An early trend towards gigantism in Triassic sauropodomorph dinosaurs

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Dinosaurs dominated the terrestrial ecosystems for more than 140 Myr during the Mesozoic era, and among them were sauropodomorphs, the largest land animals recorded in the history of life. Early sauropodomorphs were small bipeds, and it was long believed that acquisition of giant body size in this clade (over 10 tonnes) occurred during the Jurassic and was linked to numerous skeletal modifications present in Eusauropoda. Although the origin of gigantism in sauropodomorphs was a pivotal stage in the history of dinosaurs, an incomplete fossil record obscures details of this crucial evolutionary change. Here, we describe a new sauropodomorph from the Late Triassic of Argentina nested within a clade of other non-eusauropods from southwest Pangaea. Members of this clade attained large body size while maintaining a plesiomorphic cyclical growth pattern, displaying many features of the body plan of basal sauropodomorphs and lacking most anatomical traits previously regarded as adaptations to gigantism. This novel strategy highlights a highly accelerated growth rate, an improved avian-style respiratory system, and modifications of the vertebral epaxial musculature and hindlimbs as critical to the evolution of gigantism. This reveals that the first pulse towards gigantism in dinosaurs occurred over 30 Myr before the appearance of the first eusauropods.

The Late Triassic period (~237–201 million years ago (Ma)) was a crucial moment in the evolutionary history of terrestrial vertebrates, during which numerous extinctions, diversifications and faunal radiations changed the ecosystem dynamics throughout the world1–4. Among the new lineages that arose at that moment, dinosaurs had a central role, evolving into numerous forms that occupied different niches in terrestrial ecosystems. Sauropodomorpha was the first successful group of herbivorous dinosaurs, dominating most terrestrial ecosystems for more than 140 Myr, from the Late Triassic to Late Cretaceous5–11. The sauropodomorph radiation in the Late Triassic is evident by the appearance of many small, gracile and bipedal taxa recorded world-wide (a paraphyletic assemblage formerly known as ‘prosauropods’). Sauropods evolved from these smaller forms and became the largest land animals that ever lived on Earth12–17.

The evolution from small bipedal to giant quadrupedal sauropodomorphs involved numerous anatomical changes, such as decreased skull size, elongation of the neck and forelimbs, highly pneumatic vertebrae, columnar limbs, tubular metacarpi, reduction of the phalanges and acyclical bone growth12–15,18–20. The simultaneous presence of all these features characterizes the body plan of Eusauropoda (true sauropods)—the clade that evolved into giant forms reaching up to 70 tonnes in the late Mesozoic16,17,21,22. Here, we present a new non-eusauropod sauropodomorph and three new specimens of Lessemsauridae, all from the Late Triassic of Argentina, which show the presence of a novel growth strategy that allowed them to attain large body size without having the anatomical traits previously regarded as adaptations to gigantism in eusauropods.

Results
Systematic palaeontology.

Dinosauria Owen, 1842
Saurischia Seeley, 1888
Sauropodomorpha von Huene, 1932
Lessemsauridae clade nov.

Etymology. Related to L. sauropoides Bonaparte, 1999.

Definition. The clade Lessemsauridae is defined here as L. sauropoides Bonaparte, 1999 and Antetonitrus ingenipes Yates and Kitching, 2003, and all the descendants from their most common ancestor.

Diagnosis. Lessemsauridae differs from all other Sauropodomorpha dinosaurs in possessing the following unique character state combination (asterisks indicate apomorphies of the clade): robust scapulae with dorsal and ventral ends equally expanded*; bone growth characterized by the presence of thick zones of highly vascularized fibrolamellar bone, within a cyclical growth pattern*; slit-shaped neural canal of posterior dorsal vertebrae; anterior dorsal neural spines transversely expanded towards the dorsal end; and a minimum transverse shaft width of the first metacarpal greater than twice the minimum transverse shaft of the second metacarpal.

Ingentia prima gen. et sp. nov.

Etymology. ‘Ingentia’, huge (fem., Latin); ‘prima’, first (fem. Latin), referring to the large body size acquired during the early evolution of Dinosauria.

Holotype. Paleovertebrado Instituto y Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan, Argentina (PVSJ) 1086. Six articulated posterior cervical vertebrae (C5–C10), glenoid region of right scapula and right forelimb lacking all phalanges (except phalanx IV.1 and V.1–2; Fig. 1 and Supplementary Table 1).

Locality and horizon. Southern outcrops of the Quebrada del Barro Formation, Marayes–El Carrizal Basin, northwestern Argentina, late Norian–Rhaetian age17 (Supplementary Fig. 1). The type horizon is located 160 m below the top of the formation (Supplementary Information).
Fig. 1 | Skeletal anatomy of *Ingentia prima* gen. et sp. nov. from the Quebrada del Barro Formation, northwestern Argentina. a-k. Holotype (PVSJ 1086). I-s. Referred material (PVSJ 1087). a-d. Mid-posterior cervical vertebrae, C5–C10 articulated series (a), close up of the pneumatic fossa with internal subfossae on the centrodiaaphyseal fossa (cdf)26 of C8 (b) and C9 (c), and a complex of subfossae on the prcdf26 of C10 (d). e. Right partial scapula. f-i. Right forelimb: humerus (f), and the radius and ulna in proximal (g) and anterior (h) view, and distal articulation (i). j. Right manus in plantar view. k. Metacarpal I in proximal (k) and dorsal (l) view. m.n. Radius and ulnae with respective proximal ulna: right radius-ulna (m) and left radius-ulna (n) in posterior view. o. Left proximal end of fibula. p-r. Right partial pes: distal tarsal III–IV in proximal view (p), metatarsal I and II in dorsal view (q) and isolated phalanges (r). s. Four anterior caudal vertebrae and a distal one (bottom left). cen, centrum; dp, diapophysis; dt, distal tubercles of radius-ulna; f-sf, fossa-subfossa complex; ft, fibular tubercle; nc, neural canal; ol, olecranon; pm, posteromedial margin of the ulna; prz, prezygapophysis; rf, radial fossa; rib, rib. Scale bars: 10 cm in a and i–s; 2 cm in b–d; 20 cm in e–h; 120 cm for the skeleton. Red, holotype; yellow, referred specimen; orange, holotype and referred specimen.

Diagnosis. Mid-cervical neural arches almost twice as high as their respective centrum; vertebrae C6–C10 with hyposphenes as tall as the neural canal height; pneumatic structures on posterior cervical neural arches, including deep fossae on the centrodiaaphyseal fossa (cdf), with internal subfossae in C8–C9, and a complex of subfossae in the prezygapophysial centrodiaaphyseal fossa (prcdf) in C10; expanded proximal end of the ulna with a posteromedial margin 1.5 times larger than the radial fossa margin* (*autapomorphies; Fig. 1).

Osteological and histological description. The cervical vertebrae are tall, with the tallest neural arch twice as high as its posterior centrum articular surface. The postzygapophyses are developed with respect to prezygapophyses, as in other sauropods16,23. From vertebra C6, the hyposphenes are as tall as the height of the neural canal (Fig. 1), similar to *Lessemsaurus*, *Aardonyx* and *Merokeitos* (Supplementary Fig. 4). The posterior cervical vertebrae have a unique combination of pneumatic structures (Fig. 1; see Supplementary Information): in vertebrae C8–C9, the cdf26 is invaded by a deep fossa, with two shallow concavities inside it (Fig. 1b,c); and C10 has a complex of two deep subfossae within the prcdf26. Deep fossae within the cdf and prcdf are also present on the posteriormost cervical vertebrae of *Lessemsaurus* (Paleovertebrado Instituto Miguel Lillo, Tucumán, Argentina (PVL) 4822–1), although the prcdf seems to lack internal subfossae (Supplementary Fig. 4). Except for a few specimens of *Plateosaurus* that have incipient pneumatic fossae within fossa on cervico-dorsal neural arches13, the combination of well-developed pneumatic structures of the cervical vertebrae of *Ingentia* is unique among Sauropodomorpha (see Supplementary Information). The humerus has a marked distal flexor fossa, as in *Lessemsaurus* and non-sauropod sauropodomorphs. The deltopectoral crest extends 40% of the total length of the humerus, as in Sauropodiformes. The posteromedial margin of the proximal end of the ulna is more than 1.5 times longer than the anterior (that is, radial fossa) margin, differing from all non-eusaupod sauropodomorphs (for example, *Lessemsaurus*, *Antetonitrus* and *Massaurus*) in which the anterior margin is equal or larger than the posteromedial margin. The olecranon is poorly developed, as in *Lessemsaurus*, *Antetonitrus* and other sauropods. The metacarpals are proximodistally short, with a notably robust metacarpal I that is wider than it is long (Supplementary Table 1), as in other sauropodiforms such as *Aardonyx*, *Seifananosaurus*, *Lessemsaurus* and *Antetonitrus*, but different from the enlarged first metacarpal of other sauropodomorphs (for example, *Plateosaurus*, *Massaurus* and Neosauropoda).

The humeral histology of *Ingentia* preserves well-defined growth lines throughout the cortical bone that reveal a cyclical growth pattern as in non-sauropod sauropodomorphs18. However, there are remarkably thick zones of well-vascularized fibrolamellar bone indicative of high rates of bone tissue formation in the active phases of growth, as in sauropods (Fig. 2 and Supplementary Fig. 6). *Lessemsaurus sauropoides* Bonaparte 1999, Pol and Powell 2007

New referred material. Centro Regional de Investigaciones Científicas y Transferencia Tecnológica de La Rioja, La Rioja, Argentina (CRILAR) PV-303: both partial scapulae lacking distal ends; CRILAR PV-302: left ilium, articulated ischia; PVL 6580: distal third of right femur (Supplementary Fig. 2 and Supplementary Information).

Locality and horizon. Upper levels of the Los Colorados Formation (mid-Norian19), Ischigualasto–Villa Unión Basin, northwestern Argentina (see Supplementary Information).

Osteological and histological description. The scapulae have markedly expanded dorsal blades with strongly concave ante-
rior and posterior borders—apomorphies of Lessem saurus and Antetonitrus[28–31] (see Supplementary Information). Overall, the morphology of the ilium resembles other non-eusauropod sauropodomorphs, but bears two autapomorphies of Lessem saurus (medial wall of the pubic peduncle extending to the acetabulum and extended brevis crest[30]). The femur shares general features present in the type material and differs from other sauropodomorphs from the same formation mainly in the shaft and tubifibular condyle morphology (Supplementary Fig. 2; see also Supplementary Information).

Histological samples of the femora of Lessem saurus exhibit well-defined growth lines throughout the cortical bone and notably thick zones (>10 mm) of highly vascularized reticular fibrolamellar bone tissue between the growth lines (Supplementary Fig. 7), indicating a highly accelerated growth rate (see Supplementary Information). The abundance of plexiform and reticular cortical bone tissue in Lessem saurus (Supplementary Figs. 7 and 8) differs from the laminar vascularization typical of eusauropods and their closest relatives, such as Isanosaurus[32].

Despite sampling different appendicular elements for Lessem saurus (femur) and Ingentia (humerus), both have thick zones of highly vascularized fibrolamellar bone within a cyclical growth pattern, suggesting a common growth strategy that is different from that reported for Isanosaurus and eusauropod dinosaurs[33]. Previous studies have reported that the highest known values of zone thickness among eusauropods reached 4,343 μm[29], which, when used as a proxy for growth rates (that is, by dividing the thickness of these annual growth cycles by 365 d), yielded maximum values below 12 μm d−1. These zone thicknesses in the sampled femora of Lessem saurus vary between 7,200 and 13,600 μm, implying growth rates of 20–37 μm per day (Fig. 2). This unusual high growth rate detected in a lessem saurid specimen (PVL 3669), which is twice or three times faster than in other sauropods, could explain the size of the other larger specimens here referred to as Lessem saurus (that is, CRILAR-PV 302-303; see Supplementary Information). Previous body mass estimates for Lessem saurus based on the type material were ~2 tonnes[16,17], but the unfused neural arches of cervical vertebrae of the holotype[16] and the absence of the outer circumferential layer or reduction in zone thickness in the referred femur (PVL 6580) suggest that these specimens of Lessem saurus were not fully skeletally mature at the time of death. Two of the new specimens of Lessem saurus are larger than the holotype (for example, scapular proximodistal length: 80 cm; ilium anteroposterior length: 75 cm) and similar in size to that of Early Jurassic basal gravisorsians[34–36], whose body mass has been estimated in the range of 8–10 tonnes[37] (see Supplementary Information and Supplementary Table 2). Similarly, a linear regression of iliac measurements versus inferred body mass[3] in basal sauropodomorphs in fact suggests a body mass of over 7 tonnes for the specimen of Lessem saurus represented by the ilium (Supplementary Fig. 3b,c and Supplementary Table 2; see also Supplementary Information).

Phylogenetic analysis. We assessed the phylogenetic affinities of Ingentia using the dataset and protocols presented in previous studies[16,17] (see Methods and Supplementary Information). Our phylogenetic result recovered Ingentia, Lessem saurus and Antetonitrus to form a clade, named here as Lessem sauridae (Fig. 3 and Supplementary Fig. 9; see also Supplementary Information). Under the most broadly used phylogenetic definitions for sauropodomorph clade names[38] (see Methods), Lessem sauridae would be considered the basal-most sauropod clade or, alternatively, one of the closest relatives of Sauropoda if a more restrictive definition is used[39–41].

Discussion
Implications of the origin of gigantism. The mid-Norian age of Lessem saurus[29]—the oldest lessem saurid—indicates the appearance of an early trend towards large body size (equal to or approximating the body mass of basal gravisorsians such as Vulcanodon or Tazoudasaurus) at least 15 Myr earlier than previously thought (that is, Vulcanodon ~199–188 Ma[16]; Fig. 3). The combination of reticular and plexiform bone observed in Lessem saurus has recently been reported for Antetonitrus[40], which together with the presence of well-vascularized fibrolamellar bone in all lessem saurids, indicates that this clade was able to attain large body sizes through a strategy of accelerated growth distinct from that associated with gigantism in eusauropods[19,20].

Gigantism in eusauropods has been proposed as the result of a complex interplay of anatomical, physiological and reproductive intrinsic traits[12–20]. In this context, their elongated neck was interpreted as a key acquisition that—among others—improved heat loss allowed by the avian-like cervical air sacs and the neck’s high surface-to-volume ratio, as required given the high metabolic rate inferred for
The pneumatic structures present in the cervical vertebrae of *Ingentia* and *Lessemsaurus*, and in the dorsal vertebrae of *Antetonitrus*, suggest the presence of an avian-like respiratory system in lessemsaurids that was more developed in terms of invading the axial skeleton than in basal sauropodomorphs. In contrast with eusauro pods, in lessemsaurids the cervical and abdominal air sacs probably only invaded the neural arches (that is, not the vertebral centra) (Supplementary Figs. 4 and 5). Moreover, lessemsaurids also lacked an elongated neck as they had proportionately short cervical vertebrae, indicating that the neck elongation was not a prerequisite for achieving body sizes comparable to those of basal eusauro pods or gravisaurians (see Supplementary Information).

The upright position of the limbs has been highlighted as a major feature of the sauropodomorph bauplan that is considered an adaptation to gigantism [13,15,34,26,23]. Lessemsaurids have a pectoral girdle and forelimb anatomy like that of early sauropodomorphs, with the posteroventral orientation of the scapular glenoid precluding an erect posture of the humerus and a completely pronated manus [13,25,36,31,44], together with a relative flexed forelimb posture (flexor fossa of the distal humerus, shallow radial fossae and developed olecranon of the proximal ulna, and twisted digit I) [29–31,44]. Similarly, sauropodomorph plesiomorphies in the ilium, such as the reduced preacetabular process or the presence of brevis fossa, which determined the length and orientation of associated muscles (m. iliotibialis and m. caudofemoralis brevis) [13,18,45], differed from the modified features of giant eusauro pods (see Supplementary Information). Thus, lessemsaurids lacked the purported adaptations related to a fully erect forelimb and the marked modifications of the hindlimb lever arms in eusauro pods, showing that these features were not strictly necessary for the acquisition of gigantic body size. The aforementioned eusauro pod features may instead be more related to the evolution of graviportalism than body size.

**Fig. 3 | Origin of Sauropoda and its relationship with the evolution of the body mass.** a. Phylogenetic relationships of Lessemsauridae within a simplified tree of Sauropodomorpha obtained from the dataset of Cerda et al. (Methods and Supplementary Information). Numbers indicate Ma. b. Evolution of body mass among Sauropodomorpha during the Late Triassic and Early-to-Mid Jurassic. Grey circles represent the most basal sauropodomorphs, white circles the non-eusauro pod sauropodomorphs, stars the non-eusauro pod sauropodomorphs (red stars, *Lessemsaurus*) and triangles the eusauro pods. Body masses are from Benson et al. [13], with the addition of some non-eusauro pod sauropodomorph taxa [29–31,44] (Supplementary Table 2). Body mass for *Lessemsaurus* was estimated by linear regression of iliac measurements versus body mass (thick red star), and by direct comparison of the dimensions and proportions of each bone element versus body mass (thin red star; see Supplementary Information). Silhouettes indicate general morphotypes acquired by Sauropodomorpha from the Late Triassic to the Late Jurassic. Aale., Aalenian; Bajo., Bajocian; Bath., Bathonian; Call., Callovian; Hetta., Hettangian; Pliensbac., Pliensbachian.
However, lessemsaurids have sauropod-derived femoral traits—a fourth trochanter at the midshaft, ovoid in cross-section, and a tibia-to-femur ratio <0.7 (refs 20–23)—traditionally correlated with a slow but powerful hindlimb stride in response to increasing body mass15,44,66 (see Supplementary Information). Additionally, the apomorphic vertebral anatomy of lessemsaurids with remarkably tall neural arches and a high postzygapophyseal level indicate an enlarged epaxial musculature that strengthened the axial skeleton in relation to forces that held the neck at a low-to-horizontal angle12,23. The mosaic of derived and plesiomorphic traits in the skeleton of lessemsaurids highlights these derived femoral and vertebral features that may represent some of the key skeletal innovations related to the acquisition of large body masses in lessemsaurids.

In the Late Triassic, Lessemsauridae achieved body sizes comparable to those of the Early Jurassic basal gravisaurians and euasauropods while maintaining a plesiomorphic body plan through a novel growth strategy of cyclical and remarkably high growth rates. Pneumatic cervical and dorsal neural arches indicating an avian-like invasion of the axial skeleton by the respiratory system, few muscle- and leverage-related modifications, including high neural arches and an apomorphic femur, and elongated proportions of the forelimb (ulna/humerus) and hindlimb elements (tibia/femur) probably represented key elements in the mosaic of features that allowed the first pulse of gigantism in dinosaurs during the Triassic. However, this unique growth strategy and body plan of lessemsaurids continued only up to the Early Jurassic when the most recent members are recorded12, after which the euasauropod growth strategy and biomechanical design prevailed among Sauropodomorpha to subsequently evolve into the largest land animals in the history of life.

Methods

Histology: Appendicular bones of the four lessemsaurid individuals belonging to two different taxa (Lessemsaurus and Ingentia prima nov. gen. et sp.) were used in this study, including one humerus of Ingentia (PVSJ 1086) and two scapulae (PVL 4822/5 and CRILAR PV-303) and two femora (PVL 4822/64 and PVL 6580) of Lessemsaurus. The transverse thin sections from the humerus and femur PVL 4822/64 were generated from the midshaft. The cross-section of the femur PVL 6580 was obtained from a more distal portion shaft. In the case of the scapulae, incomplete transverse sections from the ventral side of the mid portion of the elements were obtained. To ensure no loss of gross morphological data, the elements were moulded before thin sectioning, and resin casts were made. Specimens were prepared for thin sections based on the methodology outlined in Chinsamy and Raath43. The preparation of the histological sections was carried out at the Egidio Feruglio Museum of Trelew (Argentina) and the Departamento de Geología de la Universidad Nacional de San Luis (Argentina). All histological specimens were analysed using a petrographic polarizing microscope (LabKlass and Nikon E200 Pol). The nomenclature and definitions of structures used in this study are derived from Franchillón-Vieillot et al.12 and de Ricqlès et al.12.

Phylogenetic analysis. To know the phylogenetic relationships of the new species Ingentia prima, we scored the new anatomical and histological information throughout the last version of the Sauropodomorpha matrix1 originally published by Yates et al.12. Some multistate characters were ordered (characters 8, 13, 19, 20, 40, 57, 69, 92, 102, 108, 117, 121, 134, 144, 147, 149, 150, 157, 167, 170, 171, 177, 205, 207, 222, 227, 242, 251, 254, 277, 294, 299, 336, 342, 349, 353 and 370). The modified dataset of 372 phylogenetic characters and 62 taxa was analysed under the elements were moulded before thin sectioning, and resin casts were made. Specimens were prepared for thin sections based on the methodology outlined in Chinsamy and Raath43. The preparation of the histological sections was carried out at the Egidio Feruglio Museum of Trelew (Argentina) and the Departamento de Geología de la Universidad Nacional de San Luis (Argentina). All histological specimens were analysed using a petrographic polarizing microscope (LabKlass and Nikon E200 Pol). The nomenclature and definitions of structures used in this study are derived from Franchillón-Vieillot et al.12 and de Ricqlès et al.12.

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All the data is provided along the manuscript or data set file.
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Please select the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences  ☐ Behavioural & social sciences  ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/authors/policies/ReportingSummary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

| Study description | The study is mainly based in the description of a new species of dinosaur from the Late Triassic of Argentina. It have implied a phylogenetic analysis and comparisons with relative taxa. Some anatomical features (pneumaticity and histological growth) were analyzed with more detail, which revealed novel adaptations and strategies of growth among primitive dinosaurs. |
| Research sample | The sample consists in an uncompleted specimen (postcranial disarticulated bones) of dinosaur (PVSJ 1086). |
| Sampling strategy | The new specimen was collected in 2015 during a fieldwork of two weeks, carried out by the researcher team of the Instituto y Museo de Ciencias Naturales, Universidad Nacional de San Juan. |
| Data collection | The data collection (morphological features observed in the new specimen) were translated to the morphological data set (Mesquite matrix) in the LAB period of work. |
| Timing and spatial scale | N/A - The data collection was produced on Lab, immediately after the mechanical preparation of the specimen. |
| Data exclusions | Data was not excluded. |
| Reproducibility | No reproducible experiments were carried out. |
| Randomization | The randomization is not a method used to evaluate new fossil species of vertebrates. |
| Blinding | Blinding is not part of the design nor methods used for the discovery and study of vertebrate fossils. |
| Did the study involve field work? | ☒ Yes  ☐ No |

Field work, collection and transport

Field conditions | The fieldwork was carried out on a desertic zone of Northwestern Argentina (Marayes - El Carrizal Basin) |
| Location | Marayes Basin is located at Northwestern of Argentina, precisely at Southeastern of San Juan Province. |
| Access and import/export | To access to the basin is possible by National routes 150, of San Juan Province (Caucete town) |
| Disturbance | No disturb was caused by this study. |

Reporting for specific materials, systems and methods

| Materials & experimental systems | Methods |
|---------------------------------|---------|
| n/a  | n/a |
| ☒ Unique biological materials | ☒ ChiP-seq |
| ☒ Antibodies | ☒ Flow cytometry |
| ☒ Eukaryotic cell lines | ☒ MRI-based neuroimaging |
| ☒ Palaeontology | |
| ☒ Animals and other organisms | |
| ☒ Human research participants | |
| Specimen provenance | The new species described here comes from Marayes Basin (Quebrada del Barro Formation), at northwestern of Argentina (South America). |
| Specimen deposition | The specimens are deposited in the palaeovertebrate collection of the Instituto y Museo de Ciencias Naturales, Universidad Nacional de San Juan (PVSN). |
| Dating methods | The new species was collected in 2015 during a fieldwork, it was studied by comparison with other known species, and it was assigned a new scientific name based on its morphological features. |

☐ Tick this box to confirm that the raw and calibrated dates are available in the paper or in Supplementary Information.