



# Biomechanical implications of the onset of walking<sup>☆</sup>

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## ARTICLE INFO

### Article history:

Received 27 October 2017

Accepted 1 June 2018

Available online 17 July 2018

### Keywords:

Locomotion

Cross-sectional geometry

Neandertals

Growth

Ontogeny

## 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,

<sup>\*</sup> Grant sponsorship: Leakey Foundation, Wenner-Gren Foundation, NSF BCS-0549925.

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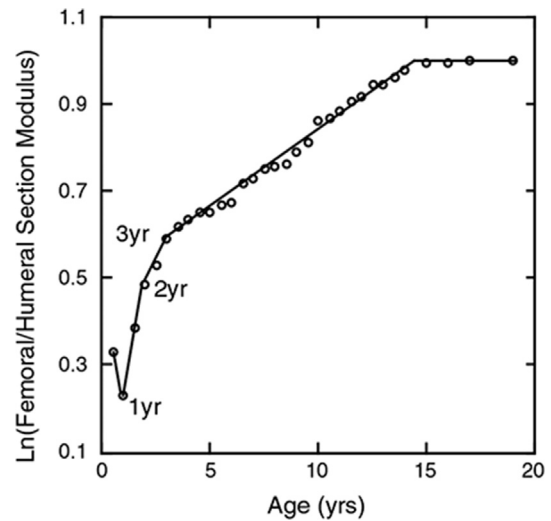
followed by a steep decline. After one year, growth in the femoral polar section modulus outpaces that of the humerus until approximately three years of age (Fig. 1). These changes in long bone strength<sup>1</sup> are not explained by increases in body mass or bone length. Therefore, such changes were 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 <sup>a</sup>	34–39	54
Bipedal walking	48	34–43	58

<sup>a</sup> 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.

<sup>1</sup> 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.

It is debatable whether physical restraint of infant body movements has an effect on the timing of major motor developmental events. While Navajo and Hopi infants spend six to 23 hours a day bound to a cradleboard from the first week of life, the examination of motor development among these infants failed to detect any deviation from American standards in the age of attainment of major stages in the motor sequence (Dennis and Dennis, 1940; Kluckhohn, 1947; Kluckhohn and Leighton, 1974; Chisholm, 1983). In contrast, perturbations, alterations, and delays in the motor sequence have been detected in infants whose movements have been reduced in other contexts. Dennis (1963) evaluated motor development in three orphanages in Tehran, Iran, and found that in the institutions with low interaction and stimulation, infant motor development was not only markedly delayed, but also deviated substantially from the pattern of development in normal infants. Between the ages of 2.0 and 2.9 years, only 8% could walk unaided; by the age of 3.9 years, this percentage only climbed to 15% of children walking independently. In addition to this substantial developmental delay, many young infants did not crawl at all, but locomoted prior to walking by “scooting,” in which infants sit erect and propel themselves with their arms, sliding on their buttocks along the substrate. This complete deviation from the normal crawling pattern was attributed to the fact that infants in the institution were always placed on their backs and never permitted to lie prone in their small cribs, thereby eliminating some of the early stimuli necessary to initiate crawling (Dennis, 1963).

The studies by Dennis (1963) and others suggest a strong environmental component to the development of the normal motor sequence. In fact, while genetic explanations have been sought, most of the evidence for delayed or precocious motor development is best explained as a product of differences in child-rearing practices. !Kung parents, for example, do not believe in the natural maturation of motor milestones; if a child is not actively taught to sit, stand, and walk, the child will fail to do so (Konner, 1976, 1977). Infants are actively trained to sit by their parents bracing their back and buttocks with sand and propping them up long before they are developmentally mature enough to sit independently (Konner, 1976, 1977). !Kung caregivers often stand infants in their laps, thereby initiating the stepping reflex and actively maintaining it beyond the age when it is lost in Western infants (circa five to six months), which results in an earlier age of successful walking among !Kung children (Takada, 2005). In contrast, motor developmental delay among Ache children has been attributed to their parents' extreme reluctance to allow infants under the age of two to explore their environment, with mothers actively discouraging the independent locomotion of infants by continually pulling the infant back to their lap before they venture out of reach (Kaplan and Dove, 1987). In all likelihood, it is this variability in parenting attitude and strategy that leads to variation in the development of motor coordination, with variables such as genetic background and subsistence economy playing a lesser or non-existent role.

Given previous success in detecting the biomechanical effects of walking in a longitudinal North American sample, it may be possible to identify this locomotor shift in archaeological and fossil populations. Therefore, this research will explore three specific areas in a large, geographically diverse set of Holocene samples, and a smaller selection of immature Late Pleistocene fossil remains. First, the general pattern of strength among long bone ratios (right humeral/femoral bending and torsional strength, right humeral/tibial bending and torsional strength, and femoral/tibial bending and torsional strength) will be evaluated between the ages of birth and 18 years in a large, geographically diverse sample. If strength changes related to the onset of walking are detectable in a cross-sectional sample, changes in the strength ratios, such as increased robusticity in lower limb elements relative to those in the

upper limb, are expected to be associated with individuals younger than three. Second, if a possible peak associated with the developmental adaptation of bipedality is detected, a closer look at population differences in the timing of the peak will be undertaken, as research on living children suggests that the onset of walking may differ among human groups. Third, long bone ratios in a small sample of immature Late Pleistocene Neandertals and modern humans will be compared to immature Holocene humans. While the Late Pleistocene sample of very young individuals is small, differences in the strength ratios between the fossil sample and Holocene groups may be suggestive, although not conclusive, of differences in developmental timing.

## 2. Materials

The primary data for this analysis consist of long bone polar second moment of area ratios constructed from femoral, tibial, and humeral cross-sectional properties from seven Holocene human skeletal samples and available Late Pleistocene specimens (Cowgill, 2010). Measurements were collected from a total of 501 immature Holocene individuals under the age of 18, although actual sample size may vary by analysis due to missing elements. The seven samples were selected to represent the broadest possible range of historical and archaeological time periods, geographic locations, and subsistence strategies. Within the comparative sample, individuals displaying indicators of obvious developmental pathology were excluded, although observations of non-specific developmental stress (Harris lines, cribra orbitalia, porotic hyperostosis) were not considered grounds for omission. In addition, while sex-related variation in development exists (Burdi et al., 1970; Garn and Burdi, 1971), it was necessary to group the sexes in this analysis due to the difficulty in determining sex in pre-pubertal skeletal remains. However, in previous studies where sex was known, no differences in the timing of the developmental onset of bipedality were detected in a longitudinal sample (Ruff, 2003a,b), so it remains unlikely that grouping the sexes in this analysis will have much effect on the results.

### 2.1. Holocene sample

While details of the comparative sample have been published elsewhere (Cowgill, 2010), and are summarized in Table 2, they are discussed briefly here for additional clarity. The California Amerindian sample used in this analysis is derived from 28 sites in the Alameda, Sacramento, and San Joaquin counties of north-central California, primarily clustered along the San Francisco Bay and the Sacramento and San Joaquin River valleys. California Amerindians of this area are best characterized as pre-contact, semi-sedentary foraging populations, reliant on deer, elk, antelope, fishing, and extensive exploitation of acorns. Indian Knoll is an Archaic Period shell-midden site located on the Green River in Kentucky (Webb, 2001). Individuals from Indian Knoll were likely semi-sedentary with prolonged residences at seasonally occupied sites, who experienced relatively high population densities, and relied heavily on a narrow spectrum of essential resources, such as deer, turkey, mussels, nuts and a variety of locally collected plant materials (Webb, 2001). The site of Kulubnarti is located in Upper Nubia in the Batn el Hajar region, approximately 130 km south of Wadi Halfa, where two medieval Christian cemeteries containing 406 burials were excavated in 1979 (Van Gerven et al., 1995). With marginal subsistence levels, individuals traditionally lived in small villages, participated in small-scale agriculture, and likely suffered from chronic nutritional difficulty combined with bouts of infectious disease during growth (Van Gerven et al., 1990). Mistihalj is a medieval burial site located on the border between Bosnia-

**Table 2**  
Sample description, size, date, and location.

Sample	Original Location	Approx. Time Period	n	Sample location
California Amerindian	Northern California	500–4600 BP	87	Phoebe Hearst Museum at the University of California, Berkeley (Berkeley, CA, USA)
Dart	Johannesburg, South Africa	20th century	72	School of Medicine, University of Witwatersrand (Johannesburg, South Africa)
Indian Knoll	Green River, Kentucky	4143–6415 BP	97	University of Kentucky, Lexington (Lexington, KY, USA)
Kulubnarti	Batn el Hajar, Upper Nubia	Medieval (6th–14th century)	97	University of Colorado, Boulder (Boulder, CO, USA)
Luis Lopes	Lisbon, Portugal	20th century	44	Bocage Museum (Lisbon, Portugal)
Mistihalj	Bosnia-Herzegovina	Medieval (15th century)	51	Peabody Museum at Harvard University (Cambridge, MA, USA)
Point Hope	Point Hope, Alaska	300–2100 BP	53	American Museum of Natural History (New York, NY, USA)

Herzegovina and Montenegro. The remains at Mistihalj are culturally associated with the Vlaxhs, an indigenous Balkan ethnic group, who primarily engaged in breeding sheep, horses, mules, and cattle, and who migrated seasonally over varied terrain (Alexeeva et al., 2003). The Dart Collection is an ethnically mixed, native African cadaver sample derived from hospitals in the Transvaal region in South Africa (Saunders and DeVito, 1991). Approximately 74% of all individuals died prior to 1950, and approximately 92% of the individuals within this sample are Bantu-speaking South African Blacks. Due to the diversity of this region, it is difficult to classify this sample area as exclusively rural or urban. The Luis Lopes skeletal collection consists of 20th century Portuguese from several cemeteries in Lisbon. In general, the sample is best categorized as an urban population of low to middle socio-economic status (Cardoso, 2005). The site of Point Hope, Alaska is situated on a peninsula in the Chuckchi Sea, approximately 200 km north of the Arctic Circle (Larsen and Rainey, 1948). Earlier periods of the Point Hope stratigraphic sequence are characterized by a reliance on caribou hunting, whereas later cultural horizons indicate a more extensive dependence on the exploitation of maritime resources such as walruses, seals, and whales (Larsen and Rainey, 1948; Rainey, 1971). Immature skeletal remains from the multiple cultural periods excavated at Point Hope were combined into a single sample for this analysis, as previous analyses of Point Hope adults and immature individuals found little biomechanical difference between the early and late periods at this site (Shackelford, 2007, 2014; Cowgill, 2014).

## 2.2. Late Pleistocene sample

The Late Pleistocene fossil sample includes seven immature Neandertals and 21 early modern humans (Table 3). The specimens included in the fossil analysis were limited to individuals under the age of four, in order to focus on the developmental period associated with the initiation of bipedal locomotion. While one of us (LWC) collected the majority of the Late Pleistocene data from the original fossil specimens, data for this analysis were also collected from published sources for two individuals (Dederiyeh 1 and 2); and from previously unpublished data provided by Erik Trinkaus for one individual (Skhul 1). Although fetal material was generally excluded from the comparative sample, less stringent criteria were employed in the Late Pleistocene fossil group in order to maximize sample size and avoid omitting Late Pleistocene individuals who may be slightly outside of modern human size ranges. At 68 and 63 mm respectively, La Ferrassie 5 and Cro-Magnon 5 possess estimated femoral lengths that are small for a full-term modern infant (Fazekas and Kósa, 1978). However, given modern human variation in long bone length at birth and the difficulty with directly applying modern human standards to Late Pleistocene infants, La Ferrassie 5 and Cro-Magnon 5 are included in this analysis (see more below on the Cro-Magnon 5 remains). The majority of the Late Pleistocene sample is from Europe and the Near East, although

multiple individuals are included from North Africa (Taforalt). The Taforalt sample is the only large immature Late Pleistocene modern human sample, and includes remains of 44 immature individuals from a Moroccan ossuary, 13 of which are included here (Ferembach et al., 1962).

The examination of original fossil descriptions and excavation reports confirms that the association of long bones within individuals is quite secure for most of the fossils included in this analysis. The exception to this is the neonatal remains of Cro-Magnon 5 (Gambier, 1986). The remains designated Cro-Magnon 5 consist of four neonatal left femora, two neonatal right tibiae, two neonatal left tibiae, and a humerus from an older immature individual. The femora and tibiae of Cro-Magnon 5 were cautiously associated by one of us (LWC) based on differences in long bone length. These individuals are labeled Cro-Magnon 5a and 5b in Table 3.

Due to issues of preservation and recognition in the human fossil record, fossil human remains under the age of four are relatively rare. The relative paucity of fossil remains in this age range makes it difficult to gain information about growth and life history in the past from the fossils themselves, forcing researchers to rely on less direct methods of inference in many cases. We argue, however, that in spite of the challenges raised by working with such small samples, the information gained can provide valuable insights into growth and activity in the past, and point the way to future studies. Nonetheless, research based on so few fossil specimens must be cautiously interpreted.

## 2.3. Determination of age

Age was undocumented for the fossil samples and for six of the seven Holocene samples used in this study. Cheek tooth crown and root formation evaluated from lateral mandibular radiographs was used whenever dental and postcranial remains were reliably associated. Crown and root formation was assessed following the developmental standards set by Smith (1991) for permanent dentition and Liversidge and Molleson (2004) for deciduous dentition. Each set of dentition was scored twice on two consecutive days, and individual teeth that produced different formation stage scores were evaluated a third time to resolve inconsistencies.

The ages for all Late Pleistocene remains are shown in Table 3. It remains possible that modern human reference samples are not appropriate for predicting dental age in archaic human populations (Ramirez-Rossi and Bermudez de Castro, 2004; Smith et al., 2007; however, also see; Dean et al., 2001; Guatelli-Steinberg et al., 2005; Macchiarelli et al., 2006), as a wide body of research has suggested that Neandertals may show accelerated dental development. Some authors have suggested that Neandertal teeth formed 15% faster than those of modern humans (Ramirez Rozzi and Bermudez de Castro, 2004) and others have found dental development, at least in one individual, to be accelerated by approximately two to three years when compared to a modern reference sample (Smith et al.,



**Table 3**

Fossil ages, element preservation, references, and designated approximate time period.

Sample	Period	Age (yrs.)	Hum.	Fem.	Tib.	References
La Ferrassie 5 <sup>a</sup>	Neandertal	Neonatal		X	X	Vandermeersch, 1965; Heim, 1982
Le Moustier 2	Neandertal	Neonatal	X	X		Maureille, 2002
Cro-Magnon 5A <sup>a,b</sup>	Early UP AMH <sup>c</sup>	Neonatal		X	X	Gambier, 1986; Henry-Gambier, 2003
Cro-Magnon 5B <sup>a,b</sup>	Early UP AMH	Neonatal		X	X	Gambier, 1986; Henry-Gambier, 2003
El Wad 10312 <sup>a</sup>	Late UP AMH <sup>d</sup>	0.05	X	X	X	McCown and Keith, 1939; Weinstein-Evron, 1998
La Ferrassie 4	Neandertal	0.15	X	X	X	Vandermeersch, 1965; Heim, 1982
Romanelli 3	Late UP AMH	0.93	X	X	X	Alessio et al., 1964; Fabbri, 1987
Dederiyeh 1	Neandertal	1.25	X	X	X	Kondo and Dodo, 2002a
Dederiyeh 2	Neandertal	1.67		X	X	Kondo and Dodo, 2002b
Arene Candide 11 <sup>a</sup>	Late UP AMH	2.4	X	X	X	Parenti, 1946; Formicola et al., 2005
Roc de Marsal 1	Neandertal	2.5	X	X		Vandermeersch, 1965; Madre-Dupouy, 1992
Arene Candide 5b	Late UP AMH	2.75	X	X	X	Parenti, 1946; Formicola et al., 2005
La Ferrassie 6 <sup>a</sup>	Neandertal	2.98	X	X	X	Vandermeersch, 1965; Heim, 1982
Skhul 1	MP AMH	3.25	X	X	X	McCown and Keith, 1939; Grün et al., 2005
La Madeleine 4	Late UP AMH	3.3	X	X	X	Oakley et al., 1971; Heim, 1991
Taforalt	Late UP AMH	0.0–1.24	12	13	13	Ferembach et al., 1962; Vallois, 1969

<sup>a</sup> Ages estimated through long bone length.<sup>b</sup> Cro-Magnon 5 consists of 4 neonatal left femora, 2 neonatal right tibiae, 2 neonatal left tibia, and a humerus from an older individual.<sup>c</sup> Approximately 35–20 ky BP, following Shackelford (2005).<sup>d</sup> Approximately 20–10 ky BP, following Shackelford (2005).

2007). This presents unique analytical difficulties. For the purposes of this study, we initially assume immature Neandertal and modern human development are approximately equivalent and that they can be dentally aged based on the same criteria. While ages have previously been determined for many immature Late Pleistocene individuals by other researchers, the present aging protocol was used in this analysis in order to maintain internally consistent ages. However, when significant differences between Neandertals and modern human populations were detected, we evaluated the results in the context of two sets of Neandertal age estimates: one where Neandertal and modern human development are equivalent and one where point estimates of Neandertal ages have been adjusted downward by 15%. This adjustment makes it possible to evaluate if potential postcranial strength differences are likely a result of erroneous dental ages.

When no dentition was directly associated with the postcranial remains (approximately 9% of the total sample), chronological age was predicted from a within-sample least squares regression of femoral, tibial, or humeral length on age for each of the comparative samples (using dental ages when chronological age was not known) in order to maximize sample size, following the methods of Cowgill (2010). As fossil sample sizes were not sufficiently large to generate their own prediction formulae, the appropriate regression formulae were selected based on body size and body proportion characteristics analogous to the target Late Pleistocene sample (see Cowgill, 2010). By developing age-prediction equations specific to each sample, difficulties arising from the application of a formula developed on individuals differing in body size or proportions to an archaeological target sample are partially mitigated.

### 3. Methods

#### 3.1. Cross-sectional geometry

The analysis of strength proportions compared three sets of ratios: humeral/femoral polar second moment of area, humeral/tibial polar second moment of area, and femoral/tibial polar second moment of area. Polar second moment of area (J) can be calculated as (twice) the average bending rigidity in any two perpendicular planes; in this analysis  $I_{max}$  and  $I_{min}$  were used. Right humeri were preferentially used, but left humeri were included if the right element was missing or damaged. Biomechanical length for

unfused elements was measured following Trinkaus and colleagues (2002a,b). Cross-sectional levels were chosen to best approximate the 50% section level in fused elements. In immature femora, however, 50% of diaphyseal length was calculated as 45.5% of femoral intermetaphyseal length, as this measurement best corresponds to the location of the 50% level in individuals with fused femoral epiphyses due to the relatively larger contribution of the distal epiphysis to biomechanical length in fused femora (Ruff, 2003a,b).

All cross-sectional properties were collected using a method similar to O'Neill and Ruff (2004) "latex cast method" (LCM) and the method used by Sakaue (1998), which rely on AP and ML radiographs combined with external bone contours derived from molding with Cuttersil Putty Plus™ silicone molding putty. Anterior, posterior, medial, and lateral cortical bone thicknesses were measured on radiographs with digital calipers, and measurements were corrected for parallax distortion by comparing external breadths measured on the radiograph with external breadths measured on the element. Once corrected for parallax, the four cortical bone thicknesses were plotted onto the two-dimensional photocopy of the original mold, and the endosteal contours were interpolated by using the subperiosteal contour as a guide. The resultant sections were enlarged on a digitizing tablet, and the endosteal and periosteal contours digitized by tracing with a digitizing pen. Cross-sectional properties were computed from the sections in a PC-DOS version of SLICE (Nagurka and Hayes, 1980; Eschman, 1992). Only polar second moment of area, which approximates overall torsional and bending rigidity, was used in this analysis, and size standardization was not necessary, as all data are ratios within individuals.

#### 3.2. Statistical analyses

While log–log bivariate regressions could be used to evaluate strength proportions during ontogeny, the relationship between strength proportions during growth is not linear (Ruff, 2003a), and this method of evaluation does not allow the interpretation of changes in strength proportions relative to age. In order to evaluate any biomechanical changes associated with the onset of walking, it is first necessary to determine what ages are affected by this locomotor transition. In order to establish the relevant window of time, unlogged strength ratios (dependent) were first plotted

against age (independent) for the entire ontogenetic period available for this analysis (birth to age 18). LOESS regressions, with a smoothing “tension value” of 20%, were used to visually determine the relevant window of time when the onset of walking had the most profound effects. Once changes related to the development of walking were visually detected in the LOESS graphs, the dataset was subsequently reduced to an age range where those patterns could be explored in detail.

In order to compare the strength ratios among Holocene populations and between fossil and Holocene groups, strength ratios must first be corrected for age. Without age corrections, differences in age structure among samples can strongly affect results if age and the strength ratios are correlated. Therefore, assuming that an appropriate regression model can be identified, strength ratios can be regressed on age to remove the effect of age, and residuals can be subsequently be used in population comparisons. Polynomial least squares regression was carried out over a limited age range (less than four years of age – see below), and model fit was evaluated through stepwise regression and  $r^2$  change in significance. Non-parametric Kruskal–Wallis tests were used to compare age-corrected residuals from these regressions among both Holocene and Late Pleistocene populations.

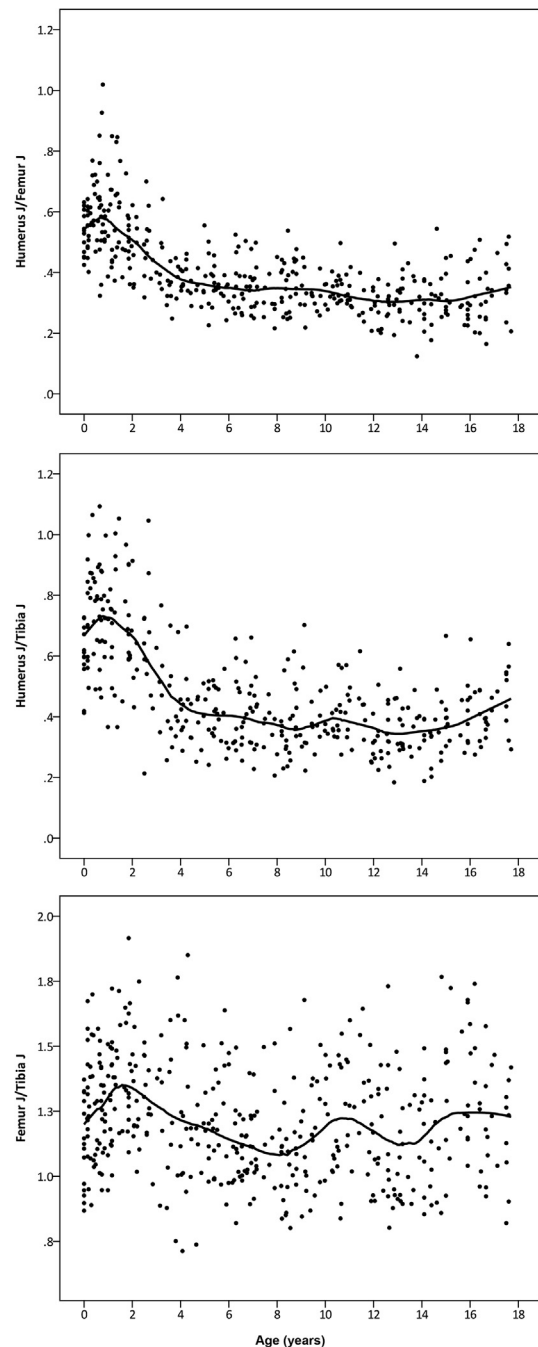
Dunn’s post hoc comparisons with Benjamini–Hochberg multiple comparison corrections were subsequently used to identify specifically which populations differed from one another (Dunn, 1964; Benjamini and Hochberg, 1995). Bonferroni corrections are frequently employed for this purpose; however, these corrections are very conservative and come with a serious loss of statistical power. In addition, they also lack standards for their application, and often penalize complex, detailed analyses (Perneger, 1998; Moran, 2003; Nakagawa, 2004; Cowgill, 2010). Due to their conservative nature, Bonferroni multiple comparisons are most appropriate when the number of comparisons is very small (such that the alpha levels are only slightly lowered) and the cost of a single false positive is quite high in terms of interpretive consequences (McDonald, 2009). An alternative procedure is the Benjamini–Hochberg correction (1995), which controls for the false discovery rate, or the proportion of significant results (“discoveries”) that are actually false positives, and is less sensitive to large numbers of comparisons in complex analyses (McDonald, 2009). However, as one of us has argued elsewhere (Cowgill, 2010), in analyses where a large number of samples are used and numerous pairwise comparisons are made, it may be best to simply carefully evaluate general trends in significant differences among groups as opposed to performing alpha level and  $p$ -value manipulation. Given these considerations, Benjamini–Hochberg adjusted  $p$ -values are displayed in all results tables (false discovery rate of 0.05) along with unadjusted  $p$ -values for comparison.

All statistical analysis was conducted in SPSS 23.0 with STATS PADJUST extension, which calculates  $p$ -values adjusted for multiple comparisons.

## 4. Results

### 4.1. Developmental pattern

Strength proportions between the humeri, femora, and tibiae during growth are presented in Figure 2. Humeral strength relative to femoral strength increases briefly prior to the age of one. This is followed by a sharp decline in relative humeral strength until age four, and a subsequent slow decline into adolescence (around 12–14 years of age). The pattern of variation in humeral to tibial torsional and bending strength is similar, but the height of the early peak is slightly more exaggerated. The peak in humeral strength



**Figure 2.** Comparative sample ratios for humeral/femoral, humeral/tibial, and femoral/tibial second polar moments on age, fit with a LOESS regression line.

relative to tibial strength is followed by a marked decline in relative humeral strength; this decline becomes shallower around the age of four, but still continues, with minor fluctuations, to mid-adolescence. The relationship between femoral and tibial strength differs from that of the upper limb/lower limb, with considerably more data scatter and a femoral strength peak closer to two years of age. The femoral/tibial strength ratio also shows a much smaller “peak” around 11 years of age. Table 4 shows raw means and confidence intervals of humeral/femoral, humeral/tibial, and femoral/tibial strength ratios for each year of life. Age-specific strength means generally support the pattern visually detected in graphical analyses.

**Table 4**

Raw means and confidence intervals of humeral/femoral, humeral/tibial, and femoral/tibial strength ratios for each year of life.

		Humerus J/Femur J	Humerus J/Tibia J	Femur J/Tibia J
0.0–0.49 years	<i>n</i>	39	39	39
	Mean	0.551	0.703	1.272
	CI	0.518–0.585	0.641–0.765	1.193–1.351
0.5–0.9 years	<i>n</i>	19	19	19
	Mean	0.602	0.738	1.243
	CI	0.519–0.685	0.646–0.830	1.158–1.328
1.0 to 1.9 years	<i>n</i>	34	34	34
	Mean	0.558	0.777	1.392
	CI	0.510–0.605	0.679–0.875	1.268–1.516
2.0 to 2.9 years	<i>n</i>	16	16	16
	Mean	0.498	0.616	1.22
	CI	0.431–0.565	0.507–0.725	1.107–1.333
3.0 to 3.9 years	<i>n</i>	16	16	16
	Mean	0.383	0.483	1.25
	CI	0.348–0.418	0.401–0.565	1.01–1.401
4.0 to 4.9 years	<i>n</i>	19	19	19
	Mean	0.366	0.414	1.131
	CI	0.343–0.389	0.365–0.464	1.029–1.233
5.0 to 5.9 years	<i>n</i>	22	22	22
	Mean	0.356	0.406	1.14
	CI	0.326–0.386	0.365–0.446	1.071–1.209
6.0 to 6.9 years	<i>n</i>	25	25	25
	Mean	0.393	0.451	1.166
	CI	0.322–0.465	0.374–0.529	1.051–1.281
7.0 to 7.9 years	<i>n</i>	14	14	14
	Mean	0.328	0.366	1.117
	CI	0.284–0.372	0.313–0.419	1.024–1.209
8.0 to 8.9 years	<i>n</i>	23	23	23
	Mean	0.362	0.377	1.046
	CI	0.327–0.398	0.330–0.424	0.958–1.133
9.0 to 9.9 years	<i>n</i>	15	15	15
	Mean	0.331	0.389	1.168
	CI	0.297–0.331	0.322–0.456	1.036–1.299
10.0 to 10.9 years	<i>n</i>	21	21	21
	Mean	0.343	0.408	1.195
	CI	0.320–0.366	0.370–0.446	1.104–1.285
11.0 to 11.9 years	<i>n</i>	12	12	12
	Mean	0.303	0.395	1.309
	CI	0.267–0.339	0.325–0.466	1.127–1.490
12.0 to 12.9 years	<i>n</i>	20	20	20
	Mean	0.282	0.323	1.151
	CI	0.239–0.324	0.270–0.376	1.036–1.265
13.0 to 13.9 years	<i>n</i>	17	17	17
	Mean	0.328	0.367	1.214
	CI	0.277–0.380	0.327–0.408	0.937–1.490
14.0 to 14.9 years	<i>n</i>	17	17	17
	Mean	0.312	0.335	1.107
	CI	0.268–0.355	0.292–0.377	0.965–1.249
15.0 to 15.9 years	<i>n</i>	19	19	19
	Mean	0.311	0.411	1.324
	CI	0.276–0.346	0.350–0.472	1.211–1.436
16.0 to 16.9 years	<i>n</i>	17	17	17
	Mean	0.328	0.437	1.354
	CI	0.282–0.375	0.367–0.506	1.206–1.502
17.0 to 17.9 years	<i>n</i>	10	10	10
	Mean	0.422	0.473	1.154
	CI	0.333–0.511	0.393–0.553	1.011–1.296

#### 4.2. Walking peak in recent humans

After visual identification of an infancy peak in humeral to femoral and tibial strength likely related to the onset of bipedality, the sample was restricted to individuals under the age of four ( $n = 184$ ) for subsequent analysis. Although correlation coefficients are somewhat low due to wide variation in these ratios, age and strength ratios are significantly correlated, and the best fit equations are quadratic regressions. Residuals from these regressions

were then used to compare strength proportions among the comparative samples. Equations,  $r^2$ , and significance across all populations are shown in Figure 3.

Boxplots of modern population-specific residuals for individuals under the age of four are shown in Figure 4. Under the age of four, Kruskal–Wallis non-parametric tests of population differences were significant for humeral/femoral, humeral/tibial, and femoral/tibial strength ratios ( $p = 0.013, 0.008, 0.001$ , respectively). The results of pairwise Dunn tests were used to determine which populations were specifically differing, and the results of these analyses are shown both uncorrected and with Benjamini–Hochberg multiple comparison corrections in Table 5. Of 63 comparisons, 18 pairwise comparisons reached significance at an alpha level of 0.05; nine remained significant once corrected for multiple comparisons. The majority of the differences found were significantly higher values for all Point Hope strength ratios, and higher values for Mistihalj in the ratio of femoral to tibial strength.

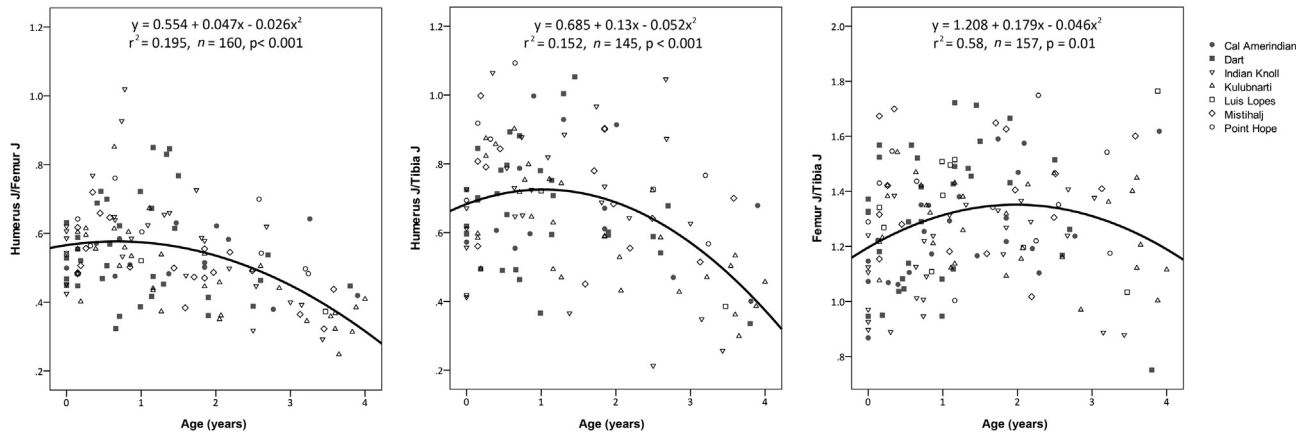
#### 4.3. Fossil samples

The positions of the Late Pleistocene individuals relative to the comparative sample are shown in Figure 5; boxplots displaying sub-sample-specific medians and interquartile ranges are illustrated in Figure 6. Kruskal–Wallis non-parametric tests were used to compare the comparative sample, Neandertals, and Late Upper Paleolithic modern humans both with all of the comparative samples combined and divided by sample. While there are no significant differences when the comparative samples are grouped (Humerus J/Femur J:  $p = 0.178$ ; Humerus J/Tibia J:  $p = 0.199$ ; Femur J/Tibia J:  $p = 0.123$ ), the Late Pleistocene samples do differ from specific Holocene samples (Humerus J/Femur J:  $p = 0.018$ ; Humerus J/Tibia J:  $p = 0.008$ ; Femur J/Tibia J:  $p = 0.001$ ).  $P$ -values for Dunn comparisons between the fossil groups and the comparative samples are shown in Table 6, with values corrected for multiple comparisons in parentheses. In spite of small samples, 10 pairwise comparisons attain significance (although only one remains so after multiple comparison corrections). The pairwise comparisons primarily highlight the differences between Point Hope, Mistihalj, and the Neandertals.

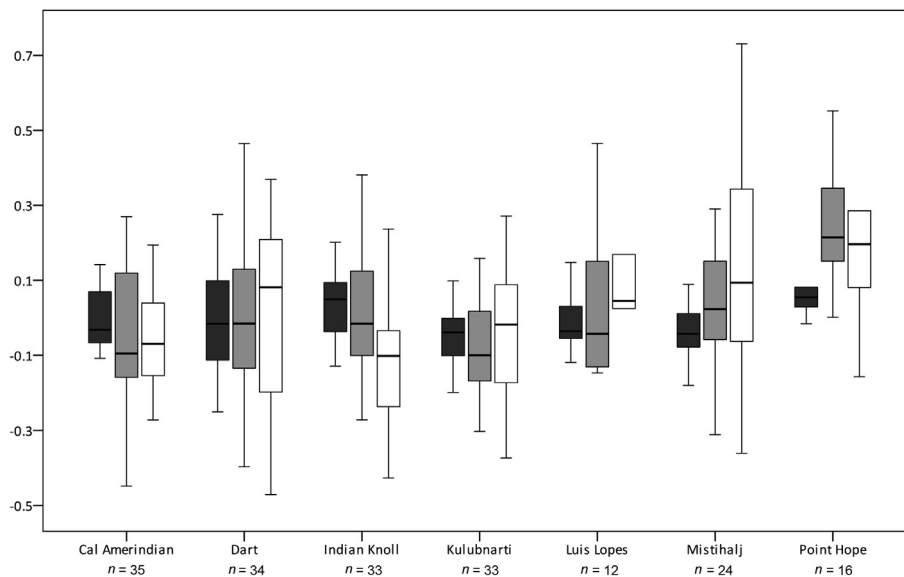
### 5. Discussion

As has been noted previously in studies of a longitudinal sample (Ruff, 2003a,b), the early developmental changes in long bone strength ratios detected here are likely related to changes in locomotor patterns, although correlation coefficients are rather low, indicating substantial developmental variation and higher levels of biological “noise.” In the ratio of humeral to femoral torsional strength, relative humeral strength increases up to the age of one and declines thereafter. This pattern is best explained by the fact that prior to the developmental advent of bipedalism, the humerus is bearing substantial body weight during crawling. Once bipedal posture is committed to, however, the humerus moves to an entirely different biomechanical milieu; its role is then primarily manipulative and the lower limbs bear all of body mass, resulting in the subsequent decline in the ratio of humeral to femoral torsional strength after the age of one as femoral strength rapidly increases relative to the now manipulative upper limb.

In light of this, it becomes easier to interpret the patterns shown by the ratios including tibial strength, which have not been previously examined in either longitudinal or cross-sectional samples. The locomotor peak seen in the ratio of humeral to tibial strength is visibly higher and better defined than that seen in the ratio of



**Figure 3.** Quadratic equations,  $r^2$ , sample sizes, and significance across all populations under age four.



**Figure 4.** Boxplots of residuals from the regression of strength ratios on age for the comparative sample under age four. Sample size for each population shown on x-axis. Humeral/femoral J in dark gray; humeral/tibial J in light gray; femoral/tibial J in white. Boxplots show the median value, the interquartile range, minimum, and maximum.

humeral to femoral strength when fit with a LOESS line. This is likely because of the relatively limited role the tibia plays in crawling: prior to upright standing and walking, the tibia experiences very little direct compressive loading via body mass, and is seldom loaded axially in the manner of the humerus and femur during crawling. Therefore, the relatively higher peak in the ratio of humeral to tibial torsional strength is probably related to the more dramatic biomechanical transition experienced by the tibia during this major locomotor shift. Unlike the femur (which switches from bearing approximately half of body weight during crawling to all during walking) or the humerus (half during crawling, none during walking), for the tibia, it is, effectively, “all or nothing.” This relationship may explain the modest early peak seen in the ratio of femoral to tibial torsional strength and its later decline as well: femoral strength increases rapidly relative to tibial strength until fully upright posture is adopted.

Explanations for the smaller, early adolescence perturbation in the ratio of femoral to tibial strength are less clear. Given the wide range of variation seen in the strength ratios, it is entirely possible that this peak may be only “noise.” Alternatively, it could be an

artifact of slightly different timing in the peak velocities of the femur and tibia during the adolescent growth spurt (Smith and Buschang, 2005), which may result in variation in relative femoral and tibial length (see below for more discussion).

### 5.1. Population differences under the age of four

**5.1.1. Holocene sample** Most of the pairwise comparisons of the Holocene samples, both corrected and uncorrected for multiple comparisons, highlight the elevated ratios at Point Hope and Mistihalj. Previous analyses of size-standardized cross-sectional properties have detected elevated levels of bone strength during development in these specific samples, even in very young age groups (Cowgill, 2008, 2010). However, long bone strength was high in these groups across all elements; there was no evidence that Point Hope and Mistihalj had exceptionally strong humeri when compared to the lower limb. In addition, while it remains possible that this reflects differences in the onset of walking, there are few plausible behavioral scenarios from which this could result based on known ethnographic information about



**Table 5**

P-values for Dunn post hoc comparisons of strength ratios. Uncorrected for multiple comparisons are shown on the bottom; corrected p-values are shown on the top.

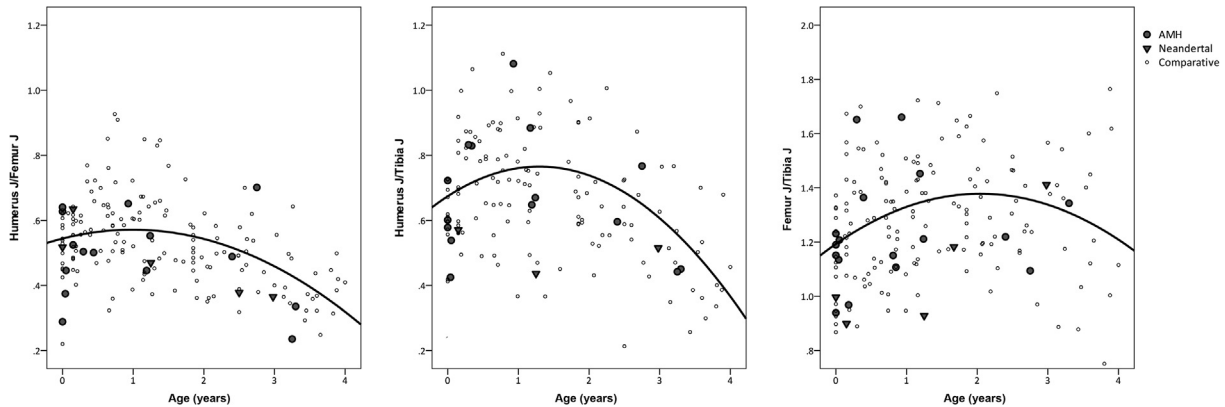
		Cal Amer-indian	Dart	Indian Knoll	Kulubnarti	Luis Lopes	Mistihalj	Point Hope
<b>Corrected with Benjamini-Hochberg</b>								
Cal Amerindian	Hum/Fem							
	Hum/Tib							0.021
	Fem/Tib							
Dart	Hum/Fem							
	Hum/Tib							0.021
	Fem/Tib			0.021				
Indian Knoll	Hum/Fem				0.042			
	Hum/Tib							0.021
	Fem/Tib		0.003				<0.001	0.011
Kulubnarti	Hum/Fem			0.006				0.021
	Hum/Tib							<0.001
	Fem/Tib							
Luis Lopes	Hum/Fem							
	Hum/Tib							
	Fem/Tib			0.020				
Mistihalj	Hum/Fem							0.042
	Hum/Tib				0.039			
	Fem/Tib	0.012		<0.001	0.032			
Point Hope	Hum/Fem	0.021	0.012		0.001		0.006	
	Hum/Tib	0.004	0.003	0.001	<0.001	0.031		
	Fem/Tib	0.022		0.001				
<b>Uncorrected for Multiple Comparisons</b>								

these populations. While an absence of evidence illustrates little, no studies to date have suggested accelerated motor development in these groups.

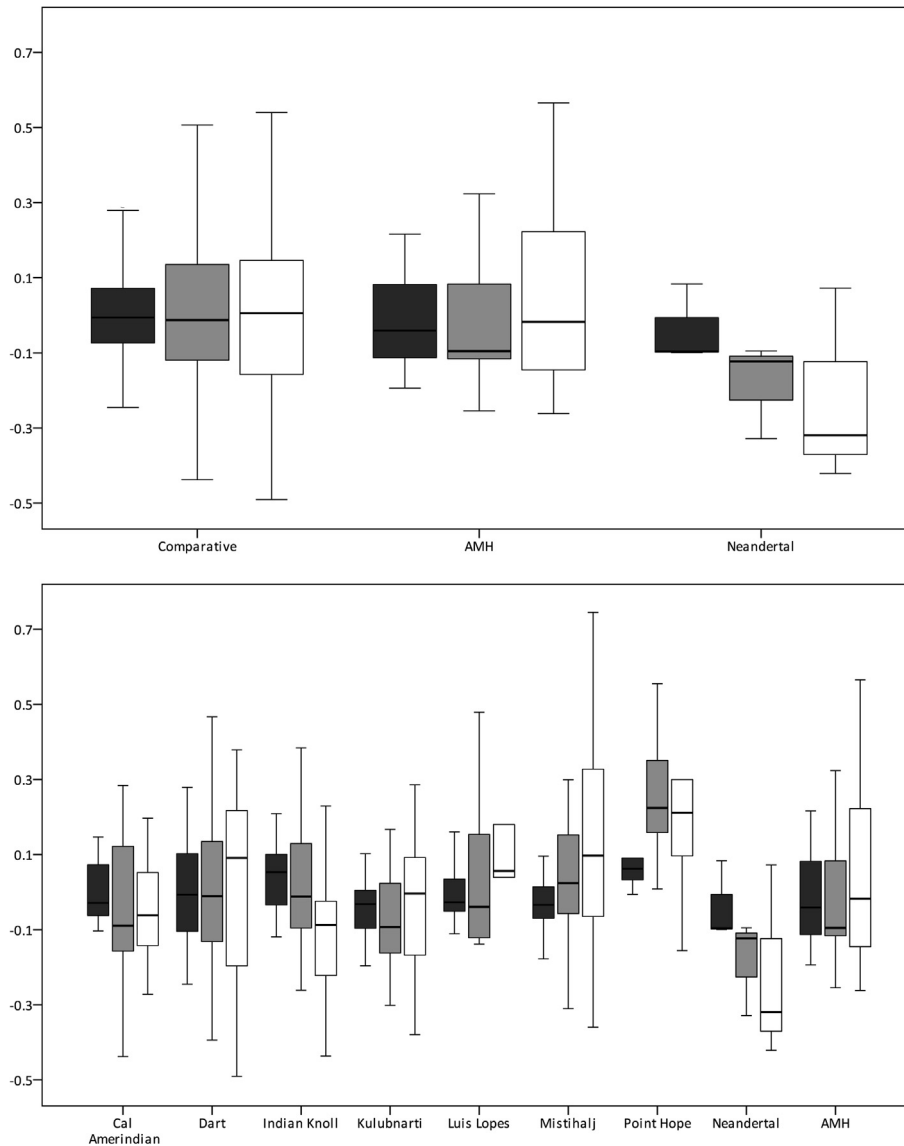
Alternatively, these contrasts could also be an artifact of differences in long bone length, particularly in the tibia. Previous analyses have found no association between limb length proportions and specific behavioral transitions during development (Ruff, 2003a; Ruff et al., 2013). In previous analyses on immature strength proportions, Ruff (2003a,b) detected changes in strength proportions associated with walking in a longitudinal sample, with no correlated changes in long bone length. However, Point Hope and Mistihalj possess some of the relatively shortest tibiae in the modern human sample. The two populations have relatively low crural indices (0.80 and 0.82, respectively), which have been shown to be consistent across development (Cowgill et al., 2012).

Figure 7 shows the crural indices for the immature samples used in this analysis, where indices were regressed on age to control for differences in age composition among samples. It is theoretically possible that the relatively shorter tibiae in these samples results in decreased bending loads through shorter bending moment arms, which, in turn, results in lower polar second moments of area when cross-sectional properties are not standardized by body mass and beam length (Gruss, 2007). The shortened distal segments of populations like Point Hope and Mistihalj result in relatively smaller denominators in the ratios of humeral to tibial and femoral to tibial torsional strength, and thus produce overall higher values.

In order to evaluate this possibility, residuals from strength ratios regressed on age were compared with residuals from the crural index regressed on age. While there is no correlation



**Figure 5.** Late Pleistocene fossil ratios for humeral/femoral, humeral/tibial, and femoral/tibial second polar moments regressed on age, with all points fit with a quadratic regression line.



**Figure 6.** Boxplots of residuals from the regression of strength ratios on age for Late Pleistocene fossils compared to the comparative sample. Humeral/femoral J in dark gray; humeral/tibial J in light gray; femoral/tibial J in white. Comparative samples grouped above, and divided below. Boxplots show the median value, the interquartile range, minimum, and maximum.

between the crural index and strength residuals for the analysis of humeral to femoral proportions ( $p = 0.602$ ), both the ratios of humeral to tibial and femoral to tibial strength show negative and significant relationships with the crural index (humeral J/tibial J:  $r^2 = 0.104$ ,  $p < 0.001$ ; femoral J/tibial J:  $r^2 = 0.132$ ,  $p < 0.001$ ). As expected, variation in tibial length is only influencing ratios where the tibia is the denominator, and not humeral to femoral ratios, which are unlikely to be effected by population differences in segment length.

**5.1.2. Late Pleistocene fossil sample** Most of the statistical differences between the Late Pleistocene fossils and recent human groups reflect the relatively low values found in Neandertal ratios where the tibial polar second moment of area serves as the denominator. This is particularly surprising given their very low crural indices; if reduced tibial length is playing a role in high strength ratios in the Holocene human groups, it is notable that Neandertals do not group with the Holocene samples displaying similar body

proportions. The very low strength ratios of Neandertals show the exact opposite of expectations based on the limb proportions patterns detected in the Holocene samples.

It remains difficult to interpret these results with only seven Neandertal data points. There are, however, a few possible explanations. First, it is possible that age estimates for Neandertals could be inaccurate. Because of the relationship between the strength ratios and age, aging estimation errors would have an effect on the magnitude of individual residuals, and subsequently, any pairwise comparisons between those residuals and ones from recent humans. While it is challenging to incorporate the results of the work on Neandertal dental development into postcranial research directly, manipulation of the ages used for the immature Neandertals in this study suggests that aging errors are not the root of the problem. When modern human aging standards are used, for example, the humeral versus tibial strength residual mean for Neandertals is  $-0.182$ . When the age of the Neandertal children is

**Table 6**

P-values for Dunn post hoc comparisons of strength ratios. Uncorrected for multiple comparisons are shown with significant corrected p-values in parentheses.

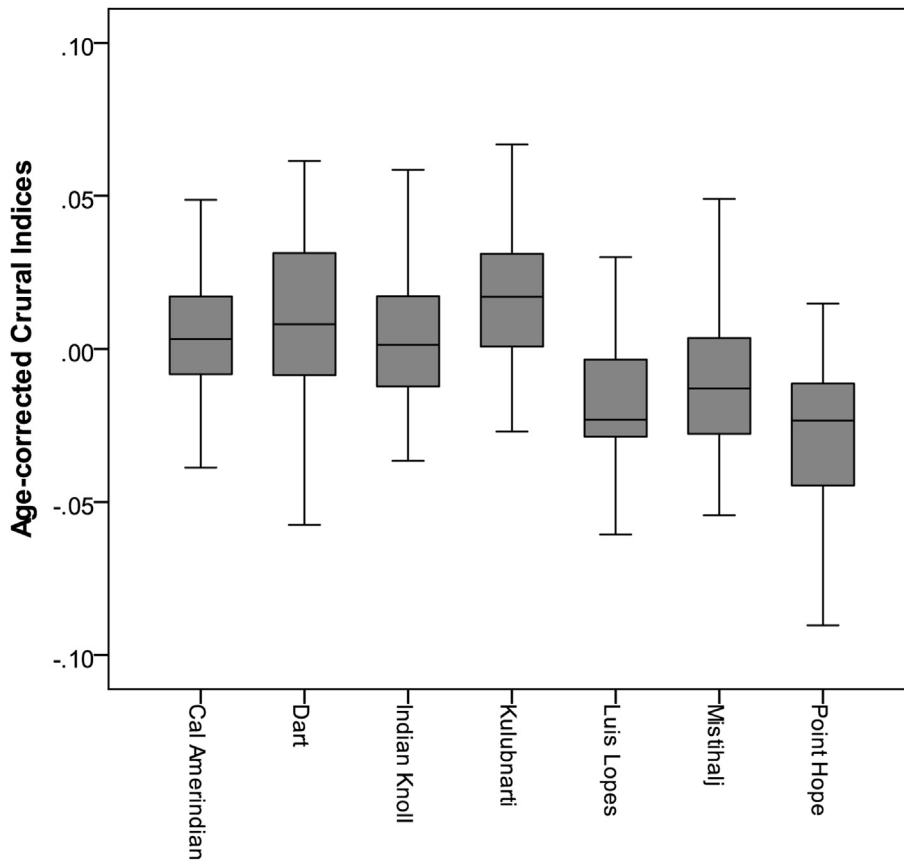
		AMH	Neandertals
<b>Cal Amerindian</b>	Hum/Fem		
	Hum/Tib		
<b>Dart</b>	Fem/Tib		
	Hum/Fem		
<b>Indian Knoll</b>	Hum/Tib	0.028	0.021
	Fem/Tib		
<b>Kulubnarti</b>	Hum/Fem		
	Hum/Tib		
<b>Luis Lopes</b>	Fem/Tib		
	Hum/Fem		
<b>Mistihalj</b>	Hum/Tib		0.027
	Fem/Tib		
<b>Point Hope</b>	Hum/Fem	0.003	0.045
	Hum/Tib	0.003	0.004
	Fem/Tib		0.011
	Fem/Tib		0.001 (0.036)

conservatively adjusted downward by 15%, the humeral versus tibial strength residual mean is  $-0.201$ , placing them even farther below the modern human regression line. Given this, it seems unlikely that the unusually low strength ratios detected in

Neandertals are primarily a product of accelerated physical development in this group.

Second, it is possible that Neandertals have extremely strong tibiae relative to more recent humans, in spite of their relatively shortened length. This would effectively enlarge the denominator in two of the ratios, possibly resulting in the low values seen for both the humerus and femur relative to the tibia. However, previous analyses of immature Neandertal tibial strength argue against this interpretation, and indicate that when properly standardized by body mass, Neandertal tibial strength is virtually indistinguishable from that of similarly-aged, non-industrial children (Cowgill et al., 2007).

Lastly, it is possible that Neandertals differed from modern human populations in the timing of the developmental shift to upright posture and bipedalism. If, for example, Neandertal infants walked at a significantly earlier age than modern humans, this could explain their low ratios of femoral and humeral to tibial torsional strength. The relatively elevated tibial strength could be caused by an earlier onset of tibial loading during walking than experienced by other individuals in the comparative sample. As the tibia is relatively unloaded during crawling, this longer interval of loading would necessitate an earlier developmental transition to upright posture. While it remains impossible to reach a firm conclusion as to the cause of the unusual pattern seen in Neandertals due to the relatively small available fossil sample, future research into strength ratios during development could lead to additional insights into the timing of this significant locomotor shift in fossil groups.



**Figure 7.** Crural indices were regressed on age to remove the slight but significant age effect ( $y = -0.0047x^2 + 0.0003X + 0.8421$ ,  $p < 0.001$ ,  $r^2 = 0.068$ ,  $n = 505$ ). Boxplots show the median value, the interquartile range, minimum, and maximum for age-corrected residuals for the entire ontogenetic sample.

## 6. Conclusions

There has been considerable success in exploring the evolutionary adaptation of bipedal locomotion in adult Pleistocene and Pliocene hominins (Ruff, 2008, 2009; Ruff et al., 2016), and previous research in several taxa has shown that the high plasticity of immature bone adequately captures biomechanical signals related to shifting locomotor regimes (Ruff et al., 2013; Sarringhaus et al., 2016). Despite wide individual developmental variation, it is clear that the effects on long bone structure of the locomotor shift to bipedality at about one year of age can be detected in immature human archaeological samples. Subtle variation in long bone strength ratios exists between populations, but it remains uncertain precisely what population-level differences in these ratios mean in a developmental context. While differences among recent human groups could be indicative of the population differences in motor development that have been reported from living children, they could also be an artifact of the techniques employed to investigate them in this analysis, and particularly, the relationship between limb length segments and bending moments. The small sample sizes of immature fossil groups further complicate interpretations. Relative to recent Holocene humans and early modern humans, immature Neandertals display low strength ratios during the period of time associated with the developmental onset of bipedality, which appear to be specifically related to elevated tibial strength, and contrast strongly with the patterns seen in Holocene samples with similar body proportions. It remains unclear, however, if the elevated tibia strength of immature Neandertals is related to a more extended period of loading related to earlier onset of bipedal walking or some other factor.

## Acknowledgements

We would like to particularly thank Christopher B. Ruff for his thoughts and comments on multiple iterations of this manuscript. His continued feedback and commentary were invaluable. As this particular paper has been an evolving work for quite some time, additional thanks for fruitful conversations and comments are owed to a variety of people, including Erik Trinkaus, Rich Smith, and Herman Pontzer. Additional thanks are owed to the two very helpful anonymous reviewers who provided their thoughts on this paper.

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