

Is Central Asia the Eastern Outpost of the Neandertal Range? A Reassessment of the Teshik-Tash Child

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KEY WORDS Late Pleistocene; dispersals; sub-adult hominin fossil; logistic regression

ABSTRACT Since its discovery in southeastern Uzbekistan in 1938, the Teshik-Tash child has been considered a Neandertal. Its affinity is important to studies of Late Pleistocene hominin growth and development as well as interpretations of the Central Asian Middle Paleolithic and the geographic distribution of Neandertals. A close examination of the original Russian monograph reveals the incompleteness of key morphologies associated with the cranial base and face and problems with the reconstruction of the Teshik-Tash cranium, making its Neandertal attribution less certain than previously assumed. This study reassesses the Neandertal status of Teshik-Tash 1 by comparing it to a sample of Neandertal, Middle and Upper Paleolithic modern humans, and recent human sub-adults. Separate examinations of the cranium and mandible are conducted using multinomial logistic regression and discriminant function analysis to assess group

membership. Results of the cranial analysis group Teshik-Tash with Upper Paleolithic modern humans when variables are not size-standardized, while results of the mandibular analysis place the specimen with recent modern humans for both raw and size-standardized data. Although these results are influenced by limitations related to the incomplete nature of the comparative sample, they suggest that the morphology of Teshik-Tash 1 as expressed in craniometrics is equivocal. Although, further quantitative studies as well as additional sub-adult fossil finds from this region are needed to ascertain the morphological pattern of this specimen specifically, and Central Asian Middle Paleolithic hominins in general, these results challenge current characterizations of this territory as the eastern boundary of the Neandertal range during the Late Pleistocene. *Am J Phys Anthropol* 138:45–61, 2009. © 2008 Wiley-Liss, Inc.

The Neandertal status of the Teshik-Tash child is important to studies of Late Pleistocene hominin growth and development as well as to characterizations of the Central Asian Middle Paleolithic and its relationship to other areas of the Old World. More specifically, the Neandertal attribution of Teshik-Tash 1 defines the eastern extent of this group's geographic distribution (but see Krause et al., 2007). Since its discovery in 1938 (Okladnikov, 1939), a handful of studies (Weidenreich, 1945; Minugh-Purvis and Lewandowski, 1994; Ritzman, 2005) have suggested that the morphology of this specimen does not justify its unequivocal classification as a Neandertal. The present study expands upon this research by reexamining Teshik-Tash 1 with respect to other Late Pleistocene sub-adult hominins in a multivariate framework. The specimen's role in the characterization of Central Asia as the eastern outpost of the Neandertal range and the impact a reassessment may have on altering interpretations of Neandertal adaptations and dispersals will also be discussed.

The consensus view in paleoanthropology identifies Teshik-Tash 1 as a Neandertal juvenile (Stringer and Gamble, 1993; Rak et al., 1994; Vishnyatsky, 1999; Stanford et al., 2006). This taxonomic assessment effectively anchors the eastern boundary of the Neandertal range in Central Asia (see Fig. 1). In addition, the fossil's association with a Middle Paleolithic industry has been the implicit basis for linking all Mousterian-like assemblages from the Central Asia to this hominin group. The Neandertal status of the Teshik-Tash child is used as taxonomic corroboration of cultural links made between Middle Paleolithic industries in Central Asia and those from

the Near East such as Shanidar Cave (Vishnyatsky, 1999). Consequently, the specimen plays an important role in the models of Late Pleistocene hominin population dynamics, including those central to the modern human origins debate (Vandermeersch, 1992; Wolpoff et al., 2001; Trinkaus, 2005).

The history of the discovery of Teshik-Tash Cave, its archaeological materials and chronological determination, as well as the stratigraphic position of the child and its interpretation as a ritual burial have been summarized in English by Movius (1953), Gargett (1989), Vishnyatsky (1999), and Schwartz and Tattersall (2003). The Teshik-Tash child (see Fig. 2) consists of 150 cranial fragments that were reconstructed to produce a relatively complete cranium, a complete mandible, and some post-cranial elements (Gremyatskii, 1949). The post-cranial elements include vertebrae (fragments of the cervical, thoracic, and lumbar), right and left clavicles, complete and fragmentary ribs, a left humeral diaphysis, a pelvic fragment, diaphyses of right femur and left tibia, and fragmentary diaphyses of the left and right fibulae (Okladnikov, 1949).

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Received 13 July 2007; accepted 19 May 2008

DOI 10.1002/ajpa.20897

Published online 18 August 2008 in Wiley InterScience (www.interscience.wiley.com).



Fig. 1. Map of the Neandertal distribution with Teshik-Tash circled. Adapted from Stanford et al., 2006.

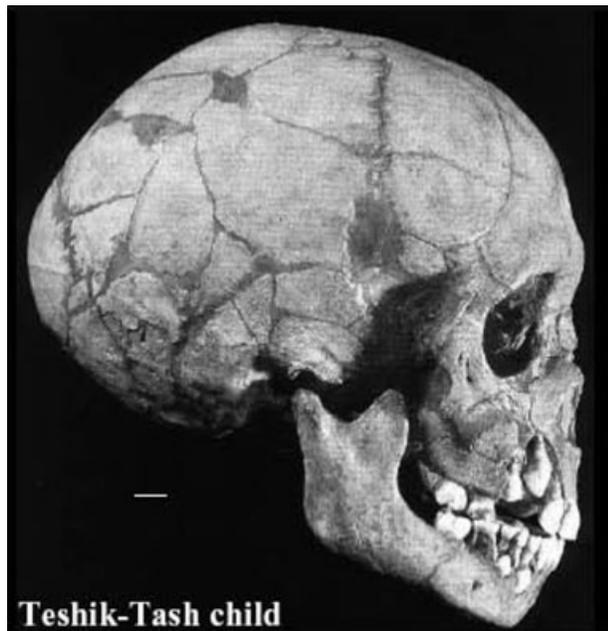


Fig. 2. Skull of Teshik-Tash. Scale bar = 1 cm.

The lithic assemblage from Teshik-Tash Cave consists of over 2,000 pieces (Vishnyatsky, 1999). Most of these were recovered from a ~50 square meter area in the central portion of the cave. The original monograph identified five “culture areas” of varying thicknesses, each of which was separated by a layer of sterile clay, sand, and coarse silt (Movius, 1953). Neither the original description (Movius, 1953) nor subsequent research (Vishnyatsky, 1999) have indicated any systematic difference between the lithic assemblages from these layers.

Vishnyatsky’s (1999) analysis of the lithic material led him to conclude that the assemblages from Teshik-Tash can be reliably characterized as Mousterian-like. Although

they contain most of the elements that define Vishnyatsky’s (1999) “ordinary Mousterian,” there is a conspicuous absence of points and limaces as well as double and convergent sidescrapers.

The remains of the Teshik-Tash child were found in a sterile clay layer 25 cm below the base of “Culture Layer I,” the thickest and archaeologically richest layer (Movius, 1953). The original workers did not note any evidence that the lithic materials or the fossil itself were intrusive. Although the proposed ritual significance of the burial has been scrutinized (Gargett, 1989), the interpretation that the Teshik-Tash child was deposited in the cave sometime during the Middle Paleolithic has never been questioned.

Movius (1953) initially relied on the faunal assemblages from the site to infer a rough age of “early Würm.” In contrast, Vishnyatsky (1999) argued that Teshik-Tash 1 should be assigned to the late interpeniglacial (roughly between 57 and 24 thousand years ago [kya]). Unfortunately, recent attempts to radiometrically date the site have been unsuccessful (P. Wrinn and B. Viola, personal communication) and attributing a secure date to the site is not possible.

PREVIOUS ASSESSMENTS OF THE MORPHOLOGY OF TESHIK-TASH 1

Aside from being part of the Neandertal sample in studies that compare Late Pleistocene hominin growth trajectories (Minugh-Purvis, 1988; Krovitz, 2000, 2003; Tillier, 2002; Williams et al., 2003; Williams, 2004; Williams and Krovitz, 2004; Ponce de León and Zollikofer, 2006), the morphology of the Teshik-Tash child itself has been the central focus of only a handful of analyses. Before the publication of the more thorough morphological assessment of Teshik-Tash 1 presented in the original Russian monograph (Gremyatskii, 1949), Hrdlička (1939) and Debetz (1940) corroborated Okladnikov’s initial claim (Okladnikov, 1939; see also Movius, 1953 for an English summary) that the child was a Neandertal.

Gremyatskii's (1949) work will be discussed in greater detail in the following section. More recently, Rak et al. (1994) relied heavily on observations of the dimensions of the foramen magnum and discrete features on the mandible of Teshik-Tash 1 to diagnose the Amud 7 infant as a Neandertal (see also Creed-Miles et al., 1996; Jabbour et al., 2002). Schwartz and Tattersall (2003: 394) have provided the most comprehensive English description of Teshik-Tash 1 and incorrectly concluded 1) "... Weidenreich (1945) concurred" (with the assessment of Teshik-Tash 1 as a Neandertal) and that 2) "nobody has demurred."

In fact, Weidenreich and a number of researchers have questioned the Neandertal status of the specimen. Weidenreich (1945) took issue with some of the features originally used to diagnose the child as a Neandertal. He provided comparative evidence to show that, contrary to previous descriptions (Hrdlička, 1939; Debetz, 1940), Teshik-Tash 1 did not possess a distinctively low cranial vault relative to a sample of similarly aged modern humans. He also questioned the observation that the fossil lacked canine fossae and instead suggested that the facial skeleton was not only badly damaged in this area but also that erupting upper canines created the illusion of a puffy or bulging alveolus. Although he concluded that the Teshik-Tash child exhibited no *mentum osseum*, Weidenreich (1945) argued that the chin should not be described as receding, noting the presence of a clear mental trigone consisting of a well-developed tuberculum at the mental symphysis and bilaterally expressed lateral tubercles. Most importantly, however, the newly described remains from the Mount Carmel caves were not part of the initial description and comparative study of Teshik-Tash 1 presented in the Gremyatskii (1949) monograph. Weidenreich observed that when the Mount Carmel sample was included in comparisons, Teshik-Tash 1 was most similar to that group.

In an unpublished study, Minugh-Purvis and Lewandowski (1994) analyzed 50 morphometric variables in a large sample of Neandertal and early modern human sub-adults. Their results indicated that the morphology of Teshik-Tash 1 was mosaic, with some aspects of its neurocranium most similar to the Neandertals and areas of its face resembling those of early modern humans. The interpretation of the morphology of Teshik-Tash 1 as mosaic has been echoed by other researchers as well, although not in the context of formal morphological analyses (e.g., the Alekseev lectures at Harvard in Reinhart-Waller, 1991; Wolpoff, 1999). Interestingly, in a study of the pattern of cranial growth and development among Neandertals and Middle and Upper Paleolithic modern humans, Coqueugniot et al., (1996) results clearly show that Teshik-Tash 1 falls among Upper Paleolithic modern humans from Předmostí with respect to a number of cranial metric variables. In an unpublished thesis using methods similar to those used here, Ritzman (2005) also provided evidence of Teshik-Tash's departure from European Neandertal sub-adult morphology.

WHY ANOTHER REASSESSMENT?

The historical context of fossil discoveries and their subsequent interpretations often set precedents that can remain fixed even as perspectives inevitably change to fit with a growing database. Even the most sincere attempts by researchers to remain unburdened by his-

tory can be confounded by the simple act of sample construction. Decisions about which specimens are placed among Neandertals, which are attributed to early modern humans, and so on, almost exclusively follow historical precedent. Sample construction in and of itself has taxonomic implications or, at a minimum, identifies assumed isolated to semi-isolated populations in the human fossil record. In this sense, the burden of historical precedents can obstruct an appreciation of variation that may in turn invalidate the existing models used to explain extinct human interaction and adaptation.

The present study aims to reevaluate the affiliation of Teshik-Tash 1 to underscore the importance of addressing variation in the Late Pleistocene fossil record. A detailed study of this fossil is warranted because a number of previous studies, as described above, have raised the point that Teshik-Tash 1 departs somewhat from the morphology of classic European Neandertals. Its continual allocation to this group, however, has provided evidence used to support the characterization of Central Asia as a Neandertal periphery, an area to which Neandertals retreated as they unsuccessfully competed with invading modern humans (see Vishnyatsky, 1999).

In addition, a thorough appraisal of the original description of Teshik-Tash 1 from an English translation that we generated from the Russian monograph (Gremyatskii, 1949) reveals problems associated with the fossil's reconstruction. To our knowledge, the present study is the first to address Gremyatskii's (1949) own assessments of his team's reconstruction efforts and how distortions and missing elements might affect morphological interpretations of the child's skull and its affiliation.

Gremyatskii (1949: p 141) suggested that the reconstruction of the facial skeleton of Teshik-Tash 1 revealed "substantial defects," with areas either completely missing or identified by him as problematic. In particular, he described the extensive reconstruction of the foramen magnum, nasal aperture, and aspects of the palate and maxillae. Gremyatskii (1949) also noted that the missing aspects of the cranial base associated with the foramen magnum significantly affected the determination of the position of important anthropometric points, the length of the foramen magnum itself, and the orientation of the plane in which it is located. Figures 3 and 4 illustrate those areas of the cranium that, following Gremyatskii (1949), were either heavily reconstructed or completely missing.

The original classification of Teshik-Tash 1 was influenced, at least in part, by the fact that fossil material from Skhul and Tabun were not used in any of Gremyatskii's comparative analyses, even though the Mount Carmel cave monograph (McCown and Keith, 1939) was published 10 years before that of the Teshik-Tash child. Given the omission of the Mount Carmel cave material, it is possible to conclude that Gremyatskii and his colleagues assumed that Mousterian assemblages were exclusively the handiwork of Neandertals. Morphology aside, this paradigm alone certainly inclined Gremyatskii (1949) to identify the Teshik-Tash fossil as a Neandertal; this assessment was ultimately the basis for defining Central Asia as the eastern outpost of the Neandertal range.

Another reason to undertake a reassessment of the Teshik-Tash fossil is that over the past 15 years Paleolithic research in Central Asia has been revitalized. Multi-disciplinary work at Anghilak Cave (Glantz et al.,

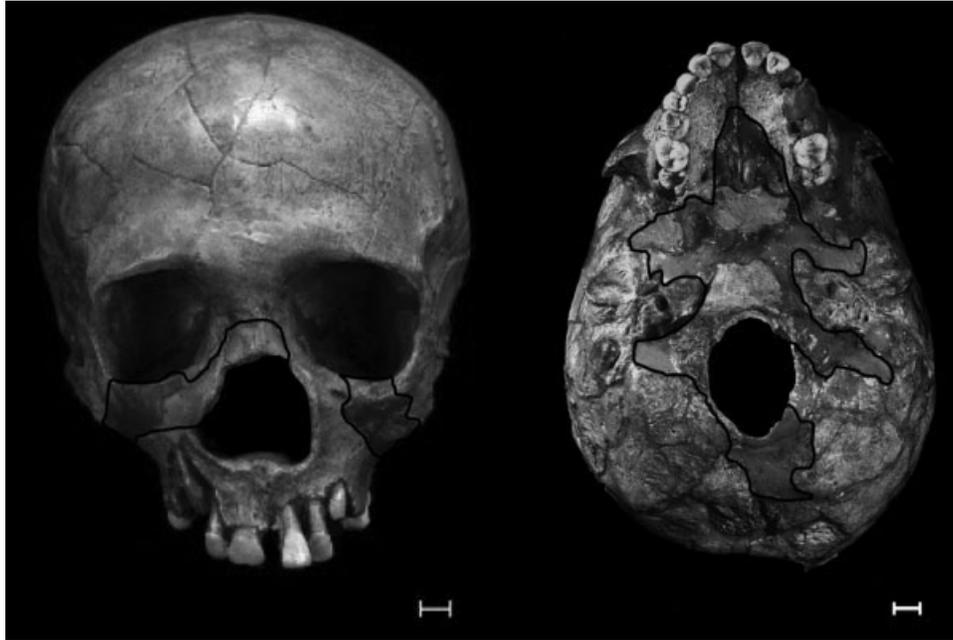


Fig. 3. Frontal and basal view of Teshik-Tash with areas substantially reconstructed or missing heavily outlined. Scale bar = 1 cm. Adapted from Schwartz and Tattersall, 2003.

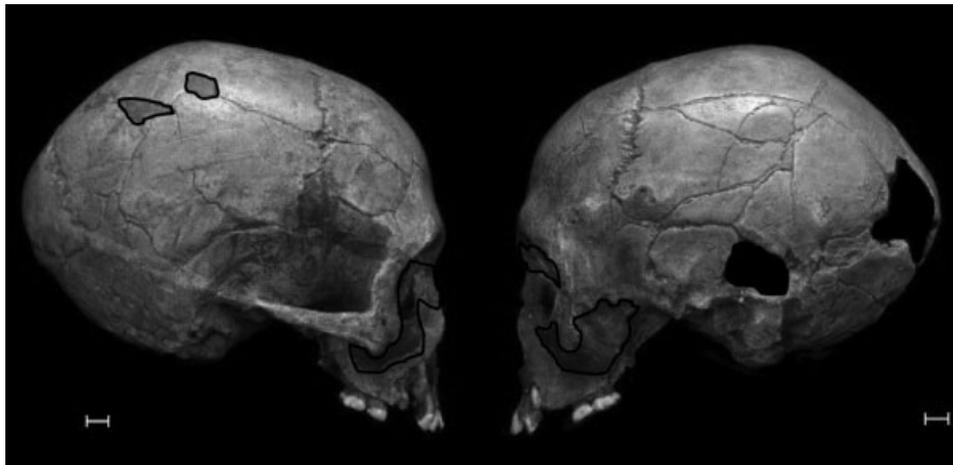


Fig. 4. Right and left lateral views of Teshik-Tash with areas substantially reconstructed or missing heavily outlined. Scale bar = 1 cm. Adapted from Schwartz and Tattersall, 2003.

2003, 2006) and Obi-Rakhmat Grotto (Derevianko et al., 2004; Glantz et al., in press) has produced provocative new archaeological and hominin materials. The results of this research suggest that it may not be appropriate to interpret data from this region within existing models of Late Pleistocene hominin evolution because these models are based largely on the evidence from Africa, Europe, and Western Asia. They tend to implicitly relegate Central Asia as a periphery, making it difficult to adequately assess the character of this region and its role in Late Pleistocene hominin population dynamics.

In the present study, we examine the affinities of Teshik-Tash 1 with respect to other Late Pleistocene sub-adult hominins. This study is different from the other reassessments in two important ways: 1) the variables analyzed here are not from areas of the cranium that were heavily reconstructed or missing on Teshik-Tash 1 and 2)

the statistical procedures used in this study are more appropriate for samples that are composed of small group sizes and have missing data. Our intent here is to use as powerful a set of analyses as possible to evaluate Teshik-Tash 1's morphological pattern in a comparative context, and discuss the meaning of any apparent departure from the Neandertal form within the framework of Late Pleistocene hominin population dynamics in general and the Central Asian Middle Paleolithic in particular.

MATERIALS AND METHODS

Sample

The comparative sample (total $N = 102$) consists of Late Pleistocene fossil ($n = 24$) and recent modern human sub-adults ($n = 78$) (Tables 1 and 2). Following

TABLE 1. Fossil and modern human sample for cranial data analysis with a priori classifications used in the MLR and DFA

Fossil sample		
Specimen	Ontogenetic age ^a	A priori classification ^b
Carigüela 2	6.5	Neandertal
Kostenki 3	6.5	UPmh
Kostenki 4	10	UPmh
Krapina A	4	Neandertal
La Quina 18	7.75	Neandertal
Le Fate 1&2	8	Neandertal
Předmostí 2	7.5	UPmh
Předmostí 22	8.5	UPmh
Předmostí 7	11.5	UPmh
Qafzeh 11	12	MPmh
Sungir 2	12	UPmh
Teshik-Tash ^c	10	Unclassified
Modern humans		
Region	Sample size	A priori classification
Central Asia	19	Recent modern human
Nubia	32	Recent modern human
Tepe Hissar	22	Recent modern human
Total cranial sample:	85	

^a Ontogenetic ages were taken from Minugh-Purvis (1988).

^b UPmh, Upper Paleolithic modern human; MPmh, Middle Paleolithic modern humans.

^c Estimated ages of Teshik-Tash range from 7 to 11 years old (see text for details).

the relevant literature, the Late Pleistocene hominins are identified as Neandertal, Middle Paleolithic modern humans, or Upper Paleolithic modern humans. The recent modern human comparative sample consists of 23 Central Asian sub-adults from skeletal collections housed at the Institute of Archaeology in Samarkand, Uzbekistan, 33 Nubians from the Kulubnarti cemetery collections at the University of Colorado-Boulder, and 22 individuals from the Bronze Age Iranian site of Tepe Hissar housed at the University of Pennsylvania Museum. In order to maximize the number of fossil specimens that could be included in the analysis, cranial and mandibular measurements were analyzed separately. For the cranial analysis, the size of the comparative sample was 84; for the mandibular analysis it was 98.

Because the nature of the question being posed in this study concerns the affinity of Teshik-Tash 1 rather than a prediction of its developmental trajectory and subsequent adult morphology, a cross-sectional comparison based on a single age cohort is appropriate. The issue of ontogenetic heterogeneity of the sample, however, inevitably plays a role in the reliability of the analysis and results. One way we addressed this problem is by restricting the sample so that it only included individuals who were at a comparable stage of dental development as Teshik-Tash 1.

A number of different ages have been attributed to the Teshik-Tash child. For example, based on its dental eruption pattern, Gremyatskii (1949) likened the fossil child to European children around the age of nine. Yet, based on an assumption that Neandertals grew more quickly than modern humans, he concluded that

TABLE 2. Fossil and modern human sample for mandibular data analysis with a priori classifications used in the MLR and DFA

Fossil sample		
Specimen	Ontogenetic age ^a	A priori classification ^b
Hortus 2 and 3	6.5	Neandertal
Isturitz 7B 1950-1955	10	UPmh
Kostenki 3	4	UPmh
Kostenki 4	7.75	UPmh
Krapina Mandible B	8	Neandertal
Krapina Mandible C	7.5	Neandertal
Ksâr 'Akil 1	8.5	UPmh
Le Fate 1&2	6	Neandertal
Les Rois 1	10.5	UPmh
Miesslingtal	9-10	UPmh
Předmostí 2	7-8	UPmh
Předmostí 24	7-8	UPmh
Předmostí 7	11-12	UPmh
Qafzeh 10 ^c	11-12	MPmh
Qafzeh 15 ^c	9	MPmh
Qafzeh 4	6.5	MPmh
Sungir' 3	11-12	UPmh
Teshik-Tash ^d	10	Unclassified
Zaskalnaya VI 1	9-10	Neandertal
Modern human sample		
Region	Sample size	A priori classification
Central Asia	23	Recent human
Nubia	33	Recent human
Tepe Hissar	22	Recent human
Total mandibular sample:	97	

^a Ontogenetic ages were taken from Minugh-Purvis (1988) unless otherwise noted.

^b UPmh, Upper Paleolithic modern human; MPmh, Middle Paleolithic modern humans.

^c Ontogenetic ages taken from Tillier (2002).

^d Estimated ages of Teshik-Tash range from 7 to 11 years old (see text for details).

its chronological age was more likely younger than nine. Weidenreich (1945); Rokhlin (1949); and Ullrich (1955) also provided younger age estimates (7-9 years old) for Teshik-Tash 1 using a variety of methods. Nevertheless, most contemporary scholars estimate the age of the Teshik-Tash child to be between 9 and 11 years (see Tillier, 1988; Krovitz, 2000; Williams et al., 2003). Minugh-Purvis (1988) relied on dental calcification and dental formation aging methods to yield an age of ~11 years for the fossil; this age falls within the maximum age range for the specimen of 9.5-11.8 determined by Skinner and Sperber (1985) using dental calcification scoring. In order to accommodate these various age estimates, the comparative sample used here includes individuals with fully erupted M1s and unerupted M2s. The dental development of the recent modern human sample was directly observed by TR, whereas the fossil specimens were chosen based on the descriptions presented in Minugh-Purvis (1988).

We computed the correlation between ontogenetic age (based on the criteria in Minugh-Purvis' (1988) dissertation as well as direct observations of the modern human specimens) and the first and second principal components in order to evaluate the effect that ontogenetic heterogeneity may have on our results. The R^2 values of this comparison (Table 3) indicate that the correlation

TABLE 3. R^2 values indicating the correlation between ontogenetic age and scores for principal components 1 and 2

	Ontogenetic age vs. PC1 total sample (R^2)	Ontogenetic age vs. PC2 total sample (R^2)	Ontogenetic age vs. PC1 fossil sample (R^2)	Ontogenetic age vs. PC2 fossil sample (R^2)
Cranial data raw	0.035	0.039	0.059	0.187
Cranial data size-standardized	<0.001	0.051	0.042	0.111
Mandibular data raw	0.206	0.171	0.410	0.048
Mandibular data size-standardized	0.001	0.165	0.226	0.175

between the ontogenetic age and the values of the most influential variables was minimal, below 0.05 for the cranial data and 0.20 for the mandibular data. When just the fossil sample was considered, the values increased in some cases with the highest correlation 0.41. Based on this result, the ontogenetic differences among specimens selected for analysis was considered to have a negligible influence on the subsequent results.

Regardless of the minor impact of ontogenetic variability of the sample, the craniofacial morphology of interest here changes in both the size and shape with age. Thus, data reduction and statistical analyses were performed based on both the raw and size-standardized variables, with size-correction following Darroch and Mossiman (1985). It should be noted here that it is arguably inappropriate to factor out size in analyses such as these because it is a key component of form differences among sub-adults. A 6-year-old and an 11-year-old scaled to the same size still do not exhibit many of the shape components that would be shared by two individuals from the same ontogenetic age. Therefore, we give greater consideration to the results based on the unstandardized variables in the discussion.

Data collection

Linear measurements of recent modern humans from the Uzbekistan and the Nubian collections were taken using standard craniometric protocols by TR. Data on the recent modern human sample from Tepe Hissar were collected from Krogman (1940). For the fossil sample, data were compiled using published measurements, the majority of which are from Minugh-Purvis (1988). Because the purpose of this study was to examine the original morphology of Teshik-Tash 1, potential variables were omitted if 1) they were associated with any aspect of skull that was missing or heavily reconstructed on the specimen following (Gremyatskii, 1949) and 2) they were poorly preserved or relatively unattainable from the comparative sample. As shown in Table 4, the resulting data set was comprised of 18 cranial and nine mandibular variables.

Imputation of missing data

Although the fossil sample examined consists of the largest number of Pleistocene sub-adults available, very few are complete individuals or preserve all of the morphologies that are captured by the variables listed in Table 4. In order to increase the sample size and perform statistical analyses, we included relatively incomplete specimens and therefore analyzed variables that were missing for many of the cases. Because of the incomplete data matrix, it was necessary to impute the missing data

TABLE 4. Variables used and percentage of missing fossil data imputed

	% missing data
Cranial variables	
Maximum cranial length	33
Maximum cranial breadth	33
Maximum frontal breadth	25
Minimum frontal breadth	8
Bistephanic breadth	42
Nasion-bregma chord	42
Nasion-bregma arc	42
Parietal sagittal chord	50
Parietal sagittal arc	58
Lambda-opisthion chord	58
Mastoid length	58
Nasal height	75
Nasal breadth	50
Biorbital breadth	42
Interorbital breadth	25
Upper facial height	58
Maxilloalveolar length	67
Facial width	58
Mandibular variables	
Bicondylar breadth	71
Minimum breadth of ascending ramus	43
Ramus height	43
Corpus height at M1	33
Corpus breadth at M1	29
Corpus breadth at symphysis	29
Symphysis height	14
M1 length	67
M1 breadth	67

before proceeding with the subsequent analyses, all of which assumed a complete data matrix.

Missing data were imputed using the expectation-maximization (EM) algorithm and multiple imputation (MI). The EM method uses a maximum likelihood estimation to predict missing values based on the covariance matrix of the complete characters. Unlike the principal components method, which also uses the covariance matrix of known characters to predict the missing values, the EM approach is an iterative algorithm which continually reestimates the parameters of the data set and uses those new parameters to reestimate the missing values until the two converge. This has been shown to be superior to PCA in estimating the missing data in the paleontological data sets (Strauss et al., 2003). MI is a general technique for fitting models to incomplete data (Rubin, 1987). Like EM, it takes advantage of the interdependence between the missing data and the unknown parameters of the data model (Schafer and Olsen, 1998). By alternately simulating the missing data and parameters,

TABLE 5. Cumulative variance of cranial and mandibular principal components

Component	Raw data			Size-standardized data		
	Eigenvalue	Proportion	Cumulative	Eigenvalue	Proportion	Cumulative
Cranial analysis						
1	6.331	0.352	0.352	5.594	0.311	0.311
2	4.137	0.230	0.582	3.417	0.190	0.501
3	2.567	0.143	0.724	3.118	0.173	0.674
4	1.553	0.086	0.811	1.948	0.108	0.782
5	1.178	0.066	0.876	1.271	0.071	0.853
Mandibular analysis						
1	3.71263	0.4125	0.4125	2.59004	0.2878	0.2878
2	1.60635	0.1785	0.591	2.1565	0.2396	0.5274
3	1.15547	0.1284	0.7194	1.49801	0.1664	0.6938
4	0.987106	0.1097	0.8291	1.16304	0.1292	0.8231
5	0.736386	0.0818	0.9109	0.729417	0.081	0.9041

a Markov chain is created that eventually converges on a stable predictive distribution from which multiple imputations of the missing data are drawn. Missing data were imputed using the software NORM 2.3 (Schafer 1999).

Previous research (Allison, 2000; Yuan, 2000) has shown that this method is superior to other imputation methods when working with smaller datasets and those with a higher percentage of missing values. In addition, the use of EM as well as the NORM programs has precedence in physical anthropological studies (Shell-Duncan, 1995; Stefan, 2004; Scherer, 2007). More common approaches used in paleoanthropological studies to deal with missing data, such as listwise or pairwise deletion, would result in a data matrix that would be so small as to be untenable for statistical analysis. Another common approach, mean substitution, has a tendency to create artificial similarities among the fossils even when applied under the strictest of conditions (Holt and Benfer, 2000). It also tends to create under-estimated variances and covariances, as does the multiple regression method of imputing missing data (Marc, 2002).

As much of statistical and methodological literature on missing data procedures has noted (e.g., Schafer and Olsen, 1998; Schafer and Graham, 2002; Wayman, 2003), the purpose of missing data imputation is not to calculate the exact value of the missing measurements, but rather to estimate the values in such a way that the parameters of the observed population are preserved, and thus subsequent complete-data analytical methods are minimally affected by the missing data points. It should be noted that whenever data are missing, any decision as to how to proceed is in essence a methodological decision. By reducing the study to only those variables and cases that are complete, one is selecting a form of complete-case analysis, which was shown as biased because complete cases are rarely a random sub-sample of the entire population (Little and Schluchter, 1985). Our decision was to use a more statistically principled means of estimating the missing data in order to proceed with the complete-data analysis. However, the extent to which data had to be imputed for certain variables is likely to have affected the results, and therefore will be taken into consideration in the discussion.

The percentage of missing variables for the fossil specimens is shown in Table 4. Cranial and mandibular datasets were imputed separately. Each final data set was created from five imputed data sets, which were

averaged to form the raw data that were analyzed. None of the values for Teshnik-Tash 1 were imputed.

Data analysis

Several recent studies have used morphometric and multivariate analyses to investigate the ontogenetic trajectory of Neandertals relative to modern humans (Ponce de León and Zollikofer, 2001, 2006; Krovitz, 2003; Williams and Krovitz, 2004). These studies are interested primarily, although not exclusively, in questions of taxonomy with respect to archaic and modern Late Pleistocene groups. As such, they use methods comparable to time-series analyses, designed to reveal heterochronic differences between these populations. In contrast, the present study is not seeking answers to questions of phylogeny or heterochrony but rather addresses the affinity and allocation of a single fossil specimen. Therefore, the analyses conducted here, while they take into consideration the issue of ontogenetic heterogeneity, are by nature cross-sectional comparisons.

Multinomial logistic regression and discriminant function analysis. Analyses were performed using Intercooled Stata 9.2 (StataCorp, 2004). The data were reduced by principal components analysis (PCA) (Tables 5 and 6) and analyzed using multinomial logistic regression (MLR) to assess the affinity of Teshnik-Tash 1 relative to the comparative sample. Like discriminant function analysis (DFA), which was originally developed to classify an unknown biological sample (Rao, 1948), MLR allows for the allocation of an unknown case to a set of *a priori* defined groups and generates posterior probabilities of group membership. DFA, which is more commonly used in paleoanthropology for this purpose, is sensitive to uneven group sizes, whereas MLR is considerably more robust against violations of the assumptions of equal group sizes (Long and Freese, 2001). In addition, while the posterior probability values of DFA and MLR are virtually identical when the assumptions of DFA are met (Efron, 1975), DFA has a tendency to produce overestimations of posterior probabilities when covariance matrices are unequal and/or data are non-normally distributed (Press and Wilson, 1978).

One limitation of MLR is that it does not allow for the evaluation of typicality probabilities. Typicality probabilities assess the likelihood that a given case is typical of a particular group without reference to the other *a priori*

TABLE 6. Factor loadings for the cranial and mandibular variables (raw and size-standardized). Size-standardized factor loadings are italicized

	PC1	PC2	PC3	PC4	PC5
Cranial variables					
Maximum cranial width	0.2468 <i>0.1541</i>	0.2516 <i>-0.1744</i>	-0.1364 <i>0.2634</i>	-0.0943 <i>0.1890</i>	-0.0474 <i>0.3655</i>
Maximum cranial breadth	0.1500 <i>0.2682</i>	0.2580 <i>0.2768</i>	0.3809 <i>0.1822</i>	-0.2062 <i>-0.1860</i>	0.2558 <i>0.2322</i>
Maximum frontal breadth	0.2630 <i>0.1407</i>	0.2384 <i>0.1103</i>	0.1821 <i>0.3974</i>	-0.1503 <i>-0.1063</i>	0.0097 <i>0.0712</i>
Minimum frontal breadth	0.2040 <i>0.2944</i>	0.3259 <i>-0.0539</i>	0.0565 <i>0.1571</i>	0.0833 <i>0.1093</i>	0.2649 <i>0.1380</i>
Bistephanic breadth	0.2697 <i>-0.3703</i>	-0.3099 <i>0.1392</i>	0.0295 <i>0.0689</i>	-0.1951 <i>-0.0925</i>	0.0657 <i>0.1345</i>
Frontal sagittal chord	0.21671 <i>-0.1929</i>	-0.0243 <i>-0.3945</i>	-0.3972 <i>-0.1349</i>	0.2496 <i>0.1488</i>	0.2336 <i>-0.1507</i>
Frontal sagittal arc	0.27353 <i>-0.1591</i>	-0.1559 <i>-0.0248</i>	-0.1900 <i>-0.0650</i>	0.1193 <i>0.4068</i>	0.3096 <i>0.5617</i>
Parietal sagittal chord	0.3467 <i>-0.3379</i>	-0.1459 <i>-0.0475</i>	-0.0685 <i>0.2517</i>	0.0810 <i>0.1135</i>	-0.2392 <i>-0.2089</i>
Parietal sagittal arc	0.2385 <i>-0.0840</i>	0.1653 <i>-0.4737</i>	-0.3617 <i>0.0388</i>	0.1821 <i>0.0433</i>	0.1685 <i>-0.1933</i>
Lambda-opisthion chord	-0.2622 <i>0.3886</i>	0.3417 <i>-0.1014</i>	-0.0460 <i>-0.1213</i>	0.1948 <i>0.1366</i>	0.0234 <i>-0.0276</i>
Mastoid length	-0.0103 <i>-0.0465</i>	-0.1181 <i>0.2613</i>	0.3133 <i>-0.2506</i>	-0.2659 <i>-0.4933</i>	0.6198 <i>0.0712</i>
Nasal height	0.17514 <i>0.1968</i>	0.2259 <i>0.1994</i>	0.3303 <i>0.2375</i>	0.2921 <i>0.1746</i>	-0.2006 <i>-0.4866</i>
Nasal breadth	0.0975 <i>0.2708</i>	0.4110 <i>-0.2863</i>	-0.1625 <i>0.1893</i>	-0.0895 <i>-0.0631</i>	0.0095 <i>0.0133</i>
Biorbital breadth	0.3690 <i>-0.201</i>	-0.0777 <i>0.2362</i>	0.1381 <i>0.3415</i>	0.0193 <i>0.2575</i>	-0.0998 <i>0.1109</i>
Interorbital breadth	0.3394 <i>-0.1322</i>	0.1322 <i>-0.1114</i>	-0.0180 <i>0.4656</i>	-0.1761 <i>-0.1235</i>	-0.1891 <i>-0.0403</i>
Upper facial height	0.10016 <i>0.1119</i>	-0.0017 <i>0.3644</i>	0.4363 <i>0.0406</i>	0.4223 <i>0.3268</i>	-0.1804 <i>-0.3055</i>
Maximum alveolar length	-0.2446 <i>0.3728</i>	0.3275 <i>-0.1041</i>	-0.0348 <i>-0.1698</i>	0.1924 <i>0.0790</i>	0.1862 <i>0.0291</i>
Facial width	0.0613 <i>-0.0419</i>	-0.2370 <i>0.2521</i>	0.1516 <i>-0.2986</i>	0.5622 <i>0.4522</i>	0.2893 <i>-0.0140</i>
Mandibular variables					
Bicondylar breadth	0.2724 <i>0.2863</i>	0.6157 <i>-0.5371</i>	-0.0592 <i>0.0955</i>	-0.0488 <i>-0.2363</i>	0.2830 <i>-0.2024</i>
Minimum ramus breadth	0.2724 <i>-0.2210</i>	0.6157 <i>0.2313</i>	-0.0592 <i>0.193</i>	-0.0488 <i>-0.6285</i>	0.2830 <i>0.4107</i>
Ramus height	0.4643 <i>-0.3074</i>	0.0990 <i>-0.382</i>	-0.1438 <i>0.2794</i>	-0.0516 <i>0.1774</i>	-0.0311 <i>0.4235</i>
Corpus height M1	0.4290 <i>-0.5314</i>	-0.0813 <i>-0.2122</i>	-0.0783 <i>-0.1055</i>	-0.4784 <i>0.0721</i>	-0.1130 <i>-0.2527</i>
Corpus breadth M1	0.2900 <i>-0.0846</i>	-0.4301 <i>0.458</i>	-0.0972 <i>0.3743</i>	0.1945 <i>-0.016</i>	0.4844 <i>-0.6191</i>
Corpus breadth at symphysis	0.3099 <i>0.5138</i>	0.5010 <i>-0.2215</i>	-0.1165 <i>0.0763</i>	0.3562 <i>0.2229</i>	-0.1949 <i>-0.0469</i>
Symphysis height	0.3263 <i>-0.1587</i>	-0.1790 <i>0.1803</i>	0.4056 <i>-0.6711</i>	-0.1654 <i>0.3221</i>	-0.6172 <i>0.0815</i>
M1 length	0.0815 <i>0.4016</i>	0.0941 <i>0.2234</i>	0.8311 <i>-0.3493</i>	0.3385 <i>-0.3374</i>	0.1907 <i>0.1534</i>
M1 breadth	0.2619 <i>0.1865</i>	-0.2963 <i>0.3547</i>	-0.2736 <i>0.3823</i>	0.6556 <i>0.495</i>	-0.2536 <i>0.3626</i>

defined groups (Albrecht, 1992). These values can only be computed from a DFA. Unlike the posterior probability values which are computed from the linear discriminant function, typicality probabilities are computed directly from the absolute value of the Mahalanobis's distance and therefore unequal covariance matrices do not influence their value (Reyment et al., 1984).

Given the small number of Neandertals in the samples analyzed, typicality probabilities are important to consider in this study. In these analyses, the typicality prob-

ability results relate something about group affinity because if Neandertals are distinct, and Teshik-Tash 1 is a Neandertal, then it should receive a low typicality probability with regard to all the groups in the analysis regardless of whether the comparative sample includes Neandertals. It would not be typical of any of the other groups. To evaluate typicality probabilities, a DFA was performed using SPSS 15.0.

Because MLR requires that the number of variables used not exceed the number of *a priori* defined groups

TABLE 7. Highest posterior and typicality probability values of group allocation for Teshik-Tash

	MLR highest group ^a	Posterior probability	DFA highest group ^b	Typicality probability	MLR posterior probability of being Neandertal
Cranial analysis raw data	UPmh ^c	76.5%	UPmh	72.2%	17.1%
Cranial analysis size-standardized data	Neandertal	61.8%	Neandertal	40.8%	
Mandibular analysis raw data	Recent modern human	54.2%	Recent modern human	21.2%	18.7%
Mandibular analysis size-standardized data	Recent modern human	87.2%	Recent modern human	49.4%	0.002%

^a MLR, multinomial logistic regression analysis.

^b DFA, discriminant function analysis.

^c UPmh, Upper Paleolithic modern human.

TABLE 8. Results of likelihood ratio (LR) post-estimation test assessing the significance of differences between groups. P-values significant at 0.05 level are italicized, indicating groups are significantly different

	UPmh	Neandertal	Recent modern human	
Cranial analysis raw				
UPmh ^a	–	0.011	<0.001	
Neandertal	–	–	<0.001	
Recent modern human	–	–	–	
Cranial analysis size-standardized				
UPmh	–	0.039	<0.001	
Neandertal	–	–	<0.001	
Recent modern human	–	–	–	
	MPmh	UPmh	Neandertal	Recent modern human
Mandibular analysis raw				
MPmh ^b	–	0.067	0.001	0.035
Upmh	–	–	0.101	<0.001
Neandertal	–	–	–	<0.001
Recent modern human	–	–	–	–
Mandibular analysis size-standardized				
MPmh	–	0.024	<0.001	0.090
UPmh	–	–	0.010	<0.001
Neandertal	–	–	–	<0.001
Recent modern human	–	–	–	–

^a UPmh, Upper Paleolithic modern human.

^b MPmh, Middle Paleolithic modern human.

being analyzed, the sample used in the cranial analysis was divided into three predefined groups (Neandertal, Upper Paleolithic modern humans, and recent modern humans). The mandibular analyses had a sufficiently large sample to include a fourth group (Middle Paleolithic modern humans). The first three principal components were used as variables in the MLR, accounting for 72% of the variance in the raw cranial data, 67% in the size-standardized cranial data, 71% for the raw mandibular data, and 70% in the standardized data.

For the computation of typicality probabilities from a DFA, five PCs were used, representing 87% of the raw and 85% of the size-standardized cranial data, and 91% of both the raw and standardized mandibular data. Separate-group covariance matrices were analyzed and prior probabilities were not set according to the group size. By setting the prior probabilities to the group size, an unclassified or ambiguous specimen has a higher chance of classifying with the largest group (i.e., recent modern humans in this study). To avoid this problem, prior prob-

abilities were made equivalent for each group (0.33 for the cranial analyses and 0.25 for the mandibular analyses).

The significance of group differences was assessed using a likelihood ratio (LR) test. The LR test evaluates the null hypothesis that two groups can be combined (Long and Freese, 2001). When the results are significant ($P \leq 0.05$), the null hypothesis can be rejected and the two groups are considered to be significantly different.

RESULTS

Cranial analyses

The results of the cranial and mandibular MLR are presented in Table 7. The percentage of the specimens that were correctly classified was above 95% for both cranial analyses. When only the fossil specimens were

TABLE 9. Results of discriminant function analysis test of variable contributions to the model. P-values significant at 0.05 level are italicized

	Wilks' lambda	F	P
Cranial analysis raw			
PC1	0.934	2.806	0.066
PC2	0.528	35.823	<0.001
PC3	0.977	0.926	0.400
PC4	0.785	10.966	<0.001
PC5	0.909	3.981	0.022
Cranial analysis size standardized			
PC1	0.88	5.443	0.006
PC2	0.876	5.659	0.005
PC3	0.713	16.108	<0.001
PC4	0.785	10.926	<0.001
PC5	0.946	2.278	0.109
Mandibular analysis raw			
PC1	0.807	7.336	<0.001
PC2	0.936	2.079	0.108
PC3	0.685	14.09	<0.001
PC4	0.965	1.097	0.355
PC5	0.979	0.669	0.573
Mandibular analysis size standardized			
PC1	0.726	11.552	<0.001
PC2	0.889	3.84	0.012
PC3	0.831	6.247	0.001
PC4	0.964	1.147	0.334
PC5	0.965	1.113	0.348

considered, the percentage of correct classification was 63% for both the cranial analyses.

For the raw cranial analysis, Teshik-Tash 1 expressed a high (76%) posterior probability and a high (72%) typicality probability of grouping with the Upper Paleolithic modern humans. Its probability of grouping with Neandertals was 17%. When size-standardized cranial data were considered, Teshik-Tash 1 had a 61% posterior probability of grouping with the Neandertals and a 40% typicality probability. As stated earlier, group size was not considered when setting prior probabilities for the DFA. A test that set prior probabilities according to group size, however, classified Teshik-Tash 1 as an Upper Paleolithic modern human with a low (0.10) typicality probability in the size-standardized analysis, indicating some ambiguity as to its allocation. A LR ratio post-estimation test assessing the significance of differences between the groups reveals that for both the raw and size-standardized analyses, all the three groups are significantly different from each other (Table 8).

Table 9 illustrates the test of the significance of each variable in contributing to the multinomial logit model. For the raw data, principal components 1 and 2 are significant at the $P = 0.05$ level ($P < 0.001$ for both variables), whereas PC 3 is not ($P = 0.74$). For the size-standardized data, all the three principal components were significant ($P < 0.001$). In the DFA used to compute typicality probabilities, five PCs were used. The results were similar to that of the MLR. Specifically, a Wilks' Lambda test revealed that the PCs 1 and 2 were the significant contributors to the model for the raw data analysis as were PCs 4 and 5, whereas PC3 was not (Table 10); for the size-standardized data, PCs 1–4 were significant. For both the raw and size-standardized data, a Wilks' Lambda test of the ability of the functions to discriminate among the groups was significant for functions one and two of the raw and size-standardized cranial data ($P < 0.001$).

TABLE 10. Results of test of ability of functions to discriminate between groups. P-values significant at $P < 0.05$ are italicized

Test of function(s)	Wilks' lambda	Chi-square	df	P
Cranial analysis raw				
1 through 2	0.239	111.651	10	<0.001
2	0.864	11.399	4	0.022
Cranial analysis size standardized				
1 through 2	0.244	110.141	10	<0.001
2	0.917	6.723	4	0.151
Mandibular analysis raw				
1 through 3	0.454	71.408	15	<0.001
2 through 3	0.840	15.807	8	0.045
3	0.936	5.961	3	0.114
Mandibular analysis size standardized				
1 through 3	0.430	76.315	15	<0.001
2 through 3	0.893	10.217	8	0.250
3	0.994	0.529	3	0.912

Mandibular analyses

The percentage of correctly classified specimens was above 85% for the raw and standardized mandibular analyses. When only the fossil specimens were considered, 34% of the cases were correctly classified in the raw mandibular analysis, and 50% in the size-standardized analysis. The results of the mandibular analyses gave Teshik-Tash 1 a higher posterior probability of grouping with the recent modern humans in both the raw and size-standardized MLR analyses, with the values of 0.54 and 0.87, respectively. In the DFA, Teshik-Tash 1 was given a relatively low typicality probability relative to recent modern humans (21%), although this was its highest value relative to any group. Its highest typicality probability was again in relation to the recent modern humans for the size-standardized analyses, and this value was higher (49%) than the reported value associated with the raw data. In the MLR of size-standardized data, Teshik-Tash 1 had a 0.19 probability of classifying with the Neandertals for the raw data, and a <0.001 probability of grouping with them for the size-standardized data.

A likelihood-ratio post-estimation test of the significance of differences between the groups indicated that, for the raw data, most pairwise comparisons of groups were significantly different except Neandertal vs. Upper Paleolithic modern humans ($P = 0.10$), and Middle vs. Upper Paleolithic modern humans (marginally above significance at $P = 0.07$). For the size-standardized data, all groups were significantly different with the exception of Middle Paleolithic modern humans and recent humans ($P = 0.09$) (Table 6). In the MLR analyses, all the three principal components significantly contributed to the differences among the groups ($P < 0.0001$ for all except PC2 in the raw analysis, $P = 0.02$). In the DFA, the first and third PCs were the significant contributors to the differences among the groups for both the raw and size standardized analyses; PCs 4 and 5 were not. Additionally, PC 2 was not a significant contributor to the model for the raw mandibular data analysis (Table 8). The Wilks' Lambda test indicates that the first and second functions successfully discriminate among the groups for the raw and size standardized data.

In order to investigate the consistency of these findings, analyses that gave Teshik-Tash 1 an *a priori* classification as a Neandertal were also conducted. This was done for both the cranial and mandibular analyses in

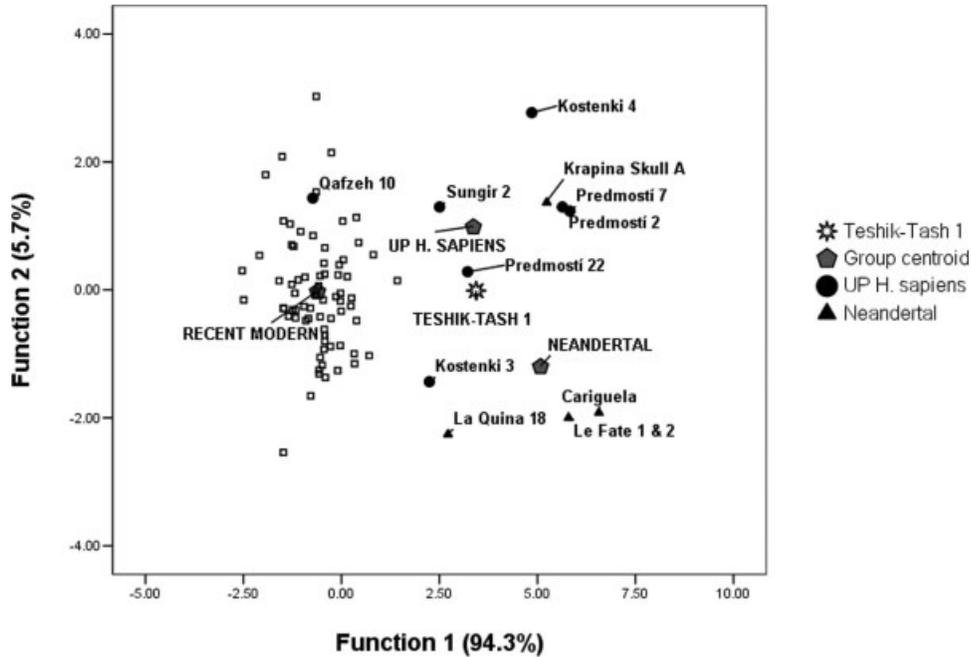


Fig. 5. Plot of discriminant functions 1 and 2 extracted from raw cranial variables.

order to explore the effect of adding one more “Neandertal” to the sample and to test the strength of Teshik-Tash’s affinities to the other groups. For the cranial analyses, the results gave Teshik-Tash 1 a higher posterior probability of grouping with the Neandertals than the Upper Paleolithic humans (54% vs. 41%, respectively, for the raw data, 69% vs. 21%, respectively, for the size-corrected data). For the mandibular analyses, Teshik-Tash 1 was consistently given a higher posterior probability of grouping with the recent modern humans than with the other three groups (48% and 83% probability of being a recent modern human for the raw and standardized data, respectively).

Plots of the discriminant function scores for the cranial and mandibular data (Figs. 5–8) reveal the position of Teshik-Tash 1 relative to the comparative sample. Although the depiction is based on analyses that, as stated earlier, are somewhat less robust than MLR, the latter method does not provide output that is suitable for plotting in two-dimensional space. These plots also reveal information about the typicality of Teshik-Tash 1 relative to its predicted groups.

DISCUSSION

The results of these analyses suggest that in certain respects Teshik-Tash 1 may depart from the Neandertal morphological pattern based on the morphology captured by the 27 linear variables examined here. In six out of the eight analyses conducted, Teshik-Tash 1 fails to group with the Neandertals. In fact, when the variables are not size standardized, an approach we advocate, Teshik-Tash 1 expresses relatively high posterior and typicality probabilities of grouping with the Upper Paleolithic modern humans in the cranial analysis (76% and 72%) and recent modern humans in the mandibular analysis (59% and 54%). However, when the cranial variables are size standardized, Teshik-Tash 1 allocates with the Neandertals, with a posterior probability of 62% and

a relatively ambiguous typicality probability of 40%. In addition, when Teshik-Tash 1 is given a *a priori* classification as a Neandertal, it “correctly” allocates with the other Neandertals in the cranial tests, although not very strongly. In both the mandibular analyses, Teshik-Tash 1 is “incorrectly” classified as a recent modern human.

There are a few possible criticisms of the general conclusion that Teshik-Tash 1 is not typical of sub-adult European Neandertals that warrant consideration. First, it could be argued that the linear variables used in this analysis do not express the morphologies that are often relied on when separating Neandertals from modern humans. However, several tests clearly indicate that the variables analyzed here are able to discriminate between a sample of developmentally similar fossil hominins and recent modern humans. In addition, the results show that ontogenetic heterogeneity has a marginal impact on the outcome of the analyses. The lack of comparably-aged, relatively complete Neandertals against which to compare Teshik-Tash 1 is also an issue here, as it is in any study of Late Pleistocene sub-adults. However, by examining the typicality probabilities it is possible to assess Teshik-Tash 1’s morphology relative to Neandertals, even in the absence of this group.

Perhaps most importantly, there are limitations in the data analysis that call into question facile interpretation of the results presented here. In particular, a high percentage of imputed data were generated in this study. Although the average percentage was below 50%, it was high for a few variables, with a maximum of 75%. It merits repeating here that the purpose of data imputation is not to estimate the values of the missing data, but rather to preserve the existing relationships among the variables and cases, given the known data points. MI allows for those relationships to be explored by statistical methods that require complete data sets. In this context, this study can be seen as an exploration of Teshik-Tash 1’s unreconstructed morphology using arguably the most statistically principled way to deal with an

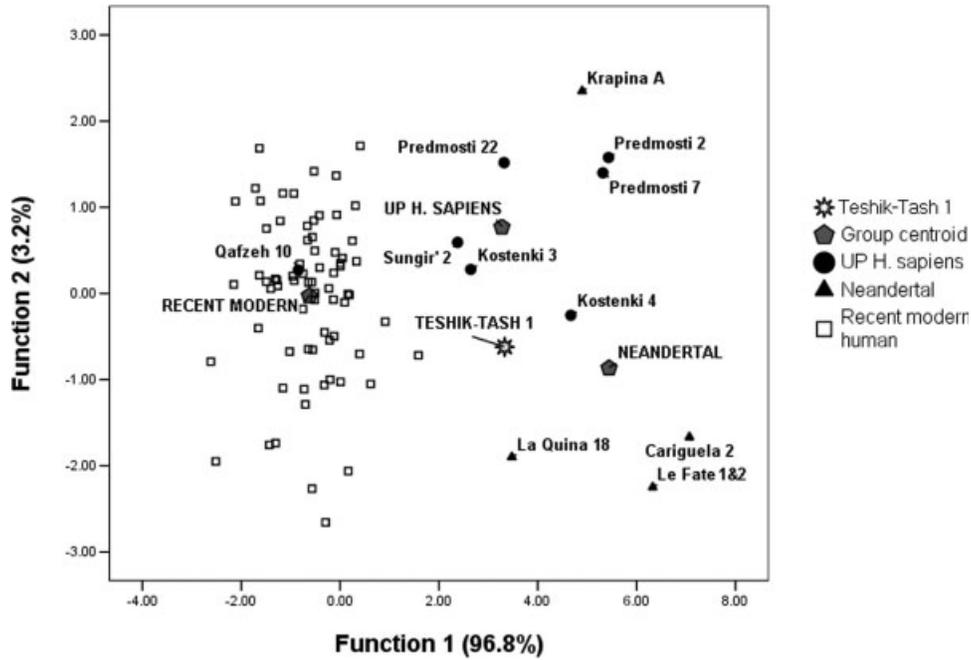


Fig. 6. Plot of discriminant functions 1 and 2 extracted from size-standardized cranial variables.

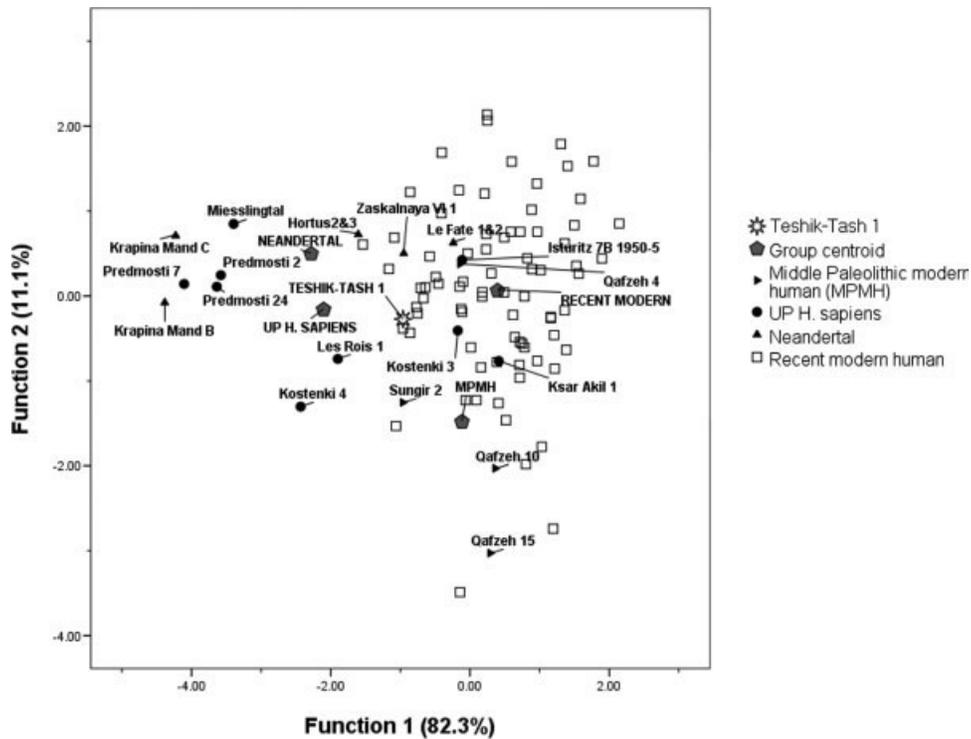


Fig. 7. Plot of discriminant functions 1 and 2 extracted from raw mandibular variables.

incomplete comparative data set. However, the methods ultimately do not solve the problem of knowing the true morphological range of the comparative sub-adult fossil sample. Without this information, it is difficult to say with certainty how Teshik-Tash 1 actually compares to these other groups.

In attempting to address the issue of the missing data, we ran a series of analyses, not included here, that used fewer variables but also had a much lower percentage of the missing data (Ritzman et al., 2006). The results were comparable to those obtained here: Teshik-Tash 1 grouped with the Upper Paleolithic humans in all cra-

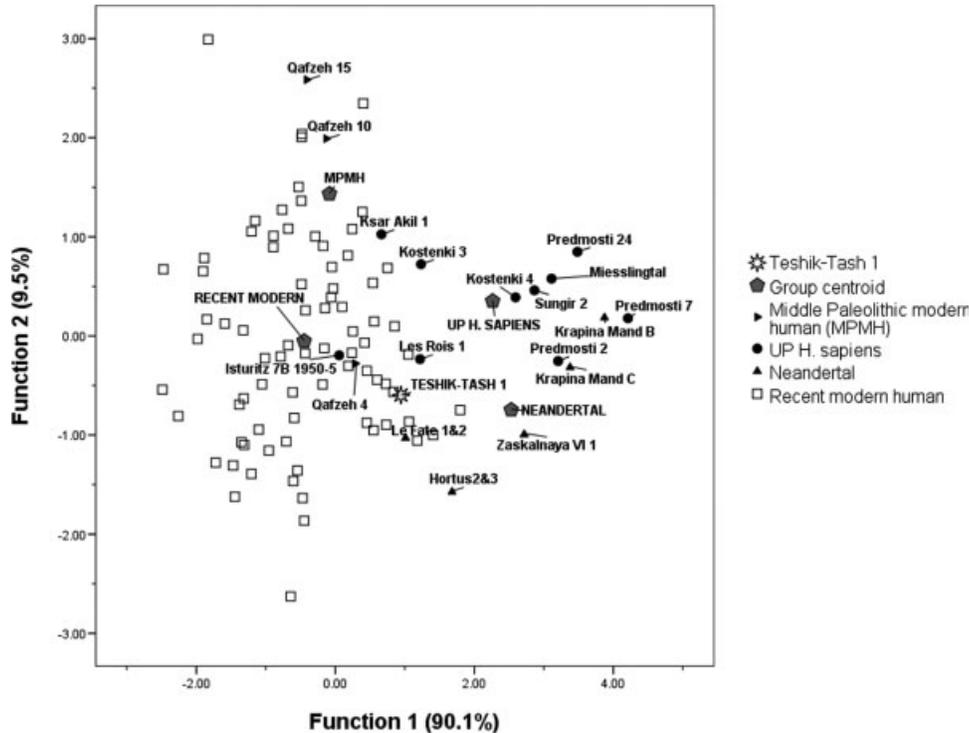


Fig. 8. Plot of discriminant functions 1 and 2 extracted from size-standardized mandibular variables.

nial analyses, and with the recent modern humans in mandibular analyses. As with this study, we ran those analyses leaving Teshik-Tash 1 ungrouped as well as giving it an *a priori* allocation as a Neandertal. In all the runs of the cranial data, Teshik-Tash 1 grouped with the Upper Paleolithic humans; with the mandibular data, it grouped with the recent human sample. Although we recognize the very real limitations of what can be said about Teshik-Tash's taxonomic allocation given the incompleteness of the comparative data set, we nonetheless take into consideration the repeatability of these results when considering its affinities.

Our results therefore beg the question: is Teshik-Tash 1 an Upper Paleolithic modern human? Or, more simply, a modern human that is somewhat more robust than the recent groups of the same age with respect to its cranium, but as gracile as those groups with regard to its mandible? Although our results suggest that Teshik-Tash 1 is metrically different from other Neandertal sub-adults in the sample, there is not sufficient evidence to support reclassifying Teshik-Tash 1 as a modern human, nor for confidently retaining its Neandertal allocation.

It is also important to consider several nonmetric assessments of Late Pleistocene hominins that include Teshik-Tash 1 in any discussion of the fossil's attribution. These studies have identified combinations of features that in a probabilistic sense align this specimen with other sub-adult and adult Neandertals. Teshik-Tash 1 has been described as possessing an *en bombe* shaped cranium, a suprainiac fossa, very low supraceutical crests, a large and long foramen magnum, medial pterygoid tubercles, and as lacking a mental eminence and canine fossae (Gremyatskii, 1949; Rak et al., 1994; Schwartz and Tattersall, 2003). The presence of specific combinations of these features has been shown to successfully discriminate between fossil hominin groups

(Jabbour et al., 2002; Trinkaus, 2003; Wolpoff and Frayer, 2005; Caspari, 2006; Gunz and Harvati, 2006), and certain authors (e.g., Rak et al., 1994, 1996) have noted the expression of some of these purportedly autapomorphic features in very young Neandertal specimens.

We are not questioning whether Teshik-Tash 1 expresses these features nor are we arguing that the results of metric analyses are more decisive vis-à-vis those concerned with discrete traits. However, the issue of whether these characters are truly biologically unique in Neandertals has been sufficiently questioned as to caution against disproportionately weighting their significance as independent characters (Trinkaus, 2006). In addition, the ontogeny of many of these characters is not well understood (Tillier, 1989; Creed-Miles et al., 1996; Jabbour et al., 2002; Minugh-Purvis, 2002).

Finally, as discussed earlier, some of the Neandertal features that are thought to be present in Teshik-Tash 1 are affected by the fragmentation of specific regions of the cranium, such as the foramen magnum, inferior portions of both the nasal bones, palate, portions of both zygoma and maxillae, and their subsequent reconstruction. These areas have been examined by several researchers (Rak et al., 1994; Franciscus and Trinkaus, 1995; Franciscus, 1999, 2003; Maureille and Bar, 1999), all of whom include Teshik-Tash 1 in their sample of Neandertals. Maureille and Bar (1999), however, concluded that the presence of the premaxillary suture of Teshik-Tash 1 (patent in Neandertals at later ages than in modern humans) is not scorable. Although the linear variables used in this study are not affected by the problems associated with the original reconstruction of the Teshik-Tash 1 cranium, we nonetheless recognize that the analyses here are not able to conclusively confirm or refute the Neandertal status of the specimen. Taken together, these issues suggest that neither the metric nor nonmet-

ric data can exclusively and unequivocally establish or resolve Teshik-Tash 1's taxonomic status. Given the fact that its Neandertal affinity has been largely unquestioned for several decades, we suggest the inconclusive nature of the results is itself informative in terms of calling into question certain existing paradigms.

The Central Asia-as-periphery paradigm

The consensus view on the affinity of Teshik-Tash 1 is that it represents a reasonable example of a European Neandertal. It has also been used to argue that Central Asia is an area to which Neandertals retreated during periods of climatic deterioration in Europe or to escape dispersing modern humans from Africa and the Levant (Vishnyatsky, 1999). It is important to note that no hominin fossils are associated with any of the known Lower Paleolithic sites in the region, some of which are relatively well dated such as Kul'dara, Tajikistan at 850–800 kya (Ranov et al., 1995; Vishnyatsky, 1999). Moreover, this archaeological evidence points to the occupation of Central Asia at least from the beginning of the Middle Pleistocene, a time that predates European Neandertal morphology. Evidence also indicates a more continuous occupation of the region during a large part of the Middle Paleolithic and across the Middle to Upper Paleolithic boundary (Ranov and Davis, 1979; Davis and Ranov, 1999; Vishnyatsky, 1999). Thus, non-Neandertal archaic groups were responsible for at least the earliest periods of Pleistocene occupation of Central Asia and Middle Paleolithic populations do not appear to be displaced in the early phases of the Upper Paleolithic. The potential interactions between these archaic groups of Central Asia and incoming Neandertals are not presently resolvable, but the archaeological evidence from the Middle and Late Pleistocene of the region suggests the possibility of a regional evolutionary trajectory, analogous to that proposed for East Asia (Etler, 1996).

In addition, the fossil records of the Altai and other areas of southern Siberia are too sparse to definitively identify the Middle Paleolithic hominin groups present there. However, if one accepts that the entire Middle Paleolithic of the southern Siberian Altai is the handwork of the Neandertals, then Central Asia is hardly the eastern periphery of this group's range. This view is supported by new genetic evidence that suggests one of the fossil hominins from Okladnikov Cave from the Siberian Altai has an mtDNA sequence similar to other Neandertals, including Teshik-Tash 1 (Krause et al., 2007).

Clinal variation in Neandertals

If we accept that our results suggest Teshik-Tash 1 differs from European Neandertal sub-adults, future interpretations of its morphology are affected by two cross-cutting issues related to Middle to Late Pleistocene hominin evolution. First, the clinal distribution of morphology among late archaic humans must be considered. And second, the impact of possible admixture with dispersing modern humans on this distribution must be addressed.

In considering the issue of clinal variation, it is possible to argue that Teshik-Tash 1 and other hominin material from the region point to a geographic variant of the Neandertals—a Central Asian Neandertal group. Certainly, it is well established that Neandertals exhibit spatio-temporal variability (Howell, 1957; Smith, 1981; Smith et al., 1989). Yet, the presence of a Neandertal

variant in Central Asia is actually very difficult to assess when most comparative frameworks lack Late Pleistocene fossil specimens from eastern Asia, noted that is essential in defining the eastern edge of a possible cline. Without this data, it is impossible to describe potential Neandertal clinal variation that would satisfactorily exclude all other Late Pleistocene hominin morphologies.

Because the geological age of the Teshik-Tash 1 fossil and the cultural layers in the cave from which it was recovered are unknown, its morphology alone cannot resolve questions concerning admixture or the timing of the appearance of modern morphologies in Asia. It is necessary to look at the Central Asian fossil hominin record as a whole. Although the record is sparse, some of the morphological attributes of other hominins from the region suggest a departure from the Neandertal condition observed in the European Middle Paleolithic. The Obi-Rakhmat juvenile from Uzbekistan has been described as possessing a mixture of Neandertal and modern human features; its dentition exhibits a suite of Neandertal characteristics (Bailey et al., in press) while its cranial morphology more closely resembles that of modern humans (Glantz et al., in press). The strata from which the hominin material at Obi-Rakhmat Grotto comes is bracketed by ESR ages of about 57,000–87,000 years BP (Blackwell et al., 2006). In addition, the Darra-i-Kur temporal bone from an area of Afghanistan only 200 km to the southeast of the Teshik-Tash cave was assessed as a modern human by Angel in 1972 (also see Trinkaus 2005) and some of the assemblages from Darra-i-Kur may be as recent as 32,000 years B.P. (Trinkaus, 2005). Both sites are associated with Middle Paleolithic traditions that slightly differ from each other with respect to the dominant technology used. In light of this and the results presented here, recharacterizing Teshik-Tash 1 as expressing a mix of features emphasizes Central Asia as an area during the Late Pleistocene to which hominin groups adapted, moving in and out of the region following unique sets of historical contingencies not necessarily dictated by hominin dispersals from Europe and the Levant.

As the preceding discussion has illustrated, the hominin material from Central Asia (e.g., Teshik-Tash, Obi-Rakhmat, and Darra-i-Kur) fit within Trinkaus's (2005: 222) description of early modern humans who, "prior to 25,000 years B.P. and outside of east Africa/southwest Asia[,] exhibit complex and varying mosaics of early modern, late archaic, and regional anatomical features." To be clear, we are not arguing that Teshik-Tash be reclassified as an early modern human because a) there is insufficient evidence for such a proposition, and b) this reassignment would be as reductionist as identifying it as a Neandertal. Rather, our intent is to highlight the metric aspects of Teshik-Tash 1's unreconstructed morphology that reflect a departure from European Neandertals and to underscore the significance of this observation in interpreting hominin population dynamics in Central Asia. Specifically, the characterization of Central Asia as the eastern periphery of the Neandertal range is likely an oversimplification of the actual pattern of regional variation across Eurasia during the Late Pleistocene.

CONCLUSIONS

Teshik-Tash 1 is the only relatively complete cranium of its developmental cohort as well as the only complete

specimen from the Middle Paleolithic associated with well represented lithic and faunal assemblages from east of the Aral Sea to the Pacific ocean. As such, its Neandertal attribution is critically important to defining this group's ontogenetic trajectory and to understanding Neandertal distribution during the Late Pleistocene. Our findings failed to support the widely held notion that Teshik-Tash 1 is typical of other European Neandertal sub-adults, but it is impossible to fully resolve the question of the affinity of this specimen because of the inherent limitations that result from a poorly preserved comparative sample. Such limitations would undoubtedly affect any multivariate analysis of Late Pleistocene sub-adults that were designed to allocate individual specimens or compare the morphological pattern among groups. Until more powerful methods are found to deal with the inevitable problems of fossil preservation, particularly of sub-adult crania, any such study will be inconclusive given the available data.

However, if we accept a less cautious interpretation of these results based on the reasoning behind certain methodological decisions made in this study as well as other multiple lines of evidence, it is possible to suggest that Teshik-Tash 1 differs from Neandertal sub-adult morphology. Such an interpretation is consistent not only with past research (Weidenreich, 1945) but also more recent studies (Bulygina and Gunz, 2008). This reemphasis allows for a more nuanced understanding of hominin population dynamics in Central Asia and adjacent regions and suggests that the characterization of Central Asia as the eastern outpost of the European Neandertal range is unsupported.

ACKNOWLEDGMENTS

The authors would like to thank Sayat Temirbekov for generating an English translation of the Teshik-Tash monograph. We would also like to thank Patrick Wrinn, Bence Viola, and Milford Wolpoff for helpful comments during manuscript preparation. In addition, MG and TR wish to express their gratitude to Rustam Suleimanov and Bahodir Pasilov and his family for their support and guidance during our field seasons in Uzbekistan and Kazakhstan.

LITERATURE CITED

- Albrecht GH. 1992. Assessing the affinities of fossils using canonical variates and generalized distances. *J Hum Evol* (Firenze) 7:49–69.
- Allison PD. 2000. Multiple imputation for missing data: a cautionary tale. *Sociological Methods Res* 28:301–309.
- Bailey S, Glantz M, Weaver T, Viola B. The affinity of the dental remains from Obi-Rakhmat Grotto, Uzbekistan. *J Hum Evol* (in press).
- Blackwell B, Mian A, Baboumian S, Blickstein J, Skinner A, Wrinn P, Krivoshapkin A, Derevianko A, Wagner J, Patchett P. 2006. Settling the age dispute for the Late Middle Paleolithic at the Obi-Rakhmat hominid site, Uzbekistan. Paper presented at the Paleanthropology Society Meeting, San Juan, April 24–26. Published online at <http://www.paleoanthro.org/journal/content/PAS2006A.pdf> (Abstract).
- Bulygina E, Gunz P. 2008. Mousterian children from Teshik-Tash and Staroselie: a 3D geometric morphometric analysis. *Am J Phys Anthropol* 135(S46):74–75 (Abstract).
- Caspari R. 2006. Are the suprainiac fossae of Upper Paleolithic Europeans homologous to those of the Neandertals? Paper presented at the Paleanthropology Society Meeting, San Juan, Puerto Rico, April 24–26. Published online at <http://www.paleoanthro.org/journal/content/PAS2006A.pdf> (Abstract).
- Coqueugnoit H, Liguora D, Tillier A-M, Chech M. 1996. L'os frontal immature de La Chaise S. 15 (Abri Suard, La Chaise de Vouthon, Charente) phylogenie et pathologie. *Paleo* 8:9–18.
- Creed-Miles M, Rosas A, Kruszynski R. 1996. Issues in the identification of Neandertal derivative traits at early post-natal stages. *J Hum Evol* 30:147–153.
- Darroch J, Mossiman J. 1985. Canonical and principal components of shape. *Biometrika* 72:241–252.
- Davis RS, Ranov V. 1999. Recent work on the Paleolithic of Central Asia. *Evol Anthropol* 8:186–193.
- Debetz GF. 1940. On anthropological peculiarities of the human skeleton from Teshik-Tash Cave. *Trans Uzbekistan Branch USSR Acad Sci* 5:1 (in Russian).
- Derevianko AP, Krivoshapkin AI, Anoikin AA, Wrinn PJ, Islamov UI. 2004. The lithic industry of Obi-Rakhmat Grotto. In: Derevianko AP, editor. *Grot Obi-Rakhmat Institute of Archaeology and Ethnography, Siberian Branch. Novosibirsk: Russian Academy of Sciences.* p 5–29.
- Efron B. 1975. The efficiency of logistic regression compared to normal discriminant analysis. *J Am Stat Assoc* 70:892–898.
- Etler D. 1996. The fossil evidence of human evolution in Asia. *Annu Rev Anthropol* 25:275–301.
- Franciscus RG. 1999. Neandertal nasal structures and upper respiratory tract “specialization”. *Proc Natl Acad Sci USA* 96:1805–1809.
- Franciscus RG. 2003. Internal nasal floor configuration in homo with special reference to the evolution of Neandertal facial form. *J Hum Evol* 44:701–729.
- Franciscus RG, Trinkaus E. 1995. Determinants of retromolar space presence in Pleistocene Homo mandibles. *J Hum Evol* 28:577–595.
- Gargett R. 1989. Grave shortcoming: the evidence for Neandertal burial. *Curr Anthropol* 30:157–190.
- Glantz M, Tostevin G, Suleimanov R, Ritzman T, Adams J, Derr K. 2006. The chronological context of Middle Paleolithic deposits at Anghilak Cave, Uzbekistan. Paper presented at the Society for American Archaeology Society Annual Meeting, San Juan, Puerto Rico, April 26–30.
- Glantz M, Viola B, Wrinn PJ, Chikisheva T, Derevianko A, Krivoshapkin AI, Islamov U, Suleimanov RH, Ritzman T. New hominin remains from Uzbekistan. *J Hum Evol* (in press).
- Glantz MM, Suleimanov R, Hughes P, Schaubert A. 2003. Anghilak Cave. Uzbekistan: documenting Neandertal occupation at the periphery. *Antiquity* 77:295.
- Gremyatskii MA. 1949. Skull of the Neandertal child from Teshik-Tash Cave, Southern Uzbekistan. In: Gremyatskii MA, editor. *Teshik-Tash: Paleolithic Man.* Moscow: Moscow State University. p 137–182.
- Gunz P, Harvati K. 2006. The Neanderthal “Chignon”: variation, integration, and homology. *J Hum Evol* 52:262–274.
- Holt B, Benfer JRA. 2000. Estimating missing data: an iterative regression approach. *J Hum Evol* 39:289–296.
- Howell FC. 1957. The evolutionary significance of variation and varieties of “Neanderthal Man”. *Q Rev Biol* 8:337–410.
- Hrdlička A. 1939. Important paleolithic find in Central Asia. *Science* 90:296–298.
- Jabbour RS, Richards GD, Anderson JY. 2002. Mandibular condyle traits in Neanderthals and other Homo: a comparative, correlative, and ontogenetic study. *Am J Phys Anthropol* 119:144–155.
- Krause J, Ludovic O, Serre D, Viola B, Prüfer K, Richards M, Hublin J, Catherine H, Derevianko AP, Pääbo S. 2007. Neanderthals in central Asia and Siberia. *Nature* 449:902–904.
- Krogman WM. 1940. Racial types from Tepe Hissar, Iran from the late fifth to the early second millennium B.C. *Verhandlungen der Koninklijke nederlandse akademie van wetenschappen. Afeeling natuurkunde (Tweede Sectie)* 39:1–87.
- Krovitz GE. 2000. Three dimensional comparisons of craniofacial morphology and growth patterns in Neandertals and modern humans. Ph.D. dissertation, Maryland, Johns Hopkins University.

- Krovitz GE. 2003. Shape and growth differences between Neandertals and modern humans: grounds for a species-level distinction? In: Thompson JL, Krovitz GE, Nelson AJ, editors. *Patterns of growth development in the Genus Homo*. Cambridge: Cambridge University Press. p 320–342.
- Little RJA, Schluchter MD. 1985. Maximum likelihood estimation for mixed continuous and categorical data with missing values. *Biometrika* 72:497–512.
- Long JS, Freese J. 2001. *Regression models for categorical dependent variables using stata*. Texas: Stata Press, College Station.
- Marc RF. 2002. Classification trees as an alternative to linear discriminant analysis. *Am J Phys Anthropol* 119:257–275.
- Maureille B, Bar D. 1999. The premaxilla in neandertal and early modern children: ontogeny and morphology. *J Hum Evol* 37:137–152.
- McCown T, Keith A. 1939. *The Stone Age of Mount Carmel*. Oxford: Clarendon Press.
- Minugh-Purvis N. 1988. Patterns of craniofacial growth and development in Upper Pleistocene hominids. Ph.D. dissertation. Pennsylvania: University of Pennsylvania.
- Minugh-Purvis N. 2002. Heterochronic change in the neurocranium and the emergence of modern humans. In: Minugh-Purvis N, McNamara KJ, editors. *Human evolution through developmental change*. Baltimore: Johns Hopkins University Press. p 479–498.
- Minugh-Purvis N, Lewandowski J. 1994. The most eastern neandertal: deciphering the morphology of Teshik-Tash. *Am J Phys Anthropol* S18:127–128.
- Movius HL. 1953. The Mousterian cave of Teshik-Tash, south-eastern Uzbekistan, Central Asia. *Bull Am School Prehistoric Res* 17:11–71.
- Okladnikov AP. 1939. Nakhodka Neandertal'tsa v Uzbekistane. *Vestnik Drevnei Istorii* 1:256–257.
- Okladnikov AP. 1949. Izuchenie mustierskoi stoyanki i pogrebenia neandertal'tsa v grote Teshik-Tash, Yuzhnyi Uzbekistan, Srednyaya Azia. In: Gremyatskii MA, editor. *Teshik-Tash: Paleolithic Man*. Moscow: Moscow State University.
- Ponce de León MS, Zollikofer CPE. 2001. Neanderthal cranial ontogeny and its implication for late hominid diversity. *Nature* 412:534–538.
- Ponce de León MS, Zollikofer CPE. 2006. Neanderthals and modern humans—chimps and bonobos: similarities and differences in development and evolution. In: Havarti K, Harrison T, editors. *Neanderthals revisited: new approaches and perspectives*. Springer. p 71–88.
- Press SJ, Wilson S. 1978. Choosing between logistic regression and discriminant analysis. *J Am Stat Assoc* 73:699–705.
- Rak Y, Ginzburg A, Geffen E. 2003. Does *Homo neanderthalensis* play a role in modern human ancestry? The mandibular evidence. *Am J Phys Anthropol* 119:199–204.
- Rak Y, Kimbel W, Hovers E. 1994. A neandertal infant from Amud Cave. *Israel. J Hum Evol* 26:313–324.
- Rak Y, Kimbel W, Hovers E. 1996. On Neandertal autapomorphies discernible in Neandertal infants: a response to Creed-Miles et al. *J Hum Evol* 30:155–158.
- Ranov VA, Carbonell E, Rodriguez XP. 1995. Kuldara: Earliest human occupation in Central Asia in its Afro-Asian context. *Curr Anthropol* 36:337–346.
- Ranov VA, Davis R. 1979. Toward a new outline of the Soviet Central Asian Paleolithic. *Curr Anthropol* 20:249–270.
- Rao CR. 1948. The utilization of multiple measurements in problems of biological classifications. *J Roy Stat Soc, Series B (Methodological)* 10:159–203.
- Reinhart-Waller G. 1991. The Alekseev manuscript. Available at www.drummingnet.com/alekseev/Tableofcontents.html.
- Reyment RA, Blackith RE, Campbell NA. 1984. *Multivariate morphometrics*. London: Academic Press.
- Ritzman T. 2005. Opening the stone: a multivariate reassessment of the neandertal status of the Teshik-Tash child. Masters thesis, Fort Collins, Colorado, Colorado State University.
- Ritzman T, Glantz M, Athreya S. 2006. Opening the stone: a multivariate reassessment of the Neandertal status of the Teshik-Tash Child. Paper presented at the Paleoanthropology Society Meetings. San Juan, Puerto Rico, April 24–26. Published online at <http://www.paleoanthro.org/journal/content/PAS2006A.pdf> (Abstract).
- Rohklin DG. 1949. Some data from the X-ray study of the child skeleton from Teshik-Tash Cave, southern Uzbekistan. In: Gremyatskii MA, editor. *Teshik-Tash: Paleolithic Man*. Moscow: Moscow State University. p 109–121.
- Rubin DB. 1987. *Multiple imputation for nonresponse in surveys*. New York: Wiley.
- Schafer JL. 1999. *NORM: Multiple imputation of incomplete multivariate data under a normal model*. State College, Pennsylvania: Pennsylvania State University.
- Schafer JL, Graham JW. 2002. Missing data: our view of the state of the art. *Psychol Methods* 7:147–177.
- Schafer JL, Olsen MK. 1998. Multiple imputation for multivariate missing-data problems: a data analyst's perspective. *Multivariate Behav Res* 33:545–571.
- Scherer AK. 2007. Population structure of the classic period Maya. *Am J Phys Anthropol* 132:367–380.
- Schwartz JH, Tattersall I. 2003. *The human fossil record (vol. I and II)*. New York: Wiley-Liss.
- Shell-Duncan B. 1995. Impact of seasonal variation in food availability and disease stress on the health status of nomadic Turkana children: a longitudinal analysis of morbidity, immunity, and nutritional status. *Am J Hum Biol* 7:339–355.
- Skinner M, Sperber G. 1985. *Atlas of radiographs of early man*. New York: A.R. Liss.
- Smith FH. 1981. Upper Pleistocene hominid evolution in South-Central Europe: a review of the evidence and trends. *Curr Anthropol* 23:667–703.
- Smith FH, Falsetti AB, Donnelly SM. 1989. Modern human origins. *Yearbk Phys Anthropol* 32:35–68.
- Stanford C, Allen JS, Anton SC. 2006. *Biological anthropology*. Upper Saddle River, NJ: Prentice Hall.
- StataCorp. 2004. *Intercooled stata 8.0*. Texas: College Station.
- Stefan VH. 2004. Assessing intrasample variation: analysis of Rapa Nui (Easter Island) museum cranial collections example. *Am J Phys Anthropol* 124:45–58.
- Strauss RE, Atanassov MN, De Oliveira JA. 2003. Evaluation of the principal-component and expectation-maximization methods for estimating missing data in morphometric studies. *J Vertebrate Paleontology* 23:284–296.
- Stringer CB, Gamble C. 1993. *In search of the Neanderthals*. New York: Thames and Hudson.
- Tillier A-M. 1989. The evolution of modern humans: evidence from young Mousterian individuals. In: Mellars P, Stringer C, editors. *The human revolution*. New Jersey: Princeton University Press. p 286–297.
- Tillier A-M. 2002. *Les Enfants Moustériens de Qafzeh: interprétation Phylogénétique et Paléoaurologique*. Paris: CNRS Editions.
- Torwalt C, Hoppa RD. 2005. A test of sex determination from measurements of chest radiographs. *J Forensic Sci* 50:785–790.
- Trinkaus E. 2003. Variability in the position of the mandibular mental foramen and the identification of Neandertal apomorphies. *Rivista di Antropologia (Roma)* 71:259–274.
- Trinkaus E. 2005. Early modern humans. *Ann Rev Anthropol* 34:207–230.
- Trinkaus E. 2006. Modern human versus neandertal evolutionary distinctiveness. *Curr Anthropol* 47:597–620.
- Ullrich, H. 1955. Paläolithische Menschenreste aus der Sowjetunion: Das Mousterian-Kind von Staroselje (Krim). *Zeitschrift für Morphologie und Anthropologie* 47:91–98.
- Vandermeersch B. 1992. The near eastern hominids and the origins of modern humans in Eurasia. In: Akazawa T, Aoki K, Kimura T, editors. *The evolution and dispersal of modern humans in Asia*. Tokyo: Hokusen-sha. p 29–38.
- Vishnyatsky L. 1999. The Paleolithic of Central Asia. *J World Prehistory* 13:69–122.
- Wayman JC. 2003. Multiple imputation for missing data: what is it and how can I use it? Paper presented at the Annual Meeting of the American Educational Research Association, Chicago, IL.

- Weidenreich F. 1945. The Paleolithic child from the Teshik-Tash Cave in southern Uzbekistan (Central Asia). *Am J Phys Anthropol* 3:237–249.
- Williams FL. 2004. Diagnosing heterochronic perturbations in the craniofacial evolution of *Homo* (Neandertals and modern humans) and *Pan* (*P. troglodytes* and *P. paniscus*). In: Thompson JL, Krovitz GE, Nelson AJ, editors. Patterns of growth development in the genus *Homo*. Cambridge: Cambridge University Press. p 295–319.
- Williams FL, Godfrey LR, Sutherland MR. 2003. Heterochrony and the evolution of Neandertal and modern human craniofacial form. In: Minugh-Purvis N, McNamara KJ, editors. Human evolution through developmental change. Baltimore: Johns Hopkins University Press. p 405–441.
- Williams F, Krovitz GE. 2004. Ontogenetic migration of the mental foramen in Neandertals and modern humans. *J Hum Evol* 47:199–219.
- Wolpoff MH. 1999. *Paleoanthropology*. Boston: McGraw-Hill.
- Wolpoff MH, Frayer DW. 2005. Unique ramus anatomy for Neanderthals? *Am J Phys Anthropol* 128:245–251.
- Wolpoff MH, Hawks J, Frayer D, Hunley K. 2001. Modern human ancestry at the peripheries: a test of the replacement theory. *Science* 291:293–297.
- Yuan YC. 2000. Multiple imputation for missing data: concepts and new developments. Proceedings of the Twenty-Fifth Annual SAS Users Group International Conference, Paper No 267–25. Cary, NC: SAS Institute.