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SHORT COMMUNICATION

**Fernando E. Novas · Silvina de Valais ·
Pat Vickers-Rich · Tom Rich**

A large Cretaceous theropod from Patagonia, Argentina, and the evolution of carcharodontosaurids

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Abstract The Cretaceous Carcharodontosauridae is the latest clade of carnosaurs, including the largest predatory dinosaurs yet recorded. Albeit spectacular for their size, the skeletal anatomy of these theropods remains poorly-known, and their diversity was until recently restricted to two Cenomanian species: the highly derived *Giganotosaurus carolinii*, from southern South America, and the incompletely known *Carcharodontosaurus saharicus*, from northern Africa. Here we describe an older and basal member of the group, *Tyrannotitan chubutensis* gen. et sp. nov., from Aptian strata of Patagonia, Argentina. The new taxon gives new insights into the systematics and evolution of carcharodontosaurids and offers a better understanding of the evolution of Southern theropod faunas. We suggest that carcharodontosaurids radiated in Gondwana sharing with spinosaurids the role of top-predators until their extinction in Cenomanian–Turonian times. During this interval, the diplodocoid sauropods and giant titanosaurians went extinct (probably as part of a global-scale crisis), and the smaller abelisaurid theropods took dominance, reigning until the end of the Cretaceous. Electronic Supplementary Material is available.

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F. E. Novas (✉)
CONICET, Museo Argentino de Ciencias Naturales
“Bernardino Rivadavia”,
Av. Angel Gallardo 470,
1405 Buenos Aires, Argentina
e-mail: fernovas@yahoo.com.ar
Tel.: +5411-4981-9282
Fax: +5411-4981-9282

S. de Valais
CONICET, Museo Paleontológico “Egidio Feruglio”,
Av. Fontana 140,
9100 Trelew, Argentina
e-mail: sdevalais@yahoo.com.ar

P. Vickers-Rich
School of Geosciences, Monash University,
Melbourne (Clayton), Victoria 3000, Australia
e-mail: prich@mail.earth.monash.edu.au

T. Rich
Museum Victoria,
GPO Box 666E, Melbourne, Victoria 3001, Australia

Introduction

The fossil record of Aptian dinosaurs from Gondwana is favourably increased with the discovery of a new carcharodontosaurid theropod. The specimens, recovered in central Patagonia, belong to the oldest carcharodontosaurid yet recorded.

Description of specimens

Two partially disarticulated skeletons found 1 km apart from each other (Rich et al. 2000).

Taxonomy

Theropoda Marsh, 1881

- Tetanurae Gauthier, 1986
- Allosauroidea Currie and Zhao, 1993
- Carcharodontosauridae Stromer 1934
- *Tyrannotitan chubutensis* gen. et sp. nov.

Etymology

The generic name is derived from the Latin words *tyrannus* (tyrant) and *titan* (giant), the specific name from the Chubut province, Argentina.

Holotype

MPEF-PV 1156 (Museo Paleontológico “Egidio Feruglio,” Trelew): Partial dentaries, isolated teeth, dorsals 3–8 and

11–14, proximal caudal vertebra, isolated ribs and haemal arches, incomplete left scapulocoracoid and right humerus and ulna; pubes, ischia, and fragments of left ilium; almost complete left femora, fibula and metatarsal II.

Paratype

MPEF-PV 1157: jugals, right dentary, isolated teeth, atlas, cervical 9?, dorsals 7?, 10 and 13, partially preserved fused centra of sacrals 1–5, isolated distal caudals, ribs, right femur, incomplete left metatarsal II, pedal phalanges 2.I, 2.II, and 3.III. Paratype specimen is approximately 7% larger than that of the holotype.

Locality and horizon

"La Juanita" farm, 28 km NE of Paso de Indios, Chubut Province, Argentina (Fig. 1a). Possibly Cerro Castaño Member, Cerro Barcino Formation, Aptian (Musacchio and Chebli 1975; Codignotto et al. 1978; Rich et al. 2000).

Diagnosis

Teeth with bilobate denticles on rostral carina, deep mental groove on dentary, posterior dorsal vertebrae with strongly developed ligament scars on neural spines (Fig. 2; see S1 for character list).

Description

As preserved, the largest specimen (MPEF-PV 1157) has a dentary 68 cm long and 14 cm deep at its rostral end. It has a deep, squared off symphyseal region, with a ventral process or "chin," as in *Giganotosaurus* (Calvo and Coria 2000) (Fig. 2). It is ornamented by oblique grooves along the ventral half of its lateral surface, passing through a band of

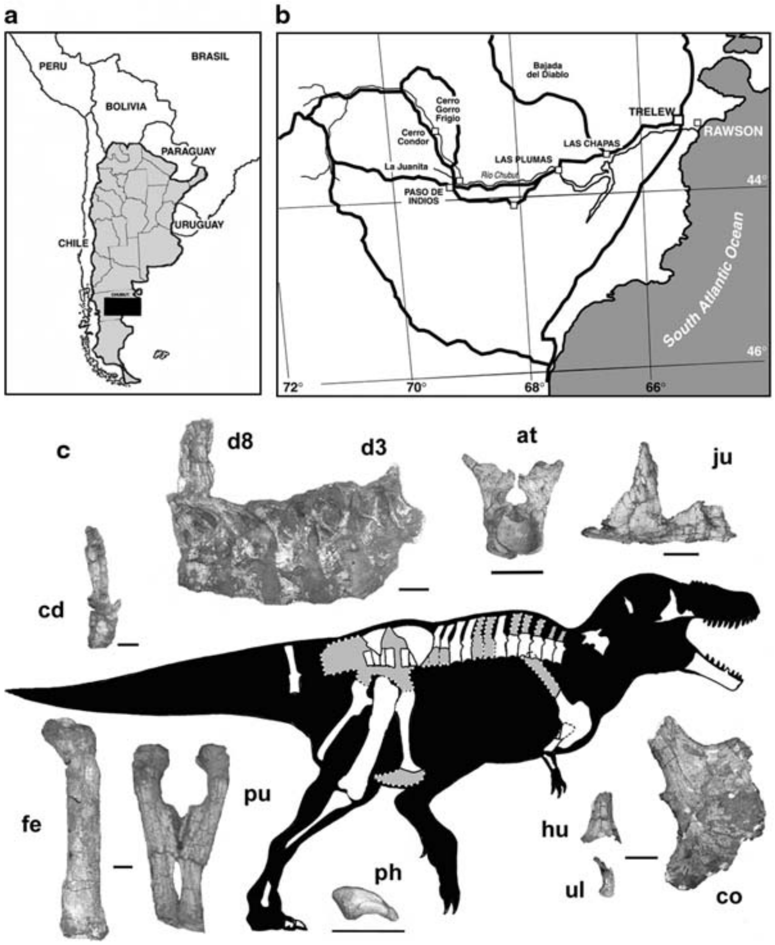

Fig. 1 (**a**) Map of Argentina, and (**b**) map of Chubut Province (Argentine Patagonia) indicating La Juanita fossil site. (**c**) Skeletal reconstruction and body shape of *Tyrannotitan chubutensis*, based on specimens MPEF-PV 1156 and 1157. Relevant bones are labelled as at (atlas in cranial view; MPEF-PV 1157), cd (anterior caudal vertebra, in lateral view; MPEF-PV 1156), co (left coracoid and proximal end of scapula in lateral view; MPEF-PV 1156), d3–d8 (sequence of dorsal vertebrae; MPEF-PV 1156), hu (right humerus in cranial view; MPEF-PV 1156), ju (right jugal in lateral view, reversed; MPEF-PV 1157), fe (left femur in cranial view; MPEF-PV 1156), pu (pubes in cranial view; MPEF-PV 1156), ph (pedal ungual of digit 2 in lateral view; MPEF-PV 1157) ul (right ulna in lateral view; MPEF-PV 1156). *Scale bar*: 10 cm

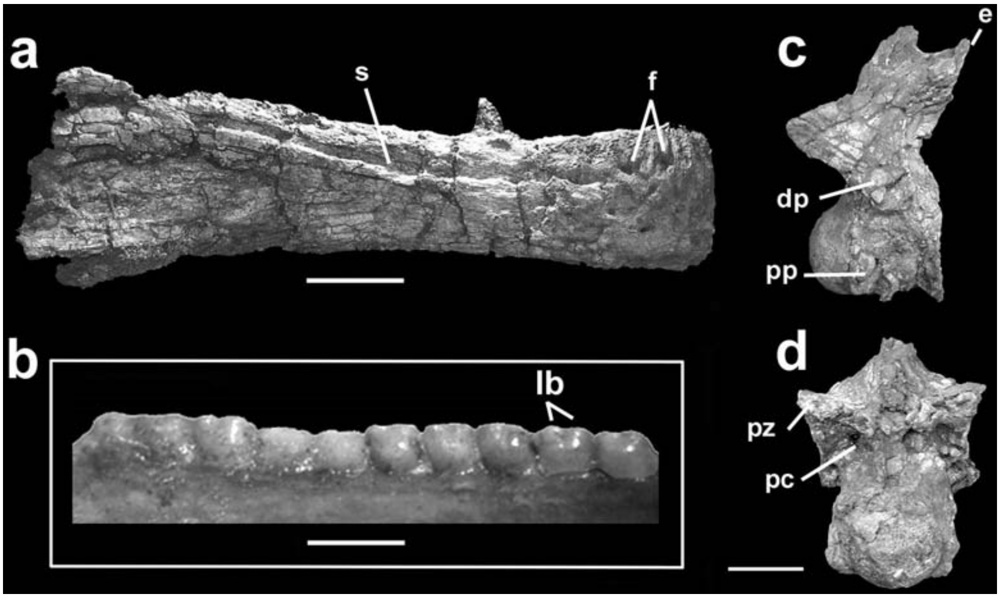

Fig. 2 *Tyrannotitan chubutensis* (MPEF-PV 1157). (**a**), Right dentary in lateral view. (**b**), detail of dental serrations. c,d, Cervical ?9th in right lateral (c) and cranial views (d). *Scale bars*: a,c,d 10 cm, and b, 1 mm. Abbreviations dp, diapophysis, e, epipophysis, f, foramina, lb, lobes, pc, pneumatic cavity, pp, parapophysis, pz, prezygapophysis, s, dentary sulcus

smooth bone surface along the dental margin, forming a pattern of ornamentation resembling that of *Giganotosaurus* and abelisaurids (e.g., *Carnotaurus*). Up to 16 alveoli are present on the dentaries. As in other carcharodontosaurids, the teeth bear marginal arcuate enamel wrinkles on the labial side of the caudal carina (Sereno et al. 1996). However, tooth denticles from the cranial carina are bilobate in side view, a character that seems unique among theropods.

Postaxial cervical vertebrae are strongly opisthocoelous. Presacral vertebrae bear well developed pneumatic foramina and fossae, in particular a pair of pleurocoels on cervical and dorsal vertebrae. Caudal centra lack pleurocoels or nutrient foramina, in contrast to the large pleurocoel reported for *Carcharodontosaurus* (Stromer 1931), and the pair of small nutrient foramina present on proximal and mid-caudals of *Acrocanthosaurus* (Currie and Carpenter 2000; Harris 1998) and *Giganotosaurus*. The neural spines of the dorsal vertebrae are craniocaudally long, dorsoventrally deep and transversely thick, and with strong ligament scars protruding both cranially and caudally.

The coracoid and scapula are fused. The scapular blade is narrow, and the acromial process rises abruptly from the scapula at an angle approaching 90°. The slender shoulder girdle of *Tyrannotitan* is sharply different from the unusually robust and highly derived one of *Giganotosaurus* (Calvo 1999), in which the coracoid is reduced. Preserved portions of humerus and ulna (MPEF-PV 1156; Fig. 2) indicate that forelimbs were short and robust in this carcharodontosaurid (as it also occurs in *Acrocanthosaurus*; Currie and Carpenter 2000). Hindlimb bones are also massive, and exhibit two remarkable carcharodontosaurid synapomorphies: the femoral head is proximomedially projected, and the fibula is proportionally short with respect to femoral length (less than 70%). The femur of MPEF-PV 1157 is almost complete; its estimated length of 140 cm is slightly shorter than that in *Giganotosaurus* (143 cm; Coria and Salgado 1995). The transverse width of the femoral shaft of *Tyrannotitan* is 16.5 cm.

Discussion

Indisputable members of Carcharodontosauridae are of Gondwanan distribution, and include the Aptian *Tyrannotitan* and the more derived *Giganotosaurus* and *Carcharodontosaurus*, both of Cenomanian age. We concur with Currie and Carpenter (2000) and Coria and Currie (2003) that *Acrocanthosaurus*, from the Aptian of North America, may not belong to Carcharodontosauridae. Opposing other authors (e.g., Sereno et al. 1996; Harris 1998; Holtz 2000; Rauhut 2003) *Acrocanthosaurus* is here united to *Allosaurus* by three unambiguous synapomorphies; moreover, nine additional steps are needed to relocate it within Carcharodontosauridae (Fig. 3; see S2 and S3 for cladistic analysis and data matrix).

Tyrannotitan helps to clarify the confusing aspects of the skeletal anatomy of its close relative *Carcharodontosaurus*. This Saharan taxon was recently diagnosed (Sereno et al. 1996) and reconstructed (Currie 1996) on the supposed overlapping characters of specimens of *Carcharodontosaurus saharicus* (Stromer 1931) and the problematic theropod "*Spinosaurus* B" (Stromer 1934). Pivotal in the purported overlap is a stout cervical vertebra, characterized by its low and very broad centrum, strong ventral keel, and reduced neural spine (Sereno et al. 1996). However, this vertebra (not found in association with specimens of *C. saharicus*; P. Sereno, personal communication) shows clear distinctions with cervicals of *Tyrannotitan, Giganotosaurus,* and the holotype specimen of *C. saharicus*. On the contrary, the cervical in question closely resembles

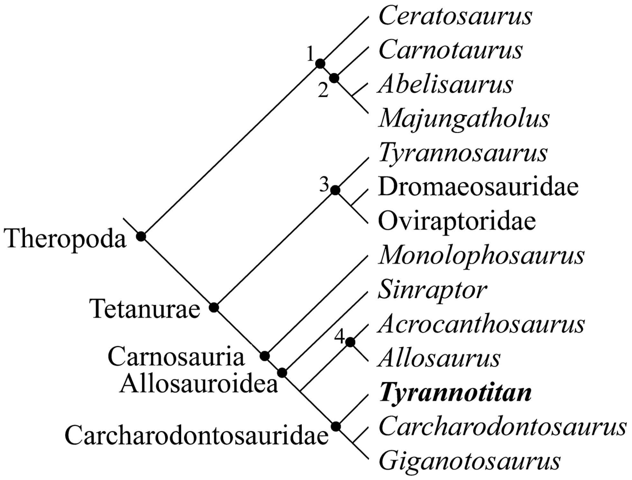

Fig. 3 Cladogram depicting phylogenetic relationships of *Tyrannotitan chubutensis* within Theropoda. A dataset of 108 characters and 15 taxa was analyzed using NONA (ver. 1.8), resulting in a single most parsimonious tree (L = 227; CI = 0.57; RI = 0.65). Tree was rooted as in Currie and Carpenter 2000. *Herrerasaurus* and Ceratosauria were taken as outgroups. *Tyrannotitan* is included in Carcharodontosauridae on the basis of the following unequivocal synapomorphies: dentary with rostral end square-shaped; teeth with wrinkles in the enamel next to the serrations; pleurocoels present in dorsal vertebrae; absence of double ventral keel in caudal vertebrae; femoral head proximo-medially angled. See S1 for Character list, S2 for Cladistic analysis, and S3 for Data matrix

that of *Sigilmassasaurus* (Russell 1996), a theropod of uncertain phylogenetic relationships. Besides, the flattened and acuminate pedal unguals of "*Spinosaurus* B" (Stromer 1934) purportedly referred as to *Carcharodontosaurus* by Sereno et al. (1996, 1998), are sharply different from the robust and curved ones of *Tyrannotitan* (Fig. 1, ph). Such differences do not correspond with digit position. Also, femur, tibia, dorsal and caudal vertebrae originally referred as to "*Spinosaurus* B" show clear distinctions from those of *Tyrannotitan* and *Giganotosaurus*. In sum, diagnosis and reconstruction of *Carcharodontosaurus* recently offered (Sereno et al. 1996; Currie 1996) are based on the chimaeric association of specimens corresponding to different theropod clades. In this context, we do not regard *Sigilmassasaurus brevicollis* as a subjective junior synonym of *C. saharicus*, as recently proposed (Sereno et al. 1998).

From Aptian through Cenomanian times Gondwana was inhabited by large theropods including carcharodontosaurids, spinosaurids, and the bizarre tetanuran *Bahariasaurus* (Stromer 1934; Sereno et al. 1998). This "mid"-Cretaceous fauna was also composed of huge titanosaurs (e.g., *Argentinosaurus, Argyrosaurus, Paralititan*), basal diplodocoids (e.g., dicraeosaurids and rebbachisaurids), and in northern Africa, crocodiles reached up to 12 m in length (e.g., *Stomatosuchus* and *Sarcosuchus*) (Stromer 1936; Smith et al. 2001; Salgado 2001; Sereno et al. 2001). In the post-Turonian, carcharodontosaurids and spinosaurids become rare or absent in South America, being replaced by smaller abelisauroids. Coincidently, the following reptiles are no longer present in the Southern landmasses after the Turonian: huge pholidosaurid crocodiles, large basal iguanodontians, and diplodocoids (following Chiappe et al. 2001; Currie Rogers and Forster 2004, and Apesteguía 2004, we interpret *Antarctosaurus wichmanianus* as a titanosaurid, thus countering Sereno et al. 1999, who envisaged this Patagonian taxon as a rebbachisaurid). After the strong decline of carcharodontosaurids and the virtual extinction of spinosaurids at the end of the Cenomanian, theropod assemblages from South America, Madagascar and India consisted mainly of comparatively smaller abelisauroids, and secondarily of a wide array of tetanurans (e.g., *Megaraptor*, coelurosaurians). Although abelisauroid diversification was underway at least from the Early Cretaceous (e.g., Carrano et al. 2002; Rauhut 2003), they become abundant and large during Late Cretaceous times.

Notably, the "mid"-Cretaceous faunal transformations described above for South America may parallel the faunal replacement that occurred in North America, where Aptian carnosaurs (e.g., *Acrocanthosaurus*), basal titanosauriforms, and large basal iguanodontians, were replaced in the Cenomanian by hadrosaurs, ceratopsians and tyrannosaurids (Bakker 1977; Kirkland 1997; Britt and Stadman 1997; Harris 1998). This suggests that a faunal replacement took place probably at a global scale at the same general time interval. Studies of the still poorly known "mid"-Cretaceous terrestrial communities will contribute to better understanding of the major ecological changes that preceded the terminal Mesozoic mass extinction event.

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