the Universidad Nacional de Tucumán, led by J. F. Bonaparte. This skeleton was originally attributed to *Antarctosaurus* sp. (Bonaparte and Gasparini, 1979), but later tentatively referred to *Argyrosaurus* by Powell (1986, 2003), who also provided a short description. Although there is some anatomical overlap between the latter individual and holotype, the referral was based on gross morphological similarities, rather than shared autapomorphies (Powell, 1986, 2003; Apesteguía, 2004a), and several subsequent studies have variously listed the referred specimen as cf. *Argyrosaurus* (Bonaparte, 1999a; Bonaparte et al., 2006) or *Argyrosaurus ‘superbis’* (Apesteguía, 2007). Salgado and Bonaparte (2007) expressed doubt as to this referral, commenting that a revision is required of the holotype and referred materials of *Argyrosaurus* (see also Martínez et al., 2004). Furthermore, Upchurch et al. (2004) could only identify a single autapomorphy of *Argyrosaurus*, with this feature restricted to the referred specimen, and therefore they cast doubt on the validity of the genus.

Several phylogenetic analyses have included *Argyrosaurus*. Sanz et al. (1999) analyzed the relationships of the taxon based only on the referred specimen (PVL 4628/MACN-CH 217) and recovered it as the sister taxon to *Saltasaurus*. Powell (2003) reran the Sanz et al. (1999) analysis, adding additional taxa; he recovered the referred *Argyrosaurus* specimen as the sister taxon to *Ampelosaurus* + *Isisaurus*. Apesteguía (2004a) coded the holotype and referred specimen separately, but recovered no resolution within his trees. He then combined the two specimens as a single operational taxonomic unit and recovered it as a lithostrotian titanosaur. Curry Rogers (2005) restricted her analysis to the type individual (although she also included scorings for a

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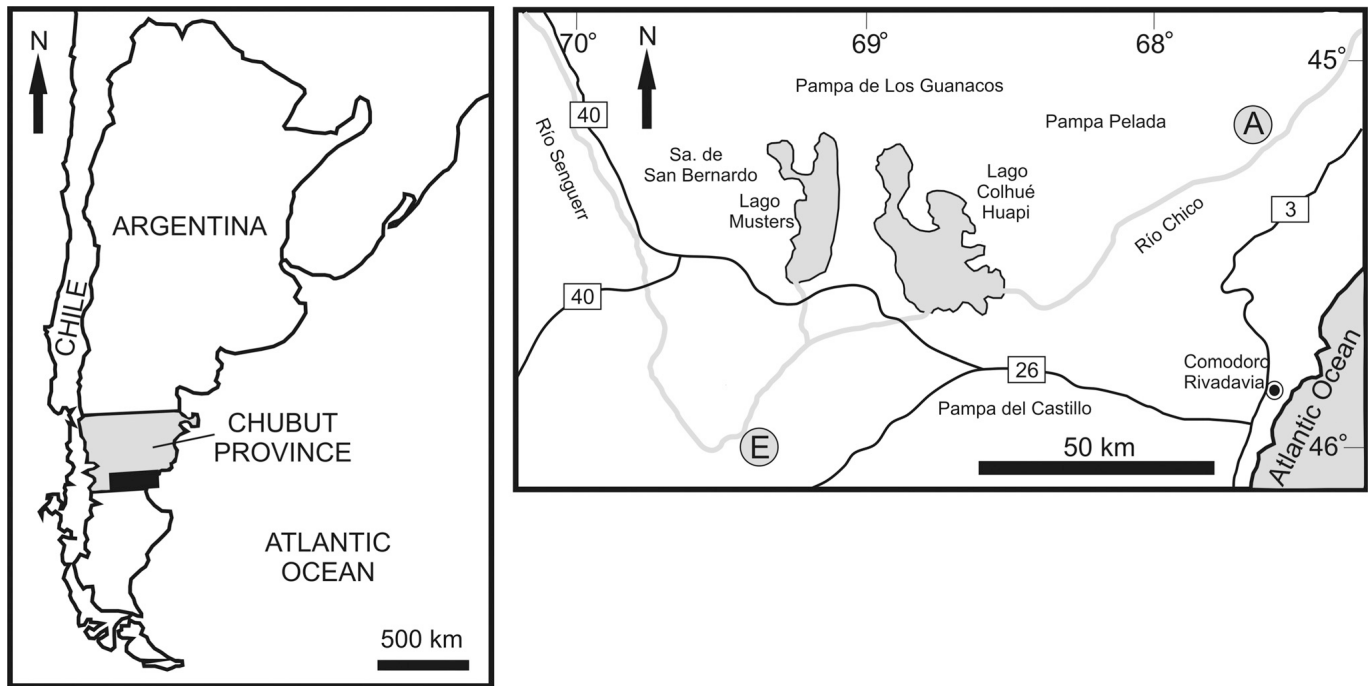


FIGURE 1. Locality map showing geographic position of Chubut Province within Argentina and a close-up (area marked with black box on map of Argentina) of the region from which *Argurosaurus superbis* (marked with an 'A') and *Elaltitan lilloi*, gen. et sp. nov. (marked with an 'E'), were recovered.

scapula, presumably of the referred specimen) and recovered it as a basal titanosaur and the sister taxon of *Paralititan* (see also Mannion, 2011:fig. 13). Mannion and Upchurch (2011) supported this placement in their reanalysis of the Curry Rogers (2005) matrix in some of their reduced consensus trees, but recovered *Argurosaurus* in a position basal to *Paralititan* (and all other titanosaurs) in others.

As well as Lydekker's (1893) original description, both Huene (1929a) and Powell (2003) briefly redescribed the *Argurosaurus* holotype and referred remains; however, the taxon has otherwise been largely overlooked. Here, the holotype of *Argurosaurus superbis* is redescribed, its validity and phylogenetic affinities determined, and the referral of remains evaluated. Of these referred materials, we place particular emphasis on the partial skeleton PVL 4628/MACN-CH 217, providing a new and detailed description.

Institutional Abbreviations—**DGM**, Dirección General de Minas, Buenos Aires, Argentina; **DMNH**, Denver Museum of Nature and Science, Denver, U.S.A.; **FMNH**, Field Museum of Natural History, Chicago, U.S.A.; **HMN**, Humboldt Museum für Naturkunde, Berlin, Germany; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **MACN**, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina; **MCF**, Museo "Carmen Funes," Plaza Huinca, Argentina; **MCS**, Museo de Cinco Saltos, Río Negro, Argentina; **MLP**, Museo de La Plata, La Plata, Argentina; **MMAB**, Museo Municipal "Alejandro Berro," Mercedes, Uruguay; **MN**, Museu Nacional, Rio de Janeiro, Brazil; **MNHN**, Muséum National d'Histoire Naturelle, Paris, France; **NHMUK**, Natural History Museum, London, United Kingdom; **PVL**, Colección de Paleontología de Vertebrados de la Fundación Instituto Miguel Lillo, Tucumán, Argentina; **USNM**, Smithsonian National Museum of Natural History, Washington D.C., U.S.A.

Anatomical Abbreviations—**ACDL**, anterior centrodiapophyseal lamina; **ACPL**, anterior centroparapophyseal lamina; **CDF**, centrodiapophyseal fossa; **CPOL**, centropostzygapophyseal lamina; **CPRL**, centroprezygapophyseal lamina; **PCDL**, posterior centrodiapophyseal lamina; **PCPL**, posterior centroparapophyseal lamina; **POCDF**, postzygapophyseal centrodiapophyseal fossa; **PODL**, postzygodiapophyseal lamina; **PRCDF**, prezygapophyseal centrodiapophyseal fossa; **PRDL**, prezygodiapophyseal lamina; **PRPADF**, prezygapophyseal parapodiapophyseal fossa; **SPDL**, spinodiapophyseal lamina; **SPOF**, spinopostzygapophyseal fossa; **SPOL**, spinopostzygapophyseal lamina; **SPRL**, spinoprezygapophyseal lamina; **TPOL**, intrapostzygapophyseal lamina.

SYSTEMATIC PALEONTOLOGY

SAUROPODA Marsh, 1878
 NEOSAUROPODA Bonaparte, 1986
 TITANOSAURIFORMES Salgado, Coria and Calvo, 1997
 TITANOSAURIA Bonaparte and Coria, 1993
ARGYROSAURUS SUPERBUS Lydekker, 1893
 (Figs. 2–3)

Holotype—MLP 77-V-29-1, a partly articulated left forelimb consisting of the humerus, ulna, radius, probably two carpals (now lost), and all five metacarpals.

Diagnosis—*Argurosaurus* can be diagnosed by five autapomorphies (marked by an asterisk), as well as a unique combination of character states: (1) medial margin of humerus forms a transversely wide ridge that projects prominently anteriorly*; (2) midshaft of humerus extremely compressed anteroposteriorly (transverse to anteroposterior width ratio = 2.6)*; (3) transverse width of distal end of radius only slightly greater than midshaft

width (ratio = 1.3)*; (4) radius is subtriangular in distal end view*; (5) presence of ossified carpals; (6) extreme elongation of metacarpals (longest metacarpal to radius length ratio = 0.6)*; (7) metacarpals II and III longest elements in metacarpus.

Locality and Horizon—Left bank (northwest) of the Río Chico, near Pampa Pelada, northeast of Lago Colhué Huapi, Chubut Province, Argentina (Fig. 1) (Lydekker, 1893; Huene, 1929a; Bonaparte and Gasparini, 1979); probably upper member of the Bajo Barreal Formation, Chubut Group (Bonaparte and Gasparini, 1979); Campanian–?Maastrichtian (Late Cretaceous) (Casal et al., 2007). Based on outcrops in the western part of the San Jorge Basin, the Bajo Barreal Formation is generally considered middle Cenomanian–Turonian in age (Bridge et al., 2000; Lamanna et al., 2002); however, recent evidence indicates that the more easterly exposures in the less well-studied Río Chico area are much younger, i.e., Campanian–?Maastrichtian (Casal et al., 2007; see also Salgado and Bonaparte, 2007; Ibiricu et al., 2010; Prieto-Marquez and Salinas, 2010).

Additional Comments—Lydekker (1893) did not provide a diagnosis for *Argyrosaurus*, merely noting several differences with *Neuquensaurus* (“*Titanosaurus*”) *australis* that he deemed worthy of generic distinction. Bonaparte and Gasparini (1979) commented that *Argyrosaurus* can be diagnosed principally by the robustness of the forelimb, whereas Powell (2003:50) provided the following diagnosis: “A huge-sized titanosaurid. Stout humerus with broad proximal end that has a straight upper edge (margin) perpendicular to the long axis of the bone. Pectoral muscle insertion far more prominent and projected forward and medially. Ulna with extremely robust proximal end showing prominent edges delimiting markedly concave facets. Stout metacarpals approximately one-third the length of the humerus.” None of these features are unique to *Argyrosaurus* and instead diagnose a wider array of titanosaurs. Other authors have proposed additional autapomorphies of *Argyrosaurus* (Upchurch et al., 2004; Novas, 2009), but these are based on elements preserved only in the referred skeleton (PVL 4628/MACN-CH 217), not the holotype; as such, these features are discussed later.

DESCRIPTION AND COMPARISONS

Humerus

The humerus is mainly complete (Fig. 2A–C), although damaged in places, and the distal end is poorly preserved. Measurements are provided in Table 1. In anterior view, the proximal and lateral margins meet at an angle close to 90° (Fig. 2A), as in other titanosaurs (Upchurch, 1999; Wilson, 2002; Otero, 2010; Mannion and Calvo, 2011). The lateral half of the proximal end is relatively horizontal in anterior view but expands proximally towards the medial edge of the humerus, forming a proximomedial bulge (the humeral head). This bulge also extends posteriorly, but does not extend distally along the posterior surface (Fig. 2B). Anteroposterior thickness of the proximal end increases medially along the lateral three-quarters, before decreasing along the remaining quarter; this gives the humerus a sub-triangular or wedge shape in proximal end view (Fig. 2C).

The medial surface of the proximal portion of the humerus forms a near right angle with the posterior surface (Fig. 2C). The anterior surface of the medial margin is composed of a transversely wide ridge that projects prominently anteriorly (Fig. 2A). This ridge becomes more rounded and less pronounced distally, but extends for most of the length of the humerus. There is no evidence of bone cracking and so this ridge does not appear to be the product of crushing. *Gondwanatitan* also possesses an anteromedial ridge (Kellner and de Azevedo, 1999:fig. 20), although this is considerably less prominent and restricted to the proximal half of the humerus (MN 4111-V; P.D.M., pers. observ., 2009). The prominence and distal extension of the ridge is unique and regarded as autapomorphic for *Argyrosaurus*. As a consequence

of this medial ridge, the anterior surface of the proximal half of the humerus is deeply concave transversely, with this concavity bounded laterally by the deltopectoral crest (Fig. 2A).

The deltopectoral crest is incomplete proximally, but is relatively narrow for most of its preserved length, expanding mediolaterally towards its distal end (Fig. 2A). This distal expansion is relatively modest, expanding medially across approximately one-third of the humerus. This is similar to the condition in most titanosauriforms, but contrasts with *Ligabuesaurus* (MCF-PHV-233; P.D.M., pers. observ., 2009), *Opisthocoelicaudia* (Borsuk-Bialynicka, 1977), *Petrobrasaurus* (Filippi et al., 2011b), and PVL 4628 (i.e., the referred *Argyrosaurus*—see below), in which the deltopectoral crest extends medially across at least half of the anterior surface of the humerus. The deltopectoral crest does not extend as far distally as the midshaft, differing from the humeri of several derived titanosaurs, i.e., *Neuquensaurus* and *Opisthocoelicaudia* (Borsuk-Bialynicka, 1977; Salgado et al., 2005). The posterolateral surface of the deltopectoral crest lacks the prominent muscle scar present in some titanosaurs, e.g., *Epachthosaurus* (Martínez et al., 2004), *Neuquensaurus* (Otero, 2010), and *Opisthocoelicaudia* (Borsuk-Bialynicka, 1977).

At midshaft, the humerus is strongly compressed anteroposteriorly, and it has the highest transverse to anteroposterior width ratio of any known sauropod (2.64 [measured on the anteroposteriorly thicker medial side]; see Table 1). Most other sauropods have ratios much lower than 2.0, with only the titanosaurs *Gondwanatitan* and *Lirainosaurus* possessing a ratio close to that of *Argyrosaurus* (see Mannion et al., 2012). As noted for the anteromedial ridge (above), there is no evidence that this strong degree of compression is a result of deformation. Although this anteroposterior compression may eventually be determined a synapomorphy of a wider clade of titanosaurs, we regard the extreme condition in *Argyrosaurus* as an autapomorphy of the genus.

The humerus displays a strong degree of torsion, with the distal half twisted laterally with respect to the proximal half. Distal to the deltopectoral crest, the lateral half of the anterior surface is relatively flat. The poor preservation of the distal end means that it is difficult to determine whether the few discernible features are genuine or the product of crushing. The ulnar condyle curves up onto the anterior surface of the humerus. Although possibly distorted by crushing, this seems to be at least partly a genuine feature based on the anteroposteriorly convex surface of the distal end, and is considered a feature of derived titanosaurs (Wilson, 2002). A moderately deep concavity is present on the medial surface of the radial condyle, but it is not possible to discern if this is the result of crushing.

The posterior surface of the proximal two-thirds of the humerus is largely featureless and flat, becoming mediolaterally convex towards its lateral and medial margins. A prominent, mediolaterally concave supracondylar fossa is present along the distal third of the posterior surface (Fig. 2B). This concavity is bounded medially by a proximodistally oriented and sharp radial condylar ridge that extends along the posteromedial margin. In contrast, the lateral margin of the supracondylar fossa is demarcated by a gently rounded ulnar condylar ridge, with little relief. A deep supracondylar fossa, bounded by ridges, is a feature of most titanosaurs (Upchurch et al., 2004).

Radius

The radius (see Table 1 for measurements) is relatively complete (Fig. 2D–E) but poorly preserved, particularly at the proximal end, which has been subjected to crushing and is missing a small portion. It is gracile (proximal end transverse width to radius length ratio = 0.23; sensu Upchurch, 1998:character 162; Curry Rogers, 2005:characters 281, 285), although this is highly variable among titanosaurs, with some taxa displaying robust radii (Curry Rogers, 2005). The anterior, lateral, and posterior

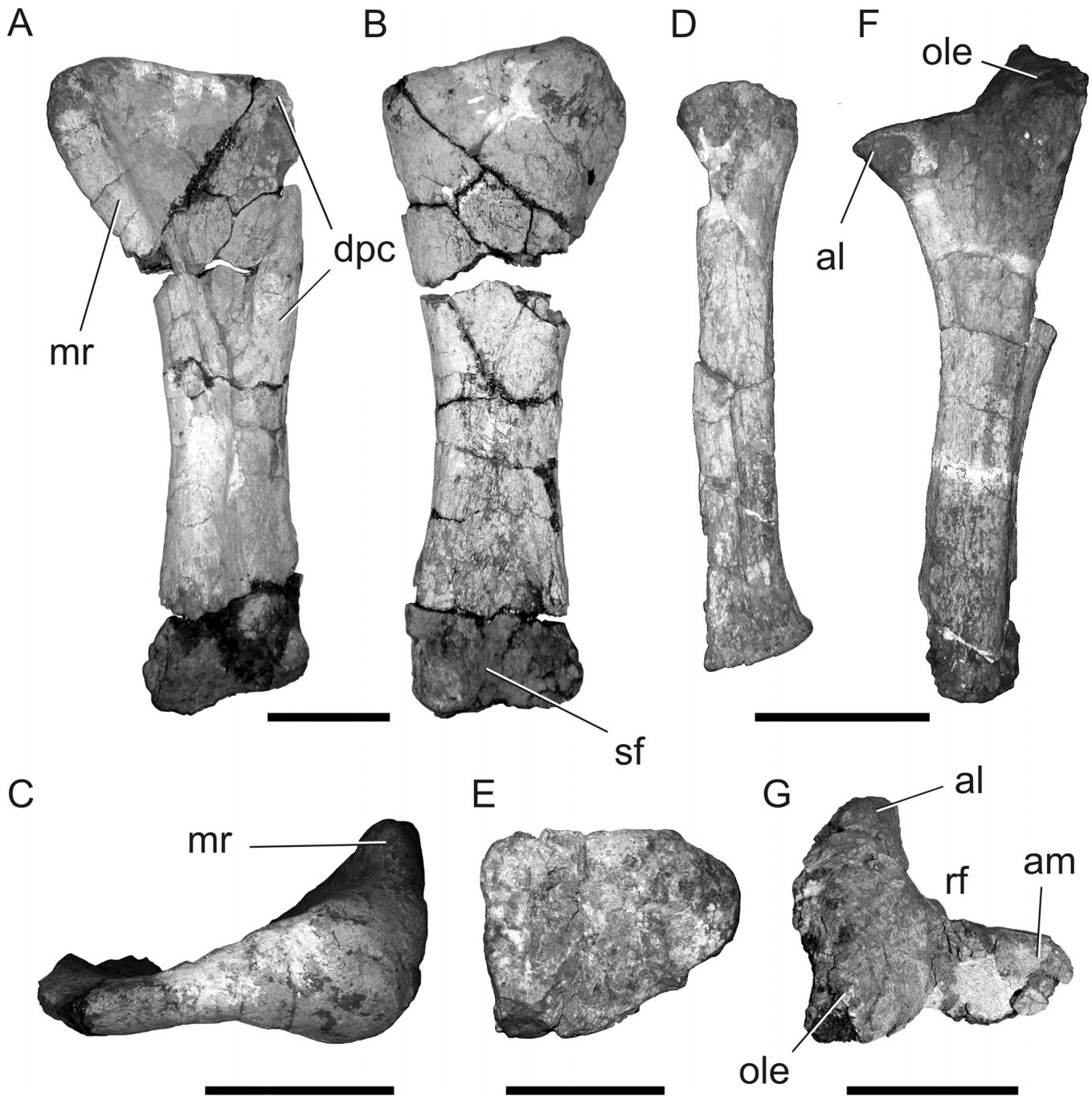


FIGURE 2. *Argyrosaurus superbus* forelimb elements (MLP 77-V-29-1). **A**, left humerus in anterior view; **B**, left humerus in posterior view; **C**, left humerus in proximal end view; **D**, left radius in anterior view; **E**, left radius in distal end view (anterior surface at top); **F**, left ulna in anterior view; **G**, left ulna in proximal end view. **Abbreviations:** al, anterolateral process; am, anteromedial process; dpc, deltopectoral crest; mr, medial ridge; ole, olecranon process; rf, radial fossa; sf, supracondylar fossa. Scale bar equals 250 mm in **A–D** and **F**, 100 mm in **E**, and 200 mm in **G**.

surfaces all curve smoothly into one another along the proximal half, whereas the medial surface is transversely concave; however, the latter feature is likely the result of severe crushing. Distally, the anterior surface curves onto the medial surface. A prominent, proximodistally oriented concavity extends along much of the anterior surface, but this is also probably the result of crushing. There is a poorly preserved ridge along the posterolateral surface that presumably would have articulated with a comparable ridge on the ulna (see below). This begins approximately

at midshaft and extends distally; its point of termination cannot be determined due to breakage.

The distal end of the radius is only slightly mediolaterally expanded in comparison to the shaft (ratio of 1.3; Table 1, Fig. 2D), with a lateral projection. In contrast, the distal width of the radius of most other titanosaurs is approximately twice the midshaft width (Wilson, 2002; Curry Rogers, 2005) and this ratio is usually at least 1.6 in other sauropods (Mannion et al., in prep.). Thus, the distal end of the radius of *Argyrosaurus* is

TABLE 1. Measurements of the humerus, ulna, and radius of the *Argyrosaurus superbus* holotype (MLP 77-V-29-1).

Element	Dimension	Measurement
Humerus	Length	1370
	Mediolateral width of proximal end	530
	Anteroposterior width of proximal end (measured on lateral margin)	62
	Anteroposterior width of proximal end (measured on medial ridge)	299
	Mediolateral width of medial ridge (measured near proximal end)	106
	Distance from proximal end to distal end of deltopectoral crest	620
	Mediolateral width at midshaft	275
	Anteroposterior width at midshaft (measured on lateral half)	85
	Anteroposterior width at midshaft (measured on medial half)	104
	Mediolateral width of distal end (partly estimated)	~ 440
	Anteroposterior width of distal end (measured on radial condyle)	~ 175
	Anteroposterior width of distal end (measured on ulnar condyle)	~ 260
	Radius	Length
Mediolateral width of proximal end		194
Anteroposterior width of proximal end		148
Mediolateral width of distal end		169
Anteroposterior width of distal end (measured along medial margin)		139
Ulna	Length	965
	Mediolateral width of proximal end (from the posterior surface to the tip of the medial process)	330
	Anteroposterior width of proximal end (from the posterior surface to the tip of the anterolateral process)	320
	Mediolateral width at midshaft	144
	Anteroposterior width at midshaft	148
	Anteroposterior width of distal end	215

All measurements are in millimeters.

autapomorphically mediolaterally narrow. The distal articular surface is sub-triangular in distal end view (Fig. 2E). It has straight anterior and medial margins that meet at a right angle, whereas the posterior and lateral margins are much more rounded. This differs from the sub-rectangular distal outlines of most sauropods, which have straight posterior margins (Wilson and Sereno, 1998), as well as the sub-circular shape of taxa such as *Cedarosaurus* and *Venenosaurus* (DMNH 39045 and DMNH 40932, respectively; P.D.M., pers. observ., 2008); consequently, this shape is regarded as diagnostic for *Argyrosaurus*. The distal surface is beveled approximately 20° to the long axis of the radius (Fig. 2D), facing distally and also laterally. This beveled morphology is restricted to titanosaurs, such as the derived forms *Neuquensaurus*, *Opisthocoelicaudia*, and *Saltasaurus* (Wilson, 2002), but is also present in more basal members, e.g., “*Pelorosaurus*” *becklesii* (NHMUK R1870; P.D.M., pers. observ., 2010).

Ulna

The ulna (Fig. 2F–G) is missing the posterolateral region of much of the proximal half and the anteromedial portion of the distal end; it is also poorly preserved. Measurements are provided in Table 1. It has a triradiate proximal end with condylar processes of approximately equal length (Fig. 2G). In most sauropods, the anteromedial process is longer than the anterolateral one, although *Malawisaurus* (along with several non-titanosaurs) apparently shares this equidimensional morphology with *Argyrosaurus* (Wilson, 2002). The proximal surface of the anterolateral process slopes slightly forward towards its anterior end. There is a prominent olecranon process that projects well above the proximal articular surface. This process is reduced or absent in most sauropods, but reappears in titanosaurs (Wilson and Sereno, 1998), although its development varies among taxa (Curry Rogers, 2009; Otero, 2010) and through ontogeny (e.g., *Venenosaurus*; Tidwell and Wilhite, 2005). The proximal surface of the anteromedial process is relatively flat and slopes so that it faces dorsally but also slightly medially; it therefore lacks the concave outline seen in most titanosaurs (Upchurch, 1995). The anteromedial process does not extend as far proximally as the remainder of the proximal surface of the ulna.

The ulna is bowed anteriorly in lateral view, with a gently concave posterior margin along the distal half. Between the two proximal condylar processes, the anterior surface of the ulna is mediolaterally concave. Distal to this concavity there is a prominent, convex bulge, which presumably represents a muscle attachment site. The anteromedial surface of the shaft is transversely convex, whereas the lateral surface is flat. Along the proximal half of the ulna, the anterior and medial/posteromedial surfaces curve smoothly into one another. Distally, these become distinct surfaces, with a relatively flat posteromedial surface. Approximately one-third of the way up from the distal end there is a proximodistally elongate, rugose ridge along the anteromedial margin: this would articulate with a comparable ridge on the radius (see above). The incompleteness of the distal end of the ulna prevents us from determining its shape, but it is strongly expanded anteroposteriorly in comparison to the shaft, as in most sauropods (Upchurch et al., 2004).

Carpus

The two carpals could not be located in the collections of the Museo de La Plata and so the following description is based solely on the figures in Lydekker (1893:pl. 5; see also Fig. 3A), Huene (1929a:pl. 37, fig. 1a), and information provided by Apesteguía (2005). Based on Lydekker (1893) and Huene (1929a), the larger carpal completely covered the proximal surfaces of metacarpals (Mc.) IV and V, as well as the lateral half of the proximal end of Mc. III, and appears to have increased in proximodistal thickness medially (Fig. 3A). However, Apesteguía (2005), noting that the smaller carpal was attached to the distal end of the ulna, proposed that the observed position of the larger carpal is a taphonomic artefact of twisting of the forearm, and that the element would instead have been situated above Mc. I–II and associated with the radius in life, as in other sauropods, e.g., *Atlasaurus* (Monbaron et al., 1999:fig. 1k), *Camarasaurus* (Osborn, 1904:fig. 1), and *Turiasaurus* (Royo-Torres et al., 2006:fig. 1a). This twisting is evident in the original photograph in Lydekker (1893:pl. 5; Fig. 3A), whereby the ulna and radius have been rotated approximately 90° counterclockwise in relation to the humerus, such that they are in lateral view; however, the metacarpus has been rotated a further 90° (note that the humerus is in posterior view and the

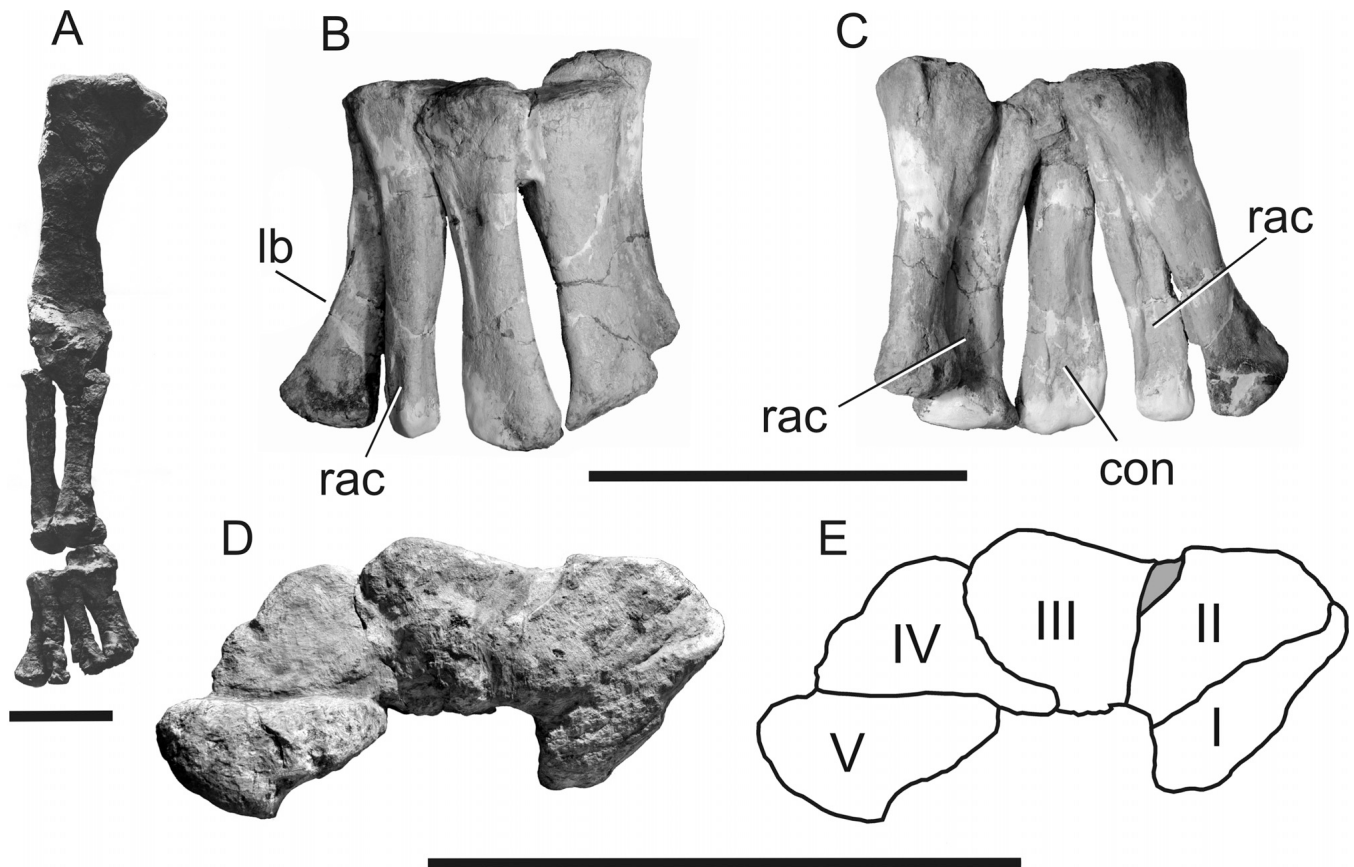


FIGURE 3. *Argyrosaurus superbis* forelimb elements (MLP 77-V-29-1). **A**, preserved left forelimb as figured by Lydekker (1893:pl. 5); **B**, left metacarpals in dorsal view; **C**, left metacarpals in ventral view; **D**, left metacarpals in proximal end view; **E**, line drawing of left metacarpals in proximal end view. **Abbreviations:** con, concavity; lb, lateral bowing; rac, ridges and concavity. Gray in-fill in **E** denotes matrix. Scale bars equal 500 mm.

metacarpus in anterior view in Lydekker 1893:pl. 5; reproduced here in Fig. 3A). Based on other sauropods, Apesteguía's (2005) proposal seems highly plausible, but must await new specimens for confirmation.

Carpal elements are otherwise unknown in titanosaurs (Borsuk-Bialynicka, 1977; Wilson and Sereno, 1998; Upchurch et al., 2004), including well-preserved and articulated forelimbs of taxa such as *Alamosaurus* (Gilmore, 1946), *Epachthosaurus* (Martínez et al., 2004), and *Opisthocoelicaudia* (Borsuk-Bialynicka, 1977). As such, we consider the probable presence of ossified carpals in *Argyrosaurus* as a local autapomorphy within Titanosauria.

Metacarpus

The articulated metacarpus (Fig. 3A–E) was complete in the original descriptions of Lydekker (1893) and Huene (1929a), but is now broken in several places. Although in life the metacarpals would have been oriented vertically, they are here described in a horizontal plane (see also Mannion and Calvo, 2011). Thus, what would be the anterior surface in life of Mc. II–IV is treated as the dorsal surface in our description. Similarly, the posteromedially facing surfaces of Mc. I and V are described as the dorsal surfaces. Measurements are provided in Table 2.

The metacarpals are articulated in a 'U'-shaped colonnade, as is the case in all neosauropods (Wilson and Sereno, 1998) and most eusauropods (Upchurch, 1998). Mc. II is the longest

metacarpal, closely followed by Mc. III (see Table 2). Mc. III is the longest metacarpal in most sauropods (Upchurch, 1998), but this is not the case in several titanosaurs: Mc. I and II are the longest in *Alamosaurus*, *Epachthosaurus*, and *Opisthocoelicaudia* (Gilmore, 1946; Borsuk-Bialynicka, 1977; Martínez et al., 2004). However, the putative basal titanosaur *Janenschia* shows

TABLE 2. Measurements of the metacarpus of the *Argyrosaurus superbis* holotype (MLP 77-V-29-1).

Dimension	Mc. I	Mc. II	Mc. III	Mc. IV	Mc. V
Length along medial margin	480	513*	504*	420	398
Length along lateral margin	460	—	—	402	398
Maximum mediolateral width of proximal end	180	124	144	136	139
Maximum dorsoventral height of proximal end	73	147	127	153	82
Mediolateral width of midshaft	79	80	90	86	73
Dorsoventral height of midshaft	55	66	58	68	65
Maximum mediolateral width of distal end	141	—	—	158	99
Maximum dorsoventral height of distal end	75	—	—	81	69

Measurements denoted with an asterisk indicate that measurements were estimated from Huene (1929a:pl. 37, fig. 1) because of present-day breakage. All measurements are in millimeters.

TABLE 3. Ratios of the length of the longest metacarpal to radius length for an array of macronarian taxa (including putative forms) preserving associated forearm elements (see also Apesteguía, 2005:table 15.1).

Taxon and reference/specimen number	Ratio
<i>Aeolosaurus</i> (Powell, 2003)	0.53
<i>Alamosaurus</i> (Gilmore, 1946)	0.51
<i>Angolatitan</i> (Mateus et al., 2011)	0.49
<i>Argyrosaurus</i> (MLP 77-V-29-1)	0.60
<i>Atlasaurus</i> (Monbaron et al., 1999)	0.38
<i>Camarasaurus</i> (Gilmore, 1925)	0.47
<i>Cedarosaurus</i> (DMNH 39045; Tidwell et al., 1999)	0.51
<i>Chubutisaurus</i> (Salgado, 1993)	0.54
<i>Epachthosaurus</i> (Martínez et al., 2004)	0.55
<i>Giraffatitan</i> (Janensch, 1961)	0.51
<i>Opisthocoelicaudia</i> (Borsuk-Bialynicka, 1977)	0.46
<i>Rapetosaurus</i> (Curry Rogers, 2009)	0.50
<i>Venosaurus</i> (DMNH 40932; Tidwell et al., 2001)	0.52
<i>Wintonotitan</i> (Hocknull et al., 2009)	0.53

the same pattern as *Argyrosaurus*, with metacarpals II and III the longest metacarpals (Janensch, 1922). Consequently, we consider this a local autapomorphy of *Argyrosaurus*. The ratio of the longest metacarpal length to radius length is 0.6. Previous authors have noted that macronarian sauropods have a greater ratio than other sauropods (0.45 or greater; Salgado et al., 1997; Upchurch, 1998; Wilson and Sereno, 1998; Apesteguía, 2005) and Table 3 demonstrates that *Argyrosaurus* has considerably more elongate metacarpals (with respect to radius length) than all other macronarians. As such, the prominent elongation of metacarpals is considered an autapomorphy of *Argyrosaurus*.

The proximal articular surface of metacarpal I is relatively flat and rugose, but becomes convex towards its medial, dorsal, and lateral margins. It has an approximately sub-triangular outline, with the narrow apex pointing laterally (i.e., anteromedially in the articulated metacarpus; see Fig. 3D–E). This dorsoventrally compressed morphology is comparable to the titanosaurs *Andesaurus* and *Rapetosaurus* (Apesteguía, 2005; Curry Rogers, 2009; Mannion and Calvo, 2011) and differs from the semicircular or ‘D’-shaped outlines of most other sauropods (Upchurch et al., 2004; Apesteguía, 2005). In proximal end view, Mc. I is dorsoventrally wider along the medial half (i.e., the posterolaterally oriented half in the articulated metacarpus; see Fig. 3D–E), although it tapers at the medial tip to form a small medial bulge. The dorsal surface (medially facing in the articulated metacarpus) of the proximal third of Mc. I is flat and featureless, whereas it becomes mildly mediolaterally convex distally. Along the proximal third there is a dorsomedial ridge, as well as a roughened ridge on the medial surface, close to the ventral margin. In dorsal view, the lateral margin (medial margin in the articulated metacarpus) is strongly concave, giving the metacarpal a bowed appearance (Fig. 3B), as in several other titanosaurs (Apesteguía, 2005; Mannion and Calvo, 2011). The lateral surface is extremely bulbous along the proximal half, whereas it forms a sharp ridge distally. The ventrolateral corner of the distal end forms a small process that would have articulated with the medial surface of the distal end of Mc. II. The distal articular surface is ‘D’-shaped, similar to *Andesaurus* (Mannion and Calvo, 2011).

Metacarpal II has a mildly convex, trapezoidal proximal articular surface, with long medial, dorsal, and lateral margins, and a short ventral margin (Fig. 3D–E). In dorsal view, the proximomedial corner of Mc. II extends medially, completely covering the proximal part of the dorsal surface of Mc. I. The dorsal, medial, and lateral surfaces all curve smoothly into one another along the proximal half of the shaft, whereas at midshaft the lateral and dorsal surfaces become slightly more distinct. There is a prominent, transversely convex ridge extending proximodistally along

the lateral half of the dorsal surface, with a concavity medial to this ridge; this concavity is bounded medially by a second, weaker ridge (Fig. 3B). Although the depth of this concavity is slightly accentuated by deformation, this morphology is a genuine feature. The distal end is mediolaterally wide and dorsoventrally narrow.

The proximal articular surface of metacarpal III is rugose and is mediolaterally convex towards the lateral margin and convex in all directions towards the ventral tip. This surface is sub-triangular in outline, with the apex projecting ventrally (Fig. 3D–E). A gentle, elongate ridge extends along the dorsal surface, a short distance from the proximal end. This begins close to the dorsomedial margin, but is deflected laterally along the shaft, fading out distally (Fig. 3B). The dorsal, lateral, and ventral surfaces of the shaft curve smoothly into one another, whereas the dorsal and medial surfaces form a sharp ridge at their point of convergence. A mild, proximodistally oriented ridge extends along the midline of the ventral surface. Along the distal third, close to the ventromedial margin, there is a small, proximodistally oriented, channel-like concavity along the ventral surface (Fig. 3C; see below). The distal end is incomplete medially, but seems to have been mediolaterally wide and dorsoventrally narrow, with the latter dimension decreasing medially (Huene 1929a:pl. 37, fig. 1a).

The proximal articular surface of metacarpal IV is much flatter than those of the other metacarpals, although it becomes rugose dorsolaterally. In proximal end view, Mc. IV has a sub-triangular outline, with the apex projecting ventrally (Fig. 3D–E). The dorsal surface is relatively flat throughout the length of the metacarpal, although it becomes convex towards the lateral and medial margins. The ventromedial corner of the proximal portion extends underneath the ventrolateral surface of Mc. III. A short distance from the proximal end, the ventromedial margin possesses a prominent roughened ridge, oriented proximodistally. The ventral surface is strongly concave mediolaterally along the proximal half; it then becomes mediolaterally convex at midshaft with a mediolaterally concave, proximodistally elongate channel along the distal half, bounded medially and laterally by ridges (Fig. 3C). A similar feature was noted on the dorsal surface of Mc. II and the ventral surface of Mc. III. It is not clear how widely distributed these ridge-bounded concavities are among sauropods: for example, a similar morphology is present along the distal two-thirds of the ventral surface of Mc. III in “*Brachiosaurus nougaredi*” (MNHN unnumbered; P.D.M., pers. observ., 2011), but is absent in the metacarpals of *Giraffatitan* and *Janenschia* (HMN MBR 2249 and 2093, respectively; P.D.M., pers. observ., 2011). As such, the presence of ridge-bounded concavities in metacarpals II–IV might be autapomorphic for *Argyrosaurus*, but for now we exclude this feature from our diagnosis. The distal end of the metacarpal expands prominently mediolaterally and a rugosity is situated on the dorsal surface, close to the distal end. A sharp, dorsomedial projection at the distal end overhangs a ventromedially facing surface into which the laterodistal corner of Mc. III fitted.

Metacarpal V has a mediolaterally convex, sub-triangular proximal articular surface. It extends further proximally than that of Mc. IV, which is ‘sunken’ in relation to the proximal surfaces of all other metacarpals (Fig. 3B–E). Mc. IV and V are only in contact along their proximal portions and very distal ends. The dorsal and lateral surfaces of Mc. V curve into one another. Near the very proximal end, these surfaces meet to form a prominent rugosity; medial to this rugosity, the dorsal surface is flatter and curves into the medial surface. The ventral surface (anteriorly facing in the articulated metacarpus) cannot be examined along the proximal half because of its articulation with Mc. IV and it is covered with matrix along its distal half. The shaft narrows along the middle third of the metacarpal and then expands distally. There is a dorsolateral flange of bone close to the distal end (Apesteguía, 2005) and the lateral surface beneath this is concave. A similar morphology occurs in *Andesaurus*

TABLE 4. Materials referred to *Argyrosaurus* by previous authors (Lydekker, 1893; Huene, 1929a, 1929b; Powell, 2003).

Specimen no.	Skeletal element	Reference	Taxonomic affinities
MLP 21	Left femur	Lydekker, 1893	Titanosauriformes indet.
MLP 22	2 posterior caudal vertebrae	Lydekker, 1893	Lithostrotia indet.
DGM (no.?)	Anterior caudal vertebra	Huene, 1929a	Lithostrotia indet.
MACN 5205	3 posterior caudal vertebrae	Huene, 1929a	Lithostrotia indet.
MLP 27	Right femur	Huene, 1929a	Titanosauriformes indet.
FMNH 13018	Right femur	Huene, 1929a	Titanosauria indet.
MACN 5017	Right humerus	Huene, 1929a	Titanosauria indet.
MACN (no.?)	Left humerus	Huene, 1929a	Titanosauria indet.
MMAB (no.?)	Humerus, radius and rib	Huene, 1929b	Sauropoda indet.
FMNH 13019–13020*	Right femur and left tibia	Powell, 2003	Titanosauria indet.
PVL 4628*	Partial skeleton	Powell, 2003	<i>Elaltitan lilloi</i>

Specimens marked with an asterisk were originally referred to *Antarctosaurus* (Huene, 1929a; Bonaparte and Gasparini, 1979) and later referred or considered comparable to *Argyrosaurus* (Powell, 2003).

(Apesteuguía, 2005; Mannion and Calvo, 2011). Additionally, there is a prominent dorsomedial flange; this increases in medial expansion distally and forms the main contribution to the transverse expansion of the distal end. At the very distal end, the metacarpal expands ventrolaterally and there is a small bulge on the midline of the dorsal surface. The distal end surface is rugose and convex.

TAXONOMIC STATUS OF MATERIALS REFERRED TO *ARGYROSAURUS*

Numerous remains from Argentina and Uruguay have been referred to *Argyrosaurus* by previous authors (Lydekker, 1893; Huene, 1929a, 1929b, 1931; Powell, 2003; see Introduction). Here we discuss each referral and determine its taxonomic status (see also Table 4).

Lydekker (1893:11) referred a left femur (MLP 21), discovered near the Río Senguerr (Chubut Province), to *Argyrosaurus*. He did not state why he considered this specimen attributable to *Argyrosaurus* but, regardless of his reasons, the lack of overlapping elements in the holotype precludes this assignment. The proximal end of the femur is missing and the distal end is poorly preserved. Based on the illustrations in Huene (1929a:pl. 38, fig. 1), the femur appears to have a lateral bulge just below the level of the proximal breakage. This prominence is a feature of titanosauriforms (Salgado et al., 1997) and consequently MLP 21 is considered an indeterminate member of that clade.

The centra of two middle–posterior caudal vertebrae (MLP 22) from Santa Cruz Province were also referred to *Argyrosaurus* by Lydekker (1893:11). Only one of these has been figured (Lydekker, 1893:pl. 4, fig. 5; Huene, 1929a:pl. 39, fig. 2). This centrum is strongly procoelous, with the posterior condyle forming a cone-like structure (Lydekker, 1893). According to Lydekker (1893), the ventral surface lacks excavations. Additionally, the base of the neural arch is situated on the anterior two-thirds of the centrum. No caudal vertebrae are known in the holotype of *Argyrosaurus*, precluding referral to that genus. Based on their strong procoely, MLP 22 is thus regarded as pertaining to an indeterminate lithostrotian.

Huene (1929a) referred an anterior caudal centrum (DGM [number unknown]) from the eastern shore of Lago Colhué Huapi (Chubut Province) to *Argyrosaurus*. The centrum is anteroposteriorly short and strongly procoelous. The base of a transverse process (caudal rib) is present on the anterodorsal corner of the lateral surface (Huene, 1929a:pl. 39, fig. 1). Little more can be said of this specimen, but its strong procoely indicates that it represents an indeterminate lithostrotian.

Three middle–posterior caudal centra (MACN 5205) from east of the Río Leona (Santa Cruz Province) were also referred to *Argyrosaurus* (Huene, 1929a). These are all procoelous and

the bases of the neural arches are situated anteriorly (Huene, 1929a:pl. 39, figs. 3–4). An anteroposteriorly elongate ridge extends along the lateral surface of two of the centra, situated approximately two-thirds of the way from the ventral margin, representing reduced transverse processes. Huene (1929a) also noted the presence of ventrolateral ridges and the absence of chevron facets. These features indicate that MACN 5205 belongs to an indeterminate lithostrotian.

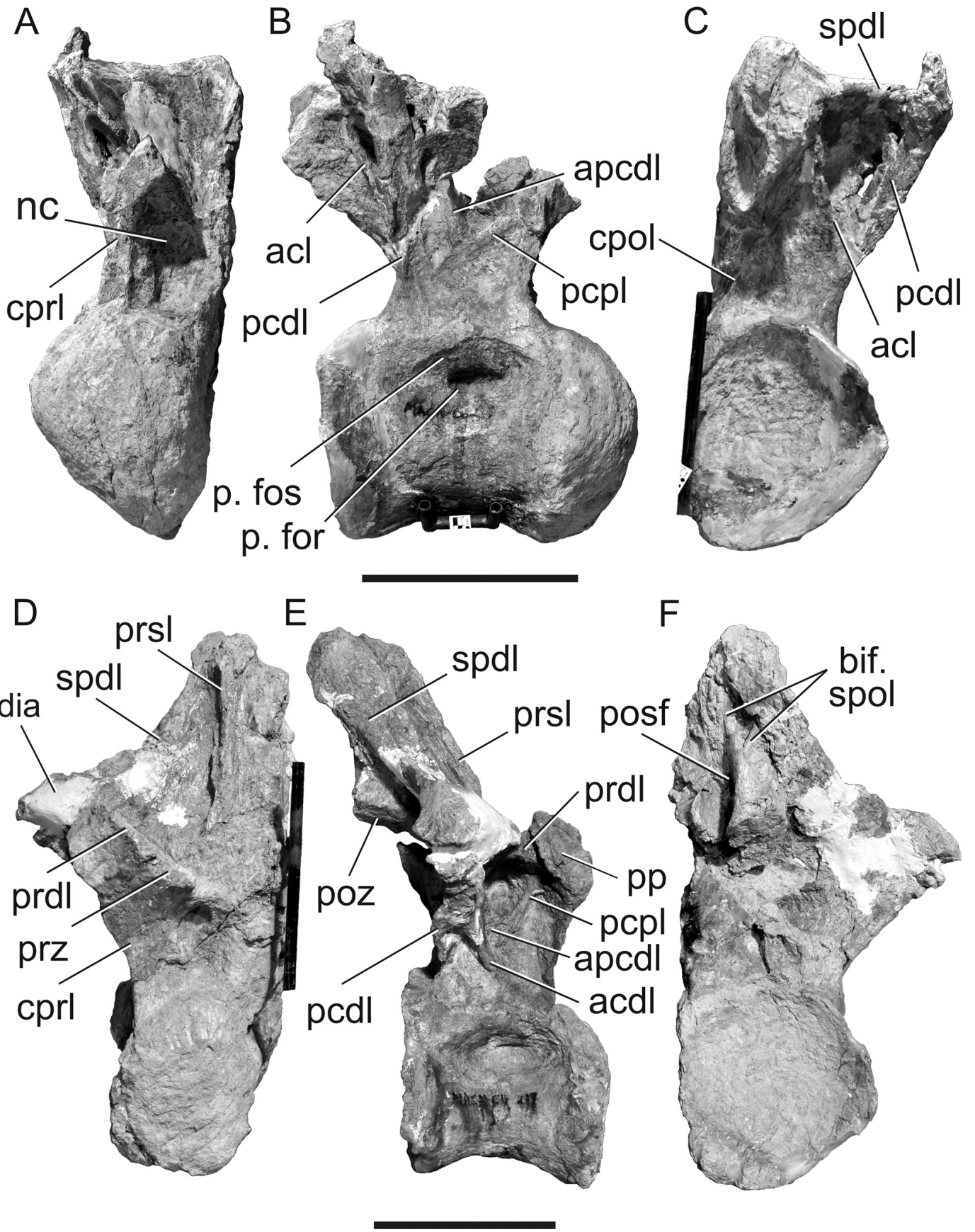
A right femur (MLP 27) found 2 km from the Southern Railway Bridge over the Río Neuquén (Neuquén Province) was referred to *Argyrosaurus* (Huene, 1929a). It is damaged proximally and distally and little information can be discerned from the illustrations in Huene (1929a:pl. 38, fig. 2), aside from the probable presence of a lateral bulge. Thus, we consider MLP 27 to represent an indeterminate titanosauriform.

A second right femur (FMNH 13018), discovered by an expedition of the Field Museum of Natural History in the Sierra de San Bernardo (Chubut Province), was also referred to *Argyrosaurus* (Huene, 1929a). This complete and well-preserved specimen is extremely long—just over 2 m—representing one of the largest known sauropod femora. The proximal third is strongly deflected medially, with a gentle lateral bulge just distal to the level of the proximal head. The distal articular surface is also strongly convex anteroposteriorly, curving up onto the anterior and posterior surfaces of the femur (P.D.M., pers. observ., 2008), a feature of derived titanosaurs (Wilson and Carrano, 1999; Wilson, 2002). As such, we regard FMNH 13018 as Titanosauria indet.

MACN 5017 is a small right humerus that Huene (1929a) thought was most probably collected from Neuquén Province and which he referred to *Argyrosaurus*. The specimen is missing the very proximal end and is also damaged distally (Huene, 1929a:pl. 37, fig. 6). It lacks the medial ridge present in the holotype of *Argyrosaurus* and so cannot be referred to that genus. The distal end of the deltopectoral crest expands medially and the supracondylar fossa appears to be prominent; thus, MACN 5017 represents an indeterminate titanosaur.

A left humerus (MACN [number unknown]) from the right bank of the Río Uruguay (Entre Ríos Province, Argentina) was also referred to *Argyrosaurus* (Huene, 1929a). This specimen is largely complete, apart from missing a portion of the shaft. As with MACN 5017, it lacks the autapomorphic medial ridge of the holotype and so cannot be referred to *Argyrosaurus*. The distal end of the deltopectoral crest expands medially and the proximolateral corner of the humerus is square in anterior view (Huene, 1929a:pl. 37, fig. 4). Consequently, we consider this specimen to represent an indeterminate titanosaur.

A complete right femur (FMNH 13019) and left tibia (FMNH 13020), also collected by the Field Museum of Natural History expedition in the Sierra de San Bernardo (Chubut Province;



see above), were originally referred to *Antarctosaurus* (Huene, 1929a). Powell (2003) subsequently described these elements as cf. *Argyrosaurus*. The femur is complete and well preserved, with a medially deflected proximal third and prominent lateral bulge (Powell, 2003:pl. 70, fig. 2). As with the larger specimen FMNH 13018, the distal articular surface curves up onto the anterior and posterior surfaces of the femur (P.D.M., pers. observ., 2008), indicating that the specimen belongs to an indeterminate titanosaur. The tibia has a mediolaterally expanded distal end (P.D.M., pers. observ., 2008), as is the case in most titanosauriforms (Salgado et al., 1997), with the exception of the autapomorphically sub-circular distal end of that of *Antarctosaurus* (Huene, 1929a:pl. 33, fig. 2), to which it clearly cannot be referred.

The distal end of a humerus, half of a radius, and a rib fragment (MMAB [number unknown]) were found close to the Río Lancha, southeast of Palmitas, Soriano Department, Uruguay, and were referred to *Argyrosaurus* (Huene, 1929b). The basis for this referral seems to be the large size of the humerus (Huene, 1929b); however, no illustrations or further information were provided, and pending restudy we consider these Uruguayan elements to represent indeterminate sauropods.

Lastly, Bonaparte and Gasparini (1979) briefly mentioned a partial skeleton from Chubut Province (collected by an expedition of the Fundación Miguel Lillo and the Universidad Nacional de Tucumán, led by J. F. Bonaparte) that they attributed to *Antarctosaurus*; subsequently, Powell (1986, 2003) tentatively referred the specimen to *Argyrosaurus*. This specimen does not share autapomorphies with either *Antarctosaurus* or *Argyrosaurus* and can be distinguished from all other sauropods; as such, it is described below as a new genus and species.

SYSTEMATIC PALEONTOLOGY

SAUROPODA Marsh, 1878

NEOSAUROPODA Bonaparte, 1986

TITANOSAURIFORMES Salgado, Coria, and Calvo, 1997

TITANOSAURIA Bonaparte and Coria, 1993

LITHOSTROTIA Upchurch, Barrett, and Dodson, 2004

ELALTITAN LILLOI, gen. et sp. nov.

(Figs. 4–8)

Antarctosaurus sp.: Bonaparte and Gasparini, 1979:402.

Argyrosaurus sp.: Powell, 1986.

Argyrosaurus superbus: Bonaparte, 1996:108–109, fig. 43.

cf. *Argyrosaurus*: Bonaparte, 1999a:165–167, fig. 35.

Argyrosaurus superbus?: Powell, 2003:50–53, pls. 67–70.

cf. *Argyrosaurus*: Bonaparte et al., 2006:369.

Argyrosaurus 'superbus': Apesteguía, 2007:542.

Etymology—*Elal* (ee-lal), the creator god of the Tehuelche people of Chubut Province; *titan*, giant in Greek mythology. Specific name in honor of Miguel Lillo, for his contribution and legacy to natural sciences in Tucumán.

Holotype—PVL 4628 and MACN-CH 217. Associated partial skeleton comprising three dorsal vertebrae, two caudal vertebrae, left scapula, left humerus, left radius, both ulnae, right pubis, proximal half of right femur, distal part of left tibia, distal two-thirds of left fibula, right astragalus, and calcaneum.

Diagnosis—*Elaltitan* can be diagnosed by a unique combination of character states, as well as one autapomorphy (marked by an asterisk): (1) spinopostzygapophyseal laminae in middle–posterior dorsal vertebrae bifurcate into medial and lateral branches; (2) dorsoventrally tall neural arch restricted to anterior half of centrum (excluding condylar ball) in anterior-most caudal vertebrae*; (3) astragalus ascending process does not extend to the posterior margin of the astragalus; (4) presence of a calcaneum. Other potentially unusual features, or characters with limited taxonomic scope, are commented upon in the text. Additionally, we place particular emphasis on highlighting features that distinguish *Elaltitan* from *Antarctosaurus* and *Argyrosaurus*, as well as other sauropods from the lower member of the Bajo Barreal Formation (i.e., *Drusilasaura* and *Epachthosaurus*).

Locality and Horizon—South (right) bank of the Río Senguerr, in the area between the bend of this river and the Pampa de María Santísima, southeast of the southernmost part of the Sierra de San Bernardo, Chubut Province, Argentina (Fig. 1) (Bonaparte and Gasparini, 1979; Powell, 2003); lower member of the Bajo Barreal Formation (Bonaparte, 1996; Bridge et al., 2000; Lamanna et al., 2002; Powell, 2003; Martínez et al., 2004); middle Cenomanian–Turonian (Archangelsky et al., 1994; Bridge et al., 2000; Lamanna et al., 2002). Bonaparte and Gasparini (1979) originally listed this specimen as having come from the Laguna Palacios Formation. However, this proposed provenance has been doubted by subsequent authors and, most significantly, the Laguna Palacios Formation does not crop out in this region (Bridge et al., 2000); therefore, the attribution of the specimen to the Bajo Barreal Formation seems secure.

Additional Comments—Although all of the material was originally accessioned as PVL 4628 (Bonaparte, 1996; Powell, 2003), the dorsal vertebrae and complete caudal vertebra were subsequently moved to the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” in Buenos Aires, where they were accessioned as MACN-CH 217 (see Bonaparte, 1999a; Bonaparte et al., 2006; Apesteguía, 2007). Two features previously described as autapomorphies of *Argyrosaurus* are based solely on PVL 4628/MACN-CH 217 (see above) and, as such, are discussed here. Novas (2009) considered the mild opisthocoely present in posterior dorsal vertebrae to be a local autapomorphy within derived titanosaurs (see also Powell, 2003), and Upchurch et al. (2004:310) listed “proximal caudal vertebrae with craniocaudally short and dorsoventrally tall neural arches” as autapomorphic for this specimen. The first of these proposed autapomorphies (Novas, 2009) is problematic, because one of the posterior dorsal vertebrae is mildly opisthocoelous, whereas the preceding dorsal vertebra retains relatively prominent opisthocoely; consequently, we reject this as a diagnostic feature. We include an amended version of the autapomorphy proposed by Upchurch et al. (2004) in our diagnosis of *Elaltitan*.

DESCRIPTION AND COMPARISONS

Dorsal Vertebrae

Three dorsal vertebrae (Dv) are preserved (Figs. 4–5), which Powell (2003) considered to correspond to Dv5, 9, and 10. Although we agree with this approximate numbering, their exact

← FIGURE 4. *Elaltitan lilloi*, gen. et sp. nov., middle–posterior dorsal vertebrae (MACN-CH 217). **A**, DvA in anterior view; **B**, DvA in right lateral view; **C**, DvA in posterior view; **D**, DvB in anterior view; **E**, DvB in right lateral view; **F**, DvB in posterior view. **Abbreviations:** **acdl**, anterior centrodiapophyseal lamina; **acl**, accessory lamina; **apcdl**, accessory posterior centrodiapophyseal lamina; **bif. spol**, bifurcated spinopostzygapophyseal lamina; **cpol**, centropostzygapophyseal lamina; **cpri**, centroprezygapophyseal lamina; **dia**, diapophysis; **nc**, neural canal; **pcdl**, posterior centrodiapophyseal lamina; **pcpl**, posterior centroparapophyseal lamina; **p. for**, pneumatic foramen; **p. fos**, pneumatic fossa; **posf**, postspinal fossa; **poz**, postzygapophysis; **pp**, parapophysis; **prdl**, prezygodiapophyseal lamina; **prsl**, prespinal lamina; **prz**, prezygapophysis; **spdl**, spinodiapophyseal lamina. Scale bars equal 250 mm.

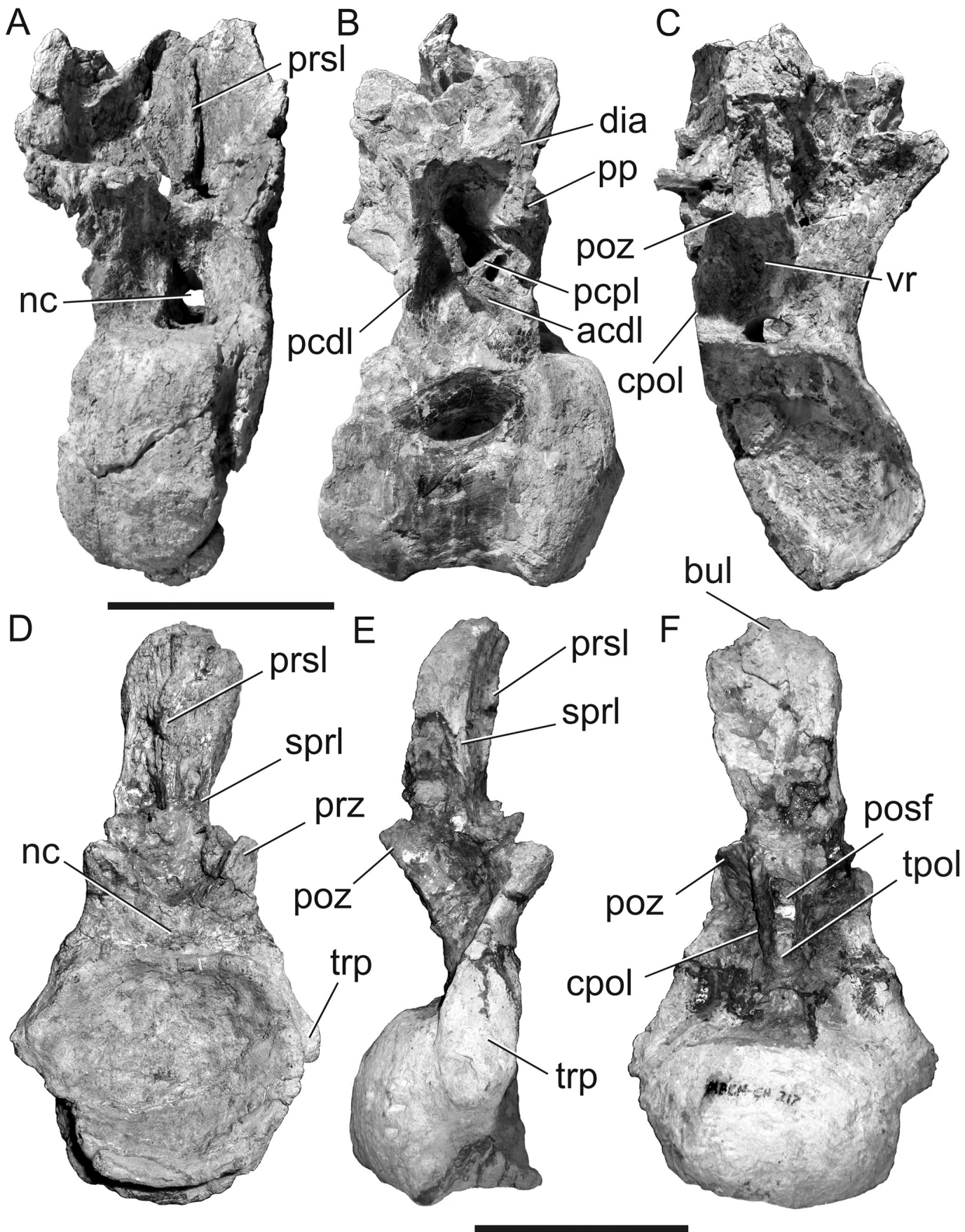


TABLE 5. Measurements of the dorsal (DvA–C) and caudal (Cd) vertebrae of *Elaltitan lilloi* (MACN-CH 217).

Dimension	DvA	DvB	DvC	Cd
Centrum length (excluding ball)	295	254	237	133
Centrum width	—	271*	—	315
Centrum height	~ 268	~ 273	~ 280	265
Neural arch height	153	203	—	~ 228
Total vertebra height	607*	749	634*	694

Centrum width and height is measured on the concave cotyle of the vertebra, i.e., the posterior surface of the dorsal centra and the anterior surface of the caudal centrum. Neural arch height is measured from the dorsal surface of the centrum up to the dorsal-most point of the postzygapophyseal articular surface. An asterisk denotes that a measurement is based on an incomplete element. All measurements are in millimeters.

positions in the dorsal sequence cannot be determined; as such we use DvA ('Dv5'), DvB ('Dv9'), and DvC ('Dv10') to refer to them in the following description. Description of vertebral laminae and fossae follow the nomenclature of Wilson (1999) and Wilson et al. (2011), respectively. Measurements are provided in Table 5.

DvA (Fig. 4A–C) possesses an anteroposteriorly elongate, opisthocoelous centrum. Although damaged anteriorly, the centrum of DvB (Fig. 4D–F) is only mildly opisthocoelous, with a much shallower posterior concavity than in DvA (Powell, 2003); in contrast, DvC (Fig. 5A–C) retains relatively prominent opisthocoely and a deep posterior cotyle. This is somewhat unusual and might suggest that DvC is actually anterior to DvB; however, although we do not outright reject this possibility, other aspects of the vertebrae suggest that Powell's (2003) sequence is correct (in particular the position of the diapophysis; see below). Novas (2009) proposed that mild opisthocoely in posterior dorsal vertebrae might represent a local autapomorphy of this specimen within derived titanosaurs; however, the variation between DvB and DvC makes this a problematic feature and so it is excluded from our amended diagnosis.

Ventral surfaces are arched dorsally and mediolaterally convex; they lack excavations or ridges. As in other titanosaurs (Salgado et al., 1997), the lateral pneumatic foramen in DvA is small and eye-shaped (Fig. 4B), with the long axis oriented anteroposteriorly. It is situated on the dorsal third of the centrum and positioned approximately centrally with regards to the long axis of the centrum (including the articular ball). The foramen is fairly shallow and does not ramify dorsally or ventrally. It is set within a lateral fossa, as in other titanosaurs (Bonaparte and Coria, 1993; Upchurch et al., 2004), that merges smoothly with the lateral surface of the centrum ventrally, but is separated dorsally from this surface by a dorsally arched ridge (Powell, 2003). In DvB, the foramen is much more elongate (Fig. 4E), but does not differ in other regards. The pneumatic foramen in DvC is also elongate (Fig. 5B), but differs from those of the other two dorsal vertebrae in that it is tilted, such that the long axis is anterodorsally oriented at approximately 20° to the horizontal.

The neural arch extends to the base of the anterior articular ball, but does not fully reach the posterior margin of the centrum. In DvA, the anterior opening of the neural canal is large

and subcircular (Fig. 4A), whereas the posterior opening is subtriangular, with the apex of this triangle pointing dorsally (Fig. 4C). DvB possesses the same anterior morphology (Fig. 4D) but the posterior surface is too poorly preserved to discern the shape of the neural canal (Fig. 4F). The neural canal of DvC is dorsoventrally elongate at its anterior end (Fig. 5A) but small and dorsoventrally flattened posteriorly (Fig. 5C).

The anterior centrodiapophyseal lamina (ACDL) is not clearly defined in DvA (Fig. 4B), but is a prominent, posterodorsally oriented lamina in posterior dorsal vertebrae (Figs. 4E, 5B). Elsewhere, this ACDL has been interpreted as a ventral bifurcation of the posterior centrodiapophyseal lamina (PCDL) (Bonaparte, 1999a; Bonaparte et al., 2006) or as a separate accessory lamina (Salgado et al., 2005) (see discussion in Wilson and Upchurch, 2009; Mannion and Calvo, 2011). In DvA, the PCDL is a near vertically oriented, plate-like structure (Fig. 4B), but it becomes more anterodorsally oriented in DvB–C (Figs. 4E, 5B). An anterodorsally oriented posterior centroparapophyseal lamina (PCPL) forms a sub-triangular prezygapophyseal parapodiapophyseal fossa (PRPADF) (the 'postparapophyseal fossa' of Bonaparte, 1999a) with the PCDL in DvA (Fig. 4B); this PRPADF is roofed by an approximately horizontal, albeit partly broken, prezygodiapophyseal lamina (PRDL). A PRPADF is present in the middle–posterior dorsal vertebrae of most somphospondyls, as well as *Diplodocus* (Mannion and Calvo, 2011), and is subdivided in *Elaltitan* by a posterodorsally oriented accessory lamina. This accessory lamina seems most similar to the 'accessory posterior centrodiapophyseal lamina' described in the dorsal vertebrae of the Argentinean titanosaur *Barrosasaurus* (Salgado and Coria, 2009:fig. 4b). The development of the ACDL in posterior dorsal vertebrae creates a small, sub-triangular centrodiapophyseal fossa (CDF) ('infradiapophyseal' cavity of Bonaparte, 1999a) between the ACDL and PCDL (Figs. 4E, 5B); this feature is also present in several other titanosaurs, e.g., *Argentinosaurus* (Bonaparte and Coria, 1993:fig. 5a; MCF-PVPH-1 [P.D.M., pers. observ., 2009]), *Neuquensaurus* (Salgado et al., 2005:fig. 3), and *Paludititan* (Csiki et al., 2010:fig. 2). In the posterior dorsal vertebrae of *Elaltitan*, a shallow prezygapophyseal centrodiapophyseal fossa (PRCDF) is present between the ACDL, CPRL, and PRDL (Figs. 4E, 5B). Towards the dorsal tip of this PRCDF in DvB, a 'V'-shaped structure is formed (Powell, 2003) by the posterodorsally inclined accessory lamina and PCPL, with a deeper sub-triangular coel present between the branches of this 'V' (Fig. 4E). In DvC, the accessory lamina is absent but the posterodorsal branch of the 'V'-shaped structure is instead formed by the ACDL (Fig. 5B). The PRCDF is present in most somphospondyls (Salgado et al., 1997; Bonaparte, 1999a), but the 'V'-shaped structure is restricted to only a few derived titanosaurs, i.e., *Barrosasaurus* (Salgado and Coria, 2009), *Neuquensaurus* (Salgado et al., 2005:figs. 3–4), *Rocasaurus* (Salgado and Azpilicueta, 2000:fig. 5), and *Saltasaurus* (Powell, 2003:pls. 26–27). The lateral surface, anteroventral to the PCPL, is shallowly concave in DvA and DvB, but forms a prominent coel in DvC (Fig. 5B).

The PRDL is a prominent, though partly broken, plate-like structure in DvA (Fig. 4B), but is reduced and anteroposteriorly shortened in the posterior dorsal vertebrae (Figs. 4E, 5B). Prezygapophyseal articular surfaces are flat and face predominantly

← FIGURE 5. *Elaltitan lilloi*, gen. et sp. nov., posterior dorsal and anterior caudal vertebrae (MACN-CH 217). **A**, DvC in anterior view; **B**, DvC in right lateral view; **C**, DvC in posterior view; **D**, anterior caudal vertebra in anterior view; **E**, anterior caudal vertebra in right lateral view; **F**, anterior caudal vertebra in posterior view. **Abbreviations:** **acdl**, anterior centrodiapophyseal lamina; **bul**, bulge; **cpol**, centropostzygapophyseal lamina; **dia**, diapophysis; **nc**, neural canal; **pcdl**, posterior centrodiapophyseal lamina; **pcpl**, posterior centroparapophyseal lamina; **posf**, postspinal fossa; **poz**, postzygapophysis; **pp**, parapophysis; **prsl**, prespinal lamina; **prz**, prezygapophysis; **spri**, spinoprezygapophyseal lamina; **tpol**, intrapostzygapophyseal lamina; **trp**, transverse process; **vr**, vertical ridge. Scale bars equal 250 mm.

medially in DvA, facing more dorsomedially in posterior dorsal vertebrae. The parapophysis is situated on the lateral wall of the prezygapophysis and is supported from below by a centroprezygapophyseal (CPRL) (or anterior centroparapophyseal lamina [ACPL]). There is some evidence to suggest that the CPRL bifurcates ventrally in DvA (Fig. 4A), but the preservation in this region is poor; the CPRL is plate-like and definitely does not bifurcate in DvB or DvC (Figs. 4D, 5A). The postzygapophyses are not well preserved in DvA, but in DvB–C their flat articular surfaces face ventrolaterally and slightly posteriorly. Dorsomedially oriented centropostzygapophyseal laminae (CPOLs) support the postzygapophyses from below (Figs. 4C, F, 5C). A transversely thin ridge extends ventrally from the midline of the postzygapophyses to the dorsal margin of the neural canal in DvC (Fig. 5C); the relevant region is too poorly preserved on DvB to determine the presence or absence of this ridge. Similar ridges are present throughout the dorsal series of *Rapetosaurus* and in the anterior dorsal vertebrae of *Malawisaurus* (Curry Rogers, 2009). There is no evidence for a postzygodiapophyseal lamina (PODL) in any of the dorsal vertebrae and this structure seems to be genuinely absent. A PODL is present in the dorsal vertebrae of nearly all sauropods (Wilson, 1999), including most titanosaurs (e.g., *Andesaurus* [Mannion and Calvo, 2011], *Drusilasaura* [Navarrete et al., 2011], *Neuquensaurus* [Salgado et al., 2005], and *Rapetosaurus* [Curry Rogers, 2009]), but is lost in several derived titanosaurs, e.g., *Ampelosaurus*, *Lirainosaurus*, *Muyelensaurus*, *Opisthocoelicaudia*, and *Paludititan* (Salgado et al., 1997; Sanz et al., 1999; Calvo et al., 2008; Csiki et al., 2010).

An extremely deep sub-triangular postzygapophyseal centrodiaepophyseal fossa (POCDF), with the apex of this triangle pointing ventrally, is present on the posterior face of DvA (Fig. 4C). This is demarcated laterally by the PCDL and dorsally by the spinodiapophyseal lamina (SPDL). It is bounded ventromedially by an additional prominent lamina that meets the PCDL ventrally. Dorsally, this accessory lamina meets the ventral side of the medial end of the SPDL. It also contributes to the formation of another coel medially, which itself is bounded medially by the CPOL. This region is poorly preserved in DvB, but an undivided POCDF, lacking the accessory lamina, is present between the PCDL and CPOL in DvC (Fig. 5C). The presence of this POCDF is typical of most eusauropods (i.e., taxa with a CPOL, PCDL, and SPDL; Upchurch, 1998; Wilson and Sereno, 1998; Wilson, 1999), whereas the accessory lamina appears to be unique to *Elaltitan*; however, it is not proposed here as an autapomorphy of this taxon because it is present in only one dorsal vertebra and can only be observed on the right side. Bilateral asymmetry is common in titanosaur dorsal vertebrae (e.g., Santucci and Bertini, 2006a; Casal and Ibiricu, 2010) and thus this feature is of doubtful use as a diagnostic character.

The diapophysis is only fully preserved in DvB and it projects laterally, dorsally, and slightly posteriorly (Fig. 4D–F). The SPDL is almost horizontal throughout much of its preserved length on DvA (Fig. 4C), although it curves upwards as it meets the spine. In contrast, the SPDL is steeply inclined posterodorsally on DvB (Fig. 4D–F). On DvC, the preserved base of the diapophysis is much more anteriorly positioned, such that it is almost directly dorsal to the prezygapophysis/parapophysis (Fig. 5B); this is also the case in the posterior-most dorsal vertebrae of several other derived titanosaurs (i.e., *Opisthocoelicaudia*, *Rapetosaurus*, *Saltasaurus*, and *Trigonosaurus*; Upchurch, 1998; Powell, 2003; Campos et al., 2005; Curry Rogers, 2005, 2009) and provides strong evidence to support the placement of DvC as posterior to DvB in the dorsal sequence (see above).

Only DvB preserves a relatively complete neural spine. The spine is sub-triangular in anterior view, with the apex pointing dorsally (Fig. 4D). A similar spinal morphology is present in the middle–posterior dorsal vertebrae of *Barrosasaurus* (Sal-

gado and Coria, 2009), *Muyelensaurus* (Calvo et al., 2008), *Paludititan* (Csiki et al., 2010), *Rapetosaurus* (Curry Rogers, 2009), and *Trigonosaurus* (Powell, 2003:pl. 15, fig. 5b). All three neural spines of *Elaltitan* project posterodorsally and a thickened, rugose prespinal lamina ascends the midline of most of the preserved length of each spine (Figs. 4D, 5A); the remaining anterior surface of the neural spine appears to be relatively featureless. A spinopostzygapophyseal (postspinal) fossa (SPOF) is present and the spinopostzygapophyseal lamina (SPOL) bifurcates into medial and lateral branches (Fig. 4F). Bifurcation of the SPOL in middle–posterior dorsal vertebrae is the plesiomorphic condition in most eusauropods, but each SPOL becomes a singular structure in titanosaurs (Wilson, 1999, 2002; Curry Rogers, 2005), with the exception of *Opisthocoelicaudia* (Borsuk-Bialynicka, 1977:fig. 2). As such, the presence of a bifurcated SPOL is considered a local autapomorphy of *Elaltitan*. The region dorsal to this is poorly preserved and few anatomical features can be discerned.

Caudal Vertebrae

Two anterior caudal vertebrae are preserved, although the anterior-most (apparently the first caudal vertebra) "... is so poorly preserved it is impossible to be sure whether or not it is biconvex" (Powell, 2003:51). The remaining caudal vertebra (Fig. 5D–F) is relatively complete and probably represents the second or third in the series (Powell, 2003). The following description is thus based entirely on this element.

The centrum is strongly procoelous, as in other lithostrotians (Upchurch et al., 2004), and is anteroposteriorly short (Fig. 5D–F; see Table 5). There are no ridges or excavations on the ventral surface and the lateral surface lacks openings. At its posterior end, the neural canal is a small, dorsoventrally compressed semicircle; the anterior opening is partly concealed by crushing, but was probably similar in size and shape. The anteroposteriorly short neural arch is restricted to the anterior half of the centrum (excluding the posterior convexity) and is dorsoventrally tall (Fig. 5E). This morphology is unusual in two ways. First, in comparison to the anterior caudal vertebrae of other sauropods with an anteriorly positioned neural arch, the anterior bias in *Elaltitan* is considerably more marked: only in middle caudal vertebrae does the same degree of anterior bias occur in other titanosauriforms (Upchurch, 1995, 1998; Salgado et al., 1997). Thus, we consider this an autapomorphy of *Elaltitan*. Second, most sauropod caudal vertebrae have dorsoventrally low neural arches (defined as the region between the dorsal surface of the centrum and the most dorsal point of the postzygapophyseal articular surface), whereas the arch of *Elaltitan* is only slightly shorter than the centrum height (Table 5). Only *Drusilasaura* (Navarrete et al., 2011; see below) and *Saltasaurus* (Powell, 2003:pl. 33) have a comparable morphology, although the anterior-most caudal vertebrae of *Mamenchisaurus youngi* (Ouyang and Ye, 2001) and *Mendozasaurus* (González Riga, 2003) also possess dorsoventrally elongate neural arches.

Transverse processes (caudal ribs) are situated on the dorsal half of the centrum and extend dorsally on to the neural arch (Fig. 5D–F). Although incomplete distally, they project laterally and slightly posteriorly. The transverse processes are dorsoventrally tall at their bases, but rapidly taper distally. Dorsally, they curve smoothly up onto the prezygapophyses, although this is not a well-defined PRDL. The prezygapophyses project anteriorly, strongly dorsally, and slightly laterally, but extend only a short distance beyond the anterior margin of the centrum (Fig. 5D–E). Their ventral surfaces are flat whereas their articular surfaces are transversely convex. The postzygapophyses are partly reconstructed but their articular surfaces are preserved and are transversely concave and dorsoventrally flat (Fig. 5F). The articular zygapophyseal surfaces of caudal vertebrae

of most other sauropods are flat (Wilson, 2002), with the exception of a concavo-convex articulation in a number of titanosaurs (e.g., *Alamosaurus* [M. D'Emic, pers. comm., 2011], *Epachthosaurus* [Martínez et al., 2004:fig. 7], and *Mendozasaurus* [González Riga, 2003:160]) and the diplodocines *Barosaurus* and *Diplodocus* (Wilson, 2002; Whitlock, 2011).

A dorsoventrally elongate spinopostzygapophyseal fossa is present between and ventral to the midline of the postzygapophyses (Fig. 5F). It is divided approximately one-third of the way up by a weak horizontal ridge. This ridge may be autapomorphic for *Elaltitan*, but we exclude this feature from our diagnosis because of the poor preservation of the postspinal region. Ventral to the level of the postzygapophyseal articular surfaces, the postspinal fossa is bounded by what appear to be prominent, near vertical CPOLs that meet ventrally to form a transversely short, 'U'-shaped intrapostzygapophyseal lamina (Fig. 5F). In other sauropods, the CPOLs are greatly reduced in caudal vertebrae, with the postzygapophyses approaching the dorsal margin of the neural canal (Wilson, 1999). However, it is difficult to distinguish where the postzygapophyses end and the CPOLs begin because of damage and restoration. Although the presence of elongate CPOLs may be a genuine feature of *Elaltitan*, it seems more likely that the upper portions of these structures are instead ventrally elongate postzygapophyses, comparable to the morphology observed in the anterior caudal vertebrae of *Neuquensaurus* (Salgado et al., 2005:fig. 6b).

It is clear that the neural spine has been broken off and then reattached; as such, its slightly anterior projection is most probably an artifact and it instead projected primarily dorsally, as in most sauropods, and differing from the posterodorsally oriented anterior caudal neural spines of saltasaurines such as *Neuquensaurus* (Salgado et al., 2005). The neural spine is approximately subrectangular in anterior view (Fig. 5D), with a prominent central bulge on the dorsal surface, near the posterior margin (Fig. 5F); this spinal morphology is similar to those of *Neuquensaurus* (Salgado et al., 2005:fig. 6a–b) and *Alamosaurus* (Gilmore, 1946:pl. 8; USNM 15560 [P.D.M., pers. observ., 2008]). Plate-like, vertical spinoprezygapophyseal laminae (SPRLs) are present, along with a midline prespinal rugosity (Fig. 5D–E). Between the prespinal lamina and each SPRL, the ventral half of the spine is excavated by a dorsoventrally elongate coel (Fig. 5D). Comparable coels are present in *Neuquensaurus*, although they do not extend as far laterally in that taxon. The posterior surface of the neural spine is too poorly preserved to determine the presence of laminae, although there is a small strut of bone that may be part of a SPOL.

Scapula

The left scapula (Fig. 6A–B) will be described with the blade oriented horizontally. Measurements are provided in Table 6. It is complete except for the distal portion of the dorsal margin of the scapular blade. It As a consequence of its fragility and stored position, it cannot be photographed in its entirety (but see Powell, 2003:pl. 67, fig. 5). The coracoid articular surface forms an angle of approximately 50° with the long axis of the scapular blade (Fig. 6A), a feature of derived titanosaurs (Wilson, 2002). The acromial (proximal) plate mediolaterally thickens towards the glenoid region, which lacks the rounded shape seen in *Neuquensaurus* (Otero, 2010). The anterodorsal portion of the lateral surface of the acromial plate is concave and bounded posteriorly by a stout, prominent acromial ridge (Fig. 6A–B). This ridge slopes posterodorsally at an angle of approximately 75° to the long axis of the scapular blade, differing from the near vertical acromial ridge of *Antarctosaurus* (Powell, 2003). As a consequence of its prominence, the area posterior to the acromial ridge is concave. There is no rugose 'shelf' such as that seen along the dorsal margin of the acromial plate of some specimens of *Neuquensaurus* (Otero, 2010) and *Saltasaurus* (PVL 4017; A.O., pers. observ.,

TABLE 6. Measurements of the pectoral and forelimb elements of *Elaltitan lilloi* (PVL 4628).

Element	Dimension	Measurement
Scapula	Length	1490
	Maximum dorsoventral height of acromial plate	915
	Minimum dorsoventral height of scapular blade	286
	Maximum dorsoventral height of scapular blade	415*
Humerus	Length	1300
	Mediolateral width of proximal end	510
	Anteroposterior width of proximal end (measured on lateral margin)	73
	Anteroposterior width of proximal end (measured on medial margin)	130
	Distance from proximal end to distal end of deltopectoral crest	585
	Mediolateral width at midshaft	245
	Anteroposterior width at midshaft	124
	Mediolateral width of distal end	~ 445
	Anteroposterior width of distal end (measured on radial condyle)	200
Anteroposterior width of distal end (measured on ulnar condyle)	275	
Radius	Length	730
	Mediolateral width of proximal end	230
	Anteroposterior width of proximal end	170
	Mediolateral width of distal end	140
	Anteroposterior width of distal end	205
Ulna	Length	827/880
	Mediolateral width of proximal end	370/340
	Anteroposterior width of proximal end	295/~250
	Mediolateral width of midshaft	154/153
	Anteroposterior width of midshaft	146/~160
	Anteroposterior width of distal end	200/200

An asterisk denotes that a measurement is based on an incomplete element. For the left and right ulnae, measurements are given for the left element first. All measurements are in millimeters.

2011). A sub-triangular process is present at the posteroventral corner of the acromial plate, although this is slightly deflected medially and thus partially obscured in lateral view (Fig. 6A–B). A similar process is present in a number of basal titanosauriforms (e.g., *Angolatitan* [Mateus et al., 2011], *Chubutisaurus* [Carballido et al., 2011], *Daxiatitan* [You et al., 2008], some specimens of *Giraffatitan* [Janensch, 1961:pl. 15], and *Ligabuesaurus* [Bonaparte et al., 2006]), as well as the derived titanosaurs *Alamosaurus*, *Mendozasaurus* (D'Emic et al., 2011), and *Paralititan* (Smith et al., 2001:1704), but tends to be absent in most other derived titanosaurs (e.g., *Antarctosaurus* [Huene, 1929a:pl. 31, fig. 1] and *Saltasaurus* [Powell, 2003:pl. 37]).

The proximal half of the scapular blade has a 'D'-shaped cross-section, with a dorsoventrally convex lateral surface. Along the distal half, the lateral surface is relatively flat. The scapular blade expands along both its dorsal and ventral margins towards the distal end (Fig. 6A). Although the dorsal margin is incomplete, the angle at which it expands is similar to that of the ventral expansion, suggesting that the scapular blade may have had a symmetrical distal end. There is a large degree of variation in the amount of scapular blade expansion among sauropods, as well as within more exclusive clades (Mannion, 2009). For example, within Titanosauria, *Neuquensaurus* lacks any ventral expansion (Salgado et al., 2005:fig. 7f; Otero, 2010:fig. 2), and there is little dorsal or ventral expansion in the scapular blade of *Rapetosaurus* (Curry Rogers, 2009). The distal end of the blade appears to have a rounded profile in lateral view (Fig. 6A), differing from the straighter margins seen in taxa such as *Rapetosaurus* (Curry Rogers, 2009:fig. 32).

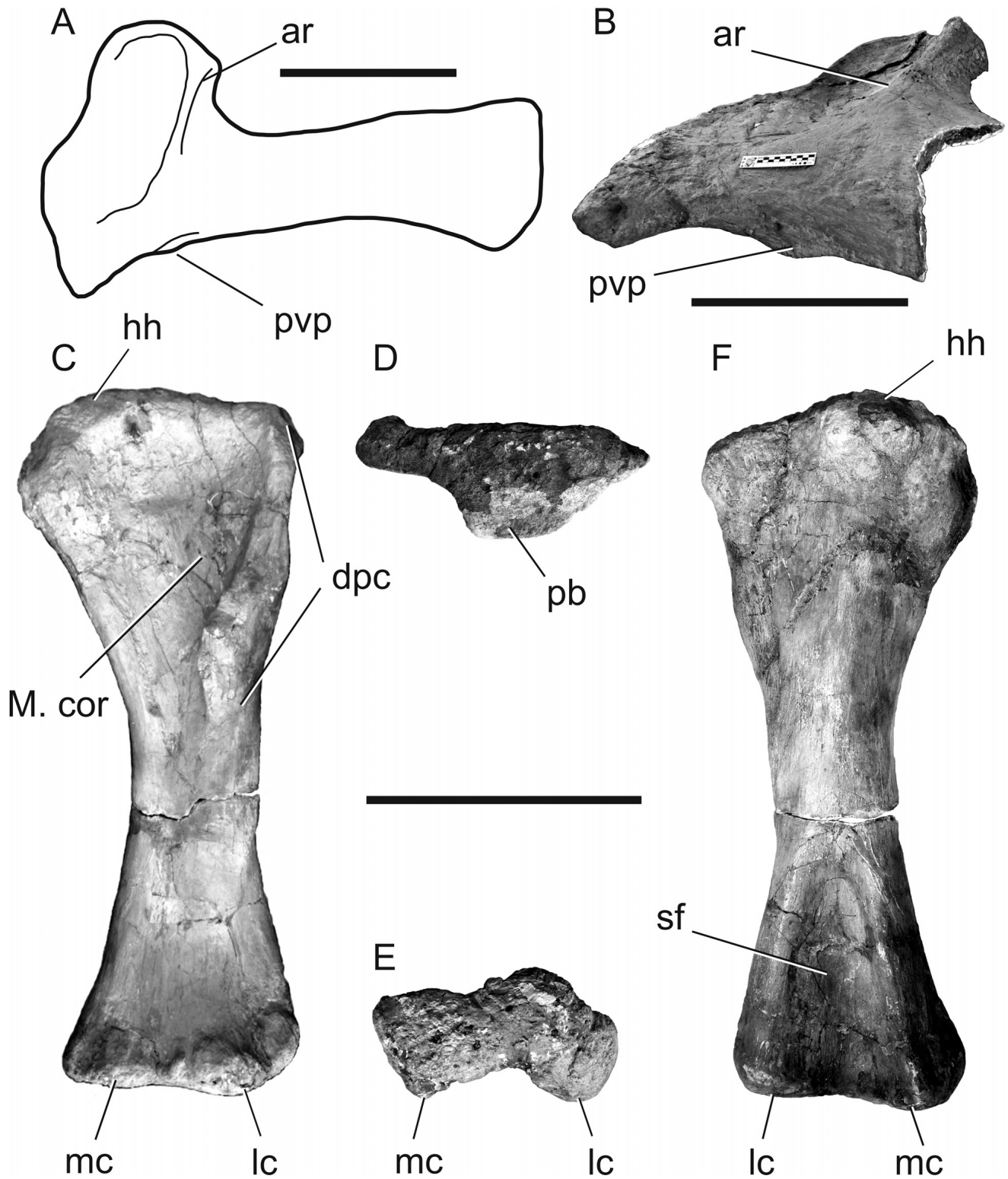


FIGURE 6. *Elaltitan lilloi*, gen. et sp. nov., pectoral and forelimb elements (PVL 4628). **A**, line drawing of left scapula in lateral view (after Powell, 2003:pl. 69, fig. 5); **B**, scapular acromial plate in ventrolateral view; **C**, left humerus in anterior view; **D**, left humerus in proximal end view (anterior surface at top); **E**, left humerus in distal end view (anterior surface at top); **F**, left humerus in posterior view. **Abbreviations:** **ar**, acromial ridge; **dpc**, deltopectoral crest; **hh**, humeral head; **lc**, lateral condyle; **mc**, medial condyle; **M. cor**, tuberosity for attachment of *M. coracobrachialis*; **pb**, posterior bulge of the humeral head; **pvp**, posteroventral process; **sf**, supracondylar fossa. Scale bar equals 500 mm in **A** and **C–F**, and 300 mm in **B**.

Humerus

The complete left humerus (Fig. 6C–F) (see Table 6 for measurements) has a sub-triangular outline in proximal end view. The proximal and lateral margins of the humerus meet at a near right angle (a titanosaur feature; see description of *Argyrosaurus* humerus above), and the lateral margin of the entire humerus is only very mildly concave in anterior view (Fig. 6C). In contrast, the medial margin is strongly concave. There is no anteromedial ridge such as that described in *Argyrosaurus*. The deltopectoral crest extends for approximately 45% of the length of the humerus. Towards its distal end it expands, extending over the medial half of the anterior surface (Fig. 6C). This morphology is present in three other titanosauriforms (*Ligabuesaurus*, *Opisthocoeleicaudia*, and *Petrobrasaurus*; see description of *Argyrosaurus* humerus above), but is absent in both *Argyrosaurus* and *Antarctosaurus* (Huene, 1929a:pl. 32, fig. 1). The posterolateral surface of the deltopectoral crest possesses a prominent muscle scar for the *M. latissimus dorsi*, a feature of several derived titanosaurs (Otero, 2010). Medial to the deltopectoral crest, the anterior surface of the proximal end is gently concave mediolaterally and displays a prominent, bulge-like tuberosity (Fig. 6C) for attachment of the *M. coracobrachialis* (Powell, 2003). Similar muscle attachment sites are present in some other titanosaur humeri, e.g., *Gondwanatitan* (Kellner and de Azevedo, 1999) and *Saltasaurus* (Powell, 2003:pl. 40), but the distribution of this feature is variable: for example, at least some specimens referred to *Neuquensaurus* lack this tuberosity (Otero, 2010:fig. 3).

The posterior surface of the proximal two-thirds of the humerus is mediolaterally convex and there is a prominent posterior bulge at the proximal end (the humeral head), although this does not extend distally as a ridge (Fig. 6D, F). At midshaft, the humerus has a transverse to anteroposterior width ratio of just under 2.0 (Table 6): this is comparable to the high end spectrum of titanosaurs, but is considerably lower than that of *Argyrosaurus* (see above). The anterior surface of the distal third is gently concave mediolaterally, whereas on the posterior surface there is a deep fossa between two prominent supracondylar ridges (Fig. 6C, F), as is the case in most other titanosaurs (Upchurch et al., 2004). As a consequence of the degree of torsion of the distal half, the lateral surface of the distal end faces posterolaterally. The undivided distal articular surface is mildly convex anteroposteriorly, but does not extend up onto the anterior or posterior surfaces of the humerus (Fig. 6E–F).

Radius

The right radius (Fig. 7A–D) is missing the posteromedial corner of the proximal end, but is otherwise relatively complete (see Table 6 for measurements). It is a relatively stout element (proximal end transverse width to radius length ratio = 0.32), with mediolaterally expanded proximal and distal ends. In anterior view, the lateral margin of the radius is strongly concave, whereas the medial margin is relatively straight (Fig. 7A–B). Although incomplete, the proximal end has a medial projection, which is also anteroposteriorly narrower than the remainder of the proximal end (Fig. 7C). The proximal articular surface is flat to mildly concave. The anterior surface of the radius is mediolaterally convex, whereas the posterior surface is predominantly flat. Along the distal two-thirds, the anterior surface has a rugose and pitted surface, which may be pathological; this also seems to continue on to the posterolateral surface (Fig. 7A–B). A posterolateral interosseous ridge is present along the distal quarter of the radius, for articulation with the anteromedial surface of the distal end of the ulna (Fig. 7B).

The distal end of the radius is mediolaterally expanded in comparison to the shaft (ratio of 1.7; see Table 6, Fig. 7A–B); this expansion is greater than in *Argyrosaurus* and is comparable to other sauropods, although it is lower than in most other ti-

tanosaurs (Wilson, 2002; Curry Rogers, 2005). The distal articular surface is convex, with a sub-rectangular outline (Fig. 7D), differing from the sub-triangular distal end of the radius of *Argyrosaurus* (Fig. 2E). Although the medial half of the distal surface is relatively flat in posterior view, the lateral half is beveled at an angle greater than 20° to the long axis of the radius (Fig. 7A–B), as in other titanosaurs (Wilson, 2002).

Ulna

Both ulnae are preserved, although the proximal processes of the right ulna are damaged (see Table 6 for measurements). As such, the following description is based on the complete left ulna (Fig. 7E–H). It is a stout element, with a proximal end transverse width to ulna length ratio of 0.45, comparable to that of titanosaurs such as *Saltasaurus* (Powell, 2003:pl. 41), and differing from the more gracile morphology seen in *Argyrosaurus* (ratio = 0.34). The proximal end is triradiate, and the anteromedial process is much longer than the anterolateral process (Fig. 7E); in *Argyrosaurus*, in contrast, the proximal processes are equidimensional. A prominent olecranon process projects above the proximal articular surface (Powell, 2003), and the proximal articular surface of the anteromedial process has a concave profile in anterior view (Fig. 7G), as in other titanosaurs (Upchurch, 1995; Wilson and Sereno, 1998).

The area between the two proximal anterior processes is mediolaterally concave for reception of the radius and possesses a proximodistally elongate, moderately rugose ridge. A similar ridge has been described in *Neuquensaurus* and was suggested to correspond to the attachment site for the *M. pronator quadratus* (Otero, 2010). Both proximal anterior processes extend distally for most of the length of the ulna as ridges. The posterior proximal process also extends distally along the posterolateral surface as a rounded ridge, fading out slightly distal to midshaft, with the surfaces medial and lateral to this ridge transversely concave. At the distal end, the anteromedial surface is gently concave for articulation with the radius. The distal end expands posteriorly and has an anteroposteriorly convex, ‘D’-shaped, or sub-rectangular distal articular surface (Fig. 7F).

Pubis

The right pubis (Fig. 7I) is largely complete, missing only a small amount of material from the posterior margin of the distal blade. It is still partly encased in its field jacket; consequently, the lateral surface cannot be observed. Measurements are provided in Table 7. The iliac articular surface is anteroposteriorly elongate and mediolaterally compressed (ratio = 2.4), a morphology that appears to be restricted to titanosaurs (Mannion and Calvo, 2011). The length of the ischiadic articulation is slightly greater than 40% of the total pubis length, comparable to the condition in most other macronarians (Salgado et al., 1997; Wilson and Sereno, 1998). As is the case in many other titanosauriforms (Mannion and Calvo, 2011), the fully enclosed obturator foramen has an oval shape and its long axis is oriented in approximately the same plane as that of the pubis (Fig. 7I). The medial surface of the pubis is largely featureless, with an anteroposteriorly convex proximal half that becomes concave towards the ischiadic plate, and a flat distal blade. There is a small degree of anteroposterior expansion of the blade at its distal end, but this condition does not approach the prominent ‘boot-like’ anterior projection seen in some other titanosauriforms, e.g., *Giraffatitan* (Janensch, 1961:Beilage G, fig. 2) and *Tastavinsaurus* (Canudo et al., 2008).

Femur

Only the proximal half of the right femur (Fig. 8A) is preserved (see Table 7 for measurements). The femoral head is deflected

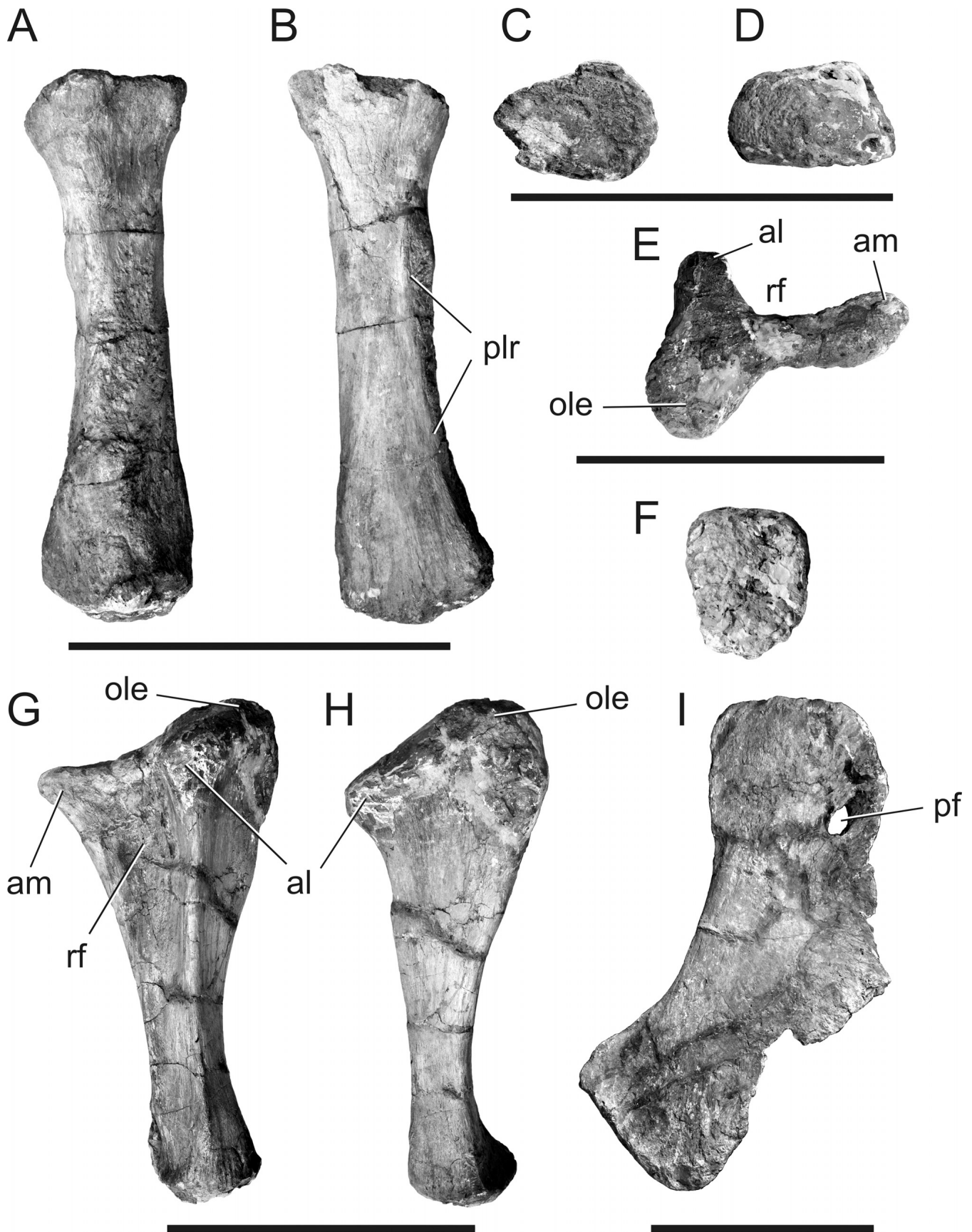


FIGURE 7. *Elalitan lilloi*, gen. et sp. nov., forelimb and pelvic elements (PVL 4628). **A**, right radius in anterior view; **B**, right radius in posterior view; **C**, right radius in proximal end view (anterior surface at top); **D**, right radius in distal end view (anterior surface at top); **E**, left ulna in proximal end view; **F**, left ulna in distal end view (anterior surface at top); **G**, left ulna in anterior view; **H**, left ulna in lateral view; **I**, right pubis in medial view. **Abbreviations:** **al**, anterolateral process; **am**, anteromedial process; **ole**, olecranon process; **pf**, pubic foramen; **plr**, posterolateral ridge; **rf**, radial fossa. Scale bars equal 500 mm.

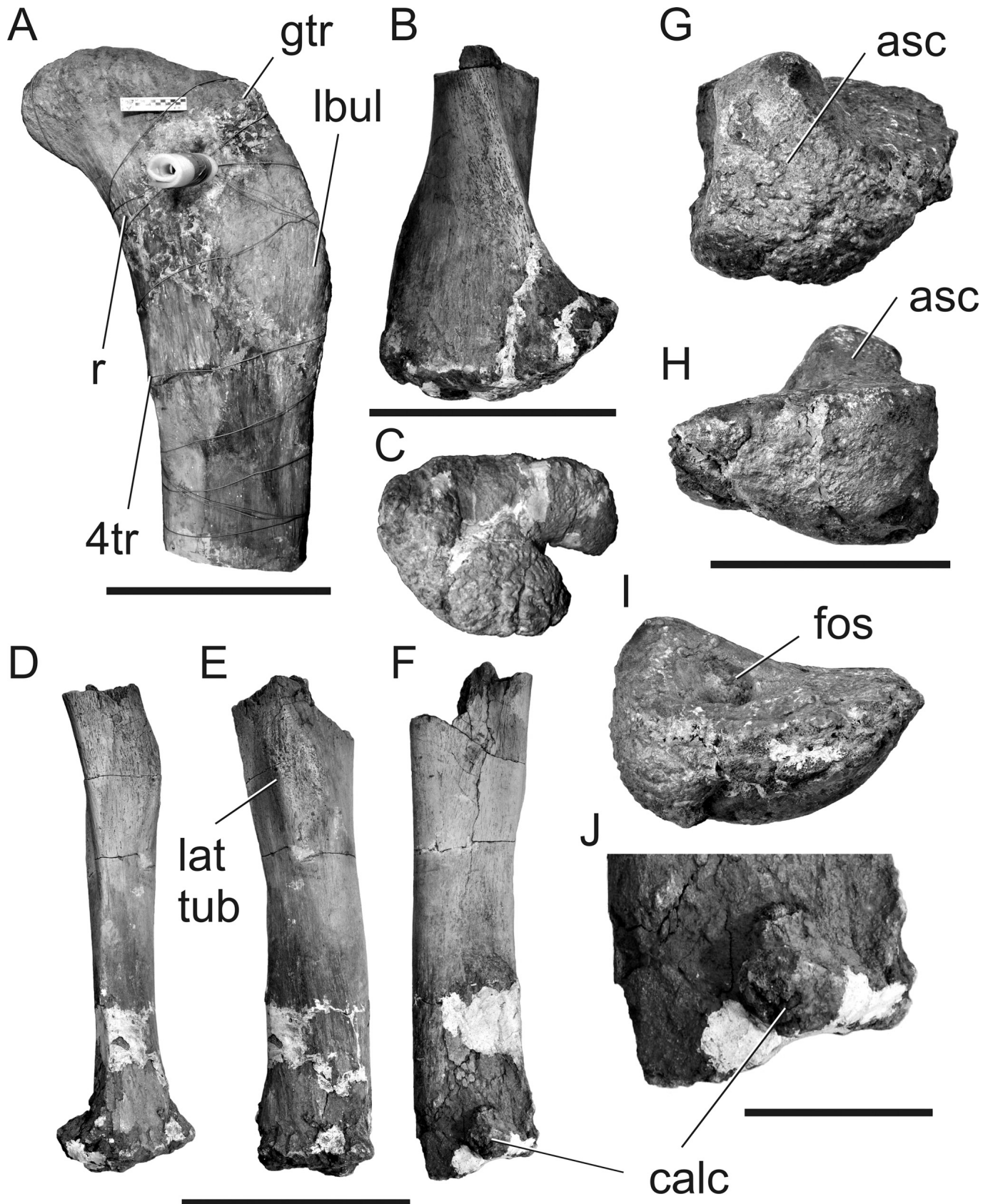


FIGURE 8. *Elaltitan lilloi*, gen. et sp. nov., hind limb elements (PVL 4628). **A**, right femur in posterior view; **B**, left tibia (distal portion) in anterior view; **C**, left tibia (distal portion) in distal end view (anterior surface at top); **D**, left fibula in anterior view; **E**, left fibula in lateral view; **F**, left fibula in medial view; **G**, right astragalus in anterior view; **H**, right astragalus in posterior view; **I**, right astragalus in medial view; **J**, calcaneum (adhered to medial surface of fibula) in distal end view. **Abbreviations:** **4tr**, fourth trochanter; **asc**, ascending process; **calc**, calcaneum; **f**, fossa; **gtr**, greater trochanter; **lat tub**, lateral tuberosity; **lbul**, lateral bulge; **r**, ridge. Scale bar equals 500 mm in **A**, 300 mm in **B–F**, 200 mm in **G–I**, and 100 mm in **J**.

TABLE 7. Measurements of pelvic and hind limb elements of *Elaltitan lilloi* (PVL 4628).

Element	Dimension	Measurement
Pubis	Length	1130
	Anteroposterior length of iliac articular surface	358
	Mediolateral width of iliac articular surface	151
	Dorsoventral height of ischiadic articular surface	500
	Straight line anteroposterior length of acetabular region	175
	Maximum anteroposterior width of distal blade	440
	Long axis of pubic foramen	103
	Width of pubic foramen perpendicular to long axis	48
Femur	Length	1150*
	Maximum mediolateral width of proximal end	530
	Maximum anteroposterior width of proximal end	250
	Mediolateral width at midshaft	317
Tibia	Anteroposterior width at midshaft	180
	Mediolateral width at midshaft	182
	Anteroposterior width at midshaft	147
	Mediolateral width of distal end	293
Fibula	Anteroposterior width of distal end	230
	Length	650*
	Mediolateral width at midshaft	97
	Anteroposterior width at midshaft	123
	Mediolateral width of distal end	145
Astragalus	Anteroposterior width of distal end	141
	Mediolateral width	222*
	Anteroposterior width	178
	Dorsoventral height	155
Calcaneum	Mediolateral width	71
	Anteroposterior width	59

An asterisk denotes that a measurement is based on an incomplete element. All measurements are in millimeters.

dorsomedially with respect to the greater trochanter. Along with the presence of a prominent lateral bulge (Fig. 8A), this femoral morphology is typical of titanosauriforms (Salgado et al., 1997). Muscle scars are also present on the surface of the lateral bulge. A vertical crest on the posterior surface, close to the medial margin (Fig. 8A), extends from the proximal end to approximately one-third of the preserved length of the femur. The fourth trochanter is situated on the posteromedial margin and is greatly reduced (Fig. 8A) (Powell, 2003), although it possesses distinctive scars for insertion of the *M. caudofemoralis pars longus* and *brevis* (Borsuk-Bialynicka, 1977; Otero and Vizcaíno, 2008). At the broken distal end (approximately at midshaft, based on comparisons with complete titanosaur femora), the femur has an anteroposteriorly compressed cross-section (transverse to anteroposterior width ratio = 1.8), although this compression is not as extreme as that seen in many derived titanosaurs, e.g., *Neuquensaurus* and *Saltasaurus* (Wilson, 2002). Based on comparisons with the morphologically similar femur of “*Antarctosaurus giganteus*,” which Huene (1929a) measured as 2310 mm in length, the complete femur of *Elaltitan* would be approximately the same size, making it one of the largest known sauropods ever to have existed.

Tibia

The distal end of the left tibia (Fig. 8B–C) is preserved (see Table 7 for measurements). Its flat anterior surface has a triangular shape (Fig. 8B), as is typical for sauropods (Upchurch et al., 2004). The distal end is mediolaterally expanded and anteroposteriorly compressed (Fig. 8C), as in most other titanosauriforms

(Salgado et al., 1997), although differing from that of *Antarctosaurus* (see above description of remains previously attributed to *Argyrosaurus*). The distal articular surface is mediolaterally convex, with this particularly marked towards the lateral margin, such that the distal surface of the lateral malleolus faces lateroventrally.

Fibula

The distal two-thirds of a left fibula are preserved (Fig. 8D–F). It lacks the strong curvature seen in taxa such as *Antarctosaurus* (Huene, 1929a:pl. 33, fig. 3) and *Neuquensaurus* (Salgado et al., 2005:fig. 7). The lateral surface is transversely convex, whereas the medial surface is transversely concave (Powell, 2003). Although the fibula is thickest anteroposteriorly along the shaft, it is only gently compressed mediolaterally. The anterior margin forms a prominent rounded ridge that becomes sharper distally (Fig. 8D). The lateral tuberosity is a well-developed, rugose, oval muscle scar (for attachment of the *M. iliofibularis*; Otero and Vizcaíno, 2008) that is divided into two proximodistally elongate ridges, either side of a gentle concavity (Fig. 8E). This bifurcated morphology is a feature traditionally thought to be restricted to derived titanosaurs (e.g., *Antarctosaurus*, *Opisthocoelicaudia*, and *Saltasaurus*; Powell, 1992; Upchurch, 1998), but is present in a wider array of titanosauriforms, including *Giraffatitan* (HMN MBR 2698 [St 149]; P.D.M., pers. observ., 2011), *Gobititan* (IVPP V12579; P.D.M. and P. Upchurch, pers. observ., 2007), and *Tastavinsaurus* (Canudo et al., 2008). The distal end is poorly preserved, but expands mediolaterally, and the distal articular surface appears to be mediolaterally convex.

Astragalus

The right astragalus (Fig. 8G–I) is almost complete, missing only a small part of its medial tip (Powell, 2003). It is a relatively small element, resembling the pyramidal shape of astragali of derived titanosaurs such as *Neuquensaurus* and *Opisthocoelicaudia* (Wilson, 2002). As in all sauropods (Wilson and Sereno, 1998), no fossae or foramina are present on the anterior surface. The distal surface is poorly preserved but is strongly convex both mediolaterally (particularly towards the medial margin) and anteroposteriorly. In anterior view, the ascending process is trapezoidal, with a sub-rectangular outline in proximal view. Unusually for a neosauropod (Wilson and Sereno, 1998), the ascending process does not extend to the posterior margin of the astragalus (Fig. 8G–H), a feature that we regard as a local autapomorphy of *Elaltitan*. The lateral surface of the ascending process is gently concave both anteroposteriorly and mediolaterally for reception of the fibula. It lacks any distinct laterally directed ventral shelf or lip, as is also absent in a number of other titanosauriforms, including *Euhelopus* (Wilson and Upchurch, 2009). Medial to the ascending process is a large oval fossa (Fig. 8I), and the remainder of the proximal surface of the medial half of the astragalus is relatively flat and rugose. Towards the medial edge, proximodistal thickness decreases and the astragalus narrows anteroposteriorly, although the latter reduction is entirely related to the anterior margin: the posterior margin of the astragalus is straight in proximal view.

Calcaneum

A small, oval to sub-circular element is adhered to the medial surface of the distal end of the fibula (Fig. 8F, J). It seems probable that this is a displaced calcaneum, with only its distal surface visible. It is similar in morphology to a calcaneum referred to *Neuquensaurus* (Huene, 1929a:pl. 17, fig. 2), with a convex distal surface that forms a distinct sub-triangular facet towards one end (Fig. 8J). In other regards, it is largely similar in size and morphology to the calcanea of basal titanosauriforms such as

Euhelopus (Wilson and Upchurch, 2009). If this element is correctly identified, then *Elaltitan* is the first example of a titanosaur skeleton to preserve an associated calcaneum (the putative titanosaur *Gobititan* [You et al., 2003] lacks clear titanosaur synapomorphies; P.D.M. and P. Upchurch pers. observ., 2007), and indicates that, in at least some titanosaurs, absence of this element may be purely artifactual.

DISCUSSION

Comparisons with Other Titanosaurs from the Lower Member of the Bajo Barreal Formation

As well as *Elaltitan lilloi*, two additional titanosaur genera have been named from the lower member of the Bajo Barreal Formation. Below, we provide more detailed comparisons with *Drusilasaura deseadensis* (Navarrete et al., 2011) and *Epachthosaurus sciuttoii* (Powell, 1990; Martínez et al., 2004).

Drusilasaura deseadensis—*Drusilasaura* is known from a poorly preserved individual, comprising dorsal and caudal vertebrae, as well as a scapula (Navarrete et al., 2011). Although both taxa preserve dorsal vertebrae, it is difficult to fully compare these elements, because only an anterior dorsal vertebra of *Drusilasaura* is preserved well enough to be described and figured, whereas *Elaltitan* only preserves middle–posterior dorsal vertebrae, and anatomical features are not always consistent along the vertebral column (e.g., Wilson, 1999; Upchurch et al., 2004; Haluza et al., 2012). However, some potentially meaningful differences can be noted. As mentioned above, the dorsal vertebrae of *Elaltitan* lack a postzygodiapophyseal lamina (PODL), whereas this is present in *Drusilasaura*. The PODL is present throughout the dorsal sequence in almost all sauropods that possess this lamina, including derived titanosaurs such as *Rapetosaurus* (Curry Rogers, 2009), or appears only in posterior dorsal vertebrae (e.g., *Trigonosaurus*; Campos et al., 2005), whereas there are no known examples in which the PODL disappears posteriorly along the sequence. *Elaltitan* also lacks the two autapomorphies of the dorsal vertebrae of *Drusilasaura* listed by Navarrete et al. (2011; presence of an anterior and posterior spinodiapophyseal lamina either side of a supradiapophyseal cavity, and presence of a circumneural lamina surrounding the posterior neural canal), although we recognize that these features may be restricted to the anterior dorsal vertebrae.

The anterior caudal vertebra of *Drusilasaura* (described as a posterior sacral vertebra by Navarrete et al., 2011) shows some general similarities with the comparable element in *Elaltitan*. Both have dorsoventrally tall neural arches, although the ratio between centrum height and neural arch height is lower in *Elaltitan* (1.16) than in *Drusilasaura* (1.36). Notable differences include the position of the neural arch with respect to the centrum: in *Elaltitan* the arch is restricted to the anterior half of the centrum, whereas in *Drusilasaura* the arch occupies almost the entire dorsal surface of the centrum. Additionally, the centrum of *Elaltitan* is strongly procoelous, whereas the comparable element in *Drusilasaura* displays only mild procoely. Lateroventral ridges bound a longitudinal depression (which is further pierced by two large foramina) on the ventral surface of the caudal centra of *Drusilasaura*, whereas the ventral surface of the comparable element of *Elaltitan* lacks excavations or ridges (as noted in the above description). The anterior caudal transverse processes also differ between the two taxa: although in both species the transverse processes are formed by a dorsal and ventral bar (Galina and Otero, 2009), *Elaltitan* presents a poorly developed bony bar contacting both dorsal and ventral structures, whereas *Drusilasaura* displays a well developed bony bar (the ‘prezygapophyseal tuberosity’ of Navarrete et al., 2011). Navarrete et al. (2011) proposed two autapomorphies of the caudal vertebrae of *Drusilasaura* relating to the prespinal and postspinal lamina, in which these two structures expand transversely up the neural spine;

however, in *Elaltitan*, the prespinal lamina remains narrow along its length (Fig. 5D), and the postspinal lamina is not preserved.

The morphology of the acromial plate of the scapula differs between the two taxa: whereas the coracoid articular surface forms an angle of approximately 50° with the long axis of the scapular blade in *Elaltitan* (Fig. 6A), this angle is close to 90° in *Drusilasaura*. Other differences are subtle; for example, the posterior margin of the acromial process is concave in *Elaltitan* but straight in *Drusilasaura*. Further comparison between the morphology of the acromial plates is not possible because of poor preservation along the dorsal and ventral margins. Both scapula blades have a comparable distal end morphology and there is some evidence to suggest that the sub-triangular process described on the posteroventral corner of the acromial plate of the *Elaltitan* scapula is also present in that of *Drusilasaura* too (Navarrete et al., 2011:fig. 7); however, the preservation of the scapula in this region of the latter taxon is too poor to be certain that this is a genuine feature and, as noted above, the distribution of this feature within Titanosauriformes is more widespread.

In conclusion, we consider *Elaltitan* to be distinct from *Drusilasaura*, with numerous anatomical differences noted in the dorsal and caudal vertebrae, as well as in the scapula. Several of these features found in *Elaltitan* seem to only be otherwise present in derived titanosaurs, i.e., the absence of a PODL in dorsal vertebrae, prominent procoely in anterior caudal vertebrae, and the posterodorsal orientation of the coracoid articular surface of the scapula (see also below). The presence of these features in *Elaltitan*, and their absence in *Drusilasaura*, suggests that despite some gross overall similarities, the two taxa may not be particularly closely related.

Epachthosaurus sciuttoii—The type individual of *Epachthosaurus* is poorly preserved (Powell, 1990); however, a referred partial skeleton (Martínez et al., 2004) preserves nearly all anatomically overlapping elements for comparison with *Elaltitan*, and additional material was described by Casal and Ibiricu (2010). Anatomical differences between *Elaltitan* and *Epachthosaurus* are much clearer than with *Drusilasaura* (see also Martínez et al., 2004:117), and below we outline some of the main features that differentiate the two taxa.

Middle–posterior dorsal and anterior caudal vertebrae of *Epachthosaurus* possess hyposphene-hypantrum articulations (Martínez et al., 2004), whereas these are absent in those of *Elaltitan*. The lateral pneumatic foramina of the dorsal vertebrae of *Epachthosaurus* are deep, leaving a thin midline septum (Martínez et al., 2004), contrasting with the shallow foramina observed in *Elaltitan*. Postzygodiapophyseal laminae (PODLs) are present on the dorsal vertebrae of *Epachthosaurus*, whereas these structures are absent in those of *Elaltitan*. The dorsal vertebrae of *Epachthosaurus* also lack the bifurcated spinopostzygapophyseal laminae (SPOLs) noted in *Elaltitan*, and the latter taxon has proportionally much taller dorsal and caudal neural arches and spines (Martínez et al., 2004). The anterior caudal neural spines of *Epachthosaurus* project posterodorsally at approximately 45° to the horizontal, whereas the caudal neural spine of *Elaltitan* projects vertically.

Notable differences can also be observed in the appendicular elements. The humeral deltopectoral crest of *Epachthosaurus* only extends a short distance medially, differing from the prominent medial expansion seen in that of *Elaltitan*. The radius of *Epachthosaurus* has a much greater distal end to midshaft transverse width ratio (2.4) than that of *Elaltitan* (1.7), whereas the latter taxon has a stouter ulna. The ascending process of the astragalus of *Epachthosaurus* extends to the posterior margin, differing from the plesiomorphic condition seen in that of *Elaltitan*. Lastly, there is no evidence for the presence of an ossified calcaneum in *Epachthosaurus*. These features, and numerous others, indicate that *Elaltitan* and *Epachthosaurus* represent distinct taxa.

Phylogenetic Affinities of *Argyrosaurus* and *Elaltitan*

The preceding descriptions have demonstrated numerous differences between the holotype of *Argyrosaurus superbis* and the previously referred specimen PVL 4628/MACN-CH 217, here designated the holotype of the new taxon *Elaltitan lilloi*. *Elaltitan* has also been demonstrated to be distinct from *Antarctosaurus* (see also Powell, 2003), to which the holotypic specimen was originally referred (Bonaparte and Gasparini, 1979), and to the spatiotemporally contemporaneous taxa *Drusilasaura* and *Epachthosaurus*. Both *Argyrosaurus* and *Elaltitan* possess a number of autapomorphies and unusual features that are absent in overlapping elements of the other genus, confirming their taxonomic distinction. Furthermore, *Elaltitan* possesses a suite of characters that indicate a derived position within Titanosauria, including the absence of postzygodiapophyseal laminae in dorsal vertebrae; diapophyses positioned dorsal to the prezygapophyses/parapophyses in posterior dorsal vertebrae; middle–posterior dorsal neural spines that are sub-triangular in anterior view; strongly procoelous anterior caudal centra; and the presence of a prominent muscle scar on the posterolateral surface of the humeral deltopectoral crest. Conversely, the tarsus of *Elaltitan* displays some plesiomorphic features, in terms of the antero-posteriorly short ascending process of the astragalus, and the presence of a calcaneum. Although *Argyrosaurus* displays some

derived titanosaur features (e.g., the distal articular surface of the humerus extends onto the anterior surface of the element), it predominantly possesses characters that are present in basal (plesiomorphic) titanosaurs as well. Moreover, *Argyrosaurus* possesses two characters that hint at a relatively basal position within Titanosauria. First, evidence from Lydekker (1893) and Huene (1929a) indicates that *Argyrosaurus* possesses carpal bones, which are unknown in all other titanosaurs. Secondly, the longest metacarpals are Mc. II and III, a feature *Argyrosaurus* shares with the putative basal titanosaur *Janenschia*.

Additional support for the generic separation of *Argyrosaurus* and *Elaltitan* comes from recent stratigraphic revision of the Bajo Barreal Formation. *Elaltitan* comes from the lower member of the formation in the area of the Río Senguerr, which is dated as middle Cenomanian–Turonian (Archangelsky et al., 1994; Bridge et al., 2000; Lamanna et al., 2002), whereas *Argyrosaurus* is probably from the upper member in the area of the Río Chico, tentatively dated as Campanian–?Maastrichtian (Casal et al., 2007).

Currently, the largest titanosaur phylogenetic data matrix (Curry Rogers, 2005) samples less than 50% of all putative titanosaur genera (Mannion and Upchurch, 2011; Mannion et al., 2011) and provides little topological resolution (Mannion, 2011). Only through the development of new data matrices can the interrelationships of titanosaurs such as *Argyrosaurus* and *Elaltitan*

TABLE 8. List of valid South American Cretaceous titanosauriform genera (only type species listed), along with their geographical and stratigraphical ranges.

Taxon	Country	Age	Reference
<i>Adamantisaurus mezzalirai</i>	Brazil	Turonian–Maastrichtian	Santucci and Bertini, 2006b
<i>Aeolosaurus rionegrinus</i>	Argentina	late Campanian–early Maastrichtian	Powell, 1987
<i>Agustinia ligabuei</i>	Argentina	Aptian–Albian	Bonaparte, 1999b
<i>Amargatitanis macni</i>	Argentina	Barremian	Apesteguía, 2007
<i>Andesaurus delgadoi</i>	Argentina	early Cenomanian	Calvo and Bonaparte, 1991
<i>Antarctosaurus wichmannianus</i>	Argentina	early–middle Campanian	Huene, 1929a
<i>Argentinosaurus huinculensis</i>	Argentina	late Cenomanian	Bonaparte and Coria, 1993
<i>Argyrosaurus superbis</i>	Argentina	Campanian–?Maastrichtian	Lydekker, 1893
<i>Atacamatitan chilensis</i>	Chile	Cenomanian–Maastrichtian	Kellner et al., 2011
<i>Barrosasaurus casamiquelai</i>	Argentina	early–middle Campanian	Salgado and Coria, 2009
<i>Baurutitan britoi</i>	Brazil	Maastrichtian	Kellner et al., 2005
<i>Bonatitan reigi</i>	Argentina	late Campanian–?Maastrichtian	Martinelli and Forasiepi, 2004
<i>Bonitasaura salgadoi</i>	Argentina	Santonian	Apesteguía, 2004b
<i>Chubutisaurus insignis</i>	Argentina	Aptian–Cenomanian	del Corro, 1975
<i>Drusilasaura deseadensis</i>	Argentina	late Cenomanian–Turonian	Navarrete et al., 2011
<i>Elaltitan lilloi</i>	Argentina	middle Cenomanian–Turonian	This study
<i>Epachthosaurus sciuttoii</i>	Argentina	late Cenomanian–early Turonian	Powell, 1990
<i>Fuataognosaurus dukei</i>	Argentina	late Turonian–early Coniacian	Calvo et al., 2007
<i>Gondwanatitan faustoi</i>	Brazil	Turonian–Maastrichtian	Kellner and de Azevedo, 1999
<i>Laplataosaurus araukanicus</i>	Argentina	early–middle Campanian	Huene, 1929a
<i>Ligabuesaurus leanzai</i>	Argentina	late Aptian–Albian	Bonaparte et al., 2006
<i>Malarguesaurus florenciae</i>	Argentina	late Turonian–early Coniacian	González Riga et al., 2009
<i>Maxakalisaurus topai</i>	Brazil	Turonian–Maastrichtian	Kellner et al., 2006
<i>Mendozasaurus neguyelap</i>	Argentina	late Turonian–Coniacian	González Riga, 2003
<i>Muyelensaurus pecheni</i>	Argentina	late Coniacian–Santonian	Calvo et al., 2008
<i>Narambuenatitan palomoi</i>	Argentina	early–middle Campanian	Filippi et al., 2011a
<i>Neuquensaurus australis</i>	Argentina	Santonian–Maastrichtian	Powell, 1992
<i>Panamericansaurus schroederi</i>	Argentina	late Campanian–?Maastrichtian	Calvo and Porfiri, 2010
<i>Pellegrinisaurus powelli</i>	Argentina	early–middle Campanian	Salgado, 1996
<i>Petrobrasaurus puestohermandezi</i>	Argentina	late Coniacian–early Santonian	Filippi et al., 2011b
<i>Pitekunsaurus macayai</i>	Argentina	early–middle Campanian	Filippi and Garrido, 2008
<i>Puertasaurus reuili</i>	Argentina	Cenomanian–early Maastrichtian	Novas et al., 2005
<i>Rinconsaurus caudamirus</i>	Argentina	early–middle Campanian	Calvo and González Riga, 2003
<i>Rocasaurus muniozi</i>	Argentina	late Campanian–early Maastrichtian	Salgado and Azpilicueta, 2000
<i>Saltasaurus loricatus</i>	Argentina	late Campanian–Maastrichtian?	Bonaparte and Powell, 1980
<i>Tapuiasaurus macedoi</i>	Brazil	Aptian	Zaher et al., 2011
<i>Traukutitan eocaudata</i>	Argentina	Santonian	Juárez Valieri and Calvo, 2011
<i>Trigonosaurus pricei</i>	Brazil	Maastrichtian	Campos et al., 2005
<i>Uberabatitan ribeiroi</i>	Brazil	Maastrichtian	Salgado and Carvalho, 2008

Information based on Mannion et al. (2011) and Mannion and Calvo (2011), with updated stratigraphical data from Leanza et al. (2004), Garrido (2010), and O’Gorman and Varela (2010). As a result of the lack of consensus for the age of the Adamantina Formation (e.g., Gobbo-Rodrigues et al., 1999; Dias-Brito et al., 2001; Santucci and Bertini, 2006b), we present the full proposed stratigraphic range (i.e., Turonian–Maastrichtian).

be fully explored; however, this is beyond the scope of the current work.

The Subfamily *Argyrosaurinae*

Powell (1986) named *Argyrosaurinae* as a new subfamily in his doctoral thesis, and it is unclear when the name was first formally published. Powell (1986) listed a number of purportedly diagnostic features (robust limb bones; dorsoventrally tall dorsal and anterior caudal vertebrae with anteroposteriorly short centra bearing small lateral foramina; dorsal and caudal neural spines taller and apically wider than in other derived titanosaurs; pubis with wide, flat anterodorsal lamina, without distal widening), but all are poorly defined (Bonaparte, 1996) and more widespread among titanosauriforms or more inclusive sauropod clades. Powell (1986) also did not provide a definition for *Argyrosaurinae*. Furthermore, the taxon for which Powell (1986) erected this subfamily (i.e., *Argyrosaurus*) has here been shown to represent two genera, and there is little evidence to suggest that these genera are closely related. *Argyrosaurinae* has been rarely used in the literature (Bonaparte and Coria, 1993; Bonaparte, 1996) and has little use as a monotypic subfamily; as such, we recommend disuse of *Argyrosaurinae* pending the discovery of taxa that form a monophyletic clade with *Argyrosaurus*.

Diversity of South American Cretaceous Titanosauriforms

Following the revision of *Argyrosaurus* and erection of the new genus *Elaltitan*, there are currently 39 Cretaceous South American titanosauriform genera considered to be valid (Table 8). The majority of these are from Argentina (31), with the remaining taxa known from Brazil (7) and Chile (1). Indeterminate titanosauriform body fossils and trackways also extend the South American titanosauriform record into the Cretaceous of Uruguay (e.g., Huene, 1929b, 1931; Powell, 2003; Soto et al., 2012), Peru (Powell, 2003), and Bolivia (Lockley et al., 2002).

South American Cretaceous titanosauriforms span a time interval of approximately 65 million years, from the Barremian through the Maastrichtian inclusive (Table 8), with many of the most recent discoveries filling gaps in previously poorly sampled time intervals (e.g., the Coniacian–Santonian). A wide array of titanosauriforms is represented, including basal forms lying outside Titanosauria (e.g., *Chubutisaurus* and *Ligabuesaurus*), basal titanosaurs (e.g., *Andesaurus*), putative nemegtosaurids (e.g., *Tapuiasaurus*), and saltasaurids (e.g., *Neuquensaurus* and *Saltasaurus*). Most of these 39 taxa have been named in the last decade, reflecting both the exponential growth of South American dinosaur paleontology, but also partly the lack of time for taxonomic revision. It seems probable that some taxa will be shown to be synonymous or non-diagnostic following restudy and/or the discovery of more complete individuals. Nevertheless, it is clear that the Cretaceous terrestrial ecosystems of South America were richly diverse and abundant in dinosaurs, particularly titanosauriform sauropods (Salgado and Bonaparte, 2007; Novas, 2009).

CONCLUSIONS

The poorly known Argentinean titanosaur *Argyrosaurus superbus* has been demonstrated to be a valid genus, based on five autapomorphies as well as a unique character combination. This genus is restricted to the holotypic specimen, with most previously referred material regarded as that of indeterminate titanosauriforms. One exception is a partial skeleton that is demonstrably distinct from *Argyrosaurus* and herein named *Elaltitan lilloi*. This taxon is diagnosed by one autapomorphy as well as an unusual combination of features, and was approximately spatiotemporally contemporaneous with two other titanosaurs, *Drusilasaura* and *Epachthosaurus*. There is some evidence to suggest that *Argyrosaurus* represents a basal titanosaur,

whereas *Elaltitan* is included within the derived clade Lithostrotia. The position of both taxa requires further investigation through new phylogenetic analyses exploring the interrelationships of titanosaurs; however, this is beyond the scope of the current work. This revision provides new information on two poorly understood and largely overlooked members of Titanosauria, and increases our knowledge of this diverse but enigmatic clade.

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