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Microfaunal remains at Middle Pleistocene Qesem Cave, Israel: Preliminary results on small vertebrates, environment and biostratigraphy[☆]

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ABSTRACT

Preliminary results of the investigation of the microfauna at the Acheulo-Yabrudian Middle Pleistocene site of Qesem Cave, Israel, are presented. Thus far the assemblage includes ca. 10,000 bone and tooth fragments, of which 50% could be identified to the generic and some hundreds to the species level. Based on the current material, the fauna includes the following squamate reptiles: *Laudakia* sp., *Chamaeleo* sp., Gekkonidae indet., Lacertidae indet., Scincidae indet., *Pseudopus* sp., *Varanus* sp., Colubroidea indet. (at least three species) and micromammals: *Suncus etruscus*, *Crociodura* cf. *leucodon*, Crocidurinae indet. (large form), Chiroptera indet., *Sciurus* cf. *anomalous*, *Cricetulus* cf. *migratorius*, *Microtus guentheri*, *Nannospalax ehrenbergi*, *Dipodillus* cf. *dasyurus*, *Meriones* cf. *tristrami*, Gerbillidae indet., *Mus* cf. *musculus*, *Apodemus* cf. *flavicollis*. These results suggest that the fauna includes only taxa that occur recently in the territory of Israel. The ecological preferences of the nearest living relatives of the recorded taxa allow us to infer a paleoenvironment with a mosaic of open and woodland habitats. However, comparing the lower with the upper levels of the microfauna-bearing profile, a slight shift towards more wooded conditions might be detectable. Biostratigraphical inferences from the recorded micromammal taxa cover a rather wide age range, whereas the radiometric (U-series and preliminary TL) dating enable a provisionally estimated date for the microfauna-bearing levels at 360–300 ka. Detailed morphometric comparisons with material from other sites in the region are necessary and may yet provide further insights.

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Introduction

The Levant, especially the strip between the rift valley and the Mediterranean coast, is crucial for the reconstruction of early (Early and Middle Pleistocene) human history, because it is a part of the corridor through which hominins departed Africa and spread to Asia and Europe. The paleoecological conditions under which these hominins lived are of great significance for any evaluation of their migration and subsistence activities. Middle Pleistocene sites are of

particular interest because it is at this time that we see the first record of many modern mammal species, as well as a modernization of the micromammal communities. The site of Qesem Cave, discovered in 2000 on the western slopes of the Samaria hills, 12 km east of the Mediterranean present coastline, holds great potential in this respect, being a rich and well-preserved site. It has already yielded very large assemblages of lithic finds in excellent condition as well as abundant vertebrate remains representing both macro- and micro-faunal elements. It has also yielded a number of hominin teeth, which are now under study. This paper presents the first results of the analysis of a microfaunal assemblage retrieved at the Acheulo-Yabrudian Middle Pleistocene site of Qesem Cave, Israel. It offers an attempt to extract information concerning the cave's surroundings and provides a first reconstruction of the ecological conditions at the time the bones were deposited, and it offers a preliminary incorporation of our finds into a more general Near Eastern and broader continental biostratigraphy.

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The assemblage presented includes approximately 10,000 bone and tooth fragments, of which some 50% could be identified to the generic level. In addition, hundreds of specimens are identifiable at the species level.

The cave

The setting

Qesem Cave has been assigned to the Acheulo-Yabrudian Cultural Complex (AYCC) of the late Lower Paleolithic. It is located about 12 km east of the Mediterranean, at an elevation 90 m asl on the moderate western slopes of the Samaria hills (Fig. 1). The area is, at present, within the Mediterranean climatic zone with an annual average precipitation of 500–600 mm. However, the natural forest vegetation has long since been destroyed by overgrazing and modern developmental projects. After discovery, two short salvage seasons were conducted during 2001 and a new series of four field seasons followed in 2004–2008.

Qesem Cave is a sediment-filled karstic chamber cave some 20 × 15 m in size and ca. 10 m high. The Samaria hills region is rich in karstic systems created by dissolution of the limestone, many of them still active. Qesem Cave is part of a larger karstic system within the limestone of the B'ina Formation of the Cretaceous Period. The cave seems to have developed as an isolated phreatic cave before the Samaria hills were uplifted to their present position without a human-accessible entrance. Later, in the Middle Pleistocene, Qesem Cave was breached by natural erosion, which allowed the entry of hominins and anthropogenic sediment deposition. An adjacent cave (50 m) that has been breached only by recent road-cutting and is still an active underground void may be used as a model to reconstruct the processes in Qesem Cave (Frumkin et al., 2009).

The excavation and the general stratigraphy

The excavation exposed a ca. 7.5 m archaeological sequence. Subsidence, erosion, fracturing, deposition of various sediments and cementation were continuous or recurrent within Qesem Cave

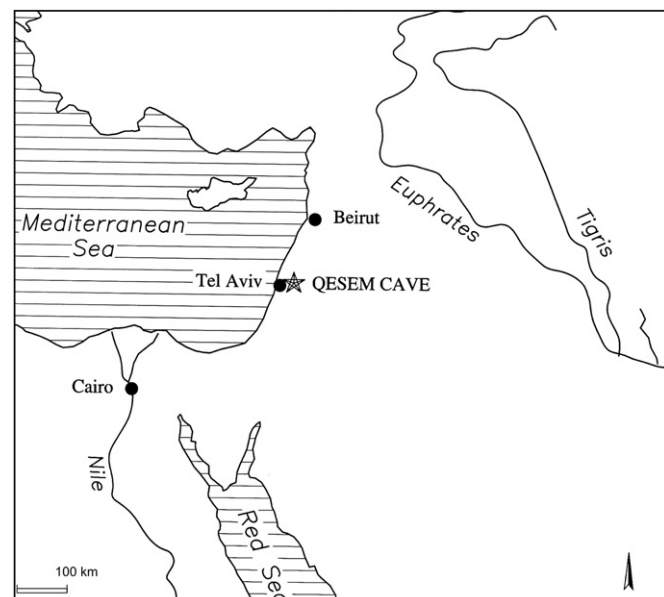


Figure 1. Location of Qesem Cave.

during the Middle Pleistocene, constantly changing the cave's landscape and conditions and finally acting as post-depositional agents shaping the present cave and its sediments (Frumkin et al., 2009).

The stratigraphic sequence has been divided into two major parts – the lower one (ca. 3 m thick), consists of sediments with clastic content and gravel (henceforth Lseq. = Lower sequence), and the upper one (ca. 4.5 m thick), including soft and cemented sediment with a large ash component (henceforth Useq. = Upper sequence). The transition from the Lseq. to the Useq. is characterized by several exposed large limestone boulders. This boundary is not yet excavated, so its detailed features are not exposed. The Lseq. was deposited in a closed karstic chamber cave, while the Useq. was deposited when the cave was more open as indicated by the presence of calcified rootlets (Karkanas et al., 2007).

The use of fire at the site is apparent not only by burnt bones and flints, but also by the presence of ash in the sediments. The micromorphological study indicates that fire was habitually used in the Useq. and present but less common in the Lseq. (Karkanas et al., 2007).

The microfauna-bearing area

During the 2004 season, we initiated an excavation at the southeastern part of the cave, at the bottom part of a talus-like feature belonging to the Useq., in squares L-M 13–14. This specific area was chosen for excavation for several reasons. First, this area seemed to be very close to the original eastern wall of the cave and the only place at the cave where sediments attached to the cave wall were easily accessible. Second, the excavation area offered the potential to study the stratigraphic relations between the Useq. and Lseq. because it included the lowermost part of the upper sequence, possibly revealing a direct connection between the two sequences. This is not yet possible in other parts of the cave. Third, the original topography of the cave in this area enabled access to the uppermost part of the stratigraphic sequence from the south, thus a southern profile within the talus-like feature was possible. This allowed us to remove the upper-cemented crust and uncover undisturbed intact layers. Subsequently, it became clear that the cemented sediments, stones and archaeological finds are actually a thick cover overlying the original stratified deposition. A similar exposure was reached following the removal of the cemented crust cover at the northern part of the Useq., at square K-10 (Lemorini et al., 2006).

As in other parts of the cave, this area was excavated in 0.5 × 0.5 × 0.05 m units. All sediments were dry sieved through a 2.4 mm mesh. Being close to the cave wall, this area was especially rich in finds including microfaunal remains. Therefore, it received special attention in recovery: large artifacts were retrieved manually during excavation and the sediments of these areas were processed by wet sieving through a 0.5–1.0 mm mesh (instead of dry sieving that might cause damage to the bones) and slowly dried in shadowed areas. The area rich in microfauna was excavated continuously by one of us (A. Barash). The sediment was then picked for microfaunal remains, which are stored in microtiter well-boxes.

Most of the micromammals and other microfaunal finds were recovered from this relatively small area in squares M-12, 13, 14; N-14, 15 at elevations 320–545 cm below datum; most of them in elevations 465–545. Altogether we excavated 2.5 square meters in this area. It is an inclining slope, and the top part was cleaned and prepared for excavation in ¼ square meter units by removing sediment and stones starting at around elevation 420 cm in square L-13, 300–320 in square M-13, ca. 350 cm in square M-14, and ca. 425–430 cm in squares N-14, 15 (a niche full of coarse grained sediments and rich in microfauna). Some of the subsquares were

dug down to elevation 545 by the end of the 2008 season while others are still higher. Altogether, some 3.80 m³ (not including the squares of strip L that yielded very few microfaunal remains) were excavated in this area. Microfauna-bearing excavation units of 0.5 × 0.5 × 0.05 m consist of 1.1 m³ of sediment (that is ca. 30% of the volume excavated in this area). This area is most probably close to the eastern cave wall and lies below the dated speleothem Q3 (see Gopher et al., 2010), although a clear stratigraphic connection between the speleothem and the microfauna-bearing layers could not be established.

From the very early stages of research, the sediment close to the eastern walls of the cave looked different from the sediment of the central parts of the cave in showing a complex stratigraphy. As seen on a section-looking north (Fig. 2), the sedimentary column in this part of the cave that yielded the microfaunal assemblage can be divided into two major parts.

The upper part consists of consolidated sediments and stone blocks of different size. Some fissures, voids (empty spaces) and small pockets of soft sediment within some of the fissures were found in this part of the sequence. One major fissure runs throughout the sequence from top to bottom in the eastern part of the area, possibly by the cave wall. Although the upper part of the sequence looks chaotic, it has a series of consolidated, relatively horizontal beds at its base down to elevation 430. This part of the sequence is rich in ash.

The lower part consists of a series of relatively thin beds and some stones inclined to the west and south. These start at elevation 430 in the east (M-13) and reach elevation 495 in the west (L-13, and see Fig. 2). The sediments are soft with small angular or sub-rounded stones and include at least two thin horizons of dark brown to black sediment, the rest appearing in different shades of brown. These inclined beds continue to the west through the sections of the excavated squares I, J/13 and at the top part of square H-13d of the deep sounding (see Fig. 3). Below these inclined beds is a thicker more massive sedimentation of light brown to gray colors similar in nature to the top sediments in the central deep pit. This part was excavated down to elevation 545. As in other studied areas, the top part of the Lseq. (Karkanas et al., 2007), especially



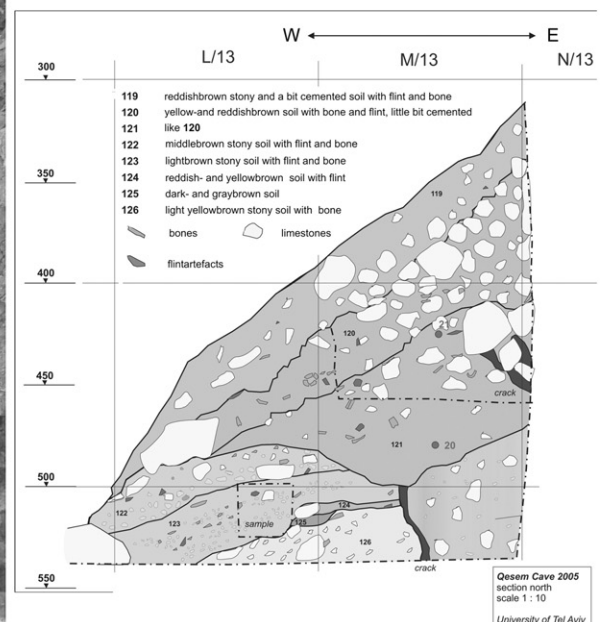
Figure 3. Levels inclined from the east (right part of the photo) towards the deep sounding.

close to the south-eastern wall, consists of a sedimentary sequence that is a mixture of loose, collapsed, gravelly material intercalating with brown clay showing some upward grading. The Lseq. as a whole is dominated by sediments that formed through mud and debris flow and includes localized hearths. The sequence is laminated, composed of brown clay and rock éboulis, and formed in a humid-closed cave environment (Karkanas et al., 2007).

A deeper look at the sediments and formation processes in the lower part of the area rich in microfaunal remains is provided by a detailed micromorphological study. An intact block of sediments (QCB-3), 25 cm thick, was collected in subsquare L-14b between elevations 495 and 520 cm below datum. The block belongs to the uppermost part of the Lseq. based on sedimentological and depositional considerations. The studied block is in close proximity (in a nearby subsquare) to the microfauna-rich area in squares M-13, 14. The macroscopic appearance of the sediments included in the block is brown laminated and it includes many pebble-sized clasts. The large clasts are both rocks and bones, and some flint of



Figure 2. Section through L, M-13, looking north (right in 2005; left in 2008) showing upper and lower parts of the microfauna-bearing area.



anthropogenic origin. The rocks are sub-rounded to sub-angular while the large bone clasts are mostly angular to sub-angular. The layers are inclined towards the west.

Infrared examination of bulk sediments from this block enabled the identification of the minerals clay, calcite and dahllite. The sources of these minerals were revealed through a micromorphological study of thin sections produced from the block (a total of three thin sections, each measuring 5×7.5 cm). The lower part of the block includes a large amount of rocky pebbles (0.3–3 cm in diameter), while its upper part is dominated by a brown clayey groundmass and includes large bone and teeth fragments. The rock clasts are composed of tufa, pure speleothem, dolomite, limestone and flint.

All rock types appear sub-rounded to sub-angular, indicating some degree of abrasion that occurred through the slow debris flow within the cave. These rock fragments are interpreted as éboulis, collapsed rocks from the cave walls and ceiling. Formation of phosphate rims around the carbonaceous rock fragments was not detected, (i.e., there is no evidence for acidic conditions related to organic matter degradation). The brown groundmass in the thin section is dominated by clay. The clay is associated with quartz sand and silt in a porphyric related distribution typical of clay-supported soils, and possesses an angular blocky microstructure (aggregates have angular edges, voids are planar and the faces of the aggregates accommodate each other). The aggregates are largely decalcified. The composition and structure of the groundmass is typical of *terra rossa* soil that is local and found outside the cave. Thus, it appears that soil material infiltrated into the cave and formed layers of sediment on the former cave floor. The clay crystals show an aligned orientation around voids and quartz grains (i.e., poro- and grano-striated arrangements, respectively). Such arrangements are indicative of cycles of wetting and drying (Jim, 1990). The clay aggregates include small black particles, most are manganese oxides and in rare occasions they have cellular structures resembling plant tissues. No calcitic ash is associated with these particles. In addition, the clay aggregates include small fragments of bones, mostly sub-rounded. Larger bone fragments, angular to sub-rounded, are found between the aggregates. One micromammal jaw with a molar was identified in the central part of the block (Fig. 4). The determination of this molar is very difficult because it is obliquely orientated to the thin section. Possibly we see a cut of a soricid molar near its outer margin. Bone fragments display

a variety of colors in plane polarized light (PPL), from pale yellow to dark reddish-brown. The latter is interpreted as burned. Some bones seem to be in the process of dissolution – they lack internal structure and appear as pale (almost transparent) gray in PPL and amorphous in cross polarized light (XPL). Such bones also frequently have rounded edges. Sometimes clear staining of bones by manganese oxides can be seen along bone edges. Secondary calcite appears as deposits along large voids, around rocky clasts, and in and around bone clasts. Calcite seems to envelop the clayey aggregates but did not precipitate in large masses within them. This observation is explained as follows: during wetting periods pore waters within the clayey aggregates are under-saturated with respect to calcite, while capillary movement of water from the clay aggregates towards large voids during drying periods resulted in saturation of the water with respect to calcite along void edges at the final stages of desiccation. Areas of dissolved secondary calcite also occur, (i.e., calcite shows evidence for cycles of dissolution and precipitation). There seems to be an increase in the amount of secondary calcite from the bottom of the sample to its top.

In summary, the source of clay in the infrared spectra is *terra rossa* soil; the source of calcite is primary rock éboulis, tufa and speleothems, and secondary calcite; the source of dahllite is the bones. Dolomite and quartz were not detected with the infrared, possibly due to their low amounts in the total sediment.

Most of the microvertebrate remains were retrieved from squares M 13–14 within the stratigraphic sequence of inclined sub-horizontal layers. In most cases the microfauna was associated with macrofauna and lithics and the general composition of these layers, apart from the abundance of microfauna, is not different from that of other layers of the cave. It thus appears that the micromammal remains were introduced to the archaeological layers during the course of deposition in a continuous manner. Microvertebrate remains were mostly retrieved from small “pockets” of soft sediments within the layers. Such bones could not be extracted from cemented or semi-cemented sediments. The fact that squares L-13 and L-14 are close to the slope of the talus-like feature affected the amount of these bones retrieved since most of the sediments were hardened or cemented. It is noted that the larger amount of microfaunal remains was excavated from the eastern most sub-squares M 13/M 14 b and M 14 d. These squares are associated with the major fissure that runs throughout the sequence from top to bottom in the eastern part of the area. The case may thus be that

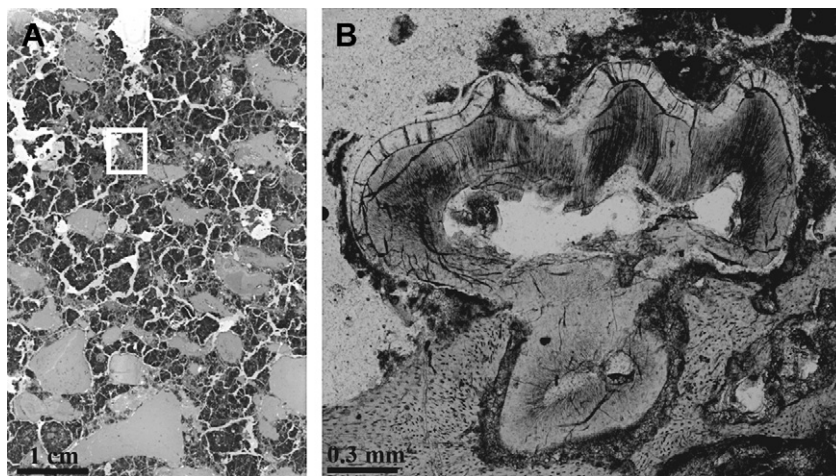


Figure 4. A) Scan of thin section QCB-3b showing the location of the oblique section of a micromammal jaw with tooth (in the white rectangle). The fragmented dark mass is the clay groundmass transected by planar voids due to desiccation. The light patches are macroscopic bone fragments. Large voids appear as elongated white features. B) Photomicrograph of the jaw with tooth. Note the preservation of both tooth dentin and enamel cap.

this fissure was one of the “channels” through which microvertebrate remains reached the above described sequence of deposition throughout the deposition sequence of this area. We reiterate the fact that most of the microfauna-rich sediments are part of the lower sequence deposited in a closed karstic cave.

A considerable number of additional microfaunal remains were found in small nooks and crevices between the fallen blocks and

the cave's eastern wall in the same area in subsquares N-14c and N-15a (see Fig. 5) and appear to be in stratigraphic correlation with excavation squares L/M 13–L/M 14. An insignificant number of microfaunal remains was recovered in another area, in squares F, G, H-10; I-8 (elevations 505–580) and J-12 (elevation 555–560), while the rest of the excavated areas in the cave yielded no microfaunal remains at all.

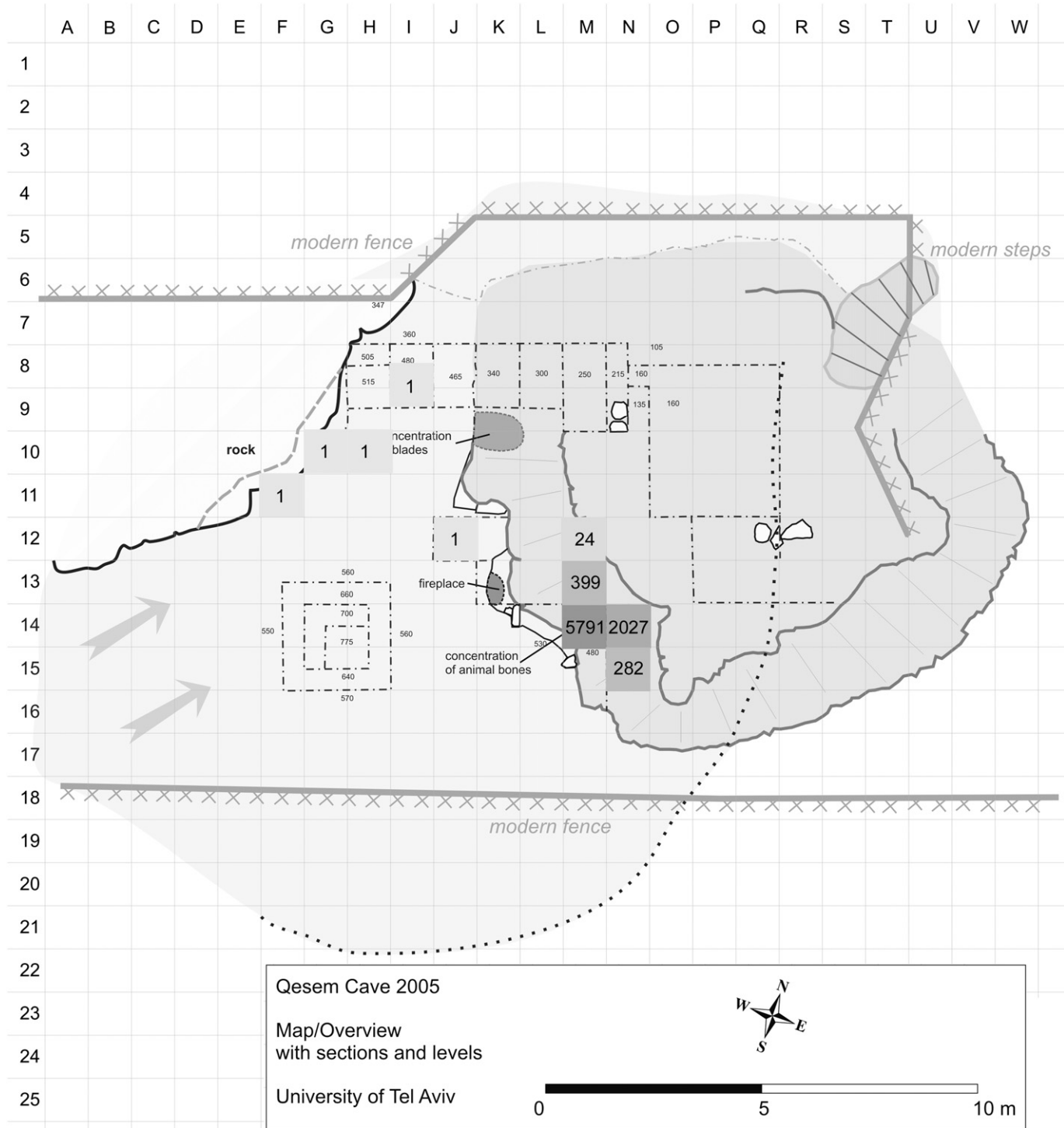


Figure 5. Spatial distribution of microfaunal remains at Qesem Cave. Numbers in gray squares indicate the number of microfaunal remains.

Archaeological finds and cultural entities

The human activity at Qesem Cave is securely assigned to the AYCC of the late Lower Paleolithic period (Barkai et al., 2003; Gopher et al., 2005). The AYCC of the Levant repeatedly appears stratigraphically above Lower Paleolithic Acheulian and below Middle Paleolithic Mousterian. Acheulo-Yabrudian sites are known from the central and southern Levant in caves and open-air sites.

At Qesem Cave, the Amudian blade industry of the AYCC dominates throughout the stratigraphic sequence and is characterized by systematic blade production. Alongside blade production, flakes also appear in the Amudian as well as some scrapers and single handaxes (Barkai et al., 2005, 2009; Boaretto et al., 2009; Barkai and Gopher, in press). Amudian blades were mostly used in cutting, butchering and defleshing activities on soft tissues and were practically conceived as disposable tools, cut and throw-away implements (Lemorini et al., 2006). Recently excavated areas at the cave revealed the presence of Yabrudian, scraper-dominated assemblages (Barkai et al., 2009).

Macrofauna

The faunal remains of Qesem cave also include a significant macrofaunal assemblage consisting of thousands of animal bones, on which cut marks and signs of burning are frequently observed (Stiner et al., 2009). According to Stiner et al. (2009), fallow deer (*Dama cf. mesopotamica*) was the main prey species at all layers of the cave (74–80% of the identified specimens); these remains are accompanied by rhinoceros (*Stephanorhinus hemitoechus*), wild ass (*Equus cf. hydruntinus*), a horse (*Equus sp.*), wild boar (*Sus scrofa*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), aurochs (*Bos sp.*), wild goat (*Capra aegagrus*) and tortoise (*Testudo graeca*).

The microvertebrate remains

Approximately 10,000 microvertebrate remains have been recovered so far, mainly belonging to micromammals and reptiles but also including a few remains of anurans and birds. Because this number includes many small bone fragments, the number of specimens precisely identified is much less. About 50% could be identified to the generic and hundreds to the species level. Reptilian remains outnumber mammalian remains, but this is partly because mammals are mainly identified by their jaws, molars, and sometimes incisors. The identification of reptiles, on the other hand, was based on all elements, and the lower species diversity of reptiles permitted the attribution of less globally diagnostic material. The preliminary faunal list from Qesem Cave is summarized in Table 1, measurements in Table 2. In the following descriptions, lower case denotes lower teeth and upper case denotes upper teeth.

Reptiles

Class “Reptilia” Laurenti 1768
Order Squamata Oppel 1811
Family Agamidae Fitzinger 1826
Genus *Laudakia* Gray 1845
Laudakia sp.

Over two hundred specimens are referred to *Laudakia*, including a premaxilla, maxillae, prefrontals, a jugal, postorbitals, a squamosal, quadrates, a nasal, frontals, parietals, a pterygoid, ectopterygoids, dentaries, an angular, compound bones, and vertebrae.

Our identification of this material as *Laudakia*, which includes the Hardun or Starred Agama (*Laudakia stellio*), rests on several newly identified apomorphies. The material is similar to members

Table 1
Microvertebrate taxa recorded from Qesem Cave.

Reptilia	<i>Laudakia</i> sp.
Squamata	<i>Chamaeleo</i> sp.
	Gekkonidae indet.
	Lacertidae indet.
	Scincidae indet.
	<i>Pseudopus</i> sp.
	<i>Varanus</i> sp.
	Colubroidea indet. (at least three species)
Mammalia	<i>Suncus etruscus</i>
Eulipotyphla	<i>Crociodura cf. leucodon</i>
	Crociodurinae indet. (large form)
Chiroptera	Chiroptera indet.
Rodentia	<i>Sciurus cf. anomalus</i>
	<i>Cricetulus cf. migratorius</i>
	<i>Microtus guentheri</i>
	<i>Nannospalax ehrenbergi</i>
	<i>Dipodillus cf. dasyurus</i>
	<i>Meriones cf. tristrami</i>
	Gerbillidae indet.
	<i>Mus cf. musculus</i>
	<i>Apodemus cf. flavicollis</i>

of the African–West Asian agamid clade Agaminae (*sensu* Macey et al., 2000; Group VI of Moody, 1980) in possessing only two anterior pleurodont loci on both maxilla and dentary (Fig. 6A–C). Most other agamids, in contrast, possess at least three such teeth on the dentary, and most also show a greater number of pleurodont teeth on the dentary than on the maxilla. Tooth morphology—simple, unicuspid crowns with a triangular labial and lingual profile (with a tendency toward weak convexity mesially and weak concavity distally), and without significant longitudinal grooves or irregularities (Fig. 6C)—is derived in the same manner as in Agaminae. The medial folding of the facial process of the maxilla creates an anterodorsally facing surface, a derived feature (Smith, 2009) also common to Agaminae. The fossil material is uniquely similar to *L. stellio* and *Acanthocercus cyanogaster*, among examined species (Appendix), in that the anterior pleurodont dentary tooth is larger than or subequal in size to the posterior one (Fig. 6A and B), whereas the posterior pleurodont maxillary tooth is larger than the anterior one (Fig. 6C); in all other examined agamids, the posterior-most pleurodont tooth is the largest on both maxilla and dentary. The postorbital possesses a weak, dorsoventrally elongate eminence for attachment of the supraorbital fascia that is separated from the frontoparietal articulation (Fig. 6D), as in *Laudakia*, but also possibly *Pseudotrapelus*. Finally, the maxilla is uniquely similar to *Laudakia* among Agaminae in having a posterior maxillary pleurodont tooth enormously enlarged in both length and girth (Fig. 6C), at least in some specimens (presumably males). The squamosal (Fig. 6E) is very similar to that seen in *L. stellio*.

A pair of jaws from Level 535–540, nearly identical in length but differing greatly in robustness, especially on the inferior margin of the jaw (Fig. 6A and B), suggests that this species showed sexual dimorphism in head size. Daan (1967) documented an intersexual difference of up to 10% in the linear dimensions of the head in populations distributed throughout the range of the species. Panov and Zykova (1997) confirmed this in Israeli populations. Sexual dimorphism of head size has also been found in North African *Agama impalearis* (Znari and el Mouden, 1997) and *Acanthocercus atricollis* (Reaney and Whiting, 2002); in the latter, larger heads in males may play a role in agonistic behavior (Reaney and Whiting, 2002).

Many presently recognized clades of Agaminae (*Acanthocercus*, *Agama*, *Laudakia*, *Pseudotrapelus*, *Trapelus*, *Xenagama*) were once included in the nominal genus *Agama*. As Delfino et al. (2008) recently noted, past referral of fossil material to “*Agama*” *sensu*

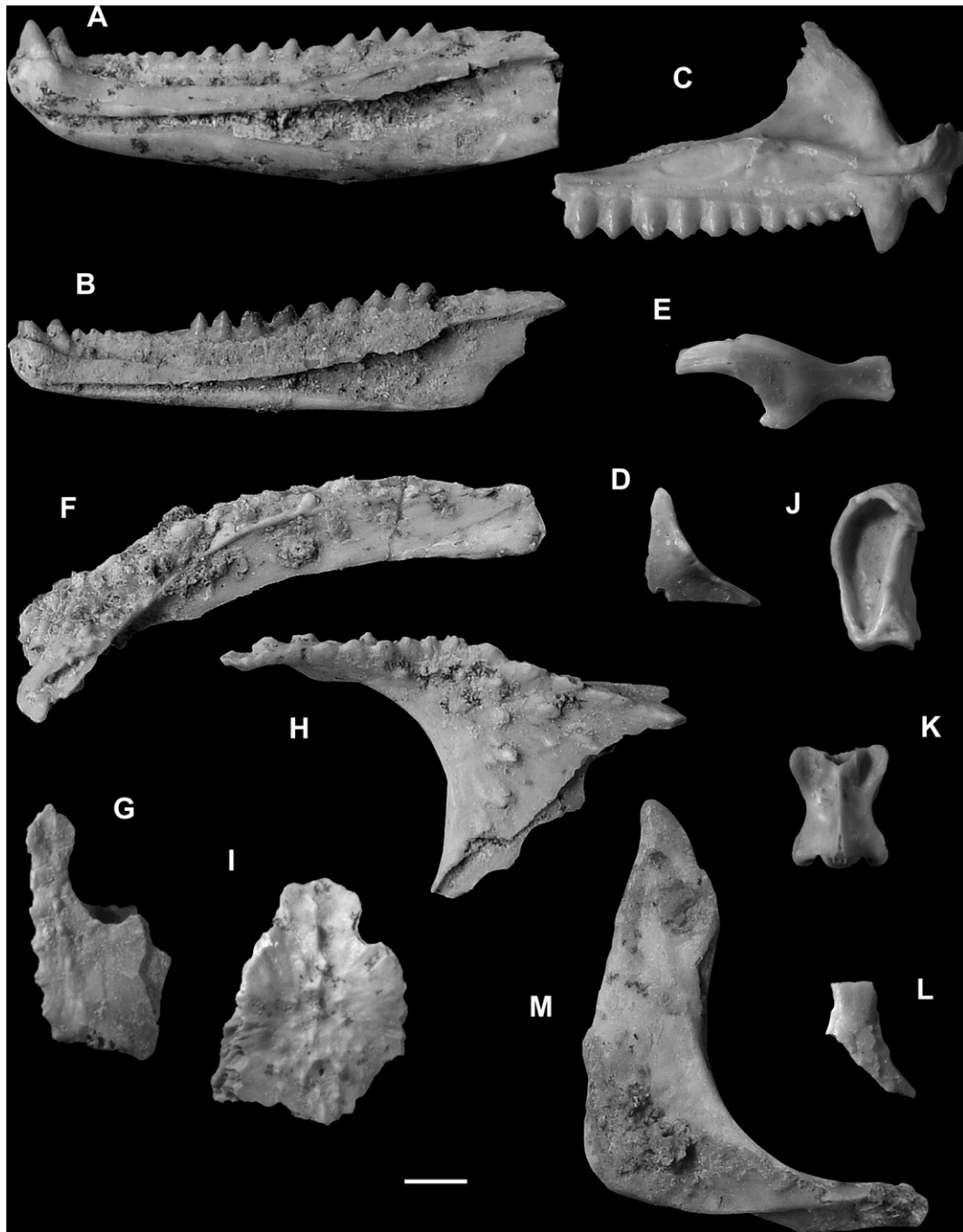


Figure 6. Squamate reptile remains from Qesem Cave. A and B), two right dentaries of *Laudakia* sp. in medial view. C) left maxilla of *Laudakia* sp. in medial view. D) right postorbital of *Laudakia* sp. in lateral view. E) left squamosal of *Laudakia* sp. in lateral view. F) parietal of *Chamaeleo* sp. in left lateral view. G) left prefrontal of *Chamaeleo* sp. in dorsal view. H) left postorbitofrontal of *Chamaeleo* sp. in lateral view. I) frontal of *Chamaeleo* sp. in dorsal view. J) left quadrate of undetermined lacertid in posterior view. K) mid-dorsal vertebra of undetermined ? lacertid in dorsal view. L) zygous frontal of undetermined scincid in dorsal view. M) right jugal of *Pseudopus* sp. in lateral view. Scale bar is 2 mm.

lato has been problematic. Species of *Agama*, *Laudakia*, *Pseudotrapelus*, and *Trapelus* occur today in or near the Levant (Baha el Din, 2006). We have suggested some new features that might help to distinguish among these species, and further study of the fossil and Recent comparative material will probably reveal more.

Only one species of *Laudakia*, *L. stellio*, occurs today in the Levant, and its range extends from Turkey east to Iraq and south to Egypt (e.g., Daan, 1967). Given the breadth of its range and habitat tolerances and the distribution of apomorphies discussed above, it is possible that the fossil material described here pertains to *L.*

stellio. Nevertheless, there are 21 nominal species of *Laudakia* (<http://www.reptile-database.org>), and skeletal preparations of species other than *L. stellio* were unavailable, so even if our identification of the fossil specimens as *Laudakia* is accurate, it would be premature to identify them to the species level.

An agamid “the size of *Agama* [= *Laudakia*] *stellio* is not rare” in the lower Pleistocene assemblage of ‘Ubeidiya (Haas, 1966:59; see also Haas, 1968). These remains were attributed to “*Agama*” (*s.l.*) sp. The extremely enlarged posterior pleurodont maxillary tooth (Haas, 1966: pl. I, fig. 6A, B) suggests that these remains also represent *Laudakia*.

L. stellio is reported to prefer “rocky, well-vegetated” habitats (Baha el Din, 2006). Indeed, except for on certain islands of the Aegean, the species is considered to show a preference for tree trunks (Beutler, 1981). Panov and Zykova (1997) observed populations in the Levant to be particularly dense in open (artificial) forest and orchards but noted also that they occur in areas of patchy, dense grass alternating with badlands. The species is excluded only from closed forest and unvegetated areas (Beutler, 1981). Shenbrot and Krasnov (1997) found *L. stellio* to be absent in most barren areas and only rare in areas with vegetation cover of 18.5%. In other words, the species appears to have a broad tolerance but is more abundant in well-vegetated areas with trees and large rocks. Tall objects may be important in the hierarchical social behavior of *L. stellio*, because dominant males perch on the highest available object for display (Disi et al., 2001). *L. stellio*, and presumably other species (like iguanians generally), is diurnal.

Family Chamaeleonidae Werner 1902
Genus *Chamaeleo* Laurenti 1768
Chamaeleo sp.

Nearly 1500 specimens are referred to a single species of *Chamaeleo*, including a premaxilla, maxillae, prefrontals, jugals, post-orbitofrontals, squamosals, quadrates, frontals, parietals, a pterygoid, ectopterygoids, basisphenoids, basioccipitals, an exoccipital, a supraoccipital, dentaries, coronoids, articulars, vertebrae, and limb and girdle elements. Vertebrae are the most common and are distinguished by the nearly parallel-sided central essentially lacking subcentral impressions, among other features (Hoffstetter and Gasc, 1969).

Chamaeleonidae is a morphologically diverse and species rich group distributed from Madagascar to India. It includes the dwarf, terrestrial, Malagasy genus *Brookesia* as its most basal member (Rieppel, 1987; Rieppel and Crumly, 1997; Townsend and Larson, 2002), as well as the following genera: African dwarf terrestrial *Rhampholeon*, African arboreal *Chamaeleo* (including the spectacular horned members of the subgenus *Trioceros*), *Bradypodion*, *Kinyongia* and *Rieppoleon*, and arboreal Malagasy *Calumma* and *Furcifer*. Of these, the fossil species shares almost exclusively with *Furcifer* (Rieppel and Crumly, 1997) and *Chamaeleo* (Rieppel et al., 1992) the presence of a strong, mediolaterally compressed parietal blade (Fig. 6F). As in *Chamaeleo* but unlike in most *Rhampholeon*, *Calumma*, and *Furcifer* (Rieppel and Crumly, 1997), the prefrontal (Fig. 6G) and postorbitofrontal (Fig. 6H) evidently met one another lateral to the frontal, as indicated by the posterior extent of the former and the anterior extent of the latter as well as the articular facets on the frontal (Fig. 6I). The specimens also share the deep emargination of the prefrontal by the prefrontal fontanelle with *Chamaeleo* (at least with the *Chamaeleo dilepis* and *Chamaeleo chamaeleon* groups) (Fig. 6G). This combination of apomorphies links the fossil species with *Chamaeleo*.

A combination of additional features suggests alliance with the *C. chamaeleon* group (the Common Chameleon and its close relatives). First, the parietal blade arches rather strongly (Fig. 6F), unlike in examined members of *Chamaeleo* (*Trioceros*) and the *C. dilepis* group (but possibly similar to what is seen in *Chamaeleo senegalensis*). The height of this structure is sexually dimorphic in close relatives of *C. chamaeleon* (Hillenius, 1959; Klaver, 1981), but there is unfortunately only one complete parietal in the assemblage. Second, the supratemporal bar of the Qesem taxon, as in *C. chamaeleon*, also appears to have arched slightly ventrally from the orbital margin, as indicated by a curvature of the postorbitofrontal (Fig. 6H); in contrast, in the *C. dilepis* group, *C. senegalensis* (Hillenius, 1988: fig. 3c; de Witte, 1965) and *Chamaeleo calyptratus* the dorsal margin of the postorbitofrontal is straight, which is

related to a relatively higher position of the supratemporal arch on the skull. The combination of a strongly arching parietal blade and a ventrally arched supratemporal bar implies the presence of a “roof-shaped parietal,” which Hillenius (1959: 43) considered distinctive of the *C. chamaeleon* group (including *Chamaeleo zeylanicus*). Finally, the frontal shows a median row of protuberances which presumably correspond with epidermal scales, suggesting that this species showed the median row of enlarged, projecting scales common to *C. chamaeleon* but lacking in *C. zeylanicus* (Hillenius, 1978) and *C. calyptratus*.

More comparative osteological study is necessary to identify the Qesem material to the species level, although its great abundance suggests this will be possible. Unfortunately, a tarsal spur has not yet been identified in the fossil material. This structure, which is present in males of *Chamaeleo africanus*, *C. calyptratus*, *C. zeylanicus* (all in the *C. chamaeleon* group), *C. gracilis*, and *C. dilepis*, but absent in other chamaeleons (Hillenius, 1959), and which is highly reduced or absent in *C. chamaeleon* (Hillenius, 1959, 1978; Baha el Din, 2006) and perhaps also *C. calcaricarenis* (Böhme, 1985; Largen and Spawls, 2006), might otherwise help to identify the fossil species.

Today, only one species of *Chamaeleo*, *C. chamaeleon*, occurs in the Levant (Barash and Hoofien, 1961; Disi et al., 2001), and apart from *C. africanus* no other species of the *C. chamaeleon* group is found within about 800 km. The curvature of the parietal blade is one feature that appears to distinguish the fossil Qesem species from populations presently living in the area. Namely, Hillenius (1978) noted that populations of *C. chamaeleon* in Sinai and the Levant differ from other populations in having a parietal crest that is nearly straight in lateral profile. Baha el Din (2006) also gives a straight parietal crest as a feature distinguishing between *C. africanus* (which forms, together with *C. calcaricarenis*, the sister-clade of *C. chamaeleon*; Townsend and Larson, 2002; Macey et al., 2008) and Egyptian populations of *C. chamaeleon*. On the other hand, Schleich et al. (1996) found that the curvature of the crest in *C. chamaeleon* is variable even within North African populations. More complete specimens will be necessary to determine how widespread a curved crest was in the Qesem population.

Species closely related to *C. chamaeleon*, like many other members of Chamaeleonidae, are generally considered arboreal. In Egypt, *C. africanus* (here, including also *C. calcaricarenis*) “inhabits cultivated areas, where it is found in orchards, often near or at the margin of wetlands (Baha el Din, 2006: 141; see also Dimaki et al., 2000). It “seems to prefer short dense trees and reeds” but has been observed on tall trees (Baha el Din, 2006: 141). *C. calcaricarenis* has been reported to occur on “small trees and shrubs” (Largen and Spawls, 2006: 37). According to Baha el Din (2006: 143), *C. chamaeleon* is found in “dry cultivations, orchards, and semi-desert with good vegetation cover and some larger bushes.” Disi et al. (2001: 163) report that the species “is restricted to regions with more or less dense vegetation: Mediterranean forests, gardens, patches of vegetation in wadis, etc.” The availability of taller vegetation appears to be particularly important for at least some populations of *C. chamaeleon*, where intraspecific cannibalism results in a vertical stratification by age-class of habitat occupation, adults occurring in bushes and trees and juveniles restricted to grass and open ground (Keren-Rotem et al., 2006). *Chamaeleo* is diurnal (e.g., Klaver, 1981; Baha el Din, 2006).

Family Gekkonidae (*sensu* Zug et al., 2001)
Gekkonidae indet.

One dentary and one compound bone are referable to Gekkonidae (geckos, pygopods, and relatives). The former is dorsoventrally short near the end of the tooth row and is

distinguished by a fused Meckelian groove and a large number of small teeth. The compound bone is identified on the basis of the morphology of the retroarticular process (see Estes et al., 1988). A small parietal fragment showing ventral origin of the adductor musculature and lacking rugosities or osteoderms on the dorsal surface possibly represents a gekkonid. Whether these represent a single species or several, and which species they might pertain to, is not yet established.

Without a more precise identification, these rare gekkonid remains have little to say about paleoenvironment.

Family Lacertidae Gray 1825
Lacertidae indet.

A complete left quadrate, as well as two partial frontal bones, are referred to Lacertidae (wall lizards and relatives). An articulation facet on the posterior frontal fragment indicates that a tab of the parietal underlapped the frontal, a diagnostic feature of lacertoids (Estes et al., 1988). The anterior frontal fragment shows similar sculpture to what is seen on the posterior fragment. The quadrate (Fig. 6J) is distinctively lacertid. Two rather elongate dorsal vertebrae showing subcentral impressions on the ventral surface on either side of the midline and accessory intervertebral articulations (the prezygapophyseal surface curving dorsally at its medial edge to form a rudimentary zygosphenes that is completely connected with the prezygapophysis; Fig. 6K) are tentatively referred to Lacertidae as well. Whether these remains represent a single species or several, and which species they might pertain to, is not yet established.

Without a more precise identification, these rare lacertid remains have little to say about paleoenvironment.

Family Scincidae Gray 1825
Scincidae indet.

A single partial frontal is tentatively referred to Scincidae (Skinks, Sandfish and relatives). Despite their diminutive size (frontals ~1.5 mm across at mid-orbit), the frontals are fully coalesced and the osteoderms are fused to the dorsal surface of the bone (Fig. 6L). The prefrontal scar extends past the mid-point of the orbit. The identity of this rare species has not yet been established.

Family Anguillidae Gray 1825
Genus *Pseudopus* Merrem 1820
Pseudopus sp.

A single right (Fig. 6M) and a single left jugal, a squamosal, and numerous vertebrae and osteoderms are referred to *Pseudopus*. Caudal vertebrae have fused hemal arches, as in many members of Anguillidae and *Amphisbaenia* (Hoffstetter and Gasc, 1969). The vertebrae, with their ventrally flattened surfaces, are characteristic of Anguillidae, and their size implies an animal far surpassing any member of the clade except the *Pseudopus apodus* (Glass Snake or Sheltopusik) lineage in this respect. The osteoderms are characteristic as well. The three skull elements all derive from the same three-cm level; their similar size and preservation (same color, heavily encrusted) suggest they could represent a single individual. A more specific identification may prove possible.

This lineage of large, limbless lizards is known since the Miocene (e.g., von Fejérváry-Langh, 1923; Klembara et al., 2010). The jugal of the Qesem taxon is more massively constructed than that of the living *Pseudopus apodus* but lacks the (plesiomorphic?) quadratojugal process seen in the fossil taxon *Pseudopus pannonicus* (von Fejérváry-Langh, 1923: pl. I, figs. 6, 6a). *Pseudopus* does not appear to be common at Qesem in comparison with the

acrodont iguanians; remains of this taxon are mostly confined to vertebrae and osteoderms, which outnumber skull bones even in taxa with unelongated bodies.

In Jordan today, living *P. apodus* “prefers light woodlands, with dry and warm hillsides” and is “often found near stream banks” (Disi et al., 2001: 165).

Family Varanidae Hardwicke et Gray 1827
Genus *Varanus* Merrem 1829
Varanus sp.

A single partial left prefrontal is tentatively referred to *Varanus* (Monitor Lizards). A species identification is probably impossible on the basis of this fragment alone.

Superfamily Colubroidea Oppel 1811
Colubroidea indet.

Several vertebrae are referred to Colubroidea, a clade including most advanced snakes (vipers, grass snakes, cobras, etc.). At least three species appear to be represented, but their identity has not yet been established. The rarity of snake vertebrae in comparison with those of other squamates at Qesem is surprising.

Mammals

Class Mammalia Linnaeus 1758
Order Eulipotyphla Waddell, Okada et Hasegawa 1999
Family Soricidae Fischer von Waldheim 1814

About 40 mandibular and maxillary fragments as well as isolated teeth are referable to white-toothed shrews (Crocidae), the largest subfamily of shrews, whose center of diversity is in Africa. Dentition within this group is rather uniform, consisting of three molars, two antemolars and the incisor in the lower jaw, and three molars, four (*Crocidae*) or five (*Suncus*) antemolars and an incisor in the upper jaw. The shape of the articular process, with a broad interarticular bridge between the two facets, is an important character in separating shrew genera. The crocidurine species are mainly distinguished by size.

Genus *Suncus* Ehrenberg 1833
Suncus etruscus (Savi 1822)

The Etruscan or Pigmy white-toothed shrew is represented by only a few fragments (Fig. 7C). The tiny dimensions of the length of the molar series in the mandible make this record unambiguous. The alveolar length of the molar tooth row m1–m3 in two available specimens is 2.68 and 2.71 mm, respectively. This size is in complete agreement with the Recent comparative material as well as the data in the literature (Spitzenberger, 1990; Harrison and Bates, 1991; Kryštufek and Vohralík, 2001). The Recent *Suncus etruscus* is adapted to grasslands (meadows, hedgerow margins) (Mitchell-Jones et al., 1999).

Genus *Crocidae* Wagler 1832
Crocidae cf. *leucodon* (Herrmann 1780)

The common field or bi-colored white-toothed shrew is represented by a dozen jaw fragments (Fig. 7A). The coronar length of m1–m3 ranges from 3.82–4.59 mm (mean 4.32 mm, $n = 5$). This size does not differ from that of Recent representatives of this species. It is larger than the two other contemporaneous species, *Crocidae russula* and *Crocidae suaveolens* (cf. Genoud and Hutterer, 1990; Vlasák and Niethammer, 1990). *Crocidae leucodon* is indicative of habitats in plains and mountains up to

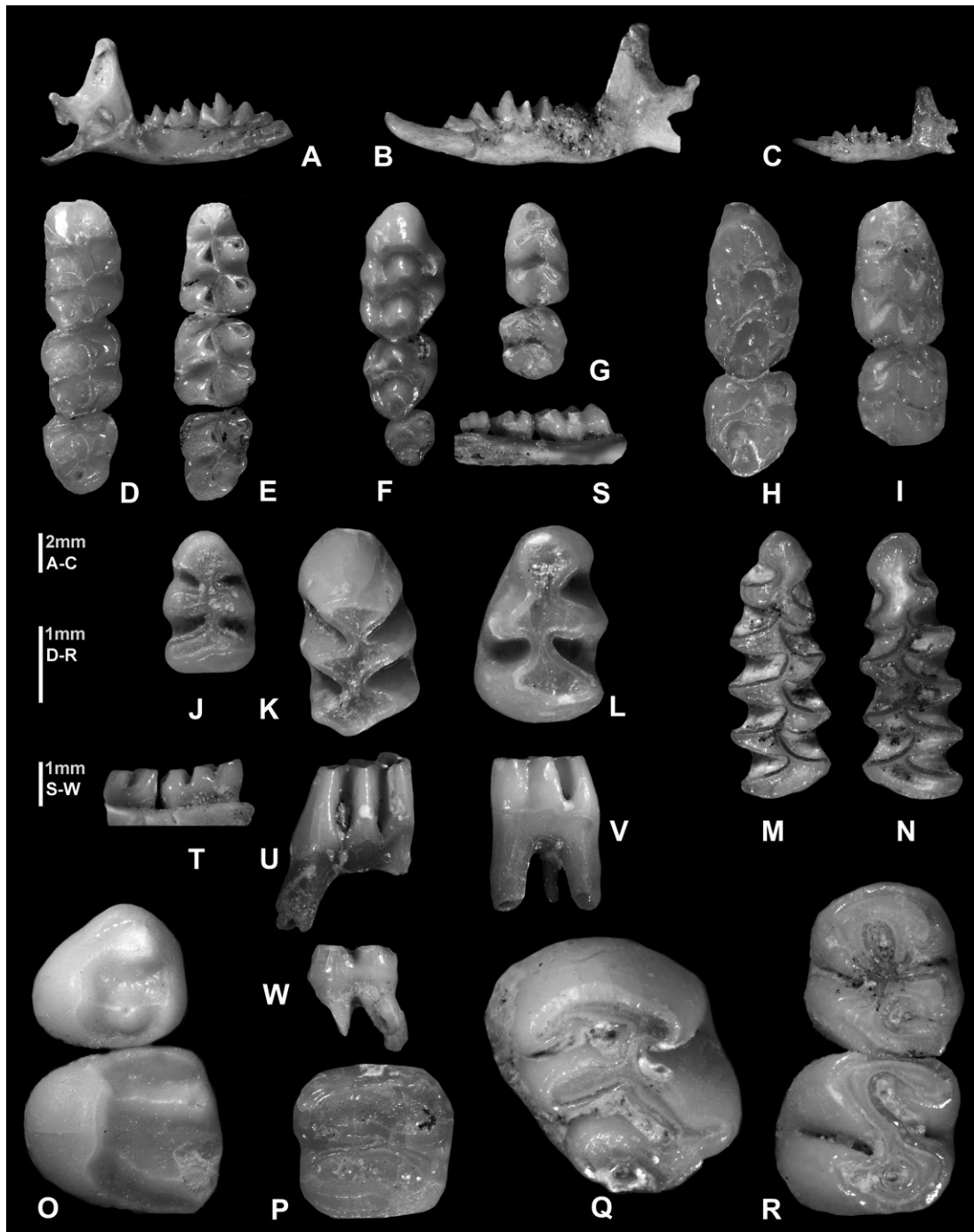


Figure 7. Micromammal remains from Qesem Cave. A) *Crocidura cf. leucodon*, right mandible. B) *Crocidurinae* indet., left mandible. C) *Suncus etruscus*, left mandible. D) *Cricetulus cf. migratorius*, left upper M1–M3. E) *Cricetulus cf. migratorius*, left lower m1–m3. F and S) *Mus cf. musculus*, right upper M1–M3. G) *Mus cf. musculus*, right lower m1–m2. H) *Apodemus cf. flavicollis*, right upper M1–M2. I) *Apodemus cf. flavicollis*, right lower m1–m2. J) *Dipodillus cf. dasyurus*, right lower m1. T) *Dipodillus cf. dasyurus*, right lower m1–m2. K and U) *Meriones cf. tristrami*, upper M1. L and V) *Meriones cf. tristrami*, lower m1. W and P) *Gerbillidae* indet., lower m2. M and N) *Microtus guentheri*, lower m1. O) *Sciurus cf. anomalus*, left upper P4–M1. Q) *Nannospalax ehrenbergi*, right upper M1. R) *N. ehrenbergi*, left lower p4–m1. A–C, S–W, buccal view and D–R, occlusal view.

3600 m and occurs in dense vegetation (Mitchell-Jones et al., 1999).

Crocidurinae indet.

A third white-toothed shrew represented by five specimens is much larger in size than the previous two species (Fig. 7B). On two mandibles an m1–m3 coronar length of 6.35 and 6.84 mm could be

measured. This attains the dimensions of *Suncus murinus* (Linnaeus 1766), the Asian house shrew. Until recently it was distributed from Afghanistan to China and in the Indo-Malayan region and was supposedly introduced by man into coastal regions of Arabia and Africa from East Asia (Butler, 1998; Wolsan and Hutterer, 1998). However, *S. murinus* is also listed in several late Middle and Late Pleistocene faunas from Israel (e.g., Tchernov, 1996), which would

weaken the hypothesis of an introduction in recent times. For now, the remains are determined as an unusually large species of a Crocidurinae indet. until more material will enable a taxonomical reexamination.

Chiroptera Blumenbach 1779
Chiroptera indet.

Several jaw and humerus fragments belong to Chiroptera. Bats can be distinguished from other micromammals by the lower mandible ramus and the particular shape of their molars. Thus far, the material is still too fragmentary for a more detailed identification.

Order Rodentia Bowdich 1821
Family Sciuridae Hemprich 1820
Genus *Sciurus* Linnaeus 1758
Sciurus cf. *anomalus* Gueldenstaedt 1785

A maxillary fragment with P4 and M1 (P4 length: 2.10 mm, M1 length: 2.39 mm) and a lower p4 (length: 2.30 mm) belong to a squirrel (Fig. 7O). The occlusal pattern with rather low cusps and crests is indicative of a tree squirrel (genus *Sciurus*), which is more brachyodont than ground squirrels (*Spermophilus*). *Sciurus* has less pronounced metaconids but a stronger entoconid than *Spermophilus*. According to the Recent distribution it can be referred to the Persian squirrel *Sciurus anomalus*. However, *S. anomalus* is usually characterized by bigger size compared to the European Red squirrel *Sciurus vulgaris* (van der Meulen and Doukas, 2001), however, that is not the case here. Additionally, van der Meulen and Doukas (2001) stress that in *S. vulgaris* the P4 is longer than M1 and M2, but in *S. anomalus* it is not. This relation can be also observed in the Qesem specimen. However, because of the paucity of material we refer the specimens tentatively to *Sciurus* cf. *anomalus*. *Sciurus* depends on trees and is therefore an indicator for wooded areas (Mitchell-Jones et al., 1999).

Family Cricetidae Fischer von Waldheim 1817
Genus *Cricetulus* Milne-Edwards 1867
Cricetulus cf. *migratorius* (Pallas 1773)

A total of twelve jaw and teeth fragments of the Qesem material are referable to a small cricetid (Fig. 7D and E). According to their morphology and size, identity with *Cricetus* and *Mesocricetus*, with clear funnel-like structures between the opposed upper molar tubercles (Savić, 1982), can be excluded. Two species similar in size remain under consideration: the Gray Hamster *Cricetulus migratorius* and *Allocricetus jezreelicus* described by Bate (1943) from level F of Tabun. She found morphological differences between these two species in features of the skull. *A. jezreelicus* can thus be distinguished from *Cricetulus* by a short, wide and deep rostrum, supraorbital ridges, and the shape of the hinder part of mandible. Unfortunately, no sufficiently complete skull material is available from Qesem.

Allocricetus and *Cricetulus* are very similar in their dental pattern (Schaub, 1930), with split anterocone and anteroconid (Fahlbusch, 1969) (nomenclature of cricetids after Kälin, 1999), and in their size (Tchernov, 1968; Fahlbusch, 1969). Tchernov (1968, citing Schaub, 1930) stressed that the posterolophid (= posterior cingulum in Tchernov, 1968) of m1 is well developed in *C. migratorius* and less prominent in *A. jezreelicus*, which, on the contrary, has an anterolophid (= anterior cingulum in Tchernov, 1968) on m1 more commonly than in *C. migratorius*. In both species, a mesostylid is developed only on m3 – which, according to Tchernov (1968), should be more frequent in *Cricetulus* than in *Allocricetus*, although Topachevskij and Skorik (1992) figure specimens of the latter with a well-developed mesostylid on m3. In the available Qesem specimens the posterolophid in m1 is well developed,

mesostylids in m3 are well developed, and tooth row lengths fall within the ranges given by Harrison and Bates (1991) for Middle East populations of *C. migratorius*. Because of the greater similarity with *C. migratorius*, we refer our material to this species, however as “confer.”

C. migratorius is characterized by considerable habitat plasticity. It prefers steppes and stony places with sparse vegetation but inhabits also desert and semi-desert (Mitchell-Jones et al., 1999).

Family Arvicolidae Gray 1821
Genus *Microtus* Schrank 1798
Subgenus *Sumeriomys* Argyropulo 1933
Microtus (*Sumeriomys*) *guentheri* (Danford et Alston 1880)

All arvicolids possess high-crowned prismatic molars. The older (mainly pre-Pleistocene) species have still rooted molars, whilst the genus *Microtus* is without roots (Fig. 7M and N). Guenther's vole belongs to the subgenus *Sumeriomys* together with *Microtus socialis*, *Microtus anatolicus*, etc. (Shenbrot and Krasnov, 2005). The species is much more derived than the rather primitive member of the *Tibericola* lineage from 'Ubeidiyah (von Koenigswald et al., 1992) in having five clearly closed dentine fields. Members of *Microtus guentheri* are distinctly larger than most other *Microtus* species (including *M. socialis*). The thickness of the enamel edges and the relative length of the anteroconid complex in the lower m1 are diagnostic of *Microtus* species (the A/L-index devised by van der Meulen, 1973). For the Qesem specimens, all these parameters are basically the same as in the living *M. guentheri*. The mean A/L-index is 55.72 (min: 51.70, max: 60.45, n: 31, sd: 1.99) and the mean length of m1 is 3.14 mm (min: 2.82 mm, max: 3.52 mm, n: 32, sd: 0.17). Morphologically and metrically (mean length of m1: 3.15 mm), the Qesem sample resembles the published specimens from the Middle Pleistocene of the island of Chios (Greece) described by Storch (1975). *M. guentheri* currently lives in grassy terrain, bushy scrub, mountain slopes and valley, open oak forests (Mitchell-Jones et al., 1999).

Family Muridae Illiger 1815
Genus *Mus* Linnaeus 1758
Mus cf. *musculus* Linnaeus 1758

The smaller of the two murid species recorded at Qesem shows all dental morphological traits of the genus *Mus* (Fig. 7F, G and S). Some authors treat *Mus domesticus* and *Mus musculus*, the Western and the Eastern house mouse, as different species, others as subspecies of *M. musculus* (Mitchell-Jones et al., 1999). Metrically, the remains from Qesem exactly match the data for *M. musculus* derived from different sources, including those of the fossil site Oumm-Qatafa (Tchernov, 1968). However, *Mus macedonicus* is also a possible candidate. In the Middle East, this species is similar in overall size to *M. musculus* (Harrison and Bates, 1991). A major diagnostic feature distinguishing these two species is the thickness of the zygomatic arch of the skull, which is not present in our material. According to Çolak et al. (2006), the m1 of *M. macedonicus* can be distinguished from that of *M. musculus* by its more prominent mesiolabial cusp. Specifically, there is a deeper incision between the buccal anteroconid and the protoconid (Çolak et al., 2006; Fig. 3) (nomenclature for murids after Freudenthal and Martín Suárez, 1999). Occasionally, some specimens of *M. macedonicus* display a mesial cusp on M1, a t3 on M2 and a lingual outline of M2 that is straight or convexly rounded (Çolak et al., 2006). Zagorodnyuk (2002), who refers *M. macedonicus* to *M. spicilegus* s.l., points to the more forward inclination of the anterior root of M1 and the relative shorter M3 of *M. musculus*. *Mus camini* described by Bate (1942) from Tabun level D–E, is another member of the genus. However, according to

her description this species is hardly to be distinguished morphologically and metrically from either of the latter species and is elsewhere considered conspecific with *M. musculus* (Wilson and Reeder, 1993).

M. musculus is characterized by an extremely wide range of ecological adaptation. Originally living in steppes and semi-deserts, its ability to live commensally in human settlements enabled it to spread throughout the whole world (Mitchell-Jones et al., 1999). *M. macedonicus* is mostly limited to the Mediterranean and is reported from a wide range of open habitats, whereas it avoids forests (Mitchell-Jones et al., 1999).

Genus *Apodemus* Kaup 1829
Apodemus cf. *flavicollis* (Melchior 1834)

A larger murid at Qesem possesses typical characters of the subgenus *Sylvaemus* (i.e., a small antero-central cusp on the m1 and a series of buccal accessory tubercles) (Fig. 7H and I). On the available M1s, neither a connection between tubercles t1–t5 nor an additional tubercle t2bis can be recognized as it is typical (Filippucci et al., 1996) in the Steppe Field Mouse *Apodemus witherbyi* (= *A. hermonensis*). Because of a greater morphological resemblance with the molars of *Apodemus flavicollis*, the yellow-necked mouse, we refer the Qesem specimens to this species, although metrically they fit the size of both *A. witherbyi* and *A. flavicollis* and are between the measurements of the smaller *Apodemus sylvaticus* and the larger *Apodemus mystacinus* (Niethammer, 1978a,b,c). On the other hand, Tchernov (1979) mentioned considerable size fluctuations within the members of the *Sylvaemus* group in Israeli fossil localities. Although small specimens of *A. mystacinus* overlap with the range of the Qesem teeth, this species (here referred to *Sylvaemus*) can be excluded since on the upper M1 the connection t12–t9 is weak, which is atypical for *A. mystacinus* (Storch, 2004).

Further species, obviously members of the subgenus *Sylvaemus*, were described by Bate (1942) from Tabun. *Apodemus caesareanus* is the size of *A. sylvaticus*, and *Apodemus levantinus* is large as *A. flavicollis*. Bate (1942) mentions diagnostic features in the skull, which are not determinable in the Qesem material. However, because of the remaining uncertainties we refer the fossil *Apodemus* from Qesem to *A. cf. flavicollis*.

In Western Europe *A. flavicollis* lives in forests, but in the East it can also occupy more open habitats (e.g., hedges) (Mitchell-Jones et al., 1999). Tchernov (1979) observed that *A. flavicollis* occurred in Pleistocene fossil sites in Israel only during colder periods.

Family Spalacidae Gray 1821
Genus *Nannospalax* Palmer 1903
Nannospalax ehrenbergi (Nehring 1898)

The enamel pattern of these rather large dental remains indicates a spalacid, subfamily Spalacinae (Blind mole rats) (Fig. 7Q and R). The oblique orientation of the re-entrant angles of the molar occlusal surface is typical for the genus *Nannospalax*, and distinguishes this taxon from members of the genus *Spalax* (Topachevskij, 1969; Savić, 1982). The size and geographic distribution enable reference of the spalacid remains to *N. ehrenbergi*.

Nannospalax lives on plains and hilly steppes. Deep, loose, well-drained (diggable) soil is preferred – true desert, forest, swamps, and marshes are avoided. It is also absent from rocky substrates (Savić, 1982; Mitchell-Jones et al., 1999).

Gerbillidae Gray 1825
Genus *Dipodillus* Lataste 1881
Dipodillus cf. *dasyurus* (Wagner 1842)

The smallest representative of the gerbils recorded at Qesem is referred to Wagner's Gerbil (Fig. 7J and T). The teeth are characterized

by rather small dimensions, rather low crowns and less symmetric cusps in comparison to the bigger genus *Meriones* (see below) (Tong, 1989). As Payne (1983) previously noted, *Gerbillus nanus* has a similar size to Wagner's Gerbil. Therefore, we refer the specimens to *Gerbillus* cf. *dasyurus*. This species lives in rocky steppe desert, whereas *G. nanus* inhabits sandy desert (Tchernov, 1975; Ferguson, 2002).

Genus *Meriones* Illiger 1811
Meriones cf. *tristrami* Thomas 1892

Tristram's Jird (Fig. 7K, L, U and V) can be distinguished from the former species by its bigger size, clearly more hypsodont teeth (see Fig. 7U and V vs. Fig. 7T), and a rather symmetric appearance caused by an opposition of the tubercles. The crown patterns of *Psammomys* and *Meriones* are not much different, but the base of the enamel (in lateral view) is fairly flat in *Meriones*, while in *Psammomys* "the embayments run much higher up each lamina and have more pointed ends" (Payne, 1983: 8). Thus, we can exclude *Psammomys*. The number of roots in our specimens (M1–4, M2–2, M3–1, m1, m2–2 and m3–1) indicate that the molars also differ from *Parameriones* recorded at 'Ubeidiyah (Tchernov and Chetboun, 1984). *Meriones* is adapted to deserts and steppes and is tolerant of wide range of soil conditions (Tchernov, 1975; Mitchell-Jones et al., 1999; Ferguson, 2002).

Gerbillidae indet.

A single m2 has a very particular appearance with unfused lophs (laminae). By this morphology and by its size (cf. Tong, 1989; Wessels, 1998) it resembles *Tatera*. Currently, the genus does not occur in the territory of Israel. However, a single specimen is not enough to prove this referral. Therefore it is assigned to Gerbillidae indet (Fig. 7P and W).

Taphonomy

The occurrence of microvertebrates in fossil deposits owes mainly to birds of prey or mammalian carnivores (Canidae, Mustelidae) (Andrews, 1990). Particularly, nocturnal birds of prey (owls) regurgitate rather well-preserved bone and teeth. The dietary spectrum of these animals consists of up to 90% of micromammals. The accumulation in Qesem Cave probably has the same origin, because several owl species roost in cave fissures or perch on promontories near cave entrances. The Barn Owl *Tyto alba* is known to prey upon *C. chamaeleon*, as are species of *Falco* and mustelids (Schleich et al., 1996). Although owls and presumably other predators are capable of bearing prey some 20 km from their source (Kowalski, 1990), Porder et al. (2003) determined that most faunal remains discovered in Porcupine Cave (Wyoming, USA) originated within a radius of about 5 km from the cave entrance. Thus, one might reasonably assume that most small animals preserved at Qesem were taken close to the cave. Nevertheless, predation is a taphonomic filter, and certain species will be overrepresented in the assemblage because of ease of capture or food preferences (Kowalski, 1990).

Paleoecological implications

Tchernov (1975), in his paleoecological analysis, referred fossil rodents recorded in Israel to particular living spaces (rock, grassland, moist steppe, woodland, sand dunes). Of the species recorded at Qesem the following can be referred to as grassland dwellers: *N. ehrenbergi*, *C. migratorius*, *Meriones tristrami*, *Microtus guentheri*. Woodland dwellers are *A. flavicollis*, and *S. anomalus*. A rock dweller is *Dipodillus dasyurus*. This suggests

Table 2

Tooth measurements of rodent taxa recorded from Qesem Cave.

		mean	min	max	N
<i>Cricetulus cf. migratorius</i>	m1–m3 coronar length	3.82	3.79	3.85	4
	m1 length	1.46	1.38	1.66	7
	m2 length	1.15	1.12	1.18	5
	m3 length	1.15	1.08	1.25	5
	M1–M3 coronar length	3.95	3.67	4.13	4
	M1 length	1.63	1.55	1.73	6
	M2 length	1.19	1.09	1.32	6
	M3 length	1.10	1.05	1.12	4
	<i>Mus cf. musculus</i>	m1–m3 coronar length	2.23	1.48	2.98
m1 length		1.44	0.90	1.69	15
m2 length		0.99	0.91	1.07	12
m3 length		0.62	0.62	0.62	1
M1–M3 coronar length		3.39	3.23	3.61	5
M1 length		1.81	1.65	2.01	10
M2 length		1.07	0.97	1.22	6
M3 length		0.73	0.66	0.82	5
<i>Apodemus cf. flavicollis</i>	m1–m3 coronar length	4.80			1
	m1 length	1.96	1.81	2.08	7
	m2 length	1.42	1.33	1.46	6
	m3 length	1.44	1.44	1.44	1
	M1 length	2.19	2.16	2.22	2
	M2 length	1.39			1
<i>Nannospalax ehrenbergi</i>	M1 length	2.92	2.91	2.93	2
	M3 length	2.01	1.78	2.24	2
	m1 length	2.34	2.29	2.36	4
	m2 length	2.12	2.09	2.16	2
	m3 length	2.31	2.10	2.52	3
<i>Dipodillus cf. dasyurus</i>	m1 length	1.88	1.62	2.22	10
	m1 crown height			0.80	8
	m2 length	1.17	1.17	1.17	1
<i>Meriones cf. tristrami</i>	M1 length	2.54	2.23	3.23	15
	M1 crown height			2.29	12
	M2 length	1.56	1.45	1.71	8
	M2 crown height			1.75	8
	M3 length	0.84	0.84	0.84	1
	m1 length	2.48	2.29	2.84	11
	m1 crown height			1.72	9
	m2 length	1.61	1.39	1.92	7
m2 crown height			2.07	7	

the existence of a mosaic of habitats in the vicinity of Qesem Cave.

The squamate assemblage is dominated by two acrodont iguanian species, *Laudakia* sp. and *Chamaeleo* sp. The specimens of *Chamaeleo* sp. in particular represent roughly 75% of the squamate

remains recovered so far. The chameleon suggests relatively dense vegetation, as might *Laudakia* sp., if it represents the same species occurring in the Levant today.

The spatial distribution of microvertebrate specimens at Qesem Cave is not homogeneous. The part of the sequence that is higher than 430 cm below datum (see above) contains only a few microfaunal remnants, at least in square M13. The only specifically determinable specimen is an m1 of *M. guentheri*, which is similar in size to the specimens from the lower part of the sequence.

The majority of the specimens derive from the part deeper than 430 cm below datum. Although remains are concentrated in particular squares and at particular levels (see above), there seem to be no major taxonomic differences between upper and lower levels, only shifts in the relative amount of the recorded specimens per taxon. Yet these shifts suffice to suggest a slight change in environment between the upper (320–525 cm below datum) and lower (525–545 cm below datum) microfauna-bearing levels. In particular, *Laudakia* sp. and *Chamaeleo* sp. are represented by nearly twice as many specimens in the upper levels as in the lower. In contrast, *Pseudopus* sp. is represented in the upper levels by only one-fourth the number of specimens. Thus, the taxa with arboreal tendencies are relatively and absolutely more common in the upper levels. The conclusion of more densely vegetated conditions during deposition of the upper levels is corroborated by the sole occurrence there of the tree squirrels (see Table 3). It should be noted that the record of large animals (Stiner et al., 2009) accords with the interpretation of a mosaic of wooded (*Sus*, *Dama*, *Cervus*, *Capreolus*) and open (*Equus*, *Testudo*, *S. hemitoechus*) areas surrounding Qesem Cave.

Stratigraphic implications

Micromammals are generally excellent biostratigraphic indicators. The species composition of an assemblage and the evolutionary level of individual species can enable a fairly precise age determination. In temperate regions of the Holarctic, particularly arvicolids are among the most useful biostratigraphic markers. They show clear evolutionary trends in dental morphology from their origin in the Late Miocene to the present. The crown height of rooted molars increases, and eventually rootless forms evolve. Such forms, including *Microtus* and *Arvicola*, have elaborate enamel patterns on the lower first and upper third molar and variation in the enamel thickness on all molars. These trends are continuous but not strictly linear, and obviously vary geographically. On the basis of such data a refined stratigraphic scheme was devised

Table 3

Spatial distribution of microvertebrates within the microfauna-bearing levels of Qesem Cave.

	indet.	Amphibia	Aves	Reptilia					Mammalia																		
				Agamidae	Chamaeleonidae	Anguidae	Varamidae	Lacertidae	Insectivora		Chiroptera		Rodentia														
									<i>Suncus</i>	<i>Crocodyra</i>			<i>Sciuridae</i>	<i>Cricetidae</i>	<i>Arvicolidae</i>	<i>Spalacidae</i>	<i>Gerbillidae</i>	<i>Dipodillus</i>	<i>Meriones</i>	<i>Muridae</i>	<i>Mus</i>	<i>Apodemus</i>					
Total	4364	11	14	2056	227	1451	331	1	4	577	40	40	4	35	5	402	2	11	136	10	52	8	40	33	13	10	
430-525 cm																											
below datum	3902	7	8	1191	135	955	67	0	4	335	16	16		16		201	2	4	82	6	27	5	21	15	6	4	
525-545 cm																											
below datum	462	4	6	865	92	496	264	1	0	242	24	24	4	19	5	201	0	7	54	4	25	3	21	18	7	6	

Table 4
Species composition of the micromammals from Qesem Cave in comparison to other Pleistocene sites of Israel (data from Tchernov, 1992; Tchernov, 1996; Goren-Inbar et al., 2000).

Locality	Chrono-cultural unit	<i>Suncus etruscus</i>	<i>Crocidura leucodon</i>	<i>Sciurus anomalus</i>	<i>Cricetulus migratorius</i>	<i>Mus macedonicus</i>	<i>Mus musculus</i>	<i>Apodemus flavicollis</i>	<i>Dipodillus dasyurus</i>	<i>Meriones tristrami</i>	<i>Nannospalax ehrenbergi</i>	<i>Microtus guentheri</i>	<i>Paramerion obediensis</i>	<i>Microtus (Tibericola) jordanica</i>	<i>Lagurodon aranka</i>	<i>Lagurodon praepannonicus</i>	<i>Kalymnomys haasi</i>
Qesem		x	cf.	cf.	cf.		cf.	cf.	cf.	cf.	x	x					
Israel	Present	x	x	x	x	x	x	x	x	x	x	x					
Shovakh		x		?			x		x	x							
Geula		x		x			x		x	x							
Hayonim Upper E		x		x			x		x	x							
Kebara	Middle	x	x	x	x	x				x	x	x					
Tabun B	Paleolithic	x	x	x	x	x	x		x	x	x	x					
Tabun C	Mousterian	x	x	x	x	x	x		x	x	x	x					
Tabun D		x	x	x	x	x	x	x	x	x	x	x					
Qafzeh XV-XVIV		x	x	x		x	x	x	x	x	x	x					
Hayonim Lower E		x	x	x	x	x	x		x	x	x	x					
Tabun E	Lower Paleolithic Acheulo-Yabrudian		x	x		x	x	x		x	x	x					
Tabun F				x			x			x	x	x					
Oumm-Qatafa			x	x		x			x	x	x	x					
Gesher Benot Ya'aqov	Lower Paleolithic					x			x		x	x		x			
Give'at Shaul (= Jerusalem)	Acheulian					cf.		x	x		x		x				x
Evron + Latamne						cf.		x	x		x		x	x	x		
'Ubeidiya			cf.			cf.		x	x		x		x	x	x	x	

decades ago (Kretzoi, 1941, 1956) and continues to be developed (e.g., Fejfar et al., 1998).

Therefore, it was hoped that the microvertebrates might help refined age estimates for the deposits at Qesem Cave. The preliminary results, however, show that all the taxa identified in the Qesem Cave assemblage also occur today in the territory of Israel. On the other hand, many taxa are not yet identified with certainty to species, and further taxonomic work could reveal differences at the specific level (Table 4).

Comparing the taxa from Qesem with those of other Pleistocene sites in Israel, one can recognize that assemblages of this composition occur since at least the Oumm-Qatafa Acheulian and the Tabun D Mousterian (cf. Tchernov, 1996). There is then a gap in the record, and the next older fauna (Gesher Benot Ya'aqov – Goren-Inbar et al., 2000), up to c. 780 ka, includes not only taxa occurring in the later parts of the Middle Pleistocene but also species wanting(?) in these younger assemblages. According to these data, the Qesem assemblage could be of any age younger than 780 ka.

Even arvicolid are not particularly helpful in this case. In Qesem Cave, there is thus far only one arvicolid species known, *Microtus guentheri*. In other *Microtus* lineages, clear morphological and morphometric differences are observed between the very early forms (at c. 1.8 Ma) and those of the early Middle Pleistocene (e.g., see Maul et al., 1998). From the later Middle Pleistocene (c. 250 ka) onwards, these forms are more or less identical in dental morphology to the Recent forms. Because Qesem is dated by other means to 400–200 ka (see below), the major differences between the Qesem and Recent forms cannot be expected. Detailed morphometric comparison with material from other sites in the region is necessary and may yet provide further constraint.

The absolute dating of the AYCC indicates a starting date of about 400 ka ago and a replacement by the Middle Paleolithic Mousterian culture around 200 ka (e.g., Barkai et al., 2003; Rink et al., 2004; Le Tensorer et al., 2007; Gopher et al., 2010). A pilot U-Th (TIMS) dating project (eight dates) of Qesem Cave indicated a range between about 380 and 200 ka (Barkai et al., 2003). An intensive program of U-series dating has recently been completed and indicates a similar range, approximately 400–220 ka (Gopher et al., 2010). Another project of TL and ESR dating accompanied by a thorough dosimetry program throughout the cave's sedimentary sequence is now underway.

We propose that the sediments bearing the bulk of the microfauna, stratigraphically positioned below the orange sediments (however not in direct contact) are older than 300 ka. This proposal is based on three observations. First, the microfauna-bearing sediments belong to the top part of the lower sequence. Second, the lower sequence is clearly below the orange sediments under the shelf in the central western part of the cave (see Gopher et al., 2010). Third, we have dated an *in situ* speleothem within the orange sediments below the shelf to ca. 300 ka (see Gopher et al., 2010). It is noteworthy that fragments of speleothems found within the talus-like feature above the microfauna-bearing unit have shown dates between 254 and 218 ka (Barkai et al., 2003). Another relevant point is that a TL project not yet published has given preliminary dates of ca. 360 ka for samples from the deep sounding in the center of the cave that are part of the lower sedimentary sequence over two meters below the microfauna-bearing unit. Thus, a provisional age range for the microfauna is 360–300 ka. Dosimeters were inserted within the microfauna-bearing layers, and we hope to be able to provide direct dates in the near future.

General remarks

As mentioned in the introduction, these results are to be seen as preliminary. Species identifications of micromammals and

squamate reptiles need to be refined based on comparison with more fossil and Recent material. Moreover, less numerous faunal elements like birds and amphibians need to be studied. Doubtlessly, both advances will contribute to a more precise environmental characterization of the surroundings of Qesem Cave. Specific identification of the mammals will permit more detailed faunal comparisons with other relevant Levantine sites (e.g., Tabun Cave). Finally, present sample sizes for particular stratigraphic units are insufficient to describe in detail the potential environmental change discussed above. The fact that many thousands of additional finds are being made every field season promises that meaningful quantitative analyses may become possible in the very near future.

Perhaps the most curious aspect of the Qesem microvertebrate fauna is the great abundance of chameleon remains. The fossil record of Chamaeleonidae is generally sparse. Outside of the Levant, the taxon is known from a few Miocene specimens from Africa (e.g., Rieppel et al., 1992), some remains from the Miocene of Europe (e.g., Moody and Roček, 1980; Böhme, 2010), and a record from the Holocene of Spain (Talavera and Sanchíz, 1983). Hooijer (1961) cites a few jaws from the site of Ksâr'Akil in Lebanon, but they are much less abundant than co-occurring *Pseudopus* remains. Haas (1952) also noted that remains "Agama", *Chamaeleo* and *Testudo* were particularly abundant in the Nafutian site of Abu Usba, but he gave no indication that *Chamaeleo* was any more abundant than the other two. The superabundance of *Chamaeleo* in Qesem Cave (roughly 75% of identified squamate specimens) is noteworthy, and we hope that ongoing taphonomic work will clarify its significance.

It is too early in the research cycle for Qesem Cave to address particular hypotheses of the relation between hominin habitat occupation and environment, since we do not know enough about the Qesem Cave hominins. It is clear, however, that even these first faunal results will inform such hypotheses as the makers of the well-studied Acheulo-Yabrudian industry at Qesem become better known.

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Appendix

Modern comparative squamate skeletons examined for this study: Agamidae: *Acanthocercus cyanogaster* (UF 50556), *Acanthosaura armata* (UF 69015), *Bronchocela cristatella* (UF 42346, 51820), *Calotes mystaceus* (SMF 69754), *C. versicolor* (UF 68490, 71577), *Draco volans* (UF 53599), *Gonocephalus grandis* (UF 61544, 61548), *Hydrosaurus amboinensis* (SMF 70930), *Japalura polygonata* (UF 63381, 63382), *L. stellio* (CM 39115, 39116, UF 68087), *Lyriocephalus scutatus* (UF 68088), *Phrynocephalus maculatus* (UF 71573, 71574), *P. interscapularis* (UF 80248), *Physignathus cocincinus* (SMF 61415, UF 71685, 71686), *Pogona vitticeps* (SMF 71829), *Pseudotrapelus sinaitus* (UF 13934), *Trapelus agilis* (UF 74674, 74675), *T. megalonyx* (UF 67819), *T. pallidus* (CM 41289), *T. ruderatus* (UF 71720, 71721); Uromastycidae: *Leiolepis belliana* (SMF 57471, UF 62046–62048), *Uromastyx acanthinurus* (UF 54136), *U. geyri* (UF 144229), *U. hardwickii* (CM 145030, 145031, 145037), *U. princeps* (CM 145043, 145044); Chamaeleonidae: *Chamaeleo hoehneli* (CM 144863, 144865).

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