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Locomotion in *Homo floresiensis*: reconstructing foot use from the internal bone structure of the metatarsals of LB1

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The enigmatic *Homo floresiensis* displays a unique combination of cranial and post-cranial morphology [1-3], distinguishing it from other species of the genus *Homo*. Although its skeletal anatomy shows clear adaptations for terrestrial bipedalism, it also retains a suite of features conducive to arboreal behaviours. Thus, exactly how the locomotor behaviours of *H. floresiensis* compare with those of other hominins remains an important research question. The foot of the holotype (LB1) is long relative to its femoral length, has a longer forefoot than hindfoot, long phalanges relative to the non-hallucial metatarsals (Mts), and a short Mt1 relative to the other Mts [3]. However, it also possesses a human-like Mt head morphology and relative robusticity pattern [2-3]. Here, we assess the internal morphology of the Mts of LB1 to further assess foot functional morphology and locomotor kinematics in *H. floresiensis*.

Using high resolution micro-CT scans of the Mts of LB1 and a comparative sample of *Homo sapiens* (N=10), *Pan troglodytes* (N=15), *Pan paniscus* (N=15), *Gorilla* spp. (N=10) and *Pongo* spp. (N=9), we conducted a cross-sectional geometric analysis at mid-shaft and analysis of trabecular bone distribution in the Mt head. As the head was only fully preserved for the right Mt5 of LB1, trabecular analysis was limited to this element.

Cross-sectional geometry of the Mts at mid-shaft distinguishes between ape-like and human-like biomechanics, with greater loading of the Mt2 and Mt3 in apes compared with more lateral loading in humans [4]. The Mts of LB1 are internally robust, having a high cross-sectional area relative to bone length. Results show that the relative strength of the Mts, based on the internal structure, differs from the previously reported human-like pattern, which was based on external measurements of midshaft circumference [2-3]. We find that, after scaling by total bone length, the robusticity pattern for the left Mts of LB1 is 1>2>5>3>4 for CSA and Z, and 1>5>2>4>3 for J. Although there is some variation among humans, in general the Mt3 and Mt2 have lower measures of robusticity than the Mt4 and Mt5 [4]. In LB1, the Mt2 is consistently more robust than is expected in humans, with the pattern being 1>2/5>3/4 compared to 1>4/5>2/3 in humans.

The distribution of trabecular bone in the Mt5 head distinguishes between locomotor groups. In *H. sapiens*, where the foot is loaded in dorsiflexion there is a dorsal concentration of bone, which is asymmetric in extending dorsomedially. In African apes, where the toes are positioned dorsally during knuckle-walking and disto-plantarly during climbing (depending on substrate size) the distribution of trabecular bone extends dorsally to plantarly on the metatarsal head. In *Pongo*, trabecular bone is distributed distally and plantarly reflecting a grasping foot. The distribution of trabecular bone in the Mt5 of LB1 is located dorsally and distally but does not extend plantarly. This distribution pattern differs from humans in being centrally located, rather than medially, and in extending further distally. This suggests that the metatarsophalangeal joint in LB1 was loaded in a more a neutral position than in humans.

Together, the results suggest that loading of the foot of *H. floresiensis* differed from modern humans. First, the distribution of load across the foot was likely higher in the Mt2, a feature that could relate to higher loading of the second ray in a foot with a relatively short first ray. Secondly, the trabecular pattern suggests loading of the Mt5 head more distally than in humans, and with less asymmetric loading. This differing position of the metatarsophalangeal joint could be related to the long, curved phalanges of LB1. Future research exploring whole-bone cortical and trabecular structure of the metatarsals will shed new light on the kinematics of locomotion in *H. floresiensis*.

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