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Giants under a microscope: revealing sauropodomorph dinosaur paleobiology through the bone and tooth microstructure

IGNACIO A. CERDA[1,2,3*]
KRISTINA CURRY ROGERS[4]
ROMINA GONZÁLEZ[1,5]
ANUSUYA CHINSAMY[6]

1. Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Buenos Aires, Argentina.
2. Instituto de Investigaciones en Paleobiología y Geología (IIPG-CONICET-UNRN), General Roca, Río Negro, Argentina.
3. Museo Provincial Carlos Ameghino, Cipolletti, Río Negro, Argentina.
4. Biology and Geology Departments, Macalester College, St. Paul, Minnesota, United States of America.
5. Centro de Ecología Aplicada del Litoral (CECOAL-CONICET-UNNE). Corrientes, Argentina.
6. Department of Biological Sciences, University of Cape Town, South Africa.
*Corresponding author

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Asociación Paleontológica Argentina
Maipú 645 1° piso, C1006ACG, Buenos Aires
República Argentina
Tel/Fax (54-11) 4326-7563
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GIANTS UNDER A MICROSCOPE: REVEALING SAUROPODOMORPH DINOSAUR PALEOBIOLOGY THROUGH THE BONE AND TOOTH MICROSTRUCTURE

IGNACIO A. CERDA[1,2,3]*, KRISTINA CURRY ROGERS[4], ROMINA GONZÁLEZ[1,5], AND ANUSUYA CHINSAMY[6]

[1]Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Buenos Aires, Argentina. *nachocerda6@yahoo.com.ar*; *romigonzl95@gmail.com*
[2]Instituto de Investigaciones en Paleobiología y Geología (IIPG-CONICET-UNRN), General Roca, Río Negro, Argentina.
[3]Museo Provincial Carlos Ameghino, Cipolletti, Río Negro, Argentina.
[4]Biology and Geology Departments, Macalester College, St. Paul, Minnesota, United States of America. *rogersk@macalester.edu*
[5]Centro de Ecología Aplicada del Litoral (CECOAL-CONICET-UNNE). Corrientes, Argentina.
[6]Department of Biological Sciences, University of Cape Town, South Africa. *Anusuya.chinsamy-turan@uct.ac.za*
*Corresponding author

IAC: https://orcid.org/0000-0001-6279-0392; **KCR:** https://orcid.org/0000-0003-3565-9780; **RG:** https://orcid.org/0000-0002-6087-7205, **AC:** https://orcid.org/0000-0002-9786-5080

Abstract. The paleobiology of sauropodomorph dinosaurs has historically garnered considerable interest, primarily because this clade includes the largest terrestrial vertebrates. Bone and tooth microstructures are crucial sources of paleobiological data, and many paleohistological studies have focused on this group. Here we review and synthesize the main advances in an understanding of sauropodomorph paleobiology derived from osteological and dental histology. We explore a wide range of topics, including age assessment, ontogenetic stages, growth rates, growth dynamics and life histories, skeletal element formation, soft tissue reconstructions, paleopathologies, paleocytology, and tooth implantation and replacement rates. We also provide a comprehensive bibliographic review of the published literature detailing sauropodomorph bone and/or tooth histology.

Key words. Paleohistology. Bone histology. Tooth histology. Sauropodomorpha. Sauropoda. Paleobiology.

Resumen. GIGANTES BAJO EL MICROSCOPIO: REVELANDO LA PALEOBIOLOGÍA DE LOS DINOSAURIOS SAUROPODOMORFOS A TRAVÉS DE LA MICROESTRUCTURA DE HUESOS Y DIENTES. La paleobiología de los dinosaurios sauropodomorfos ha suscitado un considerable interés a lo largo de la historia, principalmente porque este clado incluye a los vertebrados terrestres más grandes. Tanto la microestructura ósea y dental son fuentes cruciales de datos paleobiológicos, y muchos estudios paleohistológicos se han centrado en este grupo de dinosaurios. En este trabajo, revisamos y sintetizamos los principales avances en la comprensión de la paleobiología de los sauropodomorfos a partir de la histología ósea y dental. Exploramos una amplia gama de temas, incluyendo: determinación de la edad, estadios ontogenéticos, tasas de crecimiento, dinámica del crecimiento e historias de vida, formación de elementos esqueléticos, reconstrucción de tejidos blandos, paleopatologías, paleocitología y tasas de implantación y reemplazo dental. También proporcionamos una revisión bibliográfica exhaustiva de la literatura publicada que detalla la histología ósea y/o dental de los sauropodomorfos.

Palabras clave. Paleohistología. Histología ósea. Histología dental. Sauropodomorpha. Sauropoda. Paleobiología.

INTRODUCTION

Among sauropodomorphs, sauropod dinosaurs are the largest animals ever to evolve in terrestrial ecosystems (Sander et al., 2011a) and represent the ultimate pop culture embodiment of gigantic beasts. The diversity and evolutionary success challenge the idea that massively scaled dinosaurs were painted into an evolutionary corner by their giant bodies and doomed to extinction. The fossil record reveals that sauropods evolved their basic body plan early in their evolutionary history and maintained this *baüplan* until their extinction alongside other non-avian dinosaurs 66 million years ago (Sander et al., 2011b). Starting out as tiny individuals and reaching adult sizes in excess of 70 tons, sauropods exhibit the greatest absolute ontogenetic size difference known for any terrestrial tetrapod group (Chiappe et al., 1998; Carballido et al., 2017). Such an extreme size range raises pertinent questions about the life histories of these vertebrates. What ontogenetic growth patterns and rates underpin such trajectories, and did sauropods grow at constant or variable rates? How many years were required

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to achieve sexual and somatic maturity, and what were their lifespans? What types of diets were required to fuel their ontogenetic growth, and what adaptations may have supported these feeding patterns? When did these biological strategies evolve, and are they unique among dinosaurs? Fortunately, studies of the microscopic structure of their bones and teeth have shed critical light on these questions (*e.g.*, Erickson, 2014; Bailleul et al., 2019; Chinsamy, 2023) while also providing essential insights into other paleobiological issues, such as the origin of particular skeletal elements and the reconstruction of soft tissues.

Here we review the main advances in sauropod paleobiology obtained from paleohistology of bones and teeth. Because paleobiology is best understood within an evolutionary framework, we expand our review to include basal sauropod relatives (*i.e.*, non-sauropod sauropodomorphs). We also provide a comprehensive bibliography of publications that include histological description of sauropodomorph bones and/or teeth (see Supplementary Information).

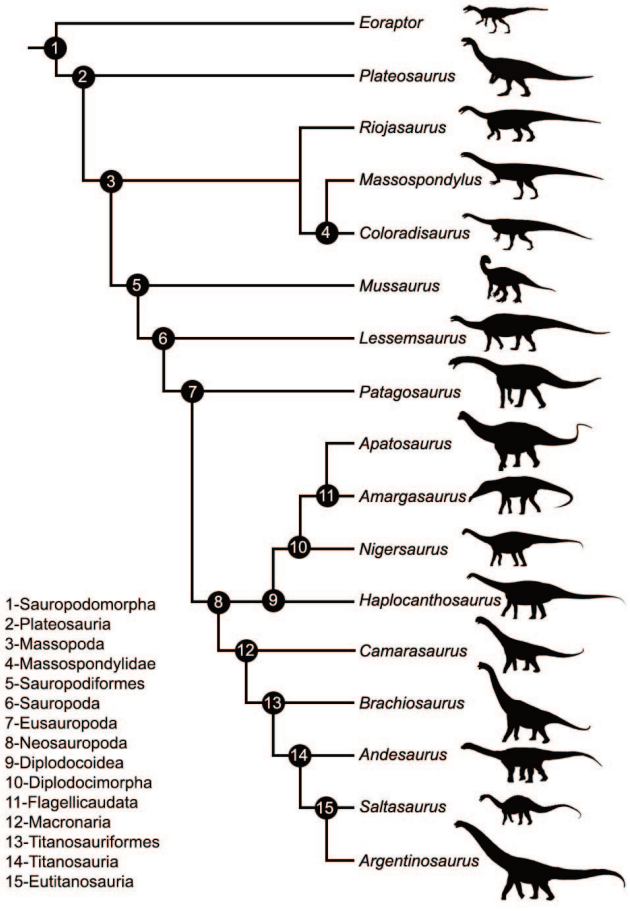


Figure 1. Simplified phylogeny of Sauropodomorpha showing several of the most important clades of the lineage. Based on the phylogenetic framework of Mannion et al. (2019), Carballido et al. (2020) and Pol et al. (2021a).

Because this review focuses specifically on paleobiological interpretations of fossilized tissues, we exclude studies that use paleohistology for other purposes, such as taxonomic assignment (*e.g.*, Nikolov et al., 2020). These contributions are included in the Supplementary Information. While tooth and bone microstructure can be analyzed using different techniques (*e.g.*, scanning electron microscopy and micro-CT scans), we largely restrict our scope to studies utilizing petrographic thin sections. This review is based on primary literature, including peer-reviewed journal articles, specialized books and books chapters. Conference abstracts and theses/dissertations (bachelor, masters, and doctoral) are excluded. For major phylogenetic relationships, we follow the topologies proposed by Mannion et al. (2019), Carballido et al. (2020) and Pol et al. (2021a; Fig. 1).

Institutional acronyms. BYU, Brigham Young University, Earth Science Museum, Provo, Utah, USA. **MACN PV,** División de Paleontología, Colección de Paleovertebrados, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina; **MCF-PVPH,** Museo Municipal "Carmen Funes" de Plaza Huincul, Vertebrate Paleontology collection, Plaza Huincul, Neuquén Province, Argentina; **MCS-Pv,** Museo de Cinco Saltos, Colección Paleovertebrados, Cinco Saltos, Argentina; **MDT-Pv,** Museo Desiderio Torres, Palaeovertebrate collection, Sarmiento, Chubut, Argentina; **MLP,** Museo de La Plata, División Paleontología de Vertebrados, La Plata, Argentina; **MPCA-Ph, MPCA-Pv,** Museo Provincial Carlos Ameghino, Paleohistological and Paleovertebrate collections, Cipolletti, Argentina; **MPEF-PV,** Vertebrate paleontology, Museo Paleontológico Egidio Feruglio, Trelew, Chubut, Argentina; **MPM-PV,** Vertebrate Paleontology collection ofthe Museo Regional Provincial Padre Molina, Río Gallegos, Santa Cruz Province, Argentina; **PVL,** Paleovertebrate collection of Instituto Miguel Lillo, San Miguel de Tucumán, Tucumán Province, Argentina; **PVSJ,** Instituto y Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan, Argentina; **UA,** Université d'Antananarivo, Antananarivo, Madagascar; **UNPSJB-PV,** Universidad

Nacional de la Patagonia San Juan Bosco, Palaeovertebrate collection, Comodoro Rivadavia, Argentina.

AGE ASSESSMENT

Determining the age of fossil and living organisms is essential for determining lifespan, growth rates, and the timing of sexual and somatic maturity (*e.g.*, Chinsamy-Turan, 2005; Erickson, 2014). Skeletochronology is a standard method for aging vertebrates using hard tissues, mostly bone (Castanet et al., 1993; Woodward et al., 2013). This technique involves counting cyclically deposited growth marks (CGMs) preserved in cortical bone (Fig. 2). CGMs originates from changes in bone rate deposition that has been commonly related with endogenous and exogenous factors that occur with annual periodicity. CGMs occur as lines of arrested growth (LAGs) and/or annuli (though other types of CGMs have also been employed, see below "Polish Lines"). LAGs and annuli can occur associated in the same tissue. While various skeletal elements can be employed, appendicular bone midshafts are typically preferred because they preserve the most complete growth record (*e.g.*, Chinsamy, 1993; Curry, 1999; Sander, 2000; Chinsamy-Turan, 2005; Klein & Sander, 2007; Klein et al., 2009, 2012a; Cerda et al., 2017). Expansion of the medullary cavity and secondary remodeling destroy early ontogeny growth marks, which means that counting preserved CGMs in subadult and adults yields only a minimum age estimate (Castanet et al., 1993; Woodward et al., 2013). To more accurately assess age, these missing growth marks must be retro-calculated (*e.g.*, Castanet et al., 1993; Woodward et al., 2013).

Age estimation using LAGs and annuli formed in appendicular bones.

Basal sauropodomorphs typically deposit CGMs in their limb bones (*e.g.*, Chinsamy, 1993; Sander et al., 2004; Klein & Sander, 2007; Cerda et al., 2017, 2022a; Woodruff et al., 2025). The presence of these CGMs throughout the cortex of both juvenile and adult individuals indicates a cyclical growth strategy, where growth interruptions (and the formation of corresponding growth marks) occur from early ontogeny. Minimum ages, calculated by counting CGMs in appendicular bones, have been estimated for several basal sauropodomorph individuals (*e.g.*, Yates et al., 2010; Cerda et al., 2017; Chapelle et al., 2019). Conversely, absolute age estimations, derived from both visible and retrocalculated growth marks, have only been established for a few taxa, including *Massospondylus carinatus* (Early Jurassic of southern Africa; Chinsamy, 1993; Chapelle et al., 2022), *Plateosaurus trossingensis* (Late Triassic of Germany and Switzerland; Sander & Klein, 2005; Klein & Sander, 2007) and *Mussaurus patagonicus* (Early Jurassic of Argentina; Cerda et al., 2022a). Maximum absolute ages of 20 (*Massospondylus*), 27 (*Plateosaurus*) and 29–34 (*Mussaurus*) years have been reported (Sander & Klein, 2005; Cerda et al., 2022a; Chapelle et al., 2022). However, discrepancies in the age estimates have been observed, depending on the skeletal element sampled as well as the method of retrocalculation. For instance, using the same retrocalculation method on a single *Mussaurus* individual yielded estimates of 32 years for the humerus and only 19 years for the femur; furthermore, applying different retrocalculation methods to the same femur resulted in estimates of 34 and 26 years (Cerda et al., 2022a). Despite these methodological challenges, larger taxa (*Mussaurus* and *Plateosaurus*) appear to have lived longer than comparatively smaller taxa like *Massospondylus*. As noted by Chapelle et al. (2022), this variation in maximum absolute age aligns with the linear relationship between body mass and life span of poikilothermic animals. Because *Mussaurus* and *Plateosaurus* attained larger body masses than *Massospondylus*, they are hypothesized to exhibit correspondingly longer lifespans.

Alternative ways of assessing age

Unlike most basal sauropodomorphs, sauropod limb bones typically lack mid-cortical growth marks (Sander et al., 2004). This absence prohibits the use of traditional skeletochronological methods, prompting researchers to rely on alternative approaches to infer the relative and absolute ages of sauropod dinosaurs. These alternative methods include: analyzing skeletal elements other than limb bones (*e.g.*, Waskow & Sander, 2014); using CGMs other than LAGs/ annuli (*e.g.*, Sander, 2000; Lehman & Woodward, 2008); and calculating rates of primary bone apposition (*e.g.*, Curry, 1999; Sander & Tückmantel, 2003; Curry Rogers & Erickson, 2005).

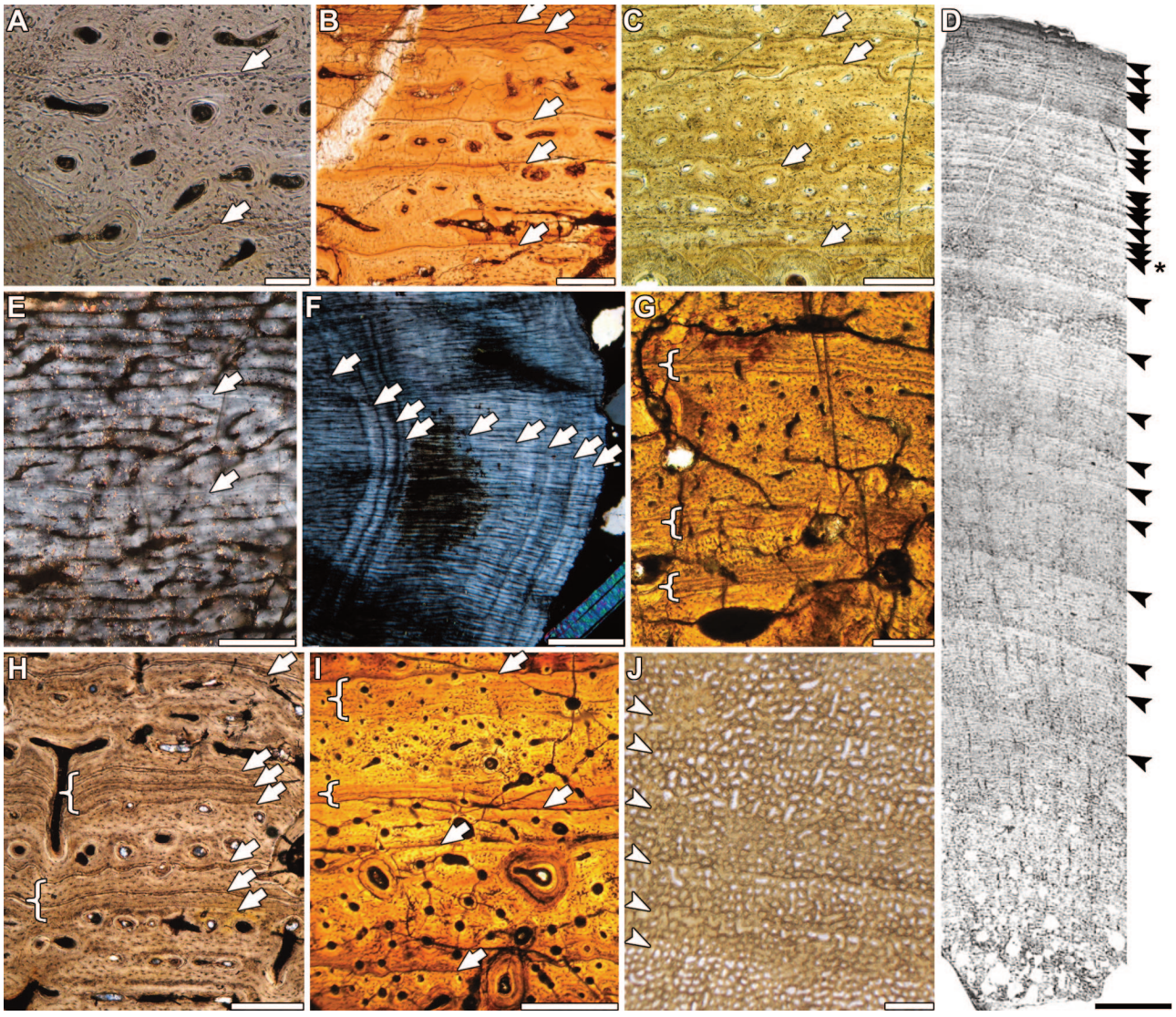


Figure 2. Different types of growth marks formed in sauropodomorph dinosaurs. A, Femur of *Neuquensaurus australis*, MCS-Pv 5/28. B, Femur of *Mussaurus patagonicus*, MLP 68-II-26-3. C, Cervical vertebra of *Amargasaurus cazaui*, MACN PV N1A. D, Femur of *Janenschia robusta*, Nr. 22 (modified from Sander, 2000). E, Femur of *Riojasaurus incertus*, PVL 3669. F, Dermal ossicle of *Saltasaurus loricatus*, PVL 4017—208. G, Dorsal rib of *Leonerasaurus taquetrensis*, MPEF-PV 1663. H, Fibula of *Mussaurus patagonicus*, MLP 61-III-20-22. I, Dorsal rib of *Katepensaurus goicoecheai*, UNPSJB-PV 1007/28. J, Scapula of *Apatosaurus*, BYU 641. asterisk = possible onset of sexual maturity; black arrowheads = polish lines; brackets = annuli; white arrows = lines of arrested growth; white arrowheads = modulations. Scales = 0.1 mm (A), 0.2 mm (B, F, G), 0.3 mm (C, E, H), 5 mm (D), 0.5 mm (I), and 1 mm (J).

Age assessment from non-appendicular bones. Because growth mark counts typically vary among skeletal elements (*e.g.*, Horner et al., 1999, 2000; Woodward et al., 2014), investigations that incorporate multiple elements provide the most useful insights into overall somatic growth strategies. Recent studies indicate that the proximal ends of sauropod dorsal ribs may offer a good record of growth marks and are useful for age estimation (Waskow & Sander, 2014; Woodruff et al., 2017), at least in non-titanosauriform sauropods, which lack costal pneumatic cavities (Wilson & Sereno, 1998). Minimum (and sometimes absolute) age estimations for sauropod dinosaurs have often been derived from different elements of the axial skeleton, mostly dorsal ribs (*e.g.*, Woodruff & Foster, 2017; Woodruff et al., 2017; Windholz & Cerda, 2021; Brum et al., Cerda et al., 2022b; 2022; Windholz et al., 2023). For example, analyzing growth

cycles in in the dorsal ribs of *Camarasaurus* and *Diplodocus* (both from the Upper Jurassic of North America) yields absolute individual age estimates of 40 and 34 years, respectively (Waskow & Sander, 2014; Woodruff & Foster, 2017; Woodruff et al., 2017).

For armored titanosaurs, osteoderms can provide valuable records of ontogenetic growth. While large osteoderms are usually intensely remodeled and/or internally occupied by large cavities (Salgado, 2003; Cerda & Powell, 2010; Curry Rogers et al., 2011, Cerda et al., 2015a; Vidal et al., 2017), smaller ossicles (less than 10 mm long) undergo less remodeling and retain more complete growth records (Cerda & Powell, 2010). To date, the most extensive growth record obtained from an osteoderm indicates the preservation of 17 LAGs in the armored titanosaur *Saltasaurus loricatus* (Late Cretaceous of Argentina; Cerda & Powell, 2010).

Age assessment using 'modulations' and 'polish lines'. "Modulations" and "polish lines" cyclically deposited in appendicular bones provide alternative methods for estimating age. Modulations (also referred to as "incremental cycles", "cycles" or "depositional cycles") are cyclical variations in the primary bone vascular pattern. Different from annuli, modulations are not related with variations in the intrinsic fiber arrangement in the matrix. Best observed under low magnification, these variations do not structurally correspond to CGMs *sensu stricto* (*i.e.*, LAGs or annuli; *e.g.*, de Ricqlès, 1983; Rimblot-Baly et al., 1995; Curry, 1999; Woodward & Lehman, 2009). Similar depositional modulations have been documented in other vertebrates, including sirenians (Fawcett, 1942), leatherback turtles (Rhodin, 1985), ichthyosaurs (de Buffrénil & Mazin, 1990) and non-sauropodomorph dinosaurs (Chinsamy et al., 2012a). In leatherback turtles, Rhodin (1985) interpreted these modulations as the result of cyclical cortical bone growth, where intervals of relatively faster and slower growth alternate.

"Polish lines" were first described by Sander (2000) in various sauropods from the Upper Jurassic Tendaguru Formation (Tanzania; Sander, 2000). A polish line is defined as a cortical bone growth mark that is visible in polished section but not in thin section (Sander, 2000). Polish lines are rarely reported in other vertebrates (*e.g.*, Klein & Sander, 2007; Erickson & Druckenmiller, 2011). Although some studies have described these lines in thin sections (Waskow & Mateus, 2017), doing so contradicts their formal definition. Sander (2000) suggested that the abrupt decrease in reflectivity which gives polish lines their appearance under bright-field illumination, might be caused by a decrease in mineralization or a change in crystallite size of bone apatite.

Despite lacking the structural hallmarks of LAGs and annuli, both modulations and polish lines have been interpreted as annually formed growth marks (*e.g.*, de Ricqlès, 1983; Curry, 1999; Sander, 2000; Sander & Tückmantel, 2003; Woodward & Lehman, 2009). Sander (2000) interpreted polish lines as an intermediate stage between modulations and LAGs; they are hypothesized to result from a growth slowdown that is more pronounced than a modulation, but not severe enough to completely arrest growth. By combining counts of modulations, polish lines, and LAGs with retrocalculation methods, researchers can estimate the ages of individual sauropods. The highest age estimates obtained using this approach are from specimens of *Janenschia robusta* (Upper Jurassic of Tanzania), *Mamenchisaurus* sp. (Upper Jurassic of China), and *Apatosaurus* sp. which reached estimated ages of 55, 43 and 41 years, respectively (Sander et al., 2011b). It is important to note, as a final point, that recent studies have revealed that there is not always a direct correlation between the number of LAGs and the age of individuals (*e.g.*, Chinsamy & Pereyra, 2026). Therefore, ages inferred from this method should be reviewed in the future.

Age assessment from periosteal bone apposition rates. Another approach for age estimation relies on applying known primary bone apposition rates derived experimentally in extant vertebrates (*e.g.*, Castanet et al., 2000). This method requires the assumption that different bone tissue types are deposited at a range of different absolute rates. Once dominant primary bone tissue type is identified in a fossil sample, experimental growth rates of the same tissue type in living vertebrates may be applied to the total cortical bone thickness (typically the radius of a long bone at midshaft) to yield the number of days required for total apposition (*e.g.*, Curry Rogers & Erickson, 2005). This method yields similar results to one that relies on estimating periosteal bone apposition rates directly from fossil bones (Curry, 1999; Sander & Tückmantel, 2003; Curry Rogers &

Erickson, 2005). This method involves: 1) measuring an average zone thickness (between LAG, or between modulation or polish line borders); 2) assuming annual deposition of the zone, divide average thickness by number of days in a year (calibrated to geological time period) to result in an estimated average daily primary bone apposition rate and; 3) this average rate can then be applied to the total cortical thickness in the same way that experimental data are, by dividing total cortical thickness by the calculated range of appositional rates to result in an estimated number of days required for growth of the cortex. Days can be converted to years when geological time period is included in the calibration (Curry Rogers & Erickson, 2005). Though infrequently used these methods have been applied to estimate the ages of sauropod taxa from the Tendaguru Formation and also for several specimens of *Apatosaurus* (Curry, 1999; Sander & Tückmantel, 2003; Curry Rogers & Erickson, 2005).

DETERMINATION OF ONTOGENETIC STAGES

In addition to chronological age, assessing relative ontogenetic stages (*e.g.*, juvenile, adult, and senescent) is highly valuable for describing fossil vertebrates, including sauropodomorph dinosaurs (*e.g.*, Curry, 1999; Sander, 2000; Klein & Sander, 2008; González et al., 2020; Zurriaguz et al., 2026). While ontogeny is a continuous process of gradual development, milestones like sexual and somatic maturation are of singular importance in an individual's life and serve to define distinct ontogenetic stages. Because the physiological shifts accompanying the onset of these stages can drastically impact skeletal growth, bone histology provides insights for determining the ontogenetic status in the individuals.

Sexual maturity

Sexual maturity can be defined as the stage at which an individual becomes capable of breeding, and can be reached before, after or simultaneously with somatic maturity, when growth becomes asymptotic (Erickson et al., 2007; Lee & Werning, 2008). In taxa that reach sexual maturity prior to attaining adult size, a coincident decrease in growth rate is observed (Erickson et al., 2007; Lee & Werning, 2008; Erickson, 2014). Histologically, the reduction in growth rate manifests as a clear change in the organization of the intrinsic collagenous fibers of the bone matrix (from poorly to well organized) and/or a decreasing in the spacing between successive growth marks if these are present. In addition, the reduction in growth rate results in a decrease in an overall reduction in the density and diameter of vascular canals (*e.g.*, Castanet & Baez, 1991; Chinsamy-Turan, 2005; Khonsue et al., 2010; Chinsamy, 2023; Fig. 3A). This reduction in growth rate reflects a shift in resource allocation from growth to reproduction as the individual became sexually mature (Sander, 2000; Erickson, 2014).

The long bone histology of non-avian dinosaurs, including sauropodomorphs, favors the hypothesis that many attained sexual maturity early in life. Furthermore, because age estimations suggest that some sauropods took roughly three decades to reach adult size, synchronous sexual and somatic maturity is unlikely (Sander et al., 2011b). In sauropodomorphs, the onset of the sexual maturity is typically inferred directly from bone histology (*e.g.*, Cerda et al., 2022a) or from reconstructed, histology-derived growth curves (Griebeler et al., 2013). When using growth curves, sexual maturity corresponds to the age at the curve's inflection point occurs.

Sexual maturity has been inferred for individuals of several basal sauropodomorph taxa (*e.g.*, Cerda et al., 2017), but it has rarely been examined in the context of chronological age or relative body size. In *Plateosaurus*, Klein and Sander (2007) estimated that the onset of sexual maturity occurred at a body length of approximately 4 m, roughly one-half to two-thirds of the size of most specimens studied using long bone histology. Griebeler et al. (2013) used histology-derived growth curve estimations to infer that *Plateosaurus* reached sexual maturity between 10 and 13 years (Fig. 3B). In contrast, an age of 23 to 31 years at sexual maturity is hypothesized for *Mussaurus* (Cerda et al., 2022a). Perhaps delayed sexual maturation, like longer lifespan is related to the larger body size of *Mussaurus* compared to *Plateosaurus*. Among sauropods, age estimates for sexual maturity are available for some taxa. For example, Waskow and Sander (2014) used growth rate reduction to estimate that *Camarasaurus* was sexually mature between 18 and 19 years. This estimate was obtained from dorsal rib growth mark counts and equates to about half the time required for this taxon to reach full body size.

Among non-avian dinosaurs, one histological indicator proposed for the attainment of sexual maturity is the presence of 'medullary bone,' a specific bone tissue formed in ovulating females of some extant avian taxa (Schweitzer et al., 2005, 2007, 2016; Lee & Werning, 2008; Hübner, 2012; Prondvai, 2017). Although a preliminary examination

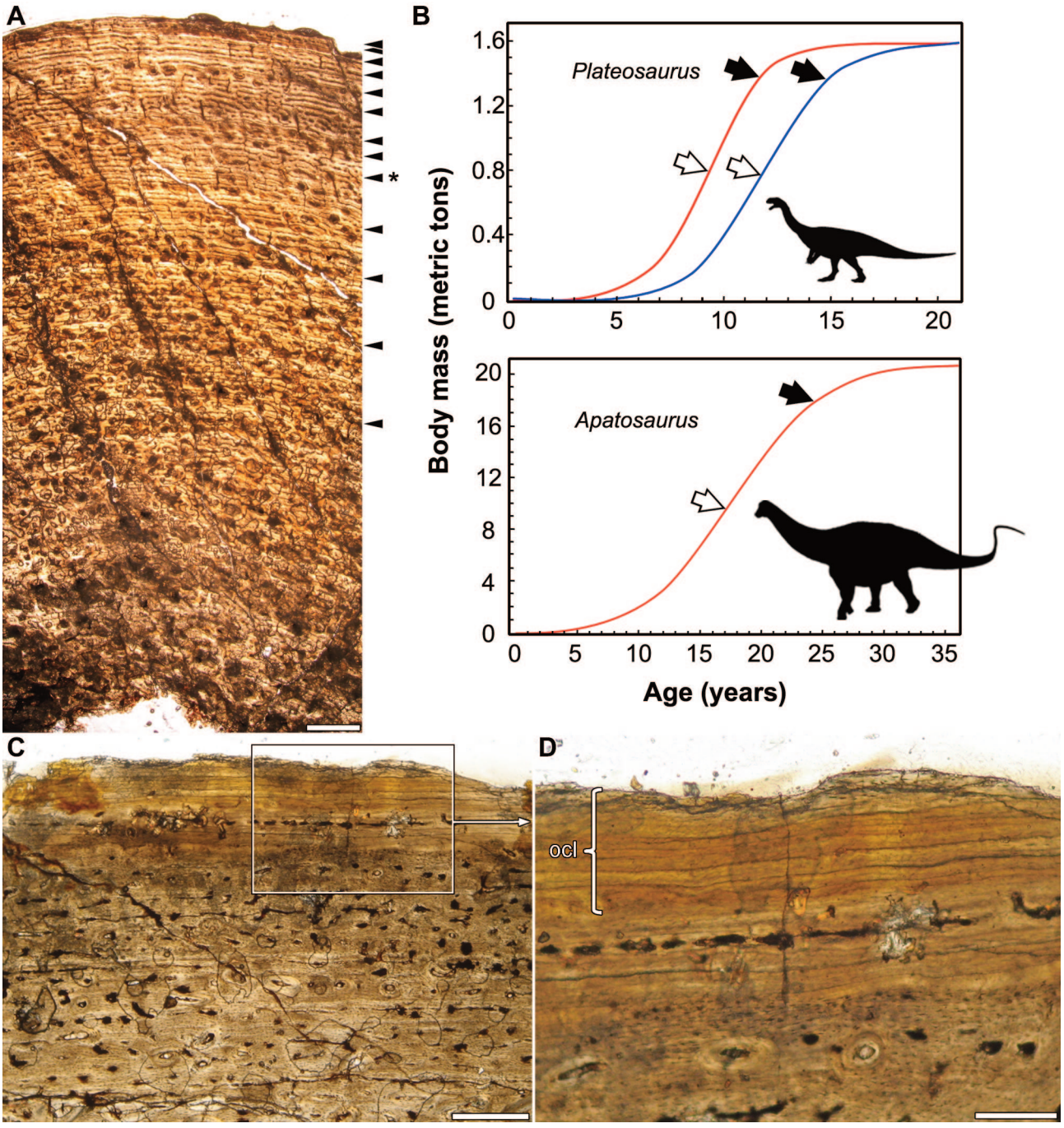


Figure 3. Sexual and somatic maturity determination in sauropodomorph dinosaurs. A, Femoral cortex of a basal sauropodomorph, PVSJ 1079, showing the distribution of growth marks. B, Logistic growth models established for two sauropodomorph dinosaurs (based on the data provided by Griebeler et al., 2013). C–D, Femur of *Mussaurus patagonicus*, MLP 61-II-20-26: C, general view; D, detail of the outer cortex displaying the presence of an outer circumferential layer (OCL). Asterisk = point in which LAGs spacing decreases; arrows = lower (white) and upper (black) limits for sexual maturity attainment; black arrow heads = growth marks; curves showed for *Plateosaurus* = two different fitting techniques (see details in Griebeler et al., 2013). Scales= 1 mm (A); 0.5 mm (C); 0.2 mm (D).

of a *Mussaurus* individual revealed a medullary bone-like tissue, this was later reinterpreted as pathological (Cerda et al., 2014b; see Prondvai, 2017 for a different interpretation). To date, there are no confident reports of medullary bone within Sauropodomorpha.

In two recent publications, Brum et al. (2021, 2022) inferred the ontogenetic stages of several titanosaurs from the Upper Cretaceous of Brazil (*Austroposeidon magnificus*, *Gondwanatitan faustoi* and *Maxakalisaurus topai* and *Aeolosaurini* indet.) by examining, among other histological features, the degree of secondary remodeling in axial bones, including cervical and dorsal ribs. They posited that sexual maturation in sauropod dinosaurs "*…can be microstructurally characterised by the transition to low bone depositional rates, advanced remodeling and* (sic) *endosteal bone*." (Brum et al., 2021, p. 4). While there is a general consensus that low bone depositional rates correlate with the onset of sexual maturity, the same cannot be said for the degree of remodeling. The causal relationship between the degree of secondary remodeling and sexual maturity proposed by Brum et al. (2021, 2022) relies heavily on earlier studies of dorsal rib histology (Waskow & Sander, 2014; Waskow & Mateus, 2017). However, when Waskow and Sander (2014) and Waskow and Mateus (2017) inferred sexual maturity from dorsal ribs, they were explicitly referencing the decrease in LAG spacing within the primary bone, rather than the extent of remodeling. Furthermore, ribs exhibit significant intra-elemental variation with regard to the degree of secondary remodeling, a phenomenon usually attributed to differing mechanical regimes acting on these elements from proximal to distal (*e.g.*, Waskow & Sander, 2014; Brum et al., 2022). Brum et al. (2021, 2022) further justify their framework by stating that "*The centrifugal advance of the secondary bone is also associated with the sexual maturity, due to the decrease in the nutrient contribution to the bone, which limits bone apposition in fast growth organisms"* (Padian et al., 2016). However, this inference stems from a misinterpretation of the work of Padian et al. (2016), who were actually discussing potential causes for inter-element variation in secondary remodeling among large animals; specifically, that secondary osteons may form to a greater degree in smaller bones compared to larger ones. Padian et al. (2016) do not address the relationship between remodeling and sexual maturity at all. The fact that most remodeled areas of sauropodomorph ribs correspond to areas of muscle attachment (Waskow & Mateus, 2017) strongly supports a biomechanical rather than ontogenetic cause for the pattern observed by Brum et al. (2021, 2022). Thus, while a general relationship between the extent of secondary remodeling and age is evident in dinosaur growth series and remains useful for inferring relative ontogenetic stages (*e.g.*, Klein & Sander, 2008), a direct causal link between secondary remodeling and sexual maturity currently lacks support.

Somatic maturity

The outer circumferential layer (OCL, also referred to as external fundamental system, the EFS) is a histological marker usually found in somatically mature (*i.e.*, full-adult size) individuals of taxa with determinate growth, meaning that an individual has lived long enough to reach asymptotic growth (Woodward et al., 2011). The OCL is a microstructural feature observed in the subperiosteal cortex. It consists of poorly vascularized (or avascular) tissue that can contain a number of closely spaced LAGs (Horner et al., 1999; Chinsamy-Turan, 2005; Woodward et al., 2011). Typically, the OCL is composed of slowly deposited parallel-fibered or lamellar tissue that usually marks an effective cessation of growth in the subperiosteal circumferential bone apposition and is one signal of somatic maturity (Woodward et al., 2011). An important exception to this has been recorded in birds, where the OCL start to form during early ontogeny (*e.g.*, Atterholt & Woodward, 2021). The OCL has been widely used to infer somatic maturity in fossil taxa (*e.g.*, Horner et al., 1999; Köhler et al., 2021; Canoville et al., 2022; Baiano & Cerda, 2023; Maho et al., 2023; D'Angelo et al., 2024; Sombathy et al., 2025; Woodward et al., 2026).

The inference of somatic maturity through the identification of unambiguous OCL has been conducted for several sauropodomorph taxa (Fig. 3C–D; *e.g.*, Klein & Sander, 2007; Carballido et al., 2011; Cerda et al., 2015b, 2017, 2022a, García et al., 2015; Woodruff et al., 2017; Krupandan et al., 2018; Chapelle et al., 2023). The feature has been used to assess growth strategies (determinate versus indeterminate growth) and even to infer phylogenetic size reduction. The absence of an OCL was interpreted as evidence

for an indeterminate growth strategy in *Massospondylus* (Chinsamy, 1993). Later, the lack of an OCL in the largest known *Massospondyus* specimen led to the hypothesis that even larger individuals of this taxon existed (Cerda et al., 2017). However, Chapelle et al. (2023) revealed that, although uncommon, an OCL can be present in *Massospondyus*. The resulting deduction of a determinate growth strategy in *Massospondylus* aligns with the general consensus for saurischian dinosaurs.

The presence of a distinct OCL has been also employed to verify small body sizes in basal sauropodomorphs. For example, Chapelle et al. (2023) studied the morphology and histology of a single humerus from the Lower Jurassic of South Africa and concluded that the same represents the smallest known (75.35 kg) sauropodomorph to have lived during the Jurassic.

As a final comment on this regard, it must be noted that, although the presence of an OCL is employed to infer the onset of somatic growth, it actually indicates only the cessation of periosteal growth and not necessarily the cessation of the growth of animal as a whole. Similar to the reported for living birds (*e.g.*, Atterholt & Woodward, 2021), growth in length of appendicular bones of the western grey kangaroo appears to continue despite the cessation of diaphyseal appositional growth (Chinsamy & Warburton, 2021).

The histologic ontogenetic stages (HOS)

The histological parameters mentioned above for sexual and somatic maturation have been employed to several vertebrate groups beyond just sauropodomorph dinosaurs. Various studies that have explored the microstructural changes occurring through ontogeny, offering histological characterizations of successive ontogenetic stages. These contributions span groups of non-avian dinosaurs, including sauropodomorphs (*e.g.*, Curry, 1999; Erickson & Tumanova, 2000; Horner et al., 2000; Sander, 2000; Klein & Sander, 2008; Hayashi et al., 2009). A study by Klein and Sander (2008) on neosauropods is of a particular note; not only did it utilize one for the largest sample sizes of non-avian dinosaurs, but it also encompassed one of most extensive array of skeletal elements. Klein and Sander (2008) defined thirteen histological ontogenetic stages (HOS) identified based on a combination of seven bone tissue types. Each tissue type was characterized by vascularization pattern, degree of secondary remodeling, and presence of growth marks (Klein & Sander, 2008). The authors proposed a correspondence between HOS and biological ontogenetic stages (*e.g.*, embryo, hatching, juvenile, etc.). For example, they hypothesized that sexual maturity is reached at HOS 8. Using this approach, the authors inferred that an individual *Apatosaurus* reached sexual maturity at ~50% of its maximum adult body size (Klein & Sander, 2008). Stein et al. (2010) revised the HOS to 13 stages to improve ontogenetic resolution, characterizing the new stages by the presence of at least two generations of cortical secondary osteons. Building on this, Mitchell et al. (2017) established 'remodeling stages' for sauropod dinosaurs based on the degree of bone remodeling.

The HOS model proposed by Klein and Sander (2008) has been widely used to ontogenetic stages in sauropods (*e.g.*, Company, 2011; Gallina, 2012; Hedrick et al., 2014; Melstrom et al., 2016; Cerda et al., 2017, 2021; Woodruff et al., 2017; Woodruff & Foster, 2017; Wiersma-Weyand et al., 2021; Windholz & Cerda, 2021; Navarro et al., 2022; Windholz et al., 2023, 2024), but the system exhibits some limitations. First, it cannot be used widely among sauropods because the histological variations that occur during ontogeny are not the same for all groups. Titanosaurs are particularly illustrative in this regard, given the enhanced degree of secondary remodeling that these sauropods experienced during early ontogeny (Woodward & Lehman, 2009; Klein et al., 2009, 2012a; Stein et al., 2010; Company, 2011; Gallina, 2012; Lacovara et al., 2014; García et al., 2015; Carballido et al., 2017; Curry Rogers & Kulik, 2018; Díez Díaz et al., 2018). In addition, González et al. (2020) analyzed the long bone histology of two small specimens assigned to Titanosauria from the Upper Cretaceous of northern Argentinean Patagonia, and found a combination of histological features that correspond to both very early (*e.g.*, predominance of highly vascularized woven fibered bone and incipient formation of primary osteons) and very advanced (*e.g.*, secondary remodeling, presence of LAGs) ontogenetic stages. These tissue inconsistencies made application the HOS problematic for Titanosauria.

While the use of bone microstructure remains one of the

most reliable parameters for establishing ontogenetic stages, it appears that in the specific case of using HOS, these must be adjusted for each group, taking into account their growth characteristics. Likewise, it is desirable that this adjustment be made considering other parameters that vary during ontogeny. In this regard, recent works such as that of have employed the bone histology (more specifically, the HOS) alongside several anatomical features that show variation during the ontogeny, including body size and fusion of skeletal sutures, among others (*e.g.*, Woodruff et al., 2017). This combined use of different parameters has allowed a more precise adjustment for the estimation of ontogenetic stages.

DEVELOPMENTAL PLASTICITY IN BASAL SAUROPODOMORPHS

A comparison of body size with age and ontogenetic data derived from long bone histology has revealed evidence of developmental plasticity in sauropodomorph dinosaurs. Plasticity is defined as a genotype's capacity to produce multiple phenotypes in response to environmental variation (Warner et al., 2018). In the case of developmental plasticity, this term refers to the ability of an organism to respond to changes in the environment by evoking different developmental programs resulting in different adult phenotypes (Smith-Gill, 1983). This phenomenon can result in widely differing growth rates and final sizes in individuals of the same species. Developmental plasticity has been reported in several living forms, including amphibians, reptiles, and birds (*e.g.*, Games, 1990; Alcobendas & Castanet, 2000; de Buffrénil & Hémery, 2002; Starck & Chinsamy, 2002), and is inferred in extinct non-avian dinosaurs (Starck & Chinsamy, 2002; Sander & Klein, 2005; Chapelle et al., 2021; Barta et al., 2022; Cerda et al., 2022a).

Histological analyses have revealed that body size and age/ontogenetic stage are poorly correlated in at least three basal sauropodomorphs: *Plateosaurus trossingensis* (Sander & Klein, 2005), *Massosspondylus carinatus* (Chinsamy, 1993; Chinsamy-Turan, 2005; Chapelle et al., 2021) and *Mussaurus patagonicus* (Cerda et al., 2022a). For example, adult *Plateosaurus* individuals range in length from 4.8 to 10.0 m due to highly variable growth rates (Sander & Klein, 2005; Klein & Sander, 2007). Although sexual dimorphism could be invoked to explain this variation, this explanation was rejected due to terminal body size in *Plateosaurus* showed a unimodal distribution, albeit with a high standard deviation, and not the bimodal distribution expected for sexual morphs (Sander & Klein, 2005). Similarly, the cortical bone of two adult *Mussaurus* specimens (representing ~48 and 100% of the taxon's maximum known size) is dominated by parallel-fibered and fibrolamellar bone, respectively (Cerda et al., 2022a). Irregular spacing between LAGs in both *Plateosaurus* and *Massopondylus*, points to significant annual fluctuations in body mass gain (Chapelle et al., 2021). This poor match between estimated age and body size has been explained as a consequence of pronounced developmental plasticity in these taxa.

Sander and Klein (2005) suggested that the developmental plasticity in *Plateosaurus* reflects a low metabolic rate and behavioral thermoregulation. The subsequent loss of this developmental plasticity in more derived sauropods, inferred from the tighter relationship between body size and relative age, is hypothesized to indicate a shift toward increased metabolic rates and endothermy (Klein & Sander, 2008; Sander et al., 2011a). While several studies support this loss of developmental plasticity in sauropods (*e.g.*, Klein & Sander, 2008; Klein et al., 2009; 2012a, Company, 2011), at least one challenges this view. Woodruff and Foster (2017) reported a somatically mature but small statured *Camarasaurus* and suggested that the assumed loss of developmental plasticity may not be uniform among all sauropods.

GROWTH RATES ASSESSMENT

Growth rate (the speed body size increase over time) is a crucial aspect of sauropodomorph dinosaur paleobiology, especially considering the group's evolutionary trend toward colossal sizes. The growth rate of a single individual varies during the ontogeny, and may halt entirely during harsh conditions (Case, 1978). Although direct measurements are impossible for extinct dinosaurs, bone histology provides reliable indirect estimations. This is achieved through both qualitative methods, such as examining bone typologies, and quantitative methods, including the calculation of apposition rates and growth curves.

Relative growth rates inferred from bone typologies

"Amprino's rule" states that the rate of bone tissue formation dictates its structure: densely vascularized bone matrix with highly disorganized intrinsic fibers (woven fibered bone) grows faster than poorly vascularized, highly organized parallel-fibered and lamellar bone (Francillon-Vieillot et al., 1990; Chinsamy-Turan, 2005; de Buffrénil et al., 2021). This principle considers the primary bone apposition rates in general, irrespective of the bone element or region. Because tetrapod bone shaft diameter usually positively correlates with body size (*e.g.*, Anderson et al., 1985; Campione & Evans, 2012), estimating periosteal bone apposition rates in these elements yields insights into overall growth rates. Consequently, primary bone typology is a standard metric for comparing relative growth rates in extinct tetrapods, including sauropodomorphs (*e.g.*, Sander et al., 2004; Klein et al., 2012a; Cerda et al. 2017).

For example, this approach has been used to assess titanosaur growth rates. The cortical bone of some small- to medium-sized titanosaurs as *Ampelosaurus* (Klein et al., 2012a), *Magyarosaurus* (Stein et al., 2010) and *Lirainosaurus* (Klein et al., 2012a) (Upper Cretaceous of France, Romania and Spain, respectively) is predominantly formed by parallel-fibered and lamellar bone. In the particular case of *Ampelosaurus*, Klein et al. (2012a) referred this bone tissue as "modified laminar bone". The prevalence of parallel-fibered and lamellar bone in these sauropods contrasts with large-bodied titanosaurs like *Alamosaurus* (Upper Cretaceous of North America) where fibrolamellar bone dominates (Stein et al., 2010; Klein et al., 2012a). For *Lirainosaurus* and *Magyarosaurus*, this slower growth is coupled with a dramatic body size reduction (and possibly a lowered metabolic rate) commensurate with dwarving on the Late Cretaceous European islands (Stein et al., 2010; Klein et al., 2012a).

A key limitation of using bone typologies to infer growth is that a specific tissue forms at a range of possible rates (*e.g.*, Castanet et al., 2000, 2004; Starck & Chinsamy, 2002; de Buffrénil et al., 2021). For example, fibrolamellar bone tissue types with different vascularity form at differing, but overlapping rates (de Buffrénil et al., 2021). In penguin humeri, radially vascularized fibrolamellar bone is deposited at rates ranging from 45 to 145 µm per day (de Buffrénil et al., 2021). In Japanese quail, longitudinally vascularized fibrolamellar bone forms at rates ranging from 10–50 µm per day (Starck & Chinsamy, 2002). In addition, considerable overlap exists among the marginal values of apposition rates that correspond to distinct tissue types (de Buffrénil et al., 2021). Despite these limitations, bone typologies remain a useful tool for making general growth rate comparisons among closely related taxa.

Bone apposition growth rates

As detailed above under "Age assessment from periosteal bone apposition rates", bone apposition rates can be estimated by measuring cortical zone thickness. Expressed in microns per day (zone thickness divided by the number of days in a year, calibrated to geological age), these allow for growth rate comparisons among groups, including sauropodomorphs (Apaldetti et al., 2018; Cerda et al., 2022a). For example, Apaldetti et al. (2018) found that lessemsaurids (depending the definition, a clade of basal sauropods or the sister group of Sauropoda) grew faster than neosauropods, reporting apposition rates of 20–37 µm per day, compared to a maximum of 12 µm per day in eusauropods. This accelerated growth may have been crucial for lessemsaurids to achieve their massive body sizes (Apaldetti et al., 2018).

As with the use of bone typologies, estimation of growth rates from bone apposition rates has limitations. Measurement location, intraskeletal variation, assumptions about the annual duration of the active growth, and stochastic growth marks can skew results (Chinsamy & Pereyra, 2026). Despite these limitations, however, it can be considered that bone apposition rates across taxa are still valuable for comparative purposes, mostly among closely related taxa.

Growth curves

Absolute growth rate values during the exponential stage of sauropodomorph development are determined by reconstructing growth curves (Erickson et al., 2001; Lehman & Woodward, 2008; Griebeler et al., 2013; Myhrvold, 2013). Erickson et al. (2001) provided early estimations for the sauropodomorphs *Massospondylus* and *Apatosaurus*, calculating which maximum growth rates were estimated at 34.6 and 5466 kg/year, respectively.

Subsequent analyses yielded different results. Lehman and Woodward (2008) found considerably lower growth rates in *Alamosaurus*, *Apatosaurus, Janenschia*, and an indeterminate sauropod from England (the same described by Reid, 1981). Griebeler et al. (2013) also estimated sauropod growth rates at ~1500 kg/year. Ultimately, these estimated growth rates have been challenged by recent authors, largely due to the inherent uncertainties in estimating dinosaur body mass (Myhrvold, 2013).

While these earlier studies derived maximum growth rates from growth curves based on both inferred age and body mass, an alternative approach relies solely on inferring body mass. If a single individual's cortical bone preserves clear growth cycles, these cyclical increments can be converted directly into body mass increments (Sander et al., 2011b). By calculating the organism's body mass at the formation of each growth mark, the maximum growth rate can be determined simply from the body mass difference between the widest consecutive growth marks (*i.e.*, the thickest cortical zone). This technique has been used to estimate peak growth rates in several sauropodomorphs including *Plateosaurus, Mamenchisaurus, Apatosaurus, Camarasaurus* and *Europasaurus* (Upper Jurassic of Germany; Sander et al., 2011b).

In summary, maximum growth rate estimates exist for only a few sauropodomorph taxa, and the consistency of these results varies by methodology. While multi-method analyses of some taxa (*e.g.*, *Plateosaurus* and *Massospondylus*) yield consistent values, others show inconsistencies. The case of *Apatosaurus* is particularly illustrative, with the values ranging widely from a low of 485 kg/year (Myhrvold, 2013), to a high of 5466 kg/year (Erickson et al., 2001), and numerous intermediate estimates (550 kg/year, Lehman & Woodward, 2008; 1468–1613 kg/year, Griebeler et al., 2013; 962–2531 kg/year, Sander et al., 2011b). These discrepancies stem from varying growth models, unrealistic assumptions of isometric bone growth, inaccurate age determinations, and/or inaccurate body mass estimation (*e.g.*, Sander et al., 2011b; Griebeler et al., 2013; Myhrvold, 2013).

Despite these challenges, some general patterns emerge. Consistent with their smaller adult body sizes, basal sauropodomorphs (*e.g.*, *Plateosaurus*, *Massospondylus*) exhibit lower maximum growth rates than large bodied, sauropod dinosaurs. Most growth estimates for sauropods fall within the range of variation reported for precocial birds and modern mega-herbivores (*e.g.*, elephants) of equivalent projected body mass (Lehman & Woodward, 2008; Griebeler et al., 2013).

EARLY GROWTH

Early growth patterns are close tied to life histories. Therefore, studying bone microstructure of taxa during these early stages is crucial for understanding issues growth rates, growth cyclicity, developmental shifts linked to hatching or birth. It also sheds light on post-hatching biology (*e.g.*, altricial versus precocial) and changes in locomotion (*e.g.*, Cerda et al., 2014a; Curry Rogers et al., 2016; Zhao et al., 2019). While histological studies focusing on early growth stages of sauropodomorph dinosaurs remain scarce, they have already yielded important paleobiological insights.

Fossils of both embryos and perinates reveal the initial phases of sauropodomorph growth (Fig. 4A–F). For example, the Lower Lufeng Formation (Sinemurian, Lower Jurassic) in China has yielded multiple sauropodomorph embryos (possibly *Lufengosaurus*) representing various stages of development (Reisz et al., 2013). Histological analysis of these individuals revealed a consistently rapid growth rate throughout embryonic development, even outpacing the rates observed in birds and other dinosaurs. These high growth rates suggest short incubation times for these basal sauropodomorphs (Reisz et al., 2013). Bone histology also indicated asymmetric radial growth of the femoral shaft and rapid expansion of the fourth trochanter, suggesting that embryonic muscle activation played an important role in the pre-hatching ontogeny of these dinosaurs (Reisz et al., 2013).

Early ontogeny has also been examined in *Massospondylus carinatus* and in *Mussaurus patagonicus*. In the former, a juvenile *Massospondylus* (femur length: 12.75 cm) revealed the presence of at least one LAG, indicating a temporary cessation of growth early in ontogeny (Chinsamy, 1993). Interestingly, histological samples from similarly-sized individuals of *Mussaurus* lack LAGs (Cerda et al., 2014a; Pol et al., 2021b). Moreover, other histological features (higher porosity of the cortical bone, predominance of



Figure 4. Early growth of sauropodomorph dinosaurs. A, Life reconstruction of a titanosaur embryo from the Upper Cretaceous of Argentina (illustration by Jorge González). B–C, Long bone histology of titanosaur embryo, MCF-PVPH 808. D, Life reconstruction of a hatching individual of *Mussaurus patagonicus* (illustration by Jorge Blanco). E, Femur of a hatching individual of *Mussaurus patagonicus*; the longitudinally oriented section of the distal end (PVL 4068) reveals a thick layer of calcified epiphyseal cartilage, which is perforated by prominent canals. F, Femur of a juvenile individual of *Mussaurus patagonicus*, MPM-PV 1813-2. G, Life reconstruction of a perinate individual of *Rapetosaurus krausei* (illustration by Demetrios Vital). H, Right femur, fibula, and left tibia (reversed) of perinate *Rapetosaurus*, UA 9998, in anterior view. I–J, Proximal tibia epiphyseal microstructure showing abundant calcified cartilage. K–L, Mid-diaphyseal tibia microstructure. Abbreviations: cc, calcified cartilage; hl, hatching line; Kl, Kastschenko's line; mc, medullary cavity. Scales = 0.5 mm (B); 0.2 mm (C); 1 mm (E); 0.5 mm (F); 30 mm (H); 5 mm (I); 0.5 mm (J); 5 mm (K); 0.3 mm (L).

woven fibered matrix, and absent or poorly developed primary osteons) indicate a relatively faster early ontogeny growth rate in *Mussaurus* compared to *Massospondylus*. Because maximum growth rate varies depending on adult size (Case, 1978), these differing growth strategies not unexpected given the larger adult body size of *Mussaurus* (Cerda et al., 2014a).

Within Sauropoda, histological insights into the earliest phases of growth are restricted to just a few specimens. These include an undetermined titanosauriform the Late Jurassic of United States and some titanosaur specimens from the Upper Cretaceous of Argentina (Schwarz et al., 2007b; García & Cerda, 2010b; González et al., 2020; Zurriaguz et al., 2026) and Madagascar (Curry Rogers et al., 2016).

The Anacleto Formation of Argentina (early–middle Campanian) has yielded embryonic titanosaurs preserved in eggs. Microstructural analysis of the cranial and limb bones of these specimens revealed a high degree of cortical porosity and dense osteocyte lacunae in a context of woven bone consistent with a rapid growth rate (García & Cerda, 2010b). A recent review of the same sections has revealed the presence of a Kastchenko's line around the medullary cavity (González et al., 2020). The line marks the start of perichondral ossification and can be used to estimate the size of the cartilage template of long bones (Francillon-Vieillot et al., 1990). The presence of a Kastchenko's line supports the hypothesis that these titanosaur embryos died at an advanced developmental stage, though not immediately prior to hatching (Chinsamy-Turan, 2005; García & Cerda, 2010b).

Examining more advanced ontogenetic stages, Schwarz et al. (2007b) studied the long bone histology of a juvenile titanosauriform (initially interpreted as a diplodocid) from the Lower Morrison Formation (Late Jurassic) of north-central Wyoming (Schwarz et al., 2007b; Carballido et al., 2012). Consistent with its small size (femur length equals 22.4 cm), the cortical histology of the femur is entirely formed by highly vascularized, azonal woven fibered bone. Although the authors originally described this tissue as fibrolamellar bone, they also noted the absence of primary osteons—structures that are, by definition, present in a true fibrolamellar complex. Overall, the described histology indicates rapid, sustained growth in this individual.

Further insight into early post-hatching ontogeny in sauropods comes from a perinatal titanosaur, *Rapetosaurus krausei*, from the Late Cretaceous of Madagascar (Fig. 4G–L; Curry Rogers et al., 2016). This specimen includes several long bones, and is ~13% adult size (femur length: 19.2 cm). Densely vascularized fibrolamellar bone tissue characterizes its cross-sectional histology, indicating rapid growth rates (Curry Rogers et al., 2016). A distinct modulation, specifically a regional change in the vascular space organization and size, was interpreted as a hatching line (Curry Rogers et al., 2016). Equivalent histological structures have been also reported in other tetrapods, including squamates, crocodilians, birds and mammals (*e.g.*, Castanet et al., 1993, 2004; Starck & Chinsamy, 2002; Chinsamy & Hurum, 2006; Curtin et al., 2012; Hugi & Sánchez-Villagra, 2012; Nacarino Meneses & Köhler, 2018; Prondvai et al., 2020; Garrone et al., 2021; Woolley et al., 2021) and signal the stressful biological moment that hatching/birth represents.

The presence of this hatching line provided a direct measurement of the midshaft circumference of the hatching *Rapetosaurus* (Curry Rogers et al., 2016). Because anatomical evidence reveals that *Rapetosaurus* limb bones grew isometrically in length and width throughout their development, Curry Rogers et al. (2016) could estimate hatching body mass (~3.4 kg) using the femoral and humeral midshaft circumferences. The perinatal *Rapetosaurus* limb elements preserve only a thin layer of hypertrophied calcified cartilage at their ends, which contrasts sharply with the thick epiphyseal cartilages known in some other non-avian dinosaurs, such as the hadrosaurid *Maiasaura* (Horner et al., 2001). Both the histological and anatomical features of the *Rapetosaurus* perinate strongly suggest an active, precocial growth strategy (Curry Rogers et al., 2016).

New information regarding early growth in titanosaurs was provided by González et al. (2020). The material consists of two small femora (ranging from 23 to 33 cm length) of indeterminate titanosaurs from the Upper Cretaceous of Argentina. Both juvenile femora exhibit predominantly fibrolamellar bone tissue with a plexiform vascularization pattern, suggesting a relatively rapid growth rate. Despite the specimens' early developmental stages, secondary remodeling was evident in one of them. In the other sample,

a growth mark is observed, which suggests unexpected cyclical growth and departs from the typically reported fast, uninterrupted growth in neosauropod long bones (*e.g.*, Sander et al., 2004).

GROWTH DYNAMICS, LIFE HISTORIES AND GIGANTISM

Gigantism is undoubtedly the most notable feature of the sauropods—the most iconic clade of sauropodomorph dinosaurs. Sauropod gigantism was enabled by a specific combination of basal features and evolutionary innovations which triggered a remarkable evolutionary cascade (Sander et al., 2011a). Elevated growth rates are considered among the most important of these innovations, acting as a prerequisite for attaining such giant body sizes (Sander et al., 2011a). Changes in growth strategies recorded by the histological organization of the intrinsic collagenous fibers, presence and distribution of growth marks and density and arrangement of vascular spaces, provide information about the rate of periosteal bone accretion (Amprino, 1947; Francillon-Vieillot et al., 1990; Chinsamy-Turan, 2005).

It has been postulated that the origin of Sauropoda may have been accompanied by a significant change in growth strategy (*i.e.*, achievement of rapid, sustained growth) that facilitated the attainment of gigantism (Sander et al., 2004, 2011b). Basal sauropodomorphs often exhibit a higher proportion of parallel-fibered bone tissue that is less vascularized, along with cyclical growth dynamics recorded by cortical growth marks, indicative of a relatively slower growth rate (Chinsamy, 1993; Sander et al., 2004; Klein & Sander, 2007; Cerda et al., 2017). That said, deviations of this growth pattern occur in sauropodomorphs, complicating the "just-so" story of evolving gigantism (Fig. 5). One important departure from this pattern is observed in *Mussaurus*, which exhibits polymorphism in its growth strategies. These strategies can vary from cyclical, as seen in other early sauropodomorphs, to continuous, as reported in later sauropods (Cerda et al., 2022a).

Another important deviation is found in the Lessemsauridae, a group which can be considered giant itself, with included taxa reaching sizes ranging from 7–10 tons for *Lessemsaurus sauropoides* (Late Triassic from Argentina), to 12 tons for *Ledumahadi mafube* (Early Jurassic of South Africa; Apaldetti et al., 2018; McPhee et al., 2018). Like basal sauropodomorphs, lessemsaurids revealed a cyclical growth strategy (Cerda et al., 2017; Apaldetti et al., 2018; Krupandan et al., 2018; McPhee et al., 2018). However, in lessemsaurids this cyclical pattern is accompanied by the presence of highly vascularized fibrolamellar bone with reticular vascularity, indicative of accelerated growth rates during active growth intervals (Cerda et al., 2017; Apaldetti et al., 2018). Relatively high

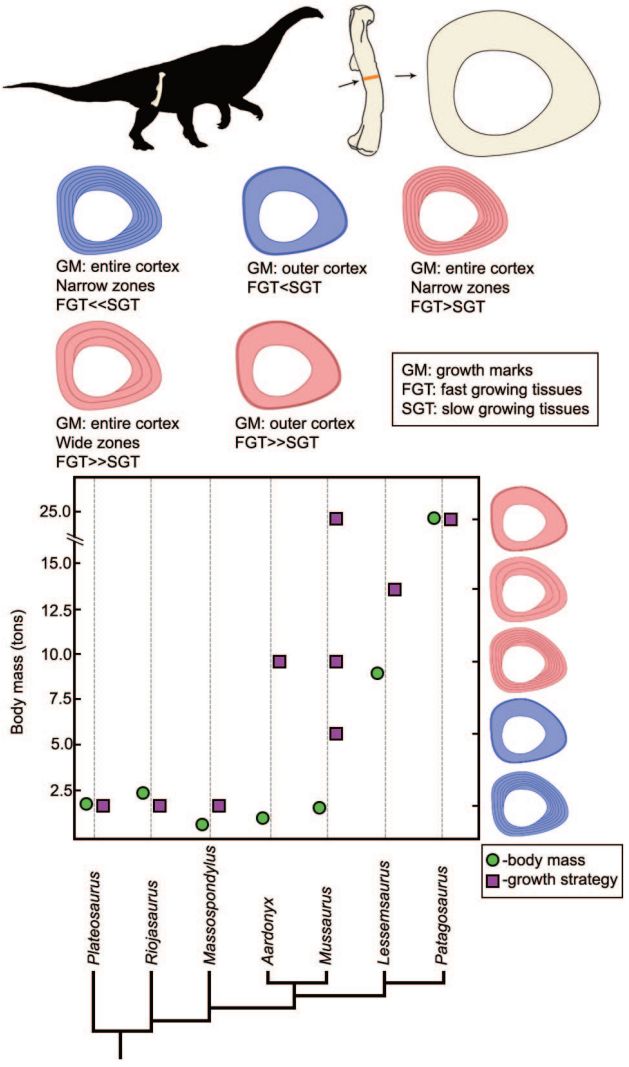


Figure 5. Diversity in the growth strategies among sauropodomorph dinosaurs (in this case, non Eusauropoda) and their relationship with body size and gigantism. The growth strategies are deduced from the presence and distribution of cyclical growth marks (lines of arrested growth) and the organization of intrinsic fibers of primary tissues (fast and slowing bone tissues, see main text) in long bone midshafts. Note the polymorphic nature of growth strategies in *Mussaurus*. Data regarding phylogenetic relationships, growth strategies and body mass obtained from Cerda et al. (2017), Apaldetti et al. (2018); Pol et al. (2021a), Otero and Pol (2021) and Botha et al. (2022).

growth rates are also evident from the wide spacing between successive growth marks (*e.g.*, 13.6 mm reported in a specimen of *Lessemsaurus*, which far surpasses the maximum values obtained for most sauropods (*e.g.*, 4 mm for *Janenschia*). Furthermore, the reticular and plexiform vascularity is another important difference between lessemsaurids and other sauropods, which usually exhibit laminar vascularity (Sander & Tückmantel, 2003; Klein & Sander, 2008; Cerda et al., 2017; Apaldetti et al., 2018; Krupandan et al., 2018). In sum, lessemsaurids reveal that sustained, uninterrupted growth is not a strict prerequisite for gigantism, but that an increase in appositional growth rates may be.

More recent studies further complicate the evolutionary narrative. The long bone histology of *Aardonyx celestae* (Early Jurassic) and *Sefapanosaurus zatronensis* (Late Triassic), two large but non-gigantic forms from South Africa closely related to the phylogenetic origin of Sauropoda (*i.e.*, non-Sauropoda Sauropodiformes), was characterized by the presence of highly vascularized fibrolamellar bone containing regular cyclical growth marks (Botha et al., 2022). These observations were interpreted as evidence for rapid, but seasonally interrupted growth. Thus, the capacity for rapid bone tissue formation, typical of sauropod dinosaurs, did not evolve specifically to enable giant body sizes but may have been a prerequisite for them (Botha et al., 2022).

A subsequent contribution by Toefy et al. (2025), which increased the sampling of non-Sauropoda Sauropodiformes, provided support for the hypothesis of high diversity in growth strategies during the early evolution of this lineage. This compendium of new publications indicates flexibility regarding growth strategies during the early evolution of Sauropodiformes. Rather than a directed and sequential evolution from a 'prosauropod model' to a 'sauropod model,' the evolution of growth strategies may be a mosaic of strategies that diversified over time, with one specific strategy eventually rising to dominance in neosauropods.

THE SMALLEST OF THE LARGEST: DWARF SAUROPODS

Bone microstructure has been extremely useful in detecting a particular biological phenomenon in sauropodomorph dinosaurs (more specifically, macronarian sauropods): phylogenetic size reduction, or dwarfism. The phenomenon was first proposed by Nopcsa (1914), who recognized that a titanosaur from the Late Cretaceous of Transylvania (later named as *Magyarosaurus dacus*) was relatively small (6 m long, 900 kg) compared to other members of the group (Jianu & Weishampel, 1999; Benton et al., 2010). This diminutive size was interpreted as a consequence of body-size effects of insular isolation, similar to the insular dwarf elephants and hippos of the Pleistocene (Jianu & Weishampel, 1999; Stein et al., 2010).

Bone histology data allowed Stein et al. (2010) to test for insular dwarfism in *M. dacus*. Although all the sampled individuals lacked an OCL, intensive remodeling and a high HOS were considered reliable indicators of the somatic maturation of the largest *M. dacus* specimens (Stein et al., 2010). Additionally, the relative abundance of parallel-fibered and lamellar bone in the non-remodeled cortical bones was interpreted as evidence of an extremely reduced growth rate of bone deposition compared to other sauropod dinosaurs. Together, these data supported the hypothesis of dwarfism in *M. dacus* (Stein et al., 2010).

A second case of phyletic nanism was hypothesized for the basal macronarian *Europasaurus holgeri* (Sander et al., 2006). As proposed for *M. dacus*, the remarkably small size of *Europasaurus* (6.2 m long, 800 kg) was also interpreted as a consequence of insular dwarfism (Sander et al., 2006). The long bone histology in an ontogenetic series of *Europasaurus* (individuals from 1.75 to 6.2 m long) was compared with that of *M. dacus*. The largest sampled specimen of *Europasaurus* revealed a distinct OCL/EFS in the outer cortex, indicating somatic maturity (Sander et al., 2006). In addition, its long bone histology departs from that of other sauropods in that cyclical growth marks are clearly differentiated in the cortex. Ultimately, the minute body size of *Europasaurus* appears to result from a reduction in primary appositional growth rate (Sander et al., 2006).

ORIGIN AND FORMATION OF SPECIFIC SKELETAL ELEMENTS

Although fossil materials do not directly record the process of ossification, the structure of the resulting primary bone (*i.e.*, the tissue first formed in the element) and

comparisons with extant groups can provide clues regarding its formation. This approach is particularly useful for identifying enigmatic osseous structures and allows testing hypothesis regarding the homology of particular elements. Among sauropod dinosaurs, paleohistological studies have provided relevant data regarding the origin of osteoderms in titanosaurs and hyper-elongated cervical ribs in neosauropods, as well as the identification of a supraspinous elastic ligament in some titanosauriforms.

Formation and functions of osteoderms

Dermal ossifications, usually known as osteoderms, dermal ossicles or dermal plates, represent the most commonly identified and documented osseous element of the integumentary skeleton among tetrapods (Vickaryous & Sire, 2009). Osteoderms are widely distributed among different groups of living and extinct tetrapods, including non-avian dinosaurs (Moss, 1969; Hill, 2005; Sire et al., 2009; Vickaryous & Sire, 2009). Among sauropodomorph dinosaurs, osteoderms are mostly restricted to derived sauropods (*e.g.*, Titanosauria; *e.g.*, Dodson et al., 1998; Salgado, 2003; D'Emic et al., 2009; Curry Rogers et al., 2011; Vidal et al., 2014, 2017; Zurriaguz, 2017; Fronimos, 2021). Although titanosaur osteoderms were identified during the nineteenth century (Depéret, 1896), their bone histology has only been studied in recent decades (*e.g.*, Salgado, 2003; Cerda & Powell, 2010).

The bone microstructure of titanosaur osteoderms has provided important clues regarding their ossification mechanism (*i.e.*, histogenesis), homology with similar structures in other tetrapods, and possible functions. Salgado (2003) provide the first attempt to infer the ossification mechanism of titanosaur osteoderms through microstructural analysis of an isolated element collected from the Upper Cretaceous of Argentina. He interpreted the abundance of mineralized fibers in the primary bone tissue as Sharpey's fibers and as evidence for metaplastic ossification. Bone metaplasia is a process in which a preexisting, non-osseous and fully developed tissue is transformed into bone (Haines & Mohuiddin, 1968). The hypothesis for a metaplastic ossification in titanosaur osteoderms was supported in subsequent publications (*e.g.*, Cerda & Powell, 2010; Cerda et al., 2015b). In these contributions, the metaplastic origin of the osteoderms was inferred by the presence of interwoven bundles of mineralized collagen fibers formally named "structural fibers" (Scheyer & Sander, 2004, 2007; Main et al., 2005; Witzmann & Soler-Gijón, 2008). These structural fibers correspond to the putative Sharpey's fibers identified by Salgado (2003). It should be noted that, although Sharpey's fibers, like structural fibers, can originate from the dermis, their spatial organization is strongly different, since they do not form a matrix of discrete and interwoven bundles that characterizes the latter. Beyond inferences about ossification mechanisms, the microstructure of titanosaur osteoderms has provided clues about the homology of these elements. In this regard, the millimeter-sized osteoderms (*i.e.*, ossicles) of *Saltasaurus loricatus* are formed by at least three orthogonal systems of structural fiber bundles: one vertical and two horizontal (Fig. 6). This arrangement is identical to that reported for the ossicles of the ankylosaur *Antarctopelta oliveroi* (de Ricqlès et al., 2001; Cerda et al., 2019; Sanchez et al., 2025). This strong resemblance suggests deep homology, wherein a common mineralization process occurs in the same integumental layer of distantly related groups and generates anatomically similar, but convergently evolved structures (Main et al., 2005; Cerda & Powell, 2010). Although the osteoderms of titanosaurs and ankylosaurs are not homologous, the capability of the dermis to produce them is homologous (Zylberberg & Castanet, 1985; Hill, 2006; Vickaryous & Hall, 2008; Vickaryous & Sire, 2009).

Function is another important question regarding titanosaur osteoderms. Different, and in several cases non-mutually exclusive, functions have been proposed for these skeletal elements, including passive and/or active defense, serving as a mineral reservoir, thermoregulation, and display and/or species recognition (*e.g.*, Powell, 1980; Sanz & Buscalioni, 1987; Le Loeuff et al., 1994; Salgado, 2003; Cerda & Powell, 2010; Curry Rogers et al., 2011; Marinho & Iori, 2011; Cerda et al., 2015a; Vidal et al., 2017; Fronimos, 2021; Silva Junior et al., 2022). Microanatomical and histological data has provided relevant information to tests these hypotheses. A mineral-storage function has been supported by the presence of both large internal cavities and several prominent vascular spaces within osteoderms (Curry Rogers et al., 2011; Cerda et al., 2015a; Vidal et al., 2017; Fronimos,

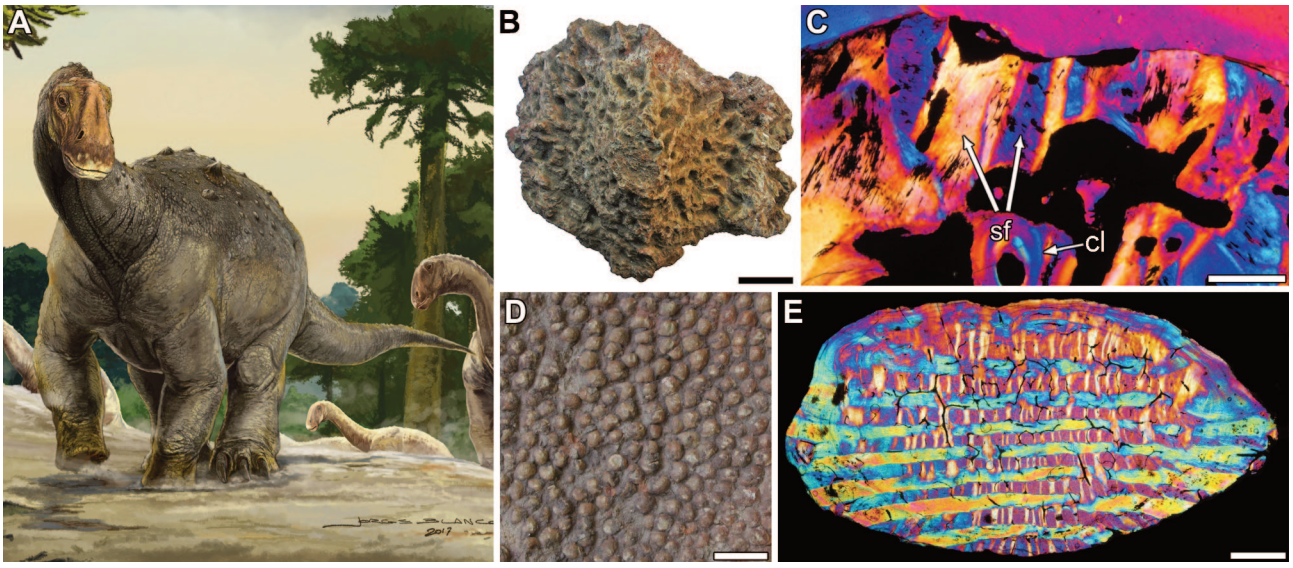


Figure 6. Osteoderm histology of titanosaurs. A, Life reconstruction of *Saltasaurus loricatus* (illustration by Jorge Blanco). B, Dermal plate in superficial view, PVL 4017—113. C, External cortex of the dermal plate showing coarse bundles of mineralized structural fibers derived from dermal tissue; secondary remodeling is evident by the presence of Haversian osteons and cementing lines. D, Dermal ossicles in deep view, PVL 4017—119. E, Complete section of a single ossicle, PVL 4017—108 formed entirely by mineralized structural fibers. Abbreviations: cl, cementing lines; sf, structural fibers. - Scales = 20 mm (B); 0.5 mm (C); 20 mm (D); 1 mm (E).

2021). These vascular canals possibly allowed rapid mobilization of the mineral reserves from the osteoderms to other parts of the body (Curry Rogers et al., 2011). A probable role of passive defense has been supported for the distribution and microstructural features found in the dermal ossicles of *Saltasaurus* (Cerda & Powell, 2010). The tight arrangement of these osteoderms, which were surrounded by the thick collagenous fiber bundles of the unmineralized portions of the dermis, likely imparted strength and resistance to the integument (Cerda & Powell, 2010; Cerda et al., 2015a).

Cervical ribs formation

Bone histology also has also been employed to determine the mechanism of formation of the hyperelongated cervical ribs found in several sauropod taxa. Cervical ribs in which the shaft extends backward to two or more vertebrae have been reported in several sauropod dinosaurs, including basal titanosauriforms, derived lithostrotians and mamenchisaurids (*e.g.*, Janensch, 1950; Young & Zhao, 1972; Wedel et al., 2000; Salgado & Carvalho, 2008; Gallina & Apesteguía, 2015; Díez Díaz et al., 2018). These skeletal structures regularly form thick bundles of superimposed elements (Fig. 7A–C). The microstructure of the primary bone tissue of the cervical ribs have provided evidence that these elements, at least in part, originated from metaplastic ossification of a tendinous structure (Cerda, 2009; Gallina, 2012; Klein et al., 2012b; Díez Díaz et al., 2018; Woodruff et al., 2018; Brum et al., 2022; Windholz et al., 2023). Specifically, the bone tissue of the cervical ribs shaft is composed of coarse bundles of mineralized collagenous fibers, which are oriented parallel to the rib main axis (*contra* Brum et al., 2021).

The only different interpretation of the primary bone tissue in sauropod cervical ribs was provided by Brum et al. (2021), who stated that the structure was formed by fibrolamellar bone with Sharpey's fibers. This interpretation lacks evidence (Cerda, 2009; Gallina, 2012; Klein et al., 2012b; Cerda et al., 2015b; Díez Díaz et al., 2018; Woodruff et al., 2018; Brum et al., 2022; Windholz et al., 2023), including from the figures provided in the publication (Brum et al., 2021, figs. 3–4). Brum et al. (2021) putative Sharpey's fibers appears to record the structure and orientation of tendinous tissues mineralized by metaplasia.

It is worth noting that a tendinous origin for the cervical rib shafts is not restricted to hyper-elongated elements,

but also applies to short ribs (Klein et al., 2012b). Histological studies indicate that the same mechanism extends to the cervical ribs shaft in other sauropodomorphs as *Plateosaurus*, and even in other archosaurs (*e.g.*, crocodylians; Preuschoft & Klein, 2013). The tendinous origin of the cervical ribs has been interpreted in mechanical terms. In this regard, Klein et al. (2012b) considered that the transformation of the cervical ribs into ossified tendons makes the sauropod neck more flexible and implies that tension forces acted mainly along the length of the neck.

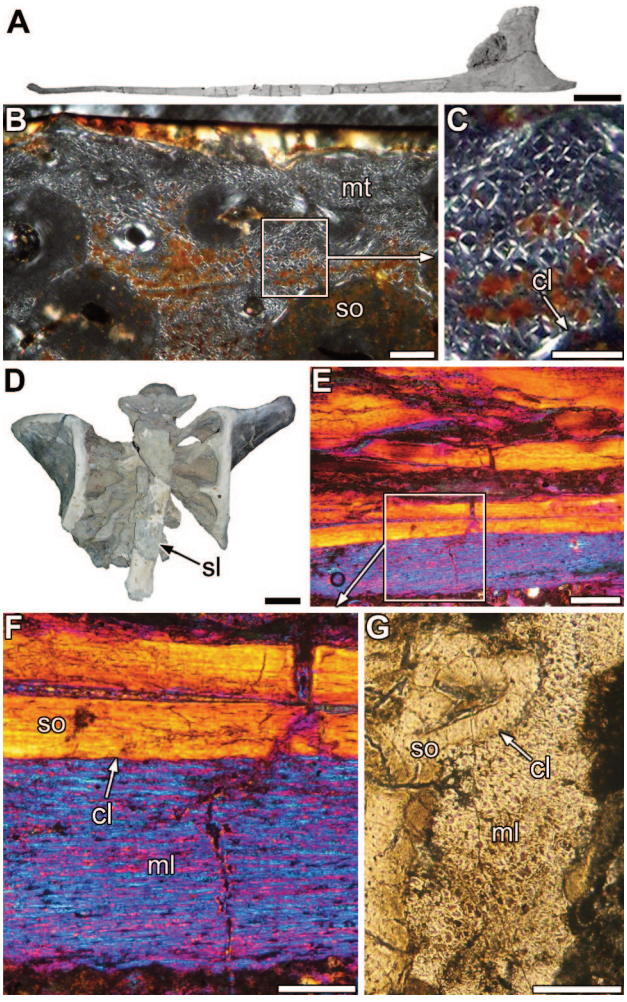


Figure 7. Examples of tendinous and ligamentous mineralizations in sauropod dinosaurs. A, Cervical rib of *Bonitasaura salgadoi*, MPCA-Pv 460 in lateral view (modified from Gallina, 2011). B, Outer cortex of a single cervical rib in cross (Titanosauria indet., MCS-Pv uncatalogued specimen); the primary bone is entirely formed by mineralized fibers of a tendinous tissue; note the presence secondary osteons. C, Detailed view of the bone tissue showed in D; distinct cementing lines indicate the boundary between primary and secondary bone. D, Sacrum of *Epachthosaurus sciuttoi*, UNPSJB-PV 920, in dorsal view, showing an ossified elastic supraspinous ligament over the sacral vertebrae spines. E, Longitudinal section of the mineralized elastic ligament from Lithostrotia indet., MDT-Pv 4. F, Detailed view of previous image showing the structure of the mineralized elastic ligament. G, Detail of the transverse section of the same specimen; the mineralized ligament has been partially replaced by secondary bone. Abbreviations: cl, cementing lines; ml, mineralized elastic ligament; mt, mineralized fibers of tendinous tissue; sl, supraspinous ligament; so, secondary osteons. Scales = 5 cm (A); 0.1 mm (B); 0.05 mm (C); 20 cm (D); 0.5 mm (E); 0.2 mm (F); 0.2 mm (G).

As a final consideration, histological analysis of both sauropod osteoderms and ribs have helped resolve the nature of particularly enigmatic osseous elements. For example, histology helped to refine the identity of putative osteoderms of the enigmatic rebbachisaurid *Agustinia ligabuei* (Lower Cretaceous of Argentina). These elements were eventually re-interpreted as cervical and dorsal ribs (Bellardini & Cerda, 2017).

Ossified tendinous and ligamentous structures. Bone histology has provided insight about the nature of other sauropod skeletal elements of unknown origin. The first was reported by Martínez et al. (2016) and corresponds to a thin (diameter of approximately 3 mm), "cable-like" structure, located ventrolateral to the right side of the cervical vertebrae and ribs of *Sarmientosaurus musacchioi*, a basal lithostrotian from the Upper Cretaceous of Argentina. The presence of longitudinally oriented mineralized fibers in the primary bone of this is long structure was interpreted as, in the cervical ribs, evidence for a tendinous origin (Martínez et al., 2016). Another structure interpreted as tendinous in origin was ported for *Camarasaurus lentus* (Upper Jurassic of USA; Organ & Adams, 2005).

Relatively more common than these isolated tendinous ossifications are the sacral 'supraspinous rods' recorded in some titanosauriforms. A 'supraspinous rod' consists of an elongated structure that runs along the apices of the neural spines of the sacral vertebrae. This structure has been identified in at least 12 specimens of several taxa (Mocho et al., 2024). The bone microstructure of the 'supraspinous rod,' analyzed in a specimen of *Epachthosaurus sciuttoi* and an undetermined lithostrotiam (both from the Upper Cretaceous of Argentina), preserved primary bone tissue that was consistent with presence of an ossified elastic ligament (Fig. 7D–G; Cerda et al., 2015b). This interpretation was later supported by Woodruff et al. (2016) based on structural characterization of fossilized soft tissues in a specimen of *Alamosaurus*. The "supraspinous rod" possibly

originated from a non-pathological ossification of the elastic supraspinous ligament, potentially induced by the continuous tensile forces applied to the element (Cerda et al., 2015b).

Mineralized ligaments in sauropodomorphs are also observed in the cervical and caudal vertebrae of *Diplodocus* (Horner et al., 2016; Woodruff, 2016). In the caudal vertebrae, sections of a neural spine revealed that the outer primary tissue consists of a mineralized fibrocartilage interpreted as the enthesial attachment of the nuchal ligament (Horner et al., 2016). Similarly, a "trident-shaped" structure in the neural arch of an immature *Diplodocus* vertebra was identified as a mineralized interspinal ligament, though without preserved fibrocartilage (Woodruff, 2016). The hypothesized ligamentous nature of the bone tissue reported in both cervical and caudal vertebra of *Diplodocus* is supported by primary microstructure as well as the presence of "secondary reconstructions" (Horner et al., 2016). Horner et al. (2016) distinguish these reconstructions from typical secondary osteons because they lack osteocyte lacunae and true cementing lines. With few exceptions (Scheyer & Sander, 2004; Wilson et al., 2016; Woodruff et al., 2018), similar "secondary reconstructions" have not been reported in other tissues of metaplastic origin (*e.g.*, Reid, 1996; de Ricqlès et al., 2001; Barrett et al., 2002; Main et al., 2005; Hill, 2006; Scheyer & Sánchez-Villagra, 2007; Witzmann & Soler-Gijón, 2008; Cerda, 2009; Cerda & Powell, 2010; Hayashi et al., 2010; Klein et al., 2012b; Sterli et al., 2013, 2020; Burns & Currie, 2014; Cerda et al., 2015a, 2015b, 2018, 2019; Chinsamy et al., 2016; Bellardini & Cerda, 2017; Ponce et al., 2017; Díez Díaz et al., 2018; Paulina-Carabajal et al., 2021; Brum et al., 2022; Windholz et al., 2023; Sanchez et al., 2025). Typically, primary tissue originating from metaplastic ossification is reconstructed with distinct secondary osteons featuring clear cementing lines and osteocyte lacunae (Figs. 6C, 7B, F). Further investigation, especially in extant taxa, is needed to determine the nature of these "secondary reconstructions."

SOFT TISSUE RECONSTRUCTIONS

Osseous microstructure provides important insights into associated soft tissues. Muscle and/or tendon attachment, for example, alters the bone microstructure by modifying vascular canal organization and producing Sharpey' fibers (*i.e.*, extrinsic fibers) at attachment sites (Jones & Boyde, 1974; Francillon-Vieillot et al., 1990; Aaron, 2012).

A soft tissue of particular interest in saurischian dinosaurs is the thin epithelium of the pneumatic diverticula derived from the lung and air sacs. These structures are documented or inferred in several ornithodiran archosaurs, including pterosaurs and saurischian dinosaurs (*e.g.*, Britt, 1997; Wedel, 2005; O'Connor, 2006; Cerda et al., 2012). Pneumatic features in sauropodomorphs have traditionally been assessed using external and internal anatomy (*e.g.*, Janensch, 1947; Britt, 1997; Wedel, 2003, 2009; Schwarz et al., 2007a; Yates et al., 2012; Zurriaguz & Cerda, 2017; Apaldetti et al., 2018; Zurriaguz, 2025; Windholz et al., 2019, 2025). More recently, histological approaches have also been applied to evaluate their relationship with bone tissue.

Lambertz et al. (2018) described thin extrinsic fibers associated with the diverticular epithelium and proposed the term "pneumosteon". Subsequent studies reported similar tissues in the axial skeletons of South American titanosaurs from the Upper Cretaceous of Brazil (*Uberabatitan ribeiroi*, *Ibirania parva*, and *Austroposeidon magnificus*; Aureliano et al., 2020, 2021a; Brum et al., 2022), and interpreted them as additional evidence of pneumatic diverticular invasion into bone. However, other histological studies of pneumatized sauropod bones (*e.g.*, *Patagotitan mayorum* (Late Cretaceous of Argentina), *Saltasaurus loricatus*, *Rapetosaurus krausei*, and an indeterminate Titanosauria from the Late Cretaceous of Spain) have not identified pneumosteal tissue (Sellés et al., 2015; Chinsamy et al., 2016; Carballido et al., 2017; Curry Rogers & Kulik, 2018). Moreover, Fernández et al. (2025) found that supposed extrinsic fibers in *Rocasaurus muniozi*, a hyperpneumatic titanosaur from the Late Cretaceous of Argentina are largely absent or restricted to diagentically altered regions, suggesting earlier identifications may be taphonomic artifacts. Together, these findings cast doubt on the widespread occurrence of pneumosteon (*e.g.*, Aureliano et al., 2020; 2021a).

Sharpey's fibers also inform muscle and ligament reconstructions. In *Patagotitan mayorum,* dense bundles of these fibers in the outer cortex of neural spines and transverse processes indicate strong ligamentous and muscular attachments (Carballido et al., 2017). Their

orientation can further reveal the direction of tensile forces and thus aspects of biomechanics (Petermann & Sander, 2013).

Histology has also informed interpretations of unusual skeletal structures. Dicraeosaurids are characterized by elongated hemispinous processes in the presacral vertebrae (*e.g.*, Salgado & Bonaparte, 1991; Coria et al., 2019; Gallina et al., 2019; Windholz et al., 2021). These structures show an extreme elongation in some taxa, including Early Cretaceous Argentinean forms as *Amargasaurus, Bajadasaurus,* and *Pilmatueia,* where they have been interpreted as supporting sails, bison-like humps, or internal osseus cores of cervical horns. These alternative hypotheses have been recently tested using both morphological and histological information mostly obtained from the holotype of the *Amargasaurus* (Cerda et al., 2022b). The hypothesis of a keratinous sheath was rejected, in part, on the basis of the distribution and orientation of Sharpey's fibers. Instead, Sharpey's fiber organization supports the presence of a system of interspinous ligaments that possibly connect successive hemispinous processes in *Amargasaurus* and indicate the presence of a "cervical sail" in *Amargasaurus* and other dicraeosaurids (Cerda et al., 2022b).

PALEOPATHOLOGY

Paleopathology examines disease and injury in fossil organisms and provides insight into behavior, population dynamics, and disease evolution (Rothschild & Tanke, 1992; Tanke & Rothschild, 2002; Rothschild & Martin, 2006). Pathologies are commonly identified through gross morphology or CT imaging (*e.g.*, Kaikaew et al., 2025), but many are only detectable histologically through deviations in the microscopic structure of bone tissue (*e.g.*, Krupandan et al., 2018; De Cerf et al., 2021). Because relatively few fossil bones are thin sectioned, it is highly likely that the frequency of palaeopathologies in extinct taxa is underestimated (Jentgen-Ceschino et al., 2020).

Sauropodomorphs exhibit a wide range of skeletal pathologies (*e.g.*, Hatcher, 1901; Gilmore, 1932; Rothschild & Berman, 1991; Reid, 1996; McWhinney et al., 2001; Chinsamy & Tumarkin-Deratzian, 2009; Butler et al., 2013; Lovelace, 2014; Xing et al., 2014; Martinelli et al., 2015; Barbosa et al., 2016, 2018, 2019; Chinsamy et al., 2016; García et al., 2017; Tschopp et al., 2016; Witzmann et al., 2016; Krupandan et al., 2018; González et al., 2017; de Cerff et al., 2021; Woodruff et al., 2022; Cruzado-Caballero et al., 2023; Tan et al., 2024; Dupuis et al., 2025; Kaikaew et al., 2025; Aureliano et al., 2026). Several of these studies have permitted the diagnosis of the disease that afflicted the dinosaur, such as osteopetrosis, enthesophytes, neoplasias, pneumonia and infections. In other cases, diagnoses are uncertain due to ambiguous morphologies or overlapping histological signatures (*e.g.*, Kaikaew et al., 2025).

Several recurring histological patterns have been described (*e.g.*, Fig. 8). Highly vascularized bone, characterized by enlarged vascular canals and resorption cavities, is often associated with tumors and/or infections. This pattern has been reported by Barbosa et al. (2016), González et al. (2017), and Aureliano et al. (2021b). Barbosa et al. (2016) reported two types of bone tumors (hemangioma and osteoma) in a caudal vertebra of an indeterminate titanosaur. Histological examination of a small vertebral bony protuberance revealed abundant "microtrabecular" bone that was densely vascularized with abundant osteocyte lacunae (Barbosa et al., 2016, fig. 3F). Aureliano et al. (2021b) described a periosteal and perimedullary lesion in a titanosaur fibula titanosaur, which documented radial and reticular vascularization in fibrolamellar bone, including regions with a notable increase of the reticular vascularization and resorption cavities.

Avascular bone tissue with abundant bundles of collagenous fibers has been linked to ossified tendons and/or enthesophytes. Tschopp et al. (2016) studied several bony spurs in phalanges of a camarasaurid sauropod. The spurs observed in the first pedal ungual were attributed to ossified tendons. Histologically, they were dominated by avascular bone, but included regions of dense Haversian bone (Tschopp et al., 2016, fig. 5). García et al. (2017) reported evidence of osteomyelitis and enthesophytes in different caudal vertebra from an indeterminate titanosaur (Fig. 8A–C). As a final example, in a study of the titanosaur *Bonitasaura salgadoi* (Upper Cretaceous of Argentina), González et al. (2017) described three different pathologies, an osteoblastic tumor (femur), an infection (vertebra) and an entesophyte (metatarsal). While the pathological bone of the femur was formed by fibrolamellar tissue with abundant

radially oriented vascular canals, the prezygapophysis of the vertebra is composed of poorly vascularized tissue formed by coarse and chaotically arranged bundles of mineralized fibers (González et al., 2017, fig. 5C).

One of the most commonly reported pathological bone tissues is the 'sunburst pattern' consisting of radially oriented bony spicules extending perpendicular to the periosteum/surface of the bone, and commonly associated

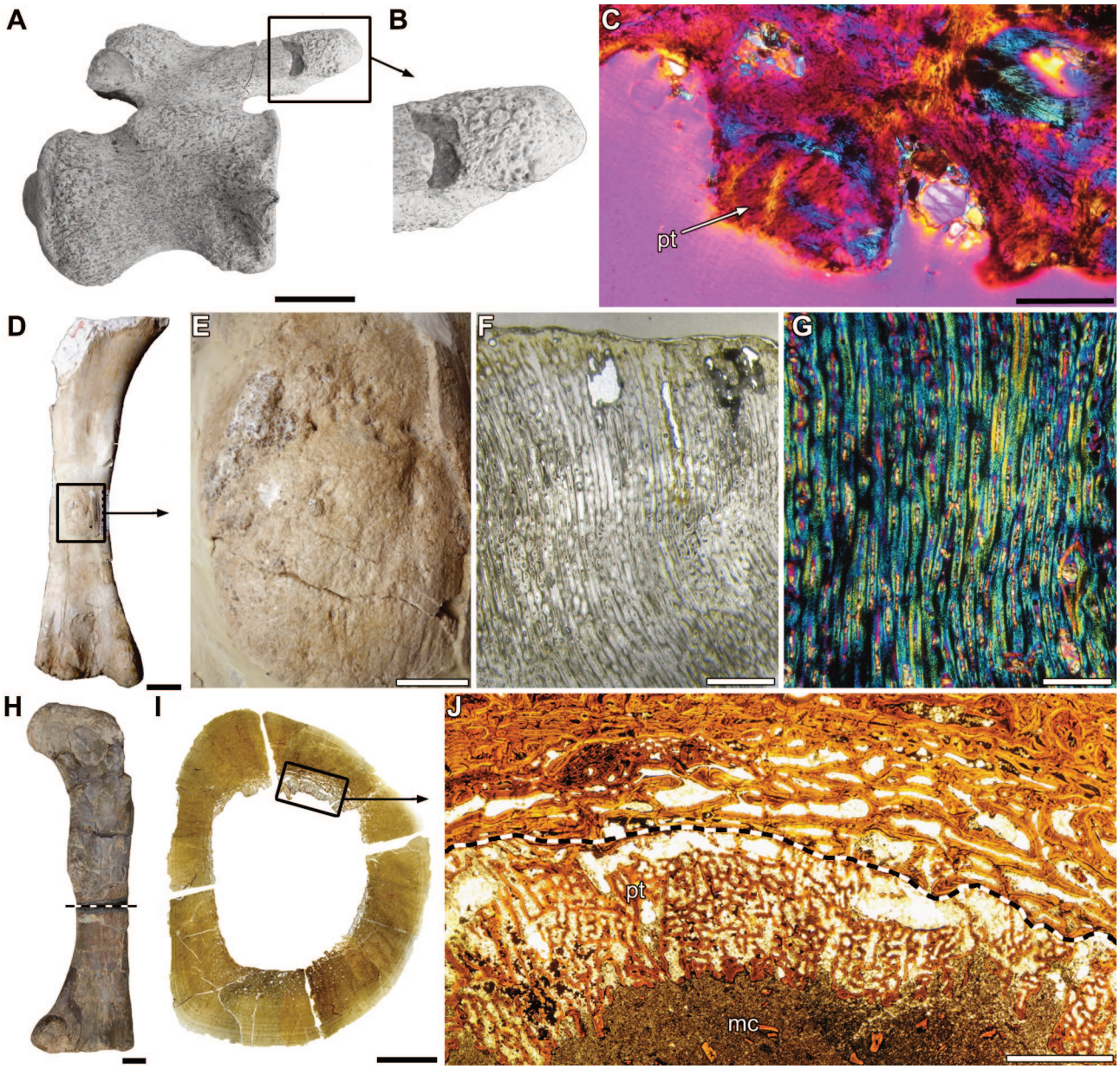


Figure 8. Examples of pathological conditions in sauropod dinosaurs. A, Caudal vertebra of indeterminate titanosaur, MCS-Pv 183/8, in lateral view (inverted image). B, Detail of the prezygapophysis showing an irregular, 'microbubbly' texture in the surface. C, Longitudinally section of a pathological prezygapophysis of the same individual. D, Left femur of *Bonitasaura salgadoi*, MPCA-Pv 460, in posterior view. E, Detail of the overgrowth inferred as an osteoblastic tumor, located at the element midshaft. F–G, General view and detail of the pathological tissue formed in the femur viewed under plane polarized light and cross polarized light with lambda filter respectively. H, Femur of *Mussaurus patagonicus,* MLP 61-III-20–22, in posterior view. I, Complete cross section of the femur. J, General view of the pathological tissue formed around the medullary cavity; Abbreviations: mc, medullary cavity; pt, pathological tissue. Dashed lines = H, position of the section showed in I; J, boundary between the pathological tissue and the normal bone. Scales = 5 cm (A); 0.5 mm (C); 10 cm (D); 5 cm (E); 2 mm (F); 1 mm (G); 5 cm (H); 2 cm (I); 0.3 mm (J).

with reactive growth and/or tumors (*e.g.*, Chinsamy & Tumarkin-Deratzian, 2009; González et al., 2017; de Cerff et al., 2021; Kaikaew et al., 2025). Brum et al. (2021) described a periosteal and endosteal outgrowth in the proximal part of a titanosaur dorsal rib. The histology of the outgrowth is formed by a fibrolamellar tissue with wide longitudinal and radial vascular canals and was hypothesized to be the result of reactive bone growth due to an intra-thoracic infection (pneumonia, probably related to tuberculosis). More recently, the presence of spiculated periosteal reactive tissue in the ulna of a mamenchisaurid from the Late Jurassic of Thailand, combined with other pathological histological features, permitted the identification of the pathology as an osteogenic tumor (Kaikaew et al., 2025). However, despite excluding several pathologies such as osteosarcoma, osteomyelitis, and intraosseous abscess, the precise etiology in the mamenchisaurid remains unknown.

Pathological tissues of endosteal origin have also been documented in sauropodomorphs. For example, an abnormal tissue characterized by a highly vascularized matrix and dense osteocyte lacunae was found within the medullary cavity and inner cortical zone of an adult *Mussaurus patagonicus* femur (Cerda et al., 2014b). Initially attributed to a retrovirus-induced disease akin to avian osteopetrosis, this tissue was later reinterpreted by Prondvai (2017) as avian-like medullary bone. Similarly, unusual endosteal tissues have been reported in titanosaur from the Upper Cretaceous of Northern Argentina (Chinsamy et al., 2016). Highly vascularized bone tissue was observed in the pneumatic cavities and intertrabecular spaces of an osteoderm, a metatarsal, and a posterior caudal vertebra. While the exact nature of the tissue in the caudal vertebra and osteoderm could not be determined, the authors concluded that the metatarsal tissue was pathological, though a specific diagnosis was not established.

Diagnosis remains challenging because different diseases can produce similar bone responses, and soft tissue indicators are usually absent (*e.g.*, Kaikaew et al., 2025). Additionally, modern clinical diagnoses rarely rely on bone histology alone, limiting direct comparisons. Despite these limitations, documenting and describing pathologies remains valuable for understanding disease in the fossil record (*e.g.*, Thompson & Dittmer, 2016; Kaikaew et al., 2025).

PALEOCYTOLOGY

Osteocytes represent the main cellular component of bone tissue and carry out important functions in bone growth and physiology (Hall, 2005; Davesne et al., 2020). They derive from bone-producing cells called osteoblasts which become incorporated into the surrounding collagen matrix during bone growth (Franz-Odendaal et al., 2006). Osteoblasts transform into osteocytes when they are enclosed within the matrix during osteogenesis (Ferretti et al., 2002; Zylberberg, 2021). Osteocytes are contained within cavities called lacunae which are interconnected via small conducts, the canaliculi. Given the small pericellular space within each lacunae, the size and shape of these a hard-tissue record of the osteocyte morphology (Franz-Odendaal et al., 2006; Zylberberg, 2021). Since osteocyte lacunae are commonly well-preserved in fossils bones, they represent a valuable source of information in paleovertebrate biology (*e.g.*, Organ et al., 2009, 2011; D'Emic & Benson, 2013; Sanchez et al., 2013). In this regard, some aspects of the sauropodomorph paleobiology have been analyzed from the study of osteocyte lacunae and associated structures as canaliculi.

Osteocyte lacunar density has been linked to growth rate and metabolic regime (Cubo et al., 2012). Stein and Werner (2013) analyzed the osteocyte lacunar density in several sauropodomorph taxa, including both basal (*e.g.*, *Plateosaurus*) and derived (*Apatosaurus*) taxa. They found that sauropods show unexpectedly high lacunar densities, comparable to, or exceeding that of mammals, though Nevertheless, similar values in squamates, complicate simple interpretations (Stein & Werner, 2013).

Rensberger and Martínez (2015) analyzed the density of osteocyte cytoplasmic surface (estimated from the measurement of the perimeters of osteocyte lacunae, the lengths of canaliculi, the number of canalicular branching points and the total canalicular and lacunar perimeters). They found that saurischian dinosaurs possessed the most densely organized bone cell cytoplasm of any of the tetrapod groups examined. Among the non-avian dinosaurs sampled, they included a femur from an undetermined diplodocid, a ti-

tanosaur "limb" bone from the Late Cretaceous of India and a dorsal rib of *Adeopapposaurus mognai*, a massospondylid from the Early Jurassic of Argentina. The elevated density of the cytoplasmic surface area found in saurischian dinosaurs was hypothesized to directly relate to high rates of osteogenesis (Rensberger & Martínez, 2015). It must be noted that the analyzed data provided in this contribution included a wide range of different skeletal elements, from rib to proximal and distal limb bones, which can significantly affect the results and interpretations (D'Emic & Benson, 2013), and the influence of diagenesis on the preservation of these microstructures was not accounted for.

It has been established that a strong correlation exists between cell size and genome size in living vertebrates (Gregory, 2001). Since the shape and size of a single osteocyte and the lacuna in which is contained are almost equal since the small pericellular space within each lacuna, genome size has been repeatedly inferred using measurements from osteocyte lacunae (*e.g.*, Organ et al., 2007, 2011; Organ & Shedlock, 2009). Using this approach, Organ et al. (2009) analyzed the genome size in 10 sauropodomorph taxa and found that this parameter does not exhibit deep variations in the evolution of the clade (different from theropods dinosaurs, in which the genome size was strongly reduced in the evolutionary transition to birds; but see D'Emic & Benson, 2013 for a different interpretation). Also, these authors also do not find a relationship between body size and estimated genome size in extinct dinosaurs. Inferences made from paleogenomic studies have been questioned by some authors, mainly considering methodological problems. In this sense, D'Emic and Benson (2013) carried out a study that included living forms of birds as well as non-avian theropod and sauropod dinosaurs. Using a different methodology to estimate the volume of osteocyte lacunae, these authors found differences with respect to previous studies (Organ et al., 2009). For example, they found that the osteocyte lacunae of the sauropods *Sauroposeidon proteles* and *Abydosaurus mcintoshi* (both from Lower Cretaceous of North America) were smaller than those of an ostrich. From the above, although methodologies still need to be refined, the preservation of osteocyte lacunae may offer a fruitful area of future research.

TOOTH HISTOLOGY AND ATTACHMENT

Tooth replacement rates in fossil vertebrates are commonly estimated from incremental lines of von Ebner (see Kosch & Zanno, 2020 for a review). Von Ebner lines are daily formed growth marks present in the dentin (Fig. 9; Erickson, 1996a, b). Paleontological studies have therefore used direct von Ebner line counts to estimates tooth formation times and replacement rates in extinct species (*e.g.*, Erickson, 1996b; Chinsamy et al., 2012b; D'Emic et al., 2019; Ricart et al., 2019; Nacarino-Meneses & Chinsamy, 2022), including sauropodomorph dinosaurs (Sereno et al., 2007; D'Emic et al., 2013, 2025; García & Zurriaguz, 2016).

In sauropodmorphs, replacement rates vary widely. D'Emic et al. (2019, 2025) analyzed the tooth formation and replacement rates in several sauropodomorph taxa using both the tooth size and the spacing of lines of von Ebner. Basal macronarians (*e.g.*, *Camarasaurus*) and brachiosaurids (*e.g.*, *Abydosaurus*) retain the ancestral sauropod condition of relatively low tooth replacement rates (2–3 months to replace a tooth in a single alveolus), whereas diplodocoids (*e.g.*, *Diplodocus*) evolved much higher rates (2–5 weeks to replace a tooth in a single alveolus). High replacement rates inferred for diplodocoids appears to be convergent for Titanosauria. These results suggest that, along with the strong morphological variation in tooth crowns in sauropod dinosaurs, the tooth replacement rates were also highly variable. Such variation in the replacement rates likely reflects disparate feeding strategies and/or food choices (D'Emic et al., 2019, 2025).

To date, the tooth histology of embryonic sauropodomorphs has been studied only in *Lufengosaurus* (Early Jurassic of China; Reisz et al., 2020). Although dental tissues such as enamel and dentine were identified in the *Lufengosaurus* embryos, the authors do not mention the presence of von Ebner lines. Histological data revealed that embryonic *Lufengosaurus* teeth were implanted in a pleurodont fashion, which contrasts with the thecodont condition in adult individuals (Reisz et al., 2020).

Tooth implantation and attachment are particularly well studied among vertebrates because of their relevance in systematics and phylogenetic relationships (Bertin et al., 2018; Reisz et al., 2020). Most of these studies have provided valuable information regarding whether tooth

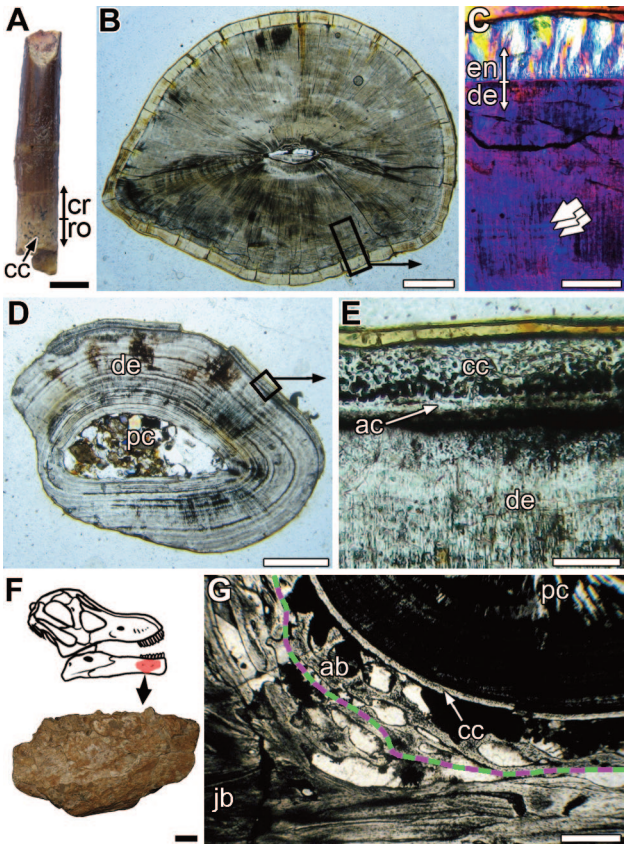


Figure 9. Tooth and tooth attachment in titanosaur sauropods. A, Indeterminate titanosaur tooth, MCS-Pv 94, in lingual view; both the crown and the root of the tooth are preserved; the root is still partially covered by a thin layer of cellular cementum. B, Indeterminate titanosaur tooth, MPCA-Ph 17, complete section at level of the crown. C, Detail of the same tooth showing dentine and enamel. D, Indeterminate titanosaur tooth, MPCA-Ph 13, complete section al level of the root; the section includes the pulp cavity. E, Detail of the cellular cementum, acelular cementum, and dentine; a thin layer of cellular cementum coats the root. F, Indeterminate titanosaur, sampled fragment of right dentary in lateral view; the upper scheme below indicates its relative position. G, longitudinal section at the level of the root tooth; the image show part of the root tooth with cellular cementum, alveolar bone, and jaw bone. Abbreviations: ab, alveolar bone; ac, acelular cementum; cc, cellular cementum; cr, crown of the tooth; de, dentine; jb, jaw bone; pc, pulp cavity; ro, root of the tooth. White arrows = presence of von Ebner lines; dashed line = boundary between the alveolar and jaw bone. Scales = 5 mm (A); 1 mm (B); 0.2 mm (C); 1 mm (D); 0.2 mm (E); 10 mm (F); 0.5 mm (G).

attachment was fused to the jaw (ankylosis) or anchored by a soft periodontal ligament (gomphosis; LeBlanc & Reisz, 2013). The histological analyses of dental attachment tissues in non-avian dinosaurs have mostly focused on ornithischian dinosaurs (*e.g.*, Erickson et al., 2015; LeBlanc et al., 2016, 2017; Bramble et al., 2017; Chen et al., 2018) and, to a lesser degree, non-avian theropods (*e.g.*, Fong et al., 2016; LeBlanc et al., 2017; Cerda & Porfiri., 2025). Sauropodomorph dental attachment tissues (*i.e.*, root cementum, alveolar bone and periodontal ligament) has only been described in few instances. Reid (1996, 1997) briefly described and figured alveolar bone from a *Camarasaurus* dentary, showing that it was entirely formed by woven fibered bone. Later, García and Cerda (2010a) and García and Zurriaguz (2016) analyzed the histology of a fragment of a dentary from a titanosaur from the Upper Cretaceous of Argentina. Results were shared with most other archosaurs with three tooth attachment tissues: root cementum, alveolar bone and the periodontal ligament. The cementum consists of a thin layer that covers the root area of the tooth. The alveolar bone occupies the inner walls of the tooth socket and is formed by a highly vascularized, woven fibered bone tissue. This tissue contains the extrinsic fibers (*i.e.*, Sharpey's fibers) that correspond to the periodontal ligament, which anchor the tooth to the alveolus. These tissues and the presence of a periodontal space between the alveolar bone and the cellular cementum were interpreted as evidence of gomphosis in this dinosaur, a feature shared among most archosaurs (*e.g.*, Fong et al., 2016; García & Zurriaguz, 2016; LeBlanc et al., 2017; Chen et al., 2018). García and Cerda (2010a) interpreted that the fine cancellous appearance of the alveolar bone and the presence of resorption lines were related to a high rate of tooth replacement in titanosaurs. Also, the absence of Sharpey's fibers in the cementum and its distinctive thinness was considered by García and Zurriaguz (2016) as evidence of a weak attachment of the tooth to the jaw. It is worth noting that, despite some differences (*e.g.*, relative thickness of the cementum), no histological modifications were found in the attachment tissues of the indeterminate titanosaur in comparison with other amniotes. Such invariability supports the idea of conservatism in the identity of the tooth attachment tissues among amniotes (LeBlanc & Reisz, 2013).

CONCLUDING REMARKS

Since the earliest descriptions in the 20th century (*e.g.*, Seitz, 1907; Nopcsa, 1914), research on sauropodomorph bone histology has expanded dramatically, transforming our understanding of sauropod biology. Histological evidence revealed rapid, determinate growth in sauropods, overturn-

ing archaic assumptions of slow, indeterminate growth histories. Despite these advances, limited sampling prohibits a comprehensive view of sauropod growth strategies and their relationship to evolution and paleobiology. Even in relatively well-studied groups like Titanosauria, only a small fraction of species has been analyzed histologically, often based on a single skeletal element or individual. Future progress depends upon broader taxonomic sampling, larger datasets, and integration of new technologies (*e.g.*, micro-CT scans). Continued discoveries and methodological advances promise significant further into sauropodomorph paleobiology.

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