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Complex and changing patterns of natural selection explain the evolution of the human hip

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ABSTRACT

Causal explanations for the dramatic changes that occurred during the evolution of the human hip focus largely on selection for bipedal function and locomotor efficiency. These hypotheses rest on two critical assumptions. The first—that these anatomical changes served functional roles in bipedalism—has been supported in numerous analyses showing how postcranial changes likely affected locomotion. The second—that morphological changes that did play functional roles in bipedalism were the result of selection for that behavior—has not been previously explored and represents a major gap in our understanding of hominin hip evolution. Here we use evolutionary quantitative genetic models to test the hypothesis that strong directional selection on many individual aspects of morphology was responsible for the large differences observed across a sample of fossil hominin hips spanning the Plio-Pleistocene. Our approach uses covariance among traits and the differences between relatively complete fossils to estimate the net selection pressures that drove the major transitions in hominin hip evolution. Our findings show a complex and changing pattern of natural selection drove hominin hip evolution, and that many, but not all, traits hypothesized to play functional roles in bipedalism evolved as a direct result of natural selection. While the rate of evolutionary change for all transitions explored here does not exceed the amount expected if evolution was occurring solely through neutral processes, it was far above rates of evolution for morphological traits in other mammalian groups. Given that stasis is the norm in the mammalian fossil record, our results suggest that large shifts in the adaptive landscape drove hominin evolution.

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1. Introduction

Hip anatomy has changed drastically over the course of human evolution. Short hip bones, laterally rotated iliac blades, and expansion of the retroauricular region are some of the most important morphological differences distinguishing the hominin (species more closely related to modern humans than any other living taxon) hip from that of other great apes (Dart, 1949a; Lovejoy et al., 1973; Stern and Susman, 1983). Other more subtle differences have been used to distinguish between hominin species. For example, when compared to australopiths, *Homo* pelvis generally have a taller posterior ilium, shorter anterior ilium, larger

retroauricular area, more robust and projecting anterior inferior iliac spine, shorter tuberoacetabular sulcus, longer pubic symphysis, and an anteroposteriorly broader birth canal (Simpson et al., 2008, 2014). Most of the differences in hominin hip morphology are hypothesized to play functional roles in bipedal locomotion (see Table 1, Fig. 1). Accordingly, causal explanations for these morphological shifts largely focus on selection for bipedal competence and efficiency (e.g., Stern, 2000; Bramble and Lieberman, 2004).

Hypotheses that morphological changes were the result of selection for bipedalism rest on two critical assumptions. The first is that those changes serve functional roles in bipedalism. Comparative and functional morphology can help to reveal the biological roles of traits by determining the functions they likely affected. Biomechanical modeling can be used to test these hypotheses (Ward, 2002), and numerous analyses show how hominin

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Table 1a

Hypothesized function for measurements believed to play major roles in bipedalism in modern humans compared to homologous traits in inferred chimpanzee-like LCA.

Distance ^a	Hypothesized functions of derived features in modern humans related to bipedalism
Anterior margin of iliac blade: H1	Along with the iliac blades rotating laterally, shortening this distance in modern humans places the lesser gluteal mm. in position to function as abductors and provide pelvic stabilization during single support phase (Sigmon, 1975).
Posterior margin of iliac blade: H2	Shortening this distance in modern humans reduces lumbar entrapment, allowing lumbar lordosis and placing the body's center of mass above the hips (see McCollum et al., 2010).
Auricular surface length: H3	Expanded in modern humans reflecting adaptation for weight bearing during bipedal behavior (Berge and Kazmierczak, 1986).
Retroauricular height: H4	Expansion in modern humans leads to increased area for attachment of interosseous sacroiliac ligaments, the size of which is significant for maintaining upright posture (Dart, 1949a,b); places the expanded gluteus maximus m. in a suitable position from which to control heel strike (Lovejoy, 2005), leads to posterior displacement of sacral articular surface relative to acetabulum allowing line of gravity of vertically oriented trunk to pass close to femoral heads instead of in front of them (Stern and Susman, 1983); provides a larger area of attachment for erector spinae mm. that control trunk flexion (Bramble and Lieberman, 2004).
Lateral iliac breadth: H5	–
Lower iliac height: H6	Shorter distance in modern humans places trunk center of gravity closer to hip joints and diminishes muscular torques needed to control balance (Stern and Susman, 1983); allows lumbar mobility not found in non-human African great apes (Lovejoy et al., 2009a,b).
Pubis length: H7	–
Pubic symphysis length: H8	–
Biomechanical moment arm of the ischium: H9	A shorter distance and dorsal placement of the ischial tuberosity in modern humans allows effective hamstring function on an extended limb, and when combined with a longer lower limb (Sokol et al., 2007), leads to a complex adapted for speed rather than power as seen in great apes (Robinson, 1972).
Femur Maximum length: F10	Longer limbs in modern humans increase locomotor efficiency by increasing step length and thus, reducing cost of traveling the same distance (Pontzer et al., 2009).
Biomechanical neck length: F11	Combined with laterally placed ilia, longer necks in modern humans provide improved mechanical advantage of hip abductors and thus, requires less force production from these muscles (Ruff, 1995).
Femoral Head diameter: F12	Larger heads in modern humans reflects greater proportion of body mass supported by the lower limbs in bipedal locomotion (Jungers, 1988), are required to withstand elevated forces produced by less optimally placed abductors (Lovejoy, 1988), and are a consequence of body size increase from earlier hominins (Ruff, 1998).
Bi-ilac breadth: O13	Combined with more laterally placed iliac blades, increasing this distance in modern humans increases the muscle moment arm at the hip that combined with gluteal muscle force counters torque generated by body mass and greater bi-acetabular breadth during upright walking (Ruff, 1995).
Bi-acetabular breadth: O14	A wider pelvis in modern humans would allow for greater effects of transverse pelvic rotation, increasing step length and decreasing the center of mass vertical displacement and thus, increasing efficiency (Rak, 1991) and/or would also leading to greater torque at the hip which must be countered by greater muscle force, a longer biomechanical neck length, or wider bi-iliac breadth (Ruff, 1995; but see Warrener, 2011).

^a Numbers correspond to traits shown in Fig. 1.**Table 1b**Character state in inferred LCA and currently described fossil hominins compared to modern humans.^a

Distance	Inferred LCA morphology	Australopiths	<i>H. erectus</i>	<i>Later Homo</i>	<i>H. neanderthalensis</i>
Anterior margin of iliac blade: H1	Much longer	Longer	NA	Similar	Slightly longer
Posterior margin of iliac blade: H2	Much longer	Similar	Similar	Similar	Longer
Auricular surface length: H3	Shorter	Shorter	Slightly shorter	Similar	Similar
Retroauricular height: H4	Much shorter	Shorter (e.g., A.L. 288-1, Sts-14); Similar (e.g., KSD-VP-1/1, MH2)	Similar	Similar	Similar
Lateral iliac breadth: H5	Slightly narrower	Wider	NA	Slightly wider	Similar
Lower iliac height: H6	Slightly longer*	Shorter	Slightly shorter	Similar	Shorter
Pubis length: H7	Longer	Longer	Longer	Longer	Longer
Pubic symphysis length: H8	Longer	Shorter	Similar	Slightly longer	Longer
Biomechanical moment arm of the ischium: H9	Much longer	Longer (Stern and Susman, 1983); Similar (Kibii et al., 2011)	Similar	Similar	Similar
Femur Maximum length: F10	Very short	Shorter (e.g., A.L. 288-1); Similar (e.g., KSD-VP-1/1)	Similar	Similar	Similar
Biomechanical neck length: F11	Shorter	Longer	Longer	Longer	NA
Femoral Head diameter: F12	Smaller	Smaller	Similar	Slightly larger	Slightly larger
Bi-ilac breadth: O13	Slightly narrower	Much wider	Wider	Much wider	Wider
Bi-acetabular breadth: O14	Narrower	Much wider	Wider	Slightly wider	Slightly wider

*Slightly longer in terms of total length—the *Pan*-like LCA has greatly increased height, but the modern human has expanded its bi-acetabular breadth, along with reducing height.^a Numbers correspond to traits shown in Fig. 1. Refer to SOM Excel Sheets 1 and 2 for list of fossils in each comparison and full references.

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