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journal homepage: www.elsevier.com/locate/jhevolBiomechanical implications of the onset of walking[☆]Libby W. Cowgill^{*}, Rob'yn A. Johnston

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ABSTRACT

Changes in long bone strength associated with the onset of bipedal walking in humans have been previously documented in a longitudinal growth sample. However, it is unclear if this transition can be detected using archaeological, cross-sectional data, which likely encompass more cultural and biological variation than a single dataset of living children. Focusing on variation in cross-sectional polar second moment of area, we evaluate the ratios of femoral, tibial, and humeral strength in seven temporally diverse samples of individuals from birth to the age of eighteen years ($n = 501$), with subsequent comparisons to immature Late Pleistocene fossils. Using these samples, we determine whether changes related to the developmental onset of bipedality can be detected in a large, multi-population sample, test for differences in long bone strength ratios among Holocene groups that may indicate developmental differences in the onset of walking, and determine whether immature Late Pleistocene samples follow the same patterns as modern humans.

Despite great variation within the Holocene sample, clear changes in these ratios are apparent around the age of the onset of walking. Humeral-to-femoral strength increases briefly prior to the age of one, with a sharp decline in relative humeral strength thereafter until age four. A similar pattern is apparent in the ratio of humeral/tibial and femoral/tibial strength. While the general pattern is consistent across all human groups sampled, these ratios vary by skeletal population, which seems to be closely related to variation in tibial length among samples. Although the extremely small fossil sample makes differences difficult to interpret, Neandertals also differ from both Late Pleistocene and Holocene modern humans in their strength ratios. Further research in this area may provide additional information about the skeletal impact of the onset of walking in the past and in additional fossil taxa.

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1. Introduction

During early human growth, biomechanical loading of the upper and lower limbs through both muscle contraction and body mass is essential to normal long bone development. In the absence of regular loading, long bones fail to ossify and develop in a normal fashion, resulting in developmental pathologies such as premature ossification and reductions in cortical thickness and area (Hall, 1972; Rodriguez et al., 1988). Given the close relationship between immature bone structure and its mechanical environment, early human postcranial growth can be conceived of as a continuous struggle to meet ever-increasing biomechanical demands placed on the maturing skeleton with the goal of constraining bone

deformation and strain to set levels. In this context, the entire process of postcranial growth is regulated by a biological “arms race” between bone strength and increasing biomechanical loads, as bone structural stability is constantly threatened during growth by increases in bone length, muscle force, and body mass (Rauch and Schoenau, 2001). Therefore, the biomechanical challenges imposed by crawling and walking are some of the earliest functional stimuli to affect the growing skeleton, and should be associated with morphological changes in human long bones. While all humans follow a basically similar developmental trajectory, the timing of these changes may differ subtly among human populations due to documented variation in the timing of motor events (Cintas, 1989).

In 2003, Ruff detected such a signal in a longitudinal sample of 20th century North American children (Ruff, 2003a,b). In an analysis of the ratio between immature femoral and humeral polar section moduli, Ruff (2003a) found that humeral polar section moduli increased most rapidly between six months and one year,

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followed by a steep decline. After one year, growth in the femoral polar section modulus outpaces that of the humerus until approximately three years of age (Fig. 1). These changes in long bone strength¹ are not explained by increases in body mass or bone length. Therefore, such changes were interpreted as the result of the cessation of crawling and the initiation of upright walking. Increases in upper limb strength prior to one year of age are probably related to the use of the humerus as a weight-bearing limb in crawling. Subsequently, the increases in femoral strength after the age of one are likely a product of the femur bearing a larger percentage of body weight in walking than in crawling. Studies of growth velocity during this time period illuminated similar patterns (Ruff, 2003b). Furthermore, additional studies of immature gorillas and chimpanzees have successfully detected comparable structural changes resulting from locomotor shifts across ontogeny as apes decrease arboreal locomotion and transition to a terrestrial gait (Ruff et al., 2013; Sarringhaus et al., 2016).

While this morphological and behavioral association has been detected in analyses of a modern longitudinal human sample, it has yet to be identified in broader cross-sectional samples of human skeletons. It remains possible that population-level behavioral variation or other factors may obscure the signal from the onset of bipedal locomotion among archaeological groups. Therefore, this analysis will attempt to identify the osteological signal of the developmental transition to walking in a large, diverse sample of immature Holocene and Late Pleistocene remains.

1.1. Variation in the timing of human locomotor events

Modern human children follow a well-established sequence of motor development. The infant progresses through a variety of locomotor stages culminating in fully bipedal walking between the ages of twelve and fifteen months (Gesell and Thompson, 1934; Shirley, 1963; Bly, 1994). Walking is preceded by sitting without support (circa four months), quadrupedal locomotion (between seven and ten months), and standing independently (by fourteen months) (Shirley, 1963; Bly, 1994). This sequence, however, varies both in timing and occasionally in order within our own species. While the timing of the hominin motor sequence has not been extensively explored within paleoanthropological literature, it is possible that the age of achievement of specific locomotor events varied during human evolution as well.

It is difficult to compare the timing of key milestones in the motor sequence across the great apes and humans because the locomotor endpoints (independent knuckle walking, quadrumanous locomotion, and bipedalism) differ so widely. However, the few attempts to compare standardized motor landmarks have yielded interesting results, in spite of the difficulty in defining equivalent states across species. Several researchers have used modifications of the Gesell Developmental Schedule, which contains developmental metrics for motor milestones in young children, to compare motor development in great apes (Gesell and Thompson, 1934). Compiled data for the timing of motor events in humans, common chimpanzees, and gorillas are shown in Table 1. Similar to dental development, the attainment of major motor skills is accelerated in chimpanzees and gorillas, although full locomotor independence from the mother is not achieved until 2.5 years in mountain gorillas and 5 years in chimpanzees (Doran, 1997). While the direct comparison of locomotor achievements among apes and humans is complicated by dissimilar adult

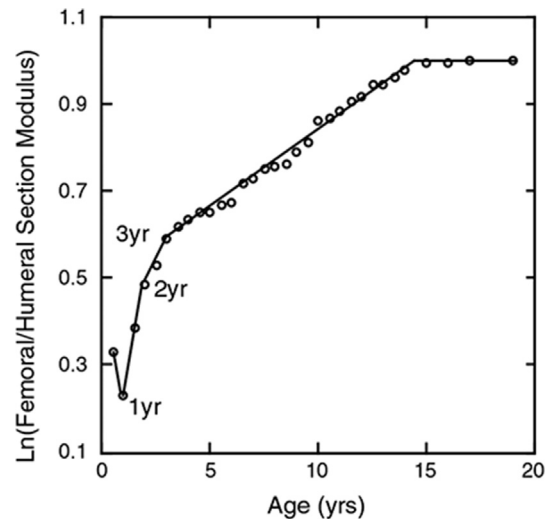


Figure 1. Age changes in the logged ratio of femoral to humeral polar section moduli in the Denver Growth Study sample. Reproduced from Ruff (2003a).

Table 1

Age of attainment of locomotor landmarks in weeks. Stages based on Gesell and Thompson (1934). Data from Gesell and Thompson, 1934; Riesen and Kinder, 1952; Hoff et al., 1983; Brakke and Savage-Rumbaugh, 1991.

	Gorillas	Chimpanzees	Humans
Arm extended (Prone)	n.d	2	20
Raises head and chest	4	2	13
Rolls to prone	12	11	40
Stands on fours	12	12–20	42
"Walks" on fours (creeps)	12	14–20	45
Sits	12	24–33	23
Bipedal standing	12 ^a	34–39	54
Bipedal walking	48	34–43	58

^a With support in gorillas.

locomotor patterns and possible alterations of the motor sequence in captive apes, it is clear that there is variation among hominoids in the attainment of general locomotor control, and that variation in motor development also could have characterized early human ancestors.

While there is substantial uniformity to the general developmental order of the motor sequence within humans, the specific timing of major landmarks such as independent walking vary across cultures. Studies of African infants originally led researchers to conclude that gross motor and locomotor development was relatively precocious in traditional, non-Western societies when compared to European infants (Geber and Dean, 1957; Ainsworth, 1967; LeVine, 1970; Liddicoat and Griesel, 1971; Goldberg, 1972, 1977; Lusk and Lewis, 1972; Leiderman et al., 1973; Konner, 1976; Super, 1976, 1980, 1981). Such studies have documented early attainment of motor sequence stages in African infants by one month or more, particularly sitting and walking (Geber and Dean, 1957; Ainsworth, 1967; LeVine, 1970; Konner, 1973, 1977; Super, 1976). Additional studies, however, have found that infants in other traditional, non-African societies may exhibit substantial developmental delay. Studies of traditional Mayan communities in Mexico indicate that general motor development is delayed compared with American norms (Brazelton et al., 1969; Solomons and Solomons, 1975), while Kaplan and Dove (1987) suggest that the Ache of eastern Paraguay learn to walk nine months later than their American counterparts, and a full year later than !Kung children.

¹ Cross-sectional second moments of area technically measure bone rigidity (Ruff, 2007). However, for convenience and ease of reading, long bone "strength" is used here.

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