

**Birth is but our death begun: A bioarchaeological assessment of skeletal emaciation in immature human skeletons in the context of environmental, social, and subsistence transition**

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**Abstract:**

The second millennium BC was a period of significant social and environmental changes in prehistoric India. After the disintegration of the Indus civilization, in a phase known as the Early Jorwe (1400–1000 BC), hundreds of agrarian villages flourished in the Deccan region of west-central India. Environmental degradation, combined with unsustainable agricultural practices, contributed to the abandonment of many communities around 1000 BC. Inamgaon was one of a handful of villages to persist into the Late Jorwe phase (1000–700 BC), wherein reliance on dry-plough agricultural production declined. Previous research demonstrated a significant decline in body size (stature and body mass index) through time, which is often used to infer increased levels of biocultural stress in bioarchaeology. This article assesses evidence for growth disruption in the immature human skeletal remains from Inamgaon by correlating measures of whole bone morphology with midshaft femur compact bone geometry and histology. Growth derangement is observable in immature archaeological femora as an alteration in the expected amount and distribution of bone mass and porosity in the midshaft cross-section. Cross-section shape matched expectations for older infants with the acquisition of bipedal locomotion. These results support the hypothesis that small body size was related to disruptions in homeostasis and high levels of biocultural stress in the Late Jorwe at Inamgaon. Further, the combined use of geometric properties and histological details provides a method for teasing apart the complex interactions among activity and “health,” demonstrating how biocultural stressors affect the acquisition and quality of bone mass.

**Keywords:** bioarchaeology | femur | emaciation | biocultural stress | childhood

## Article:

Human populations living in semi-arid environments potentially face the most significant impacts from global climate change. Human security literature seeks to understand human responses to changing resource availability and the potential impacts of specific problems, like declines in agricultural production (for example, see Metz, 2007). South Asia is a particularly important region in which to examine impacts of climate and environmental changes in the past because more than 700 million people live in semi-arid regions of rural village India today, wherein subsistence practices and technologies are diverse but there has also been remarkable continuity over the past 4,000 years (Dhavalikar, 1994a). Thus the strategies and consequences of past peoples' environmental interactions are critically important tools for predicting outcomes today. This article is part of a larger research agenda that examines the health consequences when human populations choose not to abandon their settlements in the face of climate and environmental changes.

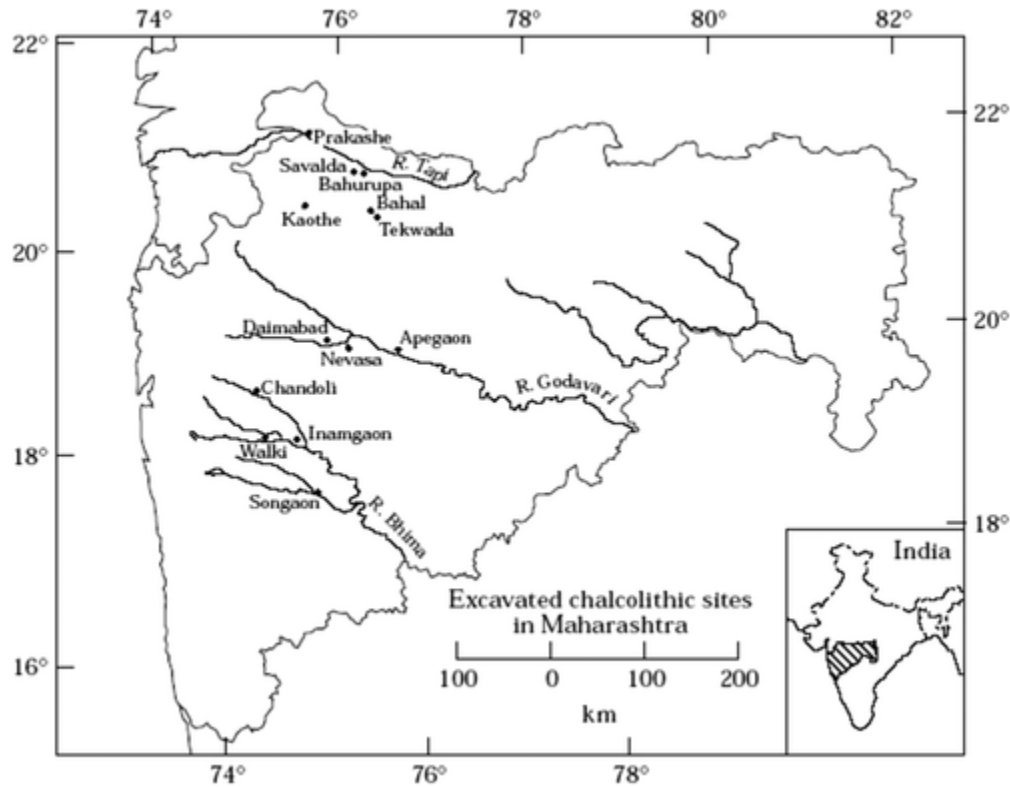
Climate and monsoon variability have had profound impacts on human populations in South Asia throughout the late Holocene, from the Late Bronze Age forward. The Indus Civilization was founded *circa* 3300 B.C. along the banks of monsoon-fed rivers in the semi-arid landscape of north-west India and Pakistan (Bryson, 1981; Wright, 1993; Enzel et al., 1999; Von Rad, 1999; Phadtare, 2000; Singh and Bengtsson, 2004; Madella and Fuller, 2006; Migowski et al., 2006). From 2200 to 1700 BC, centuries-long drought contributed to disruptions in the interaction sphere across Middle and West Asia (Mayewski et al., 2004; Staubwasser and Weiss, 2006; Fiorentino et al., 2008; Frahm and Feinberg, 2013; Masi et al., 2013). While initially this period of increasing aridity appears to have corresponded to rapid population growth at Indus urban centers (2200–2000 BC), centuries of environmental change and economic disruption contributed to the abandonment of the urban lifestyle in South Asia, beginning around 1900 BC. (Schuldenrein et al., 2004; Wright et al., 2008; Giosan et al., 2012). The human population that chose to remain in the city during the “post-urban” period (1900–1700 BC) faced significant increases in inter-personal violence (Robbins Schug et al., 2012), rates of infection, and infectious disease (Robbins Schug et al., 2013b). Eventually, Indus cities and many Indus cultural traditions were abandoned and the urban lifestyle did not recur for millennia.

A similar situation occurred in the second millennium BC in west-central peninsular India. In a period known as the “Deccan Chalcolithic” (DC) (2200–700 BC), small agrarian communities were founded along the riverbanks of stable watercourses in the contemporary state of Maharashtra (Fig. 1). Again, the DC was initially characterized by relative prosperity. Small populations in regionally connected villages coped with the semi-arid climate through adaptive diversity, maintaining a varied subsistence economy focused on hunting, fishing, foraging, pastoral, and agricultural activities (Dhavalikar, 1988a, 1988b). Following 800 years of successful colonization in this region, these rural communities began to grow relatively more rapidly (Robbins, 2007; Robbins-Schug, 2011). In the phase known as the Early Jorwe (1400–1000 BC), farmers increasingly relied on double cropping and intensive barley and wheat production to feed the growing population (Kajale, 1988). By 1000 BC, these farming practices

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were no longer sustainable; the soil became increasingly saline and farmers shifted to tolerant crops, like lentils (Kajale, 1988). Other changes in food production included a shifting emphasis from cattle keeping to sheep and goat herding (Pawankar and Thomas, 1997) and an increased reliance on wild foods (Dhavalikar, 1988a). By the opening of the phase known as the Late Jorwe (1000–700 BC), another massive emigration occurred and most of the DC villages were abandoned (Dhavalikar, 1988a). For the next 500 years, this area was largely unoccupied; it became *banajar bhumi*, a barren and unproductive land.



**Figure 1.** Map of Deccan Chalcolithic Sites, including Inamgaon.

There has been some debate as to whether climate changes or human decisions were primarily responsible for the socio-cultural and economic changes we see at the beginning of the first millennium B.C. (Dhavalikar, 1984; Lukacs and Walimbe, 2000; Robbins Schug, 2011; but see Fuller, 2013). What is clear is that the Late Jorwe population at Inamgaon, one of the few villages in this region to persist, faced significant demographic changes and biocultural challenges (Dhavalikar, 1988a; Lukacs and Walimbe, 2007; Robbins-Schug, 2011). On one hand, the subsistence transition just described represented a successful biocultural adaptation at Inamgaon, which combined with reduced population density, allowed this village population to persist for another 300 years after most villages of this region were abandoned. On the other hand, previous bioarchaeological research indicates a significant increase in fertility and infant mortality rates and a statistically significant decline in body size (stature, body mass, and BMI) for young infants and children of the Late Jorwe phase (Robbins Schug, 2011). The goal of this research is to assess the biomechanical and histological signature of small body size at Inamgaon and to determine the likelihood that declining body size in the Late Jorwe was due to skeletal emaciation and high levels of biocultural stress. The results will provide enhanced resolution of

the health consequences of choosing to stay in a rural agrarian village in peninsular India in the second millennium BC despite significant environmental degradation and the abandonment of the majority of the other villages in the region.

#### Archaeological context and previous bioarchaeological research

At the beginning of the second millennium BC, hundreds of agrarian villages sprang up at the margins of Indus territory and down into peninsular India. Despite an increasingly unpredictable monsoon and inhospitable semi-arid climate throughout the first and second millennium BC (Bryson, 1981; Enzel et al., 1999; Phadtare, 2000; Jain and Tandon, 2003), human populations thrived in west-central India from 2200 to 1000 BC. Deccan Chalcolithic villages were constructed of stone, mud-brick, wattle, and daub. People used copper and bronze technology sparingly as the raw materials were less available in this new landscape (Dhavalikar, 1988a). They pursued a mixed economic strategy that preserved drought resistant barley agriculture and stock-raising, but supplemented those traditions with South Indian crops and by exploiting local forest and lacustrine resources (Dhavalikar, 1984, 1988a, 1988b, 1997; Fuller et al., 2004). During the phase known as the Early Jorwe (1400–1000 BC) the human population expanded rapidly and far-reaching exchange relationships were established with communities on the west coast of India and post-urban Indus settlements to the northwest. After 1000 BC, most of the villages in this region were abandoned. Population growth in the Early Jorwe, combined with unsustainable agricultural practices led to local environmental degradation and crop failure throughout the region (Kajale, 1988).

In the phase known as the Late Jorwe (1000–700 BC), the people of Inamgaon adjusted their economic activities and adopted a strategy of adaptive diversity that allowed them to occupy their village despite the abandonment of most of this region. The archaeological record of the Late Jorwe is characterized by an increasingly “degenerate” ceramic style, greater numbers of hastily constructed “flimsy” round houses, declines in agricultural production, shift in species preference from drought resistant barley to saline tolerant lentils, and a shift from cattle to sheep/goat bones in the faunal remains (Dhavalikar, 1988a; Kajale, 1988; Thomas, 1988; Pawankar, 1996, 1997; Pawankar and Thomas, 1997). Changes in artifact assemblages indicate a shift in emphasis away from implements associated with farming and a new prominence of lacustrine food resources, tools, and ornamentation as trade with coastal people became increasingly important during this time (Robbins Schug, 2011). After 300 years, Inamgaon too was abandoned (Dhavalikar, 1988a).

Archaeologists have struggled to understand the impact of these changes on the human population. The *Climate and Culture Change Model* predicted dire health consequences faced the Late Jorwe people who chose to stay at Inamgaon (Dhavalikar, 1984, 1988b, 1994b). Bioarchaeologists proposed an antithetical model—that declines in agricultural production during the Late Jorwe phase would lead to an improvement in health status due to declining population density, improved sanitation, and increasingly diverse diet (the *Subsistence Transition Model*). The latter model was primarily based on comparisons of the dental anthropology profiles of Early versus Late Jorwe Inamgaon; however, support for this model was not consistently found across the biocultural stress markers examined (Lukacs, 1985, 2001; Walimbe and Kulkarni, 1994; Walimbe and Gambhir, 1997; Lukacs and Walimbe, 1998, 2000, 2005, 2007).

Significant differences between the Early and Late Jorwe have been demonstrated in changing deciduous tooth size, declining caries rates, and declining prevalence of localized hypoplasia of the primary canine (LHPC). However, evaluation of other stress markers demonstrated no systematic trend; there was no significant difference between Early and Late Jorwe in linear enamel hypoplasia (LEH) or interproximal contact hypoplasia (IPCH) through time (Lukacs and Walimbe, 2007). Declines through time in tooth size and caries rates confirm subsistence transition away from agricultural production; declining prevalence of LHPC was interpreted as evidence for reduced biocultural stress levels in the Late Jorwe but this “stress” marker has a complex etiology and thus conformational trends in other stress markers is required. Research on gross bone pathology demonstrated little evidence of “biocultural stress” and few significant differences through time (Lukacs et al., 1986).

Osseous remains serve as an excellent source of evidence to address hypotheses about human health during the Deccan Chalcolithic. Previous research on the human skeletons from Inamgaon demonstrated significant demographic changes accompanied the social and subsistence transition at Inamgaon. A biodemographic analysis of immature skeletons from Inamgaon (Robbins, 2007; Robbins Schug, 2011) suggested (1) growing settlement size and population density accompanied the increasing production of barley in the Early Jorwe; a commensurate decline in population size accompanied the abandonment of agriculture in the Late Jorwe, and (2) fertility and infant mortality rates increased to unsustainable levels at Inamgaon through time. A comprehensive analysis of subadult skeletal growth profiles (stature, body mass, and body mass index, or BMI) demonstrated significant declines in body size (stature and BMI) for infants and children 0–5 years of age in the Late Jorwe (Robbins, 2007; Robbins Schug, 2011). Although the Early Jorwe infants matched contemporary reference standards for BMI for their developmental age, there was a significant decline in BMI for infants and children who died in the Late Jorwe phase, when 22% of 0–5 year old individuals fell more than 2 standard deviations below the median for BMI for developmental age. For infants 0–1 year, the difference was most striking; average BMI for this age class was 17 in the Early Jorwe phase but only 14 in the Late Jorwe.

The present research specifically addresses whether demonstrated declines in body size through time at Inamgaon were associated with evidence of growth faltering in the cross-section geometric and histological properties. Declines in stature and body mass index through time at Inamgaon have been inferred to represent skeletal emaciation caused by the synergy among poor health, nutritional deficiencies, and reduced activity levels that accompanied the abandonment of agriculture in the Late Jorwe (Robbins, 2007; Robbins Schug, 2011). Stunting and wasting are excellent indicators of developmental stress in contemporary populations and declines in stature are commonly used as a proxy for changing health status, particularly in the context of subsistence transition (Saunders, 1992; Saunders and Hoppa, 1993; Larsen, 1995; Mummert et al., 2011; Vercellotti et al., this issue). However, based solely on an examination of stature and body mass index, it is unclear that small body size necessarily represents a decline in childhood “health,” particularly given issues of biological mortality bias (Wood et al., 1992), mortuary, and preservation biases that often characterize archaeologically derived immature skeletal assemblages (Johnson, 1968; Saunders, 1992; Ribot and Roberts, 1996; Hoppa and Fitzgerald, 1999). There are few adults in the sample and thus final adult height and body mass cannot be evaluated (Johnson, 1962). Thus, bone histomorphology is a next logical step to tease apart the

causes of small body size in ontogeny at Inamgaon and evaluate inferences about biocultural stress levels through time in the this population (Robbins Schug, 2011).

It is important to understand whether skeletal emaciation was the cause of small body size in the Late Jorwe because it relates to the consequences of subsistence transition as a strategy for coping with climate change in South Asia's rural communities today. If histological analysis confirms that Late Jorwe children were “small” but not unhealthy (Seckler, 1982, 1984; but see Martorell, 1989), it suggests abandoning dry-plough agriculture was an adaptive strategy for rural village populations coping with environmental changes in rural communities the past. Conversely, if “small” body size is associated with histological and geometric differences suggesting skeletal emaciation, this result will indicate that declining body size in the Late Jorwe was at least partially due to increasingly high levels of biocultural stress. If body size declines through time at Inamgaon are stress-related, that result would suggest that persisting in rural villages past the point of a viable agricultural base may lead to higher prevalence of starvation and poor health outcomes. Developing a better understanding of the consequences of population growth, subsistence choices, and migration in the face of environmental change has implications for bioarchaeology and anthropology more broadly.

#### Ontogeny and compact bone histology: background and predictions

This article examines cross-sectional shape and microstructural features of the midshaft femur in immature skeletons from Inamgaon. Given adequate nutritional support, genetics, body mass, and activity determine the size and shape of long bones from an early age through the processes of modeling and remodeling (Martin, 1991; Lanyon and Skerry, 2001; Auerbach and Ruff, 2004; Pearson and Lieberman, 2004; Demes, 2007; Wallace et al., 2012). During ontogeny, modeling determines the size, shape, and curvature of long bone diaphyses through coordinated patterns of deposition and resorption on complementary bone surfaces (Foote, 1916; Enlow, 1962a, 1962b, 1963; Frost, 1973; Enlow et al., 1982; Enlow and Hans, 1996); this occurs to a lesser extent throughout life (Smith and Walker, 1964; Robling and Stout, 2000; Seeman, 2003; Crowder and Stout, 2011). This modeling behavior is the most prominent feature of the cross-section in the first 10 years of life (Ruff, 2003a, 2003b, 2005a, 2005b; Cowgill et al., 2010; Crowder and Stout, 2011; Gosman et al., 2013). Bone remodeling (Enlow, 1976) refers to the process of bone turnover which occurs within Basic Structural Units (BSUs), as osteoclasts remove bone tissue and osteoblasts subsequently deposit new bone matrix within the resorption bay (Frost, 1964, 1973, 1986, 1997; Jaworski, 1976; Parfitt, 1990). Remodeling begins in the antenatal period (Burton et al., 1989; Glorieux et al., 2000) and continues throughout the lifespan to replace primary, lamellar bone tissue with reorganized material (Haversian systems or secondary osteons).

This research approaches the skeletal sample from Inamgaon using an assessment of both geometric and histological properties to tease apart the complex interactions among activity and “health” status in the femoral cross-section. By using a combined approach, we seek to demonstrate how biocultural stressors affect the acquisition and quality of bone mass in a changing biomechanical milieu. Our expectations for the Inamgaon infants are based on recent literature on the range of normal in histological and geometric properties of the immature human femur. A recent analysis of femoral midshaft geometry in 522 subadult skeletons from seven

spatially and temporally diverse populations demonstrated consistent patterns of variation in the first year of life, with the acquisition of bipedalism (Cowgill et al., 2010). Results indicated that mediolateral reinforcement was greatest in children 1–4 years of age, indicated by the ratio of AP/ML diameter; femoral  $I_x/I_y$  increased linearly with age; and the  $I_{max}/I_{min}$  ratio had a positive correlation with age. The authors inferred that the orientation of maximum bending rigidity differed in young infants and children (as opposed to adults) as a functional adaptation, whereby bone modeling adjusts the amount and distribution of bone tissue in response to biomechanical loading; femoral geometry is thereby shaped during ontogeny by the “stance, step length, cadence, and walking velocity” of the immature human gait. Similar results were obtained by Gosman et al. (2013) in their analysis of 46 femora from Norris Farms No. 36.

Using these data as a reference, the geometric properties of infants from Inamgaon will follow these established patterns if they are acquiring locomotor behaviors toward the end of the first year. Geometric properties will change in the first year of life, from roughly circular cross sections in the youngest infants (2- to 5-month-old) to cross sections that are mediolaterally reinforced as locomotor skills are acquired (6–13 months). We expect to see *theta* (a measure of the distribution of bone mass) change to an anterior-medial/posterior-lateral orientation in the infants 6–13 months. We also predict that the older infants, who are acquiring locomotor skills, will demonstrate evidence of modeling—porosity occurring in a reciprocal pattern at the endosteal and periosteal surfaces. Finally, we predict the greatest number of pores and greatest pore volume will occur in the posterior-medial quadrant.

The distribution of pores in the cross section can then be used to assay disruptions in homeostasis, as distinct from the effects of activity. Research on the distribution of porosity has confirmed age-structured variation. As young children waddle and toddle on the road to mature bipedal gait (Cowgill et al., 2010), so predictable changes should occur in the distribution of pores in ontogeny (Thomas et al., 2000, 2005). In a study of well-nourished immature individuals 1–20 years old, significantly higher levels of porosity were identified in the posterior cortex of the toddler age group (2–3 years), relative to that seen in early and late childhood (Goldman et al., 2009). Qualitative analysis suggests these differences result from changing drift patterns and geometry during growth. Given cross-sectional shape changes indicating mobility, infants should demonstrate this predictable outcome of the biomechanical environment. Derangement of the expected amount and distribution of porosity from the reciprocal arrangement typical of normal modeling in ontogeny, to a high volume of pore with a more uniform distribution in the cross section, indicates disruption in homeostasis. In this way, by combining measures of midshaft geometry with porosity, we will tease apart the effects of stress from those of activity level. We hypothesize that for those infants with evidence for skeletal emaciation—stunting and wasting—small body size resulted from a significant disruption to homeostasis that will be visible histologically. We expect that most of these infants were still acquiring locomotor skills and thus we predict geometric properties related to locomotion will vary by age but not by body size. With the acquisition of bipedalism in all of the older infants (around 1 year), we expect to see a trend toward medio-lateral reinforcement and for *theta* to be in an anterior–medial/posterior–lateral direction. For these “small” infants however, if indeed they were “stressed,” we expect to find a statistically significant difference in the histological profile, with an increase in the number and the volume of pores (relative to bone volume), and a significantly different distribution of porosity.

## MATERIALS AND METHODS

This study sample derives from the site of Inamgaon. Adult burials are rare in the Deccan Chalcolithic; infants and children were interred in sealed jars under abandoned house floors, leading to excellent preservation of even the smallest perinates (Lukacs and Walimbe, 1986; Dhavalikar et al., 1988). Of 215 skeletons recovered during excavations at Inamgaon, 199 individuals (92.5% of the assemblage) were buried in the Early and Late Jorwe layers. Sixteen individuals were recovered from the phase known as the Malwa (1600–1400 BC) but are not included in this investigation, which concerns a period of environmental and subsistence transition from the Early to the Late Jorwe. This research is based on an analysis of 182 individuals available for study at Deccan College Post-Graduate Research Institute in Pune, India. Individuals 10 years of age or under make up 73.8% of the Early Jorwe and 76.1% of the Late Jorwe assemblages; 82 of these individuals have independent dental age estimates and intact femora for which length and midshaft measurements are possible (Table 1). In a previous analysis of stature and body mass in this sub-sample (Robbins Schug, 2011), 22% of the infants and children examined demonstrated values for stature and body mass index below two standard deviations from the median (Robbins Schug, 2011). Body size declines were greatest in young infants less than 12 months of age and individuals who died in their third year of life. For infants (2- to 12-month-old), mean BMI (body mass index) declined from 17 to 14. For this research, we examined compact bone mass—total area (TA), medullar area (MA), and cortical area (CA)—estimated at the midshaft femur (at 50% the bone length) using radiographs for 26 of these individuals (46.4% of the total number of infants from this age category). Radiographs were obtained in the medio-lateral dimension at the office of Dr. Ram Tapasvi in Pune. Midshaft diameter, medullar diameter, medial, and lateral compact bone thickness measurements were made using Mitotoyu digital calipers. Measures were corrected for parallax distortion by comparing the length and midshaft diameter measurements from radiographs with those made directly on the whole bone. Cross-section geometric properties (TA, MA, and CA) were calculated based on the cylindrical model (following O'Neill and Ruff, 2004); MA was derived from TA and CA (MA=TA-CA).

**Table 1.** Sample of immature skeletons from Inamgaon

Phase	Date (B.C.)	N	n <sup>a</sup>	Humerus and femur	Femur	Femur cross-	Femur histology
				radiographs <sup>b</sup>	radiographs	sections	
				0–10 years	0–1 year	0–1 year	0–1 year
Early Jorwe	1400–1000	41	27	3	8	5	3
Late Jorwe	1000–700	141	65	13	18	9	8
Total		182	82	18	26	14	11

Individuals included in the radiographic and histological analysis were between 0 and 1 year and had independent age estimates available from dentition.

<sup>a</sup> The total number of individuals (0–;10 years) with intact long bones and dental age estimates available.

<sup>b</sup> The number of individuals with intact humerus, femur, and dental age estimates available.

We also examined whole bone geometry using the midshaft section modulus ( $Z_p$ ) from radiographs of 28 individuals for whom both the humerus and femur were available. This sample included 10 perinates (<1 month) and 18 older individuals (2–120 months), who were compared

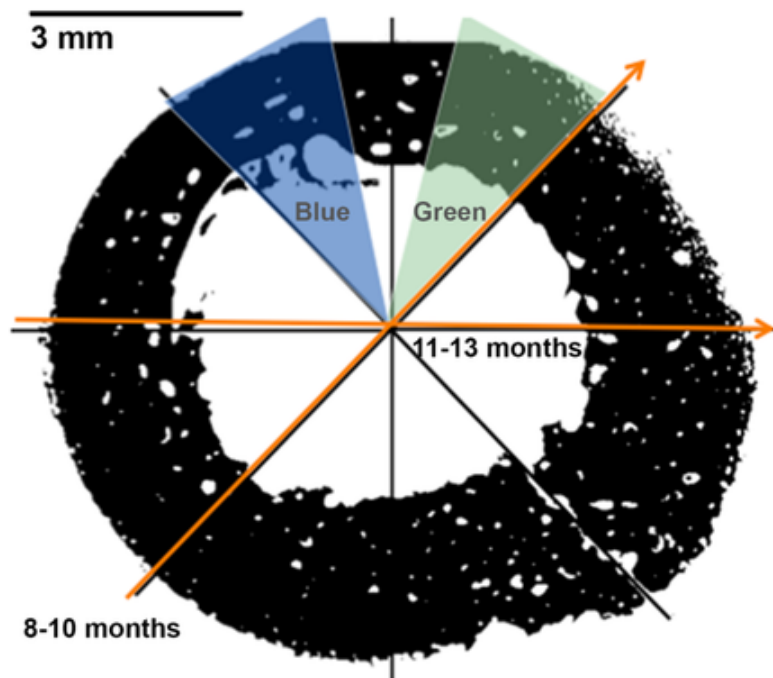


with 32 individuals (2–120 months) from the Denver Growth Study. Cross-sectional moments of inertia ( $J$ ) and the Polar Section Modulus ( $Zp$ ) were calculated (following Ruff, 1992) from measures of the total medio-lateral diameter ( $T$ ) and the medullar diameter ( $M$  = total breadth – summed medial and lateral breadths) on the radiographs. Measures were again corrected by comparing the measurement from the radiograph with that of the bone itself. Formulas for the geometric properties follow:

$$J = \pi/32 \times (T^4 - M^4)$$
$$Zp = J(T/2)$$

Because sectioning is a destructive analysis, direct measures of cross-section geometry were possible only for 14 of these individuals (25% of the infants available from this age category). Undecalcified ground thin sections were prepared at 50% femur length. Sections were ground using the Maat method: a graded series of abrasive papers and then Beuhler diamond suspensions. Images were obtained using an Optronix digital CCD camera, mounted on a Zeiss Axioplan 40 transmitted light microscope fitted with an automated  $X$ ,  $Y$ , and  $Z$  stage. These images were imported into ImageJ (<http://imagej.nih.gov/ij/>), where they were binarized and segmented. Pores were given a value of “255” (white) and bone tissue was given the value of “0” (black). Periosteal and endosteal outlines were automatically detected, and the endosteal boundary smoothed (see Feik et al., 1997; Goldman et al., 2005). Traditional 2D measures of the geometric properties were calculated (e.g., Total Subperiosteal Area (TSPA), Cortical Area (CA), and Medullary Area (MA), maximum and minimum second moments of area ( $I_{max}$  and  $I_{min}$ ), polar moment of inertia ( $J$ ) and  $theta$  (defined as the angle between the medio-lateral axis of the cross section and the orientation of maximum bending rigidity [ $I_{max}$ ]) (Ruff and Hayes, 1983). The maximum ( $I_{max}$ ) and minimum ( $I_{min}$ ) second moments of inertia were calculated using the BoneJ plug-in (Doubé et al., 2010) and the shape of the cross-section was described using the ratio of  $I_{max}/I_{min}$ . Geometric measures and cortical widths were plotted against developmental age to document changing geometric properties of the sample through ontogeny that reflect cortical and medullary expansion or contraction, and/or shifts in the axis of greatest bending rigidity.

Transmitted light microscopy (TLM) was used to evaluate evidence for diagenesis, microbial, or taphonomic damage (post-depositional mineralization, tunneling, fracturing, or erosion of the periosteal surface). Three individuals were excluded from further analysis due to taphonomic damage and histological analysis was conducted on 11 of these 14 individuals, who demonstrated sufficient preservation. Cortical drift patterns and porosity were assessed by dividing the cortex into eight equal polar sections (Fig. 2), following the methods outlined in Goldman et al. (2009). Compact bone areas and pore areas were calculated for each radial sector, the number of pores in each sector was counted, and the proportion of pore:bone volume (defined as total pore area divided by cortical bone area) was calculated. Pores were automatically detected once the input image pixels were binary classified. These measurements were made using an additional macro routine, which was integrated into ImageJ (MomentMacro, <http://www.hopkinsmedicine.org/fae/mmacro.htm>).



**Location (*theta* angle orientation)**  
**A-M to P-L (Green) = 45 to 67.5**  
**A-L to P-M (Blue) = -67.5 to -45**  
**M-L = radians < 45**  
**A-P = 67.5 to -67.5**

**Figure 2.** Femur midshaft cross-sections were divided into eight equal polar sections for analysis of bone mass and pore volume distribution. The location of theta was determined using the following scale: A-M to P-L (green triangle) = 45–67.5; A-L to P-M (blue triangle) = –67.5 to –45; A-P = 67.5 to –67.5; M-L = radians < 45.

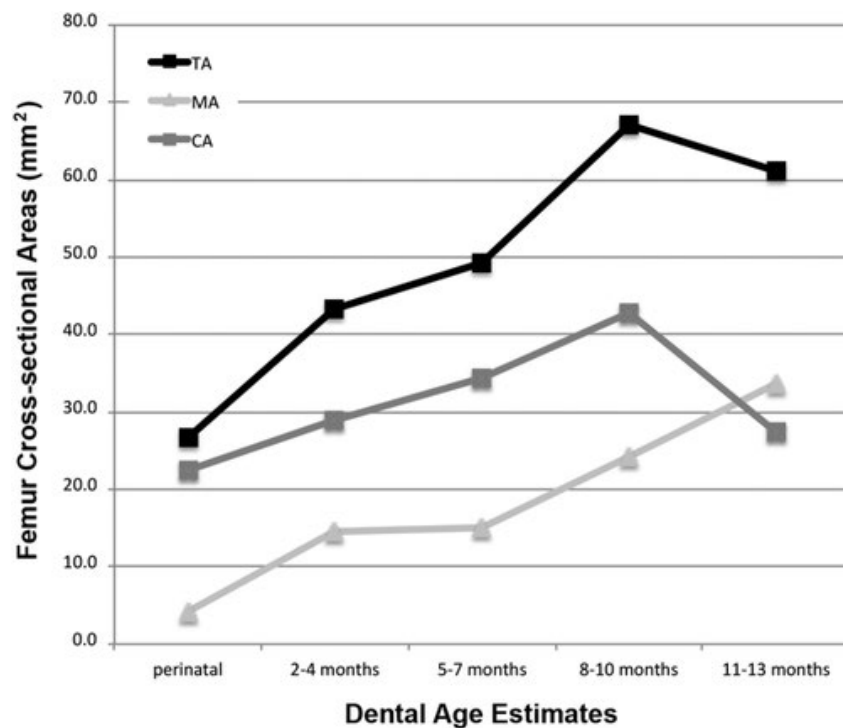
Of this sample of 11 individuals, those specimens that met growth standards for developmental age in whole bone morphology ( $n = 6$ ) were used to characterize age-structured variation in porosity due to developmental differences. This reference was then compared with five individuals who demonstrated evidence of growth suppression in long bone length, body mass, and bone mass index and were thus expected to demonstrate derangement in the histological signature. The sample of individuals who met expectations for stature and BMI for age ( $n = 6$ ) is hereafter referred to as the “average” sample, a short-hand reference to body size that falls within the range of variation expected for dental age (the 95% CI, or confidence interval); individuals with stature and BMI values below two standard deviations from the median for age (<95% CI) are hereafter referred to as “small” ( $n = 5$ ). Kruskal-Wallis (with the Bonferroni correction to compensate for multiple comparisons) and Mann-Whitney U nonparametric tests were used to evaluate the significance of differences in histological properties between “average” and “small” infants from Inamgaon. Three histological properties were evaluated in the statistical analysis: number of pores, pore:bone volume (total pores area divided by total compact bone area in the cross-section), and the distribution of pores in four different quadrants of the cortex (anterior–medial, anterior–lateral, posterior–medial, and posterior–lateral). The sample sizes for histology are small but it is important to remember, we are not testing here whether there were significant

differences between the Early and Late Jorwe in terms of body size; that has been previously demonstrated (Robbins, 2007; Robbins Schug, 2011). Here we are using bone histology to assess whether small body size in the infants from Inamgaon corresponds to altered biomechanical activity and/or histological evidence of a disruption in homeostasis. The null hypothesis then is that there will be no significant difference in geometric and histological properties among the infants of “small” versus “average” body size, or with the published reference samples (Goldman et al., 2009; Cowgill et al., 2010; Gosman et al., 2013).

## RESULTS

Total subperiosteal area (TA), medullar area (MA), and cortical area (CA)

Summary statistics for measures of femoral midshaft cross-section geometry in the first year of life are provided in Table 2. An examination of TA, MA, and CA demonstrates a strong correspondence among increasing bone mass and developmental age for the first year of post-natal life ( $n = 26$ ), with periosteal expansion and endosteal absorption occurring in proportion to one another until 11- to 13 months of age (Fig. 3). In this age category, there is a reduction in bone mass (TA and CA) on average compared with infants who died at younger ages. Bone mass in older infants from Inamgaon departs from the expected trend (Gosman et al., 2013) but the sample size in this age category is small ( $n = 2$ ) and an examination of growth trajectories in geometric properties for a longer period of growth is required to assess the implications of this departure in the context of Inamgaon sample as a whole (below).



**Figure 3.** Cortical bone areas (TA, total subperiosteal area; MA, medullar area; CA, cortical area) at the midshaft femur demonstrate that the infants from Inamgaon are acquiring bone mass with age but there is a significant drop in CA around the time when bipedalism becomes habitual.

**Table 2.** Cortical bone mass values by age category for the Inamgaon sample

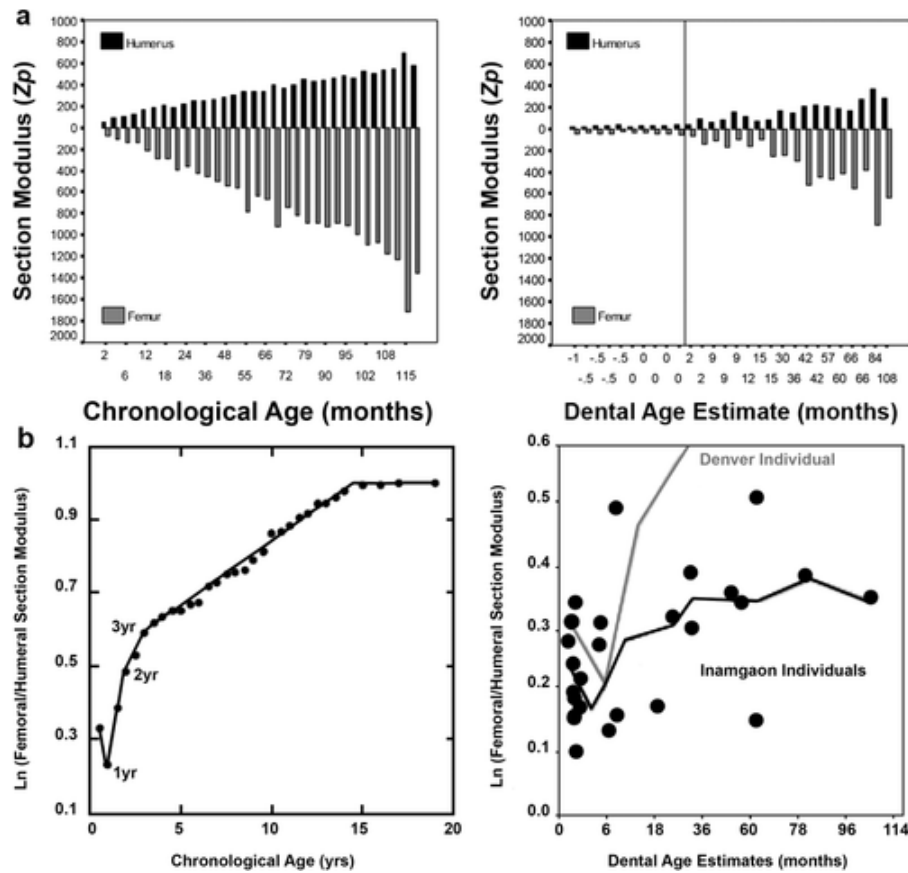
Age	<i>n</i>	TA	MA	CA
Perinatal	8	26.74	4.25	22.49
2–4 months	5	43.40	14.56	28.84
5–7 months	2	49.30	15.01	34.29
8–10 months	9	67.19	24.32	42.87
11–13 months	2	61.21	33.73	27.47

TA, total area; MA, medullar area; CA, cortical area.

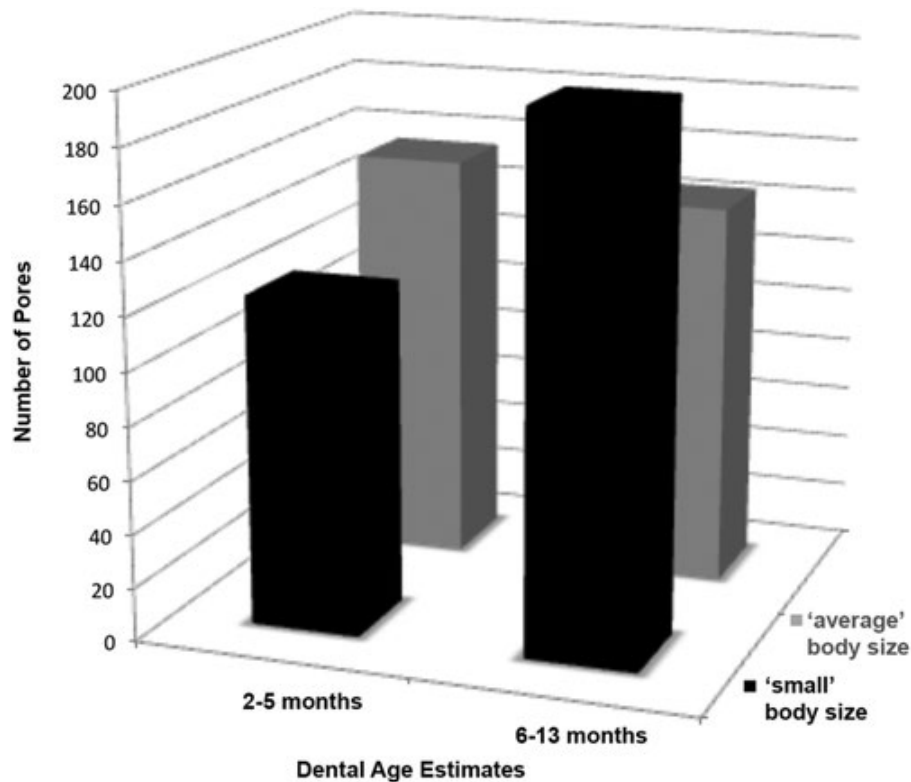
Section modulus, or bending strength ( $Zp$ ) in the humerus relative to the femur

An examination of bending strength and torsional rigidity in the humerus and femur for 28 individuals from the Early and Late Jorwe samples from Inamgaon (10 perinates and 18 individuals 2- to 120 months of age) demonstrates that bone strength in the humerus and femur is much lower than expected (Fig. 4). In a previously published comparison of femoral and humeral bending strength for a sample ( $n = 40$ ) of infants and children from the Denver Growth Study (Ruff, 2003b), bending strength (or  $Zp$ ) increased with age despite declines in %CA because mass is added at the periosteal surface, so bone diameter increases even as the medullar area also increases (Fig. 4a). In contrast, for the Inamgaon specimens (Fig. 4b), bending strength does not increase as expected in the humerus or the femur, suggesting that beyond a reduction in total bone mass, individuals from Inamgaon specifically demonstrate growth suppression at the periosteal surface.

Another way of thinking about this issue is to examine an index of femoral/humeral section moduli ( $Zp$ ). When the velocity of growth in  $Zp$  is plotted by age for a single individual from the Denver sample (following Ruff, 2003b), the strength for the femur increases quickly relative to the humerus after one year of age, with the acquisition of bipedalism (Fig. 5a). For infants and children from Inamgaon, this ratio is significantly altered (Fig. 5b). When the femoral/humeral section modulus is plotted for individuals from Inamgaon (perinatal to 120 months), it becomes apparent that the stunted acquisition of bone mass described above for the femur of 11- to 13-month-old from Inamgaon continues throughout the first 10 years of life for all children for whom both bones are available. The relative growth velocity of the humerus and femur depicted in Figure 5b resembles the pattern expected for quadrupeds. Both humeral and femoral strength are much lower than expected for age and the femoral growth velocity in  $Zp$  is much slower than expected relative to the humerus. This result indicates either (1) children from Inamgaon are not acquiring bipedal locomotion as expected, or (2) despite the acquisition of bipedalism, children from Inamgaon are not acquiring bone mass (or bone strength) as expected due to nutritional deficiency, disease, parasitism, or other biocultural stressors. A more detailed analysis of the cross-section geometry and histology was performed to address this issue further.



**Figure 4.** Bending strength in the humerus and femur of 0- to 10-year-old children from the Denver Growth Study (left) with those from Early and Late Jorwe Inamgaon (right). In 4a, values for section modulus of the humerus are on the top of the graph and the femur is on the bottom of the graph. The Denver study children (left) have a relatively faster growth velocity ( $Z_p$ ) in the femur indexed to the humerus than the children from Inamgaon (right). In 4b, when the velocity of one individual from the Denver study (left) (from Ruff, 2003b) is compared with the cross-sectional data for the children from Inamgaon (right), the Deccan Chalcolithic individuals have relative limb strengths for age more similar to a quadruped than a biped, suggesting that femoral bone mass is not acquired at the expected velocity (relative to the humerus) despite biomechanical strain.



**Figure 5.** The quantity of pores in the cross-section increases with age in young infants but does not have a straight-forward relationship with biocultural stress levels.

#### Orthogonal principal axes and theta

An examination of the distribution of bone mass in infants, using the orthogonal axes and *theta*, demonstrates that bipedal locomotion is likely part of the behavioral repertoire for these older infants from Inamgaon (Table 3). The mean  $I_{max}/I_{min}$  for the Inamgaon sample ( $n = 14$ ) was 1.31 (st. dev. = 0.15). Previous research demonstrated that the expected ratio of orthogonal principal axes ( $I_{max}/I_{min}$ ) is 1.29 (st. dev. = 0.15) for 0–2 year olds ( $n = 21$ ) (Gosman et al., 2013). This is also within the range of variation described by Cowgill et al. (2010).

**Table 3.** Measures of femur midshaft geometry for the Inamgaon sample (by age category)

Age	<i>n</i>	$I_{max}/I_{min}$	<i>Theta</i>	Orientation
Perinatal	3	1.46	30–82	Mixed
2–4 months	3	1.43	20–23	M-L
5–7 months	1	1.20	32	M-L
8–10 months	5	1.11	45–59	AM-PL
11–13 months	2	1.35	3–15	M-L

Another way of thinking about shape is to look at *theta* (the specific orientation of  $I_{max}$ , given in radians). Expectations for toddlers were developed from published reference data (Goldman et al., 2009) that predicts *theta* will shift to AM-PL radian range in toddlers. The Inamgaon specimens demonstrate a shift toward a medio-lateral orientation of bone mass after 9 months of age (Table 3); These data strongly suggest that infants who died in the first year were acquiring locomotor skills between 9 and 13 months. Thus, despite apparent reduction in the quantity of

compact bone (TA, CA, and  $Zp$ ), the bone mass for infants from Inamgaon was on average distributed in a manner that meets expectations for this age class.

#### Quantity, volume, and distribution of pores

We had predicted that there would be an increase in the number of pores for the individuals previously identified as having short stature and reduced BMI for age (the “small” category) but this relationship was not straightforward (Table 4). The quantity of pores in the cross-section was not systematically related to age or body size (Fig. 5). The median number of pores was higher for ‘average’ individuals (192.5) than for the “small” individuals (137); however, a Mann Whitney U test demonstrates the differences between the two samples were not statistically significant ( $N = 11$ ; Median = 150;  $\text{Chi}^2 = 0.110$ ;  $P\text{-value} = 0.740$ ). The number of pores increased with age for “average” infants ( $n = 6$ ), from a mean count of 124 pores in the 2- to 5-month-old category to a mean count of 198 pores in the 6- to 13-month-old category. In contrast, for the “small” infants ( $n = 5$ ), the mean number of pores declined from 155 in younger infants to 144 in the older infant age category. However, the range of variation in the number of pores was much greater in the “average” individuals (51–256) than for the “small” individuals (106–204). This result suggests that the number of pores is not systematically related to developmental age or body size, and it may not be a sensitive measure of the effects of biocultural stress, perhaps because pore formation has a complex relationship with locomotion, homeostasis, and micro-traumas as well.

When the volume of pores relative to bone mass (pore area divided by compact bone area) was compared between “average” individuals ( $n = 6$ ) and “small” individuals with low BMI ( $n = 5$ ) the difference was statistically significant in a Mann Whitney U test ( $N = 11$ ; Median = 8.8;  $\text{Chi}^2 = 11.000$ ;  $P\text{-value} < 0.005$ ). Throughout the first year of life, the mean pore volumes in the sample of “average” body size were less than or equal to 5% of the total compact bone volume (Fig. 6). In the sample of individuals with “small” body size, pores comprised 26% of the cross-section area in the younger infants (2–5 months) and 14% in the older infants (6–13 months). The significantly higher volume of pores supports our hypothesis that small body size in the Inamgaon sample corresponds to histological evidence of decoupled resorption and formation in the bone cortex.

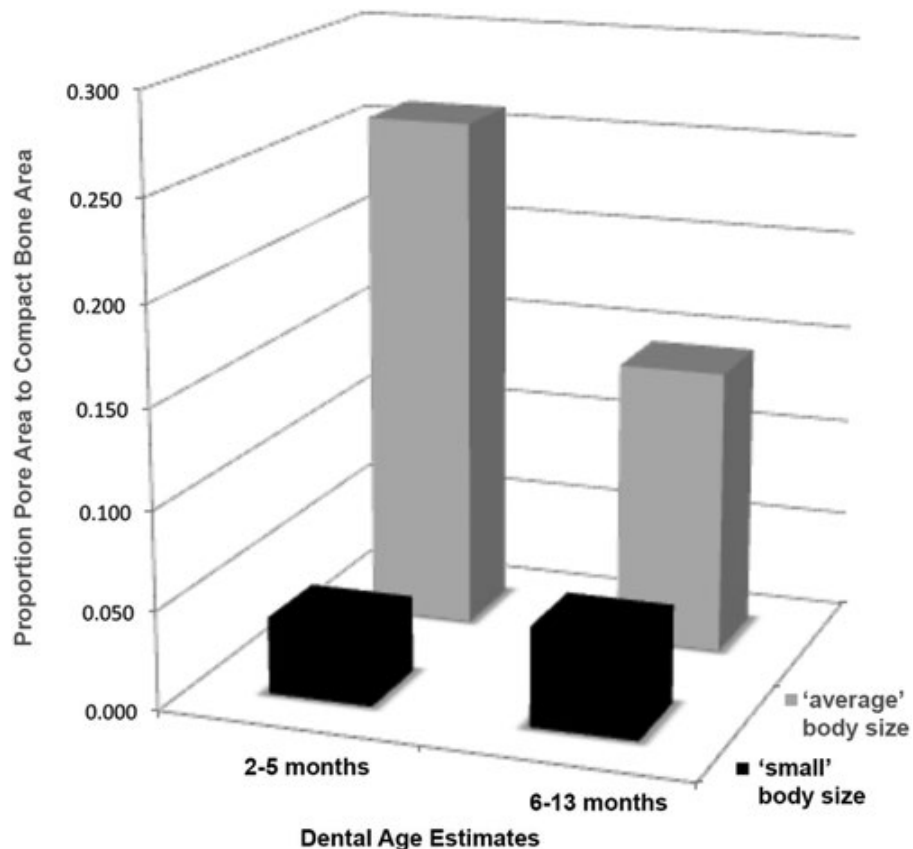
The distribution of pore volume also differs significantly between infants of “average” body size and those who demonstrate evidence of “small” body size. When the volume of pores relative to bone mass (pore area divided by compact bone area) is considered by quadrant of the cross-section, a Kruskal-Wallis test demonstrates there are significant differences among the samples in general ( $df = 3$ ;  $\text{Chi}^2 = 12.110$ ;  $P\text{-value} < 0.005$ ) and post-hoc tests suggest one significant pair-wise difference in “average” versus “small” infants 2- to 5-month-old ( $Z = 2.896$ ;  $P\text{-value} < 0.023$ ). None of the other pair-wise comparisons demonstrated differences that were statistically significant.

**Table 4.** Histological properties of the femur midshaft cross-sections from Inamgaon (by age category)

2–5 months old											
Average body size sample						Small body size sample					
	Quadrant	Number of pores	Pore area <sup>a</sup>	Compact bone area <sup>a</sup>	%pores		Quadrant	Number of pores	Pore area	Compact bone area	%pores
INM 179b	am	51	0.215	7.509	2.863	INM 212-1	am	51	0.528	5.459	9.672
	al	44	0.262	8.202	3.194		al	16	2.761	4.009	68.870
	pl	25	0.187	7.299	2.562		pl	52	0.752	6.066	12.397
	pm	30	0.205	7.685	2.668		pm	36	1.801	6.824	26.392
	total	150	0.869	30.695	2.831		total	155	5.842	22.358	26.129
INM 61	am	31	0.170	3.721	4.569						
	al	30	0.169	4.732	3.571						
	pl	22	0.352	5.674	6.204						
	pm	14	0.321	6.319	5.080						
	total	97	1.012	20.446	4.950						
6–13 months old											
Average body size sample						Small body size sample					
	Quadrant	Number of pores	Pore area	Compact bone area	%pores		Quadrant	Number of pores	Pore area	Compact bone area	%pores
INM 122	am	42	0.615	7.649	8.040	INM 105	am	22	0.738	6.946	10.625
	al	99	0.693	8.267	8.383		al	25	0.842	6.441	13.073
	pl	67	0.310	9.338	3.320		pl	26	0.750	5.637	13.305
	pm	27	0.344	10.488	3.280		pm	57	1.139	5.667	20.099
	total	235	1.962	35.742	5.489		total	130	3.469	24.691	14.050
INM 223	am	46	0.291	11.390	2.555	INM 148	am	36	1.682	7.504	22.415
	al	26	0.353	8.643	4.084		al	41	1.111	9.140	12.155
	pl	84	0.401	11.265	3.560		pl	58	1.518	9.181	16.534
	pm	100	0.907	11.749	7.720		pm	69	1.195	8.800	13.580
	total	256	1.952	43.047	4.535		total	204	5.506	34.625	15.902
INM 179a	am	33	1.224	11.160	10.968	INM 162	am	33	0.996	7.016	14.196
	al	34	0.896	11.177	8.016		al	29	2.558	6.488	39.427
	pl	90	1.019	13.092	7.783		pl	26	0.514	9.219	5.575
	pm	92	1.127	12.874	8.754		pm	49	1.096	8.265	13.261
	total	249	4.266	48.303	8.832		total	137	5.164	30.988	16.665
INM 213	am	13	0.032	5.757	0.556	INM 187	am	16	0.333	6.199	5.372
	al	2	0.006	4.563	0.131		al	15	0.286	4.192	6.823
	pl	9	0.026	7.019	0.370		pl	27	0.373	7.708	4.839
	pm	27	0.221	6.947	3.181		pm	48	1.919	8.381	22.897
	total	51	0.285	24.286	1.174		total	106	2.911	26.480	10.993

<sup>a</sup> Pore and compact bone area measurements in mm<sup>2</sup>.



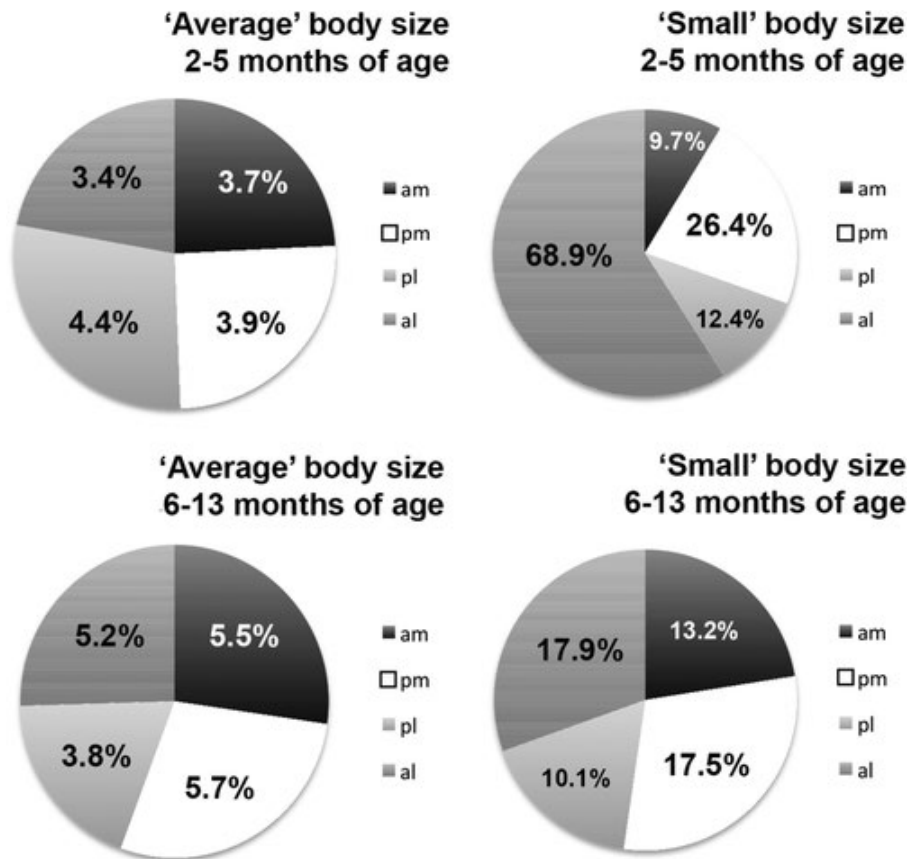


**Figure 6.** The volume of pores in the cross-section is <5% of cortical bone area for “average” individuals 2–13 months; “small” individuals have a significantly higher percent pore volume.

We graphically demonstrate the differences among age categories for the “average” and “small” samples using pie charts, in which each slice of the pie represents the percent pore area in that quadrant (Fig. 7). The sample sizes are small but for young infants (2–5 months) in the “average” sample ( $n = 2$ ), the pore volume is relatively evenly distributed across the section. This result is not inconsistent with biomechanical expectations (Goldman et al., 2009) as young infants are not regularly supporting their body weight in a way that would lead to systematic patterning in the distribution of the pores. The skeletally “small” individual ( $n = 1$ ) in this age category demonstrated a large volume of pores in the anterior-lateral quadrant. This result is difficult to interpret because of the small sample size. The range of variation for the patterning of pore volume in young infants is not fully documented and thus this result simply suggests a need for additional basic research.

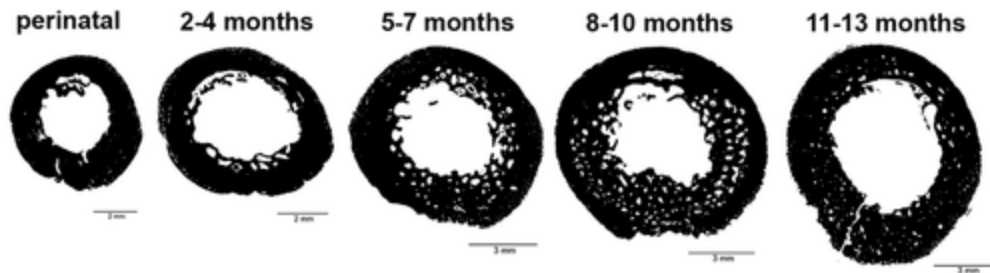
For individuals of average body size in the 6–13 month age category ( $n = 4$ ), the pores are primarily distributed in an axis perpendicular to *theta*. *Theta* was oriented AM-PL for 6- to 13-month-old; the major axis of pore distribution is AL-PM. This suggests a hypothesis that for older infants, pores will be distributed in an orientation perpendicular to the greatest biomechanical strain. This hypothesis should be addressed in future analyses. Recall that the “small” individuals in this age category ( $n = 4$ ) demonstrated a significantly greater pore volume relative to bone volume (reported above) but our analysis of the distribution of pores in the cortex demonstrates no significant difference from the “healthy” sample. This result suggests the

distribution of pores is strongly determined by locomotor behavior, which did not differ strongly among the “average” and “small” samples.

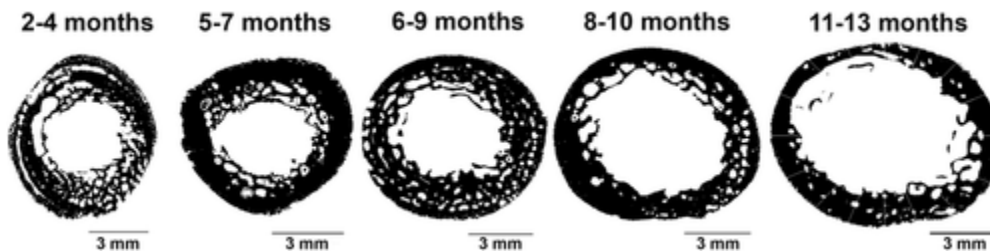


**Figure 7.** The distribution of pores is presented here as the percentage of pore area within the total subperiosteal area of each quadrant of the cross-section. Pores area is roughly equal in all four quadrants for young infants (2–5 months), although a single individual with “small” body size deviated from the expected pattern. In older infants (6–13 months), who are acquiring locomotor behavior, the pores tend to be distributed perpendicular to *theta* (the major orientation of bone mass). This is true for those older infants with “average” and “small” body size.

Figure 8 demonstrates the ontogeny of geometric properties, modeling, pore volume, and distribution for 2- to 13-month-olds from Inamgaon. These binarized images are representative of the geometric properties and pore distribution of the specimens from individuals of “average” body size ( $n = 6$ ), specimens which basically matched our expectations for midshaft geometry and histology from the literature. Figure 9 demonstrates the increased range of variation in compact bone geometric properties, pore volume, and distribution across the midshaft femur for the sample of infants (2–13 months) with “small” body size ( $n = 5$ ). These individuals had stature and body mass values below the 5th percentile for dental age (Robbins Schug, 2011) and this research demonstrates that “small” body size was also associated with increased pore volume relative to bone volume, changes in pore distribution, and reduced cortical bone mass.



**Figure 8.** Binary images of representative bone sections from individuals of “average” body size in each age category. All images are oriented such that anterior is up and posterior is down; medial is to the right.



**Figure 9.** Binary images demonstrating increasing variation in bone mass, pore volume, and distribution for individuals of “small” body size (6–13 months of age). All images are oriented such that anterior is up and posterior is down; medial is to the right.

## DISCUSSION

Bioarchaeologists seek to address questions about human lifestyles, health and functional adaptations in the past. Our ultimate goal in this research was to combine assessments of femoral midshaft geometry with compact bone histology to understand how activity, nutritional deprivation, and other biocultural stressors contributed to small body size in a prehistoric population. The results of this study demonstrate that all of the infants examined show changes in cross-sectional shape and the orientation of bone mass consistent with expectations for developmental age, given the acquisition of habitual locomotor behavior. Throughout the first year of life, the expected trajectory of shape changes was consistent with published expectations: (1) the young infants have roughly circular cross-sections until 6–9 months, when there is an obvious transition to medio-lateral reinforcement; and, (2) *theta* values demonstrate that the bone mass in older infants is distributed in an AM-PL orientation that matches expectations for infants acquiring locomotor skills (Cowgill et al., 2010; Goldman et al., 2009; Gosman et al., 2013). Results are consistent with the inference that infants from Inamgaon were acquiring a normal repertoire of locomotor activities, “waddling and toddling” as expected, by the end of the first year of life (Cowgill et al., 2010).

However, our analysis of the velocity of growth in long bone strength ( $Zp$ ) in the humerus relative to the femur suggests a significant alteration in the expected pattern of bone mass acquisition in the first ten years of life (Ruff, 2003b), such that the infants and children from Inamgaon resemble a pattern typical of quadrupeds—the femur is not increasing in strength relative to the humerus. Although changes in bone cross-sectional shape indicate infants and children from Inamgaon were mobile, they were not achieving expected levels of bone strength ( $Zp$ ) in the femur. This has important implications for understanding the role of activity in

shaping compact bone mass at the midshaft femur. In the context of adequate health and nutritional status, infants and children acquire and actively maintain bone mass in response to their biomechanical environment (Ruff 2003a, 2003b; Pearson and Lieberman, 2004; Cowgill et al., 2010). Results of our analysis indicate that despite regular activity, compact bone mass may be reduced at the midshaft femur in cases of low BMI, a relationship that has been demonstrated in animal models (Lee et al., 1986; Wronski et al., 1987; Lee et al., 1993; Lane et al., 1995; Talbott et al., 1998; Wallace et al., 2012) and is consistent with recent investigations of bone mass and body mass in the immature skeleton (McGuigan et al., 2002; Galusca et al., 2008; Robbins et al., 2010; Robbins Schug et al., 2013a).

To return to our hypothesis that “small” body size (short stature, low BMI, and reduced bone mass) was an indicator of biocultural stress, one which represented skeletal emaciation at Inamgaon, this study demonstrates small stature and low BMI were also associated with reductions in bone mass ( $CA$ ), bone strength ( $Zp$ ), and a significant increase in pore volume relative to bone volume. While individuals of “average” body size fell within the expected range of variation for the geometric and histological properties measured here, growth derangement was visible in all measures for 100% of the “small” individuals studied. Small body size at Inamgaon was associated with a decoupling of bone formation and resorption, suggesting a disruption in homeostasis significant enough to impact on bone quality. Growth disruption in linear length and appositional growth are already important biocultural stress markers in bioarchaeology (following the General Adaptation Model of Goodman et al., 1984, 1988). The use of BMI as a biocultural stress marker is a more recent innovation in bioarchaeology but it has been applied to adult (Auerbach, 2011; Siegmund and Papageorgopolou, 2011) and immature skeletons (Robbins, 2007; Robbins Schug, 2011; Robbins Schug et al., 2013a) and this project suggests its use as a stress marker (in combination with other lines of evidence) is appropriate.

We have demonstrated skeletal emaciation at Inamgaon was characterized by a combination of small stature for age, low BMI for age, decreased bone mass, and strength, and increased pore to compact bone volume. Beyond their role as stress markers, these measures are also powerful indicators of health more generally. From a lifespan epidemiology perspective (Gluckman and Hanson, 2007), osteopenia is an important risk factor for fracture (Cooper et al., 2006) and reduced peak bone mass in childhood and adolescence predisposes individuals to accelerated post-menopausal osteoporosis (Cassidy, 1998; Lane, 2006; Cooper et al., 2009). In contemporary populations, wasting is also associated with particularly profound biocultural impacts, including declines in health status. Childhood wasting is associated with commensurate increases in infant, childhood, and maternal mortality (Rose and Martorell, 1992; Pelletier et al., 1995; Black et al., 2008); psychological and intellectual impacts (Scrimshaw and Gordon, 1968; Martorell et al., 1992; Victora et al., 2008); and increased adult morbidity through impairments to immune function and predisposition toward developing cardiovascular and pulmonary diseases (Victora et al., 2008). An examination of the most common proximate causes of skeletal emaciation and wasting in contemporary populations suggests acute starvation at Inamgaon was likely due to a combination of inadequate dietary intake and high rates of infection or disease (Lutter et al., 1992; de Onis et al., 1993). Ultimate causes of wasting in human populations today are institutional, political, ideological, and economic and these include issues around food security; household composition, maternal perceptions, and child care practices; environmental circumstances; prevalence of diarrhea, parasitic infection, and infectious diseases, and variation

in health-related beliefs, practices, and access to health services (Frongillo and Hanson, 1995; Frongillo et al., 1997; Bloss et al., 2004).

Research on childhood growth and development provides important insights into the health of past populations but this research also has important implications for understanding the process of growth derangement today. Importantly, this research represents the first attempt to our knowledge to combine insights about linear growth and compact bone geometry with histological information about the process of growth disruption and growth derangement in immature skeletons. Basic research on the ontogeny of histological variation using *ex vivo* subadult specimens has been limited in the past by scarcity of appropriate samples. Ontogenetic variation is well documented in studies of subadult iliac crest bone biopsies (Parfitt, 1990; Glorieux et al., 2000; Parfitt et al., 2000; Rauch et al., 2007), archaeological (Pfeiffer, 2006) and autopsy samples of ribs (Epker and Frost, 1965; Reid and Boyde, 1987; Pfeiffer et al., 2006), and some studies on femora (Burton et al., 1989; Drapeau and Streeter, 2006; Goldman et al., 2008, 2009). However, the majority of clinical research on femur midshaft compact bone growth and osteopenia has concentrated on *in vivo* assessments of bone size and density using radiography, dual energy X-ray absorptiometry (DXA), and quantitative computed tomography (qCT) (Garn, 1970; Helin et al., 1985; Horsman et al., 1989; Lettgen, 1995; Ferretti, 1997; Binkley, 2002; Petit et al., 2005; Wren and Gilsanz, 2006). Remote sensing is most practical as a research tool but these methods cannot adequately represent the functional properties of a bone during growth—changes in geometry, structural density, and mineralization confound interpretations of BMD (Kanis et al., 1994; Nelson and Koo, 1999; Schonau, 1996, 1998)—nor capture the organizational structure of human bone tissue as precisely as histological techniques (Lazenby, 1986; Schonau, 1998; Nelson and Koo, 1999; Lane, 2006). Additional *ex vivo* research is required to answer questions about the nature of relationships between geometry and microstructure during ontogeny and how derangement of this process proceeds.

Although the sample size used in the present analysis is small, it is actually a large sample for this type of *ex vivo* research on immature femurs. Goldman et al. (2009) examined the range of variation in histological properties for 14 individuals, a sample which spanned the non-adult age range. Gosman et al. (2013) reconstructed cross-sectional shape changes and the modeling of cortical surfaces for 46 individuals, 21 of which were in the 0–2 year age category. The fact that research on compact bone ontogeny is generally performed on small samples (particularly when microstructural characteristics are studied) means the current study provides an important contribution to basic research documenting the range of variation in femoral midshaft ontogeny; this is particularly true given our focus on the first year of life, when locomotor skills are initially acquired. Basic research on human biological variation and growth disruption is important for clinicians, human biologists, bioarchaeologists, and functional morphologists interested in the effects of emaciation on bone mass. That being said, because the sample size is small, it will be important to evaluate these findings in additional samples to further test these hypotheses about growth and its derangement in young infants.

## CONCLUSIONS

This research is part of a broader investigation into human strategies for coping with climate and environmental changes in South Asia's past (Robbins, 2007; Robbins Schug, 2011; Robbins

Schug et al., 2012, 2013b). The ultimate goal is to trace the complexities of human-environmental interactions throughout the Late Holocene using a scientific and social bioarchaeology approach to the data that will clarify the strategies employed, the social forces involved, and the consequences for human communities. In the case of the Deccan Chalcolithic, and the Indus Civilization prior, the archaeological record suggests these populations initially developed highly successful biocultural adaptations to a semi-arid environment and monsoon uncertainty. Unfortunately, through time, the archaeological record demonstrates relatively rapid population growth preceded abandonment of settlements and migration to new regions of South Asia at the end of the second and the third millennium B.C. In the third millennium BC at Harappa, those human groups who remained in the city during the post-urban period saw significantly elevated levels of inter-personal violence, infection, and infectious disease (Robbins Schug et al., 2012, 2013b). In the second millennium BC, those who remained at Inamgaon when the rest of the region was abandoned in the Late Jorwe, also faced different but equally significant health consequences.

Previous research has demonstrated that the loss of a major proportion of their subsistence, when dry-plow agriculture was abandoned, led to significant reductions in body size for the infants and children of Inamgaon (Robbins Schug, 2011). The present research demonstrates that small body size in the infant population was associated with histological evidence of disruptions in homeostasis, indicating it is an appropriate indication of health status in this population through time. Thus, these results provide important new evidence about potential health consequences of environmental and climate changes in rural Indian populations. Unchecked population growth in combination with unsustainable agricultural practices led to the abandonment of this region around 1000 B.C. The population of Inamgaon decided to remain, choosing to abandon agriculture and shift to heavier reliance on sheep-goat pastoralism, saline-tolerant crops, and wild resources. Although some have suggested the abandonment of agriculture could theoretically lead to an improvement in health status (Lukacs and Walimbe, 2000), our results demonstrate that the abandonment of agriculture at Inamgaon was associated with significantly elevated levels of biocultural stress in the Late Jorwe phase. Additional research is required on the relationship between skeletal and dental markers of growth disruption, particularly in light of the conflicting patterns of dental stress markers (Lukacs and Walimbe, 2007) and the complex etiology of LHPC, which has variously been attributed to biomechanical, traumatic, and nutritional causes (Skinner, 1986; Suckling, 1986, 1989; Skinner and Hung, 1989; Taji et al., 2000; Lukacs et al., 2001; Halcrow and Tayles, 2008; McDonnell and Oxenham, 2012; Skinner et al, 2014).

Taken as a whole, this body of research suggests that several times in the Late Holocene of South Asia, climate, and environmental changes of long duration corresponded with significant reorganization of the human population. In the case of the Indus Age and the Deccan Chalcolithic, human communities initially developed social, economic, and subsistence strategies to cope with life in a semi-arid, monsoon climate. Population growth, economic transitions, and centuries of environmental change—increasing aridity in the Indus Age and environmental degradation in the Deccan Chalcolithic—eventually resulted in massive levels of migration away from settlements (and entire regions) that had been successfully occupied for centuries. Although the specific biocultural challenges differ—violence and disease in the urban context versus infant

mortality and skeletal emaciation in the rural context—ultimately the human population that remained in largely abandoned regions faced profound consequences.

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