Middle Pleistocene Dental Remains From Qesem Cave (Israel)

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ABSTRACT This study presents a description and comparative analysis of Middle Pleistocene permanent and deciduous teeth from the site of Qesem Cave (Israel). All of the human fossils are assigned to the Acheulo-Yabrudian Cultural Complex (AYCC) of the late Lower Paleolithic. The Middle Pleistocene age of the Qesem teeth (400–200 ka) places them chronologically earlier than the bulk of fossil hominin specimens previously known from southwest Asia. Three permanent mandibular teeth (C_1-P_4) were found in close proximity in the lower part of the stratigraphic sequence. The small metric dimensions of the crowns indicate a considerable degree of dental reduction although the roots are long and robust. In contrast, three isolated permanent maxillary teeth (I^2, C^1, and M^3) and two isolated deciduous teeth that were found within the upper part of the sequence are much larger and show some plesiomorphous traits similar to those of the Skhul/Qafzeh specimens. Although none of the Qesem teeth shows a suite of Neanderthal characters, a few traits may suggest some affinities with members of the Neanderthal evolutionary lineage. However, the balance of the evidence suggests a closer similarity with the Skhul/Qafzeh dental material, although many of these resemblances likely represent plesiomorphous features. Am J Phys Anthropol 000:000–000, 2010. © 2010 Wiley-Liss, Inc.

The current study presents a description and comparative study of new Middle Pleistocene permanent and deciduous dental remains from the site of Qesem Cave in Israel. The frequencies and combinations of individual dental morphological characters have proven to be important tools in defining broad patterns of dental variation within the hominin fossil record (Martinón-Torres et al., 2007). In addition, recent studies are now providing more objective criteria for comparing morphological and metric differences in the dentition of fossil hominins (Stefan and Trinkaus, 1998; Bailey, 2004, 2006; Bailey and Hublin, 2005, 2006; Quam et al., 2009). This set of diagnostic tools can also be used to evaluate taxonomic affinities in individual specimens.

ARCHAEOLOGICAL CONTEXT

Qesem Cave (32° 11′ latitude, 34° 98′ longitude) is situated on the low western slopes of the Judean Hills some 12-km east of Tel Aviv and the Mediterranean shore. It is a karstic, sediment-filled chamber in the Cretaceous/Touronian limestone B'ina Formation showing a variety of subsidence, erosion, fracturing, sediment deposition, and cementation processes during the Middle Pleistocene (Frumkin et al., 2009). The cave's floor area known at present covers about 200 m^2, with additional

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partly visible passages not yet exposed. Within the cave, about 7.5-m column of sediments constitutes two major cycles of deposition. The Lower Sequence (ca. 3-m thick) consists of sediments with clastic content and gravel with a massive stony layer at the top. It was deposited in a closed karstic chamber. The Upper Sequence (ca. 4.5-m thick) consists mostly of cemented sediments with a large ashy component. It was deposited when the cave was more open as indicated by the presence of calcified rootlets (Karkanas et al., 2007). Large fallen boulders between the two sequences indicate major event/s of roof and wall collapse. To date, some 50 m^2 have been excavated in two salvage seasons in 2001 and in a series of planned field seasons from 2004 to 2009.

All archaeological finds at Qesem Cave were assigned to the Acheulo-Yabrudian Cultural Complex (AYCC) of the late Lower Paleolithic, postdating the Acheulean complex of the Lower Paleolithic and predating the Mousterian of the Middle Paleolithic. As defined by Rust (1950), the AYCC includes three major industries—Acheulo-Yabrudian dominated by hand-axes and Quina scrapers; Yabrudian dominated by Quina scrapers; and Pre-Aurignacian/Amudian dominated by blades and shaped blades (Garrod, 1956, 1970; Jelinek, 1982, 1990; Bar-Yosef, 1994; Goren-Inbar, 1995; Copeland, 2000; Ronen and Weinstein-Evron, 2000; Monigal, 2001, 2002). The blade-dominated Amudian industry of the AYCC is consistently present throughout Qesem Cave, while the Quina scraper-dominated Yabrudian industry is less intense and appears, at the moment, in only two small areas of the cave and as distinct stratigraphic units (Barkai et al., 2009).

The faunal assemblage of the site is rich and in a good state of preservation. Fallow deer dominate the assemblages. Other species include auroch (*Bos*), horse (*Equus*), wild pig (*Sus*), tortoise (*Testudo*), and red deer (*Cervus*). Not all body parts are present, indicating that carcasses were first processed away from the site. Cut marks were found on some of the bones and indications of marrow extraction were recognized (Stiner et al., 2009). High frequencies of burning and cut marks on the bones, most likely created by blade cutting tools (Lemorini et al., 2006), were observed (Stiner et al., 2009).

A large series of $^{230}Th/^{234}U$ ages on speleothems suggest that the occupation of the cave began about 420 kyr and ended prior to about 200 kyr (Barkai et al., 2003; Gopher et al., in press). The large number of dates makes it possible to assign different dates to various contexts within the cave and/or set a terminus that facilitates establishing ranges of dates for different parts of the cave and its stratigraphy.

The human teeth were found in both the Lower and Upper Sequence and in at least three different archaeological contexts (Table 1, Fig. 1). Three teeth (C_1, P_3, P_4) were found in the Lower Sequence in an Amudian context. Although no direct dates are available for this portion of the stratigraphic sequence, an in situ speleothem postdating the whole Lower Sequence was dated to about 300 ka. This indicates a date of >300 kya for these three teeth. Of the remaining teeth, one (C^1) was recovered from a Yabrudian context (>300 kya) and four others (I^2, M^3, di_2, dm_2) were recovered from Amudian blade-dominated contexts. The di_2 and the M^3 were found in close proximity to each other. One of the Amudian teeth (dm_2) probably dates to >300 kya, while the other Amudian specimens are <300 kya (Table 1).

TABLE 1. Stratigraphic provenience, archaeological context, and chronology of the Qesem teeth

Tooth	Excavation square	Depth (cm)	Stratigraphic provenience	Sediment characteristics	Lithic industry	Chronology
Upper I2	O-8c	170–175	Upper part of upper sequence	Cemented, brown	Amudian	<300 kya
Lower di2	M-13d	360–365	Middle part of upper Sequence	Soft, brown	Amudian	<300 kya
Upper M3	M-13d	360–370	Middle part of upper sequence	Soft, brown	Amudian	<300 kya
Upper C	G-9b	520–525	Upper part of lower sequence	Hard, brown	Yabrudian	>300 kya
Lower dm2	I-12a	560–565	Upper part of lower sequence	Gray	Amudian	Probably >300 ka
Lower C	G-22	685–690	Middle part of lower sequence	Gray with bedded gravels	Amudian with Spheroids	>300 ka, probably 300–400 ka
Lower P3	G-22	705–710	Middle part of lower sequence	Gray with bedded gravels	Amudian with Spheroids	>300 ka, probably 300–400 ka
Lower P4	G-22	685–690	Middle part of lower sequence	Gray with bedded gravels	Amudian with Spheroids	>300 ka, probably 300–400 ka

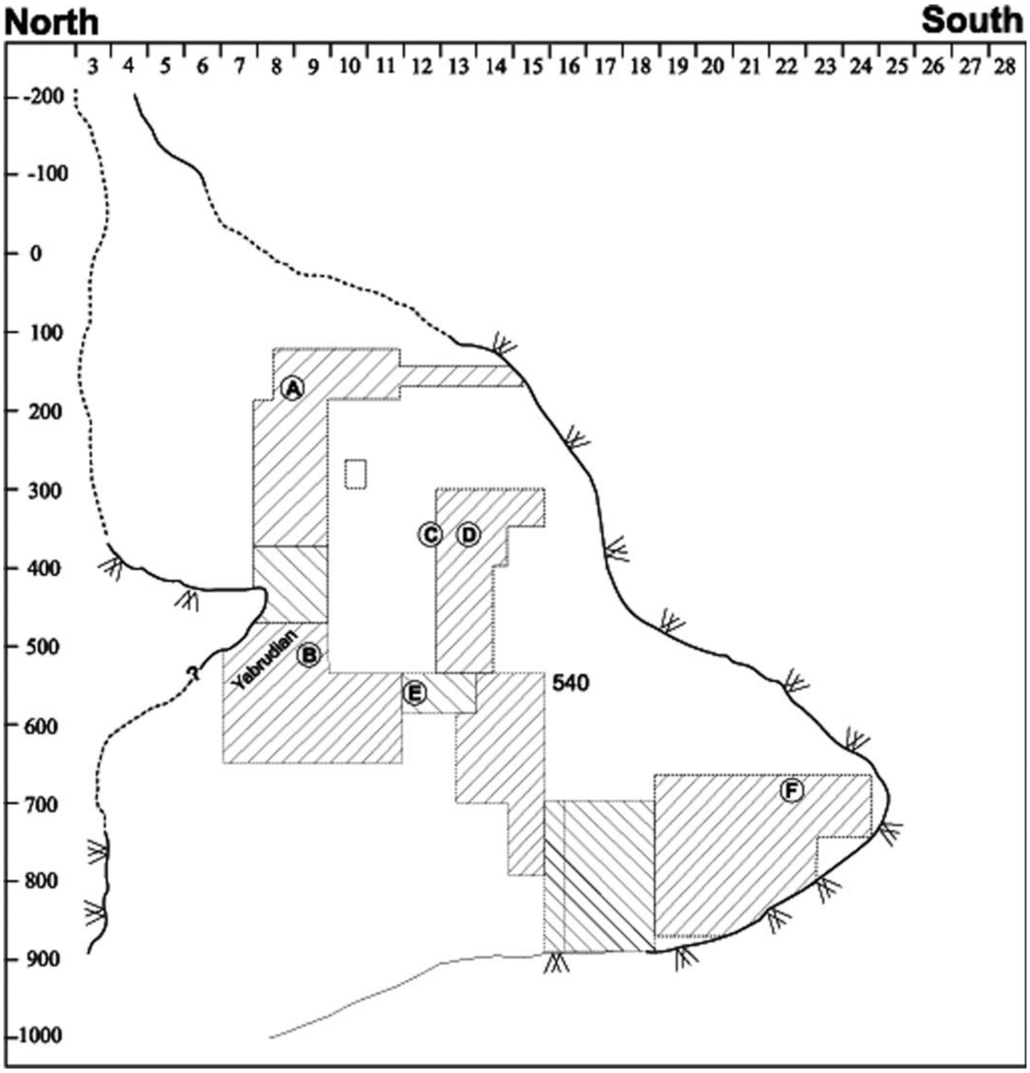

Fig. 1. A combined schematic north-south section of Qesem Cave looking east (note different scales on the *X* and *Y* axes). The location of the individual teeth are indicated as follows: (**A**) I^2, (**B**) C^1, (**C**) di_2, (**D**) M^3, (**E**) dm_2, (**F**) C_1, P_3, P_4.

MATERIALS AND METHODS

This study pertains to eight teeth found in the Qesem Cave excavations: two teeth are deciduous and six are permanent. Descriptions of the morphological features in the Qesem Cave permanent teeth include a few traits defined by Keith (1913), as well as traits included in the Arizona State University Dental Anthropology System (ASUDAS), (Turner et al., 1991; Scott and Turner, 1997). Scoring of individual features in the ASUDAS has been carried out using the standard reference plaques and published descriptions of the scoring criteria. Additional features that have recently been argued to distinguish Neanderthals from *H. sapiens* teeth are also considered (Bailey, 2002b, 2006; Bailey and Lynch, 2005; Gómez-Robles et al., 2008). Morphological features of the deciduous teeth are described qualitatively.

Mesiodistal (MD) and buccolingual (BL) dimensions of the Qesem teeth, both on the crown and at the cervicoenamel junction (CEJ), as well as root length were made with a standard sliding caliper and recorded to the nearest 0.1 mm. Because of the effects of interproximal wear in reducing the MD dimension, the comparisons with other fossil samples are limited to the BL dimension only. The measured crown area (MCA) and occlusal polygon areas were measured on occlusal photographs (Wood and Abbot, 1983; Martinón-Torres et al., 2006; Gómez-Robles et al., 2008). The Qesem teeth were compared with Middle Pleistocene *Homo* specimens from Africa and Europe, as well as European and southwest Asian Neanderthals and the early *H. sapiens* specimens from Skhul and Qafzeh (Table 2). For comparative purposes, we have relied on measurements collected on samples of Late Pleistocene *H. sapiens* populations from Israel (Natufian) as well as on recent European populations (Table 2).

Wear stages of the individual teeth were scored following Molnar (1971) and together with dental development were used for age at death estimates (Table 3). Developmental ages are based on modern human dental calcification schedules (Lunt and Law, 1974; Anderson et al., 1976). Nevertheless, studies of enamel formation and tooth eruption in Pleistocene fossil hominin taxa suggest a possible faster rate of dental formation than in liv-

TABLE 2. Comparative samples used in the present study

Taxon	Sample	Author
Recent humans	Natufian/Neolithic (Levant)	Original specimens
Recent humans	Chalcolithic (Levant)	Original specimens
Recent humans	Modern Near East	Original specimens
Recent humans	Medieval Spanish (San Pablo)	Original specimens
Recent humans	Recent Spanish	Original specimens
Recent humans	Spitalfields	Original specimens
Recent humans	Coimbra	Original specimens
Recent humans	Museu Bocage de Lisboa	Original specimens
Early *H. sapiens*	Qafzeh	Vandermeersch (1981); Tillier (1999) and original specimens
Early *H. sapiens*	Skhul	McCown and Keith (1939)
Early *H. sapiens*	Jebel Irhoud	Hublin and Tillier (1981)
Af. Mid. Pleist.	Ternifine	JMBC[a]
Af. Mid. Pleist.	Rabat	Original specimen
Af. Mid. Pleist.	Thomas Quarry III	Bermúdez de Castro (1986)
Af. Mid. Pleist.	Kabwe (Broken Hill)	Day (1965)
Eur. Mid. Pleist.	Atapuerca (Sima de los Huesos)	Bermúdez de Castro (1986,1993); JMBC*
Eur. Mid. Pleist.	Montmaurin	Bermúdez de Castro (1986)
Eur. Mid. Pleist.	Petralona	Stringer (1979)
Eur. Mid. Pleist.	Arago	de Lumley (1987)
Eur. Mid. Pleist.	Mauer	Bermúdez de Castro (1986)
Eur. Mid. Pleist.	Ehringsdorf	de Lumley (1973)
Eur. Mid. Pleist.	La Chaise (B-D)	Condemi (2001)
H. neanderthalensis	Amud	Suzuki and Takai (1970) and original specimen
H. neanderthalensis	Kebara	Smith and Tillier (1989); Tillier et al. (2003) and original specimens
H. neanderthalensis	Shanidar	Trinkaus (1983)
H. neanderthalensis	Tabun	McCown and Keith (1939) and original specimen
H. neanderthalensis	Teshik-Tash	Gremiatski (1949); Tillier (1979)[a]
H. neanderthalensis	Dederiyeh	Mizoguachi (2002); Kondo and Ishida (2002)
H. neanderthalensis	Barakai	Faerman et al. (1994)
H. neanderthalensis	Arcy-sur-Cure	Leroi-Gourhan (1958); Bailey and Hublin (2006)
H. neanderthalensis	Genay	de Lumley (1987)
H. neanderthalensis	Hortus	JMBC[a]
H. neanderthalensis	Krapina	Wolpoff (1979)
H. neanderthalensis	Gibraltar	Madre-Dupouy (1992)
H. neanderthalensis	Pech de l'Aze	Original specimen
H. neanderthalensis	La Quina	JMBC[a]
H. neanderthalensis	La Ferrassie	Original specimens
H. neanderthalensis	Engis	Madre-Dupouy (1992)
H. neanderthalensis	Le Moustier	Bilsborough and Thompson (2005)
H. neanderthalensis	Monte Circeo	Sergi and Ascenzi (1955)
H. neanderthalensis	Archi	Ascenzi and Segre 1971
H. neanderthalensis	Molare	Mallegni et al. 1989
H. neanderthalensis	Chateauneuf	Tillier, 1979
H. neanderthalensis	Regourdou	Maureille et al. (2001)
H. neanderthalensis	Roc de Marsal	Madre-Dupouy (1992)
H. neanderthalensis	Saccopastore	Condemi (1992)
H. neanderthalensis	Subalyuk	Pap et al. (1996)
H. neanderthalensis	Spy	JMBC[a] and de Lumley (1973)
H. neanderthalensis	Vindija	Wolpoff et al. (1981)
H. neanderthalensis	Valdegoba	Quam et al. (2001)
H. neanderthalensis	Combe Grenal	Garralda and Vandermeersch (2000)
H. neanderthalensis	Monsempron	Vallois (1952)
H. neanderthalensis	Zafarraya	Barroso et al. (2006)

Original specimens measured by the authors.
[a] Data provided by J. M. Bermúdez de Castro.

ing humans (Wolpoff, 1979; Dean et al., 2001; Ramirez-Rozzi and Bermúdez de Castro, 2004). Thus, the ages at death for the Qesem teeth may well be overestimates.

CT imaging of the Qesem teeth was performed to determine internal morphology of the root structure. The Qesem specimens were scanned with an YXLON Compact (Hattingen, Germany) industrial multi-slice computed-tomography (CT) scanner, at the Universidad de Burgos (Spain). The individual specimens were aligned along a longitudinal axis. Scanning parameters included a matrix size of 1024 × 1024 pixels, 160 kV and 4 mA, with dual sampling to achieve a 0.5-mm collimation, inter-slice spacing was 0.2 mm, field of view 3.7 cm. For the two complete teeth, 127 slices were obtained for the P_4 and 133 were obtained for the C_1. Data was archived on compact disk in FLT type raw data 32 bits with a final pixel size of 0.036 mm and transferred to the computer for processing using the commercially available software package Mimics 10.0 (Materialise, Belgium) to visualize the teeth.

TABLE 3. Main metric dimensions for the Qesem teeth

Tooth	Side	MD (mm)	BL (mm)	CI	CCA (mm^2)	MCA (mm^2)	CEJ MD (mm)	CEJ BL (mm)	Root Length (mm)
Lower di2	L	5.0	4.8	96.0	24.0	–	4.2	4.6	10.4
Lower dm2	L	11.3	9.5	84.1	107.4	88.1	8.8	9.0	10.5
Upper I2	L	7.4	7.6	102.7	56.2	–	6.7	4.4	–
Upper C	R	8.8	9.8	111.4	86.2	65.5	7.3	9.8	–
Upper M3	L	9.7	11.1	114.4	107.7	88.0	–	–	–
Lower C	L	7.2	8.3	115.3	59.8	41.4	6.0	8.1	18.6
Lower P3	L	7.3	7.6	104.1	55.5	42.3	5.7	7.1	–
Lower P4	L	6.6	8.1	122.7	53.5	42.4	5.8	7.2	19.7

Crown index (CI) = (BL × 100)/MD.
Computed crown area (CCA) = MD × BL.
Measured crown area (MCA) following Wood and Abbott (1983).

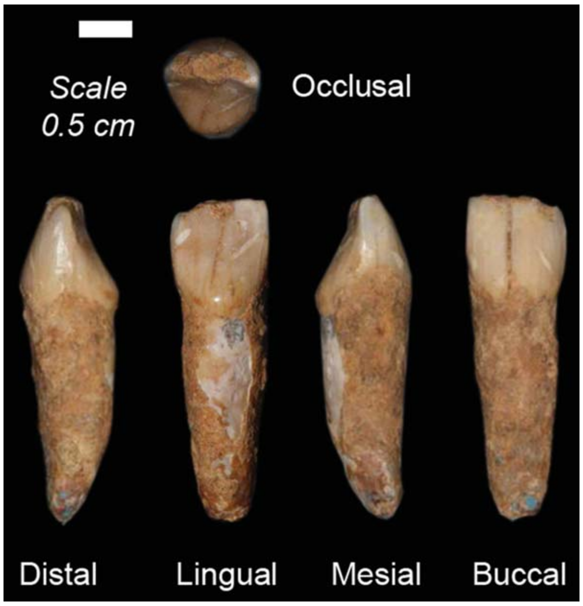

Fig. 2. The Qesem lower left lateral deciduous incisor. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

Minimum number of individuals (MNI) and age at death

Six of the specimens represent permanent teeth and two represent deciduous teeth (Table 1). All three permanent mandibular teeth from square G-22 (left C_1, P_3, and P_4) can be reliably associated, since their age at death estimates are compatible, they articulate well with each other (their interproximal facets match), and they were found in close proximity. Although the di_2 and the M^3 were both found in square M13d, one belongs to a child and one to an adolescent. The remaining teeth were recovered from different stratigraphic levels, and it is not possible to associate any of them with either the individual from G-22 or with each other. Thus, based on ages-at-death and stratigraphic criteria, there appear to be six individuals represented.

In the three teeth from G-22, the root apex is closed (Ac stage of calcification) indicating full development (Table 3), and a minimum age at death of 11.4–14.8 years based on modern human standards (Anderson et al., 1976). Attrition into dentine (Molnar Stage 3) was visible on the canine and P_3, but only enamel facets were present on the P_4, similar to that seen in Individual 23 from the Sima de los Huesos (SH) at Atapuerca and the Krapina specimens 54 and 55, all of which have been aged at 14–16 years at death (Radovcic et al., 1988; Bermúdez de Castro et al., 2004) based on modern human standards for dental development.

Among the isolated permanent teeth, the M^3 falls between the $Cr_{3/4}$-Crc calcification stage, suggesting an age at death of <12.7–13.3 years based on modern human standards (Table 3). The roots of the I^2 and C^1 are broken, but in both teeth the broken end of the root shows that the root canal is narrow; indicating that root formation was advanced if not complete. An Ac calcification stage provides minimum ages at death from 9.7 to 11.1 years and 11.9 to 13.7 years, respectively. The stage of attrition corresponds to that seen on Qafzeh 9, in whom the third molars have erupted, indicating a minimum age of 14–20 years. Both of the deciduous teeth show fully closed root apices, indicating that they were fully formed at the time of death, with no evidence of root resorption. Based on modern human deciduous dental calcification standards (Lunt and Law, 1974), minimum ages at death of 2.0 years for the di_2 and 3.0 years for the dm_2 are suggested (Table 3). The fact that an interproximal facet is present on the mesial but not the distal surface of dm_2 (implying that the first permanent molar had not yet erupted), places an upper limit to its age. The children to whom these teeth belonged must have died around this age, since both teeth show only minor attrition facets.

DESCRIPTION AND COMPARATIVE ANALYSIS

Deciduous dentition

Lower left lateral deciduous incisor. This tooth is complete and was fully formed at the time of death (see Fig. 2). Slight occlusal attrition has just exposed the dentine, and a small inciso-lingual wear facet is present. The crown also shows slight damage along the occlusal margin that appears to be postmortem. The occlusal margin and tooth root are covered by a sedimentary concretion, and the buccal crown face shows a vertical crack from the cervix to the occlusal margin. The specimen shows a slightly larger mesial than distal interproximal wear facet into enamel, but the MD dimension is unaffected.

The lingual surface is smooth, with no marginal ridges, and the tooth is not shovel-shaped. A slight lingual swelling is present at its base, rising toward the occlusal margin, but no lingual tubercle is present. In buccal view, the mesial surface is fairly straight while

TABLE 4. Dental dimensions of the Qesem deciduous teeth compared with Pleistocene and recent humans

Specimen/sample	di_2 MD (mm) Mean ± s.d. (*n*) Range	di_2 BL (mm) Mean ± s.d. (*n*) Range	dm_2 MD (mm) Mean ± s.d. (*n*) Range	dm_2 BL (mm) Mean ± s.d. (*n*) Range
Qesem	5.0	4.8	11.3	9.5
Euro. Mid. Pleist.	–	–	10.3 ± 0.5 (3) (9.8–10.7)	9.4 ± 0.1 (3) (9.3–9.5)
H. neanderthalensis	5.5 ± 0.4 (13) (4.8-6.2)	4.9 ± 0.3 (13) (4.4–5.3)	10.6 ± 0.6 (34) (9.2–11.5)	9.4 ± 0.5 (34) (8.0–10.1)
Early *H. sapiens*	5.0 ± 0.4 (4) (4.5–5.5)	4.9 ± 0.1 (4) (4.7–5.0)	11.1 ± 0.4 (8) (10.1–11.4)	9.8 ± 0.6 (8) (9.0–10.7)
Recent Humans-Europe	4.5 ± 0.4 (48) (3.4–5.5)	4.1 ± 0.4 (48) (3.0–4.8)	9.7 ± 0.5 (57) (8.6–11.3)	8.3 ± 0.6 (57) (7.1–9.5)

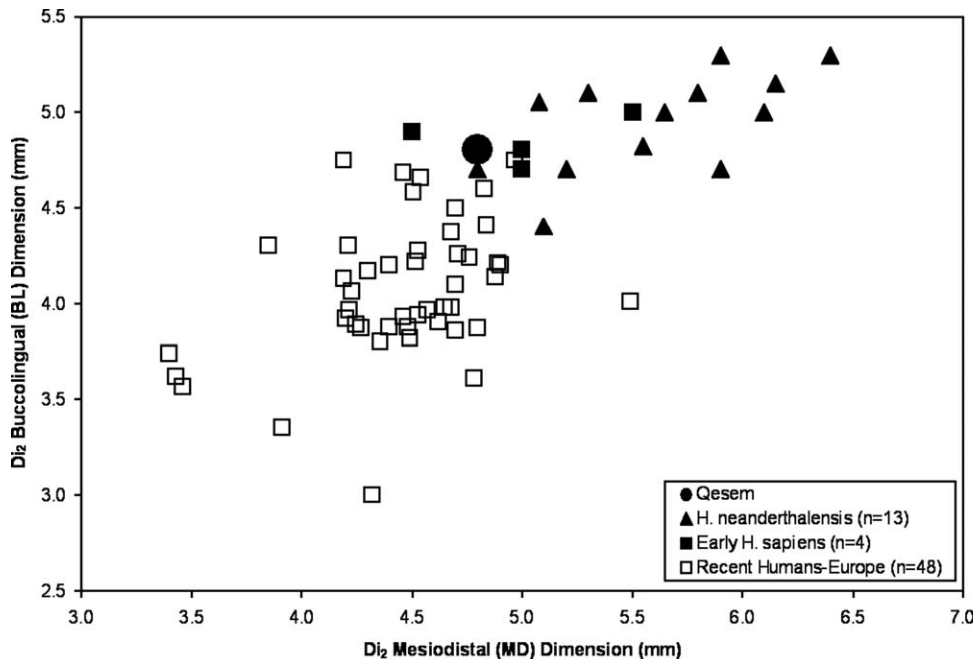

Fig. 3. MD and BL dimensions in the Qesem di_2 compared with Pleistocene and recent humans.

the distal margin is slightly convex. Although the occlusal margin slopes slightly from mesial to distal, the tooth lacks the reduced distal lobe characteristic of the Neanderthals (Smith and Arensburg, 1977; Quam et al., 2001; Bailey and Hublin, 2006) and resembles more closely the specimens from Qafzeh.

The BL dimension in Qesem is similar to the mean values found among early modern humans and Neanderthals (Table 4). When both BL and MD dimensions are considered, the Qesem tooth falls (together with the Qafzeh/Skhul teeth) within an overlap zone between recent *H. sapiens* and Neanderthals (see Fig. 3).

Lower left second deciduous molar. This specimen is largely complete, although the tips of the divergent roots show some damage (see Fig. 4). A sedimentary concretion, like that on the di_2, adheres to its roots. The pulp chamber is expanded, showing marked taurodontism, while the roots were fully formed and the root canals seem to be constricted. A slight occlusal attrition facet is noticeable on the mesio-buccal cusp. In occlusal view, the BL breadth is wider distally, in the region of the talonid, than toward its mesial portion. The distal marginal ridge is bisected by a shallow groove, but the mesial marginal ridge is uninterrupted. The crown surface has been severely altered by postdepositional taphonomic factors, leading to a loss of the enamel in a number of places, and the main intercusp fissures are difficult to identify. The anterior cusp tips are internally placed. While an anterior fovea is present, a mid-trigonid crest appears to be absent. Further crown details are obscured by damage to the enamel surface. A pronounced line of enamel decalcification is clearly visible on the buccal and distal surfaces, most likely the result of postdepositional alteration.

The extreme taurodontism seen in Qesem has long been considered a Neanderthal characteristic (Keith, 1927), but it is also present in earlier African hominins (Skinner and Sperber, 1982) as well as in specimens from Qafzeh (Qafzeh 4), and in the *H. erectus* sample from Zhoukoudian (Weidenreich, 1937). The lack of a mid-trigonid crest would differentiate the Qesem tooth from Neanderthal specimens (Bailey and Hublin, 2006).

The BL dimension in the Qesem dm_2 is large compared with recent *H. sapiens* but is similar to the mean

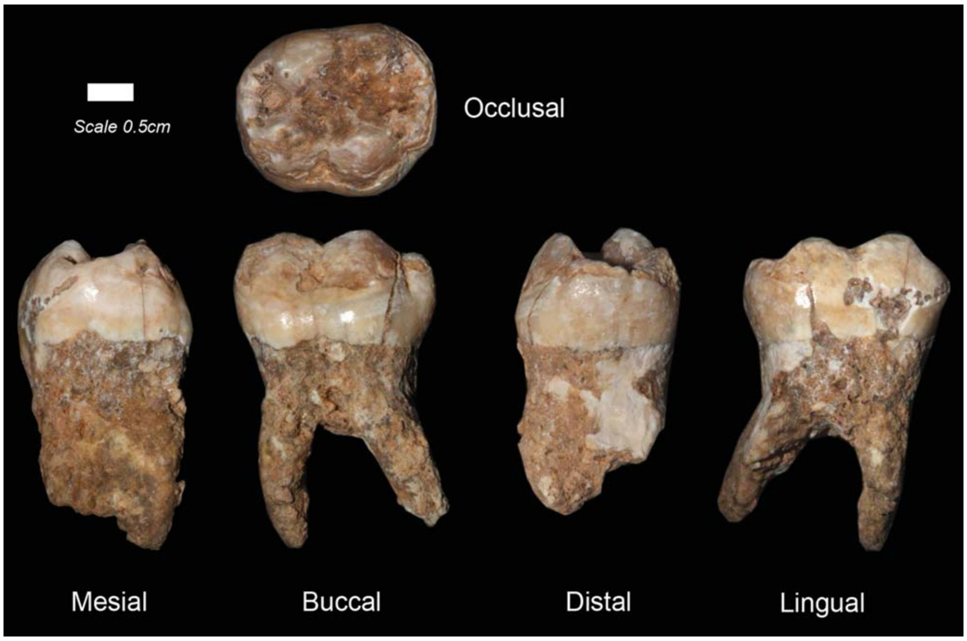

Fig. 4. The Qesem lower left second deciduous molar. Note the lack of a mid-trigonid crest, the taurodont pulp chamber and the marked line of enamel decalcification. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

values among the comparative fossil samples (Table 4, Fig. 5). The measured crown area (MCA = 88.1 mm^2) is larger than Kebara 1 (72.5 mm^2), Pech de l'Aze (72.4 mm^2), and La Ferrassie 8 (75.6 mm^2). At the same time, it is near the mean value in the early *H. sapiens* sample from Qafzeh and Skhul (mean ± S.D. = 85.2 ± 10.6 mm^2; range = 75.3–98.1 mm^2; n = 4), being closest to Qafzeh 10. Thus, it is clear that the Qesem dm_2 is a relatively large tooth.

Permanent dentition

Upper left lateral incisor. This specimen has a complete crown and a broken root (see Fig. 6). A small chip of enamel is missing on the mesial tooth crown and a larger fragment of the enamel is missing distally. This damage affects the MD measurement, making estimation necessary. Occlusal wear corresponds to Molnar's (1971) Stage 2–3. A horizontal hypoplastic line is present at the middle of the buccal crown, and there are scratches (possibly post depositional) oriented from the disto-cervical to mesio-incisal surface.

The tooth shows slight lingual shoveling (ASUDAS Grade 3) and a small lingual tubercle with a free apex at the base of the lingual face (ASUDAS Grade 4). The buccal face is convex, with no evidence of double shoveling. A degree of labial curvature is also present in the Qesem tooth. If the ASUDAS reference plaque for the I^1 is used, the curvature would correspond to Grade 4 or above, the maximum expression for this feature.

A similar small lingual tubercle is present in one of the upper lateral incisors from Qafzeh (Qafzeh 5) as well as in earlier African hominins (e.g., KNM-WT 15,000). While this trait is well developed in Neanderthals and is also found in some of the Atapuerca (SH) specimen (Bermúdez de Castro, 1988, 1993), it is associated with marked bucco-lingual expansion, a feature absent from the Qesem incisors. The African Middle Pleistocene specimen from Rabat shows a less pronounced degree of lingual shoveling and lacks a lingual tubercle. The combination of lingual tubercle and a cusp with a free apex is common in Neanderthals but is absent in the Skhul and Qafzeh samples (Trinkaus, 1995; Bailey, 2006). It is present in only 13% of Upper Paleolithic modern humans (Bailey and Hublin, 2006) but is found in many recent populations (Scott and Turner, 1997).

The BL crown dimension (see Fig. 7) is identical to the mean value in the early *H. sapiens* sample from Skhul and Qafzeh (Table 5). At the same time, it falls slightly more than one S.D. below the means of Neanderthals and European Middle Pleistocene specimens and below or just within the range of variation in African Middle Pleistocene specimens. Although there is clearly overlap among the samples, the Qesem tooth does not appear to show the BL expansion seen in Neanderthals.

Upper right canine. This specimen has a complete crown, but the root is broken just below the CEJ (see Fig. 8). Slight wear is present along the occlusal margin corresponding to Stage 2 (Molnar, 1971), and a small fragment of the enamel is missing on the mesiobuccal corner. A well-developed horizontal hypoplastic line is present 5.4 mm above the CEJ. Based on modern human dental calcification, this hypoplastic line would have developed at 2.5–3.0 years postnatal.

In lateral view, the buccal face is relatively straight and inclines lingually from base to apex. There is no trace buccally of either a basal swelling or cingulum. In lingual view, the crown is asymmetrical, with the mesial margin slightly taller than the distal margin. The lingual face shows well-developed mesial and distal marginal ridges, with the mesial ridge more strongly developed, and this tooth is shovel-shaped (similar to ASUDAS Grade 6 for the I^1 and Grade 4–5 for the I^2 plaques). A central depression is present on the lingual face, bounded by the marginal ridges, and a vertical crest, located slightly mesially, rises toward the apex within the central depression. A small lingual tubercle,

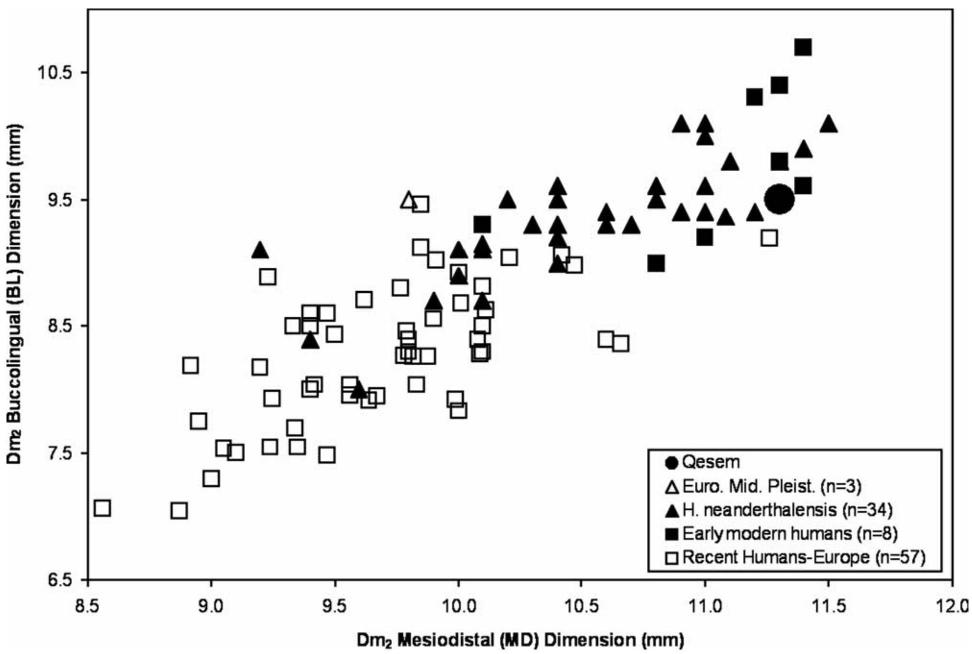

Fig. 5. MD and BL dimensions in the Qesem dm_2 compared with Pleistocene and recent humans.

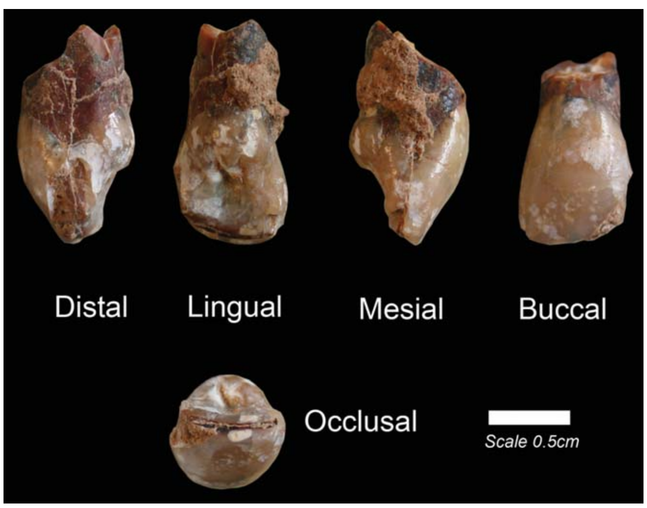

Fig. 6. The Qesem upper left lateral incisor. Note the presence of a lingual cusp with a free apex at the base of the crown. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

in the form of a cusp with a free apex, is present at the base of the lingual face where it fuses with the mesial marginal ridge (ASUDAS Grade 2 for Canine Mesial Ridge). There is no trace of a distal accessory ridge.

The BL crown dimension falls above the range of variation in our European modern human reference sample (Table 5) and slightly above the mean value in the Skhul/Qafzeh sample, but within the range of variation. At the same time, the Qesem specimen is at or very near the mean values seen in European Middle Pleistocene specimens and Neanderthals, but just within the lower limit of the range of variation among African Middle Pleistocene individuals (see Fig. 9). The MCA in Qesem (65.5 mm^2) is similar to the largest specimen (Qafzeh 6) within the Qafzeh sample (mean ± S.D. = 56.4 ± 7.0 mm^2; range = 48.6–63.0 mm^2; n = 4) but smaller than the African Middle Pleistocene specimen from Rabat (72.2 mm^2).

Upper left third molar. This specimen is represented by a developing tooth with ~4/5 of the crown present (see Fig. 10). Three well-developed main cusps (metacone ASUDAS Grade 4) are present, but there is no distinct hypocone. Only a weak oblique ridge is observed, and the occlusal surface is wrinkled. A small cusp (metaconule) is present along the distal margin (ASUDAS Grade 3). In contrast, no accessory cusps are present along the mesial marginal ridge nor is there any trace of a Carabelli structure.

Hypocone reduction or loss is commonly associated with reduction in crown size, thus it occurs both in Neanderthals and early *H. sapiens*. In Neanderthals, 37% of the specimens essentially lack a hypocone and the presence of cusp 5 occurs in about one third (ca. 35%), (Bailey, 2006). The absence of any mesial accessory cusps in Qesem differentiates this tooth from most Neanderthals, who show a high frequency (70%) of this trait. Nevertheless, the frequencies of most of these features are similar in early *H. sapiens* samples from Africa, southwest Asia, and Europe, and their expression in the Qesem tooth is not particularly informative.

Since the growth of the crown was not completed, the full convexity of the lingual lobe is absent. The BL diameter as measured is therefore underestimated and cannot be used for comparative purposes.

Lower left canine. Two distinct wear patterns can be seen on the occlusal surface of this tooth, reflecting attrition from the upper canine and first premolar (see Fig. 11). Small mesial and distal interproximal facets are present. There are no hypoplastic defects. The enamel is thin, and the root canal is constricted (see Fig. 11).

This tooth is markedly asymmetrical, but it is not shovel-shaped and there is no distal accessory ridge. The

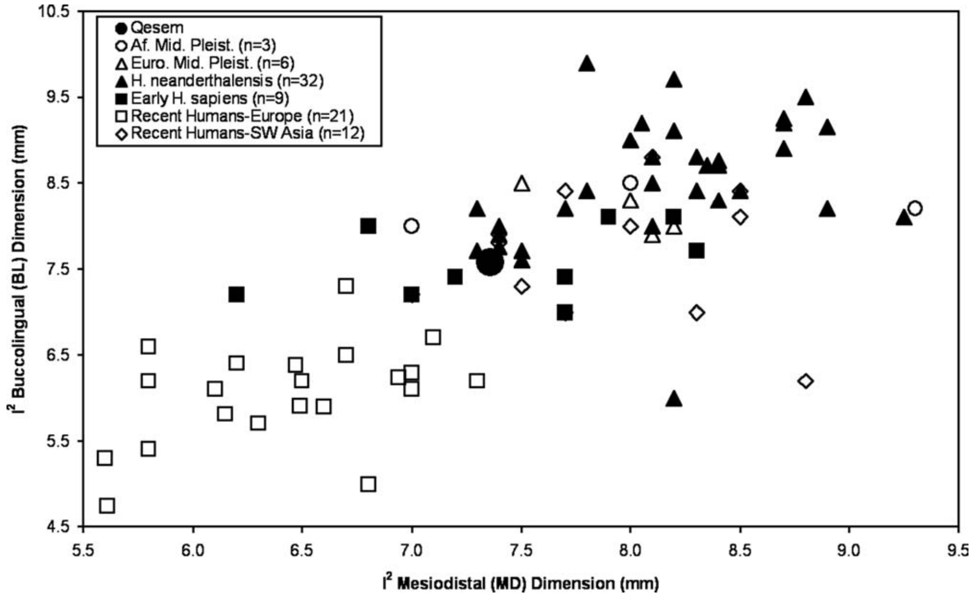

Fig. 7. MD and BL dimensions in the Qesem I^2 compared with Pleistocene and recent humans.

TABLE 5. Dental dimensions of maxillary teeth in Qesem compared with Pleistocene and recent humans

	I^2		C^1		M^3	
Specimen/sample	MD (mm) Mean ± s.d. (*n*) Range	BL (mm) Mean ± s.d. (*n*) Range	MD (mm) Mean ± s.d. (*n*) Range	BL (mm) Mean ± s.d. (*n*) Range	MD (mm) Mean ± s.d. (*n*) Range	BL (mm) Mean ± s.d. (*n*) Range
Qesem	7.4	7.6	8.8	9.8	9.7	11.1
Afr. Mid. Pleist.	8.1 ± 1.2 (3) (7.0–9.3)	8.2 ± 0.3 (3) (8.0–8.5)	9.4 ± 0.5 (4) (8.7–10.0)	10.2 ± 0.5 (4) (9.8–11.0)	9.2 (1) –	13.2 (1) –
Euro. Mid. Pleist.	7.9 ± 0.3 (6) (7.5–8.2)	8.1 ± 0.3 (6) (7.6–8.5)	8.8 ± 0.7 (12) (8.1–9.8)	9.7 ± 0.7 (12) (8.8–10.7)	9.0 ± 0.6 (8) (8.0–10.1)	11.8 ± 0.9 (8) (10.1–13.0)
H. neanderthalensis	8.1 ± 0.5 (32) (7.3–9.3)	8.5 ± 0.8 (32) (6.0–9.9)	8.7 ± 0.7 (33) (7.3–10.0)	9.9 ± 0.7 (33) (8.8–11.4)	9.9 ± 0.7 (24) (8.3–11.4)	12.3 ± 1.0 (24) (9.4–14.0)
Early *H. sapiens*	7.4 ± 0.7 (9) (6.2–8.3)	7.6 ± 0.4 (9) (7.0–8.1)	8.5 ± 0.7 (8) (7.5–9.7)	9.4 ± 0.7 (8) (8.5–10.2)	9.5 ± 0.7 (6) (9.0–10.9)	11.5 ± 0.7 (6) (10.4–12.1)
Recent Humans-Europe	6.4 ± 0.5 (21) (5.6–7.3)	6.0 ± 0.6 (21) (4.7–7.3)	7.4 ± 0.5 (17) (6.5–8.2)	7.7 ± 0.7 (17) (6.8–9.3)	8.9 ± 1.0 (13) (7.1–11.0)	10.1 ± 1.0 (13) (8.0–11.9)
Recent Humans-SW Asia	7.9 ± 0.5 (12) (7.0–8.8)	7.7 ± 0.7 (12) (6.2–8.8)	8.4 ± 0.5 (11) (7.5–9.3)	9.3 ± 0.6 (11) (8.7–10.5)	9.0 ± 0.5 (15) (8.3–10.4)	11.3 ± 1.0 (15) (9.4–12.5)

distal marginal ridge is more strongly developed than the mesial one, producing a small fovea in the distal lingual face. A small tubercle is located on the distal marginal ridge, just below the worn occlusal surface. This specimen has a single long, robust and mesiodistally compressed root. The buccal root face is broader than the lingual, and the apex tapers to distal. There is a single pulp chamber.

Its BL dimension is outside the European modern human range of variation (Table 6, Fig. 12). Qesem compares most favorably with the Natufian and Qafzeh/Skhul means and falls slightly below the Neanderthal and European Middle Pleistocene means. In contrast to the upper canine, the MCA of the Qesem lower canine (41.4 mm^2) is more modest. It is smaller than the Skhul/Qafzeh specimens (range = 43.8–53.8 mm^2), the African Middle Pleistocene specimen from Rabat (55.8 mm^2) and the Petit Puymoyen 3 Neanderthal (52.9 mm^2). It is, however, within the range of variation of the Atapuerca (SH) sample (mean ± S.D. = 49.7 ± 7.4 mm^2; range = 37.1–65.7 mm^2; n = 14) as well as a pooled-sex contemporary *H. sapiens* sample (mean ± S.D. = 37.3 ± 4.8 mm^2; range = 25.0–49.3 mm^2; n = 216), (Bermúdez de Castro et al., 2001).

Root length in the Qesem canine (18.6 mm) is relatively long compared with recent humans (mean ± S.D. = 14.6 ± 1.9 mm; range = 11.9–19.3 mm; n = 34), being surpassed by only about 9% of our modern European comparative sample. Longer roots (21.0–26.2 mm) can be found among the *H. erectus* specimens from Zhoukoudian (Weidenreich, 1937), and a nearly identical value (18.5 mm) is reported in *H. antecessor* (Bermúdez de Castro et al., 1999). The Qesem specimen compares more favorably with Neanderthals (mean = 19.4 mm; range = 16.3–23.2 mm), (Bailey and Hublin, 2006) but is clearly longer than the value reported in Skhul 2 (14.5–15.0 mm), (McCown and Keith, 1939) and just within the upper limit of a European Upper Paleolithic range of

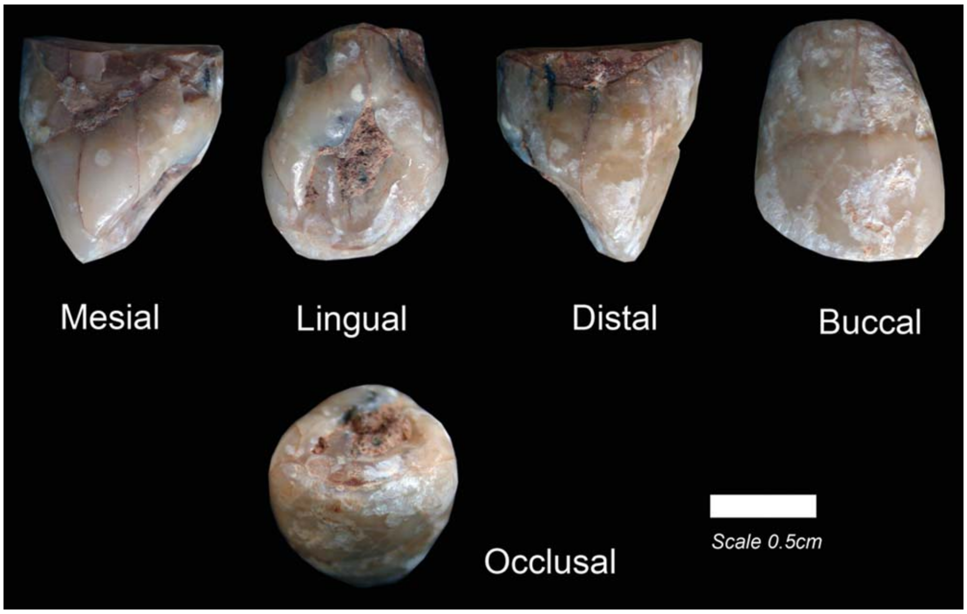

Fig. 8. The Qesem upper right canine. Note the pronounced shoveling and the presence of a cusp with a free apex fused with the mesial marginal ridge. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

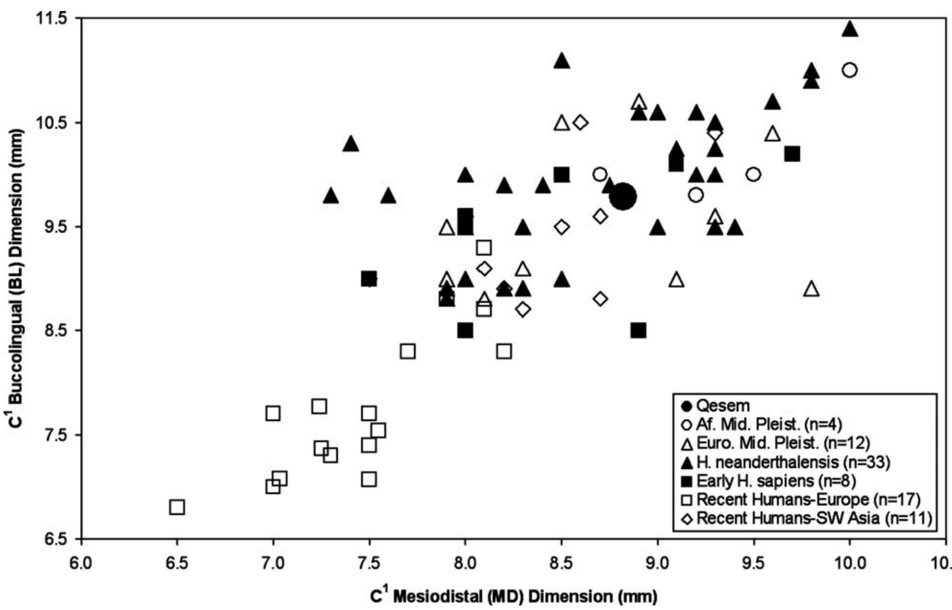

Fig. 9. MD and BL dimensions in the Qesem C^1 compared with Pleistocene and recent humans.

variation (mean = 16.2 mm; range = 13.1–19.0 mm), (Bailey and Hublin, 2006).

Lower left first premolar. This specimen is represented by a complete crown and approximately half of the broken root (see Fig. 13). The broken root reveals a single root canal. Radiographic analysis reveals a thin enamel layer, with a constriction of the root canal in the cervical area. Slight tooth wear on the tip of the buccal cusp corresponds to Stage 2 of Molnar (1971). This is a bicuspid tooth, with the buccal cusp being significantly larger than the lingual one. The buccal surface of the buccal cusp takes up a large portion of the occlusal view, and neither mesial nor distal buccal grooves are present on the buccal face. The lingual cusp is located mesially, approximately opposite the tip of the protoconid. A very small distal accessory cusp (ASUDAS Grade 3) is present on the distal marginal ridge, separated from the metaconid by a distal lingual groove. The distal marginal ridge slopes downward from the distobuccal angle of the crown toward the lingual cusp forming a distal accessory ridge. A weak transverse crest joins the main buccal and lingual cusps and divides the central basin into mesial and distal fossae.

In occlusal view, the crown presents only a slight asymmetry in the external contour, being closer to a round shape. The distal portion of the lingual contour is convex, while the mesial portion is slightly concave. The

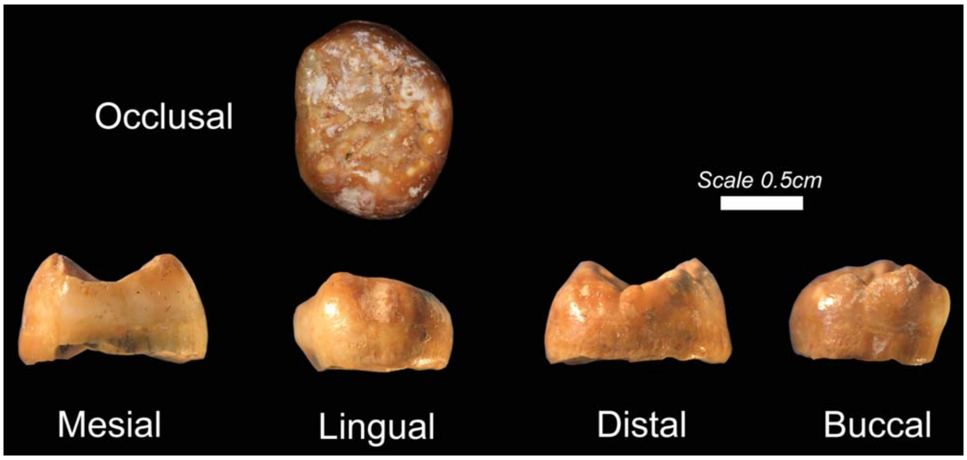

Fig. 10. The Qesem upper left third molar. Note the weakly expressed oblique ridge, absence of a hypocone and presence of a metaconule along the distal margin. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

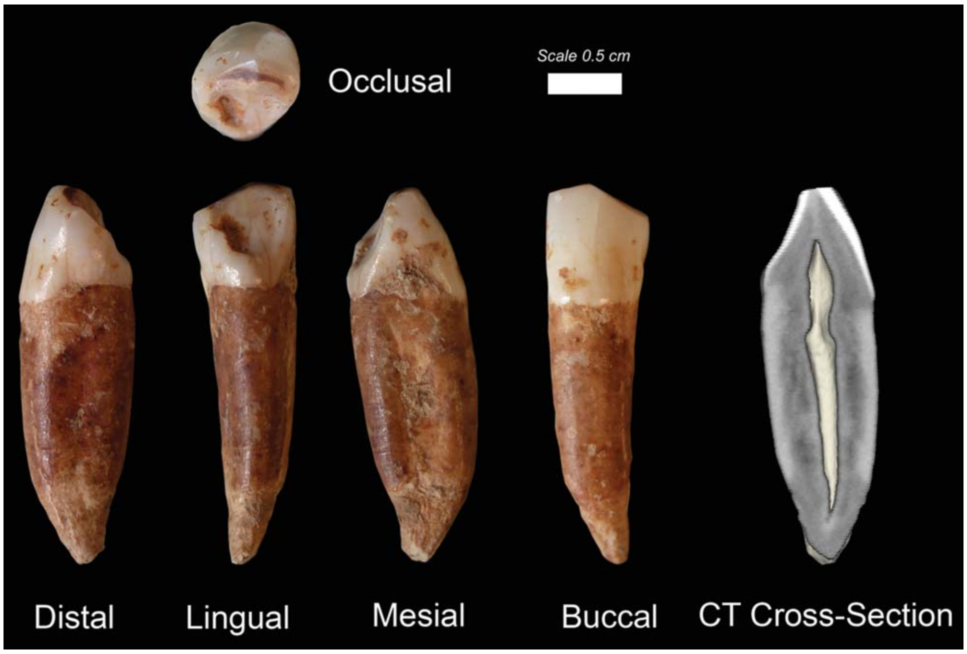

Fig. 11. The Qesem lower left canine. Note the lack of both shoveling and the distal accessory ridge. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

relative occlusal polygon area (7.71) was measured according to Gómez-Robles et al. (2008). Although we have not performed a geometric morphometric analysis, the placement of the protoconid and metaconid cusp tips and the mesial and distal fossae suggest that the Qesem P_3 shows an occlusal polygon (Gómez-Robles et al., 2008) that is reduced and displaced toward the lingual half of the tooth.

The combination of morphological features in the Qesem P_3 does not provide a clear indication of its taxonomic affinities, since many of these features occur in Neanderthals and early modern humans in similar frequencies (Bailey, 2006). Size as well as the absence of buccal grooves would seem to differentiate the Qesem P_3 from *H. erectus* specimens from both Zhoukoudian and Java (Kaifu et al., 2005; Xing et al., 2009). The slight asymmetry of the external crown outline and the reduced and lingually placed occlusal polygon in Qesem resemble some Neanderthals and European Middle Pleistocene specimens (Martinón-Torres et al., 2007; Gómez-Robles et al., 2008).

The BL crown dimension in the Qesem P_3 is very modest (Table 6), falling easily within the ranges of variation of the European modern human and Natufian samples (see Fig. 14), but at the lower limit or outside the ranges of variation in all the fossil samples. The MCA in the Qesem P_3 is also quite diminutive, falling well below the values of the Early Pleistocene European specimen from Atapuerca (TD) and the African Middle Pleistocene specimen from Rabat (Table 7). The MCA in Qesem also falls below the lower limit of the range of variation seen in Neanderthals and the Skhul/Qafzeh sample but is similar to some of the smallest specimens from Atapuerca (SH) site. The small size of the Qesem P_3 compares most favorably with recent humans.

TABLE 6. Dental dimensions of mandibular teeth in Qesem compared with Pleistocene and recent humans

	C_1		P_3		P_4	
Specimen/sample	MD (mm) Mean ± s.d. (*n*) Range	BL (mm) Mean ± s.d. (*n*) Range	MD (mm) Mean ± s.d. (*n*) Range	BL (mm) Mean ± s.d. (*n*) Range	MD (mm) Mean ± s.d. (*n*) Range	BL (mm) Mean ± s.d. (*n*) Range
Qesem	7.2	8.3	7.3	7.6	6.6	8.0
Afr. Mid. Pleist.	7.8–8.5 (2)	9.5–10.3 (2)	8.6 ± 0.2 (4)	10.4 ± 0.5 (4)	8.6 ± 0.5 (4)	10.4 ± 0.7 (4)
	–	–	(8.5–8.8)	(10.0–11.2)	(8.2–9.2)	(9.9–11.4)
Euro. Mid. Pleist.	7.8 ± 0.6 (14)	8.8 ± 0.7 (14)	7.7 ± 0.5 (13)	8.7 ± 1.0 (13)	7.4 ± 0.6 (18)	9.0 ± 1.1 (18)
	(7.0–9.0)	(7.3–9.9)	(7.0–9.0)	(7.4–11.5)	(6.6–8.8)	(7.2–11.5)
H. neanderthalensis	7.9 ± 0.5 (33)	9.1 ± 0.8 (33)	7.8 ± 0.7 (33)	9.2 ± 0.6 (33)	7.7 ± 0.8 (37)	9.2 ± 0.7 (37)
	(6.8–8.8)	(7.5–10.3)	(6.5–9.2)	(8.0–10.3)	(5.4–9.4)	(7.1–10.5)
Early *H. sapiens*	7.8 ± 0.8 (9)	8.5 ± 0.6 (9)	7.4 ± 0.9 (7)	8.6 ± 0.7 (7)	7.6 ± 0.4 (7)	8.8 ± 0.7 (7)
	(6.9–9.4)	(7.8–9.8)	(5.8–8.6)	(7.7–9.6)	(7.0–8.3)	(7.8–10.0)
Recent Humans-Europe	6.5 ± 0.4 (18)	7.1 ± 0.7 (18)	6.9 ± 0.4 (27)	7.6 ± 0.5 (27)	6.8 ± 0.7 (14)	7.8 ± 0.8 (14)
	(5.8–7.5)	(5.5–8.0)	(5.7–7.5)	(6.2–8.5)	(5.7–8.2)	(6.5–9.4)
Recent Humans-SW Asia	7.4 ± 0.7 (15)	8.4 ± 0.5 (15)	7.1 ± 0.7 (12)	8.2 ± 0.8 (12)	7.6 ± 0.6 (15)	8.5 ± 1.0 (15)
	(6.3–8.6)	(7.6–9.6)	(6.2–8.4)	(7.3–9.5)	(6.5–8.5)	(6.1–9.8)

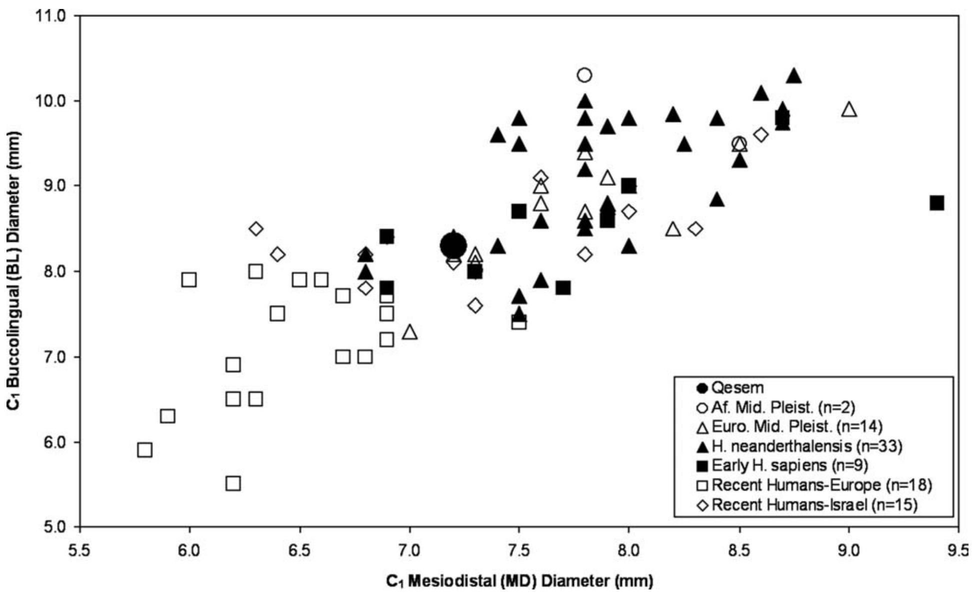

Fig. 12. MD and BL dimensions in the Qesem C_1 compared with Pleistocene and recent humans.

Lower left second premolar. This specimen is represented by a complete crown and root (see Fig. 15). Only the slightest wear is present on the occlusal surface, corresponding to Molnar's (1971) Stage 1. A larger distal and a smaller mesial interproximal wear facet indicate articulation with the M_1 and P_3, respectively. The Qesem P_4, then, was fully in occlusion at the time of death.

The enamel surface shows a relatively simplified occlusal morphology, generally lacking the enamel crenulations and extra furrows, deemed characteristic of Neanderthals (Bailey, 2002a,b). The protoconid and metaconid are approximately equal in height and are joined by a transverse crest which is crossed by the longitudinal fissure. The groove pattern, then, corresponds to an H-pattern (Hillson, 1996). Neither mesial nor distal buccal grooves are present on the buccal surface of the protoconid. The metaconid is well-developed, and its tip is located approximately opposite but slightly mesial to the protoconid. Only a small distal accessory cusp (ASUDAS Grade 2) is present along the lingual margin of the tooth, but no lingual groove is present. Only a weak distal accessory crest is present. In occlusal view, the crown outline presents weak asymmetry, more closely resembling a rounded square shape. The root is flattened MD and has a distal shallow longitudinal groove. In buccal view, the root is nearly straight, and the apex inclines slightly distally. There is a single pulp chamber, corresponding to the 1R category (Wood et al., 1988).

The presence of both a distal accessory crest and distal accessory cusp occurs more frequently in Neanderthal specimens, but the weak asymmetry of the crown outline, the discontinuous transverse crest and the slight mesial placement of the metaconid tip suggest a departure from the Neanderthal dental pattern (Bailey, 2002a; Bailey and Lynch, 2005; Martinón-Torres et al., 2006). The African Middle Pleistocene specimen from Rabat differs from Qesem in showing a stronger asymmetry of the crown outline and more mesial placement of the metaconid but resembles it in the discontinuous transverse crest. In these three features, the Qesem tooth approximates more closely the morphology seen among the

Qafzeh specimens as well as one of the Xichuan *H. erectus* specimens (PA 528) from China (Xing et al., 2009).

The BL dimensions is modest, falling within the Natufian and European modern human ranges of variation (Table 6; Fig. 16) but toward the lower extremes of the variation in Neanderthals and European Middle Pleistocene specimens. All of the African Middle Pleistocene specimens show much larger dimensions (Table 6). The MCA in the Qesem premolar falls below the lower limit of the Neanderthal and Skhul/Qafzeh variation but is similar to some of the smallest specimens from Atapuerca (SH). The small size of the Qesem P_4 compares most favorably with recent humans.

The size ratio of the P_3 and P_4 has been argued to be a useful criterion for distinguishing Neanderthals and European Middle Pleistocene specimens from other *Homo* taxa (Bermúdez de Castro, 1993; Bermudez de Castro and Nicolás, 1996). In particular, Neanderthal lineage specimens are generally characterized by $P_3 > P_4$, perhaps related to the expansion of the anterior dentition. Nevertheless, this same pattern of P_3 predominance is also found in 40% (two of five individuals) of the *H. erectus* sample from Zhoukoudian (Weidenreich, 1937), obscuring the phylogenetic polarity of this feature. Although some variation is present, the P_3/P_4 MCA ratio in Neanderthals and the Atapuerca (SH) sample (Table 7) suggests a predominance of the P_3 (i.e. $P_3>P_4$). The values in the Qafzeh/Skhul sample, however, suggest a slight predominance of the P_4, and these specimens resemble living humans in this regard. The ratio in Qesem (99.6) indicates that the premolars in this individual are nearly equal in size. A nearly identical ratio (99.5) is found in the European Early Pleistocene specimen from Atapuerca (TD) and a slightly lower ratio (94.3) characterizes the African Middle Pleistocene specimen from Rabat (Table 7). Thus, the Qesem specimen does not appear to show the $P_3>P_4$ size sequence.

The occlusal polygon area was measured according to Martinón-Torres et al. (2006). When adjusted for crown size, the relative occlusal polygon area in the Qesem specimen (15.2) is large, indicating that the lingual portion of the tooth crown is not truncated. The Qesem specimen falls 1 S.D. above the African Middle Pleistocene mean value (12.7 ± 2.5), but falls further from the European Middle Pleistocene (10.9 ± 1.9), Neanderthal (11.3 ± 2.6) and *H. sapiens* (11.0 ± 1.9) means (Martinón-Torres et al., 2006).

Root length in the Qesem P_4 (19.7 mm) is long compared with European modern humans (mean ± S.D. = 14.7 ± 1.9 mm; range = 10.6–18.7 mm; n = 22). However, a similar value (19.2 mm) has been reported for the Zhoukoudian GI individual (Weidenreich, 1937), and the Qesem root length falls above the mean value but within the range of variation reported for Neanderthals (mean = 18.7 mm; range = 14.5–22.6 mm), (Bailey and Hublin, 2006). In contrast, root length in Skhul 2 (13.5 mm), (McCown and Keith, 1939) is considerably shorter, and

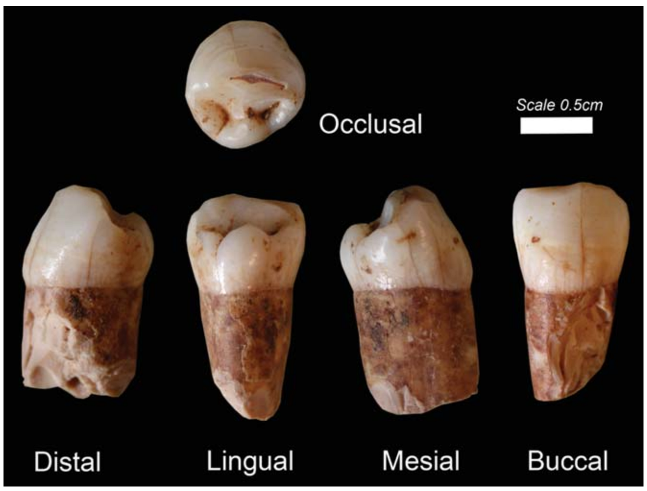

Fig. 13. The Qesem lower left third premolar. Note the slight asymmetry of the crown outline and the weak transverse crest joining the main buccal and lingual cusps. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

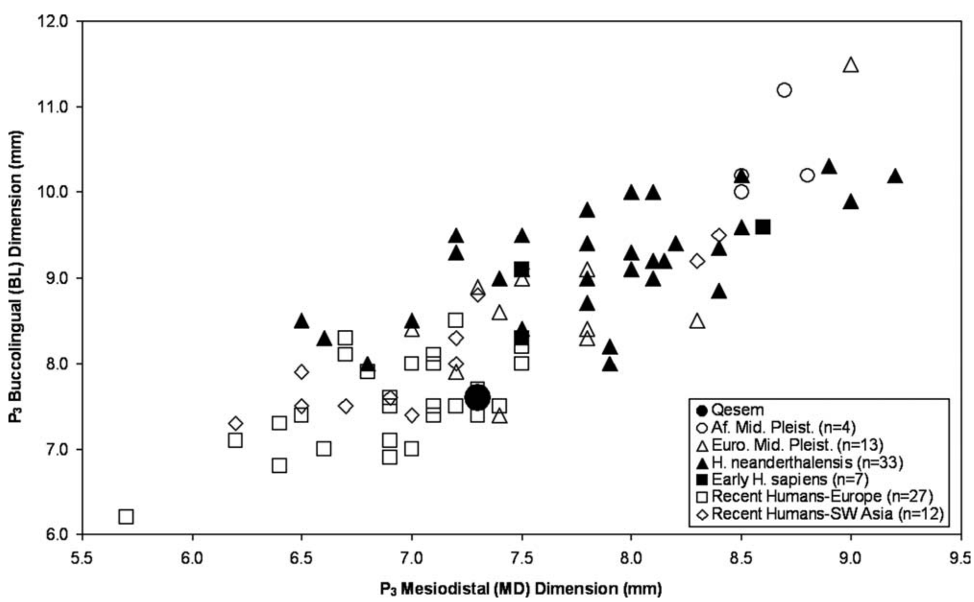

Fig. 14. MD and BL dimensions in the Qesem P_3 compared with Pleistocene and recent humans.

TABLE 7. Measured crown areas (mm²) in the Qesem P_3 and P_4 and some comparative samples

Specimen/sample	Lower P3	Lower P4	P3/P4 Ratio	Reference
Qesem	42.3	42.4	99.6	Original specimen
Atapuerca (TD)	65.8	66.1	99.5	Bermúdez de Castro et al. (1999)
Rabat	63.2	67.0	94.3	Original specimen
Atapuerca (SH) mean ± s.d. (*n*)	53.1 ± 6.6 (14)	50.6 ± 7.3 (14)	105.4 ± 5.5 (14)	Bermúdez de Castro et al. (2001)
Atapuerca (SH) (range)	(40.5–64.6)	(35.5-63.4)	(97.3–114.7)	
Neandertal mean ± s.d. (*n*)	53.2 ± 6.4 (11)	56.9 ± 10.3 (8)	104.0 ± 14.0 (5)	Original specimens
Neandertal range	(43.5–64.3)	(43.2–67.7)	(95.7–128.8)	
Skhul/Qafzeh mean ± s.d. (*n*)	55.8 ± 6.3 (5)	57.5 ± 5.0 (5)	96.9 ± 3.3 (5)	Original specimens
Skhul/Qafzeh range	(48.0–65.3)	(51.4–65.2)	(93.4–100.2)	
H. sapiens (male) mean ± s.d. (*n*)	39.5 ± 4.4 (131)	45.1 ± 5.2 (117)	87.6[a]	Bermúdez de Castro et al. (2001)
H. sapiens (male) (range)	(29.8–50.4)	(31.7–55.9)		
H. sapiens (female) mean ± s.d. (*n*)	37.0 ± 3.8 (93)	42.5 ± 5.0 (87)	87.1[a]	Bermúdez de Castro et al. (2001)
H. sapiens (female) (range)	(27.9–46.8)	(31.4–57.4)		

[a] Calculated from mean MCA values.

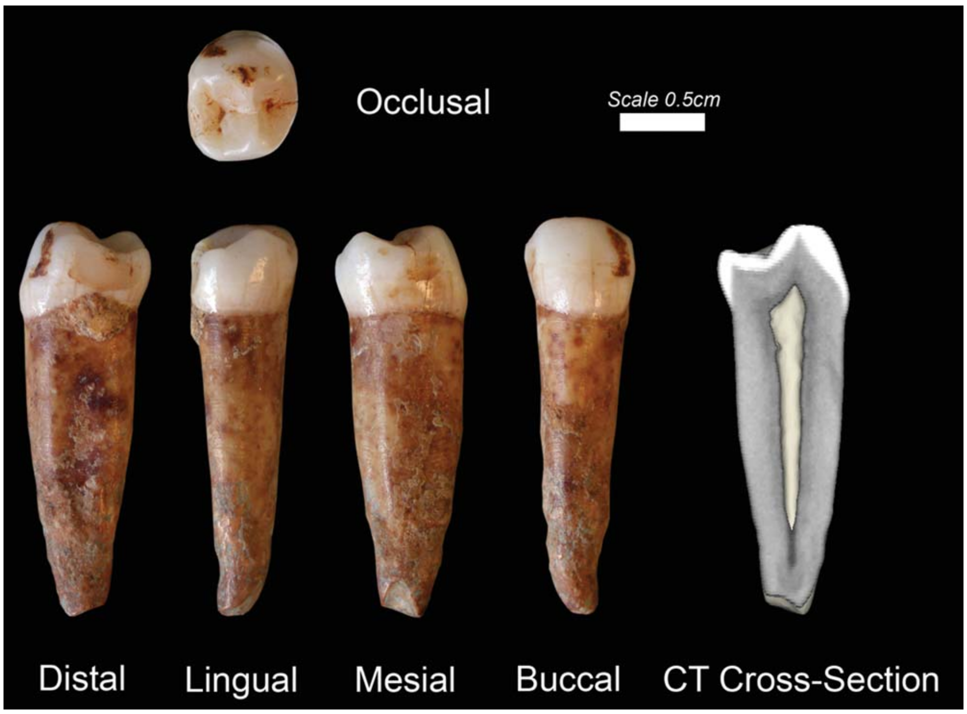

Fig. 15. The Qesem lower left fourth premolar. Note the weak asymmetry of the crown outline, the presence of a well-developed and medially placed lingual cusp, the discontinuous transverse crest and the single root canal. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

the Qesem specimen falls outside the range of variation reported for Upper Paleolithic modern humans from Europe (mean = 15.0 mm; range = 12.6–17.1 mm), (Bailey and Hublin, 2006).

DISCUSSION

The Qesem teeth originate from a secure and well-dated stratigraphic context of the Lower Paleolithic (400–200 ka). The cultural complex from which the teeth were recovered (AYCC) is a unique Levantine, local phenomenon spread from Central Syria to Central Israel with no evidence of African and/or European cultural affinities.

The Middle Pleistocene age of the Qesem specimens places them chronologically earlier than the bulk of fossil hominin specimens known from southwest Asia. Both Neanderthal and early *H. sapiens* specimens are known from the Late Pleistocene at a number of sites across the region (McCown and Keith, 1939; Suzuki and Takai, 1970; Vandermeersch, 1981; Trinkaus, 1983; Bar-Yosef and Vandermeersch, 1991; Hovers et al., 1995; Tillier, 1999; Akazawa and Muhesen, 2002; Tillier et al., 2003). In Europe, the emergence of the Neanderthal evolutionary lineage has been documented early in the Middle Pleistocene (Arsuaga et al., 1993, 1997; Bischoff et al., 2007), while *H. sapiens* specimens are known from Africa in the late part of the Middle Pleistocene (White et al., 2003; McDougall et al., 2005) and are present in southwest Asia around 100,000 years ago (Valladas et al., 1988; Stringer et al., 1989).

Specimens from Israel contemporaneous with the Qesem teeth include a femoral diaphysis and an isolated and worn lower molar from Layer E at Tabun (McCown

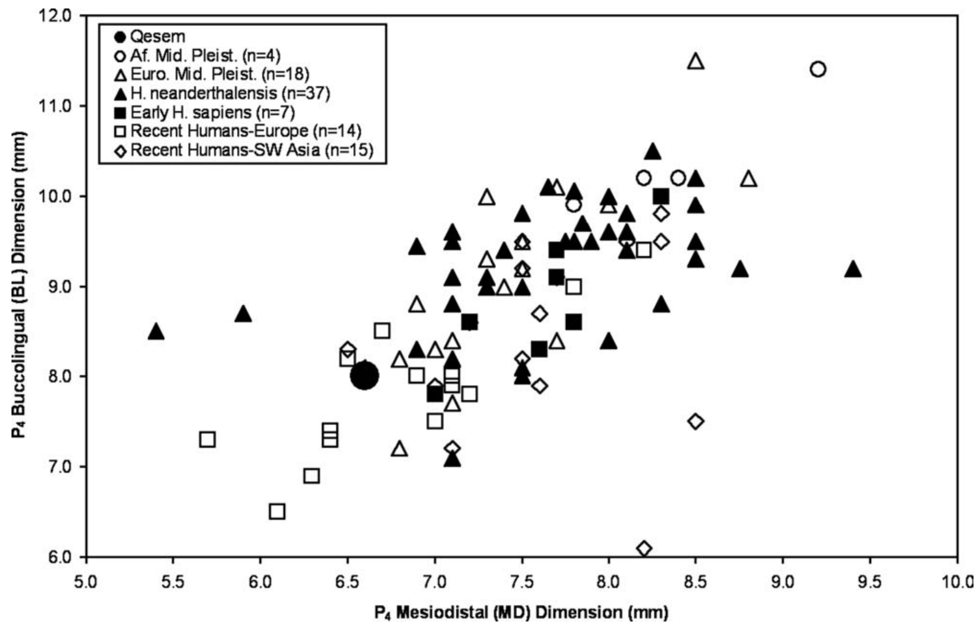

Fig. 16. MD and BL dimensions in the Qesem P_4 compared with Pleistocene and recent humans.

and Keith, 1939) and the partial cranium from the site of Zuttiyeh (Turville-Petre, 1927). The Tabun Layer E fossils have been described as showing features which align them with archaic members of the genus *Homo* (Trinkaus, 1995). The taxonomic affinities of the Zuttiyeh specimen have been a matter of considerable debate, with opinions ranging widely between a form of Neanderthal (Keith, 1927), a direct ancestor of the early *H. sapiens* population from Skhul and Qafzeh (Vandermeersch, 1989, 1995), a generalized archaic *Homo* taxon (Rak, 1986; Trinkaus, 1989; Simmons et al., 1991) or as showing affinities with the *H. erectus* specimens from Zhoukoudian (Sohn and Wolpoff, 1993). However, this specimen has no teeth, limiting its relevance for the present study.

Given the chronology of the Qesem individuals, and the lack of consensus on the identity of the Middle Pleistocene occupants of southwest Asia, the most relevant question surrounding the taxonomic affinities of the Qesem population concerns the possible identification of derived features that would align the specimens more closely with the Neanderthal evolutionary lineage or the earliest *H. sapiens* from the region. Alternatively, a genetic influence from North African Middle Pleistocene populations must also be considered.

Regarding the permanent maxillary teeth, the lateral incisor lacks the BL expansion seen in the Neanderthal dentition, but resembles Neanderthals in the marked degree of labial convexity. Similarly, the presence of a lingual tubercle with some degree of shoveling, the lack of a distal accessory ridge, and the mesial marginal ridge morphology of the C^1, although regarded as "Neanderthal-like" characteristics, fall within the range of variation seen in both Skhul/Qafzeh individuals and the North African Middle Pleistocene hominins. This resemblance to the Skhul/Qafzeh specimens is also evident from the crown dimensions. Albeit strikingly modern in appearance, the morphology of the M^3 is undiagnostic as to its taxonomic affinities. Dental traits considered characteristic of Neanderthals represent an increased frequency and expression of traits already found in African ancestral populations. Despite the fact that the phylogenetic polarity for many of the dental features studied is obscure, it is the combination of metric and morphological features that leads us to conclude that the Qesem teeth from the upper strata show stronger affinity to the Skhul/Qafzeh population than to the Neanderthals.

Regarding the mandibular dentition (C_1, P_3, P_4), the crown size is surprisingly small, but they are otherwise generally plesiomorphous. This presents some problems in evaluating their relationship to other specimens described here, especially Skhul/Qafzeh. The morphology of the C_1 is not diagnostic as to taxonomic affinity, although the long tooth root would appear to represent a plesiomorphous feature. Morphology of the P_3 is likewise inconclusive, and the P_4 is lacking most of the features which characterize the Neanderthal P_4. In contrast, the long root length and large occlusal polygon in the P_4 both resemble archaic members of the genus *Homo*, while the $P_3 = P_4$ size ratio indicates only that Qesem lacks the $P_3 > P_4$ size sequence.

The P_4 has been argued to be one of the most diagnostic teeth for distinguishing between human groups in the Middle and Late Pleistocene (Bailey and Lynch, 2005). Thus, its morphology in Qesem may be particularly revealing for diagnosing its taxonomic affinities. A suite of features have been identified in the Neanderthal P_4 (marked crown asymmetry, well-developed and mesially placed lingual cusp and a well-developed and continuous transverse crest), (Bailey, 2002a, 2006; Bailey and Lynch, 2005). All of these features occur in high frequencies in Neanderthals, but can also be found individually in other fossil human taxa at variable frequencies. Thus, the Neanderthal P_4 morphological pattern may comprise a combination of ancestral and derived features. However, the phylogenetic polarity of the individual features is a matter of debate (Bailey, 2002a, 2006; Bailey and Lynch, 2005; Martinón-Torres et al., 2006). The absence of most of these features in the

Qesem P_4, then, would indicate a departure from the Neanderthal morphological pattern, approaching more closely the condition seen in at least one Chinese *H. erectus* specimen as well as the Qafzeh/Skhul specimens.

Regarding the deciduous teeth, the lack of a reduced distal lobe in the Qesem di_2 differs from the condition seen in several Neanderthal individuals from Europe and southwest Asia. Taphonomic damage has obscured most morphological details in the dm_2. The taurodont pulp chamber is a feature that is characteristic of Neanderthal molars, but which is also found among the *Homo erectus* specimen from Zhoukoudian as well as in Qafzeh 4 (Weidenreich, 1937; Zilberman et al., 1992). The probable absence of a mid-trigonid crest differentiates the Qesem tooth from Neanderthals (Bailey and Hublin, 2006).

There are three scenarios that might account for the morphological details in the Qesem teeth. The first one is of a local archaic *Homo* population occupying southwest Asia during the Middle Pleistocene, to which the Qesem specimens would be attributed. Perhaps relevant in this regard, the Qesem lithic assemblages studied to date indicate a local origin, with no evidence of African and or European cultural affinities (Barkai et al., 2005; Gopher et al., 2005; Barkai et al., 2009). Albeit the lack of other diagnostic Middle Pleistocene SW Asian teeth, considering the evidence in its entirety, we believe that the Qesem "package" is more Skhul/Qafzeh like, even if some of its features are plesiomorphous.

The second scenario is one of long-term in situ evolution of Neanderthals in southwest Asia. The presence of shoveling and a lingual tubercle in the stratigraphically younger maxillary teeth may be indicating the emergence of the Neanderthal morphological pattern during the Middle Pleistocene in southwest Asia. This would parallel the situation documented in Europe, where the Neanderthal evolutionary lineage has been shown to have roots extending deep into the Middle Pleistocene (Arsuaga et al., 1997; Stringer and Hublin, 1999; Bischoff et al., 2007). Under this scenario, southwest Asia would represent one regional subpopulation within the wider geographic range of the evolving Neanderthal lineage. Nonetheless, the large and well dated samples of fossil humans from Skhul/Qafzeh that post date the Qesem specimens but predate most of the Neanderthal specimens from the region do not show an accentuation of Neanderthal features.

The third scenario is that more than one Pleistocene human taxon is represented within the Qesem dental sample. The mandibular teeth are stratigraphically deeper (older) but are smaller and lack plesiomorphous features identified in the chronologically later specimens. The differences between these chronologically disparate samples may reflect a population or species level distinction, and may involve population replacement on a local scale.

Resolution of these alternative scenarios must await further discoveries of additional and more complete Middle Pleistocene remains from southwest Asia. Nevertheless, the Qesem specimens represent an important contribution to the growing sample of Pleistocene human fossils from this circum-Mediterranean region of the Old World.

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