

# Skeletal Variation Among Early Holocene North American Humans: Implications for Origins and Diversity in the Americas

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**KEY WORDS** limb proportions; bi-iliac breadth; stature; Paleoindian; Beringian Standstill Hypothesis

**ABSTRACT** The movement of humans into the Americas remains a major topic of debate among scientific disciplines. Central to this discussion is ascertaining the timing and migratory routes of the earliest colonizers, in addition to understanding their ancestry. Molecular studies have recently argued that the colonizing population was isolated from other Asian populations for an extended period before proceeding to colonize the Americas. This research has suggested that Beringia was the location of this “incubation,” though archaeological and skeletal data have not yet supported this hypothesis. This study employs the remains of the five most complete North American male early Holocene skeletons to examine patterns of human morphology at the earliest observable time period. Stature, body mass, body breadth, and limb proportions are examined in the context of male skeletal

samples representing the range of morphological variation in North America in the last two millennia of the Holocene. These are also compared with a global sample. Results indicate that early Holocene males have variable postcranial morphologies, but all share the common trait of wide bodies. This trait, which is retained in more recent indigenous North American groups, is associated with adaptations to cold climates. Peoples from the Americas exhibit wider bodies than other populations sampled globally. This pattern suggests the common ancestral population of all of these indigenous American groups had reduced morphological variation in this trait. Furthermore, this provides support for a single, possibly high latitude location for the genetic isolation of ancestors of the human colonizers of the Americas. *Am J Phys Anthropol* 149:525–536, 2012. ©2012 Wiley Periodicals, Inc.

This study utilizes dimensions of the most complete skeletons of humans dating to the early Holocene of North America to examine hypotheses concerning the peopling of the Americas. The investigation of the modern human colonization of the Americas during the terminal Pleistocene has been a major research focus for well over a century (Fewkes et al., 1912; Meltzer, 2009). This pursuit rests on resolving three central issues: when humans arrived in the New World; what routes they took in migrating; and their group composition. Ultimately, these inquiries focus on ancestor-descendent relationships and population movement. Investigators have utilized diverse data sources in this endeavor, including paleopalynology (Newby et al., 2005), faunal analysis (Leonard et al., 2000), landscape learning (Anderson and Gilliam, 2000; Meltzer, 2002), and resource procurement (Cannon and Meltzer, 2004; Hofecker and Elias, 2007), in addition to the often-cited evidence from lithic, human skeletal, and molecular biological sources (Goebel et al., 2008; Dillehay, 2009; Sassa-man, 2010).

Despite, or perhaps because of the variety of research approaches taken (Sassaman, 2010), as well as increasing amounts of data, no strict consensus has emerged regarding the three central questions (Waguespeck, 2007; Goebel et al., 2008). Genetic, archaeological, and skeletal data almost exclusively agree on an Asian origin for the colonizing humans (Kemp and Schurr, 2010; Hubbe et al., 2011; but see Stanford and Bradley, 2012). However, when the original occupying peoples arrived and how they dispersed cannot yet be resolved.

Recent genetic analyses, though, point to an extended, millennia-long pause, or standstill, in the migration of the first New World human groups before spreading throughout the Americas. This has been evidenced by the accumulation of shared single nucleotide polymorphisms in the mitochondrial genome largely exclusive to indigenous peoples of the Americas (Tamm et al., 2007; Kitchen et al., 2008; Mulligan et al., 2008; Kemp and Schurr, 2010). Investigators proposing this hypothesis—which they have termed the “Beringian Standstill” or “Beringian Incubator Model” (BIM) (Tamm et al., 2007; Kemp and Schurr, 2010)—have favored a model wherein the isolation of New World human ancestors occurred in Beringia, the now-submerged landmass that once con-

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nected and included modern northeastern Siberia and modern Alaska. Furthermore, using molecular clocks, researchers have proposed that this isolation event and an associated population bottleneck must have ended between 17,000 and 15,000 years before present (yBP) (Tamm et al., 2007; Mulligan et al., 2008; Fagundes et al., 2008).

While archaeological data to directly support the BIM are still lacking, current data do not refute the validity of this model. There is no evidence for the long-term colonization of northeastern Siberia or Alaska toward the end of the Pleistocene, and most reported sites date *after* the proposed end of the standstill (Goebel et al., 2003, 2008); this calls into question the likelihood that these regions were locations of the proposed isolation of human populations necessitated by genetic arguments. However, some recent archaeological researchers have investigated possible migratory scenarios to allow for the BIM (Anderson et al., 2010; Sassaman, 2010). One example involves the occupation of a set of island archipelagos along the southern coast of Beringia and far north of the Aleutian chain that may have been conducive to water travel and a lengthy maritime subsistence (Brigham-Grette et al., 2004; Erlandson et al., 2007, 2008; Anderson, 2010). As these islands are now submerged and have not been archaeologically surveyed or excavated, archaeological evidence of human occupation following this model remains hypothetical. It is worth noting that sites like the ca. 10,000 yBP (calibrated calendar years) On-Your-Knees-Cave, found on Prince of Wales Island, present compelling evidence that humans consumed a diet heavily dependent on maritime resources (Dixon, 2002), which likely had been established for some time (Erlandson et al., 2008). In addition to evidence for maritime resource utilization, the climate of Beringia would have supported human habitation. Paleoclimate studies have indicated that parts of Beringia varied between slightly warmer to the same temperature range as found in modern southern Alaska (Elias, 2000; Hoffecker and Elias, 2003), and that the southern coast of Beringia had a milder climate than the interior (Mandryk et al., 2001; Brigham-Grette et al., 2004), though there was climatic volatility throughout the Last Glacial Maximum (Hoffecker and Elias, 2007). Ultimately, though a scenario for millennia-long human colonization of Beringia may be suggested from these and related discoveries (Hoffecker and Elias, 2007; Erlandson et al., 2008; Anderson, 2010), no incontrovertible archaeological evidence has been found.

The examination of human skeletal remains provides an alternative source of evidence with which to assess these colonization hypotheses. If isolated human groups did occupy the high latitude Beringian region for millennia, it is conceivable that a combination of drift and selection pressures would have shaped their morphology. This morphology would have mutually diverged between the Beringian isolated populations and their Asian ancestors. Unfortunately, no human remains dating to the time period of interest (i.e., between 20,000 and 11,000 yBP) have been recovered from Alaska or Siberia, and the most ancient remains recovered to date were cremated (Potter et al., 2011).

It is possible, however, that the earliest available well-preserved human skeletons retain the morphological traits of their colonizing ancestors, despite the millennia that separate these skeletons from the first colonizing humans (Meltzer, 2002). Most of these skeletons date to

the early Holocene (between 10,500 and 8,000 yBP). This argument has formed the basis of many studies of early human variation in the Americas, which have mostly focused on metrics of the crania (e.g., Jantz and Owsley, 2001; Powell, 2005; Neves et al., 2007; Hubbe et al., 2011). These articles have generally concluded that the earliest humans in the Americas exhibit morphological distinctions from more recent populations, though these distinctions are variable in magnitude and somewhat dependent on comparative samples. Researchers have further argued from their cranial analyses for a model of rapid movement of populations from Asia followed by replacement by other human groups (Jantz and Owsley, 2001; Chatters, 2010; Hubbe et al., 2011), though others suggest that the observed cranial differences are the result of drift and gene flow (Powell, 2005; Gonzalez-Jose et al., 2008). A rapid Pacific Rim coastal migration of humans at the end of the Pleistocene fits well with some archaeological evidence (Bever, 2006; Erlandson and Braje, 2011), explaining early occupation dates for sites like On-Your-Knees-Cave (Dixon, 2002; Erlandson et al., 2008), Paisley Caves (Gilbert et al., 2008), and Monte Verde (Dillehay et al., 2008).

Reconciling cranial and molecular studies, however, is difficult. Researchers concluding that humans migrated rapidly along the Pacific coastal rim from Asia argue that cranial morphologies of early Holocene American skeletons (EHAS) do not exhibit characteristics associated with more recent human groups living in cold climates (Jantz and Owsley, 2001; Hubbe et al., 2011). However, later Holocene American groups do have these morphologies, even in warm temperate environments, which skeletal biologists interpret as a signature for discontinuity between early Holocene and more recent (e.g., Archaic) individuals. This contradicts genetic evidence (such as the BIM), unless the colonizers represented by EHAS: 1) do not possess the mitochondrial DNA polymorphisms that uniquely identify all living (and many past) groups from the Americas, or; 2) emerged from one population that was already genetically isolated from other Asian populations, with a portion (not expressing morphologies associated with cold climate populations) splintering off and colonizing lower latitudes while a later group (characterized with cold climate morphologies) followed them. Recent studies of ancient DNA from some EHAS falsify the hypothesis of genetic discontinuity between early and middle Holocene humans, despite craniometric differences between them (Stone and Stoneking, 1998; Bever, 2006; Kemp et al., 2007; Kemp and Schurr, 2010; Raff et al., 2011). While not all early Holocene skeletons have been sampled, the building evidence suggests that a single population with a shared, unique genetic pool was the fundamental source of all humans who colonized the Americas, despite craniometric differences among them.

This presents a conundrum: If the earliest humans in the Americas were cranially distinct from later groups, did they share the same source population, and was that population the genetically isolated group proposed by the BIM? As stated above, cranial morphological differences between earlier and later groups do not exclude the possibility for a shared genetic source population. Three scenarios may explain the observed phenotypic and genetic variation. The groups represented by the EHAS could have separated from their source population early, but after the establishment of common New World molecular polymorphisms, and drift then differentiated the mor-

phologies of these human groups over the initial millennia of colonization. Alternatively, if cranial differences were related to cold climate adaptations in the later groups, then a shared source population would have been genetically isolated, followed by the departure of groups represented by the EHAS *before* evolutionary forces shaped the observed cranial morphologies found among later Holocene skeletons. A third possibility is that the groups represented by EHAS underwent morphological changes *after* inhabiting Beringia (or another location), while later waves of colonizers retained a derived suite of cranial morphologies that could have come about from drift, selection, gene flow, or a combination of these.

One potential complication to using crania dating over millennia is the potential for adaptation, drift, and secular change to shape differences among groups or individuals, though these effects do not disguise underlying population differences (Ackermann and Cheverud, 2004; Relethford, 2004; Carson, 2006; Roseman et al., 2010). However, minor their effect, teasing apart these factors has complicated the interpretations of cranial diversity among EHAS and later American groups. Therefore, the analyses in this article instead focus on morphologies hypothesized to be stable over long temporal periods, namely the shape and proportions of postcranial morphology (Holiday and Falsetti, 1995; Holliday, 1997, 1999; Temple et al., 2008; Auerbach and Ruff, 2010; Auerbach, 2011a; Cowgill et al., 2012).

### Body size and shape variation

The size, shape, and proportions of modern humans have been shown globally—especially in Eurasian and African populations—to roughly correspond with ecogeographic expectations (Roberts, 1978; Trinkaus, 1981; Ruff, 1994; Holliday, 1997; Auerbach and Ruff, 2010) relating to biological rules attributed to Bergmann and Allen (Bergmann, 1847; Allen, 1877; Mayr, 1956). These patterns may be generalized into a model where size and proportions, especially of the postcrania, trend toward efficient dissipation or retention of heat by changing the ratio of heat-producing volume to surface area (Ruff, 1994, 2002). Empirically, this is demonstrated by cold environment-dwelling human populations' tendency to have wide body breadths, generally measured as bi-iliac breadth of the pelvis, and short limbs or distal limb elements relative to overall stature or proximal limb elements, respectively (e.g., Ruff, 1994; Holliday, 1997, 1999; Temple et al., 2008). Relatedly, and important to this study, research into the movement of modern humans from Africa into Europe has indicated that postcranial morphology may be retained from ancestral groups for millennia (Holliday, 1997, 1999; Ruff, 2002), and so studies of the EHAS likely reflect the phenotypes of early North American colonizing human populations.

Yet, as noted by Mayr (1956), there are multiple factors that likely influence morphology. For example, positive allometry in limb element lengths increases limb-to-trunk length proportions in especially tall human populations (Auerbach, 2010; Auerbach and Sylvester, 2011). Terrain and ranging behavior likewise could influence limb proportions (Higgins and Ruff, 2011). Obstetrical sufficiency and locomotor efficiency shape the pelvis in addition to thermoregulatory requirements (e.g., Kurki, 2011), though research has indicated that bi-iliac breadth may be independent from true pelvis dimensions

that relate to obstetric size and shape (King et al., 2011; Grabowski, in press). Furthermore, a recent study comparing limb proportions with bi-iliac breadth among skeletons in the Goldman Data Set has indicated that these morphologies are independent, and so are potentially subject to different evolutionary forces (Betti et al., 2012). Without modeling and experimentation, the relative effects of each of these factors, among others, remain uncertain. Nonetheless, the patterns of human postcranial morphological variation documented in Europe, Africa, and Asia correspond with climatic factors. Moreover, recent studies have indicated that humans living for millennia in the highest (and therefore coldest) latitudes exhibit morphological extremes that correspond with thermoregulatory expectations, and therefore may skew analyses that include them (Harvati and Weaver, 2007; Auerbach, 2007; King, 2010). Thus, while thermoregulation is one of many variables shaping postcranial morphology, it remains an important factor in the phenotypic variation found among humans as they colonized new environments.

### Hypotheses

Based on the evidence presented, what can be hypothesized about comparisons of postcranial size and shape among EHAS? Cranial studies suggest a discontinuity, or at least a morphological distinction between the EHAS and more recent (Archaic and later) inhabitants of North America. These studies have assumed that climatic selection or other forces led to this difference in cranial shape, which in turn would imply that the ancestors of the EHAS experienced a different population history from more recent indigenous North American groups, argued by some to indicate separate ancestry for the EHAS and more recent groups. In contrast, molecular evidence argues for a shared ancestor population for all indigenous American groups (including the EHAS), and would support continuity or discontinuity in skeletal morphology. This is because the DNA used in the molecular argument (generally mitochondrial DNA) does not relate to the skeletal phenotype, which itself is only in part determined by genes. Therefore, in examining postcranial morphology, this study assesses whether the evidence for discontinuity in morphology—as argued from cranial studies—exists throughout the skeleton. The central hypothesis is that the EHAS will have postcranial morphologies that are dissimilar from morphological variation (e.g., fall outside of the range) found in more recent North American groups. Shared postcranial phenotypic characteristics between EHAS and later skeletons, moreover, could argue for a shared ancestral population for both groups, despite cranial differences between them.

Regardless of morphological continuity in postcranial size and shape between EHAS and more recent skeletons, this study cannot test where the morphologies of these groups emerged. Arguably, one may hypothesize that the earliest humans to enter into the Americas would have developed morphologies associated with colder climates: wide body breadths, short distal limb elements relative to proximal limb elements, and short lower limb lengths relative to total stature. These morphologies could have developed in Asia, among the ancestors of American colonizers, or in Beringia should humans have inhabited that region for a long enough

time to undergo morphological adaptation to cold climates or drift due to isolation.

## METHODS

The five early Holocene male skeletons chosen for this study represent the most complete human remains available from the earliest time periods in North America. Both the Spirit Cave and Kennewick skeletons are nearly complete, and the other skeletons preserved the necessary elements (i.e., limb long bone lengths) to allow for their inclusion in analyses. While not exhaustive, the comparative samples used in this study were chosen to best represent human morphological variation in the late Holocene based on previous studies (Ruff et al., 1994; Holliday and Falsetti, 1995; Holliday, 1997, 1999; Temple et al., 2008). Late Holocene samples were favored in order to maximize the time for humans to adapt to environments in the Americas, and therefore provide a best-case scenario for contextualizing the variation observed among the EHAS. Compared with a much larger (>1,300 males) sample of skeletons (Auerbach, 2007), the 14 sites chosen herein encapsulate the total range of morphological variation present in North America during the last millennium. More information about the American samples, including their provenience and curating institutions, may be found in Section 1 of the Supporting Information.

Measurements used in this study were taken from complete adult, nonpathological individuals determined to be male using methods in Phenice (1969) and Bruzek (2002). A Paleo-Tech portable field osteometric board (Paleo-Tech Concepts, Inc.) and Mitutoyo Absolute Digimatic 150 mm Sliding Calipers (Mitutoyo America Corp.) were used to obtain metric data. Six dimensions were used for most skeletons: maximum lengths of the humerus, radius, and tibia; bicondylar length for the femur; femoral head anteroposterior diameter; and bi-iliac breadth. Maximum femoral lengths were converted to bicondylar length for Gore Creek and the Kenyan & Ugandan samples using formulae in Auerbach (2011b). Measurements were taken bilaterally to reduce the effects of bilateral directional asymmetry, especially in the upper limb (Auerbach and Ruff, 2006). The author measured all of the American skeletons used in this study with the exception of Gore Creek and Wizard's Beach, the source data for which are cited in Table 1. Likewise, all of the African, Eurasian, and Australian skeletal samples were measured by the author as part of the Goldman Data Set (Auerbach and Ruff, 2004) (available at: <http://web.utk.edu/~auerbach/GOLD.htm>) except samples from Kenya and Uganda; Christopher Ruff shared those African skeletal data. All bi-iliac breadths were taken from rearticulated pelvises stabilized using rubber bands, except for the early Holocene Kennewick skeleton; details of the Kennewick skeleton's pelvic reconstruction are detailed in Auerbach (in press). All measurement errors for the author were less than 1% for the dimensions used herein.

These measurements were used to calculate the morphologies compared. Intralimb indices were calculated as proportions of the radial maximum length to humeral maximum length (brachial index) and of the tibial maximum length to femoral bicondylar length (crural index) after Davenport (1933), Trinkaus (1981), and Ruff (1994). Body mass was calculated from femoral head diameter following the procedures recommended in Auer-

bach and Ruff (2004) for Old World samples and Auerbach (2007, 2011a) for American samples. Statures for Old World samples were calculated following procedures in Auerbach and Ruff (2004), except the Nubian sample, wherein statures were calculated by multiple regression following Raxter et al. (2008). Multiple regression estimations from the femur and tibia were also used for the later Holocene North American samples following Auerbach and Ruff (2010); these equations were also used to estimate statures for Gore Creek, Horn Shelter 2, and Wizard's Beach, following the recommendations made in that article. The statures for Kennewick and Spirit Cave were determined using the revised Fully anatomical method (Raxter et al., 2006, 2007).

Bi-iliac breadth could not be taken on Horn Shelter 2 or Wizard's Beach, so a multiple regression formula for predicting bi-iliac breadth from stature and femoral head diameter was generated using non-pygmoid males from the Goldman Data Set and the indigenous North American males in Auerbach and Ruff (2010). This equation [Eq. (S1)] and its associated statistics are presented in Section 3 in the Supporting Information. Generally, the equation is an imprecise estimator of bi-iliac breadth—its standard error of the estimate is  $\pm 13.41$  mm (4.94% SEE), and its Pearson's  $r = 0.58$ . The equation, then, produces provisional, but informative estimates of Horn Shelter 2's and Wizard Beach's body breadths.

As the EHAS represent individuals that cannot be pooled into a single sample, most statistical comparisons are not applicable. Therefore, comparative descriptive statistics were chosen over methods like discriminant function analysis, which makes assumptions about the underlying data distribution. Mixture analyses (e.g., Kramer and Konigsberg, 1999) were not used, as this study is not attempting to associate morphologies of the earliest North American male skeletons with those of more recent indigenous groups. Any statistical tests performed used individual data for comparative (non-EHAS) samples, and not group means. Comparisons between later Holocene North American and Old World samples were made using Student's  $t$ -tests for nonratio data (e.g., stature and bi-iliac breadth), while ratios were compared with nonparametric Wilcoxon rank-sum tests. The Welch's  $t'$  statistic was used when homogeneity of variances between samples were violated (Welch, 1947). All statistics were calculated using Stata 12.0 for Macintosh.

## RESULTS

Tables 1 and 2 respectively present dimensions directly measured, estimated, or calculated from skeletal measurements taken on the five observed male EHAS. The means of these dimensions for males from 14 later Holocene New World sites are also presented in Tables 1 and 2. It should be noted that all of these are sites from North America except for the Ayalán, which were recovered from equatorial Ecuador; they are included to provide an example of morphologies found among indigenous Americans dwelling in tropical regions. The Ayalán have among the narrowest bi-iliac breadths of any group sampled in the Americas. Additional details on the comparative sample groups may be found in the Supporting Information. Table 3 presents mean data for comparable dimensions from African, Eurasian and Australian (here-

TABLE 1. Measured and estimated dimensions of the male North American EHAS (shaded cells) and mean dimensions of later Holocene male samples<sup>a</sup>

Individual/sample group	N <sup>b</sup>	Date (BP) <sup>c</sup>	Average humerus maximum length (mm) (SD)	Average radius maximum length (mm) (SD)	Average femur bicondylar length (mm) (SD)	Average tibia maximum length (mm) (SD)	Average femoral head anteroposterior diameter (mm) (SD)	Bi-iliac breadth (mm) (SD)
Gore Creek <sup>d</sup>	1	8,250 ± 115	N.O.	251.00	436.24 <sup>e</sup>	368.50	N.O.	N.O.
Horn Shelter 2	1	9,500 ± 200	315.25	249.25	429.00	359.00	46.58	276.08 [250–302] <sup>f</sup>
Kennewick	1	8,370 ± 60	340.75	258.75	464.25	400.00	48.57	281.00
Spirit Cave	1	9,415 ± 25	297.50	236.00	424.50	352.00	43.27	279.00
Wizard's Beach <sup>g</sup>	1	9,515 ± 155	339.00	261.00	460.00	396.59	50.00	288.79 [263–314] <sup>f</sup>
Windover Pond	23	ca. 7,400	314.51 (13.55)	250.16 (11.70)	445.54 (17.72)	380.64 (17.18)	44.75 (2.38)	265.12 (12.76)
Point Hope Tigara	22	750–250	302.07 (15.69)	226.23 (12.49)	429.43 (21.75)	355.85 (20.49)	47.15 (2.66)	280.14 (11.21)
Sadlermiut	28	950–100	305.14 (15.39)	219.71 (9.17)	434.92 (22.54)	350.06 (19.43)	48.37 (2.24)	273.31 (13.03)
Aleut	29	ca. 1,500–1,000	302.13 (20.36)	230.35 (13.90)	414.66 (27.66)	336.34 (23.01)	45.47 (2.09)	261.65 (13.85)
Ikogmiut	27	500–100	313.32 (17.41)	233.94 (13.79)	422.06 (25.88)	347.19 (21.87)	45.73 (2.26)	263.90 (16.25)
Lillooet Salish	10	Precontact	304.88 (12.33)	237.68 (10.42)	422.18 (12.58)	349.48 (9.69)	44.29 (2.22)	266.19 (10.60)
Grasshopper Pueblo	27	650–500	314.84 (16.72)	245.76 (12.40)	429.57 (21.41)	370.69 (19.58)	43.20 (2.57)	264.69 (9.97)
Mobridge I Arikara	21	350–250	322.96 (13.23)	254.63 (8.86)	449.36 (18.68)	384.40 (14.44)	46.41 (3.01)	283.82 (15.71)
Polley-Secret	6	1,310 ± 60	301.92 (9.54)	238.42 (8.74)	414.54 (12.31)	358.63 (11.19)	43.50 (1.42)	263.17 (12.29)
Fremont								
Montague Delaware	8	400–200	326.19 (11.72)	256.59 (6.12)	452.38 (13.71)	388.72 (12.60)	45.80 (2.04)	263.50 (12.79)
Ledford Island	21	600–450	321.49 (15.52)	250.89 (9.74)	446.50 (16.37)	376.22 (14.76)	22.25 (2.02)	269.88 (13.51)
Mississippian								
Ryan Mound	40	1,235 ± 65–835 ± 90	312.88 (13.31)	243.76 (9.37)	431.86 (16.45)	364.88 (14.22)	44.74 (2.12)	269.47 (15.22)
Santa Cruz Island	12	400–200	310.38 (12.89)	245.88 (12.04)	428.56 (15.58)	363.54 (13.32)	45.30 (1.69)	260.73 (12.20)
Ayalán	3	1,220 ± 115	302.75	242.50	418.91	355.33	43.62	245.00

<sup>a</sup> The author measured all skeletons except Gore Creek and Wizard's Beach. Standard deviation values for group means from later Holocene samples are presented in parentheses.

<sup>b</sup> Reported number reflects total individuals with intact limb bones; number of individuals with measurable bi-iliac breadths is generally smaller than total reported.

<sup>c</sup> Dates for the five EHAS are in uncalibrated radiocarbon years. More recent Holocene samples are reported in calibrated years BP; associated sigma values are included when available. Sources: Gore Creek (Cybulski et al., 1981); Horn Shelter (Watt, 1978); Kennewick (Chatters, 2000); Spirit Cave (Tuohy and Dansie, 1997); Wizard's Beach (Kirner et al., 1997); Windover Pond (Doran, 2002); Point Hope Tigara (Larsen and Rainey, 1948); Sadlermiut (Merbs, 1983); Aleut (Coltrain et al., 2006); Ikogmiut (de Laguna, 1936); Interior Salish (Smith, 1899); Grasshopper Pueblo (Graves et al., 1982); Mobridge Arikara (Owsley et al., 1982); Polley-Secret Fremont (Kopp, 2006); Montague Delaware (Hrdlička, 1916); Ledford Landing Mississippian (Boyd and Boyd, 1989); Ryan Mound (Leventhal, 1993); Santa Cruz Island (Lambert, 1993); Ayalán (Ubelaker, 1981).

<sup>d</sup> Data obtained from Cybulski et al. (1981).

<sup>e</sup> Calculated from maximum length and converted after Auerbach (2011).

<sup>f</sup> Estimated from femoral head diameter and stature, following Eq. (S1) in the Supporting Information; 95% confidence limits of the estimate are given in brackets.

<sup>g</sup> Data shared by Dr. Douglas Owsley and Richard Jantz.

TABLE 2. Calculated morphologies of the male North American EHAS (shaded cells) and mean dimensions of later Holocene male samples<sup>a</sup>

Individual/ sample group	N <sup>b</sup>	Date (BP) <sup>c</sup>	Brachial index (×100)	Crural index (×100)	Estimated living stature (cm) <sup>d</sup> (SD)	Estimated body mass (kg) <sup>e</sup> (SD)	Bi-iliac breadth/stature (×100)
Gore Creek <sup>f</sup>	1	8,250 ± 115	N.O.	84.47	162.13	N.O.	–
Horn Shelter 2	1	9,500 ± 200	79.06	83.68	162.07	69.14	17.03 [15.4–18.6] <sup>g</sup>
Kennewick	1	8,370 ± 60	75.94	86.16	171.74	73.66	16.36
Spirit Cave	1	9,415 ± 25	79.33	82.92	160.84	61.63	17.35
Wizard's Beach <sup>h</sup>	1	9,515 ± 155	76.99	86.22	170.68	76.90	16.92 [15.4–18.4] <sup>g</sup>
Windover Pond	23	ca. 7,400	79.54	85.43	166.36 (4.85)	65.00 (4.97)	15.94
Point Hope Tigara	22	750–250	74.91	82.86	159.66 (5.25)	69.52 (4.38)	17.55
Sadlermiut	28	950–100	72.00	80.49	159.64 (5.22)	73.20 (5.08)	17.12
Aleut	29	ca. 1,500–1,000	76.29	81.12	155.32 (6.37)	66.75 (4.85)	16.85
Ikogmiut	27	500–100	74.70	82.28	157.63 (5.94)	67.29 (5.11)	16.74
Lillooet Salish	10	Precontact	77.97	82.79	157.93 (2.78)	63.96 (5.04)	16.89
Grasshopper Pueblo	27	650–500	78.09	86.30	162.55 (5.79)	61.49 (5.82)	16.28
Mobridge I Arikara	21	350–250	78.90	85.57	167.82 (4.52)	70.65 (5.19)	16.91
Polley-Secret Fremont	6	1,310 ± 60	78.97	86.51	158.62 (3.28)	62.17 (3.21)	16.59
Montague Delaware	8	400–200	78.72	85.96	168.47 (3.28)	67.67 (4.84)	15.64
Ledford Island	21	600–450	78.11	84.26	165.95 (4.30)	64.34 (4.07)	16.26
Mississippian							
Ryan Mound	40	1,235 ± 65–835 ± 90	77.94	84.50	162.18 (4.29)	64.97 (4.81)	16.62
Santa Cruz Island	12	400–200	79.22	84.83	161.49 (4.02)	66.25 (3.84)	16.15
Ayalán	3	1,220 ± 115	80.14	84.81	–	62.37	–

<sup>a</sup> The author measured all skeletons except Gore Creek and Wizard's Beach. Standard deviation values for group means from later Holocene samples are presented in parentheses.

<sup>b</sup> Reported number reflects total individuals with intact limb bones; number of individuals with measurable bi-iliac breadths is generally smaller than total reported.

<sup>c</sup> Dates for the five EHAS are in uncalibrated radiocarbon years. More recent Holocene samples are reported in calibrated years BP; associated sigma values are included when available. Sources: Gore Creek (Cybulski et al., 1981); Horn Shelter (Watt, 1978); Kennewick (Chatters, 2000); Spirit Cave (Tuohy and Dansie, 1997); Wizard's Beach (Kirner et al., 1997); Windover Pond (Doran, 2002); Point Hope Tigara (Larsen and Rainey, 1948); Sadlermiut (Merbs, 1983); Aleut (Coltrain et al., 2006); Ikogmiut (de Laguna, 1936); Interior Salish (Smith, 1899); Grasshopper Pueblo (Graves et al., 1982); Mobridge Arikara (Owsley et al., 1982); Polley-Secret Fremont (Kopp, 2006); Montague Delaware (Hrdlička, 1916); Ledford Landing Mississippian (Boyd and Boyd, 1989); Ryan Mound (Leventhal, 1993); Santa Cruz Island (Lambert, 1993); Ayalán (Ubelaker, 1981).

<sup>d</sup> Gore Creek, Horn Shelter 2, and Wizard's Beach statures calculated using formulae from Auerbach and Ruff (2010). Kennewick and Spirit Cave statures estimated using the revised Fully Anatomical Method (Raxter et al., 2006, 2007).

<sup>e</sup> Estimated from femoral head diameter using the formulae of Grine et al. (1995), following Auerbach (2007).

<sup>f</sup> Calculations from measures obtained from Cybulski et al. (1981).

<sup>g</sup> Using BIB estimated from femoral head diameter and stature, following Eq. (S1) in the Supporting Information. Ratios calculated using 95% confidence interval bi-iliac breadth estimations (Table 1) are given in brackets.

<sup>h</sup> Calculations from data shared by Drs. Douglas Owsley and Richard Jantz.

after “Old World”) males to place the American variation into a global context.

In general, the early Holocene male skeletons have heterogeneous morphologies when compared with each other. Moreover, individuals present a mosaic of morphologies; both Spirit Cave and Horn Shelter 2 have high brachial indices with low crural indices, while Kennewick and Wizard's Beach present the opposite pattern. The early Holocene individuals except Spirit Cave have estimated body masses toward the higher end of the range of means for all more recent human samples included in this study. Both Spirit Cave and Kennewick have wide body breadths, both absolutely and in proportion with stature, an observation considered further below.

Before comparing the EHAS with more recent variation among indigenous American groups, it is useful to assess how variable morphologies among the later Holocene American groups are in the context of established variation among groups from Old World samples. A comparison of the ranges in intralimb (brachial and crural) indices among all of the later Holocene groups demonstrates that males from the Americas have the same range in both indices as is found in the Old World; indigenous American male samples and Old World male sam-

ples are not significantly different in intralimb indices ( $P = 0.131$ , brachial;  $P = 0.735$ , crural). All other dimensions reported in Tables 1 to 3, however, do significantly differ between males in America compared with Old World males. Most notably, indigenous American males are significantly wider-bodied, both in absolute bi-iliac breadth (an overall mean of 1.8 cm greater) and bi-iliac breadth relative to stature (a difference of 1.17% in medians). Relatedly, indigenous American males are significantly more massive ( $t'_{(280,0.05,2)} = 4.323$ ). Excluding North American arctic samples from these comparisons does not change these results.

All five of the EHAS present morphologies within the range of variation found in later Holocene indigenous American groups. Notably, though, both Kennewick and Spirit Cave have observed bi-iliac breadths wider than males that fall one standard deviation above the mean of each indigenous American sample group except for the high-latitude arctic samples (Point Hope Tigara, Sadlermiut, and Ikogmiut) and northern Great Plains Arikara (Mobridge I). Box plots of American male sample bi-iliac breadths in Figure 1 illustrate this. Furthermore, based on a multiple regression using all of the recent Holocene male samples to estimate bi-iliac breadth from femoral head diameter and estimated statures [see Eq. (S1) in

TABLE 3. Dimensions from select late Holocene male human samples from Africa, Eurasia, and Australia

Sample group	N	Average humerus maximum length (mm) (SD)	Average radius maximum length (mm) z(SD)	Brachial index ( $\times 100$ )	Average femur bicondylar length (mm) (SD)	Average tibia maximum length (mm) (SD)	Crural index ( $\times 100$ )	Estimated living stature (cm) <sup>a</sup> (SD)	Average femoral head AP diameter (mm) (SD)	Estimated body mass (kg) <sup>a</sup> (SD)	Bi-iliac breadth (mm) (SD)	Bi-iliac breadth/stature ( $\times 100$ )
Australian Aborigine	18	318.44 (16.12)	249.38 (16.41)	77.99	443.86 (25.39)	376.14 (27.81)	84.71	166.42 (5.56)	43.93 (2.14)	60.19 (4.97)	248.70 (11.17)	14.96
Modern Kenya and Uganda	27	322.56 (23.42)	256.04 (19.51)	79.38	454.08 <sup>b</sup> (33.67)	392.85 (32.39)	86.48	166.69 (8.93)	43.34 (2.65)	58.82 (6.16)	241.67 (15.36)	14.51
Kerma and Sayala (Nubia)	23	317.63 (21.97)	248.76 (18.67)	78.02	442.24 (33.02)	379.42 (29.89)	85.80	165.48 (7.89)	44.75 (3.16)	62.09 (7.34)	258.50 (15.48)	15.64
19th-century Sicily	19	308.41 (15.10)	234.21 (13.94)	75.93	425.88 (21.10)	360.21 (22.60)	84.55	163.63 (5.02)	44.70 (3.03)	61.97 (7.04)	255.58 (12.65)	15.62
Medieval Bavaria, Germany	40	334.59 (19.88)	252.67 (15.82)	75.52	465.28 (27.34)	387.53 (26.17)	83.28	173.00 (6.51)	47.74 (2.92)	69.03 (6.80)	277.27 (19.04)	16.05
Medieval Orkney Islands	6	326.17 (14.06)	251.58 (12.45)	77.16	453.67 (21.90)	372.50 (13.32)	82.22	170.24 (5.21)	46.80 (2.57)	66.84 (5.97)	268.60 (4.45)	15.87
Edo period Japan	29	296.34 (9.99)	226.72 (10.22)	77.05	410.97 (17.03)	336.40 (15.11)	81.86	163.53 (4.21)	45.59 (2.17)	64.04 (5.05)	254.54 (13.52)	15.56

All samples are measured by the author and taken from the Goldman Data Set (Auerbach and Ruff, 2004) except the modern Kenya and Uganda sample, which has been shared by Christopher B. Ruff.

<sup>a</sup> Statures and body masses are estimated using methods described in source Auerbach and Ruff (2004).

<sup>b</sup> Calculated from maximum length and converted after Auerbach (2011).

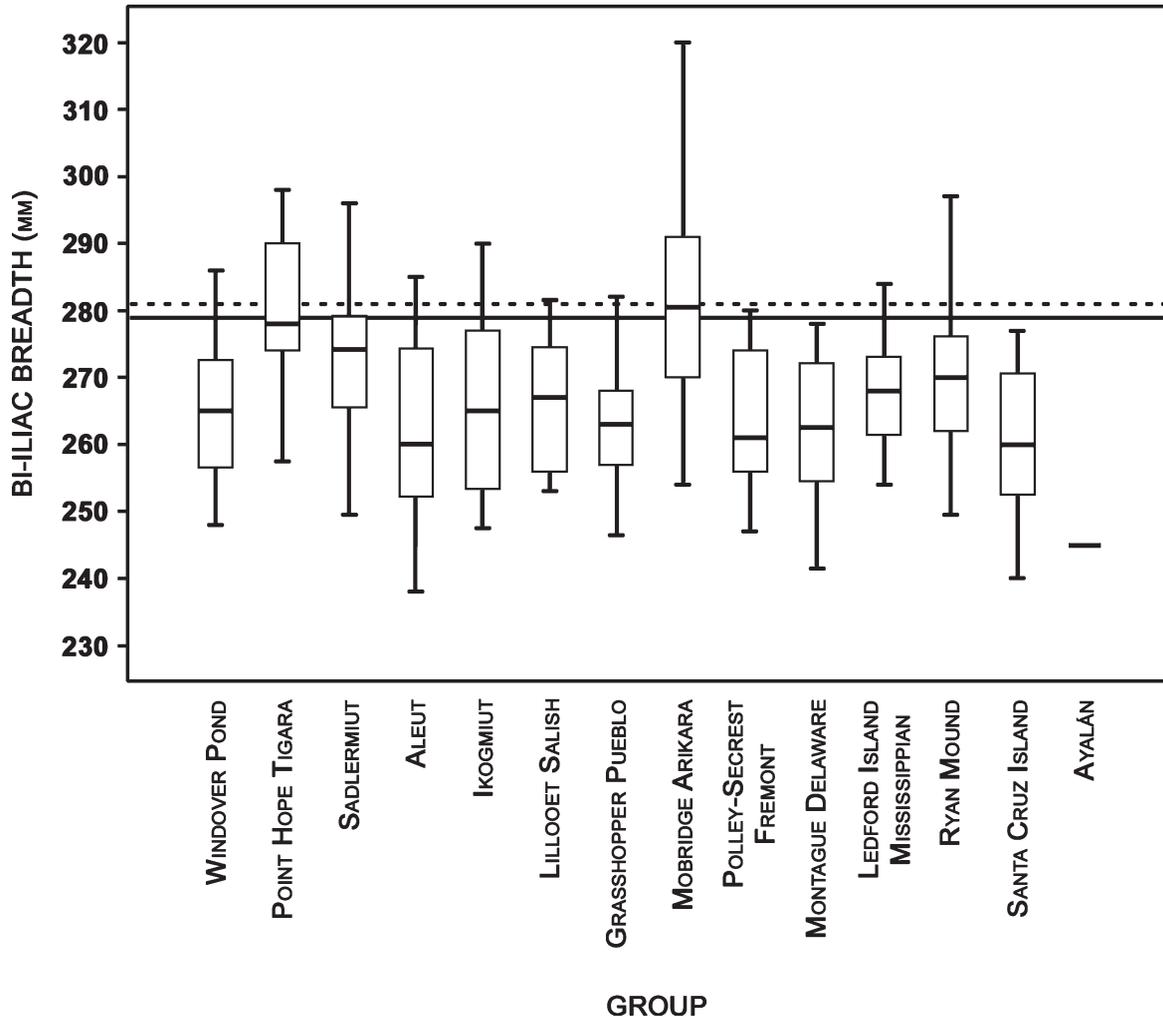
the Supporting Information], the Horn Shelter 2 and Wizard's Beach male EHAS would be predicted to have equally wide bi-iliac breadths (Table 1). Further consideration of these estimates may be found in the Discussion. Thus, the early Holocene males had relative bi-iliac breadths greater than 16 (i.e., body breadth is more than 16% of total stature), all therefore falling outside of the range of means for the Old World male samples but within the range of more recent Holocene North American samples.

The discordance of upper and lower intralimb indices within the EHAS warrants additional analysis. Figures 2 and 3 respectively present scatterplots of brachial and crural indices of the early Holocene males (indicated by letters) superimposed on the individuals from recent indigenous American male samples. Arctic male samples, represented by small black x's, fall toward the low end of the overall intralimb index range, which is expected given these groups' low indices as well as shorter statures (especially reflected in shorter femoral and tibial lengths). It is notable in both scatterplots that the Kennewick and Horn Shelter males have nearly identical intralimb indices, though their brachial indices are more similar to those observed in more recent arctic groups, while their crural indices are not. As noted above and in Table 2, the Spirit Cave male skeleton has a high brachial index, while his crural index is within the cluster of arctic groups, as exemplified in Figure 3.

## DISCUSSION

The morphological variation observed in both the EHAS and more recent Holocene male indigenous American samples has important implications about human variation in the Americas. Some morphologies have as much variation as observed in the Old World sample, while others have restricted variation. In general, the North American males sampled herein, excluding the equatorial Ayalán, exhibit as great a range of intralimb indices as found throughout the Old World. This is interesting, as humans in North America have occupied the continent for a far shorter temporal period than humans in the Old World, and the regions inhabited in North America do not encompass the climatic range represented by the Old World sample (see Section 2 of the Supporting Information for climatic data for the North American samples). In contrast, North American males are wider-bodied than the Old World males sampled and, concurrently, are more massive. As a cylindrical model of human form (Ruff, 1994; Auerbach and Ruff, 2004) relates body mass to two variables—body breadth and stature—this relationship is not surprising. While the very small equatorial Ayalán sample does present a body breadth similar to low latitude Old World samples (Tables 1 and 3), it should be noted that additional low-latitude indigenous American samples do not have such narrow bi-iliac breadths (Eveleth and Tanner, 1976; Auerbach, 2007). In addition, relative body breadths calculated from anthropometrically measured indigenous male populations in the Americas (Eveleth and Tanner, 1976) present results comparable to those reported in Table 2.

In this morphological context, what can be concluded about the EHAS? By the beginning of the Holocene, humans living in North America were *not* morphologically homogeneous postcranially, matching previous analyses that show considerable craniomorph variation



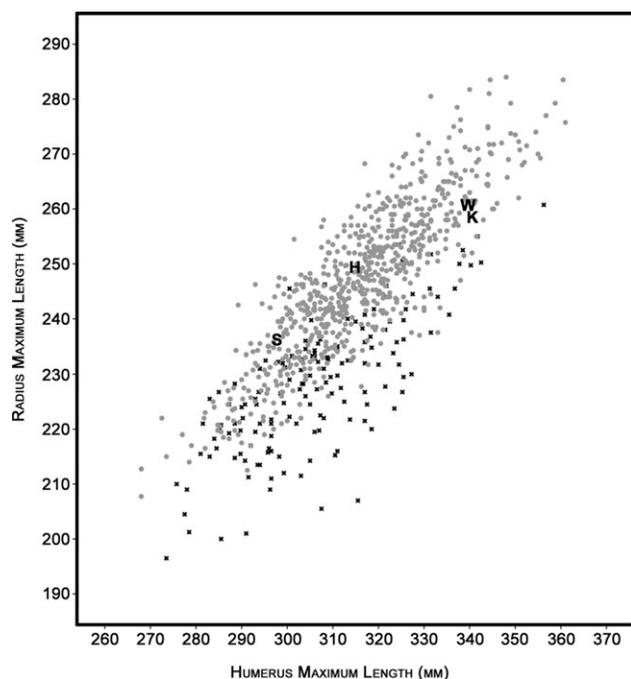
**Fig. 1.** Box-plots of bi-iliac breadths of comparative later Holocene American male samples. Solid horizontal line, bi-iliac breadth for the Spirit Cave EHAS. Dashed line, bi-iliac breadth for the Kennewick EHAS.

when the earliest skeletons' crania are placed into a modern context (Jantz and Owsley, 2001; Powell, 2005; Neves et al., 2007; Hubbe et al., 2011). Yet, importantly, the four male skeletons preserving dimensions from which to estimate body mass and stature exhibit the same high body masses, especially relative to stature, observed in general among all North American indigenous male samples. Furthermore, all of these males had or are estimated to have had wider bodies than is typically observed in all humans except those living at the highest latitudes later in the Holocene, despite their burials in locations far from arctic climates. This pattern would support the hypothesis that these individuals retain a common ancestral morphology, namely wide body breadths, and that this morphology has generally been retained throughout the Holocene in North American indigenous humans.

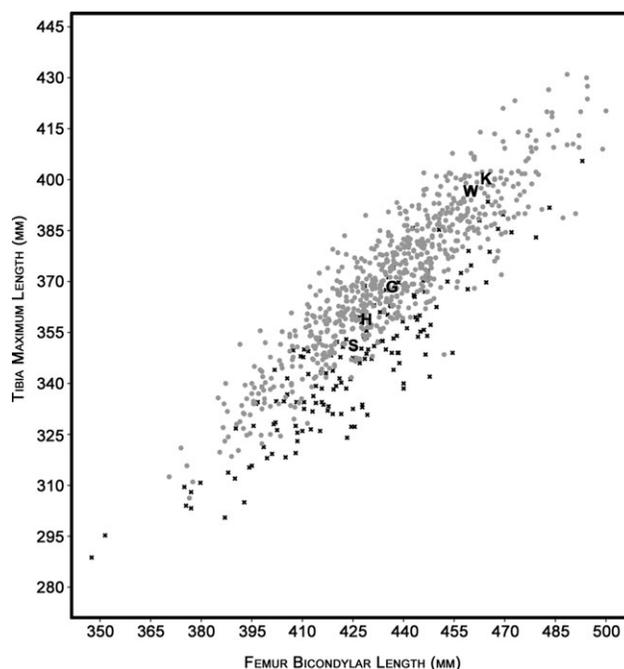
Perhaps this mosaic pattern is best demonstrated by comparing the Wizard's Beach and Spirit Cave early Holocene skeletons. These two individuals were buried within 150 km and arguably within a century of each other. Both had wide bodies, especially relative to stature. Even at the most conservative estimate (263 mm; see Table 1), Wizard's Beach would have had a bi-iliac breadth relative to

stature of 15.4%, but it is likely that his body breadth was closer to the estimate (288.79 mm) given his high mass relative to stature (see Table 2), following the principles of the cylindrical model (Ruff, 1994). Yet, though both individuals were buried (and presumably lived) in the same region, they have considerably different intralimb indices, statures, and body masses. A more limited but similar argument could be made in comparing the Gore Creek skeleton with the Kennewick skeleton, as both were recovered from the Western Plateau but had differing crural indices. Indeed, Wizard's Beach is considerably more similar to the Kennewick skeleton, despite being buried centuries and hundreds of kilometers apart.

This highlights the main biological implication of this study: bi-iliac breadth did not respond to evolutionary forces in tandem with limb lengths, namely intralimb proportions, in the Americas. This mirrors patterns found in examinations of Neandertals from the Levant; these groups have higher intralimb indices, as would be expected in warm environments, while retaining a purportedly ancestral trait of wide body breadths (Trinkaus, 1981; Ruff, 1994). One might therefore conclude that bi-iliac breadth may better reflect long-term evolutionary effects due to thermoregulation than intralimb indices,



**Fig. 2.** Scatterplot of brachial indices for comparative later Holocene North American male samples and EHAS. Black x's, arctic samples; grey dots, subarctic (temperate) North American samples. EHAS proportions are indicated by letter: H, Horn Shelter 2; K, Kennewick; S, Spirit Cave; W, Wizard's Beach.



**Fig. 3.** Scatterplot of crural indices for comparative later Holocene North American male samples and EHAS. Black x's, arctic samples; grey dots, subarctic (temperate) North American samples. EHAS proportions are indicated by letter: G, Gore Creek; H, Horn Shelter 2; K, Kennewick; S, Spirit Cave; W, Wizard's Beach.

or these morphologies are responding to different evolutionary forces, a trend found in other studies (e.g., Betti et al., 2012). Why bi-iliac breadth remained comparatively wide until the late Holocene among the indigenous populations of the Americas cannot be addressed in this study. However, an analysis of obstetric dimensions in comparison with bi-iliac breadth among high- and low-latitude indigenous humans from late Holocene North America shows independence between these sets of dimensions, potentially eliminating obstetric constraint as a selective factor restricting decreases in bi-iliac breadth (King et al., 2011). The shape of the pelvis, as well as intralimb indices, may be subject to evolutionary forces tied to locomotor efficiency (Ruff, 1995; Weaver, 2001; Weaver and Stuedel-Numbers, 2005; Higgins and Ruff, 2011), and so thermoregulation should not be considered to be the only factor influencing their morphologies. Indeed, it is possible that limb proportions ultimately reflect colonization and migration history in the Americas (Jantz et al., 2010, but see Betti et al., 2012), and so demonstrate a mitigated relationship with climate or mechanics. Only additional study of these morphologies and factors in concert will better model their interactions, and thus the evolutionary processes involved.

It is not possible to conclude whether the individual EHAS represent different breeding populations, but the contrast in their morphologies itself has important additional implications for the influence of environmental factors and population history on human morphology after the colonization of the Americas. There is strong evidence, both from the EHAS and recent comparative sample, that variation in intralimb indices and body breadth are morphologically independent among indigenous Americans.

(Arctic groups, such as the Inuit, are a notable exception.) Studies of ecogeographic variation in Old World humans have not shown morphological integration in these morphologies, though they demonstrate more similar trends in relation to climate than these North American results support. The mosaic of intralimb proportions among the EHAS further shows differences in the responses of the upper limb and lower limb to the same environmental effects within these individuals, a pattern that is atypical in the later Holocene samples. For example, of the later Holocene American sample ( $n = 277$ ), only 22 (approximately 8%) males have the high brachial indices ( $>79$ ) and low crural indices ( $<84$ ) found in both the Horn Shelter 2 and Spirit Cave EHAS. Even fewer males ( $n = 12$ , or approximately 4%) have the low brachial and high crural indices found in the Kennewick and Wizard's Beach EHAS. From these patterns, the following inferences are made:

1. All early Holocene male skeletons from North America observed herein have or are estimated to have wide body breadths and high body masses, both in a global and North American archaeological context. In contrast, by the early Holocene, intralimb indices were variable among these individuals. This pattern further suggests that a selection pressure, founder effect, or drift led to relative fixation of wide bodies in all of the colonizers of North America; this is a shared ancestral characteristic.
2. The shared wide body breadth and high body masses among the early and late Holocene American groups, compared with Old World variation, argue against separate ancestral populations for them. This moreover supports genetic evidence, as outlined in the Introduction, which argues for a common ancestry for

all populations that colonized the Americas. However, the shared morphology does not exclude the possibility for separate earlier and later colonizing populations that emerged from this shared ancestral population. Variation in other morphologies among the EHAS indicates local morphological differences among humans had manifest by the beginning of the Holocene.

3. The influence of drift and selection on the intralimb indices compared with bi-iliac breadth is unknown. It is evident that these evolutionary forces affected intralimb proportions differently from body breadth, effectively decoupling them in most North American populations. Moreover, there is evidence for independence in the response of brachial and crural indices to evolutionary forces. It is also possible that rapid movements of colonizing populations (Meltzer, 2002; Anderson and Gillam, 2006) might have not afforded enough time or environmental consistency to equally affect intralimb proportions, or that selection was too weak to influence their variation. This in turn would argue that bi-iliac breadth was much less responsive to these evolutionary forces than the limbs, or was constrained by evolutionary forces.
4. Given that wide bi-iliac breadths have been argued to be a product of human adaptation to cold environments (Ruff, 1994), and are found only among high latitude or some maritime modern humans, the shared wide body breadth trait among all North American samples fails to reject Beringia or another high latitude area as a location for the "standstill" that occurred during human migration to the Americas. This assumes that the ancestral population of all of the colonizers of the Americas did not already have a high mean bi-iliac breadth, a morphological state that cannot be eliminated based on current evidence. High body mass estimations (>70 kg) are indicative of wide bodies, and some Pleistocene modern humans in Eastern Asia had masses in excess of 80 kg (Shang and Trinkaus, 2010). Contrastingly, some Late Pleistocene colonizers of Japan had much lower body masses than the EHAS [e.g., Minatogawa 1's femoral head body mass estimate is 58.6 kg (from measurements in Baba and Endo, 1982)]. Ultimately, it is not known which populations gave rise to the humans that colonized the Americas. The mosaic morphology of limb proportions among the EHAS, furthermore, does not argue against the BIM, as there was an apparent decoupling in the response of brachial and crural indices with evolutionary forces and with variation in bi-iliac breadth.

In conclusion, the earliest male human skeletons from North America indicate that varying morphologies were already present by 9,000 years ago. All of these individuals appear to have been comparatively invariant in their wide body breadths. In contrast, intralimb indices, which among most humans follow the same patterns in both upper and lower limbs, instead follow atypical patterns and are variable among the EHAS. Together, these suggest morphological restrictions in the variation possible in bi-iliac breadth, a trait that continues into indigenous groups from the late Holocene, coupled with more variable intralimb proportions. The relative influence of genetic drift, selection, and gene flow awaits the development of genetic models and additional data from the early Holocene. Regardless, this evidence altogether lends support to the molecular argument for a single source population, possibly located in high latitudes, as the ancestor for all of the colonizers of North America.

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