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ISABELLE CREVECOEUR, ERIK TRINKAUS

FROM THE NILE TO THE DANUBE: A COMPARISON OF THE NAZLET KHATER 2 AND OASE 1 EARLY MODERN HUMAN MANDIBLES

ABSTRACT: A discrete trait and morphometric analysis of the earliest oxygen isotope stage 3 modern human mandibles from around the eastern Mediterranean, the Egyptian Nazlet Khater 2 and the Romanian Oase 1 specimens, confirms their status as early modern humans. However, both specimens exhibit distinctly archaic morphological aspects in their mandibles and/or molars, and their expressions of these archaic features vary. These specimens therefore emphasize both the persistence of non-modern morphological aspects in these early "modern" humans, and the variable natures of the mosaics of derived modern human and retained archaic human features in these human populations on the cusp of the modern human dispersal throughout the Old World.

RESUMÉ: La variabilité de l'homme anatomiquement moderne des époques paléolithiques a été particulièrement étudiée durant deux périodes distinctes de l'évolution humaine: celle des stades isotopiques 6 et 5e avec les plus vieux hommes modernes d'Afrique et du Proche-Orient et celle des stades isotopiques 2 et 1 avec l'expansion des hommes modernes dans toutes les parties du monde. C'est durant le stade isotopique 3 que les hommes modernes semblent se confronter pour la dernière fois avec les populations archaïques ou non anatomiquement modernes. Cependant, le manque de restes bien datés entre 30 ka et 100 ka limite la connaissance de l'anatomie moderne aussi bien en Afrique, qu'en Asie et en Europe.
Les restes humains de Nazlet Khater 2 (Egypte) et d'Oase 1 (Roumanie), ont été datés par association pour le premier à 37 ka et directement pour le second à 35 ka. Ces fossiles offrent une occasion unique d'appréhender une part de la variabilité de la morphologie moderne durant le stade isotopique 3.
L'étude morphométrique des mandibules et des molaires de ces deux spécimens circumméditerranéens confirme leur statut d'hommes anatomiquement modernes. La présence de certains caractères archaïques mandibulaires et dentaires varie suivant les individus. Ces deux spécimens témoignent donc de la persistance de traits primitifs au sein des premiers hommes modernes et également de l'expression en mosaïque des caractères apomorphes et plésiomorphes au sein des populations humaines modernes qui sont à l'origine du peuplement de l'Ancien Monde.

KEY WORDS: Human paleontology – Mandible – Dentition – Europe – Africa – Late Pleistocene

INTRODUCTION

A consensus has emerged that the appearance and spread of modern human biology in the western Old World involved two distinct stages. The initial stage occurred during oxygen isotope stages (OIS) 6-5e, and it involved the evolutionary emergence of craniofacially robust modern humans in sub-Saharan Africa (Day, Stringer 1982, Fleagle *et al.* 2003, White *et al.* 2003, Haile-Selassie *et al.* 2004), with a brief range expansion into the southern Levant (Vandermeersch 1981, Stefan, Trinkaus 1998a, Holliday 2000, Kaufman 2002). During this stage, early modern humans appear to have been restricted to ecologically African geographical regions, and they were contemporaneous with late archaic humans in other portions of the Old World through OIS 5, 4 and 3b. The second stage took place through OIS 3, and it consisted of the dispersal of early modern humans out of their ecologically African geographical range into portions of Africa and Eurasia previously occupied by late archaic humans. During this process, the expanding early modern human populations appear to have variably absorbed regional groups of late archaic humans, although the degree to which that absorption took place remains contentious (Holliday 1997, 2003, Jorde *et al.* 1998, Smith *et al.* 1999, Hublin 2000, Wolpoff *et al.* 2001, Bräuer 2001, Eswaran 2002, Stringer 2002, Trinkaus, Zilhão 2002, Templeton 2002, White *et al.* 2003, Tattersall 2003).

While considerable attention has been focused on both the OIS 6-5e emergence of the earliest modern humans and the degree to which late archaic humans were absorbed by the OIS 3 range expansion of modern humans, the biological nature of OIS 3 early modern humans has remained only partially investigated. This has been due to both the dearth of diagnostic and well-dated OIS 3 modern human remains prior to 30,000 BP, and to a general assumption that, once humans were cladistically "modern" (possessed derived modern human traits), they were also phenetically "modern" (exhibited the full suite of modern human morphology). This issue has been brought into focus by three recent sets of findings.

First, several purportedly early modern humans from Europe have been shown to be late OIS 2 or OIS 1 in age (Smith *et al.* 1999, Terberger *et al.* 2001, Svoboda *et al.* 2002) and others to be post-30,000 (30 ka) BP in age (Orschiedt 2003, Henry-Gambier 2003). As a result, only the fragmentary but directly dated Cioclovina, Kent's Cavern and Muierii remains (all between 29 and 31 ka BP) (Keith 1927, Stringer 1990, Păunescu 2000, 2002), the indirectly dated Brassempouy, La Quina, Mladeč and Vogelherd remains (Svoboda *et al.* 2002, Conard, Bolus 2003, Dujardin 2003, Henry-Gambier *et al.* 2004, Trinkaus pers. observ.), and the undated remains from Fontana Nuova and Les Rois (Vallois 1958, Chilardi *et al.* 1996) remain reasonable candidates to document the anatomy of the earliest modern humans in Europe (see also Churchill, Smith 2000). The western Asian Ksar Akil child may be ca. 35 ka BP (Bergman, Stringer 1989), but it is unavailable for confirmation. Of these, the best dated all post-date 32 ka BP, making the anatomy of pre-32 ka BP early modern humans uncertain across most of western Asia and Europe.

Second, the early modern human partial skeleton from Nazlet Khater, Egypt (Thoma 1984) has been radiocarbon dated by association to ca. 37,000 BP (Vermeersch 2002), making it the oldest OIS 3 mature modern human remains from northern Africa. Only the immature partial skeleton from Taramsa Hill, probably of an early modern human, is older (Vermeersch *et al.* 1998). The other OIS 3 remains from north Africa are either chronologically considerably younger or, such as the Aterian remains from Dar-es-Soltane and Témara (Vallois, Roche 1958, Ferembach 1976, 1998, Ménard 1998, 2002), are best seen as north African late archaic humans, despite their incomplete preservation. It seems likely (Débénath *et al.* 1982, Débénath 1994, Wengler 1997) that these northwest African Aterian remains bracket the northeast African Nazlet Khater remains in geological age.

And third, early modern human remains have been discovered in the Peştera cu Oase, Romania (Trinkaus *et al.* 2003a, 2003b). Directly dated to ca. 35,000 BP, the Oase 1 mandible is the oldest securely dated modern human from Europe, and the Oase sample provides a mix of archaic and modern human features.

In light of these considerations, we present here a comparison of the mandibles of the two last specimens, Nazlet Khater 2 and Oase 1. The former has been compared to African and a few western Asian later Pleistocene human remains (Thoma 1984, Pinhasi 1998, 2002), and the latter has been assessed in the context of European and west Asian Late Pleistocene remains (Trinkaus *et al.* 2003a). However, as roughly contemporaneous human remains, from either side of the Mediterranean, from the approximate time of the early Upper Paleolithic dispersal of early modern humans into Eurasia, it is appropriate to reassess their affinities to at least the circum-Mediterranean remains, which bracket them in time.

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MATERIALS AND METHODS

The analysis presented here is principally a comparison of the largely complete mandibles and dentitions of Nazlet Khater 2 and Oase 1. The Nazlet Khater 2 mandible is essentially complete, having sustained only marked dental occlusal attrition and some minor abrasion to the margins (especially to the alveolar process). The Oase 1 mandible lacks only the posterior margin of the right ramus, but all of the teeth except for five molars were lost post mortem. The areas of comparison therefore consist of overall mandibular size and proportions, molar crown proportions, and a series of discrete traits of the corpus and ramus.

The comparative samples, given the geological ages of the specimens, are predominantly Middle Paleolithic late archaic humans of north Africa, western Asia and Europe, the OIS 5 Middle Paleolithic early modern humans from south-western Asia (Qafzeh and Skhul), and OIS 3 Upper Paleolithic early modern humans from western Asia and Europe. Data on sufficiently intact remains from elsewhere during this time period that brackets the Nazlet Khater and Oase remains are absent. The late archaic humans are separated into Neandertals from Europe and western Asia and Aterian humans from northwest Africa. The latter consist of the Aterian remains from Témara and Dar-es-Soltane, for which incomplete data sets are available.

A set of discrete traits of the mandible (*Table 1*), most of which are indirect reflections of facial spatial proportions (Stefan, Trinkaus 1998a), exhibit variation across Late Pleistocene human samples with significant frequency differences principally between the Neandertals and other samples (Stefan, Trinkaus 1998b). They are compared individually across the samples. Note that the loss through attrition of the occlusal morphology of the Nazlet Khater 2 teeth prevents dental discrete trait comparisons.

The linear and angular morphometrics are limited to those which are available on the Oase and Nazlet Khater remains and for which sufficiently large and representative comparative samples remain. They consist of five linear mandibular measurements (*Table 3*), five molar crown diameters constrained by those available for Oase 1 (*Table 4*) and one external angular assessment of the symphysis (*Table 2*). The Oase and Nazlet Khater observations were taken by us; the comparative data come from either personal examination of the remains or primary published descriptions of them.

In addition, the symphyseal cross sections of the mandibles were compared by modelling the anterior mandibles as solid beams and computing second moments of area from the digitized subperiosteal contours using SLICE (Nagurka, Hayes 1980, Eschman 1992, see Dobson, Trinkaus 2002). The Oase 1 and Nazlet Khater 2 cross sections were transcribed using polysiloxane putty and projected enlarged onto a Summagraphics 1812 tablet, oriented with respect to the alveolar plane. Other cross-sections, as discussed in Dobson and Trinkaus (2002), were either transcribed in a similar manner or obtained from scaled and similarly oriented published symphyseal cross-sections. As previously argued (Dobson, Trinkaus 2002), anteroposterior second moments of area should be scaled to mandible length and vertical second moments of area to dental arcade breadth (for which the external breadth at the M_2s is employed). In addition, the angle of the maximum second moment of area to the alveolar plane provides an indication of the overall symphyseal orientation. The orientation of the maximum second moment of area was computed for the Témara 1 mandible from the unscaled cross section provided by Vallois and Roche (1958).

The linear and angular measurements are compared initially as univariate values, with the Oase, Nazlet Khater and Témara values assessed relative to the three reference samples. In this, each measurement and one ratio are assessed using adjusted z-scores following Houët in Maureille *et al.* (2001), in which the interval of –1.00 to 1.00 includes the 95% confidence interval of the reference sample in question. Therefore a specimen value outside of this range has a $P<0.05$ of belonging to the reference sample. As with the adjusted z-scores of Sokal and Rohlf (1981), this accounts for means, standard deviations and sample sizes of the reference samples.

The discrete traits are evaluated relative to the percentage distributions of the reference samples, which were compared using Kruskal-Wallis P-values computed as exact probabilities through StatXact 4 (Mehta, Patel 1999). The linear and angular measurements are compared across the reference samples using ANOVA. Levels of significance are assessed using a sequentially reductive Bonferroni multiple comparison correction within data sets (Proschan, Waclawiw 2000).

The univariate analyses were followed, for those specimens which preserve all five mandibular or dental crown linear dimensions, by principal component analyses (PCA) computed using Statistica (StatSoft France 2002). The dental crown measurements were analyzed as raw measurements, since absolute crown size, as well as proportions along the dental arcade, are morphometrically relevant in the Late Pleistocene (Maureille 2001, Trinkaus 2004). However, since there are significant differences in overall mandibular length through the Late Pleistocene (Trinkaus 2003), the mandibular data were size-standardized using the technique of Darroch and Mosimann (1985; see also Jungers *et al.* 1995). These principal component analyses were combined with discriminant functional analysis using cross-validation (jackknife option), computed with SPSS (SPSS Inc. 2002). The Oase, Nazlet Khater, Témara and Dar-es-Soltane specimens were treated as unknowns in the discriminant function analysis.

RESULTS

Mandibular discrete traits

The Nazlet Khater 2 and Oase 1 mandibles both exhibit a distinctive trait of recent humans, a prominent *tuber symphyseos* or the clear development of a "chin". Following the *mentum osseum* ranks of Dobson and Trinkaus (2002), their anterior symphyses are both stage 4, the clear prominence of the *tuber symphyseos* but with little development of the lateral tubercles. This is the pattern, which is prevalent among Middle and earlier Upper Paleolithic early modern humans (Trinkaus 2002). Moreover, stage 4 is absent among earlier archaic humans, even though a clear (but non-projecting) mentum osseum is present among a number of them. This trait is sufficient to categorize Oase 1 as an early modern human and supports the similar designation of Nazlet Khater 2 based on its cranium and associated postcrania (Thoma 1984).

At the same time, there is a suite of mandibular discrete traits that can be scored on Nazlet Khater 2 and Oase 1, for which there are comparative data from other Late Pleistocene human samples (*Table 1*). These traits provide a relatively consistent separation of the reference samples, with only the frequency of mandibular foramen lingular bridging (or the horizontal-oval form) not significantly different across the samples. However, in every trait there is some overlap in the morphological ranges of the samples,

TABLE 1. Discrete traits of the mandibular corpus and ramus of Oase 1, Nazlet Khater 2 and Dar-es-Soltane 5, compared to samples of western Asian and European Late Pleistocene human mandibles. The Oase 1, Nazlet Khater 2 and Dar-es-Soltane 5 configurations are presented, along with the frequencies of the character states indicated in the column headings. P-values are from Kruskal-Wallis tests across the comparative samples; * = significant P<0.05 with a sequentially reductive multiple comparison correction. EUP: earlier Upper Paleolithic.

	Mental foramen: % Anterior of P_4/M_1	**Retromolar space: % Absent**	**Mandibular incisure: % Symmetrical**	**Incisure crest: % Lateral on condyle**	**Mandibular foramen: % Lingular bridging**
Oase 1	P_4	absent	symmetrical	lateral	abs / pres
Nazlet Khater 2	P_4	absent	symmetrical	lateral	absent
Dar-es-Soltane 5	P_4	absent	symmetrical	–	–
Neandertals	7.4% (27)	25.0% (28)	28.6% (14)	62.5% (16)	40.9% (22)
Qafzeh-Skhul	66.7% (6)	60.0% (5)	100% (2)	100% (2)	0.0% (3)
EUP	80.8% (26)	77.1% (24)	88.2% (17)	100% (17)	20.0% (15)
Kruskal-Wallis P	<0.001*	<0.001*	<0.001*	0.005*	0.069

TABLE 2. Symphyseal angles relative to the alveolar plane and ramus breadth to mandible length indices for the Oase 1, Nazlet Khater 2 (NK 2) and Témara 1 mandibles and comparative samples. Mean ± standard deviation (N) provided for sufficiently large comparative samples. P-values are from ANOVAs across the comparative samples; * = significant P<0.05 with a sequentially reductive multiple comparison correction. For the adjusted z-scores, ±1.00 encompasses the 95% limits of the reference sample (see Methods); values which exceed the 95% limits of the reference samples are in bold face. EUP: earlier Upper Paleolithic.

	Anterior symphyseal angle	**Cross–sectional symphyseal angle**	**Ramus breadth to length index**
Oase 1	91°	84°	44.7
Nazlet Khater 2	89°	81°	47.4
Témara 1	80°	78°	–
Neandertals	80.8° ± 7.3° (18)	75.7° ± 6.5° (18)	38.0 ± 2.4 (15)
Qafzeh-Skhul	89.3° ± 0.5° (4)	85°, 88°, 91°	33.7, 37.3, 39.4
EUP	96.3° ± 6.2° (12)	93.3° ± 8.5° (10)	38.2 ± 3.0 (13)
ANOVA P	<0.001*	<0.001*	0.714
Adjusted z–scores			
Oase 1 vs. Nean.	0.630	0.585	**1.245**
NK 2 vs. Nean.	0.499	0.326	**1.758**
Témara vs. Nean.	–0.071	0.146	–
Oase 1 vs. EUP	–0.387	–0.108	0.993
NK 2 vs. EUP	–0.547	0.281	**1.412**
Témara vs. EUP	**–1.239**	–0.793	–

and one Neandertal (La Quina 9) presents the complete suite of early modern human character states (Stefan, Trinkaus 1998b). Therefore these traits provide a distributional separation of the samples rather than a categorical one.

The Nazlet Khater 2 mandible is aligned with the early modern human samples in all five of its features, even though only its mesially placed mental foramen separates it from almost all of the Neandertals. Oase 1 is similarly aligned with the early modern humans, except in the unilateral asymmetrical presence of lingular bridging of the mandibular foramen; this trait has been considered to be a derived Neandertal feature, since it is only known from Neandertal lineage specimens prior to the Upper Paleolithic (Lebel, Trinkaus 2002); its partial presence in Oase 1 and several European earlier Upper Paleolithic specimens may be interpreted as indicating an undefined degree of gene flow between them.

Nonetheless, these discrete traits of the anterior symphysis, lateral corpus and ramus are sufficient to align these two mandibles with the early modern human samples of western Asia and Europe. However, the configurations of the three of these features observable on the published photographs (Ferembach 1976) of the Aterian Dar-es-Soltane 5 mandible align it with early modern humans rather than with the Neandertals, even though both

Dar-es-Soltane 5 and Témara 1, from published information (Vallois, Roche 1958, Ferembach 1976) exhibit little development of the *mentum osseum* and would probably be scored as having *mentum osseum* rank 3, a common arrangement among late archaic humans but rare among early modern humans.

It should also be noted that the Nazlet Khater 2 mandible has a pronounced inferior mandibular torus across the lingual symphysis, one that is similar to many late archaic humans, including Témara 1 (Vallois, Roche 1958), and contrasts with the pattern seen in all early modern humans. Oase 1, in contrast, has a very modest inferior torus indistinguishable from those of early modern humans.

Mandibular symphyseal comparisons

Even though Nazlet Khater 2 and Oase 1 have prominent chins, their anterior symphyseal angles are essentially vertical, providing infradentale-pogonian to alveolar plane angles within a degree of 90° (*Table 2*). As such, they fall very close to the Qafzeh-Skhul mean and between the means of the Neandertal and earlier Upper Paleolithic samples. Their symphyseal cross-sectional angles are similarly between the Neandertal and earlier Upper Paleolithic means, but also below those of the small Qafzeh-Skhul sample. However, given the degree of variation in these angles in the Neandertal and earlier Upper Paleolithic samples, none of the adjusted z-scores reaches significance despite the significant P-values across the three reference samples.

The two Aterian mandibles, Dar-es-Soltane 5 and Témara 1, provide contrasting anterior symphyseal orientations, with the former having a nearly vertical profile but the latter has a retreating surface. The Témara 1 angles (ca. 80° and 78°) are close to the Neandertal means, but only the anterior symphyseal angle is significantly different from a reference sample (*Table 2*).

Mandibular morphometrics

In the context of these assessments of the Nazlet Khater 2 and Oase 1 mandibles, the raw mandibular measurements under consideration provide variable degrees of contrast between the reference samples, with mandibular length, corpus breadth and ramus breadth providing significant differences (*Table 3*). In overall length, the Oase 1 and Nazlet Khater 2 mandibles fall between the means of the Middle and Upper Paleolithic samples. The lateral corpus of Nazlet Khater 2 is very broad, similar to the Neandertals (and two of the Qafzeh-Skhul specimens) and contrasting with the earlier Upper Paleolithic sample. Oase 1, on the other hand, has a narrow corpus similar to those of earlier Upper Paleolithic modern humans.

Yet, both of these mandibles have very broad rami, with the Nazlet Khater 2 one being significantly different from all of the reference samples and the Oase 1 ramus being minimally less distinct. This is evident in their absolute ramal breadths (*Table 3*) and in indices of ramal breadth to mandible length (*Table 2*). Among the reference samples, only the Pataud 1 mandible (Billy 1975) approaches Oase 1 in relative ramus breadth, making Oase 1 trivially less than significantly different at the $P < 0.05$ level from the earlier Upper Paleolithic sample in the ramus breadth index. The one other mandible which appears to have a relatively broad ramus is the Dar-es-Soltane 5 specimen – measurements are not available, but assessment of the published photograph (Ferembach 1976) places its ramus breadth to length index near the upper limits of the reference samples and below those of Oase 1 and Nazlet Khater 2.

TABLE 3. Osteometrics of the Oase 1 and Nazlet Khater 2 (NK 2) mandibles and comparative samples, in mm. Mean ± standard deviation (N) provided for sufficiently large comparative samples. Right / left provided for Oase 1 and Nazlet Khater 2 as preserved; right and left values as available are averaged for specimens prior to comparisons. P-values are from ANOVAs across the comparative samples; * = significant $P<0.05$ with a sequentially reductive multiple comparison correction. For the adjusted z-scores, ±1.00 encompasses the 95% limits of the reference sample (see Methods); values which surpass the 95% limits of the reference samples are in bold face. EUP: earlier Upper Paleolithic.

	Mandible superior length	Symphyseal height	Mental foramen height	Mental foramen breadth	Ramus minimum breadth
Oase 1	103.5	34.5	33.5 / 32.9	11.9 / 12.4	46.2
Nazlet Khater 2	107.6	37.5	35.3 / 35.2	16.1 / 15.5	51.0
Neandertals	109.3 ± 6.7 (15)	35.1 ± 3.8 (21)	32.9 ± 3.3 (23)	15.7 ± 1.8 (23)	41.5 ± 2.7 (15)
Qafzeh-Skhul	109.0, 118.0, 126.0	37.3 ± 3.2 (4)	35.0, 36.0, 40.5	13.2, 15.0, 16.6	42.5, 43.0, 44.0
EUP	99.9 ± 7.3 (13)	32.3 ± 3.6 (15)	32.2 ± 4.1 (12)	12.1 ± 1.4 (11)	38.2 ± 3.4 (13)
ANOVA P	<0.001*	0.029	0.106	<0.001*	0.006*
Adjusted z-scores					
Oase 1 vs. Nean.	–0.450	–0.276	0.011	**–1.094**	0.786
NK 2 vs. Nean.	–0.157	0.301	0.319	0.107	**1.635**
Oase 1 vs. EUP	0.218	0.283	0.116	0.017	**1.084**
NK 2 vs. EUP	0.483	0.669	0.344	**1.221**	**1.732**

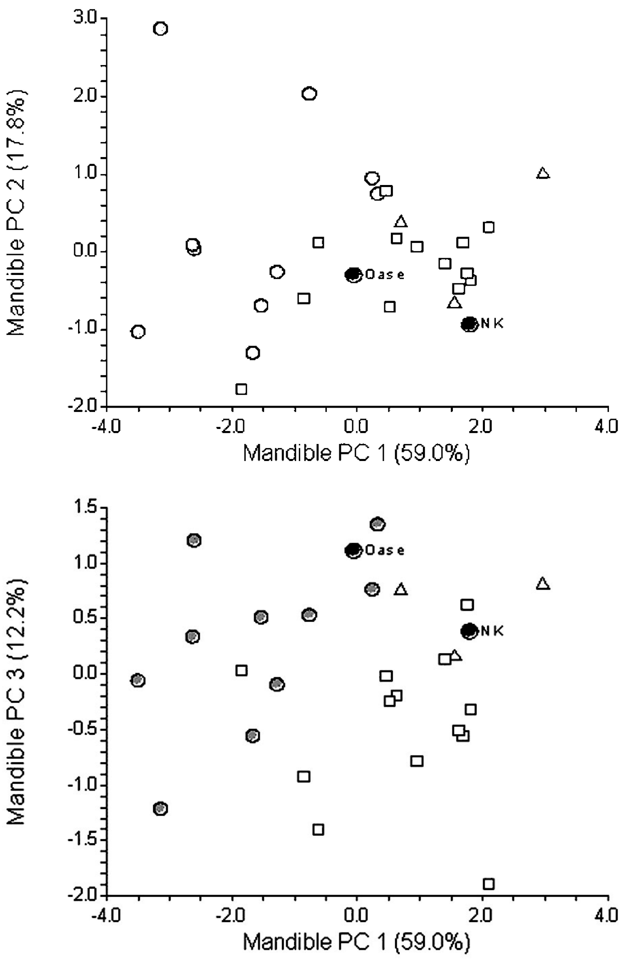

FIGURE 1. Bivariate plots of mandibular size-adjusted principal component (PC) axes for Nazlet Khater 2, Oase 1 and comparative samples. Gray circle – earlier Upper Paleolithic Europe and western Asia; triangle – Qafzeh-Skhul; square: Neandertal. Oase 1 (Oase) and Nazlet Khater 2 (NK) are individually labelled.

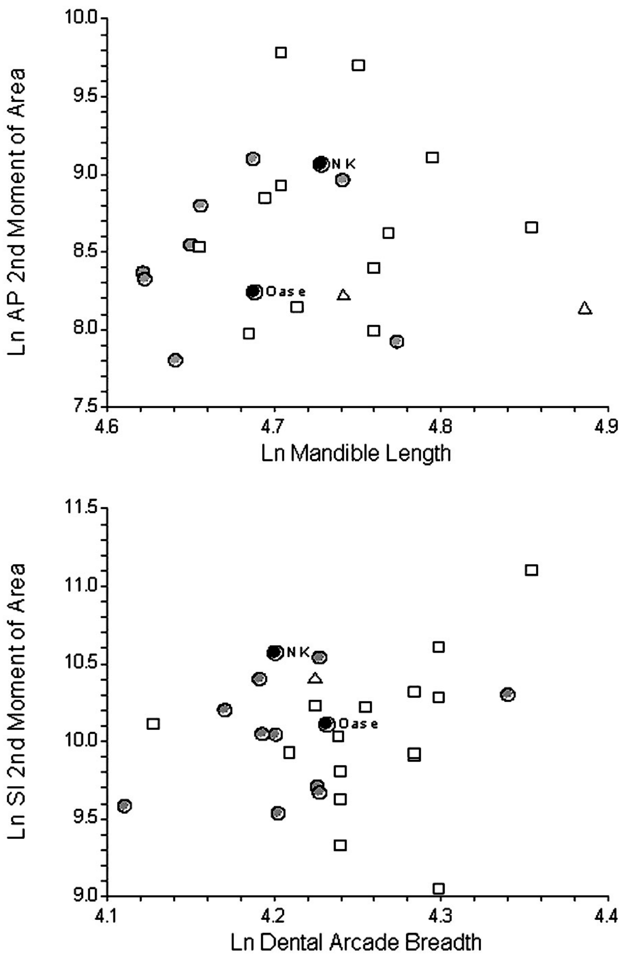

FIGURE 2. Bivariate plots of ln_e mandibular symphyseal second moments of area versus mandibular dimensions for Nazlet Khater 2, Oase 1 and comparative samples. gray circle – earlier Upper Paleolithic Europe and western Asia; triangle – Qafzeh-Skhul; square: Neandertal. Oase 1 (Oase) and Nazlet Khater 2 (NK) are individually labelled.

To assess these proportions in a more integrated fashion, the size-adjusted linear measurements were analyzed using principal components analysis (PCA), and axes 2 and 3 are compared graphically to axis 1 in *Figure 1*. In axis 1 (59% of the variation), the two Eurasian Middle Paleolithic samples are clustered together with minimal overlap with the Upper Paleolithic sample, whereas there is complete overlap of the reference samples in axis 2 (18% of the variation) and a high degree of overlap in axis 3 (12% of the variation).

In the first two axes, Oase 1 falls in the middle of the overall distribution, but with respect to axis 3 it is aligned with the earlier Upper Paleolithic sample, and to a lesser extent with the Qafzeh-Skhul sample. It falls particularly close to the Dolní Věstonice 14 and 16 and Předmostí 3 mandibles and to the Skhul 4 and 5 ones. On the other hand, the Nazlet Khater 2 mandible is distinct from the earlier Upper Paleolithic sample and falls in all three axes well within the distributions of the Neandertal and Qafzeh-Skhul mandibles.

These graphic PCA assessments are reinforced by discriminant function analysis. With cross validation, there is a 73.9% correct classification of the specimens in the reference samples (N=23). All nine earlier Upper Paleolithic specimens are correctly classified with posterior probabilities >0.95, but only three Middle Paleolithic specimens (Kebara 2, Shanidar 4 and Regourdou 1) are correctly classified with posterior probabilities >0.80. The misclassifications are entirely between the two Middle Paleolithic samples, with Qafzeh 9 and Skhul 5 being classified as Neandertals and La Ferrassie 1, La Quina 9 and Saint-Césaire 1 appearing as Qafzeh-Skhul specimens. However, Skhul 5 and La Quina 9 have posterior probabilities of 0.533 and 0.503 of being in the wrong sample, making their assignments ambiguous.

In the context of these classifications and posterior probabilities, Oase 1 is classified as an earlier Upper Paleolithic specimen, with a posterior probability of 0.989. Nazlet Khater 2, however, is classified as Neandertal but with a lower posterior probability (0.586) and with posterior

TABLE 4. Mandibular molar mesiodistal (MD) and buccolingual (BL) crown diameters in mm, for the five diameters preserved for Oase 1, Nazlet Khater 2 (NK 2), Témara 1, Dar-es-Soltane 5 (D-e-S 5) and the comparative samples. Areas are length x breadth and in mm^2. Right / left values given for the the first four specimens as available. The summary statistics for the reference samples and the Oase 1, Nazlet Khater 2, Témara 1 and Dar-es-Soltane 5 comparisons to the reference samples are based on the average dental dimension for those measurements provided by both antimeres. Mean ± standard deviation (N) are provided for sufficiently large comparative samples. ANOVA P-values are across the comparative samples; none are significant after a sequentially reductive multiple comparison correction. For the adjusted z-scores, ±1.00 encompasses the 95% limits of the reference sample (see Methods); values which surpass the 95% limits of the reference samples are in bold-face. EUP: earlier Upper Paleolithic; Q-S: Qafzeh-Skhul.

	M_1 BL	M_2 MD	M_2 BL	M_2 Area	M_3 MD	M_3 BL	M_3 Area
Oase 1	11.7 / –	12.9 / 13.2	12.1 / 11.7	156.1 / 154.4	14.2 / 14.1	12.1 / 12.0	171.8 / 169.2
NK 2	11.8 / 11.7	– / 11.9	– / 11.5	– / 136.9	– / 11.7	– / 11.1	– / 129.9
Témara 1	12.0 / 12.0	12.3 / 12.1	12.1 / 12.2	148.8 / 147.6	– / 11.5	– / 11.2	128.8
Dar-es-Soltane 5	– / 12.5	– / 12.8	– / 12.4	– / 158.7	– / 11.7	– / 11.5	– / 134.6
Neandertals	10.9 ± 0.6 (49)	11.7 ± 0.5 (37)	11.0 ± 0.7 (35)	127.8 ± 12.0 (35)	11.7 ± 0.6 (40)	10.9 ± 0.8 (42)	127.3 ± 14.8 (40)
Qafzeh-Skhul	11.4 ± 0.6 (15)	11.1 ± 0.8 (9)	10.9 ± 0.7 (10)	121.1 ± 15.5 (9)	11.9 ± 0.8 (7)	10.8 ± 0.7 (7)	128.1 ± 15.5 (7)
EUP	11.1 ± 0.7 (39)	11.3 ± 0.8 (33)	10.9 ± 0.7 (34)	123.8 ± 16.3 (33)	11.3 ± 0.8 (20)	10.7 ± 0.8 (21)	120.1 ± 18.4 (20)
ANOVA P	0.029	0.032	0.936	0.419	0.057	0.491	0.221
Adjusted z-scores							
Oase vs. Nean.	0.694	**1.260**	0.670	**1.132**	**1.908**	0.672	**1.444**
NK 2 vs. Nean.	0.694	0.216	0.388	0.373	0.035	0.100	0.086
Témara vs. Nean.	0.960	0.488	0.846	0.841	–0.117	0.160	0.050
D-e-S 5 vs. Nean.	0.004	0.022	0.023	0.007	0.472	0.247	0.314
Oase 1 vs. Q-S	0.229	**1.027**	0.640	0.956	**1.112**	0.791	**1.120**
NK 2 vs. Q-S	0.229	0.434	0.394	0.441	–0.093	0.201	0.046
Témara vs. Q-S	0.453	0.588	0.792	0.759	–0.191	0.263	0.018
D-e-S 5 vs. Q-S	0.049	0.036	0.031	0.021	0.414	0.157	0.346
Oase vs. EUP	0.440	**1.079**	0.640	0.945	**1.623**	0.768	**1.303**
NK 2 vs. EUP	0.440	0.371	0.376	0.391	0.243	0.231	0.252
Témara vs. EUP	0.656	0.556	0.804	0.733	0.131	0.288	0.225
D-e-S 5 vs. EUP	0.023	0.034	0.029	0.020	0.308	0.175	0.222

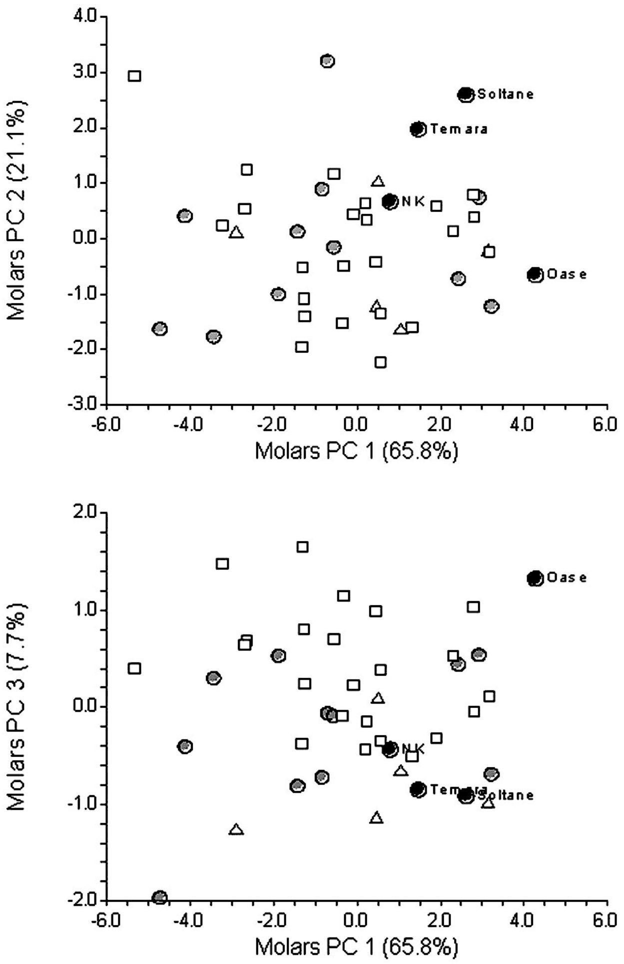

FIGURE 3. Bivariate plots of molar diameter principal component (PC) axes for Nazlet Khater 2, Oase 1 and comparative specimens. Gray circle - earlier Upper Paleolithic Europe and western Asia; triangle – Qafzeh-Skhul; square: Neandertal. Oase 1 (Oase), Nazlet Khater 2 (NK), Dar-es-Soltane 5 (Soltane) and Témara 1 (Temara) are individually labelled.

probabilities of being earlier Upper Paleolithic of 0.365 and Qafzeh-Skhul of 0.049.

These morphometric assessments of the Nazlet Khater 2 and Oase 1 mandibles highlight two similarities between the specimens (their wide mandibular rami and intermediate symphyseal orientations) and a contrast between them (corpus breadth). Yet, when taken in the context of overall mandibular proportions, Oase 1 is Upper Paleolithic in form, whereas Nazlet Khater 2 is considerably more archaic.

Symphyseal cross-sectional assessments

The symphyseal cross-sectional parameters are plotted against appropriate measures of mandible size in *Figure 2*. As previously documented (Dobson, Trinkaus 2002), there is little difference between the late archaic and early modern human samples in absolute second moments of area at the symphysis despite changes in anterior symphyseal morphology (ANOVA P-values of 0.149 and 0.680 for the anteroposterior and superoinferior second moments of area across the reference samples). The modest differences in distributions between the samples are largely due to differences in mandible length and dental arcade breadth, plus a couple of high values for Neandertals (Kebara 2 in both measurements and Shanidar 4 in the anteroposterior second moment of area).

The absolute values for Nazlet Khater 2 and Oase 1 are within the ranges of variation of the reference samples. Yet, the former has among the highest values, except for the two Neandertal high outliers, reflecting its large mandibular torus. The latter is average in the superoinferior comparison, but moderately gracile in the anteroposterior comparison.

Dental morphometric comparisons

In the molar crown metric comparisons, there are few differences across the reference samples, as has been previously documented (e.g., Frayer 1978, Maureille 2001, Trinkaus 2004). The principal differences noted here are in the M_1 breadth (in which the Neandertals have slightly smaller teeth) and the M_2 length (in which the Neandertals have slightly larger teeth) (*Table 4*); yet, with a multiple comparison correction their P-values do not reach significance. The considerable overlap in the individual ranges of variation of these dental metrics is reflected in the size and shape (raw measurement) PCA plots (*Figure 3*), in which there is complete overlap of the distributions on axis 1 (66% of the variation), largely reflecting overall dental size. There is some separation of the samples on axes 2 and 3 (21% and 8% of the variation respectively), but considerable congruity of the distributions exists on those axes as well. This is reflected in a correct classification rate of only 61.5% (N=39) in the discriminant function analysis using cross validation. The misclassifications are across all three samples, with eleven (28.2%) between the Neandertals and the earlier Upper Paleolithic sample. Of those correctly classified, only nine (23.1%) have posterior probabilities >0.80.

In this messy context, the Nazlet Khater 2, Dar-es-Soltane 5 and Témara 1 molars are classified principally with the early modern humans. None of their individual dental measurements are distinct from the reference samples (*Table 4*). They fall well within the overall distributions on PCA axis 1. Dar-es-Soltane 5 and Témara 1 are relatively high on axis 2, being exceeded only by the Hortus 5 Neandertal and the Arène Candide 1 earlier Upper Paleolithic specimen. All three north African specimens are moderately low on axis 3 (*Figure 3*). And they have, respectively, posterior probabilities of being Qafzeh-Skhul of 0.588, 0.969 and 0.840 and of being earlier Upper Paleolithic of 0.350, 0.030 and 0.145. Their posterior probabilities of being Neandertals on this basis are therefore 0.062, 0.001 and 0.015.

In contrast, Oase 1 is separate from these three specimens. Its M_2 and M_3 lengths are distinct from the reference samples. In the context of M_2 and M_3 breadths that are non-significantly above the reference sample means, its M_2 and M_3 areas (length × breadth) are significantly different from all three samples. On PCA axis 1, which reflects in large part size, it is a high outlier. It is average on axis 2, but it is high on axis 3, bracketted by the Neandertals from Saint-Césaire and Zaskalnaya above and from Arcy-Hyène, Le Moustier and Regourdou below. Its posterior probabilities also place it among the Neandertals (0.727) and separate from the earlier Upper Paleolithic (0.250) and especially Qafzeh-Skhul (0.023) samples.

DISCUSSION

These morphological and morphometric assessments of these two early Upper Paleolithic human mandibles, from either side of the Mediterranean, illustrate an anatomical mosaic at the time of the spread of modern humans across Africa and into and across Eurasia. Both of these specimens can easily be classified overall as "early modern humans". This is evident in derived features of the mandibles, and it is confirmed by the remainder of the Nazlet Khater 2 skeleton and the associated Oase 2 and 3 cranial remains. Yet, they both possess unusually wide mandibular rami (*Table 3*), an archaic feature in which they are approached by only two OIS 3 specimens (Dar-es-Soltane 5 and Pataud 1) and in which they recall several Middle Pleistocene European and African specimens (Arago 2, KNM-BK 67, Loyangalani 1, Mauer 1 and Tighenif 3). The Nazlet Khater 2 mandible is exceptional among early modern humans for the robustness of its mandibular corpus, both anteriorly and laterally, and this is probably most responsible for its alignment with the Neandertals in the multivariate analyses of mandibular metrics (*Figure 1*). Yet, its molar dimensions are most similar to those of early modern humans (plus the Aterian Dar-es-Soltane 5 and Témara 1) (*Table 3*). The Oase 1 mandible, despite its bridging of one mandibular foramen, is proportionately separate from the Neandertals, and it is aligned with the earlier Upper Paleolithic humans. However, its molars contrast with those of early modern humans, Nazlet Khater 2, Dar-es-Soltane 5 and Témara 1, and appear closest to the Neandertals among Late Pleistocene humans (*Figure 3*).

Although limited anatomically and morphometrically, given the preservation of these fossils and the available data on samples of Late Pleistocene human mandibles, these considerations are sufficient to emphasize the complex morphological mosaic that accompanied the spread of early modern humans during OIS 3. They document that the earliest "anatomically modern" humans from OIS 3 were not particularly "modern" in a variety of aspects. Although limited in time, space and sample size, they are also sufficient to emphasize that the biological processes through which humans became "modern" were geographically, temporally and probably individually significantly more variable than the neo-typological characterizations of what it means to be "modern" usually imply.

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Isabelle Crevecoeur
UMR 5809 du CNRS
Laboratoire d'Anthropologie des Populations du Passé
Université de Bordeaux 1
33405 Talence, France
E-mail: isabelle.crevecoeur@etu.u-bordeaux1.fr

Erik Trinkaus
Department of Anthropology
Campus Box 1114, Washington University
St. Louis MO 63130, USA
E-mail: trinkaus@artsci.wustl.edu

Note: Since this paper was written, it has been shown (Conard N. J., Grootes P. M., Smith F. H. 2004: Unexpectedly recent dates for human remains from Vogelherd. *Nature* 430: 198–201) that the Vogelherd 1 mandible is Holocene in age. Deleting it from the EUP sample has little effect on the morphometric comparisons and most of the discrete trait frequencies. However, it was the only morphologically secure example of lingular bridging of the mandibular foramen in the EUP sample (the other two are based on casts of Předmostí mandibles). Its deletion produces a P=0.027 across the reference samples (P=0.004 if the Předmostí remains are also deleted). This makes the secure presence of this feature in Oase 1 unique among European early modern humans.