LETTERS

# Bone histology indicates insular dwarfism in a new Late Jurassic sauropod dinosaur

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**Sauropod dinosaurs were the largest animals ever to inhabit the land, with truly gigantic forms in at least three lineages[1–3]. Small species with an adult body mass less than five tonnes are very rare[4,5], and small sauropod bones generally represent juveniles. Here we describe a new diminutive species of basal macronarian sauropod, *Europasaurus holgeri* gen. et sp. nov., and on the basis of bone histology we show it to have been a dwarf species. The fossils, including excellent skull material, come from Kimmeridgian marine beds of northern Germany[6,7], and record more than 11 individuals of sauropods 1.7 to 6.2 m in total body length. Morphological overlap between partial skeletons and isolated bones links all material to the same new taxon. Cortical histology of femora and tibiae indicates that size differences within the specimens are due to different ontogenetic stages, from juveniles to fully grown individuals. The little dinosaurs must have lived on one of the large islands around the Lower Saxony basin[8]. Comparison with the long-bone histology of large-bodied sauropods suggests that the island dwarf species evolved through a decrease in growth rate from its larger ancestor.**

Sauropoda Marsh, 1878
Neosauropoda Bonaparte, 1986
Macronaria Wilson and Sereno, 1998
***Europasaurus holgeri*** gen. et sp. nov.

**Etymology.** The generic name means 'reptile from Europe', after Europe and the Greek *sauros* for lizard; *holgeri* after Holger Lüdtke, who discovered the first bones.

**Holotype.** DFMMh/FV 291: disarticulated left premaxilla; right maxilla; right quadratojugal; occipital region; left laterosphenoid–orbitosphenoid complex; right surangular; right angular; left dentary; teeth; cervical and sacral vertebrae; and cervical and dorsal ribs of one individual (see Fig. 1 and Supplementary Information). DFMMh/FV: Dinosaurier-Freilichtmuseum Münchehagen/Verein zur Förderung der Niedersächsischen Paläontologie (e.V.), Germany.

**Referred material.** Cranial and postcranial elements of at least ten individuals, preserved as isolated bones to partially articulated skeletons, including young juveniles (estimated body length 1.7 m) to adults (body length 6.2 m).

**Horizon and locality.** Late Jurassic, middle Kimmeridgian marine carbonate rock, bed 93 of section at Langenberg quarry[7], Lower Saxony basin, Oker near Goslar, Niedersachsen, northern Germany (see Supplementary Information).

**Diagnosis.** *Europasaurus holgeri* gen. et sp. nov. shows the following unambiguous autapomorphies (see also Supplementary Information): nasal process of premaxillary projecting anterodorsally; medial notch on posterior dorsal margin of cervical vertebral centra; scapular acromion with a prominent posterior projection; and transverse width of astragalus twice its dorsoventral height and anteroposterior length. *Europasaurus* differs from *Camarasaurus* in the wing-shaped posterior process of the postorbital being slightly longer and wider than the anterior process, whereas it is much shorter in *Camarasaurus*. *Europasaurus* also differs from *Camarasaurus* in its short nasal–frontal contact; rectangular parietal in posterior view; and undivided presacral neural spines. *Europasaurus* differs from *Brachiosaurus* in the shorter muzzle, quadratojugal contacting squamosal; participation of jugal in ventral margin of skull; short nasal–frontal contact; and humerus flat anteromedially with proximal and distal epiphyses not aligned. *Europasaurus* differs from *Lusotitan atalaiensis*[25] in the shape of the ilium and the astragalus, and from the potentially valid '*Cetiosaurus*' *humerocristatus*[4] in its shorter and less prominent deltopectoral crest. *Europasaurus* differs from almost all known neosauropods in its diminutive adult body size.

Phylogenetic analysis (see Supplementary Information) indicates that *Europasaurus holgeri* gen. et sp. nov. is a macronarian that is more derived than *Camarasaurus*, and is the sistergroup of Brachiosauridae and all (more-derived) Titanosauromorpha. It also indicates that the diminutive body size of *Europasaurus* is derived.

Six individuals that represent the full body-length range known for *Europasaurus* were sampled histologically from one or two long bones each. The bones selected were femora and tibiae, and the bone tissues examined were those of the cortex (see Supplementary Information). The bone cortex of the smallest individual (body length 1.75 m; DFMMh/FV 009) is primary bone of the fibrolamellar complex with a reticular vascular network that grades into a laminar network (Fig. 2a). The bone matrix consists of fibrous tissue with plump osteocyte lacunae. Only a thin veneer of lamellar bone lines the vascular canals (incipient primary osteons). There are no growth marks in the cortical bone. The inner cortex lacks any indication of secondary remodelling, except for large erosional cavities. These features indicate a rapidly growing juvenile[9–11].

The next-largest individual (body length 2 m; DFMMh/FV 291.9) differs from the previous one in that the fibrolamellar bone is of the laminar type, the vascular network being organized into a predominantly circumferential pattern. The vascular canals have a lining of lamellar bone, forming primary osteons. In the next-largest individual (body length 3.5 m; DFMMh/FV 001), the primary osteons in the fibrolamellar complex are mature with a narrow central vascular canal. Notably, there are two cyclical growth marks (annuli) in the fibrolamellar bone of the outer cortex.

A slightly larger individual (body length 3.7 m; DFMMh/FV 495) was sampled from its tibia and femur. Both bones have the same histology of laminar fibrolamellar bone interrupted by growth marks (Fig. 2b), the spacing of which diminishes towards the outer bone surface, indicating a decrease in growth rate. However, the vascular canals in the outermost cortex are large and open to the bone surface, indicating active growth at the time of death. The next-largest individual (body length 4.6 m; DFMMh/FV 153) has the same primary bone histology as the previous ones, preserving five growth

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marks with decreasing spacing. It differs in having isolated secondary osteons in the inner cortex.

The largest individual (body length 6.2 m; DFMMh/FV 415) was sampled from a distal femur fragment. Because of the distal position of the sample, the cortex is relatively thinner than in the other specimens (Fig. 2c). In the inner part, the laminar fibrolamellar bone is heavily remodelled by secondary osteons with little primary bone remaining. The outer cortex has three closely spaced lines of arrested growth (LAGs). Vascular canals are longitudinal, and the tissue is predominantly lamellar. Vascularity decreases outwards, with the last cycle being nearly avascular and consisting of lamellar bone only. This histology is typical of an external fundamental system (ESF), and indicates that the individual was fully grown[9,11–13]. Because only one cycle of purely lamellar bone was laid down, the animal must have died soon after reaching full size.

Four size-related trends in the cortical histology of the *Europasaurus* long bones indicate that the fossils represent a growth series from juveniles to subadults to fully grown adults[9,11,12]: (1) only medium-sized and larger individuals have growth marks (annuli and LAGs) that diminish in spacing towards the outer surface, recording a decreasing growth rate; (2) only the largest individual was fully grown; (3) vascularization decreases from the smallest to the largest individuals, which is coupled with increased organization of the vascular network; and (4) haversian remodelling increases with increasing body size, from none in the four smallest specimens to many secondary osteons in the largest.

Palaeogeography[8] suggests insular dwarfing as the explanation for the diminutive body size of *Europasaurus*. The largest palaeo-islands surrounding the locality in the Lower Saxony basin had areas of $<$200,000 km$^2$ (calculated from ref. 8). Such islands would not have been able to support large-bodied sauropods. The ancestor of *Europasaurus* would have dwarfed rapidly on immigrating to the island, or as a response to shrinking land masses caused by rising sea levels. Previous hypotheses about island dwarfs among dinosaurs have focused on the Cretaceous of southeastern Europe[14–17], in particular on the sauropod *Magyarosaurus dacus* and the hadrosaur *Telmatosaurus transylvanicus* from the latest Cretaceous of the Hateg basin in Romania[14,15,18]. Fusion of cranial bones suggests that *Telmatosaurus* was fully grown[18], but the ontogenetic status of *Magyarosaurus* remains uncertain[16,19] in the absence of histological or bone fusion evidence.

The development of growth marks in the long bone cortex of *Europasaurus* suggests that it grew more slowly than larger less-derived neosauropod dinosaurs, including *Camarasaurus*[12,20–22]. Thus, an evolutionary decrease in growth rate was important in the dwarfing of *Europasaurus*. This is a reversal of the accelerated growth in the evolution of giant body size in sauropod and theropod dinosaurs[20,23,24].

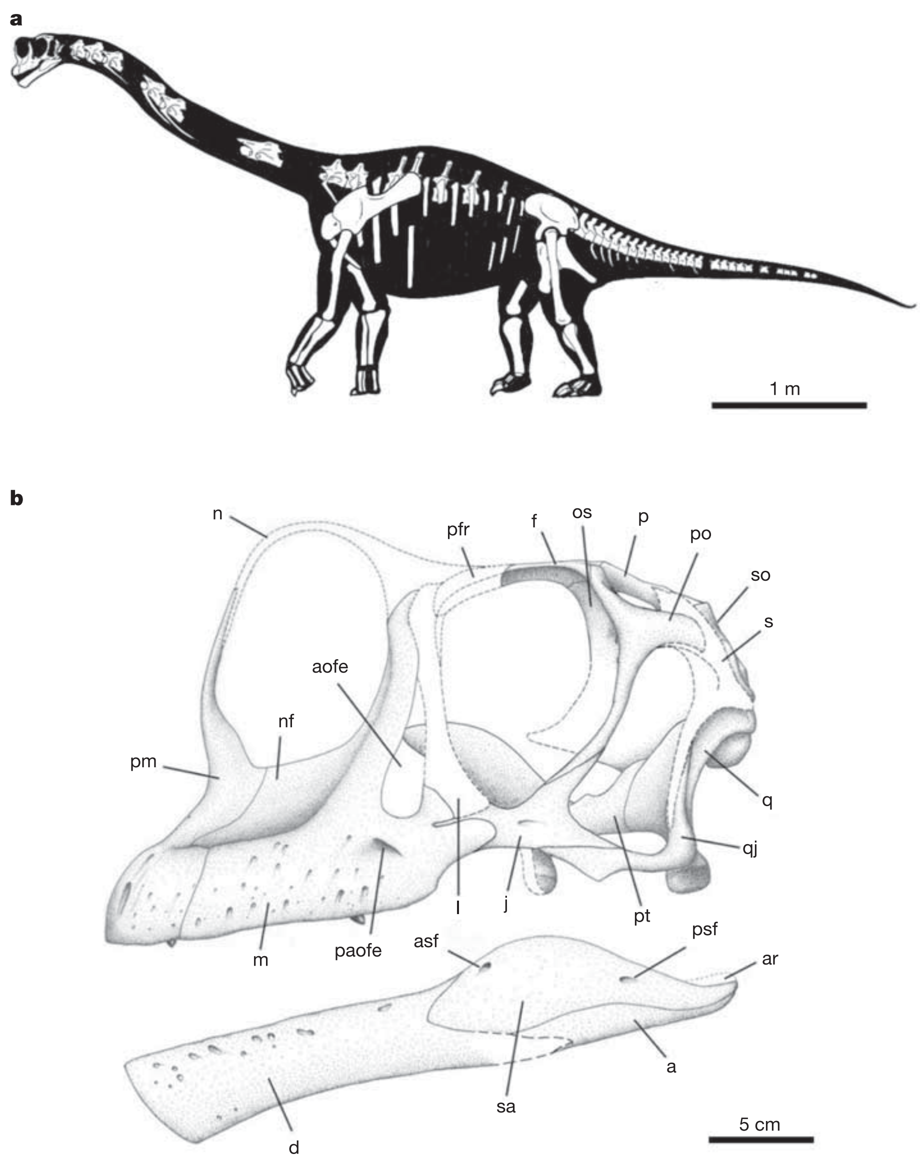


**Figure 1** | ***Europasaurus holgeri* gen. et sp. nov.** **a**, Reconstruction of the skeleton (known parts shown in white) and outline (black) scaled to the largest individual (body length 6.2 m). **b**, Skull reconstruction based on several individuals but scaled to the holotype. Abbreviations: a, angular; aofe, antorbital fenestra; ar, articular; asf, anterior surangular foramen; d, dentary; f, frontal; j, jugal; l, lacrimal; m, maxilla; n, nasal; nf, narial fossa; os, orbitosphenoid; p, parietal; paofe, preantorbital fenestra; pfr, prefrontal; pm, premaxillary; po, postorbital; psf, posterior surangular foramen; pt, pterygoid; q, quadrate; qj, quadratojugal; s, squamosal; sa, surangular; so, supraoccipital.

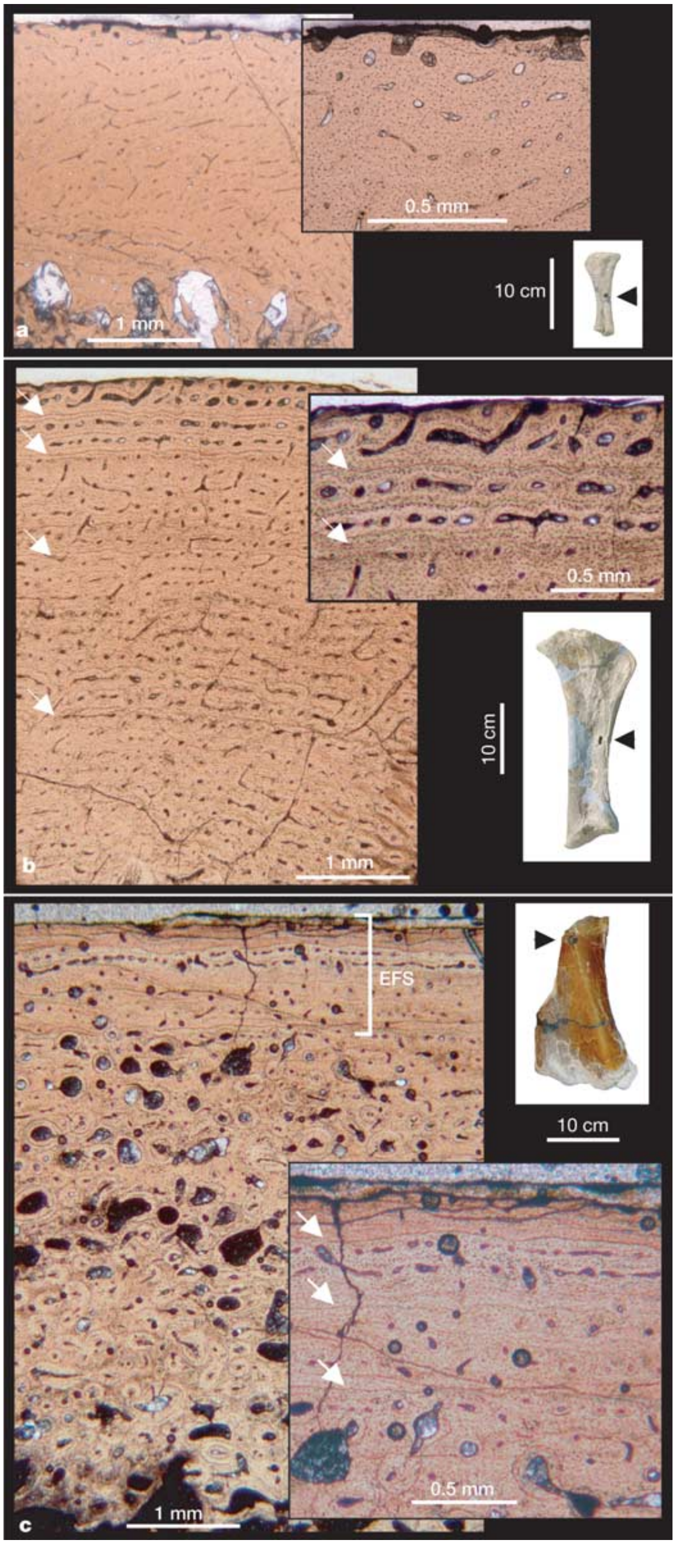


**Figure 2** | **Histological growth series and sampled bones of *Europasaurus holgeri* gen. et sp. nov. a**, Tibia from DFMMh/FV 009, the smallest individual (body length 1.75 m). The reticular fibrolamellar tissue, which grades into laminar fibrolamellar tissue (inset), and the absence of growth marks indicate its juvenile status. **b**, Tibia from DFMMh/FV 459.5, a mid-sized individual (body length 3.7 m). The cortex consists of laminar fibrolamellar bone interrupted by growth marks (arrows). Wide vascular canals opening to the outer bone surface (inset) indicate that this animal was still actively growing. **c**, Distal femur from DFMMh/FV 415, the largest individual (body length 6.2 m). The external fundamental system (ESF; inset) indicates that it was fully grown. Bone surface is at the top of all photomicrographs. Black arrows indicate sample locations; white arrows indicate growth marks.

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**Supplementary Information** is linked to the online version of the paper at www.nature.com/nature.

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