A new giant basal titanosaur sauropod in the Upper Cretaceous (Coniacian) of the Neuquén Basin, Argentina

Leonardo S. Filippi a, *, Leonardo Salgado b, c, Alberto C. Garrido d, e

a Museo Municipal Argentino Urquiza, Jujuy y Chaco s/n, 8319 Rincon de los Sauces, Neuquén, Argentina
b CONICET, Argentina
c Instituto de Investigación en Paleobiología y Geología, Universidad Nacional de Río Negro-Conicet, Av. Gral. J. A. Roca 1242, 8322 General Roca, Río Negro, Argentina
d Museo Provincial de Ciencias Naturales “Profesor Dr. Juan A. Olsacher”, Dirección Provincial de Minería, Eteléz y Ejército Argentino, 8340 Zapala, Neuquén, Argentina
e Departamento Geología y Petróleo, Facultad de Ingeniería, Universidad Nacional del Comahue, Buenos Aires 1400, Neuquén 8300, provincia del Neuquén, Argentina

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Abstract
A new basal sauropod titanosaur, Kaijutitan maui gen. et sp. nov., is described. The holotype of this species, which comes from the Sierra Barrosa Formation (upper Coniacian, Upper Cretaceous), consists of cranial, axial, and appendicular elements presenting an unique combination of plesiomorphic and apomorphic characters. The most notable characteristic observed in Kaijutitan is the presence of anterior cervical vertebrae with bifid neural spines, a condition that would have evolved several times among sauropods. The phylogenetic analysis places Kaijutitan as a basal titanosaur, the sister taxon of Epachthosaurus + Eutitanosauria. The new species supports the coexistence, in the Late Cretaceous (Turonian-Santonian), of basal titanosaurs and eutitanosaurian sauropods, at least in Patagonia.

1. Introduction
Sauropods are among the most abundant non-avian dinosaurs in the fossil record. These quadrupedal megaherbivores include the largest terrestrial animals that have ever existed on the planet (Wilson, 2002; Wilson and Curry Rogers, 2005; Barrett et al., 2010; Sander et al., 2011), with truly gigantic forms, such as the basal titanosauriforms Brachiosaurus altithorax Riggs (1903), Giraffatitan brancai Janensch (1914) and Ruyangosaurus giganteus Lu et al. (2009), and the titanosaur Argentinosaurus huinculensis Bonaparte and Coria (1993), Puertasaurus reuili Novas et al. (2005), Futalognkosaurus dukei Calvo et al. (2007a,b), Dreadnoughtus schrani Lacovara et al. (2014), Notocolossus gonzalezparejasi González Riga et al. (2016) and Patagotitan mayorum Carballido et al. (2017). Their remains have been found on all continents, including Antarctica (Cerda et al., 2012). Sauropods, defined as the most inclusive clade that includes Saltasaurus loricatus but not Melanorosaurus readi (Yates, 2007) would have originated in the Late Triassic and predominated up to end of the Cretaceous (Upchurch et al., 2004); however, only titanosaurs survived until the end of the Cretaceous. This group of sauropods reached its greatest diversity in Gondwana, especially in South America (Bonaparte, 1986; Powell, 2003).

Late Cretaceous continental deposits in the area of Rincon de los Sauces (Neuquén, Argentina) have yielded, in the last fifteen years, numerous and important findings of titanosaur sauropods (Calvo and González Riga, 2003; Calvo et al., 2007b; Coria et al., 2013; Filippi and Garrido, 2008; Filippi et al., 2011a,b; 2013; González Riga, 2003, 2005). Here, we present a new basal, giant titanosaur, which is the first basal titanosaur described for the Coniacian (Upper Cretaceous) of North Patagonia.

The holotypic material of the new species was found by a team of researchers from the Museo Municipal “Argentino Urquiza” and the Museo Provincial de Ciencias Naturales “Prof. Dr. Juan
Oltsacher”. The new species, one of the few sauropods from the Sierra Barrosa Formation, preserves part of the skull, which is virtually unknown in large titanosaurians.

2. Materials and methods

2.1. Anatomical abbreviations

al, accessory lamina; alp, anterolateral process; amp, ante-
romedial process; ap, acromion process; asp, ascending process; Bsp, basi-epiphysial, bpi, basipterygoid process; bt, basal tuber; ca, cristata antotica; cap, capitulum; c, crest; cc, cranial cavity; cdl, centrodiaphyseal lamina; cf, coracoid foramen; cnc, enial crest; cprf, centropostzygapophyseal fossa; cprf, centroprezygapophyseal fossa; cr, cervical rib; cr.pro; crista prootica; ct, cista tuberalis; dp, diaphysis; dpc, deltopectoral crest; eo, exoccipital, Eo-op, exoccipital-opisthotic complex; ep, epio-
physes; eprl, epiphysial-prezygapophyseal lamina; f, frontal; fh, femoral head; fo, foramen; ft, fourth trochanter; gc, ghenoide cavity; ic, internal carotid; icp, pterosphenoid; if, infrapostzygapophyseal fossa; ir, interosseous ridge; lb, lateral bulge; lshp, laterosphenoid; lpp, lateroposterior process; mdcpml, medial division of the centrodiaphyseal lamina; mf, metotic foramen; mt, medial tubercle; nc, neurapophyes; nc, nasal neural; nc, neural spine; oc, occipital condyle; of, oval fenestra; ol, olecranon; orb, orbitosphenoid; p, parietal; pas, pascalang ear surface; pcdl, posteri or centrodiaphyseal lamina; pcpl, posterior centroparaphyseal lamina; plb, posterolateral bulge; pnf, pneumatic foramen; po, postorbital; podf, postzygodiaphyseal fossa; podl, postzygodiaphyseal lamina; pop, parapophyseal process; posl, postspinal lamina; poz, postzygapophyseal process; pp, parapophysis; ppdp, pubic peduncle; prap, preacetabular process; prs, prezygoepipophyseal lamina; prs, prootico; prsl, prespinal lamina; prz, prezygapophysis; ps, pre-
sonphoid; ptc, pituitary cavity; rac, radial condyle; scb, scapular blade; sdf, spinodiaphyseal fossa; spof, spinopostzygapophyseal fossa; spof, spinoprezygapophyseal fossa; spol, spinopostzygapophyseal lamina; sprl, spinoprezygapophyseal lamina; t, tuberosity; tp, transverse process; tpdl, intraprezygapophyseal lamina; tpri, intraprezygapophyseal lamina; ts, trochanteric shelf; tu, tuberculum; ulc, ulnar condyle; vf, ventral fossa; vk, ventral keel.

2.2. Institutional abbreviations

FWMSH, Fort Worth Museum of Science and History, Fort Worth, Texas, U.S.A.; MAU-Pv-CM, Museo Municipal Argentino Urquiza, Paleontología de Vertebrados, Canadón Mistriga, Neuquén, Argentina; MGCPFD, Museo de Geología y Paleontología del Instituto de Formación Docente Continua de General Roca, Río Negro; MMl, Museo Municipal de Lamarque, Río Negro, Argentina; MPCA, Museo Provincial Carlos Ameghino, Cipolletti, Río Negro, Argentina; MUCPv, Museo Universidad Nacional del Comahue, Neuquén, Argentina; NMMNH, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, U.S.A.; SMA, Sau-
riermuseum Aathal, Aathal, Switzerland.

3. Systematic paleontology

Saurischia Seeley, 1888
Sauropoda Marsh, 1878
Titanosauriformes Salgado et al., 1997
Sauropodomorpha Wilson and Sereno, 1998
Titanosauria Bonaparte and Coria, 1993

Kaijutitan maui gen. et sp. nov.

Derivation of the name. From Kaiju, Japanese word that means “strange beast”, usually translated into English as “monster”, and titan, from the Greek “giant”. The species name maui refers to the acronym of the Museo Municipal Argentino Urquiza, Rincon de los Sauces, Neuquén, Argentina.

Holotype. MAU-Pv-CM-522. (Figs. 2-10) Incomplete neurocranium MAU-Pv-CM-522/1 composed of supraoccipital, exoccipitals, left parapophysis process, left exoccipital-opisthotic-prootic complex, left laterosphenoid and orbitosphenoid, basioccipital-basiphenoid complex; MAU-Pv-CM-522/2, anterior cervical vertebra; MAU-Pv-CM-522/9, incomplete posterior cervical vertebra: proximal fragment of cervical rib; MAU-Pv-CM-522/6, fragments from cervical ribs; MAU-Pv-CM-522/11, left second dorsal; MAU-Pv-CM-522/8, incomplete dorsal rib; MAU-Pv-CM-522/18, fragment of dorsal rib; MAU-Pv-CM-522/35, anterior caudal vertebra; MAU-Pv-CM-522/17, left sternal plate; MAU-Pv-

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The specimen of Kaijutitan maui gen. et sp. nov. was dis-articulated but its bones associated and distributed in an area of 20 m².

The fossiliferous level is characterized by a monotonous suc-
cession of massive and reddish mudstones, in which thin horizons (less than 5 cm of thickness) alternate with greenish limestones and tabular sandy bodies (less than 12 cm of thickness) charac-
terized by the presence of undulitic stratification, horizontal
stratification and/or low-angle cross-stratification, which are attributed to floodplain deposits.

4. Description

4.1. Skull

Cranial elements of this specimen include the complete neurocranium (MAU-Pv-CM-522/1) (Fig. 2), composed of the supraoccipital, exoccipital, left paraoccipital process, left exoccipital-opisthotic-prootic complex, left laterosphenoid and orbitosphoid, and basioccipital-basisphenoid complex. The impossibility of recognizing clear sutures between the different bony elements that make it up indicates an ontogenetic adult stage of the specimen.

4.1.1. Supraoccipital

The supraoccipital (Fig. 2A-B) is completely fused to the exoccipitals, forming, as in other sauropods, the posterodorsal margin of the skull and the dorsal margin of the foramen magnum. Although the borders of the foramen magnum are badly preserved, a subcircular contour is inferred, similar to that of the basal sauropod *Shunosaurus* (Chatterjee and Zheng, 2002), the basal macronarian *Europosaurus* (Marpmann et al., 2014; Fig. 13A) and the basal titanosauriform *Giraffatitan brancai* (Paul, 1988; Janensch, 1935, Fig. 2). Instead, in titanosaurians as *Antarctosaurus* (Huene, 1929); *Saltasaurus* (Bonaparte and Powell, 1980); *Bonatitan* (Martinelli and Foriasepi, 2004); *Muyelensaurus* (Calvo et al., 2007b); *Pitaksaurus* (Filippi and Garrido, 2008); *Narambuennatitan* (Filippi et al., 2011b); *Rapetosaurus* (Curry Rogers and Forster, 2004); *Nemegtosaurus* (Nowinski, 1971; Wilson, 2005); *Vahiny* (Curry Rogers and Wilson, 2014), the dorsoventral diameter is markedly larger than the transverse diameter. In *Kaijutitan*, as in *Narambuennatitan*, the height of the supraoccipital is slightly greater than the dorsoventral diameter of the foramen magnum (see Table S1). In turn, in *Saltasaurus* (Powell, 1992, 2003) and *Jainosaurus* (Wilson et al., 2009), the height of the supraoccipital is twice the height of the foramen magnum. The supraoccipital protuberance, laterally limited by deep depressions, is lower and wider than in titanosaurs such as *Bonatitan*, *Narambuennatitan*, *Sarmientosaurus* (Martinez et al., 2016) and *Tapuiasaurus* (Zaher et al., 2011; Wilson et al., 2016), slightly surpassing the dorsal border of the exoccipitals. In *Jainosaurus* (Wilson et al., 2009), *Phuwiangosaurus* (Suteethorn et al., 2009) and the MML-194 specimen (García et al., 2008), the supraoccipital protuberance is relatively narrow and prominent. The supraoccipital lacks a midline ridge and a medial sulcus present in titanosaurians such as *Quaesitosaurus* (Kurzanov and Bannikov, 1983), *Saltasaurus*, *Rapetosaurus*, *Bonatitan*, *Muyelensaurus* and the MML-194 specimen (García et al., 2008).

4.1.2. Exoccipital–opisthotic–prootic complex

The prootic is completely fused with the exoccipital-opisthotic complex. A shallow prominence on the dorsolateral margin of the foramen magnum is observed as in the dicraeosaurid *Amargasaurus cazui* (Salgado y Calvo, 1992), and other titanosaurian as
Fig. 2. Skull of *Kaijutitan maui* gen. et sp. nov. MAU-Pv-CM-522/1 (A-B), in posterior, (C-D), anterior, (E-F), lateral, (G-H), and ventral views. Scale bar: 10 cm.
Quaesitosaurus, Nemegtosaurus, Saltasaurus, MUCPv-334 specimen (Calvo and Kellner, 2006) and MML-194 specimen (García et al., 2008). This structure was interpreted as a ligament insertion area probably related to the neck (Calvo and Kellner, 2006), while other authors interpreted it as an articular surface for the proatlas (Berman and Jain, 1982; Salgado and Calvo, 1992; Wilson et al., 2005). The rugose occipital condyle (Fig. 2A-B) is noticeably larger than the foramen magnum (see Table S12), a condition present in the eusauropod Turiasaurus riodevensis (Royo-Torres and Upchurch, 2012; Fig. 3C and 5A), basal sauropods such as Shunosaurus lii (Chatterjee and Zheng, 2002; 5B) and titanosaurs such as Nemegtosaurus and Quaesitosaurus. In contrast, a similar proportion can be observed in titanosaurs such as Bonatitan, MUCPv-334 specimen (Calvo and Kellner, 2006, Fig. 1A), MGPID-FR-118 specimen (Paulina Carabajal and Salgado, 2007, Fig. 2D) and, to a lesser extent, in Antarcotosaurus. Only the left paraoccipital process, incomplete distally, has been preserved; it is robust, wide and lateroventrally curved. Despite it is incomplete, the preserved morphology allows to infer the presence of the ventral non-articular process that characterizes most titanosaurs. Anterior to the position where the exit of cranial nerve XII should be (this foramen is not preserved), the ventral edge of the paraoccipital process, Fig. 7Cute ridge that corresponds to the ventral form branch of the opisthotic. This ridge separates this last foramen from the metotic foramen, which is big and elliptical, being visible in lateral view, and corresponding to the exit of cranial nerves IX, X, XI, and the jugular vein (Chatterjee and Zheng, 2002, 2005). Anterior to the metotic foramen and separated by a thin wall of bone, there is the oval fenestra (Fig. 2E-F), as in the basal macronarian Euro-Saurus (Marpmann et al., 2014, Fig. 13B) and many titanosaurids (Powell, 2003; Martinelli and Forasiepi, 2004; Paulina Carabajal and Salgado, 2007; García et al., 2008). It is elliptical and has half of the size of the metotic foramen. On the contrary, in Saltasaurus the oval fenestra opens in the same duct than the metotic foramen (Powell, 2003). The crista prootica (Fig. 2 A-B), although not complete, is inferred to be very pronounced laterally, as observed in MUCPv-334 specimen (Calvo and Kellner, 2006, Fig. 3B), the MML-194 specimen (García et al., 2008; Fig. 1B, D) and in Pitekunsaurus (Filippi and Garrido, 2008; Fig. 3.3). The foramen for the exit of nerve VII is not observable. The poor preservation in the sector between the prootic and the orbitosphenoid makes difficult to locate the exit foramen of nerve V. However, between the orbitosphenoid-laterosphenoid and the prootic, along a crack in the bones (Fig. 2E-F), there is observed a foramen delimited rostrally by the crista antotica and caudally by the crista prootica, which would correspond to the exit foramen of nerve V. All the branches of nerve V (ophthalmic, maxillary and mandibular) would come out through this single opening. The exit foramen of nerve V is bounded rostrally by the crista antotica, which separates it from the exit foramen of nerve III.

4.1.3. Orbitosphenoid—laterosphenoid complex

The left orbitosphenoid-laterosphenoid complex (Fig. 2E-F) articulates caudally with the exoccipital-opisthotic-prootic complex. The presphenoid-parasphenoid complex, which forms the cultriform process, has been partially preserved, allowing the pituitary fossa to be observed anteriorly. The crista antotica presents an anteroposteriorly compressed and posteriorly oriented morphology. The foramen exit of nerve III is located rostrally with respect to the crista antotica, being elliptical as in Bonatitan (Martinelli and Forasiepi, 2004, Fig. 7C), and different from the subcircular foramen present in the MML-194 specimen (García et al., 2008). Rostrally to the exit foramen of nerve III, there is the exit foramen of nerve II, which, although the ventral wall of bone is not preserved, would have been large and subcircular in shape. The foramen of nerve IV is not observable, although it could be included in a crack located on the foramen of nerve III. In Bonatitan, as in the specimen MML-194 (García et al., 2008), this foramen is located between the suture of the orbitosphenoid and the laterosphenoid at the bottom of a rostrocaudally extended fossa, being the smallest of all the foramina preserved (Martinelli and Forasiepi, 2004).

4.1.4. Basiooccipital-basisphenoid complex

This complex forms the floor of the braincase (Fig. 2) and is composed of the occipital condyle, the basal tuberosities, and the proximal portion of the left basipectyroid process. The cultriform process has not been preserved. The occipital condyle is subcircular, rugose, and has a prominent notch on its dorsal aspect, at the level of the ventral edge of the foramen magnum, which gives it a kidney-like appearance (Fig. 2A-B). The occipital condyle presents laterally on the neck, a fossa that does not extend towards the basal tuberosities, as in some sauropods (Tschopp et al., 2015; Character 80). If the supraoccipital is oriented vertically, which is considered the normal orientation (Salgado and Calvo, 1997), and if the foramen magnum is located on in the same plane, the occipital condyle inclines posteroverally, as in most sauropods. As in the MML-194 specimen (García et al., 2008), the angle between the occipital condyle and the supraoccipital is nearly 140°. If the supraoccipital is oriented horizontally, based on the preserved proximal portion of the left element, the basipectyroid processes project ventrally, unlike the MML-194 specimen (García et al., 2008), where they are projected rostroventrally. The proximal portion of left basipectyroid processes presents a subcircular shape in cross-section. Basal tuberosities in Kaijutitan are large both dorsoventrally and mediolaterally, and are clearly differentiated from the basipectyroid processes. The basal tuberosities of Kaijutitan are not bordered laterally. Ventrally they are bordered by a thick lip, as in Rapetosaurus (Curry Rogers and Forster, 2004), Pitekunsaurus, Narambuenatitan, Saltasaurus and MML-194 specimen, Antarcotosaurus, Mongolosaurus (Mannion, 2010), Malawisaurus and Muyelensaurus. The posterior surface of the basal tuberosities are slightly concave, as in Giraffatitan, Phuwiangosaurus (Suteethorn et al., 2009), Malawisaurus (Gomani, 2005), Tapuiasaurus (Wilson et al., 2016), Pitekunsaurus and Narambuenatitan, and different from Camarasaurus and diplodocids, where this surface is convex. The anteroposterior depth of basal tuberosities are nearly the half of the dorsoventral height, as in Brachiosaurus, Rapetosaurus and Lirainosaurus (Díez Díaz et al., 2011), different from Narambuenatitan, Pitekunsaurus, Muye- lensaurus, Nemegtosaurus and Saltasaurus, which present sheet-like basal tuberosities, whose anteroposterior depth is nearly 20% of its dorsoventral height. The transverse width of basal tuberosities of Kaijutitan represents approximately half the diameter of the occipital condyle; they are very prominent and project laterally, as in Pitekunsaurus, although in the latter they are smaller and different from the basal tuberosities of Narambuenatitan (Filippi et al., 2011a, b; Fig. 3C) and Saltasaurus (Powell, 2003; Plate 19, A), where they are reduced. The width of both basal tuberosities (Fig. 2A-B) is almost four times the width of the foramen magnum (see Table S12), which doubles that of basal tita nosauriforms such as Giraffatitan brancai (Janensch, 1935), Phuwiangosaurus sirindhornae (Suteethorn et al., 2009), and many titanosaurids as Pitekunsaurus, Muyelensaurus, Narambuenatitan, Bonatitan, Antarcotosaurus, Sar- mientosaurus, Mongolosaurus (Gilmore, 1933; Mannion, 2011), Saltasaurus, Malawisaurus (Jacobs et al., 1993; Gomani, 2005), Vahliny and Tupaiasaurus (Zaher et al., 2011; Wilson et al., 2016). Unlike Kaijutitan, its diplodocoid sauropods such as in Phuwiangosaurus (Suteethorn et al., 2009), and Suuwassea emiliae (Harris and Dodson, 2004; Fig. 1C3), the tuberosities are very close to each other, being fused in the dicraeosaurid Amargasaurus cazae (Salgado and Bonaparte, 1991, Fig. 1, Salgado and Calvo, 1992, Fig. 1B). However, the...
Fig. 3. Anterior cervical vertebra of Kaijutitan maui gen. et sp. nov. MAU-Pv-CM-522/2 (A-B), in left lateral, (C-D), right lateral, (E-F) anterior, (G-H) and posterior, views. Scale bar: 10 cm.
ventral projection of the tuberosities is less pronounced than in most titanosaurs (e.g. Muyelensaurus, Pitekunsaurus, Antarctosaurus, Rapetosaurus, Sarmientosaurus, Tapuiasaurus). In Kaijuititan, the occipital condyle dorsoventral height/occipital condyle plus basal tuberosities dorsoventral height (Mannion et al., 2013, character 7) is 0.6, as in Nigersaurus and Aptosaurus, whereas in Europasaurus, Mongolosaurus, Giraffatitan and Phuwiangosaurus is greater than 0.6. This value for Kaijuititan may be interpreted as intermediate or even as a primitive state. Between the basal tuberosities, and below the occipital condyle, there is a basisphenoidal depression, similar to that present in Naranbuenaittian (Filippi et al., 2011a; b; Fig. 3C). In Kaijuititan the basisphenoidal depression lacks a well-developed notch in the ventral midline, as is observed in Pitekunsaurus and, incipiently, in the MUCPv-334 specimen (Calvo and Kellner, 2006). The basal tuberosities lacks a foramina, present in Lirainosaurus (Díez Díaz et al., 2011; Fig. 3 and 4). The foramen for the internal carotid artery (Fig. 2C-D and G-H) is located posteriory to the basipterygoid processes, almost at the middle of the distance between these processes and the basal tuberosities, differing from most titanosaurs, where it is located medially to these processes. In Jainsaurus (Wilson et al., 2011a), Lirainosaurus astibiae (Díez Díaz et al., 2011; Figs. 2 and 4) and Vahiny (Curry Rogers and Wilson, 2014; Fig. 3C, D), the foramen is located laterally to the basipterygoid processes, a primitive condition among non-titanosaurian sauropods (Paulina Carabajal, 2012; Curry Rogers and Wilson, 2014), such as Amargasaurus (Paulina Carabajal et al., 2014; Fig. 1B) and Phuwiangosaurus (Suteethorn et al., 2009; Fig. 9D). Because the presphenoid-parasphenoid complex is eroded and incomplete, it is possible to observe the pituitary fossa, partially exposed anteriorly, which is oval transversally and dorsoventrally compressed (Fig. 2C-D). The pituitary cavity is located as in the MML-194 specimen (García et al., 2008, Fig. 1C), anteriorly to the foramina of the internal carotids, which penetrate the cavity posteroventrally.

4.2. Axial skeleton

4.2.1. Cervical vertebrae

A complete and well-preserved anterior cervical vertebra (MAU-Pv-CM-522/2) (Figs. 3 and 4), probably the third one, was found near the neurocranium. Its centrum is opisthocoelous, elongated, with an elongation index lesser than 3.0 (see Table S1A), as in Alamosaurus (Gilmore, 1922, 1946; Lehman and Coulson, 2002), Europasaurus and Saltasaurus; and very compressed laterally, especially in the middle region. This laterally compressed is interpreted as natural. Ventrally, at the level of the parapophyses, which are located posteromedially to the metapophyses. This bony structure, as in most titanosaurs, is divided by a septum, and present a lesser development. The PODL is single, different from the central cervical and posterior cervical vertebrae.

The foramen for the internal carotid artery (Fig. 3), consisting of two structures (metapophyses) that are lateral surface of the neural spine is slightly concave anteroposteriorly from the TPRL up to a prominent bony structure (Fig. 3), generating between them deep and anteroposteriorly elongated pneumatic cavities (Figs. 3, 4A-B, and 4C-B). Similar structures are observed in the anterior and middle cervical of the titanosaur Pitekunsaurus (Filippi and Garrido, 2008), although in the latter such structures are paired or divided by a septum, and present a lesser development. The PODL is single, different from the

ventral projection of the tuberosities is less pronounced than in most titanosaurs (e.g. Muyelensaurus, Pitekunsaurus, Antarctosaurus, Rapetosaurus, Sarmientosaurus, Tapuiasaurus). In Kaijuititan, the occipital condyle dorsoventral height/occipital condyle plus basal tuberosities dorsoventral height (Mannion et al., 2013, character 7) is 0.6, as in Nigersaurus and Aptosaurus, whereas in Europasaurus, Mongolosaurus, Giraffatitan and Phuwiangosaurus is greater than 0.6. This value for Kaijuititan may be interpreted as intermediate or even as a primitive state. Between the basal tuberosities, and below the occipital condyle, there is a basisphenoidal depression, similar to that present in Naranbuenaittian (Filippi et al., 2011a; b; Fig. 3C). In Kaijuititan the basisphenoidal depression lacks a well-developed notch in the ventral midline, as is observed in Pitekunsaurus and, incipiently, in the MUCPv-334 specimen (Calvo and Kellner, 2006). The basal tuberosities lacks a foramina, present in Lirainosaurus (Díez Díaz et al., 2011; Fig. 3 and 4). The foramen for the internal carotid artery (Fig. 2C-D and G-H) is located posteriory to the basipterygoid processes, almost at the middle of the distance between these processes and the basal tuberosities, differing from most titanosaurs, where it is located medially to these processes. In Jainsaurus (Wilson et al., 2011a), Lirainosaurus astibiae (Díez Díaz et al., 2011; Figs. 2 and 4) and Vahiny (Curry Rogers and Wilson, 2014; Fig. 3C, D), the foramen is located laterally to the basipterygoid processes, a primitive condition among non-titanosaurian sauropods (Paulina Carabajal, 2012; Curry Rogers and Wilson, 2014), such as Amargasaurus (Paulina Carabajal et al., 2014; Fig. 1B) and Phuwiangosaurus (Suteethorn et al., 2009; Fig. 9D). Because the presphenoid-parasphenoid complex is eroded and incomplete, it is possible to observe the pituitary fossa, partially exposed anteriorly, which is oval transversally and dorsoventrally compressed (Fig. 2C-D). The pituitary cavity is located as in the MML-194 specimen (García et al., 2008, Fig. 1C), anteriorly to the foramina of the internal carotids, which penetrate the cavity posteroventrally.

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A complete and well-preserved anterior cervical vertebra (MAU-Pv-CM-522/2) (Figs. 3 and 4), probably the third one, was found near the neurocranium. Its centrum is opisthocoelous, elongated, with an elongation index lesser than 3.0 (see Table S1A), as in Alamosaurus (Gilmore, 1922, 1946; Lehman and Coulson, 2002), Europasaurus and Saltasaurus; and very compressed laterally, especially in the middle region. This laterally compressed is interpreted as natural. Ventrally, at the level of the parapophyses, which are located anteriorly, there is a pronounced concavity (Fig. 4C-D) that lacks the medially crest observed in Mongolosaurus (Mannion, 2011). In the probably dicraeosaurid Suvuwaasen (Harris, 2006, Fig. 5F), and in titanosaur such as Pitekunsaurus, this ventral concavity extends practically along the entire length of the vertebral centrum. On the ventral side, two ridges develop from the posterior border of the parapophyses and converge posteriorly in a median keel, which reaches the posterior edge of the vertebral centrum (Fig. 4C-D). Although the anterior condyle is slightly deformed, it is oval, wider than high, and presents a groove or median notch on its dorsal border. The posterior cotyle lacks the notch, is quadrangular with a dorsal edge concave and a ventral plane flat. The lateral surface of the vertebral centrum is anteroposteriorly concave, lacking true pleurocoel but having, mostly on the left side, two small pneumatic foramina. At both sides of the neural canal, there are the centroprezygapophyseal fossae (cprf). These are subtriangular and delimited by the medial division of the centroprezygapophyseal lamina (mdCPRL), the intra-prezygapophyseal lamina (TPRL) and a robust
Fig. 4. Anterior cervical vertebra of *Kaijutitan maui* gen. et sp. nov. MAU-Pv-CM-522/2 (A-B) in dorsal, (C-D) and ventral views. Scale bar: 10 cm.
diaphyseal and zygapophyseal segments observed in *Bonitasaura* (Gallina y Apesteguía, 2015), *Uberabatitan riberoi* (Salgado and Carvalho, 2008) and the specimen "Serie A" of Peirópolis (Powell, 1987). Postzygapophyses present epipophyses, as in *Erketu ellisoni* (Ksepka and Norell, 2006), but less developed that in *Euhelopus zdanskyi* (Wilson and Upchurch, 2009), *Mongolosaurus* and *Phuwiangosaurus*. The cervical vertebra lacks of an epipophyseal-prezygapophyseal lamina (EPRL). Posteriorly, between the postzygapophyses and the roof of the neural canal, there is a deep and transversely wide spinopostzygapophyseal fossa (SPOF), which

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Fig. 5. Posterior cervical vertebra of *Kaijutitan maui* gen. et sp. nov. MAU-Pv-CM-522/9 (A-B) in left lateral, (C-D), dorsal, (E-F) and posterior views. Scale bar: 10 cm.
Fig. 6. Anterior caudal vertebra of Kaijutitan maui gen. et sp. nov. MAU-Pv-CM-522/35 (A-B) in right lateral, (C-D), posterior, (E-F) and anterodorsal views. Scale bar: 10 cm.
reaches the mid-length of the vertebral centrum. The articular sector of the right cervical rib has been preserved fused to the parapophysis and diapophysis, while the left proximal portion of the process was unconnected but associated with it. Posteromedially, between the capitulum and the tuberculum, both cervical ribs have a pneumatic foramen. The anterior process of both cervical ribs is short and curved medially. The posterior process of the left rib, at least in the preserved portion, is straight, laminar and presents a ridge at its lateroventral edge that confers a “T” morphology in cross section.

The posterior cervical vertebra (MAU-Pv-CM-522/9), probably the C12, is very incomplete (Fig. 7). Only part of the left diapophysis and the posterodorsal region of the vertebral centrum are preserved. The dorsoventral inclination of the diapophysis (Fig. 5A-B and E-F) suggests that, as in the anterior cervical, the parapophysis would be ventrally projected, meaning that the cervical rib is located below the level of the vertebral centrum. The vertebra presents well-developed sprf and spof, the latter being the deepest. Although the neural spine has not been preserved, the structure of the base suggests that it would have been transversely wide and anteroposteriorly compressed. Therefore, like the previous cervical vertebra, it could have been bifid with two metapophyses, as in Phuwiangosaurus (Suteethorn et al., 2009). Posteriorly to the SPRL, there is a short lamina attached to it and projected posterodorsally, here interpreted as the EPRL, based on Wilson et al. (2011b) (Fig. 5A-D). The EPRL divides two deep and subtriangular supradiapophyseal fossae, sdf1 and sdf2. As in the anterior cervical, posteriorly, on the left margin of the neural canal, a large, subtriangular cpof is observed. It is delimited by the medial division of the centropostzygapophyseal lamina (mdCPOL), the centropostzygapophyseal lateral lamina (lCPOL), and the TPOL. The cpof fossae are also present in the posterior cervicals of Overosaurus paradasorum (Coria et al., 2013). On the other hand, the posterior cervical vertebrae of Saltasaurus (personal obs), Bonitasaura (Gallina and Apesteguía, 2015) and Trigonosaurus pricei (Campos et al., 2005) present only the cpof.

Fig. 7. Anterior dorsal rib of Kaijutitan maui gen. et sp. nov. MAU-Pv-CM-522/8 (A-B) in posterior views. Scale bar: 10 cm.

Fig. 8. Kaijutitan maui gen. et sp. nov. (A-B), left sternal plate (MAU-Pv-CM-522/17) in anterior views; (C-D), left coracoid (MAU-Pv-CM-522/19) in left lateral views; (E-F) and left scapula (MAU-Pv-CM-522/21) in left lateral views. Scale bar: 10 cm.
Fig. 9. Kaijutitan muii gen. et sp. nov. MAU-Pv-CM-522/34 (A-B) right humerus in anterior view; left ulna MAU-Pv-CM-522/12 (A) in proximal, (B-C), medial, (D) and distal views; right radius MAU-Pv-CM-522/31 (G-H) in posterior, (I), and distal views; right metacarpal II MAU-Pv-CM-522/32 (J), in anterior, (K), proximal, (L), distal, (M), lateral, (N), medial, (O) and posterior views; right metacarpal III MAU-Pv-CM-522/33 (P), in anterior, (Q), proximal, (R), distal, (S), lateral, (T), medial, (U) and posterior views. Scale bar: 10 cm.
4.2.3. Dorsal ribs

The anterior caudal vertebra of *Kaijutitan maui* (MAU-Pv-CM-522/35) is procoelous, with the centrum being slightly wider than high (see Table S14) and with a prominent condyle (Fig. 6C-D). The lateral faces of the centrum are slightly concave anteroposteriorly. They lack of pleurocoels and any other excavations. In posterior view (Fig. 6C-D) is observed a prominence on the left ventral edge, which corresponds to the articular facet for the chevrons. The right transverse processes are well developed and project lateroposteriorly. The tubercle on the dorsal margin present in *Baurutititan* (Kellner et al., 2005) is not observed in *Kaijutitan*. The left transverse process presents an indeterminate fused bone that prevents observing its morphology. The neural arch is on the anterior half of the vertebral centrum, almost on the anterior border. The prezygapophyses have subcircular articular surfaces; these are short, robust, and projected anterodorsally with an angle of nearly 45° with respect to the horizontal. The prezygapophyses lack the expanded articular surfaces that characterize some aeolosaurs, and their curvature in lateral view is interpreted as a preservation artefact. The prezygapophyses are connected to the spine by short spinoprezygapophyseal laminae. The neural spine is incomplete distally; it is compressed anteroposteriorly as in *Patagotitan* (Carballido et al., 2017; Fig. 2 I and J) and *Bonitasaurus* (Gallina and Apesteguía, 2015; Fig. 7C), and widens towards its distal end as in *Patulognkosaurus* (Calvo et al., 2007c, Figs. 16 and 17). It is subsequently tilted at an angle of approximately 95°-100° with respect to the horizontal, as in *Giraffatitan* (Janesch, 1950; Fig. 3), *Phuwiangosaurus* (Suteethorn et al., 2009; Fig. 16C), *Mendozaosaurus* (Fig. González Riga, 2003; Fig. 5A, B and E), *Malawisaurus* (Gomani, 2005, Fig. 14), *Baurutititan* (Kellner et al., 2005; Fig. 16), *Petrobrasaurus* (Filippi et al., 2011a; Fig. 5C and E), *Rapetosaurus* (Curry Rogers, 2009, Fig. 27C and D), *Bonitasaurus* (Gallina and Apesteguía, 2015, Fig. 7C), *Myelensaurus* (Calvo et al. 2007b, Fig. 9) and *Saltasaurus* (Powell, 1992, Fig. 21B). In *Narrosuenbatitan* (Filippi et al., 2011b; Fig. 8A-D), *Epachthosaurus* (Martínez et al., 2004; Fig. 6A) and * Neuquensaurus* (Salgado et al., 2005; Fig. 6B and C), the anteriormost caudal vertebrae have neural spines with a very marked posterior inclination angle of approximately 140°-145° with respect to the horizontal. Conversely, *Trigodonosaurus* presents anterior caudal vertebrae (Camps et al., 2005, Fig. 25), with the neural spine inclined forward at an angle of approximately 80°-85° with respect to the horizontal. The neural spine presents well-developed, robust prespinal and postspinal laminae (Fig 6C-F), as in *Mendozaosaurus* (González Riga, 2003; Fig. 4E and 5A), *Patagotitan* (Carballido et al., 2017, Fig. 2H and J) and *Bonitasaurus* (Gallina and Apesteguía, 2015; Fig. 7A and B), which extend to the distal end of the neural spine. The postspinal lamina widens distally. The anterior caudal vertebra of *Kaijutitan* presents a short SPRL similar to that observed in *Mendozaosaurus* and *Patagotitan*. The articular surfaces of the postzygapophyses are subtriangular and are united to the spine by short SPOL. Both postzygapophyses are united ventrally forming an angle of nearly 45°, delimiting a deep postspinal fossa. The vertebrae lack the hyposphene-hypantrum complex present in the anterior caudals of *Epachthosaurus* (Martínez et al., 2004, Fig. 7B). Laterally, the neural spine presents a depression (Fig. 6A-B), the spinoprezygapophyseal fossa (sdf), delimited anteriorly by the SPRL and later by the SPOL. Ventrally in this depression, there is evidence of the existence of a thin accessory lamina that join prezygapophyses and postzygapophyses.

4.2.2. Caudal vertebra

The anterior caudal vertebra of *Kaijutitan maui* (MAU-Pv-CM-522/11), probably the 2nd one, has been preserved (Fig. 7). This assignment is based on comparisons with the titanosaur *Oversaurus* (Coria et al., 2013; Fig. 7), which preserves the first four pairs of articulated dorsal ribs. The rib preserves the proximal two thirds, lacking the distal end. As in the 2nd dorsal rib of *Oversaurus*, the capitulum is twice as long as the tubercle, and is relatively more gracile. The element, formed by the capitulum and the tubercle, has a convex anterior face and a concave posterior face, as in rebbachissaurids, *Camarasaurus* and *Europatitan* (Torcida Fernández-Baldor, 2017, Fig. 9), a character interpreted as a neosauropod synapomorphy (sensu Wilson and Sereno, 1998). No pneumatic foramina are observed, unlike most Titanosauriformes. The rib shaft is almost straight with a subtriangular cross section in the proximal sector.

In addition, another dorsal rib has been recovered from the quarry (MAU-Pv-CM-522/27), which is incomplete proximally. Other fragments are MAU-Pv-CM-522/8 and 18. They are compressed and slightly curved lateromedially.

4.3. Apendicular skeleton

4.3.1. Sternal plate

The left sternal plate of *Kaijutitan* (MAU-Pv-CM-522/17) is incomplete at its distal end. In spite of this, an oval morphology is inferred (Fig. 8A-B), similar to that present in basal macronarians such as *Camarasaurus*, basal titanosauriforms such as *Giraffatitan*, and in other titanosaurids such as *Sauvantanosaurus* (Poropat et al., 2016; Fig. 4j). This morphology differs from the typical semilunar shape present in most titanosaurids. The medial border is clearly convex while the lateral border is practically straight or subtly concave. The ventral crest, present in many titanosaurids (e.g. *Saltasaurus*, *Epachthosaurus*, *Librofaciens*), is absent. The sternal plate/humerus length ratio is approximately 0.63 (0.65 or less is state 0 for Character 154 in Upchurch, 1998) as in *Camarasaurus*, *Brachiosaurus*, *Petrobrasaurus* (0.53) and *Narrosuenbatitan* (0.65). In derived titanosaurids such as *Alamosaurus*, *Opisthocoelicaudia* and *Mendozaosaurus*, the sternal plate/humerus length ratio is 0.75 or greater (Character 154, state 1; Upchurch, 1998).

4.3.2. Coracoid

The left coracoid of *Kaijutitan* (MAU-Pv-CM-522/19) is incomplete in the sector of the articulation with the scapula and in its dorsal sector (Fig. 8C-D). It is deeper dorsoventrally than long anteroposteriorly, as in the titanosaurid *Sauroposeidon proteus* Wedel et al. 2000 (D'Emic, 2013; FWMSH 938-10-39), “*Paluxysaurus jonesi*” Rose, 2007; Fig. 21). It has a rounded anteroventral rim, as in *Sauroposeidon*, *Euhelopus*, *Giraffatitan*, *Brachiosaurus* (Riggs, 1903, Fig. 3), *Ruyangosaurus*, *Dreadnougthus* (Lacovara et al., 2014, Fig. 28), *Malawisaurus* (Gomani, 2005, Fig. 19C), *Rapetosaurus* (Curry Rogers, 2009; Fig. 33B), *Tupaiasaurus* (Zaher et al., 2011; Fig. 5A), also present in most non-somphospondylan sauropods (Wilson, 2002), unlike the quadangular edge observed in *Cedarosaurus* (Tidwell et al., 1999, Fig. 6), *Rincosaurus*, *Quetecosaurus* (González Riga and Ortíz, 2014, Fig. 10) and saltasaurids. As in *Camarasaurus*, *Europasaurus*, *Euhelopus*, *Malawisaurus*, *Rapetosaurus* and the non-neosauropod sauropods (i.e., *Shunosaurus*, *Patagosaurus*, *Haplocanthosaurus*), the anteroventral border lacks the lip and the infraglenoid fossa observed in the basal macronarian *Tehuelchesaurus* benitezzi (Rich et al., 1999), the titanosaurids *Rincosaurus*, *Quetecosaurus* and *Patagotitan* (Carballido et al., 2017; Fig. 2P) and saltasaurids. The poor preservation of the articulation with the scapula prevents to observe whether the coracoid foramen was open or closed.

4.3.3. Scapula

The material corresponds to the right scapula (MAU-Pv-CM-522/10), incomplete in its anterior edge, the sector of the glenoid cavity and the supraglenoid fossa. The poor preservation impedes to know if the glenoid cavity was deflected medially as many
Fig. 10. Kaijutitan maui gen. et sp. nov. MAU-Pv-CM-522/25 (A-B) ilium in medial views; (C-D), right femur MAU-Pv-CM-522/29 in anterior view; right tibia MAU-Pv-CM-522/28 (E), in proximal, (F-G), lateral, (H), and distal views; left astragalus MAU-Pv-CM-522/11 (I-J), in anterior, (K-L), proximal, (N-M), lateral, (O-P), posterior, (K-R), medial, (S-T) and distal views; right metatarsal II MAU-Pv-CM-522/3 (U-V), in anterior, (W), and distal views. Scale bar: 10 cm.
titanosaurs. In the same way, it is not possible to observe ridges or processes on the scapular blade. The acromial process and the distal end of the scapular blade are not preserved (Fig. 8E-F). Both the anterodorsal and posteroventral edges of the scapular blade are slightly concave, as in Pitekunsaurus (Filippi and Garrido, 2008, Fig. 8) and Myurelensaurus (Calvo et al., 2007b, Fig. 12). The cross-section of the scapular blade presents a “D” shape morphology, as in Ligabuesaurus (Bonaparte et al., 2006), Chubutisaurus (del Corro, 1975) and Antarctosaurus. The medial ventral process observed in Chubutisaurus (Carballido et al., 2011, Fig. 9), Wintonotitan (Hocknull et al., 2009, Fig. 16), Ligabuesaurus (Bonaparte et al., 2006), Vouivria (Mannion et al., 2017, Fig. 16), and Patagotitan (Carballido et al., 2017, Fig. 2P), is absent in Kaijutitan.

4.3.4. Humerus

The right humerus of Kaijutitan (MAU-Pv-CM-522/34) is incomplete in its proximal portion (Fig. 9A–B). The shaft is ante-roposteriorly compressed in cross section. The deltopectoral ex-tends almost to the mid-length of the diaphysis crest, maintaining the same mediolateral width throughout its entire extension, unlike Isisaurus colberti (Jain and Bandyopudh, 1997; Fig. 20), where the crest is very short and restricted to the proximal third of the humerus. The deltopectoral crest is strongly inclined medially, as in Opiosthoecolicaudia, Gondwanatitan (Reidner and Azpeitia, 1999; Fig. 20), Mendozasaurus (González Riga, 2003; Fig. 51; González Riga et al., 2018; Fig. 14B) and Petrobrasaurus (Filippi et al., 2011a, Fig. 6A), differing from the slight mediolateral inclination observed in Malawisaurus and Chubutisaurus. In many sauropods such as Ligabuesaurus (Bonaparte et al., 2006; Fig. 6A), Alamosaurus, Naranbumenatitan (Filippi et al., 2011b; Fig. 10B), Rinconsaurus, Muyelen-Lensaurus (Calvo et al., 2007b; Fig. 12B), Malawisaurus, Rapetosaurus (Curry Rogers, 2009; Fig. 35A) and Saltasaurus, the deltopectoral crest is anteriorly projected. On the anterior surface of the proximal third, a slightly tuberosity is observed, which is interpreted as attachment of the M. coracobrachialis, as in Patagotitan (Carballido et al., 2017, Fig. 2Q), Ruyangosaurus, Diamantinasaurus (Poropat et al., 2015; Fig. 10A) and Neuquensaurus (Otero, 2010). On the lateral margin of the posterior surface, leveled with the most prominently developed portion of the deltopectoral crest, a strong bulge is observed, which is interpreted as the area for insertion of the M. scapulohumeralis anterior, as in Opisthoecolinauda (Borsuk-Bialynicka, 1977; Fig. 7C and D), Notocolossus (González Riga et al., 2016; Fig. 4A), Patagotitan (Carballido et al., 2017, Fig. 2R), Wintonotitan (Poropat et al., 2014; Fig. 8C), Mendozasaurus (González Riga et al., 2018) and Naranbumenatitan. The distal end of the humerus presents a slight medial torsion with respect to the proximal end. Distally, the radial condyle is more developed than the ulnar condyle, as in Petrobrasaurus and Neuquensaurus. In Rapetosaurus, the ulnar condyle is slightly larger than the radial condyle (Curry Rogers, 2009). The condyles are separated by a shallow groove as in Chubutisaurus and different to the well development fossa present in saltasaurines (Otero, 2010).

4.3.5. Ultra

The left ulna of Kaijutitan (MAU-Pv-CM-522/12) (Fig. 9C-F) is moderately robust, with a robustness index of 0.24, similar to Rapetosaurus (0.23), lesser than Neuquensaurus (0.29) and Yongjinglong datangi (Li–Guo Li et al., 2014; Fig. 13 and 14) (0.33) and greater than Argyrosaurus (0.19). In proximal view, the ulna is triradiate, a configuration conferred by the olecranon and the anteromedial and anterolateral processes. The olecranon process is not prominent, and it is located approximately at the level of the anteromedial and anterolateral processes (Fig. 9D–E), as in Camarasaurus, Europasaurus, Bonitasaurus and Dreadnoughtus schrani (Lacovara et al., 2014). The anteromedial process have a similar length than the anterolateral process (Fig. 9C), as in Diamantinasaurus (Poropat et al., 2015; Fig. 11F), Malawisaurus and Argyrosaurus superbus Lydekker (1893) and different from Rapetosaurus, Elantitan illioi (Mannion and Otero, 2012; Fig. 7E), Nar-bunmenatitana (Filippi et al., 2011a,b; Fig. 10A1), Pitekunsaurus, Myurelensaurus and Neuquensaurus (Otero, 2010; Fig. 4A5) where the anteromedial processes is longer than the anterolateral process. The anteromedial process is concave in medial and lateral views, a condition that is present in several Titanosauriforms (Poropat et al., 2014). The anterolateral process is almost parallel to the olecranon process. This position might have been affected by crushing. The radial surface of the ulna is concave. The distal end is oval, as in Naranbumenatitana (Filippi et al., 2011a,b; Fig. 10 A3) and different from Rapetosaurus (Curry Rogers, 2009; Fig. 37E), Diamantinasaurus (Poropat et al., 2015; Fig. 11H), Elantitan (Mannion and Otero, 2012; Fig. 7F) and Pitekunsaurus, where it is rather circular. The distal end of the ulna has a depression on its anteromedially face (Fig. 9F), where it would articulate with the radius.

4.3.6. Radius

The distal two-thirds of the right radius of Kaijutitan (MAU-Pv-CM-522/31) is preserved (Fig. 9G–I). The distal end of the radius is robust and widened in relation to the narrow and slender shaft, which is subelliptic in cross-section. The distal articular face is oval, with the major axis lateromedially oriented, as in Diamantinasaurus (Poropat et al., 2015, Fig. 12B), Mendozasaurus (González Riga et al., 2018, Fig. 16D), Bonitasaurus (Gallina and Apesteguía, 2015; Fig. 12C) and Neuquensaurus (Otero, 2010; Fig. 5A7), and different from Argyrosaurus (Mannion and Otero, 2012; Fig. 2E), where it is sub-triangular and slightly expanded. The distal end is approximately twice the minimum width of the diaphysis as in Chubutisaurus (Carballido et al., 2011). The distal lateral end is beveled as in Diamantinasaurus (Poropat et al., 2015; Fig. 12) and Bonitasaurus salgadoi (Gallina and Apesteguía, 2015; Fig. 12A and B). This beveling is also present in several somphospondyls (Wilson, 2002; Mannion et al., 2013) and in several basi-eusauropterygids (Mannion et al., 2013; Mateus et al., 2014). In the distal third of the diaphysis, on the posterior face, a short ridge is observed, which would corre-pond to the interosseous ridge present in other titanosaurs, as Rapetosaurus (Curry Rogers, 2009; Fig. 36), Mendozasaurus (González Riga et al., 2018; Fig. 16 C), Bonitasaurus (Gallina and Apesteguía, 2015; Fig. 12 B) and Neuquensaurus (Otero, 2010; Fig. 5).

4.3.7. Metacarpus

Only the right metacarpals II and III (MAU-Pv-CM-522/32 and 33) (Fig. 9J–U), have been recovered, complete and in a very good state of preservation (Fig. 14). Metacarpal III is longer than metacar-pal II, as in Sauroposeidon (“Paluxysaurus jonesi” Rose, 2007), Rapetosaurus (Curry Rogers, 2009, Fig. 38), Wintonotitan (Poropat et al., 2014) and many other sauropterygids (Upchurch, 1998). On the contrary, in Camarasaurus sp. SMA 0002 (Tschopp et al., 2015), Alamosaurus (Gilmore, 1946), Argyrosaurus (Mannion and Otero, 2012, Fig. 3) and Petrobrasaurus (Filippi et al., 2011a, Fig. 6D), metacarpal II is the longest. In Mendozasaurus (González Riga et al., 2018) the longest metacarpal is metacarpal IV, followed by metacar-pals II and III, of equal length. The distal end of metacarpals II and III does not show the presence of joint surfaces for phalanges, as in Camarasaurus (Tschopp et al., 2015) and Giraffatitan (“Bra-chiosaurus”: Janesch, 1914).

Metacarpal II (Fig. 9J–O) Metacarpal II of Kaijutitan presents a straight diaphysis with relations proportionally widened, as in Diamantinasaurus (Poropat et al., 2015; Fig. 13 M and N), and Rinconsaurus (Calvo and González Riga, 2003), while metacarpal II of Bonitasaurus (Gallina and Apesteguía, 2015; Fig. 12), Neuquensaurus and Petrobrasaurus (Filippi et al., 2011a; Fig. 6D), shows a slight
widening only at its proximal end. The proximal end, which is slightly convex, and the flat distal end have rough surfaces. In cross-section, the proximal end is subtriangular and the distal end is subrectangular, as in Petrobrasionaurus, Wintonotitan (Poropat et al., 2015; Fig. 15 B), and Mendozasaurus (González Riga et al., 2018; Fig. 18G), unlike the distal quadrangular end observed in Bonitasaura. The postero medial face for the articulation with metacarpal I is proximally concave as in Bonitasaura and Rinconsaurus, as well as the postero lateral face for the articulation with metacarpal III. The anterior face is practically flat. On the proximal third of the postero medial face there is a tuberculum, which is probably for the insertion of the ligaments of the flexor muscles of the hand (M. flexores digitorum profundi, sensu Otero, 2018).

Metacarpal III. (Fig. 9P-U) Like metacarpal II, metacarpal III of Kaijuttan has a straight diaphysis with its ends widened, as in Diamantinasaurus (Poropat et al., 2015; Fig. 13M and J), Mendozasaurus (González Riga et al., 2018; Fig. 18P) and Chubutisaurus (Carballido et al., 2011; Fig. 12). The proximal and distal ends have rough surfaces, while the proximal surface is slightly convex and the distal surface relatively flat. The proximal end is subtriangular in cross-section, while the distal end is subquadrangular, as in Chubutisaurus, Epachthosaurus (Martinez et al., 2004, Fig. 10) and Argynosaurus (Mannion and Otero, 2012, Fig. 3D), and unlike Diamantinasaurus (Poropat et al., 2015; Fig. 13P), Wintonotitan (Poropat et al., 2014; Fig. 16B), Aeolosaurus sp. MPCA-27100 (Salgado et al., 1997; Fig. 4A) and Mendozasaurus (González Riga et al., 2018; Fig. 18M), where it is subrectangular. The postero medial face for the articulation with metacarpal II is slightly concave, as in Rinconsaurus, while the postero lateral face for the contact with metacarpal IV is slightly convex as in Bonitasaura. On the proximal third of the postero medial face, there is the tuberculum for the insertion of ligaments for the flexor muscles of the hand (Mm. flexores digitorum profundi, sensu Otero, 2018), also observed in metacarpal II.

4.3.8. Ilium

A fragment of bone (MAU-Pv-CM-522/25) is interpreted as part of a left ilium (Fig. 10A-B). The fragment consists in part of the preacetabular process, the proximal sector of the pubic pedicle and part of the iliac blade. Although the bad preservation of the material prevents a detailed description, it is possible to infer that the preacetabular process was recurved and expanded laterally, as in other titanosauriforms such as Ruyangosaurus (Lu et al., 2014; Fig. 3-14A), Epachthosaurus (Martinez et al., 2004; Fig. 11A), Rapetosaurus (Curry Rogers, 2009; Fig. 39), Trigonosaurus (Campos et al., 2005; Fig. 21), Rinconsaurus (Calvo and González Riga, 2003; Fig. 3B) and Óverosaurus (Coria et al., 2013; Fig. 5A). The pubic pedicle is relatively long. Its anterior surface is convex and its posterior surface, which is part of the acetabulum, is concave. On the dorsal edge of the pubic pedicle there is a prominent crest, which corresponds to the articulation with the second sacral rib, as observed in Rapetosaurus (Curry Rogers, 2009; Fig. 39A), Muyelensaurus (MAU-Pv-LL-432) and Rinconsaurus (MAU-Pv-CRS-275/2).

4.3.9. Femur

The left femur of Kaijuttan (MAU-Pv-CM-522/29) is incomplete in two sectors: laterodistally and in the area of the greater trochanter (Fig. 10C-D). The diaphysis is anteroposteriorly compressed and elliptical in cross-section, but also has undergone some crushing. The femoral head projects dorsomedially: it is prominent, robust, with the rough articular surface. In the proximal portion, on the postero lateral surface, the femur presents a ridge, which corresponds to the trochanteric shelf, present in sauropods such as Neuquensaurus (Otero, 2010, Fig. 1A3 and A4), Mendozasaurus, Petrobrasinosaur, Rapetosaurus (Curry Rogers, 2009; Fig. 43C) and Peteckunusaurus. The lateral protuberance, very noticeable, is placed on the lateral edge of the diaphysis, below the position where the greater trochanter would be, as in other titanosauriformes (Salgado et al., 1997; Wilson and Sereno, 1998). The fourth trochanter is located posteriorly on the caudomedial margin of the shaft. Although the femur is not complete, it would be placed near to the middle of the shaft, as in Giraffatitan, Chubutisaurus (Carballido et al., 2011; Fig. 14A and B), Ligabuesaurus, Ruyangosaurus (Lu et al., 2014; Fig. 3-19B), Epachthosaurus (Martinez et al., 2004; Fig. 12A), Rinconsaurus (Calvo and González Riga, 2003; Fig. 3C) and Mendozasaurus. On the contrary, in Brachiosaurus, Phuwiangosaurus (Martin et al., 1999; Fig. 18-2), Rapetosaurus (Curry Rogers, 2009; Fig. 43B and C), Bonitasaurus, Patagotitan (Carballido et al., 2017, Fig. 2S), Petrobrasaurus, Naranbuenatitan (Filippi et al., 2011b, Fig. 11A), Neuquensaurus (Otero, 2010, Fig. 10A3 and A4) and Saltasaurus, the fourth trochanter is located on the proximal third of the diaphysis. There is no evidence for a midline ridge (intermuscularis cranialis line) on the anterior surface of the shaft.

4.3.10. Tibia

The right tibia of Kaijuttan (MAU-Pv-CM-522/28) is almost complete, lacking only part of the distal end (Fig. 10E-H). Both ends are well developed, with the proximal end enlarged as in other sauropods. It is a relatively robust bone (see robustness index in Table S1S, Supplementary information), like that of Chubutisaurus (Carballido et al., 2011), Ophisthocoelaicudia, Neuquensaurus (Otero, 2010) and Saltasaurus, unlike the gracile tibia of other sauropods such as Iainosaurus (Wilson et al., 2011a) and Laplatasaurus (Gallina y Otero, 2015). The proximal end is lateromedially compressed, with the articular surface subrectangular (Fig. 10E), different from the oval contour present in Ruyangosaurus (Lu et al., 2014; Fig. 3.21B), Petrobrasaurus (Filippi et al., 2011a; Fig. 6G), Rapetosaurus (Curry Rogers, 2009; Fig. 44E), Bonitasaurus (Gallina and Apesteguía, 2015; Fig. 15E) and Mendozasaurus (González Riga, 2003; Fig. 6A), and the subcircular contour observed in other sauropods such as Tastavinsaurus (Canudo et al., 2008; Fig. 14E), Gobititan (You et al., 2003; Fig. 2), Ligabuesaurus, Chubutisaurus (Carballido et al., 2011, Fig. 15C), Diamantinasaurus (Poropat et al., 2015; Fig. 20B), Iainosaurus (Wilson et al., 2011a; Fig. 7E), Laplatasaurus (Gallina y Otero, 2015; Fig. 2S), Überabatitan (Salgado and Carvalho, 2008, Fig. 19B) and Neuquensaurus (Otero, 2010, Fig. 11A6). The cnemial crest is triangular (Fig. 16D-E), as in Laplatasaurus, Bonitasaurus (Gallina and Apesteguía, 2015; Fig. 15D) and Neuquensaurus, different from the curved cnemial crest present in Chubutisaurus (Carballido et al., 2011, Fig. 15A), Lirainosaurus (Díez Diaz et al., 2013; Fig. 5, 6 and 7), Diamantinasaurus (Poropat et al., 2015; Fig. 20C and E), Petrobrasaurus (Filippi et al., 2011a, Fig. 6H-L) and Bonatitan (Salgado et al., 2014; Fig. A and B). The cnemial crest is anteriorly projected, as in Turiasaurus (Royo-Torres et al., 2006) and Patagosaurus fariasi (Bonaparte, 1979), and different from the anterolateral projection observed in most eusauropods (Wilson and Sereno, 1998). Postero laterally to the cnemial crest, the tibia lacks the protubercans present in Überabatitan (Salgado and Carvalho, 2008, Fig. 19B) and Ophisthocoelaicudia (Borsuk-Bialynicka, 1977: pl. 14). Laterally on the cnemial ridge, there is a concave depression corresponding to the articular surface for the proximal end of the fibula. The distal end is similar to Chubutisaurus, with the posteroventral process reduced and the articular surface for the ascending process of the astragalus well developed, forming a step-like shape (Carballido et al., 2011).

4.3.11. Astragalus

The left astragalus of Kaijuttan (MAU-Pv-CM-522/13) (Fig. 10I-T) is well preserved but incomplete in its medial portion. The astragalus exhibits the wedge morphology observed in other
Neosauropoda (Upchurch, 1995, 1998). It is wider (mediolaterally) than high (proximodistally), as in Janeschia robusta (Bonaparte et al., 2000; Figs. 6 and 7), Camarasaurus grandis (Wilson and Sereno, 1998; Fig. 33), Giraffatitan and Lusotitan atalaiensis (Mannion et al., 2013; Fig. 19), lacking the pyramidal morphology present in most titanosaurids (Wilson, 2002). In proximal view, the astragals is subtriangular, tapering medially. The anterior and lateral edges are rounded, differing from the straight edges observed in Bonitasaura and Diamantinasaurus. The surface of the astragals, especially its distal surface, is rugose probably due to the presence of cartilage. The ascending process, although distally incomplete, is relatively prominent, but not so as in Uberabatitan (Salgado and Carvalho, 2008) and Savannasaurus elliptorum (Poropat et al., 2016). Because the ascending process is distally incomplete, it is not possible to know if it was posteriorly projected. At the base of the ascending process, the astragals presents a wide, undivided subcircular pit, within which there is a single foramen, as in Giraffatitan, Bonitasaura, Neuquensaurus, Opisthocoelicaudia, Epachthosaurus and Notocotolus, a different condition from the divided fossa present in basal macronarians and diplodocoids (Gallina and Apestegua, 2015). The lateral side of the ascending process presents a slightly concave surface for the contact with the distal end of the tibia (Wilson, 2002). A lateral view (Long, 2002, Fig. 2) also as observed in most sauropods (e.g. Notocotolus, Uberabatitan, Diamantinasaurus) and absent in several titanosaursiformes like Euhelopus, Giraffatitan and Cobitititan (Mannion, 2013). In specimen MUCPV-1533 (González Riga et al., 2008), this concavity is present but is less marked. The articular surface for the tibia is inclined medially in a relatively marked angle, as in Aeolosaurus sp. (Salgado et al., 1997), although at a lower angle than in Uberabatitan and Savannasaurus. While in saltasaurids the astragals is transversely reduced, covering only a part of the surface of the distal end of the tibia (e.g. Opisthocoelicaudia 54% and Neuquensaurus 56%, Salgado and Carvalho, 2008), the astragals of Kaijutitan would cover a larger surface, probably 80%, being similar to that observed in Cobititen shenzhouiensis (You et al., 2003; Fig. 2; and Erketu (Ksepka and Norell, 2006; Fig. 10). In Euhelopus (Wilson and Upchurch, 2009, Fig. 25), the astragals covers completely the distal end of the tibia. Ventrally, the astragals presents a convex rough surface, as in Giraffatitan, Euhelopus, Erketu, Cobititan, Opisthocoelicaudia and Bonitasaura, probably for articulation with the metatarsals II and III.

4.3.12. Metatarsus

Only the distal portion of the right metatarsal II of Kaijutitan has been preserved (MAU-Pv-CM-522/3) (Fig. 10U-W). Although it is incomplete, it is observed that the preserved portion of the diaphysis is dorsoplantarily compressed, as in the basal macronarian Camarasaurus (SMA 0002, Tschopp et al., 2015) and the titanosaurus Cobititan, Muyelensaurus and the specimen NMMNH P-4996 (D'Emic et al., 2011). The distal articular surface is rugose, as in most sauropods (e.g. Ligabuesaurus, Muyelensaurus, MUCPV-1533 and Notocotolus), probably owed to the existence of cartilage. The distal articular surface is quadrangular and has a projection in its ventromedial corner, which is visible in distal view, similar to that observed in metatarsal II of the NMMNH P-4996 (D’Emic et al., 2011, Fig. 2) and Notocotolus (González Riga et al., 2016; Supplementary Fig. S7). Also in distal view, the articulation surface for the phalanx is asymmetric, with the dorsal edge more extended medially than laterally, as in most sauropods, for instance Apatosaurus ajoy (Upchurch et al., 2004), Cobititan (You et al., 2003; Fig. 2) and Notocotolus (González Riga et al., 2016, Supplementary Fig. S7). As in other sauropods (e.g. Rapetosaurus, Muyelensaurus, Notocotolus, NMMNH P-4996, MUCPV-1533), the distal articular surface has a convex dorsal region and a concave plantar region.

5. Discussion

5.1. Phylogenetic analysis

In order to establish the phylogenetic relationships of Kaijutitan, an analysis was performed based on the data matrix published by Carballido et al. (2017), consisting of 87 taxa and 405 characters. From this matrix, thirteen unstable taxa (Isanosaurus, Tehuelchesaurus, Venenosaurus, Cederosaurus, Tastavinsaurus, Lusotitan, Padillasaurus, Malarguesaurus, Quetcasaurus, Drusilasauro, Puertasaurus, Bonitasaura and Trigonosaurus) were excluded a priori. On the other hand, a number of existing characters were modified (see Supplementary information). The character scores for Ruyangosaurus were revised based on Lü et al. (2014), Tapuiasaurus based on Wilson et al. (2016), while the rest of the specimens were revised based on the original bibliography and direct observations on the materials. The program used to analyze the data was the software T.N.T. 1.5 (Goloboff and Catalano, 2016). Characters were ordered as in the original analysis. The chosen parameters included the algorithm of Tree bisection reconnection (TBR), with 10000 replications of Wagner trees and 10 trees to save per replication. This procedure retrieved 40 most parsimonious trees (MPTs) of 1296 steps (CI = 0.38, RI = 0.71), found in 1223 of the replicates. (The strict consensus of both analyses is illustrated in the Supplementary information).

The strict consensus shows a polytomy at the base of Saltasauridae, but it is resolved pruning Nemegtosaurus. Kaijutitan maui is recovered as a basal titanosaur, the sister taxon of Epachthosaurus + Eutitanosaurus (sensu Salgado, 2003) (Fig. 11). Only one character supports this group: procoelous anterior caudal vertebra (character 231, state 3). Whereas the group of Epachthosaurus + Eutitanosaurus, is supported by astragalus shape with subequal anteroposterior and transverse dimensions (character 372, state 1).

Other positions of Kaijutitan were tested. First, a position within Lithostrotia was forced, resulting in 80 trees of 1303 steps, that is, seven steps longer than the most parsimonious tree. When Kaijutitan was forced into a position within Eutitanosaurus, resulted 40 trees of 1297 steps, only one step longer than the most parsimonious tree. In sum, the hypothesis that Kaijutitan is a basal titanosaur is weakly supported, since with a single step it is located within Eutitanosaurus.

The inclusion of Kaijutitan in the matrix of Carballido et al. (2017) has affected other taxa: Wintonotitan is recovered as a basal Titanosauria, but closely related as a sister taxon of Andesaurus. In turn, Ruyangosaurus is located in a more derived position as a basal Eutitanosaurus, different from the proposal hypothesis of Carballido et al. (2017), where Ruyangosaurus is recovered as a basal Titanosaurus. This phylogenetic positions differs from the one presented by Lü et al. (2014), in which Ruyangosaurus is a basal Somphospondylid. The new topology with Ruyangosaurus in a new position is probably due to the character modification and the inclusion of Kaijutitan.

5.2. Body mass estimation

The body mass of quadrupedal dinosaurs can be estimated using femoral and humeral circumferences, through scaling equations and volumetric methods (Campione and Evans, 2012; Benson et al., 2014). Unfortunately, the femur and humerus of Kaijutitan maui are incomplete, which makes impossible to make such a calculation. However, by comparisons with measurements taken from other titanosaurs (Giraffatitan, Brachiosaurus, Sauroposeidon, Ligabuesaurus, Ruyangosaurus, Sarmientosaurus, Antarctosaurus, Narambanisaurus, Epachthosaurus, Notocotolus, Dreadnoughtus, Patagotitan, see measurements table 2 and 3 in Supplementary information), it is possible to estimate the probable body mass of Kaijutitan.
Ten skeletal elements were compared: neurocranium, posterior cervical vertebrae, coracoid, sternal plate, scapula, humerus, ulna, femur, tibia and astragalus. According to the comparative measurements (see Table SI2 and SI3, Supplementary information), *Kaijutitan* would have had a body mass similar or intermediate to that of *Giraffatitan* (38.000 kg; Gunga et al., 2008) and *Notocolossus* (60.398 kg; González Riga et al., 2016) However, better preserved materials of the *Kaijutitan* are necessary to corroborate this.

5.3. Anatomical traits

The neurocranium of *Kaijutitan* present some titanosaurian features (sensu Paulina Carabajal et al., 2008), as the anteroposteriorly compressed and posteriorly oriented morphology of the crista antotica of the laterosphenoid, the complete fusion between the prootic and the exoccipital-opisthotic complex, an oval metotic foramen that is as large as the exit of cranial nerve V, and that is visible in lateral view, and an oval fenestra that is separated from the metotic fenestra by a thin wall of bone.

The internal carotids, positioned posteriorly to the basipterygoid processes, almost at the mid-way between these and the basal tuberosities, are intermediate between the lateral location present in the primitive sauropods and the medial location present in more derived forms. In this work, this intermediate condition is considered as an autapomorphy.

*Kaijutitan* also presents a combination of plesiomorphic characters such as: oval sternal plate (character 293, state 0), proximodistal length of the coracoid less than the joint length scapular (character 287, state 0), non-quadrangular coracoid (character 288, state 0), proximal compressed condyle of tibia, narrow with anteroposterior long axis (character 363, state 0), and apomorphic characters such as procoelous anterior caudal vertebra (character 231, state 3), manual phalanges absent in digits II and III (character 324, state 2) and extremely reduced fourth trochanter of femur (character 353, state 2).
Among the most notable autapomorphies exhibited by Kaijuittit is the anterior cervical vertebra with bifid neural spine. In sauropods, bifid presacral neural spines evolved several times independently: they are present in some manchenschuarias, all known diplodocids and dicraeosaurids, the basal macronarian Camarasaurus and Don- gungysaur (Lü et al., 2010), in the Euhelopodidae, and in the derived titanosaur Ophiococcolaia (Wedel y Taylor, 2013).

The basal macronarian sauropod Camarasaurus and the diplodocoid Suuwassea emiliae (Harris and Dodson, 2004), present anterior cervical vertebrae with shallow bifurcate spines, middle cervical vertebrae with spines moderately bifurcated, and posterior cervical vertebrae with spines deeply bifurcated. In the euhelopo- did Phuwiangosaurus sirindhornae (Martin et al., 1994), the middle cervicals are moderately bifurcated and posterior cervicals are deeply bifurcated. Kaijuittit is different since moderate bifurcation begins in the anterior cervical neural spines. Although the neural spine of the posterior cervical of Kaijuittit has not been preserved, it is inferred that it would have been deeply bifurcated, based on these other sauropods.

The presence of an epipophyseal-prezygapophyseal lamina in the posterior cervical vertebra of Kaijuittit is recovered in the phylogenetic analysis as an autapomorphy. This lamina is observed in many basal macronarians (e.g. Camarasaurus and Galvesaurus), rebbachisaurids (e.g. Nigersaurus, Zapalasaurus and Limaysaurus), Euhelopodidae (e.g. Erketu and Phuwiangosaurus) and in the tita- nosaur Patagotitan. In its most basic form, it divides the spinodia- physeal fossa (sdf) into upper (sdf1) and lower (sdf2) subfossae (Wilson, 2012; Fig. 6). This condition is observed in Kaijuittit, Bra- chiosaurus and Phuwiangosaurus (Suteethorn et al., 2009; Fig. 12).

5.4. Evolutionary implications

During the Early Cretaceous, diplodocoids declined globally and different titanosauriform groups became predominant in different continents: brachiosaurids in North America, euhelopodids in Asia, and titanosaurids in Gondwana and Eurasia. In the Latest Cretaceous, the only sauropods recorded throughout the world are derived titanosaur (D’Emic, 2012). Specifically in South America, at least until the Turonian-Santonian, basal titanosaurans with amphiplaty- cald neural spines are recorded, such as Traukutit (Juarez Valieri and Calvo, 2011) and the Loma de los Jotes titanosaur specimen (MAU-Pv-LJ-472; Filippi et al., 2008), with slightly procuneal caudal vertebrae in the anterior and posterior half of the tail. Kaijuittit extends the record of basal titanosaurans up to the late Con- cacion. We ignore whether all these basal forms represent a single lineage or a clade; however, it is evident that the evolutionary picture of titanosaurans is more complex than previously thought.

6. Concluding remarks

The new giant sauropod, Kaijuittit maui gen. et sp. nov., is the latest basal titanosaur ever recorded. It presents a singular combi- nation of plesiomorphic and apomorphic characters, among them, the presence of bifid cervical neural spines, an unusual feature among titanosaurans. Finally, Kaijuittit maui expands the scarce knowledge about the sauropod dinosaurs from the Sierra Barrosa Formation and provides new evidence of the coexistence of basal titanosaurans and eutitanosaurans sauropods in the Late Creta- ceous (Turonian–Santonian) at least for Patagonia (Leanza et al., 2004; Salgado and Bonaparte, 2007).

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Zb, Atlanticus

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cretres.2019.03.008.