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Evolutionary timing and relationships of the talar facets: implication for hominin talus

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With the rise of terrestrial bipedalism operating as a selective force, hominins evolved a suite of specialized skeletal adaptations (e.g., anteriorly placed foramen magnum, S-shape vertebral column, broad and flattened ribcage, wide and short pelvis, long lower limb, stable knee, relatively long and robust ankle region, arched foot) which together facilitate efficient bipedal gait as well as upright standing [1]. Among locomotor adaptations, the human foot is unique compared to other primates because it is highly specialized for bipedal walking. Specifically, the talus occupies a pivotal position between the leg and foot, as 1) it sustains the weight of the body while distributing load anteriorly (i.e., to the navicular) and inferiorly (i.e., to the calcaneus), 2) it contributes importantly to plantar and dorsi flexion of the foot, and 3) it is part of the medial longitudinal arch. Importantly, the talus is relatively frequently found element in the fossil records and therefore can be used to reconstruct locomotor patterns among fossil hominoids [2]. For all these reasons, there is a vast literature addressing the evolution of bipedalism based on talar morphology [3]. Until now, however, no work has addressed the evolutionary timing and functional significance of relationships of variation in talar facets among hominins. Here, we analyze hominoid talar morphology as a whole, as well as individual and combined talar facets 1) to determine the evolutionary timing for the appearance of the human-like talar facets, and 2) to evaluate the discriminatory power in recognizing bipedal features in single and combined talar facets. A template of 251 (semi)landmarks was used to analyze 81 Homo sapiens, 31 Gorilla, 29 Pan, and 20 fossil hominin specimens (Australopithecus afarensis, A. africanus, A. sediba, Paranthropus robustus, H. habilis, early Homo, H. erectus sensu lato, H. floresiensis, H. neanderthalensis). The advantage in using semi-landmarks is that they allow more robust estimation of missing data in incomplete specimens [4] that are frequently omitted from analyses due to their fragmentary conditions. We used digital reconstructions to estimate missing (semi)landmarks on damaged fossils with cracks and/or gaps in order to include as many as possible. Generalized Procrustes analysis was used to convert the (semi)landmark configurations to shape coordinates, and talar shape variation was explored by Principal Component Analysis [5]. The results of the whole talus analysis show wide separation between H. sapiens and African apes. No hominins fall inside the range of ape morphospaces suggesting that all extinct hominins had acquired bipedal locomotion even if there may variation between species. The analysis of individual facets reveals different levels in distinguishing bipeds versus knuckle-walkers. The navicular facet appears human-like in A. afarensis, while more recent fossils, such as A. africanus and A. sediba retain more ape-like navicular facet morphology. The lateral malleolar facet seems to most effectively discriminate bipedal species from more arboreal species, suggesting that this facet evolved toward a bipedal form already in Australopiths. When combining articular surfaces, the combined head, trochlea and posterior calcaneal facets perform the best, with a net separation between Australopiths and Homo. Therefore, we suggest that the relative position of the major articular facets of the talus might inform about the presence of the medial longitudinal arch. Overall, this study points out that individual and combined talar facets vary in discriminatory power in recognizing bipedal forms, and that analysis of articular facets can contribute to the taxonomic and functional assessment of fragmentary fossil tali.