

Osteology and phylogenetic relationships of *Tyrannotitan chubutensis* Novas, de Valais, Vickers-Rich and Rich, 2005 (Theropoda: Carcharodontosauridae) from the Lower Cretaceous of ⁶⁰ Patagonia, Argentina

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The theropod clade Carcharodontosauridae is a broadly distributed group of large allosauroid theropods. The carcharodontosaurids recorded in the Albian–Cenomanian of Gondwana are the youngest and most derived members of this clade. *Tyrannotitan chubutensis*, from the Cerro Castaño Member of Cerro Barcino Formation (Albian; Chubut Group), Central Patagonia, Argentina, is of prime interest among Gondwanan carcharodontosaurids as it represents the oldest record of the group. Here we offer a detailed osteological comparative description of the holotype and paratype of *Tyrannotitan chubutensis* together with a new diagnosis of the species. The new information results in a better understanding of this taxon and Carcharodontosauridae. Furthermore, a comparative study of the anatomy of the pectoral girdle of *Giganotosaurus* is reinterpreted as very similar to that of *Tyrannotitan* and *Mapusaurus*. We also present a phylogenetic analysis of Carcharodontosauridae that recovers *Tyrannotitan* as a derived carcharodontosaurid, being the sister group of the clade formed by *Giganotosaurus* and *Mapusaurus*, all nested in the clade Giganotosaurini.

Keywords: Theropoda; Carcharodontosauridae; Tyrannotitan; Patagonia; Argentina

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1. Introduction

Allosauroid theropods, and particularly carcharodontosaurids, have been the focus of recent research (Novas et al. 2005; Coria and Currie 2006; Brusatte and Sereno 2008; Sereno and Brusatte 2008; Brusatte et al. 2009; Ortega et al. 2010). Although Carcharodontosauridae was formerly interpreted as a group of gigantic Gondwanan predatory dinosaurs, this clade is now known to be present in both the southern and northern hemispheres (Brusatte et al. 2009, 2012; Ortega et al. 2010). New carcharodontosaurid taxa have been recovered from different localities in the northern hemisphere, such as Spain (Ortega et al. 2010) and China (Brusatte et al. 2009; Brusatte et al. 2012), distant from the 'classic' localities in South America and Africa (Stromer 1931; Coria and Salgado 1995; Sereno et al. 1996; Sereno and Brusatte 2008). Recently, Benson et al. (2010) considered that some 'problematic' carnivorous dinosaurs from southern continents, including Megaraptor, Orkoraptor, Australovenator and Aerosteon (all grouped in a clade called Megaraptora), with the European form *Neovenator* as their sister group, constitute a monophyletic clade that conform the sister group of Carcharodontosauridae: the Neovenatoridae. In this way, these authors established the new clade Carcharodontosauria, which includes Neovenatoridae and Carcharodontosauridae. This

proposal was recently challenged by Novas et al., which considered Megaraptora as more closely related to tyrannosauroid coelurosaur theropods (Novas et al. 2013) than to carcharodontosaurids.

The phylogenetic relationships within carcharodontosaurids have been highly debated, in spite of the few detailed anatomical descriptions available for most carcharodontosaurids (Coria and Currie 2006; Brusatte and Sereno 2007; Eddy and Clarke 2011). Therefore, the 90 description in detail of carcharodontosaurid remains is necessary in order to understand the basic osteology, as well as, the phylogenetic relationships of this group.

The aim of this paper was to provide a detailed osteological description of *Tyrannotitan chubutensis* ⁹⁵ Novas, de Valais, Rich and Rich, 2005, including a new and revised diagnosis of the genus and species. We also present and discuss a phylogenetic analysis of carchar-odontosaurids, including the anatomical information obtained from the study of both specimens of *Tyrannotitan* ¹⁰⁰ and new data of other carcharodontosaurid taxa.

2. Institutional abbreviations

MACN: Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; MCF-PVPH:

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Museo Municipal 'Carmen Funes', Plaza Huincul, Provincia de Neuquén, República Argentina; MMCh-PV: Museo Paleontológico 'Ernesto Bachmann', colección Paleontología Vertebrados, Villa El Chocón, Provincia de 115 Neuquén, Argentina; MNN IGU: Musée National du Niger, Iguidi collection. Níger; MPEF-PV: Museo Paleontológico 'Egidio Feruglio', colección Paleontología Vertebrados, Trelew, Provincia de Chubut, Argentina; MUCPv: Museo de la Universidad del Comahue, Ciudad 120 de Neuquén, Provincia de Neuquén, Argentina; MUCPV-Ch: Museo de la Universidad del Comahue, Colección Chocón, Villa El Chocón, Provincia de Neuquén, República Argentina; NCSM: North Carolina State Museum of Natural Sciences, Raleigh, North Carolina, 125 USA; SGM-Din: Ministére de l'Energie et des Mines, dinosaur collection, Rabat, Marruecos; UMNH-VP: Utah Museum of Natural History, Vertebrate Paleontology collection, Salt Lake City, Utah, USA.

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3. Anatomical abbreviations

abr, articular brace; ac, acetabulum; acd, anterior centrodiapophyseal lamina; af, antorbital fossa; al, accessory lamina; ap, acromion process; avp, anteroven-135 tral process; bict, biceps tubercle; cf, coracoid foramen; cfu, collateral furrow; cp, collateral pit; cprf, centroprezygapophyseal fossa; cprl, centroprezygapophyseal lamina; ctf, crista tibiofibularis; dc, distal carina; df, dorsal 140 fossa; dia, diapophysis; dpc, deltopectoral crest; ep, epipophysis; f, foramen; ff, fibular fossa; fh, femoral head; flf, flexor fossa; foc, facet for occipital condyle; ft, fourth trochanter; gf, glenoid fossa; hya, hypantrum; hys, hyposphene; idp, interdental plates; ift, iliofibularis 145 tubercle; il, ilium; ilped, iliac peduncle; iprf, infraprezygapophyseal fossa; jaf, articular facet for jugal; jpr, jugal pneumatic recess; lc, lateral condyle; lf, lateral fossa; lmf, lateromedial furrow; ls, ligament scar; lt, lesser trochanter; mc, mesial carina; mco, mesial condyle; mf, Meckelian 150 fossa; mfp, medial fibular pocket; mg, Meckelian groove; nc, neural canal; nvf, neurovascular foramen; nvg, neurovascular groove; on, obturator notch; op, obturator process; paf, articular facet for postorbital; pcd, posterior centrodiapophyseal lamina; pec, prezygoepipophyseal 155 crest; pf, pubic foramen; pl, pleurocoel; po, pneumatic opening; pvp, posteroventral process; poz, postzygapophysis; pp, parapophysis; ppdl, paradiapophyseal lamina; pped, pubic peduncle; prz, prezygapophysis; ps, pubic symphysis; pvp, posteroventral process; r, ridge; rcl, ridge 160 for cruciate ligaments; spol, spinopostzygapophyseal lamina; spof, spinopostzygapophyseal fossa; sprl, spinoprezygapophyseal lamina; sprf, spinoprezygapophyseal fossa; tp, transverse process; tub, tuberosity; vf, ventral fossa.

Systematic paleontology 4.

Dinosauria Owen, 1842	
Saurischia Seeley, 1888	170
Theropoda Marsh, 1881	
Allosauroidea Marsh, 1878	
Carcharodontosauridae Stromer, 1931	
Carcharodontosaurinae Stromer, 1931 (nomen	
translatum Brusatte and Sereno, 2008)	

Giganotosaurini Coria and Currie, 2006 (nomen translatum Brusatte and Sereno, 2008)

Tyrannotitan chubutensis Novas, de Valais, Vickers-Rich and Rich, 2005

4.1 Holotype

MPEF-PV 1156: Partially articulated skeleton, composed of right dentary with two complete teeth, left dentary, articulated dorsal vertebrae 2nd to 7th, 8th? to 11th? 185 dorsals, 14th? dorsal, 1st? sacral vertebra, anterior caudal vertebra, left scapula and coracoid, right humerus, both radii, fragments of left ilium, both ischia, both pubis, both femora, left fibula, six haemal arches and fragments of gastralia. 190

4.2 Paratype

MPEF-PV 1157: Composed by right jugal, right quadratojugal, right dentary, two isolated teeth, 7th 195 cervical vertebra, 1st dorsal vertebra, 4th dorsal, 6th to 8th dorsals, 12th to 14th dorsals, isolated neural spine of a posterior dorsal vertebra, incomplete sacrum, distal caudal vertebra, proximal fragment of dorsal rib, right dorsal rib 14, haemal arch, right femur, left metatarsal II and left 200 pedal phalanges II-2, II-3, IV-2, IV-3. The specimen was found 1 km from the holotype material.

4.3 Referred material

MPEF-PV 10821: 19 isolated teeth found in this locality, which are housed at the MPEF collections but have not been assigned to the holotype or paratype. Only two isolated teeth have been catalogued as part of the paratype (MPEF-PV 1157; see above).

4.4 Locality and horizon

'La Juanita' farm, 28 km north-west of Paso de Indios town, Chubut Province, Argentina (Figure 1). Precise GPS 215 data of the fossiliferous localities are deposited at the MPEF collection and available upon request. Cerro Castaño Member, Cerro Barcino Formation, Albian (Musacchio and Chebli 1975; Codignotto et al. 1978; Rich et al. 2000; Marveggio and Llorens 2013). 220

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Figure 1. Tyrannotitan chubutensis (Novas et al. 2005) locality map: (A) Argentina and (B) detail of Chubut province with the Tyrannotitan locality indicated by a star.

245 Cerro Barcino Formation is the upper unit of the Chubut Group and its age has been regarded as Hauterivian to Senonian (Campanian?) in age (Page et al. 1999), and is subdivided into several members. The basalmost member is Puesto La Paloma and is 250 characterised by pyroclastic and fluvial sediments, with dunes intercalated deposited under arid conditions. This unit contains chelid and meiolaniform turtles (Gaffney et al. 2007; de la Fuente et al. 2011; Sterli et al. 2013), as well as abelisaurid theropod and titanosauriform sauropod 255 dinosaurs (Rich et al. 2000; Rauhut et al. 2003). Overlying La Paloma Member is the Cerro Castaño Member, formed mainly by fluvial sediments. Sedimentological evidence indicates that during deposition of the Cerro Castaño Member, a return to wetter conditions occurred over the 260 previous unit. Apart from Tyrannotitan (Novas et al. 2005), this member has provided a variety of vertebrate remains, including crocodiles (Leardi and Pol 2009), sphenodontians (Apesteguía and Carballido in press), sauropod eggs (Argarañaz et al. 2013) and possibly the 265 ceratosaur theropod Genvodectes serus (Rauhut et al. 2003; Rauhut 2004). Cerro Barcino Formation culminates with Bayo Overo Member, in which the titanosauriform sauropod Chubutisaurus insignis was found (Del Corro 1975; Carballido et al. 2011). 270

4.5 Emended diagnosis

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A carcharodontosaurid theropod diagnosed by the following autapomorphic characters: teeth with bilobated

300 denticles in the mesial carinae; dentary with vertical symphyseal margin in lateral view; second and third dorsal vertebrae with well-developed accessory lamina connecting anterior and posterior centrodiapophyseal laminae; fibular fossa extended over the proximal end of the crista 305 tibiofibularis in the femoral shaft; proximomedial fossa of the fibula with posteriorly projected anterior border. Modified from Novas et al. (2005) (see Section 6).

5. Description

5.1 Jugal

The right jugal of the paratype (MPEF-PV 1157/1) is well preserved, but lacks a fragment of its anterior portion, the surface for the maxilla/lacrimal contact surface and the 315 quadratojugal processes.

The jugal is a transversely flattened bone that has an anterior projection for articulation with the maxilla, a dorsal process to contact the postorbital and a double posterior projection for articulation with the quadratoju-320 gal. In lateral view the ventral margin of the bone is straight to slightly convex (Figure 2), as in Carcharodontosaurus saharicus (SGM-Din 1) and Mapusaurus (MCF-PVPH 108,167), but differing from that of Allosaurus (UMNH 9085, UMNH 9086) where the ventral 325 margin is sigmoid in lateral view, with a strong convexity ventral to the level of the postorbital process. In ventral view, the jugal has a sigmoidal shape, with the anterior region laterally concave and the posterior portion laterally convex. 330

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Figure 2. Tyrannotitan chubutensis right jugal (MPEF 1157) photographs and line drawings in (A) lateral view and (B) medial view. Note: Scale bar is 10 cm; see text for abbreviations.

The anterior end of the jugal is thin and laminar, incompletely preserved in some areas, and bears on its lateral surface the posteroventral corner of the antorbital fossa (Figure 2(A)). The edge of this fossa is curved, with a similar position and morphology to that of Mapusaurus (MCF-PVPH 108.167) and Allosaurus (Madsen 1976). A large jugal pneumatic recess is also present, and is as expanded as in Mapusaurus (MCF-PVPH 108.167) and Acrocanthosaurus (NCSM 14345).

A prominent horizontal ridge runs along most of the lateral surface of the jugal, which extends from the notch between the two quadratojugal processes towards few centimetres anteriorly to the anterior margin of the postorbital process. This crest, also present in Mapusaurus (MCF-PVPH 108.167), was probably an insertion area for the m. pterygoideus ventralis (Holliday 2009).

Ventrally to the ventral edge of the orbital margin, the jugal is pierced by a foramen of about 1 cm in diameter, which penetrates into the bone internal structure (Figure 2 (A)). Posteriorly to this foramen, there is a much smaller and rounded blind depression.

The postorbital process of jugal is triangular in lateral view, with the anterior margin nearly straight and subvertically oriented. In cross section this process has a rounded and robust anterior end and tapers posteriorly 375 becoming a thin lamina at its posterior margin. The base of this process is anteroposteriorly long, as in Mapusaurus (MCF-PVPH 108167-168), but differing from the condition of Carcharodontosaurus saharicus (SGM-Din 1) in which the process is anteroposteriorly short. On the anterior 380 margin the oblique and anterolaterally oriented postorbital facet occupies the dorsal three-quarters of the postorbital process (Figure 2(A)). The laminar posterior margin of the process bears a slight depression, corresponding to the 385 anterior edge of the infratemporal fossa.

The articulation for the quadratojugal is forked into dorsal and ventral quadratojugal processes. Both processes have their posterior end broken, being the ventral process the most completely preserved. The latter is subcircular in cross-section and bears a dorsal concavity. The dorsal 410 process is laminar in cross-section. The posterior region of the jugal of Tyrannotitan lacks, both laterally and medially, a third medial process or accessory prong (contra Eddy and Clarke 2011), as was described for Acrocanthosaurus (Eddy and Clarke 2011), Sinraptor 415 (Currie and Zhao 1993) and Mapusaurus (MCF-PVPH 108 168).

Quadratojugal 5.2

The right quadratojugal has been preserved in MEFP-PV 1157 (Figure 3). The jugal process is dorsoventrally high, and becomes narrower towards its anterior end. The squamosal process has a fairly constant anteroposterior width along the dorsoventral axis throughout its entire 425 length. In lateral view, the height of the jugal process is larger than the anteroposterior width of the squamosal process, unlike Allosaurus (UMNH 8944, UMNH 8946) and Acrocanthosaurus (NCSM 14345) in which an inverse relationship is present. In the posteroventral corner, this 430 bone has a posterior process similar to that of other theropods. In medial view, a shallow depression is present at the dorsal sector of the jugal process. This depression represents the area for the articulation of the posterodorsal process of the jugal. 435

5.3 Dentary

The three available dentaries are preserved in a fairly good condition, lacking only the posteriormost portion that 440

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Figure 3. *Tyrannotitan chubutensis* right quadratojugal (MPEF 1157) photographs and line drawings in (A) lateral view and (B) medial view. Note: Scale bar is 10 cm; see text for abbreviations.

contacts the postdentary bones. The following description is based on the three elements.

460 In dorsal view, the dentary is transversely compressed, and slightly widens anteriorly towards the symphyseal area (Figure 4(C)). This feature is reminiscent to that of other allosauroids, such as in Giganotosaurus (MUCPv-Ch 1), Acrocanthosaurus (NCSM 14345), Allosaurus 465 (UMNH-PV 9351), but differs from abelisaurids (e.g. Carnotaurus (MACN-CH 894), Ekrixinatosaurus (MUCPv-294), Skorpiovenator (MMCH-PV 48) in which the dentary has a constant transverse width throughout its entire length. The dentary of Tyrannotitan 470 is nearly straight along most of its length, showing a slight medial curvature near its anterior end, at the level of the anterior edge of the third alveolus. In Giganotosaurus (MUCPv-Ch 1, MUCPv 95), the medial curvature of the anterior region is more marked and starts more posteriorly, 475 approximately at the anterior border of the sixth alveolus,

whereas in Acrocanthosaurus (NCSM 14345), the dentary is straight and in Allosaurus (UMNH-PV 9351) the dentary is gently curved medially along its entire length. In 515 lateral view, the dentary is posteriorly high and progressively tapers anteriorly, but has a dorsoventrally higher anterior end, creating a constriction at its central portion (Figures 4 and 5). This condition is also found in Giganotosaurus (MUCPv-Ch 1, MUCPv 95) and Mapu-520 saurus (Coria and Currie 2006). In Acrocanthosaurus (NCSM 14345), Allosaurus (UMNH-VP 9351, UMNH-VP 6476) and the purported carcharodontosaurid Kelmayisaurus petrolicus (Brusatte et al. 2012), the dorsoventral dentary height is nearly homogeneous along 525 the entire length of the bone. In Tyrannotitan the minimum height of the dentary occurs at the level of the seventh alveolus. The dentary has 15 alveoli, the anteriormost of which is subcircular while all others are ellipsoidal and 530 anteroposteriorly elongated; a morphology that is more



Figure 4.Tyrannotitan chubutensis left dentary (MPEF 1156) photographs in (A) lateral view, (B) medial view, (C) dorsal view and (D)detail of the symphysis in medial view. Note: Scale bar is 10 cm in A–C and 2 cm in D; see text for abbreviations.550



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Figure 5. Tyrannotitan chubutensis right dentary (MPEF 1157) photographs and line drawings in (A) lateral view and (B) medial view. Note: Scale bar is 10 cm; see text for abbreviations.

pronounced in the posterior alveoli. This contrasts with the condition of Neovenator and in most ceratosaurs, in which the alveoli have a subrectangular outline (Sereno et al. 2004; Brusatte et al. 2008; Canale et al. 2009). Anterior alveoli are 570 arranged obliquely to the anteroposterior axis of the dentary. The anterior end of the dentary has a subrectangular contour in lateral view, with the angle between the anterior end of the ventral margin and the symphyseal edge nearly straight. The same subrectangular outline is present in Giganoto-575 saurus (MUCPv-Ch 1, MUCPv-95), Carcharodontosaurus iguidensis (MNN IGU 5), Acrocanthosaurus (NCSM 14345) and in a large specimen of Allosaurus (UMNH-PV 6476). However, in Tyrannotitan the symphyseal anterior edge is completely vertical with respect to its 580 ventral margin. Moreover, the anteroventral end is more anteriorly projected than the anterodorsal margin, so that the symphyseal edge has a slight anteroventralposterodorsal orientation, which constitutes an autapo-585 morphy of Tyrannotitan. In the anterior end of the ventral margin, there is a ventral process ('chin') that is also present in Giganotosaurus (MUCPV-Ch 1), Carcharodontosaurus iguidensis (MNN IGU 5), Acrocanthosaurus (NCSM 14345) and Mapusaurus 590 (Coria and Currie 2006). This character is only present in the dentary of the paratype specimen, and has not been preserved in remaining available dentaries of Tyrannotitan (Figure 5).

The anterior margin of the dentary in lateral view bears 595 large and rounded neurovascular foramina. Some of these foramina are located within a longitudinal neurovascular groove, which is located dorsally on the lateral surface of the dentary at its anterior region. This groove bends ventrally at the level of the fourth and fifth alveoli, and 600 more posteriorly it curves dorsally (reaching the alveolar margin at the level of the posteriormost alveolus, Figure 5 (A)). Therefore, the groove follows a sigmoidal pattern, a feature considered as diagnostic of carcharodontosaurids by Sereno and Brusatte (2008). A similar pattern is present 605 not only in Carcharodontosaurus iguidensis (MNN IGU 5),

Giganotosaurus (MUCPV-Ch 1, MUCPv-95) and Acrocanthosaurus (NCSM 14345), but also in Allosaurus (UMNH-PV 6476). In Sinraptor (Currie and Zhao 1993), the lateral neurovascular groove is relatively straight and is 625 located more dorsally than in the above-mentioned taxa. In Tyrannotitan, this lateral neurovascular groove follows the same path and is similarly positioned to a groove located on the medial surface of the dentary, where the ventral ends of the fused dental plates are placed. 630

The symphyseal area is only well preserved in the right dentary of MPEF-PV 1156. It has two smooth concavities separated by a central ridge at its mid-height. In the ventral concavity there is a small rounded process; also observed in Carcharodontosaurus iguidensis ('articular brace' sensu 635 Brusatte and Sereno 2007) (Figure 4(D)). The symphyseal surface is set at a wide angle with respect to the medial surface of the dentary, observable in dorsal view. This angle gives a rounded appearance to the symphyseal region of the dentary, but not as rounded as in 640 Carcharodontosaurus iguidensis (Brusatte and Sereno 2007). Dorsal to the symphysis a small anterodorsal process is present, as in Carcharodontosaurus iguidensis (MNN IGU 5).

Along the medial face of the dentary of *Tyrannotitan*, 645 a thickened bar of bone is present, being more prominent in the anterior sector. This bar forms the dorsal limit of the Meckelian groove and is dorsally limited by a deep neurovascular groove that receives the ventral edge of the dental plates. This medial groove, as mentioned above, 650 follows a similar path as the neurovascular groove of the lateral surface of the dentary. Within this groove, it can be observed in dorsal view two foramina located approximately at the level of the second and third alveoli, as in Carcharodontosaurus iguidensis (MNN 655 IGU 5). The dental plates are fused together, and have variable height along the dentary. Its maximum height is located at the level of the central constriction of the dentary, decreasing both anteriorly and posteriorly (Figure 5(B)). 660

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The Meckelian groove in Tyrannotitan, as in other

carcharodontosaurids, is deep and well defined. As in Carcharodontosaurus iguidensis (MNN IGU 5) and Giganotosauurs (MUCPv-Ch 1, MUCPv-95), the Meck-

elian groove in Tyrannotitan ends anteriorly at the level of

first and second alveoli, whereas in Acrocanthosaurus (NCSM 14345) it ends more posteriorly, at the level of third and fourth alveoli. Anteriorly to the Meckelian groove, the dentary bears an anteroposteriorly elongated

oval fossa that is preceded anteriorly by a small round

foramen (Figure 5(B)). At the level of the dorsoventral constriction of the dentary, the Meckelian groove expands ventrally, forming a broad and subtriangular Meckelian fossa, which receives the anterior process of the splenial.

Dorsally to this fossa, the medial surface of the dentary is smooth and flat, as also occurring in Tyrannosaurus (Brochu 2003), whereas anteriorly this surface is gently convex. This transition occurs at the level of the 9th to 10th

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5.4 Teeth

alveoli.

The right dentary of the holotype (MPEF-PV 1156) has the sixth and seventh teeth preserved in their alveoli. The collected materials also include 21 isolated teeth, 2 of which had been referred to the paratype specimen (MPEF-PV 1157). The following description is based on the general characteristics present in all the available teeth.

The teeth are transversely compressed, with a crown 690 base ratio (crown base width/crown base length) that varies between 0.33 and 0.63 (values taken from 13 teeth) (Appendix S4, Table 2). The mesial margin is convex and the distal is in general straight, except for a few teeth that have concave distal margin (Figure 6(D)). In eight of the 695 teeth recovered, the mesial and distal carinae are centrally located, giving the tooth crown a symmetrical cross section. These teeth may have occupied a middle-posterior position in the toothrow. In the remaining seven teeth that have preserved both carinae, the mesial and distal carinae 700 are displaced from the mesiodistal axis, giving the tooth crown an asymmetrical cross section. Probably these teeth were positioned at the anterior region of the toothrow. The specific position of the isolated teeth (i.e. whether they represent upper or lower teeth, left or right) is difficult to 705 determine, given the variation observed in other theropods. For example, in the abelisaurid Majungasaurus crenatissimus (Fanti and Therrien 2007), the anterior teeth have both carinae lingually displaced. However, in the dentary of Giganotosaurus (MUCPv-Ch 1), the anteriorly 710 located teeth have their carinae labially displaced, creating a greater convexity on the lingual surface of each tooth. For this reason, in the case of the isolated teeth of Tyrannotitan, we have decided not to use the carinae displacement as a parameter to assign the teeth of



735 Tyrannotitan chubutensis isolated teeth (MPEF Figure 6. 10821) photographs in (A) lateral view, (B) mesial view and (C) distal view of a 'anterior' tooth, (D) lateral view, (E) mesial view and (F) distal view of a 'middle-posterior' tooth. Note: Scale bar is 5 cm; see text for abbreviations.

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asymmetric cross section to a particular placement of the toothrow (left or right side), except for identifying them as positioned anteriorly or middle-posteriorly in the toothrow. The complete teeth, which have preserved their crown 745 and root, have a sigmoid shape when observed in anterior or posterior view (Figure 6(C)), as in *Giganotosaurus* (MUCPV-Ch 1), Mapusaurus (MCF PVPH 108.9) and Carcharodontosaurus saharicus (SGM-Din 1).

The denticles are 'chisel-like' (Currie et al. 1990), with 750 poorly developed blood-grooves. In the central sector of both carinae, there are two denticles per mm, as in Giganotosaurus (MUCPV-Ch 1), Carcharodontosaurus saharicus (SGM-Din 1), Carcharodontosaurus iguidensis (MNN IGU 6), but differing from Acrocanthosaurus 755 (Currie and Carpenter 2000) that has three denticles per mm. Close to the base the denticles are smaller, and the denticle density raises to three per mm. Of the 23 teeth studied, only 5 have preserved a complete mesial carina. Out of those five teeth, only three have bilobulated 760 denticles (the sixth tooth of the right dentary of the holotype plus two isolated teeth). In one of the isolated teeth, the mesial carina extends only over the apical half of the crown. Its ventral half has a smooth and rounded mesial border, lacking a carina or denticles. 765

At least five teeth have preserved enamel wrinkles, which are present in a wide variety of theropod species (Brusatte et al. 2007; Canale et al. 2009). In Tyrannotitan chubutensis, the wrinkles occur variably in each tooth, being located on the mesial carina, on the distal carina or 770



Figure 7. Reconstruction of the lateral side of the skull of *Tyrannotitan chubutensis* based on elements of the paratype (MPEF 1157). Note: Scale bar is 10 cm.

in both carinae. The four teeth preserving the root have a constriction on both the labial and lingual sides, creating an eight-shaped cross section of the root.

5.5 Vertebral column

Combining the vertebral elements of both specimens recovered, the available material of *Tyrannotitan* contains representatives of all sections of the vertebral column.

Novas et al. (2005) identified a cervical vertebra of the paratype of Tyrannotitan as the ninth cervical. Through comparisons with the cervical series of Giganotosaurus (MUCPV-Ch 1), this element is reinterpreted here as the seventh cervical vertebra, given the presence of characters such as a marked opisthocoely of the centrum, a transverse process directed more ventrally than laterally and a neural arch anteroposteriorly extended. Novas et al. (2005) also identified a sequence of articulated vertebrae of the holotype (MEFP-PV 1156), exposed only on its right lateral side, as the segment of third to eighth dorsals. Here, this series is reinterpreted as the sequence of second to seventh dorsals, based on comparison of the neural arch of the first of these articulated elements with the dorsal series of Allosaurus (Madsen 1976). The transverse process of this neural arch is laterally directed, its dorsal surface being exposed in lateral

view. This is consistent with the morphology of the second dorsal of *Allosaurus* (Madsen 1976), whereas in the third dorsal of this taxon, the transverse process has a slight dorsal orientation, so that its dorsal surface is not exposed in lateral view. Another character that supports this interpretation is the location of the parapophysis in the middle of the centrum, as in the second dorsal of *Allosaurus* (Madsen 1976), whereas in the third dorsal the parapophysis is located on the base of the neural arch (Figure 7).

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5.5.1 Atlas

The atlas (MEFP-PV 1157) is an anteroposteriorly short element. In anterior view, the vertebral body has a square 840 contour at its ventral half. The anterior surface of the centrum has a deep concavity that articulates with the occipital condyle. Within this concavity, the dorsal sector bears an oval perforation separated from the neural canal by a thin bridge of bone (Figure 8(A),(C)). In posterior 845 view, the centrum is dorsally concave and ventrally convex. The dorsal concavity corresponds to the articulation with the odontoid process of the axis. The neural arch is as high as the centrum. Anteriorly and laterally to the neural canal there is a pair of rounded prominences. 850 Ventrally to each postzygapophysis, the neural arch bears a rounded and well-marked fossa. The postzygapophyses are oriented medioventrally (Figure 8(C)). The epipophyses are well developed (Figure 8), as in Torvosaurus (BYU 725/4884), Majungasaurus (O'Connor 2007) and 855 Acrocanthosaurus (NCSM 14345).

5.5.2 Seventh cervical

The centrum of this vertebra (MPEF-PV 1157) is strongly opisthocoelic, having a hemispherical anterior articular surface (Figure 9), as in *Giganotosaurus* (MUCPV-Ch 1), but unlike that of *Allosaurus* (UMNH-PV 8354) in which the opisthocoely is less developed. The ventral surface is concave in lateral view. The parapophysis is large and rounded, and located at the anteroventral corner of the lateral surface of the centrum, immediately behind the



Figure 8. *Tyrannotitan chubutensis* atlas (MPEF 1157) photographs in (A) anterior view, (B) right lateral view, (C) posterior view and (D) left lateral view. Note: Scale bar is 10 cm; see text for abbreviations.

785

790



800

805

810 [Q1]

825



Figure 9. *Tyrannotitan chubutensis* seventh cervical vertebra (MPEF 1157) photographs and line drawings in (A) anterior view, (B) right lateral view, (C) posterior view and (D) left lateral view. Note: Scale bar is 10 cm; see text for abbreviations.

anterior articular face. This vertebra has two pleurocoels 905 on its lateral surface (Figure 9(B)), as in Carcharodontosaurus saharicus (NCSM 18166) and Giganotosaurus (MUCPV Ch 1). The anterior pleurocoel is located dorsally to the parapophysis, is larger than the posterior pleurocoel and is separated from the posterior pleurocoel 910 by a thin oblique sheet of bone. The posterior surface of the centrum is nearly circular, except for its flattened dorsal margin below the neural canal. The prezygapophyses are wide and dorsomedially oriented. The medial 915 edge of each prezygapophysis is ventrally curved forming a rudimentary hypantrum (Figure 9(A)), which is not as developed as in the dorsal vertebrae.

he diapophysis is triangular in lateral view (Figure 9 (B),(D)), as in Giganotosaurus (MUCPV Ch 1), 920 Mapusaurus (MCF-PVPH 108.90) and Carcharodontosaurus saharicus (NCSM 18166), and is lateroventrally directed. The prezygodiapophyseal lamina is supported by two accessory laminae: the anterior of which is more developed. In posterior view, dorsal to the neural canal, 925 there is a small vertical lamina that supports the base of the 'U-shaped' hyposphene. On each side of this lamina, over the neural canal, the neural arch bears small circular fossae that are bounded laterally by a curved lamina, which comes from the vertebral centrum and connects to the 930 lateral wall of the hyposphene (Figure 9(C)). Dorsal to postzygapophyses, a rhomboid deep depression occupies the entire posterior surface of the neural spine, at the centre of which is distinguished the ligament scar. The epipophyses are pointed and well developed on the dorsal 935 surface of each postzgapophysis (Figure 9(D)). The robust

neural spine has a quadrangular cross section at its base, as 960 in *Giganotosaurus* (MUCPV Ch 1) and *Mapusaurus* (MCF-PVPH 108.90). At the base of its anterior surface there are ligament scars.

5.5.3 First dorsal

The centrum of the first dorsal (MPEF-PV 1157) is larger but less opisthocoelic than in the seventh cervical. The kidney-shaped parapophyses are located anteroventrally on the lateral sides of centrum. Dorsally to each 970 parapophysis, the centrum bears a large oval pleurocoel (Figure 10(B),(D)). The posterior surface of the centrum has a perfectly circular outline. The ventral surface is concave in lateral view. The neural arch is higher and anteroposteriorly shorter than that of the seventh cervical 975 vertebra. The neural canal is oval, being higher than wide. The prezygapophyses are dorsally positioned, on the neural arch, with a wide hypantrum developed ventral to them (Figure 10(A)). The neural spine is robust, with a square-shaped base in cross section. The transverse 980 processes are more laterally than ventrally directed. The prezygapophyses, as the postzygapophyses, face dorsally as in the rest of the dorsal vertebrae. The hyposphene is well developed and has a short medial lamina at its ventral end that extends down to the dorsal edge of the neural 985 canal. On both sides of the above-mentioned lamina, deep fossae are present. These are laterally bounded by a pair of curved laminae that have a similar disposition to that described of the seventh cervical, but are proportionally more robust (Figure 10(C)). These same laminae are 990



Figure 10. *Tyrannotitan chubutensis* first dorsal vertebra (MPEF 1157) photographs and line drawings in (A) anterior view, (B) right lateral view, (C) posterior view and (D) left lateral view. Note: Scale bar is 10 cm; see text for abbreviations.

1015 present in *Mapusaurus* (MCF PVPH 108.82) but in this taxon they are less developed than in *Tyrannotitan*.

5.5.4 Second dorsal

In the second dorsal vertebra, only the neural arch has been 1020 preserved (MPEF-PV 1156), lacking neural spine. The transverse process is laterally directed, so that its dorsal surface is exposed in lateral view. The centroprezygapophyseal lamina is subvertically oriented and merges with 1025 the anterior centrodiapophyseal lamina. The resultant lamina extends along the neural arch towards the parapophysis (Figure 11), as in the second dorsal of Acrocanthosaurus (Harris 1998), Allosaurus (Madsen 1976) and in an anterior dorsal of Mapusaurus (MCF-1030 PVPH 108.82). The parapophysis is located at mid height of the neural arch. The centroprezygapophyseal fossa (sensu Wilson et al. 2011) is shallower than in more posterior dorsal vertebrae. The posterior centrodiapophyseal lamina is more robust than the anterior centrodiapo-1035 physeal lamina and is vertically oriented. Both laminae delimit a triangular and deep centrodiapophyseal fossa. At the ventral region of this fossa there is a low accessory lamina that runs anteroposteriorly (Figure 11).

1040

1045

5.5.5 Third dorsal

In this vertebra (MPEF-PV 1156) only the neural arch and part of the centrum have been preserved. The neural arch is anteroposteriorly longer than that of the second dorsal, in part because the transverse process becomes more 1070 posterodorsally oriented and the prezygapophysis is more anteriorly projected, surpassing the anterior border of the vertebral centrum. This trend among the transverse processes and prezygapophysis is accentuated in subsequent vertebrae. Consequently, along this series the 1075 centroprezygapophyseal fossa becomes progressively wider and deeper in posterior dorsal vertebrae. The parapophysis is located at the base of the neural arch. As in the second dorsal, the anterior centrodiapophyseal lamina merges with the centroprezygapophyseal and the resultant 1080 lamina extends over the neural arch dorsal to the parapophysis. The accessory lamina is more prominent and better defined than in the second dorsal (Figure 11). This lamina is absent in the anterior dorsal vertebra of Mapusaurus (MCF PVPH 108.82) and Allosaurus 1085 (UMNH-VP 8334). In Acrocanthosaurus (SMU-74646 4-17: Harris 1998), there are two thin accessory laminae in the third dorsal vertebra, which resemble that of Tyrannotitan, although they are much less developed. The parapophysis is dorsoventrally elongated. 1090

5.5.6 Fourth dorsal

The fourth dorsal vertebra is represented by fragments of the centrum and neural arch in both holotype and paratype 1095 (Figures 11 and 12). The centrum is tall, with flat and ovoid articular surfaces, dorsoventrally elongated and with a concave margin under the neural canal. The centrum is spool shaped, ventrally concave in lateral view and without a ventral keel. The centrum bears two pleurocoels 1100



Figure 11. *Tyrannotitan chubutensis* articulated second dorsal to seventh dorsal vertebrae (MPEF 1156) photographs and line drawings in right lateral view. Note: Scale bar is 10 cm; see text for abbreviations.

on its lateral surface, which are anteroposteriorly aligned and separated by a thin oblique lamina (Figure 12), as in *Giganotosaurus* (MUCPV-Ch 1) and *Acrocanthosaurus* (Harris 1998). The neural canal is dorsoventrally elongated. The prezygapophysis faces dorsomedially.
The hypantrum is thin walled, and delimits the medial margin of the deep centroprezygapophyseal fossae. These fossae are laterally limited by the centroprezygapophyseal laminae (Figure 12(A)). The neural arch has the same height as the centrum. The centroprezygapophyseal lamina is shorter and more robust than in the preceding vertebrae. The anterior centrodiapophyseal lamina reaches 1200 the dorsal border of the parapophysis and does not merge to the centroprezygapophyseal lamina. Therefore, in the fourth dorsal (and in more posterior vertebrae), this lamina is referred as parapodiapophyseal lamina (Figure 11). In this vertebra, and in the subsequent dorsal vertebrae, there is no evidence of the accessory laminae described for the second and third dorsals. The centroprezygapophyseal fossa is wider than the centrodiapophyseal fossa, whereas in the second dorsal both fossae are similarly developed. This trend is accentuated in the subsequent posterior 1210



Figure 12. *Tyrannotitan chubutensis* fourth dorsal vertebra (MPEF 1157) photographs in (A) anterior view, (B) right lateral view, (C) posterior view and (D) left lateral view. Note: Scale bar is 10 cm; see text for abbreviations.

1230

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1260

vertebrae. The parapophysis is dorsoventrally elongated and is located at the anterior border of the neural arch.

5.5.7 Fifth dorsal

The fifth dorsal vertebra lacks the neural spine (MPEF-PV 1156) (Figure 11). It has two aligned pleurocoels on each lateral side of the centrum. In lateral view, the tip of the transverse process surpasses the posterior border of the centrum. The centroprezygapophyseal lamina is as robust as the same in the fourth dorsal, expanding to the base of the prezygapophysis. As in the precedent vertebrae, the centrodiapophyseal lamina is vertically oriented. The parapophysis has a circular outline.

5.5.8 Sixth dorsal

¹²⁴⁵ Two centra with part of the neural arch have been preserved of the sixth dorsal, belonging to holotype and paratype (Figures 11 and 13). The centrum is tall, amphyplatyan and ventrally concave in lateral view. Both pleurocoels are anteroposteriorly elongated and located on the dorsal region of the lateral surface of the centrum. The neural canal is dorsoventrally elongated. The prezygapophysis faces dorsally and below them there are two deep cenotroprezygapophyseal fossae, limited laterally by the 1285 robust centroprezygapophyseal laminae and medially by the hypantrum walls (Figure 13(A)). Over the anterior border of the prezygapophysis there are two rounded pneumatic pits, which are also present in Giganotosaurus (MUCPv-Ch 1), Mapusaurus (MCF-PVPH 108.84) and 1290 Allosaurus fragilis (UMNH-VP 10108). The hyposphenehypantrum facets are well developed and dorsoventrally elongated. The parapophysis is located at the anteroventral border of the neural arch (Figure 11). The centrodiapophyseal lamina is robust and the parapodiapophyseal is 1295 very reduced. The transverse process is strongly posterodorsally directed.

1280

1300

5.5.9 Seventh dorsal

Remains of the seventh dorsal have been preserved on both the holotype and the paratype. The transverse process is more posterodorsally oriented and the centroprezygapo-



Figure 13. *Tyrannotitan chubutensis* sixth dorsal vertebra (MPEF 1157) photographs in (A) anterior view, (B) right lateral view, (C) posterior view and (D) left lateral view. Note: Scale bar is 10 cm; see text for abbreviations. 1320



Figure 14. *Tyrannotitan chubutensis* eighth dorsal vertebra (MPEF 1157) photographs in (A) anterior view, (B) right lateral view, (C) posterior view, (D) left lateral view of the isolated neural spine and (E) anterior view of a fragment of the neural arch. Note: Scale bar is 10 cm; see text for abbreviations.

physeal lamina is shorter and more robust than in the sixth dorsal vertebra (Figure 11). The parapodiapophyseal lamina is weakly developed in comparison with the posterior centrodiapophyseal lamina. The neural spine is as high as the centrum plus the neural arch. The neural spine has strongly developed ligament scars on the dorsal region of its anterior surface, as in *Mapusaurus* (MCF PVPH 108) and *Acrocanthosaurus* (Harris 1998). The centrum bears two pleurocoels on the dorsal region of its lateral surface.

1360

5.5.10 Eighth? dorsal

An isolated neural spine (MPEF-PV 1156) (Figure 14(A)-(D)) and part of a neural arch (MPEF-PV 1157) (Figure 14 (E)) were assigned with doubts to the eighth dorsal 1365 vertebra. The centroprezygapophyseal fossae are strongly reduced and restricted to the base of the parapophysis (Figure 14(E)). The hypantrum is rhomboid shaped, being wider at its central sector than in the sixth dorsal. The parapophysis is laterally directed, and has a pointed 1370 projection at its dorsal end. The neural spine is subrectangular in lateral view, with a central anteroposterior and lateromedial constriction. The ligament scars are strongly developed, having rounded anterolateral projec-1375 tions and being restricted to the dorsal half of the neural

spine. The spinoprezygapophyseal laminae ventrally delimit a wide spinoprezygapophyseal fossa (Figure 14 ¹⁴⁰⁵ (A),(C)). The posterior ligament scars are not as developed as those of the anterior surface.

5.5.11 Nineth? dorsal

An isolated neural spine (MPEF-PV 1156) was assigned with doubts to the ninth dorsal vertebra. The overall morphology is very similar to that assigned to the eighth dorsal vertebra, but is higher and more slender. The pneumatic openings are well developed under each prezygapophysis. The right spinoprezygapophyseal lamina has a bifurcation with a small anterolateral lamina. The transverse process is dorsally oriented, but only a fragment of this process has been preserved. The anterior ligament scar is strongly developed and restricted to the dorsal half of the spine.

5.5.12 Tenth dorsal

The 10th dorsal vertebra has been almost completely preserved (MPEF-PV 1156) (Figure 15). The centrum is spool shaped and bears two ovoid pleurocoels. These are anteroposteriorly aligned and, unlike in the anterior dorsals, located within a deep and anteroposteriorly 1430

1400

1410

elongated fossa. The transverse process is laterally directed, as in the last dorsal vertebra of Allosaurus (Madsen 1976). The posterior centrodiapophyseal lamina is robust and reaches the anterior margin of the postzygapophysis. The lateral border of the postzygapo-1435 physis is ventrally curved, covering laterally the prezygapophysis of the subsequent vertebra (preserved in articulation), as in Giganotosaurus (MUCPV Ch 1), Acrocanthosaurus (Harris 1998), Majungasaurus 1440 (O'Connor 2007) and Carnotaurus (MACN-CH 894). The morphology of the neural spine is very similar to that of the preceding dorsal vertebrae.

5.5.13 Eleventh dorsal 1445

1450

1455

1460

The 11th dorsal vertebra (MPEF-PV 1156) is almost completely preserved and articulated with the 10th dorsal (Figure 15). In posterior aspect, the articular surface has a subcircular outline as in the posterior dorsal vertebrae of Giganotosaurus (MUCPv-CH 1) and Allosaurus (Madsen 1976). As in the 10th dorsal, the pleurocoels are located within a deep and anteroposteriorly elongated fossa. The parapophyses are dorsoventrally elongated. The transverse processes are laterally directed. The centroprezygapophyseal lamina is short and robust. The parapodiapophyseal lamina is an oblique and very thin sheet of bone. The posterior centrodiapophyseal lamina is vertically oriented and thinner than in the 10th dorsal. The postzygapophysis

has its lateral margin ventrally curved, as in the 10th dorsal. The spinopostzygapophyseal laminae are markedly robust at their base, and both delimit a deep spinopostzygapophyseal fossa. Between both postzygapophyses, only a fragment of the hyposphene has been preserved in this vertebra.

5.5.14 Twelfth dorsal

1495

1490

1505

dorsal vertebra (MPEF-PV 1157). The posterior articular surface has a circular contour. The anterior pleurocoel is larger than the posterior pleurocoel. The left side of the 1500 centrum has preserved the base of an oblique anterior centrodiapophyseal lamina and a vertical posterior centrodiapophyseal lamina. Unlike the more anterior dorsal vertebrae, this vertebra has a wide ventral furrow.

Only an isolated vertebral centrum is known from the 12th

Thirteenth dorsal 5.5.15

Only the isolated centrum of the 13th dorsal vertebra has been preserved (MPEF-PV 1157). As in the 12th dorsal vertebra, the articular surfaces have a subcircular 1510 outline, the anterior pleurocoel is more developed than the posterior, and the centrum has a wide ventral furrow. The neural canal is rounded, instead of being

1515



Figure 15. Tyrannotitan chubutensis articulated 10th and 11th dorsal vertebrae (MPEF 1156) photographs and line drawings in right 1485 lateral view. Note: Scale bar is 10 cm; see text for abbreviations.



Figure 16. Tyrannotitan chubutensis 14th dorsal vertebra (MPEF 1157) photographs in (A) anterior view, (B) right lateral view, (C) posterior view and (D) left lateral view. Note: Scale bar is 10 cm; see text for abbreviations.

1555

dorsoventrally elongated as in the most anterior dorsal vertebrae.

1560 5.5.16 Fourteenth dorsal

The isolated vertebral centrum of the 14th vertebra has been preserved (MPEF-PV 1157) (Figure 16), as well as an isolated neural spine (MPEF 1156) (Figure 17). The centrum is anteroposteriorly shorter than in the 12th and 1565 13th vertebrae. Both anterior and posterior articular surfaces are rounded, but the posterior one is smaller, which matches the size of the first sacral centrum. There is only one rounded pleurocoel on each lateral surface of the centrum (Figure 16(B),(D)). The posterior centrodiapo-1570 physeal lamina (only preserved on the left side) is anterodorsally directed, as in the 14th dorsal of Allosaurus (Madsen 1976) (Figure 16(B)). The hypantrum is well

1595



Figure 17. Tyrannotitan chubutensis articulated neural spines of 14th dorsal vertebra and 1st sacral vertebra (MPEF 1156) photographs in left lateral view. Note: Scale bar is 10 cm; see text for abbreviations.

developed and dorsomedially elongated. The neural spine is anteroposteriorly shorter than that of the 10th and 12th dorsal vertebrae, as in Allosaurus (Madsen 1976) and Tyrannosaurus (Brochu 2003). The anterior ligament scar 1615 is strongly developed in this vertebra. The neural spine is anterodorsally oriented (Figure 17), as in the 14th dorsal vertebra of Allosaurus (Madsen 1976), Sinraptor (Currie and Zhao 1993) and Aerosteon (Sereno et al. 2008).

1620

1610

5.5.17 Sacrum

A neural spine, found in articulation with the neural spine of the 14th dorsal (MPEF 1156) (Figure 17), has been preserved from the sacrum of the holotype, as well as two 1625 fragments of fused sacral centra of the paratype (MPEF-PV 1157) (Figure 18).

The lateral surface of the neural spine is partially covered by a fragment of the left ilium. The spine is anteroposteriorly wider than in the 14th dorsal and has the 1630 posterior ligament scar strongly developed. As in Giganotosaurus (MUCPV-Ch 1), there is no evidence of fusion between the sacral neural spines.

The two preserved sacral fragments of the paratype include the left half of the first and a small part of the 1635 second sacral centrum, which are fused and have clear evidence of deformation, and a fused sequence of the third, fourth and fifth sacral centra. The sacrum is ventrally concave and medially compressed, as in Giganotosaurus (MUCPV Ch 1), Carnotaurus (MACN-CH 894) and 1640 Ceratosaurus (Gilmore 1920) (Figure 18(A)-(C)). The lateral surface of the first sacral centrum bears a medial longitudinal ridge. The base of the neural arch has been preserved and is located over the posterior half of the centrum. This vertebra lacks pleurocoels, but it has a 1645 pneumatic recess and small opening at the base of the neural arch (Figure 18(A)). The ventral surface, although incomplete seems to be transversely compressed. The third centrum is the smallest of the sacral series. The contact between the third and fourth centra is the lateromedially 1650

narrowest contact of the sacral series. The fourth sacral has the posterior surface expanded with respect to the anterior surface and has a pleurocoel on the posterodorsal region of the left lateral surface of the centrum (located within a anteroposteriorly elongated fossa) (Figure 18(A)). Sacral pleurocoels are known also in *Mapusaurus* (MCF PVPH 108.209) and *Giganotosaurus* (MUCPV Ch 1). The fifth sacral vertebra is the highest of the sacral series; its posterior articular surface is also expanded, and has a conspicuous pleurocoel on its lateral surface (as in the fourth sacral). The postzygapophysis preserved in this sacral centrum faces ventrally (Figure 18(D)).

1665 5.5.18 Anterior caudal

1670

1675

There is an almost complete anterior caudal vertebra (MPEF 1156) (Figure 19), which has slight deformation at the tip of its neural spine. This element is interpreted as belonging to the series between the 5th and 10th caudal vertebrae, giving the size difference between its centrum and that of the last sacral and the orientation of the zygapophyses.

The centrum is amphyplatyan. The margins of its articular surfaces are not complete, and they likely were

more expanded than preserved, creating a spool-shaped centrum. There are anteroposteriorly elongated depressions ('pleurocoelic fossae') on the dorsal region of its lateral surface, as in Giganotosaurus (MUCPV-Ch 1) and Mapusaurus (MCF PVPH 108.81). This differs from 1710 the condition of Carcharodontosaurus saharicus (Stromer 1931), which have actual pleurocoels in the anterior caudal vertebrae. The prezygapophysis faces dorsomedially, at an [Q3] angle of approximately 45th with the horizontal plane 1715 (Figure 19(A)). The spinoprezygapophyseal fossa is shallow between both spinoprezygapophyseal laminae. Over the dorsal half of the anterior surface of the neural spine, there is a ligament scar, which is less developed than in the posterior dorsal vertebrae. The transverse processes 1720 are robust and posterolaterally oriented. The anterior surface of the transverse process bears a longitudinal wide fossa, as in the anterior caudal vertebrae of Giganotosaurus (MUCPV-Ch 1). The postzygapophysis faces ventrolaterally. Dorsal to the postzygapophysis and 1725 between both spinopostzygapophyseal laminae there is a deep spinopostzygapophyseal fossa, limited dorsally by a ligament scar, which is much more developed than the anterior scars (Figure 19(B),(D)). The neural spine is twice as tall as the centrum. There is no preserved hypantrum in 1730







Figure 19. Tyrannotitan chubutensis anterior caudal vertebra (MPEF 1156) photographs in (A) anterior view, (B) right lateral view, (C) posterior view and (D) left lateral view. Note: Scale bar is 10 cm; see text for abbreviations.

this element, but there is a small hyposphene between the 1790 postzygapophyses, as in Giganotosaurus (MUCPV-Ch 1) and possibly in cf. Veterupristisaurus (MB R 1940: Rauhut 2011).

1795

1800

1815

5.5.19 Distal caudal

There is a fragmentary and isolated distal caudal vertebra preserved (MPEF-PV 1157) (Figure 20). Based on comparisons with the caudal series of Allosaurus (Madsen 1976), this element was interpreted as belonging to the series between the 30th and 35th caudal vertebrae. The centrum is laterally compressed, ventrally concave in



Figure 20. Tyrannotitan chubutensis distal caudal vertebra (MPEF 1157) photographs in (A) anterior view and (B) right lateral view. Note: Scale bar is 10 cm; see text for abbreviations.

lateral view and expanded at its articular surfaces. The 1845 anterior articular surface (the only one preserved) is wider than high. The lateral surface of the centrum bears an anteroposteriorly long depression. The preserved right prezygapophysis is laterodorsally projected and seems to have the spinoprezygapophyseal lamina extending as 1850 anteriorly as in Veterupristisaurus (to the midwidth of the base of the prezygapophysis; Rauhut 2011). In addition, the lamina that extends over the lateral surface of the prezygapophysis, which characterises Veterupristisaurus (Rauhut 2011), is absent in Tyrannotitan. The neural spine 1855 is low and anteroposteriorly extended.

5.5.20 Ribs

Several ribs, mostly fragments, were recovered. They have 1860 no major differences with those of Giganotosaurus (MUCPV Ch 1) and Allosaurus (Madsen 1976). A proximal fragment of an anterior dorsal rib (MPEF-PV 1157) lacks evidence of pneumatisation, as in Mapusaurus (Coria and Currie 2006) and Sinraptor 1865 (Currie and Zhao 1993). A complete posterior dorsal rib was recovered (MPEF-PV 1157), probably the 14th dorsal rib, based on the comparisons with Allosaurus (Madsen 1976). It is a short and recurved element with a flattened shaft. The capitulum is also flattened and its dorsomedial 1870

5.5.21 Haemal arches



Figure 21. Tyrannotitan chubutensis left scapulocoracoid (MPEF 1156) photographs in (A) lateral view and (B) medial view. Note: Scale bar is 10 cm; see text for abbreviations.

margin is formed by a lamina that connects to the subcylindrical tuberculum.

1890

1885

Seven haemal arches have been recovered from both the holotype and paratype specimens, five anterior and two distal. They are proximodistally long and laterally 1895 compressed elements. The haemal arch interpreted as the most anterior element is straight in lateral view, whereas the rest are posteriorly concave. The haemal canal is triangular in anterior view, and occupies approximately less than one-fifth of the total height of the bone, differing 1900 from the condition of the first 10 haemal arches of Tyrannosaurus in which the canal occupies at least onefourth of their height (Brochu 2003). The haemal canal is dorsally closed by two oblique articular facets for the caudal vertebrae. Over the anterior and posterior margins 1905 of both proximal rami, there are rounded processes. The posterior process occupies a more distal position over the ramus than the anterior process.

1910 5.6 Scapulocoracoid

A left coracoid with the proximal third of the scapula fused was preserved (MPEF-PV 1156). Although this element is damaged, it has preserved the subcircular outline of the coracoid (Figure 21). The coracoid is a robust bone near 1915 the glenoid cavity, and becomes thinner towards the anterior and dorsal margins. The posteroventral process is well developed, as in Giganotosaurus (MUCPv-Ch 1), Allosaurus (UMNH 9822), Piatnitzkysaurus (Bonaparte 1986) and Carnotaurus (MACN-CH 894). The antero-1920 ventral sector of the lateral surface of the coracoid bears a long biceps tubercle (Figure 21(A)), as in Tyrannosaurus (Brochu 2003). This tubercle is represented by a straight low crest of about 9 cm long, being more pronounced at its 1925 posterodorsal end. The coracoid foramen is large and

rounded, positioned in a central position on the lateral surface of the coracoid, as in Giganotosaurus (MUCPv-Ch 1), but unlike Mapusaurus (MCF-PVPH 108.71) in which the foramen is located near the glenoid cavity. This 1945 foramen perforates the bone obliquely, so that the medial opening is more posteriorly positioned than the lateral one. A broad fossa occupies most of the anterior region of the medial surface of the coracoid. This fossa is subdivided in two smaller fossae: one located dorsally and another 1950 located ventrally, being separated from each other by a low anteroposterior crest (Figure 21(B)).

Only the proximal scapula part was preserved, which, unlike Mapusaurus (MCF-PVPH 108-50; MCF-PVPH 1955 108-71), is completely fused to the coracoid. The acromial process projects abruptly forming a straight angle with the dorsal margin of the scapular blade, as in Mapusaurus (Coria and Currie 2006), Acrocanthosaurus (Harris 1998) and most non-avian theropods. The anterolateral region of 1960 the acromion process is occupied by the subacromial fossa. The preserved portion of the scapular blade has a wide and rounded ventral border and a sharp dorsal margin.

5.7 Humerus

Only the distal half of a right humerus has been preserved (MPEF-PV 1156). The distal end is preserved of the deltopectoral crest at the proximal end of the preserved anterior surface, which is anteromedially oriented as in 1970 Mapusaurus (MCF-PVPH 108.45). In contrast, Allosaurus (UMNH-PV 8157) and Acrocanthosaurus (NCSM 14345) have an anteriorly projected distal end of the deltopectoral crest. The humerus is lateromedially expanded at its distal end (Figure 22(A),(C)). At the medioventral region of the 1975 anterior surface, the humerus bears the proximal end of the fossa located between the radial and ulnar condyles (Figure 22(A)). This fossa has a triangular outline, as in Mapusaurus (MCF-PVPH 108-45) and Torvosaurus (BYU-VP 2002). In lateral view, it can be seen that the

1965

1940

2060

2070



1995

2000

1985

1990

Figure 22. *Tyrannotitan chubutensis* right humerus (MPEF 1156) photographs in (A) anterior view, (B) lateral view, (C) posterior view and (D) medial view. Note: Scale bar is 10 cm; see text for abbreviations.

distal articular condyles are anteriorly projected (Figure 22 (B),(D)).

expansion is laterally projected. The region of the radius on the medial surface where the ulna articulates is smooth and slightly depressed. The distal of the radius end is only moderately expanded.

5.8 Radius

The right ulna cited by Novas et al. (2005) is reinterpreted here as a right radius, based on comparisons with *Acrocanthosaurus* (NCSM 14345) and *Allosaurus* (Madsen 1976; UMNH-PV unnumbered). In addition, a fragment of left radius has been preserved in the holotype.

The radius is a short and robust bone that is strongly 2010 curved, being posteriorly concave (Figure 23), as in *Acrocanthosaurs* (NCSM 14345) and *Mapusaurus* (MCF PVPH-108.46), but unlike that of *Allosaurus* (Madsen 1976; UMNH-PV unnumbered). In anterior view the radius is straight. The shaft is subcircular in cross section 2015 and the proximal end is expanded. The proximal articular surface, although partially eroded, has preserved an ovoidal contour, as in *Acrocanthosaurus* (NCSM 14345) and *Mapusaurus* (MCF PVPH-108.46). The proximal

5.9 Ilium

Two fragments of the left ilium were preserved (MPEF 1156). One of them, preserved attached to the posteriormost dorsal and first sacral neural spines (Figure 17), corresponds to part of the preacetabular blade. The other fragment is interpreted here as the lateral wall of the 2065 postacetabular blade, which is lateromedially narrow. The posterior sector of this fragment is ventrally directed.

5.10 Pubis

Both pubic shafts have been preserved, lacking their proximal end and distal foot (MPEF 1156) (Figure 24). The pubic shafts are straight in lateral view (Figure 24(B)),





as in Giganotosaurus (MUCPV Ch 1), but unlike Carcharodontosaurus saharicus (Stromer 1931) and Acrocanthosaurus (Harris 1998) in which these elements are anteriorly curved. In anterior or posterior view the pubic shaft has a sigmoid shape (Figure 24(A),(C)). The 2095 pubic symphysis is laminar and occupies the central third of the preserved region of the pubis. Distally to the symphysis and proximally delimited by pubic foot, a proximodistally enlarged pubic foramen is present. 2100 Proximal to the pubic symphysis the medial margins of the shaft are sharp, giving a tear-shaped cross section to this region of the pubic shaft. The distance between both iliac processes of both pubes and both ischia is approximately 40 cm, indicating the width of the hip in the holotype of Tyrannotitan.

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5.11 Ischium

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Both ischia have been almost completely preserved and articulated along their shafts (MPEF 1156) (Figure 25). The ischia are not fused to each other, but in some parts the limit between the left and right element is not clear because of their poor preservation. The iliac peduncles, although incomplete, have a rectangular outline at their base. Based on the available material, it cannot be confirmed whether they had the pocket for the isquiatic peduncle of the ilium, as in Giganotosaurus (MUCPv-Ch 1) or Mapusaurus (Coria and Currie 2006). The pubic process is subrectangular, lateromedially compressed and has the distinct 'neck' between the ischial body and the articular surface for the pubis, a feature also present in Sinraptor (Currie and Zhao 1993), Allosaurus (UUPV 40-

273) and Carcharodontosaurus saharicus (Rauhut 1995). The obturator processes are incompletely preserved on both ischia, but it can be observed that they were prominent and distally expanded, as in Allosaurus fragilis (UUPV 40-273). The ischia also have preserved the 2150 obturator notch that separates the distal end of the obturator process and the ischiatic shaft (Figure 25(A), (C)), cited by Rauhut (1995) for Sinraptor, Allosaurus, Carcharodontosaurus saharicus and basal theropods.

Distally to the obturator processes, the ischiatic shafts 2155 are parallel to each other, as in Allosaurus fragilis (UUPV 40-273), but unlike Giganotosaurus (MUCPV Ch 1) in which the contact between both ischia is restricted to their distal ends. The ischiatic shaft is subcircular in cross section, and slightly expanded at its distal end. 2160 Tyrannotitan, however, lacks the distinct ischiatic foot present in Neovenator (Brusatte et al. 2008), Concavenator (Ortega et al. 2010) and Acrocanthosaurus (Harris 1998).

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5.12 Femur

The femur is known by both femora of the holotype, and the right femur of the paratype. The femur is robust, 2170 straight in anterior view and anteriorly convex in lateral view (Figure 26). The femoral head is strongly upturned dorsomedially, as in Giganotosaurus (MUCPv-Ch 1), Carcharodontosaurus saharicus (Stromer 1931) and Mapusaurus (MCF-PVPH 108.203). The lesser trochanter 2175 is proximally projected, but does not surpass the level of the greater trochanter (Figure 26(A)), as in Concavenator (Ortega et al. 2010) and Carcharodontosaurus saharicus



Figure 24. Tyrannotitan chubutensis articulated pubes (MPEF 1156) photographs in (A) anterior view, (B) right lateral view and (C) 2145 posterior view. Note: Scale bar is 10 cm; see text for abbreviations. 2200



2220 2275 Figure 25. Tyrannotitan chubutensis articulated ischia (MPEF 1156) photographs in (A) left lateral view, (B) anterior view and (C) right lateral view. Note: Scale bar is 10 cm; see text for abbreviations.

(Stromer 1931). In contrast, the lesser trochanter of Giganotosaurus (MUCPV Ch 1) is strongly reduced. Both 2225 lesser and greater trochanters are separated by a deep vertical notch. The lesser trochanter has a similar morphology to that of Allosaurus fragilis (UMNH-PV 12231), being subtriangular in lateral view and lateromedially robust. Distal to the lesser trochanter there is a 2230 rugose surface, probably for insertion of the ilifemoralis muscle. Distal to that surface there is a low pyramidshaped elevation: the 'trochanteric shelf' sensu Brochu (2003). The femoral shaft is lateromedially wider than anteroposteriorly long. The fourth trochanter is placed on 2235

the upper half of the posterior surface of the femoral shaft (Figure 26(B)), being a well-developed proximodistally 2280 elongated crest that is posteromedially projected. The fourth trochanter is more posteriorly projected and proximodistally longer than in Mapusaurus (MCF PVPH 108.203) and Giganotosaurus (MUCPV Ch 1), in which 2285 the fourth trochanter is reduced to a low crest. In Tyrannotitan, the fourth trochanter delimits posteriorly a distinct ovoid and proximodistally elongated fossa; the insertion point of the M. caudifemoralis longus (Coria and Currie 2006). 2290

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Figure 27. *Tyrannotitan chubutensis* left fibula (MPEF 1157) photographs in (A) anterior view, (B) lateral view, (C) posterior view, (D) medial view and (E) proximal view. Note: Scale bar is 10 cm; see text for abbreviations.

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Almost one-fourth of the anterior surface of the distal end of the femur is occupied by a well-developed mediodistal crest, as in Mapusaurus (Coria and Currie 2006) and Giganotosaurus (MUCPV Ch 1), bounded by a 2335 low and wide depression with a medial projection. The fibular fossa, delimited by the lateral tibial condyle and the tibiofibular crest, extends proximally over the femoral shaft up to the proximal limit of the tibiofibular crest. This wide and shallow fossa has not been reported in other 2340 allosauroid theropods. In distal view, the posterior projections of the medial condyle and the tibiofibular crest are rounded (Figure 26(F)), differing from the pointed posterior projections of Mapusaurus (MCF PVPH 108.55). The extensor fossa is shallow and broad, as in 2345 Mapusaurus (MCF PVPH 108.55), and different from the narrow and deep fossa of Allosaurus (UMNH-VP 12231) and Acrocanthosaurus (Harris 1998; Currie and Carpenter 2000). The flexor fossa has a low ridge for the attachment of the cruciate ligaments, as in Allosaurus (UMNH-VP 2350 12231) and Acrocanthosaurus (Harris 1998; Currie and Carpenter 2000). The lateral condyle is strongly developed and has a circular outline, as in Mapusaurus (MCF PVPH 108.55). The lateral condyle and the tibiofibular crest are separated by a deep and very narrow fibular fossa as in 2355 Mapusaurus (MCF PVPH 108.55), a condition absent in other allosauroid theropods.

2360 **5.13 Fibula**

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The preserved left fibula lacks its distal end (MPEF-PV 1156) (Figure 27). The proximal end is anteroposteriorly expanded, although the posterior projection is less developed than in *Giganotosaurus* (MUCPv-Ch 1) and *Mapusaurus* (Coria and Currie 2006: fig. 30; right fibula

figured as left). The proximal articular surface is smooth, as in Giganotosaurus (MUCPv-Ch 1). The proximomedial fossa is subovoid and tear-shaped, resembling the condition of Giganotosaurus (MUCPv-Ch 1), Mapusaurus 2390 (Coria and Currie 2006) and Allosaurus fragilis (UMNH-VP 6400). The anterior margin of the proximomedial fossa is posteriorly projected, covering a small part of the fossa (Figure 27(E)), a character absent in other allosauroids. The fibular shaft has a D-shaped cross section, with a flat 2395 medial surface. The *iliofibularis tubercle* is located on the distal region of the dorsal half of the anterior surface of the fibula (Figure 27(B),(D)). This tubercle is a proximodistally elongated ridge, resembling that condition of Giganotosaurus (MUCPv-Ch 1). Distal to the iliofibularis 2400 tubercle the anteroposterior width of the fibular shaft is constant.

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5.14 Metatarsal II

Only the distal half of the left metatarsal II was preserved (MPEF-PV 1157) (Figure 28). This element is robust and has and expanded distal end, similar to that of Allosaurus (UMNH-VP 10142). The shaft has a subcircular cross section, with a slightly flattened medial surface for the 2410 contact with metatarsal III. On the ventral surface, the trochlea is separated from the shaft by a distinct lateromedial furrow (Figure 28(B)). Proximal to this furrow there are two tuberosities, a rounded distal tuberosity and an elongated proximal tuberosity. The 2415 collateral pits are deep and well delimited (Figure 28(D), (E)). The medial pit is deeper than the lateral pit, and is located at the distal sector of a marked fossa that occupies the entire lateral surface of the trochlea. The flexor fossa is deep and laterally displaced (Figure 28(C)), as in 2420



Figure 28. *Tyrannotitan chubutensis* left II metatarsal (MPEF 1157) photographs in (A) dorsal view, (B) ventral view, (C) distal view, (D) lateral view and (E) medial view. Note: Scale bar is 10 cm; see text for abbreviations.

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Allosaurus fragilis (UMNH-VP 10142) and Sinraptor (Currie and Zhao 1993), but unlike in *Torvosaurus* (BYU 5147) in which this fossa is much shallower.

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5.15 Pedal phalanges

We have reinterpreted the identity of the four preserved pedal phalanges of *Tyrannotitan* (see Novas et al. 2005) as the phalanges II-2, II-3, IV-2 and IV-3, all of which belong to the left pes of the paratype specimen.

5.15.1 Phalanx II-2

This phalanx is robust and proximally expanded (Figure 29). The proximal articular surface is higher than wide and has a pronounced medial vertical sulcus. The ventral surface is flat and is separated from the trochlea by a transversal and laterally extensive furrow. On the proximal region of the lateral surface, there are two subcircular depressions, one dorsal and another ventral. The colateral ligamental pits are deep and located centrally on the lateral surfaces of the trochlea. In dorsal view, the lateral hemicondyle is more developed and distally projected than the medial hemicondyle.

5.15.2 Phalanx II-3

This phalanx is a robust and recurved ungual that lacks the distal tip and part of the proximodorsal tubercle (Figure 30). It is asymmetrical in anterior view: the medial surface is located slightly dorsally with respect to the lateral surface. The ventral surface is mostly flat, except for the presence of a transverse elongated furrow located on its proximal region. The collateral grooves are well marked, the lateral groove being positioned more ventrally that the medial groove. These grooves run parallel to the ventral margin of the phalanx until the proximal third of this element, in which they are abruptly deflected ventrally. There is no evidence of proximal bifurcation of the colateral grooves, contrasting with the condition of abelisaurids (Novas and Bandyopadhyay 2001). The proximal



Figure 29. *Tyrannotitan chubutensis* phalange II-2 (MPEF 1157) photographs in (A) medial view, (B) lateral view, (C) ventral view, (D) dorsal view, (E) proximal view and (F) distal view. Note: Scale bar is 10 cm; see text for abbreviations.



Figure 30. Tyrannotitan chubutensis phalange II-3 (MPEF 2550 1157) photographs in (A) lateral view, (B) medial view, (C) proximal view, (D) dorsal view and (E) ventral view. Note: Scale bar is 10 cm; see text for abbreviations.

2555 articular surface is subcircular and bears a rounded proximodorsal tubercle.

5.15.3 Phalanx IV-2

2560 This phalanx is short and robust and lacks part of the trochlea (Figure 31). The proximal articular surface is almost twice as wide as high. The ventral surface has a marked transversal furrow just proximal to the trochlea. Although this element is incompletely preserved, it can be 2565 determined that the medial hemicondyle was more developed than the lateral hemicondyle, as in Allosaurus (Madsen 1976) and Sinraptor (Currie and Zhao 1993).

2570 5.15.4 Phalanx IV-3

> This phalanx is extremely short and lacks almost all the trochlea (Figure 32). The proximal articular surface has a straight ventral margin and continuous and curved lateral, medial and dorsal margins. As in the other non-terminal phalanges, it has ventral and dorsal transversal furrows that separate the trochlea from the rest of the phalanx.

Discussion 6. 2580

The combined elements of both holotype and paratype specimens of Tyrannotitan chubutensis (MPEF-PV 1156-MPEF-PV 1157) offer new information about the anatomy of this taxon and its diagnostic features, which improves our knowledge about poorly known anatomical regions in



Figure 31. Tyrannotitan chubutensis phalange IV-2 (MPEF 2610 1157) photographs in (A) medial view, (B) lateral view, (C) ventral view, (D) dorsal view, (E) proximal view and (F) distal view. Note: Scale bar is 10 cm; see text for abbreviations.

derived carcharodontosaurids. In this section we first discuss the diagnostic characters of Tyrannotitan, then we discuss the new data on the axial skeleton and the scapular girdle of carcharodontosaurids, and finally we present a phylogenetic analysis of Carcharodontosauridae (Figure 33).

6.1 Diagnostic features of Tyrannotitan

Novas et al. (2005) diagnosed Tyrannotitan based on three characters, only one of which is left in the emended 2625 diagnosis. These three characters are first discussed here, followed by a discussion of the four new autapomorphies found in this study.

6.1.1 Characters in the original diagnosis

6.1.1.1 Teeth with bilobated denticles in the mesial carinae. This condition occurs in the teeth preserved in the holotype material of Tyrannotitan (MEFP-PV 1156) (Figure 34(A)) and some of the isolated teeth recovered 2635 at the site. Bilobated denticles are not present in all Tyrannotitan teeth and, therefore, this condition should be regarded as polymorphic among the available material. The reasons for this polymorphism could be intraspecific variation or it could represent a pathologic feature of the 2640

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[<u>Q5]</u> 2620



Figure 32. Tyrannotitan chubutensis phalange IV-3 (MPEF 1157) photographs in (A) medial view, (B) lateral view, (C) ventral view, (D) dorsal view and (E) proximal view. Note: Scale bar is 10 cm; see text for abbreviations.

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holotype. Although we consider further material is needed to determine the degree of variation of this character in Tyrannotitan, we have left for the moment this feature among the autapomorphies of Tyrannotitan following previous authors (Novas et al. 2005; Sereno and Brusatte 2008; Carrano et al. 2012), given that this condition has not been recorded in any other known theropod.

6.1.1.2 Deep mental groove on the dentary. The morphology, depth and orientation of the anterior end of the Meckelian groove in *Tyrannotitan* do not significantly differ from those of other theropod species, such as Carcharodontosaurus iguidensis (MNN IGU 5), Giganotosaurus carolinii (MUCPV Ch 1) or Allosaurus fragilis (UMNH VP 9351) (Appendix S1: Figure 1). Therefore, we have excluded this feature as an autapomorphy of Tyrannotitan, in contrast to previous proposals (Novas et al. 2005; Carrano et al. 2012).

6.1.1.3 Posterior dorsal vertebrae with strongly developed ligament scars on neural spines. In Tyrannotitan, the 2690 neural spines of the posterior dorsal vertebrae have welldeveloped ligament scars, ornamented with rounded and anterolaterally oriented projections. This character, originally noted in a preliminary study of Tyrannotitan 2695 (Rich et al. 2000), was considered as an autapomorphy of



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this genus by Novas et al. (2005). However, the same condition was described for Acrocanthosaurus atokensis (Harris 1998), and is present in Mapusaurus roseae (MCF 2725 PVPH 108) and Giganotosaurus carolinii (MUCPV Ch 1) (Appendix S1: Figure 2). In consequence, this character has been excluded from the emended diagnosis of Tyrannotitan.

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6.1.2 New autapomorphic characters of Tyrannotitan Based on observations made in this study, four new

characters were identified as autapomorphic features of Tyrannotitan. 2735

6.1.2.1 Symphyseal margin of dentary with anteroventral-posterodorsal inclination in lateral view. Several allosauroids have a characteristic squared anterior end and 2740 subvertical symphyseal margin in the dentary (Sereno and Brusatte 2008). However, in Tyrannotitan the anteroventral corner of the symphyseal margin is slightly anterior to the anterodorsal corner, which gives a very slight anteroventral-posterodorsal inclination to this margin 2745 (Figure 34(B)). This condition is absent in other theropods, including all known carcharodontosaurids (Brusatte and Sereno 2007; Sereno and Brusatte 2008), and is present in both the holotype and the paratype specimens of Tyrannotitan. 2750

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Figure 34. Autapomorphic characters of *Tyrannotitan chubutensis*. (A) detail photograph of the teeth with bilobated denticles, (B) photograph of the left dentary in lateral view, showing the vertical symphyseal margin, (C) photograph and line drawing of the second and third dorsal vertebrae in lateral view, showing the accessory laminae, (D) photograph of the right femur in medial view with a detail of the fibular fossa extended on the shaft and (E) photograph of the left fibula in medial view with a detail of the fibular fossa posteriorly projected. Note: Scale bar is 1 mm in (A) and 10 cm in (B)–(E).

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6.1.2.2 Second and third dorsal vertebrae with accessory lamina connecting anterior and posterior centrodia-pophyseal laminae. This character is also present in Acrocanthosaurus atokensis (Harris 1998), although in Tyrannotitan this is a very well-developed lamina. This character has been preserved only in the holotype, given that the paratype has not preserved these dorsal vertebrae (Figure 34(C)).

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6.1.2.3 Fibular fossa extended over the proximal end of the crista tibiofibularis in the femoral shaft. In *Tyrannotitan* the fibular fossa is laterally delimited by the lateral tibial condyle and the crista tibiofibularis, as occurring in most theropods. However, in *Tyrannotitan* this fossa extends proximally in the form of a groove that approaches the proximal margin of the tibiofibular crest in the femoral diaphysis (Figure 34(D)). This character is a unique feature of *Tyrannotitan*, and is present in both holotype and paratype.

6.1.2.4 Proximomedial fossa of the fibula with posteriorly projected anterior border. In Tyrannotitan the anterior edge of the proximomedial fossa is developed as a posteriorly oriented projection, covering part of the fossa in medial view (Figure 24(E)). In allosauroids, such as *Allosaurus* (UMNH-VP 6400), *Neovenator* (Brusatte et al. 2860

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2008), Giganotosaurus (MUCPV Ch 1) and Mapusaurus (MCF PVPH 108.202), this margin is smooth and lacks any type of projection or well-developed margin.

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6.2 Remarks on carcharodontosaurid anatomy

6.2.1 Vertebral anatomy

The vertebral anatomy of carcharodontosaurids has not been fully analysed yet. For instance, the derived carcharodontosaurid Giganotosaurus carolinii (Coria and Salgado 1995) has preserved a complete vertebral series, but these remains are still undescribed in detail. The study of the vertebrae of Tyrannotitan revealed striking similarities with those of Giganotosaurus, Carcharodontosaurus and Mapusaurus, and to a lesser degree with the vertebrae of Acrocanthosaurus.

The cervical vertebrae in Tyrannotitan are strongly opisthocoelic, with the anterior articular face subspherical, as in Giganotosaurus (MUCPV-Ch 1) and Carcharodon-2880 tosaurus (NCSM 18166). The neural spines are robust and 'pyramid-shaped' in anterior view, a feature that can also be seen in Giganotosaurus (MUCPV-Ch 1) and Mapusaurus (MCF PVPH 108.90). The cervical centra have two pleurocoels on their lateral sides, as in Giganotosaurus 2885 (MUCPV-Ch 1), Carcharodontosaurus (NCSM 18166) and Acrocanthosaurus (Harris 1998). At least the posterior cervicals have rudimentary hyposphene-hypantrum accessory articulations, resembling the condition of Giganotosaurus (MUCPV-Ch 1) and Carcharodonto-2890 saurus (NCSM 18166). All the dorsal vertebrae also bear two pleurocoels on each side of the centrum (except for dorsal 14, which has a single pleurocoel) and the prezygapophyses have pneumatic openings or pits on their anterior borders as in Mapusaurus (MCF-PVPH-2895 108.80) and Giganotosaurus (MUCPV-Ch 1). The neural spines are high, robust and rectangular in cross section, with strongly developed and prominent ligament scars and spinopre- and spinopostzygapophyseal fossae below them, as in Acrocanthosaurus (Harris 1998), Mapusaurus (MCF-2900 PVPH-108.80) and Giganotosaurus (MUCPV-Ch 1). The sacrum is composed of five fused vertebrae, ventrally concave in lateral view, laterally compressed at its anteroposterior midpoint, and with unfused neural spines, as in Giganotosaurus (MUCPV-Ch 1). The posterior sacral 2905 centra have a single pleurocoel on each lateral side as in Giganotosaurus (MUCPV-Ch 1) and Mapusaurus (MCF-PVPH-108.209). Finally, the anterior caudal vertebrae only have pneumatic depressions (lacking true pleurocoels) on the lateral surfaces of their centra, as in 2910 Giganotosaurus (MUCPV-Ch 1) and Mapusaurus (MCF-PVPH-108.81).

The absence of pleurocoels in the first sacral centrum and the presence of pleurocoels in the last dorsals and in 2915 the fourth and fifth sacral vertebrae suggest the presence of a caudosacral pneumatic hiatus (Wedel 2009). A pneumatic hiatus is an apneumatic portion of the vertebral column bracketed between pneumatic vertebrae, which has been interpreted as indicative of different air sacs or diverticula that pneumatise different parts of the skeleton. 2920 In the case of Tyrannotitan, the position of the hiatus suggest that different diverticula of the abdominal air sac pneumatised the last dorsals and the last sacral vertebrae independently. This interpretation is reinforced by the 2925 presence of only one pleurocoel in the posteriormost dorsal vertebra compared with the double opening of the preceding dorsal vertebrae, suggesting that the source of the presacral pneumatisation is not completely expanded posteriorly. The presence of this hiatus has not been 2930 previously reported in theropods but has been described for the sauropod Haplocantosaurus (Wedel 2009). Its presence provides further evidence for inferring the development of abdominal air sacs with different diverticula, in addition to the cervical and clavicular air 2935

sacs in theropods, as occurring in birds (Wedel 2009).

6.2.2 Scapular girdle

The study of the scapulocoracoid in Tyrannotitan allows 2940 reinterpreting the morphology of this anatomical region in the closely related Giganotosaurus (Coria and Salgado 1995; Calvo 1999; Calvo et al. 2004; Novas et al. 2005; Novas 2009). In the original description, Coria and Salgado (1995) cited the following character as part of the 2945 diagnosis of Giganotosaurus: 'proximal end of the scapula forwardly projected over the coracoid'. In the description of the specimen they detailed that 'the coracoid is small and hook shaped with an externally open coracoid foramen'. This particular morphology was cited in 2950 subsequent contributions (Calvo 1999; Calvo et al. 2004, Novas et al. 2005) as a derived condition of Giganotosaurus that was absent in related forms.

A detailed comparison between the scapulocoracoid of Tyrannotitan and Giganotosaurus reveals that in the 2955 coracoid of the holotype of Giganotosaurus, the dorsal and anterior borders are damaged and only the sector over the glenoid cavity is preserved. The scapula of the type specimen of Giganotosaurus also has the acromial process broken, which was previously interpreted as a low 2960 acromial process (Calvo et al. 2004). The character 'externally open coracoid foramen' is also produced by a misinterpretation of the type material of this taxon. The coracoid foramen is present, but in a fragment of the left coracoid that is fused and preserved and attached to the 2965 scapula (Figure 35(A)). This fragment of the coracoid was interpreted as part of the scapula by previous authors, but the suture scar between the coracoid and scapula is visible in the type material. The position of the coracoid foramen is almost the same as in *Tyrannotitan*, located centrally on 2970



Figure 35. Scapulocoracoids in lateral view of (A) Giganotosaurus carolinii (MUCPV Ch 1) and (B) Tyrannotitan chubutensis (MPEF 2990 1156). Note: Scale bar is 10 cm; see text for abbreviations.

the lateral surface of coracoid. The interpretation of the fragment of the coracoid as part of the scapula led previous authors to postulate the autapomorphic character of 2995 Giganotosaurus 'proximal end of the scapula forwardly projected over the coracoid' (Coria and Salgado 1995) or, as expressed by Calvo et al. (2004), the 'articular margin of the scapula-coracoid oblique with respect to the long axis of the scapula'. 3000

In sum, the pectoral girdle of the type material of Giganotosaurus (Coria and Salgado 1995) is incompletely preserved and led to a misinterpretation of its anatomy. We interpret the scapula and coracoid of Giganotosaurus as similar to that of Tyrannotitan (Novas et al. 2005) and 3005 Mapusaurus roseae (Coria and Currie 2006), having a wide coracoid, well-developed coracoid foramen, scapula and coracoid fused, and the contact between these two elements is oriented perpendicular to the long axis of scapula. Although the acromion is only partially preserved 3010 in the holotype of Giganotosaurus, the available remains suggest its morphology did not differ from that of Tyrannotitan.

6.3 Phylogenetic analysis

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The phylogenetic position of Tyrannotitan chubutensis within Carcharodontosauridae has been debated in recent phylogenetic analyses (Novas et al. 2005; Brusatte and Sereno 2008; Sereno and Brusatte 2008; Smith et al. 2008; 3020 Eddy and Clarke 2011). Previous analyses have retrieved Tyrannotitan as a basal carcharodontosaurid (Novas et al. 2005; Brusatte and Sereno 2008; Eddy and Clarke 2011) or in a polytomy with other derived carcharodontosaurids (Brusatte et al. 2008; Carrano et al. 2012). Probably this 3025

lack of agreement came from the limited anatomical information available, given the lack of a detailed anatomical description of this taxon. The study of cranial 3050 and postcranial remains of Tyrannotitan chubutensis and comparisons with other carcharodontosaurids provided valuable information, which allows us testing more thoroughly their phylogenetic relationships.

The phylogenetic relationships of the clade Allosaur-3055 oidea, and in particular Carcharodontosauridae, have been the subject of intense research and debate, counting with more than 15 phylogenetic analyses published in recent years (Sereno et al. 1996; Harris 1998; Forster 1999; Currie and Carpenter 2000; Holtz 2000; Allain 2002; 3060 Coria and Currie 2002; Rauhut 2003; Holtz et al. 2004; Novas et al. 2005; Coria and Currie 2006; Smith et al. 2007; Brusatte and Sereno 2008; Sereno and Brusatte 2008; Smith et al. 2008; Brusatte et al. 2009; Benson 2010; Benson et al. 2010; Ortega et al. 2010; Eddy and Clarke 3065 2011; Carrano et al. 2012; Cau et al. 2012a, 2012b; Novas et al. 2013). Here we present a phylogenetic analysis of Carcharodontosauridae based on the original data-set of Canale (2010), expanding the character sampling regime and changing some previous scorings (Table S1: Character 3070 re-scoring table). This data-set is an updated version of that presented in a recent review by Novas et al. (2013). The data matrix includes 16 taxa scored across 169 anatomical characters, 106 of which are cranial and 63 postcranial (Appendix S2: List of Anatomical Characters 3075 and S3: Data Matrix). The data matrix was analysed with TNT v1.1 (Goloboff et al. 2008). A heuristic search was [Q7] carried out with 1000 replicates of Wagner trees (using random addition sequence) followed by tree bisection and reconnection (TBR) branch-swapping, saving 10 trees per 3080



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replication, to find the most parsimonious trees (MPTs). A final round of TBR was applied to the best trees found in 3100 the replicates to ensure that all MPTs were found. Twelve MPTs of 308 steps were recovered (CI = 0.633; IR = 0.726).

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6.3.1 Giganotosaurini

The strict consensus tree places Tyrannotitan in a derived position within Carcharodontosauridae, it being the sister group of Giganotosaurus and Mapusaurus (Figure 36). 3110 These three taxa form the clade Giganotosaurini, as also noted by Novas et al. (2013). In this phylogenetic analysis, the clade Giganotosaurini is diagnosed by three two unambiguous synapomorphies.

The first of these is the presence of a postorbital 3115 process of the jugal with a wide base (char. 60:0), a character recently recognised by Novas et al. (2013). In Allosaurus (UMNH-VP 9085), Monolophosaurus (Zhao [Q8] and Currie 1993), Sinraptor (Currie and Zhao 1993), Acrocanthosaurus (NCSM 14345) and Carcharodonto-3120 saurus saharicus (SGM Din1), the postorbital process of the jugal is rod-like, its height being equal or more than twice the anteroposterior length of its base. In Mapusaurus (MCF-PVPH 108.168) and Tyrannotitan (MPEF-PV 1157), the postorbital process of jugal is subtriangular in 3125 lateral view, its height being less than twice the length of its base (Figure 37).

The second synapomorphy of Giganotosaurini is the presence of a shallow and broad extensor groove on distal femur (char. 161:1). This character was originally 3130 proposed by Harris (1998) and later Coria and Currie (2006) considered state 1 as a synapomorphy that unites Giganotosaurus and Mapusaurus. A shallow and broad extensor groove is also present in Tyrannotitan (MPEF-PV 3135 1156).

The clade Giganotosaurini has minimal Bremer support values (BS = 1); however, this is mainly due to 3155 the unstable behaviour of Carcharodontosaurus iguidensis in suboptimal trees. When the alternative positions of the highly incomplete Carcharodontosaurus iguidensis (76% missing data) are ignored among the suboptimal trees, the





Figure 37. Illustration of character 60. Right jugals of (A) Allosaurus fragilis (UMNH-VP 9085) and (B) Tyrannotitan chubutensis (MPEF 1157). Note: Scale bar is 10 cm.

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monophyly of the clade Giganotosaurini is only rejected in trees that are three steps longer than the MPTs (BS = 3). This demonstrates that despite the uncertainties on the phylogenetic position of Carcharodontosaurus iguidensis due to its fragmentary nature, the clustering of the three South American taxa (Tyrannotitan, Mapusaurus and Giganotosaurus) to the exclusion of Carcharodontosaurus saharicus and other carcharodontosaurids is moderately well supported.

32.00 Tyrannotitan is placed basally within Giganotosaurini (Figure 36) because it lacks two derived features present in the femur of Mapusaurus and Giganotosaurus, which are interpreted in the context of this analysis as unambiguous synapomorphies of the clade formed by these two taxa. 32.05 These are the strongly reduced fourth trochanter on femur (char. 160:1) and the absence of the ridge for cruciate ligaments in flexor groove of femur (char. 162:0).

3210 6.3.2 Carcharodontosaurinae

Giganotosaurini and the African genus Carcharodontosaurus are retrieved as sister taxa (Figure 36), forming the clade Carcharodontosaurinae: a group of giant-sized, derived, gondwanan carcharodontosaurids. The mono-3215 phyly of this clade is supported by the four cranial characters proposed in previous studies that are interpreted here as unambiguous synapomorphies: the maxilla with only promaxillary foramen on the antorbital fossa (char. 7:3), external sculpturing of maxilla covering the main 3220 body of the bone (char. 13:1), strong rugosities and projections over the anterior half of the nasal (char. 25:1) and interorbital septum present and well ossified (char. 77:1). It is worth noting that the condition of Tyrannotitan for these four cranial synapomorphies is unknown. 3225 However, the support for the inclusion of this taxon deeply nested within Carcharodontosaurinae comes from the derived features shared with Mapusaurus and Giganotosaurus noted above (see Giganotosaurini; chars. 60, 161). 3230

The support value for Caracharodontosaurinae is higher than that for the clade Giganotosaurini within the context of the analysed data matrix. In trees that are three to seven steps longer than the most parsimonious topology, both Shaochilong and Eocarcharia get nested within this clade, but not other carcharodontosaurid taxa. This indicates that despite the uncertainties on the position of Shaochilong and Eocarcharia (both of which are fragmentary and with large amounts of missing data in this data-set), the clade Carcharodontosaurinae has strong character support within Carcharodontosauridae.

The monophyly of this Gondwanan clade of giant theropods and its internal divergence between the clades Carcharodontosaurus (recorded in the Cenomanian of northern Africa) and Giganotosaurini (recorded from the Albian to the Cenomanian in southern South America) are compatible with a vicariant explanation of their distribution, given that the separation between both continents was apparently effective at some point during the Aptian-Albian (Gheerbrant and Rage 2006).

6.3.3 Carcharodontosauridae

The monophyly of Carcharodontosauridae is supported by 3255 18 synapomorphies: maxilla with fully co-ossified posterior interdental plates (char. 14:1), squared anterior margin of maxillary antorbital fossa (char. 20:1), maxilla with sinuous shape of ridge across interdental plates in medial view (char. 22:1), nasals parallel sided throughout 3260 its length in dorsal view (26:1), frontals co-ossified (char. 35:1), frontals co-ossified with parietal (char. 36:1), paired frontals mediolaterally wider than 4/3 of frontal length (char. 37:2), lacrimal and postorbital in contact (char. 41:1), transversely broad interlocking suture between 3265 postorbital and squamosal (char. 42:1), postorbital with suborbital flange (char. 43:1), postorbital with bulbous swelling extensively overhanging the orbit (char. 46:1), postorbital with vascular groove present and limited to anterior half of dorsal boss (char. 49:1), postorbital with 3270 expansion of supratemporal fossa close to posterior margin of main body in dorsal view (char. 50:1), large axial epipophyses (char. 109:1), cervicals with interior structure of centrum camellate (char. 118:2), dorsal vertebrae with hyposphene laminae parallel and sheet like (char. 122:1), 3275 ischium with a boot-shaped distal expansion (absent in more derived forms) (154:2) and tibial lateral malleolus distal extension beyond medial malleolus more than 5% tibial length (char. 167:1).

7. Conclusions

The carcharodontosaurid theropod Tyrannotitan chubutensis is here described improving our knowledge of the anatomy, the phylogenetic position of this taxon and the 3285 internal relationships of carcharodontosaurid dinosaurs. The original diagnosis of the species was revised and emended with four new autapomorphic characters. The available material of Tyrannotitan has provided new information on the axial skeleton, allowing a comparison 3290 with related forms on vertebral anatomy. The presence of a pneumatic hiatus in the sacrum of Tyrannotitan adds evidence to the presence of abdominal air sacs; with different diverticula pneumatising different parts of the skeleton, in addition to the cervical and clavicular air sacs, 32.95 as occurring in birds. Tyrannotitan shares several derived characters with Giganotosaurus and Mapusaurus, and to a lesser degree, with Carcharodontosaurus (for which there is limited vertebral information) and Acrocanthosaurus. The analysis of the pectoral girdle of *Tyrannotitan* allowed 3300

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a reinterpretation of the scapula and coracoid anatomy of the related carcharodontosaurid Giganotosaurus. Features of the latter genus previously interpreted as a derived morphology actually respond to misinterpretations of broken surfaces. The new anatomical information on Tyrannotitan and related forms was incorporated in a phylogenetic analysis that reinforces the hypothesis of Tyrannotitan being a derived carcharodontosaurid. In our results, this taxon is depicted as the sister group of Giganotosaurus plus Mapusaurus, forming the South American clade Giganotosaurini. The close affinities of Tyrannotitan with other South America forms and the position of the African Carcharodontosaurus as their sister group are concordant with previous hypotheses on the vicariant pattern of southern dinosaurs that resulted from the break up of Gondwana during the Cretaceous.

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