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Epipaleolithic human appendicular remains from Ein Gev I, Israel

Restes de membres du squelette humain de l'Épipaléolithique d'Ein Gev I, Israël

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ABSTRACT

The Upper Paleolithic (Early Epipaleolithic/Kebaran; ∼ 19,000 cal BP) human skeleton, from Layer 3 of Ein Gev I on the western flanks of the Golan Heights adjacent to the Sea of Galilee, retains sufficient limb remains to permit assessment of its body size and proportions, as well as diaphyseal reflections of skeletal hypertrophy. The individual was of modest stature but average mass for a later Upper Paleolithic individual, providing it with the body mass-to-stature body proportions characteristic of later Upper Paleolithic and more recent circum-Mediterranean humans. The humeri exhibit unexceptional diaphyseal asymmetry and robustness for an Upper Paleolithic human, and the femur exhibits similar relative diaphyseal hypertrophy. The humeral midshafts are relatively round, but the femoral and tibial midshafts are pronounced anteroposteriorly. As such, Ein Gev 1 provides additional paleobiological data on the appendicular remains of these Southwest Asian humans prior to the increasing sedentism of the terminal Pleistocene.

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RÉSUMÉ

Le squelette humain du Paléolithique supérieur (Épipaléolithique ancien/Kébarien ; ∼ 19 000 cal BP) du niveau 3 d'Ein Gev I, sur les bords du Massif de Golan, à côté de la mer de Galilée, comprend suffisamment de vestiges du système appendiculaire pour permettre une analyse de sa taille, de ses proportions corporelles, et pour mener une réflexion concernant son hypertrophie squelettique. L'individu était de petite taille, mais d'une masse moyenne pour le Paléolithique supérieur récent, lui donnant des proportions de la masse à la taille caractéristiques des populations circum-méditerranéennes du Paléolithique supérieur final et des périodes plus récentes. Les humérus ont une asymétrie et une robustesse normales pour le Paléolithique supérieur, tout comme la robustesse du fémur. A mi-diaphyse, les humérus sont relativement ronds, alors que les mi-diaphyses du fémur et du tibia sont allongées antéro-postérieurement. Cette étude d'Ein Gev 1 enrichit le corpus des données paléobiologiques pour les restes appendiculaires des hommes d'Asie du Sud-Ouest avant l'apparition de la sédentarité à la fin du Pléistocène.

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1. Introduction

The human fossil record for the southwestern Asian Epipaleolithic prior to the Natufian has been relatively poor, lacking the plethora of associated skeletons and isolated elements that are well known from the neighboring regions of northern Africa and Europe. However, ongoing field research and reassessment of some long-known elements are increasingly documenting the nature and variation of those human populations, especially those dating to the time of the Last Glacial Maximum (LGM) and the subsequent Epipaleolithic (Kebaran and Geometric Kebaran) period.

The currently known human remains are from the sites of Ein Gev I, Kharaneh IV, Mataha, Neve David, Ohalo II, and 'Uyun Al-Hammam, plus the earlier remains from El-Wad, Eshkaft-e Gavi, Hayonim, Kebara, Nahal Ein Gev I, and Qafzeh (Arensburg, 1977; Arensburg and Bar-Yosef, 1973; Arensburg et al., 1990; Hershkovitz et al., 1995; Mahler, 2007; McCown and Keith, 1939; Rolston, 1982; Scott and Marean, 2009; Stock et al., 2006; Trinkaus, 2018; Vandermeersch et al., 2013).

The focus has been primarily on assessments of morphological relationships using craniofacial features, and primarily with respect to the subsequent Natufian samples. With a few exceptions (e.g., Hershkovitz et al., 1993; Stock et al., 2006; Trinkaus, 2018), there has been little attention to the postcranial paleobiology of these human remains, with other postcranial assessments mostly restricted to general comments and limited sets of standard osteometrics (e.g., Arensburg, 1977; Hershkovitz et al., 1995; Rolston, 1982). Appropriate assessment of the available Epipaleolithic human postcranial remains, and their potential implications for the paleobiology and behavior of these Upper Paleolithic *sensu lato* foragers, would be aided by the detailed descriptions of these relatively rare, and often fragmentary, human remains.

With these considerations in mind, the appendicular remains of the adult female skeleton from the site of Ein Gev (Ein Guev, 'En Gev) I, Ein Gev 1, are described and assessed paleobiologically in the context of available data from penecontemporaneous western Eurasian and North African humans remains. The Ein Gev 1 cephalic remains have been described by Arensburg (Arensburg and Bar-Yosef, 1973), but only a few diaphyseal and articular measurements of the limb bones have been provided previously (Arensburg, 1977; Shackelford, 2005; Sparacello et al., 2017; Trinkaus and Patel, 2016), in the contexts of other fossil descriptions or comparative analyses.

2. Materials and methods

2.1. The Ein Gev 1 Limb Remains

The Ein Gev 1 remains were discovered *in situ* during excavations at the site of Ein Gev I in 1964, within a burial pit immediately below Layer 3 (Arensburg and Bar-Yosef, 1973; Bar-Yosef, 1970). The site is on the eastern shore of the Sea of Galilee, ~150 m bsl, on the talus slope of the flanks of the Golan Heights (32° 46′ N, 35° 39′ E). The body had been laid on its right side with the legs strongly flexed at the knees and partially flexed at the hip, such that the left hand and femur were in contact. The grave was within a hut structure dug into the hillside and adjacent to a concentration of lithic and faunal remains (Arensburg and Bar-Yosef, 1973; Bar-Yosef, 1970; Stekelis and Bar-Yosef, 1965). Layer 3 yielded a rich Kebaran lithic assemblage (Bar-Yosef, 1970; Stekelis and Bar-Yosef, 1965) and a diverse faunal assemblage dominated by *Gazella*, *Dama mesopotamica* and *Capra aegagrus* (Davis, 1974; Marom and Bar-Oz, 2008). Charcoal adjacent to the burial in Layer 3 provided a radiocarbon date of 15,700 ± 415 ^{14}C BP (GrN-5576) or 18,910 ± 465 cal BP (calibrated using www.calpal.de v.1.5). This date places the remains about four millennia younger than the Ohalo 2 burial (Hershkovitz et al., 1995) and probably 7-8 millennia after the 'Atlitian' Nahal Ein Gev 1 individual (Arensburg, 1977; Belfer-Cohen and Goring-Morris, 2014; Belfer-Cohen et al., 2004).

The burial was removed *in situ* as a block, and subsequently excavated in 1968 by B. Arensburg. The human remains were originally described as "almost complete but seriously damaged and covered by a thick sandy calcareous incrustation" and that "the only complete bones of the postcranial skeleton were a left femur, a left ulna and some segments of the hand and the foot. All the other long bones were present, but lacked epiphyses" (Arensburg and Bar-Yosef, 1973: 202). The original publication provided little further postcranial information, but a limited set of osteometrics (mostly diaphyseal diameters) were provided subsequently (Arensburg, 1977). My analysis of the remains in 1995, as part of a comparative analysis of Southwest Asian late Pleistocene appendicular remains, revealed the potential to obtain substantial additional paleobiological data from the Ein Gev 1 limb bones, which are provided here.

The humeri consist of an essentially complete right diaphysis and distal epiphysis; it retains the distal lesser tubercle, thereby permitting accurate length estimation (Supplementary data, Table S1; Fig. 1). The left humerus is less complete but retains much of the shaft and a partial cubital area. The left ulna provides direct measurement lengths, and both ulnae and radii provide diaphyseal diameters (Fig. 2; Supplementary data, Table S1). The left os coxae preserves a damaged antero-inferior ilium with the femoral head and neck crushed into the acetabulum; the acetabular rim is nonetheless sufficiently complete to provide a height measurement of ~54.5 mm. The left femur retains the intact diaphysis from the lesser trochanter to the distal condyles with minor damage to the distal epiphysis (Fig. 3); it is sufficiently complete to estimate its original lengths (Supplementary data, Table S4). The right femur is eroded anteriorly, twisted proximally and compressed anteroposteriorly distally, and provides little additional data. The tibiae retain a largely complete, but heavily encrusted, left diaphysis and the proximal two-thirds of the right diaphysis (Fig. 4), with the tibial tuberosities preserved for orientation and alignment. The distal right tibia is cemented to its talus and distal fibula. These long bones are joined by scattered and variably complete manual and pedal remains, some of which are cemented to adjacent bones at their articulations (Supplementary data, Tables S3 and S6 to S10).

Fig. 1. Anterior and posterior views of the Ein Gev 1 right (left) and left (right) humeri, with the mid-distal (35%) and midshaft (50%) cross-sections. The cross-sections are viewed distally, and anterior is above.

Fig. 1. Vues antérieures et postérieures de l'humérus droit (à gauche) et gauche (à droite) d'Ein Gev 1, avec les sections mi-distale (à 35 %) et mi-diaphysaire (à 50 %). Les sections sont en vue inférieure et la face antérieure est en haut.

The only observed pathological lesion on the Ein Gev 1 limb remains is an osteoarthritic degeneration of the left metatarsal 5 proximal epiphysis, which has osseous changes around the cuboid facet. The lesion may be related to a probable healed fracture of the lateral half of the facet. The lesions are minor and would not have affected the individual's gait.

The Ein Gev 1 skeleton has been described as female and 30–40 years of age (Arensburg and Bar-Yosef, 1973), apparently on the basis of the craniofacial remains. It is here considered as a prime-age adult, probably female, and its sex is of concern only with respect to overall body size.

2.2. Comparative samples

The Ein Gev 1 remains are compared to Upper Paleolithic *sensu lato* human remains from western Eurasia and North Africa. Note that the Southwest Asian assemblages from ∼25 to ∼13 ka BP are normally referred to as Epipaleolithic, which is broadly equivalent to the Late Upper Paleolithic in European terminology; penecontemporaneous northern African assemblages are usually subsumed within the Later Stone Age. For convenience, despite its eurocentrism (no more so than "Levant" or "Near East"), the term Upper Paleolithic is employed here to include these circum-Mediterranean Marine Isotope Stage (MIS) 3 and MIS 2 assemblages and samples of their early modern human remains.

Despite the growing sample of Southwest Asian Epipaleolithic human remains (see 1.0), only a few provide postcranial comparative data. The comparative sample therefore includes Southwest Asian human remains from the sites of Mataha, Neve David, Ohalo II and Kharaneh IV, plus the modestly older Nahal Ein Gev I (SWA). Additional data are from the Later Stone Age (mostly late MIS 2) remains from the Nile Valley (NEA) and Northwest Africa (NWA), and Upper Paleolithic remains from Europe. Although Ein Gev 1 is dated to after the LGM, the usual Early/Mid-to-Late Upper Paleolithic boundary (e.g., Holt and Formicola, 2008), and changes have been noted in crania, body proportions and stature in Europe and

Fig. 2. Medial view of the Ein Gev 1 left ulna (left), and anterior view of its right radius (right).

Fig. 2. Vue médiale de l'ulna gauche d'Ein Gev 1 (à gauche), et vue antérieure de son radius droit (à droite).

Northeast Africa across the LGM (e.g., Brewster et al., 2014; Crevecoeur, 2008; Holliday, 1997; Holt and Formicola, 2008), reflections of appendicular hypertrophy changed little (Sparacello et al., 2017; Trinkaus, 2015). The European Upper Paleolithic sample is nonetheless separated into earlier (EUP) and later (LUP) Upper Paleolithic samples; the NEA sample includes limited upper limb data from the MIS 3 Nazlet Khater 2, but it is otherwise dominated by the large late MIS 2 Jebel Sahaba and Wadi Halfa samples. The NWA sample includes the MIS 2 Later Stone Age Afalou and Taforalt remains.

The sexes are separate for body size assessments but are otherwise pooled for body proportion and robustness comparisons; the degree of sexual dimorphism in the latter features is unclear (Trinkaus, 2015, 2018; Sparacello et al., 2017); previous analyses noting a sexual difference in robustness are biased through the use of ratios.

The complete list of sites providing specimens for which comparative data are available is in Supplementary data, Table S14. The majority of the European and northern African data are available in Shackelford (2005), Crevecoeur (2008), Sparacello et al. (2017) and Trinkaus and Ruff (2012). Linear osteometrics are available through these sources and/or the primary descriptions of the remains. The cross-sectional geometric parameters for the comparative southwest Asian Upper Paleolithic humeri, femora

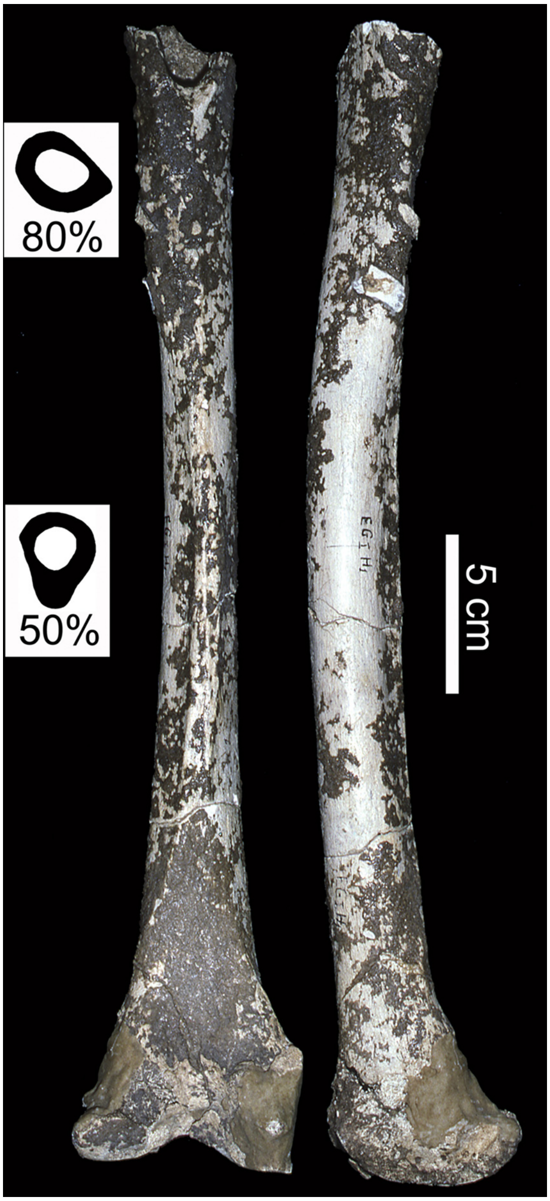

Fig. 3. Posterior (left) and lateral (right) views of the Ein Gev 1 left femur. The proximal (80%) and midshaft (50%) diaphyseal cross-sections are provided, such that anterior is above, and they are viewed distally.

Fig. 3. Vues postérieure (à gauche) et latérale (à droite) du fémur gauche d'Ein Gev 1. Les sections diaphysaires proximale (à 80 %) et à mi-hauteur (à 50 %) sont en vue distale et de telle sorte que la face antérieure soit en haut.

and tibiae, only some of which have been published, are in Supplementary data, Table S13.

3. Methods

The Ein Gev 1 quantitative data (Supplementary data, Tables S1 to S11) consist of standard osteometrics (Bräuer, 1988; Trinkaus et al., 2014), pedal discrete traits (Trinkaus, 1975), and diaphyseal cross-sectional geometry (O'Neill and Ruff, 2004). The cross-sectional

Fig. 4. The Ein Gev 1 right proximal tibial diaphysis in medial (left) and posterior (right) views, with the midshaft (50%) diaphyseal cross-section. The cross-section is viewed distally, and anterior is above.

Fig. 4. Diaphyse proximale de tibia droit d'Ein Gev 1 en vues médiale (à gauche) et postérieure (à droite), avec la section à mi-hauteur (à 50 %), en vue distale, la face antérieure vers le haut.

parameters (Supplementary data, Tables S2, S5 and S13) were generated from reconstructed diaphyseal cross-sections (Figs. 1, 3 and 4) at standard percentages of "biomechanical" lengths (Ruff and Hayes, 1983; Trinkaus et al., 1994). The subperiosteal contours were replicated with Cuttersil Putty-plus (Unitek Corp), considering the ubiquitous carbonate encrustations on the bones. Anterior, posterior, medial and lateral cortical thicknesses were measured on radiographs obtained at the Greenburg Institute of Forensic Medicine, Tel Aviv, courtesy of J. Hiss, H. Pink, and B. Arensburg. The parallax-corrected cortical thicknesses were used to interpolate the endosteal margins following the subperiosteal contours (and not solely fitting an ellipse to them), and the resultant cross-sections were digitized enlarged ~10× on a Summagraphics 1812 tablet. The cross-sectional parameters were computed using SLICE/SLCOMM (Eschman, 1992).

Humeral and femoral midshaft diaphyseal hypertrophy (robusticity) is assessed as (ln) second moments of area versus (ln) bone length × body mass, in which body masses are estimated from the femoral head diameter following Ruff et al. (2018). Humeral asymmetry comparisons employ both the midshaft (50%) and the mid-distal shaft (35%), but the humeral diaphyseal hypertrophy comparisons, as well as the diaphyseal shape ones, employ the midshaft rather than the mid-distal shaft. It is possible to reasonably accurately estimate midshaft second moments of area from the standard midshaft diameters using a Late Pleistocene reference sample (Sparacello et al., 2017; see Supplementary data, Table S13), and use of the midshaft permits the inclusion of the Kharaneh 1 humeri, as well as some of the European Upper Paleolithic ones (e.g., the lost Předmostí ones). The effect of the deltoid tuberosity is minimal, especially because the 50% section is normally located at the distal end of that tuberosity.

Diaphyseal shape is compared, for the midshaft humerus, femur and tibia (50%) and the proximal femur (80%), using the perpendicular maximum/minimum (humerus, tibia and proximal femur) and antero-posterior/medio-lateral (midshaft femur) (ln) second moments of area. Given often pronounced humeral asymmetry, dominant and non-dominant sides are assessed separately; the dominant side is based on the midshaft polar moment of area or assumed to be right for unilaterally preserved humeri. Given the low levels of femoral and tibial asymmetry (Auerbach and Ruff, 2006; Trinkaus, 2018), right and left values as available are averaged in the lower limb comparisons. Percent asymmetry for the mid-distal (35%) and midshaft (50%) humeri is computed as an absolute value (max – min)/[(max + min)/2] (Auerbach and Ruff, 2006).

The locations of the cross-sections on the incomplete Ein Gev 1 humeri and femora were determined initially at percentages of the estimated lengths. The humeral 50% and femoral 65% and 80% sections were then morphologically verified, as the first is normally at the distal end of the deltoid tuberosity, the second at the proximal linea aspera, and the last in the middle of the gluteal buttress. The remaining humeral and femoral sections were positioned according to the length estimates given the verified positions of the other sections. For mid-distal humerus and midshaft femur, proximo-distal inaccuracy on the location of the section should have little effect on the resultant cross-sectional parameters (Sládek et al., 2010; Trinkaus et al., 1999). Tibial parameters are more sensitive to section location (Sládek et al., 2010); for Ein Gev 1 the accuracy of its midshaft section position depends on the largely complete (tibial tuberosity to distal metaphysis) encrusted left tibia and morphological alignment of the right one to it. The resultant 50% section may be slightly proximal of midshaft, which would modestly exaggerate the maximum second moment of area.

The quantitative comparisons are based principally on the graphic positions of Ein Gev 1 (and other southwest Asian remains) relative to the comparative samples (Figs. 5–8). Although inappropriate for a descriptive assessment (Smith, 2018; Wasserstein and Lazar, 2016), Kruskal-Wallis p-values across the comparative samples and Z-scores for Ein Gev 1 are provided in Supplementary data, Table S12. These values are based on the distributions of individual values (in the contexts of the box plots) or on the individual deviations from the reduced major axis lines through the pooled non-southwest Asian Upper Paleolithic distributions (for the bivariate comparisons). The resultant p-values and Z-scores are evaluated using sequentially reductive multiple comparison corrections within sets of measurements (Proschan and Waclawiw, 2000; Rice, 1989).

4. Results

4.1. Body size and proportions

The body size and proportions of Ein Gev 1 are assessed using its (albeit estimated) femoral bicondylar length and head diameter (Fig. 5), the former reflecting stature and

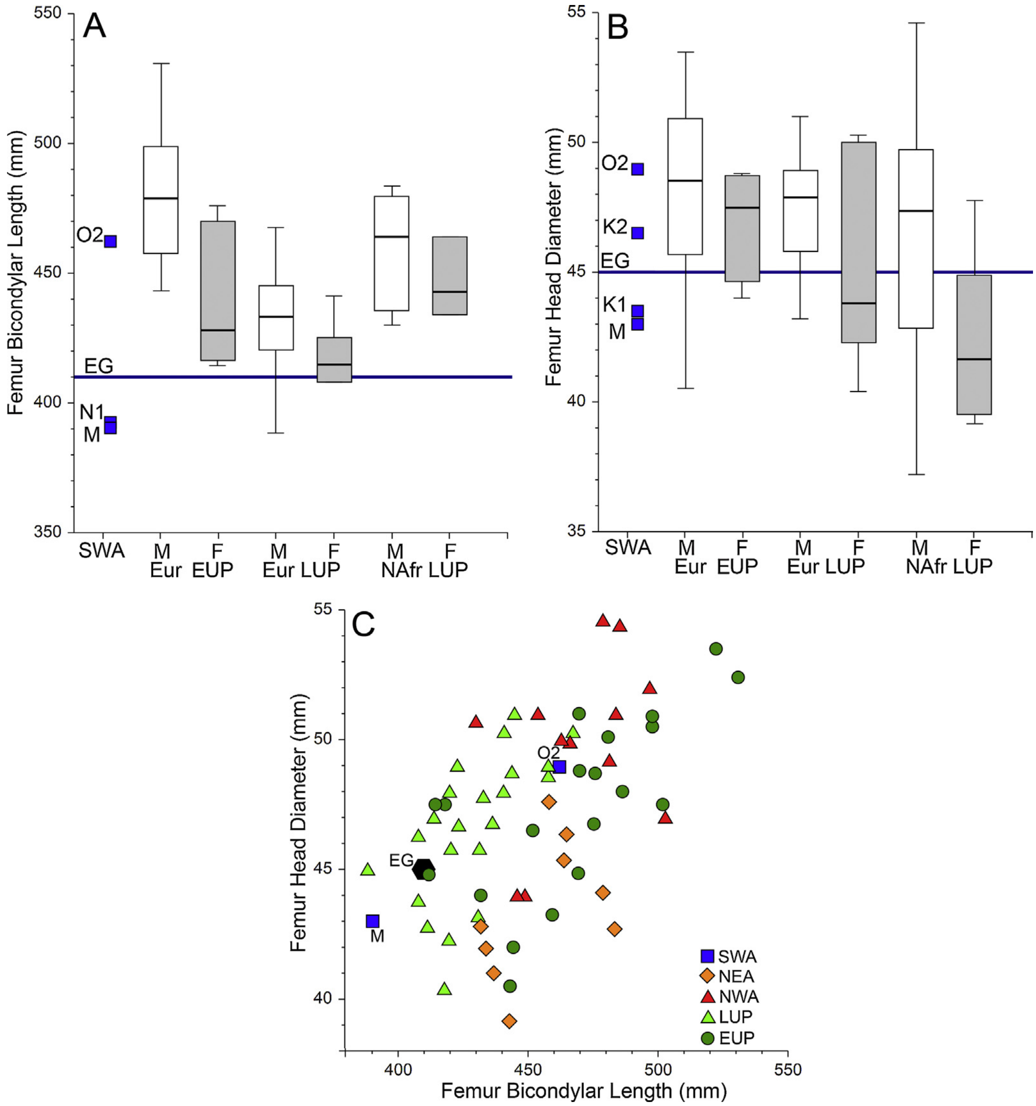

Fig. 5. Body size and proportions for Ein Gev 1 (EG) and the comparative samples. Box plots of femoral bicondylar length (A) and head diameter (B); the European and northern African samples are separated by sex (M vs. F), and the northeastern and northwestern African samples are pooled. C. Bivariate plot of femoral head diameter versus bicondylar length for those specimens providing both dimensions. K1 and K2: Kharaneh 1 and 2; M: Mataha F-81; N1: Nahal Ein Gev 1; O2: Ohalo 2; SWA: southwest Asian; NEA: northeast African; NWA: northwest African; NAfr: northern African; LUP: European later Upper Paleolithic; EUP: European earlier Upper Paleolithic.

Fig. 5. Taille et proportions corporelles d'Ein Gev 1 et échantillons de comparaison. *Boxplots* de la longueur fémorale bicondylaire (A) et du diamètre de la tête fémorale (B) ; les échantillons européens et africains sont séparés selon le sexe (M et F), et les échantillons d'Afrique du Nord-Est et du Nord-Ouest sont regroupés. C. Distribution bivariée du diamètre de la tête fémorale en fonction de la longueur fémorale pour les restes humains sur lesquels les deux mesures sont possibles. K1 et K2 : Kharaneh 1 et 2 ; M : Mataha F-81 ; N1 : Nahal Ein Gev 1 ; O2 : Ohalo 2 ; SWA : Asie du Sud-Ouest ; NEA : Afrique du Nord-Est ; NWA : Afrique du Nord-Ouest ; NAfr : Afrique du nord ; LUP : Paléolithique supérieur tardif européen ; EUP : Paléolithique supérieur ancien européen.

the latter reflecting body mass (Feldesman et al., 1990; Ruff et al., 2018). Following Ruff et al. (2018), the femoral head diameter provides a mean body mass estimate of 63.1 kg.

The femoral length of Ein Gev 1 is modest for an Upper Paleolithic human, falling among the smaller of the European LUP specimens and below the ranges of the European EUP and especially the pooled North African sample (Fig. 5A). It is well below the high value for Ohalo 2, yet above the low values for Mataha F-81 and Nahal Ein Gev 1. Its femoral head diameter, however, is moderate for an Upper Paleolithic human (Fig. 5B), among the smaller of the EUP specimens and the LUP males, moderately large for a North African female, but well within the ranges of variation of the comparative samples. Incorporation of the error ranges for the Ein Gev 1 dimensions (Supplementary data, Table S5) would have little effect on these comparative assessments.

The combination of the articular and length dimensions (or "mass-to-stature" proportions) (Fig. 5C) provides

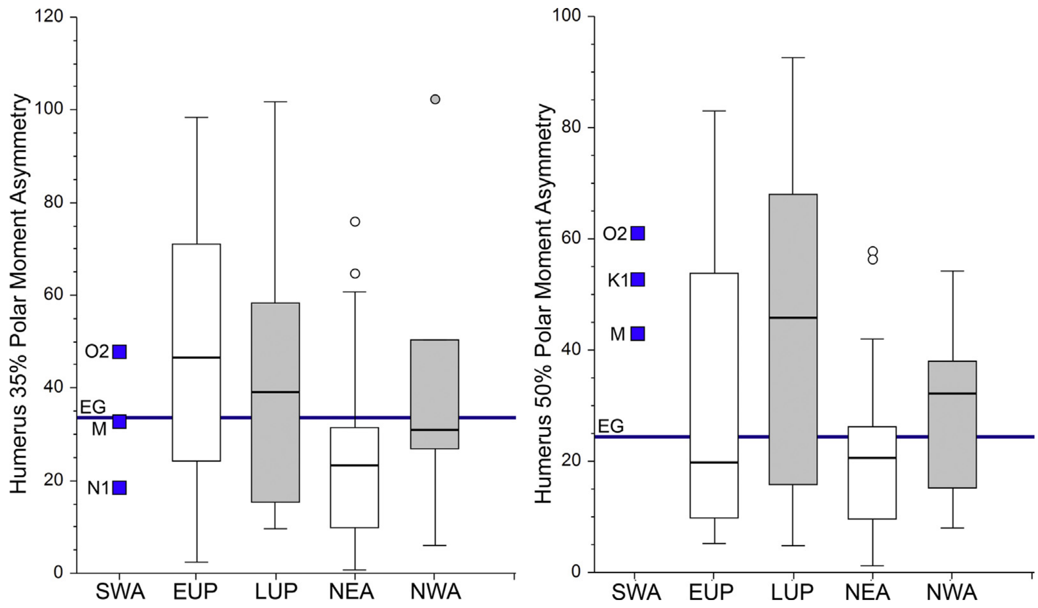

Fig. 6. Box plots of humeral mid-distal (35%) and mid (50%) diaphyseal polar moment of area absolute asymmetry for Ein Gev 1 (EG) and the comparative samples. K1: Kharaneh 1; M: Mataha F-81; N1: Nahal Ein Gev 1; O2: Ohalo 2. Sample abbreviations as in Fig. 5.

Fig. 6. *Boxplots* de l'asymétrie du moment polaire de la diaphyse humérale en mi-distale (35 % ; à gauche) et mi-diaphysaire (50 % ; à droite) pour Ein Gev 1 (EG) et les échantillons de comparaison. K1 : Kharaneh 1 ; M : Mataha F-81 ; N1 : Nahal Ein Gev 1 ; O2 : Ohalo 2. Voir la légende de la Fig. 5 pour ce qui concerne les abréviations pour les échantillons.

a largely complete (and highly significant; Supplementary data, Table S12) separation of the more linear (relatively low mass-to-stature, from narrow trunks and long limbs, as reflected in femoral head to length proportions) Northeast African and earlier European samples from the Northwest Africa and later European samples (see also Holliday, 1997, 2015). Ein Gev 1, along with Mataha F-81 and (to a lesser extent) Ohalo 2, falls with the less linear circum-Mediterranean samples, it is substantially different only from the NEA sample. These stockier (higher mass-to-stature; "mid-latitude") body proportions, which are evident in terminal Pleistocene/early Holocene Natufian remains (Holliday, 2015), were therefore present close to the LGM in southwest Asia.

It is also possible to estimate the brachial (radio-humeral) index for Ein Gev 1; the mean length estimates for the humerus and radius (Supplementary data, Tables S1 and S3) provide an index of ~71.5, using the mean length estimates minus and plus two standard errors of the humerus and radius respectively raises the brachial index to ~76.7. These values bracket those of 73.2 for Ohalo 2 and 76.6 for Mataha F-81. They are similar to the male and female average values of 72.9 and 74.8 for the Northwest African Taforalt sample (Ferembach, 1962), and modestly lower than the European EUP and LUP means of 77.9 (±2.3, n = 21) and 78.5 (±2.7, n = 15). Although recent human brachial indices vary with climate (Holliday, 1999; Trinkaus, 1981), there is little patterning among them in these Upper Paleolithic samples.

4.2. Humeral asymmetry and hypertrophy

As with most other late Pleistocene humans (Sparacello et al., 2017) and relative to most Holocene humans (Sládek et al., 2016; Trinkaus et al., 1994), the western Eurasian and Northwest African Upper Paleolithic humeri exhibit an elevated level of diaphyseal asymmetry (Fig. 6); the Northeast African sample has less pronounced asymmetry, producing the modest but minimally significant differences across the samples (Supplementary data, Table S12). The Ein Gev 1 humeral asymmetry is unexceptional at the mid-distal (35%) level, moderately low but still above the EUP and NEA medians at the midshaft (50%) level. The Ohalo 2, Kharaneh 1 and Mataha F-81 humeri are clearly asymmetrical at midshaft, but they are unexceptional more distally.

In this context, the Kharaneh 1 and Mataha F-81 dominant humeral midshafts fall among the majority of the Upper Paleolithic humeri in robustness (Fig. 7A), whereas Ohalo 2 is among the more gracile (predominantly EUP) of them (see also Trinkaus, 2018). The same pattern is evident for the non-dominant humeri (Fig. 7B). The Ein Gev 1 humeri are average, moderately gracile on the right (dominant) side and in the middle of the overall distribution on the left. Although the comparative samples are significantly different with respect to humeral hypertrophy, Ein Gev 1 is unexceptional for any of these samples (Supplementary data, Table S12).

Because midshaft humeral hypertrophy is commonly reflected in an increase in the antero-lateral to postero-medial (or maximum) dimension, the relative maximum versus minimum second moments of area should also reflect general humeral hypertrophy (Fig. 7C and D). There is more scatter in these proportions in the non-dominant side, with little separation of the comparative samples (Supplementary data, Table S12). The comparative SWA humeri fall well within the comparative distributions, but the Ein Gev 1 humeri are both relatively round.

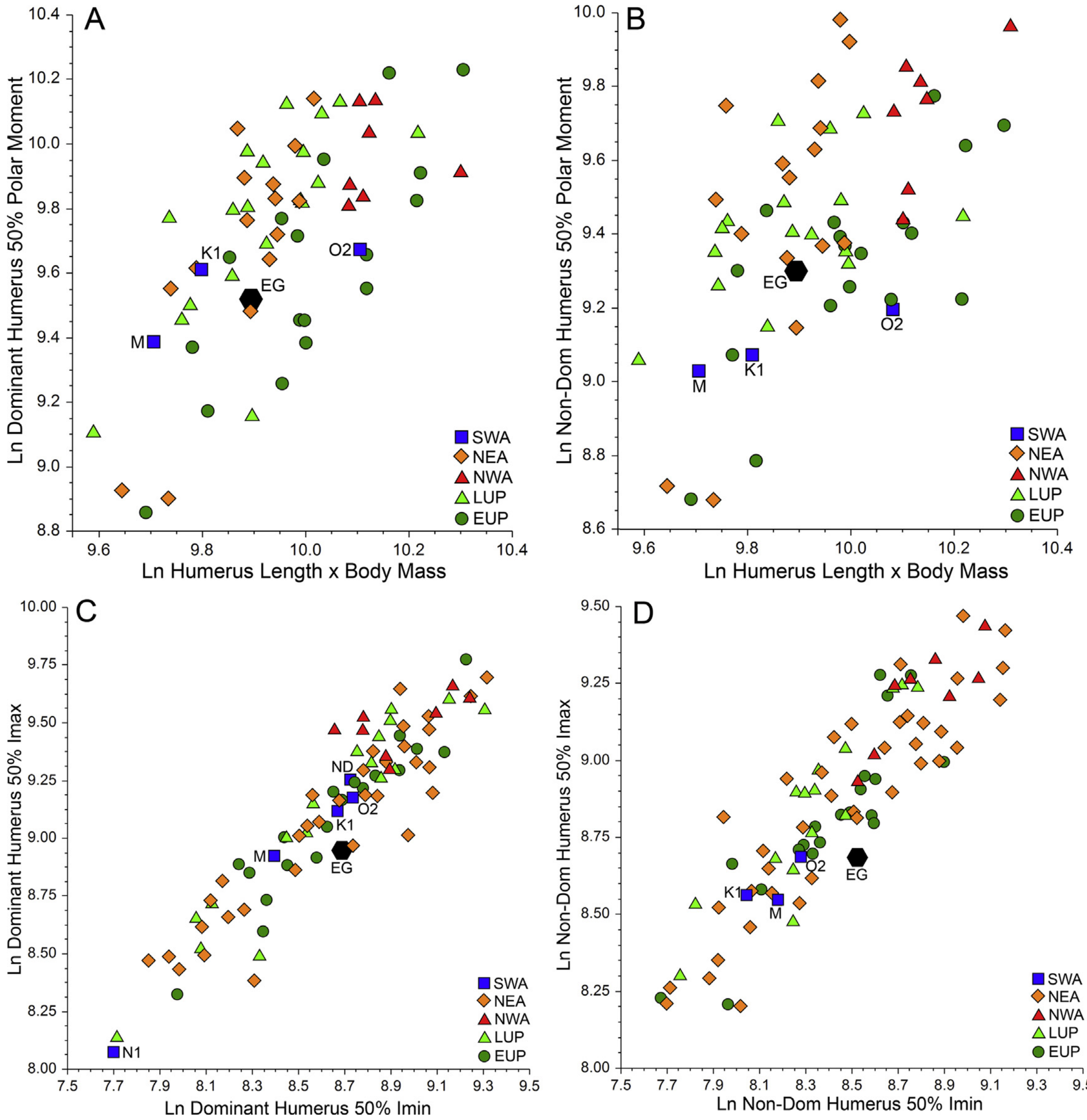

Fig. 7. Bivariate plot assessments of humeral midshaft (50%) hypertrophy, separately for dominant (A and C) and non-dominant (B and D) sides, for Ein Gev 1 (EG) and the comparative samples. Robustness (A and B) is assessed as the (ln) polar moment of area versus the (ln) humeral length × body mass; diaphyseal shape (C and D) is assessed as maximum versus minimum second moments of area. Southwest Asian specimen and sample abbreviations as in Fig. 5.

Fig. 7. Distributions bivariées pour l'hypertrophie de la mi-diaphyse humérale (50 %), séparées entre côtés dominants (A et C) et non dominants (B et D), pour Ein Gev 1 et les échantillons de comparaison. La robustesse (A et B) est évaluée en portant le logarithme népérien du moment polaire de la zone en fonction du logarithme népérien du produit de la longueur humérale par la masse corporelle. La forme diaphysaire (C et D) est évaluée en comparant les moments polaires maximaux et minimaux. Voir la légende de la Fig. 5 pour les abréviations concernant les spécimens d'Asie du Sud-Ouest et l'échantillonnage.

4.3. Femoral and tibial hypertrophy

Lower limb hypertrophy can be assessed for the femoral midshaft, along with indirect reflections from femoral and tibial diaphyseal proportions (Fig. 8). In the comparison of femoral midshaft polar moment of area to body mass times length, there are modest differences across the comparative samples, with the LUP and NWA samples being generally more robust. Ein Gev 1, Mataha F-81 and Ohalo 2 all fall in the middle of the overall distribution (Fig. 8A).

There is also little difference in femoral midshaft second moment of area proportions across the comparative samples (Fig. 8C). Ein Gev 1, however, has a pronounced pilaster through midshaft (Fig. 3), which places it (along with Ohalo 2) among the Upper Paleolithic femora with the larger anteroposterior second moments of area relative to their medio-lateral ones (Fig. 8C). It contrasts primarily with the LUP sample. There are more differences across the proximal femur and tibial midshaft, with especially the NEA sample having less prominent femoral gluteal buttresses and less tibial anteroposterior expansion. The Ein

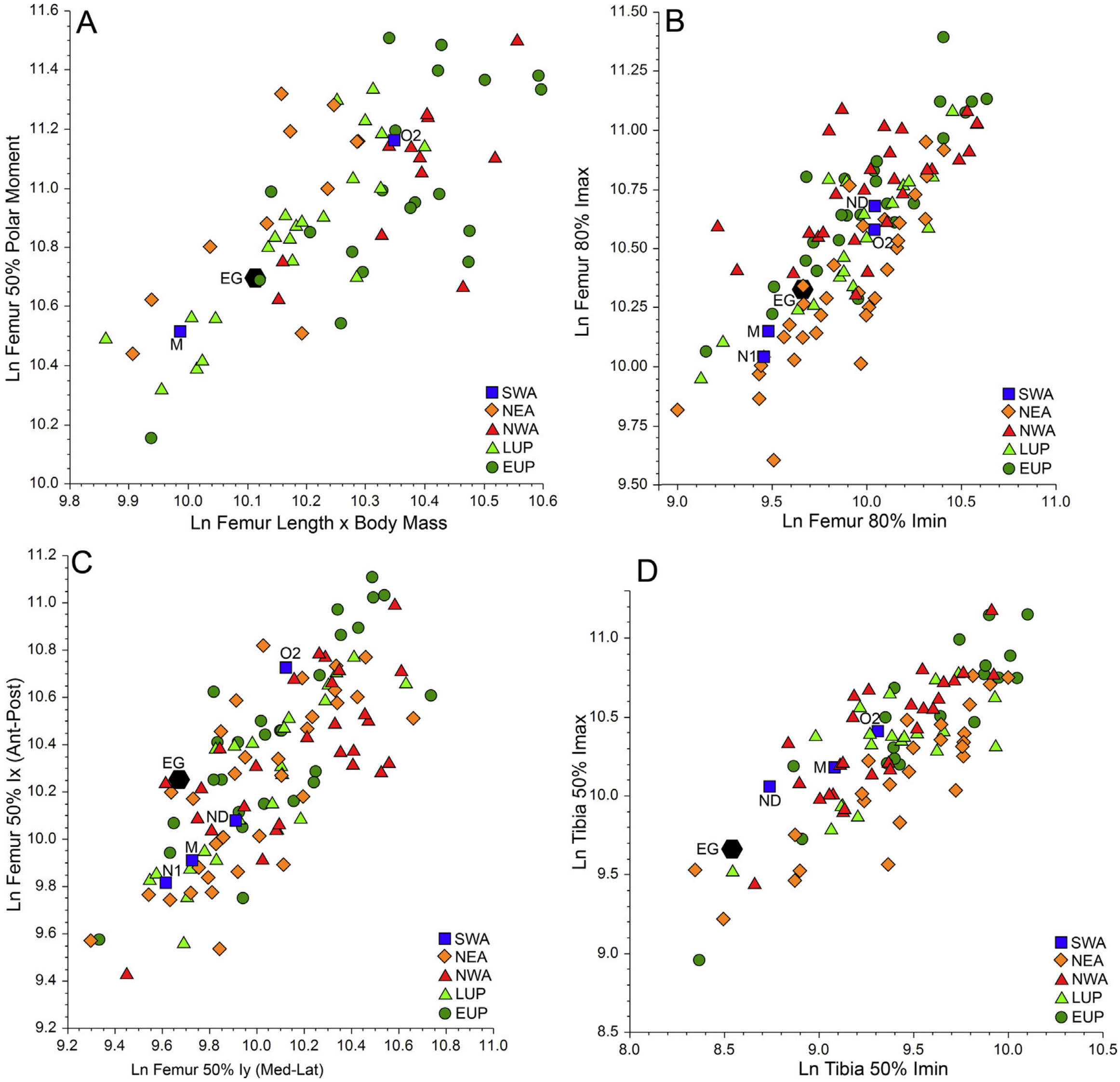

Fig. 8. Bivariate plot assessments of lower limb diaphyseal hypertrophy, for Ein Gev 1 (EG) and the comparative samples. A. Femur midshaft (50%) (ln) polar moment of area versus (ln) femoral length × body mass. B and C. Femoral proximal (80%) and midshaft (50%) perpendicular second moments of area. D. Tibial midshaft (50%) perpendicular second moments of area. Southwest Asian specimen and sample abbreviations as in Fig. 5.

Fig. 8. Distributions bivariées pour l'hypertrophie diaphysaire du membre inférieur, pour Ein Gev 1 (EG) et les échantillons de comparaison. A. Logarithme népérien du moment polaire de la mi-diaphyse (50 %) fémorale en fonction du logarithme népérien du produit de la masse corporelle par la longueur fémorale. B et C. Moments secondaires perpendiculaires pour la diaphyse proximale (80 %) et à mi-hauteur (50 %) du fémur. D. Moments secondaires perpendiculaires au milieu (50 %) de la diaphyse du tibia. Voir la légende de la Fig. 5 pour les abréviations pour les spécimens d'Asie du Sud-Ouest et l'échantillonnage.

Gev 1 proximal femur is unexceptional in these proportions (Fig. 8B). Its tibial midshaft proportions contrast primarily with the NEA sample, but they are similar to those of the other Southwest Asian Epipaleolithic specimens (Fig. 8D). It is possible that the tibial 50% section is modestly too proximal (see 2.3), but any reduction in its I_{max} would place it more in the middle of the overall distribution.

4.4. *Cubital, forearm, manual and pedal aspects*

The distal humeri of Ein Gev 1 are unexceptional for a late Pleistocene human (Fig. 1). They have moderately prominent medial epicondyles and medial flanges to the trochlea. A comparison of the summed medial and lateral pillar thicknesses versus olecranon breadth, a feature which varies through Pleistocene humans (Trinkaus, 2012), provides an index of 97.8 for the Ein Gev 1. Comparative Upper Paleolithic samples provide a wide range of values (European EUP: 107.3 ± 20.9, $n = 21$; Northeast Africa: 88.3 ± 14.6, $n = 45$; Northwest Africa: 86.8 ± 15.6, $n = 37$), such that Ein Gev 1 and Ohalo 2 (89.7) are in the middle of the variation, whereas Nahal Ein Gev 1, with an index of 69.4, is among the specimens with narrower pillars.

The largely complete left ulna and the right radius are notable for their modest degrees of dorsal or lateral curvature and their small interosseous crests (Fig. 2). Their proximal portions are too eroded to provide trochlear notch or radial tuberosity orientations. The right hamate bone exhibits a relatively pronounced hamulus, similar in projection (Ein Gev 1: 9.8 mm; Ohalo 2: 9.3 and 9.1 mm) and length (Ein Gev 1: 9.6 mm; Ohalo 2: 11.2 and 10.0 mm) to those of the larger Ohalo 2 (cf. Trinkaus et al., 2014; Supplementary data, Table S4). The tuberosity of the left trapezium exhibits little projection (1.5 mm), similar to those of Ohalo 2 (2.8 and 1.8 mm). The metacarpal 3 has minimal projection of the styloid process, extending only 0.8 mm from the mid-capitate facet, a pattern which characterizes Ohalo 2 (1.0 and 0.6 mm) and most Pleistocene human third metacarpals (Trinkaus et al., 2014; Ward et al., 2014).

The right and left pedal remains are variably eroded and cemented to each other (and to the distal tibia/fibula), but they provide discrete trait observations in addition to morphometrics (Supplementary data, Tables S7 to S11). The right talus exhibits anterior extensions of medial malleolar facet and lateral trochlea, along with a lateral squatting facet, indicating habitual hyperdorsiflexion of the talocrural articulation. The anterior and medial talo-calcaneal facets are fully fused, but there is no evidence of a sulcus tali facet. Naviculo-cuboid facets are present, and the cuboid bone has a distinct facet on the proximal margin of the peroneus longus sulcus. The hallux would have exhibited normal hallux valgus, as reflected in its metatarsal 1 horizontal head angle of 9°. The proximal phalanx 2 has modest diaphyseal diameters (5.9 and 6.0 mm), similar to those from Ohalo 2 and other Upper Paleolithic sites (Trinkaus and Patel, 2016); reflecting habitual use of footwear (Trinkaus, 2005).

5. Discussion and conclusion

The Ein Gev 1 appendicular skeleton therefore adds substantially to the data available for other Southwest Asian Epipaleolithic (pre-Natufian) human skeletal remains, with respect to patterns of appendicular hypertrophy, as well as body size and proportions. Its femoral head dimension falls in the middle of the regional range of variation, in between the male Mataha F-81 and Ohalo 2 remains, as well as between the two individuals from Kharaneh IV. Yet, its femoral length is modest, albeit above Mataha F-81 and Nahal Ein Gev 1.

Most importantly, the femoral proportions of Ein Gev 1 and Mataha F-81, and to a lesser degree Ohalo 2, indicate that the non-linear body proportions of more recent circum-Mediterranean humans were present in the pre-Natufian Epipaleolithic populations of Southwest Asia. In combination with the more linear body proportions of the terminal Pleistocene Jebel Sahaba and Wadi Halfa samples, it reinforces the dichotomy in body proportions between circum-Mediterranean and sub-Saharan populations (see also Holliday, 1995, 2015). Moreover, given the MIS 3 spread of modern humans from equatorial Africa, presumably with linear body proportions given the linear natures of European MIS 3 modern humans (Holliday, 1997; Trinkaus, 1981), the stockier proportions of Ein Gev 1 and other Kebaran humans argue for a transition through the Upper Paleolithic of Southwest Asia in this aspect, similar to the EUP-to-LUP changes documented for Europe.

The appendicular hypertrophy of Ein Gev 1, reflected in scaled midshaft polar moments of area and humeral asymmetry, is unexceptional for an Upper Paleolithic (or Pleistocene *Homo*) forager. Despite the presence of sequential hut foundations at Ein Gev I (Bar-Yosef, 1970), as well as the earlier structural evidence at Ohalo II (Nadel and Werker, 1999), any degree of sedentism among these southwestern Asian Upper Paleolithic humans is not likely to have had an effect on their habitual locomotor activity levels (and by implication mobility). Indeed, the elevated midshaft femoral I_x/I_y and tibial I_{max}/I_{min} proportions of Ein Gev 1 (in the context of an overall unexceptional level of diaphyseal hypertrophy) might imply a mobility-related elevated level of antero-posterior loading of the lower limb. Although similar to those of other late Pleistocene humans, its level of humeral diaphyseal asymmetry is high for a Holocene human.

The Ein Gev 1 female Kebaran limb remains therefore reinforce and expand upon the patterns evident in the other Southwest Asian late MIS 3 to earlier MIS 2 Epipaleolithic (Kebaran) human remains (Stock et al., 2006; Trinkaus, 2018). It is hoped that ongoing analyses of the additional human remains from penecontemporaneous sites in the region will help to fill out these patterns and their variations.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.crpv.2018.03.002.

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