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# A Gigantic, Exceptionally Complete Titanosaurian Sauropod Dinosaur from Southern Patagonia, Argentina

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**Titanosaurian sauropod dinosaurs were the most diverse and abundant large-bodied herbivores in the southern continents during the final 30 million years of the Mesozoic Era. Several titanosaur species are regarded as the most massive land-living animals yet discovered; nevertheless, nearly all of these giant titanosaurs are known only from very incomplete fossils, hindering a detailed understanding of their anatomy. Here we describe a new and gigantic titanosaur, *Dreadnoughtus schrani*, from Upper Cretaceous sediments in southern Patagonia, Argentina. Represented by approximately 70% of the postcranial skeleton, plus craniodental remains, *Dreadnoughtus* is the most complete giant titanosaur yet discovered, and provides new insight into the morphology and evolutionary history of these colossal animals. Furthermore, despite its estimated mass of about 59.3 metric tons, the bone histology of the *Dreadnoughtus* type specimen reveals that this individual was still growing at the time of death.**

T he sauropod dinosaur clade Titanosauria includes the most massive terrestrial animals yet discovered[1,2]. Nevertheless, with the exception of *Futalognkosaurus*—known from much of the vertebral column and pelvis[3]—all truly gigantic titanosaurs (*sensu* Sander et al.[4]; i.e., those with an adult body mass exceeding 40 metric tons) are represented by very fragmentary fossils[5–9]. The incomplete understanding of the anatomies of colossal titanosaurs has frustrated attempts to characterize important aspects of their evolutionary history and palaeobiology. For example, it is presently uncertain whether extreme gigantism evolved multiple times or only once within Titanosauria[4]. Furthermore, it is not even clear how large the largest titanosaurs were, with different studies yielding widely divergent estimates of body dimensions[7,10–13].

Here we report a new and gigantic titanosaur from Upper Cretaceous (Campanian–Maastrichtian[14,15]; ~84–66 Ma[16]) rocks exposed in south-western Patagonia, Argentina (Supplementary Fig. 1), some 1,200 km from the best-known South American dinosaur localities, which occur in northern Patagonia[17]. Represented by all major skeletal regions (see Supplementary Information), *Dreadnoughtus schrani* nov. gen. nov. sp. (Figs. 1, 2, Supplementary Figs. 2–18) offers new insight into the skeletal anatomy, bone histology, phylogenetic relationships (Fig. 3, Supplementary Figs. 19, 20), and body shape and mass of an enormous titanosaur. Most bones are exquisitely preserved, with details such as muscle scars and other osteological correlates of soft-tissues clearly discernible.
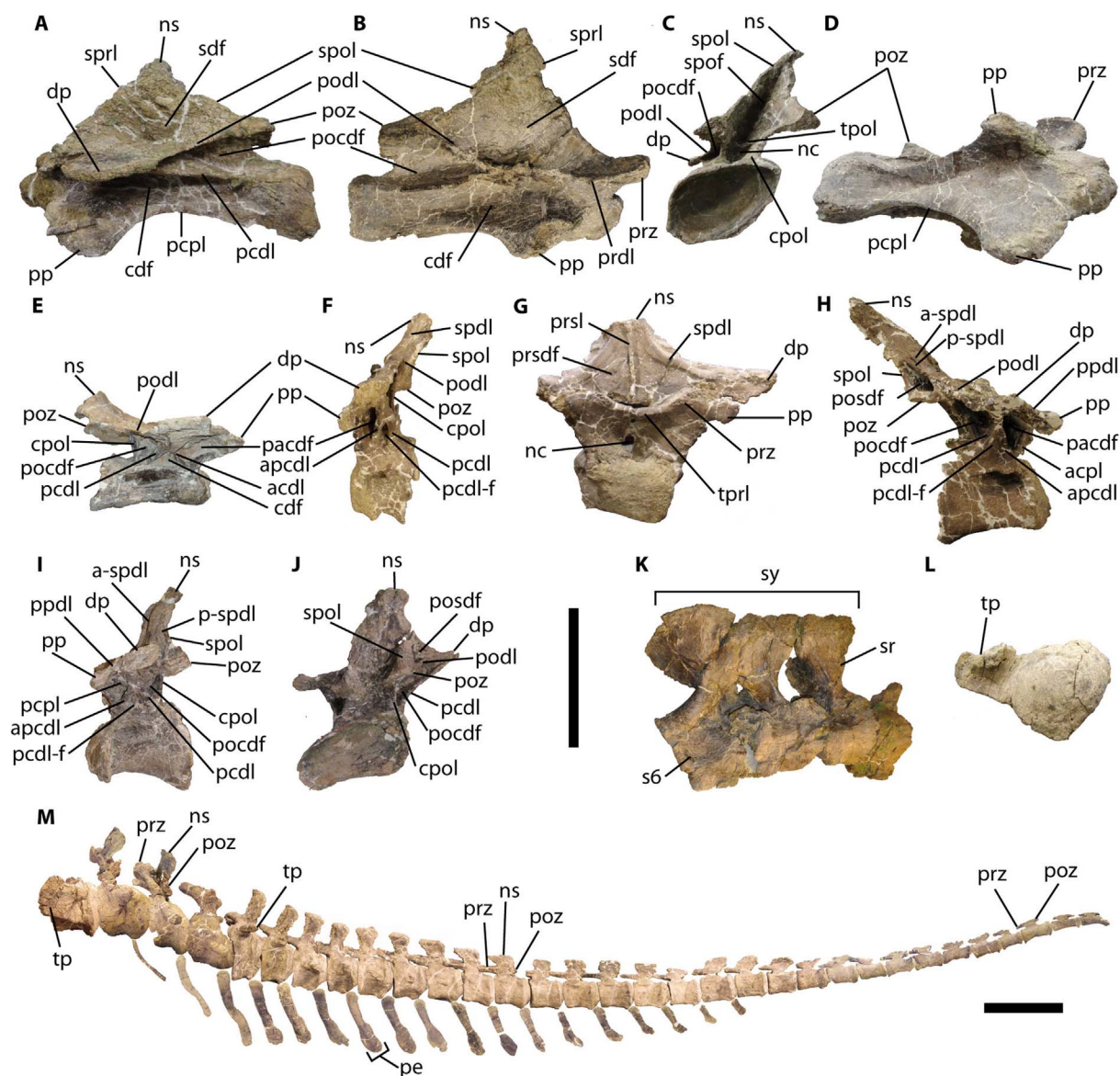
**Figure 1 | Axial skeletal anatomy of the gigantic titanosaur *Dreadnoughtus schrani*.** Posterior (~9th) cervical vertebra in (A) left lateral, (B) right lateral, (C) posterior, and (D) ventral views. (E) Anterior (~4th) dorsal vertebra in right lateral view. Middle (~6th) dorsal vertebra in (F) left lateral and (G) anterior views. (H) Posterior (~7th) dorsal vertebra in right lateral view. Posterior (~8th) dorsal vertebra in (I) left lateral and (J) posterior views. (K) Partial sacrum in ventral view. (L) Biconvex first caudal vertebra in posterior view. (M) First 32 caudal vertebrae and 18 haemal arches in left lateral view (positions of first 21 caudal vertebrae and haemal arches 4 to 18 known with certainty). All depicted elements definitively pertain to the holotype (MPM-PV 1156), with the possible exceptions of the dorsal vertebrae in (E) and (H) to (J), which belong to either the holotype or the paratype (MPM-PV 3546). Abbreviations: acpl, anterior centroparapophyseal lamina; apcdl, accessory posterior centrodiapophyseal lamina; a-spdl, anterior ramus of spinodiapophyseal lamina; cdf, centrodiapophyseal fossa; cpol, centropostzygapophyseal lamina; dp, diapophysis; nc, neural canal; ns, neural spine; pacdf, parapophyseal centrodiapophyseal fossa; pcdl, posterior centrodiapophyseal lamina; pcdl-f posterior centrodiapophyseal fossa, pcpl, posterior centroparapophyseal lamina; pe, paddle-shaped distal expansion; pocdf, postzygapophyseal centrodiapophyseal fossa; podl, postzygodiapophyseal lamina; posdf, postzygapophyseal spinodiapophyseal fossa; poz, postzygapophysis; pp, parapophysis; ppdl, paradiapophyseal lamina; prdl, prezygodiapophyseal lamina; prsdf, prezygapophyseal spinodiapophyseal fossa; prsl, prespinal lamina; prz, prezygapophysis; p-spdl, posterior ramus of spinodiapophyseal lamina; s6, sixth sacral vertebra; sdf, spinodiapophyseal fossa; spdl, spinodiapophyseal lamina; spof, spinopostzygapophyseal fossa; spol, spinopostzygapophyseal lamina; sprl, spinoprezygapophyseal lamina; sr, sacral rib; sy, sacricostal yoke; tp, transverse process; tpol, intrapostzygapophyseal lamina; tprl, intraprezygapophyseal lamina. Scale bars equal 50 cm.

## Results

**Systematic palaeontology.** Dinosauria Owen 1842. Saurischia Seeley 1887. Sauropoda Marsh 1878. Titanosauriformes Salgado, Coria, and Calvo 1997. Titanosauria Bonaparte and Coria 1993. *Dreadnoughtus schrani* nov. gen. nov. sp.

**Etymology.** *Dreadnought* (Old English), fearing nothing; genus name alludes to the gigantic body size of the taxon (which pre-sumably rendered healthy adult individuals nearly impervious to attack) and the predominant battleships of the early 20th century (two of which, ARA [Armada de la República Argentina] *Riva-davia* and ARA *Moreno*, were part of the Argentinean navy). Species name honours the American entrepreneur Adam Schran for his support of this research. **Holotype.** MPM-PV 1156, a par-tially articulated partial skeleton that comprises a maxilla fragment, a tooth, a posterior cervical vertebra, cervical ribs, multiple dorsal
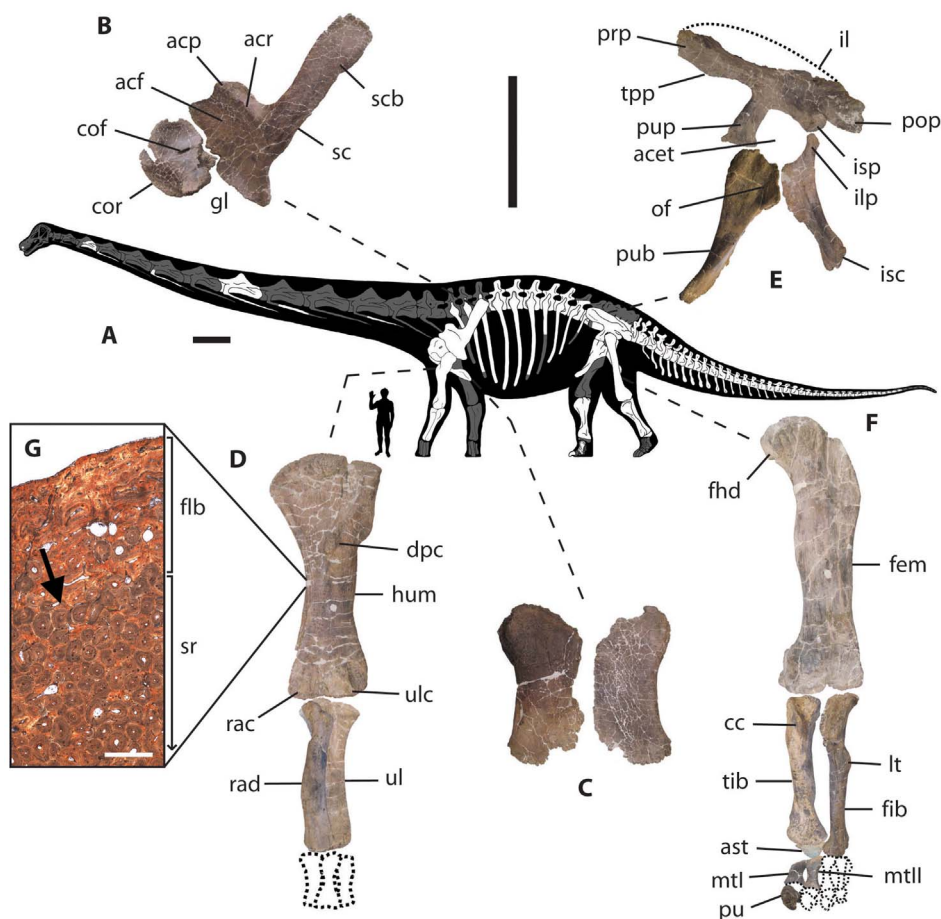
**Figure 2 | Reconstruction, appendicular skeletal anatomy, and bone histology of *Dreadnoughtus schrani*.** (A) Reconstructed skeleton and body silhouette in left lateral view with preserved elements in white. (B) Left scapula and coracoid in lateral view. (C) Sternal plates in ventral view. (D) Left forelimb (metacarpus reconstructed) in anterior view. (E) Left pelvis (ilium partially reconstructed) in lateral view. (F) Left hind limb in anterior view (metatarsus and pes partially reconstructed and reversed from right). (G) Transverse ground thin section of humeral shaft, showing heavy secondary remodelling (arrow indicates extent of dense osteon formation), a thick layer of well-vascularized fibrolamellar bone, and a lack of lines of arrested growth or an external fundamental system. Abbreviations: acet, acetabulum; acf, acromial fossa; acp, acromial process; acr, acromial ridge; ast, astragalus; cc, cnemial crest; cof, coracoid foramen; cor, coracoid; dpc, deltopectoral crest; fem, femur; fhd, femoral head; fib, fibula; flb, fibrolamellar bone; gl, glenoid; hum, humerus; il, ilium; ilp, iliac peduncle; isc, ischium; isp, ischial peduncle; lt, lateral trochanter; mtI, metatarsal I; mtII, metatarsal II; of, obturator foramen; pop, postacetabular process; prp, preacetabular process; pu, pedal ungual; pub, pubis; pup, pubic peduncle; rac, radial condyle; rad, radius; sc, scapula; scb, scapular blade; sr, secondary remodelling; tib, tibia; tpp, tuberosity on preacetabular process; ul, ulna; ulc, ulnar condyle. Scale bars equal 1 m in (A) to (F) and 1 mm in (G). (Skeletal reconstruction by L. Wright, with G. Schultz.)

vertebrae and ribs, the sacrum, 32 caudal vertebrae and 18 haemal arches (including an articulated sequence of 17 anterior and middle caudal vertebrae and their corresponding haemal arches), the left pectoral girdle and forelimb minus the manus, both sternal plates, all pelvic elements, the left hind limb lacking the pes, and the right tibia, metatarsals I and II, and pedal ungual I. **Paratype.** MPM-PV 3546, a partially articulated postcranial skeleton of a slightly smaller individual that includes a partial anterior cervical vertebra, multiple dorsal vertebrae and ribs, the sacrum, seven caudal vertebrae and five haemal arches, all pelvic elements, and the left femur. The specimens are catalogued in the collection of the Museo Padre Molina (MPM; Río Gallegos, Argentina; see Supplementary Information for other institutional abbreviations). **Type locality.** Cerro Fortaleza, east bank of the Río La Leona, Santa Cruz Province, south-western Patagonia, Argentina (coordinates on file at MPM). **Horizon.** Cerro Fortaleza Formation, approximately 350 m below the top of the formation. **Age.** Late Cretaceous, Campanian–Maastrichtian, ~84–66 Ma.

**Diagnosis.** A gigantic titanosaurian sauropod diagnosed by the following autapomorphies (* = character observable in both known specimens): (1) first caudal centrum with axial ventral keel;

(2) anterior caudal neural spines with extensively subdivided pneumatocoel between spinoprezygapophyseal and spinopostzyga-pophyseal laminae*; (3) anterior caudal neural spines with hyper-trophied prespinal and postspinal laminae*; (4) middle caudal neural spines with triangular anterodorsal process that extends well beyond anterior margin of centrum*; (5) anterior haemal arches with paddle-shaped distal expansion*; (6) posterodorsally–anteroventrally oriented ridge on medial surface of anterior end of scapular blade; (7) posteromedial surface of radius concave in proximal view; (8) distal end of radius nearly square, with subequal anteroposterior and mediolateral dimensions. (See Supplementary Information for detailed comparisons with *Puertasaurus reuili*, a fragmentary, similarly-sized titanosaur from the same lithostratigraphic formation).

**Description.** The *Dreadnoughtus* maxilla houses elongate, peg-like teeth typical of derived titanosaurians (Supplementary Fig. 2). Cervical vertebrae have opisthocoelous centra that lack lateral pneumatic fossae ('pleurocoels'), though they are internally comprised of highly pneumatized camellate tissue. The centrum of a nearly complete posterior (approximately the ninth) cervical verte-bra of the *Dreadnoughtus* holotype (MPM-PV 1156) (Fig. 1A–D,
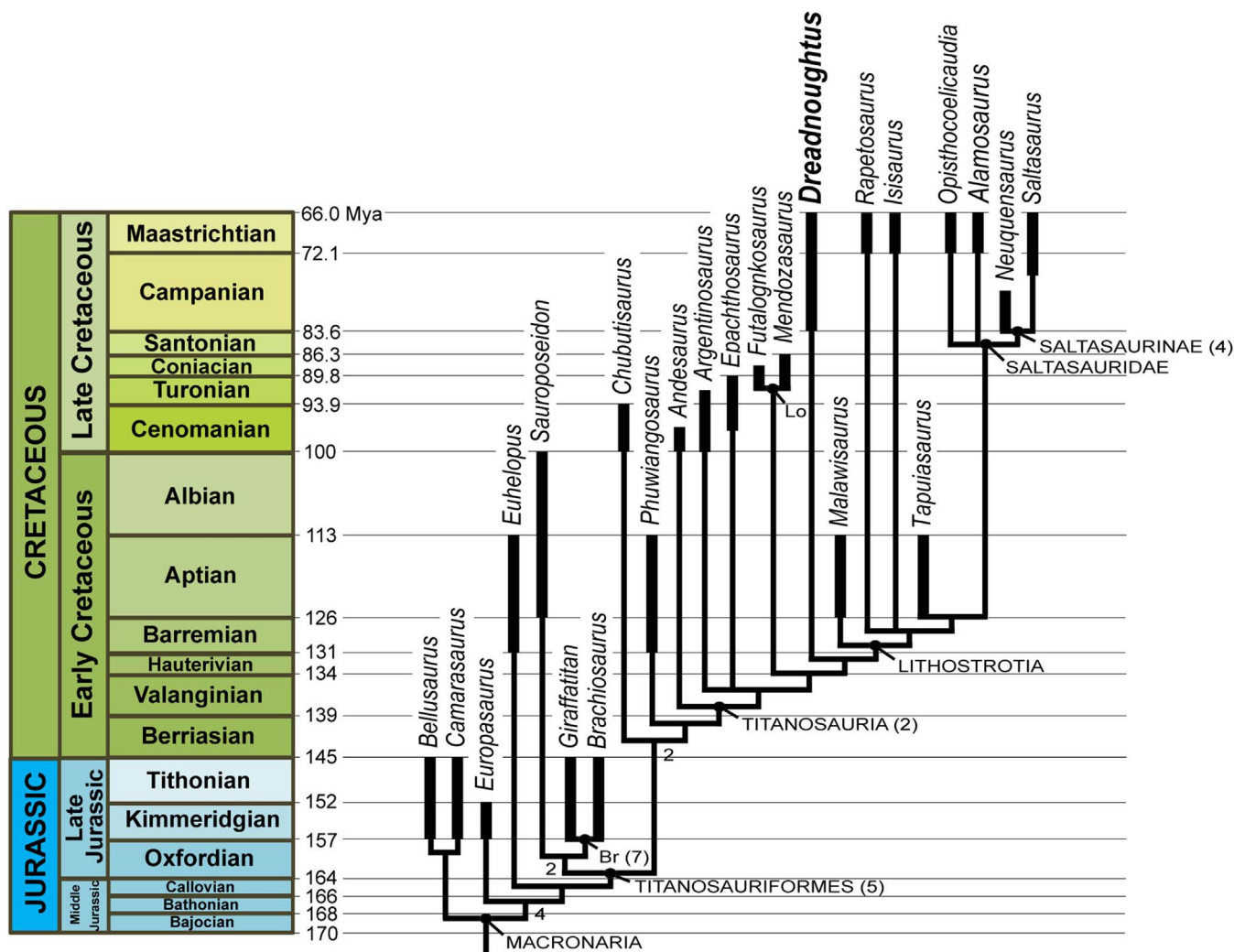
**Figure 3 | Time-calibrated hypothesis of phylogenetic relationships of *Dreadnoughtus schrani* (Consistency Index = 0.42, Retention Index = 0.76, Rescaled Consistency Index = 0.32) with relevant clades labelled.** Geologic timescale after Walker et al.[16]; stratigraphic ranges (indicated by thick black bars) for most taxa follow Wilson[27], D'Emic[20], and Mannion et al.[30]. In instances where these sources disagree on the age of a particular taxon, we follow the most recent source that includes that taxon. Additional age sources are as follows: *Dreadnoughtus*[14,15]; *Epachthosaurus*[70]; *Futalognkosaurus*[17]; *Mendozasaurus*[62]; *Neuquensaurus*[17]. Numbers beside nodes are Bremer decay indices. Abbreviations: Br, Brachiosauridae; Lo, Lognkosauria; Mya, million years ago. See Supplementary Fig. 20 for an unabridged version of this tree that presents the entire topology and also includes bootstrap and jack-knife support values.

Supplementary Figs. 3, 10) is 1.13 m in length (Supplementary Table 1). This vertebra exhibits a tall, laterally compressed neural spine that differs dramatically from the transversely expanded spine of the single known posterior cervical vertebra of *Puertasaurus*. (See Supplementary Information for further osteological information.)

The *Dreadnoughtus* dorsal series is represented by eight partial to nearly complete vertebrae that pertain to the anterior, middle, and posterior parts of the sequence (Fig. 1E–J, Supplementary Figs. 5, 11, 12). All dorsal centra are camellate and strongly opisthocoelous with well-developed lateral pneumatic fossae. The anterior (~4th) dorsal vertebra (Fig. 1E, Supplementary Figs. 5A, 11) is nearly complete but strongly dorsoventrally compressed. The neural arch is anteriorly placed, and short, thin spinoprezygapophyseal laminae merge with the much more robust prespinal lamina just dorsal to the base of the neural spine. Middle dorsal vertebrae (Fig. 1F–G, Supplementary Fig. 5B–C) closely resemble those of *Rapetosaurus*[18] in anterior view, with prominent spinopostzygapophyseal laminae and a correspondingly expanded neural spine apex. Posterior dorsal vertebrae (Fig. 1H–J, Supplementary Figs. 5D–F, 12) have elevated, posterodorsally inclined neural spines, the lateral surfaces of which possess spino-

diapophyseal laminae that are divided into paired rami by a deep coel. Along with the spinopostzygapophyseal laminae, the posterior rami of the spinodiapophyseal laminae terminate dorsally in rugose projections that are oval in posterolateral view (Fig. 1I, Supplementary Fig. 5E). On the transverse process, immediately dorsomedial to the diapophyseal facet, there is a distinct, slightly raised area ornamented by mediolaterally-oriented striations. A comparable condition is reported in the lithostrotian titanosaurs *Epachthosaurus*, *Lirainosaurus*, *Saltasaurus*, *Trigonosaurus*, and other somphospondylans, and has been hypothesized to indicate soft-tissue attachment at this site[19,20]. Dorsal ribs are plank-like, especially distally, and have proximal pneumatocoels (Supplementary Fig. 6A). The six sacral centra are firmly coossified and lack external pneumatic fossae (Fig. 1K, Supplementary Fig. 13). Sacral centra and ribs exhibit camellate internal tissue structure.

The caudal series of *Dreadnoughtus* is nearly completely preserved, lacking only a few of the posterior-most vertebrae (Fig. 1M, Supplementary Figs. 6B–G, 7, 14). The first 21 caudal vertebrae of MPM-PV 1156 are known from a closely associated sequence; caudal vertebrae 5 to 21 and their associated haemal arches were recovered

Table 1 | Selected maximum measurements (cm) of appendicular elements of *Dreadnoughtus schrani* compared to other titanosauriform sauropods, including other gigantic taxa. Non-titanosaurian titanosauriforms (*Brachiosaurus*, *Giraffatitan*, *Ligabuesaurus*, *Ruyangosaurus*) are listed first and arranged alphabetically; remaining taxa are titanosaurs, listed alphabetically. Measurements in bold are the longest known within Titanosauriformes for each element in question. * = estimate; − = element not preserved; NR = measurement not reported. Anatomical abbreviations: C-cl, mid-posterior cervical centrum length; C-cw, mid-posterior cervical centrum width; Fe, femur; Fi, fibula; Hu, humerus; Il, ilium; Ra, radius; Sc, scapula; Ti, tibia; Ul, ulna. Institutional abbreviations see Supplementary Information

| Taxon | Specimen | C-cl | C-cw | Sc | Hu | Ul | Ra | Source |
|---|---|---|---|---|---|---|---|---|
| *Brachiosaurus* | FMNH P 25107 | - | - | - | 204 | - | - | 71 |
| *Giraffatitan* | HMN SII | 87 | 44 | NR | **213** | **130** | **124** | 40 |
| *Ligabuesaurus* | MCF-PVPH-233 | - | 35 | 144 | 149 | - | - | 72 |
| *Ruyangosaurus* | 41HIII-0002 | 18 | **51*** | - | - | - | - | 73 |
| '*Antarctosaurus*' giganteus | MLP 26-316 | - | - | - | - | - | - | 5 |
| *Alamosaurus* | USNM 15560 | - | - | 148 | 136 | 89 | 80 | 65 |
| *Argentinosaurus* | MCF-PVPH-1 | - | - | - | - | - | - | 6 |
| *Argyrosaurus* | MLP 77-V-29-1 | - | - | - | 137 | 97 | 86 | 37 |
| *Diamantinasaurus* | AODF 603 | - | - | 140* | 112 | 73 | - | 42 |
| *Dreadnoughtus* | MPM-PV 1156 | **113** | 42 | **174** | 160 | 101 | 95 | This paper |
| *Elaltitan* | PVL 4628 | - | - | 149 | 130 | 88 | 73 | 37 |
| *Epachthosaurus* | UNPSJB-PV 920 | - | - | NR | 94 | 61 | 55 | 61 |
| *Futalognkosaurus* | MUCPv-323 | NR | 40* | - | - | - | - | 3 |
| *Opisthocoelicaudia* | ZPAL MgD-I/48 | - | - | 118 | 100 | 78 | 64 | 35 |
| *Paralititan* | CGM 81119 | - | - | NR | 169 | - | - | 7 |
| *Rapetosaurus* | FMNH PR 2209 | 26 | 10 | 54 | 52 | 37 | 37 | 18 |

| Taxon | Specimen | Il | Pu | Fe | Ti | Fi | Source |
|---|---|---|---|---|---|---|---|
| *Brachiosaurus* | FMNH P 25107 | 124 | - | 203 | - | - | 71 |
| *Giraffatitan* | HMN SII | - | 121 | NR | NR | 119 | 40 |
| *Ligabuesaurus* | MCF-PVPH-233 | - | - | 166* | 104 | 108 | 72 |
| *Ruyangosaurus* | 41HIII-0002 | - | - | 200* | **127** | - | 73 |
| '*Antarctosaurus*' giganteus | MLP 26-316 | - | **145** | **231** | - | - | 5 |
| *Alamosaurus* | USNM 15560 | - | - | - | - | - | 65 |
| *Argentinosaurus* | MCF-PVPH-1 | - | - | - | - | **155** | 6 |
| *Argyrosaurus* | MLP 77-V-29-1 | - | - | - | - | - | 37 |
| *Diamantinasaurus* | AODF 603 | 87 | 110 | 133 | 80 | 71* | 42 |
| *Dreadnoughtus* | MPM-PV 1156 | **131** | 126 | 191 | 120 | 103 | This paper |
| *Elaltitan* | PVL 4628 | - | 113 | 115* | NR | 65* | 37 |
| *Epachthosaurus* | UNPSJB-PV 920 | 77 | 67 | 110 | 70 | 73 | 61 |
| *Futalognkosaurus* | MUCPv-323 | NR | 137 | - | - | - | 3 |
| *Opisthocoelicaudia* | ZPAL MgD-I/48 | 114 | 112 | 140 | 81 | 83 | 35 |
| *Paralititan* | CGM 81119 | - | - | - | - | - | 7 |
| *Rapetosaurus* | FMNH PR 2209 | NR | 48 | 66 | 50 | 47 | 18 |

in articulation (Fig. 1M, Supplementary Figs. 6B–E, 7, 14). The first caudal centrum (Fig. 1L–M, Supplementary Figs. 7, 14) has a well-developed ventral keel, a character that, among titanosaurs, is otherwise known only in a more posteriorly-positioned anterior caudal vertebra of the possible saltasaurine *Bonatitan*[21]. This *Dreadnoughtus* vertebra is biconvex, as in derived titanosaurs such as *Alamosaurus*, *Baurutitan*, and *Pellegrinisaurus*[22,23], and has elongate, plate-like transverse processes reminiscent of those of *Saltasaurus*[24]. The complete left transverse process curves posteriorly before arcing anterolaterally, and a prominent roughened tubercle adorns its posterodorsal edge. Digital reconstruction (Supplementary Fig. 9) demonstrates that these processes would not have contacted the ilia in life, and as such that this biconvex vertebra is not an unfused seventh sacral vertebra as in the saltasaurine *Neuquensaurus*[23,25]. All remaining caudal vertebrae have strongly procoelous centra that lack pneumatic fossae (Fig. 1M, Supplementary Fig. 6B, D, F, Supplementary Figs. 7, 14). Anterior caudal centra are pierced by small vascular foramina ventral to the transverse processes, as in *Adamantisaurus*[26], *Alamosaurus*[27], *Andesaurus*[28], *Paralititan*[7], *Pellegrinisaurus*[29], and other sauropods[30]. Their neural spines are distinctive in possessing hypertrophied prespinal and postspinal laminae (presumably indicative of robust interspinal ligament attachments) and deep, extensively subdivided pneumatocoels between the spinoprezygapophyseal and spinopostzygapophyseal laminae (occupying the position of the conjoined postzygapophyseal spinodiapophyseal and postzygapophyseal centrodiapophyseal fossae of Wilson et al.[31]). Comparable but less complex coels occur on the first caudal neural spine in *Alamosaurus* and *Opisthocoelicaudia*[27] and in some anterior caudal spines of *Adamantisaurus*[26], *Bonatitan*[21], *Dongyangosaurus*[32], and *Mendozasaurus*[33]. Middle caudal vertebrae have elongate prezygapophyses, as in *Aeolosaurus* spp.[8] and closely related taxa, and neural spines with triangular anterodorsal processes; the latter are especially pronounced on caudal vertebrae 11 to 13, extending well beyond the anterior margins of the centra (Fig. 1M, Supplementary Figs. 7, 14). Among titanosaurs, the anterior haemal arches of *Dreadnoughtus* are unique in possessing paddle-shaped anteroposterior expansions of the distal shaft (Fig. 1M, Supplementary Figs. 7, 14).

The appendicular skeleton of *Dreadnoughtus* is completely represented except for the manus and part of the pes (Fig. 2A, Supplementary Fig. 9). The 1.74 m scapula of MPM-PV 1156 (Fig. 2B, Supplementary Fig. 15) is the longest yet reported for any titanosaur (Table 1). An oblique, textured ridge, probably indicative of muscle attachment, extends anteroventrally–posterodorsally along the med-

ial face of the blade, posterior to the scar for the M. subscapularis. The coracoid (Fig. 2B, Supplementary Fig. 15) is rectangular with a robust infraglenoid lip, as in many macronarians. The sternal plates are mediolaterally wide with rounded anterolateral and posterolateral ends (Fig. 2C, Supplementary Fig. 15). The massive 1.60 m left humerus of MPM-PV 1156 (Fig. 2D, Supplementary Fig. 16) is greater in minimum shaft circumference (785 mm) than that of all other described titanosaurs, and is longer than all other titanosaur humeri except that of *Paralititan* (Table 1). Its proximal articulation is convex in anterior view, lacking the proximolateral expansion characteristic of saltasaurids[34]. The deltopectoral crest is prominent, less medially twisted (after accounting for taphonomic distortion) than in *Mendozasaurus*[33] and *Opisthocoelicaudia*[35], and extends distally to about one-third the length of the humerus. It remains narrow in width and has a prominent lateral bulge along its distolateral edge, a feature shared with *Alamosaurus*, *Jainosaurus*, *Qingxiusaurus*, and *Saltasaurus*[36]. The ulna (Fig. 2D, Supplementary Fig. 16) is stout with a prominent olecranon process, and possesses a deep medial depression that renders its proximomedial process concave in proximal view, a condition that is otherwise known only in *Elaltitan*[37]. The radius (Fig. 2D, Supplementary Fig. 16) is gracile with an autapomorphically large concavity on the posteromedial aspect of its proximal end. As in *Rapetosaurus*[18], there is a distinct scar on the anteromedial surface of the distal end of the bone.

The preacetabular processes of the *Dreadnoughtus* ilia (Fig. 2E, Supplementary Fig. 17) are less laterally directed than in many titanosaurs (e.g., *Isisaurus*[38], *Saltasaurus*[8], *Trigonosaurus*[39]), and are not strongly canted towards the horizontal. A small, rounded tuberosity, seen elsewhere only in the brachiosaurid *Giraffatitan*[40], arises from the ventrolateral edge of the preacetabular process. The robust pubes (Fig. 2E, Supplementary Fig. 17) have proportionately short ischial articulations, as in all titanosaurs more derived than *Andesaurus*[22]. The distal pubic blade is dorsoventrally thick and tapers medially, similar to the condition in *Opisthocoelicaudia*[35] but unlike that of most other titanosaurs. The ischia (Fig. 2E, Supplementary Fig. 17) are short and laminar with a moderately expanded distal blade. As in many sauropods (e.g., rebbachisaurids, most macronarians), a tuberosity for attachment of M. flexor tibialis internus III[30] is located near the posterior margin of the lateral ischial face.

The left femur of MPM-PV 1156 (Fig. 2F, Supplementary Fig. 18) measures 1.91 m (Table 1). The femoral head is not as proximomedially directed as in many other titanosaurs (e.g., *Jainosaurus*, *Rinconsaurus*, *Rocasaurus*). The fourth trochanter is positioned proximal to midshaft and is comparatively better developed than in most lithostrotians (e.g., *Tapuiasaurus*[41]). Unlike the condition in saltasaurids[27], the distal condyles are not bevelled dorsomedially. The tibia (Fig. 2F, Supplementary Fig. 18) possesses a large proximolateral bulge similar to that in *Diamantinasaurus*[42], *Gobititan*[43], and *Uberabatitan*[44]. The fibula (Fig. 2F, Supplementary Fig. 18) is strikingly robust, with a prominent lateral trochanter and a posteriorly curved distal half that renders the bone slightly sigmoid in lateral view. This sigmoid character is shared with *Tastavinsaurus*[45] and *Aeolosaurus* sp.[46], and is also reported in one *Neuquensaurus* fibula[25]. The astragalus (Fig. 2F, Supplementary Fig. 18) is comparable to that of *Camarasaurus*[47] and *Elaltitan*[37], differing from the tall, pyramidal astragali of many other titanosaurs (e.g., *Diamantinasaurus*, *Neuquensaurus*). Pedal ungual I (Fig. 2F, Supplementary Fig. 18) retains a large flexor process at the proximal end of its plantar surface, a character shared only with *Opisthocoelicaudia*[35].

## Discussion

Based on a phylogenetic analysis (Fig. 3, Supplementary Figs. 19, 20; see Supplementary Information for details), we posit *Dreadnoughtus* as a member of Titanosauria, intermediate in phylogenetic position between basal representatives of the clade such as *Andesaurus* and the comparatively derived titanosaurian subclade Lithostrotia. The

enormous forms *Argentinosaurus* and *Futalognkosaurus* are also recovered as non-lithostrotian titanosaurs. Future fossil discoveries and phylogenetic analyses of Titanosauria are needed to clarify the relationships of these taxa.

*Dreadnoughtus* is among the largest known titanosaurs. Conclusively establishing the size of the taxon relative to those of most other gigantic representatives of the clade (e.g., '*Antarctosaurus*' *giganteus*, *Argentinosaurus*, *Paralititan*, *Puertasaurus*) is presently not possible due to the fragmentary nature of the latter forms. Nevertheless, elements of MPM-PV 1156 are comparable in linear dimensions to their counterparts in other huge titanosaurs (Table 1). Furthermore, a recently-refined equation for calculating body mass in quadrupedal tetrapods based on humeral and femoral circumference[13,48,49] yields an estimate of 59.3 metric tons for this individual (Supplementary Information)—approaching twice the value previously estimated for the large brachiosaurid *Giraffatitan* (34.0 metric tons), and approximately four times that estimated for the diplodocid *Diplodocus* (14.8 metric tons)—using the same method[13]. Reconstruction of the *Dreadnoughtus* skeleton (Fig. 2A, Supplementary Fig. 9) with the mostly missing cervical series restored after that of *Futalognkosaurus*[3] produces an approximate body length of 26 m (Supplementary Information).

Remarkably, multiple lines of evidence indicate that, despite its enormous size, MPM-PV 1156 was not osteologically mature at death. The scapula remains unfused to the coracoid (Fig. 2B, Supplementary Fig. 15), and the posteromedial margin of the coracoid foramen abuts the scapula; both of these morphologies have been cited as indicators of osteological immaturity in sauropods[50,51]. Moreover, although histological analysis of the humerus indicates that its cortical bone has undergone extensive secondary remodelling, the element retains a thick layer of vascularized fibrolamellar bone between the remodelled inner cortex and the periphery of the periosteal surface (see Supplementary Information). It also lacks lines of arrested growth or an external fundamental system[52] (Fig. 2G), which may indicate osteological immaturity[53] (although Company[54] proposed this as a synapomorphy of Titanosauria rather than an indicator of ontogenetic stage). A similar pattern is observed in the dorsal ribs, which are extensively remodelled but retain primary fibrolamellar bone tissue towards the periosteal surface. Recent analyses[55,56] have suggested that titanosaurs may have developed extensively remodelled tissues after reaching sexual maturity but prior to attaining their maximum size. Thus, the presence of unremodelled fibrolamellar bone in the outer cortex of the MPM-PV 1156 humerus suggests that this massive *Dreadnoughtus* individual was still growing at the time of its death.

*Dreadnoughtus schrani* is the most completely known giant titanosaur. Completeness metrics (Supplementary Table 2) indicate that the new Patagonian taxon has preserved approximately 45.3% of the bones expected in a complete titanosaurian skeleton, and (depending on how bones are counted) up to 70.4% of the postcranial elements. By comparison, these same values are 15.2% and 26.8% for *Futalognkosaurus*, 7.8% and 12.7% for *Paralititan*, 5.1% and 9.2% for *Argentinosaurus*, 2.3% and 3.5% for '*A.*' *giganteus*, and 1.6% and 2.8% for *Puertasaurus*. *Dreadnoughtus* is also among the most anatomically informative titanosaurs of any body size. The new taxon can be definitively evaluated for 57.5% of the morphological characters included in the data matrix recently published by Carballido and Sander[57]. Furthermore, *Dreadnoughtus* is dramatically more informative than the other gigantic titanosaurs included in our phylogenetic analysis, *Futalognkosaurus* and *Argentinosaurus*, which were scored for only 18.5% and 12.6% of the available characters, respectively (Supplementary Table 3). *Dreadnoughtus* therefore offers important new osteological data for future investigations of the anatomy, biomechanics, and evolution of the most massive land animals that have ever existed.

## Methods

**Phylogenetic analysis.** We conducted a phylogenetic analysis to assess the affinities of *Dreadnoughtus schrani* within Titanosauria. We added the new Patagonian taxon to a recently-published matrix of 70 sauropod taxa and 341 morphological characters[57] that contains a broad diversity of titanosaurian and non-titanosaurian titanosauriform genera, including the gigantic form *Argentinosaurus*. We also added *Futalognkosaurus* to the matrix (the scoring of which was based on the description by Calvo et al.[3], and is presented in the Supplementary Information) to more thoroughly investigate relationships between *Dreadnoughtus* and other giant titanosaurians. We analysed the augmented matrix using the methods outlined in Carballido and Sander[57]. Specifically, the multistate characters 12, 58, 95, 96, 102, 106, 108, 115, 116, 119, 120, 154, 164, 213, 216, 232, 233, 234, 235, 256, 267, 298, 299, and 301 were treated as ordered, and the matrix was subjected to a heuristic search in TNT (Tree Analysis Using New Technology) v. 1.1[58] (1,000 replicates of Wagner trees, random addition sequence, tree bisection reconnection branch swapping algorithm, ten trees saved per replicate). The initial trial yielded ten most parsimonious trees of 1,028 steps, the strict consensus of which recovered numerous taxa traditionally considered to be basal titanosauriforms as members of Titanosauria, and provided little resolution within Lithostrotia (Supplementary Fig. 19).

Based on numerous aspects of its morphology, the titanosaurian affinities of *Dreadnoughtus* are not in doubt; the aim of our analysis was therefore to ascertain the position of the new taxon within Titanosauria. Consequently, in an attempt to better resolve titanosaurian interrelationships, we inspected the matrix using the program TAXEQ3 (Safe Taxonomic Reduction Based on Taxonomic Equivalence[59]). The TAXEQ3 examination did not find taxa that could be safely deleted via safe taxonomic reduction, but did underscore the high proportion of missing data in the matrix. Although *Dreadnoughtus* lacked only 42.5% of the available character information, 47 (of 72 total) taxa lacked more than 50% of these data. We reanalysed the matrix after pruning 18 of the 20 fragmentary and unstable taxa pruned by Carballido and Sander[57], retaining *Andesaurus* (to define the node-based clade Titanosauria) and *Argentinosaurus* (another giant titanosaurian). This second iteration recovered 30 most parsimonious trees of 943 steps. The strict consensus of these trees (Fig. 3, Supplementary Fig. 20; Consistency Index = 0.42, Retention Index = 0.76, Rescaled Consistency Index = 0.32) yields considerably greater resolution within Titanosauria, and posits *Dreadnoughtus* as a non-lithostrotian titanosaur more derived than *Andesaurus*, *Epachthosaurus*, *Argentinosaurus*, and lognkosaurians (i.e., *Futalognkosaurus*, *Mendozasaurus*) but less derived than all other Campanian–Maastrichtian titanosaurs.

**Phylogenetic character states of *Dreadnoughtus schrani*.** Scores for *Dreadnoughtus schrani* for the 341 morphological characters employed by Carballido and Sander[57] are as follows:

?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? 1231?202?? 1110-30102 ??0?110001 00-?10102(01) 1121-11111
1200101011 (01)111101111 000211??11 31????013 ?030000001 00000-1003
10(12)000100? ??0-111011 ?0?0011001 1100011101 0110120111 1001101???
???????11 1101101000 0110110011 2111?001?1 1111010110 0??11101?? ????1?11?? ?

**Body dimensions.** Among many other elements, the *Dreadnoughtus schrani* holotype (MPM-PV 1156) includes the complete left humerus and femur. Because the minimum midshaft circumferences of these bones have been found to scale with body mass in quadrupedal terrestrial tetrapods[13,48,49], the preservation of these bones in MPM-PV 1156 permits an estimate of the mass of this specimen. The midshaft circumference of the humerus is 785 mm and that of the femur is 910 mm. Using the scaling equation recently proposed by Campione and Evans[49] ($\log BM = 2.749 * \log C_{H+F} - 1.104$, where BM is body mass and $C_{H+F}$ is combined humeral and femoral circumference), these values yield an estimated body mass of 59,291 kg (~59.3 metric tons, or 65.4 short tons) for this *Dreadnoughtus* individual. By comparison, the estimated masses of other medium- and large-bodied titanosaur specimens for which humeral and femoral shaft circumferences have been published are as follows: *Opisthocoelicaudia* ZPAL MgD-I/48[35], 25,418 kg; *Alamosaurus* TMM 41541-1[60], 35,164 kg; and *Elaltitan* PVL 4628[8], 42,798 kg. Additionally, Benson et al.[13] provide an estimate of 38,139 kg for *Futalognkosaurus*[3], based on an undescribed humerus and femur. Large individuals of the diplodocid *Diplodocus* (USNM 10865) and the brachiosaurid *Giraffatitan* (HMN SII) have been estimated at 14,813 and 34,003 kg, respectively, using the same equation[13,49]. It therefore appears that the *Dreadnoughtus schrani* holotype was considerably more massive than most other titanosaurian specimens, and indeed, most other sauropods.

Due primarily to uncertainty in the morphology of the cervical series, it is currently not possible to definitively establish the total body length of *Dreadnoughtus*. Nevertheless, the elongate nature of the two preserved cervical vertebrae implies that the taxon had a long neck, more similar to those of titanosaurs such as *Futalognkosaurus*[3] and *Rapetosaurus*[18] than to comparatively short-necked forms such as *Isisaurus*[38] and *Mendozasaurus*[62]. The centrum of the complete posterior cervical vertebra of MPM-PV 1156 is 113 cm in anteroposterior length. Assuming that the neck proportions of *Dreadnoughtus* were similar to those of *Futalognkosaurus*[3,63], and that this complete *Dreadnoughtus* cervical vertebra corresponds to the ninth vertebra in the series, this yields a neck length of approximately 11.3 m for MPM-PV 1156.

The holotype of *Tapuiasaurus* (MZSP-PV 807) is the only adult titanosaurian specimen known to preserve a complete skull associated with appendicular ele-

ments[41]. Using the radius length of MPM-PV 1156 (95 cm), and scaling up from the relative lengths of the skull and radius in *Tapuiasaurus*, we estimate the length of the mostly unknown skull of this *Dreadnoughtus* specimen at 88 cm. Thus, the total combined length of the skull and neck of MPM-PV 1156 is estimated at roughly 12.2 m.

The remainder of the axial skeleton is well-represented in *Dreadnoughtus*, permitting more precise estimates of its length. The majority of titanosaurs for which the dorsal series is completely known (e.g., *Futalognkosaurus*, *Rapetosaurus*, *Trigonosaurus*, *Overosaurus*) possess ten vertebrae in this region[3,18,39,64]; with 11 dorsal vertebrae, *Opisthocoelicaudia* is the only known exception in this regard[35]. We therefore assume that ten dorsal vertebrae were present in *Dreadnoughtus*. The only described titanosaurian specimen with a completely preserved caudal series is the holotype of *Opisthocoelicaudia* (ZPAL MgD-I/48); this includes 34 vertebrae[35]. Nevertheless, evidence indicates that the tail may have been longer in some other titanosaurian taxa. For example, exceptional specimens of *Epachthosaurus* (UNPSJB-PV 920) and *Alamosaurus* (USNM 15560) preserve the first 30 and 29 caudal vertebrae, respectively, all of which are strongly procoelous[61,65]. In both of these caudal sequences, the posterior-most preserved vertebra is clearly not the terminal caudal vertebra; moreover, Wilson et al.[66] demonstrated that the posterior-most ~seven to eight caudal vertebrae of at least some titanosaurs were biconvex. Furthermore, an as-yet undescribed titanosaurian skeleton from northern Patagonia is reputed to include approximately 65 caudal vertebrae[67]. Taking all of the above into account, we provisionally estimate that the complete caudal series of *Dreadnoughtus* would have included approximately 40 vertebrae. Digital reconstruction of the dorsal, sacral, and caudal vertebral sequences that incorporates these assumptions (Supplementary Fig. 9) yields a combined length of 13.8 m for these parts of the axial skeleton. When added to the skull and neck length estimated above, this yields an approximate total body length of 26 m for MPM-PV 1156.

**Calculating completeness vs. other giant titanosaurs.** We quantified the skeletal completeness of *Dreadnoughtus* and other enormous titanosaurs using the following method. (We chose to devise an un-weighted metric that counts the presence of each element equally. See Mannion and Upchurch[68] for an alternative, weighted method.) First, we used material of the most completely known titanosaurs of any size (e.g., *Epachthosaurus*, *Nemegtosaurus*, *Opisthocoelicaudia*, *Overosaurus*, *Rapetosaurus*, *Saltasaurus*, *Tapuiasaurus*, *Trigonosaurus*) to estimate the total number of bones in a representative titanosaurian skeleton at 256 (Supplementary Table 2). We then counted the total number of non-duplicated elements preserved between both known *Dreadnoughtus* specimens (MPM-PV 1156 and MPM-PV 3546) at 116, and used the literature to tally the elements preserved for five other giant titanosaurs: '*Antarctosaurus*' *giganteus* (six bones)[8], *Argentinosaurus* (13 bones)[6], *Futalognkosaurus* (39 bones)[3], *Paralititan* (20 bones)[7,69], and *Puertasaurus* (four bones)[9]. These numbers were then divided by 256 to yield completeness percentages for each taxon (Supplementary Table 2).

Because the six titanosaurs under consideration are represented exclusively ('*A.*' *giganteus*, *Argentinosaurus*, *Futalognkosaurus*, *Paralititan*, *Puertasaurus*) or almost exclusively (*Dreadnoughtus*) by postcranial bones, we then explored the postcranial completeness of each taxon. We calculated the total number of postcranial elements expected in a representative titanosaur and then counted all such bones for each taxon in question. We divided the elements preserved by the elements expected to produce percentages of postcranial completeness for each titanosaur (Supplementary Table 2).

Finally, because, from a morphological standpoint, the preservation of one bilaterally symmetrical element is effectively as informative as is the preservation of both, we calculated what we term the 'mirrored postcranial completeness' of each of these giant titanosaurs (Supplementary Table 2). When determining mirrored postcranial completeness, bilateral elements are treated as equivalents; in other words, if at least one of a pair of bilaterally symmetrical bones is preserved in a given taxon, that element is counted as fully preserved in that taxon. (As an example, in mirrored postcranial completeness, the humerus of *Dreadnoughtus* is treated as completely represented, even though only the left humerus of this titanosaur is actually preserved.)

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## Author contributions

K.J.L. directed the project; K.J.L., M.C.L., L.M.I., J.C.P., V.M.E., A.E.M., C.L.C. and J.P.S. collected specimens in the field; K.J.L., M.C.L. and J.C.P. supervised fossil preparation, and preparators included M.C.L., L.M.I., J.C.P., E.R.S., P.V.U., K.K.V., Z.M.B., A.M.C., E.K.F. and V.M.E.; fossils were described by K.J.L., M.C.L., L.M.I., E.R.S., P.V.U., K.K.V., Z.M.B. and J.D.H.; 3D scanning was accomplished by E.R.S., P.V.U., K.K.V., Z.M.B., A.M.C. and E.K.F.; histology was conducted by E.R.S. and Z.M.B.; mass estimates and completeness metrics were calculated by M.C.L. and P.V.U.; 3D PDFs were generated by K.K.V. and E.K.F.; phylogenetic analysis was done by M.C.L., P.V.U. and K.K.V.; permitting was accomplished by K.J.L., R.D.M. and F.E.N.; R.D.M. and F.E.N. gave logistical and analytical advice; K.J.L., M.C.L., E.R.S., P.V.U., K.K.V. and Z.M.B. wrote the paper.

## Additional information

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