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Abstract

The bony labyrinth has received growing attention in the field of human evolution as it is a useful phylogenetic indicator in hominins, and is particularly useful for distinguishing anatomically modern humans and Neanderthals. The partial adult skeleton of Qafzeh 25 dated to 92 ± 5 ka B.P. suffers from serious post-mortem taphonomic damage that has limited its anatomical description and metrical analysis. However, the two petrosal bones are preserved and the bony labyrinths are not affected by post-mortem deformations. In this study, the methodology developed by Spoor (1993) is used to analyze and compare the morphometric data from Qafzeh 25 semi-circular canals and cochlea to that of other fossils from the site and more generally to the published hominin sample (Middle and Late Pleistocene hominins). While this analysis reveals that the Qafzeh 25 bony labyrinth resembles that other Qafzeh individuals, it extends the range of variation within the sample for some variables.

Keywords: Bony labyrinth; Southwestern Asia; Morphometrics; Early anatomically modern humans

Declarations

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Authors' contributions:

- Dany Coutinho Nogueira: Conceptualization; Data curation; Formal analysis; Funding acquisition; Writing
- Hélène Coqueugniot: Conceptualization; Formal analysis; Writing
- Frédéric Santos: Conceptualization; Formal analysis
- Anne-marie Tillier : Conceptualization; Formal analysis; Writing

1. Introduction

The Mediterranean Levant provides an important fossil record dated between 250–and 45 ka. that, since the first discoveries in the 1930s, has been the subject of major debate over the phylogenetic relationships of the hominins. While all of the hominins are associated with Mousterian assemblages (Levallois-dominated industries), they document a highly anatomically heterogeneous group (Tillier et al. 1989; Rak, 1991; Vandermeersch, 1991; Mann 1995; Arensburg and Belfer-Cohen 1998; Quam et Smith 1998; Wolpoff 1999; Tillier et al., 2003; Tillier, 2005; Moskovitz et Smith, 2005; Tillier et al., 2008; Harvati et Nicholson-lopez, 2017; Tillier et Arensburg, 2017).

Based on previous studies, two scenarios of settlements in the Levant are generally evoked to explain this anatomical variability:

- an alternation of two distinct populations, Neanderthals (e.g. Tabun C1, Amud 1, Dederiyeh 1; McCown and Keith 1939; Suzuki and Takai 1970; Akazawa et al. 1995) and early anatomically modern humans (e.g. Qafzeh, Skhūl; McCown and Keith, 1939; Vandermeersch 1981; Tillier 1999)

- a more complex pattern of human peopling with regional and/or multiple influences (Arensburg and Belfer-Cohen 1998; Tillier and Arensburg 2017, Arensburg and Tillier 2019).

In this context, the present study of Q25 bony labyrinth can bring new information to the discussion of the different scenarios.

Qafzeh Cave, located in Lower Galilee, is of special interest as its collections contain a unique corpus of individuals documenting all age groups from infancy and childhood to adulthood, some of which exhibit evidence of unique funerary practices (Vandermeersch 1969, 1970; Tillier 1995, 2011). Dated to 92 ± 5 ka (Schwarcz et al. 1988; Valladas et al. 1988), the Qafzeh hominins represent early anatomically modern humans (Vandermeersch 1981; Tillier 1999) and are generally aligned with the Skhūl hominins recovered from the Mount Carmel (McCown and Keith 1939). However, a recent study based on dental traits has led to uncertainty around the taxonomic attribution of some fossils from the site (Ackermann et al. 2019).

Qafzeh 25 is not yet fully described as taphonomic processes have heavily damaged the skeletal remains. The skull, nearly complete, is crushed, deformed and fragmented. A previous study on the mandible (Schuh et al. 2017), based on 3D imaging and virtual reconstruction techniques, showed morphometric differences between Qafzeh 25 and all Levantine mandibles including those of Qafzeh 9 and Skhūl 5. This first analysis raises the question of the taxonomic attribution of the specimen and leads us to investigate other anatomical structures not deformed by post-mortem damages. The only structures unaffected by taphonomic damage are the two bony labyrinths, as assessed by measurements taken from 3D reconstructions of these structures in this study.

Previous studies of the petrosal bone have described features of the bony labyrinth and suggested that they reflect taxonomic differences between Neanderthals and modern humans (Spoor 1993, Spoor and Zonneveld 1995; Hublin et al. 1996). The bony labyrinth reaches its adult size and shape before birth (Spoor 1993) making possible to compare adults and non-adults/juveniles within the hominin Qafzeh sample, which contains the largest available bony labyrinth sample (7 immatures and 3 adults) for South West Asia. This important sample thus allows the analysis of intrasite variation and, to date, represents the second largest fossil sample behind that of Sima de los Huesos in Spain (Quam et al. 2016).

The aim of our analysis is to test the hypothesis that Qafzeh 25 is an anatomically modern human by (i) analyzing the morphometric anatomy of the bony labyrinth, and (ii) comparing the results to other Qafzeh specimens and other Southwestern Asian hominins in order to evaluate the biological relationships among the samples. Our analyses will also allow us to assess whether Qafzeh specimens exhibit an inner ear morphology close to that of recent populations, which is generally considered to be the ancestral morphology.

2. Material and methods

2.1. Qafzeh 25 specimen

Qafzeh 25 was discovered during the last excavation season directed by B. Vandermeersch in 1979, in layer XVII, square C10. All of the skeletal elements have suffered in situ from taphonomical alterations and this could explain why most of the lower part of the skeleton was destroyed in 1934 by a survey made during the first excavations conducted by R. Neuville and M. Stekelis. The remains consist of the skull (fig. 1), the mandible, and some postcranial elements, including vertebrae, ribs and upper limbs (Schuh et al. 2017; Tillier pers. comm.). The observation and description of the CT-scan images and the 3D reconstruction of the mandible (Schuh et al. 2017) allowed for a complete examination of the lower dentition. The authors suggested that Qafzeh 25 died in early adulthood [all observable root apices are closed; tooth wear of most individuals was scored 2 following Molnar (1971)]. It does not appear to be possible to use the partial skeleton to reliably assign a sex to Qafzeh 25. However, the overall robustness of the skull and mandible places Qafzeh 25 closer to Qafzeh 3 and 6 adults previously described as males (Vallois and Vandermeersch 1972; Vandermeersch 1981).

2.2. CT-scanning procedure

The two Qafzeh 25 petrosal bones are preserved but suffered from minor postmortem alteration and in particular, compression. CT scanning of Qafzeh 25 (Fig. 2) was conducted at the Sheba Medical Center in Ramat Gan (Israel) with a GE Medical system (CT-scan parameters: pixel size = 540 µm; slice thickness = 625 µm; X-ray tube current = 590 mA; exposure time = 1277 ms).

2.3. Comparative sample

In order to avoid preconceived phylogenetic attributions for the specimens from the Levant, we have clustered them together in a sample called Southwestern Asian fossils (Late Pleistocene). The other fossils are grouped by taxonomic affinities, except for the North Eastern-Asian fossils with debated phylogenetic relationships that were grouped in the same sample (Table 1).

2.4. Measurements

The analysis of the images of the bony labyrinths was performed using TIVMI software v2.3 (Dutailly et al., 2009). Measurements were taken following Spoor (1993) and Spoor and Zonneveld (1995; 1998), directly from the 2D images. To make sure that measurements were collected from the right slices, the sagittal and transverse planes were constructed using TIVMI software. Following previous studies (Hublin et al. 1996; Bouchneb and Crevecoeur 2009), we selected the dimensions and their derivatives that are most frequently used (Table 2). They include data from all regions of the bony labyrinth (shape index and radii of curvature of the three semicircular canals and cochlea; the sagittal labyrinthine index).

2.5. Statistical analyses

Several statistical analyses are carried out with the objective of better understanding the potential biological diversity among the Qafzeh hominins, and more generally, the variation among Southwestern Asian hominins and other human groups. All statistical analyses are performed using the software R 4.0.4 (R Core Team, 2021).

First, a correlation matrix was created to identify strongly correlated pairs of variables in order to avoid duplication of information that could disrupt further analyses (package 'corrplot' 0.84; Wei and Simko 2017). The results from the remaining dimensions were visualized using box plots. For each variable, a Kruskal-Wallis test was conducted to compare the medians of the different groups studied. If the test revealed significant differences, post hoc comparisons were performed using the Holm method correction for *p*-values implemented in the R package 'agricolae' 1.3.3 (De Mendiburu et al. 2020). Principal component analyses (PCA) were performed in order to highlight possible relationships between individuals and/or groups using the package 'FactoMineR' 2.4 (Lê et al. 2008) and MissMDA 1.18 (Josse and Husson 2016) following the methods employed by Coutinho

Nogueira et al. (2017). For the different PCAs, the variables used are: SLI, ASCh.w, LSCh.w, PSCh.w, ASC.R, LSC.R, PSC.R and CO.R.

In addition, cluster analyses (K-means clustering and hierarchical clustering analyses) were also carried out (‘FactoMineR’; Lê et al. 2008), and their quality was assessed using the v-measure (Rosenberg & Hirschberg, 2007). Student's t-tests were also performed in order to compare Holocene modern humans with the fossil groups.

Results

The two bony labyrinths of Qafzeh 25 were not affected by taphonomic distortion (Fig. 3), but are partly filled with sediment that has the same density in CT-scan images as the bony tissue, mainly affecting the left inner ear. Consequently, we excluded measurements that were potentially compromised by this effect (e.g. ASCw of the left bony labyrinth). There is some sediment in the cochlea of left bony labyrinth, but it does not affect measurements in this region. The Qafzeh 25 metrical results of the bony labyrinth are summarized in Table 3 (and in supplementary information). All measurements are mean values except for ASCw (right value). Right and left bony labyrinths present very similar values, in agreement with the observation made previously by Spoor (1993) in recent human populations, meaning that there is a high degree of symmetry between left and right sides in an individual. Osipov et al. (2013) noted some asymmetry for the ASCw variable, we could not verify this observation in Qafzeh 25 as we could not take this measurement on the left side. However, we noted a slight difference between left and right side for the LSCh/w index.

The correlation matrix reveals a strong correlation between the radii of the three canals (R) and their relative size (%R) (Fig. 4). Consequently, for further analysis, the data concerning the relative size of the canals of the radii were removed because they were also highly correlated.

Qafzeh 25 within the Qafzeh sample

Qafzeh 25 is notable within the Qafzeh sample for having the highest value for ASCh/w (100.91) but is not an outlier since Qafzeh 9 and 13 exhibit roughly similar values. Qafzeh 25 also has the lowest value for the variable CO-R, and a relatively low value for the radius of the anterior canal. Despite these slight peculiarities, all of the values fall within an acceptable range of variation for the Qafzeh sample. Due to the very small sample size, the acceptable range of values may be defined either by the classic Tukey (1977) boxplot rule: [q1-1.5IQR; q3+1.5IQR]; or by using the MAD (Leys et al., 2013) rule: [m - 2MAD; m+2MAD]. In both cases, Qafzeh remains within the acceptable range for all variables. However, due to the very small sample size, a statistical criterion may not be relevant here.

Qafzeh 25 within the Southwestern Asian sample

A PCA was performed that included only the Southwestern Asian individuals in order to detect biological similarities and/or differences within this group. The first principal component (PC1) expresses 40.59% of the variance and is mainly influenced by ASC.R, ASCh.w, PSC.R, CO.R, and SLI. PC2, which explains 18.62% of the variance, is mainly influenced by the variables concerning the lateral canal (Fig. 5).

The PCA reveals a continuum and a gradation in morphology rather than a clear separation of the fossils along PC1, except for Tabūn C1 which presents the most negative value. A few Southwestern Asian individuals classically described as Neanderthals (Amud 1 and 7, Kebara 1, Dederiyeh 1) fall on the negative side of PC1 because of their high values for ASCh/w and SLI; however, they stay close to some Qafzeh individuals (especially Qafzeh 9, 13, 21 and 25) that also fall on the negative side of the PC1. On PC2, some fossils fall on the positive side or very near to it with high values for LSC.R, LSCh/w and PSCh/w (Amud 1 and 7, Kebara 1, Dederiyeh 1, Qafzeh 6, 7, 6, 21 and 25, Skhūl 1 and 5), while others fall on the negative side (Tabūn C1, Qafzeh 3, 11, 12, 13 and 15). Overall, there seems to be more variability within the Qafzeh-Skhūl group than between some Qafzeh individuals and Amud 1 and 7, Kebara 1 and Dederiyeh 1.

The unsupervised clustering analyses do not provide homogeneous groups, and a certain number of fossils from Qafzeh and Skhul (that may vary depending on the algorithm used, k-means or hierarchical clustering) fall within the same cluster as “archaic fossils” (see Supplementary Information 3 for full details). These two analyses thus support the hypothesis of a continuum between the Qafzeh/Skhūl individuals and other Southwestern Asian fossils, although the latter are often commonly described in the literature as showing different phylogenetic affinities based on their overall skeletal morphology.

Qafzeh 25 is positioned near both Kebara 1 and Qafzeh 9 on the negative side of PC1 because of the high values for ASCh/w and SLI and the low ones for CO.R. Tabūn C1 occupies a marginal position in the PCA, far from other individuals. Its position can be explained by its low values for the radii (ASC.R, PSC.R and LSC.R) and the high value for SLI. The distribution of Qafzeh specimens seems wider than that of other individuals from Amud, Dederiyeh and Kebara sites. Indeed, several Qafzeh individuals (Q3, Q11, Q12, Q13, and Q15) are separated along the PC2 and seem to be disconnected from the rest of the Qafzeh sample. This slight separation is due to their lower values in the lateral canal variables.

Qafzeh within the available fossil sample

Two other PCAs were performed. The first one includes as many individuals as possible but excludes the radius of the cochlea (CO.R) because it is missing in many specimens. The second one (Fig. 6, Table 5 and 6) includes CO.R but excludes individuals for whom this data is lacking; the overall distribution remains the same. We describe the latter in more details as it shows a higher number of variables and higher percentage of variance.

The analysis with PC1 and PC3 was selected because the separation of undebated taxonomic groups is much clearer than with PC2 which allows us to discuss the position of fossils whose affinities are uncertain. PC1 explains 33.54% of the variance and PC3 14.37%. PC3 is mainly influenced by the sagittal labyrinthine index (SLI) and to a lesser extent by radius of the lateral canal (LSC.R) and the shape index of the posterior canal (PSCh/w), while PC1 is influenced by the remaining variables.

Anatomically modern humans separate from Neanderthals and European Middle Pleistocene individuals (e.g. Sima de los Huesos) along PC1. However, the distribution of individuals seems to be more complex, as some specimens of the Neanderthal lineage (e.g. Le Moustier 1 and Aroeira 3) fall within the distribution of modern humans as previously noticed (Hublin et al. 1996; Conde-Valverde et al. 2018). Aroeira 3 lacks some Neanderthal traits so its position, outside the 'classical Neanderthal' variability, is thus expected (Conde-Valverde et al., 2018). On the other hand, the position of Le Moustier 1, already highlighted in previous publications (Hublin et al. 1996; Uhl et al, 2016) questions its phylogenetic affinities.

Qafzeh 25 is positioned near some Southwestern Asian fossils and Asian (Early and Middle Pleistocene) specimens such as Qafzeh 9, Kebara 1 and the Chinese Liujiang 1 specimen. Most of the Qafzeh specimens are located on the positive side of PC1, with the exception of Qafzeh 15 and 12 (two specimens which have high values for SLI), and have values close to the mean on the PC2. The Qafzeh group is close to three other Southwestern Asian specimens (Kebara 1, Skhūl 1 and 5), to the African specimens of Dar-es-Soltane II H5, Nazlet Khater 2 and the Chinese fossil from Liujiang. This whole group stands apart from European Late Pleistocene fossils (Abri Pataud 3, Laugerie Basse 1 and Cro Magnon 1), positioned in the negative side along PC2 and which present lower SLI values .

Unlike in the first PCA, three Southwestern Asian individuals (Dederiyeh 1, Amud 1 and 7) stand out from the Qafzeh-Skhūl-Kebara group. These fossils are close to 'so-called classic' Neanderthals, especially those of La Ferrassie and La Quina. On the other hand, Tabūn C1 keeps a marginal position. If we compare Tabūn C1 with Neanderthals, we note that the specimen shows the lowest value for the sum of the radii of the three canal (ASC.R + PSC.R + LSC.R) as well as for CO.R, without being considered as a clear outlier among this sample for these variables (respectively p = 1 and p = 0.68 in the Grubbs test for detecting outliers).

The unsupervised clustering analyses do not provide homogeneous groups, and the fossils generally considered as modern humans fall within the same cluster as several other fossils from the Neanderthal lineage (see Supplementary Information 5 for full details).

Position of the posterior canal

According to Spoor et al. (2003), the relative position of the posterior canal (SLI) displays significantly different features between Neanderthals and anatomically modern humans.

The box plot (Fig. 7) shows higher values for Neanderthals and several Southwestern Asian fossils (Amud 1 and 7, Dederiyeh 1, Kebara 1 and Tabūn C1) compared to the Qafzeh-Skhūl individuals and Late Pleistocene specimens. One can also notice that Qafzeh and Skhūl individuals have higher SLI than European Late Pleistocene fossils, with half of them falling in the range of the Neanderthal variation, including Qafzeh 25. A Kruskal-Wallis test confirms significant differences among groups (Kruskal-Wallis chi-squared = 39.755, df = 5, $p < 0.001$). A *post hoc* analysis for multiple group comparisons (with adjustment of *p*-values by the Holm method, following de Mendiburu 2020) shows that Neanderthals and so-called 'archaic' Southwestern Asian fossils differ significantly from all other groups including Qafzeh-Skhūl (Table 7).

When we compare these fossil groups with the Holocene sample studied by Spoor (1993) using a Student's t-test, we notice that there is no significant difference between Qafzeh-Skhūl fossils and sub-actual humans for the SLI. Furthermore, the archaic fossils from both the Levant and Europe show substantial differences (Table 8).

Discussion

As already highlighted in previous studies (Spoor et al. 2003; Quam et al. 2016), the PCA shows overlapping areas of different groups (e.g., in the center of the graphs), and a distinctive position of some individuals (e.g. Le Moustier 1). The first PCA and the clustering analysis do not clearly separate groups (e.g., modern humans vs. Neanderthals).

It must be noted that the Qafzeh hominin group shows wide variation in the PCA, a feature that Southwestern Asian specimens share with two European samples, including individuals from La Ferrassie and Sima de Los Huesos. This relative heterogeneity in the bony labyrinth anatomy documented at Qafzeh challenges previous assumptions about the relative homogeneity of the group based on the observed expression of skeletal variants and/or dental anomalies used in studies of genetics and population affinities (Tillier 1999; Shuh et al. 2017). As an example, three individuals (Qafzeh 11, 15, and 25) that share evidence of tooth rotation, a trait usually considered to be hereditary (e.g. Evensen and Ǿgaar 2007; Souza da Souza, 2007), appear quite distant in the principal component analysis of their bony labyrinths.

With the exception of the shape index of the three canals, Qafzeh 25 and Dar-es-Soltane II-5 have very similar values for all of the dimensions of the bony labyrinth. The proximity of the fossils supports a previous study (Harvati and Hublin 2012) which revealed similarities in facial morphology between Qafzeh 6 and the Aterian fossil. Dated to 80 ka (Raynal and

Occhietti 2012) Dar-es-Soltane II-5 appears to be morphologically and chronologically the most similar African representative to the Qafzeh early modern humans.

Liujiang also presents a bony labyrinth morphology similar to Qafzeh 25 and more generally to the Qafzeh-Skhūl group, following the same distribution pattern as the Southwestern Asian fossils. Liujiang is described as an anatomically modern human with dates close to or even contemporary with Qafzeh and Skhūl samples (Shen et al., 2002).

Spoor et al. (2003) noted that Holocene populations are more similar morphologically to Neanderthals than were the European Late Pleistocene populations. Modern specimens from the Late Pleistocene of the Levant and Africa appear to differ slightly from the European populations. Indeed, the bony labyrinth of individuals from Qafzeh, and more generally early anatomically modern humans from Africa and Asia, seems to present few characteristics shared with Neanderthals, such as high SLI. On this basis, we can propose that the ancestral morphology was probably closer to that of Southwestern Asian and African specimens than to that of more recent European specimens, as previously noted (Spoor et al. 2003; Conde-Valverde et al. 2018). This means that the derived character would be a low SLI. Also, the fact that extant European populations do not show low SLI provides an additional morphometric argument suggesting a discontinuity of settlement between the Late Pleistocene and the present in Europe. In this context, it would have been fruitful to test if Late Pleistocene populations dated to more recent chronological phases in Southwestern Asia (Vandermeersch et al. 2013, Hershkovitz et al. 1995) share similarities in bony labyrinth morphology. However, the petrosal area is not preserved in Qafzeh 1 and 2 Upper Palaeolithic individuals, while CT-scans from the Early Epipaleolithic Ohalo II H2 bony labyrinths have not yet been performed.

Conclusions

This research brings a new set of data to the debate concerning human diversity in the Southwestern Asian hominin record. The Qafzeh 25 bony labyrinth, in different analyses, stands among early anatomically modern humans from the Levant, but extends the known range of variation in the sample. Indeed, the fossil occupies an eccentric position on the PCAs due to high values for ASCh/w and SLI (two variables that have a significant influence on an axis), putting it close to Neanderthal individuals without following the derived condition, i.e., small vertical canals and large lateral canal observed by Spoor et al. (2003). In sum, the mosaic of morphological traits, including plesiomorphic and modern human-like features, present in the fossil sample from Israel provides a critical perspective on the regional model of evolution, which proposes the exclusive presence of two human groups in Southwestern Asia.

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Figure captions

Figure 1. Left side of Qafzeh 25 cranium.

Figure 2. CT slices and 3D reconstruction of Qafzeh 25 skull: A) sagittal; B) axial; C) coronal; D) Rendering of the 3D reconstruction.

Figure 3. Rendering of the 3D reconstruction of the two bony labyrinths of Qafzeh 25. A: right, B: left.

Figure 4. Correlation matrix of the bony labyrinth data, abbreviations are defined in table 2. Variables highly corrected are indicated with dark blue and dark red.

Figure 5. Principal component analysis for the bony labyrinth of Southwestern Asian hominins, abbreviations of the variables are defined in table 2. A: morphospace with the distribution of the Southwestern Asian fossils. B: correlation circle

Figure 6. Principal component analysis including the entire available comparative sample, abbreviations of the variables are defined in table 2. A: morphospace with the distribution of the all available fossils. B: correlation circle

Figure 7. Box-and-whisker plot of the sagittal labyrinthine index (SLI). The whiskers represent the lowest and largest data point excluding any outliers, the limits of the boxplots represent the first and third quartile and the strong lines represent the median.