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The microvertebrates of Qesem Cave: A comparison of the two concentrations

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ABSTRACT

Middle Pleistocene Qesem Cave, Israel, contains one of the richest known deposits of microvertebrate remains in the Near East, nearly a quarter of a million specimens. The remains have been excavated from two main concentrations, and over 16,000 have been identified to genus level. The faunal content of the two concentrations is broadly similar, and only a few taxa are restricted to the one or the other; most notably, the *Myomimus judaicus/setzeri* group and *Rattus* cf. *haasi* are only known from the chronologically older Concentration 2. The identification of *Stellagama stellio* is presented as an example of tree-thinking in the Quaternary; a phylogenetic tree is an epistemic structure that provides a non-arbitrary means to determine the minimum number and phylogenetic position of extant comparative specimens required to identify an extinct population. The new mammal data show that the total proportion of lower vertebrates in the microfauna is lower than previously thought, although *Chamaeleo chamaeleon* remains by far the second most-abundant prey species. The assemblages from the two concentrations are significantly different from each other in terms of relative abundances: lower vertebrates, shrews, and bats are less abundant in the Concentration 2, and several rodents, most notably *Microtus guentheri*, are more abundant there. However, rank-order abundance between the two assemblages is strongly correlated, suggesting that the surrounding community was largely stable. The taphonomic data obtained so far suggest a Barn Owl as the predominant accumulator in Concentration 1, although natural history observations on Barn Owls and chameleons are strongly at odds with this actualistic inference. We suggest that this represents an example of non-analog behavior in the extinct Barn Owl population. Barn Owls, in turn, are sensitive to disturbance and unlikely to have occupied the cave at precisely the same time as the hominins. These observations suggest new ways to study human occupation patterns and behavioral adaptation.

1. Introduction

Qesem Cave is a sediment-filled karst chamber cave on the moderate western slopes of the Samaria hills in Israel some 12 km east of the present-day Mediterranean coast (Fig. 1) and 90 m above sea level. It is some 20 × 15 m in size and ~10 m high. The Samaria hills are underlain by limestone rich in dissolution cavities, many of which are still active. Qesem Cave is part of a larger karst system within the B'ina Formation of Turonian (Late Cretaceous) age (Frumkin et al., 2009, 2016) and has been excavated systematically since its literal discovery in 2001, producing a wealth of archeological finds. All layers of the sequence have been securely assigned to the Acheulo-Yabrudian Cultural Complex of the late Lower Paleolithic (Barkai et al., 2003; Gopher et al., 2005; Mercier et al., 2013; see also Maul et al., 2016; Falgueres et al., 2016).

In addition to a large number of artifacts (Barkai et al., 2006; Lemorini et al., 2006; Barkai et al., 2009, 2010; Shimelmitz et al., 2011; Blasco et al., 2013; see also papers in in this volume), large mammal bones (Stiner et al., 2009, 2011; Blasco et al., 2014, 2016), and some human teeth (Hershkovitz et al., 2011), Qesem Cave is very rich in microvertebrate remains (Maul et al., 2011; Horáček et al., 2013; Smith et al., 2013). The fossils separate readily from the matrix, enabling an unprecedented level of attention to these small vertebrate remains. The assemblage was first discovered in

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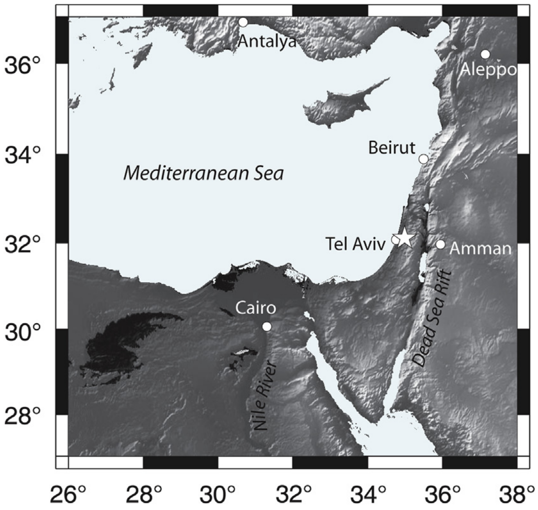

Fig. 1. Location of Qesem Cave (indicated by star) in the Levant.

2006 and now comprises some 250,000 specimens, making it one of the largest such assemblages in the Near East. It is of major importance for bridging the well-known Lower and Upper Pleistocene records. Qesem Cave may thus give new insights into human adaptation and cultural evolution as well as into microvertebrate biological evolution.

Nearly all of the microvertebrates derive from two relatively small concentration areas. Maul et al. (2011) presented a summary of the microvertebrate fauna from one concentration, and significant new collections have been made there since that report. Additionally, the richer second concentration has been excavated and studied, but has not yet been reported on. The purpose of this paper is to provide a taxonomic overview of both concentrations, including refined identifications and newly unearthed taxa. Comparison of the two assemblages may enable additional insights into the stratigraphy and biochronology of the cave deposits (Maul et al., 2016) and perhaps into the history of the cave structure and the retreat of the ceiling, based on the spatial positioning of the concentrations. We also show how tree-thinking (O'Hara, 1988, 1997) in the Quaternary can be used to compensate for a dearth of comparative material, especially in herpetology. We then present detailed quantitative comparisons of the faunal content of the two concentrations. Finally, we review the taphonomy of the site.

2. Materials and methods

2.1. Spatial distribution

In this paper we consider the material from the 2006–2012 excavation seasons. Excavation of the site is based on a 1-m grid system, with sides labeled B–N and 2–17 in the focal area. Sediment was removed in units (subsquares) measuring 50 × 50 × 5 cm (i.e., 4 excavation units per square for every 5-cm layer of sediment, labeled a, b, c and d). In the microvertebrate areas the fossil-bearing sediment was screenwashed using a 0.8 mm mesh size (after first using finer mesh to determine that important fossils do not pass through the 0.8-mm mesh). All bone from screenwash concentrate was picked in the field and sorted taxonomically in the lab. The density of microvertebrate remains was visualized using the "triangulate," "grdfilter" and "grdview" programs in Generic Mapping Tools (Wessel and Smith, 1998).

The stratigraphy of Qesem Cave is complex, and the physical relation between the two microfossil-bearing layers has not been fully established by excavation. However, a well-dated central hearth feature (Shahack-Gross et al., 2014; Falgueres et al., 2016) separates the overlying Concentration 1 (the "Eastern Microfauna-Bearing Area" of Mercier et al., 2013) from Concentration 2 (Falgueres et al., 2016), which is consistent with older age estimates for the latter concentration based on arvicolid biometrics and biostratigraphy (Maul et al., 2016). Accordingly, Concentration 1 is thought to be roughly 250–280 ka (Mercier et al., 2013), and Concentration 2 older than 300 ka (Falgueres et al., 2016; Maul et al., 2016).

2.2. Taxonomy

For the lower vertebrates, skeletal elements from the entire skeleton were identified and inventoried; for small mammals, mainly the teeth. Identification of reptile remains follows as far as possible a tree-thinking approach (Appendix B. Supplementary data). Bird remains are also found in these concentrations but will be the subject of future studies.

2.3. Diversity

Given the apparent age difference between the two concentrations, it is of interest to know whether the faunal content differs between them. Belmaker and Hovers (2011) presented a detailed analysis of diversity and abundance among small mammals at Amud Cave using established ecological methods, and we build to a great extent on their study.

Observed species richness (number of species) depends in part on sample size, and various methods have been developed to compare richness among samples. A distinction has always been drawn between interpolation methods like rarefaction, which calculate expected richness at lower sample sizes, and extrapolation methods, which estimate richness at greater-than-observed sample sizes (e.g., Gotelli and Colwell, 2001). Recently, Colwell et al. (2012) developed a unified system for rarefaction-extrapolation, which is implemented in EstimateS v.9 (Colwell, 2013). We used this system to compare the two concentrations. We further used the abundance-based coverage estimator (ACE; Chao, 2005) to calculate the minimum asymptotic species richness of the two assemblages. ACE is based on an approach that regards the rare species in an assemblage as crucial for estimating total minimum species richness (Chao, 2005; Gotelli and Chao, 2013). In this case, we take the default cut-off value of $\kappa = 10$ individuals (i.e., ACE is based on the taxa with 10 or fewer individuals each). Preliminary estimates of the distribution of individuals among taxa in Colubroidea and Lacertidae had to be made as follows. Lacertidae (2 species total): 15/5 and 10/3 individuals for Concentrations 1 and 2, respectively; Colubroidea (3 species total): 15/4/1 and 15/10/2.

The Shannon and Simpson indices are also frequently employed in studies of species diversity. They incorporate the number of species present as well as their relative abundance, but are not directly comparable. They are also sample-size dependent, and methods allowing for extrapolation of these indices are now becoming available (Chao et al., 2014). We calculated the (natural-log) Shannon, H, and (inverse) Simpson, $1/D$, indices for the two assemblages. To determine whether any differences in the indices between the two assemblages are statistically significant, we used two approaches, both based on subsampling. First, we took a bootstrap approach, creating 1000 resamples of each data set with