Chapter 13
Dental Evidence from the Aterian Human Populations of Morocco

J.-J. Hublin, C. Verna, S. Bailey, T. Smith, A. Olejniczak, F. Z. Sbihi-Alaoui, and M. Zouak

Abstract The Aterian fossil hominins represent one of the most abundant series of human remains associated with Middle Stone Age/Middle Paleolithic assemblages in Africa. Their dates have been revised and they are now mostly assigned to a period between 90 and 35 ka. Although the Aterian human fossil record is exclusively Moroccan, Aterian assemblages are found throughout a vast geographical area extending to the Western Desert of Egypt. Their makers represent populations that were located close to the main gate to Eurasia and that immediately predated the last out-of-Africa exodus. In this chapter, we present an analysis of the Aterian dental remains. The sizes of the Aterian dentitions are particularly spectacular, especially for the post-canine dentition. This massiveness is reminiscent of the Middle Paleolithic modern humans from the Near East, but also of the early *Homo sapiens* in North and East Africa. Morphologically, this megadontia is expressed in the development of mass-additive traits. The Aterian dentition also displays relatively thick enamel. These features help to set some of the traits observed in Neandertals in perspective and highlight their primitive or derived nature. The Aterian morphological pattern is also important to consider when interpreting the dental morphology of the first modern humans in Eurasia.

Keywords Aterian • *Homo sapiens* • Middle Stone Age • Modern humans • Morocco • Neandertal • Sahara • Teeth

Introduction

Moroccan sites have yielded the richest Middle and Late Pleistocene human fossil record in North Africa. This material has often been discovered in the course of archaeological excavations and is mostly associated with Acheulean, Mousterian, Aterian, or Iberomaurusian assemblages. The oldest and the youngest parts of this fossil record have attracted the attention of scholars, but the Aterian associated human remains are poorly described and mostly unpublished. However, they represent one of the

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J.-J. Hublin and S. P. McPherron (eds.), *Modern Origins: A North African Perspective*, Vertebrate Paleobiology and Paleoanthropology, DOI: 10.1007/978-94-007-2929-2_13,

most abundant series of human remains associated with a Middle Stone Age/Middle Paleolithic assemblage in Africa.

In 1939, Howe and Movius discovered the first human remains assigned to an Aterian assemblage in the cave of Mugharet el 'Aliya near Tangier. They were represented by an immature fragmentary maxilla and some isolated teeth (Senyürek 1940). Later, at the "Grotte des Pigeons" (Taforalt), another site in northern Morocco, a fragmentary human parietal was discovered by Roche in 1951 in a "late Aterian" context (Roche 1953). Subsequent discoveries of human fossils associated with Aterian artifacts occurred in sites along the Moroccan coast south of Rabat in the 1960s and 1970s.

The "Grotte des Contrebandiers" at Temara, south of Rabat, was first explored by Roche, who conducted some test excavations between 1955 and 1957. A human mandible yielded by the site was then described by Vallois (Vallois and Roche 1958). The unusual robusticity of the bone and dentition led these authors to assign it to an early stage of human evolution, contemporary to Acheulean assemblages that ultimately were never identified in the archaeology of the site. Subsequently, the excavation by Roche developed mostly from 1967 to 1975 and yielded several other specimens assigned to Aterian contexts.

Another series of discoveries resulted from the work by Debénath in other cave sites along the Atlantic coast. In the cave of Dar es-Soltan II, in the suburb of Rabat (Dar es-Soltan I is a distinct cave located nearby and the eponym site for the Soltanian), a partial skull associated with a hemimandible as well as an immature calvaria and a mandible were found in 1975 at the bottom of the stratigraphy, in a marine sand deposit (layer 7). This sterile layer was overlaid by a distinct reddish layer (layer 6), in which a hearth and some Aterian elements have been described (Debénath 1976).

Finally, another discovery was made in the cave of Zouhrah at El Harhoura, between Dar es-Soltan and Grotte des Contrebandiers. The Zouhrah site is usually called "El Haroura I" in the literature as there is an El Haroura II which, so far, has not yielded Pleistocene hominins. There, another mandible and an isolated canine were unearthed during a salvage excavation in 1977 (Debénath 1980).

In line with the notion that the Aterian was a North African late Middle Paleolithic industry, the Mugharet el 'Aliya material was initially said to display "Neandertal-like" features (Senyürek 1940), as was the case in the mid-twentieth century for virtually any Middle Paleolithic or Middle Stone Age associated human specimen from the Old World. However, these very fragmentary remains looked to many scholars to be "nearly indecipherable" (Piveteau 1957). It was not before the 1970s, when more complete specimens from Dar es-Soltan II and El Haroura I were first described, that some authors started to emphasize the primarily anatomically modern nature of these fossils. By 1976, Ferembach (Ferembach 1976) assigned the newly discovered Dar es-Soltan specimens to "*Homo sapiens sapiens*," although they displayed remarkably wide facial dimensions and strong supraorbital reliefs. Minugh-Purvis (1993) re-examined the Mugharet el 'Aliya specimen and also rejected the notion that it displayed any Neandertal facial features, supporting instead that few diagnosable features were observable on the specimen and that it could instead be a representative of "*Homo sapiens sapiens.*"

Another issue on which opinions and interpretations have widely varied is the age of these specimens. In northwestern Africa, the Aterian has long been considered a local late Middle Paleolithic assemblage, widely overlapping in time with the first Upper Paleolithic assemblages in Europe between ca. 40 and 20 ka (e.g., Debénath et al. 1986). This chronological assignment was mostly based on ^{14}C dates, which were later revealed to be mostly infinite dates. However, in the last two decades, the development of new methods based on luminescence has led to the production of a new set of dates that pushed the chronology of the Aterian outside of and later in Morocco much further back in time (for review, see Bouzouggar and Barton 2012; Raynal and Occhietti 2012; Richter et al. 2012). Today, the Aterian assemblages are mostly assigned to a period between 90 and 35 ka and could well be rooted further back in time. This evolution of our perception of the Aterian and their makers occurred in the context of a complete change of view on recent human evolution in Africa, putting an increasing emphasis on the African origins of non-African extant humans (Bräuer 1984; Cann et al. 1987; Stringer and Andrews 1988), and more recently highlighting the early occurrence in the African archaeological record of behavior unique to recent modern humans (McBrearty and Brooks 2000; Henshilwood et al. 2004; Texier et al. 2010). We have gradually shifted from a situation where Aterians were seen as Neandertal-like hominins still producing a delayed Middle Paleolithic at a time when fully anatomically modern humans were producing the Upper Paleolithic in Europe, to a scheme in which they are essentially modern humans producing a Middle Stone Age with features such as the production of personal body ornaments (d'Errico et al. 2009) at a time when Neandertals were still producing Mousterian assemblages in Europe.

In its original form and still in many debates around it, the out-of-Africa model for the origin of non-African modern populations emphasizes a hypothesized sub-Saharan source of an ancestral group. However, it is important to underline that the present day distribution of African populations might be very different from their original location in the late Pleistocene. The episodes of high aridity and extensions of the Sahara during MIS 4 and 2 resulted in the displacement of many human groups further south and their almost complete separation from Maghreb populations. There are also clues to the ancient structure of early modern populations and for more complex scenarios that were once thought to account for the out-of-Africa exodus (Gunz et al. 2009). In this context, elucidating the affinities of North African populations older than 50 ka is of major importance. To date, the Aterian human fossil record is exclusively Moroccan. However, the archaeological record demonstrates that Aterian populations occupied a very large geographical area extending from the Atlantic coast to the Western Desert of Egypt, and from the Mediterranean to south of the modern Sahara (Bouzouggar and Barton 2012; Hawkins 2012). The makers of these assemblages can therefore be seen as (1) a group of *Homo sapiens* predating and/or contemporary to the out-of-Africa exodus of the species, and (2) geographically one of the (if not *the*) closest from the main gate to Eurasia at the northeastern corner of the African continent. Although Moroccan specimens have been discovered far away from this area, they may provide us with one of the best proxies of the African groups that expanded into Eurasia. Comparing them with the European and Near-Eastern human groups that immediately pre- and post-dated this exodus is therefore of crucial importance in order to elucidate the nature of the populations involved in it.

Dental material represents a large portion of the Aterian hominins available for study, either in the form of isolated teeth or more or less complete jaws. Although this material is fragmentary, it is most helpful in elucidating the biological affinities of these populations. Dental development seems to depend little on environmental conditions and mostly on genetic control and several recent studies have demonstrated that when combining metrical and non-metrical approaches, dental morphology is a useful tool to assess taxonomic affinities of Pleistocene hominins (Bailey 2006a; Martinón-Torres et al. 2007; Olejniczak et al. 2008a, b; Bailey et al. 2009; Smith et al. 2009). In this chapter, we present a systematic analysis of the Aterian dental remains. This includes dental metric and morphological analyses, as well as an analysis of the internal dental structures, specifically enamel thickness. Each of these aspects of the dentition provides important information on the affinity of these early North African humans. Ultimately, we compare these variables with those of other Late Pleistocene as well as more recent humans.

Material

Table 13.1 lists the Aterian dental material included in this study and images of the specimens can be found in Figs. 13.1 and 13.2. At the time that this text was written, this material was housed in either the Musée Archéologique de Rabat or the Institut National des Sciences de Archéologie et du Patrimoine (Rabat). This list includes 51 teeth. In most cases the human remains were found directly in association with Aterian assemblages. However, in the case of the site of Dar es-Soltan II, it should be noted that the human remains were in fact found in a sterile layer immediately underlying an Aterian archaeological layer and are therefore considered to be intrusive from this overlying layer (Debénath 1976). Recent dates in the site (Bouzouggar and Barton 2012; Raynal and Occhietti 2012) as well as geological evidence indicate that this sterile layer is a transgressive horizon corresponding to the MIS 5 interglacial, which therefore represent a *terminus post quem* for the specimens. A similar situation is encountered at the Grotte des Contrebandiers in Temara, where archaeological layers immediately preceding the "genuine" Aterian layers have been identified either as MIS 5 "Ouljian breccias" (Vallois and Roche 1958) or "Mousterian" layers post-dating MIS 5e. However, these uncertainties should also be considered in the broader context of the debate around the age of the initial Aterian and the lack of sharp separation with underlying Mousterian assemblages within MIS 5 (Bouzouggar and Barton 2012; Richter et al. 2012).

A different problem results from the presence of six teeth in the Grotte des Contrebandiers series that Ménard (1998) assigned to the Iberomaurusian (IBM) (i.e., belonging to an epipaleolithic assemblage). Unfortunately, there is no consistency between the numbering and identification provided by Ménard (1998) and the current labeling of the specimens at the Musée Archéologique de Rabat. However, we could identify that an Upper M1 and M2 attached to a maxilla and reported by Ménard as "T4" is today numbered IB19 (Fig. 13.1). Our initial observations suggest that Menard was correct in attributing this specimen to the IBM. The teeth from this individual are smaller and morphologically simpler than the rest of the teeth in our sample. Moreover, one has a well-developed carious lesion. The frequency of caries in samples older than the Holocene is rather low, especially root-type caries of this size. Therefore, this specimen has been excluded from the Aterian sample in this study. For the remaining teeth, the specimen reported by Ménard (1998) as "T6" is today labeled "T1" and is most likely the lower M3 missing on the right side of the Grotte des Contrebandiers 1 Aterian mandible. The specimens reported as "T3" by Ménard do not correspond to the specimens today labeled "T3a" and "T3b," which display a size that clearly matches the rest of the Aterian series and is out of the IBM variation.

For our metrical study, the comparative database encompasses original and bibliographical data for three dental reference samples:

- Neandertals (NEAN) (from MIS 7 to MIS 3) (Maximun number of individuals, i.e., individuals plus unrelated isolated teeth (N = 157)) from the sites of: Abri Agut, Amud, Arcy-sur-Cure, Bau de l'Aubésier, Biache-Saint-Vaast,

Table 13.1 List of the dental material

Site	Specimen	Anatomical part	Analysed teeth
Dar es-Soltan II	Mandible H4	Mandible	Left: C, M1-M3; right: I2-P3, M1-M3
Dar es-Soltan II	Mandible H5	Mandible fragment (left)	Left: C, P4-M3
Dar es-Soltan II	NN	Isolated tooth	UM1 r
Dar es-Soltan II	H5	Maxilla fragment (right)	Right: M2-M3
Dar es-Soltan II	H6	Maxilla fragment (left)	Left: P3-M1
Dar es-Soltan II	H9	Isolated tooth	UM2 l
Dar es-Soltan II	H10	Isolated tooth	UM2 l
Contrebandiers	Mandible	Mandible	Left: I1, P4-M3; right: I1-M2
Contrebandiers	T1	Isolated tooth	LM3 r
Contrebandiers	T5	Isolated tooth	UP4 r
Contrebandiers	T2	Isolated tooth	Udm2 l
Contrebandiers	T4	Isolated tooth	UM3 l
Contrebandiers	H7	Isolated tooth	UM1 r
Contrebandiers	T3b	Isolated tooth	UM1 l
Contrebandiers	T3a	Isolated tooth	LM1 l
Contrebandiers	IB19	Maxilla fragment (left)	Left : M1, M2
El Haroura	Mandible	Mandible	Left: P4-M3; right M1-M3

In Dar es-Soltan, the maxilla fragment H5 likely belongs to the same individual as the mandible H5. The maxilla H6, the mandible H4, and the tooth H9 are also likely from the same individual. In Temara, the LM3 T1 likely belongs to the mandible

Grotta Breuil, Châteauneuf-sur-Charente, Columbeira, Combe Grenal, Dederiyeh, Devil's Tower, Croze del Dua, Le Fate, Fenera, Fossellone, Guattari, Genay, Hortus, Kebara, Krapina, Kůlna, La Chaise–Abri Suard, La Chaise–Bourgeois-Delaunay, La Ferrassie, Le Moustier, La Quina, Macassargues, Monsempron, Montmaurin, Ochoz, Payre, Le Placard, Le Portel, Petit-Puymoyen, Regourdou, les Rivaux, Rochelot, Saccopastore, Shanidar, Sipka, Soulabé-las-Maretas, Spy, Subalyuk, Tabun, Teshik-Tash, Vergisson, Vindija, Grotte Vaufrey, Zafarraya.

- Middle Paleolithic modern humans from Qafzeh and Skhul (MPMH) (N = 13).
- European Upper Paleolithic modern humans (UPMH) from Aurignacian to Solutrean (N = 75): les Abeilles, Les Battut, Bacho-Kiro, Brassempouy, El Castillo, La Crouzade, Dolní Věstonice, La Ferrassie, Kent, Mladeč, Les Rois, Les Vachons, Abri Pataud, Brno, Cro-Magnon, Grotte des Enfants, Lagar Velho, Peştera cu Oase, Paglicci, Pavlov, Předmostí, Isturitz, Lafaye, Cap Blanc, Le Morin, Saint-Germain-la-Rivière, Le Peyrat, Pech de la Boissière, Oberkassel.
- Similar groups were used for the comparison of non-metrical features:
- Neandertals (from MIS 7 to MIS 3; N = 101 specimens, individuals, or isolated teeth): Arcy-sur-Cure, Ciota Ciara, Combe Grenal, Devil's Tower, Ehringsdorf, Guattari, Hortus, Grotta Taddeo, Krapina, Kůlna, La Fate, La Ferrassie, La Quina, Malarnaud, Marillac, Monsempron, Montgaudier, Obi Rakhmat, Ochoz, Petit-Puymoyen, Pontnewydd, Regourdou, Roc de Marsal, Saccopastore, Spy, St Cesaire, Subalyuk, Taubach, Vindija.
- Middle Paleolithic modern humans from Qafzeh and Skhul (N = 11).
- Upper Paleolithic modern humans from Europe (Aurignacian and Gravettian) (N = 42): Abri Labatut, Abri Pataud, Dolní Věstonice, Derava Skala, Font de Gaume, Fontéchevade, Grotte des Abeilles, Grotte des Rois, Istallosko, Le Ferrassie, Lagar Velho, La Gravette, Lespugue, Les Vachons, Miesslingtal, Mladeč, Peştera cu Oase, Pavlov.

In addition to the European UPMH groups, it was also possible to take measurements on a series of Moroccan IBM specimens from Afalou and Taforalt (N = 106) from the collections of the Institut de Paléontologie Humaine in Paris. Also, Middle Stone Age specimens from Die Kielders, Klasies River Mouth, and Blombos (South Africa) (N = 9) were plotted in our distributions.

Three-dimensional enamel thickness studies require that the entire volume of enamel is unbroken and unworn, and none of the teeth examined here met these criteria. Two-dimensional enamel thickness measurements require that, at most, only minimal wear appears on the mesial cusps, and two of the molar teeth we examined met this condition (H7 and T3b, both maxillary first molars). To assess enamel thickness in these specimens, data describing first maxillary molar enamel thickness in other taxa were taken from the literature on modern humans (Smith et al. 2006a), Neandertals (Olejniczak et al. 2008a), australopiths (Olejniczak et al. 2008b), and chimpanzees (Smith et al. 2005).

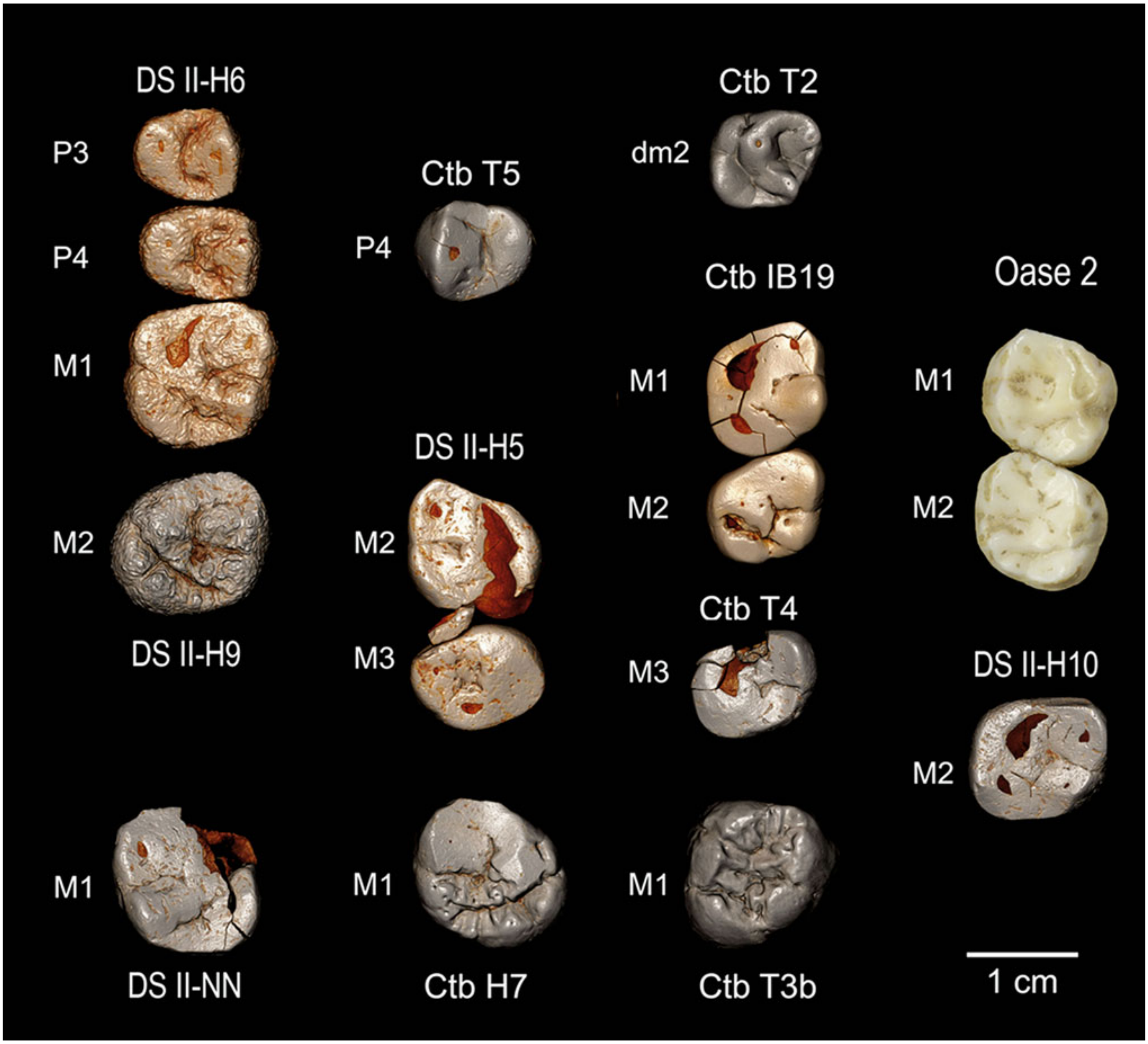

Fig. 13.1 Upper teeth from the Aterian layers of Dar es-Soltan II (DeS II) and Grotte des Contrebandiers (Ctb). Note that "Temara IB19" is not part of the Aterian sample

Methods

To assess the variations in size of the teeth, maximum mesiodistal and bucco-lingual crown diameters (M81 and M81(1)) (Braüer, 1988) were measured with calipers. In the case of the Dar es-Soltan "mandible H4" (Dar es-Soltan II-4), these measures were obtained from 3D reconstructions using Amira software 4.1.2. A bivariate assessment of these metrics was made by plotting the crown diameters for each tooth for the different groups; ellipses, including 95% of the population variation, were computed using Statistica 7.0 software for each reference population.

The non-metric analysis is based on 15 traits (4 in the upper dentition and 11 in the lower dentition) that are preserved on the Aterian specimens (see Table 13.4). Many are included in the Arizona State University Dental Anthropology System (ASUDAS) and have been chosen because they are easy to score and can be scored even in worn teeth (Turner et al. 1991). Additional traits found by Bailey (2002, 2006b) to show meaningful differences among fossil hominin groups and which are particularly important to the study of Middle-Late Pleistocene hominins have been added (maxillary premolar accessory ridges or MxPAR: Burnett 1998; lower P4 asymmetry, lower P4

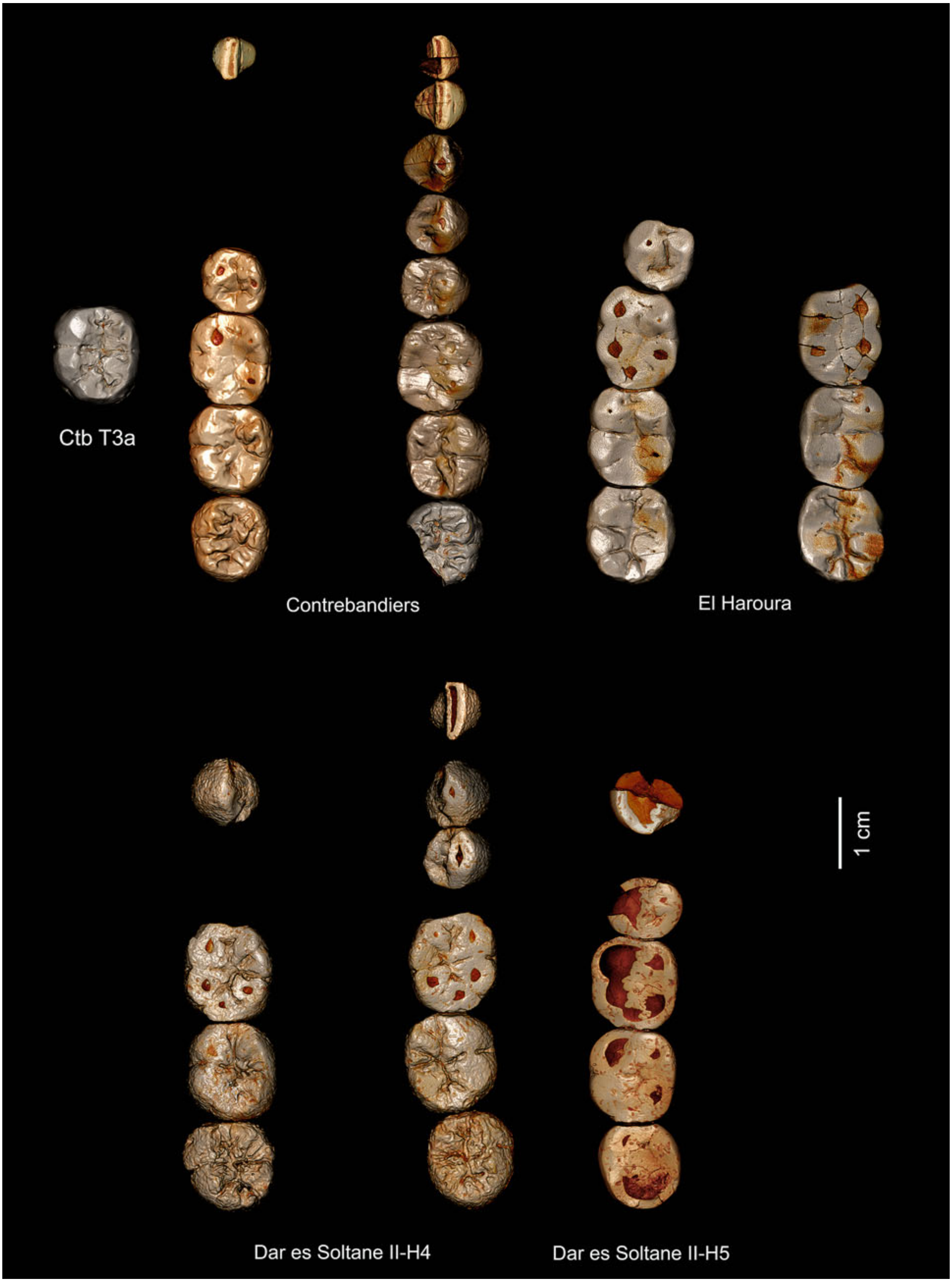

Fig. 13.2 Lower teeth from the Aterian layers of Dar es-Soltan II, Grotte des Contrebandiers (Ctb), and El Harhoura. Note that the specimen T1 (M3) is positioned behind the lower right M2 of the Temara mandible since it likely belongs with it

transverse crest, and the lower molar mid-trigonid crest). These traits are also easy to score and tend to be preserved even on moderately worn teeth.

In order to analyze enamel thickness, the molars were microCT scanned using a BIR Arctis 225/300 high-resolution industrial CT scanner with X-ray energy at 130 kV, 100 μA, and a 0.25 mm brass filter. Isometric voxel dimensions were kept below 30 microns. Mesial planes of section were produced from the microCT scans using VoxBlast software (Vaytek, Inc.), following techniques described by Olejniczak (2006). We therefore produced virtual planes of section through the mesial cusps to perform traditional, two-dimensional enamel thickness measurements, consistent with those of previous studies (e.g., Martin 1985; Smith et al. 2005). Measurements of mesial sections that were recorded on printed images using a digitizing tablet are defined following Martin (1985) and appear in Fig. 13.3: the area of the enamel cap (mm^2), the coronal dentine area (mm^2), and the length of the enamel-dentine junction (mm). Average enamel thickness (mm), the average straight-line distance between the enamel-dentine junction and the outer enamel surface, is calculated as enamel area divided by enamel-dentine junction length. Relative enamel thickness, a scale-free measurement facilitating inter-specific comparisons when tooth sizes differ among taxa, is calculated as average enamel thickness divided by the square root of the coronal dentine area.

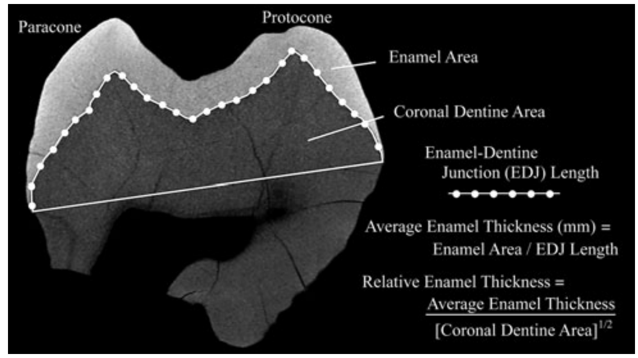

Fig. 13.3 MicroCT-based virtual mesial cusp cross-section of the Aterian maxillary first molar T3b, demonstrating the enamel thickness measurements and calculations performed in this study

Results

Metrical Analysis

We analyzed 51 teeth from the site of Dar es-Soltan II, Grotte des Contrebandiers, and El Haroura. Of these 51 teeth, 10 are isolated and 41 are attached to 4 mandibles or 3 fragmentary maxilla.

Upper Teeth

The UP3 from "Dar es-Soltan H6" (Dar es-Soltan II-6) is mesio-distally wide, falling outside the range of the IBM and close to the limit of the NEAN and UPMH range (see Figs. 13.1, 13.4; Table 13.2). Its bucco-lingual diameter, however, falls well within the overlap area of the comparative samples.

The two UP4s from Dar es-Soltan II and the Grotte des Contrebandiers are robust. They plot well outside the range of variation of IBM and UPMH but also rather far from the MPMH. Dar es-Soltan II-6 falls close to some specimens from Krapina, and is included in the 95% ellipse of the NEAN. The UP4 Grotte des Contrebandiers T5 has even higher diameters and falls outside the NEAN range.

All the UM1s fall well outside the range of variation of NEAN, UPMH, and IBM. It should be noted that this does not apply to the Grotte des Contrebandiers IB19 specimen, confirming its IBM assignment by Ménard (1998). The latter has lower diameters and falls well within the range of the reference groups.

Although large, UM2 and UM3 from Dar es-Soltan II and Grotte des Contrebandiers 1 are relatively less robust than UM1. When compared to our reference samples, two of them fall within the ranges of variation of NEAN, MPMH, UPMH, and IBM but above the means. Dar es-Soltan II H9 UM2 is very robust, with a BL higher than any other individual included in our analysis. It plots at the upper limit of the NEAN range, and is interestingly close to the UM2 from Peştera cu Oase 2. The UM2 of Grotte des Contrebandiers IB19 is much more gracile, which supports its assignment to the IBM group.

There is little separation between our comparative samples for the Udm2, and the single deciduous tooth, Grotte des Contrebandiers T2, falls well within their range of variation.

Lower Teeth

The two lower incisors from the Grotte des Contrebandiers mandible are not particularly large, and fall within the range of IBM and UPMH, with rather low bucco-lingual diameters compared to Neandertals (see Figs. 13.2, 13.5, 13.6; Table 13.3). The lower I2 from Dar es-Soltan, however, falls outside the range of all the reference groups due to its very large MD.

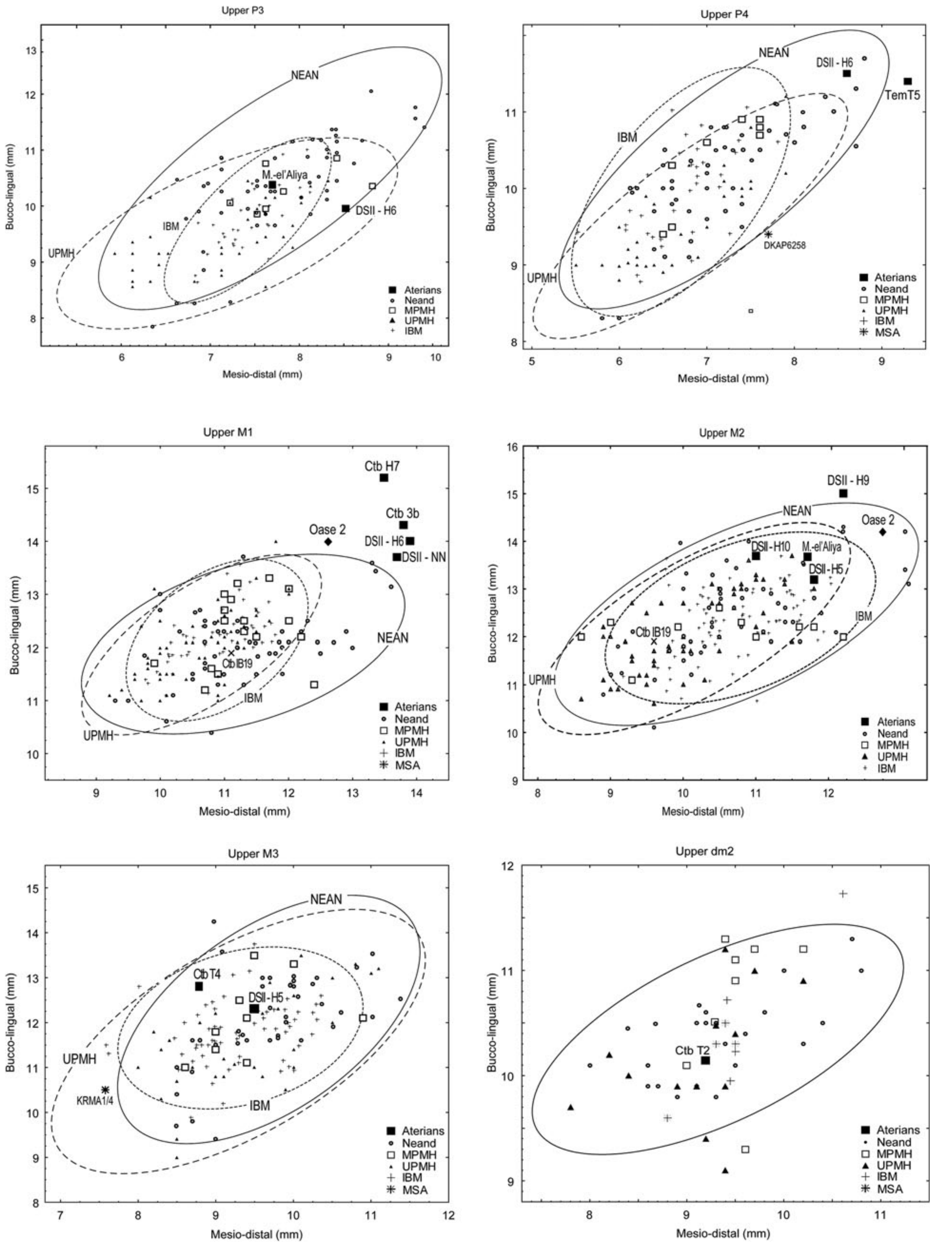

Fig. 13.4 Bivariate plots of the crown diameters of the upper teeth The graph includes equiprobable ellipses (95%) of Neandertals (Neand), Upper Paleolithic modern humans (UPMH) and Iberomaurusians (IBM), as well as individual dots for Middle Paleolithic modern humans (MPMH) and South-African Middle Stone Age modern humans (MSA)

Table 13.2 Crown diameters of the upper teeth

Site	N°	Side	Udm2		UP3		UP4		UM1		UM2		UM3	
			MD	BL	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL
Contrebandiers	T2	L	8.6	10										
Contrebandiers	T3b	L							14	14				
Contrebandiers	T4	L											8.8	13
Contrebandiers	T5	R					9.3	11						
Contrebandiers	T7	R							14	15				
Contrebandiers	IB19	L							11	12	9.6	12		
Dar es-Soltan II	H5	R									12	13	9.5	12
Dar es-Soltan II	H6	L			8.4	10	8.6	12	14	14				
Dar es-Soltan II	H9	L									12	15		
Dar es-Soltan II	H10	L									11	14		
Dar es-Soltan II	NN	R							14	14				

The lower canines from Dar es-Soltan are large, with high bucco-lingual diameters falling among the highest values of our comparative samples. Their mesio-distal diameters are even higher and exceed the values of all the individuals included in our analysis. The LC from the Grotte des Contrebandiers mandible is slightly smaller, and falls at the limit of the IBM range and within the range of the NEAN and UPMH. Large canines are also found on the MPMH Qafzeh 9.

Due to their large mesio-distal diameters, the two lower P3s from Dar es-Soltan and Grotte des Contrebandiers fall outside the UPMH and IBM ranges and at the higher limit of the NEAN range. They also plot close to Qafzeh 9. Only three specimens from Krapina show higher mesio-distal diameters.

The lower P4s are very large, falling outside the range of all the comparative samples (Dar es-Soltan H5, El Haroura) or close to their upper limit (Grotte des Contrebandiers mandible).

The lower molars are also very robust, falling either outside or at the limit of the 95% confidence limits of the reference groups. Interestingly, the LM1s stand out the most, followed by the LM2 and the LM3, which are more variable and relatively less robust compared to our reference samples. Once again, the mandible from Grotte des Contrebandiers shows smaller teeth than the Dar es-Soltan and El Haroura specimens. We also found that the LM2 and LM3 from Dar es-Soltan and El Haroura are close to those of the Peştera cu Oase 1 specimen, whereas Nazlet Khater is more gracile and plots closer to the Grotte des Contrebandiers 1 mandible.

None of the specimens preserve the entire dentition but the two mandibles from Grotte des Contrebandiers and Dar es-Soltan H4 allow us to assess dental proportions. We plotted the ratios of the summed I2 to P3 versus P4 to M2 BL diameters (Fig. 13.7a). The results show the known contrast between Neandertals and modern humans for the relative anterior dental size. The mandible from Grotte des Contrebandiers plots within the range of the IBM, UPMH, and MPMH but outside the Neandertal range (Fig. 13.7a), which shows higher relative anterior dentition size. Interestingly, the ratio of the Grotte des Contrebandiers mandible dentition falls among the highest values of the IBM but among the lowest values of the MPMH and UPMH. We also plotted the ratio [I2-C]/[M1-M2] (Fig. 13.7b) which shows a similar trend across our comparative samples. Again, the two North African specimens plot far from the Neandertals for this ratio, and well within the IBM range. The Grotte des Contrebandiers mandible ratio falls within the distribution of the MPMH and at the lowest limit of the UPMH one. The Dar es-Soltan H4 ratio is lower and outside the range of the UPMH and just at the lower limit of the MPMH.

Non Metrical Traits

In Table 13.4, we present the trait frequencies observed in the Aterians and comparative groups. It is important to point out that the Aterian sample is quite small, ranging from two to five individuals for any given trait.

The single upper P4 shows well-developed accessory ridges, a trait that is frequently observed in Neandertals and other archaic humans (Bailey 2006b). Both permanent upper M1s that preserve the lingual surface show the cusp form of Carabelli's trait (ASUDAS grades 6 and 5). A moderately- to well-developed Carabelli's trait is relatively common in the other fossil hominin permanent M1s, particularly those in the Neandertal group. The upper dm2 (Grotte des Contrebandiers T2) also possesses a Carabelli's

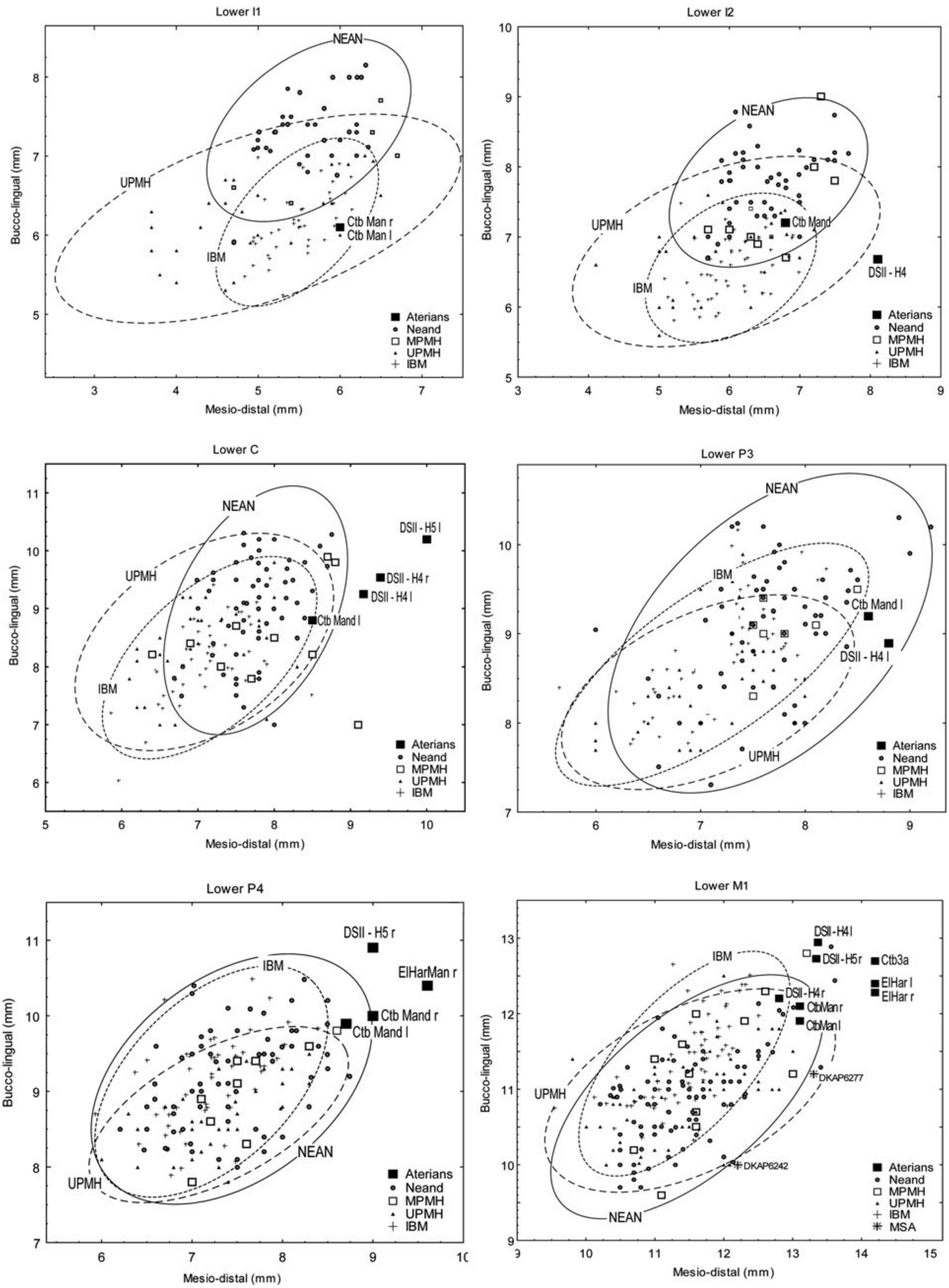

Fig. 13.5 Bivariate plots of the crown diameters of the lower teeth (I1 to M1)

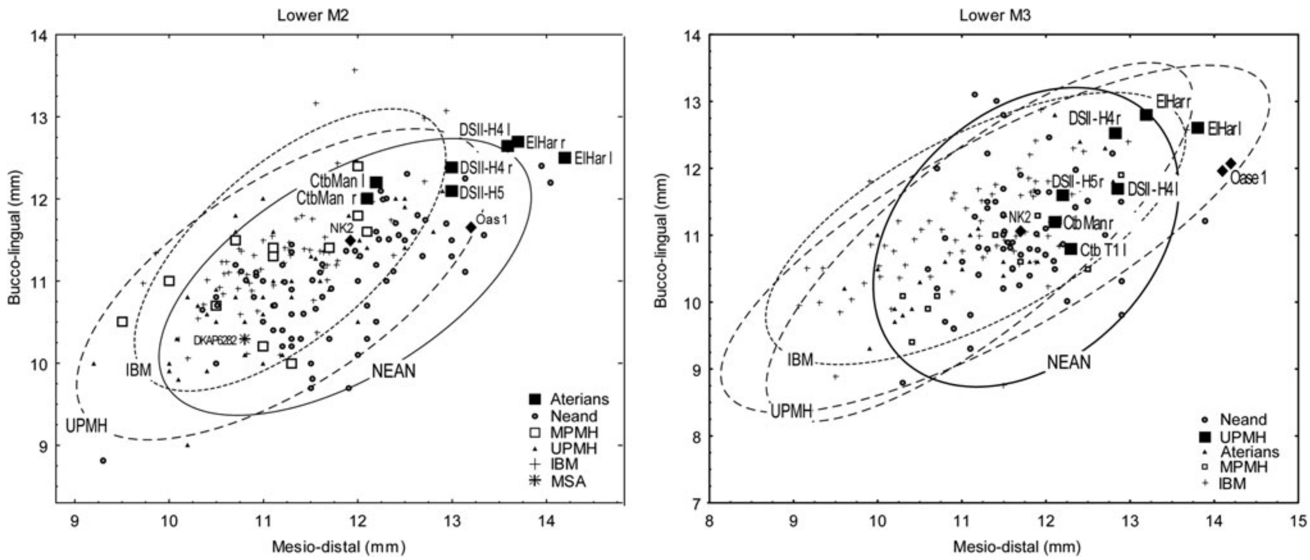

Fig. 13.6 Bivariate plots of the crown diameters of the lower M2 and M3

cusp (ASUDAS grade 6). In this case, it displaces the protocone in a buccal direction and is continuous with the hypocone. Our comparative morphological sample for deciduous dm2s is small but both fossil hominins (*Homo sapiens* from Die Kelders and Neandertal from Subalyuk) show moderately sized Carabelli's cusps, although slightly smaller than that seen in the Grotte des Contrebandiers tooth. Two of the three M1s also show an accessory distal cusp (Cusp 5 or hypoconule), which is also relatively common in other fossil hominins in our sample, particularly the early Upper Paleolithic and Neandertal groups. Neither of the M2 possesses a reduced hypocone. This is the condition found in most fossil hominins, although the early Upper Paleolithic group shows higher frequencies than the other groups for this trait. In addition, two new variants are observed on the upper molars. The first variant is found in one UM1 from Grotte des Contrebandiers (3b), which possesses a large accessory cusp between the protocone and the paracone. This may be an exceptionally large protoconule or perhaps an entocone, although the latter is usually expressed as a ridge not a cusp. The second variant is seen in two of UM (H7 from Grotte des Contrebandiers and H9 from Dar es-Soltan). Both of these teeth express exceptionally large hypocones that appear to be divided into two or more cusps (Fig. 13.1). This trait is not scored by the ASUDAS and it was not one of the traits studied in Bailey (2002) so comparative data are unavailable.

In the lower dentition, the single P4 that can be scored for the trait possesses multiple lingual cusps. However, neither P4 possesses a transverse crest or marked asymmetry. This is similar to the condition found in nearly all fossil *Homo sapiens* samples, which is strikingly different from the Neandertal condition, where all three traits occur in high frequency and are often expressed on the same tooth (Bailey 2002). One of the M1s (Dar es-Soltan H4) possesses a Cusp 7 and one individual (El Harhoura) possesses a mid-trigonid crest, while Cusp 6 and the deflecting wrinkle are both absent. On the M2, the Y-groove pattern is present on four of the five teeth and one tooth exhibits an asymmetrical expression (Y pattern on the left and X on the right). The Y-groove pattern is the primitive pattern and the most frequently observed condition in the comparative groups with the exception of the early Upper Paleolithic group, in which 50% of the teeth possess either an X or + pattern. One of the five M2s possesses four, instead of five, cusps. This is similar to the frequency found in the comparative groups, except for the Neandertals, who lack this feature. As is the case with the other *Homo sapiens* in our comparative sample, none of the Aterian M2s and M3s possess a mid-trigonid crest. This feature appears to be present on these teeth only in the Neandertal sample.

Enamel Thickness

The results of enamel thickness measurements in the Aterian maxillary first molars and the comparative sample are presented in Fig. 13.8 and Table 13.5. In terms of relative (size-scaled) enamel thickness, the Aterian molars fall within the range of recent *Homo sapiens* individuals, and do not overlap with the thinner Neandertal molars. Likewise, average enamel thickness (expressed in mm units) shows that the Aterian molars have thicker enamel than the Neandertal sample; specimen H7 falls within the range of recent *Homo sapiens*, and specimen T3b is above the range of recent *Homo sapiens*. Compared to other hominins (all of

Table 13.3 Crown diameters of the lower teeth

Site	N°	Side	LI1		LI2		LC		LP3		LP4		LM1		LM2		LM3	
			MD	BL	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL
Contrebandiers	Mand.	L	6.0	6.1							9.0	10.0	13.1	12.1	12.2	12.2	12.1	11.2
		R	6.0	6.1	6.8	7.2	8.5	8.8	8.6	9.2	8.7	9.9	13.1	11.9	12.1	12.0		
Contrebandiers	T1	L															12.3	10.8
Dar es-Soltan II	Mand. H5	L					10.0	10.2			9.0	10.9	12.8	12.2	13.0	12.1	12.2	11.6
Dar es-Soltan II	Mand. H4	R			8.3	6.8	9.3	9.3	8.8	8.9			13.4	12.9	13.6	12.6	12.9	11.7
		L					9.5	9.5					13.4	12.7	13.0	12.4	12.8	12.5
Contrebandiers	T3a	R											14.2	12.7				
El Haroura	Mand.	L									9.6	10.4	14.2	12.3	13.7	12.7	13.2	12.8
		R											14.2	12.4	14.2	12.5	13.8	12.6

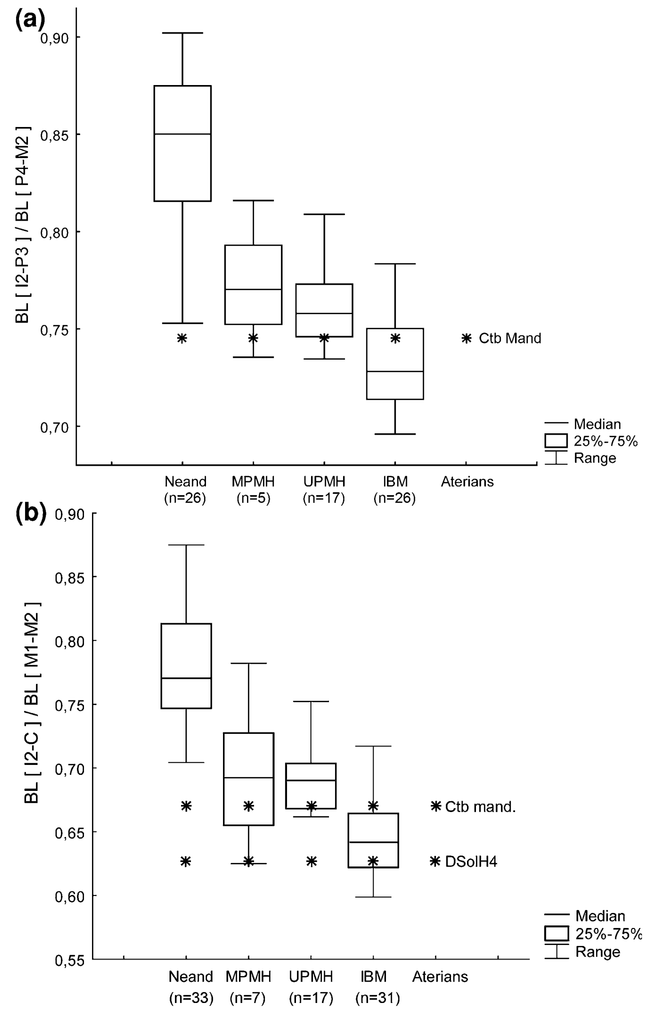

Fig. 13.7 Box plots showing the ratio of the summed bucco-lingual breadths for our comparative samples. On the left is the ratio of the summed I2 P3 versus P4 M2 bucco-lingual breadths for our comparative samples and the values of the Aterian mandible from Grotte des Contrebandiers. On the right is the ratio of I2 C versus M1 M2 bucco-lingual breadths between our samples and those from both Dar es-Soltan H4 and Grotte des Contrebandiers

which have absolutely and relatively thicker enamel than the *Pan troglodytes* comparative sample), the Aterian molars demonstrate similar relative and absolute enamel thickness values to those of recent *Homo sapiens*, are thinner-enameled than those of *Australopithecus africanus* and *Paranthropus robustus*, and are thicker-enameled than Neandertals.

Discussion

Overall, the Aterians show large or very large teeth. In several instances, their dimensions lie outside the ranges of our comparatives samples. Most noticeable in this respect

Table 13.4 Trait frequencies in Aterians and comparative samples. Sample sizes/number with trait presence in parentheses

	Homo sapiens			*H. neanderthalensis*
	Aterian	Qafzeh/ Skhul	Upper Paleolithic modern	
Upper Dentition				
P4 MxPAR + = grades 1–2	100 (1/1)	50.0 (2/1)	0.0 (2/0)	77.8 (18/14)
M1 Carabelli's trait + = grades 3–7	100 (2/2)	40.0 (5/2)	60.0 (10/6)	72.0 (25/18)
M1 C5 + = grades 1–5	66.7 (3/2)	40.0 (5/2)	72.7 (11/8)	63.6 (22/14)
M2 Hypocone reduction + = grades 0–2	0.0 (1/0)	0.0 (6/0)	25.0 (12/3)	2.9 (34/1)
Lower Dentition				
P4 asymmetry + = grade 2	0.0 (2/1)	0.0 (4/0)	0.0 (5/0)	75.0 (32/24)
P4 transverse crest + = grades 1–2	0.0 (2/0)	33.3 (3/1)	0.0 (5/0)	90.6 (32/29)
P4 lingual cusps + = grades 2–9	100 (1/1)	66.7 (3/2)	66.7 (6/4)	93.9 (32/30)
M1 Cusp 6 + = grades 1–5	0.0 (1/0)	0.0 (4/0)	20.0 (15/3)	36.4 (22/8)
M1 Cusp 7 + = grades 2–4	25.0 (4/1)	14.3 (7/1)	5.3 (19/1)	16.7 (36/6)
M1 Mid-trigonid crest + = grades 1–2	25.0 (4/1)	33.3 (3/1)	0.0 (15/0)	93.5 (31/29)
M1 Deflecting wrinkle + = grades 2–3	0.0 (2/0)	50.0 (2/1)	7.7 (13/1)	3.8 (26/1)
M2 Groove pattern + = Y	80.0 (5/4)	100 (3/3)	50.0 (14/7)	75.0 (33/27)
M2 Cusp No. + = 4 cusps	20.0 (5/1)	16.7 (6/1)	36.4 (11/4)	0.0 (40/0)
M2 Mid-trigonid crest + = grades 1–2	0.0 (2/0)	0.0 (2/0)	0.0 (15/0)	96.3 (27/26)
M3 Mid-trigonid crest + = grades 1–2	0.0 (3/0)	0.0 (2/0)	0.0 (10/0)	93.3 (93.8)

Table 13.5 Mean 2D average and relative enamel thickness in hominoid upper first molars (mesial sections)

Taxon	N	Mean AET	Range	Mean RET	Range
Pan troglodytes	6	0.66	0.61–0.73	10.3	8.5–12.2
Homo neanderthalensis	5	1.04	0.97–1.19	15.4	14.8–16.9
Modern *Homo sapiens*	37	1.22	0.98–1.50	18.8	14.0–23.9
Aterian *H. sapiens* (Ctb H7 & T3b)	**2**	**1.42**	**1.25–1.58**	**19.6**	**18.3–20.9**

are the UP4 and UM1 and the LC, LP4, and LM2. The LC, UP3, LP3, and LM1 are close in size to some MPMH specimens. In our modern human comparative samples, the only specimen close to the Aterian values is Peştera cu Oase 2. In particular, the size of the very large UM1s and LM3 from El Harhoura are reminiscent of the Peştera cu Oase 1 and 2 values. Within the Neandertal sample, one finds similarly large post-canine dentition only in some very robust MIS 5 Neandertals from Krapina. However, the most complete Aterian specimens (the mandibles Grotte des Contrebandiers and Dar es-Soltan H4) display a pattern of dental proportions clearly different from that of the Neandertals and closer to that of the modern series (which show reduced anterior dentitions relative to the post-canine dentitions). This is confirmed by the lack of bucco-lingual expansion of the anterior dentition that is observed in the Neandertals.

Morphologically, the Aterian teeth possess mass-additive traits including extra crests, distal cuspules, Carabelli's cusp, as well as large, often divided, hypocones on the upper teeth. Mass-additive traits are found in other fossil hominin groups as well, and contribute to the overall primitive morphology of the Aterians. They do not, however, possess in any appreciable frequencies the traits or trait combinations that are diagnostic of Neandertals. For example, the lower fourth premolars are symmetrical and lack a transverse crest. Likewise, with a single exception, the lower molars lack the mid-trigonid crest that is consistently present in Neandertals. More importantly, the M2s and M3s all lack this feature, which occurs nearly ubiquitously in Neandertals. Instead, the dental pattern observed in the Aterians is closer to that of the early *Homo sapiens* from Qafzeh/Skhul and to early Upper Paleolithic modern humans. In particular, the specimens from Peştera cu Oase

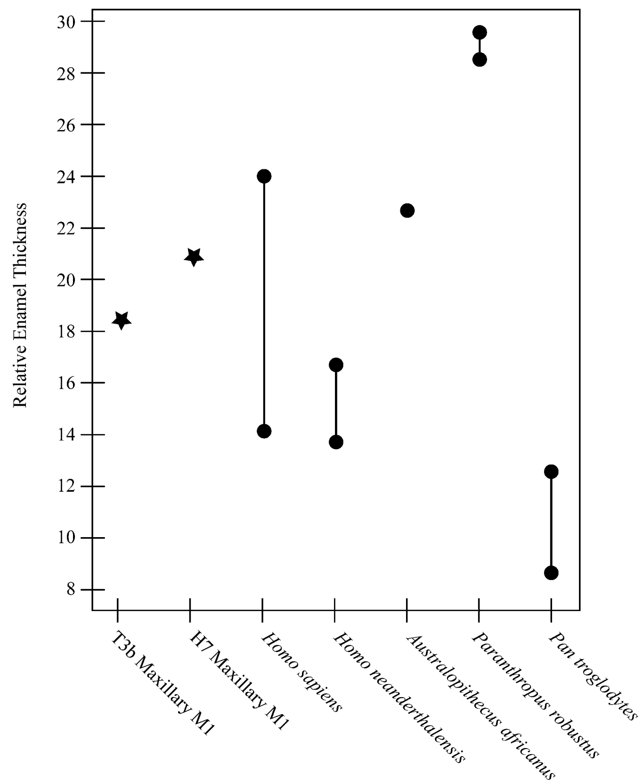

Fig. 13.8 Ranges of relative enamel thickness in mesial sections of hominin maxillary first molars. The Aterian molars measured here (*stars*) fall within the range of values reported for recent human molars (Smith et al. 2006a, b) and are above the range of values reported for Neandertals (Olejniczak et al. 2008a)

are morphologically similar in several ways. Like the permanent Aterian upper M1s, the upper M1s of Peştera cu Oase 2 possess the large cusp form of Carabelli's trait. In addition, the Peştera cu Oase 2 left UM1 exhibits several distal cusps somewhat contiguous with the hypocone that, while not identical, are similar to the divided hypocones of the Grotte des Contrebandiers UM1 and Dar es-Soltan UM2.

Molar enamel thickness has a long history of study among scholars of hominoid evolution (e.g., Martin 1985; Kono 2004; Smith et al. 2005), and recent studies have demonstrated that hominin taxa exhibit important differences in enamel thickness as well. Specifically, Neandertals have thinner molar enamel than both modern humans (Olejniczak et al. 2008a) and Plio-Pleistocene hominins (Olejniczak et al. 2008b; Smith et al. 2009). A sample of South African Middle Stone Age human molars was previously found to be similar to modern humans in terms of enamel thickness (Smith et al., 2006b) and the authors of that study concluded that enamel thickness in *Homo sapiens* "has remained stable for at least 60,000 years" (p. 516). None of the molars in that study were from the maxillary dentition, and thus were not directly comparable to the data presented here, but the present study can be taken as additional evidence that enamel thickness has remained relatively constant within *Homo sapiens*, and that enamel thickness in fossil *Homo sapiens* is similar across a wide geography: northern and southern African Middle Paleolithic specimens demonstrate similar enamel thicknesses, which is comparable to recent humans. In light of limited data describing fossil *Homo sapiens,* the relatively thin enamel of Neandertals has been cautiously interpreted as a derived condition relative to other hominins (Olejniczak et al. 2008a). This relatively thin enamel stems from a difference in tooth conformation between *Homo sapiens* and Neandertals, wherein Neandertal molars are characterized by a larger volume of coronal dentine underlying a similar volume of enamel, resulting in absolutely thinner enamel. It is unclear whether there is an adaptive significance to this unique molar tissue conformation, and perhaps it is a trait that has been fixed by neutral evolution (e.g., Weaver et al. 2008). Nonetheless, differences between Neandertals and contemporaneous *Homo sapiens* such as the Aterian molars measured here are of taxonomic utility in the assessment of isolated dental remains. These differences in dental conformation also underscore the importance of sampling earlier *Homo* taxa and populations (e.g., African *Homo erectus*) to assess the evolutionary polarity of this character.

Conclusion

The human remains associated with Aterian assemblages provide us with a sample of the populations living in the region of the extant Sahara and Magreb where this assemblage is represented, between the Atlantic coast of Morocco, the Mediterranean, and the Nile Valley roughly between 90 and 35 ka. Although today this area is largely unpopulated, this was not always the case. The Sahara, like the Kalahari further south, witnessed episodes of expansion and retraction that directly impacted the landscapes, fauna, and human populations. Isotopic composition of the Sahara-derived dust in marine sediments demonstrates the occurrence of wet periods during which C3 plants (likely trees) developed in the Central Sahara. These wet episodes occurred during the Late Pleistocene and the Holocene, more precisely during MIS 5 (ca. 120–110 ka), MIS 3 (ca. 50–45 ka), as well as during the early Holocene (Castañeda et al. 2009). In contrast, arid episodes are documented during MIS 6 (ca. 170–135 ka) and MIS 4 (ca. 65–55 ka). During the wetter periods, Saharan megalakes developed and considerably extended (Armitage et al. 2007) and river channels extended across what is today a desert to the Mediterranean Coast (Osborne et al. 2008). To what extent these fluctuations could drive groups of early representatives of our species out of Africa and into the Levant and, later, Eurasia is still debated. However, the extant geographical conditions present a biased picture of the situation before and during the last out-of-Africa movement. Much emphasis has been placed on Sub-Saharan populations, who live in areas that are often regarded to be where non-African modern humans originated. In fact, some of the extant sub-Saharan populations might be displaced populations whose hunter-gatherer ancestors lived further north. Circa 50 ka, at a key date for the colonization of the planet by *Homo sapiens*, Africa north of 15° latitude was not empty. It was much greener and more populated than today, mostly occupied by the makers of the Aterian assemblages, whose settlements are found throughout the Sahara and the Magreb.

The dental remains found in the Moroccan Aterian sites provide us with important information on populations that may have played a significant role in the colonization of Eurasia. Our comparative analysis confirms the essentially modern nature of these humans. Until 50 ka, Europe and Africa represented distinct bio-geographical barriers that were peopled by well-separated entities. In terms of metrical as well as non-metrical traits, the dental morphology displayed by the Neandertals can be easily distinguished from that of the Aterians and the UPMH (Bailey et al. 2009). Dental tissue proportions also display a different pattern, with Neandertals characterized by thinner enamel than the Aterians and other modern groups. However, although the Aterian teeth clearly group with modern samples because they lack the traits or trait combinations that are diagnostic of Neandertals, they also display distinctive features. Most spectacular is the size of the Aterian dentitions, especially for the post-canine dentition. Although the comparative sample is very small, this very large size is not observed in the South African MSA teeth, which display much variability. However, to some extent, it is reminiscent of the MPMH of the Near East but also of early *Homo sapiens* in North and East Africa predating the Aterian (Hublin and Tillier 1981; White et al. 2003). Morphologically, this megadontia is expressed in the development of mass-additive traits including extra crests, distal cuspules, Carabelli's cusp, as well as large, often divided, hypocones on the upper teeth. This helps us to set some of the features observed in Neandertals in perspective, highlighting their primitive nature (see discussion in Bailey et al. 2009). The Aterian morphological pattern is also important to consider when interpreting the dental morphology of the first modern humans in Eurasia. Strikingly, a reminiscent pattern is observed on the Peştera cu Oase 1 and 2 specimens, which are the oldest directly dated modern individuals found in Europe to date (Trinkaus et al. 2003; Rougier et al. 2007). These individuals are also missing diagnostic Neandertal features such as the mid-trigonid crest of the lower molars, but display very large post canine dentition with additional cusps such as hypoculids on the lower molars. This observation supports the view that the exceptional dental post-canine robusticity observed on Peştera cu Oase 1 and 2 could be primarily inherited from the immediate African ancestors of the first modern Europeans.

Acknowledgments We are grateful to M. A. El Hajraoui, A. Ben-Ncer, S. Raoui, the "Institut National des Sciences du Patrimoine et de l'Archéologie," and the "Direction du Patrimoine Culturel" (Rabat, Morocco) for allowing and/or facilitating the CT scanning of the fossil material at the "Musée Archéologique de Rabat," and A. Winzer and H. Temming for assistance with scanning, reconstructing computed tomographic data, and illustration.

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