Small body size and extreme cortical bone remodeling indicate phyletic dwarfism in *Magyarosaurus dacus* (Sauropoda: Titanosauria)

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Sauropods were the largest terrestrial tetrapods ($>10^5$ kg) in Earth's history and grew at rates that rival those of extant mammals. *Magyarosaurus dacus*, a titanosaurian sauropod from the Upper Cretaceous (Maastrichtian) of Romania, is known exclusively from small individuals ($<10^3$ kg) and conflicts with the idea that all sauropods were massive. The diminutive *M. dacus* was a classical example of island dwarfism (phyletic nanism) in dinosaurs, but a recent study suggested that the small Romanian titanosaurs actually represent juveniles of a larger-bodied taxon. Here we present strong histological evidence that *M. dacus* was indeed a dwarf (phyletic nanoid). Bone histological analysis of an ontogenetic series of *Magyarosaurus* limb bones indicates that even the smallest *Magyarosaurus* specimens exhibit a bone microstructure identical to fully mature or old individuals of other sauropod taxa. Comparison of histologies with large-bodied sauropods suggests that *Magyarosaurus* had an extremely reduced growth rate, but had retained high basal metabolic rates typical for sauropods. The uniquely decreased growth rate and diminutive body size in *Magyarosaurus* were adaptations to life on a Cretaceous island and show that sauropod dinosaurs were not exempt from general ecological principles limiting body size.

bone histology | Sauropoda | secondary osteon | nanism | island fauna

Sauropod dinosaurs were the largest animals that ever roamed the surface of the Earth (1, 2). Gigantic size was acquired early in the evolutionary history of the group, in the Late Triassic (3). Recent studies of bone histology have shown that sauropods attained their gargantuan sizes by an evolutionary increase in their growth rate to levels comparable to those of extant endothermic mammals (4, 5). However, not all sauropods were multi-ton animals. Some titanosaurs are known to have had relatively small body sizes by sauropod standards; e.g., the South American *Neuquensaurus australis* reached a body length of about 7–9 m (6, 7), and its body mass is estimated at 3,500 kg. The recently described basal macronarian *Europasaurus holgeri* from the Late Jurassic of Germany (8) was even smaller, with a total estimated adult body length of approximately 6.2 m and a body mass of 800 kg.

Another small-bodied titanosaurian sauropod, *Magyarosaurus dacus*, is known from the Upper Cretaceous (Maastrichtian) continental formations of the Haţeg Basin of Romania (9, 10). These strata contain an array of relatively small-bodied dinosaur taxa, including the basal hadrosaurid *Telmatosaurus* (11), and two species of the noniguanodontian euornithopod *Zalmoxes* (12). In a famous early evolutionary hypothesis involving dinosaurs, the small body size of these taxa prompted the brilliant Hungarian paleontologist Franz Baron Nopcsa to hypothesize that, like Mediterranean dwarf proboscideans (13), the Haţeg dinosaurs evolved their diminutive body size on a paleo-island (14, 15). Later, however, rare larger titanosaur bones were recovered from the Haţeg Basin as well and described (16) as "*M.*" *hungaricus*.

At present, all titanosaur bones from the Haţeg basin are tacitly grouped together as *M. dacus* (9, 17). Morphological work (by Z.C.)

suggests that the larger taxon is different from *M. dacus*, we will hence use the name *M. dacus* to the exclusion of these large specimens. A full redescription, however, is beyond the scope of this paper. Today, *M. dacus* is known form numerous but mostly isolated bones of different-sized individuals, representing a growth series (Fig. 1). *Magyarosaurus* has been incorporated in only one phylogenetic analysis (18), in which the position of *Magyarosaurus* is resolved relatively high within the Titanosauria, inside the lithostrotian *Rapetosaurus* clade. This suggests that *Magyarosaurus* is closely related to taxa such as *Rapetosaurus*, *Nemegtosaurus*, *Malawisaurus*, and *Trigonosaurus*. Neither of these taxa shows any significant size reduction compared with members of less derived outgroups (*SI Text*). Small body size in *M. dacus* would thus represent an autapomorphic feature.

Morphological and Morphometric Evidence for a Nanoid Fauna. Modern work on this classical dinosaur fauna suggests that phylogenetic size reduction [nanism *sensu* (19)] through paedomorphosis (20) had occurred in *Telmatosaurus* (11) and *Zalmoxes robustus* (12), based on patterns of heterochronic shifts in the morphology and morphometry in these taxa. Similarly, morphometric analysis of a wide range of sauropod humeri indicated that *M. dacus* bones were more similar to the bones of subadult than adult representatives of other, more typical sauropod taxa. These results were considered consistent with the interpretation of *M. dacus* as a heterochronic dwarf (21).

Alternative Hypothesis: Small Size Reflects Juvenile Status. The co-occurrence of the rare large-bodied titanosaurian elements (*M. hungaricus*) (16) with *M. dacus* (22) and uncertainty about the paleogeographic setting of the Haţeg Basin (23), have drawn the insular nanism interpretation for *Magyarosaurus* into question. This has led to the suggestion that the small titanosaurian remains collected in the Haţeg Basin are not dwarfs at all, but represent merely juveniles of a sauropod with a more typical, massive adult body size (22) such as *M. hungaricus*. Historically, the ontogenetic status of dinosaurs has been difficult to resolve based on bone morphology alone because, unlike mammalian long bones, dinosaur long bones lack morphological indicators of full size having been attained. However, fossil bone histology has evolved into a powerful tool for detecting the ontogenetic status of nonmammalian tetrapods (reviewed in refs. 24 and 25; recent applications discussed in refs. 26–28). Because sauropod dino-
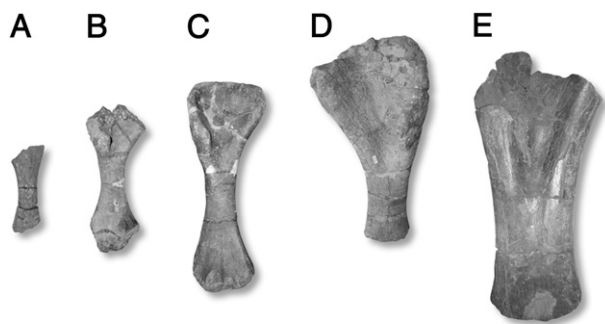
Fig. 1. Photographs of some of the sampled titanosaur bones from the Maastrichtian of Romania. (*A–D*) *Magyarosaurus dacus* humeri, specimens (*A*) MAFI Ob. 3092 (smallest recorded body size, 45% maximum size), (*B*) FGGUB R.1246 (65% maximum size), (*C*) MAFI v.13492 (76% maximum size), (*D*) FGGUB R.1048 (largest known specimen), and (*E*) "*Magyarosaurus*" *hungaricus*, MAFI Ob.3104. (Scale bar, 100 mm.)

saurs are one of the two histologically best sampled clades of dinosaurs (the other being Theropoda), we use long bone histology to resolve the controversy surrounding *Magyarosaurus dacus* and test the competing hypotheses of insular nanism vs. juveniles of a large-bodied species. We sampled a growth series of the small *M. dacus*, as well as one of the two long bones of *M. hungaricus,* available for study (Table 1).

Size and Age in Dinosaurs. Sauropods as well as theropods [and ornithischian dinosaurs, where sample size is sufficient (29–31)] follow a narrow growth trajectory, i.e., they lack developmental plasticity. In sauropods, this is documented by a close correlation between histologic ontogenetic stage (HOS) and body size (32–38).

In theropods, which commonly show good quantifiable growth records, growth curves vary little between individuals (39–45). This indicates that dinosaurs, like mammals, showed little intraspecific variation in asymptotic body size. Hence, large differences in adult size, in otherwise morphologically similar fossils, suggests that these individuals represent different biological species.

Results

***M. dacus* Long Bone Histology.** Like those of other sauropods (34, 35, 38, 46), *M. dacus* long bones are characterized by a small medullary cavity and relatively thick cortex (Fig. 2*A*). The medullary cavity merges into the cortex via cancellous bone that surrounds large erosion cavities. The cancellous bone is secondary in origin, and the erosion cavities become smaller as they grade into the innermost cortex. The cortical bone histology, however, represents a radical departure from that seen in any other sauropod, with the exception of the very largest and oldest of normal-sized sauropods. In all but the smallest individuals of *M. dacus* and irrespective of type of skeletal element, the primary bone of the cortex is completely replaced by dense secondary osteons or Haversian bone (Fig. 2 *A, B, E,* and *F*). The smallest individual (MAFI Ob.3092, less than 46% the length of FGGUB R.1048, the largest *M. dacus* humerus and 24% the length of the *M. hungaricus* humerus) retains primary bone in the outer cortex that, however, is also disrupted by numerous secondary osteons (Fig. 2 *C* and *D*). This primary bone is of the laminar fibrolamellar type with circumferential vascular canals and primary osteons. Unlike in typical laminar fibrolamellar bone of large mammals and other dinosaurs, the bone matrix between the vascular canals in *M. dacus* consists mostly of parallel-fibered and lamellar bone, with a minimal amount of woven bone. This well-organized primary bone matrix suggests that primary bone deposition rates were relatively slow (47–49), although the bone retained the extensive network of

Table 1. List of sampled titanosaur specimens, with dimensions

Specimen	Collection	Locality	Taxon	Bone type	Side	Length (mm)	Minimal shaft circumference (mm)	Percentage maximum size	Standardized length (to humerus)	Standardized percentage maximum size	HOS
R.1220	FGGUB	Groapa	*Magyarosaurus*	Femur	R	(346)	176	64	266	54.5	13
R.1511	FGGUB	Groapa	*Magyarosaurus*	Femur	L	(466)	179	86	358	73	13
R.1046	FGGUB	Ciula	*Magyarosaurus*	Femur	L	525	193	97	403.5	82.5	14
R.1992	FGGUB	Ciula	*Magyarosaurus*	Femur	R	(540)	195	100	414.5	85	14
Ob.3092	MAFI	Vălioara	*Magyarosaurus*	Humerus	L	(222)	115	46	222.5	46	12
R.1246	FGGUB	Groapa	*Magyarosaurus*	Humerus	R	(320)	122	65.5	320	65.5	14
R.1195	FGGUB	Scoaba	Titanosauria indet. (?*Magyarosaurus*)	Humerus	L	(346)	150	71	346	71	13
Ob.3089	MAFI	Vălioara	*Magyarosaurus*	Humerus	L	(365)	136	75	365	75	14
v.13492	MAFI	Vălioara	*Magyarosaurus*	Humerus	R	372	140	76	372	76	13
Ob.3128	MAFI	Vălioara	*Magyarosaurus*	Humerus	L	(432)	151	88	432	88	14
R.1047	FGGUB	Ciula	*Magyarosaurus*	Humerus	R	403	183	82.5	403	82.5	13
R.1048	FGGUB	Sînpetru	*Magyarosaurus*	Humerus	L	(488)	194	100	488	100	14
Ob.3104	MAFI	Vălioara - Budurone	"*M.*" *hungaricus*	Humerus	R	(914)	365		914	—	12
R.1252	FGGUB	Groapa	*Magyarosaurus*	Tibia	L	(354)	105	79	—	—	12
Ob.4212	MAFI	Vălioara	*Magyarosaurus*	Tibia	L	(323)	109	72	—	—	12.5
R.1380	FGGUB	Cărare	*Magyarosaurus*	Tibia	L	(402)	134	89	—	—	13
R.1045	FGGUB	unknown	*Magyarosaurus*	Tibia	R	450	181	100	—	—	14
Ob.3087	MAFI	Vălioara	*Magyarosaurus*	Tibia	L	(858)	260		—	—	14
Ob.3086a	MAFI	Vălioara	*Magyarosaurus*	Fibula	L	(388)	100		—	—	14
Ob.3086b	MAFI	Vălioara	*Magyarosaurus*	Fibula	L	(384)	101		—	—	14
R.1598	FGGUB	Groapa	*Magyarosaurus*	Ulna	L	(219)	95	65	—	—	14
Ob.3099	MAFI	Vălioara	*Magyarosaurus*	Ulna	R	337	128	100	—	—	14

Data in parentheses indicate estimated total length, provenance, relative size, and histologic ontogenetic stage (HOS). L, left; R, right.
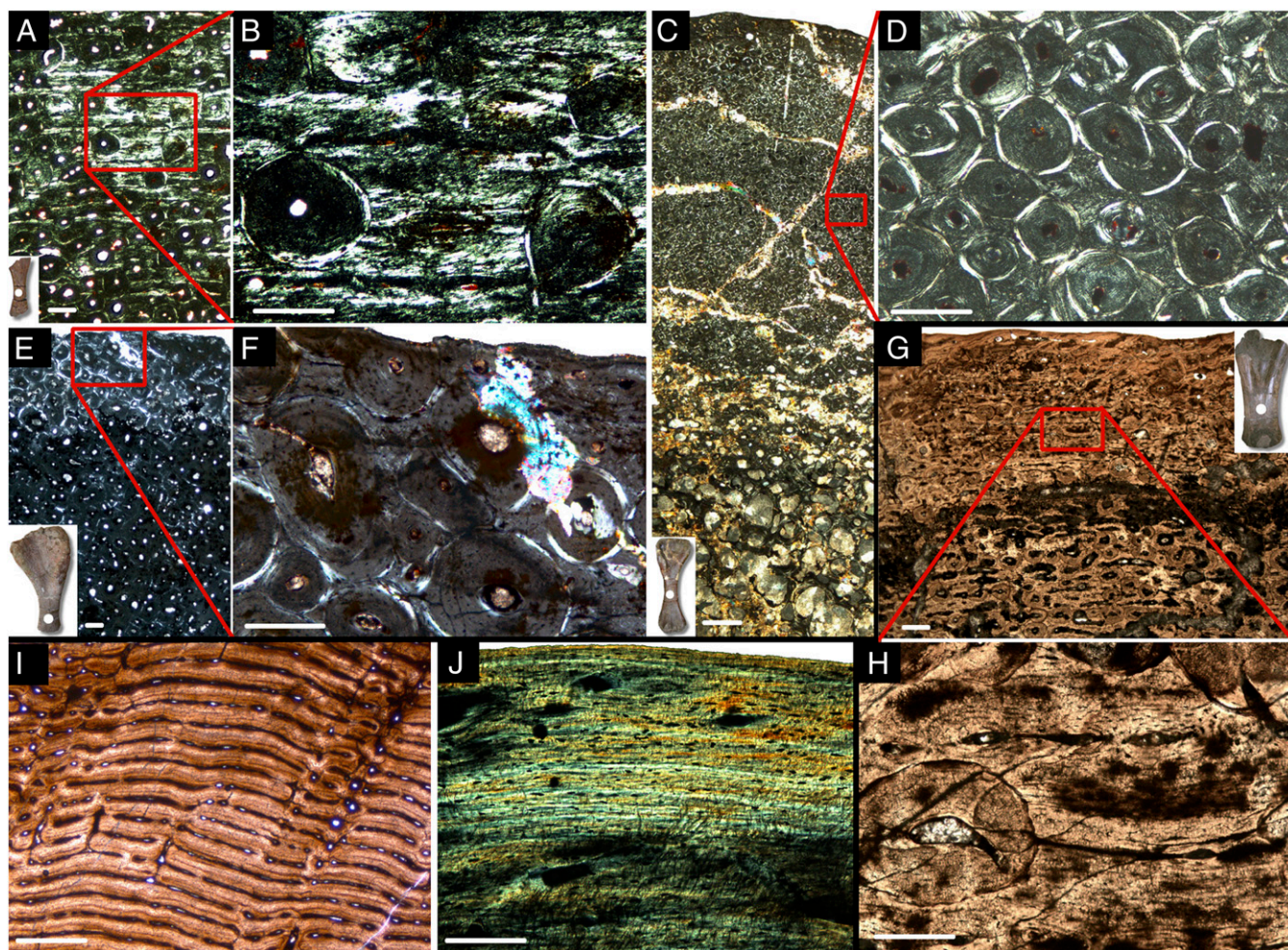
Fig. 2. Micrographs of long bone histology. (*A–E*) Long bone histology of *Magyarosaurus dacus* under crossed polarizers. (*A*) Micrograph of a midshaft section of the smallest available specimen of *Magyarosaurus dacus* (MAFI Ob.3092, 46% max size). (*B*) Close-up of *A*: largely interstitial laminar primary bone in the outermost cortex. The vascular canals are oriented circumferentially as in laminar fibrolamellar bone, but the bone matrix between the vascular canals consists largely of parallel-fibered and lamellar bone, with only a minute fraction of fibrous (or woven) bone tissue. (*C*) Micrograph of a midshaft section of MAFI v.13492 (76% max. size). The cortex is completely remodeled, in some areas several generations of secondary osteons can be seen crosscutting each other. (*D*) Closeup of *C*: cortex dominated by several generations of secondary remodeling. (*E*) Micrograph of a midshaft section of the largest available *M. dacus* humerus (FGGUB R.1048). (*F*) Close-up of *E*: Note the secondary osteons of the third generation, and truncated secondary osteons at the outer bone surface. (*G* and *H*) Long bone histology of '*M*.' *hungaricus* under polarized light. (*G*) Micrograph of a midshaft section of '*M*.' *hungaricus* (MAFI Ob.3104). The specimen is strongly remodeled, but the interstitial primary tissue is of the highly vascularized laminar fibrolamellar kind, with well developed primary osteons in the middle cortex, and poorly developed primary osteons with no lamellar bone infilling in the outermost cortex. Note that secondary osteons of the first generation are less well developed than in the largest *M. dacus* specimens. (*H*) Close-up of *G*: Secondary osteons crosscutting well developed primary osteons in the middle cortex. (*I*) Laminar fibrolamellar bone of *Apatosaurus* (BYU 72517014). (*J*) Alligator (SMNS 10481) long bone histology showing lamellar-zonal bone. (Scale bars: *A*, *B*, and *D–H*, 200 μm; *C*, 1,000 μm; *I* and *J*, 500 μm).

vascular canals typical of fibrolamellar bone seen in other sauropods and fast-growing extant vertebrates (48–50).

An external fundamental system (EFS, outer circumferential lamellae *sensu* 51) was not observed in any of the *Magyarosaurus dacus* individuals in this study. In the smallest individuals, those that retain some primary bone in their outermost cortex, an EFS could have been observed, if present. In the larger, completely remodeled specimens (HOS 13 or more), an EFS, if present, would have been obscured by this remodeling. An additional agent of destruction of an EFS is preparation. Some specimens showing secondary osteons truncated by the outer bone surface (Fig. 2 *E* and *F*) suggest that bone has been removed by rough preparation methods, possibly leading to the loss of the micrometer-thin EFS.

Histologic Ontogenetic Stages in the *M. dacus* Sample. We emphasize again that, in its extreme degree of cortical remodeling even in very

small individuals, the long bone histology of *Magyarosaurus* is unique among sauropods. In some larger individuals, three to four generations of secondary osteons can be observed (FGGUB R.1048; Fig. 2 *E* and *F*). However, the *Magyarosaurus dacus* sample is still amenable to relative age determination of individuals using histologic ontogentic stages (HOS) (35). The smallest individual, represented by specimen MAFI Ob.3092, records HOS 12 (Fig. 3). The bone microstructure of specimens FGGUB R.1220, FGGUB R.1511, FGGUB R.1246, FGGUB R.1195, MAFI v.13492, and FGGUB R.1047 corresponds to HOS 13, where the cortex is completely or almost completely remodeled. In a number of femora and humeri (FGGUB R.1046, FGGUB R.1992, MAFI Ob.3089, MAFI Ob.3128, FGGUB R.1048), at least one additional generation of secondary osteons, crosscutting secondary osteons of the first or subsequent generations are present in the outer cortex. The microstructure of these specimens corresponds to tissue type H,
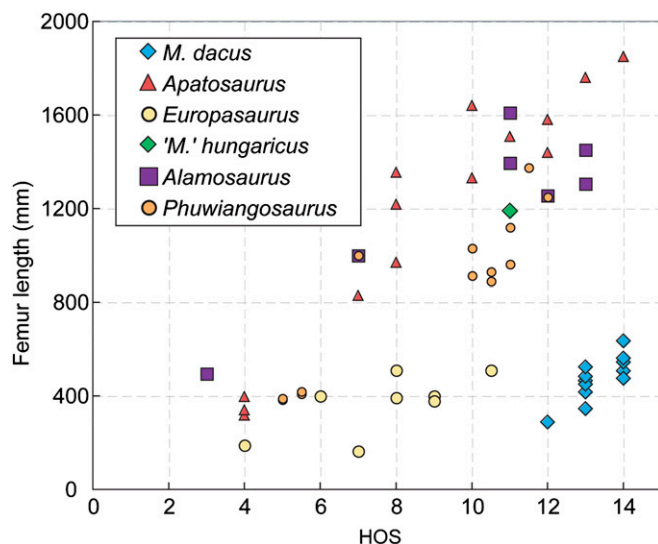
Fig. 3. Plot of histologic ontogenetic stage (HOS) (35) vs. body size as expressed by femur length in *Magyarosaurus dacus*, compared with *Europasaurus, Apatosaurus, Alamosaurus,* and *Phuwiangosaurus*. The samples of *Magyarosaurus dacus* derive from humeri that were normalized to femur length. The single "*M*'" *hungaricus* sample is also included. Data for *Alamosaurus* were obtained from a previous report (38), supported by own data. Data for *Phuwiangosaurus* were obtained from another report (37).

and is thus assigned to HOS 14 (35) (Fig. 3, *Materials and Methods,* and *SI Text*).

Titanosaur long bone histology has received only limited study so far. However, specimens of the basal titanosaur *Phuwiangosaurus* and the advanced titanosaur *Alamosaurus* that are the size of the smallest *M. dacus* show HOS 3–5 (35, 37, 38) (Fig. 3). HOS 14 has not been observed in *Alamosaurus* and *Phuwiangosaurus*, but fully remodeled specimens (HOS 13) have femur lengths of 1,400 mm, nearly 2.5 times the size of the largest *M. dacus* (Fig. 3).

Long Bone Histology and HOS of *M. hungaricus*. The histology of the large titanosaurian bone (MAFI Ob.3104) is different from the *Magyarosaurus dacus* bones (Fig. 2 *G* and *H*). The inner and outer cortex are dominated by secondary osteons, but with laminar primary bone still present in the outermost cortex. The primary bone is of the fibrolamellar kind, with a thick lining of lamellar bone in the vascular canals. These vascular canals, however, are not as narrow as in the *M. dacus* bones. Erosion cavities, but also mature secondary osteons, are visible in the outermost primary cortex. The outer bone surface is intact in MAFI Ob.3104, but there is no EFS, indicating that the animal was not fully grown. The bone microstructure of MAFI Ob.3104 corresponds to bone tissue type F (35) and is assigned to HOS 11 (Fig. 3). This is a lower stage than in the smallest bones in the *M. dacus* sample. However, this MAFI Ob.3104 is more than four times larger than the *M. dacus* specimens showing a later HOS (Figs. 1 and 3 and Table 1).

The histological sample of *M. hungaricus* shows a bone microstucture identical to that of *Phuwiangosaurus*, and a histology similar to that of the advanced titanosaur *Alamosaurus* (refs. 35, 37, 38) (Fig. 3). *M. hungaricus* thus displays a typical titanosaur long bone microstructure. A general observation of these titanosaur taxa compared to more basal neosauropods (e.g., *Apatosaurus*), is their accelerated remodeling rates (37, 38), which may be a result of continued peramorphic processes in Sauropodomorpha (34, 38, 51).

Interpretation. Both, the comparison of bone tissue types and of HOS (Fig. 3) indicates that the small (*M. dacus*) and large titanosaur bones (*M. hungaricus*) cannot be placed on the same

growth trajectory. This suggests that two distinct titanosaur taxa are present in the Haţeg Basin, with the great majority of bones belonging to a growth series of the diminutive *M. dacus*. We therefore reject the hypothesis (22) that the small titanosaur bones from the Haţeg Basin are merely juveniles of the large-bodied sauropod taxon, and we conclude that *M. dacus* is a dwarf taxon.

Discussion

Potential Problems: Lack of EFS. The lack of an EFS in any of the studied long bones represents a weakness in our argument for *M. dacus* having been a dwarf taxon. An EFS would most convincingly indicate that growth had terminated (24, 25). However, we see the evidence as conclusive that the *M. dacus* sample does not represent juveniles of the larger *M. hungaricus*. First, as noted earlier, the advanced remodeling reaching the outer bone surface in the larger specimens of *M. dacus* would have obliterated any EFS, the lack of which thus cannot be cited as evidence for the *M. dacus* specimens being juveniles. Second, *M. hungaricus,* having been the adult of *M. dacus* would mean that an earlier HOS is present in specimens differing 4-fold in size. Such an extreme variability in size at a given HOS is not seen in any other sauropod (35, 37, 38) and runs counter to the general observation of a close correlation between body size and histology in dinosaurs in general (32–36, 38). The only known exception to this pattern appears to be the Triassic basal sauropodomorph *Plateosaurus* (53), but this taxon is much more basal in the saurischian phylogeny than *Magyarosaurus*. Third, the completely remodeled cortex of the larger *M. dacus* specimens is wholly inconsistent with a juvenile status, not only in comparison with other sauropods (as seen in the HOS comparisons) but also with amniotes in general. Even in slow-growing mammals such a humans, complete remodeling of the long bones is a sign that full size has been reached (25, 47, 54–57).

Co-occurrence of Large and Small Titanosaurs on an Island. The very rare fossils of the larger titanosaur *M. hungaricus* in the Haţeg fauna are an interesting exception to the general dwarfing of other dinosaurs on Haţeg island. The presence of a few individuals of a larger titanosaurian species might relate to a time of lower sea level, for example, when the effective island size increased and allowed the survival of a larger-sized subsequent immigrant population, or they represent the remains of stray animals from nearby larger land masses. A similar example comes from the Pliocene–Pleistocene from Sulawesi, where the presence of the large *Stegodon* among smaller proboscideans was explained as the result of a late immigration event (58). Alternatively, the large bones may represent an early immigrant population before it reduced in size or went extinct. Nanism is known to occur very rapidly (59), at a time scale of 10^3 years, which is well below the time resolution in terrestrial sedimentary deposits, potentially making early colonists and later dwarfs seem comtemporaneous.

However, determining the most likely scenario is beyond the scope of this contribution, and will ultimately rely on future paleobiogeographic and phylogenetic work on the Haţeg dinosaur assemblage.

Significance of the Unique Long Bone Histology of *M. dacus*. The nanoid status of *M. dacus* is unique among titanosaurs, all of which have body masses an order of magnitude greater (1, 60). The only other island nanoid sauropod known is *Europasaurus* from the Upper Jurassic of Germany (8). At 900 kg, *M. dacus* had a similar adult body mass as *Europasaurus*, but the two taxa show distinctive histologies and ontogenetic growth trajectories (Fig. 3). *Europasaurus* does not have as intensely remodeled bone cortices as *M. dacus*, even in the largest known individual, which shows a clear EFS (8). The fully grown *Europasaurus* individuals are HOS 10.5, and the smallest ones (34% maximum size) are only HOS 4. *Europasaurus*, like large-bodied sauropods, also shows fibrolamellar bone in its long bone cortex (Fig. 2*I*), and only late in its

ontogeny, growth marks and Haversian remodeling started to appear (8). The primary bone in the smallest individual of *M. dacus* (46% maximum size) shows a large proportion of parallel-fibered bone, and our sample of *M. dacus* exhibits HOS ranging from 12–14. These observations suggest a reduced growth rate of *M. dacus*, in comparison not only with large sauropods but also with *Europasaurus* (Fig. 3).

Implications for Metabolic Rate. The highly vascularized fibrolamellar tissue in the long bones of *M. dacus*, albeit with a strong lamellar component, suggests that the high metabolic rate of sauropods (5, 53, 61) has been retained in *Magyarosaurus*, because the phyletic nanism did not result in the reversal to a bone histology seen in similar-sized ectothermic vertebrates (62). In ectotherms such as crocodiles (Fig. 2*J*) and large pseudosuchians (63), lamellar-zonal bone predominates, and these ectotherms lack strongly vascularized primary bone and Haversian bone of the kind observed in *Magyarosaurus*. That this is an evolutionary option for endothermic amniotes in a resource-limited habitat is shown by the Neogene dwarf goat *Myotragus* from the Balearic islands, which shows typical lamellar–zonal bone (ref. 64). Instead, *Magyarosaurus* reduced both adult body size and overall ontogenetic growth rate, presumably to adapt to island dwelling with its resource limitations.

Materials and Methods

Materials. Since Nopcsa's time, much new material has been recovered, and *M. dacus* is now known from numerous small-sized long bones and vertebrae. We sampled limb bone material (humeri, ulnae, femora, tibiae, fibulae) (Table 1 and Fig. 1) from the collections at the Faculty of Geology and Geophysics of the University of Bucharest, Romania (FGGUB) and the Geological Survey of Hungary in Budapest (MAFI). A total of 21 specimens were sampled, representing 18 *M. dacus* individuals, and one *M. hungaricus*. The humeral growth series of the diminutive *M. dacus* covers a size range from ≈22 cm to 49 cm in humerus length, whereas the large specimens are twice this large, with a sampled *M. hungaricus* humerus having an estimated length of 91 cm. For comparative purposes, we also sampled 5 individuals of *Alamosaurus sanjuanensis* to augment previous data (38). We sampled the specimens with a histological coring technique (34, 65). Samples were processed into thin sections, which were then studied histologically under a Leica DMLP polarized light microscope. Images were acquired with a Leica DFC420 digital camera and processed with Imagic Imageaccess software.

Mass Estimates. Most of the bones were found in isolation and come from a number of different localities within the Haţeg Basin. However, in a few cases, associated material allowed the sampling of multiple appendicular elements from the same skeleton (FGGUB R.1046, FGGUB R.1047, FGGUB R.1992). The length of the fragmentary femora was estimated from FGGUB R.1046; the length of fragmentary humeri from FGGUB R.1047; that of the tibiae from FGGUB R.1045; all ulnae and fibulae are virtually complete. We used a bone size estimation method based on identification of morphological landmarks and estimation of the preserved percentage of total length. Size standardization was performed for femora relative to humeral

length. The humerus to femur ratio (0.768) is calculated from associated specimens FGGUB R.1046 and FGGUB R.1047. Unlike in most other studies, the humerus was chosen because it represents the largest subset of our samples and histology is better preserved than in femora. Note, however, that humerus length was scaled to femur length in the HOS diagram (Fig. 3).

The masses of *Neuquensaurus* and *Magyarosaurus* were estimated using an equation for calculating large quadrupedal animal masses based on humerus and femur circumference (66, 67). Humerus and femur data for *Neuquensaurus* were obtained from the literature (7). For *M. dacus*, measurements were directly taken from an associated humerus (FGGUB R.1047) and femur (FGGUB R.1046) (Table 1).

Aging Sauropod Long Bones Using Histologic Ontogenetic Stages. Hundreds of individuals of different ontogenetic stages from close to 20 taxa across the entire sauropod phylogeny have been sampled so far [reviewed in (46)]. This breadth of sampling has led to the identification of histologic indicators of ontogenetic stage (32–34), formalized in the histologic ontogenetic stage (HOS) scheme (35). This scheme allows qualitative ontogenetic comparisons between humeri and femora of different sauropod taxa (37, 38). The previously used HOS scale ranges from HOS 1, representing embryonic bone, to HOS 13, representing individuals with a completely or almost completely remodeled long bone cortex (35) (*SI Text*). Histologic ontogenetic stages 12 and 13 are only seen in very old and large sauropod individuals that had lived for many years after reaching asymptotic body size, such as in the 1.58 and 1.76 m femora (BYU 601–17328, OMNH 01991) of *Apatosaurus* (Fig. 3). Some sauropod individuals, however, are characterized by a completely remodeled cortex, displaying successive crosscutting relations of secondary osteons in the outer bone cortex, with the inner and middle cortex displaying this feature anyway, as remodeling progresses from the medullary region outward (32–35). This feature is seen only in the largest and oldest sauropod individuals, such as in a 1.8-m femur (OMNH 4020) of *Apatosaurus*. Degrees of remodeling in large sauropod individuals have not previously been distinguished (35), but we believe that it is necessary to make this distinction for comparative histological purposes, as is done in forensic science (54, 55, 57). Therefore, we define a tissue type with a completely remodeled cortex and at least two generations of crosscutting secondary osteons in the outer cortex as tissue type H, representing HOS 14. Although it is tempting to define additional HOSs for every generation of secondary osteons, this is problematic. Eventually, as remodeling continues, it will have obscured earlier generations of secondary osteons, making it impossible to detect the precise number of generations of secondary osteons. The introduction of HOS 14 thus serves to refine the histologic ontogenetic staging of sauropods.

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Supporting Information

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Ancestral Character State Optimization for Body Size. We have optimized the ancestral character state for size on the only current phylogeny including *Magyarosaurus dacus* (1). We took femur length as a proxy for body size, as it is readily measurable with relatively high accuracy, or easily obtained from the literature. Mass estimates vary greatly even for the same skeleton depending on method and inherently have large errors. We also added *Europasaurus* to the optimization as a basal macronarian (2). Femur length of *Magyarosaurus* was measured on specimen FGGUB R.1046 and femur lengths of other taxa were taken from the literature (2–7 (Table S1). These lengths were mapped as a continuous character on the phylogeny in TNT. Fig. S1 illustrates the marked size decrease of *Europasaurus* and *Magyarosaurus*, compared to its close relatives. Even though *Magyarosaurus* is part of a clade of generally smaller titanosaurs, its femur length is significantly smaller than that of its sister taxa, indicating an autapomorphic size decrease.

Ontogenetic Bone Tissue Types in Long Bones. The following bone tissue types (types A–G) have been previously recognized in sauropods (9).

Type A bone tissue is embryonic tissue, with nonlaminar organization of vascular canals.

Type B bone tissue is fibrolamellar bone that is dominated by woven or fibrous bone. The vascularization is not laminar but mainly longitudinal, and the density of the vascular canals is very high. The vascular canals are large and essentially circular in cross section, but with an irregular margin, similar to small erosion cavities of the remodeling zone. Type B bone tissue normally has no true primary osteons developed and only a thin sheath of lamellar bone lines the vascular canals, indicating that primary osteon formation has started. No secondary osteons or growth marks are developed in the type B bone tissue.

Type C bone tissue consists of a primarily laminar fibrolamellar bone with a still very high vascular canal density. The type C bone tissue usually also starts with longitudinal vascular canals that later grade into vascular canals with a more circumferential appearance. However, longitudinal vascular canals in type C bone tissue are easy to distinguish from those in type B bone tissue by a more regularly round margin compared to the irregular longitudinal vascular canals in type B bone tissue and an already laminar organization even of the longitudinal vascular canals.

The transition from type C bone tissue to type D bone tissue is also gradual and not abrupt. The change is again indicated by the increase in lamellar bone in the primary osteons, and the vascular canals in the type D bone tissue have a thick lining of lamellar bone. However, vascularization is still high in type D bone tissue: the vascular canals are large but smaller compared with that seen in type C bone tissue. Vascularization is primarily laminar, but a few areas have vermiform or more reticular organization. In the type D bone tissue, the formation of secondary osteons starts. Thus, incompletely filled ("young") large secondary osteons are developed mainly between larger erosion cavities of the remodeling zone and are closely associated with the medullary cavity. Growth marks are rather rare in this tissue type.

Type E bone tissue represents a still relatively fast-growing tissue. The transition between type D bone tissue and type E bone tissue is gradual. These bone tissue types, in fact, differ only in organization and degree of vascular density. The vascular spaces in type E bone tissue are still present but are smaller in comparison with type D bone tissue because the thickness of the layer of lamellar bone lining the vascular canals increases, resulting in very distinctive primary osteons. The secondary osteons between the erosion cavities in the inner cortex are more densely spaced in type E bone tissue. In addition, the spread of secondary osteons into the primary cortex has started by now, resulting in scattered secondary osteons that may extend in some specimens up to the middle of the primary cortex. Growth marks may occur, but remain rare and are not typical for type E bone tissue.

Type F bone tissue is characterized by a clear decrease in vascularization, resulting finally in a nearly complete infilling of the primary vascular canals by lamellar bone. In some specimens, a change in bone tissue type from fibrolamellar to lamellar–zonal bone and the deposition of an EFS is initiated. The EFS indicates that a growth plateau has been reached. The vascular canals of primary osteons are more or less completely filled by lamellar bone tissue . Remodeling by secondary osteons has increased significantly, and dense secondary osteons are deposited at least up to the middle to inner two thirds of the primary cortex. In type F bone tissue, growth marks are usually present, including the closely spaced LAGs of the EFS. However, some specimens do not show growth marks or an EFS in the type F bone tissue.

Type G bone tissue is characterized by an almost complete or complete remodeling of the primary cortex by secondary osteons.

Type H bone tissue is characterized by a complete remodeling of the cortex, with multiple generations of secondary osteons crosscutting each other in the outer cortex, with interstitial laminae as a result. As the remodeling front commences at the medullary cavity–cortex transition, the inner cortex will automatically have been successively remodeled also.

The succession of these bone tissue types throughout ontogeny resulted in a scheme of 13 histologic ontogenetic stages (9), to which a 14th stage is added here (Table S2).

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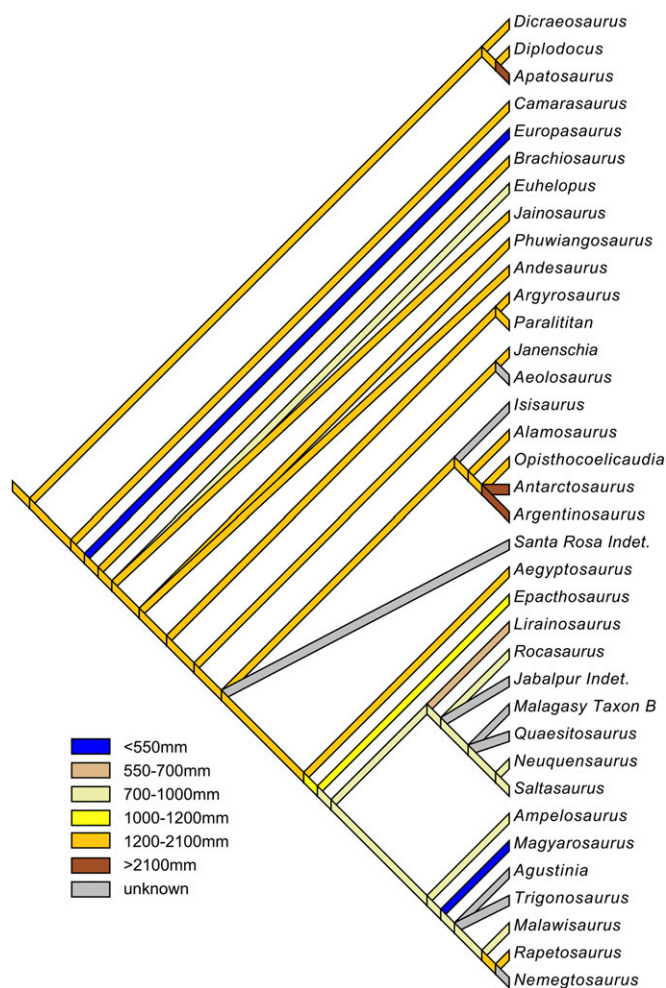
Fig. S1. Femur length as a proxy for body size, mapped on the only phylogeny that includes *Magyarosaurus* (1). *Europasaurus* was inserted as a basal macronarian (2). Both *Magyarosaurus* and *Europasaurus* unequivocally illustrate the phenomenon of autapomorphic size decrease. Even though *Magyarosaurus* is part of a generally smaller clade of derived titanosaurs, it is still significantly smaller than its sister taxa. Class determination is summarized in Table S1. Character optimization analysis was performed in TNT (8).

Table S1. Femur lengths used in ancestral character state optimization as proxy for body size for taxa included in phylogenetic tree used in the current analysis (1)

Taxon	Femur length (mm)	Specimen	Data source	Length class cutoff	Length class
Argentinosaurus	2,557	MLP-DP 46-VIII-21–3	Mazzetta et al. (2004)	0.22	5
Apatosaurus	2,500	YPM 1860	Carrano (2005)	0.60	5
Antarctosaurus	2,350	MLP 23–316	Mazzetta et al. (2004)	1.26	5
Paralititan	2,054	Est by Smith et al. (2001)	Smith et al. (2001)	0.26	4
Brachiosaurus	2,000	FMNH P25107	Carrano (2006)	0.45	4
Argyrosaurus	1,910	PVL 4628	Carrano (2006)	0.58	4
Camarasaurus	1,800	AMNH 5761a	Carrano (2006)	0.86	4
Diplodocus	1,645	YPM 1920	Carrano (2006)	0.21	4
Alamosaurus	1,610	TMM-HW16	Carrano (2006)	0.37	4
Andesaurus	1,550	MUCPv-132	Carrano (2006)	0.32	4
Rapetosaurus	1,500	Est by Curry Rogers (2009)	Curry Rogers (2009)	0.70	4
Opisthocoelicaudia	1,395	ZPAL MgD-I/48	Carrano (2006)	0.47	4
Janenschia	1,330	HMN IX	Carrano (2006)	0.30	4
Aegyptosaurus	1,290	BSP 1912 VIII 61	Carrano (2006)	0.31	4
Phuwiangosaurus	1,250	P.W. 1–1/1–21	Carrano (2006)	0.24	4
Dicraeosaurus	1,220	HMN m	Carrano (2006)	1.02	4
Epacthosaurus	1,095	UNPSJB-PV 920	Carrano (2006)	1.28	3
Euhelopus	955	PMU R234	Carrano (2006)	0.05	2
Malawisaurus	950	Mal-201	Gomani (2006)	0.79	2
Saltasaurus	875	PVL 4017–80	Carrano (2006)	0.83	2
Ampelosaurus	802	MDE uncat. 1	Carrano (2006)	0.04	2
Neuquensaurus	799	MLP-Cs 1094	Carrano (2006)	0.39	2
Rocasaurus	768	MPCA-Pv 56	Carrano (2006)	1.07	2
Lirainosaurus	686	MCNA 7468	Carrano (2006)	2.13	1
Magyarosaurus	540	FGGUB R.1046	This study	0.56	0
Europasaurus	510	DFMMh/FV415	Sander et al. (2006)	—	0
Agustinia	Unknown				
Aeolosaurus	Unknown				
Trigonosaurus	Unknown				
Jabalpur indet.	Unknown				
Jainosaurus	Unknown				
Malagasy Taxon B	Unknown				
Nemegtosaurus	Unknown				
Quaesitosaurus	Unknown				
Santa Rosa indet.	Unknown				
Isisaurus	Unknown				

The six femur length classes were devised on the basis that the greatest gaps in the length distribution should be used as class boundaries. We used the following procedure to identify these class boundaries: taxa were first ranked by increasing femur length, with the largest femur length available for each taxon being entered, whenever possible. In a pairwise comparison and starting with the largest femur, i.e., that of *Argentinosaurus*, the length of the smaller femur was subtracted from the larger. The difference was then divided by the length of the larger of the two and multiplied by 10. The resulting cutoff values for the successive pairs vary from 0.11 to 2.06, and a previously uncharacterized size class was established for cutoff values >1. Est, estimated.

Table S2. Fourteen histologic ontogenetic stages (HOSs) in sauropod long bones

Bone tissue type	HOS
Cortex consists of type A bone tissue.	Stage 1
Cortex consists primarily of type A bone tissue with type B bone tissue laid down in the outer cortex.	Stage 2
Cortex consists primarily of type B bone tissue, whereas in the inner cortex remains of type A bone tissue can be preserved.	Stage 3
Cortex consists primarily of type B bone tissue with type C bone tissue laid down in the outer cortex.	Stage 4
Cortex consists primarily of type C bone tissue, whereas in the inner cortex remains of type B bone tissue can be preserved.	Stage 5
Cortex consists primarily of type C bone tissue with type D bone tissue laid down in the outer cortex.	Stage 6
Cortex consists primarily of type D bone tissue, whereas in the inner cortex remains of type C bone tissue can be preserved.	Stage 7
Cortex consists primarily of type D bone tissue with type E bone tissue laid down in the outer cortex.	Stage 8
Cortex consists primarily of type E bone tissue, whereas in the inner cortex remains of type D bone tissue can be preserved.	Stage 9
Cortex consists primarily of type E bone tissue with type F bone tissue laid down in the outer cortex.	Stage 10
Cortex consists primarily of type F bone tissue, whereas in the inner cortex remains of type E bone tissue can be preserved.	Stage 11
Cortex consists primarily of type F bone tissue, whereas in the outer cortex an EFS is deposited.	Stage 12
Cortex consists of type G bone tissue which means it is nearly completely remodeled by secondary osteons.	Stage 13
Cortex consists of type H bone tissue, which means that multiple generations of secondary osteons with interstitial laminae are visible in the outer cortex.	Stage 14

Thirteen HOSs have been recognized in sauropod long bones by previous study (9), and a 14th HOS is added here. There are more HOSs than ontogenetic bone tissue types (type A–H) because in any one growth series there are specimens that preserve more than one bone tissue type in sequence. Of course, the preservation of successive bone tissue types depends on remodeling and resorption activity because strong resorption will result in a relatively thin cortex and strong remodeling activity will obliterate the primary growth record. This is why the HOSs that are based on the transition from one bone tissue type to the next are set up based on this transition occurring in the outer cortex, which is least affected by variability in resorption and remodeling.