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# The Skeletal Phenotype of "Negritos" from the Andaman Islands and Philippines Relative to Global Variation among Hunter-Gatherers

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## **Abstract**

The "negrito hypothesis" suggests that populations of small-bodied foragers in South and Southeast Asia who share common phenotypic characteristics may also share a common, ancient origin. The key defining characteristics of the "negrito" phenotype, small body size, dark skin, and tightly curled hair, have been interpreted as linking these populations to sub-Saharan Africans. The underlying assumption of this interpretation is that the observed phenotypic similarities likely reflect shared ancestry rather than phenotypic convergence. Current genetic evidence is inconclusive, as it both demonstrates that negrito populations have genetic affinities with neighboring populations but also rare and ancient variation that suggests considerable isolation. This study investigates the skeletal phenotype of Andaman Islanders and Aeta foragers from the Philippines in the context of the phenotypic variation among other hunter-gatherers globally, to test whether they show a common, unique physique apart from small body size. Particular emphasis is placed on the comparison of negrito phenotypes to African, Asian, and Australian hunter-gatherer diversity to investigate phenotypic similarities to other populations globally. The results demonstrate that despite sharing small adult stature, the Andaman Islanders and Aeta show variation in body dimensions. In particular, the Andaman Islanders share a pattern of narrow bi-iliac breadth and short upper limbs with the Khoisan (Later Stone Age Southern Africans), whereas the Aeta and Efé show broader bi-iliac breadths relative to lower limb lengths. Although general similarities in size and proportions remain between the Andamanese and Aeta, differences in humero-femoral indices and arm length between these groups and the Efé demonstrate that there is not a generic "pygmy" phenotype. Our interpretations of negrito origins and adaptation must account for this phenotypic variation.

## **Keywords**

Body Proportions, Phenotypic Variation, Human Adaptation, Plasticity

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## ***The Skeletal Phenotype of “Negritos” from the Andaman Islands and Philippines Relative to Global Variation among Hunter-Gatherers***

JAY T. STOCK<sup>1</sup>

*Abstract* The “negrito hypothesis” suggests that populations of small-bodied foragers in South and Southeast Asia who share common phenotypic characteristics may also share a common, ancient origin. The key defining characteristics of the “negrito” phenotype, small body size, dark skin, and tightly curled hair, have been interpreted as linking these populations to sub-Saharan Africans. The underlying assumption of this interpretation is that the observed phenotypic similarities likely reflect shared ancestry rather than phenotypic convergence. Current genetic evidence is inconclusive, as it both demonstrates that negrito populations have genetic affinities with neighboring populations but also rare and ancient variation that suggests considerable isolation. This study investigates the skeletal phenotype of Andaman Islanders and Aeta foragers from the Philippines in the context of the phenotypic variation among other hunter-gatherers globally, to test whether they show a common, unique physique apart from small body size. Particular emphasis is placed on the comparison of negrito phenotypes to African, Asian, and Australian hunter-gatherer diversity to investigate phenotypic similarities to other populations globally. The results demonstrate that despite sharing small adult stature, the Andaman Islanders and Aeta show variation in body dimensions. In particular, the Andaman Islanders share a pattern of narrow bi-iliac breadth and short upper limbs with the Khoisan (Later Stone Age Southern Africans), whereas the Aeta and Efé show broader bi-iliac breadths relative to lower limb lengths. Although general similarities in size and proportions remain between the Andamanese and Aeta, differences in humero-femoral indices and arm length between these groups and the Efé demonstrate that there is not a generic “pygmy” phenotype. Our interpretations of negrito origins and adaptation must account for this phenotypic variation.

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KEY WORDS: BODY PROPORTIONS, PHENOTYPIC VARIATION, HUMAN ADAPTATION, PLASTICITY.

The indigenous inhabitants of the Andaman Islands, the Agta, Aeta, Mamanwa, and Zambales of the Philippines, and the Semang of the Malay Peninsula have frequently been considered to be “negrito,” due to their short stature, dark skin, and “frizzy” hair (Barrows 1910; Banerjee et al. 1984; Hanihara 1989; Bhasin et al. 1994). These phenotypic similarities among negrito hunter-gatherer populations of Southeast Asia have led to a long-standing speculation that these groups share a common, ancient ancestry. Although these populations are separated by considerable geographic distance, they share common physical features that are often presumed to be the result of common ancestry.

The negrito populations are characterized by small body size, dark skin, and tightly curled hair that is unusual within the context of phenotypic variation within Southeast Asia. Early genetic research in the 1980s linked these groups closely to other Asian populations and suggested that they were not closely related to Africans (Omoto 1984). Subsequent research using mitochondrial DNA (mtDNA) variation provided evidence for a link between negrito groups of the Andaman Islands and sub-Saharan African foragers (Mukerjee 1999). More recent research has enhanced our understanding of the genetics of this group, suggesting that genetic variation among the Andaman Islanders may reflect considerable isolation of this population following initial dispersal out of Africa (Thangaraj et al. 2003, 2006; Thangaraj and Chaubey 2005). Although this plausibly fits an interpretive framework where the Andaman Islanders and other negrito populations represent relict populations of this early dispersal, recent evidence suggests that genetic variation among negritos is complex (Reich et al. 2009). The genetic evidence for negrito origins now illustrates the complex population histories of these populations, which at once show that they share genetic variation with other populations in their immediate surroundings while possessing more “ancient” genetic variants that attest to some level of long-term isolation (Barik et al. 2008; Chaubey and Endicott this issue).

Although future genetic research will further clarify the relationships between these South and Southeast Asian populations, the phenotypic similarities of negritos remain a question of interest. The “negrito hypothesis” was initially formulated to explain observed phenotypic similarities: small body size, dark skin, and tightly curled hair. However, the majority of research has used genetic approaches without reconsidering whether the phenotypic basis for the hypothesized links among negrito groups is more systematic than similarities in body size, skin color, and characteristics of hair. In recent years our understanding of the mechanisms influencing human phenotypic variation has improved considerably, with evidence for both genetically conservative variation and phenotypic plasticity in expression of traits (for reviews, see Stock 2012; Wells and Stock 2007, 2011). This article provides the first comparison of human postcranial skeletal variation to test whether two negrito populations, the Andaman Islanders and the Aeta of the Philippines, show a pattern of skeletal variation that is unique among small-bodied hunter-gatherers, thus providing evidence of a distinctive postcranial skeletal phenotype. Here, Andaman Islander and Aeta postcranial osteometric data are

compared with a globally representative range of hunter-gatherer populations to investigate whether there are common features of the negrito phenotype beyond small body size.

**Negrito Populations and Their Origins.** There are several plausible models to account for the origins of the negritos. A classic anthropological interpretation suggests that negritos are the only surviving descendants of the first human occupants of southern Asia (Bhasin et al. 1994; Myka 1993). This model, based initially upon the physical similarities between the negritos and African “pygmies” and Bushmen (Howells 1973), suggests that the negritos are the direct descendants of African populations who were replaced in most areas by subsequent migrations into Southeast Asia (Carey 1976). This would likely place the origin of the negritos prior to occupation of Melanesia and Australia, around 5 kya. In an earlier model, Coon (1965) proposed that the negritos were a subpopulation of his “Australoid” population, which inhabited much of Southeast Asia during the last glaciation. He suggested that the phenotypic similarities of the negritos to sub-Saharan Africans were the result of adaptation to similar environments. It is also possible that the negritos are descended from other Southeast Asian or Oceanic populations, with distinctive characteristics evolving in the past several thousand years through isolation and convergent adaptation in response to similar environmental conditions and subsistence strategies (tropical rain forest hunter-gatherers), thus leading to similarities with small-bodied African populations.

However, archaeological evidence for the early occupation of the Andaman and other Southeast Asian Islands is lacking, due to the poor conditions for organic preservation in tropical rain forests. Although several authors have argued for the great antiquity of occupation in the Andaman Islands (Radcliffe-Brown 1964; Cipriani 1962; Dutta 1963), the oldest radiocarbon date from an archaeological context is  $2,280 \pm 90$  years ago (Cooper 1993). This does not necessarily refute the possibility of earlier settlement, but it provides no empirical support of it. Regardless of the approach taken to test these models, results are confounded by the recent history and small size of these populations. Among the Andaman Islanders, the Great Andaman tribe has approximately 30 remaining individuals, the Onge fewer than 100, and the Jarawa approximately 200 (Myka 1993; Stock and Migliano 2009). The populations of the Semang and Aeta are larger, but so is the potential for recent gene flow from surrounding populations.

Despite and perhaps in light of these caveats, the genetic evidence for the origins of the negrito groups is suggestive of both ancient lineages and uniqueness of these populations, but also of closer relationships with neighboring populations than would be expected of an “isolation” model. Early analyses of Aeta mtDNA demonstrated that their maternal genetic diversity is broadly similar to that of other Asian groups but is distinct on the basis of several morphs, with low affinity to African populations (Harihara et al. 1988). Later work suggested that the presence of a 9-base-pair (9-bp) deletion in high frequencies among the Aeta is suggestive of a genetic relationship with the populations of Polynesia and Micronesia (Harihara et

al. 1992). This variability supports a model in which the early original inhabitants of Melanesia and Australia arrived at least 40 kya without the 9-bp deletion, with a migration of individuals carrying the 9-bp deletion through Melanesia sometime in the last 5,000 years (Hagelberg et al. 1999). However the 9-bp deletion is highly variable in frequency and occurs on different haplogroup backgrounds to haplogroup B, which contains the dominant Polynesian mtDNA, suggesting that interpretations should be made with extreme caution (Watkins et al. 1999). Matsumoto et al. (1999) found that three distinct Gm haplotypes among the Aeta and Zambales of the Philippines link these groups to Asian populations, although one specific haplotype was found to be prevalent among these groups and those of Africa, New Guinea, and North Australia populations. A study of HLA antigens among the Aeta and Mamanwa found similarities with other Asian groups and differences in specific antigens compared with Europeans and Africans (Horai et al. 1981). Further variation in red cell enzymes (CA<sub>1</sub>, AK, and ESD) and serum proteins among the Aeta and Mamanwa have demonstrated rare variants among these populations (Omoto et al. 1978; Omoto 1980; Mitsui et al. 1992), although the interpretation of this variation is challenging.

There is some evidence that genetic variation among the Andaman Islanders may reflect considerable isolation following initial dispersal out of Africa (Kashyap et al. 2003; Thangaraj et al. 2003, 2006; Thangaraj and Chaubey 2005). Although this plausibly fits an interpretive framework where the Andaman Islanders and other negrito populations represent relict populations of this early dispersal, recent evidence suggests that genetic variation among these populations is much more complex than previously thought (Reich et al. 2009). Current genetic evidence is beginning to highlight more recent relationships between negrito populations and other, non-negrito populations in the same region, while maintaining some evidence for deeper genetic roots of these populations (Barik et al. 2008; Chaubey and Endicott this issue). These deep lineages may not reflect a common ancestry concurrent with the dispersal out of Africa, as predicted by the negrito hypothesis, but a degree of long-term genetic isolation from neighboring populations. The first study to integrate genotype and phenotype data of a negrito population (Migliano et al. this issue) suggests that, based on genetic variation, the Aeta, Batak, and Agta cluster with other South Asian populations and that their small body size evolved independently of other pygmy populations in Africa or Papua New Guinea.

The different models of negrito origins have implications for our understanding of phenotypic variation. An early and common ancestry of these groups implies a very long period of morphological stasis characterized by the negrito and African pygmy/bushman pattern of small body size and dark skin. Genetic similarities would have to be accounted for by founder effect and long-term canalization of phenotypic traits, or convergent evolution occurring over tens of thousands of years. Recent convergence from local populations would predict relatively rapid morphological change of either the Polynesians, from a “negrito-like” ancestor, or the negritos, from a morphologically Polynesian ancestor. Morphological similarities among Polynesians, combined with relative genetic homogeneity, suggest that the recent

origin model of the negritos must account for their distinctive phenotype through convergence, based upon one of two different models: (a) recent natural selection among the negritos in their respective environments or (b) phenotypic plasticity and relatively rapid change in the phenotypic characteristics in question.

**Skeletal and Dental Morphology.** Several studies have investigated morphological affinities of negrito populations on the basis of dental morphometrics and crown morphology, which are under tight genetic control. Hanihara (1989, 1990, 1992) demonstrates that the Aeta are similar to the Semang negritos and share the Sundadont dental pattern that is closely related to other Asian populations (Hanihara 1989). He later suggested that their crown morphology is specifically "proto-Sundadont" and shared with the Australians, which he interpreted as indicative of common ancestry (Hanihara 1992). This research is contradicted somewhat by a study of the crown morphology of living Andamanese (Pal 1987), which suggests that their dental morphology was intermediate between that of African and Asian populations; however, the emerging evidence suggests that Andamanese dental morphology most closely resembles variation within South Asia (Bulbeck this issue). Research on dental nonmetric traits of the Batak place this population within the Southeast Asian "Sundadont" pattern (Turner and Eder 2006).

Early craniometric studies of the Aeta, Semang, and Andamanese have illustrated a closer affinity of the negritos with Southeast Asian populations rather than Australian Aborigines (Hanihara 1993). A recent investigation of South Asian craniofacial variation within the context of global diversity revealed a relatively unique position of the Andaman Islanders (Stock et al. 2007), who were morphologically distinct from other South Asian populations, including the Vedda, while still situated broadly within the range of variation found within the Indian subcontinent. This would seem to suggest that the Andamanese morphology is best interpreted as linked to the genetic history of South Asia. A more recent and systematic analyses of craniofacial variation among negrito populations suggests that the Andaman Islanders share closer affinities to African populations than they do to Asian (Bulbeck this issue). Although these studies differ in aims, methods, analyses, and interpretations, neither directly support a model of common, ancient ancestry between the Andaman Islanders and other negritos.

**Variation in Human Phenotype, and among Negrito Populations.** Relationships between climate and mammalian body form, such as those described by Bergmann's (1847) and Allen's (1877) rules, are relatively consistent among all mammals. Both Bergmann's and Allen's rules refer to the relationship between surface area and body mass, which tends to be higher in species inhabiting hot climates and lower in species from cold climates. Within humans, stature, limb lengths, body mass, and body linearity show approximate clinal distributions, varying with mean annual temperatures (Roberts 1978; Eveleth and Tanner 1990; Katzmarzyk and Leonard 1998). Human body mass and the ratio of sitting height to stature appear to be negatively correlated with mean temperatures

(Roberts 1978). Although there is variability in human stature within different climates, body breadth appears to be more tightly correlated with temperature. Body breadth is an important factor in human adaptation to climate, due to the relationship between body breadth and the surface-to-volume ratio (Ruff 1991, 1994). Using a cylindrical model to approximate human surface area and volume, the ratio of surface area to volume stays the same for a given breadth, regardless of the height of the cylinder (Ruff 1991, 1994). This trend is highlighted by the observation that tropical populations may have either tall or short stature, but this is generally accompanied by narrow pelvises (Hiernaux 1975) as variation in body breadth has much greater effect on surface-area-to-volume ratios than does variation in stature (Ruff 1994). Despite this apparent relationship to climate, there is emerging evidence that bi-iliac breadth (BIB) (Auerbach 2012) and other aspects of pelvic morphology (Betti et al. 2013) are relatively canalized and reflective of population history. This suggests that pelvic morphology may track either neutral genetic history (Auerbach 2012; Betti et al. 2013) or previous adaptation (Auerbach 2012).

Limb proportions, approximated by brachial and crural indices, also correlate with mean annual temperatures. High brachial and crural indices indicate longer distal limb segments of the arm and leg, respectively. They tend to be higher in people of the tropics, where there is a higher mean annual temperature (Trinkaus 1981), a trend that has most commonly been interpreted in relation to Allen's (1877) rule and thermoregulatory constraints. The small physique of modern pygmies and negritos is less linear than the that of Nilotic Africans, and the limb lengths are relatively shorter, but small body size also results in a high surface-area-to-mass ratio, as well as lower metabolic rates and heat production. This suggests that both may be adaptations to heat stress, but in humid and dry environments, among pygmies and Nilotic Africans, respectively.

There is considerable global variation in human body size and proportions, some of which has been interpreted as phylogenetically conservative and heritable (Holliday 1997; Holliday and Falsetti 1999; Pearson 2000; Holliday and Ruff 2001), thus providing information about long-term adaptation to environmental variation. Most recent analyses continue to interpret variation in human limb proportions as being adaptive in response to environmental stress (Temple et al. 2008) and relatively stable throughout development (Cowgill et al. 2012). This sits somewhat at odds with evidence for plasticity of human body size and limb proportions (Tanner et al. 1982; Bogin et al. 2002), and evidence that environmental plasticity of many phenotypic characteristics can influence heritability estimates (Wells and Stock 2011). A comparison of variation in physique among the Andaman Islanders and Later Stone Age (LSA) Southern Africans (Khoisan) demonstrates that these populations share small body size and adaptations characteristic of other low-latitude populations (Kurki et al. 2008); however, it is unclear whether other negrito populations share these phenotypic characteristics. There is evidence that the very first humans to occupy Southeast Asia had very small adult body size (Détroit et al. this issue). This underscores the importance of our understanding of

the mechanisms that drive body size variation within our species and the extent to which size correlates with other phenotypic characteristics.

Phenotypic similarities between specific groups inspired the negrito hypothesis, yet much of this variation can be seen to be relatively superficial: dark skin and hair pigmentation, tightly curled or peppercorn hair, and small body size. These characteristics may reflect common ancestry, but they may also be evolutionarily convergent; phenotypically “plastic” and hence convergent due to recent environmental similarities; or morphologically “integrated” as pleiotropic effects acting upon other traits (Wells and Stock 2011). Research by Bulbeck (this issue) suggests that there is phenotypic variation among negritos. However, testing hypotheses about negrito variation is complicated by several factors: (a) very few studies have provided new original phenotypic data; (b) where data exist, it is very difficult to obtain comparable data from other negrito groups; and (c) we still know very little about the mechanisms that control the human phenotype, genetic or otherwise.

This study extends our understanding of phenotypic similarities among negrito populations, by comparing postcranial skeletal variation between Andaman Islanders and Aeta negritos from the Philippines with a globally representative range of hunter-gatherers. Of particular interest is the comparison of these groups with LSA foragers from Southern Africa (ancestral to Khoisan-speaking peoples), LSA populations from East Africa, Central African pygmies (Efé) from the Congo, and hunter-gatherers from Australia and Tasmania, as each of these regions has been invoked in models of negrito origins.

At present we know very little about the relationship between genetic variation and human phenotypic variation. Genetic studies provide the best evidence for the population history of these groups; however, morphological data may either correlate strongly with genetic data where it tracks neutral variation (Betti et al. 2013) or differ where it tracks adaptation or plasticity (Stock 2006). In this context, it is premature to invoke a direct relationship between general phenotypic data and genetic phylogenies, as morphological similarities between negrito groups could reflect ancient common ancestry and neutral genetic variation combined with “canalization” of traits, recent convergent evolution in response to similar environmental stresses, or plasticity in response to environmental conditions over several generations or within the life span. In this context, this study does not directly address questions of population history; rather, it asks whether phenotypic similarities among negrito populations extend to general aspects of physique and limb proportions. In other words, are there more phenotypic similarities between negrito groups than body size?

Although small body size has been considered a central feature of the typical negrito phenotype, our current understanding of the mechanisms controlling body size is inconclusive. There is considerable evidence for genetic factors influencing the body size of pygmies (Becker et al. 2011), but human body size also shows considerable plasticity in response to environmental variation (Wells and Stock 2011; Stock 2012). Life history parameters appear to be involved in the mechanisms

that influence size variation (Migliano et al. 2007), and they may be a factor driving variation in size between generations of Andaman Islanders (Stock and Migliano 2009) and Barinneans. This study compares basic skeletal indicators of phenotype among a global range of hunter-gatherers to examine whether the Andaman Islanders and Aeta show unique characteristics of body size compared with other modern human foragers. If consistent morphological similarities are found, it implies that similar biological mechanisms influence the human phenotype, whether they are canalized or plastic. The identification of variation among the negritos and other small-bodied foragers would suggest that their small size may be convergent and subject to developmental plasticity, or at least responsive to local conditions or population history.

## Materials and Methods

Osteometric data representing humeri, radii, ulnae, ossa coxae, femora, and tibiae were compared and used to calculate indices that represent commonly used body dimensions and ratios. Skeletal samples used in this study are presented in Table 1. Skeletal measurements of one Tasmanian, four “Eastern pygmies,” and 16 Philippine “negritos” were provided by Auerbach and Ruff (2004, 2006); the remainder were measured by the author. The pygmy samples most likely represent the Efé, based upon their geographical provenance, whereas the Philippine negritos were derived from southern Luzon (Genet-Varcin 1951) and most likely represent Aeta foragers. They will be referred to as the “Efé” and “Aeta” in the text, although these attributions should be treated with caution. Univariate measures of skeletal dimensions were first compared using analysis of variance, with Games-Howell post hoc tests for population level differences. This test, which does not assume equal variances, is useful because of the differences in sample sizes between populations. Many of the populations include individuals of indeterminate sex. Because sexual dimorphism is lower in magnitude than population-level differences, and relatively consistent across populations, the sexes have been pooled in univariate analyses to test for population-level differences. However, population-specific sex ratios were used to weight the data in all analyses, to ensure that uneven sex ratios did not bias the results. A Bonferroni correction was used to adjust the confidence intervals for multiple pairwise comparisons of populations. Box and scatter plots of individual variables by population, however, illustrate differences between sexes and those individuals of indeterminate sex, for each population. To investigate more general patterns of skeletal variation within the limbs, canonical variates analysis was used.

## Results

Initial comparisons are provided using analysis of variance and Games-Howell post hoc tests to explore variation in skeletal dimensions, which provides information about general variation in body size and form. Tables 2 and 3 summarize results of post hoc pairwise comparisons between Andaman Islanders and Aeta, respectively.

**Table 1. Samples Used in This Study**

POPULATION	SUBSISTENCE CONTEXT	N	SEX <sup>a</sup>			REFERENCE
			M	F	IND.	
Aeta negrito, Luzon, Philippines	Hunter-gatherer	16	11	5	0	Goldman data set (Auerbach and Ruff, 2004, 2006)
Australian Aborigine	Hunter-gatherer	31	9	6	16	Present study
Andaman Islanders	Hunter-gatherer- fisher	38	19	19	0	Stock and Pfeiffer 2001; Stock 2006
Archaic, Great Lakes, Canada	Hunter-gatherer	20	9	7	4	Stock 2006
Eastern (Efé) pygmy, Congo	Hunter-gatherer	4	2	2	0	Auerbach and Ruff, 2004, 2006
Egyptian, Predynastic Early	horticulturalist	10	3	3	4	Stock et al. 2011
Epipaleolithic (early- middle), Levant	Hunter-gatherer	5	0	2	3	Stock et al. 2005
Fuegian (Yahgan), Tierra del Fuego	Protohistoric hunter-gatherer- fisher	47	23	16	8	Stock 2006
Iberomaurusian, North Africa	Hunter-gatherer	94	22	12	59	Present study
Inuit, Canada	Hunter-gatherer- fisher	46	20	18	8	Present study
Jebel Sahaba	Hunter-gatherer	18	7	3	8	Stock et al. 2011
Jomon, Japan	Hunter-gatherer- fisher	44	19	14	11	Present study
Kitoi, Siberia	Hunter-gatherer- fisher	59	33	19	7	Stock et al. 2010
LSA, Kenya	Hunter-gatherer	30	9	8	13	Present study
LSA, Southern Africa	Hunter-gatherer	64	30	32	2	Stock and Pfeiffer 2001; Stock 2006
LSA, Tanzania	Hunter-gatherer	17	2	4	11	Present study
Masai, Tanzania	Pastoralist	12	11	1	0	Stock 2006
Mesolithic, France	Hunter-gatherer- fisher	8	5	3	0	Present study
Natufian (late Epipaleolithic), Levant	Hunter-gatherer	34	14	8	12	Stock et al. 2005
Nubian, Sudan	Agriculturalist	28	12	13	3	Stock et al. 2011
Serovo-Glazkovo, Siberia	Hunter-gatherer- fisher	37	19	17	1	Stock et al. 2010
Tasmanian	Hunter-gatherer	2	2	0	0	Present study; Goldman data set (Auerbach and Ruff, 2004, 2006)

All data were collected by author except those cited as Auerbach and Ruff (2004, 2006).

<sup>a</sup>M, male; F, female; Ind., indeterminate sex.

**Table 2. Andaman Islander Mean Phenotypic Measurements**

Population	Phenotypic Measurement <sup>a</sup>												
	FXL	TXL	FHD	BIB	ARM	LEG	BRACH	CRUR	FHD:FXL	HUM:FEM	ARM:LEG	BIB:FXL	BIB:CRUR
Andaman Islander													
Mean	384.3	324.9	37.81	207.7	488.1	706.4	80.7	85.2	9.84	70.3	68.7	52.43	2.32
SD	17.01	14.18	2.53	15.13	26.87	30.37	3.83	1.86	0.577	3.11	2.12	4.24	0.119
N	31	29	31	15	28	29	28	29	31	31	26	9	8
<i>p</i> -Values <sup>b</sup>													
Aeta, Philippines	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	.043	.003
Efé pygmy, Congo	NS	NS	NS	NS	NS	.048	NS	NS	NS	.001	.007	.015	.046
Aborigine, Australia	.019	NS	NS	.001	NS	NS	NS	NS	.010	NS	NS	NS	.001
Archaic, Great Lakes	.001	.001	.001	NS	.002	.003	NS	NS	NS	NS	NS	NS	NS
Egyptian, Predynastic	NS	—	NS	—	—	—	—	—	NS	NS	—	—	—
Epipaleolithic	NS	NS	NS	—	NS	NS	NS	NS	NS	NS	NS	—	—
Fuegian	NS	NS	.002	.001	NS	NS	NS	NS	.001	.022	NS	.001	.001
Iberomausian	.001	.001	.001	.001	.001	.001	NS	NS	.001	NS	NS	NS	.008
Inuit	.001	NS	.001	.001	NS	.002	.001	.001	.001	NS	NS	.001	.001
Jebel Sahaba	.005	—	.032	—	NS	—	NS	—	NS	NS	—	—	—
Jomon	.001	.005	.001	.001	NS	.001	NS	NS	.026	NS	NS	.005	.001
Kitoi	.001	.001	.001	.001	.001	.001	.004	.001	.001	NS	.010	.010	.001
Later Stone Age (LSA), Kenya	.001	.001	.014	—	.001	NS	NS	NS	NS	NS	NS	—	—
LSA, Southern Africa	.001	.001	NS	NS	NS	.001	.004	NS	NS	NS	NS	NS	NS
LSA, Tanzania	NS	—	NS	—	—	—	—	—	—	—	—	—	—
Masai, Tanzania	.050	.016	NS	NS	—	.009	—	NS	NS	NS	—	NS	.004
Mesolithic, France	.019	NS	.014	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Natufian	.001	NS	.001	NS	.005	.030	.027	NS	NS	NS	NS	—	—
Nubian, Sudan	.001	.001	.001	—	.001	.001	NS	NS	NS	NS	NS	—	—
Serovo/Glazkovo	.001	.001	.001	.001	.001	.001	.003	.001	.017	NS	NS	.014	.001
Tasmanian	—	—	—	—	—	—	—	—	—	—	—	—	—

<sup>a</sup>Measurement abbreviations: FXL, femur maximum length; TXL, tibia maximum length; FHD, femoral head diameter; BIB, bi-iliac breadth; ARM, arm length; Leg, leg length; Brach, brachial index; Crur, crural index.

<sup>b</sup>*p*-Values are for comparisons with other populations. All reported *p*-values indicate significant results of Games-Howell pairwise post hoc comparisons. NS, nonsignificant; —, sample size too low to allow pairwise comparison.

**Table 3. Aeta Mean Phenotypic Measurements**

Population		Phenotypic Measurement <sup>a</sup>													
		FXL	TXL	FHD	BIB	ARM	LEG	BRACH	CRUR	FHD:FXL	HUM:FEM	ARM:LEG	BIB:FXL	BIB:CRUR	
Aeta		379.4	322.4	36.73	223.8	480.3	699.3	77.57	85.81	9.67	71.4	68.8	60.12	2.62	
Mean		21.48	20.49	3.49	6.75	27.89	42.1	2.23	1.45	5.93	1.29	1.43	4.09	0.081	
SD		15	16	15	10	16	15	16	15	15	15	14	9	9	
N															
<i>p</i> -Values <sup>b</sup>															
Andaman Islanders		NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	.043	.003	
Efé pygmy, Congo		NS	NS	NS	NS	NS	NS	NS	NS	NS	.001	.011	NS	NS	
Aborigine, Australia		.010	NS	NS	.001	NS	.047	NS	NS	NS	NS	NS	NS	.001	
Archaic, Great Lakes		.001	.001	.001	NS	.001	.001	NS	NS	NS	NS	NS	NS	NS	
Egyptian, predynastic		NS	—	NS	—	—	—	—	—	NS	NS	—	—	—	
Epipaleolithic		NS	NS	NS	—	NS	.928	NS	NS	NS	NS	NS	—	—	
Fuegian		NS	NS	.005	.001	.047	.837	NS	NS	.002	NS	NS	NS	.001	
Iberomantuan		.001	.001	.001	.001	.001	.001	NS	NS	.005	NS	NS	NS	.048	
Inuit		.001	NS	.001	.001	NS	.013	.001	.001	.001	NS	NS	NS	.001	
Jebel Sahaba		.001	—	.013	—	NS	—	NS	—	NS	NS	—	—	—	
Jomon		.005	NS	.001	.004	NS	.022	NS	NS	.035	.007	NS	NS	.001	
Kitoo		.001	.033	.001	.001	.001	.002	NS	.001	.013	NS	.012	NS	.001	
Later Stone Age (LSA), Kenya		.001	.001	.005	—	.001	.036	NS	NS	NS	NS	NS	—	—	
LSA, Southern Africa		.013	.043	NS	.035	NS	.038	NS	NS	NS	NS	NS	.003	NS	
LSA, Tanzania		—	—	NS	—	—	—	—	—	—	—	—	—	—	
Masai, Tanzania		.030	.013	NS	NS	—	.002	—	NS	NS	NS	—	.022	NS	
Mesolithic, France		.011	NS	.005	NS	NS	.047	NS	NS	NS	NS	NS	NS	NS	
Natufian		.001	NS	.001	NS	.002	.006	NS	NS	NS	NS	NS	—	—	
Nubian, Sudan		.001	.001	.001	—	.000	.001	NS	NS	NS	NS	NS	—	—	
Serovo/Glazkovo		.001	.003	.001	.001	.000	.001	NS	.001	.021	NS	NS	NS	.001	
Tasmanian		—	—	—	—	—	—	—	—	—	—	—	—	—	

<sup>a</sup>Measurement abbreviations: FXL, femur maximum length; TXL, tibia maximum length; FHD, femoral head diameter; BIB, bi-iliac breadth; Arm, arm length; Leg, leg length; Brach, brachial index; Crur, crural index.

<sup>b</sup>*p*-Values are for comparisons with other populations. All reported *p*-values indicate significant results of Games-Howell pairwise post hoc comparisons. NS, nonsignificant. —, sample size too low to allow pairwise comparison.

Femur length (Figure 1) and tibia length are among the most highly correlated with stature and body length and show similar patterns across populations. The mean femur length (FXL) of the Efé pygmies (360.6 mm) is the lowest among all of the groups. The Andaman Islander (384.2 mm) and Aeta (379.4 mm) means are also very low compared with other groups. Although they do not significantly differ from the smallest Efé group, or each other, FXL of Andaman Islanders is significantly shorter than all populations with the exception of the Fuegians, Egyptian Predynastic, Epipaleolithic, and LSA Tanzanian samples (the latter three had very small sample sizes). The Aeta FXL showed a similar pattern of significant differences. When tibial length is considered, the Andaman Islander (325 mm) and Aeta (322 mm) means are significantly different from a number of other populations, but there were fewer significant differences than with FXL.

Body mass, a second component of body size, correlates strongly with femoral head diameter (FHD) (Auerbach and Ruff 2004) and bi-iliac breadth (BIB) (Ruff 1994). When we compare FHD among the groups (Figure 2), the Andaman Islanders and Aeta have small values similar to those of the Efé and LSA Southern Africans but significantly different from most other populations. Although the lack of significance of some of these results is driven by the small sample sizes involved, these populations have notably lower body mass than the East African LSA groups and the Australian and Tasmanian Aborigines. Differences in physique and body mass are often driven by variation in body breadth, the best measure of which is BIB. Andaman Islander BIB is the narrowest of all global hunter-gatherers but most similar to the LSA of Southern Africa (Figure 3). The Aeta have BIB measures that are somewhat larger among males and females, but not significantly so. It is noteworthy that, despite their small stature, the Efé have greater bi-iliac breadths than the Andaman Islanders, Aeta, or LSA Southern Africans and that the LSA of Kenya and the two individuals from Tasmania have considerably greater bi-iliac breadths, similar to other hunter-gatherers globally.

Comparisons of lengths of upper limbs (humerus plus radius) and lower limbs (femur bicondylar plus tibia; Figure 4) highlight very similar trends toward shorter limbs and stature among the Andaman Islanders, Aeta, and Efé pygmies. These groups are not significantly different in upper limb length, but the Andaman Islanders have significantly longer lower limbs than the Efé. The Aeta males have somewhat longer lower limbs than the Efé, but a high level of sexual dimorphism among the Aeta is reflected in similar leg lengths between the Aeta women and the Efé. Although there is a variable pattern of significant differences in pairwise comparisons with the other groups, somewhat short leg lengths are also found among the LSA of Southern Africa and the female Fuegians, but not among the Australian or Tasmanian groups.

Intralimb segment lengths (the proportion of distal segment to proximal segment length) are variable among human populations and can be a sensitive indicator of adaptation to climatic environments (Trinkaus 1981; Holliday 1997). Distal limb segments (radii, tibiae) that are shorter relative to proximal elements (humeri, femora) are generally associated with populations adapted to cold climates,

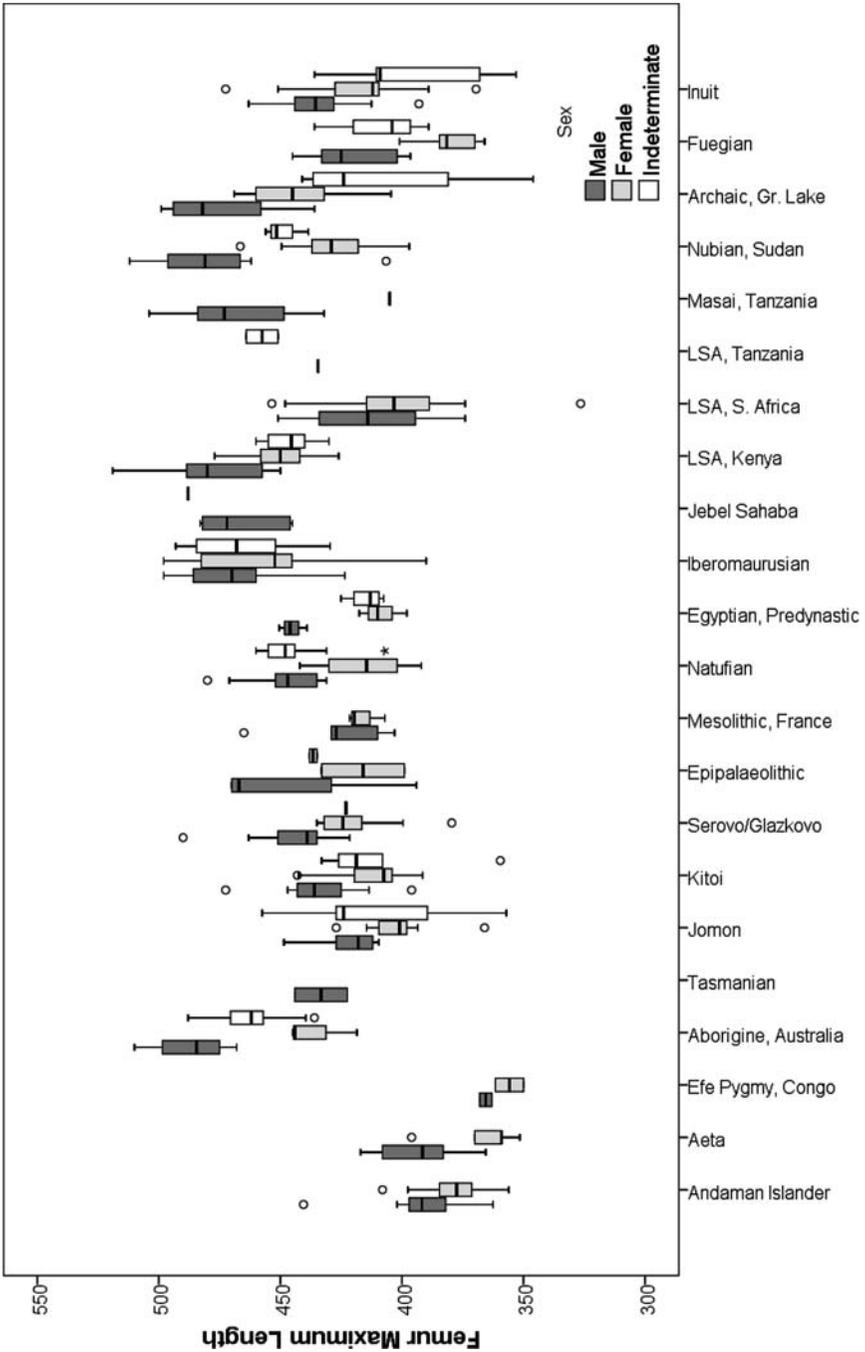
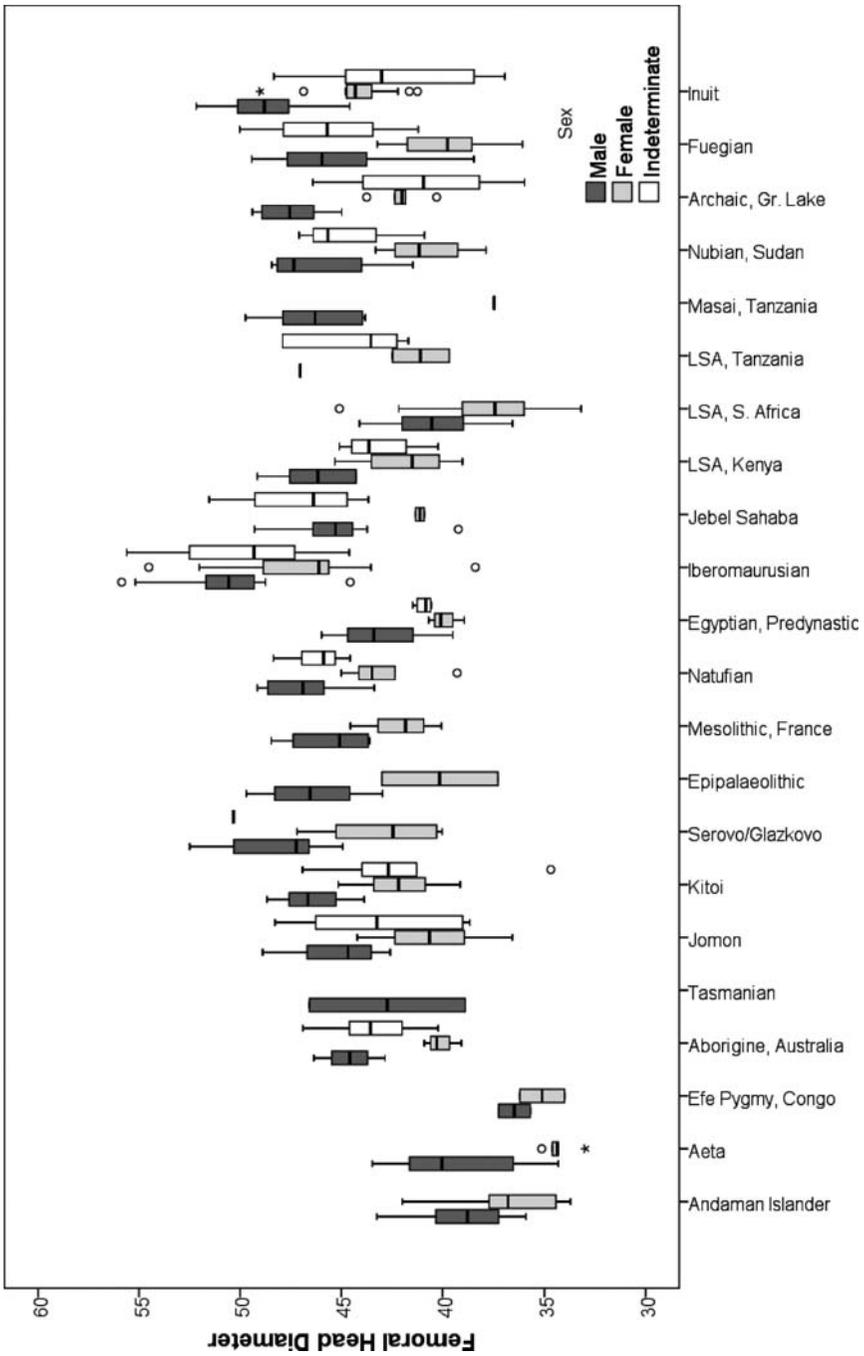


Figure 1. Global variation in femur maximum length among hunter-gatherers and other groups.



**Figure 2.** Variation in femoral head diameter (a proxy for body mass) among hunter-gatherers and other groups.

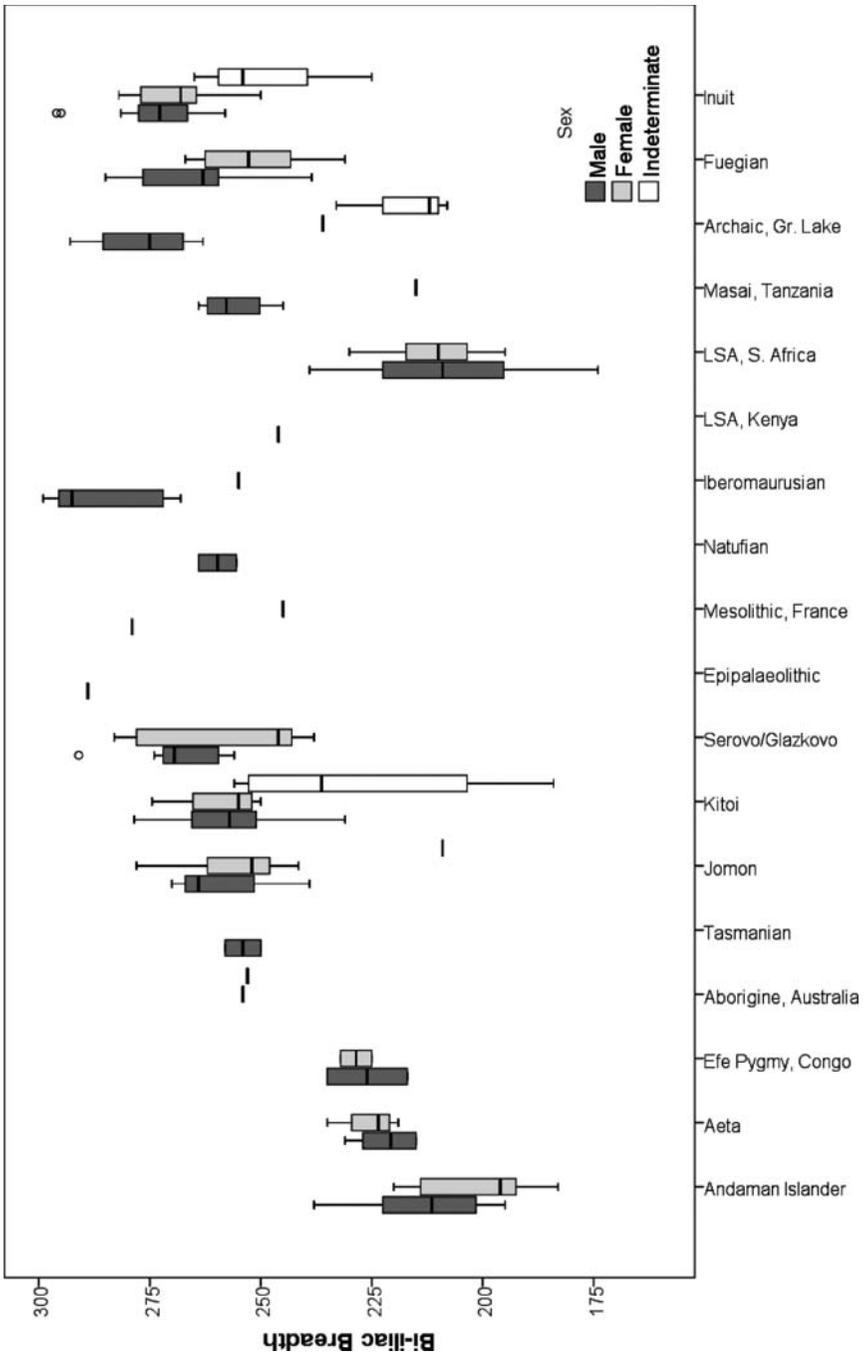
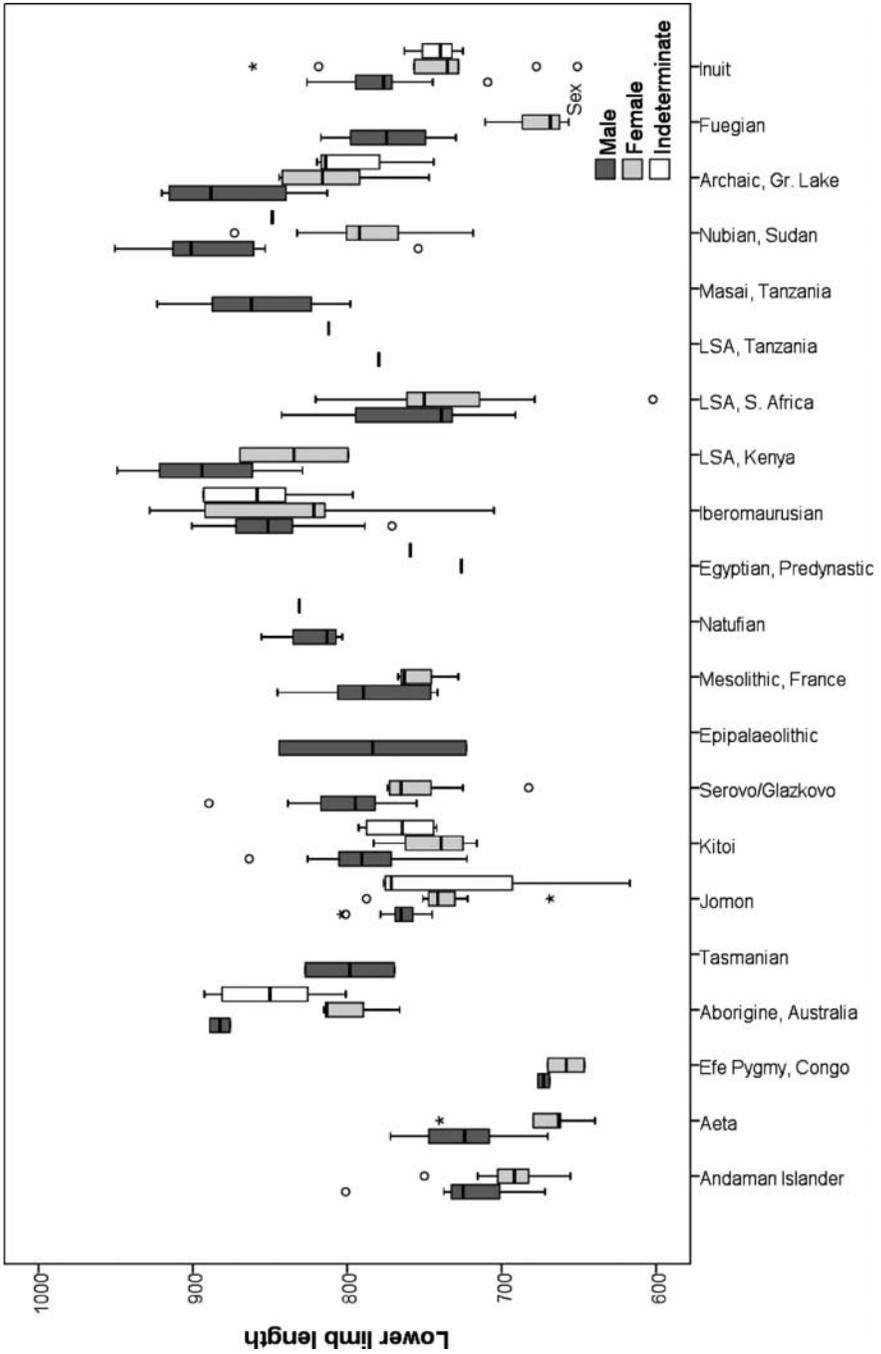


Figure 3. Variation in bi-iliac breadth among hunter-gatherers and other groups.



**Figure 4.** Variation in lower limb length (femur bicondylar length + tibia maximum length) among hunter-gatherers and other groups.

and thus they generally correspond with latitude. The brachial index (radius length / humerus length  $\times$  100) of the Andaman Islanders is quite high (Figure 5), demonstrating that despite having relatively short upper limbs, the Andaman Islanders have proportionately long forearms. The mean brachial index of the Andaman Islanders (80.7) is the highest found among the comparative samples, although this difference is nonsignificant in most cases. Many of the other groups are characterized by much smaller sample sizes, which may be driving the lack of statistical significance. The Aeta and Efé have brachial indices that are broadly similar to other populations and within the ranges exhibited by populations of very different latitudes and body sizes, thus showing a marked contrast with the phenotype of the Andaman Islanders. It is also interesting to note that the Inuit have brachial indices significantly lower than most populations, a likely consequence of living at the highest latitude. The Inuit also have significantly lower crural indices, but in these dimensions the Andaman Islanders, Aeta, and Efé are very similar and within the range exhibited by most other populations. The only pairwise post hoc tests that showed significant differences between populations are those with the Inuit, Kitoi, and Serovo-Glazkovo, all high-latitude populations of central Siberia or the high Canadian Arctic (Tables 2 and 3). This suggests that crural indices do not show any particularly relevant patterning among these populations apart from separating those that are cold adapted. It is more difficult to interpret the unusually high brachial indices of the Andaman Islanders because they appear to be atypical compared with other small-bodied foragers, such as the LSA Southern Africans, who show morphological affinities with the Andaman Islanders in other characteristics.

A range of further, but less commonly used, indices can help investigate phenotypic variation among these populations. The ratio of FHD to femur maximum length (Figure 6) gives an indication of body mass relative to stature. Here, the Andaman Islanders, Aeta, and Efé sit at the very low end of the range of variation found among other hunter-gatherers, because of their small stature and body mass. This is reflected in a predominance of nonsignificant pairwise comparisons for this variable (Tables 2 and 3). Perhaps the main trend is that these “small-bodied” foragers have relatively lower body mass for size than might be predicted from a global regression, whereas some other populations such as the Inuit, Kitoi, Serovo-Glazkovo, and Fuegians have higher body mass relative to stature. Although these groups all inhabit particularly cold climates at high latitudes, the late Pleistocene Iberomaurusians from North Africa also show particularly high body mass relative to FXL.

The ratio of upper limb to lower limb length (Figure 7) and the humerofemoral index were used to investigate the length of the upper limb, and its components, relative to the lower limb. In both cases, there is broad homogeneity among the populations, suggesting that this is a relatively canalized feature of the human phenotype. The one exception is the high values found among the Efé in both comparisons, which differ significantly from both the Andaman Islanders and Aeta.

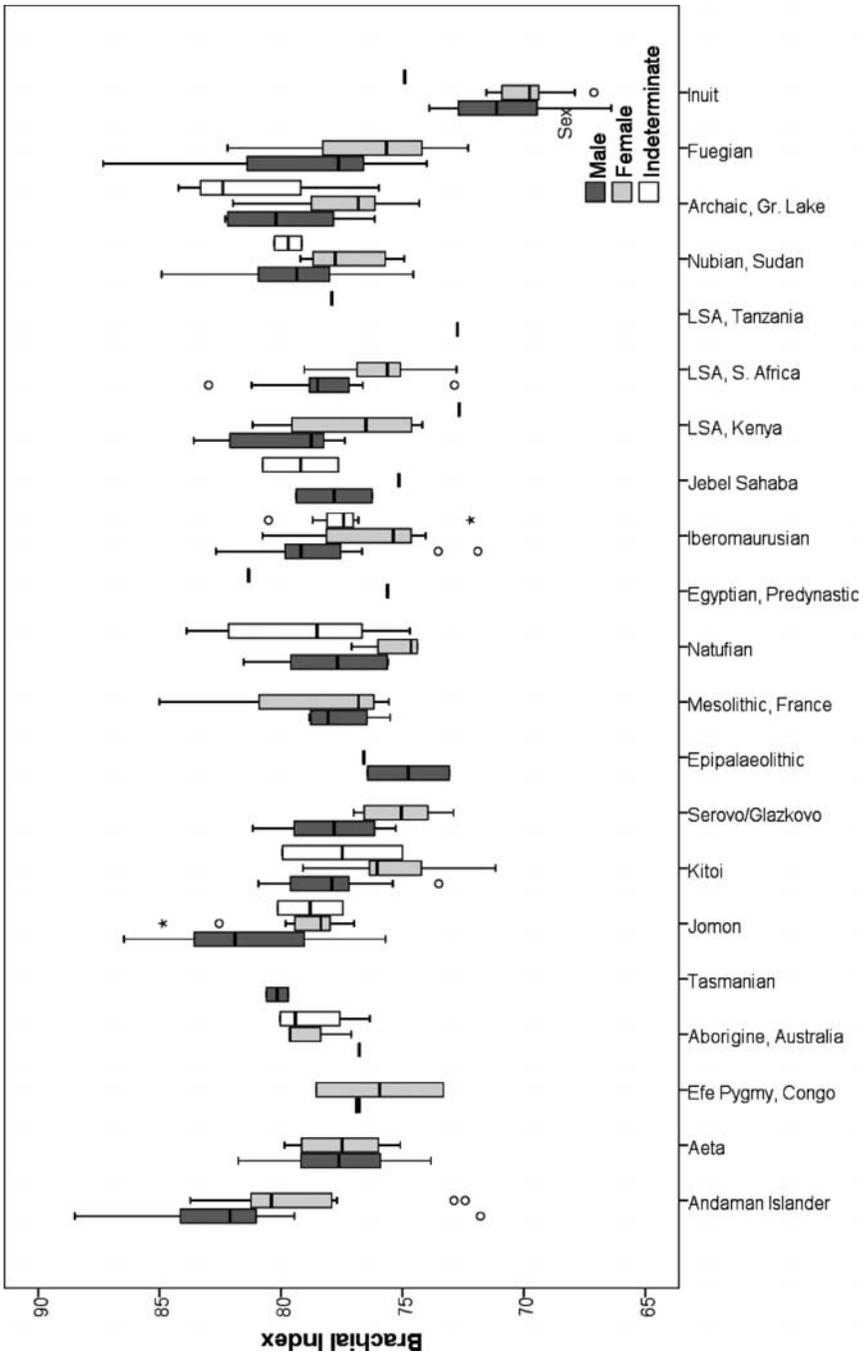
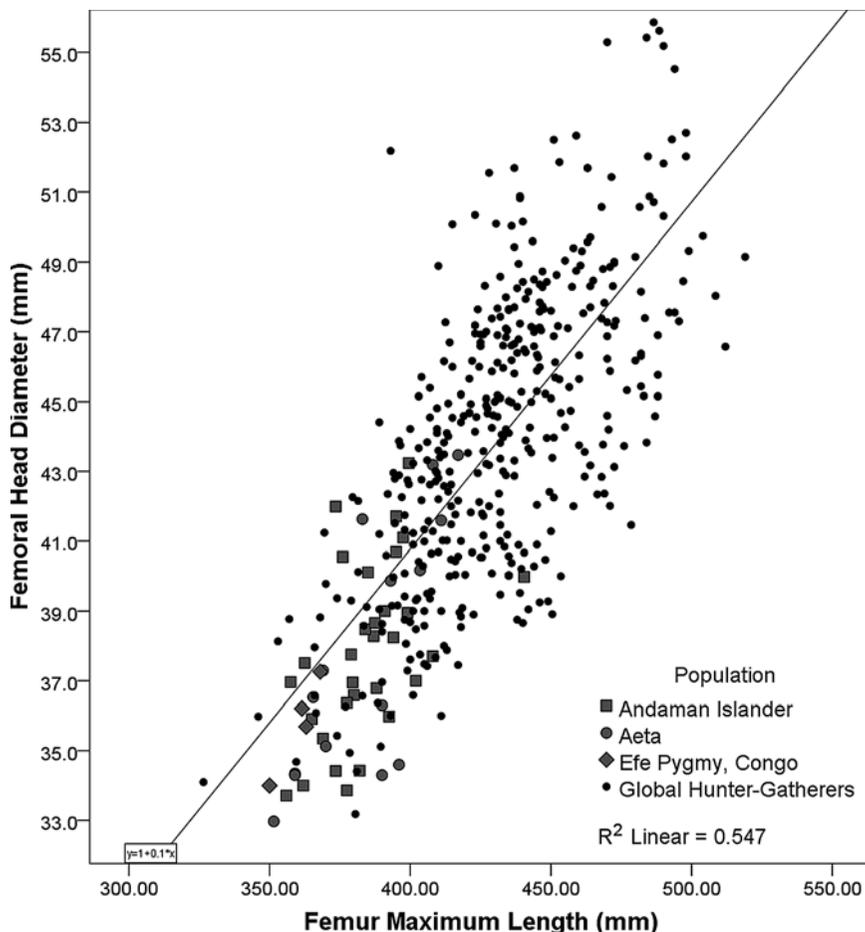
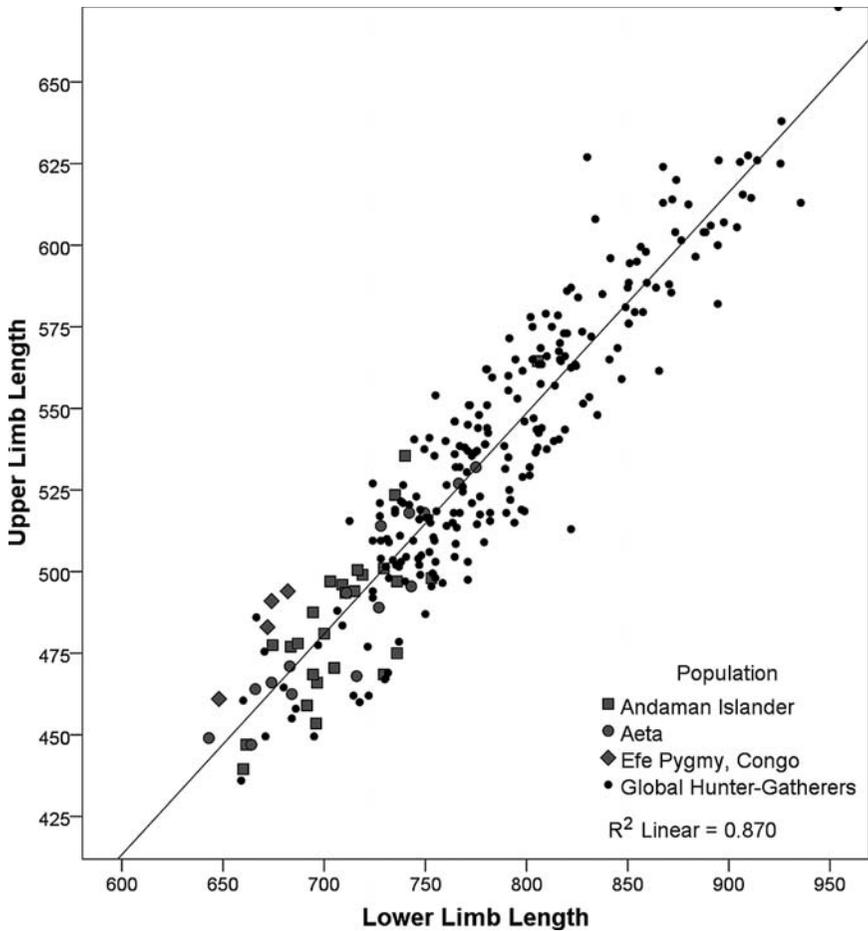


Figure 5. Variation in brachial index among hunter-gatherers and other groups.



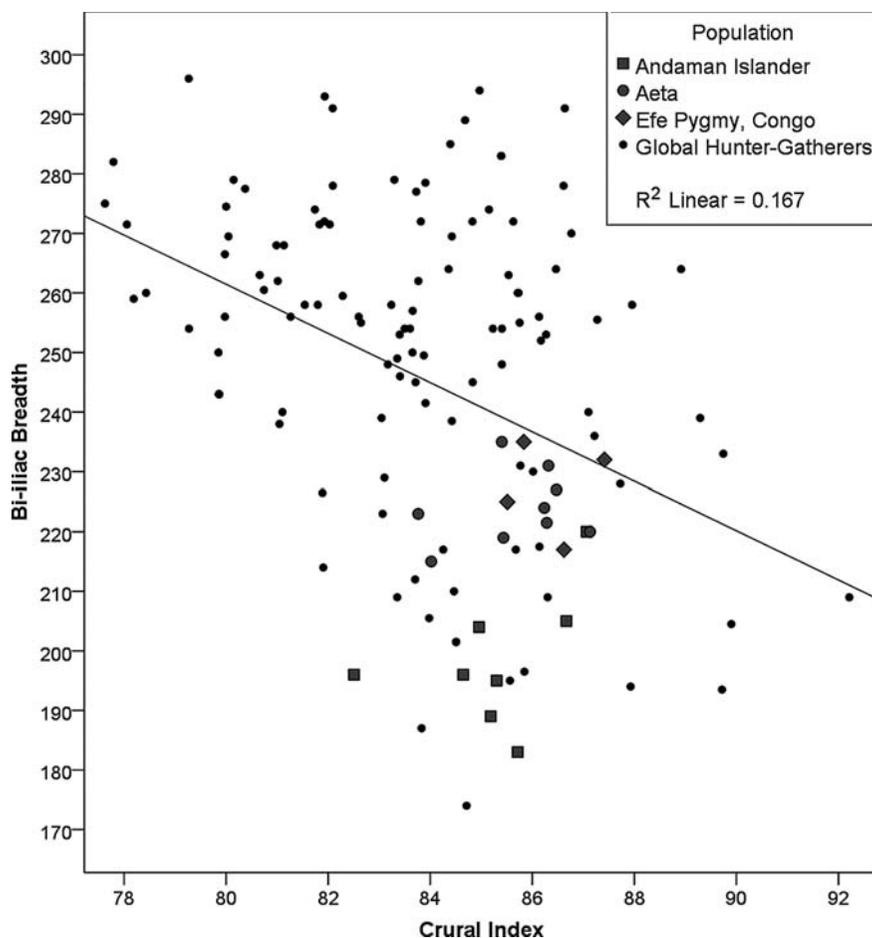
**Figure 6.** Variation in femoral head diameter relative to femur maximum length among hunter-gatherers and other groups.

Finally, two ratios involving BIB were used to investigate relative variation in body breadth. The BIB:FXL ratio provides a general measure of body breadth relative to stature. Here the Andaman Islanders and LSA Southern Africans had smaller ratios than all other groups. Although these differences are nonsignificant in most cases, the Aeta have significantly higher BIB:FXL ratios compared with Andaman Islanders or LSA Southern Africans (Table 3). The BIB:crural index ratio (Figure 8) was used to further investigate variation in body breadth relative to intralimb proportions. In this case there were more significant pairwise differences. Very low values among the Andaman Islanders (representing the combination of a relatively narrow pelvis with proportionately long tibiae) are significantly different from the Aeta and Efé but quite similar to the LSA Southern Africans.



**Figure 7.** Upper limb length relative to lower limb length among hunter-gatherers.

Canonical variates (discriminant) analysis of phenotypic parameters used in the previous analyses provides a general exploration of the Andaman Islander and Aeta phenotypes relative to other populations. Only raw measurements were used in the analysis to avoid problems associated with entering the same variables into the model as part of a ratio. Results of the analysis are provided in Table 4. Canonical variates analyses typically separate a size component of variation on function 1. In this case, the structure matrix for the analysis suggests that the first function is primarily driven by pelvic breadth (BIB) and body mass (FHD), representing a “body mass” component of size rather than stature. The second function further weights BIB as well as upper limb length, as represented by humeral and radial lengths. The first functions seem to separate the Efé and Andaman Islanders as



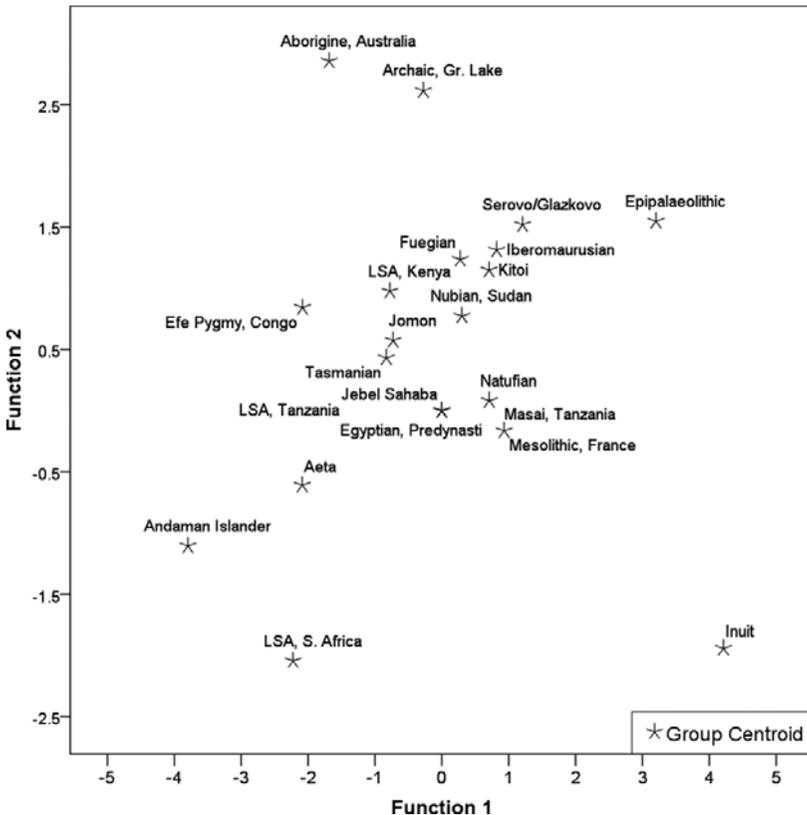
**Figure 8.** Variation in bi-iliac breadth relative to crural index among hunter-gatherers.

having particularly low body mass, followed by low centroid positions of the LSA Southern Africans, Aeta, and Tasmanians on this axis (Figure 9). In this context, the clearest morphological distinction is that of the Inuit, which sits at the high end of function 1 and the extreme low end of function 2, representing a combination of high body mass and shorter upper limb (and particularly forearm) lengths. The Inuit show a morphological pattern that appears to be highly derived and characterized by particularly broad pelvic breadth and very short radii. Functions 1 and 2 seem to be best at distinguishing the Inuit, suggesting that their body proportions are driven by recent directional selection, but the functions are less effective at discriminating among other populations. Despite this, the relative position of centroids of the “small-bodied” foragers is of interest. The LSA Southern Africans

**Table 4. Canonical Variates Analysis: Skeletal Phenotype/Structure Matrix**

	FUNCTION 1	FUNCTION 2	FUNCTION 3	FUNCTION 4
Bi-iliac breadth (BIB)	0.710 <sup>a</sup>	0.542	0.300	0.294
Tibia maximum length	0.249	0.262	0.786 <sup>a</sup>	0.455
Femur maximum length (FXL)	0.082	0.279	0.773 <sup>a</sup>	0.255
Radius length	0.033	0.551	0.558 <sup>a</sup>	0.413
Humerus length	0.259	0.400	0.506 <sup>a</sup>	0.495
Femoral head diameter (FHD)	0.486	0.175	0.333	0.361
<i>Significance</i>				
Eigenvalue	6.359	2.806	0.923	0.617
	(57.7%)	(25.5%)	(8.4%)	(5.6%)
Canonical correlation	0.930	0.859	0.693	0.618
Wilk's <i>L</i> (before function)	0.009	0.064	0.243	0.466
Chi squared (Wilk's <i>L</i> )	422.7*	245.0	126.1	67.9*
	(df = 90)	(df = 70)	(df = 52)	(df = 36)

<sup>a</sup>Largest absolute correlation between each variable and any discriminant function.  
 \**p* = 0.001.



**Figure 9.** Canonical variates analysis centroid locations (asterisks), functions 1 and 2.

and Andaman Islanders are the most similar and differ the most from other foragers, with a combination of small body mass (low BIB, FHD) and relatively long forearms, particularly the Andamanese. Both of these groups, however, are more clearly distinguished on the basis of function 2, which is weighted heavily by the combination of BIB and radius length. It is important to note that although the components of upper limb length (radius and humerus length) correlate strongly with function 2, limb length was not a component of the analysis. The Efé also occupy a unique position, with very small body mass combined with longer humeri relative to the size of other elements. Neither function 3 nor 4 discriminated the Andaman Islanders or Aeta from other populations of hunter-gatherers, suggesting that variation in the measurements weighted in these functions does not capture phenotypic variation characteristic of negritos.

## **Discussion**

The analyses presented above highlight a number of trends in hunter-gatherer phenotypic variation and, in particular, the question of morphological similarities between the negrito populations of the Andaman Islands and Philippines. They suggest that there are both similarities in measures of body size between the Andaman Islanders and the Aeta and numerous differences in the components of size and proportions between elements. Osteological indicators of stature, such as femoral and tibial lengths, are very similar between the negritos, highlighting the previously noted similarities in adult stature on which the negrito hypothesis is partly based. However, the results also identify phenotypic variation among the negritos, particularly in the form of narrower pelves among the Andaman Islanders compared with the Aeta, but also higher brachial indices. Differences in the Andaman Islander and Aeta lower limbs were reflected in the length of the femur, the proximal limb segment, rather than the more “plastic” distal limb segment (tibia), which appears to be more sensitive to environmental stress (Pomeroy et al. 2012). In general, the characteristics of narrow bi-iliac breadths and short crural indices are shared with Southern African hunter-gatherers and not other Asian populations. These observations suggest that there is considerable phenotypic variation among negrito populations, despite similarities in the “classic” phenotypic characteristics such as small body size. Overall, these differences, which are primarily reflected in body mass, body breadth, and upper limb morphology, demonstrate that the Andaman Islanders and Aeta do not share a generic negrito phenotype. Despite some general similarities in size among the Andaman Islanders, Aeta, Efé, and LSA (Khoisan) Southern Africans, the results also suggest that there is no generic, morphologically integrated phenotype that is typical of small-bodied foragers/pygmies. This supports recent evidence for the independent origins of small body size among small-bodied foragers (Migliano et al. this issue).

The concept and definition of the “pygmy” phenotype is relevant to consider here. Despite the small body size of these populations, the Andaman Islanders showed morphological affinities with the Southern African LSA population. These

represent mid-Holocene hunter-gatherers along the southern and eastern capes of Southern Africa, the ancestors of the contemporary Khoisan who possess some of the most ancient genetic lineages yet identified. Although this cannot be interpreted as evidence for close common ancestry of these populations, it provides some phenotypic predictions that require testing among other negrito populations. It also supports analyses of cranial variation among the Andaman Islanders (Bulbeck this issue), which suggests that they show affinities to African groups; however, it is interesting to note that the postcranial affinities noted in this study are not shared with the East African or North African groups. In the present analyses, neither the Andaman Islanders nor Aeta show any particular morphological similarities with either Asian foragers such as the Jomon or Australian or Tasmanian populations.

The differences highlighted by these analyses suggest that consideration of hypotheses of negrito origins needs to go beyond stature as phenotypic indicator. This study has highlighted considerable variation in phenotype among “small-bodied” hunter-gatherers; however, it is worth considering the extent to which phenotypic characteristics are canalized or plastic in response to environmental variation (Stock and Buck 2010). Human paleontologists often make assumptions about the genetic basis for skeletal traits, and hence their evolutionary stability, but the interpretation of skeletal variation is confounded by aspects of developmental and environmental plasticity (Stock 2012). The variables used in this study relate to stature and body mass, aspects of physique that can be both highly heritable and susceptible to intergenerational plasticity (Wells and Stock 2011). The Andaman Islanders exhibit a very narrow pelvis (BIB) similar to the Khoisan, which is both absolutely narrow and narrow relative to limb lengths. Previous studies have investigated the narrow pelvic dimensions of the Andaman Islanders and Khoisan/LSA Southern Africans (Kurki 2007, 2011) but it is somewhat surprising that this characteristic is not shared with other small-bodied foragers such as the Aeta. Pelvic dimensions have recently been shown to carry phylogenetic information relevant to human population history (Betti et al. 2012, 2013); however, we know very little about the mechanisms controlling other skeletal dimensions. Pelvic dimensions, for example, may vary with ecological parameters, diet, and other aspects of phenotype (Wells et al. 2012). In addition, lower limb length, in particular, the dimensions of the tibia, appears to be relatively sensitive to environmental variation (Trinkaus 1981; Holliday 1997; Stock 2012). It remains to be determined whether the morphology of the upper limb is as sensitive to the environment as is that of the lower limb, or is more genetically stable.

Although we cannot directly test the ancestry of negrito populations using postcranial morphology, any theory attempting to explain the phenotypic characteristics of these populations needs to account for their phenotypic variation, through mechanisms of either long-term natural selection or shorter-term plasticity. Future research is required to understand the mechanisms controlling this variation in the human phenotype. This will ultimately help us to resolve our understanding of the phenotypic characteristics that form the basis of the negrito hypothesis.

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