Chapter 15
A 3-D Look at the Tabun C2 Jaw

Katerina Harvati and Elisabeth Nicholson Lopez

Abstract The Tabun cave is among the most important paleoanthropological sites in the Near East. It has yielded a long sequence of archeological record, as well as important fossil human remains, notably the Tabun C1 partial skeleton and the Tabun C2 mandible. The chronology of these specimens, as well as their respective provenience, has been intensely debated. Most recent estimates place the C1 skeleton at oxygen isotope stage 5 or 6, while the C2 mandible is thought to be significantly older. The affinities of the C2 remains are unresolved. While general consensus sees the Tabun C1 skeleton as a lightly built Neanderthal, the Tabun C2 mandible has variably been attributed to early modern humans and to Neanderthals based on both metric and non-metric traits. We conducted a comparative analysis of the three-dimensional shape of the C2 mandible using the methods of geometric morphometrics, with the goal of helping to resolve its taxonomic affinities. Results show that Tabun C2 cannot be easily accommodated either within the early modern human or the Neanderthal sample. This finding is consistent with the proposed great geological age of the specimen.

Keywords Geometric morphometrics • Mandible • Modern human origins • Neanderthals

Introduction

Excavated by Garrod between 1929 and 1934 (Garrod and Bate 1937), the Tabun cave is one of the most important paleoanthropological sites in the Near East. It has yielded both a long sequence of archeological record, now a reference sequence for Levantine Paleolithic archeology, and important fossil human specimens. The most complete of these include the Tabun C1 partial skeleton and the Tabun C2 mandible. Both specimens were recovered from stratigraphic layer C, but their exact provenance and association are uncertain (Garrod and Bate 1937; Bar-Yosef and Pilbeam 1993; see below). The striking differences in the morphology of the Tabun C1 and C2 mandibles were noted early on (see Bar-Yosef and Callander 1999). While Tabun C1 is generally considered a lightly built Neanderthal, most likely a female, opinions differ on the taxonomic affinities of the Tabun C2 specimen (e.g., Quam 1995; Quam and Smith 1998; Stefan and Trinkaus 1998; Rak 1998; see below).

The exact provenience of Tabun C1 and C2, as well as their respective chronology, is not fully resolved. Although both individuals were found within layer C of the stratigraphic sequence, Tabun C1 may have been an intrusive burial from the overlying layer B and was found in the West sector of the excavation (Garrod and Bate 1937; Bar-Yosef and Pilbeam 1993; Bar-Yosef and Callander 1999; Grün and Stringer 2000). Tabun C2 came from the deeper part of layer C and from the East sector of the cave (Garrod and Bate 1937; Bar-Yosef and Callander 1999). Early attempts at absolute dating of layer C of the Tabun cave by radiocarbon dating indicated an age of approximately 50 ka (Jelinek 1982). However, as this date was at the ^{14}C method's limit, it likely underestimated the true age by many millennia. Later dating attempts using more recent dating methods (Electron Spin Resonance [ESR], Thermoluminescence [TL], coupled ESR-Uranium series) have since obtained, for the most part, much older ages for this layer. The Tabun C1 skeleton was initially dated directly through ESR by Schwarcz et al.

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(1998), who found it to be very young (between 24 ± 5 and 19 ± 2 ka). Schwarcz et al. (1998) concluded that Tabun C1 represented a very late intrusion into layer C, indicating a very late Neanderthal survival in the Levant. However, these late dates are considered problematic based on both methodological and stratigraphic issues (Millard and Pike 1999; Alperson et al. 2000). They are not supported by more recent direct dating of the Tabun C1 specimen to between 112 ± 29 and 143 ± 37 ka (also by ESR; Grün and Stringer 2000). Grün and Stringer (2000) agreed with Schwarcz et al. (1998) that Tabun C1 was likely intrusive from layer B, as initially suggested by Garrod and Bate (1937), albeit an intrusion from a much earlier layer than previously thought. Tabun C1 was therefore probably broadly contemporaneous with the Skhul and Qafzeh early modern human populations roughly between 100 and 130 ka (Grün et al. 2005). If these latest assessments of the chronology of the Tabun sequence are correct, then the Tabun C2 mandible (coming from the lower part of layer C) would likely date to as early as 135–170 ka (Grün and Stringer 2000; Mercier and Valladas 2003).

Because of this specimen's possible association with a commonly recognized Neanderthal and its probable broad contemporaneity with the earliest modern human populations outside of Africa, the interpretation of its taxonomic affiliation and its phylogenetic position play a crucial role in the understanding of modern human origins in the region. We aim to contribute to this discussion by conducting a three-dimensional geometric morphometrics analysis of the shape of the Tabun C2 mandible using a comparative sample of early and Upper Paleolithic modern human, Neanderthal (including Tabun C1) and *Homo heidelbergensis* mandibular specimens. The use of these methods can potentially be informative, as 3-D geometric morphometrics have several advantages over traditional morphometrics. In addition to providing a means for visualization of shape differences, these techniques enable a better representation of shape than traditional linear and angle measurements and permit the quantitative assessment of traits previously described qualitatively (e.g., Rohlf and Marcus 1993; Harvati 2003). Although the mandible is considered less taxonomically informative than parts of the cranium, an analysis of modern human and Neanderthal mandibular shape was able to discriminate between the two groups and to quantitatively evaluate their described morphological differences (Nicholson and Harvati 2006).

The Tabun C2 Mandible – Previous Interpretations

Tabun C2 is a large, rather robust mandible. On the basis of its size and robusticity it is likely a male. Even though it was recovered in several pieces, it has been reconstructed and it is virtually complete (Garrod and Bate 1937; Fig. 15.1). No agreement exists on its taxonomic placement. In her unpublished field notes, Garrod noted its marked departure from the Tabun C1 mandibular morphology soon after its discovery. This morphological dissimilarity led her to believe that two human taxa were present at the site (see Bar-Yosef and Callander 1999).

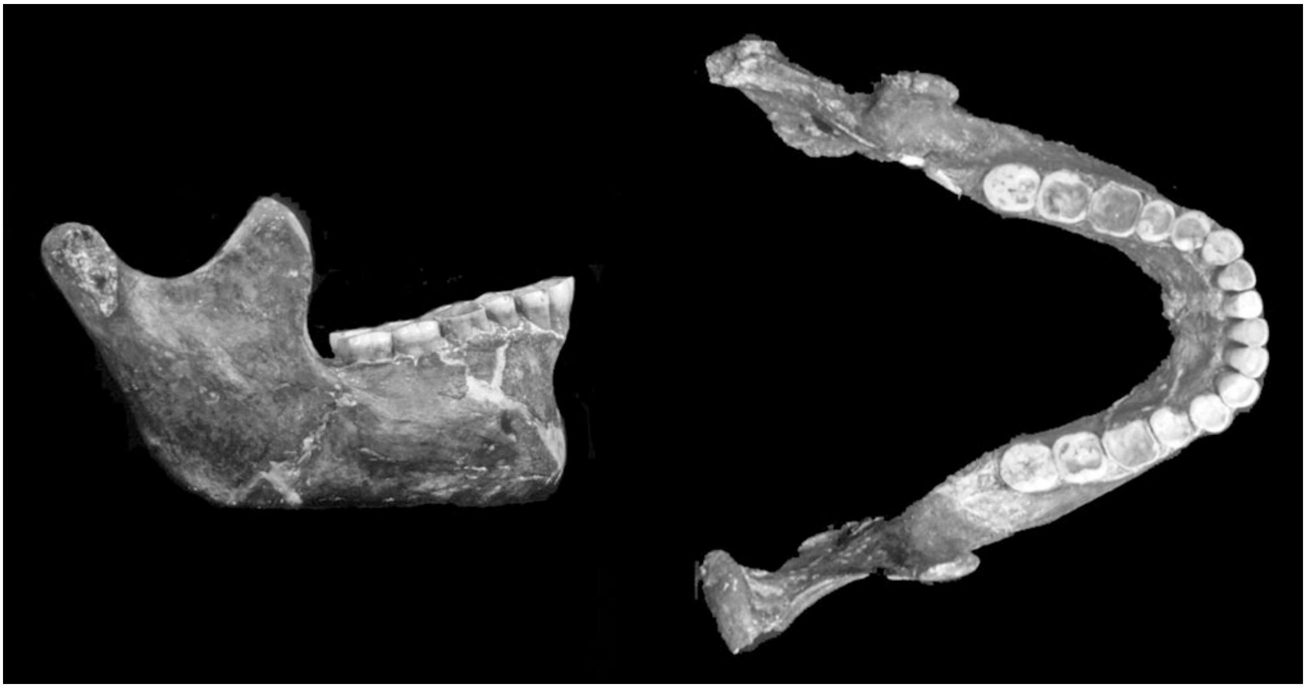

Fig. 15.1 Tabun C2 mandible. Lateral and occlusal views. Image courtesy and copyright © Jeffrey H. Schwartz

More recent analyses have also reached no consensus. Tabun C2 has been attributed to early modern humans by some authors (e.g., Vandermeersch 1981; Bar-Yosef and Pilbeam 1993; Rak 1998; Rak et al. 2002), and has often been described as possessing a distinct chin (McCown and Keith 1939; Vandermeersch 1981; Quam and Smith 1998; Rak 1998), although the lower part of the symphysis is not preserved. Rak (1998) and Rak et al. (2002) pointed out that the ramus and mandibular notch morphology of this specimen lack typical Neanderthal features. He argued that the lateral placement of the mandibular notch crest relative to the condyle, the symmetric shape of the notch, and the presence of a chin align this specimen with early modern humans rather than with Tabun C1 and Neanderthals (Rak 1998). In their analysis of the mandibular notch outline, Rak et al. (2002) found that its morphology clearly distinguishes Neanderthals from modern humans and earlier *Homo erectus* specimens. Tabun C2 fell within the ‘generalized’ fossil group, including modern humans, early modern specimens from Skhul and Qafzeh, and *H. erectus* specimens, and away from Tabun C1 and the Neanderthal sample.

Other investigations, however, have assigned Tabun C2 to Neanderthals. Stefan and Trinkaus (1998) examined a series of discrete traits and analyzed dental metrics in an effort to elucidate the specimen’s affinities. They found that Tabun C2 exhibited an unusual combination of discrete traits, with two features (mental foramen position, mandibular foramen form) aligning it with Neanderthals. Two further features (retromolar space, mandibular notch shape) were found to be ambiguous. *Contra* Rak (1998), Stefan and Trinkaus (1998) considered the notch crest position not to be taxonomically informative. Furthermore, they affirmed that the Tabun C2 symphyseal region is not sufficiently preserved to properly evaluate the presence of a chin. Their analysis of dental crown dimensions, driven by the size of the anterior teeth, classified Tabun C2 as Neanderthal. The authors concluded that their overall results indicate that Tabun C2 should be considered a Neanderthal (Stefan and Trinkaus 1998).

A detailed investigation of the Tabun C2 chin by Schwartz and Tattersall (2000; see also Schwartz and Tattersall 2010) found the preserved portions of the symphysis in this specimen to be neither modern human-like, nor similar to the morphology shown by some of the early modern humans from Skhul. The authors concluded that the specimen is not a *Homo sapiens*, but also hesitated to classify it as a Neanderthal (Schwartz and Tattersall 2000), instead suggesting the possibility of a third taxon. The ambiguous nature of Tabun C2 was also noted by Quam and Smith (1998; see also Quam 1995), who suggested that the ambiguous combination of features might be interpreted as the result of hybridization between Neanderthals and modern humans (Quam and Smith 1998). A more recent analysis of the morphology and size of the anterior dental roots (Le Cabec et al. 2013) was also unable to resolve the controversy. Le Cabec et al. (2013) found that Tabun C2 aligned with Neanderthals in the large size and shape of its anterior tooth roots, but with modern humans in its cynodont molar roots. Since the authors found that Middle Pleistocene specimens show anterior roots similar to those of Neanderthals the morphology exhibited by Tabun C2 could be a primitive retention. However, Le Cabec et al. (2013) could not reject the hypothesis that the specimen might represent a hybrid individual.

Materials and Methods

Samples Our comparative sample comprised 26 fossil mandibles (Table 15.1; see also Nicholson and Harvati 2006). Four European Middle Pleistocene specimens commonly assigned to *Homo heidelbergensis* (HH), eight Neanderthal (NEA), thirteen Upper Paleolithic/Later Stone

Table 15.1 Samples

Comparative fossil samples	Total: 26
Neanderthals (NEA) Amud 1*, Krapina J*, La Ferrassie 1, Shanidar 1*, Tabun C1*, Zafarraya*, Regourdou 1	7
Middle Pleistocene Europeans (MPE) Arago 13*, Mauer 1, Montmaurin, Sima de los Huesos 5*	4
Early Anatomically Modern Humans (EAM) Skhul 5, Qafzeh 9*	2
Upper Paleolithic/Later Stone Age (UP) Grimaldi-Grotte-Des-Enfants 6*†, Isturitz 1950-4-1, Dolní Věstonice 3, 13, 14, 15, 16, Oase, Abri Pataud, Ohalo II, Upper Cave 101* and 103*, Wadi Kubbaniya	13

*Asterisks indicate specimens for which high-quality casts from the AMNH, NYU and MPI-EVA collections were used

†Grimaldi-Grotte-Des-Enfants 6 is a subadult

Age (UP), and two Late Pleistocene early anatomically modern human (EAM) specimens were included. In cases where we were not able to measure the original fossils, high quality casts were measured from the collections of the Division of Anthropology at the American Museum of Natural History (AMNH), the Department of Anthropology, New York University (NYU), and of the Department of Human Evolution, Max Plank Institute for Evolutionary Anthropology (MPI-EVA). All individuals included were adult (with the exception of Grimaldi 6, an adolescent), as determined by a fully erupted permanent dentition. Due to the lack of secure sex assignments for fossil specimens, sexes were pooled in the analysis and shape differences attributed to sexual dimorphism were not explored.

Data The data were collected in the form of three-dimensional coordinates of 26 landmarks using a Microscribe 3DX digitizer, by ENL and KH (Fig. 15.2; for inter- and intra-observer error assessments and landmark definitions see Nicholson and Harvati 2006). Because morphometric analysis does not accommodate missing data, and since many of the fossil specimens were incomplete, some data reconstruction was found to be necessary (see Nicholson and Harvati 2006).

Since Tabun C2 is virtually complete, landmarks were selected to represent the overall shape of the mandible as preserved in this specimen. Although the lower part of the symphysis is missing in Tabun C2, we felt that the reconstruction of this area was reasonable enough for us to measure gnathion. This point (in conjunction with infradentale) provides an assessment of the corpus supero-inferior height at the symphysis and of symphyseal slope, but does not bear on the evaluation of the chin, one of the proposed modern human-like features of Tabun C2. Since it has been claimed that the impression of a modern human-like chin is partially due to the way that the anterior aspect of the symphysis was reconstructed (Stefan and Trinkaus 1998), we avoided using landmarks or semilandmarks describing the shape of the symphysis in the mid-sagittal plane. Effectively, therefore, we did not include the chin among the features examined, thus removing one of the possible traits indicating modern human affinities for Tabun C2. We also repeated the analysis excluding any landmarks in the symphysis region (for a total of 22 landmarks), so as to assess the impact of this partially reconstructed morphology on our results.

Analysis Landmark coordinates were superimposed using generalized Procrustes analysis (GPA) in Morphologika (O'Higgins and Jones 2004). GPA superimposes the specimen landmark configurations by translating them to a common origin, scaling them to unit centroid size (the square root of the sum of squared distances of all landmarks to the centroid of the object; the measure of size used here), and rotating them according to a best-fit criterion. This procedure allows for the separate analysis of 'shape' and

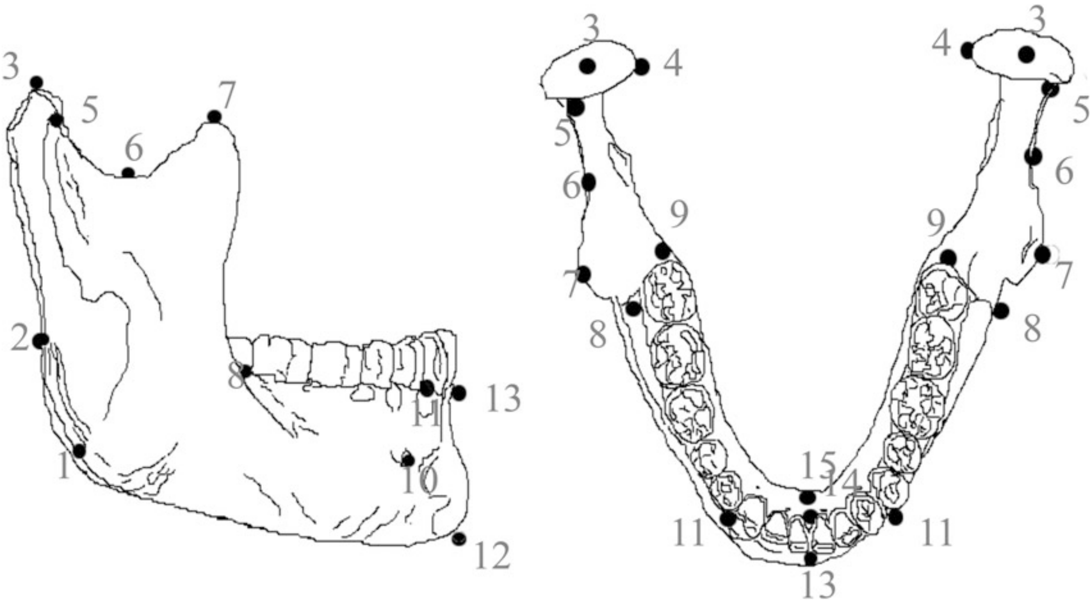

Fig. 15.2 Mandibular landmarks. 1. gonion (right & left), 2. posterior ramus (right & left), 3. condyle tip (right & left), 4. condylion mediale (right & left), 5. root of sigmoid process (right & left), 6. sigmoid notch (right & left), 7. coronion (right & left), 8. anterior ramus (right & left), 9. M3 (right & left), 10. mental foramen (right & left), 11. canine (right & left), 12. *gnathion*, 13. *infradentale*, 14. *mandibular orale*, 15. *superior transverse torus* (Nicholson and Harvati 2006). Landmarks excluded in the 22 landmarks analysis are shown in italics

'size' (although size-related shape differences may remain; Rohlf 1990; Rohlf and Marcus 1993; Slice 1996; O'Higgins and Jones 1998). Procrustes methods have been shown to have higher statistical power than alternative geometric morphometric approaches (Rohlf 2000).

A principal components analysis (PCA) was conducted on the fitted coordinates so as to reduce the variables and explore the patterns of variation present in the data. An ANOVA was performed on centroid size and on the PCA scores to determine the significance of taxonomic effects. For this analysis the two EAM specimens were grouped together with the UP sample as *H. sapiens* (HS). Shape changes along the PC axes were visualized using Morphologika. A discriminant and classification analysis was undertaken using the first 3 principal components (61.07% [26 landmarks] and 63.11% [22 landmarks] of the total variance, chosen on the basis of a scree plot) treating Tabun C2 as unknown, and using UP, EAM, NEA and HH as the a priori groups. Cross-validation classification was performed to evaluate the robustness of the results. All statistical analyses and plots were performed in the Morphologika, SAS and PAST software packages.

Results

Centroid Size

UP and EAM were generally smaller than the two archaic taxa, although the ranges overlapped. Tabun C2's centroid size falls at or close to the upper limit of the UP and EAM range, and within the centroid size range of NEA and HH for both the 26 and the 22 landmarks analyses (Fig. 15.3).

Principal Components Analysis

In the PCA, PC1 (32.83% of the total variance) partially separated the EAM from all other samples, while PC2 (18.64% of total variance) separated the UP from the NEA and HH samples. EAM plotted in an intermediate position but closer to the archaic specimens along these axes (Fig. 15.4, top). Tabun C2 plotted in between Skhul 5 and Qafzeh 9 on the one hand and NEA and HH on the other, though it fell outside the convex hulls of the latter two samples. PC1 was not significant for taxonomic effects. Qafzeh 9 showed a very positive PC1 score and was removed from all other specimens on this axis. The shape changes along PC1 reflected, on the positive end, a narrow, antero-posteriorly (hereafter a-p) elongated mandible with an anteriorly projecting gnathion and symmetrical mandibular notch; and at the negative end, a wide, a-p shortened mandible, with posteriorly placed gnathion and asymmetric mandibular notch (Fig. 15.4 top).

PC2 was the only axis significant for taxonomic effects ($p < 0.0001$), separating HS from NEA and HH (although EAM fell with the latter samples along this axis). It was also correlated with centroid size ($r = 0.78$, $p < 0.0001$). The correlation between PC2 and centroid size was no longer significant when the taxa were examined separately for either HH ($r = -0.07363$, $p = 0.9264$) or NEA ($r = 0.58679$, $p = 0.1661$), but remained close to significant for the combined UP and EAM sample ($r = 0.50852$, $p = 0.0529$), suggesting that some of the mandibular differences separating the taxa might be allometric. Shape changes along PC2 include many of the described differences between modern humans and Neanderthals, including, on the positive (Neanderthal) end, an asymmetric mandibular notch, a retromolar gap, a more posterior placement of the mental foramen and a posteriorly inclined symphysis (Fig. 15.4 bottom).

Neanderthals were further partially separated from HH along the third principal component (Fig. 15.4 bottom; 9.6% of the total variance). This component approached significance for taxonomic effects ($p = 0.07$). On these two axes Tabun C2 fell outside the convex hulls of any of the samples, but plotted closest to the HH range, and away from the NEA, EAM and UP (Fig. 15.4, bottom). PC3 was not correlated with centroid size. The shape differences along this axis included, on the negative (HH) end, a more posteriorly inclined symphysis, a (antero-posteriorly) broader ramus, a more posterior placement of gonion and a shallow mandibular notch (Fig. 15.4 bottom).

When the PCA was repeated with the reduced dataset of 22 landmarks, results remained essentially the same (Fig. 15.5).

Discriminant Analysis

When asked to classify to either HH, UP, EAM or NEA, Tabun C2 was classified as HH. However, the cross-validation classification revealed several misclassifications, especially between the HH group and Neanderthals, with two out of seven Neanderthal specimens (La Ferrassie 1 and Tabun C1) being misclassified as HH and two HH (Sima 5 and Arago) misclassified as Neanderthal. One of the two EAM specimens, Skhul 5, was also misclassified as Neanderthal. Results were virtually identical in the 22 landmarks analysis. Summary cross-validation classification results are shown in Table 15.2.

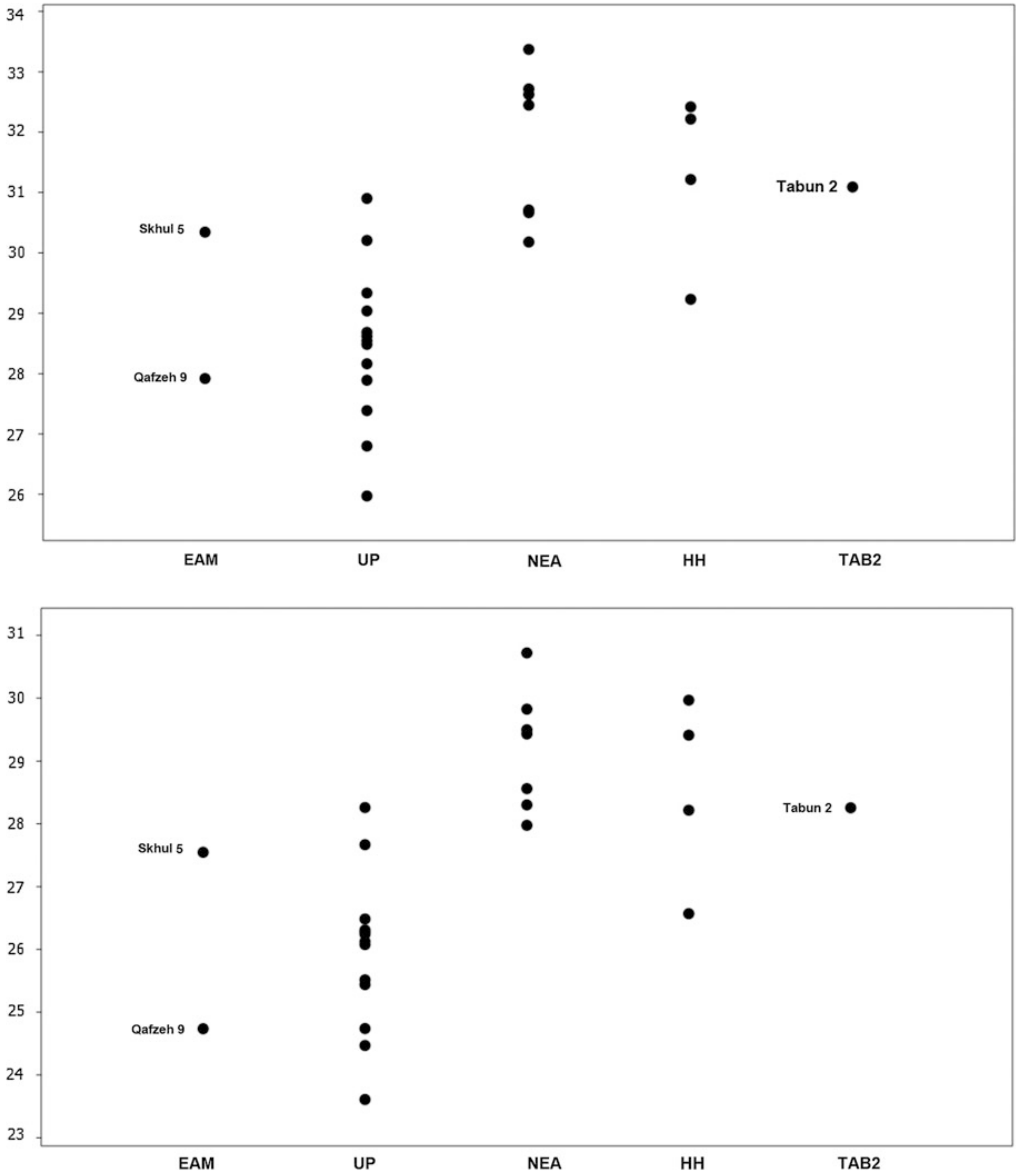

Fig. 15.3 Distribution of centroid size among groups. Labels as in Table 15.1. Top: 26 landmarks analysis; Bottom: 22 landmarks analysis

Procrustes Distances

In terms of Procrustes distances, Tabun C2 was closest to the Sima 5 and the Montmaurin mandibles (0.0880 and 0.1017 respectively), and next closest to Skhul 5 (0.1024). The same specimens were the three closest specimens to Tabun C2 in the 22 landmarks analysis. The Procrustes distances between Tabun C2 and each specimen included in our comparative sample for both the 26 and the 22 landmarks analyses are reported in Table 15.3.

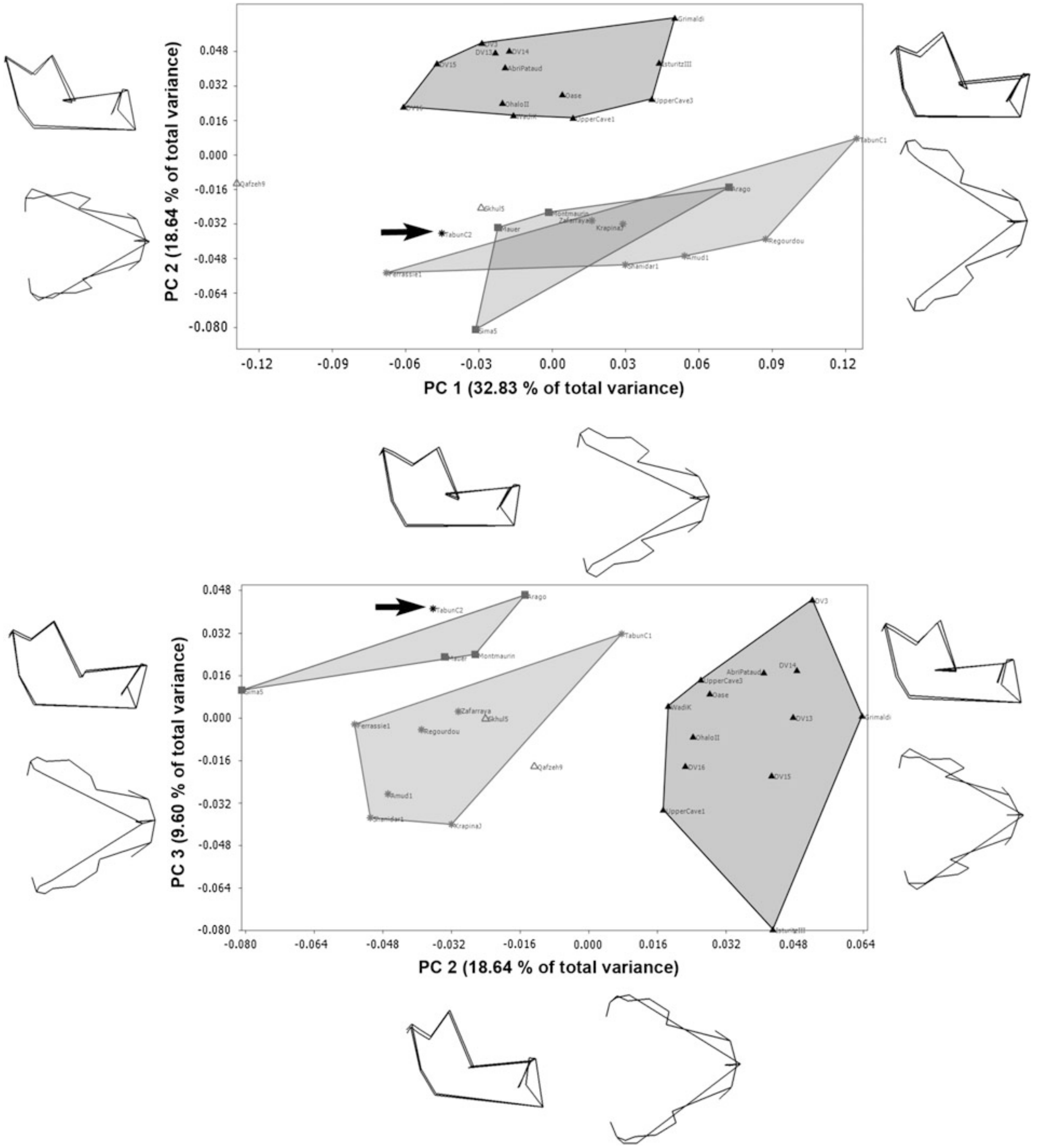

Fig. 15.4 Principal components analysis, 26 landmarks analysis. Top: PC 1 plotted against PC 2. Bottom: PC 2 plotted against PC 3. Shape changes along the principal components are also shown. Black triangles: UP; Grey stars: NEA; Open triangles: EAM; Grey squares: HH; Black start: Tabun C2

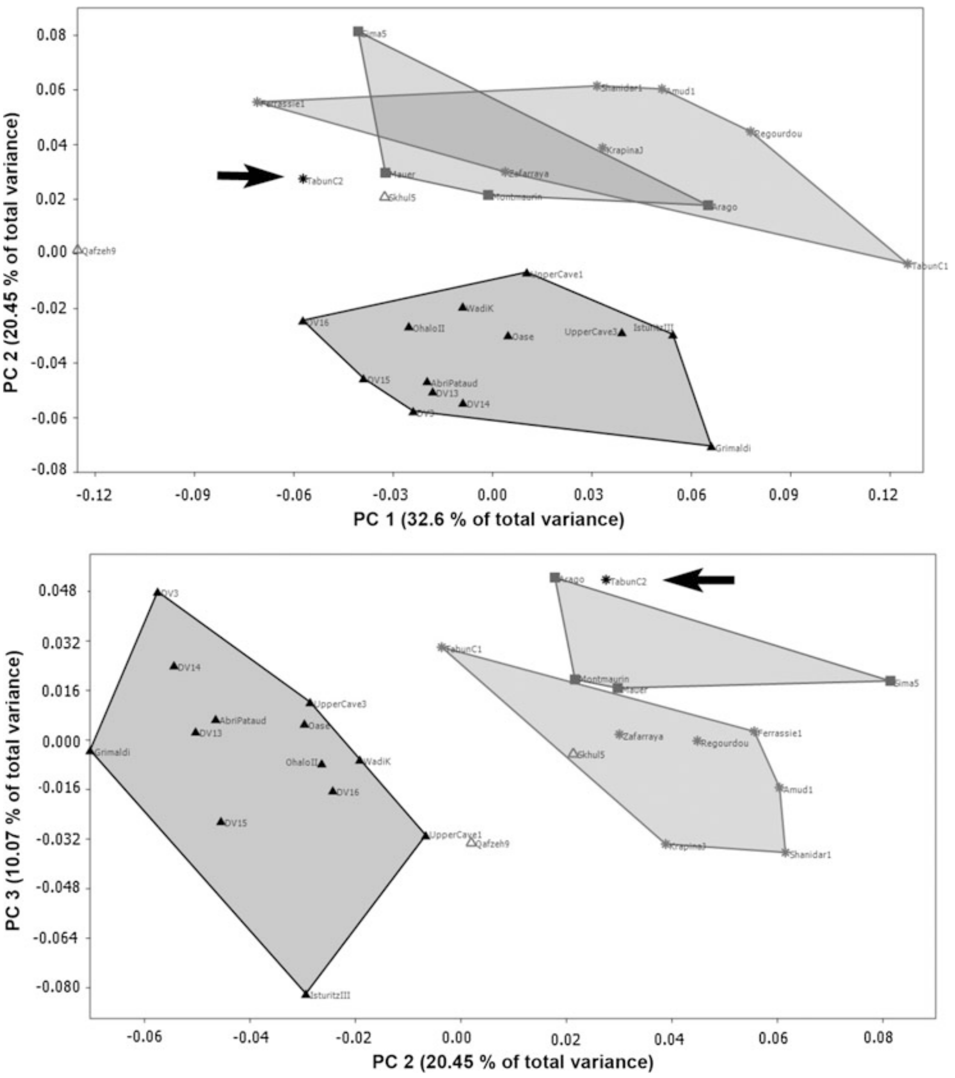

Fig. 15.5 Principal components analysis, 22 landmarks analysis. Top: PC 1 plotted against PC 2. Bottom: PC 2 plotted against PC 3. Symbols as in Fig. 15.4

Table 15.2 Cross validation classification summary. The values are the same for both the 26 and the 22 landmarks analyses

Number of observations and percent classification into group					
From	EAM	HH	NEA	UP	Total
EAM	0	0	1	1	2
	0.00	0.00	50.00	50.00	100.00
HH	0	2	2	0	4
	0.00	50.00	50.00	0.00	100.00
NEA	0	2	5	0	7
	0.00	28.57	71.43	0.00	100.00
UP	0	0	0	13	13
	0.00	0.00	0.00	100.00	100.00
Total	0	4	8	14	

Table 15.3 Procrustes distances between Tabun C2 and each of the specimens included in the comparative sample

26 Landmarks			22 Landmarks		
Specimen	Distance from Tabun 2	Group	Specimen	Distance from Tabun 2	Group
Sima 5	0.0880	HH	Sima 5	0.0903	HH
Montmaurin	0.1017	HH	Montmaurin	0.0945	HH
Skhul 5	0.1024	EAM	Skhul 5	0.1024	EAM
Ohalo II	0.1084	UP	Zafarraya	0.1070	NEA
DV 14	0.1101	UP	Ferrassie 1	0.1084	NEA
DV 16	0.1108	UP	Ohalo II	0.1115	UP
Zafarraya	0.1119	NEA	DV 3	0.1115	UP
Ferrassie 1	0.1122	NEA	DV 16	0.1123	UP
Mauer	0.1124	HH	DV 14	0.1137	UP
DV 3	0.1132	UP	Mauer	0.1142	HH
DV 13	0.1144	UP	DV 13	0.1186	UP
DV 15	0.1220	UP	DV 15	0.1249	UP
Abri Pataud	0.1294	UP	Wadi K.	0.1308	UP
Wadi K.	0.1304	UP	Abri Pataud	0.1320	UP
Oase	0.1306	UP	Upper Cave 101	0.1354	UP
Upper Cave 101	0.1341	UP	Oase	0.1368	UP
Krapina J	0.1343	NEA	Upper Cave 103	0.1396	UP
Upper Cave 103	0.1352	UP	Qafzeh 9	0.1425	EAM
Amud 1	0.1384	NEA	Amud 1	0.1441	NEA
Shanidar 1	0.1441	NEA	Krapina J	0.1458	NEA
Qafzeh 9	0.1477	EAM	Shanidar 1	0.1497	NEA
Arago 13	0.1504	HH	Arago 13	0.1509	HH
Regourdou	0.1557	NEA	Regourdou	0.1605	NEA
Grimaldi	0.1694	UP	Grimaldi	0.1827	UP
Isturitz	0.1825	UP	Isturitz	0.1917	UP
Tabun C1	0.2022	NEA	Tabun C1	0.2055	NEA

Discussion

The results presented should be interpreted with caution. Our approach required relatively complete specimens, and thus limited the sample available for comparison, especially for the early modern humans. It was also based on general mandibular shape, and used relatively few landmarks, thus representing overall, rather than detailed, mandibular shape. Furthermore, the region of the anterior symphysis was not represented by our landmarks, so as to avoid the partially reconstructed chin of Tabun C2. This region is, however, highly informative taxonomically. Finally, the relatively high levels of misclassification between HH and NEA, but also between EAM and NEA, further advise against over-interpretation of our findings.

Nevertheless, our results show that the Tabun C2 overall mandibular shape cannot be easily accommodated either within the Neanderthal or the early modern human range of variation. Although not clearly aligning with either Neanderthals or EAM, Tabun C2 obviously differed from the later UP modern human sample, and generally grouped with the older (including early anatomically modern human) specimens. PC 2, the only axis significant for taxonomic effects, separated the later UP modern human sample from early anatomically modern humans (EAM), Neanderthals (NEA), European Middle Pleistocene specimens (HH) and Tabun C2, and was correlated with centroid size in both analyses. This indicates that, as also found previously (Nicholson and Harvati 2006), some of mandibular shape differences between modern and archaic humans are influenced by allometry. It also suggests that Tabun C2's large size could be a contributing factor to its archaic-like morphology.

Tabun C2 and Neanderthals Stefan and Trinkaus (1998) concluded that Tabun C2 is best regarded as Neanderthal, although they found its morphology to be ambiguous. Our analyses, however, found no obvious affinity between this specimen and the Neanderthal sample used here. Our PCA could separate Neanderthals from modern humans along PC2, which reflected features commonly described as Neanderthal (e.g., retromolar space, a low condyle relative to the coronoid process, a relatively posterior position of the deepest point of the mandibular notch). Although Tabun C2 generally grouped with the older samples, including HH, EAM and NEA in this analysis, it neither plotted clearly with the NEA sample in the PCA, nor was it classified as Neanderthal in the discriminant analysis.

These findings remained the same when the dataset was reduced to 22 landmarks, indicating that the symphyseal region, which was partly reconstructed in this specimen, plays a minor role in determining our findings. Furthermore, none of the specimens closest to Tabun C2 in total shape, as reflected in Procrustes distance, were Neanderthal (Table 15.2), although some Neanderthals are closer to Tabun C2 in the 22 landmarks analysis. Tabun C2 also showed no particular similarity with Tabun C1, which derives from the same site and, possibly, the same layer (C). It generally plotted away from this specimen in the PCA. Indeed the greatest observed Procrustes distance between Tabun C2 and any of the specimens in both analyses was the Tabun C2 – Tabun C1 distance (0.2022; Table 15.2). While this large distance could be at least in part due to sexual dimorphism (Tabun C1 generally is considered female), it further illustrates the lack of affinities of Tabun C2 for the Neanderthal sample.

Tabun C2 and the Early Modern Human Sample Tabun C2 has also been interpreted as an early modern human (e.g., Rak 1998). Perhaps the clearest result reported here is that Tabun C2 differs from the Upper Paleolithic/ Later Stone Age sample included in our analysis. However, the relationship of Tabun C2 with the early modern human specimens from Skhul and Qafzeh is more difficult to evaluate. This is due in part to the very small number of specimens that could be included in our analysis: only two, Skhul 5 and Qafzeh 9. The interpretation of our results with respect to this sample is further complicated by the extreme position of Qafzeh 9 on PC1, which suggests that distortion affects this mandible's shape (Vandermeersch 1981; see also Nicholson and Harvati 2006). Beyond taphonomic considerations, Qafzeh 9 has recently been described as exhibiting severe malocclusion (Sarig et al. 2013), which may have also affected its shape. Tabun C2 did not plot consistently with the EAM specimens in the PCA. It was also not classified as EAM in the discriminant analysis. Nevertheless, the third closest specimen to Tabun C2 in Procrustes distance was Skhul 5 in both analyses.

Our results therefore do not clearly support an affinity with early modern humans either. However, given the extremely small number of EAM specimens that could be included here, as well as the likely distorted nature of one of them, we consider this outcome inconclusive.

Tabun C2 and the European Middle Pleistocene Sample Our most surprising result was the alignment of Tabun C2 with the European Middle Pleistocene Homo heidelbergensis sample included in our study. It fell closest to HH along PC3 and was classified as HH in both analyses. It also showed the two smallest Procrustes distances, and therefore closest similarity in total shape, with two of the four HH specimens included here (Sima 5 and Montmaurin; Table 15.2). This result is perplexing, as the HH specimens are much older than the purported possible age of Tabun C2. However, it suggests that Tabun C2's morphology might best be regarded as preserving primitive features. Indeed the features that are reflected by the extreme PC3 scores characteristic of Tabun C2 and HH mandibles include a relatively long ramus antero-posteriorly, a subequal height of the coronoid and condyle, and a relatively receding symphyseal orientation (Fig. 15.5), traits described as characteristic for middle and early Pleistocene specimens (e.g., Mounier et al. 2009). Such a finding is consistent with that of Le Cabec et al. 2013, who also described a mix of archaic, likely primitive, and modern traits in its dental root morphology. A similar pattern of mosaic morphology has been reported for the Middle Pleistocene human dental remains from Qesem cave (Hershkovitz et al. 2011), while generalized primitive morphology has also been proposed for the partial cranial remains from Zuttiyeh (Freidline et al. 2012).

Tabun C2 as a Neanderthal-Early Modern Human Hybrid? Tabun C2 has also been proposed to reflect admixture between Neanderthals and early modern humans. This hypothesis is difficult to evaluate, as there are no clear expectations of how hybridization may be reflected in skeletal morphology (see Harvati et al. 2007; Ackermann 2010; Kelaita and Cortes-Ortiz 2013). Although large, Tabun C2 is not greatly different in size than either proposed parent populations, as might be expected from a hybrid (Ackermann et al. 2006; Harvati et al. 2007) nor does it show any peculiar dental anomalies (Ackermann et al. 2006; Ackermann 2010). Although it has been described as showing a mixture of Neanderthal-like and modern human-like features (e.g., Quam and Smith 1998; Le Cabec et al. 2013), it was not consistently intermediate in overall mandibular shape between the two taxa in our study. We feel, however, that our analysis cannot adequately address this hypothesis.

Conclusions

Our results do not indicate a clear affinity of Tabun C2 with either Neanderthals or early modern humans, and therefore do not support assignment to either taxon. Rather, our findings point to similarity of Tabun C2 with geologically older specimens, and suggest that the large size of the specimen may be a contributing factor to its archaic morphology. We tentatively conclude that Tabun C2 may retain a primitive overall mandibular shape, as might be consistent with its proposed great geological age. Our findings also suggest a possible presence of a third taxon in this region during the later part of the middle Pleistocene.

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