

Deciphering evolutionary dynamics in the hands and feet of modern humans

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The morphology of human hands and feet has distinct features that distinguish us from apes. The human foot exhibits a relatively long and robust fully adducted and non-opposable hallux, short and straight pedal phalanges from digits II-V, medial longitudinal and tarsal transverse arches, which, together with the well-developed plantar aponeurosis and intrinsic muscles, provide necessary stiffness against the tarsal break. The hand is distinguished by a long thumb relative to fingers, built with an enlarged thenar muscular complex, providing a unique range of rotation, stabilization, and grasping capacities. Additionally, the human hand displays short and straight metacarpals and non-pollical digits, along with a reoriented carpal-metacarpal articulation of the wrist via the first metacarpal-trapezium-scaphoid.

These autapomorphies enable humans to achieve two distinctive hallmarks: fully bipedal locomotion and unique manipulation abilities. Classic literature proposed the evolution of human autopods as an adaptive independent response to hand manipulation abilities for tool use and the acquisition of committed bipedalism, respectively. However, later investigations proposed different hypotheses, including the possibility that the modern human hand and feet co-evolved [1]. Specifically, this hypothesis suggests that the proportions of the hand represent a by-product of morphological adaptations for bipedalism in the foot. This hypothesis is based on the principle that hands and feet are serially homologous elements, sharing similar genetic and developmental architecture, and thus are initially strongly integrated [2]. Patterns and magnitudes of integration can be relatively modified due to functional factors [3], however, the shared genetic structure of the autopods constrains their ability to evolve independently.

In this study, we aim to shed light on the coevolution of hands and feet by quantifying the ability of modern human hands and feet to respond to selection demands in a coordinated manner. To do so, we apply a framework developed for evolutionary quantitative genetics to each homologous metapodial and phalanx skeletal element ($n = 19$) using nine linear variables. We subjected the autopods to three different evolutionary selection regimes: 1) random selection acting on both elements, 2) relaxation of selection in the hands, and 3) a scenario of no selection in the feet. The preliminary results indicate that, except for the second digit, all other digits exhibit significant negative values of coevolvability, indicating divergent random selection. However, the first two digits show increased positive coevolvability values when selection is acting only on the foot, while the third to fifth digits display even higher negative values. When analyzing individual skeletal elements, under random selection, all metapodials exhibit positive coevolutionary values, with the exception of the first metapodial, which shows low negative values in three selective regimes. Phalanges generally demonstrate negative coevolvability values, except for the II proximal phalanx, V middle phalanx, and I distal phalanx.

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References:[1] Rolian, C., Lieberman, D.E., Hallgrímsson, B., 2010. The coevolution of human hands and feet. *Evolution*. 64, 1558-1568. [2] Young, N.M., Hallgrímsson, B., 2005. Serial homology and the evolution of mammalian limb covariation structure. *Evolution*. 59, 2691-2704. [3] Rolian, C., 2009. Integration and evolvability in primate hands and feet. *Evolutionary Biology*. 36, 100-117.