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A new giant titanosaur sheds light on body mass evolution among sauropod dinosaurs

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Titanosauria was the most diverse and successful lineage of sauropod dinosaurs. This clade had its major radiation during the middle Early Cretaceous and survived up to the end of that period. Among sauropods, this lineage has the most disparate values of body mass, including the smallest and largest sauropods known. Although recent findings have improved our knowledge on giant titanosaur anatomy, there are still many unknown aspects about their evolution, especially for the most gigantic forms and the evolution of body mass in this clade. Here we describe a new giant titanosaur, which represents the largest species described so far and one of the most complete titanosaurs. Its inclusion in an extended phylogenetic analysis and the optimization of body mass reveals the presence of an endemic clade of giant titanosaurs inhabited Patagonia between the Albian and the Santonian. This clade includes most of the giant species of titanosaurs and represents the major increase in body mass in the history of Titanosauria.

1. Introduction

The origin of titanosaur dinosaurs was inferred to date back to the latest Jurassic [1] (*ca* 150 Ma) and recent analyses place their time of diversification during the Early Cretaceous (Barriasian–Barremian *ca* 140–125 Ma) [2–7]. Titanosauria is a diverse clade (approx. 90 genera) of sauropods and also the only one that survived until the end-Cretaceous. In addition to their taxonomic diversity (approx. 30% of valid sauropod genera) this clade has a remarkable variation on body size among its members, including the largest known sauropods (e.g. *Argentinosaurus*, *Puertasaurus*; with rough estimates of body mass above 60 tonnes [8]) and the smallest sauropods known to date (e.g. *Rinconsaurus*, *Saltasaurus*; with estimated body masses of approximately 6 tonnes [8]). Understanding the evolution of body mass in this clade is key for understanding many aspects of sauropod evolution, including changes in their palaeoecology and growth strategies. Studies on dinosaur body mass evolution have noted an increase in variation of body size among titanosaurs during the Cretaceous in comparison with other sauropod groups, and some previous studies noted an overall trend to body mass decrease [8–10]. Nonetheless, recent studies failed to find any exceptional body mass shifts in sauropod evolution during the Cretaceous, a result interpreted as a product of niche saturation achieved during the Triassic–Jurassic [8]. A common problem in studies on the evolution of body size in Titanosauria has been the lack of well-sampled phylogenetic studies of the group [11,12], especially those considering
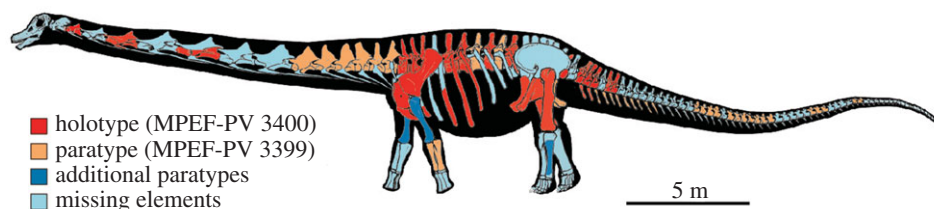
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Figure 1. Reconstructed skeleton and body silhouette of *Patagotitan mayorum* showing preserved elements from the holotype and paratypic specimens.

large-bodied titanosaurs, whose record has been extremely fragmentary for many years [13,14]. Recent discoveries of more complete remains of giant titanosaurs [12,15,16] have revealed new and relevant anatomical data, such as the pre-caudal axial skeletal anatomy of *Futalognkosaurus* with expanded neural spines in posterior cervical vertebrae [15] (as in *Puertasaurus* [14] and *Mendozasaurus* [17]) or the pes of *Notocolossus* showing adaptations for gigantism, such as the reduction in the number of phalanges and the compact construction of its metatarsus [16]. However, the phylogenetic relationships of these forms among titanosaurs are still uncertain, and it is not clear if they are related to each other and how many lineages experienced a drastic increase in body size among titanosaurs.

Here we describe a new giant titanosaur, which not only represents the largest sauropod described so far but also one of the most complete titanosaur taxa recovered to date. The new taxon is represented by at least six different specimens. Based on the taphonomical, histological and ecological data available, we interpret this monospecific sauropod association as the first evidence of social behaviour among giant titanosaurs. The new taxon is included in an expanded phylogenetic analysis that recovered a diverse clade of giant Patagonian titanosaurs, indicating that one major event of extreme gigantism took place in the evolution of this clade during the 'middle' Cretaceous, representing the major deviation from the ancestral sauropod body size.

2. Systematic palaeontology

Dinosauria Owen, 1842
Sauropoda Marsh, 1878
Titanosauria Bonaparte and Coria, 1993
Eutitanosauria Sanz *et al.*, 1999
Lognkosauria Calvo *et al.* 2007
Patagotitan mayorum n. gen. et sp.

(a) Etymology
Patago from Patagonia (southern South America) and *titan* (Greek divinity) symbolic of strength and large size. The species name honours the Mayo family for their hospitality during fieldwork at the 'La Flecha' ranch.

(b) Holotype
MPEF-PV (Museo Paleontológico Egidio Feruglio, Trelew, Argentina) 3400. A single individual preserving an anterior and two middle cervical vertebrae, three anterior, two middle and two posterior dorsal vertebrae, six anterior caudal vertebrae, three chevrons, dorsal ribs, both sternal plates, right scapulocoracoid, both pubes and both femora (figure 1). This specimen is the best preserved and also the one with the largest amount of diagnostic characters.

(c) Paratypes
The repeated elements recovered at this site include both axial and appendicular bones that lack morphological differences, with size variation less than 5%. Furthermore, some of these elements share the presence of autapomorphies (in the two most complete specimens and in the multiple isolated femora and humeri). Based on this evidence all sauropod material collected in the quarry is here identified as belonging to the same taxon, forming a monospecific assemblage (see the electronic supplementary material). One of the paratypic specimens corresponds to a partially associated specimen (MPEF-PV 3399) composed of six posterior cervical vertebrae, one anterior, one middle and two posterior dorsal vertebrae, one anterior and 16 posterior caudal vertebrae, ribs and chevrons, left ulna and radius, both ischia, left pubes and one left femur. Additional paratypic specimens include an isolated tooth (MPEF-PV 3372), an isolated posterior caudal vertebra (MPEF-PV 3393), two left humeri (MPEF-PV 3395, 3396) and one right humerus (MPEF-PV 3397), one left (MPEF-PV 3375) and one right (MPEF-PV 3394) femur, and two partially preserved fibulae (MPEF-PV 3391, 3392) (figure 1).

(d) Type locality and horizon
'La Flecha' ranch, Chubut Province, Argentina. Cerro Barcino Formation, latest Albian (101.62 ± 0.18 Ma; see electronic supplementary material for a detailed description of U-Pb geochronology).

(e) Taphonomy
A minimum of six individuals were found in the same quarry, distributed in three distinct but closely spaced horizons, which corresponds to three different burial events (see electronic supplementary material). The fossiliferous sequence is 3.43 m thick and composed of interbedded muddy sandstones and sandy mudstones, with thin intercalations of fine-grained sandstone bodies (indicative of a fluvial floodplain with recurrent episodes of flooding). The low-energy depositional setting and taphonomical data indicates that the specimens were not transported prior to their burial. The negligible size variation of repeated elements and the histological data (see below) indicate that they were young adult individuals (prime-age animals [18]). The deaths of young adults at the same place in different events indicates site fidelity of individuals that died close to water bodies (floodplain), as seen in sites with recurrent deaths of prime-age male elephants [18].

(f) Diagnosis
Anterior dorsal vertebrae (D1–D3) with vertical prezygodiapophyseal lamina, due to the elevated position of the prezygapophysis respect to the diapophysis; anteriormost dorsal vertebrae (D1–D2) with ventral bulge in prespinal

lamina; hyposphene-hypantrum restricted to the articulation between D3 and D4; middle and posterior dorsal vertebrae with vertical neural spine (reversal to the condition of non-titanosauriforms, convergently acquired in some lithostrotian titanosaurs); first caudal vertebra with flat anterior and convex posterior articular surfaces; anterior caudal vertebrae with neural spines four to six times mediolaterally wider than antero-posteriorly long; anterior caudal neural spines incipiently bifid with anteriorly directed tips; marked bulge on the posterolateral surface of the humerus (convergently acquired in some derived lithostrotians); straight lateral edge on distal femur.

(g) Comparative diagnosis

Dorsal vertebrae preserved in *Patagotitan*, *Argentinosaurus* and *Puertasaurus* allows distinguishing the new taxon from these more fragmentary previously known giant titanosaurs from 'mid-Cretaceous' of Patagonia. (i) The dorsal vertebrae of *Argentinosaurus* and *Puertasaurus* have robust but low (poorly developed) laminae, whereas the dorsal vertebrae of *Patagotitan* have thin and highly developed laminae. (ii) The prezygodiapophyseal lamina of anterior dorsal vertebrae of *Patagotitan* is vertically oriented whereas in *Argentinosaurus* and *Puertasaurus* this lamina projects anteriorly from the diapophysis (as in other sauropods). (iii) The neural spines of anterior dorsal vertebrae of *Patagotitan* are high and vertically directed with an arrow-shaped end (product of the lateral expansion of the spine, as in *Argentinosaurus*), whereas in *Puertasaurus* (and other lognkosaurians) these neural spines are short with lateral margins converging dorsally. (iv) The neural spine of middle and posterior dorsal vertebrae of *Patagotitan* are vertically oriented, differing from the poster-odorsally directed neural spine of *Argentinosaurus* and most titanosauriforms. Other characters from the diagnosis of *Patagotitan* are unknown in *Puertasaurus* and *Argentinosaurus*, and some of them might have a more widespread distribution within Lognkosauria, such as the hyposphene-hypantrum system present exclusively between the third and fourth dorsal vertebrae (unknown for closely related taxa, such as *Argentinosaurus*, *Puertasaurus*, *Drusilasaura*). The more completely known anatomy of *Dreadnoughtus* allows identifying multiple differences from *Patagotitan*: (i) short and posteriorly directed neural spine in anterior and middle dorsal vertebrae, differing from the much higher and vertical neural spine of *Patagotitan*; (ii) biconvex first caudal centrum, whereas in *Patagotitan* the centrum is anteriorly flat; (iii) neural spine of anterior caudal vertebrae slightly anteroposteriorly longer than mediolaterally wide, whereas in *Patagotitan* it is wider than long; (iv) anterior caudal vertebrae lacks the dorsoventrally high transverse processes present in *Patagotitan*; (v) scapular blade lacks the distal expansion present in *Patagotitan*; (vi) marked bulge on the posterolateral surface of the humerus of *Patagotitan* is absent in *Dreadnoughtus*.

3. Description

Nine cervical vertebrae have been preserved, including anterior, middle and posterior elements. The posteriormost elements were poorly preserved and anteroposteriorly crushed. Anterior and middle cervical centra are highly elongated (elongation index greater than 5; *sensu* [19]) (figure 2a) and lack pleurocoels (*sensu* [20]) but bear small pneumatopores on their lateral surface, which open into the

internal camellate bone tissue. Neural spines of anterior and middle cervical vertebrae are single and mediolaterally compressed. The presence of laterally expanded neural spines in posterior cervical vertebrae (as in *Futalognkosaurus* [15], *Mendozasaurus* [17] and *Ligabuesaurus* [21]) cannot be determined in *Patagotitan* due to poor preservation. Posterior cervical vertebrae and all dorsal vertebrae bear deep pleurocoels that open into the internal camellate bone tissue. Based on the morphological differences among the dorsal vertebrae of *Patagotitan*, we identify that nine distinct vertebral positions are represented. Based on comparisons with dorsal series of other titanosaurs (and assuming a total number of 10 dorsal vertebrae, as in the closely related titanosaur *Futalognkosaurus* [15] and most titanosaurs for which complete dorsal series is known), the dorsal series of *Patagotitan* is probably complete except for the fourth dorsal vertebra. Two dorsal vertebrae (one from the holotype and the other from the most complete paratypic specimen) are interpreted as the third dorsal vertebra of *Patagotitan* (figure 2d,e). They share general morphological features (e.g. parapophysis position, laminae development and orientation) and have a peculiar combination of features: the absence of hypantrum on the anterior surface and the presence of hyposphene on its posterior surface. The absence of hyposphene-hypantrum in all other preserved middle and posterior dorsal vertebrae (figure 2f,g) indicates that this extra articulation was solely present between the third and fourth dorsal vertebrae of *Patagotitan* (assuming the presence of a hypantrum in the unpreserved fourth dorsal vertebra). Although the hyposphene-hypantrum was convergently lost in the history of sauropods [22], the retention of the plesiomorphic hyposphene-hypantrum articulation between the third and fourth dorsal vertebra is an unreported condition among sauropods. The preservation of this accessory articulation in anterior-middle dorsal vertebrae of *Patagotitan* is intriguing, but it could be biomechanically related to its extreme gigantism as this region coincides with the anatomical position of the scapular blade [23] (figure 1) and the peak of torsional stress noted for other sauropods (evidenced by the maximum neurocentral sutural complexity [24]). The prezygodiapophyseal lamina of the first, second and (to a lesser degree) third dorsal vertebra is vertically oriented in *Patagotitan* (figure 2b,c), differing from other known titanosaurs, including *Argentinosaurus*, *Futalognkosaurus*, *Puertasaurus*, *Dreadnoughtus* and *Notocolossus*. Lamination in dorsal vertebrae is well developed, clearly differing from the much less developed laminae of *Argentinosaurus*. Dorsal neural spines are high, and bear thin and long prespinal and postspinal laminae and arrow-shaped triangular aliform processes, similar to that of *Argentinosaurus* (figure 2b,c,f,g). The middle and posterior dorsal vertebrae bear an anterior and posterior spinodiapophyseal laminae and a bifurcated posterior centrodiapophyseal lamina (figure 2g), as in many other titanosaurs [25].

The first caudal vertebra has a flat anterior articular surface and a prominently convex posterior one (observed in both first caudal vertebrae recovered), whereas subsequent preserved caudal centra are procoelous (figure 2h–o). The articular morphology of the first caudal vertebra of the two most complete specimens of *Patagotitan* (MPEF-PV 4000 and MPEF-PV 3399) is unique among titanosaurs, differing from the procoelous anterior caudal vertebrae of other basal titanosaurs (e.g. *Futalognkosaurus*) and the biconvex caudal vertebrae observed in many lithostrotians and related forms
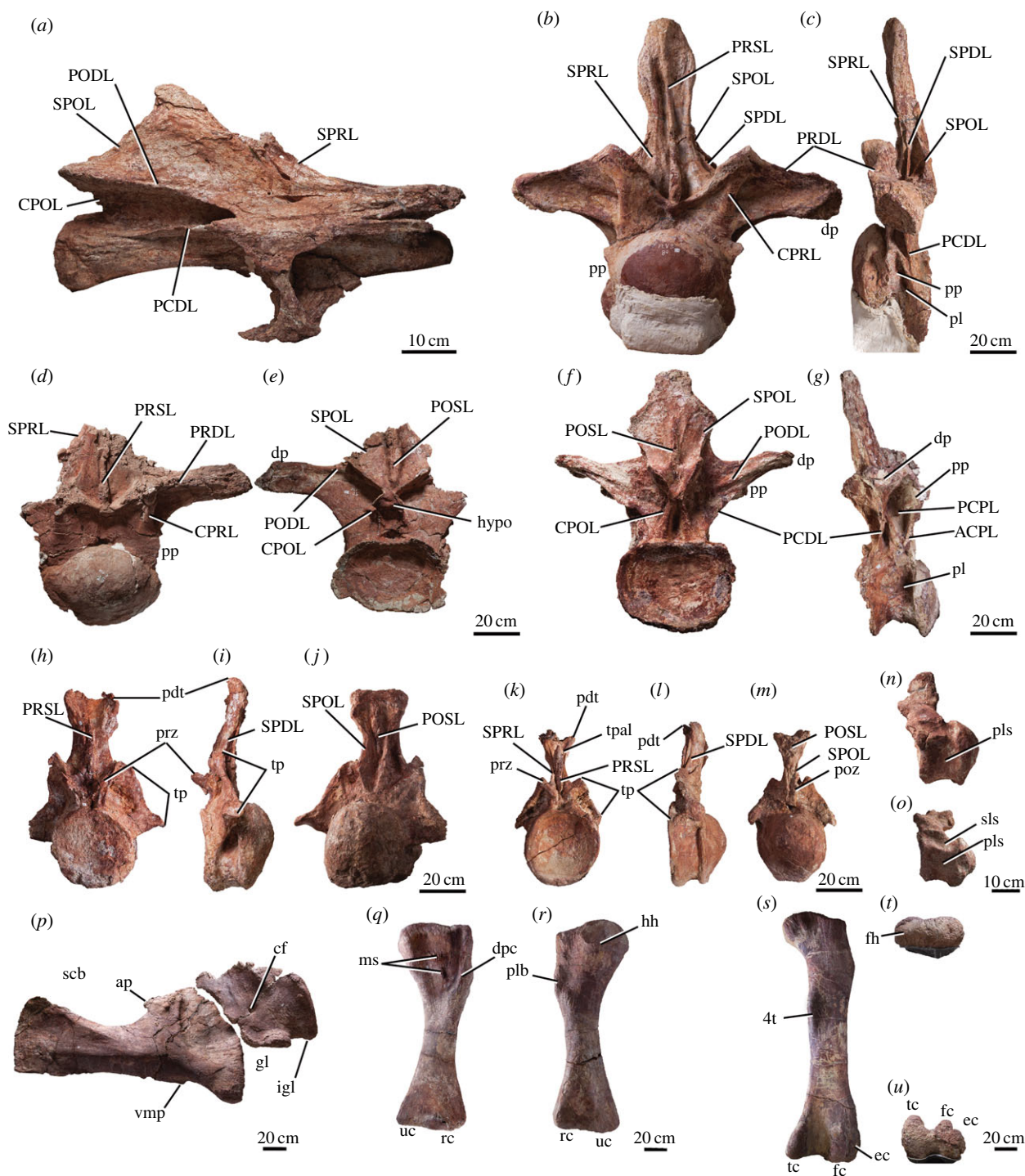
Figure 2. Representative elements of *Patagotitan mayorum*. (*a*) Middle cervical vertebra (MPEF-PV 3400/2; 5th?) in right lateral view. (*b,c*) Anterior dorsal vertebra (MPEF-PV 3400/5; 2nd) in anterior (*b*) and left lateral (*c*) views. (*d,e*) Anterior dorsal vertebra (MPEF-PV 3400/6; 3rd) in anterior (*d*) and posterior (*e*) views. (*f,g*) Posterior dorsal vertebra (MPEF-PV 3400/10; 10th?) in posterior (*f*) and right lateral (*g*) views. (*h–j*) First caudal vertebra in anterior (*h*), left lateral (*i*) and posterior (*j*) views. (*k–m*) Anterior caudal vertebra (MPEF-PV 3400/16; 8th?) in anterior (*k*), left lateral (*l*) and posterior (*m*) views. (*n*) Middle caudal vertebra in left lateral view. (*o*) Posterior caudal vertebra in left lateral view. (*p*) Right scapula (MPEF-PV 3400/23) and coracoid (MPEF-PV 3400/24) in lateral view. (*q,r*) Left humerus (MPEF-PV 3397) in anterior (*q*) and posterior (*r*) views. (*s–u*) Right femur (MPEF-PV 4400/26) in posterior (*s*), proximal (*t*) and distal (*u*) view. Vertebrae elements were oriented with their neural canal horizontally placed. 4t, fourth trochanter; ap, acromion process; cf, coracoid foramen; CPOL, centrpopostzygapophyseal lamina; CPRL, centroprezygapophyseal lamina; dp, diapophysis; dpc, deltopectoral crest; ec, epicondyle; fc, fibular condyle; fh, femur head; gl, glenoid; hh, humeral head; igl, infraglenoid lip; ms muscle scar; PCDL, posterior centrodiapophyseal lamina; pdt, posteriorly directed tips; pl, pleurocoel; plb, posterolateral bulge; pls, primary lateral surface; PODL, postzygodiapophyseal lamina; POSL, postspinal lamina; poz, postzygapophysis; pp, parapohysis; PPDL, paradiapophyseal lamina; PRDL, prezygodiapophyseal lamina; PRSL, prezigapophyseal lamina; prz, prezygapophysis; rc, radial condyle; scb, scapular blade; sls, secondary lateral surface; SPOL, spinopostzygapophyseal lamina; SPRL, spinoprezygapophyseal lamina; tc, tibial condyle; tp, transverse process; tpal, thin paired anterior laminae; uc, ulnar condyle; vmp, ventromedial process.

(e.g. *Dreadnoughtus*). Anterior and middle caudal vertebrae have a markedly concave primary lateral surface [26] of the centrum (figure 2*n*). The anteriormost eight caudal vertebrae

bear a distinctively high transverse process, which is formed by a broad sheet of bone that extends laterally, from the centrum up to the dorsoventral midpoint of the neural arch

(figure 2*h*−*m*). This process is present at least up to the eighth caudal vertebra and is definitively absent in middle caudal vertebrae, but its presence cannot be determined in between these two regions due to the lack of preserved elements. The transverse process of *Patagotitan* is somewhat similar to the wing-like process of diplodocoids, but differs from those in certain aspects. The dorsal margin of the transverse process is much shorter than the ventral margin in *Patagotitan* (figure 2*h*−*k*), whereas diplodocoids have a remarkably long dorsal margin, which is similar in length to the ventral margin and is dorsolaterally oriented [27]. The morphology of the dorsoventrally high and anteroposteriorly narrow transverse process of the anterior caudal vertebrae of *Patagotitan* resembles that of the large titanosaurs *Futalognkosaurus* and *Mendozasaurus* from the early Late Cretaceous of Patagonia. However, it differs from the dorsoventrally low processes of basal macronarians (e.g. *Camarasaurus*, *Brachiosaurus*, *Tastavinsaurus*) and other titanosaurs, including the large-bodied *Dreadnoughtus* and *Notocolossus*. The neural spines of the anterior caudal vertebrae are remarkably high (approx. 1.5 times the centrum height) and broad (more than twice as mediolaterally wide as anteroposteriorly long), differing from the narrow neural spines widespread in non-lognkosaurian titanosaurs (titanosaurs recovered outside Lognkosauria), such as *Dreadnoughtus*, *Malawisaurus* or *Epachthosaurus*. The anterior caudal vertebrae have thin longitudinal laminae that diverge dorsally from the prespinal and postpinal laminae, a character previously proposed as an autapomorphy of *Bonitasaura* [28] (figure 2*k*). The anterior caudal vertebrae also bear a spinodiapophyseal lamina, which is well developed and runs from the dorsal surface of the transverse process up to the lateral aspect of the neural spine. The presence of this lamina in anterior caudal vertebrae is an uncommon character among sauropods, but this lamina can be recognized in some rebbachisaurids (e.g. *Demandasaurus*), and among titanosaurs it is present in *Drusilasaura*, *Futalognkosaurus*, *Mendozasaurus* and *Patagotitan*. The dorsal margin of the neural spine of anterior caudal vertebrae is markedly concave, creating an incipient bifid spine with the lateral tips anteriorly directed (a distinctive character of *Patagotitan*, observed in MPEF-PV 3400 and 3399).

The caudal vertebrae morphology of *Patagotitan* shows multiple modifications from the ancestral condition of Titanosauria related to the insertion areas of the caudal musculature (e.g. large primary lateral surface of centra, high and broad neural spines, high transverse processes). Histological sections taken from the high transverse processes and dorsal tip of the neural spine of caudal vertebrae revealed the primary bone of their cortex consists of avascular tissue formed by coarse Sharpey's fibres (for a more detailed description, see electronic supplementary material, figure S1). The apomorphic shape of the transverse process of *Patagotitan* provides an expansion of the attachment areas for the tail muscles (*m. caudofemoralis longus*, *m. ilio-ischiocaudalis* and *m. spinalis*, respectively [29,30]), which evidences modifications on muscular architecture and may imply and increase in caudal muscular mass in this giant titanosaur (see electronic supplementary material for a more detailed description).

The sternal plates, scapula, coracoid, humerus, ulna and radius are preserved. The coracoid is proximodistally shorter than its scapular articulation (figure 2*p*). The acromion process of the scapula is well developed and distally oriented. The scapular blade is distally expanded and set at an angle of 45°

with respect to the coracoid articulation. The humerus (figure 2*q*,*r*) is robust, with a square proximolateral corner, a straight lateral margin along its proximal third, and flat distal condyles. One distinctive character observed in the three recovered humeri is the presence of a well-developed bulge on the posterolateral surface (figure 2*r*), resembling that of some derived lithostrotians (e.g. *Neuquensaurus*, *Opisthocoelicaudia* [31]). The triradiate ulna has a deep radial fossa, and the olecranon process is weakly developed. The distal condyles of the radius are perpendicular to its long axis.

The pubis is larger than the ischium, and the puboischial articulation is almost half the pubic length. The ischium has a marked ischial tuberosity and a robust distal blade that ends at the level of the pubic peduncle. Although robust, the ischial blade is not as proportionally short as that of most lithostrotians, in which the ischium blade is no more than twice its maximum width (e.g. *Neuquensaurus*, *Malawisaurus*). The femur (figure 2*s*−*u*) has well-marked muscle insertion scars and a massive head. The lateral bulge is well developed in the proximal one-fourth of its length, and the fourth trochanter is positioned at the proximal one-third of its length. The five preserved femora have a straight lateral edge along the distal one-quarter of its length, forming a prominent epicondyle. In distal view, the fibular condyle is anteroposteriorly shorter than the tibial one (figure 2*u*), as in *Bonitasaura*.

4. Ontogenetic stage

In order to assess the ontogenetic stage of the different specimens recovered at the quarry, thin sections were made in five femora (including both femora from the holotype and the specimens MPEF-PV 3399, 3394 and 3375) and one humerus (MPEF-PV 3397). All samples were taken at midshaft and, when possible, with surrounding sedimentary matrix. All thin sections of long bones show that cortical bone is mostly composed of dense Haversian (secondary) tissue with remains of unremodelled fibrolamellar primary tissue in the outer cortex (see electronic supplementary material for a more complete histological description; electronic supplementary material, figure S1). This indicates that individuals died during a deceleration of growth rate phase [32] but that they had not stopped growing, given the absence of an outer external fundamental system [33]. The absence of an outer circumferential layer (OCL) was suggested as a titanosaur feature given its absence in a few titanosaur species [34]. However, the presence of OCL in at least two titanosaur taxa (e.g. *Saltasaurus*, *Neuquensaurus* [35]) contradicts this hypothesis and suggests that alternative explanations (e.g. sampling of not fully grown specimens, extensive secondary remodelling) may account for the absence of OCL in some titanosaurs [36].

5. Body mass

The body mass of quadrupedal dinosaurs can be estimated through scaling equations (using femoral and humeral circumferences [37]) and volumetric methods [38–40] (see electronic supplementary material for a detailed description on both methods and results). Applying the scaling equation for *Patagotitan* yields an estimated body mass of 69 tonnes (±17 tonnes standard error [37]), which is 10 000 kg (over 15%) more than the mass estimate obtained with the same equation for the largest titanosaur in which femur and

humerus have been preserved (*Dreadnoughtus* [12]) and twice the estimated body mass of several large Jurassic sauropods using the same equation (e.g. *Giraffatitan, Apatosaurus* [8]). Uncertainties in large dinosaur body mass estimations from scaling equations are notably large and error bars in the cases of *Patagotitan* and *Dreadnoughtus* overlap between 59 tonnes (minimal body mass for *Patagotitan*) and 74 tonnes (maximal body mass for *Dreadnoughtus*). The completeness of *Patagotitan* allowed the reconstruction of volumetric models (following the method described by [38]), and yielded even larger differences between *Patagotitan* and other sauropods (including *Dreadnoughtus*). Volumetric body mass estimates also have uncertainties related to the amount of soft-tissue reconstructed [37], and resulted in estimates of 45, 51 and 77 tonnes (depending on the amount of soft-tissue reconstructed; see the electronic supplementary material). These estimates represents approximately twice (or more) the body mass inferred by the same volumetric methods for other sauropods, such as *Camarasaurus, Giraffatitan, Sauroposeidon* and *Dreadnoughtus* [39]. In addition to the uncertainties of each method, the estimates from volumetric models and scaling equations can be markedly different, as recently noted for *Dreadnoughtus* (with volumetric body mass estimates ranging between 37 and 64% of the scaling estimates [39]). The incongruence between these two methodologies is not as marked when applied to other sauropods [39], including *Patagotitan* (with volumetric mass estimates largely overlapping with those of scaling equations when their respective errors are considered; see the electronic supplementary material). The discrepancy among methods found in *Dreadnoughtus* is probably related to the robustness of its limb elements and it is higher than expected, however, the agreement in *Patagotitan* shows estimates from the two methods do not necessarily diverge with increasing body mass in giant titanosaurs [16].

Body mass estimates for giant titanosaurs such as *Argentinosaurus* [13] and *Puertasaurus* [14] cannot be calculated using scaling equations due to the absence of limb elements; nonetheless, anterior dorsal vertebrae have been preserved in all of them (as well as in *Notocolossus*) and can therefore be directly compared. Comparing the area of these vertebrae (a two-dimensional equivalent to the volumetric method [38]) yields values that are approximately 10% smaller for these other taxa in comparison with *Patagotitan* (see electronic supplementary material, figure S3). The above-mentioned body mass estimates, as well as these vertebral comparisons, place *Patagotitan* as the largest known dinosaur species (especially considering those for which a reliable mass estimation can be made).

6. Phylogenetic analysis

The phylogenetic position of *Patagotitan* was tested through an equally weighted parsimony analysis in TNT v. 1.1 [41] and using a dataset of 405 characters scored across 87 sauropodomorphs (including 50 macronarians, 28 of which are titanosaurs; see the electronic supplementary material for further information and characters list). The heuristic tree search consisted of 10 000 replicates of Wagner trees (with random addition sequence of taxa) followed by tree bisection-reconstruction (TBR) branch swapping. This procedure retrieved 920 most parsimonious trees (MPTs) of 1328 steps in 143 replicates. The MPTs were subjected to a final round of TBR and a total of 5500 trees were found. Owing to the

instability of some taxa among the MPTs a reduced consensus is used for summarizing the MPTs (figure 3; see electronic supplementary material).

The analysis resolved *Patagotitan* as the titanosaur sauropod most closely related to *Argentinosaurus*, a clade that is supported by a single unambiguous synapomorphic character, the presence of anterior dorsal vertebrae with elongated neural spines (neural spine is more than twice as dorsoventrally high as mediolaterally wide; character (ch.) 174). These two giant titanosaurs are nested within Lognkosauria, a diverse clade that includes most of the largest titanosaurs known. The successive sister taxa of Lognkosauria are *Notocolossus* [16] and *Bonitasaura* (a titanosaur known from a juvenile mid-sized specimen [42,43]). In contrast with previous analyses [15,17,28], Lognkosauria is here recovered as a non-lithostrotian clade of titanosaurs. Lognkosaurians share three derived features found in the anterior caudal vertebrae: (1) the presence of a highly developed spinodiapophyseal lamina (ch. 244, present in *Mendozasaurus, Futalognkosaurus, Drusilasaura* and *Patagotitan* [17,44,45]); (2) the presence of small accessory spinoprezygapophyseal laminae that ventrally contact to the prespinal lamina (ch. 236; described as an autapomorphic bifurcated prespinal laminae for *Futalognkosaurus* [44]; absent in the basal *Mendozasaurus*); and (3) dorsoventrally high transverse process (ch. 247; absent in the basal *Mendozasaurus*).

The recently described giant titanosaur from the Late Cretaceous of western Argentina, *Notocolossus*, was suggested to be the sister taxon of *Dreadnoughtus* and closely related to Lithostrotia [16]. Our analysis places *Notocolossus* as the sister taxon of Lognkosauria, whereas *Dreadnoughtus* is recovered as closely related to Lithostrotia, as in previous studies [12,46]. The monophyly of *Notocolossus* plus Lognkosauria is supported by a single synapomorphy: the presence of reduced spinoprezygapophyseal laminae in anterior caudal vertebrae (ch. 243). This feature is present in *Notocolossus, Mendozasaurus, Futalognkosaurus, Drusilasaura* and *Patagotitan*, and differs from the morphology of other eutitanosaurs that bear well-developed spinoprezygapophyseal laminae in anterior caudal vertebrae (e.g. *Aeolosaurus, Dreadnoughtus, Neuquensaurus* [12,47,48]). *Bonitasaura* was recovered as closely related to Lognkosauria, as suggested in previous analyses (e.g. [49]). This position is supported by six unambiguous synapomorphies: (1) expanded neural spines in posterior cervical vertebrae (ch. 150); (2) high neural spines in posterior cervical vertebrae (ch. 153); (3,4) anterior and middle to posterior dorsal vertebrae with vertical or slightly inclined neural spines (ch. 172 and ch. 185); (5) distally expanded neural spine in anterior caudal vertebrae (ch. 248); and (6) femur with tibial and fibular condyles having similar posterior projections (ch. 350).

Branch support of clades, evaluated using Bremer and bootstrap support, retrieved low values for most of the nodes inside Macronaria. Bremer values higher than one were recovered for Macronaria (6), the clade formed by *Europasaurus* and More Derived Sauropods (MDS; 4), *Galvesaurus* and MDS (3), and Lithostrotia (2). Bootstrap values higher than 50% were not recovered for any node inside Macronaria. Given the low support, and in order to further test the robustness of the monophyly here recovered for the clade of giant titanosaurs formed by *Notocolossus* + Lognkosauria, alternative positions were tested by constraining different taxa outside this clade. The position of *Patagotitan* (49% missing data) inside
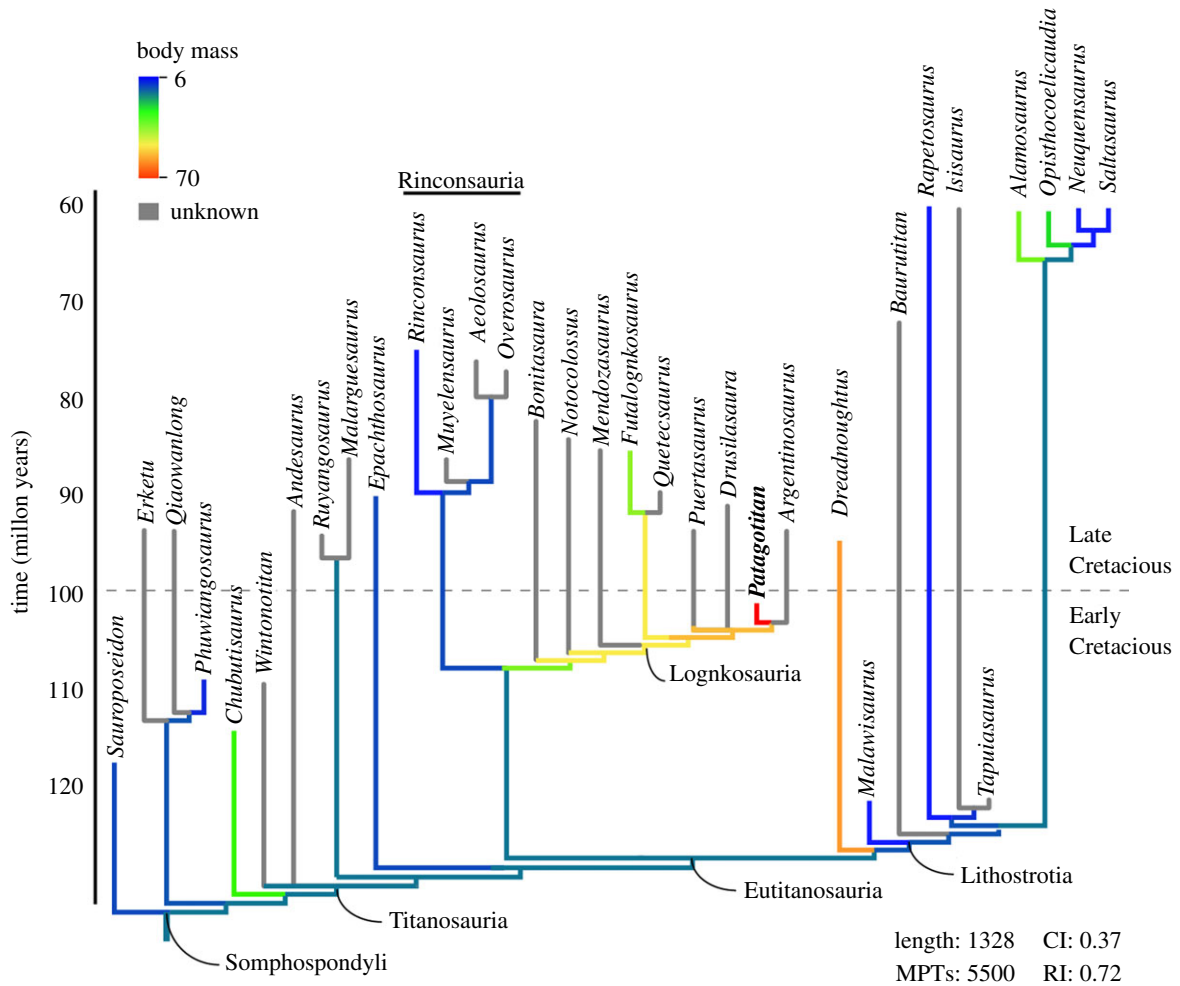
Figure 3. Phylogenetic relationships of *Patagotitan mayorum* and body mass evolution in Somphospondyli. Reduced strict consensus tree (excluding *Sauroposeidon*, *Ligabuesaurus* and *Trigonosaurus*) calibrated against age. Branch colours indicates body mass inferred through scaling equation [37] and continuous character optimization in TNT (ancestral branches). See electronic supplementary material for complete phylogenetic analysis, body mass optimization and taxon definitions followed here.

Lognkosauria is well supported, requiring 12 extra steps to place this taxon as the sister lineage to Lognkosauria, and 22 extra steps if *Patagotitan* is forced to be a lithostrotian titanosaur. Despite the amount of missing data in *Argentinosaurus* (87%), six extra steps are needed to place this taxon as the sister lineage to Lognkosauria, and eight extra steps if it is forced to be inside Lithostrotia. *Puertasaurus* and *Quetecsaurus* (approx. 90% missing data) are the most unstable lognkosaurian taxa, and with one extra step they can be placed as sister taxa to Lognkosauria. Six extra steps are needed if these taxa are forced into Lithostrotia. *Drusilasaura* (94% missing data) was also found to be unstable in suboptimal trees, as it requires three extra steps to place it as sister taxa to Lognkosauria and eight extra steps if it is forced as the sister lineage to Lithostrotia. A large number of extra steps are needed to force *Futalognkosaurus* (73% missing data) or *Mendozasaurus* (67% missing data) inside Lithostrotia, with 10 extra steps needed to move *Mendozasaurus* and 18 for *Futalognkosaurus*. Moving *Notocolossus* (80% missing data) inside Lithostrotia requires only two extra steps. This analysis reveals that Lognkosauria is relatively well supported except for *Quetecsaurus*, *Drusilasaura* and *Puertasaurus*, an expected instability given the large amount of missing data in these taxa (more than 90%). Finally, placing Lognkosauria inside Lithostrotia (as in previous analyses [15,16,49]) requires nine extra steps, indicating that the more basal position here obtained for this clade is well supported.

In the present analysis, *Alamosaurus*, from the Maastrichtian of North America, is recovered as a derived lithostrotian. This taxon was recently recovered as closely related to Lognkosauria [46]. Nevertheless, in our data set (which includes character scorings based on [46]) this position is highly suboptimal, requiring 36 extra steps to place *Alamosaurus* as the sister taxon to Lognkosauria.

Rinconsauria, the sister clade of the lineage formed by Longkosauria + *Notocolossus* + *Bonitasaura*, is supported by three unambiguous synapomorphies: (1) anterior caudal vertebrae with the anterior face of the centrum anteriorly directed (ch. 254); (2) posterior caudal vertebrae with flattened centra (ch. 262); and (3) gracile humerus (ch. 304). The original definition of Aeolosaurinae (as titanosaurs more closely related to *Aeolosaurus* and *Gonwanatitan* than to *Saltasaurus* and *Opisthocoelicaudia* [50]; see the electronic supplementary material) points to the clade formed by Rinconsauria plus Lognkosauria. Nevertheless, this clade was traditionally used to include a small clade of derived titanosaurs closely related to the genus *Aeolosaurus*, and a new definition (node based) of Aeolosaurinae is here proposed in order to keep the original aim of the definition (see the electronic supplementary material).

Dreadnoughtus was here recovered as the sister taxon to Lithostrotia [12], and therefore not related to the other giant titanosaurs from Patagonia. The clade formed by *Dreadnoughtus*

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and Lithostrotia is supported by four unambiguous synapomorphies: (1) dorsoventrally compressed cervical centra (ch. 132); (2) first caudal vertebra with convex anterior articular surface (ch. 224); (3) the absence of ventral bulge in anterior caudal vertebrae (ch. 227); and (4) the absence of a deep infraglenoid groove in the coracoid (ch. 290). Ten extra steps are needed to place *Dreadnoughtus* (46% missing data) within Lognkosauria, indicating a markedly suboptimal hypothesis. Characters present in Lognkosauria that increase their length when *Dreadnoughtus* is forced in this clade include: (1) the more rounded cervical centra (ch. 132); (2) the vertically oriented neural spine in anterior dorsal vertebrae (ch. 172); (3) the non-biconvex first caudal vertebra (ch. 224); (4) the presence of a ventral bulge in anterior caudal vertebrae (ch. 227); (5) laterally expanded neural spines in anterior caudal vertebrae (ch. 237); (6) dorsally expanded neural spine in anterior caudal vertebrae (ch. 248); (7) anterior caudal vertebrae with vertical neural spine (ch. 257); (8) the presence of an infraglenoid grove in the coracoid (ch. 290); and (9) femur with similarly developed condyles (ch. 350).

7. Discussion

Our analysis reveals the presence of a previously unrecognized diverse lineage of Patagonian titanosaurs that includes most of the largest known titanosaur sauropods (e.g. *Notocolossus*, *Patagotitan*, *Argentinosaurus*, *Puertasaurus*; figure 3). This clade is placed basally within Titanosauria and depicted as the sister clade to Rinconsauria, a lineage that includes some of the smallest titanosaurs known so far (e.g. *Rinconsaurus*, *Aeolosaurus*). In order to evaluate the evolution of body size we used mass estimates from the scaling equation [37] inferred in previous studies [8,12] and optimized them as a continuous character using parsimony [41,51]. The optimization reveals that body mass was largely stable along sauropod evolution during the Jurassic and Cretaceous (as previously noted [8,10,47,52]). Inferred body masses for most of the basal nodes of Eusauropoda range between 12 and 15 tonnes (see the electronic supplementary material), and within Macronaria a large part of the internal nodes are optimized with a range of 12–20 tonnes. The latter values are maintained in most internal nodes within somphospondylians and Titanosauria (green-blue colour in figure 3). Within Titanosauria, however, multiple events of body mass changes are inferred based on the optimization, as expected given the clade includes some of the largest and smallest known sauropod species [8]. Our analysis reveals a single major event of body mass increase at the base of the clade formed by *Notocolossus* and Lognkosauria, implying a threefold body mass increase (38–60 tonnes) with respect to the body mass reconstruction of most nodes within Titanosauria (12–20 tonnes; figure 3). The acquisition of gigantism in this clade was not the only marked increase in body mass, as two other titanosaur lineages (*Dreadnoughtus* and *Alamosaurus* [12,46]; figure 3) independently acquired large body masses, although without reaching to the extreme gigantism recorded in Lognkosauria (e.g. *Patagotitan*). The evolutionary dynamics of titanosaur body masses also includes events of marked body mass decrease in Rinconsauria and three lineages within Lithostrotia (probably including dwarfism events [34,36,53]; figure 3).

The age of *Patagotitan* indicates that the radiation of lognkosaurians (and related forms) started in the late Early Cretaceous, temporally coincident with the diversification of lithostrotians [4,54,55], the other major clade of titanosaurs. The phylogenetic diversification event of the major clades of eutitanosaurs in the Aptian–Albian involved major changes in body mass, indicative of ecological differentiation among titanosaurs during this time. This includes the inferred events of mass decrease in some lithostrotians (figure 3) and the maximum increase known to date for titanosaurs (in lognkosaurians, exemplified by *Patagotitan*; figure 3). This phylogenetic and ecological diversification in titanosaurs coincides with similar events noted for other archosaurian clades in the Southern Hemisphere, such as theropods and crocodyliforms [56,57]. Furthermore, these events took place during a global period of major environmental changes that include a warmer climate [58], the onset of the dominance of angiosperms in continental environments [59] and the establishment of the particular 'mid-Cretaceous' fauna in Gondwana [60,61] that lasted until the Turonian [61].

References

1. Wilson JA, Carrano MT. 1999 Titanosaurs and the origin of 'wide-gauge' trackways: a biomechanical and systematic perspective on sauropod locomotion. *Paleobiology* **25**, 252–267. (doi:10.1666/0094-8373-25.2.252)

2. Wilson JA. 2002 Sauropod dinosaur phylogeny: critique and cladistic analysis. *Zool. J. Linn. Soc.* **136**, 215–275. (doi:10.1046/j.1096-3642.2002.00029.x)

3. Upchurch P, Barrett PM, Dodson P. 2004 The Dinosauria. In *The Dinosauria* (eds DB Weishampel, P Dodson, H Osmólska), pp. 259–322. Berkeley, CA: University of California Press.

4. Zaher H *et al.* 2011 A complete skull of an early cretaceous sauropod and the evolution of advanced titanosaurians. *PLoS ONE* **6**, e16663. (doi:10.1371/journal.pone.0016663)

5. D'Emic MD. 2012 The early evolution of titanosauriform sauropod dinosaurs. *Zool. J. Linn. Soc.* **166**, 624–671. (doi:10.1111/j.1096-3642.2012.00853.x)

6. Gorscak E, O'Connor PM. 2016 Time-calibrated models support congruency between Cretaceous continental rifting and titanosaurian evolutionary history. *Biol. Lett.* **12**, 20151047. (doi:10.1098/rsbl.2015.1047)

7. Mannion P, Upchurch P, Barnes RN, Mateus O. 2013 Osteology of the Late Jurassic Portuguese sauropod dinosaur *Lusotitan atalaiensis* (Macronaria) and the evolutionary history of basal titanosauriforms. *Zool. J. Linn. Soc.* **168**, 98–206. (doi:10.1111/zoj.12029)

8. Benson RBJ, Campione NE, Carrano MT, Mannion PD, Sullivan C, Upchurch P, Evans DC. 2014 Rates of dinosaur body mass evolution indicate 170 million years of sustained ecological innovation on the avian stem lineage. *PLoS Biol.* **12**, e1001853. (doi:10.1371/journal.pbio.1001853)

9. De Souza LM, Santucci RM. 2014 Body size evolution in Titanosauriformes (Sauropoda, Macronaria). *J. Evol. Biol.* **27**, 2001–2012. (doi:10.1111/jeb.12456)

10. Hone DWW, Keesey TM, Pisani D, Purvis A. 2005 Macroevolutionary trends in the Dinosauria: Cope's rule. *J. Evol. Biol.* **18**, 587–595. (doi:10.1111/j.1420-9101.2004.00870.x)

11. Sander PM *et al.* 2011 Biology of the sauropod dinosaurs: the evolution of gigantism. *Biol. Rev.* **86**, 117–155. (doi:10.1111/j.1469-185X.2010.00137.x)

12. Lacovara KJ *et al.* 2014 A gigantic, exceptionally complete titanosaurian sauropod dinosaur from Southern Patagonia, Argentina. *Sci. Rep.* **4**, 6196. (doi:10.1038/srep06196)

13. Bonaparte JF, Coria RA. 1993 Un nuevo y gigantesco saurópodo titanosaurio de la Formación Rio Limay (Albiano-Cenomaniano) de la provincia del Neuquén, Argentina. *Ameghiniana* **30**, 271–282.

14. Novas FE, Salgado L, Calvo J, Agnolin F. 2005 Giant titanosaur (Dinosauria, Sauropoda) from the Late Cretaceous of Patagonia. *Rev. Museo Argentino Cienc. Nat.* **7**, 37–41. (doi:10.22179/REVMACN.7.344)

15. Calvo JO, Porfiri JD, González-Riga BJ, Kellner AWA. 2007 A new Cretaceous terrestrial ecosystem from Gondwana with the description of a new sauropod dinosaur. *Ann. Acad. Brasileira Cienc.* **79**, 529–541. (doi:10.1590/S0001-37652007000300013)

16. González Riga BJ, Lamanna MC, Ortiz David LD, Calvo JO, Coria JP. 2016 A gigantic new dinosaur from Argentina and the evolution of the sauropod hind foot. *Sci. Rep.* **6**, 19165. (doi:10.1038/srep19165)

17. González Riga B. 2005 Nuevos restos fósiles de *Mendozasaurus neguyelap* (Sauropoda, Titanosauria) del Cretácico Tardío de Mendoza, Argentina. *Ameghiniana* **42**, 535–548.

18. Conybeare A, Haynes G. 1984 Observations on elephant mortality and bones in water holes. *Quat. Res.* **22**, 189–200. (doi:10.1016/0033-5894(84)90039-5)

19. Upchurch P. 1998 The phylogenetic relationships of sauropod dinosaurs. *Zool. J. Linn. Soc.* **124**, 43–103. (doi:10.1111/j.1096-3642.1998.tb00569.x)

20. Carballido JL, Sander PM. 2014 Postcranial axial axial skeleton of *Europasaurus holgeri* (Dinosauria, Sauropoda) from the Upper Jurassic of Germany: implications for sauropod ontogeny and phylogenetic relationships of basal Macronaria. *J. Syst. Palaeontol.* **12**, 335–387. (doi:10.1080/14772019.2013.764935)

21. Bonaparte JF, González Riga B, Apesteguía S. 2006 *Ligabuesaurus lenzai* gen et sp. nov. (Dinosauria, Sauropoda), a new titanosaur from the Lohan Cura Formation (Aptian, Lower Cretaceous) of Neuquén, Patagonia, Argentina. *Cretaceous Res.* **27**, 364–376. (doi:10.1016/j.cretres.2005.07.004)

22. Carballido JL, Salgado L, Pol D, Canudo JI, Garrido A. 2012 A new basal rebbachisaurid (Sauropoda, Diplodocoidea) from the Early Cretaceous of the Neuquén Basin; evolution and biogeography of the group. *Hist. Biol.* **24**, 631–654. (doi:10.1080/08912963.2012.672416)

23. Schwarz D, Frey E, Meyer C. 2007 Novel reconstruction of the orientation of the pectoral girdle in sauropods. *Anat. Rec.* **290**, 32–47. (doi:10.1002/ar.20405)

24. Fronimos JA, Wilson JF. 2017 Neurocentral suture complexity and stress distribution in the vertebral column of a sauropod dinosaur. *Ameghiniana* **54**, 36–49. (doi:10.5710/AMGH.05.09.2016.3009)

25. Salgado L, Powell JE. 2010 Reassessment of vertebral laminae in some South American titanosaur sauropods. *J. Vertebr. Paleontol.* **30**, 1760–1772. (doi:10.1080/02724634.2010.520783)

26. Salgado L, García RA. 2002 Variación morfológica en la secuencia de vértebras caudales de algunos saurópodos titanosaurios. *Rev. Esp. Paleontol.* **17**, 211–216.

27. Whitlock JA, D'Emic MD, Wilson JF. 2011 Cretaceous diplodocids in Asia? Re-evaluating the phylogenetic affinities of a fragmentary specimen. *Palaeontology* **54**, 351–364. (doi:10.1111/j.1475-4983.2010.01029.x)

28. Gallina PA, Apesteguía S. 2015 Postcranial anatomy of *Bonitasaura salgadoi* (Sauropoda, Titanosauria) from the Late Cretaceous of Patagonia. *J. Vertebr. Paleontol.* **35**, e924957. (doi:10.1080/02724634.2014.924957)

29. Persons WS, Currie PJ. 2011 The tail of *Tyrannosaurus*: reassessing the size and locomotive importance of the *M. Caudofemoralis* in non-avian Theropods. *Anat. Rec.* **294**, 119–131. (doi:10.1002/ar.21290)

30. Persons WS, Currie PJ. 2011 Dinosaur speed demon: the caudal musculature of *Carnotaurus sastrei* and

31. implications for the evolution of South American Abelisaurids. *PLoS ONE* **6**, e257631. (doi:10.1371/journal.pone.0025763)

31. Otero A. 2010 The appendicular skeleton of *Neuquensaurus*, a Late Cretaceous saltasaurine sauropod from Patagonia, Argentina. *Acta Paleontol. Pol.* **55**, 399–426. (doi:10.4202/app.2009.0099)

32. Klein N, Sander M. 2008 Ontogenetic stages in the long bone histology of sauropod dinosaurs. *Paleobiology* **34**, 247–263. (doi:10.1666/0094-8373(2008)034[0247:OSITLB]2.0.CO;2)

33. Chinsamy-Turan A. 2005 *The microstructure of dinosaur bone*. Baltimore, MD: Johns Hopkins University Press.

34. Company J. 2010 Bone histology of the titanosaur *Lirainosaurus astibiae* (Dinosauria: Sauropoda) from the Latest Cretaceous of Spain. *Naturwissenschaften* **98**, 67–78. (doi:10.1007/s00114-010-0742-3)

35. García R *et al.* 2015 Paleobiology of titanosaurs: reproduction, development, histology, pneumaticity, locomotion and neuroanatomy from the South American fossil record. *Ameghiniana* **52**, 29–68. (doi:10.5710/AMGH.16.07.2014.829)

36. Klein N *et al.* 2012 Modified laminar bone in *Ampelosaurus atacis* and other Titanosaurs (Sauropoda): implications for life history and physiology. *PLoS ONE* **7**, e36907. (doi:10.1371/journal.pone.0036907)

37. Campione NE, Evans DC. 2012 A universal scaling relationship between body mass and proximal limb bone dimensions in quadrupedal terrestrial tetrapods. *BMC Biol.* **10**, 60. (doi:10.1186/1741-7007-10-60)

38. Sellers WI, Hepworth-Bell J, Falkingham PL, Bates KT, Brassey CA, Egerton VM, Manning PL. 2012 Minimum convex hull mass estimations of complete mounted skeletons. *Biol. Lett.* **8**, 842–845. (doi:10.1098/rsbl.2012.0263)

39. Bates KT, Falkingham PL, Macaulay S, Brassey C, Maidment SCR. 2015 Downsizing a giant: re-evaluating *Dreadnoughtus* body mass. *Biol. Lett.* **11**, 20150215. (doi:10.1098/rsbl.2015.0215)

40. Bates KT *et al.* 2016 Temporal and phylogenetic evolution of the sauropod dinosaur body plan. *R. Soc. open sci.* **3**, 150636. (doi:10.1098/rsos.150636)

41. Goloboff PA, Farris JS, Nixon KC. 2008 TNT, a free program for phylogenetic analysis. *Cladistics* **24**, 774–786. (doi:10.1111/j.1096-0031.2008.00217.x)

42. Apesteguía S. 2004 *Bonitasaura salgadoi* gen. et sp. nov.: a beaked sauropod from the Late Cretaceous of Patagonia. *Naturwissenschaften* **91**, 493–497. (doi:10.1007/s00114-004-0560-6)

43. Gallina PA. 2012 Histología ósea del titanosaurio *Bonitasaura salgadoi* (Dinosauria: Sauropoda) del Cretácico Superior de Patagonia. *Ameghiniana* **49**, 289–302. (doi:10.5710/AMGH.v49i3(519))

44. Calvo JO, Porfiri JD, González Riga B, Kellner AWA. 2007 Anatomy of *Futalognkosaurus dukei* Calvo, Porfiri, González Riga & Kellner, 2007 (Dinosauria, Titanosauridae) from the Neuquén Group (Late

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rspb.royalsocietypublishing.org   Proc. R. Soc. B 284: 20171219

Cretaceous), Patagonia, Argentina. *Arquivos do Museu Nacional, Rio de Janeiro* **65**, 511–526.

45. Navarrete C, Casal G, Martínez R. 2011 *Drusilasaura deseadensis* gen. et sp. nov., un nuevo titanosaurio (Dinosauria-Sauropoda), de la Formación Bajo Barreal, Cretácico Superior del norte de Santa Cruz, Argentina. *Rev. Brasilera Paleontol.* **14**, 1–14. (doi:10.4072/rbp.2011.1.01)

46. Tykoski RS, Fiorillo AR. 2016 An articulated cervical series *of Alamosaurus sanjuanensis* Gilmore, 1922 (Dinosauria, Sauropoda) from Texas: new perspective on the relationships of North America's last giant sauropod. *J. Syst. Paleontol.* **15**, 339–364. (doi:10.1080/14772019.2016.1183150)

47. Santucci RM, De Arruda-Campos AC. 2012 A new sauropod (Macronaria, Titanosauria) from the Adamantina Formation, Bauru Group, Upper Cretaceous of Brazil and the phylogenetic relationships of Aeolosaurini. *Zootaxa* **3085**, 1–33.

48. Salgado L, Apesteguía S, Heredia SE. 2005 A new specimen of *Neuquensaurus australis*, a Late Cretaceous saltasaurine titanosaur from north Patagonia. *J. Vertebr. Paleontol.* **25**, 623–634. (doi:10.1671/0272-4634(2005)025[0623:ansona]2.0.co;2)

49. Gallina PA, Apesteguía S. 2011 Cranial anatomy and phylogenetic position of the titanosaurian sauropod *Bonitasaura salgadoi*. *Acta Palaeontol. Pol.* **56**, 45–60. (doi:10.4202/app.2010.0011)

50. Franco-Rosas AC, Salgado L, Rosas CF, Carvalho IDS. 2004 Nuevos materiales de titanosaurios (Sauropoda) en el Cretácico Superior de Mato Grosso, Brasil. *Rev. Brasileira Paleontol.* **7**, 329–336. (doi:10.4072/rbp.2004.3.04)

51. Goloboff PA, Mattoni CI, Quinteros AS. 2006 Continuous characters analyzed as such. *Cladistics* **22**, 589–601. (doi:10.1111/j.1096-0031.2006.00122.x)

52. Carrano MT. 2006 Body-size evolution in the Dinosauria. In *Amniote paleobiology: perspectives on the evolution of mammals, birds, and reptiles* (eds MT Carrano, RW Blob, TJ Gaudin, JR Wible), pp. 225–268. Chicago, IL: University of Chicago Press.

53. Stein K, Csiki Z, Curry Rogers K, Weishampel DB, Redelstorff R, Carballido JL, Sander PM, Stanley SM. 2010 Small body size and extreme cortical bone remodeling indicate phyletic dwarfism in *Magyarosaurus dacus* (Sauropoda: Titanosauria). *Proc. Natl Acad. Sci. USA* **107**, 9258–9263. (doi:10.1073/pnas.1000781107)

54. Wilson JA, Pol D, Carvalho AB, Zaher H. 2016 The skull of the titanosaur *Tapuiasaurus macedoi* (Dinosauria: Sauropoda), a basal titanosaur from the Lower Cretaceous of Brazil. *Zool. J. Linn. Soc.* **178**, 611–662. (doi:10.1111/zoj.12420)

55. Gomani EM. 2005 Sauropod dinosaurs from the Early Cretaceous of Malawi, Africa. *Paleontol. Electron.* **27A**, 37.

56. Pol D, Nascimento PM, Carvalho AB, Riccomini C, Pires-Domingues RA, Zaher H. 2014 A new notosuchian from the Late Cretaceous of Brazil and the phylogeny of advanced notosuchians. *PLoS ONE* **9**, e93105. (doi:10.1371/journal.pone.0093105)

57. Novas FE, Agnolín FL, Ezcurra MD, Porfiri J, Canale JI. 2013 Evolution of the carnivorous dinosaurs during the Cretaceous: The evidence from Patagonia. *Cretaceous Res.* **45**, 174–215. (doi:10.1016/j.cretres.2013.04.001)

58. Huber BT, Norris RD, MacLeod KG. 2002 Deep-sea paleotemperature record of extreme warmth during the Cretaceous. *Geology* **30**, 123–126. (doi:10.1130/0091-7613(2002)030<0123:DSPROE>2.0.CO;2)

59. Upchurch Jr GR, Dilcher DL. 1990 Cenomanian angiosperm leaf megafossils, Dakota Formation, Rose Creek locality, Jefferson County, southeastern Nebraska. *US Geological Survey Bulletin* **1950**, 1–55.

60. Sereno PC, Wilson JA, Conrad JL. 2004 New dinosaurs link southern landmasses in the Mid-Cretaceous. *Proc. R. Soc. B* **271**, 1325–1330. (doi:10.1098/rspb.2004.2692)

61. Coria RA, Salgado L. 2005 Mid-Cretaceous turnover of saurischian dinosaur communities: evidence from the Neuquén Basin. *Geol. Soc. Lond. Spec. Publ.* **252**, 317–327. (doi:10.1144/GSL.SP.2005.252.01.16)

62. Carballido JL, Pol D, Otero A, Cerda IA, Salgado L, Garrido AC, Ramezzani J, Cúneo NR, Krause MJ. 2017 Data from: A new giant titanosaur sheds light on body mass evolution among sauropod dinosaurs. Dryad Digital Repository. (http://dx.doi.org/10.5061/dryad.5k05t)