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

Kenneth J. Lacovara1, Matthew C. Lamanna2, Lucio M. Ibiricu3, Jason C. Poole4, Elena R. Schroeter1, Paul V. Ullmann1, Kristyn K. Voegele1, Zachary M. Boles1, Aja M. Carter1, Emma K. Fowler1, Victoria M. Egerton5, Alison E. Moyer6, Christopher L. Coughenour7, Jason P. Schein8, Jerald D. Harris9, Rubén D. Martínez10 & Fernando E. Novas11

1Department of Biodiversity, Earth and Environmental Science, Drexel University, 3141 Chestnut Street, Philadelphia, PA 19104, USA, 2Section of Vertebrate Paleontology, Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, PA 15213, USA, 3Laboratorio de Paleontología, Centro Nacional Patagónico (CENPAT–CONICET), Boulevard Almirante Brown 2915, (9120) Puerto Madryn, Chubut, Argentina, 4Academy of Natural Sciences of Drexel University, 1900 Benjamin Franklin Parkway, Philadelphia, PA 19103, USA, 5Faculty of Life Sciences, The University of Manchester, Dover Street, Manchester, M13 9PL, UK, 6Department of Marine, Earth, and Atmospheric Sciences, North Carolina State University, 2800 Faucette Drive, Raleigh, NC 27695, USA, 7University of Pittsburgh at Johnstown, 450 Schoolhouse Road, Johnstown, PA 15904, USA, 8New Jersey State Museum, 205 West State Street, Trenton, NJ 08608, USA, 9Dixie State College, 225 South 700 East, St. George, UT 84770, USA, 10Laboratorio de Paleovertebrados, Universidad Nacional de la Patagonia San Juan Bosco, (9000) Comodoro Rivadavia, Chubut, Argentina, 11Museo Argentino de Ciencias Naturales, Avenida Angel Gallardo 470, (1405) Buenos Aires, Argentina.

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 titanosaurians 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 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.
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 presumably 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 partially articulated partial skeleton that comprises a maxilla fragment, a tooth, a posterior cervical vertebra, cervical ribs, multiple dorsal
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 pneumatocoele between spinoprezygapophyseal and spinopostzygapophyseal laminae*; (3) anterior caudal neural spines with hypertrophied pre- 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–anteroven-trally oriented ridge on medial surface of anterior end of scapular blade; (7) postero-medial 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 vertebra of the *Dreadnoughtus* holotype (MPM-PV 1156) (Fig. 1A–D,

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**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 (ilia 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; acr, acromial process; acs, 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; mtl, metatarsal I; mtII, metatarsal II; of, obturator foramen; pop, postacetabular process; prp, preacetabular process; pu, pedal ungual; pub, pubis; 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.)
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 Figs. 5B–C) closely resemble those of *Rapetosaurus* 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 spinopodiaphyseal laminae that are divided into paired rami by a deep coel. Along with the spinopostzygapophyseal laminae, the posterior rami of the spinopodiaphyseal 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 pneumatocoeles (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...
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 other-...
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. The deltopectoral crest is prominent, less mediolaterally twisted (after accounting for taphonomic distortion) than in *Mendozaerasaurus* 23 and *Opisthocoelicaudia* 26, 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*, *Qingxiansaurus*, and *Saltasaurus* 26. The ulna (Fig. 2A, 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 *Paralititan* (Table 1). The radius (Fig. 2D, Supplementary Fig. 16) is gracile with an autopomorphically large concavity on the postero medial 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 titanosaur species (e.g., *Lisiansaurus* 38, *Saltasaurus*, *Trigonosaurus*) 39, and are not strongly cantled towards the horizontal. A small, rounded tuberosity, seen elsewhere only in the brachiosaurid *Giraffatitan* 38, 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 titanosaur species more derived than *Andesaurus* 27. The ischial tubisch is dorsoventrally thick and tapers medially, similar to the condition in *Opisthocoelicaudia* 30 but unlike that of most other titanosaur species. The ischial tubisch is dorsoventrally thick and tapers medially, similar to the condition in *Opisthocoelicaudia* 30, unlike that in *saltasaurids* 37, the distal condyles are not bevelled dorsomedially. 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 described titanosaurs, and is longer than all other titanosaur species (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 39. Reconstruction of the *Dreadnoughtus* skeleton (Fig. 2A, Supplementary Fig. 9) with the mostly missing cervical series restored after that of *Futalognkosaurus* 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 postero medial margin of the coracoid foramen abuts the scapula; both of these morphologies have been cited as indicators of osteological immaturity in sauropods 40, 41. 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 periiphery of the periosseous surface (see Supplementary Information). It also lacks lines of arrested growth or an external fundamental system 42 (Fig. 2G), which may indicate osteological immaturity 43 (although Company 44 proposed this as a synapomorphy of *Titanosaurus* 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 45, 46 have suggested that titanosaur species may have developed extensively remodelled tissues after reaching sexual maturity but prior to attaining their maximum size. Thus, the presence of un remodelled 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 titanosaur species 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 titanosaur species 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.

**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 titanosaur species. Future fossil discoveries and phylogenetic analyses of Titanosauria are needed to clarify the relationships of these taxa.

*Dreadnoughtus* is among the largest known titanosaur species. 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 33, 36, 49 yields an estimate of 39.3 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 39. Reconstruction of the *Dreadnoughtus* skeleton (Fig. 2A, Supplementary Fig. 9) with the mostly missing cervical series restored after that of *Futalognkosaurus* produces an approximate body length of 26 m (Supplementary Information).
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 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. 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. Specifically, the multistate characters 12, 58, 95, 96, 102, 106, 108, 115, 116, 119, 120, 154, 164, 213, 216, 232, 233, 234, 253, 256, 267, 298, 299, 301 and 302 were treated as ordered, and the matrix was subjected to a heuristic search in TNT (Tree Analysis Using New Technology) v. 1.1.1 (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 Titanosauria as members, 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 TAXEO3 (Safe Taxonomic Reduction Based on Taxonomic Equivalence). The TAXEO3 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 (67 of 72 total taxa lacked more than 30% of these data), we analysed the matrix after pruning 18 of the 20 fragmentary and unstable taxa pruned by Carballido and Sander, retaining *Andesaurus* (to define the node-based clad 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*, *Mendozatosaurus*) but less derived than all other Campanian–Maestrichtian titanosaurians.

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

| Character State | Score |
|-----------------|-------|
| 0.76, Retention Index | 0.42, Retention Index |
| 0.76, Rescaled Consistency Index | 0.32 |

Calculating completeness vs. other giant titanosaurians. We quantified the skeletal completeness of *Dreadnoughtus* and other enormous titanosaurians using the following method. We chose to devise an un-weighted metric that counts the presence of each element equally. See Mannion and Upchurch for an alternative, weighted method.

First, we used material of the most completely known titanosaurids of any size (e.g., *Epachthosaurus*, *Nemegtosaurus*, *Opisthocoelicaudia*, *Overosaurus*, *Rapetosaurus*, *Saltasaurus*, *Tupaiasaurus*, *Trigonosaurus*) to estimate the total number of bones in a representative titanosaurian skeleton at 256 (Supplementary Table 2). We then computed the total number of non-duplicated elements preserved between the two 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 titanosaurans: *Antarctosaurus giganteus* (six bones); *Argentinosaurus* (13 bones); *Futalognkosaurus* (39 bones); *Paralititan* (20 bones); and *Puertasaurus* (four bones). These numbers were then divided by 256 to yield completeness percentages for each taxon (Supplementary Table 2). Because the six titanosaurans 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 bilateral element is as effectively as informative as the preservation of both, we calculated what we term the ‘mirrored postcranial completeness’ of each of these giant titanosaurid skeletons (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, 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., A.M.C. and E.K.F.; phylogenetic analysis was done 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.; etymology was accomplished by M.C.L., P.V.U., K.K.V.; collecting 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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