

Manot 1 calvaria and Recent Modern Human Evolution: an Anthropological Perspective*

La calvaria de Manot 1 et l'évolution de l'Homme moderne : une perspective anthropologique

I. Hershkovitz · B. Latimer · O. Barzilai · O. Marder

Received: 5 August 2016; Accepted: 24 February 2017
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Abstract The time range between 60 ka and 50 ka is one of the most dramatic phases in human biological evolution. In this period, the western part of Eurasia (Europe and the Near East) was populated by Neanderthals, whereas the eastern part (Central Asia and Siberia) was populated by Denisovans. However, by 30 ka, these two populations were replaced by anatomically modern humans (AMH). When did these newcomers arrive and from where? There is accumulating archaeological and genetic evidence suggesting that this demographic shift occurred at the end of MIS 4 [1–3]. Moreover, it is quite clear that a major dispersal of AMH out of Africa was the source of the new populations [4–7]. In this study, we examined specific morphological characteristics of Manot 1 (e.g., suprainiac fossa), and assessed their similarities to the corresponding traits found

among Neanderthals. We will show that although the terminology is similar, the traits in each hominin group are of different entities. We also show that Manot 1 and Early Upper Palaeolithic skulls of Europe have many traits in common (e.g., suprainiac fossa, bunning), although Manot 1 is much more gracile. Finally, some of the archaic traits (e.g., suprainiac fossa) seen in Manot 1 can be traced to the Late Pleistocene Aduma skull (~79–105 ka) from Ethiopia or even Eyasi 1 (~200–400 ka) from Tanzania.

Keywords Manot Cave · Human evolution · Upper Palaeolithic · Neanderthals · Modern human · Out of Africa origin

Résumé La période comprise entre 60 000 et 50 000 ans BP est l'une des phases les plus importantes de l'évolution biologique humaine. Au cours de celle-ci, la partie occidentale de l'Eurasie (l'Europe et le Proche-Orient) a été peuplée par les Néandertaliens, tandis que la partie orientale (Asie centrale et Sibérie) l'a été par les Denisoviens. Cependant, il y a plus de 30 000 ans, ces deux populations ont été remplacées par des Hommes anatomiquement modernes. Quand sont apparus ces nouveaux arrivants, et d'où venaient-ils ? Des données archéologiques et génétiques suggèrent que ce changement démographique a eu lieu à la fin du stade isotopique marin 4 [1–3]. Une dispersion importante d'Hommes anatomiquement modernes en dehors du continent africain serait à la source de ces nouvelles populations [4–7]. Dans cette étude, nous examinons la possibilité que Manot 1 appartienne à la population de base qui a donné lieu à l'Homme moderne. En outre, les relations entre Manot 1 et la population du Paléolithique supérieur d'Europe et les Néandertaliens levantins contemporains sont abordées. Dans cette étude, nous avons examiné les caractéristiques morphologiques particulières de Manot 1 (e.g. la fosse sus-iniacque) et évalué leurs similitudes avec les caractères homologues présents chez les Néandertaliens. Nous avons montré que, bien que la terminologie soit identique, les caractères de chaque groupe d'homininés

I. Hershkovitz (✉)
The Dan David Center for Human Evolution and Biohistory Research,
The Shamunis Institute for Anthropology,
Department of Anatomy and Anthropology,
Sackler Faculty of Medicine,
and the Steinhardt Museum of Natural History and National Research Center,
Tel Aviv University, P.O. Box 39040, Tel Aviv 6997801, Israel
e-mail : anatom2@post.tau.ac.il

B. Latimer
Departments of Anatomy and Orthodontics,
Case Western Reserve University,
2124 Cornell Rd, Cleveland, OH 44106, USA

O. Barzilai
Israel Antiquities Authority, P.O. Box 586,
Jerusalem 91004, Israel

O. Marder
Archaeology Division, Ben-Gurion University of the Negev,
P.O. Box 653, Beer-Sheva 8410501, Israel

* Cet article est une note correspondant à une conférence inaugurale d'un congrès de la SAP.

représentent des entités différentes. Nous avons aussi mis en évidence que Manot 1 et les crânes du Paléolithique supérieur ancien d'Europe ont beaucoup de caractères en commun, bien que Manot 1 soit plus gracile. Pour finir, certains des caractères archaïques observés sur le spécimen de Manot 1 sont aussi visibles sur le crâne éthiopien d'Aduma daté du Pléistocène final ou même celui d'Eyasi 1, en Tanzanie.

Mots clés Grotte de Manot · Évolution humaine · Paléolithique supérieur · Néandertaliens · Origine africaine de l'homme moderne

The Site, Its Contents, and the Characteristics of the Nearby Environment

Manot is a nearly sealed, active karstic cave located on the hilly landscape of Western Galilee, Israel (Fig. 1). It contains numerous archaeological artifacts attributed to the early phase of the Upper Palaeolithic (UP) period as well as evidence of the Middle Palaeolithic (MP) period [8]. The cave consists of an elongated main hall (80 m long, 10–25 m wide) and two

small chambers (Fig. 2). Rock falls and colluvium apparently blocked the cave's original entrance ~30 kya. During the initial survey of the cave (2008), a nearly complete calvaria (Manot 1) was found on a stone shelf in the chamber north of the main hall [9]. The skull was dated to 54.7 ± 5.5 kya by the U–Th method [9]. Numerous Middle Palaeolithic artifacts (e.g., Levallois cores, Levallois flakes, and blades) were found in secondary depositions. They manifested characteristics similar to other Late Middle Palaeolithic assemblages in the region [10,11].

The UP sequence at Manot includes two cultural traditions: the Ahmarian and the Levantine Aurignacian. The Ahmarian, radiocarbon dated to 46–42 ka, was found at the center of the cave superimposed by Aurignacian layers. It is characterized by long and narrow uni- and bidirectional lithic technology. The Ahmarian toolkit consists of retouched blades, end scrapers, and burins on blades and el-Wad points. The Levantine Aurignacian remains, recorded at the cave's entrance and center, are radiocarbon dated to 39–33 ka cal BP. The lithic industry is characterized by the production of flakes, massive blades, and bladelets. Distinctive tools include carinated and nosed end scrapers, Aurignacian blades, and curved–twisted

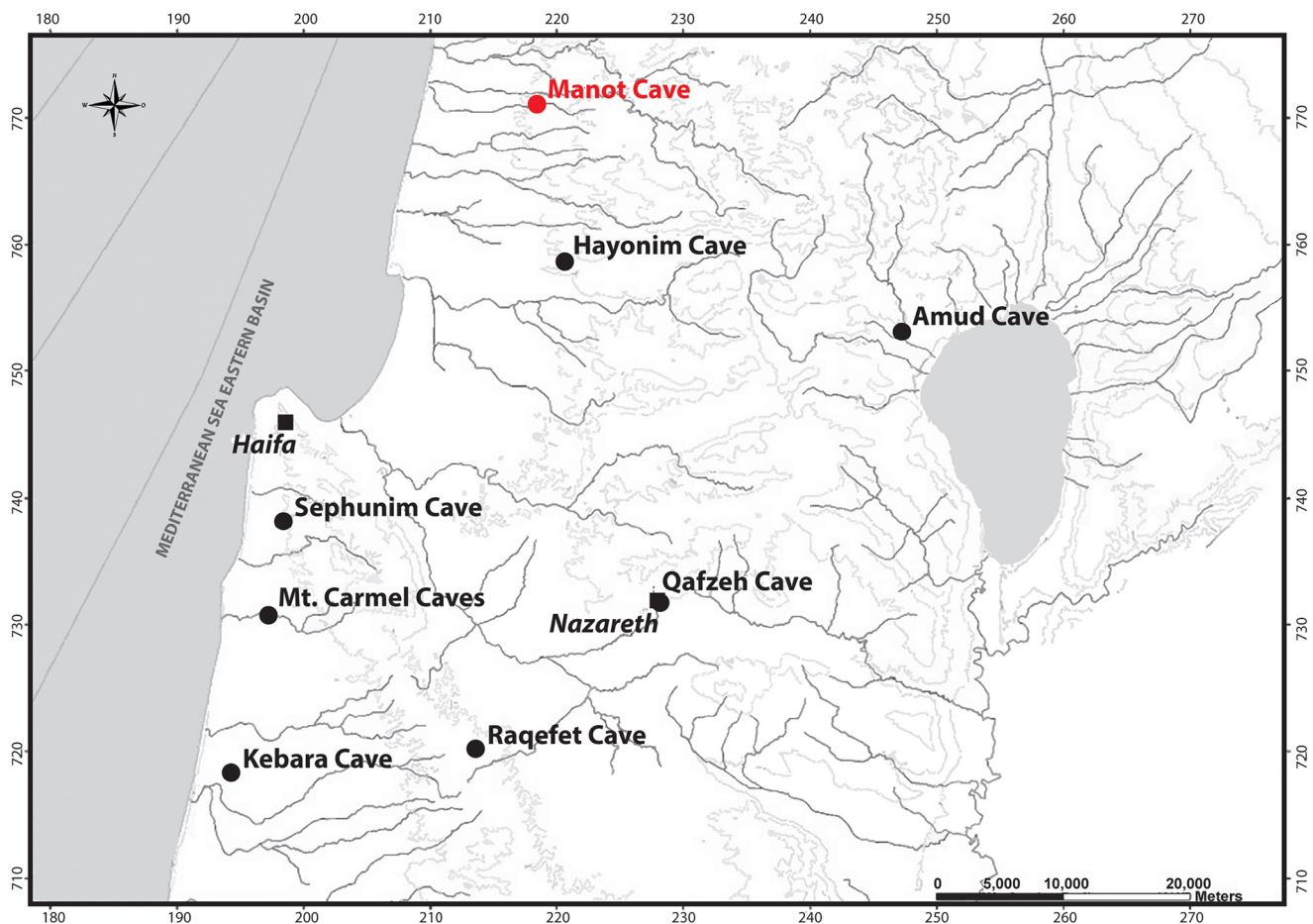


Fig. 1 Location of Manot Cave, Western Galilee, Israel / Localisation de la Grotte de Manot, Galilée de l'Ouest, Israël

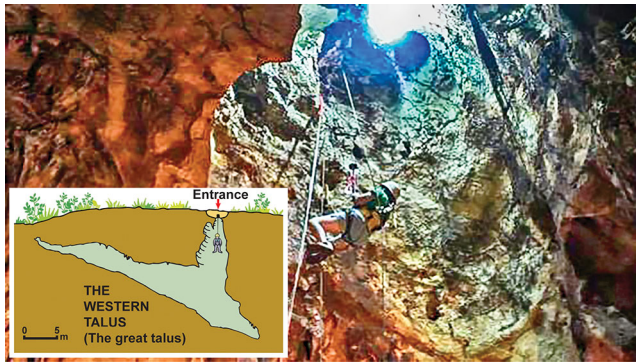


Fig. 2 Interior view of the Manot Cave / *Vue de l'intérieur de la grotte de Manot*

bladelets. Other characteristic features include an abundance of bone and antler tools, especially antler spear points [12].

The faunal record of the Manot Cave indicates that its early human inhabitants exploited large prey (ungulates), small game (birds, tortoises, and possibly snakes), and mollusks. Among the ungulates, mountain gazelle (*Gazella gazella*) and Mesopotamian fallow deer (*Dama mesopotamica*) are dominant. Between human occupations, the cave was also occupied by carnivores, as attested by carnivore gnawing marks on some of the bones. Botanical remains were identified as *Prunus* sp. and *Quercus ithaburensis*, indicating an open park and Mediterranean forest environments [8,9,12].

The Manot 1 Skull Morphology

The Manot 1 calvaria shape and size have been described elsewhere [9]. Here we will focus on some of the skull's unique morphological characteristics. The calvaria is gracile in its general appearance with moderate bone thickness (Table 1). The general profile of the skull is somewhat archaic in nature, since it lacks the smooth, uniform curvatures typically seen in modern skulls (Fig. 3). The parietals are moderately convex (parietal bone convexity angle 140°), a condition similar to that seen in the Neanderthals ($139.3^\circ \pm 6.2^\circ$), but different from the Qafzeh/Skhul specimens ($136.6^\circ \pm 1.7^\circ$). The maximum cranial breadth is positioned high, close to the vertex (Fig. 4), as in modern humans; below this point, the lateral walls of the braincase are almost parallel (Fig. 4). The parallel side walls stand in contrast to the lateral protrusion of the calvaria seen in classic Neanderthals (Fig. 4, top right). The parietals are also extremely short (arc = 118 mm, chord = 105 mm), outside the range of modern human populations (males: arc = 130.5 ± 9.7 mm, females: arc = 128.1 ± 9 mm) as well as Near East Middle Paleolithic skulls (132.5 ± 10.3 mm; 124.7 ± 9.3 mm) (Fig. 5). Their curvature is notable, although less pronounced than in modern humans (Fig. 3). The biasterio-

Table 1 Cranial vault thickness in Manot 1 calvaria and other groups of hominins / *Épaisseur de la voûte crânienne chez Manot 1 et d'autres groupes d'homininés*

Hominin	Bregma	Parietal eminence
Manot	6.0	6.5
<i>H. erectus</i>	9.4 ± 2.0	9.7 ± 2.3
	<i>N</i> = 25	<i>N</i> = 21
Early archaic humans	9.0 ± 2.2	10.3 ± 2.4
	<i>N</i> = 14	<i>N</i> = 13
Neanderthals	6.7 ± 1.4	8.3 ± 2.2
	<i>N</i> = 13	<i>N</i> = 30
Pleistocene modern humans	7.4 ± 2.0	7.4 ± 2.5
	<i>N</i> = 17	<i>N</i> = 27
Holocene modern humans	6.5 ± 0.7	5.8 ± 1.4
	<i>N</i> = 16	<i>N</i> = 17
Comparative data from Lieberman 1996		

nic breadth in Manot 1 is extremely small (95 mm), falling outside the range of modern Mediterranean populations (males = 106.9 ± 4.8 mm; females = 102.3 ± 4.4 mm) [9]. Occipital bone convexity is considerably more marked (occipital plane convexity index = 22.3) (Fig. 3) compared with modern human populations (sex combined = 16.7 ± 1.7), and very similar to European Neanderthals (22.8 ± 3.2) (Table 2). Two characteristics of the Manot 1 interior occipital surface are noteworthy: the low placement of the transverse sulcus (Fig. 6) and the location of the endinion above the inion (Fig. 6). The Manot 1 skull also manifests a well-developed superior nuchal line that extends transversely across the occipital bone (Fig. 4).

The Manot 1 Skull's Major Features

Bunning

The marked convexity (bunning) of the occipital bone of Manot 1 is common in Middle and Upper Pleistocene human fossils from Africa and Eurasia, that is, both specimens from Jebel Irhoud in Morocco manifest bunning [13] and so do most European Neanderthals (e.g., La Chapelle-aux-Saints). Bunning is also present in the majority of European Early Upper Palaeolithic modern humans (e.g., Mladeč 1).

The presence of bunning in Manot 1 at ~55 ka suggests that this feature, or a more modest version of it, sometimes called hemi-bun, exhibited in earlier UP skulls of central Europe (e.g., Mladeč 26–32 ka BP; Oase 35 ka BP) [14], is not necessarily related to interbreeding between Neanderthals and AMHs, as advocated by some studies [13]. Since Neanderthals of the Middle East (e.g., Amud 1) do

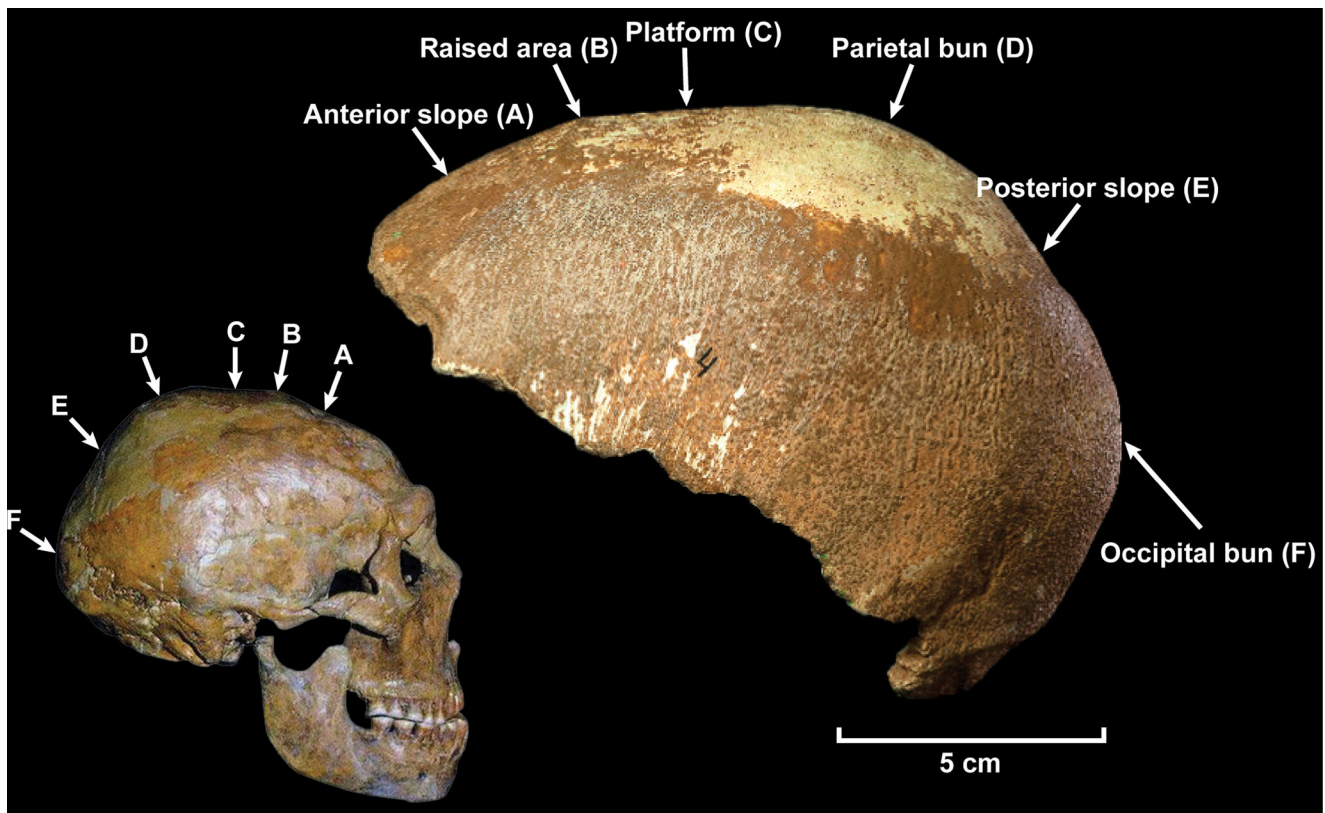


Fig. 3 Lateral view of Manot 1 calvaria. Note the archaic profile of the skull, mainly the double arched-shape profile (parietal and occipital concavities) / *Vue latérale de la calvaria Manot 1. Notez le profil archaïque du crâne, en particulier le profil en forme de double arche (concavités pariétale et occipitale)*

not exhibit bunning, it is reasonable to assume that this morphological trait originated either in the Near East AMH, or even earlier, in some African populations such as Aduma (~79–105 ka), which later migrated to the Levant. Among recent human populations, posterior projection of the occipital is uncommon and if present, it is not as pronounced as in Early European UP skulls: only 13% of modern humans manifest moderate (type III) bunning [15].

Transverse sulcus

The groove for the transverse sinus, sometimes called the transverse sulcus, is a fundamental anatomical landmark of the interior of the occipital bone. In modern humans, towards the posterior part of the parietal and the superior part of the occipital, the groove for the superior sagittal sinus becomes more marked and descends right to the midline crest. To the right of the internal occipital protuberance, the groove runs laterally. The groove for the left transverse sinus is less well developed than the right one, and originates directly from the internal occipital protuberance. These two grooves divide the occipital interior surface into two stratigraphic units: the upper and lower parts. At about the region of the asterion

(at the postero-inferior (mastoid) angle of the parietal bone) the two grooves arc inferiorly. It is noteworthy that there is large variation among modern humans with regard to patterns of the transverse sinuses. In archaic humans (*Homo heidelbergensis*, *Homo neanderthalensis*, *Homo rhodesiensis*), the transverse sulcus passes to the sigmoid sinus directly from the occipital without crossing the parietal bone [16,17]. However, the Manot 1 pattern does not resemble either of these conditions: the right and left grooves bifurcate right above the internal occipital protuberance and are both similarly developed (Fig. 6).

Inion–endinion relationships

In Manot 1, the inion is located below the endinion, contrary to the condition in Neanderthals, where the inion is located superior to the endinion. The separation between inion and endinion is a long-debated characteristic in human evolution. Since Weidenreich [18], this trait had been considered as a classical anatomical trait of *Homo erectus*, wherein the endinion is situated at a considerably lower level than the torus [19]. This spatial relationship between these two anatomical landmarks has been routinely used for taxonomic

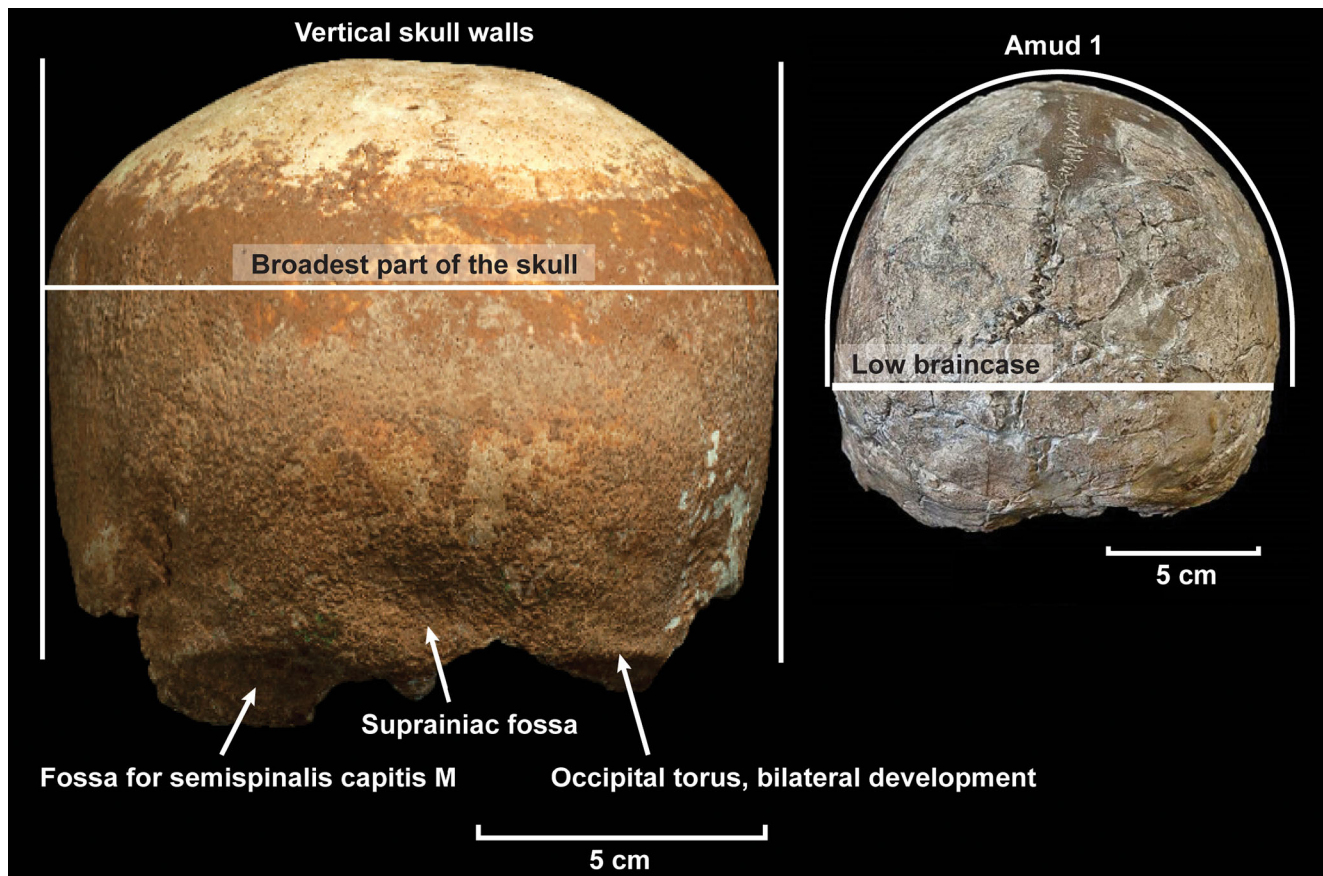


Fig. 4 Posterior view of Manot 1 calvaria. Note the presence of rounded suprainiac fossa, the position of maximum cranial breadth, and the near vertical orientation of the lateral walls of the skull / *Vue postérieure de la calvaria Manot 1. Notez la présence d'une fosse suprainiac arrondie, la position de la largeur maximale du crâne et l'orientation subverticale des parois latérales du crâne*

purposes and for determining the population affinity [18,20]. In the past two decades, the taxonomic value of this feature has been debated (e.g., [21]), since both conditions (endinion above and below the inion) occur occasionally in *Homo erectus*, Neanderthals, and Archaic Humans [22]. It is noteworthy that in early modern humans (e.g., Skhul, Qafzeh), the feature of endinion above inion occurs exclusively [22].

Suprainiac fossa

The Manot 1 external occipital table exhibits a shallow, rounded suprainiac fossa. For many years, this anatomical feature was considered a defining trait of the “classic” Neanderthal posterior neurocranium morphology [19,23,24]. Following Smith et al. [13], suprainiac fossae appear in all Neanderthal skulls (100%). However, a broad, transversely elliptical suprainiac fossa was also reported in AMH specimens from UP of Europe [25,26], Middle Palaeolithic of the Levant [13,25,27], and the Upper Pleistocene of East Africa [28]. In view of these observations, it seems questionable whether this anatomical feature really characterizes Nean-

derthal autapomorphy. Recently, it has been suggested that this feature is not homologous in Neanderthals and other humans, since they are probably derived from two different developmental processes [29]. The suprainiac fossa in Manot 1 is most similar to those seen in anatomically modern humans (AMH) and is not like the ones usually encountered in Neanderthals. The proportion of bone composition at the depression (external table/diploe/internal table) in Manot 1 is 33%/40%/27%, whereas in Neanderthals, it is 26%/52%/22%, respectively [data from 29]. This indicates that the thickness of the external table at the center of the suprainiac fossa relative to the diploic layer thickness is much greater in Manot 1 (0.82) compared with Neanderthals (0.50).

Note that the shape of the suprainiac fossa in Manot 1 is different from what we usually encounter among Neanderthals. While in Manot 1, it takes the shape of a small rounded depression (Fig. 4), in Neanderthals, the fossa is transversely elongated, its height being much shorter than its breadth. The anatomical location of the fossa is also different: in Manot 1, it is situated much higher on the occipital

Table 2 Subtense of the occipital bone with respect to the lambda-inion chord in Manot 1 calvaria and other groups of hominins / *Projection maximale de l'os occipital relativement à la corde lambda-inion chez Manot 1 et d'autres groupes d'homininés*

Specimen	Subtense of occipital ^a	Source
Manot	21.3 (24)	Authors' data
Atapuerca 1	17.2	Arsuaga et al. 2002
Atapuerca 5	14.8	Arsuaga et al. 2002
Atapuerca IV	18.6	Arsuaga et al. 2002
Swanscombe	19.7	Arsuaga et al. 2002
Sacopastore 1	20.9	Arsuaga et al. 2002
Mladeč 1	25.0	Arsuaga et al. 2002
Neanderthals (<i>n</i> = 9)	22.8 ± 3.2	Hublin 1988
Recent humans	12.7 ± 3.5	Hublin 1988
Amud	21.4	Authors' data
Qafzeh 9	13.6	Authors' data
Ohalo II	15.5	Authors' data

^a Perpendicular projection from lambda-inion chordX100)/ lambda-inion chord

bone, opposite the sagittal sinus bifurcation, whereas in Neanderthals, it is found inferior to the internal occipital protuberance [22]. The differences in shape, structure, and location clearly suggest that the suprainiac fossa in Manot 1 is probably a different entity than those observed in many European Neanderthals and some early UP skulls (e.g., Mladeč 5) [24]. It is developmentally similar to the ones seen in the upper Pleistocene East African skull from Aduma [29] and some North African Mesolithic skulls from Afalou and Tatoralt, as well as in some early modern humans such as Qafzeh 6 [27] and Skhul IX [13].

The superior nuchal line and external occipital protuberance

In modern humans, the superior nuchal lines originate from the region below the asterion and curve up toward the external occipital protuberance, with which they are usually confluent. They are less marked laterally and grow in thickness medially. In Manot 1, the pronounced arched-shaped superior nuchal lines are well-developed throughout their full length, resembling the lines seen in some European UP specimens such as Cioclovina [30,31]. Compared to Manot 1, the Neanderthal's superior nuchal lines are much thicker and run transversally. In addition, the external occipital protuberance in Neanderthals is more distinct, expressed as a wide, triangular, and irregular tuberculum [17], whereas in Manot 1, it merges with the lines. The pronounced fossae between

the superior and inferior nuchal lines for attaching the semi-spinalis capitis muscle is seen both in Neanderthals [32] and Manot 1 skulls.

Discussions and Conclusions

Summary of the Manot 1 skull's major features

The Manot 1 calvaria exhibits a mosaic of “archaic” and modern traits. Although the taxonomic significance of this combination of features is not clear [33,34], it is nevertheless notable that hominins, with a similar combination of archaic and modern features, persist in fossil records across sub-Saharan African and the Middle East until after ≈35 ka [33,35]. For example, the two Iwo Eleru skulls from southwestern Nigeria (11.7–16.3 ka BP) possess neurocranial morphologies intermediate in shape between archaic hominins (Neanderthals and *Homo erectus*) and modern humans [36], as well as the Late Stone Age Ishango skulls from the Congo region [37].

Finally, Crevecoeur et al. [38] demonstrated a large extent of cranial diversity in the late Pleistocene of Africa and Eurasia, suggesting that living humans in these regions represent a diminished relic of what was once a much greater range of past human natural variability.

In light of this, it is noteworthy that our three-dimensional geometric morphometric (GM) analysis [9] revealed that the Manot 1 calvaria represents a modern human and that its closest relatives are modern African skulls and Early UP skulls from Europe.

The contribution of Manot 1 to human evolutionary theory

During the last two decades, genetic and anthropological studies have provided us with several important insights regarding modern human evolution. These include the following: (1) that anatomically modern humans originated in Africa (≈ 200 ka) and eventually dispersed to all inhabited parts of the world [35,39]; (2) that a variety of transitional forms with various combinations of archaic and modern features lived in Africa between 200 and 35 ka [33,35,40,41]; (3) that population divergence of non-African and sub-Saharan Africans occurred over a prolonged period of time [42,43], and (4) that in the African populations, an admixture between archaic and more modern forms of AMH took place until very recent times [44–46]. The Manot 1 calvaria [9] supplements the aforementioned observations by adding four additional insights: (1) that some archaic traits appearing in early Upper Palaeolithic AMHs in Europe (previously attributed to interbreeding with Neanderthals) such as suprainiac fossa could have originated in ancient African

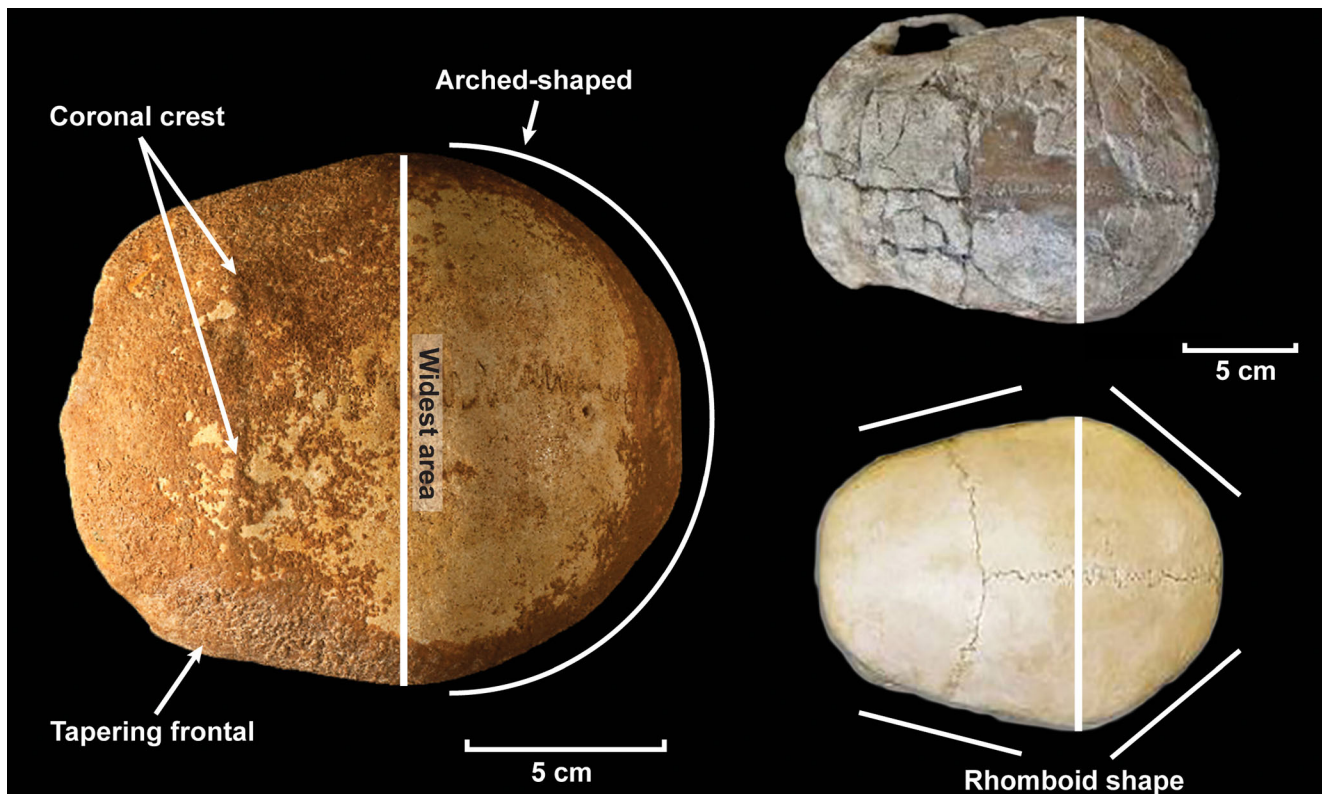


Fig. 5 Superior view of Manot 1 calvaria. Note the presence of the coronal keel and the rounded, basin-like appearance of the posterior part of the calvaria / *Vue supérieure de la calvaria Manot 1. Notez la présence d'une carène coronale et l'apparence arrondie, en forme de cuvette de la partie postérieure de la calvaria*

and/or Levantine populations, (2) that AMHs and Neanderthals shared the Levantine corridor between 60 ka and 50 ka, (3) that the Late Middle Palaeolithic AMHs of the Levant possess strong morphological affinity with African populations, and finally (4) that a population discontinuity exists between Late MP and later UP populations in the Levant.

The Manot 1 Calvaria and the Neanderthal enigma

The hypothesis of a variable genetic admixture between early modern humans dispersing into Europe and local Neanderthal populations was popular among many researchers prior to the DNA era (e.g., [47–50]). Duarte et al. [51], for example, have claimed that the 4-year-old child from Abrigo do Lagar Velho (Portugal) manifests mosaic morphology indicative of an admixture between regional Neanderthals and early modern humans migrating into southern Iberia. However, it should be recognized that such evidence, if based solely on skull morphology is, at best, equivocal. Harvati et al. [31] restudied the Cioclovina skull (28–29 ka BP, Romania), which also has been proposed to represent a Neanderthal–modern human hybrid [52], and instead suggested that it is entirely modern with respect to cranial

shape. Nevertheless, the slightly older cranium from Romania, Oase 2 (35 ka BP), shows an unusual combination of modern and archaic features that made it difficult to attribute it to a recognized taxa [14].

The notion of interbreeding runs counter to the idea that in Western Europe, the transition from the (MP to the UP period involved the extinction of the Neanderthals and their complete replacement by early modern humans, with their more elaborate technological and sociocultural systems [53–55]. The specimen from Manot Cave enabled us to progress beyond this overly simplistic model. Clearly, the reliance and use of a single characteristic, and whether it is absent or present is not adequate enough to make logical taxonomic judgments. This is especially true when the characteristic in question is highly variable and subject to different definitions. For example, the simple presence or absence of the suprainiac fossae among Neanderthals and anatomically modern humans fails as an effective discriminator. This characteristic and the degree to which it is displayed has been interpreted by various researchers [13,25,26,56,57] as supporting evidence for the existence of local interbreeding between Neanderthals and anatomically modern humans in Europe. However, the presence of a similar occipital depression in the Manot calvaria (~55 ka) and the Aduma skull

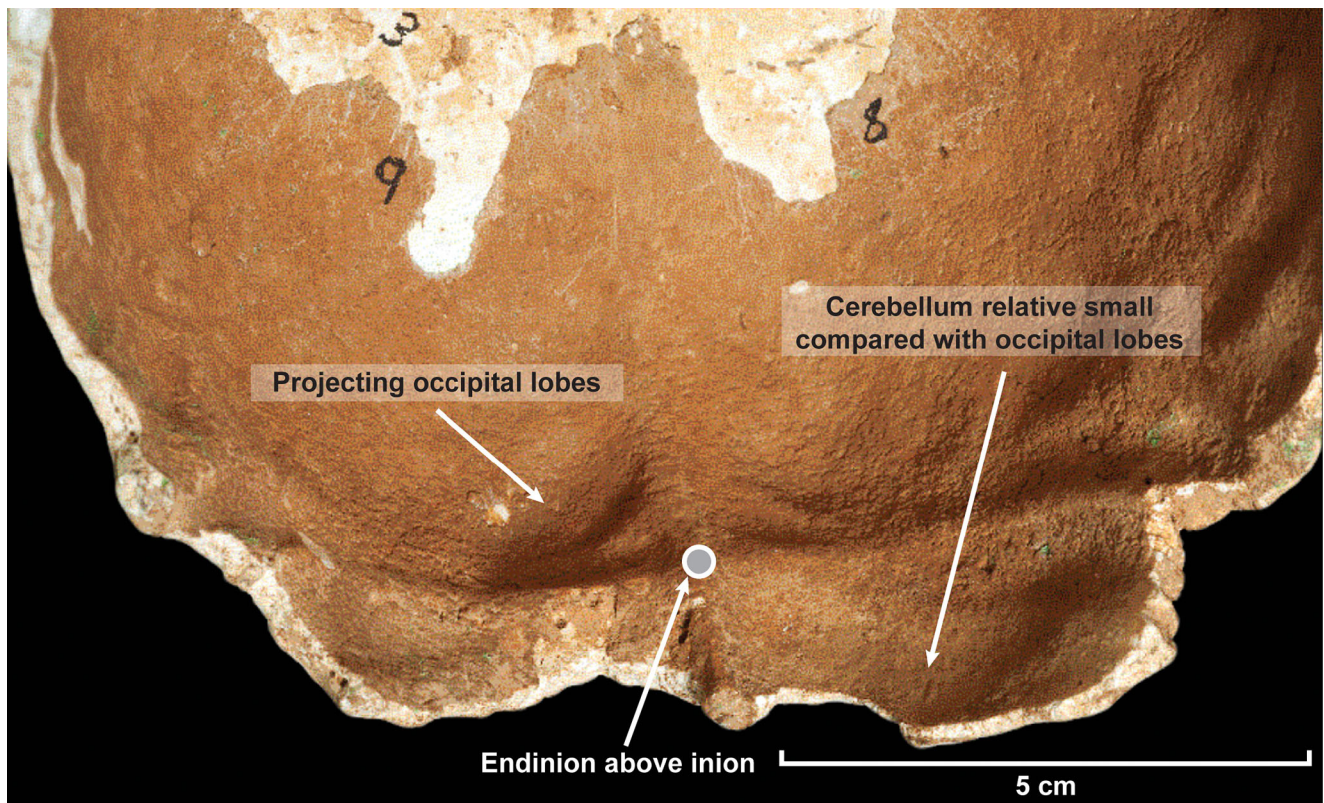


Fig. 6 The interior of the occipital region. Note the deep occipital fossae, the location of the transverse sinuses, and the low position of the endinion / *L'intérieur de la région occipitale. Notez les fosses occipitales profondes, la position des sinus transverses et la position basse de l'endinion*

(ADU-VP-1/3) [28] from East Africa (~79–105 ka) makes this “evidence” for European interbreeding questionable, since this trait was already present in the core population that later established the European UP population. Furthermore, consider the following facts: (1) some early European UP skulls manifest a type of occipital depression similar to those reported for some North African Epipalaeolithic and Mesolithic skulls [e.g., Afalou Bou Rhummel (~11–13 ka); Taforalt (~11 ka)], (2) the depression described for Qafzeh 6, Skhul V, IX, and Aduma may not be homologous to the Neanderthal suprainiac fossa [29], and (3) the Neanderthal skull Amud 1 does not possess this trait (Fig. 4), (4) the fact that Eyasi 1 cranium (400–200 ka BP, Tanzania) also manifest an oval suprainiac fossa indicates that this trait is not limited to the European and western Asian Neanderthals [58]. This suggests that the presence of this characteristic within the UP populations of Europe may not necessarily reflect interbreeding of Neanderthal/*H. sapiens*. Rather, it most likely indicates an intrusion of anatomically modern populations from Africa that migrated, through the Levantine corridor, into Europe some 45–35 ka cal BP [59–62].

Recent genetic studies leave little doubt that interbreeding between Neanderthals and modern humans did occur [63–

65]. Nevertheless, we remain skeptical whether this hybridization model adequately explains the presence of certain “archaic” traits in populations that otherwise show an abundance of modern characteristics.

Accepting the fact that genetic exchange did occur between Neanderthals and modern humans, necessarily raises several important questions: When did it occur? Where did it occur? And between what populations?

In view of the fact that modern humans evolved in Africa, migrated north, and encountered Neanderthals, a logical place where interbreeding might have occurred is the Levant, the major land corridor between Africa and Eurasia. Indeed, we find a succession of Neanderthals and anatomically modern humans in this area, but always appearing at different times. It appears as if each group remained on their respective side of the Levant and occupied it as the outermost margin of their territories. There is no fossil evidence that Neanderthals and AMHs were sympatric anywhere before between ~60 ka and 50 ka, except in Manot Cave. Thus, Manot Cave is presently the only locality suggesting chronological and spatial overlapping of Neanderthals and AMH in the Levant or anywhere else. The Manot Cave population lived contemporaneously with the Neanderthals of

the region (50–60 ka BP) (e.g., Amud, Kebara), and probably represents the last wave of AMH that had an opportunity to meet Neanderthals in the Levant.

In the absence of DNA information, one of the great obstacles in attempting to address the question: Can Manot 1 be a hybrid between a Neanderthal and a modern human, is the nearly complete inability to predict, in morphological terms, what a Neanderthal/modern human hybrid would look like. Manot 1 possesses some traits (e.g., bunning, suprainiac fossa) that are commonly found in Neanderthals, and it possesses even more traits (e.g., widest part of the braincase at the parietal bossing, parallel side walls) that are typical of AMH. This combination of traits is also seen in early Upper Palaeolithic skulls from central Europe, such as Mladeč I and Cio-clovina (“hemibun”). How much this combination of modern and archaic features can assist in addressing the aforementioned question is not clear. Different traits are likely to have different diagnostic values and the combination of different characteristics further confounds this issue. For instance, vertical cranial side walls and a broader skull region high on the parietal are quite reliable indicators of a modern neurocranial shape. In contrast, Neanderthal typical traits, such as an occipital bun or the suprainiac fossa, appear occasionally in modern humans as well. In addition, it is not clear whether these last two features are developmentally homologous in Neanderthals and modern humans [28]. We think that the distinct morphology of Manot 1 is not necessarily the result of hybridization; however, we cannot exclude this possibility. At present, no Neanderthal fossils have been discovered in Africa. However, there is clear fossil evidence of the presence of AMHs in the Levant (Qafzeh/Skhul) and possibly even in Eastern Asia [66,67]. Interestingly, prior to Manot, there has been no concrete evidence that they have ever overlapped with Neanderthals, thus excluding the possibility of earlier interbreeding between Neanderthals and AMHs.

The Manot 1 calvaria and African populations

Unfortunately, human remains from Africa that date from 60 ka to 50 ka are virtually unknown. The two reasonably complete crania that can be used for comparison are from Nazlet Khater in Egypt and from Hofmeyr in South Africa, both dated from 38 ka to 36 ka. Although these two crania present a suite of features that align them with modern humans, they also exhibit several archaic features [38,68,69]. Comparing the Manot 1 hominin to these two African skulls is very limited because the Manot 1 specimen does not possess most of the anatomical parts preserved in these skulls.

The Manot 1 skull, Levantine MP, and UP populations

At present, Levantine fossils contemporaneous with Manot 1 do not exist. The Manot 1 hominin is sandwiched between

the MP Skhul/Qafzeh group, which is ca. 50 ka earlier, and the two specimens from UP Qafzeh cave, which are 30 ka later. The skull parts available from the UP Qafzeh caves H1 and H2 do not anatomically overlap with the Manot specimens, thus hindering meaningful morphological comparisons. The only fossils, besides Manot 1, that may be chronologically intermediate between the Middle and Upper Palaeolithic human populations from the Levant, are the few fragments discovered by Wreschner [70] in the Late Mousterian layers of Geula Cave. These fragments appear to be morphologically modern [71], although little information could be gleaned from them. Since specimens earlier or contemporaneous with Qafzeh UP fossils consist either of isolated teeth or are of a very young developmental age (e.g., Abri Antelias, Ksar Akil “Egbert” skeleton; e.g., Bergman and Stringer 1989), a comparison can be made only with later UP Levantine specimens such as the female from Nahal Ein Gev I (ca. 27–25 kya BP) [72] and Ohalo II (19–21 ka BP) [73]. Our geometric morphometric analysis [9] clearly revealed that early UP skulls are morphologically more closely related to Manot 1 than are later UP Levantine skulls.

The Qafzeh and Skhul specimens represent earlier migration waves of modern morphology into the Levantine corridor around 90–110 ka. A population divergence of non-African and sub-Saharan Africans is predicted to have occurred from 90 ka to 130 ka, according to one study [74], but more reliable upper boundaries (62–95 ka) were recently published by another research team [43]. Although these dates are somewhat problematic (the first result is based on nuclear DNA, whereas the second is based on mtDNA), we can generally conclude that these genetically predicted dates are important since they remove the Qafzeh/Skhul fossils from the modern population scenario. The notion that the Qafzeh/Skhul populations interbred with the Neanderthals and gave birth to the Early UP population of Europe [75] currently seems unlikely.

The possible origin of the Manot Cave people

There are two major scenarios to explain the presence of AMH at Manot Cave ca. 50–60 ka. The first, which has been discussed in our previous paper [9], suggests a large out-of-Africa migration of AMH between 90 ka and 60 ka. Manot 1 is currently the only known Levantine fossil that represents this time period. Following this scenario, this is the core population from which all modern human populations evolved. An alternative evolutionary scenario is that Manot 1 could be an evolved version of an early local Levantine AMH. The notion of a continuous morphological transition from archaic to more modern forms in the Levant goes back to McCown and Keith’s [76] study of the Mount Carmel hominins. Impressed by the great morphological variability, they grouped the fossils from Skhul and Tabun into a

distinct species named *Palaeoanthropus palestinensis* and suggested a morphological continuum from more archaic (Neanderthal-like Tabun) to more fully modern (Skhul) *H. sapiens*. More recent studies have suggested that the evolutionary chain of AMH in the southern Levant began with the Zuttiyeh (possibly >150 kya) hominin [77–79]. One of the major problems in deciphering the lineage of modern humans in the Levant is their great morphological variability. Many anthropologists have concluded that the Skhul/Qafzeh hominins represent a single population that was almost, if not fully, anatomically modern [79–81]. However, it was clearly demonstrated that these two hominin groups differ considerably and that within-group variation is large enough to represent more than one morph (Qafzeh 6 vs. Qafzeh 9). Moreover, even the unequivocal representatives of our species in these groups (e.g., Qafzeh 6) lack some key taxon-specific features (apomorphies) such as a bipartite brow. In addition, none of the Skhul specimens possess a glabellar “butterfly”, considered a characteristic of *H. sapiens* [82]. This and other characteristics of the mandibles led the latter authors to conclude that “...Skhul adults are characteristic neither of *H. sapiens* nor of Neanderthals” (p. 114). Most of the Skhul/Qafzeh hominins do not possess occipital bun or a suprainiac fossa. Although some of the Skhul/Qafzeh skulls manifest isolated traits seen in Manot 1, none present the full battery of features that characterize Manot 1. In light of the large unexplained variations, it is therefore impossible to determine the exact relationship of Manot 1 to the Qafzeh/Skhul hominins since the results largely depend on what skull from this assemblage is being compared to Manot 1.

The fact that only very few hominin fossils have been found between the time of Qafzeh/Skhul (90–120 ka) and the time of Manot 1 (55 ka) is not surprising since there are almost no archaeological sites in Israel from this time period (probably due to extreme climate fluctuations during MIS 5 and 4). The few sites known are contemporaneous with Manot (50–60 ka), and contained mostly Neanderthal remains (e.g., Kebara, Amud). This suggests that Neanderthals and modern humans arrived at the Levant roughly at the same time, somewhere around 60 ± 5 ka. Considering all of the aforementioned facts, it seems unlikely that Manot 1 is a by-product of local evolution from the Qafzeh/Skhul stock. Finally, recent genetic data suggest the rise of a completely new branch of mitochondrial DNA (haplogroup L3) in Africa after 100 ka [83] lending additional support to our notion that Manot 1 has not evolved in situ.

Throughout modern human evolution, the Levant has served as the major land corridor for AMH populations migrating from Africa to southwestern Asia (e.g., [1]). It has also served as the avenue for the cultural transition from the Middle to the Upper Palaeolithic, which played a critical role in the appearance and expansion of modern

humans. The Manot Cave is probably among the first localities outside of Africa where fully modern humans (AMH) established themselves, replacing both archaic anatomically modern humans and Neanderthals.

Acknowledgments Financial support for the Manot Cave project was received from the Dan David Foundation, the Irene Levi-Sala CARE Archaeological Foundation, the Leakey Foundation, the Israel Science Foundation (grant no. 338/14), and the Binational Science Foundation (grant. no. 2015303). Additional financial support was retrieved from Case Western University and the Israel Antiquities Authority. We wish to thank all the students and volunteers who participated in the cave excavations over the years. Thanks goes to Clara Amit for the pictures. Special thanks go to the late Dan David and his son, Ariel David, for their inspiration and financial support over the years.

Links of Interest: None.

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