The Appendicular Remains of the Kiik-Koba 2 Neandertal Infant

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ABSTRACT

The appendicular skeleton (scapula, humerus, ulnae, radii, metacarpals, pollical phalanges, hip bone, femora, tibiae and fibula) of the Neandertal infant from Kiik-Koba (Crimea), Kiik-Koba 2, are reassessed in the context of Late Pleistocene archaic and modern human infant remains. Based on long bone lengths, it should have been 4–6 months old at death, of indeterminate sex. The infant resembles (most) older Neandertals in its scapular dorsal sulcus axillary border, medially oriented radial tuberosity, radial curvature, large pollical opponens flange, and low crural index. It lacks the mediolateral pubic elongation seen in some older Neandertals, its brachial index is average for a Late Pleistocene or recent human, and its femoral neck-shaft angle is low for its developmental age. The percent cortical areas of its humerus and especially femur are average for its age, but its tibial one is unusually low. Yet, when scaled to intermetaphyseal lengths, the midshaft rigidities of all three long bones are unexceptional for a Late Pleistocene or non-mechanized recent human infant. The Kiik-Koba 2 infant limb bones thus provide additional data and inferences concerning the mosaic of Neandertal early postnatal development of postcranial features and appendicular hypertrophy, when assessed in the broader context of both Late Pleistocene and recent human infant remains.

INTRODUCTION

Since the 1980s, there have been a number of studies of Neandertal and early modern human infant and young child remains (e.g., Akazawa and Muhesan 2002; Cowgill et al. 2007; Gambier 1986; Golovanova et al. 1996; Heim 1982a; Henry-Gambier 2001; Madre-Dupouy 1992; Maureille 2002; Ponce de León et al. 2008, 2016; Tillier 1999; Tillier et al. 2003; Trinkaus 2008; Vacca et al. 2012; Weaver et al. 2016; Zilhão and Trinkaus 2002), as well as the accumulation of appropriate comparative data for recent human children (e.g., Frelat 2007; Cowgill 2008). These studies have to a large extent focused on craniofacial remains. Moreover, many of them have been concerned with assessing the degree to which distinctive Neandertal features appear early in development, in order to assess both possible behavioral influences on the skeleton and/or the degree to which skeletal elements might primarily reflect population history. In these assessments, there has been considerable variation in the extent to which infantile Neandertal remains have been seen to be distinct from those of early and/or recent modern humans.

In this context, we have undertaken a reassessment of the Kiik-Koba 2 infant postcranial remains. Kiik-Koba 2, af-ter being ignored for half a century, was described by Vlček in the 1970s (1972, 1973, 1975, 1977), although with very limited comparative data. Given additional data for other Neandertal, as well as Late Pleistocene and recent modern human, immature (and adult) remains, it appears appropriate to reassess the well-preserved Kiik-Koba 2 appendicular remains. Although one infant skeleton, of unknown cause of death, cannot resolve many of the developmental issues related to Late Pleistocene human paleobiology, it is hoped that this well-preserved appendicular infantile partial skeleton will shed some light on the ongoing issues regarding the extent to which the infantile morphology of the Neandertals foreshadows the patterns evident in their mature remains.

KIIK-KOBA AND THE KIIK-KOBA HUMAN REMAINS

THE SITE OF KIIK-KOBA
The site of Kiik-Koba in the Crimea (45° 03′ N, 34° 18′ E) was excavated by G.A. Bonch-Osmolovski in 1924–1926, at which time he uncovered three Middle Paleolithic levels (Levels III, IV, and VI), the deepest Level VI resting on bed-

rock (Bonch-Osmolovski 1940). Level III was overlain by the largely sterile deeper portion of Level II, and Levels IV and VI were separated by a largely sterile Level V. Level I contained recent material. The site provided abundant evidence for Middle Paleolithic anthropogenetic alterations, including hearths, shallow pits, deep pits and the human burials. The lithic assemblage of the lowest level (Level VI) has been attributed to the "Eastern Taubachian" and the upper levels to the "Eastern Micoquian" (Cohen and Stepanchuk 1999); it has more generally been subsumed within the "Crimean Micoquian Tradition" and referred to as the "Kiik-Koba Mousterian" (Chabai and Marks 1998; Demidenko 2015). Based on the associated assemblages, the Kiik-Koba Mousterian assemblages have been inferred to indicate "short-term primary and secondary butchery camps" (Demidenko 2015).

The Kiik-Koba 1 adult was buried into a depression, which was excavated through Level VI and apparently into the underlying limestone. The Kiik-Koba 2 infant was buried in close proximity to the adult in a separate grave, similarly excavated through Level VI and covered by higher Middle Paleolithic levels. The burials should therefore have been associated with the upper level Middle Paleolithic assemblages, probably Level IV.

On the basis of the Middle Paleolithic (Kiik-Koba Mousterian) association of the burials and the presence of both temperate and cold climate fauna (e.g., *Sus*, *Cervus*, *Saiga*, and *Marmota* in Levels IV and VI, plus *Rangifer* in Level IV), the burial level of Kiik-Koba 1 and 2 had been attributed to the early last glacial or possibly late last interglacial (early MIS 4 or late MIS 5) (Bonch-Osmolovski 1940; Klein 1965). Although radiometric dates are not available for the Middle Paleolithic levels at Kiik-Koba, reassessments of the Crimean Middle Paleolithic (e.g., Chabai and Marks 1998; Chabai et al. 2004; Cohen and Stepanchuk 1999) indicate that the various forms of the Crimean Middle Paleolithic (including the Kiik-Koba variety) persisted from at least the Last Interglacial (MIS 5) through the Early Last Glacial (MIS 4) to the earlier Interpleniglacial (MIS 3b). The presence of *Saiga*, *Rangifer* and *Marmota* suggest one of the colder phases of MIS 4 or earlier MIS 3.

THE KIIK-KOBA HUMAN REMAINS
In 1924, Bonch-Osmolovski (1925, 1940) discovered the disturbed burial of the older adult (Kiik-Koba 1) and the more intact burial of the human infant (Kiik-Koba 2). The former is represented by a canine, 17 hand elements, the well preserved right patella, tibia and fibula, and 53 bilateral foot remains. They were treated to extensive morphometric analysis by Bonch-Osmolovski (1941, 1954) and have been integrated into morphometric assessments of Neandertal leg and especially pedal remains (e.g., Pablos et al. 2013; Trinkaus 1975; Trinkaus and Rhoads 1999; Trinkaus and Shang 2008). They have also been assessed from a paleopathological perspective (Trinkaus et al. 2008), and the manual phalanges have been reassessed in comparative radiological analyses (Mednikova 2013, 2016; Mednikova et al. 2012). The infant remains, discovered adjacent to the

adult one, for a long time received little consideration (e.g., Anon. 1925; Bonch-Osmolovski 1925; Boule 1925; Ullrich 1958). They were described as being of little value [e.g., "almost useless" ("à peu près inutilisables") (Boule 1925: 404); "the destroyed skeleton of a child" (Yakimov 1970: 268)].

This situation was remedied in the 1970s by a series of articles by Emanuel Vlček (1972, 1973, 1975, 1977), in which he documented the preservation (excellent for a Middle Paleolithic infant) of substantial postcrania for Kiik-Koba 2. He provided photographs, radiographs, a morphological description with a few measurements, a reconstruction of overall body size and proportions, and general assessments as to its affinities to the Neandertals. In particular, Vlček emphasized the robustness of the limb bones (including cortical thickness) and the presence of a series of inferred Neandertal features (e.g., femoral and radial diaphyseal curvature, tibial retroversion) in this very young child's skeleton. However, Vlček compared the Kiik-Koba 2 remains to one modern European child's skeleton, thereby not taking into account normal variation or the changes in skeletal hypertrophy that have come with sedentism and mechanization (see Chirchir et al. 2015; Ruff et al. 2015).

More recently, two of us (ET and MBM) have been able to reassess the remains in the Kunstkamera, Saint Petersburg, and combine our observations with the comparative data of LWC. In this context, the axillary border of the Kiik-Koba 2 scapula has been reconsidered (Trinkaus 2008), the cross-sectional geometry of the partial humerus was included in an analysis of Late Pleistocene diaphyseal development (Cowgill 2008, 2010), and a possible paleopathological condition has been suggested in the context of Neandertal bioarcheology (Mednikova 2015). However, despite the attention by the three of us, the Kiik-Koba 2 remains have not been properly evaluated since the studies of Vlček.

THE KIIK-KOBA 2 REMAINS

PRESERVATION
Kiik-Koba 2 consisted of major portions of the skeleton in anatomical position *in situ*, but the cranium was crushed such that only fragments were recovered. The postcrania is variably preserved, with the long bone diaphyses being the most intact.

The vertebral column is currently represented by 22 partial neural arches and spinous processes, plus a dozen vertebral centra (probably 3 cervical, 5 thoracic and 4 lumbar). There are 16 fragments identified as ribs, of which 11 are morphologically costal and vary in preserved lengths from 11.8mm to 17.0mm. Available dimensions are in Table 1.

There is an eroded acromial end of a clavicle, plus additional fragments. The right scapula (see Figure 3 below) retains the lateral spine to the acromion, the suprascapular notch, the glenoid fossa metaphysis and most of the axillary border. The right humerus (see Figure 4 below) consists of 47mm of the proximal half of the bone, from the slightly eroded head metaphysis to the midshaft. The right

TABLE 1. DIMENSIONS OF A PROBABLE MANUBRIUM, THE SUFFICIENTLY COMPLETE VERTEBRAL CENTRA, AND TWO RIBS (measured laterally) OF KIIK-KOBA 2.

	Dorsoventral	*Transverse*	*Craniocaudal*
Manubrium	3.6	11.1	7.3
Thoracic	11.0	15.0	11.0
Lumbar 2–4	11.8	17.0	7.4
Lumbar 4–5	12.4	17.7	7.7
Rib 1	--	7.5	4.0
Rib 3/4	--	7.0	4.0

forearm is preserved in a sediment block (see Figure 7 below). The radial diaphysis is intact from the tuberosity to the eroded distal metaphysis, and the bone continues proximally through the neck to the lateral corner of the head metaphysis. There is a largely complete but crushed ulna. The left ulna is a complete intermetaphyseal bone (see Figure 6 below), with some distal displacement of the olecranon process and proximal edge abrasion. The left radius (see Figure 6 below) extends from the mid tuberosity to the distal metaphysis, with a mid-proximal break creating a minor curvature distortion in the rejoining (visually corrected in Figure 6).

The right forearm block retains intermetaphyseal sections of metacarpals 1 to 4 with dorsal bone loss, and the pollical proximal phalanx (see Figure 9 below). The left hand retains its pollical metacarpal and proximal phalanx, the former missing all of the proximal metaphysis but the ulnar-palmar corner and the latter being a complete intermetaphyseal bone. There are additional partial manual phalanges, only one of which (a middle phalanx) preserves a length (7.2mm).

The left coxal bone retains portions of all three elements (see Figure 10 below). The surviving portions of the ilium have all of the internal surfaces and the inferior external surfaces, with the ventral and dorsal thirds of the blade extending to the crest metaphysis. The iliac acetabular metaphysis is essentially complete, as is the greater sciatic notch and adjacent region of the arcuate line. The ventral and superior margins of the auricular surface are intact, but the actual surface is eroded and has fragments of the sacrum adherent to it. The ischium has most of the acetabular metaphysis and that of the tuberosity, but the pelvic surfaces are absent. The pubic bone preserves most of the symphysis and the superior pubic ramus to the acetabular margin of the obturator foramen, and then the internal surface to a corner of the acetabular metaphysis.

Both femora retain complete diaphyses, with variable metaphyseal preservation (see Figure 12 below). The right one has an oblique break through the lesser trochanter surface, and distally it extends close (1mm to 2mm) to the medial condylar metaphyseal surface. The left one has most of the anterior proximal metaphysis but lacks the posterior surface above the lesser trochanter. Distally it is broken off obliquely well above the condylar metaphysis. The tibiae

are less complete (see Figure 14 below). The right one retains the diaphysis from just distal of the tuberosity to the beginning of the distal metaphyseal flare. The left one has the tuberosity and a portion of the proximal diaphysis, but it lacks metaphyseal surface bone. There is also a piece of distal metaphysis, but it cannot be connected to the right diaphysis. Finally, there is a right fibular diaphysis with the complete intermetaphyseal length, albeit with four glue joins (see Figure 14 below). It is missing portions of the shaft cortical bone, especially anteriorly.

LONG BONE LENGTHS

Evaluation of a number of aspects of Kiik-Koba 2 depends on the intermetaphyseal lengths (IML) of its long bones, but only two of them (the left ulna and the right fibula) can be directly measured. The former has an IML of 71.4mm, but since the olecranon process was pressed slightly into the coronoid area, it is rounded off to 72mm (the same as Vlček 1973). The latter has an IML of 71.7mm (72mm for Vlček 1973), since there is continuous bone across the multiple glue joins, especially posteriorly. It is also possible to measure the IML of the right radius, in its block of matrix. The lateral third of the head metaphysis is present, and the distal metaphysis, although anteriorly eroded, has its mid-transverse border evident. The mid-proximal break does not seem to have altered either its length or its curvature. The resultant measureable IML is 64.2mm, which is rounded off to 65mm given the usually more proximal medial head metaphysis.

To determine the femoral lengths, the two bones were aligned along the clear distal margins of their lesser trochanter metaphyses. They were then measured from the proximal left femur to the distal medial right femur. Because the metaphyseal bicondylar angle of pre-ambulatory children is very close to 0° (Tardieu and Trinkaus 1994), measurements to the medial versus lateral condylar metaphysis should give similar results. Furthermore, because the distal right femur does not quite extend to the metaphyseal surface, it is estimated that the original lengths were 2mm beyond the preserved bone. These considerations provide a maximum IML of ≈102mm, and a "biomechanical" or diaphyseal length (from the intersection of the diaphyseal axis with the proximal metaphysis (or neck) to the tangent to the distal metaphysis) of ≈100mm. These values

are slightly longer than the length of 98mm provided by Vlček (1973).

For the tibial length, a least squares regression based on paired recent human immature tibiae and fibulae (from Indian Knoll, KY) was determined (TibIML=1.031 x FibIML+1.9, r^2=0.998, n=29); it provides a mean tibial maximum IML of 75.9±2.2mm, rounded off to 76mm (95% CI: 71.3–80.4mm), compared to the estimate of 78mm for Vlček. It is not possible to reliably estimate the humeral length directly from the preserved portion, but humero-femoral length proportions are consistent among recent human infants (age 0 to 2 years) across populations (HumMxIML=0.693 x FemMxIML + 13.1, r^2=0.981, n=108), as they are for adults (Trinkaus 1981). The resultant regression provides a humeral IML estimate of 83.8±2.4mm for Kiik-Koba 2 (95% CI: 79.0–88.7mm), rounded off to ≈84mm; it is modestly higher than Vlček's estimate of ≈78mm.

Bearing in mind the estimation present in some of these length measurements, they are employed in limb segment (brachial and crural) indices and to scale the hypertrophy of the humeral, femoral and tibial diaphyses.

VITAL STATISTICS

The Kiik-Koba 2 bones represent a very young child. Based on comparisons of estimated stature to recent humans, Vlček placed Kiik-Koba 2 in the middle of first year postnatal (5–7 months), and more recently Tillier (1999) estimated an age-at-death ≈12 months. Using the EuroAmerican tables of Maresh (1970), the maximum intermetaphyseal length of the femora (≈102mm) and the ulnar intermetaphyseal length of ≈72mm both provide an age-at-death of ≈3 months (cf. Scheuer et al. 2000). Regression of the same femoral length on age (0 to 2 years) for the pooled comparative skeletal sample (see below) provides an age estimate of 0.4±0.3 years (r^2=0.736, n=126).

Dentally-aged Neandertal infant remains that include long bones of a similar size are few. The neonatal Mezmaiskaya 1 and Le Moustier 2 have femoral IMLs of 78mm and 72mm respectively, and radial IMLs of 52mm and 54mm respectively. They are all distinctly shorter than those of Kiik-Koba 2, as is the radius of the ≈2 month old La Ferrassie 4 (IML of ≈56mm). The next oldest Neandertals providing long bone lengths and dental ages are Dederiyeh 1 and 2 and Roc de Marsal 1 (≈1.5 – ≈2.5 years), and their intermetaphyseal lengths are substantially greater. Even though the appropriate reference sample is unknown for the long bone length to age relationship for Kiik-Koba 2, an age at death in the middle of the first year postnatal, or probably slightly younger, appears most likely.

Vlček also commented on the very tight, semicircular greater sciatic notch of Kiik-Koba 2, and he concluded that it "was very probably a male" (1973: 540). Based on adult criteria (cf. Brůžek 2002), the left ilium of Kiik-Koba 2 does conform to the "male" pattern in both the greater sciatic notch shape and the composite arch. The notch is indeed semicircular (see Figure 10 below). A perpendicular from the line between the piriform tubercle and the notch surface adjacent to the acetabular metaphysis to the superior notch falls close to the auricular surface, the mature "male" configuration. The composite arch from the anterosuperior notch to the superior auricular surface is largely continuous, also "male" in adults. However, application of these criteria to recent immature skeletons of known sex provides unreliable results (Cardoso and Saunders 2008; Vlak et al. 2008), meaning that the sex of Kiik-Koba 2 is indeterminate.

COMPARATIVE ISSUES

AFFINITIES OF THE KIIK-KOBA HUMANS

Considerations of the Kiik-Koba 2 appendicular remains require assignment to one of the Late Pleistocene human groups, at least as a working hypothesis. The Kiik-Koba human remains have been considered to be Neandertals (or at least non-modern) since their discovery (e.g., Bonch-Osmolovski 1925; Boule 1926), even though they consist almost entirely of postcrania; the Kiik-Koba 1 heavily worn and pathological canine is morphologically undiagnostic. The affinities of the Kiik-Koba 1 manual, pedal and leg remains lie with late archaic humans generally (Bonch-Osmolovski 1941, 1954), but primarily with respect to the pattern of hypertrophy of the hand remains (especially the expanded opponens pollicis crest and distal phalangeal apical tufts). Moreover, the elevated diaphyseal robustness of the tibia (Lovejoy and Trinkaus 1980) suggests the "arctic" body proportions of the Neandertals, given similar levels of lower limb robustness through Pleistocene *Homo* (Trinkaus and Ruff 2012). The features aligning Kiik-Koba 2 with late archaic humans / Neandertals include the dorsal sulcus of its scapula (Trinkaus 2008; see below) and the opponens pollicis crest of its metacarpal 1 (Vlček 1975; see below). None of these features is distinctive of the Neandertals, and individual "Neandertal" features are known to be present in non-Neandertal late archaic humans and early modern humans (Trinkaus 2006, 2007; Wu et al. 2014).

The Kiik-Koba remains are also securely associated with a Middle Paleolithic assemblage, which are only associated with Neandertals in Europe and in the more northern portions of southwest Asia, as well as at the Crimean site of Zaskalnaya and the northern Caucasian site of Mezmaiskaya (Golovanova et al. 1999; Yakimov 1980). The molars from further east at Akhshtyr and Rozhok are similar to Neandertal maxillary molars, although the Akhshtyr metatarsals are undiagnostic (ET personal observation; cf. Golovanova et al. 1999). The anatomically modern child's cranium from Starosel'e is of uncertain stratigraphic provenience (Marks et al. 1997). The Kiik-Koba human remains will therefore be considered generally as "Neandertals."

COMPARATIVE FRAMEWORK

The evaluation of the Kiik-Koba 2 remains entails comparisons to other Late Pleistocene infantile postcranial remains, of which there is a growing number but for which there are variable amounts of information available. The primary specimens are other Neandertals from western Eurasia, principally those ≤2 years of age. These include the variably complete associated skeletons of Amud 5, 7 and 16, Dederi-

yeh 1 and 2, La Ferrassie 4 and 5, Kebara 1, Mezmaiskaya 1, Le Moustier 2 and 2b, Saint-Césaire 2 and 3, and Shanidar 7 and 10 (Colombet 2012; Colombet et al. 2012; Cowgill et al. 2007; Kondo and Dodo 2002; Kondo and Ishida 2002; Heim 1982a; Maureille 2002; Rak et al. 1994; Smith and Arensburg 1977; Tillier et al. 2003; Trinkaus 1983; Weaver et al. 2016), not all of which currently provide comparative data. Included with these remains are limited data from the apparently late fetal Sesselfelsgrotte 1 (Rathgeber 2006). Additional data are available for the slightly older (2–4 year old) La Ferrassie 6 and Roc de Marsal 1 children (Heim 1982a; Madre-Dupouy 1992).

Kiik-Koba 2 and these remains are also compared to samples of early modern humans. Those of southwest Asian Middle Paleolithic modern humans (MPMH) include the neonatal Qafzeh 13, plus the 2–4 year old Qafzeh 21 and Skhul 1 (McCown and Keith 1939; Tillier 1999); the Qafzeh 12 limb bones are pathological (Tillier et al. 2001) and are not included. Data on associated infantile remains for pre-last glacial maximum (pre-LGM) Upper Paleolithic early modern humans currently derive from the neonatal Kostenki-Volkovskaya 7 (ET personal observation), the Mladeč 102 partial femur (Trinkaus et al. 2006), the femur and tibia of Pataud 2 (Billy 1975), and humeral, femoral and tibial diaphyses from Cro-Magnon (Gambier 1986). The last are numbered 5A to 5H, and following Gambier (1986) they are associated as Cro-Magnon 5 (5A), 6 (5B, 5E and 5F), 7 (5C, 5G and 5H), and 8 (5D). The older Lagar Velho 1 remains also provide relevant data (Zilhão and Trinkaus 2002), as does the late fetal Ostuni 1b partial skeleton (Vacca et al. 2012).

Upper Paleolithic remains are usually separated into pre- and post-LGM samples (or E/MUP versus LUP), and differences have been noted between the samples (e.g., Brewster et al. 2014; Churchill 1994; Holt and Formicola 2008; Shackelford 2007). However, re-assessment of adult appendicular remains (Trinkaus 2015) suggests that there are only subtle differences in postcranial morphology between the samples, affecting primarily body shape (heavier for stature post-LGM) and the frequency distributions of axillary border shapes and radial tuberosity orientations. Given the dearth of infantile remains from the E/MUP, additional data are included for LUP immature remains from Arene Candide, Fauroux, Le Figuier, Grotte-des-Enfants, La Madeleine, Maritza, Romanelli, and Vado all'Arancio (Billy 1979; Fabbri 1987; Heim 1991; Henry-Gambier 2001; Paoli et al. 1980). These Upper Paleolithic modern humans are therefore considered as a single sample in the comparisons, designated UPMH.

A number of these infantile remains are provided with an age-at-death of zero, indicating a neonatal age. These assessments are based, as with Kiik-Koba 2, primarily on their dimensions relative to recent humans. All of them, with the exception of Ostuni 1b (Vacca et al. 2012), are *ex utero* and thus postnatal, although the modest femoral lengths of some (e.g., Sesselfelsgrotte 1) may indicate prematurity and hence "fetal" remains.

The osteometrics on these immature remains derive from the references provided, supplemented by personal assessment of a few of the specimens. The cross-sectional geometric parameters were derived principally by LWC (Cowgill 2008, 2010), with observations from Trinkaus et al. (2002a, b, 2006), Kondo and Dodo (2002), Kondo and Ishida (2002), Cowgill et al. (2007), and Colombet (2012). In a couple of cases for discrete traits, those which appear to be consistent through development, immature and mature remains are combined in the comparative samples.

In order to provide a recent human context for long bone diaphyses, data are included from the infant remains in six recent human samples, from birth to ≈2 years of age. They include remains from southern Africa (Dart Collection, Johannesburg), Kulubnarti (Sudan), Mistihalj (Serbia), Indian Knoll (Kentucky), California Native Americans, and Point Hope (Alaska) (for sample details, see Cowgill 2008, 2010). Only the southern African sample derives from a recent urban population, and any mechanization does not appear to have affected their level of appendicular hypertrophy (Cowgill 2008). The other samples are archaeological. Similar data are also provided, from prehistoric North American Native Americans (Tompkins and Trinkaus 1987), for the assessment of pubic bone length.

LIMB SEGMENT PROPORTIONS

Since Kiik-Koba 2 provides reliable estimates of three of its limb segment lengths and a more tenuous one for the fourth, it is appropriate to compare its limb segment proportions to those of other Pleistocene and recent human infants. Similar lengths (many with estimation) for all four elements are rare for Pleistocene infants (<2 years old: Dederiyeh 1, Grotte-des-Enfants 2, Mezmaiskaya 1, Le Moustier 2b, and Romanelli 3), but available for eight other 2–6 year olds. However, a substantial number of individuals preserve humeral and radial IMLs or femoral and tibial IMLs.

Intralimb segment proportions (brachial and crural indices) appear to be largely consistent among populations through development in recent humans, although values for both brachial and crural indices are highest in neonates and very young infants (Cowgill et al. 2012). It is nonetheless unclear whether the variation in indices is due more to proximal or distal limb segment length variation, given the absence of reliable body core size baselines for these fragmentary remains. Yet, among adults it is the distal segments which provide the greater variation, especially in the lower limb (Holliday and Ruff 2001).

In radiohumeral (brachial) proportions (Figure 1), there is little patterning across the recent human samples, with no consistent trend from high (Point Hope) to low (Kulubnarti) latitude samples. This pattern is in contrast to recent human adults, in which mean brachial indices are inversely correlated with latitude (Holliday 1999; Trinkaus 1981). Across Late Pleistocene adults, the samples are only marginally significantly different (p=0.042); the contrast is produced by Neandertal indices that are on average lower than those of the Upper Paleolithic samples. Among the immature specimens, most of the Neandertals, Qafzeh 10, and
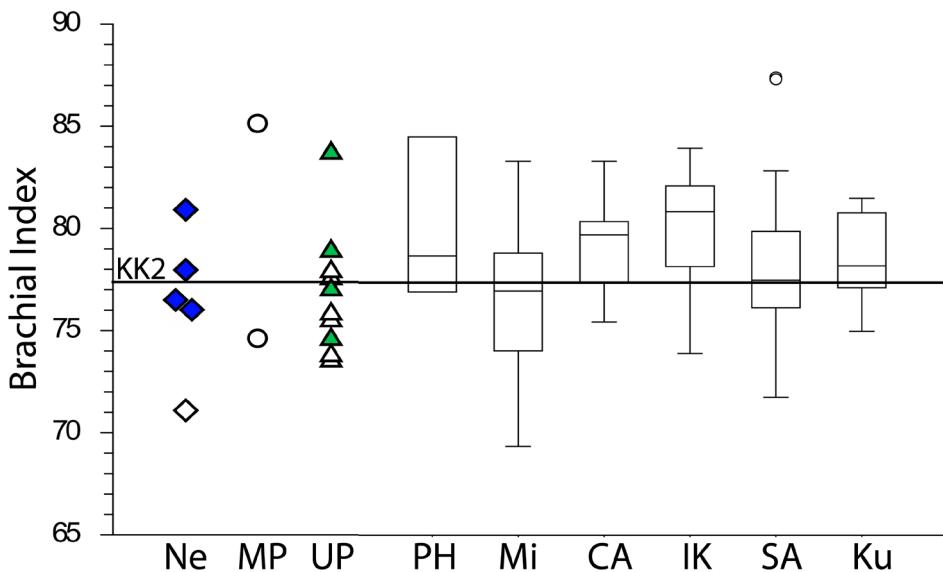
Figure 1. Brachial (radius/humerus) indices for Late Pleistocene and recent humans. For the Late Pleistocene samples: KK2: Kiik-Koba 2; Ne: Neandertals; MP: Middle Paleolithic modern humans; UP: Upper Paleolithic modern humans; solid symbols: <2 years; open symbols: 2 to 6 years. For the recent human samples: PH: Point Hope; Mi: Mistihalj; CA: California Amerindians; IK: Indian Knoll; SA: South Africans; Ku: Kulubnarti.

Upper Paleolithic specimens are well within the recent human distributions. The high outliers are the slightly older Skhul 1 and the late fetal Ostuni 1b; the low Neandertal is Roc de Marsal 1. The estimate for Kiik-Koba 2 (77.4; using the mean humeral length estimate) is unexceptional; using the 95% CI for the humeral length provides a range of 73.3 to 82.2, which bracket most of the variation.

The recent tibiofemoral (crural) proportions (Figure 2) show a contrast between the arctic Point Hope sample and the lower latitude ones. Most of the Neandertal and early modern human infants span the recent human ranges of variation, with one lower (and older) Neandertal (La Ferrassie 6) and three very high Upper Paleolithic specimens. One of those high values is Cro-Magnon 6, which may combine a femur and tibia from different individuals, but the other two are from the perinatal Ostuni 1b and the slightly older Pataud 2; neonates often have very high values. Kiik-Koba 2 has a very low index, below all of the others except La Ferrassie 6, whose values may be lower due to its older developmental age. It is possible that the low crural index of Kiik-Koba 2 is in part a product of the estimations of its femoral and tibial intermetaphyseal lengths. Decreasing its femoral length 2mm (right-left matching does not permit more of an adjustment (see Figure 12 below) and using the upper 95% CI limit for the tibial length estimate provides a crural index of ≈80, close to those of the older Dederiyeh 1 and 2 and Roc de Marsal 1. It remains well below the high values of 85.9, 86.5 and 88.2 for the neonatal Mezmaiskaya 1, Le Moustier 2, and La Ferrassie 5, respectively.

Despite the preservation of a largely complete ilium for Kiik-Koba 2 (see below, Figure 10), it is not possible to assess its overall pelvic (bi-iliac) breadth. The extensive cartilage in an infantile pelvis (Scheuer et al. 2000) prevents ac-curate iliac orientation. It is therefore unknowable whether Kiik-Koba 2 (and other neonatal/infantile Late Pleistocene humans) exhibited the wide pelves present in recent human cold climate infants (Cowgill et al. 2012) and in at least one adult Neandertal [but not all of them (Trinkaus 2011)].

THE SCAPULA

The Kiik-Koba 2 right scapula (Figure 3) provides observations on its glenoid metaphysis and axillary border. It is not clear how the proportions of the glenoid metaphysis relate to adult glenoid proportions, but the metaphyseal height (15.3mm) and breadth (9.1mm) for Kiik-Koba 2 provide a relatively low index of 59.5. This value is similar to those of the older Roc de Marsal 1 (60.9) and Qafzeh 10 (62.1) and well below the value of 71.5 for the infantile Dederiyeh 1. A sample of 0 to 6 year old UPMH provides a mean of 67.3 (±4.4, 60.3–71.4, n=8); there is no relationship with age (r^2=0.095).

Similarly, the metaphyseal axilloglenoid angle of Kiik-Koba 2 (145°) is unexceptional. Three Neandertals <3 years have values of 148°, 154°, and 154°, and three early modern human infants provide angles of 142°, 143°, and 145°.

The axillary border of Kiik-Koba 2, however, as previously described (Trinkaus 2008), exhibits an infantile version of the dorsal sulcus pattern [Vlček (1973: 543) noted that "the axillary border is thicker and there is a suggestion of the development of *sulcus marginalis*," but he did not specify whether the sulcus was ventral or dorsal]. The axillary border region retains a complete ventral surface and lateral margin, as well as a complete dorsal bar (see Figure 3). There is a longitudinal fossilization break between the lateral margin and the dorsal bar, the piece retaining the dorsal bar has been reattached to the remainder of the scap-
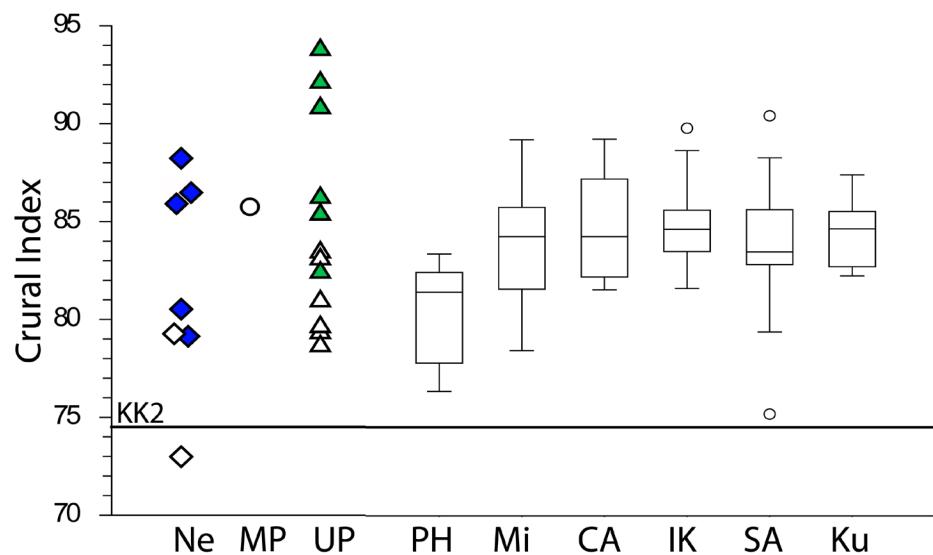
Figure 2. Crural (tibia/femur) indices for Late Pleistocene and recent humans. Symbols and abbreviations as in Figure 1.
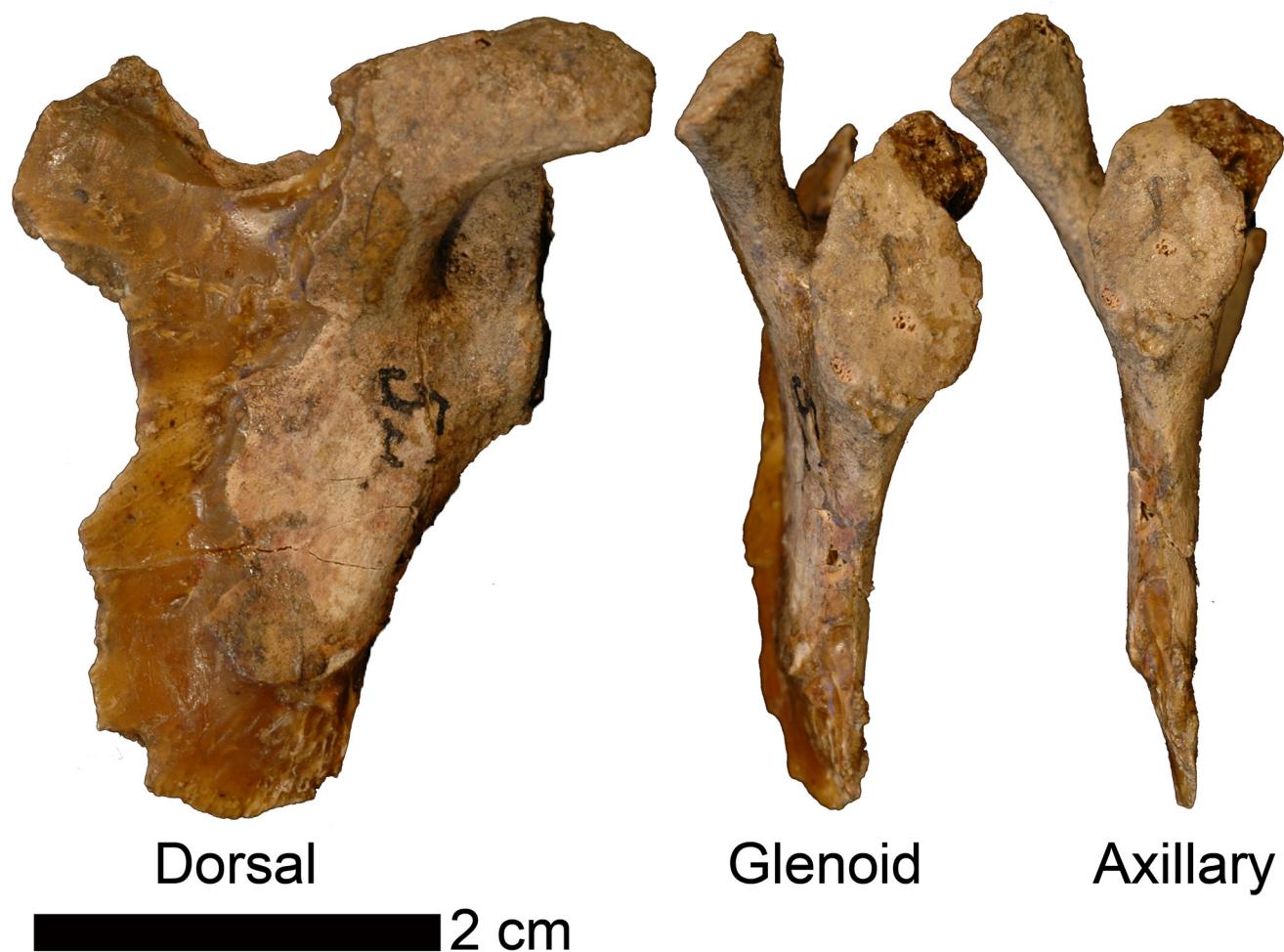

Figure 3. The Kiik-Koba 2 right scapula in dorsal, glenoid, and axillary views.

ula, and there is wax filling the missing portions of bone. However, there is excellent contact between the piece of the infraspinatus surface and the dorsolateral surface adjacent to the lateral spine and glenoid fossa metaphysis, and there is no distortion with respect to the mediolateral position of the dorsal bar relative to the ventral axillary margin, given continuous bone from the infraspinatus surface up to the glenoid metaphysis. There are small pieces of bone between the dorsal bar and the ventral margin, especially through the middle of the axillary border. Therefore, even though there is damage with some filling of missing bone with wax along the sulcus, the damage and its restoration do not affect the morphological interpretation of this anatomical region.

In the middle of the axillary border, the ventral surface from the lateral margin to the subscapularis surface is smooth and gently convex. The lateral margin is either at the ventral side of the axillary border or three-quarters of the distance from the dorsal to the ventral sides of the border; the precise assessment depends upon scapular orientation. Dorsal of the lateral margin, the bone has a longitudinal sulcus, which is evident from just caudal of the infraglenoid tubercle to the caudal break of the bone at the cranial end of the teres major attachment area. The lateral margin then rounds onto the dorsally convex dorsal bar and medially onto the infraspinatus surface.

The configuration of the Kiik-Koba 2 axillary border is therefore developed beyond the generally convex cross-section previously described for very young (<3 years postnatal) Neandertals (e.g., Kondo and Dodo 2002) and the minimally developed axillary border morphology documented by Busby (2006) for very young recent humans. Kiik-Koba 2 reveals a clear lateral margin and a clear sulcus along the margin. It is distinct from the ventral sulcus pattern, both in terms of the position of the lateral margin and the presence of a dorsal concavity. It is also difficult to subsume it within the bisulcate pattern. It is therefore an incipient dorsal sulcus pattern, with or without the lateral margin fully ventral. In the system of Churchill (1994), it would probably be classified as Stage 6. Among older immature and adult remains, the dorsal sulcus pattern is present in 75.0% of Neandertals (n=28), in 15.6% of UPMH (n=48), and absent from five MPMH.

THE ARM BONES

The proximal half of the right humerus (Figures 4 and 5) tapers from a broad partial metaphysis to the largely transverse break slightly distal of midshaft (56% of the estimated intermetaphyseal length). The proximal diaphysis is notable for its broad but pronounced bicipital sulcus, which is accentuated by an anterolateral crest for the pectoralis major insertion. The tuberosity for pectoralis major is clearly delineated from the adjacent subperiosteal bone, and reaches a maximum breadth of 3.7mm.

The midshaft (at the distal break; see Figure 4) is triangular in cross-section with rounded corners, especially anteriorly. The anteroposterior to mediolateral second moments of area (Table 2) provide a ratio (I_x/I_y) of 1.059, which

Figure 4. The Kiik-Koba 2 right humerus in anterior, posterior,r and medial views, plus a distal view of the near midshaft break. The smaller scale is only for the distal section.

is in the middle of the Late Pleistocene infant values (Table 3); only the older Roc de Marsal 1 and Arene Candide 11 humeri have much higher values, foreshadowing more ellipsoid adult cross-sections. Using only the external diameters (Table 4), there is considerable variation cross the Late Pleistocene infant humeri, and little difference across samples (right only: p=0.630; pooled sides: p=0.353). Kiik-Koba 2, with an index of 102.9, is among the rounder of the humeri.

The left ulna, although the most complete of the long bones, provides little morphological information. It is dorsally curved, especially in its proximal third, and there is a distinct line for the interosseus membrane along its lateral length (Figure 6). The diaphysis at midshaft has dorsovolar and mediolateral diameters of 4.9mm. The right ulna is too crushed to provide information (Figure 7).

The two radii, and especially the more complete right one (see Figures 6 and 7) exhibit relatively strong lateral curvature, with the maximum lateral extent distal of midshaft. The right midshaft is modestly broader than the left one (6.2mm versus 5.7mm). To the extent that it is visible in matrix (see Figure 7), the right radial tuberosity is medially facing; on the left radius, it is distinctly medially facing, in that the proximal extension of the interosseus crest bisects the radial tuberosity (Figure 8). Among Late Pleistocene humans, 74.1% of the Neandertals (n=29, 7 of which are im-
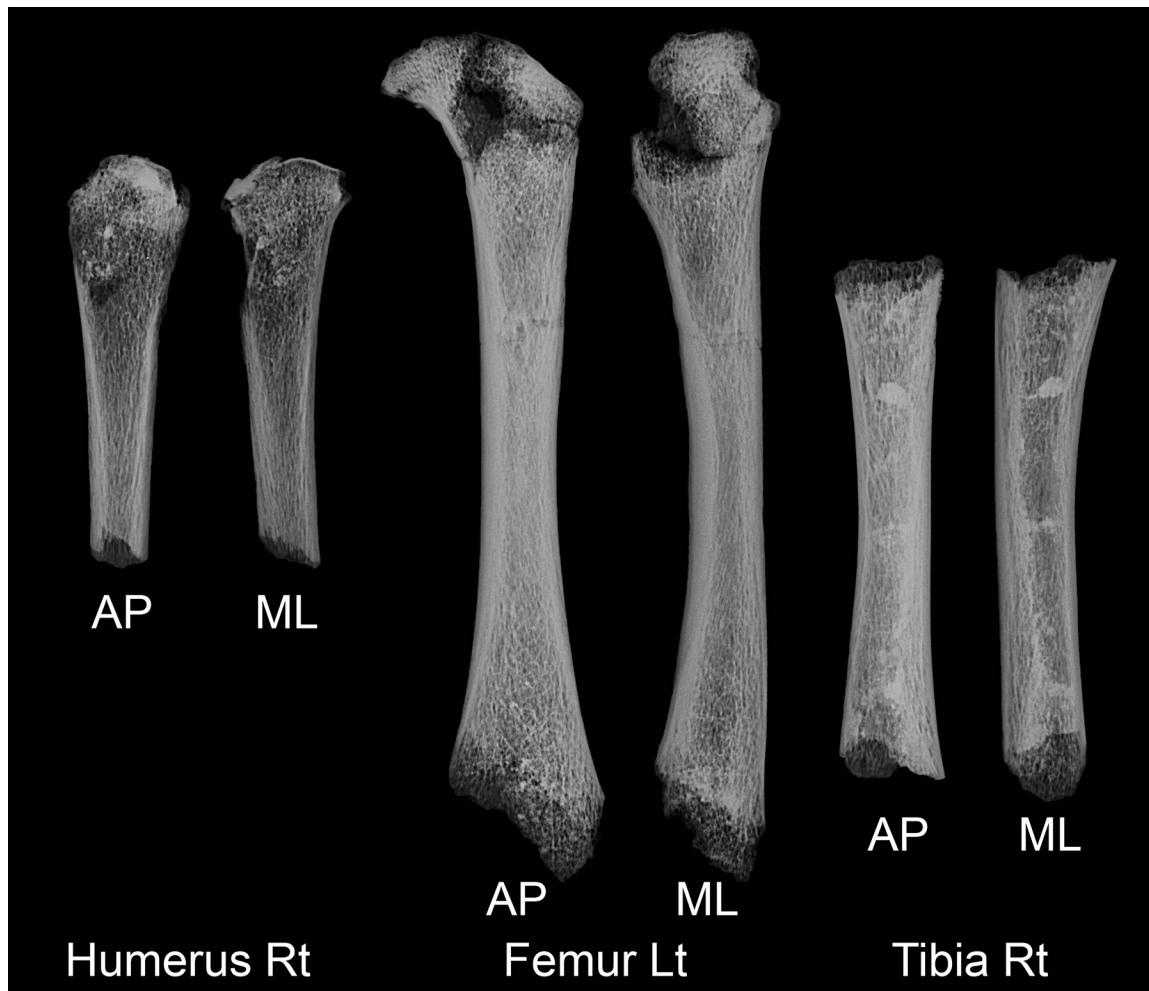
Figure 5. Anteroposterior (AP) and mediolateral (ML) radiographs of the Kiik-Koba 2 right humerus, left femur, and right tibia.

mature) have medially oriented radial tuberosities; in contrast, 8.3% of MPMH (n=6) and 5. 9% of UPMH (n=51, 3 of which are immature) have medially oriented tuberosities.

The other feature of note on the radii is a pathological growth of new bone on the anterior and lateral surfaces of the proximal left radius (see Figure 8), at the level of the distal tuberosity. It consists of slightly porous new bone laid down over the subperiosteal surface, with clear margins anteriorly and laterally. It extends up to 4.6mm from the proximal break. Similar changes are absent from the proximal ulna.

THE HAND REMAINS

Kiik-Koba 2 provides lengths for three of its right metacarpals and more complete data for its left pollical metacarpal and proximal phalanx (Table 5; Figure 9). The right second to fourth metacarpals provide intermetaphyseal lengths of ≈18.4mm, 18.3mm, and 16.1mm, respectively, and the right proximal pollical phalanx has an intermetaphyseal length of ≈8.8mm. The last is substantially shorter than the 9.4mm length of the left phalanx, providing an unusual level of asymmetry. It is possible that the right one has been foreshortened against the metacarpal 1 (see Figure 9).

The pollical metacarpal is notable for the distinct radial projection of the opponens pollicis insertion, foreshadowing the pronounced opponens pollicis flanges present on almost all adult Neandertal first metacarpals (Maki and Trinkaus 2011). Pronounced insertions for opponens pollicis are evident on the immature pollical metacarpals from Zaskalnaya (Vlček 1975), as well as those of Shanidar 7, Dederiyeh 1, and especially the modestly older La Ferrassie 6; it is absent from Roc de Marsal 1 (Kondo and Dodo 2002; Heim 1982a; Madre-Dupouy 1992; Trinkaus 1983). The Kiik-Koba 2 flange is among the largest known for a Neandertal infant.

It is also possible to compare intermetaphyseal lengths between the first and third metacarpals, the pollical proximal phalanx and metacarpal, and the last two to humeral length for Kiik-Koba 2 and a limited number of Late Pleistocene infants (most >2 years of age) (Table 6). With the infants and young children, as with the adults (Trinkaus 2016b), there is no difference in first to third metacarpal length indices across the Late Pleistocene samples. Kiik-Koba 2, however, has a rather short pollical metacarpal, although its low index of 61.2 is approached by that of the older Skhul 1. It also has a relatively high pollical proximal

TABLE 2. LONG BONE LENGTHS AND MIDSHAFT PROPERTIES,
IN MM, MM² (areas) AND MM⁴ (second moments of area).[1]

	Humerus-Right	Femur-Right	Femur-Left	Tibia-Right
Maximum IML[2]	((84))	(102)		(76)
Diaphyseal IML	((84))	(100)		(75)
Anteroposterior diameter	7.1	9.2	8.9	9.6
Anterior cortical thickness	2.0	--	2.1	1.5
Posterior cortical thickness	1.0	--	3.1	1.2
Mediolateral diameter	6.9	8.5	8.4	8.5
Medial cortical thickness	1.7	--	2.2	1.3
Lateral cortical thickness	1.3	--	1.8	1.1
Total area (TA)	38.5	--	58.7	64.1
Cortical area (CA)	12.7	--	46.0	31.2
Medullary area (MA)	25.8	--	12.7	32.9
Ant-post 2nd moment of area (I_x)	108.1	--	279.6	270.8
Med-lat 2nd moment of area (I_y)	102.1	--	244.1	213.5
Ant-post section modulus (Z_x)[3]	30.5	--	62.8	56.4
Med-lat section modulus (Z_y)[3]	29.6	--	58.1	50.2
Polar moment of area (J, I_p)[4]	210.2	--	523.7	484.3
Polar section modulus (Z_p)[4]	60.1	--	120.9	106.6

[1]Areas and second moments of area are calculated from external diameters and cortical thicknesses using standard ellipse formulae (O'Neill and Ruff 2004). External diameters are from the original bones; cortical thicknesses are from radiographs, scaled using the external diameters.

[2]See text for length estimations. IML: Intermetaphyseal length. Single parentheses indicate modest estimation; double parentheses indicate more tenuous estimation.

[3]Section moduli computed from second moments of area by dividing the latter by half of the external diameter.

[4]The sum of the perpendicular second moments of area or section moduli.

phalanx to metacarpal index, although the two values from the right and left pollical phalanges bracket those of the older Roc de Marsal 1 and Qafzeh 10, and the lower right index is close to those of Qafzeh 21 and Grotte-des-Enfants 1. Yet, there is considerable variation in these indices across the samples. When the pollical lengths are scaled to humeral length, the Kiik-Koba 2 metacarpal 1 index (estimated given humeral length uncertainty) is in the middle of the other Late Pleistocene values, and its phalangeal ones are moderately high (again, they bracket those of Roc de Marsal 1 and Qafzeh 10). In none of these indices do the infants and children exhibit the differences in relative pollical phalangeal lengths evident in mature Late Pleistocene hand remains, but those differences are driven mostly by differential distal phalanx lengths (Trinkaus 2016b).

THE PELVIC REMAINS

The left hip bone of Kiik-Koba 2 retains portions of all three elements (Figure 10). Rounding out the arc of the iliac crest metaphysis provides a maximum iliac height of ≈38.5mm and a height from the greater sciatic notch of ≈31mm; the dorsoventral dimension is ≈43mm, and the minimum distance from the acetabular metaphysis to the auricular sur-

face is 17.8mm. The acetabulo-symphyseal pubic length is ≈23.2mm, and the superior ramus breadth and minimum height are 4.8mm and 6.3mm respectively. As noted above, the greater sciatic notch forms a tight semicircle, but sexual attribution based on its shape in so young an individual is unreliable.

Given the tendency for mature Neandertals (especially males) to have elongated superior pubic rami (Trinkaus 1984; Rosenberg 1988) and the presence of some elongation in older immature Neandertals (Kondo and Dodo 2002; Tompkins and Trinkaus 1987), the Kiik-Koba 2 and comparative pubic lengths were plotted again femoral lengths (Figure 11). The two older Neandertals (Dederiyeh 1 and La Ferrassie 6) are modestly above the recent human distribution, whereas the neonatal Mezmaiskaya 1 proportions fall in line with the recent human distribution [differences in assessment (Kondo and Dodo 2002; Majó 1995; Tompkins and Trinkaus 1987; Weaver et al. 2016) probably reflect contrasting recent human reference samples, differences in the measurement of immature pubic bones, and evaluations of the degrees to which the fossil infants' proportions diverge from the reference samples]. The pubic proportions of the two early modern humans (Lagar Velho 1 and Qafzeh 10)

TABLE 3. RATIOS OF PERPENDICULAR ANTEROPOSTERIOR (I_x) AND MEDIOLATERAL (I_y) MIDSHAFT SECOND MOMENTS OF AREA FOR KIIK-KOBA 2, LATE PLEISTOCENE INFANT REMAINS AND POOLED RECENT HUMANS (Specimens are arranged in their orders of maturity within the samples, based on their approximate ages-at-death [in years]).

	Age	Humerus-Right	Femur	Tibia
Kiik-Koba 2	0.4	1.059	1.145	1.268
Neandertals				
Amud 16	0	--	0.862	--
La Ferrassie 5	0	--	0.822	1.400
Le Moustier 2	0	1.103	0.758	--
Le Moustier 2b	0	--	--	1.406
Saint-Césaire 2	0	--	0.908	--
Saint-Césaire 3	0	--	0.894	--
La Ferrassie 4	0.15	--	0.953	1.048
Kebara 1	0.45	--	--	1.458
Amud 5	0.6	--	--	1.260
Dederiyeh 1	1.5	0.778	0.930	1.451
Shanidar 10	1.5	--	--	1.092
Dederiyeh 2	2	--	1.186	1.707
La Ferrassie 6	2.5	--	0.939	1.246
Roc de Marsal 1	2.5	1.268	0.943	--
MPMH				
Skhul 1	3	--	1.118	1.368
UPMH				
Cro-Magnon 6 (5BEF)	0	--	1.010	1.579
Cro-Magnon 7 (5CGH)	0	--	0.833	--
Cro-Magnon 8 (5D)	0	--	0.765	--
Romanelli 3	0.95	--	0.910	0.974
Mladeč 102	1.2	--	0.984	--
Cro-Magnon 5 (5A)	1.6	1.152	--	--
Arene Candide 11	2.4	1.359	0.819	1.155
Arene Candide 5B	2.8	1.156	--	--
Recent Humans (0–2 years)		1. 104±0.173 (110)	0. 872±0.143 (125)	1.209±0.199 (114)

are within or along the lower portion of the recent distribution. The Kiik-Koba 2 proportions are in the middle of the very small recent humans and close to those of Mezmaiskaya 1. To the extent indicated by these comparisons, the pubic elongation of older immature Neandertals does not appear to have been present in at least these Neandertal infants.

It is also possible to assess iliac height relative to femur length for Kiik-Koba 2 and a few other Late Pleistocene infants, although it cannot be determined whether any contrasts reflect overall pelvic versus crural dimensions (see above). An index of iliac height to femur length is ≈37.3 for Kiik-Koba 2, which is below those of the Dederiyeh 1 (39.7) and 2 (40.1), La Ferrassie 4b (42.5), Mezmaiskaya 1 (41.0) and Le Moustier 2 (41.9) Neandertals. It is close to those of the LUP Grotte-des-Enfants 1 (38.0) and 2 (37.3). Older (2–6 year old) Late Pleistocene children tend to have lower indices (La Ferrassie 6: 34.2; Qafzeh 10: 30.2; UPMH: 35.5±2.2, n=6). Within the younger or the older samples, there appears to be little difference in relative iliac-to-femur dimensions.

**TABLE 4. ANTEROPOSTERIOR TO MEDIOLATERAL DIAPHYSEAL DIAMETER INDICES
FOR KIIK-KOBA 2 AND COMPARATIVE LATE PLEISTOCENE HUMAN REMAINS
(Specimens are arranged in their orders of maturity within the samples,
based on their approximate ages-at-death [in years]).**

	Age (yrs)	*Humerus Right Midshaft*	*Radius Midshaft*	*Femur Midshaft*	*Femur Proximal*	*Tibia Midshaft*
Kiik-Koba 2	0.4	102.9	70.2	107.1	80.4	112.9
Neandertals						
Sesselfelsgrotte 1	-0.1	82.5	--	93.8	--	--
Amud 16	0	--	--	92.9	--	--
La Ferrassie 4	0	103.6	--	91.2	--	--
La Ferrassie 5	0	151.7	--	92.1	--	--
Le Moustier 2	0	101.8	--	94.3	--	--
Le Moustier 2b	0	--	--	92.6	--	--
Saint-Césaire 2	0	--	--	85.8	--	--
Saint-Césaire 3	0	--	62.9	94.7	--	--
La Ferrassie 4b	0.15	--	--	93.5	--	--
Amud 7	0.5	105.3	--	--	--	--
Dederiyeh 1	1.5	96.9	74.3	98.1	86.5	119.6
Shanidar 10	1.5	--	--	--	--	108.4
Dederiyeh 2	2	--	--	98.0	88.7	106.9
La Ferrassie 6	2.5	133.3	66.7	93.9	77.0	105.7
Roc de Marsal 1	2.5	113.4	68.4	92.1	93.0	--
MPMH						
Skhul 1	3	104.1	78.9	112.9	83.3	118.2
Qafzeh 10	6	121.7	81.8	105.6	88.5	--
UPMH						
Ostuni 1b	-0.1	95.9	88.3	87.7	--	111.3
Cro-Magnon 6 (5BEF)	0	--	--	92.6	100.0	112.5
Cro-Magnon 7 (5CGH)	0	--	--	91.3	80.0	112.5
Cro-Magnon 8 (5D)	0	--	--	88.7	60.0	--
Kostenki 7	0	112.5	--	90.8	--	104.8
Pataud 2	0.4	--	--	100.0	95.5	126.7
Romanelli 3	0.95	--	--	101.8	--	--
Mladeč 102	1.2	--	--	95.7	81.8	--
Fauroux 1	1.25	--	--	84.5	84.0	--
Grotte des Enfants 2	1.5	120.4	78.5	103.3	93.6	--
Vado all'Arancio 2	1.5	--	82.9	--	--	--
Cro-Magnon 5 (5A)	1.6	104.7	--	--	--	--
Figuier 1	2.1	133.3	--	--	--	--
Arene Candide 11	2.4	136.8	75.0	94.6	79.4	121.1
Arene Candide 5B	2.8	133.0	72.8	104.2	84.1	109.5
Grotte des Enfants 1	3	127.0	82.1	103.8	78.7	117.6
La Madeleine 4	3.3	128.0	--	97.2	93.7	--
Lagar Velho 1	4.75	123.9	80.2	94.5	83.0	115.8
Arene Candide 8	5.5	123.2	78.5	109.6	89.0	118.8
Romanelli R44	5.5	130.0	--	--	--	--
Maritza 2	6	128.0	72.3	98.8	82.9	116.4

Figure 6. The forearm bones of Kiik-Koba 2. From left to right: medial view of the left radius; dorsal view of the left radius; dorsal view of the right radius (see also Figure 7), lateral view of the left ulna. The right radius image was digitally extracted from the image of the right forearm and hand block (see Figure 7); the diaphyseal and proximal metaphysis margins are above the matrix and clear, but the distal margins of the eroded distal metaphysis are less precise.

Figure 7. The Kiik-Koba 2 right forearm and hand as preserved in matrix in dorsal view.

THE LEG BONES

The femora and tibiae of Kiik-Koba 2 are incomplete (see Figure 5; Figures 12 to 14; see Table 2), but combining sides and the length from the fibula provides substantial information in addition to length proportions. Each femur has a broad and slightly roughened area for the linea aspera, which is more accentuated on the mid to proximal diaphysis. The gluteal tuberosities are raised rugose ridges, but the margins are insufficiently distinct to provide breadths. The femora are longitudinally evenly concave on their posterior surfaces (see Figure 13), but their anterior contours are straight with a slightly concavity just proximal of the distal metaphysis.

The tibiae and fibula (see Figure 14) are straight and have little musculoligamentous subperiosteal relief. The proximal half of the right anterior tibial crest has a muscular line, extending distally from the tibial tuberosity, and the left tibial tuberosity provides a breadth of ≥8.8mm. The fibula does not provide any longitudinal sulci, and the interosseus line is barely perceptible.

It is possible to estimate the femoral neck angle at ≈134°. Femur neck angles normally decrease with age as loads increase (Anderson and Trinkaus 1998), and that change is evident in the pooled recent human sample (Figure 15; least squares regression (LSR) slope: –5.5, r= –0.420, n=119). The three Late Pleistocene neonatal femora have moderately high angles, but the older infant ones have average or modestly low ones. The Kiik-Koba 2 femoral neck angle, for its age, falls along the lower margin of the recent human distribution. Slightly older (2 to 5 year old) immature Neandertal angles (129°, 130°) and Upper Paleolithic ones (130°, 134°, 140°) follow the same pattern, but the Qafzeh 10 one (139°) remains high, similar to the MPMH adults (Trinkaus 1993). All except the last value indicate a normal decrease in the angle toward the lower values evident in mature Neandertals and Upper Paleolithic humans.

The tibial midshaft cross-sectional diaphyseal proportions of Kiik-Koba 2 are similar to those of other Late Pleistocene infants (see Tables 3 and 4), in that they have anteroposterior to mediolateral diameter indices that are mostly between 100 and 120 and second moment of area ratios between 1.0 and 1.5. The Kiik-Koba ones of 112.9 and 1.268 fall in the middles of each of the ranges. The Kiik-Koba 2 femoral midshaft second moment of area ratio of 1.145 is relatively high, since most infant femoral midshafts are wider than deep; it is exceeded only by Dederiyeh 2.

Figure 8. The Kiik-Koba 2 left proximal radius. Left: medial view with the interosseus crest indicated by black arrows and the volar and dorsal margins of the radial tuberosity indicated by the white arrows. Right: enlarged view of the new bone formation on the anterolateral proximal radius; the arrow indicates its distal extent. The scale is for the medial view only.

The midshaft diameter index is also high, and it is exceeded only by the older Skhul 1 and Arene Candide 8. At the same time, the Kiik-Koba 2 subtrochanteric diameters (antero-posterior: 10.0mm and 9.7mm; mediolateral: 12.2mm and 12.3mm) provide an average index (80.4) that is among the lower values for Late Pleistocene infants. Yet, the infant (≤2

years) midshaft index and ratio values are insignificantly different across these samples for the femur (p=0.818 and 0.751) and tibia (p=0.233 and 0.579), despite substantial differences in adult femoral (but not tibial) shaft shapes (Trinkaus and Ruff 2012).

DIAPHYSEAL HYPERTROPHY

In addition to considerations of individual bone morphology and proportions, it is possible to assess the relative cortical thicknesses and scaled rigidities of the humeral, femoral and tibial midshafts [the Kiik-Koba 2 humeral and femoral metaphyseal dimensions are a reflection of body size (Ruff 2007) and are not reflections of limb robustness]. Relative cortical thickness, or percent cortical area (%CA), is not strictly a measure of hypertrophy, since it reflects both the relationship between endosteal resorption and subperiosteal deposition during development and the quantity of cortical bone resisting loads on the diaphysis (Ruff et al. 1994). Midshaft polar moments of area relative to body size should reflect resistance to both bending and torsional loads, ones that are nonetheless likely to be small in very young infants. Midshaft rigidity should be scaled to bone length times body mass (Ruff 2003). However, damage to the Kiik-Koba 2 distal femora, and hence the absence of distal metaphyseal breadth or other reliable indicators of body mass (see Ruff 2007), means that these values can be scaled only to bone length. The comparisons therefore assume that body proportions were similar across these samples, which should be valid for the proximal limb segments but less so for the tibia (Cowgill et al. 2012).

Percent cortical area decreases during early development in recent human infants, especially for the humerus and femur (Figures 16 to 18). In the pooled recent human sample, slopes are –14.1 and –10.5 for the right humerus and the femur respectively (r= –0.696, n=111; r= –0. 622, n=125). The decrease is less in the tibiae (slope: –5.6, r= –0.387, n=114). The few available %CAs for Late Pleistocene humeri <2 years of age fall within the recent human distribution, with Kiik-Koba 2 and Dederiyeh 1 having

TABLE 5. DIMENSIONS OF THE KIIK-KOBA 2 LEFT POLLICAL METACARPAL AND PROXIMAL PHALANX, IN MILLIMETERS.

	Metacarpal 1	Proximal Phalanx 1
Intermetaphyseal length	11.2	9.4
Midshaft height	3.8	2.2
Midshaft breadth	5.3	4.2
Opponens breadth[1]	5.4	--
Proximal breadth[1]	5.1	--
Proximal metaphyseal height	--	3.8
Proximal metaphyseal breadth	--	5.9
Distal metaphyseal height	4.8	2.2
Distal metaphyseal breadth	4.9	4.5

[1]The maximum breadth across the shaft and opponens pollicis crest, and the minimum breadth of the proximal diaphysis.
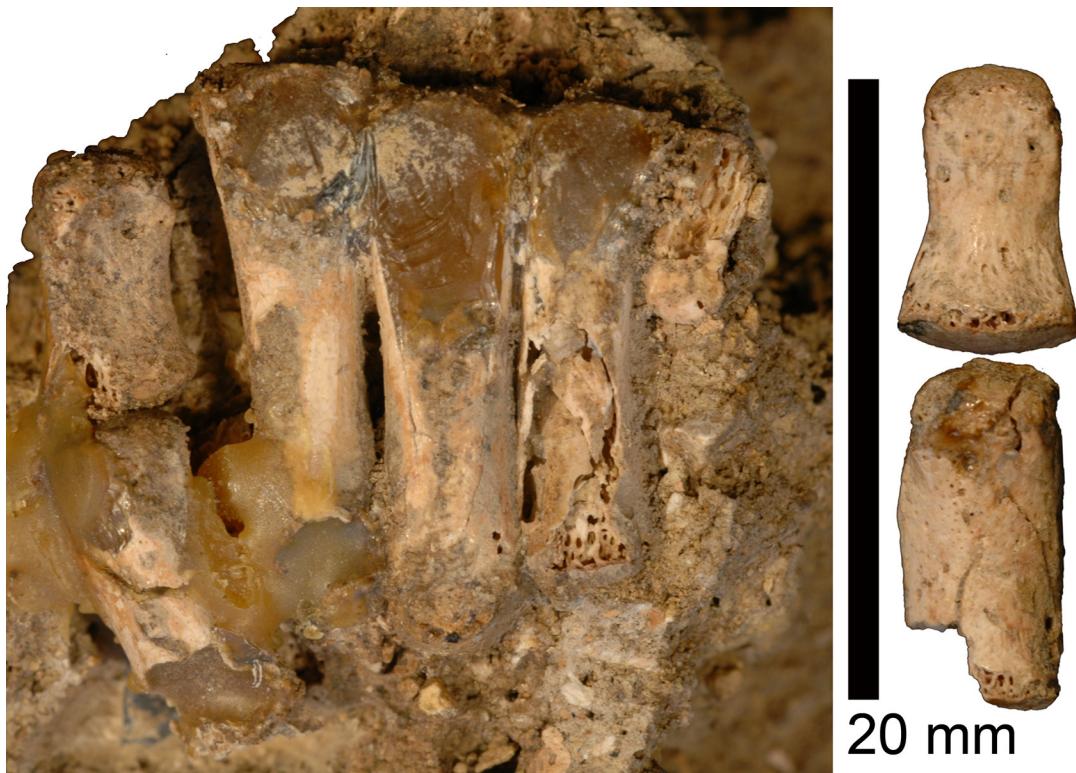
Figure 9. Left: dorsal view of the Kiik-Koba 2 right metacarpals and proximal pollical phalanx, as preserved en bloc. Right: palmar views of the left pollical metacarpal and proximal phalanx.

Figure 10. Internal views of the Kiik-Koba 2 left ilium and superior pubic ramus.

**TABLE 6. METACARPAL (MC#) AND POLLICAL PROXIMAL PHALANX (PP1)
INTERMETAPHYSEAL LENGTH PROPORTION RATIOS, EXPRESSED AS PERCENTAGES
(Specimens are arranged in their orders of maturity within the samples, based on their
approximate ages-at-death [in years]).**

	Age	MC1/MC3	PP1/MC1	MC1/Humerus	PP1/Humerus
Kiik-Koba 2	0.4	61.2	(78.6)/83.9[1]	(13.3)	(10.5)/(11.2)[1]
Humerus 95% CI[2]		--	--	(12.6) – (14.2)	(11.9) – (10.6)[3]
Humerus 95% CI[2]		--	--	--	(11.1) – (9.9)[4]
Neandertals					
Dederiyeh 1	1.5	--	72.2	13.5	9.8
La Ferrassie 6	2.5	67.0	--	--	--
Roc de Marsal 1	2.5	70.2	80.8	13.4	10.9
MPMH					
Qafzeh 13	0	66.4	--	14.0	--
Qafzeh 21	3	--	76.7	--	--
Skhul 1	3	63.7	--	12.2	--
Qafzeh 10	6	77.0	80.7	13.5	10.9
UPMH					
Grotte des Enfants 2	1.5	--	72.3	12.6	9.1
Arene Candide 5B	2.8	--	--	--	10.3
Grotte des Enfants 1	3	66.0	78.4	12.6	9.9
La Madeleine 4	3.3	--	--	--	9.8
Lagar Velho 1	4.7	70.2	68.4	13.9	9.5
Arene Candide 8	5.5	72.3	72.2	13.5	9.7
Maritza 2	6	--	53.2	18.8	10.0

[1]The two values are from using the right (8.8mm) and left (9.4mm) proximal phalanx 1 lengths. An average of the right
and left intermetaphyseal lengths (≈9.1mm) provides a PP1/MC1 index of ≈81.4 and PP1/humerus index of ≈10.8.
[2]The Kiik-Koba 2 indices using the 95% CI for humeral length (79.0 – 88.7mm); see text.
[3]The indices using the humeral 95% CI and the left proximal phalanx length of 9.4mm.
[4]The indices using the humeral 95% CI and the right proximal phalanx length of ≈8.8mm.

relatively low values (see Figure 16). The modestly older Roc de Marsal 1 has an appropriately similar value (67.1%). In the femur, the Late Pleistocene %CA values follow the recent human distribution (the modestly low UPMH value is Romanelli 3), with decreasing values with age (see Figure 17). Kiik-Koba 2 is in the middle of the distribution. In the tibial midshaft, however, three of the Late Pleistocene infants have rather low values for age, Kiik-Koba 2, Romanelli 3, and Dederiyeh 2 (see Figure 18). These %CA values for Kiik-Koba 2 are evident in the radiographs of the long bones (see Figure 5), in which the tibia has markedly thinner cortical bone than the humerus or the femur. Yet, it is joined in these comparisons by other Late Pleistocene infants.

In the right humeral and the femoral polar moment of area versus bone length comparisons (Figures 19 and 20), as previously documented (Cowgill 2010), all of the Late Pleistocene values fall comfortably within the pooled re-

cent human distributions. Kiik-Koba 2 is proportionately indistinguishable from either the recent or the Late Pleistocene human samples. In the tibial comparison (Figure 21), Kiik-Koba 2 and several small Neandertals fall among the more robust of the recent humans, despite the low %CA for the Kiik-Koba 2 tibia. It is joined by Kebara 1. The very low crural index of Kiik-Koba 2 (see Figure 2) may contribute to its relative tibial position, but this does not account for the more robust proportions of smaller Neandertal femora.

DISCUSSION

The Kiik-Koba 2's appendicular remains therefore largely follow Vlček's conclusion that it represents a Neandertal infant. However, it has been possible to expand on his observations and modify some of them, given the use of a diverse recent human sample and Late Pleistocene immature comparative materials.
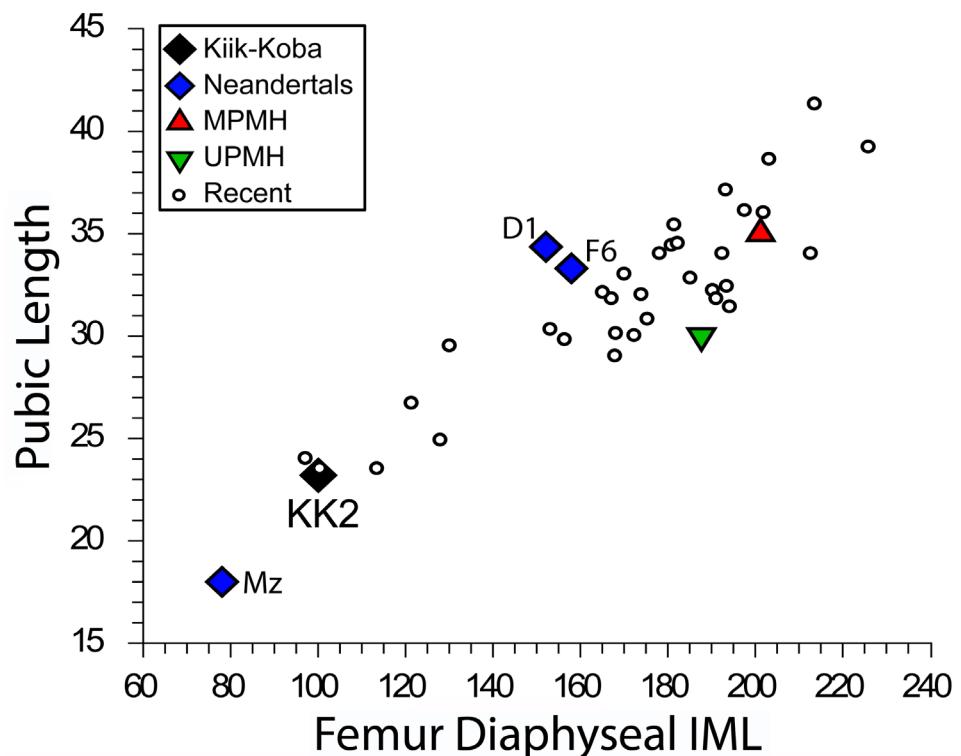
The features of Kiik-Koba 2 that align it principally

Figure 11. Bivariate plot of pubic acetabulo-symphyseal length versus femoral diaphyseal intermetaphyseal length (in mm) for Kiik-Koba 2 (KK2), the Dederiyeh 1 (D1), La Ferrassie 6 (F6), and Mezmaiskaya 1 (Mz) Neandertals, the Qafzeh 10 Middle Paleolithic modern human (MPMH), and the Lagar Velho 1 Upper Paleolithic modern human (UPMH).

Figure 12. The Kiik-Koba 2 femora in anterior (left) and posterior (right) views.

Figure 13. The Kiik-Koba 2 femora in medial view.

Figure 14. The Kiik-Koba 2 tibiae and fibula in anterior view.

with the Neandertals, as opposed to early and recent modern human infants, include its low crural index (but not brachial index, given minimal distinction in it across the comparative samples), the dorsal sulcus pattern of its scapular axillary border, the directly medial orientation of its radial tuberosity, the (apparently, given that it is metaphyseal) narrow scapular glenoid fossa, and the distinct opponens flange on the first metacarpal. One of these features, the relatively narrow glenoid fossa, appears to be ancestral for the genus *Homo*, at least with respect to mature individuals (Di Vincenzo et al. 2012). The polarities of the axillary border form and the radial tuberosity orientation are less clear (Carretero et al. 1997, 1999; Trinkaus 2007, 2016a; Trinkaus and Churchill 1988), but the forms evident in Kiik-Koba 2 reach their highest frequencies among the Late Pleistocene Neandertals. The same considerations apply to the presence of a distinct opponens pollicis flange (Trinkaus 2016b). Low crural indices are likely to reflect primarily ecogeographical patterning through the Pleistocene (Trinkaus et al. 1999), even if they remain stable for evolutionary sort periods of time (Roseman and Auerbach 2015; Ruff et al. 2002; Trinkaus 1981).

One feature that appears to characterize both Neandertals and earlier *Homo*, including older immature individuals, is a mediolaterally long superior pubic ramus (Kondo and Dodo 2002; Rosenberg et al. 2006; Tompkins and Trinkaus 1987). Kiik-Koba 2 (and apparently Mezmaiskaya 1) does not exhibit this elongation, suggesting that this fea-

ture was absent from very young Neandertals.

At the same time, the Kiik-Koba 2 (and other Neandertal infant) long bones are not especially robust [contra Vlček (1973) and Weaver et al. (2016)], when they are appropriately compared to both Late Pleistocene and recent non-mechanized humans. As such, they follow the pattern of hypertrophied diaphyses relative to largely sedentary recent humans, which are now evident for both immature and mature Neandertals and early modern humans (and more mobile non-mechanized recent humans) (Cowgill 2010; Ruff et al. 2015; Shackelford 2007; Trinkaus and Ruff 2012). The same pattern is evident in the Kiik-Koba 2 femoral neck angle, which is moderately low but unexceptional for its age, as are those of mature Neandertals, most Upper Paleolithic humans, and mobile recent humans (Trinkaus 1993, 2015; Trinkaus et al. 2014). These reflections of general Late Pleistocene hypertrophy are also evident in its pectoralis major and gluteus maximus tuberosities. [It is unclear how Vlček (1973) determined a tibial retroversion angle of 24°, since neither proximal metaphysis is (or was) preserved (see Figure 14; see also Vlček 1973: Plate 2)].

As noted by Vlček (1973), the Kiik-Koba 2 radii are relatively curved, and in this they follow the pattern in the older La Ferrassie 6 radius (Heim 1982a). However, the Dederiyeh 1 and Roc de Marsal 1 radii are substantially straighter (Kondo and Dodo 2002; Madre-Dupouy 1992), reflecting the variation in radial curvature evident among adult Neandertals (Heim 1982b; Trinkaus et al. 2014). The Kiik-Koba 2 femora, however, are not particularly bowed anteriorly (contra Vlček 1973), being straight anteriorly (especially the right one) but expanding proximally and distally for the metaphyses producing some degree of posterior concavity (see Figure 13).

CONCLUSION

To the extent that adult morphology is a product of developmental pathways, the infant Kiik-Koba 2 postcranial skeleton provides a further window into the mosaic developmental trajectory of Neandertal morphology. Although incomplete and providing mostly appendicular data, it reinforces the early appearance of a few Neandertal (or ancestral *Homo*) features, but it indicates that others emerge only later in development. It also conforms to the generally robust nature of these Pleistocene *Homo* individuals and the early development of that hypertrophy; yet its similarity to other Late Pleistocene infants, both Neandertal and early modern human, in this aspect helps to establish the developmental basis for the emerging robustness among all Pleistocene humans.
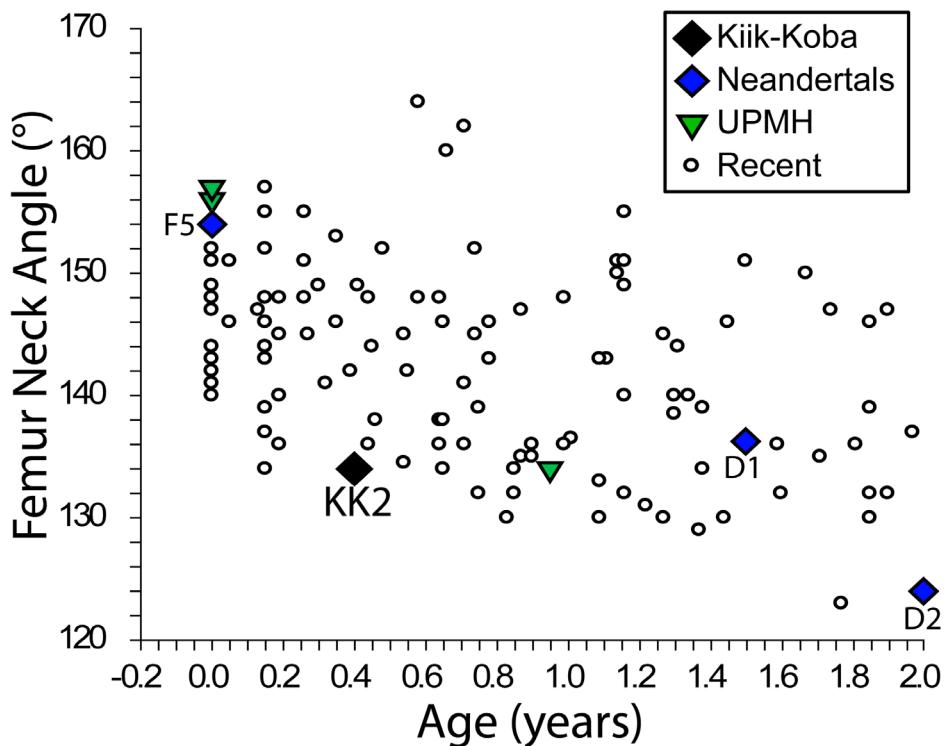
Figure 15. *Femoral neck-shaft angle versus age for Kiik-Koba 2 (KK2), Neandertals, Upper Paleolithic modern humans (UPMH), and recent humans. F5: La Ferrassie 5; D1 and D2: Dederiyeh 1 and 2.*
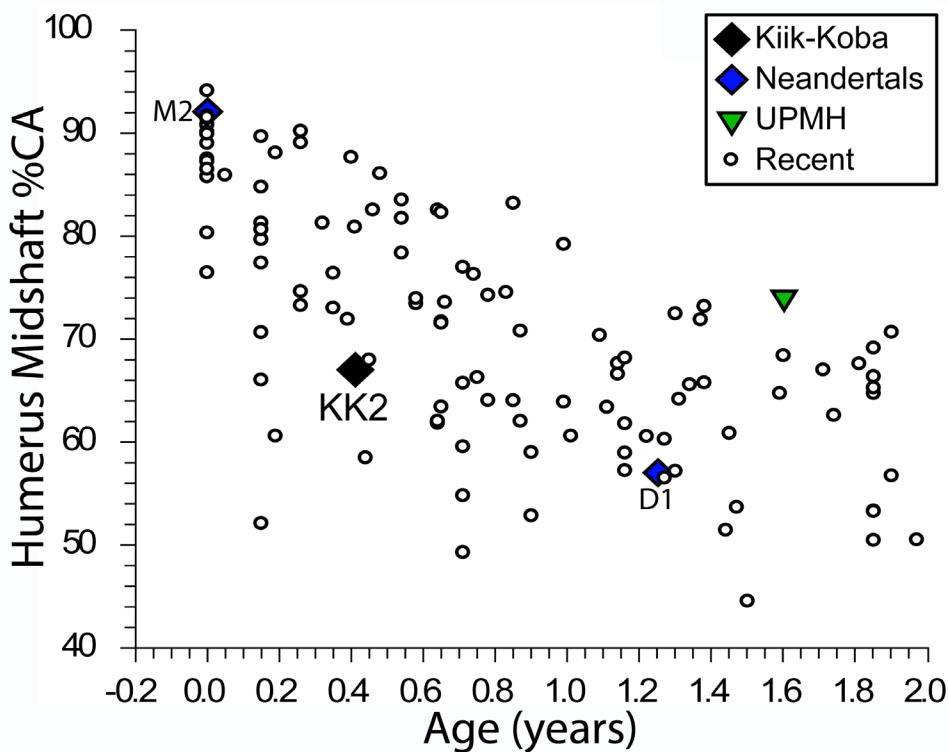

Figure 16. *Humeral midshaft percent cortical area (%CA) for Kiik-Koba 2 (KK2), Neandertals, Upper Paleolithic modern humans (UPMH), and recent humans. M2: Le Moustier 2; D1: Dederiyeh 1.*
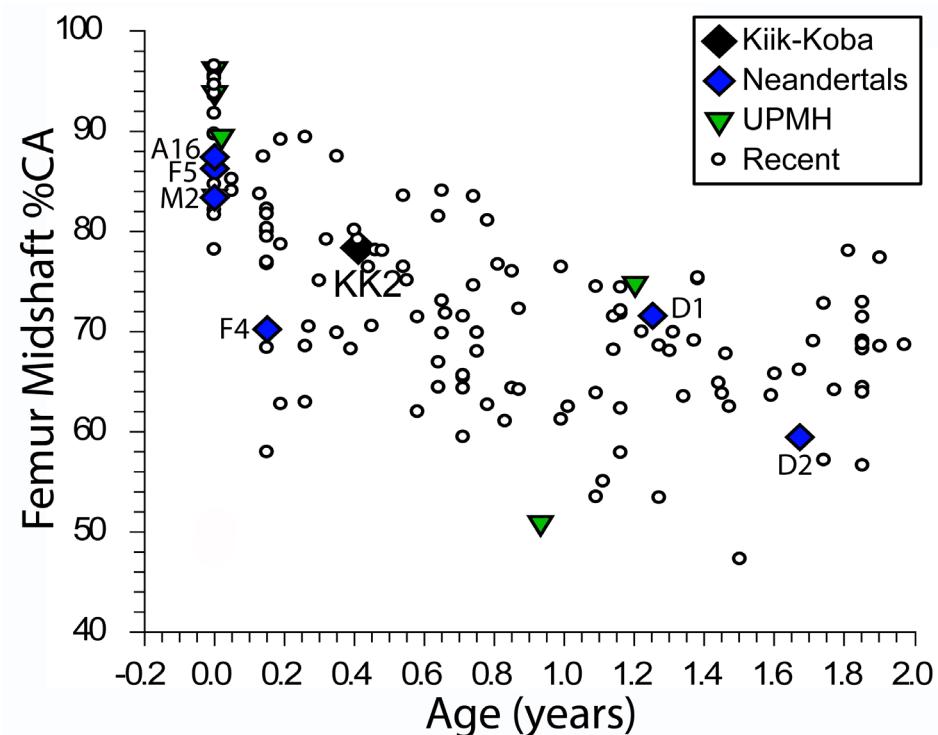
Figure 17. Femoral midshaft percent cortical area (%CA) for Kiik-Koba 2 (KK2), Neandertals, Upper Paleolithic modern humans (UPMH), and recent humans. A16: Amud 16; F4 and F5: La Ferrassie 4 and 5; D1 and D2: Dederiyeh 1 and 2.
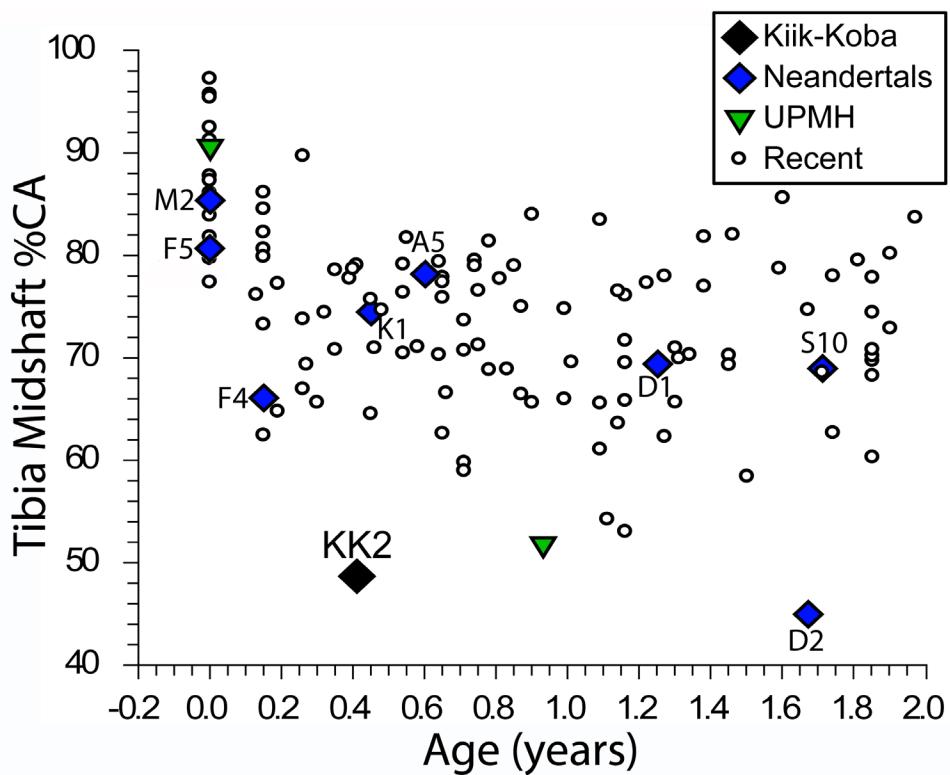

Figure 18. Tibial midshaft percent cortical area (%CA) for Kiik-Koba 2 (KK2), Neandertals, Upper Paleolithic modern humans (UPMH), and recent humans. A5: Amud 5; M2: Le Moustier 2; F4 and F5: La Ferrassie 4 and 5; K1: Kebara 1; D1 and D2: Dederiyeh 1 and 2; S10: Shanidar 10.
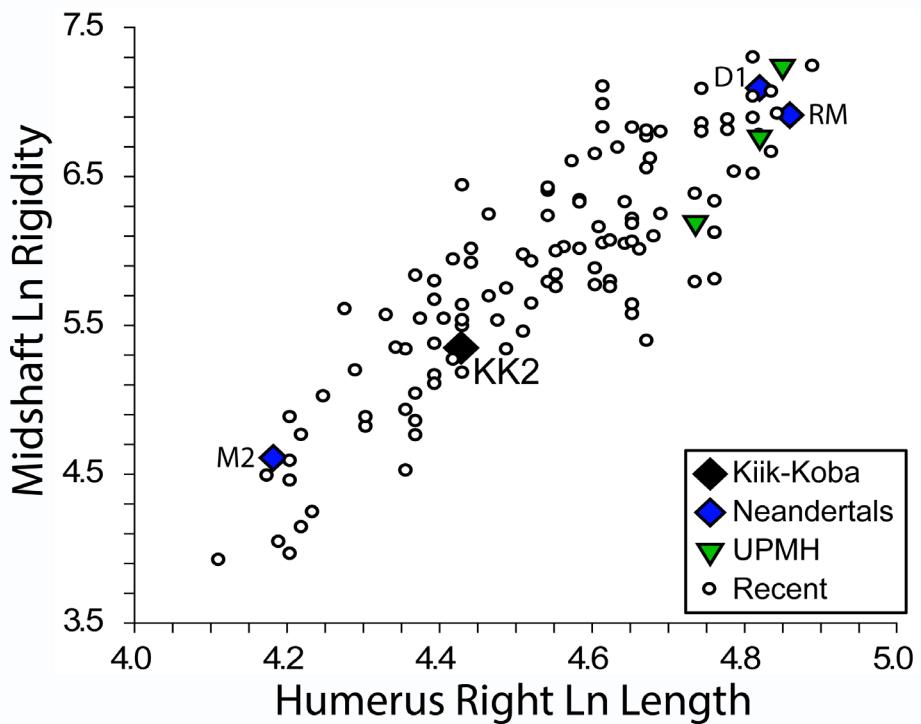
Figure 19. Humeral midshaft polar moments of area versus diaphyseal lengths for Kiik-Koba 2 (KK2), Neandertals, Upper Paleolithic modern humans (UPMH), and recent humans. M2: Le Moustier 2; D1: Dederiyeh 1; RM: Roc de Marsal 1.
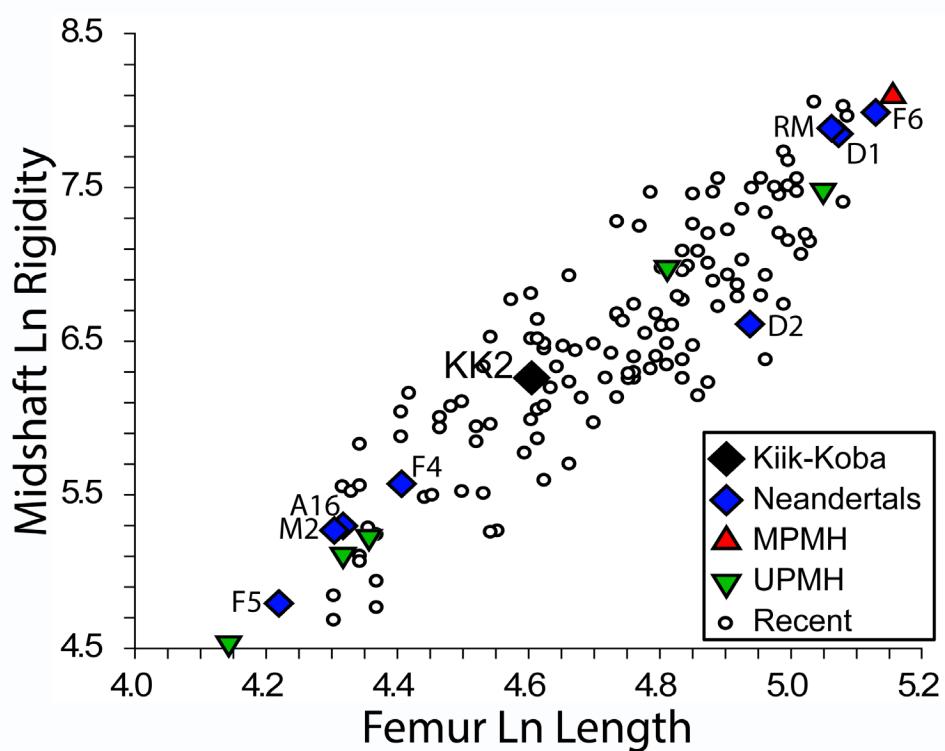

Figure 20. Femoral midshaft polar moments of area versus diaphyseal lengths for Kiik-Koba 2 (KK2), Neandertals, Middle Paleolithic modern human (MPMH), Upper Paleolithic modern humans (UPMH), and recent humans. F4, F5, and F6: La Ferrassie 4, 5, and 6; A16: Amud 16; M2: Le Moustier 2; D1 and D2: Dederiyeh 1 and 2; RM: Roc de Marsal 1.
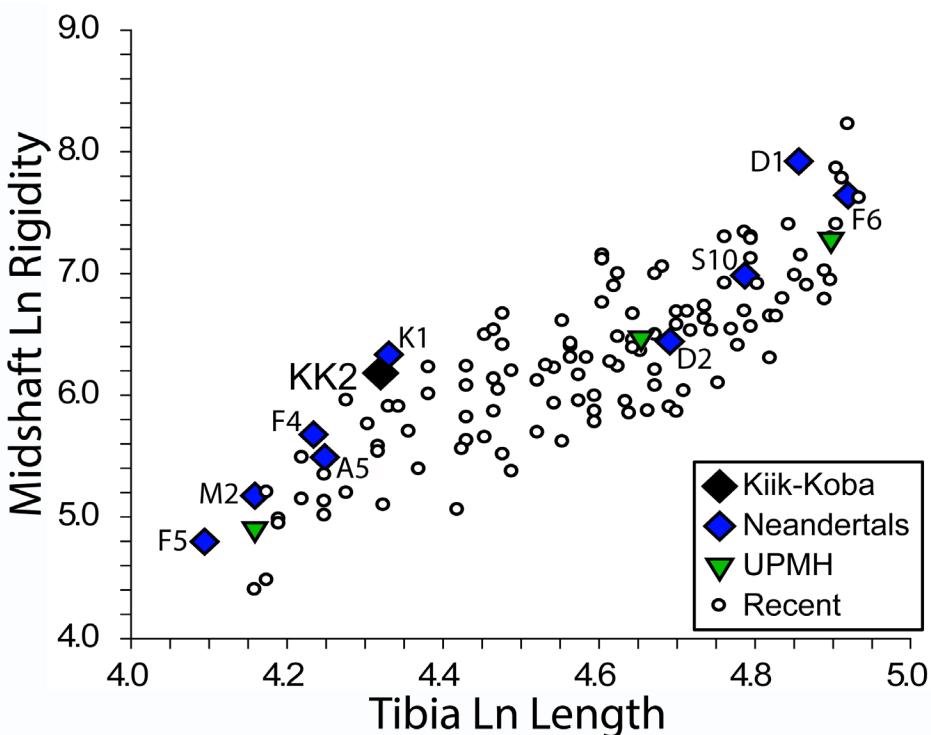
Figure 21. Tibial midshaft polar moments of area versus diaphyseal lengths for Kiik-Koba 2 (KK2), Neandertals, Upper Paleolithic modern humans (UPMH), and recent humans. F4, F5, and F6: La Ferrassie 4, 5, and 6; A5: Amud 5; M2: Le Moustier 2; K1: Kebara 1; D1 and D2: Dederiyeh 1 and 2; S10: Shanidar 10.

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