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Additional Information

Bone histology of the titanosaur *Lirainosaurus astibiae* (Dinosauria: Sauropoda) from the Latest Cretaceous of Spain

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Abstract The titanosaur *Lirainosaurus astibiae* is the only sauropod species known from the Late Cretaceous of the Iberian Peninsula. *Lirainosaurus* did not reach a gigantic body size and is one of the smallest sauropods discovered to date. Histological analysis of *Lirainosaurus* bones, focused on diaphyseal transverse sections of appendicular elements, reveals that *Lirainosaurus* did not exhibit the osseous microstructure typical for large sauropods, but is comparable with that of the coeval titanosaurs *Alamosaurus sanjuanensis*, *Ampelosaurus atacis*, and *Magyarosaurus dacus*, and also shares histological traits with other small to medium-sized sauropodomorph dinosaurs. *Lirainosaurus* limb bones exhibit a laminar fibrolamellar bone microstructure interrupted by growth marks, fully obliterated in adulthood by intense secondary remodeling processes which tend to replace completely the primary cortex. *Lirainosaurus* attained smaller sizes than typical sauropods reducing the rate of primary periosteal osteogenesis and developing an extensive secondary remodeling well before the adult size was reached. Histological organization of *Lirainosaurus* long bones is more mature than observed in basal neosauropods at similar ontogenetic stage, documenting a case of peramorphosis by pre-displacement. This

heterochronic growth would be a reversal of the accelerated pattern of bone deposition typical for the sauropod lineage.

Keywords Titanosauria · *Lirainosaurus* · Bone microstructure · Growth · Peramorphosis · Dwarfism

Introduction

Lirainosaurus astibiae was a small to medium-sized gracile titanosaur (about 8–10 m in length and estimated body mass of approximately 1.5 t) first discovered in the Upper Cretaceous Laño Quarry of Burgos province, northern Spain (Sanz et al. 1999). Recent fieldwork carried out in Late Campanian–Early Maastrichtian beds at Chera Basin (Iberian Ranges, eastern Spain) has produced new material referable to *L. astibiae*, consisting mainly of disarticulated vertebrae, pectoral girdle elements, and associated limb bones of individuals at or near full adult size (Company et al. 2009). Bones have been collected from three different fossiliferous horizons placed within a narrow stratigraphic interval in the upper part of the Sierra Perenchiza Formation, which represents palustrine deposits accumulated in a coastal plain paleoenvironment (Martín-Chivelet et al. 2002).

Lirainosaurus is one of the smallest sauropod taxa exclusively reported from the Iberian Peninsula and phylogenetically represents a derived titanosauriform (Upchurch et al. 2004). It has been previously related with the Saltosaurinae of South America (Sanz et al. 1999; Wilson 2002; Curry-Rogers 2005) but clear phylogenetic affinities can be recognized only within a more inclusive clade, the Eutitanosauria (Company et al. 2009) (Fig. 1).

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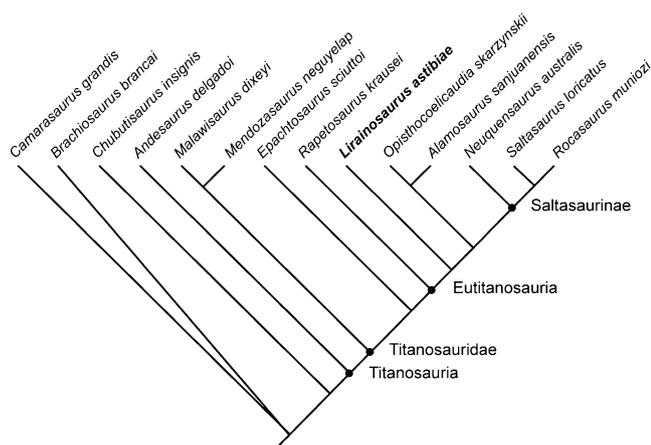


Fig. 1 Phylogenetic position of *Lirainosaurus astibiae* within Titanosauria, according to Calvo et al. (2007) (simplified from Csiki et al. 2010)

64 *Lirainosaurus* maximum body mass was comparable
 65 with that of late juveniles or subadult specimens of the
 66 largest sauropods (Lehman and Woodward 2008) and was
 67 slightly larger than minute sauropods considered as dwarf
 68 dinosaurs (Sander 2006; Klein and Sander 2008; Stein et al.
 69 2008, 2010; Benton et al 2010). The aim of this study is to
 70 describe in detail the histology of *Lirainosaurus* long bones
 71 and determine the growth strategy by which *Lirainosaurus*
 72 attained a modest body size with respect to other sauropod
 73 families. This work expands upon a preliminary study
 74 carried out previously (Company 2005).

75 Institutional abbreviations are as follows: MCNA,
 76 Museo de Ciencias Naturales de Alava, Alava, Spain;
 77 MGUV, Museo de Geología de la Universidad de Valencia,
 78 Valencia, Spain; MNHN, Muséum National d’Histoire
 79 Naturelle, Paris, France.

80 **Materials and methods**

81 Eleven complete or fragmentary fore- and hindlimb bones
 82 from at least six mature or close-to-adult individuals were
 83 selected for histological analysis (humeri, ulnae, femora,
 84 metapodial) (see Table 1). Transverse thin sections were
 85 made from samples removed from the diaphyseal region of
 86 the bones. When possible, samples were taken from
 87 standardized locations for each element, approximately
 88 halfway down the shaft (Curry 1999; Sander 2000;
 89 Chinsamy-Turan 2005; Klein and Sander 2008). Thin
 90 sections were examined at 20× to 100× magnification
 91 under a petrographic microscope, in ordinary and polarized
 92 light. Captured images were mounted and processed with
 93 Adobe© Photoshop CS4©.

94 When possible, bone tissue types and histological
 95 ontogenetic stages (HOS) of Klein and Sander (2008) have

been applied to the studied samples. Percentage of adult 96
 size and mass estimates were obtained according to 97
 Alexander (1989), Lehman (2007), and Lehman and 98
 Woodward (2008). 99

Material studied is housed at the Museum of Geology of 100
 the University of Valencia (Spain). 101

Long bone histology 102

General structure 103

Lirainosaurus long bones are slender and relatively 104
 flattened elements characterized by a relatively thin bone 105
 wall (10–20 mm thick at midshaft in femora; thicker in 106
 lateral sides and thinner in anterior and posterior sides) 107
 composed mostly of compact bone, enclosing a narrow 108
 medullar cavity almost completely filled with secondary 109
 cancellous tissue (Fig. 2b). In nearly all specimens, the 110
 spongy bone of the medullar region is somewhat crushed 111
 and the compressed trabeculae are partially broken and 112
 packed together. 113

Histological examination of transverse thin sections 114
 reveal bone walls composed of both primary (i.e., periost- 115
 eal) and secondary (remodeled) bone tissue in diverse 116
 proportions, reflecting ontogenetic variations. In this sense, 117
 two advanced ontogenetic stages can be distinguished from 118
 the histovariability observed in the studied specimens, 119
 which differ mainly in the development of the secondary 120
 reconstruction of the primary bone. None of the sampled 121
 specimens pertain to young individuals since no juvenile 122
 tissues have been preserved and all bones exhibit post- 123
 juvenile histological features. 124

Young adult individuals 125

The young adult growth stage is represented by two 126
 incomplete humeri (MGUV 17166, MGUV 17552) from 127
 individuals of approximately 69% and 62% maximum 128
 known length (Fig. 2a). The compact bone of the inner 129
 cortex exhibits a well-vascularized primary fibrolamellar 130
 tissue with predominantly laminar to locally subplexiform 131
 vascularity, partially obliterated by abundant secondary 132
 osteons and large resorption cavities (Figs. 3 and 4a). The 133
 longitudinal and circular vascular canals of the primary 134
 osteons are arranged in circular rows, resulting in 135
 concentric layers. Such vascular canals are not completely 136
 infilled by centripetally deposited lamellar bone, indicat- 137
 ing bone tissue is not mature. This type of bone tissue 138
 suggests high rates of periosteal osteogenesis (Reid 1996; 139
 Sander and Tüchtmantel 2003; Chinsamy-Turan 2005 and 140
 references therein; de Ricqlès et al. 2008; Klein and 141
 Sander 2008). 142

Table 1 Summary of sampled appendicular elements of *L. astibiae*, providing sampling location, bone tissue summary, histological type, and histologic ontogenic stage (HOS, Klein and Sander 2008)

Specimen number	Element	Sampling location (bone side)	Position in diaphysis	Bone tissue summary	Bone tissue types	HOS	% Adult size	
t1.3	MGUV 17165	Humerus	Posterior	Midshaft	Nearly 100% dense Haversian bone. Scarce primary bone	G	13	86%
t1.4	MGUV 17166	Humerus	Anterior	Midshaft	Laminar fibrolamellar bone grading to lamellar xzonal bone with LAGs. Rows of secondary osteons. Scattered resorption cavities	E–F	11–12	69%
t1.5	MGUV 17721	Humerus	Lateral, anterior	Midshaft	Nearly 100% dense Haversian bone. Scarce primary bone	G	13	–
t1.6	MGUV 17045	Ulna (l)	Lateral	Midshaft	Nearly 100% dense Haversian bone. Scarce primary bone	G	13	–
t1.7	MGUV 16450	Femur (r)	Anterior	Distal third	Nearly 100% dense Haversian bone. Scarce primary bone	G	13	100%
t1.8	MGUV 16454	Femur (d)	Posterior, lateral	Proximal third, distal third	100% dense Haversian bone	G	13	97%
t1.9	MGUV 17194	Femur (r)	Posterior	Distal third	Nearly 100% dense Haversian bone. Scarce primary bone	G	13	97%
t1.10	MGUV 17235	Femur (l)	Anterior	Proximal third, midshaft	Nearly 100% dense Haversian bone. Scarce primary bone	G	13	96%
t1.11	MGUV 17294	Femur (l)	lateral	Distal third	Abundant dense Haversian bone. Little primary bone	F, G	13	–
t1.12	MGUV 17279	Metapodial	Complete section	Midshaft	Abundant secondary cancellous bone. Cortex nearly 100% with dense Haversian bone	F, G	13	–
t1.13	MGUV 17239	Diaphysis indet.	Complete section	Midshaft	Nearly 100% dense Haversian bone. Scarce primary bone	G	13	–

Percentage adult lengths were estimated with respect to the largest (presumably oldest) humerus and femur of *Lirainosaurus* (Humerus MCNA 7464; Femur MNHN, no specimen number)



Fig. 2 Sampled bones of *Lirainosaurus* cf. *astibiae* from the Late Cretaceous of Chera locality (Valencia, Spain). *Arrows* indicate sampling locations. **a** Left humerus (MGUV 17166) in posterior view. **b** Cross section of right femur MGUV 16450 at midshaft showing bone structure. **c** Left femur (MGUV 17294) in anterior view. **d** Right femur (MGUV 16454) in anterior view. **e** Left femur (MGUV 17235) in anterior view. *Scale bar* for **a**, **c**–**e**=10 cm; **b** not to scale

Middle to outer regions of the cortex display an additional type of stratification into layers due to the presence of well-defined lines of arrested growth (LAGs) which mark pauses in bone deposition. LAGs appear to be irregularly distributed, but there is a tendency to reduce gradually their spacing towards the bone periphery, indicating a slowing down in bone deposition. Vascular density slightly decreases towards the cortical periphery. Rows of primary osteons occur in the outermost part of the cortex (Fig. 4c), and even vascular canals open to the periosteal (external) surface, indicating that the animal was actively growing at the time of death (Fig. 4d). Nevertheless, in this region, bone fibers change their spatial organization, and the fibrolamellar bone with woven-fibred matrix of the middle cortex grades into a parallel-fibred pseudolamellar bone (Fig. 4b, e), an intermediate to slow-growing tissue type (Benton et al. 2010). In the inner cortex, the primary fibrolamellar bone has been replaced by a coarse cancellous tissue formed by large open secondary osteons with remnants of primary bone in between.

Bone remodeling processes are well developed, as denoted by the presence of large erosion cavities and

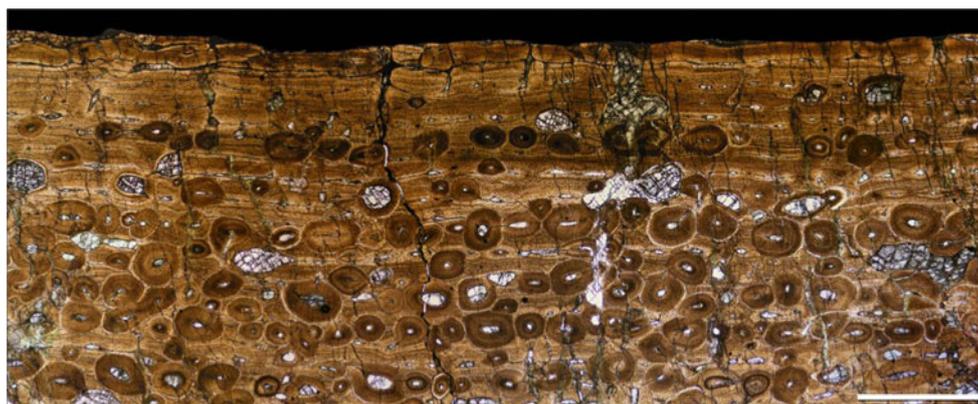


Fig. 3 Bone histology of young adult *Lirainosaurus* humerus (MGUV 17166). Image is restricted to the outer cortex. Primary vascular canals are generally longitudinal, with occasional radial

anastomoses opening to the bone surface. Note the rows of tangential secondary osteons parallel to bone surface. *Scale bar*=1 mm

164 abundant secondary osteons scattered throughout the
 165 cortex, even in the vicinity of bone surface. Secondary
 166 osteons form rows parallel to the bone surface, indicating
 167 an initial organized pattern of bone resorption and recon-
 168 struction (Fig. 3). This arrangement of secondary osteons
 169 has been recently described in bones of the Maastrichtian
 170 titanosaur *Alamosaurus sanjuanensis* from North America
 171 (Woodward and Lehman 2009). This linear fashion is found
 172 even in specimens of about 80% adult length with intense
 173 secondary remodeling. These microstructural types are
 174 comparable to types E–F bone tissue of Klein and Sander
 175 (2008), but provided with a more extensive secondary
 176 reconstruction throughout the entire cortex.

177 The presence of growth lines in the external cortex of an
 178 actively growing individual, combined with the noticeable
 179 development of Haversian systems in the inner and middle
 180 cortex, suggests that the individual had already reached
 181 sexual maturity well before final body size would be
 182 attained (Sander et al. 2004; Klein and Sander 2008; Lee
 183 and Werning 2008). In this sense, the observed micro-
 184 structural bone type can be referred to ontogenetic stage 11
 185 of Klein and Sander (2008).

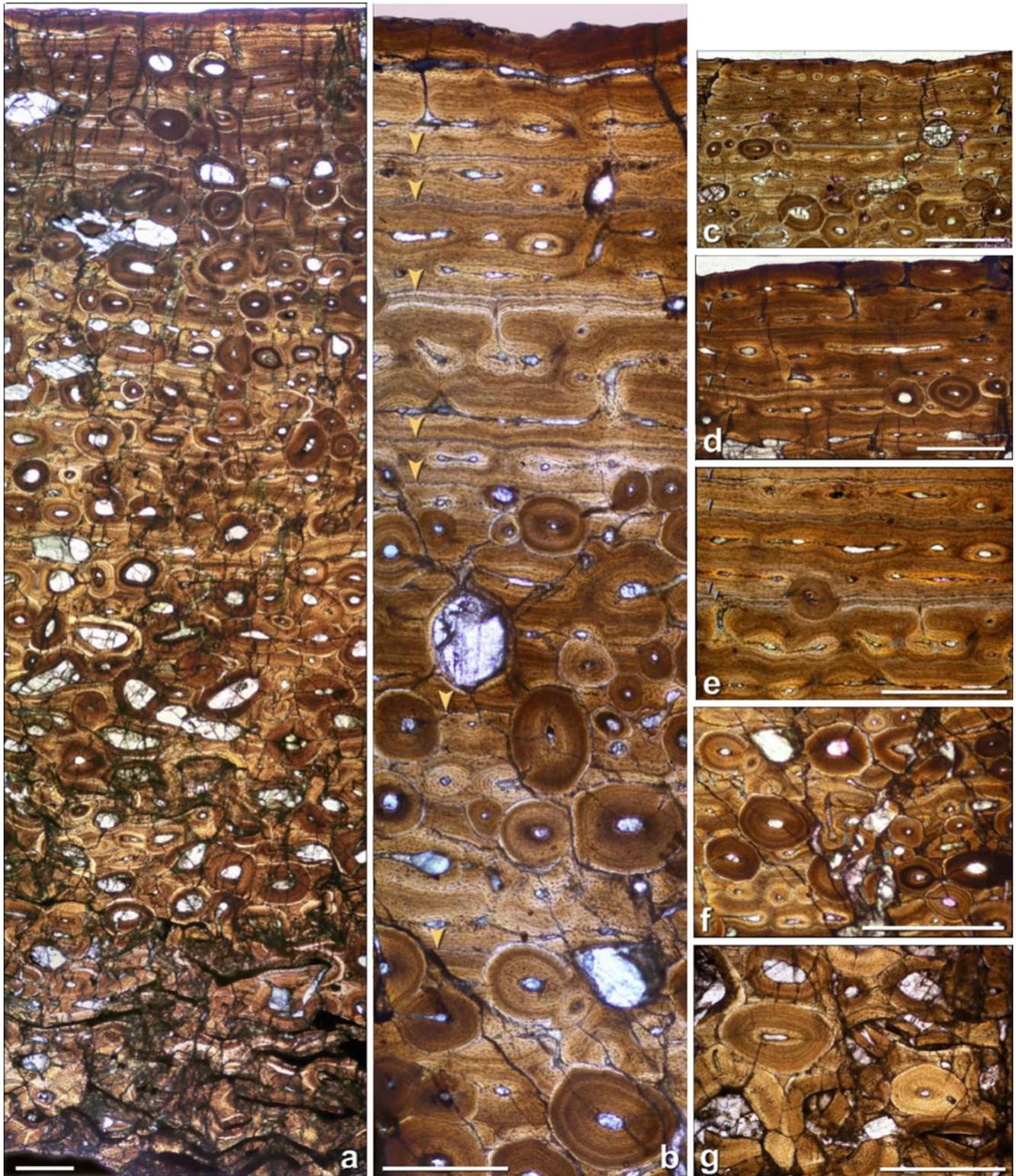
186 **Adult individuals**

187 Histological sections of cortical bone of a number of
 188 specimens (humerus—MGUV 17165; ulna—MGUV
 189 17045; femora—MGUV 16450, MGUV 16454, MGUV
 190 17194, MGUV 17235, MGUV 17294; metapodial—
 191 MGUV 17239) show extensive processes of secondary
 192 remodeling, resulting in a dense Haversian bone which
 193 tends to obliterate almost completely the primary complex
 194 of the cortex (Fig. 5a–d). In these specimens, little primary
 195 bone is present, and only interstitial areas of the outermost
 196 cortex with remnants of primary periosteal bone tissue are

preserved (Fig. 5b, c). The scarce remaining primary bone
 exhibits rows of primary osteons, and there is no evidence
 of deposition of the non-vascularized external fundamental
 system (EFS), which documents skeletal maturity and
 effective cessation of growth in tetrapods (Cormack 1987;
 Chinsamy-Turan 2005 and references therein). Where
 dense Haversian bone is developed, successive generations
 of secondary osteons overlap each other, and these osteons
 tend to be considerably larger than the primary ones and
 contain a large number of centripetally deposited layers of
 new lamellar bone (see Fig. 5d).

According to Klein and Sander (2008) and Stein et al.
 (2010), the presence of an almost completely remodeled
 cortex (type G bone tissue), which is usually accompanied

Fig. 4 Transverse thin sections of actively growing adult *Lirainosau- ▶*
rus humerus. **a** General view of a complete transverse section of left
 humerus MGUV 17166. The external cortex is at the top, and the
 beginning of the medullar cavity is visible at the bottom. **b** Detail of
 middle to outer cortex showing fibrolamellar bone tissue (*bottom*)
 grading upwards to lamellar zonal bone. *Lines* of arrested growth
 (*arrowheads*) are partially obliterated by secondary osteons. The
 vascular network is predominantly laminar to locally longitudinal.
 Vascular spaces of the primary osteons are clearly unfilled, indicating
 that bone corresponds to a young adult individual. Note the large
 cavities eroded in the primary bone, indicating the beginning of
 intense osteoclastic resorption. **c** General view of the outer cortex
 provided with longitudinal vascularization. Note the primary canals in
 form of well-defined primary osteons embedded in a lamellar fibered
 bone matrix and clusters of fully formed secondary osteons. **d** Detail
 of the outermost cortex showing radial vascular canals open to bone
 surface, indicating active growth. **e** Detail the mid-cortex showing
 parallel fibered bone (*up*). The vascular network is predominantly
 longitudinal, with some weak anastomoses. Occasionally, LAGs are
 composed of multiple rest lines. **f** Detail of inner cortex composed
 of primary fibrolamellar bone partially obliterated by secondary osteons.
g Trabecular bone filling the perimedullary cavity showing partly and
 fully formed secondary osteons. *Arrowheads* indicate the position of
 lines of arrested growth. *Scale bar*=0.5 mm



211 by the development of a peripheral EFS deposited late in
212 life, characterizes the last stages of the life history of
213 sauropod dinosaurs (HOS-13/14; see note added in revision).
214 Nevertheless, the studied samples appear to represent

individuals that were still slowly growing since no
avascular lamellar-zonal bone is present in the cortical
periphery. As growth lines are obliterated by Haversian
remodeling, it is not possible to discern the age at time of

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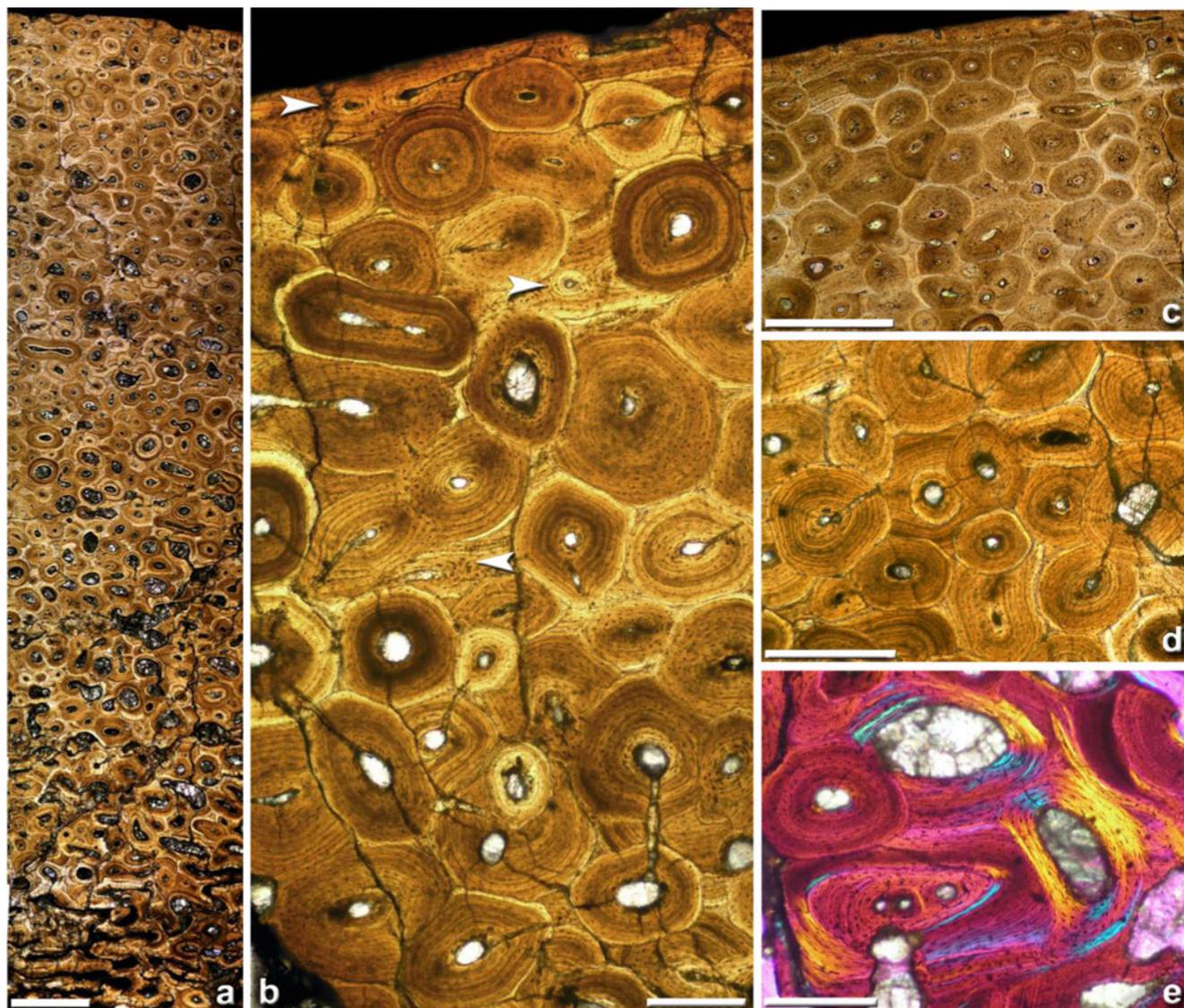


Fig. 5 Histology of adult *Lirainosaurus* limb bones. **a** Complete transverse section of *Lirainosaurus* humerus MGUV 17165. The bone comprises a distinctive cortical region of dense Haversian bone surrounding a narrow medullar cavity filled by coarse cancellous tissue. The primary (periosteal) bone tissue is almost fully obliterated by extensive Haversian reconstruction which occurs throughout the cortex. **b** Close-up of dense Haversian bone in adult *Lirainosaurus* humerus, showing fully formed secondary osteons. Each Haversian system is bounded by a peripheral cementing line, which marks the outward limit of resorption. Secondary osteons contain up to 14 centripetally deposited layers of lamellar bone. *Arrowheads* indicate

the presence of interstitial primary fibrolamellar bone. **c** Outer cortex showing dense Haversian bone and a subperiosteal layer of primary bone provided with longitudinal vascularity. Note the tangential arrangement of the secondary osteons, indicating an early phase of secondary reconstruction. **d** Dense Haversian bone in the middle cortex showing several superimposed generations of secondary osteons. **e** Close-up of secondary cancellous bone from the perimedullar region of a *Lirainosaurus* femur (MGUV 17235) showing the lamellated appearance of the secondary cancellous bone (polarized light; 1 λ filter)

219 death of these individuals, which represent still actively
 220 growing adults (HOS-11 of Klein and Sander 2008) but not
 221 fully mature (i.e., full-sized) individuals (HOS-12). Several
 222 bones (MGUV 16450, MGUV 16454) lack any evidence of
 223 primary bone. All the cortices are composed of secondary
 224 Haversian bone, denoting the most advanced stage of
 225 maturity in full-sized *Lirainosaurus* bones (HOS 14, after
 226 Stein et al. 2010).

It is also not possible to discern if secondary remodeling
 took place during pauses in periosteal bone deposition, or
 gradually, as the periosteal growth rate slowed down.
 However, it seems clear that in terms of energetic and
 developmental costs, secondary reconstruction already
 equaled or even exceeded the energy requirements for
 deposition of primary bone well before the growth plateau
 was reached.

235	Discussion		
236	Intense secondary remodeling		
237	<i>Lirainosaurus</i> documents a case in which secondary osteo-	of the dwarf sauropod <i>M. dacus</i> , as mentioned above, a	286
238	genesis is at least as important as the primary periosteal bone	diminutive titanosaur coeval with <i>Lirainosaurus</i> .	287
239	formation. The presence of dense Haversian bone, extending	This paper enhances the information reported in previous	288
240	completely throughout the cortex (type G bone tissue of Klein	works (Stein et al. 2008; Stein and Sander 2009; Benton et	289
241	and Sander 2008), is a histological feature documented only	al 2010) and concludes that bone histology confirms that	290
242	in the largest (i.e., oldest) specimens of basal neosauropods	<i>M. dacus</i> is a dwarf dinosaur. Detailed descriptions confirm	291
243	and basal macronarians (Curry 1999; Sander 2000; Klein	the idea that <i>Magyarosaurus</i> shares the main histological	292
244	and Sander 2008; Stein et al. 2010). Consequently, this	features described for <i>Lirainosaurus</i> (this paper), <i>Ampelo-</i>	293
245	histological feature has been traditionally interpreted as a	<i>saurus</i> (Klein et al. 2006), <i>Phuwiangosaurus</i> (Klein et al.	294
246	sign of maturity and senescence in sauropods (Klein and	2009), and <i>Alamosaurus</i> (Woodward and Lehman 2009).	295
247	Sander 2008; Stein et al. 2008; Benton et al. 2010).	Therefore, the presence of slowly formed primary bone	296
248	Nevertheless, heavy remodeled <i>Lirainosaurus</i> bones still	tissues, the extensive development of Haversian bone	297
249	show evidence of certain active growth. According to this	throughout most of the cortex, even in not fully grown	298
250	observation, specimens with great development of type G	individuals, and the apparent absence of the outer circum-	299
251	bone tissue may not necessarily represent fully grown	ferential lamellae support the idea herein presented that	300
252	individuals. Recently, Woodward and Lehman (2009) also	titanosaur dinosaurs exhibit a particular bone histology	301
253	observed a nearly complete replacement of primary compact	different than that of other sauropods. Furthermore, the fact	302
254	bone by secondary Haversian bone in most specimens of	that “even the smallest <i>Magyarosaurus</i> specimens exhibit a	303
255	<i>Alamosaurus</i> of less than 80% adult size. Similarly to	bone microstructure identical to fully mature or old	304
256	<i>Lirainosaurus</i> , secondary reconstruction initiated early in life	individuals of other sauropod taxa” (Stein et al. 2010, page	305
257	and is the dominant bone tissue even in immature	1 of 6) supports the idea expressed in this work that	306
258	individuals that scarcely exceed half of the adult length.	histology of <i>Lirainosaurus</i> and other Late Cretaceous	307
259	Therefore, the presence of intense Haversian remodeling in	titanosaurs may be explained in terms of heterochrony.	308
260	young bones of titanosaurs may represent a morphologically	The authors also introduce a more advanced histologic	309
261	advanced character.	ontogenetic stage (HOS-14) for fully remodeled primary	310
Q3 262	<i>Magyarosaurus dacus</i> , a diminutive titanosaur from the	bone with several superimposed generations of secondary	311
263	Late Cretaceous of Romania (Nopcsa 1914), was initially	osteons. This new stage has been applied to the <i>Liraino-</i>	312
264	regarded as a pedomorphic dwarf dinosaur on the basis of	<i>saurus</i> histological description.	313
265	its reduced skeletal size. Moreover, supposed adult <i>Mag-</i>	Intense Haversian remodeling can change the biome-	314
266	<i>yarosaurus</i> bones seem to be morphologically similar to	chanical properties of the bones (see Chinsamy-Turan 2005	315
267	“juvenile” bones of large sauropods, reinforcing this	for extensive bibliography). Morphologically, <i>Lirainosau-</i>	316
268	assumption (Jianu and Weishampel 1999). Histological	<i>rus</i> had slender and compressed limb bones (Sanz et al.	317
269	analysis of <i>Magyarosaurus</i> long bones (Stein et al. 2008,	1999; Company et al. 2009), especially the humerus and	318
270	2010; Benton et al. 2010; see note added in revision)	femora, which, in general, attained in titanosaurs a notable	319
271	revealed the presence of a nearly complete secondary	eccentricity much greater than in other sauropods (Wilson	320
272	(Haversian) reconstruction in all the specimens, even in	and Carrano 1999). As noted above, other titanosaurs	321
273	those of 45% adult length, suggesting these bones pertain to	exhibited strong secondary remodeling early in ontogeny	322
274	fully grown dwarf individuals, even though these bones	(Klein et al. 2006, 2008; Stein et al. 2008; Woodward and	323
275	lack EFS. In light of new observations, and according to Le	Lehman 2009; Benton et al. 2010; Meter 2010). Haversian	324
276	Loeuff (2005) who documented the existence of large-sized	reconstruction perhaps could offer biomechanical advan-	325
277	bones tentatively referable to this species, the small bones	tages to animals with slender bones just when weight	326
278	of <i>Magyarosaurus</i> , heavily remodeled, could represent, if	increases greatly during life (Curry 1999). Such intense	327
279	not juveniles, at least still growing adult individuals which	Haversian remodeling has also been observed in fully	328
280	could attain larger size in life (10–15 m in length).	grown individuals of large-bodied sauropods provided with	329
281	Alternatively, these large sauropod remains might represent	a more robust architecture, as <i>Apatosaurus</i> (Curry 1999;	330
282	another titanosaur taxon (Csiki and Grigorescu 2007;	Klein and Sander 2008), <i>Lapparentosaurus</i> (Rimblot-Baly	331
283	Benton et al. 2010), as a large bone sampled exhibits a	1995), <i>Barosaurus</i> , or <i>Brachiosaurus</i> (Sander 2000), just	332
Q4 284	less mature histology than the small bones of <i>M. dacus</i> .	when they get the maximum body size and mass.	333
285	Stein et al. (2010) reported a detailed study on the histology	Absence of “senescent” tissues	334
		Although all examined limb bones of <i>Lirainosaurus</i> exhibit	335
		moderate to intense secondary remodeling, none of them	336

337	records the non-vascularized EFS at the periosteal surface	layer of bone is missing in a number of specimens	389
338	that characterizes adult-sized individuals. This is not the	(Woodward and Lehman 2009; Benton et al. 2010; see	390
339	general pattern observed in ontogenetically mature tetrapod	note added in revision).	391
340	bones since this structure documents a growth plateau in		392
341	adulthood of animals with a determinate growth strategy		
342	(Padian et al. 2004; Chinsamy-Turan 2005 and references	Age estimation	393
343	therein). According to Klein and Sander (2008), sauropod		
344	bones completely remodeled by Haversian reconstruction	The less remodeled specimen (humerus, MGUV 17166)	394
345	represent senescent individuals in the latest histological	preserves a minimum of ten evident lines of arrested	395
346	developmental stage (HOS-13/14). These animals had	growth. Assuming that growth rings are deposited	396
347	already developed a peripheral EFS in a previous ontoge-	annually (Castanet et al. 1993; Chinsamy-Turan 2005;	397
348	netic stage (HOS-12) as a consequence of a dramatic	Curry-Rogers and Erickson 2005 and references therein),	398
349	slowdown in bone deposition and presumably cessation of	and considering that the outermost layer of periosteal bone	399
350	growth. Several alternative hypotheses can be proposed to	records complete or partially the last year of growth, a	400
351	explain the absence of peripheral tissues indicative of	conservative estimate of the age of the animal can be	401
352	skeletal maturity in fully remodeled long bones of	obtained from the number of rings present. Thus, this bone	402
353	<i>Lirainosaurus</i> :	records a minimum of 11 years of growth. Therefore, bone	403
		microstructure reveals that at least 11 years of life were	404
354	– <i>Lirainosaurus</i> had an indeterminate growth strategy.	required to <i>Lirainosaurus</i> to grow to about 69% adult	405
355	Consequently, there are no histological features of	length. The slowing down of growth (deposition of	406
356	cessation of growth. This hypothesis seems improbable	parallel-fibered and lamellar bone) must have occurred at	407
357	because indeterminate growth in amniotes results in	least during the last 6 years of life.	408
358	cortices composed entirely of slowly deposited lamel-	It is not possible to count growth lines in mature	409
359	lar–zonal bone tissue. Even though this growth strategy	<i>Lirainosaurus</i> bones because secondary reconstruction	410
360	has been documented in other sauropodomorphs	obliterated nearly completely the primary periosteal bone.	411
361	(Chinsamy 1993), it does not correspond with <i>Lirai-</i>		
362	<i>nosaurus</i> growth pattern.	A titanosaurian histological type?	412
363	– The secondary (i.e., Haversian) osteogenesis erased		
364	completely the primary bone, including the external	Previous studies on sauropod bone histology (de Ricqlès	413
365	fundamental system of the peripheral cortex. This	1983; Curry 1999; Sander 2000; Sander et al. 2004; Curry	414
366	assumption does not hold because, in several speci-	and Erickson 2005; Klein and Sander 2008) described the	415
367	mens, preserved areas of the outermost cortex with	“typical” sauropod long bone microstructure as consisting	416
368	remnants of primary bone not only lack evidence of an	of a thick cortex of well-vascularized laminar fibrolamellar	417
369	externalmost circumferential layer indicative of termi-	bone devoid of growth marks (except in the cortical	418
370	nal growth but contain rows of primary osteons,	periphery), affected by remodeling processes only late in	419
371	indicating active growth (Fig. 5b, c).	ontogeny. This type of bone tissue would reflect a	420
372	– The animals were still actively growing at time of	continuous, accelerated skeletal growth which made the	421
373	death. Therefore, there are no fully grown individuals	gigantism of such bulky dinosaurs possible (Sander et al.	422
374	in the sample, and secondary remodeling processes	2004; Sander and Clauss 2008). Nevertheless, good	423
375	spread out well before primary osteogenesis had	examples of zonal bone with clear growth rings in sauropod	424
376	finished. Indeed, old sauropods are generally poorly	bones have been documented by Reid (1981, 1990), de	425
377	represented in the fossil record (Klein and Sander	Ricqlès (1983), Sander (2000), Sander and Tückmantel	426
378	2008). This gap in the fossil record appears to be	(2003), and Sander et al. (2006), indicating probably a	427
379	common in other dinosaur taxa. According to Erickson	cyclical osteogenesis.	428
380	et al. (2004), only 2% of the individuals in several	On the contrary, the long bone histology of <i>Lirainosau-</i>	429
381	studied populations of tyrannosaurids lived long	<i>rus</i> consists mainly of primary laminar fibrolamellar bone	430
382	enough to reach maximum size and age for the species.	grading to lamellar–zonal tissue with growth lines, strongly	431
383	This is the most plausible hypothesis unless the	remodeled by secondary reconstruction as maturity	432
384	periosteal bone tissues formed late in life in all	approached.	433
385	<i>Lirainosaurus</i> samples have been eroded away. <i>Ala-</i>	The cyclical growth pattern observed in <i>Lirainosaurus</i>	434
386	<i>mosaurus</i> and <i>Magyarosaurus</i> mature limb bones also	bones is reminiscent of that seen in other small to medium-	435
387	lack evidence of the external fundamental system,	sized sauropodomorphs, as the Triassic prosauropods <i>Mas-</i>	436
388	albeit in this case, it is recognized that the externalmost	<i>sospondylus</i> , (Chinsamy 1993), <i>Thecodontosaurus</i> (Sander	437

438 et al. 2004), and *Plateosaurus* (Klein and Sander 2007), also
 439 characterized by intermittent growth, and is broadly similar
 440 to the cortical structure observed in limb bones of the
 441 Jurassic dwarf sauropod *Europasaurus holgeri* (Sander et al.
 442 2006). *Europasaurus* long bones also exhibit a cortex with
 443 clear growth lines and a noticeable degree of secondary
 444 remodeling increasing in adulthood. The moderate or even
 445 diminutive size of all these taxa was a consequence of slow,
 446 intermittent overall skeletal growth rates.

447 Recent histological studies focused on titanosaur materi-
 448 al shed light on a “titanosaur histology” somewhat
 449 different from the general histological organization of
 450 non-titanosaurian sauropods. Bones of the derived European
 451 titanosaurs *Ampelosaurus atacis* (Klein et al. 2006) and
 452 *M. dacus* (Stein et al. 2008; Galton et al. 2010) also exhibit
 453 cortices provided with (1) laminar fibrolamellar organiza-
 454 tion, (2) substantial development of slowly deposited
 455 parallel- and lamellar-fibered tissues, (3) presence of
 456 growth marks (not observed in the strongly remodeled
 457 bones of *Magyarosaurus*), (4) extensive Haversian remodel-
 458 ing placed early in ontogeny, and (5) absence of EFS at
 459 bone periphery. Even the basal titanosauriforms *Malargue-*
 460 *saurus florenciae* (González-Riga et al. 2009), *Phuwiango-*
 461 *saurus sirindhornae* (Klein et al. 2009), and
 462 *Lapparentosaurus madagascarensis* (Rimblot-Baly et al.
 463 1995) exhibit a similar histological pattern.

464 Particularly noticeable are the results of the above-
 465 mentioned study carried out by Woodward and Lehman
 466 (2009) on *Alamosaurus* histology. *Alamosaurus* shares with
 467 *Lirainosaurus* an intense secondary remodeling initiated
 468 early in ontogeny, the deposition of periosteal parallel-
 469 fibered bone tissues throughout adulthood, the apparent
 470 absence of EFS in presumably old individuals, and, in
 471 general terms, the presence of mature tissues in not fully
 472 grown individuals. The absence of lines of arrested growth
 473 in *Alamosaurus* bone fabric indicates a continuous growth
 474 which enabled fully grown adults to attain a mass over
 475 32,000 kg (Lehman and Woodward 2008).

476 None of the abovementioned European titanosaurs
 477 seemed to have reached gigantic proportions. *Ampelosau-*
 478 *rus* was a medium-sized titanosaur. *Europasaurus* and
 479 *Magyarosaurus* (roughly 6 m in total length) were even
 480 smaller than *Lirainosaurus* and would represent propor-
 481 tioned dwarf dinosaurs which inhabited insular environ-
 482 ments (Sander et al. 2006; Stein et al. 2008; Benton et al.
 483 2010; see note added in revision). In all cases, their
 484 histological depositional pattern reflects an overall growth
 485 rate which would have been lower than that of larger
 486 sauropods with continuous “relatively fast” growth, thus
 487 resulting in a relatively small final body size.

488 As has been stated, gigantism in sauropods is caused by
 489 accelerated growth (Sander et al. 2004; Sander and Clauss
 490 2008), whereas sauropod nanism may be a heterochronic

491 reversal, a consequence of low growth regimes (Sander et al. 491
 492 2006; Benton et al. 2010). If this reversal is a 492
 493 consequence of living in resource-limited environments 493
 494 such as islands, it could be tested by extending histophys- 494
 495 iological studies to other dinosaur taxa which inhabited the 495
 496 same areas (Benton et al. 2010). In fact, cortical bone with 496
 497 growth marks and parallel-fibered (i.e., slowly formed) 497
 498 tissues deposited seasonally are histological traits charac- 498
 499 teristic of slow-growing ectotherms, but are also observed 499
 500 in endotherms which have developed reptile-like physio- 500
 501 logical traits, as a consequence of living in resource-limited 501
 502 ecosystems. This is the case of the recently extinct giant 502
 503 Moa from New Zealand (Turvey et al. 2005) and the Plio- 503
 504 Pleistocene bovid *Myotragus* from the Mediterranean 504
 505 Balearic Islands (Köler and Moyà-Solà 2009). None of 505
 506 these are dwarf taxa, but the zonal bone would reflect the 506
 507 effects of seasonal fluctuations in resource conditions. 507

508 Therefore, apart from the presence of seasonal growth lines 508
 509 which mark pauses in growth that may be caused by living in 509
 510 energy-poor insular ecosystems, there are several histological 510
 511 characters (i.e., intense secondary remodeling, possible 511
 512 absence of EFS, and generalized presence of parallel-fibered 512
 513 tissues in the cortices) that are extended among titanosaurs 513
 514 and may be plesiomorphic traits of the group. These traits are 514
 515 size-independent morphological characteristics and are present 515
 516 in giant titanosaurs (*Alamosaurus*) as well as in 516
 517 diminutive forms (*Lirainosaurus*, *Magyarosaurus*). 517

518 A heterochronic process? 518

519 As noted above, bones of young adult specimens of 519
 520 *Lirainosaurus* show clear histological variations with 520
 521 respect to other sauropod bones in a similar ontogenetic 521
 522 stage. These differences are as follows: (1) greater 522
 523 development of strong secondary remodeling, (2) earlier 523
 524 appearance of growth marks, and (3) deposition of slowly 524
 525 formed parallel-fibered and lamellar tissues. Such features 525
 526 initiated earlier in *Lirainosaurus* ontogeny than in adults of 526
 527 neosauropod taxa. The early morphological development of 527
 528 organs or structures in an organism with respect to 528
 529 ancestors is a peramorphic (i.e., heterochronic) process 529
 530 termed pre-displacement, and it results in a greater 530
 531 development of such organs or structures (McNamara 531
 532 1986). 532

533 Thus, the early onset of the abovementioned histomor- 533
 534 phological structures in *Lirainosaurus* life history, espe- 534
 535 cially the Haversian reconstruction, allows a longer period 535
 536 for its development. The result is a peramorphic bone 536
 537 tissue, histomorphologically more advanced than that of 537
 538 other sauropods at the same growth stage. 538

539 Similarly, young titanosaurs *Phuwiangosaurus* and 539
 540 *Ampelosaurus*, besides showing a similar precocious 540
 541 development of Haversian remodeling, also exhibit a 541

542 periosteal bone with more mature primary osteons than
 543 other non-titanosaurid sauropods in a similar ontogenetic
 544 stage (Klein and Sander 2008). A number of *Alamosaurus*
 545 specimens exhibit mature tissues although they are estimat-
 546 ed to be slightly more than half adult length (Woodward
 547 and Lehman 2008), supporting the view that histological
 548 peramorphic processes by pre-displacement extended
 549 among titanosaurs.

550 *M. dacus* limb bones are likewise intensely remodeled,
 551 even the smallest (i.e., younger) specimens sampled (see
 552 note added in revision).

553 **Conclusions**

554 Histological studies focused on appendicular elements of
 555 the Late Cretaceous titanosaur *Lirainosaurus* indicates that
 556 all specimens belong to mature or nearly mature individu-
 557 als. *Lirainosaurus* bone microstructure suggests “relatively
 558 rapid” and sustained growth early in ontogeny (deposition
 559 of well-vascularized laminar fibrolamellar bone tissue),
 560 followed by a gradual slowing down in bone deposition
 561 approaching maturity (appearance of LAGs and deposition
 562 of lamellar tissues), combined with an intense secondary (i.
 563 e., Haversian) reconstruction in adulthood as body mass
 564 increased. Thus *Lirainosaurus* limb bone histology differs
 565 from the general sauropod long bone microstructure, little
 566 affected by interruptions of bone deposition, and with
 567 secondary remodeling restricted mainly to fully grown
 568 individuals, indicating a continuous, non-interrupted accel-
 569 erated growth.

570 If definitively not removed by weathering, the absence of a
 571 non-vascularized fundamental system at the periosteal surface
 572 of larger *Lirainosaurus* bones is noteworthy. The absence of
 573 such peripheral resting lines in long bones of individuals of
 574 presumably adult size has been observed to date only in
 575 tetrapods with slow, indeterminate growth strategy. In animals
 576 with a determinate growth pattern, this fact might indicate
 577 that these specimens belonged to active growing individuals
 578 which may have attained greater sizes. Nevertheless, the
 579 presence of mature tissues and bone proportions suggest that
 580 the sampled animals were close to final body size.

581 The intense secondary remodeling, as important as primary
 582 osteogenesis in terms of energetic costs and volume of bone
 583 reconstructed, initiated in *Lirainosaurus* life history well
 584 before adult size, was attained. This process was extensive
 585 before the phase of active growth was completed, as denoted
 586 by the absence of EFS in bones almost completely
 587 reconstructed. The strong bone remodeling, combined with
 588 a slowing down in periosteal deposition, may have contrib-
 589 uted to *Lirainosaurus* not reaching a large final body size.
 590 Thus, intense osteogenesis (mostly secondary) took place
 591 even though the individuals scarcely increased in size.

Similarly to *Lirainosaurus*, other small-sized sauropods, 592
 such as *Europasaurus* and *Magyarosaurus*, also exhibited 593
 reduced growth rates which led them to attain reduced adult 594
 sizes (Sander et al. 2006; Stein et al. 2008; Stein and Sander 595
 2009; Benton et al. 2010). *Ampelosaurus* histology is 596
 somewhat different, but is also characterized by the presence 597
 of slow-growing tissues and secondary remodeling starting 598
 early in ontogeny (Klein et al. 2006). Larger titanosaurs, 599
 such as *Alamosaurus* and *Phuwiangosaurus*, also shared 600
 many histological features with *Lirainosaurus*, although they 601
 showed no cyclical structures of cessation of growth. 602

The presence of highly organized bone tissues (parallel- 603
 fibered and lamellar types) with lines of arrested growth is a 604
 consequence of low growth rates, and so are common 605
 features of dwarf and small to medium-sized sauropods. 606
 The presence of heavily reconstructed primary bone is 607
 present in the smallest (*Magyarosaurus*), in the medium- 608
 sized (*Lirainosaurus*, *Ampelosaurus*) as well as in the 609
 largest titanosaurs (*Alamosaurus*), and may be a clade- 610
 related feature. The absence of the external fundamental 611
 system is extended among titanosaurs. 612

According to several authors (Sander et al. 2006; Klein 613
 and Sander 2006; Stein et al. 2008; Benton et al. 2010), the 614
 small size of the nanoid European sauropods can be 615
 explained in terms of reduction of growth rates caused by 616
 insular dwarfing. Therefore, these taxa could be considered 617
 pedomorphic species with respect to the ancestral forms. 618
 Alternatively, *Lirainosaurus* would be a small to medium- 619
 sized peramorphic taxon whose submature individuals 620
 displayed adult characters. 621

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AUTHOR QUERIES

AUTHOR PLEASE ANSWER ALL QUERIES.

- Q1. “Sander 2006”, “Reid 1996”, “Klein et al. 2008”, “Meter 2010”, “Rimblot-Baly 1995”, “Klein and Sander 2007”, “Galton et al. 2010”, “Woodward and Lehman 2008”, and “Klein and Sander 2006” are cited in text but did not appear in the reference list. Please provide details in the list or delete the citations.
- Q2. Please check the relevance of the text “see note added in revision” found in the article.
- Q3. Please check the second paragraph under “Intense secondary remodeling” section for correctness and completeness.
- Q4. The text “[Note added in submission: After this work was initially submitted for publication, an article by Stein and others was published in Proc. Natl. Acad. Sci. U. S. A.” has been deleted. Please check.
- Q5. “Francillon-Vieillot et al. 1990”, “Gould et al. 2004” and “Wilson 2005” were not cited anywhere in the text. Please provide citations or, alternatively, delete these items from the list.

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