

THE OSTEOLOGY OF *CHUBUTISAURUS INSIGNIS* DEL CORRO, 1975 (DINOSAURIA: NEOSAUROPODA) FROM THE ‘MIDDLE’ CRETACEOUS OF CENTRAL PATAGONIA, ARGENTINA

JOSÉ L. CARBALLIDO,^{*1} DIEGO POL,¹ IGNACIO CERDA,² and LEONARDO SALGADO²

¹Consejo Nacional de Investigaciones Científicas y Técnicas—Museo Paleontológico Egidio Feruglio, Fontana 140 9100, Trelew, Argentina, jcarballedo@mef.org.ar; dpol@mef.org.ar;

²Instituto—Consejo Nacional de Investigaciones Científicas y Técnicas, Museo de Geología y Paleontología, Universidad Nacional del Comahue, Buenos Aires 1400 8300, Neuquén, Argentina, nachocerda6@yahoo.com.ar; lsalgado@uncoma.edu.ar

ABSTRACT—Titanosauriform sauropods were one of the most widely distributed groups of dinosaurs during the Cretaceous. In contrast to most derived forms from the Upper Cretaceous, the most basal taxa of the group are poorly known. Thus, studies on these forms are of special interest for understanding the origin and early evolution of Titanosauria. *Chubutisaurus insignis* del Corro, 1975, is known from postcranial remains found in the Bayo Overo Member of the Cerro Barcino Formation (Chubut Group), which is commonly regarded as Aptian–Cenomanian in age. Phylogenetic analyses that include *Chubutisaurus* recovered this taxon as the sister group to Titanosauria. Nevertheless, most published studies have not included this taxon, probably due to its brief description and fragmentary remains. Fieldwork conducted in the quarry where the holotype was found yielded new materials that are regarded as part of the same specimen. These new materials, together with additional undescribed, and briefly described elements, originally collected by G. del Corro, are described here. The new information allows the recognition of a more extensive diagnosis of this taxon. The phylogenetic analysis presented here resolves *Chubutisaurus* as the most basal somphospondyliian.

INTRODUCTION

Titanosauriforms have been recovered from every major landmass except for Antarctica, and are particularly well known in South America (see Upchurch et al., 2004). In Patagonia, most titanosauriform taxa come from the Upper Cretaceous of the Neuquén Basin (northwestern Patagonia), which represent derived titanosaurs from post-Cenomanian rocks (e.g., *Neuquensaurus*, Powell, 1992; *Rocasaurus*, Salgado and Azpilicueta, 2000; *Mendozasaurus*, González Riga, 2003; *Futalognkosaurus*, Calvo et al., 2008; *Barrosasaurus*, Salgado and Coria, 2009). In contrast, titanosauriforms from the Lower Cretaceous to lower Upper Cretaceous are scarce and poorly known. Camarasauromorphs from this age come from the Neuquén Basin and Cañadón Asfalto-Somuncurá Basin. The basal-most titanosaurs come from the Neuquén Basin (i.e., *Andesaurus*, Calvo and Bonaparte, 1991; *Argentinosaurus*, Bonaparte and Coria, 1993; *Ligabuesaurus*, Bonaparte et al., 2006), whereas the basal-most camarasauromorphs (i.e., non-titanosaur camarasauromorphs) were found in the Cañadón Asfalto-Somuncurá Basin (i.e., *Chubutisaurus*, del Corro, 1975; *Tehuelchesaurus*, Rich et al., 1999). Both of the last two genera could represent the most basal camarasauromorphs known from South America, and both have been only briefly described up to now.

Chubutisaurus insignis is known from postcranial remains found in the Bayo Overo Member of the Cerro Barcino Formation. Since its original description, *Chubutisaurus* was reexamined by Salgado (1993), who reinterpreted some elements and described new materials not described by del Corro (1975). Most recent phylogenetic analyses that include *Chubutisaurus* resolve it as a non-titanosaur titanosauriform (e.g., Salgado et al., 1997; González Riga, 2003; Bonaparte et al., 2006).

Chubutisaurus was considered to be a basal titanosaur by Wilson (2002) and Upchurch et al. (2004), based on of the presence of synapomorphic characters of this clade recovered in their respective analyses. The probable relationship of *Chubutisaurus* with basal titanosaurs or closer forms to this group (e.g., *Andesaurus*, *Ligabuesaurus*) makes this taxon an important element for understanding the early evolution and radiation of this widespread group of sauropods. Moreover, Upchurch et al. (2004) stated that future studies may wish to consider *Chubutisaurus* as nomen dubium, prompting a full revision and diagnosis of this taxon.

Several new materials recently collected in the holotypic quarry, as well as other undescribed elements originally collected by del Corro, are presented and described here for the first time. The new information, together with the reexamination of the previously described elements, allows us to make a more extensive diagnosis of this taxon, including the recognition of autapomorphic characters and of a unique combination of characters. Additionally, a histological analysis was conducted with the purpose of determining the growth pattern and the ontogenetic stage of the *Chubutisaurus* holotype. Finally, the phylogenetic position of *Chubutisaurus* was analyzed using a data matrix incorporating several basal macronarians, especially those forms previously interpreted to be closely related to Titanosauria.

COLLECTION HISTORY

Chubutisaurus insignis is known from a single specimen found near El Escorial village, Chubut Province, Central Patagonia, Argentina (Fig. 1). The material was found by Mr. Martínez (a local farmer) in 1961 and later collected by del Corro in 1965, who used dynamite to extract the bones (del Corro, 1975). All the materials collected in this field trip were deposited at the Museo Argentino de Ciencias Naturales (MACN 18222). Several collected

*Corresponding author

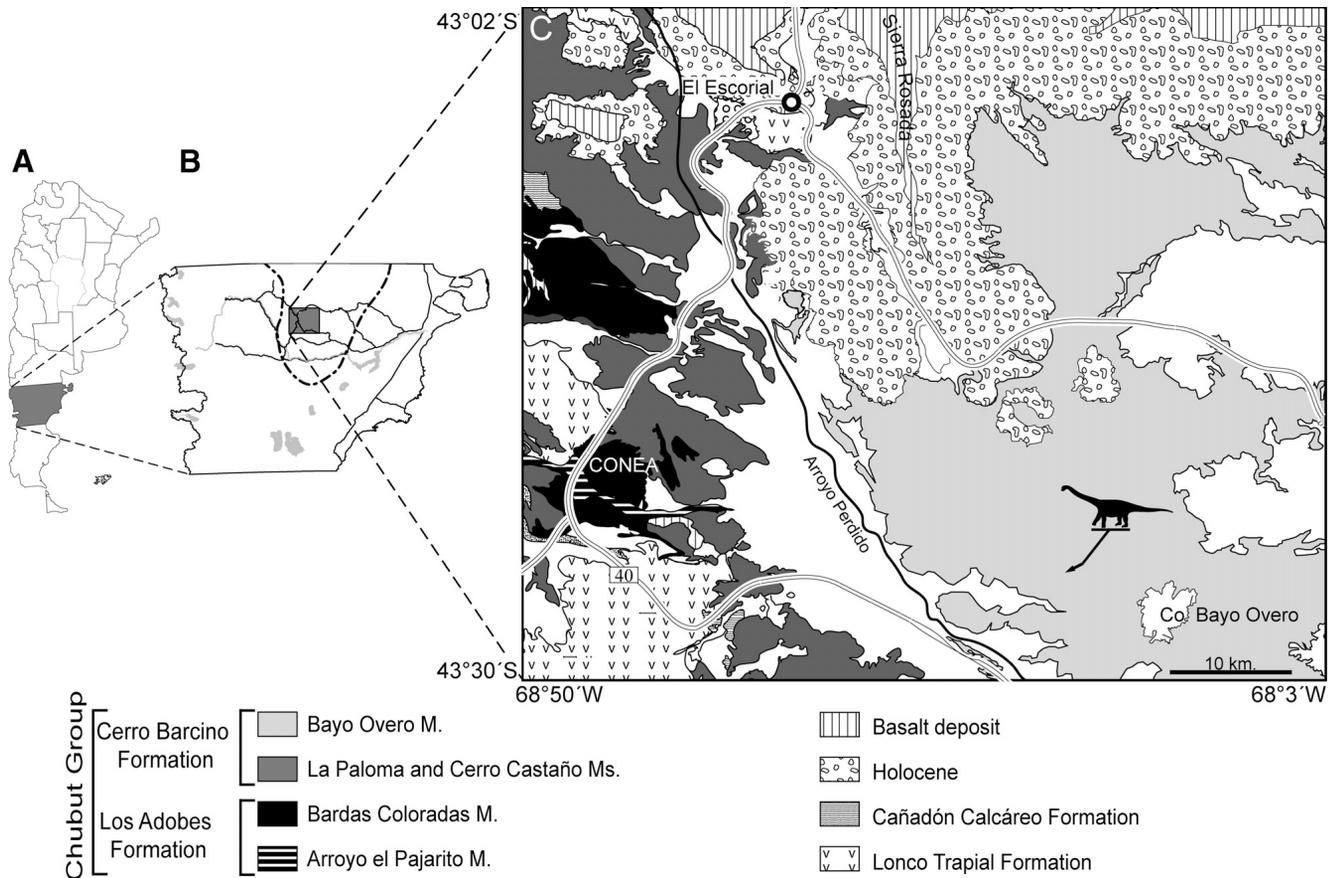


FIGURE 1. *Chubutisaurus insignis* locality map. **A**, Argentina; **B**, Chubut province, showing, with dashed line, the limits of the Somuncurá-Cañadón Asfalto basin (Cortiñas, 1996); **C**, geological map of El Escorial zone, showing the type locality position.

elements were not been described by del Corro (1975) or Salgado (1993), including fragments of caudal vertebrae, chevrons, ribs, an almost complete left scapula, a fragment of the right scapula, and a left ischium. Besides the caudal vertebrae, only the scapulae were briefly mentioned by del Corro (1975). Additionally, a fragmentary right tibia and femur, collected by del Corro and originally housed in MACN collection (as MACN 18222) were donated in the 1970s to the Museo Provincial de Ciencias Naturales y Oceanografía (CHMO). These bones are still housed there (under the numbers CHMO-565 and CHMO-901), but also retain the original MACN numbers on them.

In 1991, a field trip carried out by the Museo Paleontológico Egidio Feruglio (MPEF) relocated the quarry of the holotype of *Chubutisaurus insignis*, which was possible due to the help of Mr. Martínez' son (who was there when del Corro extracted the bones) and the large size of the quarry. A reopening of the quarry in 1991 and again in 2007 yielded several new sauropod remains. Some of them were found out of their original position, between large blocks at the base of the quarry, whereas others were collected in situ at the fossiliferous level. The new materials are housed at the MPEF (MPEF-PV 1129) and include several dorsal vertebral fragments, a caudal vertebra, ribs, and chevrons. Given the fact that all materials were collected at the same quarry, that there is no duplication of elements (contra del Corro, 1975; see below), and that the size of all the elements is consistent, we consider all available elements belong to a single individual, which is currently deposited in three different institutions (MACN, MPEF, and CHMO).

SYSTEMATIC PALEONTOLOGY

SAURISCHIA Seeley, 1887

SAUROPODA Marsh, 1878

NEOSAUROPODA Bonaparte, 1886

TITANOSAURIFORMES Salgado, Coria and Calvo, 1997

SOMPHOSPONDYLI Wilson and Sereno, 1998

CHUBUTISAURUS INSIGNIS del Corro, 1975

Figures 2–16

Holotype—Two anterior dorsal vertebrae (MACN 18222/01 and MPEF-PV 1129/A), four middle to posterior dorsal vertebrae (MACN 18222/02, MACN 18222/03, MACN 18222/05, and MPEF-PV 1129/B), a complete dorsal centrum (MPEF-PV 1129/B), two dorsal neural spines (MACN 18222/04 and MPEF-PV 1129/D), 11 anterior caudal centra (MACN 18222/06–13), fragments of four anterior caudal vertebrae (MACN 18222/14–17), four middle caudal centra (MACN 18222/18–21), two posterior caudal centra (MACN 18222/22 and MPEF-PV 1129/E), two caudal neural arches (MACN 18222/23–24), fragments of the cervical and dorsal ribs (MACN 18222/42 and MPEF-PV 1129/I), two anterior chevrons (MACN 18222/25–26) and isolated chevron fragments (MACN 18222/27 and MPEF-PV 1129/F–G), a nearly complete left scapula (MACN 18222/28) and fragments of the right one (MACN 18222/29), a left humerus (MACN 18222/30), left ulna and radius (MACN 18222/31–32), four complete and two incomplete metacarpals (MACN 18222/33–38), a left ischium (MACN

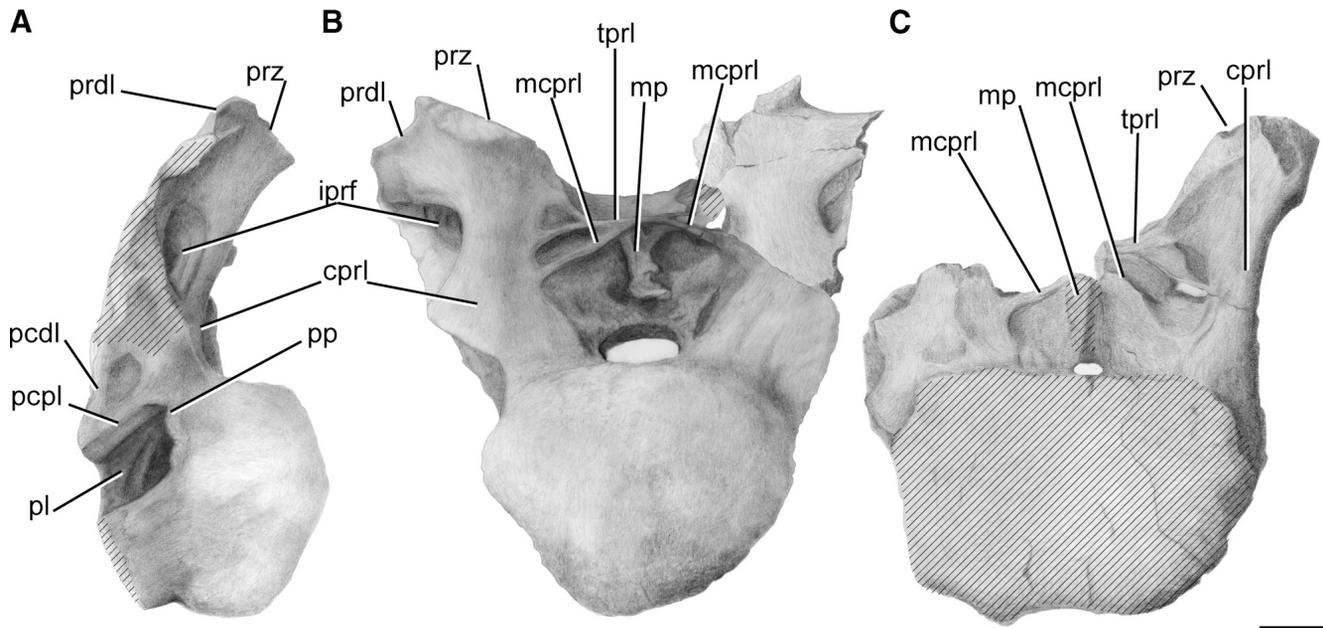


FIGURE 2. *Chubutisaurus insignis*, anterior dorsal vertebrae. MPEF-PV 1129/A in **A**, right lateral view; **B**, anterior view; MACN 18222/01 in **C**, anterior view. **Abbreviations:** **cpri**, centroprezygapophyseal lamina; **iprf**, infraprezygapophyseal fossa; **mcprl**, medial cpri; **mp**, medial pillar; **pcdl**, posterior centrodiaepophyseal lamina; **pcpl**, posterior centroparapophyseal lamina; **pl**, pleurocoel; **pp**, parapophysis; **prdl**, prezygodiaepophyseal lamina; **prz**, prezygapophysis; **tpri**, intraprezygapophyseal lamina. Scale bar equals 10 cm.

18222/39), a complete right femur (MACN 18222/40) and the dorsal half of the left one (CHMO-901), a complete right tibia (MACN 18222/41) and fragments of the left one (CHMO-565), and three histological samples of the right femur (MPEF-PV 1129/K1–K3).

Emended Diagnosis—Large titanosauriform sauropod characterized by the following autapomorphies: (1) anterior dorsal vertebrae with a medial centroprezygapophyseal lamina that connects the medial part of the centroprezygapophyseal lamina with the ventral half of the intraprezygapophyseal lamina, forming the ventromedial edge of the associated subrectangular fossa; (2) anterior dorsal vertebrae with a stout and internally pneumatized medial pillar between the neural canal and the ventral edge of the intraprezygapophyseal lamina; (3) middle dorsal vertebrae with large and deep pleurocoels that present three inner laminae. A further autapomorphy could be (4) the unusual arrangement present in the neural spine, in which the spinodiapophyseal lamina contacts the spinoprezygapophyseal lamina medially to form a composite anterior lamina. However, because of the poor preservation of this element, we prefer not to include it as a solid autapomorphic character.

Chubutisaurus also differs from other derived camarasauromorphs and basal titanosaurs in the following characters. The anterior caudal vertebrae are platycoelous/distoplastyan instead of amphicoelous or platycoelous as in both *Brachiosaurus* species and *Paluxysaurus* or the slightly procoelous caudal vertebrae present in *Andesaurus*. The unexpanded distal scapular blade differs from the expanded distal end present in *Euhelopus*, *Brachiosaurus*, and *Paluxysaurus*, whereas its D-shaped section differs from that flat scapular blade of *Euhelopus*. The humerus of *Chubutisaurus* differs from that of *Euhelopus* in that it is more slender (but not as in *Brachiosaurus*), from *Paluxysaurus* in that its proximolateral corner is square, and from *Wintonotitan*, *Ligabuesaurus*, and *Phuwiangosaurus* in that the distal condyles are not anteriorly directed. The ischium of *Chubutisaurus* shows the plesiomorphic condition in which the distal blade is large, emarginating distal to pubic peduncle, differing in that from *An-*

desaurus. *Chubutisaurus* differs from *Euhelopus* in its more anteroposteriorly compressed femur.

Locality and Horizon—‘Estancia El Dinosaurio,’ Chubut Province, Patagonia, Argentina (Fig. 1; precise GPS location of this site is deposited at the MPEF collection and can be obtained from the senior authors upon request). This locality has been mapped in the Bayo Overo Member of the Cerro Barcino Formation, Chubut Group (Proserpio, 1987; Fig. 1C). The Chubut Group is a thick succession of fluvial and volcanoclastic sediments deposited in the Somuncurá-Cañadón Asfalto Basin, extensively exposed in the northern region of Chubut Province (central Patagonia). Although different stratigraphic schemes have been proposed, most authors follow that of Codignotto et al. (1978), who recognized two formations, Los Adobes and the overlying Cerro Barcino. The Los Adobes Formation is considered to be late Valanginian to Hauterivian in age (see Rauhut et al., 2003), although Geuna et al. (2000) considered the base of this group as not earlier than Barremian, based on paleomagnetic data. The uppermost formation, Cerro Barcino, is subdivided into four members: La Paloma, Cerro Castaño, Las Plumas, and Bayo Overo (Codignotto et al., 1978). The Bayo Overo Member represents the uppermost part of the Chubut Group and was traditionally considered as Aptian–Albian (e.g., Bonaparte, 1996), although several authors noted that the Bayo Overo Member could be early Late Cretaceous in age (Rauhut et al., 2003; Anselmi et al., 2004), probably Cenomanian (as originally suggested by Codignotto et al., 1978). Although more geological studies are necessary in the Chubut Group, we ascribe a Cenomanian age to *Chubutisaurus insignis*, as is the age recently proposed in the geological revision of the area (Anselmi et al., 2004).

DESCRIPTION

Dorsal Vertebrae

The presacral vertebral column of *Chubutisaurus insignis* is represented by several fragments of dorsal vertebrae including two anterior, three medial, and one posterior dorsal vertebra.

Although some of these elements could be part of the same vertebra, there is no evident contact between them. Therefore, for descriptive purposes, these elements will be treated independently. Furthermore, some of the new information presented here allows reinterpreting the position in the vertebral series of some previously described elements (see below). As in all camellate vertebrae, the centra and the neural arches are entirely filled up with numerous and irregularly arranged pneumatic spaces (Wedel et al., 2000). The internal air spaces are generally anteroposteriorly longer than wide, being large in the middle and posterior part of the vertebra and small in the anterior part, near the anterior articular surface. The largest space (measured in MACN 18222/05) is approximately 4 cm long and 3 cm wide; the smallest spaces in this vertebra are on the order of a few millimeters wide. A similar pattern was observed in computed tomography images of MPEF-PV 1129/A, but the hardness of the rock and the low resolution of the equipment made impossible to measure precisely the proportions occupied by the air spaces.

Anterior Dorsal Vertebrae—A recently discovered element (MPEF-PV 1129/A; Fig. 2A, B) is interpreted as an anterior dorsal vertebra. This vertebra is composed of an almost complete centrum and a partially preserved neural arch, lacking the neural spine, postzygapophyses, and diapophyses (although the laminae that attach it to the centrum and prezygapophyses are preserved; see below). The posterior articular surface is mostly damaged and only a small area of this surface is preserved in the middle of the centrum, representing the deepest zone of the posteriorly concave articular surface. The anterior articular surface is only slightly damaged. As in the anterior dorsal vertebrae of all eu-sauropods, the centrum is strongly opisthocoelous (Wilson, 2002; Upchurch et al., 2004). Although its posterior end is broken, the centrum is anteroposteriorly short in relation to its height. Its length/height ratio would have been nearly equal to 1 or perhaps slightly less. The parapophysis is still connected to the centrum and forms the anterodorsal margin of the pleurocoel (or lateral foramina sensu Wedel et al., 2000; Fig. 2A). As is more evident on the left side, the parapophysis extends from the centrum to the lower section of the neural arch. The position of the parapophysis of this element resembles that of the third dorsal vertebra of *Malawisaurus*, which is anteroposteriorly longer than high, and is located between the centrum and the neural arch forming the anterodorsal edge of the pleurocoel in this taxon (Gomani, 2005:fig. 11B). Based on these similarities, this element is tentatively considered to be the third dorsal vertebra of *Chubutisaurus*, being the anterior-most preserved element in this taxon. The ventral surface of the centrum is flat and flanked by two weakly developed ventrolateral ridges. Two small (1 cm in diameter), dorsally directed openings are located on the ventral surface of the centrum, just posteriorly to the anterior articular surface.

The major axis of the pleurocoel is anteroventrally projected, forming an angle of 60° with the longitudinal axis of the centrum (Fig. 2A). A similar orientation is present in the anterior dorsal pleurocoels of titanosaurs such as *Mendozasaurus* (González Riga, 2003) and *Malawisaurus* (Gomani, 2005). As in all titanosaurs (e.g., Salgado et al., 1997; Wilson, 2002), the pleurocoel is posteriorly acuminate, a feature that is most notable on the left side. Given the above-mentioned position of the parapophysis, the pleurocoel has an almost vertical anterior edge (Fig. 2A). Posterodorsally, the pleurocoel is delimited by the posterior centroparapophyseal lamina (pcpl). Several pneumatopores open from the pleurocoel to the internal cavities of the centrum, most of which are positioned dorsally and medially within the pleurocoel.

As usual in anterior dorsal vertebrae of sauropods, in which the parapophysis is in a low position, the pcpl is weakly inclined, running from the posterior part of the centrum to the parapophysis. The pcpl joins posteroventrally with the posterior centrodipophyseal lamina (pcdl), and above the contact between these

two laminae a very small and shallow fossa is present. The pcdl has only its anterior edge preserved and seems to run almost vertically from the contact with the pcpl to the diapophysis. An infradiapophyseal fossa is present in *Chubutisaurus*, and as in most sauropods (e.g., *Patagosaurus*, *Tehuelchesaurus*, *Mendozasaurus*) and other saurischian dinosaurs (Makovicky, 1997), this fossa is delimited by the pcpl and the pcdl (Fig. 2A). The anterior centrodipophyseal lamina (acd1) that usually forms the anterior margin of this fossa is not preserved in *Chubutisaurus*. In contrast to more basal forms (e.g., *Patagosaurus*, *Tehuelchesaurus*), this fossa is very weakly developed, as in the anterior dorsal vertebrae of titanosaur sauropods (e.g., *Malawisaurus*, Gomani, 2005; *Mendozasaurus*, González Riga, 2003).

The right prezygapophysis is ventromedially inclined and set at an angle of approximately 45° with the sagittal plane (Fig. 2B), as in most titanosauriforms (e.g., *Opisthocoelicaudia*, Borsuk-Bialynicka, 1977:fig. 2; *Malawisaurus*, Gomani, 2005:fig. 10; *Neuquensaurus*, Salgado et al., 2005:figs. 3, 4). The prezygapophysis is supported by two robust laminae, the prezygodipophyseal lamina (prdl), which runs laterally from the ventrolateral edge of the prezygapophysis, and the centroprezygapophyseal lamina (cp1), which runs from the prezygapophysis to the centrum (Fig. 2B). In anterior view, the cp1 is mediolaterally broad at its ventral end (Fig. 2B), indicating that this lamina must be linked to the centrum but also, in some degree, to the parapophysis, a condition found in the anterior dorsal vertebrae of sauropods. These two laminae (cp1 and prdl), together with the pcdl, enclose a deep infraprezygapophyseal fossa that can be observed in anterior and lateral views (Fig. 2A, B), a feature also present in almost all saurischians (Makovicky, 1997).

Both prezygapophyses are connected by an almost horizontal intraprezygapophyseal lamina (tprl), coinciding with the orientation of this lamina in the anterior dorsal vertebrae of sauropods (Wilson, 1999). A thin but well-developed lamina runs from the medial edge of the cp1 to the mid-ventral part of the tprl. This lamina is clearly present in both sides of this vertebra, although badly preserved on the right side, and also present in MACN 18222/01 (see below). The position of this lamina resembles the medial cp1 (mcprl) present in the anterior dorsal vertebrae of diplodocids (the bifurcated cp1 of Harris, 2006:character 135). Although in *Chubutisaurus* this lamina is not bounding the neural canal, we prefer to use the term mcprl to refer to it. This lamina is not observed in other non-diplodocid sauropod dorsal vertebrae and is considered here as an autapomorphic trait of *Chubutisaurus* (Fig. 2B). The mcprl, together with the tprl and cp1, encloses an almost subrectangular fossa that extends dorsally from the posterior opening of the neural canal. Another small and triangular shallow fossa is located just above this subrectangular fossa, above the mcprl. A stout medial pillar runs vertically above the neural canal towards the tprl, being internally pneumatized. A medial pillar was also described in *Mendozasaurus* (González Riga, 2003). In *Chubutisaurus* the medial pillar is much more developed than in *Mendozasaurus*, in which is only a very weakly developed ridge, as also occurs in anterior dorsal vertebrae of other sauropods (e.g., *Europasaurus*, *Neuquensaurus*). The neural canal is ovoid and dorsoventrally compressed. Dorsally, the tprl is well preserved and does not present any sign of a prespinal lamina. When is present and well developed, this lamina commonly contacts the dorsal edge of the tprl in the anterior dorsal vertebrae (e.g., *Mendozasaurus*, González Riga, 2003; *Neuquensaurus*, Salgado et al., 2005).

Another centrum (MACN 18222/01; Fig. 2C) was previously interpreted as a posterior dorsal centrum by del Corro (1975:fig. 3), or as a caudosacral centrum by Salgado (1993:fig. 3). In its general shape and size, this element is very similar to the anterior dorsal centrum described above (Fig. 2B, C). A left prezygapophysis was found among the isolated elements in the MACN collection but fits in the prezygapophyseal process of MACN 18222/01

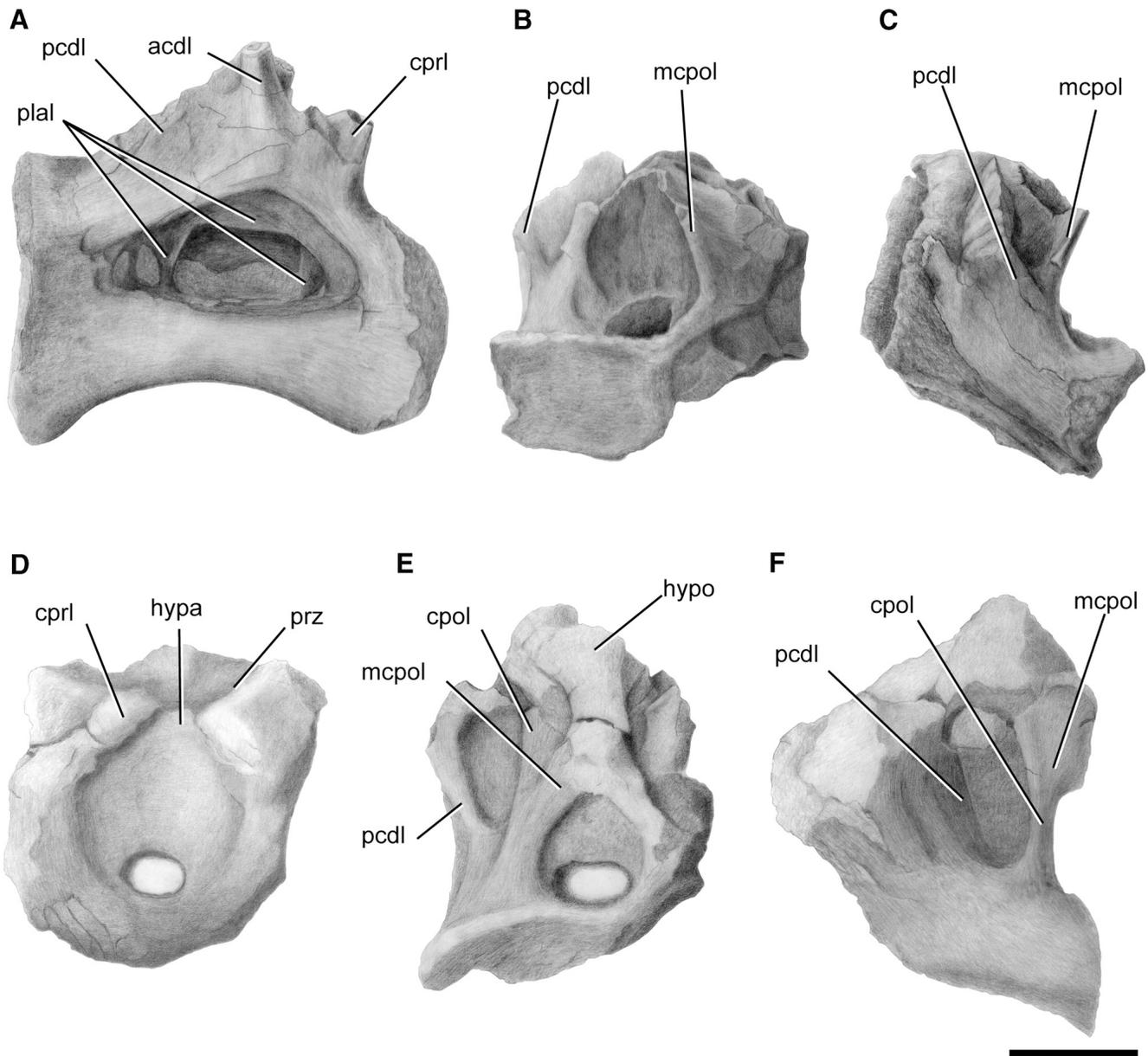


FIGURE 3. *Chubutisaurus insignis*, middle to posterior dorsal vertebrae. MPEF-PV 1129/B in **A**, right lateral view; MPEF-PV 1129/C in **B**, posterior view; **C**, left lateral view; MACN 18222/02 in **D**, anterior view; **E**, posterior view; **F**, left lateral view. **Abbreviations:** **acdl**, anterior centrodiapophyseal lamina; **cpol**, centropostzygapophyseal lamina; **cprl**, centroprezygapophyseal lamina; **hypa**, hypantrum; **hypo**, hyposphene; **mcpol**, medial centropostzygapophyseal lamina; **pcdl**, posterior centrodiapophyseal lamina; **plal**, accessory pleurocoel laminae; **prz**, prezygapophysis. Scale bar equals 10 cm.

and therefore belongs to this vertebra. Thus, this vertebra has a horizontal *trpl*, indicating that this element is in fact an anterior dorsal vertebra. Furthermore, the pleurocoel of MPEF-PV 1129/A and MACN 18222/01 have the same size and shape and differ from those of the posterior dorsal centra (see below). Finally, the autapomorphic lamina, the medial pillar (badly preserved, but clearly as developed as in MPEF-PV 1129/A, and internally pneumatized), and the two fossae present in the anterior view of MPEF-PV 1129/A are also present in MACN 18222/01 (Fig. 2C). Therefore, this vertebra is reinterpreted here as an anterior dorsal centrum, and the transverse process identified by Salgado (1993:266) as a badly preserved parapophysis, still connected to the centrum. Additionally, the flat anterior articular surface of MACN 18222/01 is interpreted as product of the poor

preservation of this region, which may have been damaged during its extraction. Some differences exist, however, in MACN 18222/01 and MPEF-PV 1129/A, suggesting a more posterior position for MACN 18222/01, being probably the fourth dorsal vertebra. Although the position of the parapophysis is not clear in MACN 18222/01, due to its poor preservation, it seems to be higher than in MPEF-PV 1129/A. Additionally, MACN 18222/01 seems to be shorter than MPEF-PV 1129/A, as commonly observed in the fourth or fifth dorsal centra of sauropods (e.g., *Camarasaurus*, Osborn and Mook, 1921; *Trigonosaurus*, Campos et al., 2005).

Middle to Posterior Dorsal Vertebrae—In addition to the middle and posterior dorsal vertebrae previously described (del Corro, 1975; Salgado, 1993), new elements collected in the

holotype quarry are described here. Due to their fragmentary nature, their precise position in the dorsal series is hard to determine, but some comments on the inferred position and the most relevant characters of the MACN and MPEF elements are noted below.

A complete dorsal centrum (MPEF-PV 1129/B) was recently recovered in the holotype quarry and represents the most complete dorsal centrum of *Chubutisaurus* (Fig. 3A). The neural arch is broken slightly above the neurocentral suture, so that only the base of the pedicels and the ventral part of some laminae are preserved (Fig. 3A). The absence of parapophysis on the centrum indicates that this element is not an anterior dorsal vertebra. The ventral surface of the centrum is transversely flat but lacks the lateral ridges present in the anterior dorsal centra described above. Longer dorsal centra are commonly observed in mid-dorsal vertebrae of other macronarian sauropods (e.g., *Trigonosaurus*, Campos et al., 2005; *Brachiosaurus brancai*, Janensch, 1950; *Camarasaurus*, Osborn and Mook, 1921). Thus, this element is considered as a mid- to anterior-posterior dorsal vertebra.

This centrum is opisthocoelous, with well-developed convex and concave anterior and posterior articular surfaces. The presence of opisthocoelous middle to posterior dorsal centra in *Chubutisaurus* was noted by Salgado (1993) on the basis of the only available and damaged centrum (MACN 18222/02; Salgado, 1993:fig. 2C), which had been described as a cervical centrum by del Corro (1975:figs. 1, 2). The smaller size of this centrum (compared to MPEF-PV 1129/B) may indicate a slightly posterior position, given the trend of centrum length decrease observed in the dorsal series of other macronarian vertebrae. An additional element (MACN 18222/05) is very similar to MACN 18222/02 and is thus regarded as middle to posterior dorsal centrum. MACN 18222/05 preserves the ventral half of the centrum, which is broken at the level of the margin of the pleurocoel. This broken surface has allowed us to measure the length and width of the air spaces described above.

As in other titanosauriforms (Upchurch, 1998), the MPEF-PV 1129/B centrum is anteroposteriorly longer (29 cm) than wide (27 cm, measured at its posterior face), and wider than high (21 cm) at its posterior end, being dorsoventrally compressed. The dorsoventral compression of this element is intermediate between the condition of most basal titanosauriforms (e.g., *Brachiosaurus brancai*, Janensch, 1950; *Phuwiangosaurus*, Martin et al., 1999) and the highly dorsoventrally compressed centra of derived titanosaurs (e.g., *Saltasaurus*, Powell, 1992).

As in most neosauropods, the centrum has well-developed pleurocoels with their long axis nearly horizontal (Fig. 3A), instead of being inclined as those of the anterior dorsal centra. The pleurocoel is positioned slightly anterior on the centrum with an acuminate caudal end as in titanosaurs (Salgado et al., 1997; Upchurch et al., 2004). Both pleurocoels penetrate deeply on the centra, leaving only a very narrow median septum of no more than 1 cm wide. The deeper zone is delimited by two vertically oriented laminae, one anterior and one posterior, and a horizontally oriented lamina dorsally positioned in the pleurocoel (Fig. 3A). These internal laminae are not observed in any other sauropod and are regarded as an autapomorphic feature of *Chubutisaurus insignis*.

Although the identification of the laminae is difficult, comparison of this centrum with the anterior dorsal vertebrae of *Chubutisaurus* and other taxa allows identification of some laminae (Fig. 3A). The *pcdl* lacks the accessory posterior centrodiapophyseal lamina or the ventral expansion, the presence of which has been considered a synapomorphic character of Titanosauria (Salgado et al., 1997).

Another element recently recovered in the holotypic quarry consists of a dorsal vertebra with the ventral portion of the neural arch, which has a broken posterior and anterior articular surfaces

(MPEF-PV 1129/C; Fig. 3B, C). This vertebra is very similar to MACN 18222/3 (Fig. 3D–F) described by Salgado (1993:fig. 2A) and therefore the two are described together.

Although very incomplete, the posterior articular surface is clearly concave (Fig. 3B, E). A well-developed lamina runs dorso-medially from the lateral edges of the neural canal (Fig. 3B, C, E, F). In sauropods, there are two distinct paired laminae that are oriented relatively parallel to one another that run from the centrum to the postzygapophysis (Apesteguía, 2005a): the centropostzygapophyseal lamina (*cpol*; Wilson, 1999) and the medial centropostzygapophyseal lamina (*mcpol*; Apesteguía, 2005a). The *mcpol* has been distinguished from the *cpol* because it contacts the medial-most region of the postzygapophysis and laterally bounds the neural canal (Apesteguía, 2005a). Both laminae (the *mcpol* and the *cpol*) are present in some neosauropods (e.g., *Camarasaurus*, *Brachiosaurus*, *Malawisaurus*, *Argentinosaurus*; Apesteguía 2005a). In taxa with only one of these laminae, its identification is difficult to establish (Apesteguía, 2005a); nevertheless, some differences in their position can be used to distinguish them. The medial-most paired laminae observed in *Chubutisaurus* bound the neural canal and project dorso-medially towards the medial region of the postzygapophysis (Fig. 3E), matching the topological criteria upon which the homology of the *mcpol* was established (Fig. 3B, E). The *mcpol* is particularly developed in middle dorsal vertebrae of *Camarasaurus*, in which they contact the ventral end of the hyposphene (Osborn and Mook, 1921:pl. 51). The *cpol* is less developed than the *mcpol* in both elements, but is more developed in MACN 18222/03 than in MPEF-PV 1129/C, indicating a slightly different position for these elements in the dorsal series. In MACN 18222/03, a stout lamina is present above the contact point of both *mcpol*. This lamina runs vertically from this point and broadens dorsally, and is interpreted here as the ventral end of the hyposphene (Fig. 3E).

The *pcdl* is well developed on both dorsal centra (MACN 18222/03 and MPEF-PV 1129/C; Fig. 3C, F). As is also observed in the dorsal centrum (MPEF-PV 1129/B), both vertebrae lack any sign of the accessory posterior centrodiapophyseal lamina. A large and very deep subcircular infrapostzygapophyseal fossa, well visible in lateral view (Fig. 3F), is completely preserved in MACN 18222/03, and is enclosed by the *cpol* and the *pcdl*.

Anteriorly, in MACN 18222/03, a large depression is enclosed by the two robust *cpol* (Fig. 3D). Dorsally, this depression creates a broad hypantrum. The probable presence of a hyposphene-hypantrum articulation in *Chubutisaurus* was already noted by Salgado (1993). Although a complete hyposphene-hypantrum complex is not preserved in any of the MPEF (or MACN) elements, the large rhomboidal fossa observed in MACN 18222/02 clearly shows the presence of this structure in *Chubutisaurus insignis* (Fig. 3D).

An almost complete neural spine (MPEF-PV 1129/D; Fig. 4) was recovered in del Corro's quarry. This element is very similar to MACN 18222/04. MPEF-PV 1129/D is better preserved, and therefore the following description is based on the recently recovered neural spine.

Both postzygapophyses are well preserved and in both elements (MACN 18222/04 and MPEF-PV 1129/D). They are dorso-laterally oriented forming an angle of almost 45° with the horizontal plane. The separation between postzygapophyses is clearly smaller than the separation between the prezygapophyses of the anterior dorsal vertebra described above (MPEF-PV 1129/A). This difference, coupled with the much higher angle of its postzygapophyses, suggests that MPEF-PV 1129/C and MACN 18222/04 are posterior dorsal vertebrae. A single and rhomboid-shaped fossa is ventrally enclosed by both postzygapophyses (Fig. 4B). This fossa is here referred as the supra-postzygapophyseal fossa (*spzf*). The shape of this fossa is very similar to that present in mid-posterior dorsal vertebrae of some

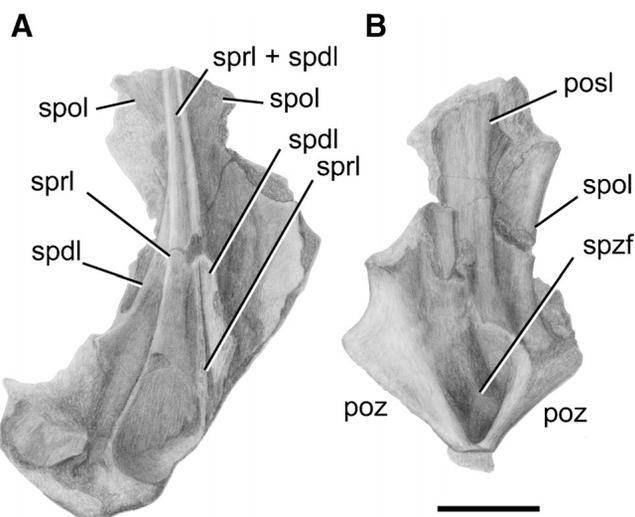


FIGURE 4. *Chubutisaurus insignis*, posterior dorsal neural spine (MPEF-PV 1129/D) in **A**, anterior view; **B**, posterior view. **Abbreviations:** *posl*, postspinal lamina; *poz*, postzygapophyses; *spdl*, spinodiapophyseal lamina; *spol*, spinopostzygapophyseal lamina; *sprl*, spinoprezygapophyseal lamina; *spzf*, suprapostzygapophyseal fossa. Scale bar equals 10 cm.

titanosaurs (e.g., *Andesaurus*, *Neuquensaurus*). Out of this group the *spzf* seems to be absent or slightly developed, as in *Tastavinsaurus* (Canudo et al., 2008). Above the *spzf* a robust postspinal lamina (*posl*) is present and bounded by the spinopostzygapophyseal laminae (*spol*). The *spol* arise in the medial-most part of the *spzf* and slightly diverge from the *posl* (Fig. 4B).

In anterior view, the laminae of this neural spine are heavily deformed toward the right side (Fig. 4A). This deformation has made the left postzygapophyses and the *spol* visible in anterior view. In addition to the *spol*, two paired laminae are observed in anterior view (Fig. 4A). The paired lateral laminae are interpreted as the spinodiapophyseal laminae (*spdl*) and the paired medial laminae as the spinoprezygapophyseal laminae (*sprl*) (Fig. 4A). The *sprl* is a very well developed and thin lamina, which runs almost vertically from its base and contacts the *spdl* dorsally, which is much more robust than the *sprl*. The ventral margin of the *sprl* is also preserved in anterior dorsal vertebrae (e.g., MPEF-PV 1129/A) where it is also a thin lamina. Dorsally, both laminae are fused to form a single and composite medial lamina (Fig. 4A). In fact, at its dorsal end, the neural spine of *Chubutisaurus* is formed anteriorly by the single *sprl*+*spdl* lamina, laterally by the *spol*, and posteriorly by the single *posl*. The *sprl*+*spdl* fusion, as is present in *Chubutisaurus*, could be regarded as an additional autapomorphy of this taxon, but due to the fragmentary nature of this neural spine, it is preferred to not include it in the diagnosis of *Chubutisaurus*. No prespinal lamina is observed in this element. Anteriorly the neural spine is clearly longer than the posterior part, a difference that is interpreted as the posterior orientation of the neural spine, a synapomorphic character of Somphospondyli (Wilson, 2002).

Caudal Vertebrae

Thirteen almost complete and four fragmentary caudal centra are preserved. Four fragments and 12 complete anterior to middle caudal centra were originally collected by del Corro (MACN 18222/06–22), and one additional distal caudal vertebra has been recently collected (MPEF-PV 1129/E). As was previously noted by Salgado (1993), del Corro (1975) misinterpreted

the prezygapophysis as a posteriorly inclined and forked neural spine. Only one posterior caudal vertebra (MPEF-PV 1129/E) preserves the neural spine. Additionally, two rather incomplete and isolated neural arches have the ventral part of the neural spine (MACN 18222/23–24). The caudal centra lack pleurocoels, fossae, or any other pneumatic feature. Salgado (1993) noted the plesiomorphic condition of the articular surfaces of the centra, lacking the procoelous condition of most titanosaurs (e.g., *Saltasaurus*, Powell, 1992; *Malawisaurus*, Gomani, 2005) or the opisthocelous condition of other titanosaurs (e.g., *Opisthocoelecaudia*, Borsuk-Bialynicka, 1977).

Sauropod vertebrae have been traditionally classified as platycoelous (slightly hollowed at each end), amphicoelous (well concave anterior and posterior articular surfaces), procoelous (anteriorly concave and posteriorly convex), or opisthocelous (anteriorly convex and posteriorly concave) (definitions follow Romer, 1956). However, Tidwell et al. (2001) noted that these terms fail to adequately describe the variation present in many sauropod caudal vertebrae, as is the case of *Chubutisaurus*. These authors defined a new term, procoelous/distoplastyan, to describe the condition observed in the anterior caudal vertebrae of some non-titanosaur titanosauriforms (e.g., *Venenosaurus*, Tidwell et al., 2001). Procoelous/distoplastyan vertebrae are anteriorly concave and posteriorly flat or slightly concave. The condition of *Chubutisaurus* anteriormost caudal vertebrae fits this category, and we follow Tidwell et al. (2001) in the use of this new term and in the recognition of a new character state as was used recently by González Riga et al. (2009).

For descriptive purposes, the complete caudal centra were ordered into three different regions, anterior (with comments on the inferred first or second caudal vertebra), middle, and posterior caudal vertebrae (see Table 1). The distinction in these categories was made based on several morphological changes, as will be described below.

Anterior Caudal Vertebrae—Besides the seven more complete caudal vertebrae, four fragmentary centra are interpreted as fragments of anterior caudal vertebrae, based on their general size and shape. Taking into account the complete centra (MACN 18222/06–13; Table 1) plus the four fragments (MACN 18222/14–17), 11 anterior caudal vertebrae are preserved.

From caudal vertebrae MACN 18222/06 to MACN 18222/13, the centra gradually increase in length and decrease in posterior width, ranging from elements that are almost twice as wide as long in the anteriormost vertebrae, to centra that are almost as long as wide (see Table 1). Thus, the length/width ratio of all these elements is less than 1, especially in the anteriormost preserved caudal vertebra (see below), in which the centrum is anteroposteriorly shorter than in the other caudal vertebrae. The anterior caudal centra also share the presence of a well-developed transverse process that gradually decreases from the anterior-most preserved caudal vertebra (MACN 18222/06) towards the posterior-most preserved anterior caudal elements (MACN 18222/13).

As noted above, the anterior-most caudal vertebrae of *Chubutisaurus* are procoelous/distoplastyan (Fig. 5). In the anterior-most preserved caudal vertebrae (MACN 18222/06–10), the depth of the anterior concave surface decreases gradually, and the posterior surface remains flat or slightly convex (Table 1). The posterior-most anterior caudal vertebrae (MACN 18222/11–13) are platycoelous, with slightly concave anterior and posterior articular surfaces, instead of procoelous/distoplastyan (Fig. 6; Table 1).

The element MACN 18222/06 (Fig. 5A–C) is interpreted as one of the anterior-most caudal vertebrae of *Chubutisaurus*, probably the first or second caudal vertebra, and some special comments on it are made here. This centrum lacks facets for the chevrons, which commonly appear between the first and the third caudal vertebrae in other sauropods (e.g., *Tastavinsaurus*,

TABLE 1. Measurements of the most complete caudal vertebrae of *Chubutisaurus insignis*.

Specimen number	AW	AH	PW	PH	APL	AS	PS	APL/PW	PH/PW
Anterior caudal vertebrae									
MACN 18222/06	20	23	20	23	11	CC (3.0)	FL	0.55	1.15
MACN 18222/07	23	28	20	20	12	CC (3.0)	SCx	0.60	1.00
MACN 18222/08	20	23	20	21	14	CC (4.0)	SCx	0.70	1.05
MACN 18222/09	24	16	22	18	13	CC (4.0)	SCx	0.60	0.81
MACN 18222/10	18	18	17	19	13	CC (2.5)	FL	0.76	1.15
MACN 18222/11	18	18	19	20	13	CC (1.0)	CC (1.5)	0.68	1.05
MACN 18222/12	18	15	17	15	13	CC (0.6)	CC (1.3)	0.76	0.88
MACN 18222/13	16	18	16	18	14	CC (1.0)	CC (1.0)	0.87	1.12
Middle caudal vertebrae									
MACN 18222/18	13	12	12	11	13	—	CC (0.5)	1.10	0.95
MACN 18222/19	11	12	11	13	14	FL	CC (1.5)	1.08	1.13
MACN 18222/20	10	12	—	10	14	FL	CC (0.8)	—	—
Posterior caudal vertebrae									
MACN 18222/21	—	—	7	5	12	—	FL	1.70	0.71
MPEF-PV 1129	7	6	7	5	10	CC (0.5)	CC (0.5)	1.42	0.78

Abbreviations: **AH**, anterior height; **APL**, anteroposterior length; **AS**, anterior articular surface; **AW**, anterior width; **PH**, posterior height; **PS**, posterior articular surface; **PW**, posterior width. The anterior and posterior articular surfaces can be **CC**, concave (with the measured depth in cm); **FL**, flat; **SCx**, slightly convex.

Royo-Torres, 2009; *Alamosaurus*, Gilmore, 1946). The transverse process, which is only partially preserved in this vertebra, is ventrally supported by a slightly anteroventrally projected lamina (Fig. 5A, B). This lamina is interpreted as the acdl. The acdl is only present in the first caudal vertebra of other macronarians (e.g., *Tastavinsaurus*, Canudo et al., 2008), reinforcing the interpretation of this element as the first or second caudal vertebra of *Chubutisaurus*. Dorsally, the transverse process is supported by a broken lamina that is interpreted as the prdl (Fig. 5A, B), a lamina that is also present only in the first and second caudal vertebrae of other sauropods (e.g., *Tastavinsaurus*, Canudo et al., 2008; *Mendozasaurus*, González Riga, 2003).

In addition to the anterior-most caudal centrum (MACN 18222/06), MACN 18222/07 (Fig. 5D–F) is the best-preserved element of the anterior series, and some general features of the

anterior caudal series are described based on this vertebra. The transverse process is cylindrical. This process is projected posterolaterally instead of anteriorly inclined as figured and interpreted by del Corro (1975:figs. 4, 5). The lateral end of the transverse process is positioned caudally to the posterior articular surface of the centrum. Ventrally the transverse process is rounded and lacks the laminae present in MACN 18222/06. A weakly developed prdl projects dorsally from the transverse processes and connects it with the prezygapophysis. The neural arch is slightly anteriorly positioned on this centrum and in the following anterior caudal centra. The prezygapophyses are anterodorsally oriented and surpass the anterior articular surface of the centrum (Fig. 5D).

Mid-Caudal Vertebrae—Three middle caudal vertebrae are preserved (MACN 18222/18–21), although none of them is complete. These vertebrae are longer than wide and lack the well-developed transverse processes present in anterior caudal centra. The anterior articular surface is flat, whereas the posterior surface is slightly concave. The ventral surface of these vertebrae is transversely convex. The neural arch is positioned anteriorly on the centrum, being more anteriorly located in comparison with those of the anterior caudal vertebrae.

The size of the two isolated neural arches (MACN 18222/23–24) suggests that they correspond to mid-caudal vertebrae. Both fragments are broken along the pedicels and only a ventral part of the neural arch is preserved. The preserved neural spine is much longer than wide (6 cm × 2.5 cm) and only the origins of the sprl and spol are preserved.

Posterior Caudal Vertebrae—Two posterior caudal vertebrae are preserved (MACN 18222/22 and MPEF-PV 1129/F).

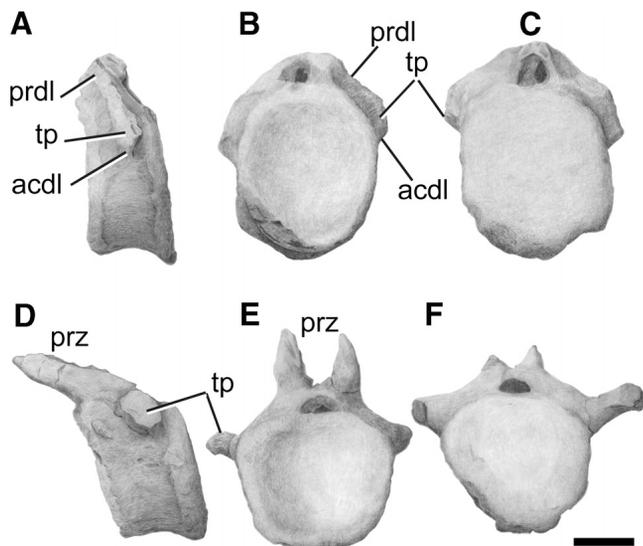


FIGURE 5. *Chubutisaurus insignis*, anterior caudal vertebrae. MACN 18222/06, first or second? caudal vertebra in **A**, left lateral view; **B**, anterior view; **C**, posterior view; MACN 18222/07, anterior caudal vertebra in **D**, left lateral view; **E**, anterior view; **F**, posterior view. **Abbreviations:** **acdl**, anterior centrodiaepophyseal lamina; **prdl**, prezygodiapophyseal lamina; **prz**, prezygapophysis; **tp**, transverse process. Scale bar equals 10 cm.

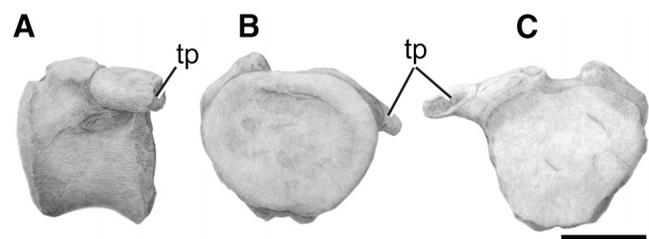


FIGURE 6. *Chubutisaurus insignis*, posterior-most anterior caudal vertebra (MACN 18222/12) in **A**, left lateral view; **B**, anterior view; **C**, posterior view. **Abbreviation:** **tp**, transverse process. Scale bar equals 10 cm.

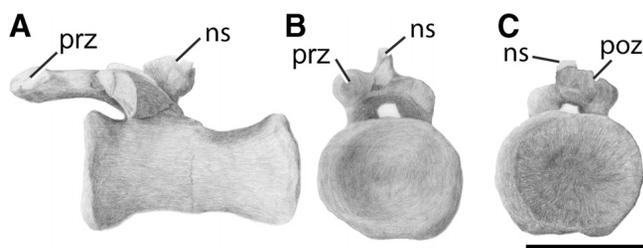


FIGURE 7. *Chubutisaurus insignis*, posterior caudal vertebra (MPEF-PV 1129/E) in **A**, left lateral view; **B**, anterior view; **C**, posterior view. **Abbreviations:** prz, prezygapophysis; poz, postzygapophysis; ns, neural spine. Scale bar equals 10 cm.

MPEF-PV 1129/F is the most complete element but lacks the left pre- and postzygapophysis (Fig. 7A–C), whereas MACN 18222/22 is broken at approximately mid-length. Thus, the description is based on MPEF-PV 1129/F. The centrum is platycoelous, with both articular surfaces slightly concave (Fig. 7). The ventral surface of the centrum is transversely flat with chevron facets on both the anterior and the posterior ends. The neural arch is even more anteriorly positioned on this vertebra than in preceding elements. Only the right prezygapophysis is preserved, being anteriorly directed with its distal half surpassing the anterior articular surface of the centrum (Fig. 7A). The anterior part of the neural spine of this vertebra is very short and thin, but its posterior end has not been preserved.

Ribs

Several rib fragments were recovered by del Corro (MACN 18222/42). Although these fragments are very incomplete, several tubular and large fragments, interpreted as cervical ribs, are also present in the MACN collection. The largest rib is 52 cm long, and is broken proximally and distally, thus it is very likely that the cervical ribs were longer than the cervical centra, as is common in non-diplodocoid sauropods (Wilson, 2002). Dorsal rib fragments are plank-like, with the proximal-most fragments heavily pneumatized as in titanosauriforms (Wilson, 2002) and in two taxa retrieved here as basal camarasauromorphs (*Venenosaurus* and *Tastavinsaurus*; see below).

Chevrons

Many partially preserved chevrons were collected by del Corro and deposited in the MACN collection (MACN 18222/25–27). Two additional chevrons were later collected from the type quarry and are stored in the MPEF collection (MPEF-PV 1129/E–F). All the preserved chevrons are Y-shaped. Among Titanosauriformes, *Alamosaurus* and *Opisthocoelicaudia* present complete series of chevrons (Gilmore, 1946; Borsuk-Bialynicka, 1977). In these taxa the Y-shaped chevrons are only present from the first to the fifteenth caudal vertebrae. Thus, all the preserved chevrons of *Chubutisaurus* are interpreted as pertaining to the anterior section of the tail. The chevrons are proximally open (MPEF-PV 1129/G), as in all camarasauromorph sauropods (e.g., Wilson, 2002; Upchurch et al., 2004).

The first chevrons of *Malawisaurus* (Gomani, 2005) and *Tastavinsaurus* (Royo-Torres, 2009:fig. 4.92) are clearly different from the subsequent Y-shaped chevrons, in that they are wider mediolaterally than long anteroposteriorly. A partially complete chevron collected by del Corro (MACN 18222/25) is clearly wider mediolaterally than long anteroposteriorly and is interpreted as the first chevron of *Chubutisaurus* (Fig. 8A). Likewise, another chevron fragment preserved (MACN 18222/26) is as long antero-

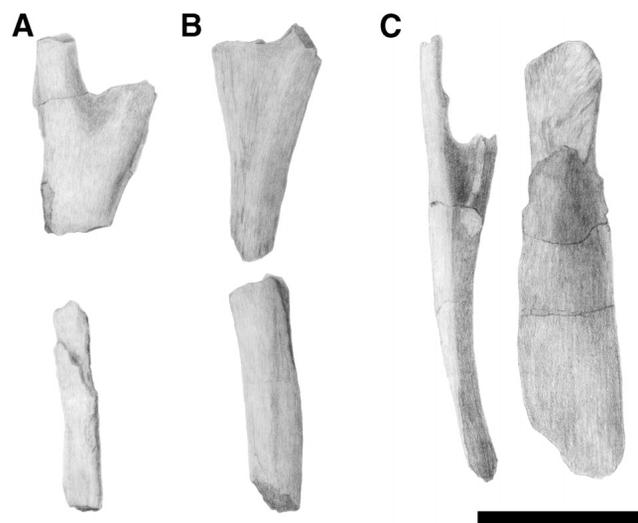


FIGURE 8. *Chubutisaurus insignis*, chevrons. **A**, anterior-most (first?) chevron (MACN 18222/25) in anterior and lateral views; **B**, second? Chevron (MACN 18222/26) in anterior and lateral views; **C**, Y-shaped chevron (MPEF-PV 1129/F) in anterior and lateral views. Scale bar equals 10 cm.

posteriorly as wide mediolaterally (Fig. 8B). A similar morphology can be seen in the second chevron of *Tastavinsaurus* (Royo-Torres, 2009:fig. 4.93) and in the third and fourth chevrons of *Brachiosaurus* (Janensch, 1950:figs. 109–110, 123–124). Thus, this element is interpreted as a second to fourth chevron of *Chubutisaurus*. Two distal process fragments, a complete distal process (MACN 18822/27), and an almost complete chevron with a broken right branch (MPEF-PV 1129/F; Fig. 8C) have the typical Y-shape with a mediolaterally compressed distal process. MPEF-PV 1129/F is the most completely preserved Y-shaped chevron. Its anteroposterior length is almost 5 times its mediolateral width. The anteroventral end of the distal process is rounded and the posteroventral part shows an almost right angle.

Scapula

Del Corro (1975) reported the existence of two scapulae, one of which was included as part of the holotype. He only mentioned that the proximal end of a second scapula is smaller than that of the holotype, inferring it may belong to a juvenile specimen. In fact, there are no differences in size or shape between the preserved parts of these elements (MACN 18222/28 and MACN 18222/29), which are right and left. Thus, both scapulae are here referred to the same individual. The right scapula (MACN 18222/29) is much damaged and only its anteroventral portion has been preserved, whereas the left scapula (MACN 18222/28) is almost complete. The description is based on MACN 18222/28 (Fig. 9; Table 2). For convenience of the description, the scapula is treated as if it were oriented with its long axis horizontal (i.e., the actual anterodorsal side is here referred to as the dorsal side).

The general aspect of the scapula (Fig. 9) is similar to that of non-titanosaur titanosauriforms or basal titanosaurs (e.g., *Ligabuesaurus*, Bonaparte et al., 2006:fig. 6; *Phuwiangosaurus*, Martin et al., 1999:fig. 10; *Wintonotitan*, Hocknull et al., 2009:fig. 16G). The scapula is long (132 cm), and its general shape resembles that of most eusauropods, in which the scapular length exceeds the minimum breadth of the scapular blade by around 6 times or more. This condition differs from that of some basal forms (e.g., *Cetiosaurus*, Upchurch and Martin, 2003) and from derived

TABLE 2. Principal measurements (in cm) of the girdle and limb bones of *Chubutisaurus insignis*.

Element	Measurement (cm)
Left scapula (MACN 18222/30) 28	
Total length	131.0
Mid-shaft breadth	20.5
Distal breadth	34.7
Left humerus (MACN 18222/30)	
Total length	146.0
Proximal breadth	49.5
Mid-shaft breadth	22.5
Distal breadth	38.5
Mid-shaft transverse length	12.5
Left radius (MACN 18222/32)	
Total length	85.5
Proximal breadth	23.0
Mid-shaft breadth	12.0
Distal breadth	24.0
Left ischium (MACN 18222/39)	
Total length	77.5
Mid-shaft breadth	13.0
Pubic articulation length	28.0
Right femur (MACN 18222/39) 40	
Total length	170.0
Mid-shaft breadth	28.2
Mid-shaft transverse length	10.0
Left tibia (MACN 18222/39) 41	
Total length	101.0
Maximum proximal breadth	36.0
Mid-shaft maximum breadth	17.0
Maximum distal breadth	30.6

titanosaurs (e.g., *Saltasaurus*, Powell, 1992:fig. 28; *Alamosaurus*, Gilmore, 1946:fig. 6), in which the scapula is more robust (i.e., the scapular length is around 5 times or less the blade width). A new character reflecting these differences was added to the phylogenetic data matrix (character 190 in Supplementary Data 1; available online at www.vertpaleo.org/jvp/JVPcontents.html).

The dorsal margin of the scapular blade is not expanded, but due to the slightly divergence among the ventral and dorsal margins, it is slightly wider at its distal end than at mid-blade length (Fig. 9A). The absence of expansion at the end of the scapular blade differs from some basal camarasauromorphs, in which the dorsal edge of the blade has a rounded expansion (e.g., *Camarasaurus*, Ostrom and McIntosh, 1966:pl. 46; *Brachiosaurus brancai*, Janensch, 1914:fig. 5). The lateral surface of the scapular blade is dorsoventrally convex, whereas the medial one is slightly concave, especially at mid-shaft length. Thus, the scapular blade is D-shaped in cross-section. This character was considered as a synapomorphy of *Jobaria* plus neosauropods, missing in some somphospondylians, and convergently acquired in opisthocoelicaudines (Wilson, 2002). Its presence in *Chubutisaurus* indicates that this character is also present in at least some basal somphospondylians. Actually, the most parsimonious hypotheses obtained here (see below) show that this character is a synapomorphy of *Jobaria*+Neosauropoda, with convergent reversals in *Europasaurus*, *Euhelopus*, and the group formed by *Isisaurus* plus saltasaurines. At its distal end, both surfaces became flat. The long axis of the scapular blade forms an angle of almost 50° with respect to the coracoid-scapular articular surface, which only preserves its ventral region. An angle of approximately 45° was interpreted by Wilson (2002) as a synapomorphy of Nemegtosauridae plus more derived titanosaurs. The presence of this character in *Chubutisaurus* suggests a broader distribution among titanosauriform sauropods. The acromion process arises close to the midpoint of the scapular length. This condition (new character 191 in Supplementary Data 1) is also observed in some other basal camarasauromorphs (e.g., *Camarasaurus*, Osborn and Mook, 1921:fig. 10; *Tehuelchesaurus*, Rich et al.,

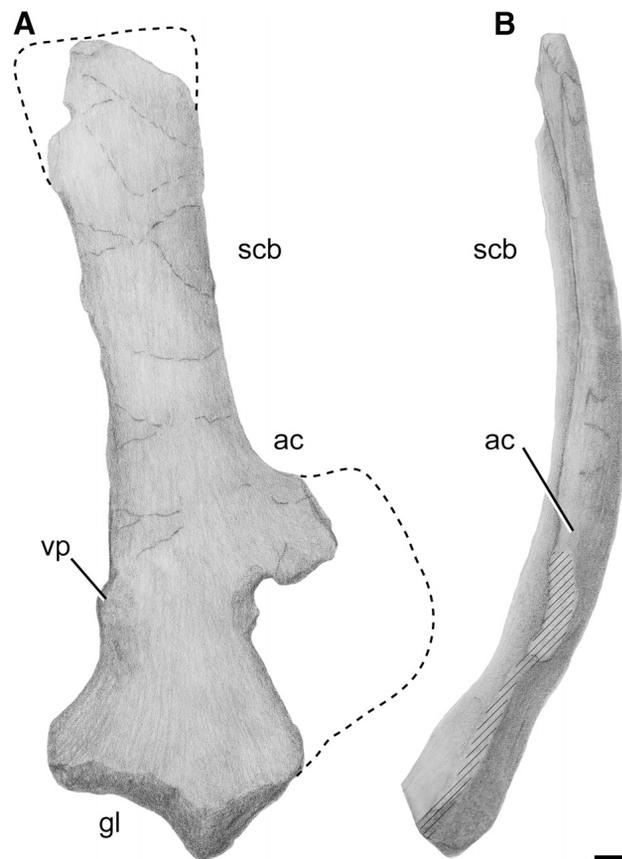


FIGURE 9. *Chubutisaurus insignis*, left scapula (MACN 18222/28) in **A**, medial view; **B**, dorsal view. **Abbreviations:** ac, acromion; gl, scapular glenoid; scb, scapular blade; vp, ventromedial process. Scale bar equals 10 cm.

1999:fig. 10; *Ligabuesaurus*, Bonaparte et al., 2006:fig. 6), and contrast with the more proximal position observed in most non-camarasauromorph sauropods (e.g., *Patagosaurus*, Bonaparte, 1986:fig. 49) and titanosaurs (e.g., *Saltasaurus*, Powell, 1992:fig. 28). The scapular glenoid facet is flat oriented and not medially exposed as it is in Titanosauria (Wilson, 2002). A weakly developed ventromedial process is observed near the glenoid, on the ventral edge of the scapula (Fig. 9A). The strong development of this process (new character, character 202, in Supplementary Data 1) produces a concave region between it and the ventral-most extension of the glenoid. Among Macronaria, a marked ventromedial process seems to be present in *Wintonotitan* (Hocknull et al., 2009) and *Ligabuesaurus* (Bonaparte et al., 2006), although it is clearly more developed in the latter taxon.

Humerus

The left humerus of *Chubutisaurus* (MACN 18222/30) was only mentioned by del Corro (1975), and briefly described by Salgado (1993:fig. 4B). Its general shape resembles the humerus of the juvenile specimen of *Alamosaurus* (Lehman and Coulson, 2002:fig. 7) and that of *Wintonotitan* (Hocknull et al., 2009:fig. 16E, F). The humerus is 3 times longer than its proximal width (Fig. 10) and more slender than that of *Opisthocoelicaudia*, *Camarasaurus*, and *Euhelopus* (Wilson and Upchurch, 2003, 2009), but more robust than that of *Brachiosaurus* (Taylor, 2009). Its robustness index (sensu Wilson and Upchurch, 2003) is low (0.24;

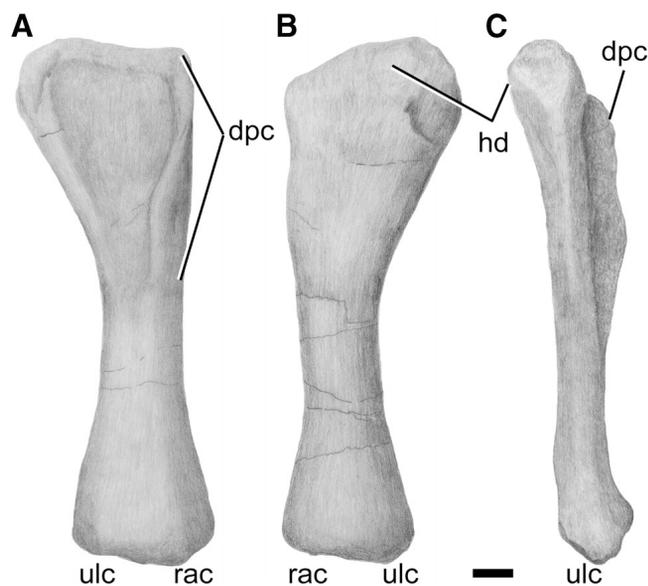


FIGURE 10. *Chubutisaurus insignis*, left humerus (MACN 18222/30) in **A**, anterior view; **B**, posterior view; **C**, lateral view. **Abbreviations:** dpc, deltopectoral crest; hd, humeral head; rac, radial condyle; ulc, ulnar condyle. Scale bar equals 10 cm.

Table 2), being similar to that of *Phuwiangosaurus* and *Antarctosaurus* (Wilson and Upchurch, 2003). The humeral head bears a rugose surface and is positioned slightly more medially than laterally (Fig. 10B). The diaphysis is long and its cross-section is elliptical, with its anteroposterior length almost 0.6 times its mediolateral width (Fig. 10).

The proximal surface of the humerus is markedly flat, and the proximolateral corner is projected at an almost right angle (Fig. 10A, B), a condition regarded as a titanosaur synapomorphy (Wilson, 2002). The deltopectoral crest is long (Salgado, 1993), almost reaching half length of the diaphysis. At its distal end, the deltopectoral crest gradually decreases, ending in a narrow and unexpanded medial end.

The distal end of the humerus is transversely and anteroposteriorly expanded, but less so than the proximal end (the proximal mediolateral width is about 1.20 times the width of the distal mediolateral expansion; Fig. 10A, B). The condyles are not distally restricted, but are anteriorly expanded (Fig. 10C). Although a shallow groove separates the condyles, they are not as clearly divided as they are in titanosaurs. The distal end of *Chubutisaurus* humerus is flat and resembles that of non-titanosaur sauropods (e.g., Wilson, 2002; Fig. 10A, B).

Ulna and Radius

An almost complete left ulna and a complete left radius are preserved (MACN 18222/31 and MACN 18222/32, respectively; Table 2). These elements were not mentioned by del Corro (1975), but Salgado (1993:fig. 4A) commented on their most relevant characters. Only the distal two-thirds of the robust left ulna are preserved (Salgado, 1993). Although the radial fossa is not preserved, the anteromedial and anterolateral processes arise at almost half of the estimated ulnar length (based on radius length). The posterior ridge is well marked, and also arises at half of the estimated ulnar length (Fig. 11). The distal articular surface of the ulna is almost triangular, with its longer edge positioned anteriorly.

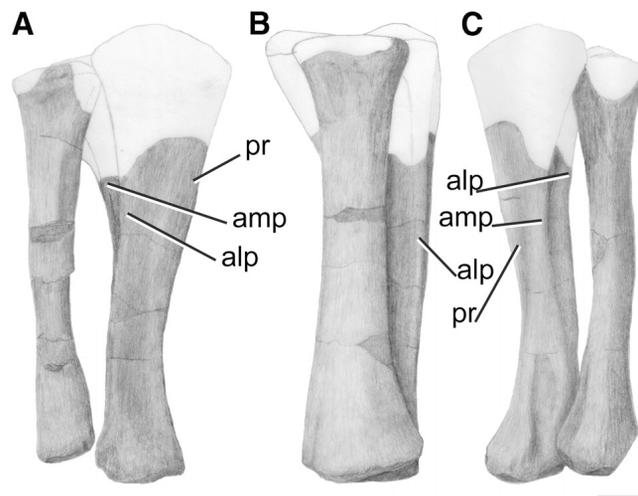


FIGURE 11. *Chubutisaurus insignis*, left ulna and radius (MACN 18222/31–32) as are articulated in MACN collection in **A**, lateral view; **B**, anterior view; **C**, posterior view. In white are the reconstructed proximal parts of both bones. **Abbreviations:** alp, anterolateral process; amp, anteromedial process; pr, posterior ridge. Scale bar equals 10 cm.

The radius is almost complete; only small anterodorsal and posterodorsal parts of the proximal articulation are not preserved (Fig. 11). The radius/humerus length ratio is 0.6 (Salgado, 1993), which agrees with the condition of most adult macronarians. These values are low compared to those of other sauropods, as a result of the relative shortening of the radius in titanosaurs (Wilson and Upchurch, 2003). The radius robustness index is very low (0.22), being similar to the values observed in *Brachiosaurus* and *Cedarosaurus* (Wilson and Upchurch, 2003). Both the proximal and distal ends are almost equally mediolaterally expanded, being approximately twice the minimum mediolateral width of the diaphysis.

Metacarpals

One right and five left metacarpals were recovered by del Corro. Four complete metacarpals and one distal fragment were described by Salgado (1993). Recently the complete elements were identified, described, and figured by Apesteguía (2005b:figs. 5–7). Thus, only some comments on these elements will be made here. As was previously noted, *Chubutisaurus* metacarpals are robust (Salgado, 1993; Apesteguía, 2005b), with a robustness index (RI; defined as the minimum circumference divided the total length; Apesteguía, 2005b) of 0.6 (in metacarpal I) and 0.5 (in metacarpals III and IV) (Apesteguía, 2005b). These values are intermediate between the RI present in *Venenosaurus* and the more robust metacarpals of titanosaurs (e.g., *Epachthosaurus*, *Aeolosaurus*; Apesteguía, 2005b). As in titanosaurs, *Chubutisaurus* shows reduced proximal and distal intermetacarpal contacts (Apesteguía, 2005b). Left metacarpal I (MACN 18222/33; Fig. 12) is complete and is very similar in size and in shape to the mirror image of another element preserved (MACN 18222/34). Thus, this latter element is recognized as the right metacarpal I. A distal portion of metacarpal II is also preserved (MACN 18222/35; Fig. 12). As in the second metacarpal of *Epachthosaurus* (Martínez et al., 2004), the distal end of this element is trapezoidal, with its lateral face slightly longer than the medial face. Metacarpal III (MACN 18222/36; Fig. 12) was described by Salgado (1993) and tentatively identified as the second (Salgado, 1993:fig. 4F). The complete left metacarpal IV (MACN 18222/37; Fig. 12) was also described by Salgado

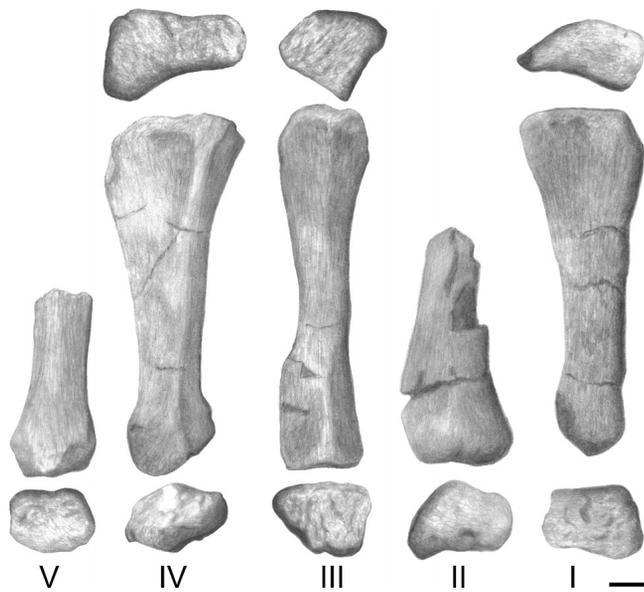


FIGURE 12. *Chubutisaurus insignis*, left metacarpals (from right to left) I (MACN 18222/33), II (MACN 18222/34), III (MACN 18222/35), IV (MACN 18222/36), and V (MACN 18222/37). Scale bar equals 5 cm.

(1993:fig. 4H) as the probably metacarpal V. Another metacarpal fragment (MACN 18222/38; Fig. 12) is here interpreted as the left metacarpal V. The preserved length of this element is 22.5 cm and as in *Epachthosaurus*, its distal end is almost square with a rounded lateral border.

Ischium

A left ischium (MACN 18222/39; Table 2) was collected by del Corro but was not previously mentioned. For descriptive convenience, the element is described as if it was oriented with its long axis horizontal, consequently, the actual anterodorsal side is regarded here as the dorsal side. The ischium is almost complete, but broken in three different parts. The shaft is broken at nearly its mid-length, and although there is not doubt on its position, the contact of both parts is not perfect (Fig. 13). The other broken area is at the pubic peduncle, but the contact in this region is perfectly preserved (Fig. 13). The iliac peduncle is not complete, so it is impossible to know its total length. The ischium has the plesiomorphic condition of Camarasauromorpha in which the

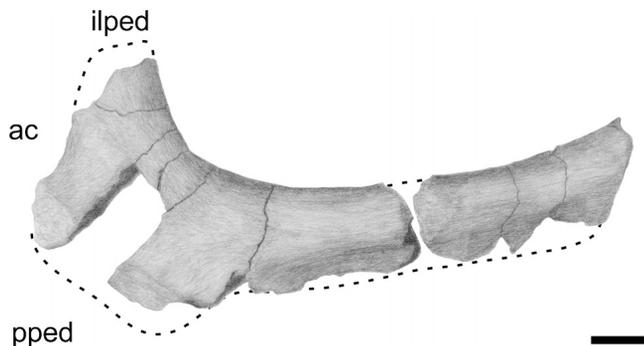


FIGURE 13. *Chubutisaurus insignis*, left ischium (MACN 18222/39) in lateral view. **Abbreviations:** ac, acetabulum; ilped, iliac peduncle; pped, pubic peduncle. Scale bar equals 10 cm.

pubic articulation is longer than the anteroposterior length of the pubic peduncle (Salgado et al., 1997). The acetabular region is laterally concave and medially straight. The shaft is mediolaterally broad on its dorsal margin, but becomes narrow on its ventral margin. As in non-titanosaur sauropods (Wilson, 2002), the shaft is large and emarginated distal to the pubic peduncle, but the total length of the ischium divided by the width of the pubic pedicle is less than 0.5. A new character (242 in Supplementary Data 1) was included in the data matrix to represent the relatively reduced ischial length of basal titanosauriforms, which is probably an intermediate condition between the large shaft present in non-titanosauriforms and the extremely short shaft present in titanosaurs.

The distal end of the ischial shaft is not dorsoventrally expanded, a character only present in *Aeolosaurus* (Salgado and Coria, 1993:fig. 9) and Flagellicaudata (Wilson, 2002). When anatomically oriented, the shaft is posteroventrally directed forming a 35° angle with respect to the horizontal plane.

Femur

In addition to the complete right femur mentioned by del Corro (1975; MACN 18222/40) and described by Salgado (1993:fig. 4C), a distal fragment of a left femur was also collected by del Corro (CHMO-901). CHMO-901 is broken just below the fourth trochanter. The length of the complete right femur is 168 cm, and the humerus-to-femur length ratio is 0.86 (Salgado, 1993; Table 2). In Macronaria, values higher than 0.9 are present in taxa closely related to *Brachiosaurus* or the node Titanosauriformes (e.g., *Cedarosaurus*, *Brachiosaurus*, *Atlasaurus*), whereas values smaller than 0.8 are commonly present in both basal camarasauromorphs (e.g., *Tehuelchesaurus*, *Camarasaurus*, Rich et al., 1999; Osborn and Mook, 1921) and derived titanosaurs (e.g., *Epachthosaurus*, Martínez et al., 2004; *Neuquensaurus*, Salgado et al., 2005; *Opisthocoelicaudia*, Borsuk-Bialynicka, 1977). Similar ratios to that of *Chubutisaurus* are observed in non-titanosaur titanosauriforms (e.g., *Paluxysaurus*, Rose, 2007; *Ligabuesaurus*, Bonaparte et al., 2006) and forms closer to this node (e.g., *Andesaurus*, Calvo and Bonaparte, 1991).

In medial view, the femur is straight along most of its length but deflected medially in its proximal part (Fig. 14A). In anatomical position, the femur head is medially directed (Fig. 14B) as in Titanosauriformes (e.g., Wilson, 2002; Upchurch et al., 2004). The femur head is dorsomedially oriented (Fig. 14B), as is also observed in other macronarians (e.g., *Euhelopus* Wiman, 1929; *Tastavinsaurus*, Canudo et al., 2008), but having a smaller angle than in derived titanosaurs (e.g., *Rapetosaurus*, Curry Rogers and Foster, 2001; *Saltasaurus*, Powell, 1992). As noted by Salgado (1993), the femur of *Chubutisaurus insignis* presents the lateral bulge synapomorphic of Titanosauriformes (Salgado et al., 1997). The mediolateral width at the level of the lateral bulge is approximately 1.5 times the minimum mediolateral width of the diaphysis. Above this bulge, the lateral margin of the femur is strongly deflected medially (Fig. 14B). The minimum mediolateral width of the femur is positioned near the beginning of the distal end. In cross-section, the shaft of the femur is elliptical. Its anteroposterior length is approximately the half of the mediolateral width. The presence of highly anteroposteriorly compressed femora in other titanosauriforms (e.g., *Brachiosaurus brancai*, Taylor, 2009; *Paluxysaurus*, Rose, 2007; *Phuwiangosaurus*, Martin et al., 1999) indicates that this condition is present in a more inclusive group than Saltosauridae (as was suggested by Wilson, 2002).

The fourth trochanter is posteriorly positioned, and the lesser trochanter is not developed (Fig. 14A, B). In the right femur, the distal condyles are broken just at their base (Fig. 14A, B). The left femur (CHMO-901) shows that the tibial and fibular condyles are well developed and restricted to the distal portions of the femur. Both condyles are equally developed in posterior view, whereas

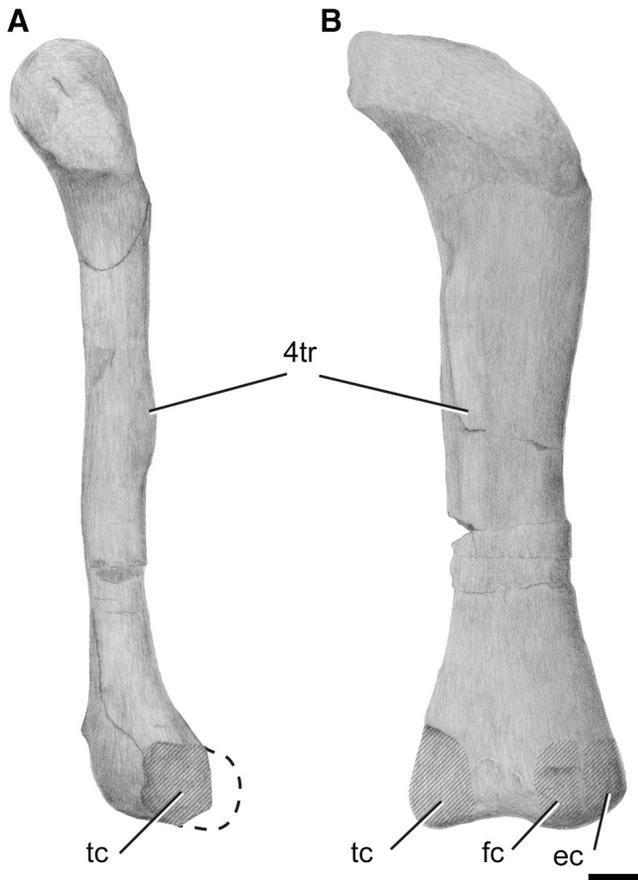


FIGURE 14. *Chubutisaurus insignis*, right femur (MACN 18222/40) in **A**, medial view; **B**, posterior view. **Abbreviations:** **4tr**, fourth trochanter; **ec**, epicondyle; **fc**, fibular condyle; **tc**, tibial condyle. Scale bar equals 10 cm.

in ventral view the tibial condyle is transversely broader than the fibular condyle.

Tibia

A right complete tibia (MACN 18222/41) was previously described by Salgado (1993:fig. 4D). In addition to this element, an incomplete left tibia was also collected by del Corro (CHMO-565). Only the proximal and distal parts of CHMO-565 are preserved. Thus, the description is based on MACN 18222/41 (Table 2). The robustness index, calculated as the average of the greatest widths of the proximal end, mid-shaft, and distal end divided by the total length of the right tibia (sensu Wilson and Upchurch, 2003), is 0.27. Therefore, *Chubutisaurus* presents an intermediate value between that of *Camarasaurus* (0.29) and *Phuwiangosaurus* (0.25) (Wilson and Upchurch, 2003).

The tibia is straight with proximal anteroposterior and distal mediolateral expansions. In proximal view, the proximal articular surface of *Chubutisaurus* tibia is almost circular, with a well-developed anterolaterally projected cnemial crest. The cnemial crest is mediolaterally broad (Salgado, 1993) and well developed throughout the proximal half of the tibia, with a moderately developed circular outline in lateral view (Fig. 15A). At mid-length, the tibial shaft is ovoid, with its anteroposterior width twice its mediolateral width. The distal end is mediolaterally expanded (Salgado, 1993; Salgado et al., 1997), and the posteroventral process is reduced, as is common in eusauropods (Wilson and

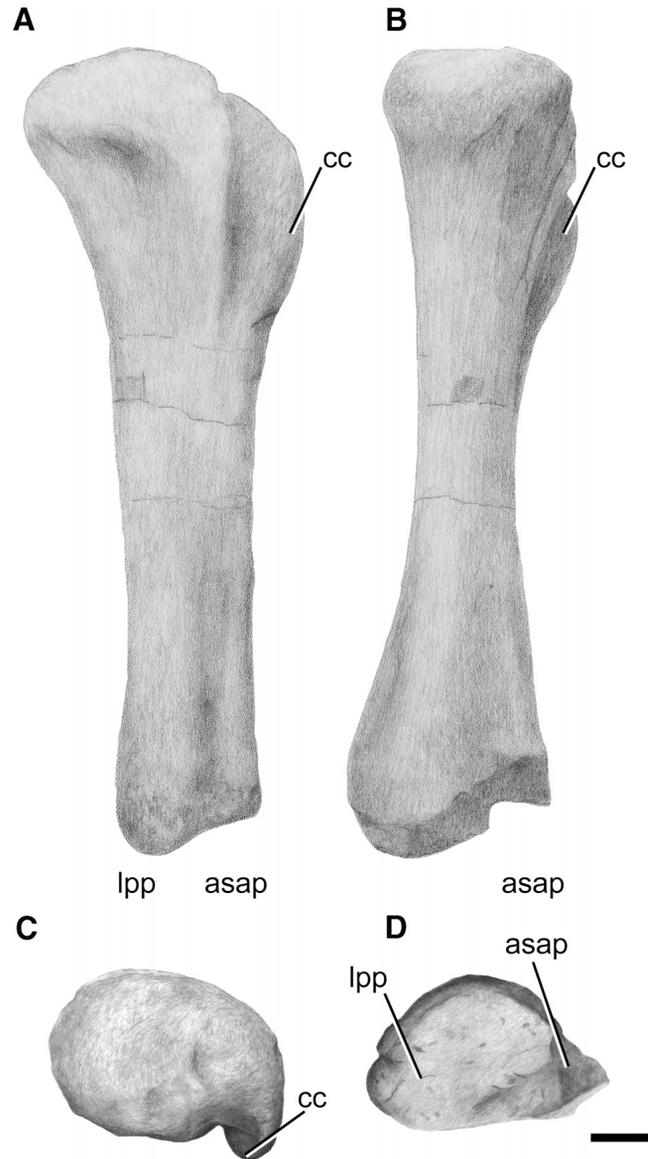


FIGURE 15. *Chubutisaurus insignis*, right tibia (MACN 18222/41) in **A**, lateral view; **B**, posterior view; **C**, proximal view; **D**, distal view. **Abbreviations:** **asap**, articular surface for the ascending process; **cc**, cnemial crest; **lpp**, lateroposterior process. Scale bar equals 10 cm.

Sereno, 1998). The articular surface for the ascending process of the astragalus is well developed, forming a step-like shape (Fig. 15B).

Metatarsus

A complete isolated metatarsal was recovered from the holotypic locality (MPEF-PV 1129/H). Based on material of other sauropods (e.g., *Tastavinsaurus*, Royo-Torres, 2009:fig. 5.186; *Ligabuesaurus*, Bonaparte et al., 2006; *Epachthosaurus*, Martínez et al., 2004), this metatarsal of *Chubutisaurus* is interpreted as the left metatarsal IV. The maximum length of this element is 23 cm, the maximum proximal width 14.5 cm, and the maximum distal width is 9.5 cm.

Both the proximal and distal ends are expanded. The proximal articular surface is almost triangular with its plantaromedial

vertex expanded and almost flat plantarolateral edge. At mid-length, the diaphysis is almost triangular in cross-section, with a rounded superior vertex and a slightly concave plantar base. The proximal end is rectangular with slightly concave plantar and convex superior edges.

Bone Histology

Bone histology has been demonstrated to be a very useful source of information regarding the growth dynamics of extinct vertebrates (Chinsamy-Turan, 2005; Erickson, 2005). With the purpose of determining the growth pattern and the ontogenetic stage of the *Chubutisaurus* holotype specimen, mid-diaphyseal petrographic thin sections were made from the right femur (CHMO-901). The sections include part of the anterior and posterior cortex (MPEF-PV 1129/K1–3). All cross-sections were prepared using standard paleohistologic techniques (Chinsamy and Raath, 1992) and studied under transmitted light, both normal and polarized. The terminology used follows the general terminology of bone histology described in Francillon-Vieillot et al. (1990) and Chinsamy-Turan (2005).

At mid-shaft, the medullary region is badly crushed (possibly diagenetic) and the original cancellous structure, made up of bony trabeculae, is destroyed and pressed together. The perimedullary cortex is also altered by diagenesis, containing many fragments of compact tissue. Only a relatively thin portion (around 10 mm) of the external cortex remains unaltered. The cortical bone is composed almost entirely of dense Haversian bone tissue (Fig. 16A). Secondary osteons are abundant and reach the outermost portion of the cortex. Remnants of fibrolamellar tissue persist between secondary osteons at the outer cortex (Fig. 16B). At the subperiosteal region, a thin layer of non-reconstructed periosteal bone is present. This bone tissue consists of avascular lamellar bone with annuli and representing an outer circumferential layer (OCL; Chinsamy-Turan, 2005), called also external fundamental system (Fig. 16C). The tissue that forms the OCL contains discontinuities; however, they do not appear to correspond with true LAGs. Instead, these marks probably are the limits between successive bony lamellae in the annuli.

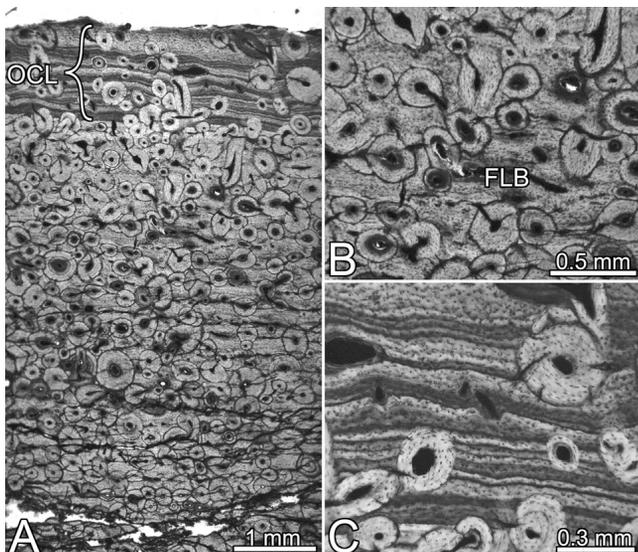


FIGURE 16. Histological section from the femoral shaft of *Chubutisaurus insignis* (MPEF-PV 1129/K1), shown in normal light microscopy. **A**, external cortex composed mainly of Haversian tissue. The outer circumferential layer (OCL) indicates that it was fully grown. **B**, remains of fibrolamellar bone tissue (FLB) are present interstitially between secondary osteons. **C**, avascular lamellar bone with annuli at the OCL.

Sharpey's fibers oriented perpendicular to the external surface are present at the lamellar matrix of the OCL.

DISCUSSION

Taxonomy and Phylogeny

Chubutisaurus insignis is here comprehensively described for the first time, increasing the knowledge of basal titanosauriforms from Patagonia. Contrary to del Corro (1975), no duplicated elements are present among the collected material and there are no size differences among the elements that can justify the recognition of more than one individual. Therefore, all the materials collected at the type quarry are here considered as belonging to the same individual, thus forming part of the holotype. Recently, Upchurch et al. (2004) cast doubt on the validity of *Chubutisaurus*, given the lack of a proper diagnosis for this taxon. The study of *Chubutisaurus insignis* presented here reveals several autapomorphies and a unique combination of characters that confirms the validity of this taxon and allows a proper diagnosis.

In the original description of *Chubutisaurus*, del Corro (1975) erected the family "Chubutisauridae," a monotypic taxon that has never been used since then. Salgado (1993) noted similarities of *Chubutisaurus* with "Brachiosauridae" and with titanosaurids, but considered *Chubutisaurus* to be Sauropoda *incertae sedis*, pending a complete phylogenetic analysis. Later, Salgado et al. (1997) included *Chubutisaurus* in a cladistic analysis for the first time, recovering it as a non-titanosaur titanosauriform, a position also obtained in subsequent analyses (e.g., Bonaparte et al., 2006; Calvo et al., 2008). Other phylogenetic analyses of macronarian sauropods, however, have not included *Chubutisaurus* among the sampled taxa (e.g., Upchurch, 1998; Wilson and Sereno, 1998; Wilson, 2002; Upchurch et al., 2004).

The new materials of *Chubutisaurus* described here reveal an interesting combination of plesiomorphic and apomorphic characters in comparison with other titanosauriforms. In order to test the most parsimonious phylogenetic information of these features and the affinities of *Chubutisaurus*, the phylogenetic relationships of this taxon were tested here through a cladistic analysis of a modified version of the data matrix published by Wilson (2002). The modified matrix includes 289 characters and 41 taxa (Supplementary Data 1 and 2; available online at www.vertpaleo.org/jvp/JVPcontents.html). In order to obtain a more thorough assessment on the plesiomorphic optimization at the base of Neosauropoda, we used as outgroup five non-neosauropod taxa, as well as all diplodocoid taxa used by Wilson (2002). Several camarasauromorphs were added to the Wilson (2002) data set, especially those forms related with the origin of Titanosauriformes (see below). Characters were mainly taken from previous studies (Salgado et al., 1997; Upchurch, 1998; Wilson and Sereno, 1998; Wilson, 2002; Upchurch et al., 2004; Canudo et al., 2008; González Riga et al., 2009), with the addition of several new characters (Supplementary Data 1). Most characters are binary, but eight were multistate characters (8, 66, 78, 100, 111, 158, 174, 189), which we treated as ordered. The equally weighted parsimony analysis was carried out using TNT v.1.1 (Goloboff et al., 2008a, 2008b). A heuristic tree search was performed consisting of 1000 replicates of Wagner trees (with random addition sequence of taxa) followed by branch swapping (TBR; saving 10 trees per replicate). This procedure retrieved 12 most parsimonious trees of 587 steps (CI = 0.478; RI = 0.689), found in 440 of the replicates. These trees were submitted to a final round of TBR that failed to find additional optimal trees. The strict consensus tree of the 12 most parsimonious trees is shown in Figure 17.

In general terms, the position of the added taxa is in accordance with at least some of the previous analyses of these forms. Nevertheless, the position of *Tehuelchesaurus*, *Tastavinsaurus*, and *Venosaurus* differs from previous studies: these taxa are

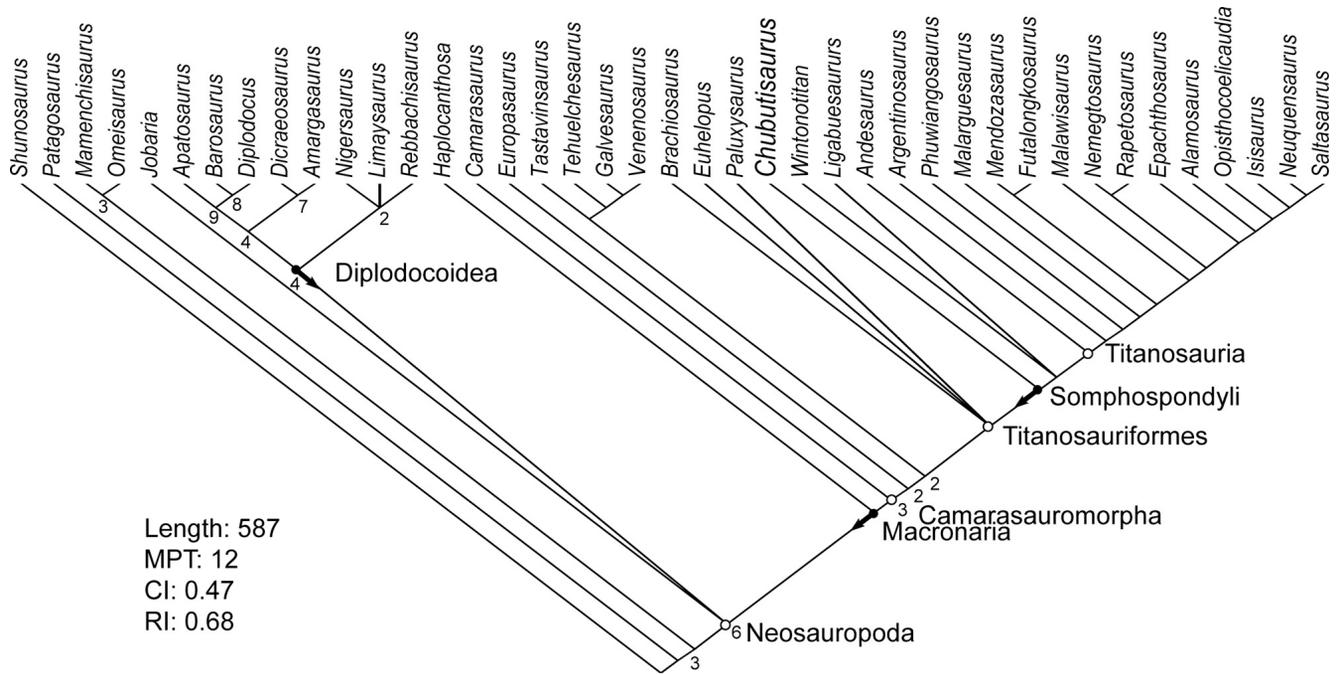


FIGURE 17. Phylogenetic relationships of *Chubutisaurus insignis* within Neosauropoda, showing the strict consensus tree of the 12 most parsimonious trees of 587 steps each. Stem-based groups are symbolized by arrows and node-based groups with open circles. Bremer values greater than 1 are indicated below the nodes.

clustered as a clade of basal camarasauromorphs. The nodal support for this clade is, however, very low (as well as those of most macronarian nodes), suggesting that future analysis can easily overturn this hypothesis. An extensive discussion on the position and support of these basal camarasauromorphs lies outside the scope of this contribution and will be discussed elsewhere. It should be noted, however, that a similar position for *Tastavinsaurus* and *Venosaurus* was recovered by Royo-Torres (2009), who also added characters and taxa to the data matrix published by Wilson (2002). Although *Tehuelchesaurus* was originally regarded as a “cetiosaurid,” the macronarian affinities of this taxon were advanced by Rauhut (2002) and Rauhut et al. (2005), who retrieved *Tehuelchesaurus* as a basal titanosauriform.

All most parsimonious trees depict *Chubutisaurus* in a basal position among titanosauriforms (Fig. 17), in broad agreement with previous proposals (e.g., Salgado et al., 1997; González Riga et al., 2009). In the present analysis, however, the basal titanosauriform position of *Chubutisaurus* has been more thoroughly tested by more extensive taxon sampling within Macronaria that includes several titanosauriform outgroups (i.e., *Galvesaurus*, *Tastavinsaurus*, *Tehuelchesaurus*, *Europasaurus*), basal titanosauriforms (i.e., *Euhelopus*), titanosaur outgroups (i.e., *Ligabuesaurus*, *Wintonotitan*), and basal titanosaurs (i.e., *Andesaurus*, *Argentinosaurus*, *Mendozasaurus*, *Phuwiangosaurus*, *Malarguesaurus*).

All most parsimonious trees recovered *Chubutisaurus insignis* as the basal-most member of Somphospondyli (sensu Wilson and Sereno, 1998) (Fig. 17). In the present analysis, Somphospondyli is supported by only one unambiguous synapomorphy: The scapular blade of *Chubutisaurus* and more derived taxa forms an angle of approximately 45° with respect to the scapularoacoid articulation (character 188, state 1).

The exclusion of *Chubutisaurus* from more derived somphospondylians (Fig. 17) is supported by two unambiguous synapomorphies recovered for this group: presence of prespinal lamina (character 125, state 1), and divided and well-

differentiated distal humeral condyles (character 209, state 0). One of the new elements of *Chubutisaurus* described here (MPEF-PV 1129/D) lacks a prespinal lamina, the plesiomorphic condition found in basal macronarians and non-neosauropods (e.g., *Camarasaurus*, *Tehuelchesaurus*, *Patagosaurus*). *Chubutisaurus* and more basal forms have flattened humeral distal condyles (character 209, state 1; Fig. 10A, B). In addition to these two unambiguous synapomorphies, missing data in *Andesaurus* or *Wintonotitan* produces five more ambiguous synapomorphies: absence of an infradiapophyseal pneumatic foramen in dorsal vertebrae (character 102, state 0); the anterior surface of the dorsal neural arches are flat or shallowly excavated (character 108, state 0); the pcdl is ventrally expanded as product of an accessory pcdl in titanosaurs (character 134, state 1; Salgado et al., 1997); the presence of ventrolateral ridges in anterior and middle caudal vertebrae (character 149, state 1); and the scapular glenoid is strongly beveled medially (character 192, state 1) in titanosaurs (Wilson, 2002).

Up to now different node-based and stem-based phylogenetic definitions have been proposed for Titanosauria (see for example Upchurch et al., 2004; Wilson and Sereno, 1998). Most stem-based definitions use *Euhelopus zdanskyi* as an external specifier. Due to the position of *Euhelopus* obtained here (Fig. 17), we prefer to use a node-based definition of Titanosauria as was recently proposed by Wilson and Upchurch (2003) and Curry Rogers (2005): *Andesaurus delgadoi* (Calvo and Bonaparte, 1991), *Saltasaurus loricatus* (Bonaparte and Powell, 1980), their most recent common ancestor, and all descendants. Following this definition, Titanosauria is supported by one unambiguous synapomorphy: absence of a strongly developed ventromedial process in the scapula (character 202, state 0). This process seems to be highly developed only in titanosaur outgroups (i.e., *Chubutisaurus*, *Wintonotitan*, *Ligabuesaurus*). Another possible synapomorphy of Titanosauria, not preserved in *Ligabuesaurus* and therefore recovered as an ambiguous synapomorphy, is the short ischial blade present in *Andesaurus*

and more derived forms, in which the blade does not surpass the pubic peduncle. Part of the problem related to choosing a phylogenetic definition for Titanosauria is found in the incompleteness of basal titanosaurs and related forms. Given the new information presented here, *Chubutisaurus* represents one of the most informative taxa of basal titanosauriforms, having almost 46% of scored characters in the data matrix presented here.

In order to test the robustness of the phylogenetic results obtained here, Bremer support values were calculated in TNT. Only a few basal nodes were recovered with Bremer values higher than one (Fig. 17). Absolute bootstrap (with standard replacement) and jackknife values (with 36% of removal probability) were examined, but both failed to find values higher than 50% in any macronarian node. Given the lack of robustness for macronarian relationships, the character support of the phylogenetic position of *Chubutisaurus* was examined using constrained parsimony analyses that forced this taxon in alternative positions, following an identical heuristic search to that described above. Only two extra steps are needed to place *Chubutisaurus* outside Titanosauriformes (as sister group to Titanosauriformes). However, forcing *Chubutisaurus* to take an even more basal position requires a minimum of six extra steps (as the sister group to the clade formed by *Tehuelchesaurus*, *Galvesaurus*, *Tastavinsaurus*, and *Venenosaurus*). On the other hand, when *Chubutisaurus* is forced to take a more derived position, the resulting trees are markedly less parsimonious. If *Chubutisaurus* is positioned as the sister taxon to *Andesaurus* and more derived titanosauriforms, six extra steps are needed, and nine extra steps are required to place *Chubutisaurus* within Titanosauria. In sum, although there is some uncertainty regarding to the position of *Chubutisaurus* and a slightly more basal position is only marginally less parsimonious, the present data set clearly rejects topologies that depict it as the sister taxon of Titanosauria, within Titanosauria, or as a basal camarasauromorph.

Histological Features

The mid-diaphyseal histological sections described here provide valuable information regarding the life history and the ontogenetic stage of the only known specimen of *Chubutisaurus*. Remains of interstitial fibrolamellar bone tissue in some areas of the cortex indicate active growth and osteogenesis, at least in some periods of the ontogeny. Due to the high remodeling of the primary bone, it is not possible to determine if the fibrolamellar bone tissue was deposited continuously or it was interrupted by lines of arrested growth (LAGs) and/or annuli. For this reason, we cannot establish if *Chubutisaurus* had a cyclical growth strategy or grew continually, at a constant, rapid rate throughout the year. Regarding the presence of an OCL in the studied samples, this structure is usually formed at the external cortex of animals that have reached their mature body size and is typical of vertebrates with determinate growth (Chinsamy-Turan, 2005). Well-developed OCL, such as that described in *Chubutisaurus*, have been identified in several sauropod taxa, including *Apatosaurus* (Curry Rogers, 1999), *Janenschia robusta*, *Dicraeosaurus* sp., *Brachiosaurus brancai* (Sander, 2000), *Europasaurus holgeri* (Sander et al., 2006), and *Alamosaurus sanjuanensis* (Woodward and Lehman, 2009), revealing that the determinate growth is a widespread feature in neosauropod dinosaurs. Besides the deposition of an OCL at the femoral cortex of *Chubutisaurus*, the degree of secondary reconstruction also indicates an advanced ontogenetic stage in the specimen. Following the definition of successive histological ontogenetic stages in sauropod dinosaurs proposed by Klein and Sander (2008), our sample coincides with the most advanced histological ontogenetic stage, which is characterized by an almost complete remodeling of the primary cortex by secondary osteons.

CONCLUSIONS

The complete osteological study, together with the new elements described here, allows us to make a solid diagnosis of *Chubutisaurus*. The particular combination of plesiomorphic and apomorphic characters observed in this taxon is reflected in the phylogenetic results that depict this taxon in a basal position among titanosauriforms, as the basal-most somphospondyl. Although low support values characterize all macronarian nodes, the present phylogenetic data set clearly rejects the inclusion of *Chubutisaurus* in Titanosauria or even as its sister group. Given its phylogenetic affinities and the fact that it currently is one of the most complete titanosaur outgroups, its inclusion in phylogenetic analyses is critical to correctly diagnose Titanosauria and to understand the origins and early evolution of this clade.

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LITERATURE CITED

- Anselmi, G., M. T. Gamba, and J. L. Panza. 2004. Hoja Geológica 4369-IV, Los Altares. Provincia del Chubut. Instituto de Geología y Recursos Minerales, Servicio Geológico Minero Argentino. Boletín 312, 98 pp.
- Apesteuña, S. 2005a. Evolution of the hyposphene-hypantrum complex within Sauropoda; pp. 248–267 in V. Tidwell and K. Carpenter (eds.), *Thunder-Lizards: The Sauropodomorph Dinosaurs*. Indiana University Press, Bloomington, Indiana.
- Apesteuña, S. 2005b. Evolution of the titanosaur metacarpus; pp. 321–345 in V. Tidwell and K. Carpenter (eds.), *Thunder-Lizards: The Sauropodomorph Dinosaurs*. Indiana University Press, Bloomington, Indiana.
- Bonaparte, J. F. 1986. Les dinosaures (Carnosaures, Allosauridés, Sauropodes, Cétiosauridés) du Jurassique moyen de Cerro Cándor (Chubut, Argentine). *Annales de Paléontologie* 72:325–386.
- Bonaparte, J. F. 1996. Cretaceous tetrapods of Argentina. *Münchener Geowissenschaftliche Abhandlungen A* 30:73–130.
- Bonaparte, J. F., and R. Coria. 1993. Un nuevo y gigantesco saurópodo titanosaurio de la Formación Río Limay (Albiano-Cenomaniano). *Ameghiniana* 30:271–282.
- Bonaparte, J. F., B. J. González Riga, and S. Apesteuña. 2006. *Ligabuesaurus leanzai* gen. et sp. nov. (Dinosauria, Sauropoda), a new titanosaur from the Lohan Cura Formation (Aptian, Lower Cretaceous) of Neuquén, Patagonia, Argentina. *Cretaceous Research* 27:364–376.
- Borsuk-Bialynicka, M. 1977. A new camarasaurid sauropod *Opisthocoelecaudia skarzynskii* gen. n. sp. n. from the Upper Cretaceous of Mongolia. *Paleontologia Polonica* 37:5–64.
- Calvo, J. O., and J. F. Bonaparte. 1991. *Andesaurus delgadoi* gen. et sp. nov. (Saurischia-Sauropoda), dinosaurio Titanosauridae de la Formación Río Limay (Albiano-Cenomaniano), Neuquén, Argentina. *Ameghiniana* 28:303–310.

- Calvo, J., J. Porfiri, B. González Riga, and A. W. Kellner. 2008. A new Cretaceous terrestrial ecosystem from Gondwana with the description of a new sauropod dinosaur. *Anais da Academia Brasileira de Ciências* 79:529–541.
- Campos, D. A., A. W. Kellner, R. J. Bertini, and R. M. Santucci. 2005. On a titanosaurid (Dinosauria, Sauropoda) vertebral column from the Bauru Group, Late Cretaceous of Brazil. *Arquivos do Museu Nacional, Rio de Janeiro* 63:565–593.
- Canudo, J. I., R. Royo-Torres, and G. Cuenca-Bescós. 2008. A new sauropod: *Tastavinsaurus sanzi* gen. et sp. nov. from the Early Cretaceous (Aptian) of Spain. *Journal of Vertebrate Paleontology* 28:712–731.
- Chinsamy, A., and M. A. Raath. 1992. Preparation of fossil bone for histological examination. *Paleontologia Africana* 29:39–44.
- Chinsamy-Turan, A. 2005. *The Microstructure of Dinosaur Bone: Deciphering Biology with Fine-Scale Techniques*. Johns Hopkins University Press, Baltimore, 195 pp.
- Codignotto, J., F. Nullo, J. Panza, and C. Proserpio. 1978. Estratigrafía del Grupo Chubut entre Paso de Indios y Las Plumas, Provincia del Chubut, Argentina. VII Congreso Geológico Argentino, Neuquén, 9–15 April 1978. *Actas* 1:471–480.
- Cortiñas, J. S. 1996. La Cuenca de Somuncurá—Cañadón Asfalto: Sus límites, ciclo evolutivo del relleno sedimentario y posibilidades exploratorias. XIII Congreso Geológico Argentino y III Congreso Exploración de Hidrocarburos, Buenos Aires, 13–18 October 1996. *Actas* 1:147–163.
- Curry Rogers, K. A. 1999. Ontogenetic histology of *Apatosaurus* (Dinosauria: Sauropoda): new insights on growth rates and longevity. *Journal of Vertebrate Paleontology* 19:654–665.
- Curry Rogers, K. 2005. Titanosauria, a phylogenetic overview; pp. 50–103 in K. Curry Rogers and J. A. Wilson (eds.), *The Sauropods: Evolution and Paleobiology*. University of California Press, Berkeley, California.
- Curry Rogers, K., and C. A. Forster. 2001. The last of the dinosaur titans: a new sauropod from Madagascar. *Nature* 412:530–534.
- del Corro, G. 1975. Un nuevo saurópodo del Cretácico *Chubutisaurus insignis* gen. et sp. nov. (Saurischia-Chubutisauridae nov.) del Cretácico Superior (Chubutiano), Chubut, Argentina, 12–16 August 1974. *Actas I Congreso Argentino de Paleontología y Bioestratigrafía, Tucumán*. 2:229–240.
- Erickson, G. M. 2005. Assessing dinosaur growth patterns: a microscopic revolution. *Trends in Ecology and Evolution* 20:677–684.
- Francillon-Vieillot, H., V. de Buffrénil, J. Castanet, J. Géraudie, J. F. Meunier, J. Y. Sire, L. Zylberberg, and A. J. de Ricqlès. 1990. Microstructure and mineralization of vertebrate skeletal tissues; pp. 471–530 in J. G. Carter (ed.), *Skeletal Biomineralization: Patterns, Process and Evolutionary Trends*. Van Nostrand Reinhold, New York.
- Geuna, S. E., R. Somoza, H. Vizán, E. G. Figari, and C. A. Rinaldi. 2000. Paleomagnetism of Jurassic and Cretaceous rocks in central Patagonia: a key to constrain the timing of rotations during the breakup of southwestern Gondwana. *Earth and Planetary Science Letters* 181:145–160.
- Gilmore, C. W. 1946. Reptilian fauna of the North Horn Formation of central Utah. U.S. Geological Survey Professional Paper 210:29–51.
- Goloboff, P. A., S. Farris, and K. Nixon. 2008a. TNT: Tree Analysis Using New Technology, vers. 1.1 (Will Henning Society Edition). Program and documentation available at www.Zmuc.Dk/Public/Phylogeny/Tnt. Accessed November 22, 2009.
- Goloboff, P. A., S. Farris, and K. Nixon. 2008b. TNT, a free program for phylogenetic analysis. *Cladistics* 24:774–786.
- Gomani, E. M. 2005. Sauropod dinosaurs from the Early Cretaceous of Malawi, Africa. *Palaeontologia Electronica* 1:1–37.
- González Riga, B. J. 2003. A new titanosaur (Dinosauria, Sauropoda) from the Upper Cretaceous of Mendoza Province, Argentina. *Ameghiniana* 40:155–172.
- González Riga, B., E. Previtara, and C. Pirrone. 2009. *Malguesaurus florenciae* gen. et sp. nov., a new titanosauriform (Dinosauria, Sauropoda) from the Upper Cretaceous of Mendoza, Argentina. *Cretaceous Research* 30:135–148.
- Harris, J. D. 2006. The significance of *Suuwassea emiliae* (Dinosauria: Sauropoda) for flagellicaudatan intrarelationships and evolution. *Journal of Systematic Palaeontology* 4:185–198.
- Hocknull, S. A., M. A. White, T. R. Tischler, A. G. Cook, N. D. Calleja, T. Sloan, and D. A. Elliott. 2009. New mid-Cretaceous (latest Albian) dinosaurs from Winton, Queensland, Australia. *PLoS ONE* 4:e6190.
- Janensch, W. 1914. Übersicht über die Wirbeltierfauna der Tendaguru-Schichten, nebst einer Kurzen Charakterisierung der neu aufgestellten Arten von Sauropoden. *Archiv für Biontologie* 3:81–110.
- Janensch, W. 1950. Die Wirbelsäule von *Brachiosaurus brancai*. *Paleontographica*. 3(Supplement 7):27–93.
- Klein, N., and P. M. Sander. 2008. Ontogenetic stages in the long bone histology of sauropod dinosaurs. *Paleobiology* 34:247–263.
- Lehman, T. M., and A. B. Coulson. 2002. A juvenile specimen of the sauropod dinosaur *Alamosaurus sanjuanensis* from the Upper Cretaceous of Big Bend National Park, Texas. *Journal of Paleontology* 76:156–172.
- Makovicky, P. 1997. Postcranial axial skeleton, comparative anatomy; pp. 579–590 in P. Currie and K. Padian (eds.), *Encyclopedia of Dinosaurs*. Academic Press, San Diego.
- Marsh, O. C. 1877. Notice of a new gigantic dinosaur. *American Journal of Science (Series 3)* 14:87–88.
- Marsh, O. C. 1878. Principal characters of American Jurassic dinosaurs. Pt. I. *American Journal of Science* 16:411–416.
- Martin, V., V. Suteethorn, and E. Buffetaut. 1999. Description of the type and referred material of *Phuwiangosaurus sirindhornae* Martin, Buffetaut and Suteethorn, 1994, a sauropod from the Lower Cretaceous of Thailand. *Oryctos* 2:39–91.
- Martínez, R. D., O. Gimenez, J. Rodríguez, M. Luna, and M. C. Lamanna. 2004. An articulated specimen of the basal titanosaurian (Dinosauria: Sauropoda) *Epachthosaurus sciutoi* from the Early Cretaceous Bajo Barreal Formation of Chubut Province, Argentina. *Journal of Vertebrate Paleontology* 24:107–120.
- Osborn, H. F., and C. C. Mook. 1921. *Camarasaurus*, *Amphicoelias* and other sauropods of Cope. *Memoirs of the American Museum of Natural History* 3:247–387.
- Ostrom, J. H., and J. S. McIntosh. 1966. *Marsh's Dinosaurs. The Collections from Como Bluff*. Yale University Press, New Haven, Connecticut, 388 pp.
- Powell, J. E. 1992. Osteología de *Saltasaurus loricatus* (Sauropoda-Titanosauridae) del Cretácico Superior del noroeste Argentino; pp. 166–230 in J. L. Sanz and A. D. Buscalioni (eds.), *Los dinosaurios y su entorno biótico*. Instituto “Juan Valdes,” Cuenca, Spain.
- Proserpio, C. A. 1987. Descripción geológica de la hoja 44e, Valle General Racedo. *Boletín de la Dirección Nacional de Minería y Geología* 210:1–102.
- Rauhut, O. W. M. 2002. Dinosaur evolution in the Jurassic: a South American perspective. *Journal of Vertebrate Paleontology* 22(3, Supplement):89A.
- Rauhut, O. W. M., G. Cladera, P. Vickers-Rich, and T. H. Rich. 2003. Dinosaur remains from the Lower Cretaceous of the Chubut Group, Argentina. *Cretaceous Research* 24:487–497.
- Rauhut O. W. M., K. Remes, R. Fechner, G. Cladera, and P. Puerta. 2005. Discovery of a short-necked sauropod dinosaur from the Late Jurassic period of Patagonia. *Nature* 435:670–672.
- Rich, T. H., P. Vickers-Rich, O. Gimenez, R. Cúneo, P. Puerta, and R. Vacca. 1999. A new sauropod dinosaur from Chubut Province, Argentina. *National Science Museum Monographs* 15:61–84.
- Romer, A. S. 1956. *Osteology of the Reptiles*. University of Chicago Press, Chicago, Illinois, 772 pp.
- Rose, P. 2007. A new titanosauriform sauropod (Dinosauria: Saurischia) from the Early Cretaceous of Central Texas and its phylogenetic relationships. *Palaeontologia Electronica* 10:1–65.
- Royo-Torres, R. 2009. El saurópodo de Peñarroya de Tastavins. Instituto de Estudios Turolenses-Fundación Conjunto Paleontológico de Teruel-Dinópolis, *Monografías Turolenses* 6, 548 pp.
- Salgado, L. 1993. Comments on *Chubutisaurus insignis* del Corro (Saurischia, Sauropoda). *Ameghiniana* 30:265–270.
- Salgado, L., and C. Azpilicueta. 2000. Un nuevo saltasaurino (Sauropoda, Titanosauridae) de la provincia de Río Negro (Formación Allen, Cretácico Superior), Patagonia, Argentina. *Ameghiniana* 37:259–264.
- Salgado, L., and R. A. Coria. 2009. *Barrosasaurus casamiquelai* gen. et sp. nov., a new titanosaur (Dinosauria, Sauropoda) from the Anacleto Formation (Late Cretaceous: early Campanian) of Sierra Barrosa (Neuquén, Argentina). *Zootaxa* 2222:1–16.
- Salgado, L., S. Apesteguía, and S. E. Heredia. 2005. A new specimen of *Neuquensaurus australis*, a Late Cretaceous saltasaurine

- titanosaur from north Patagonia. *Journal of Vertebrate Paleontology* 25:623–634.
- Salgado, L., R. A. Coria, and J. O. Calvo. 1997. Evolution of titanosaurid sauropods. I: phylogenetic analysis based on the postcranial evidence. *Ameghiniana* 34:3–32.
- Sander, M. P., O. Mateus, L. Thomas, and N. Knötschke. 2006. Bone histology indicates insular dwarfism in a new Late Jurassic sauropod dinosaur. *Nature* 441:739–741.
- Sander, P. M. 2000. Long bone histology of the Tendaguru sauropods: implications for growth and biology. *Paleobiology* 26:466–488.
- Seeley, H. G. 1887. On the classification of the fossil animals commonly called Dinosauria. *Proceedings of the Royal Society of London* 43:165–171.
- Taylor, M. P. 2009. A re-evaluation of *Brachiosaurus altiithorax* Riggs 1903 (Dinosauria, Sauropoda) and its generic separation from *Girafatitan brancai* (Janensch 1914). *Journal of Vertebrate Paleontology* 29:787–806.
- Tidwell, V., K. Carpenter, and S. Meyer. 2001. New titanosauriform (Sauropoda) from the Poison Strip Member of Cedar Mountain Formation (Lower Cretaceous), Utah; pp. 139–165 in D. Tanke and K. Carpenter (eds.), *Mesozoic Vertebrate Life*. Indiana University Press, Bloomington, Indiana.
- Upchurch, P. 1998. The phylogenetic relationships of sauropod dinosaurs. *Zoological Journal of the Linnean Society* 124:43–103.
- Upchurch, P., and J. Martin. 2003. The anatomy and taxonomy of *Cetiosaurus* (Saurischia, Sauropoda) from the Middle Jurassic of England. *Journal of Vertebrate Paleontology* 23:208–231.
- Upchurch, P., P. M. Barrett, and P. Dodson. 2004. Sauropoda; pp. 259–354 in D. B. Weishampel, H. Osmólska, and P. Dodson (eds.), *The Dinosauria*, 2nd edition. University of California Press, Berkeley and Los Angeles.
- Wedel, M. J., R. L. Cifelli, and K. Sanders. 2000. *Sauroposeidon proteles*, a new sauropod from the Early Cretaceous of Oklahoma. *Journal of Vertebrate Paleontology* 20:109–114.
- Wilson, J. A. 1999. A nomenclature for vertebral laminae in sauropods and other saurischian dinosaurs. *Journal of Vertebrate Paleontology* 19:639–653.
- Wilson, J. A. 2002. Sauropod dinosaur phylogeny: critique and cladistic analysis. *Zoological Journal of the Linnean Society* 136:215–275.
- Wilson, J. A., and P. Upchurch. 2003. A revision of *Titanosaurus* Lydekker (Dinosauria-Sauropoda), the first dinosaur genus with a “Gondwanan” distribution. *Journal of Systematic Palaeontology* 1:125–160.
- Wilson, J. A., and P. Upchurch. 2009. Redescription and reassessment of the phylogenetic affinities of *Euhelopus zdanskyi* (Dinosauria: Sauropoda) from the Early Cretaceous of China. *Journal of Systematic Palaeontology* 7:199–239.
- Wilson, J. A., and P. C. Sereno. 1998. Early evolution and higher-level phylogeny of sauropod dinosaurs. *Memoir of the Society of Vertebrate Paleontology* 5:1–68.
- Wiman, C. 1929. Die kreide-dinosaurier aus Shantung. *Palaeontologia Sinica (Series C)* 6:1–67.
- Woodward, H. N., and T. M. Lehman. 2009. Bone histology of and microanatomy of *Alamosaurus sanjuanensis* (Sauropoda: Titanosauria) from the Maastrichtian of Big Bend National Park, Texas. *Journal of Vertebrate Paleontology* 29:807–821.

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