

Special Issue: Personal Ornaments in Early Prehistory

Location, Location, Location: Investigating Perforation Locations in *Tritia gibbosula* Shells at Ksâr 'Akil (Lebanon) Using Micro-CT Data

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ABSTRACT

Perforated shells are often used to study socially mediated behavior in past hunter-gatherer groups. The assumption is that their exclusive symbolic function makes them ideally suited to investigate social networks, dispersal activity, and social interaction. Before making any statements regarding human behavior, however, it needs to be established whether perforated shells from archaeological assemblages were used as personal ornaments. One of the key issues regarding beach-collected marine taxa is whether beached specimens were purposefully collected, e.g., preferentially selected naturally holed specimens, or whether human-made perforations may be identified. Past studies have investigated these questions by comparing datasets from modern death assemblages of shells with archaeological collections and through manufacture and use-wear analysis (e.g., Bouzouggar et al. 2007; Vanhaeren et al. 2006). This study introduces a novel approach using μ CT scans of pristine shells to create a three-dimensional model of shell thickness in *Tritia (Nassarius) gibbosula*. This model is used to map robust and fragile zones on shells of this taxon. The goal of this approach is to identify structurally weak zones that would be prone to natural perforations. Heat maps of shell thickness are then used to investigate perforation locations in modern natural death and archaeological assemblages. Our results show that in natural death assemblages, most perforations occur in structurally weak zones, and that their distribution is random. In our archaeological samples, from early Upper Paleolithic contexts at Ksâr 'Akil, (Lebanon), we found that perforations in *T. gibbosula* mainly occur in structurally weak zones, but their distribution within these zones is not random and favors locations facilitating easy suspension (e.g., on cordage). This suggests that at Ksâr 'Akil, *T. gibbosula* shells were used as beads, and that shells with conveniently located natural perforations were intentionally sought for, that humans perforated the shells themselves, or that they used a combination of both. This in turn, warrants investigations into the social and behavioral implications of these perforated beads. Further aspects of human involvement with the shells should be explored, for example, through use-wear analysis.

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INTRODUCTION

All living humans practice symbolic activity, i.e., the ability to store, share, and transmit information that is coded in material culture within and across groups (e.g.,

d'Errico and Stringer 2011). In general, symbolically mediated behaviors are essential in the creation and maintenance of beliefs, conventions, and identities. Ethnographic studies demonstrate that personal ornaments including

body paint, beads, and headdresses, are recognized in traditional communities as strong markers of identity (e.g., Vanhaeren and d'Errico 2006). This behavior strengthens group-internal coherence and establishes and maintains boundaries with neighboring groups (e.g., Hodder 1977). While a large part of material culture may be symbolically imbued, personal ornaments are one of the few archaeological objects whose function is exclusively symbolic (e.g., d'Errico and Stringer 2011; d'Errico and Vanhaeren 2007; White 2007). Personal ornaments have therefore often been used to study socially mediated behavior in past hunter-gatherer groups. For example, in the recent past, shell beads have featured in debates concerning modern human behavior (e.g., Bouzouggar et al. 2007; d'Errico et al. 2005, 2009; Henshilwood et al. 2004; Marean et al. 2007; McBrearty and Brooks 2000; Vanhaeren et al. 2006, but see Zilhão et al. 2010), social networks (e.g., Álvarez Fernández and Jöris 2008; Bar-Yosef Mayer 1997; Gamble 1998; Kuhn et al. 2001; Rigaud et al. 2018; Shennan 2001; Vanhaeren and d'Errico 2006), and dispersal activity (e.g., d'Errico and Vanhaeren 2007; d'Errico et al. 2009; Hovers and Belfer-Cohen 2006; Klein 2008; Vanhaeren et al. 2004; Álvarez Fernández 2016).

Marine shells may be perforated at various stages. For example, through bioerosion, e.g., attacks by carnivorous snails, crabs, and other predators, damage by boring sponges, or damage resulting from being in an active beach environment (e.g., wave action, abrasion). Archaeological specimens may have been intentionally perforated, broken during use, pierced by post-depositional taphonomic processes such as trampling, rock fall, or processes of sediment reworking, which might also lead to crushing, and/or damaged during excavation (e.g., during sieving) and curation (Claassen 1998; White personal communication 2017). To investigate socially mediated behaviors, it is important to establish which perforations can be linked with human decision making. Areas in which human actions can be identified concern transport decisions, signs of selection of specific specimens, human modifications, and use (e.g., Bouzouggar et al. 2007; d'Errico et al. 1993; Perlès and Vanhaeren 2010; Vanhaeren et al. 2006, 2013). In the past studies have investigated these questions by comparing modern death assemblages with archaeological datasets and through manufacture and use-wear analyses (e.g., Bar-Yosef Mayer et al. 2009; Bouzouggar et al. 2007; d'Errico et al. 2009; Vanhaeren et al. 2006). We add to this by investigating how shell damage, including perforations, relates to the shell's structure both in natural (thanatocoenosis) and anthropogenic (archaeological) contexts using shell thickness as a proxy for structural resistance. In broad chronological terms, it appears that during the Levantine Middle Paleolithic and the onset of the Upper Paleolithic shells have been purposefully collected and naturally perforated shells may have been used for ornamental purposes without the need for modification. Others may have been intentionally pierced (e.g., Bar-Yosef Mayer 2005). Here we investigate *Tritia gibbosula* shells from Initial and Early Upper Paleolithic contexts from Ksâr 'Akil (Lebanon). Our goal is to contribute to a better understanding of whether a perfora-

tion is the result of natural or anthropogenic processes. We predict that most natural taphonomic processes affect thinner presumably structurally weaker zones in a shell's outer wall to a higher degree than thicker more robust zones. Moreover, damage in similarly weak zones should be randomly distributed. If our predictions are correct, deviation from these patterns needs an explanation and could suggest human involvement in either the manufacture (perforation) or the selection of perforated shells from a beach.

MATERIAL AND METHODS

Here we present a novel approach, which uses μ CT data to create three dimensional models of shell thickness to better understand the shell's biomechanical properties. Using heat maps to demonstrate thickness via CT data is common practice in different fields (e.g., Guignard et al. 2013; Jaume et al. 2003; van Uitert and Summers 2007). First, we μ CT-scan intact shell specimens to create a virtual model of *Tritia gibbosula*. Second, from this virtual model we derive a shell thickness heat-map. We then investigate natural perforation distributions from a modern death assemblage with regard to shell-thickness and test our predictions regarding the location of natural perforations. Next, we compare these data with perforation location patterns of archaeological shell assemblages from the Initial Upper Paleolithic and Early Ahmarian of Ksar 'Akil. Differences between the modern and archaeological shell assemblages are statistically evaluated.

μ CT-SCANS OF RECENT SPECIMENS

Tritia gibbosula specimens from the Eastern Mediterranean (i.e., Cyprus) were obtained from the collection Mollusca at Naturalis Biodiversity Center (RMNH.Mol.204910). Shells were selected for their pristine preservation and care was taken to avoid specimens that suffered damage from, e.g., attacks by predators, bioeroders, and wave-action. Several specimens were selected to make sure density patterns are similar species-wide and to exclude specimen-specific abnormalities.

μ CT (or microCT) stands for micro-computed tomography. CT is an X-ray attenuation-based imaging technique analogous to combining many traditional radiographs to digitally recreate a three-dimensional (3D) volume of an object based on the radio-densities of its constituent materials (Abel et al. 2012; Zollikofer et al. 1998). In the last several decades, CT imaging techniques have become widely used in fields such as Zoology, Archaeology, Geology, and Anthropology (e.g., Abel et al. 2011; Asher et al. 2017; Criswell et al. 2017; Sayab et al. 2016; Seidler et al. 1997; Weber et al. 2001). Using geographical and species-specific variations in tool morphology scientists attempt to understand the evolution of cognition, culture and human behavior. However, the dispersal of artifact collections around the globe in a large number of institutions makes direct study and comparison of the artifacts problematic, and therefore dependant on published drawings and photographs. The present study aims to determine whether CT could be used to create computerized (virtual) models with

the advantage of non-destructive visualization of internal structures and the protection of delicate original specimens from repeated handling. CT data also enable sophisticated visualization and exploration of surfaces and volumes, such as the mapping of shell thickness in the current study. The main division in the types of CT data used in archaeology is between data collected on μ CT and medical CT scanners. These types of scanner work in slightly different ways—in a medical CT scanner, the patient (or specimen) remains stationary and the X-ray source and detector panel spins around them collecting images; in a μ CT scanner, it is normal for the source and detector to remain stationary whilst the specimen rotates. The relevant difference, however, is in the resolution of the scan. A μ CT such as the Metris X-Tek HMX ST 225 CT scanner (Nikon®) used in this study has a resolution up to 0.005mm^3 (in μ CT the voxels, 3D pixels, are isometric), whereas medical CT scans rarely have a greater resolution than 0.2mm in any plane. Thus, μ CT data are preferable for visualizing and characterizing small objects, such as the shells in the current study.

The shells were μ CT scanned at the Cambridge Biotechnology Centre, University of Cambridge. The scan parameters were optimized for individual scans (consisting of three to four scans per shell) and were reconstructed with voxel sizes ranging from $0.01\text{--}0.03\text{mm}$ (isotropic). Segmentation of each shell was performed automatically using thresholds optimized for best segmentation results in Avizo 8.1 (Thermo Fisher Scientific - FEI). The removal of non-shell material, such as attached grains and finer sediments, was done manually. A virtual surface (i.e., cloud of three-dimensional points connected by triangles) was then extracted from the segmented volume, allowing for maximal and unconstrained smoothing (level 9 in the function 'Surface Gen').

Shell thickness was computed for each virtual surface as the distance along the vertex normal to the normal's intersection with the closest triangle (using the function 'Surface thickness' in Avizo 8.1). The resulting scalar field was then mapped into the surface using three different color ranges from thin to thick: 1) black to white, 2) blue to red with green representing intermediate thickness, and, 3) purple via white, purple, blue, green, yellow, and black to red for the thickest parts. Shell thickness was evaluated with regard to the shell's internal structures using orthoslices. Color ranges are unique to each shell. For subsequent analyses, the second color range was used as it emphasizes thickness variation in the areas of interest. The final images were obtained in six views (i.e., ventral, dorsal, both lateral sides, apical, and basal).

THANATOENOSIS

For our modern natural death assemblage, we used published modern thanatocoenosis data from Djerba Island, Tunisia (Bouzouggar et al. 2007; d'Errico et al. 2009; Vanhaeren et al. 2006). Descriptions of perforation locations in Bouzouggar et al. (2007) were used and expanded to record perforation damage in both the thanatocoenoses and archaeological assemblages.

ARCHAEOLOGICAL SAMPLES

As archaeological datasets, we selected samples from Initial and Early Upper Paleolithic contexts at Ksâr 'Akil, Lebanon. Ksâr 'Akil is one of the key archaeological sites on the eastern Mediterranean coast, with a 23-meter-long sequence containing Middle Paleolithic to Epi-Paleolithic deposits. The site is located roughly 10km north of Beirut, about 3km from the present-day coast. The Ksâr 'Akil rockshelter is an ideal case study because of the large mollusk assemblage recovered during the 1930s and 1940s excavation campaigns by Doherty and Ewing (Ewing 1947, 1948, 1949). The total mollusk assemblage counts 3571 specimens, over a third of which consist of beach collected taxa which may have been used as ornaments. The collection was originally described by van Regteren Altena (1962) and subsequently by Bosch et al. (2015a). The latter included a highly fragmentary assemblage recovered during the curation of the vertebrate remains. The mollusk assemblage recovered during the 1960s and 1970s campaigns led by Tixier are not included here, as these did not reach the Early and Initial Upper Paleolithic deposits (Inizan and Gaillard 1978; Tixier and Inizan 1981). Currently, the studied material is housed in the Department of Fossil Mollusca at the Naturalis Biodiversity Center, Leiden, the Netherlands. As a case-study, we selected *T. gibbosula* specimens from two archaeological layers (Layers XXII and XVII) of Ksâr 'Akil. Layer XXII is attributed to the Initial Upper Paleolithic, which dates to $>45,900\text{--}43,200$ calibrated years before present (cal BP). Layer XVII is attributed to the Early Ahmari and dates between $43,300\text{--}42,800$ cal BP (Bosch et al. 2015b); but see (Douka et al. 2015 vs. Bosch et al. 2015c).

All statistical analyses were conducted using the R statistical package (version 3.5.0; R Core Team 2018). Graphics were produced using the R package ggplot2 (Wickham 2009). Comparisons between thanatocoenosis and archaeological assemblages are statistically evaluated as follows. Relationships between counts of categorical data were tested using Pearson's chi-squared test. If sample sizes were small and one or more expected cell counts were less than five, we used a Monte Carlo simulation method with 10,000 iterations to compute the p-value (Patefield 1981). For continuous data, the Shapiro-Wilk test was used to test for the normality of the distribution. When the data were normally distributed, student t-tests were used to test for significance of results, otherwise Mann-Whitney U tests were employed. In all cases, a p-value <0.05 is considered to indicate a significant difference. When using boxplots, outliers are defined as data points which are located outside $1.5\times$ the inter-quartile range above the upper quartile and below the lower quartile.

RESULTS

THICKNESS MODELS

Shell thickness ranges from 0.17mm to 14mm . To get a better idea of the frequency distribution of the computed shell thickness we plotted it against the cumulative frequency of the number of observations (Figure 1). The number of ob-

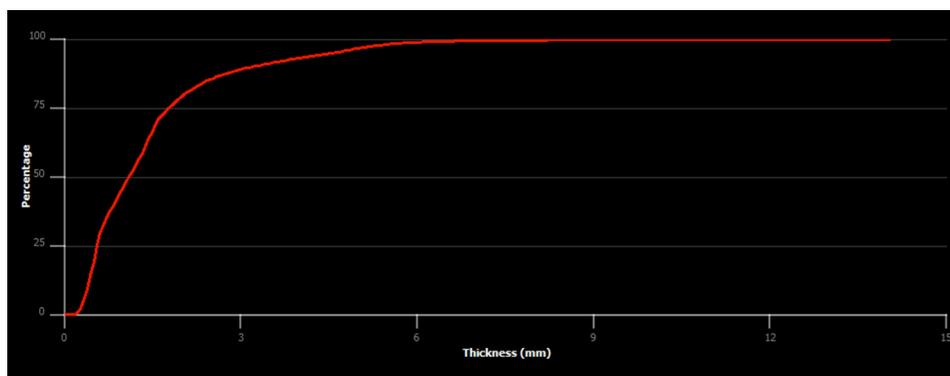


Figure 1. Histogram showing shell thickness of *Tritia gibbosula* (RMNH.Mol.204910.a) against the frequency of the number of observations.

servations clearly tails off between six and seven mm. Three sets of heat maps displaying six views were produced from the virtual models of μ CT-scanned modern, pristine *Tritia gibbosula* (Figure 2). Three different color ranges were chosen to display the data. The first is a grey scale, the second a traditional color map with red to blue (thick to thin areas), and the third a multiple-linear scale using red and black for thick zones and purple, white, and pink for thin zones. All three sets of heat maps show that the parietal rim is the thickest part of the shell and the apex and body whorls are the thinnest parts. The two dorsal humps characteristic of *T. gibbosula* are clearly visible as areas of intermediate thickness. The parietal rim is thinnest at the basal side of the aperture and on the opposite side of the aperture's shoulder. A further weak zone is visible on the mid-ventral plain between the parietal rim and the aperture's shoulder. This location is often targeted by carnivorous gastropods during predation (Claassen 1998).

The multiple-linear scale shows the complete range of shell thickness as observed in Figure 1. This model also displays linear bands, thicker than the surrounding surface, in certain locations, e.g., on the specimens' shoulder and sutures. These bands are best explained by considering the internal shell structure as well as its external surface. Very thick zones (>6mm), occur in areas where internal shell structures align. To visualize this phenomenon, we provide orthogonal slices (or orthoslices) through the shell's volume at locations where these internal structures align (see Figure 2.4). See also Appendix I for a video displaying the μ CT-scan data in series of orthoslices through the specimen in three planes and their relation to the virtual 3-D model.

In some instances, especially in the spire, thick bands occur adjacent to very thin (ca. <1mm) zones. The abrupt changes in thickness create a rheological scenario in which the so-called flow of the shell carbonates is disrupted reducing the shell's plasticity in these locations. In other words, thick and thin zones behave differently under simple directional, or shear stress. Therefore, fractures would preferentially occur on the intersection of extreme thin and thick bands. This offers a biomechanical explanation for the frequent apical damage in both natural and archaeological assemblages, both of which are commonly exposed to shear-

ing stress in the form of wave action and post-depositional crushing, respectively.

The aim of this paper is to distinguish natural perforation patterns from those mediated by human action. Most perforations occur in the thinner (ca. <1mm) parts of the shell such as the parietal shield. To focus on thickness variation in the areas of interest, we therefore use the second set of heat maps emphasizing changes in thickness between 0mm and 1.6mm, for subsequent analyzes. The grey-scale maps employ the same range of variation.

COMPARISON BETWEEN THANATOCOENOSIS AND ARCHAEOLOGICAL ASSEMBLAGES

The specimens from Ksâr 'Akil Layers XXII and XVII are similar in maximum height and height aperture, while the maximum diameter is significantly different (Wilcoxon test, $W=760.5$, $p<0.05$). This might be caused by changes in the thickness of the parietal rim in different environmental regimes (e.g., d'Errico and Vanhaeren 2007). Overall, the shells in both Ksâr 'Akil assemblages are larger than the Djerba thanatocoenosis specimens (Table 1; Figure 3; Djerba data from d'Errico et al. 2009). The range of the Ksâr 'Akil assemblages encompasses other archaeological specimens from North Africa and the Near East, namely Tavoralt, Contrebandiers, Ifri n'Ammar, Rhafas (Morocco), Djebbana (Algeria), and Skhul (Israel) (Bouzouggar et al. 2007; d'Errico et al. 2009; Vanhaeren et al. 2006).

To test our predictions regarding the relationship between perforation locations and shell thickness, we overlay the Djerba Island thanatocoenosis data published by Vanhaeren and colleagues (2006) onto our shell thickness model. The vast majority of the reported natural damage in the Djerba dataset overlaps with the thinner zones identified in our heat maps (Figure 4).

There is a significant difference in the proportion of damaged versus intact shells between the thanatocoenosis and Ksâr 'Akil archaeological assemblages (Layer XXII - Djerba: $\chi^2=71.723$, $p<0.001$; Layer XVII - Djerba: $\chi^2=58.708$, $p<0.001$). Aside from the few complete specimens, the majority of the Ksâr 'Akil assemblage is pierced and semi-intact with or without the apex preserved. Some specimens

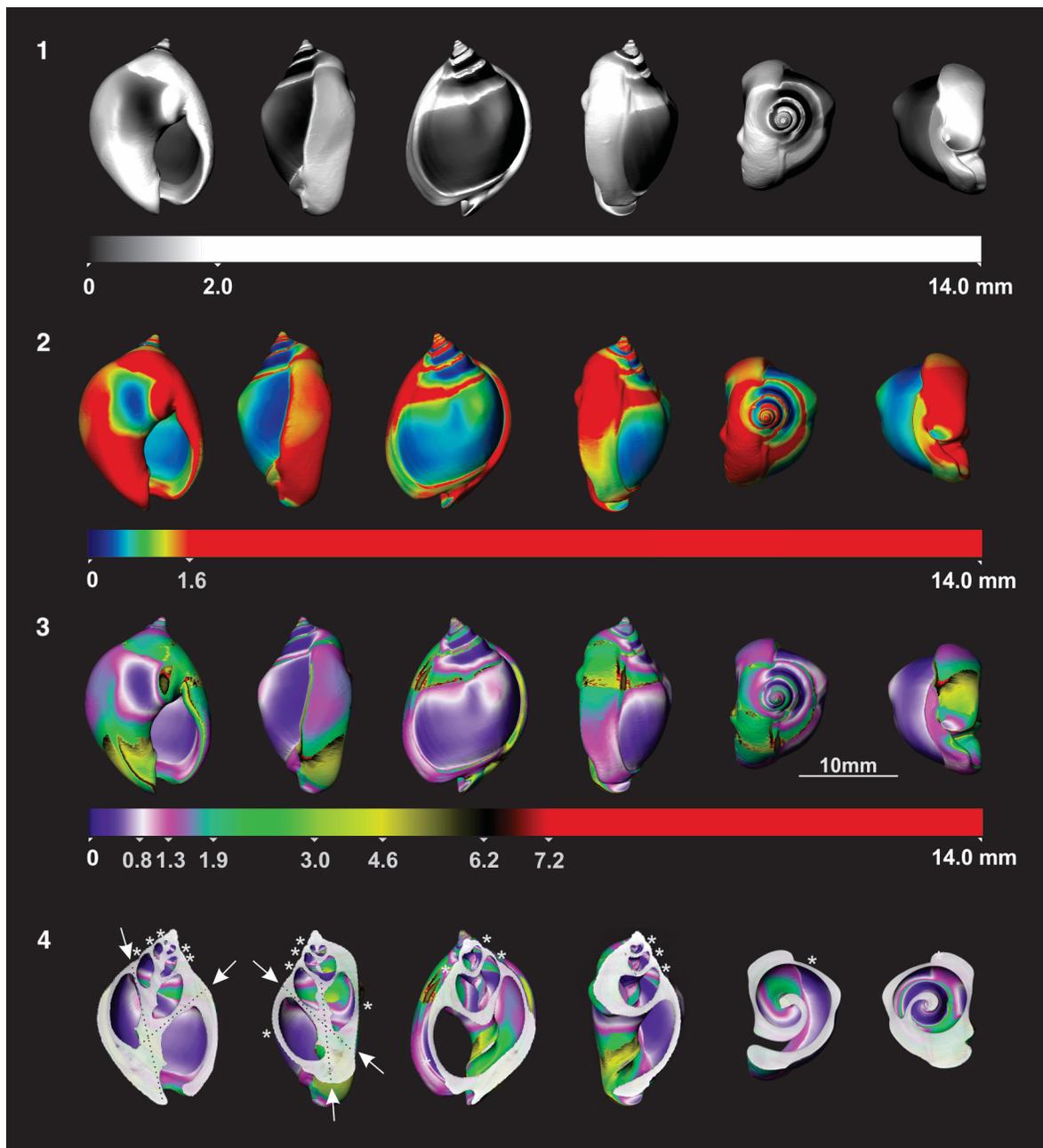


Figure 2. Heat maps of shell thickness in *Tritia gibbosula* (RMNH.Mol.204910.a). 1) grey-scale maps, ranging from white (thick) to black (thin); 2) traditional heat map, ranging from red (thick) to blue (thin). This color scale is also used in Figure 4. Note the two dorsal humps characteristic for this species in green; 3) heat maps using a multiple-linear scale, ranging from red (thick) to purple (thin); 4) orthoslices depicting thin (stars) and thick areas (arrows) where internal shell structures align (dotted lines).

display damage, which did not lead to perforations (Figure 5). The majority of the Ksâr 'Akil specimens show traces of beach erosion or other marine taphonomic alterations indicating that the shells were collected empty at the beach (Table 2).

The damage observed in both archaeological assemblages largely overlaps with the thinner parts of the shell identified using the virtual shell models. At face value, this pattern is very similar to that observed in the Djerba thanatocoenosis. However, when comparing the type of damage in our archaeological specimens with those in the mod-

ern death assemblage, there are some distinct differences (see Table 2; see Figure 4). Both the Ksâr 'Akil Layer XXII and Layer XVII assemblages show higher proportions of dorsal perforations on the side of the aperture (dorsal e), also more common are highly abraded rings formed by the parietal wall and columella (dorsal o), holes on the mid-ventral plain (ventral c), and specimens missing their apex (dorsal c). The latter may be explained by post-depositional crushing. Observed damage, further, results significantly more frequently in a perforation in the archaeological specimens (Layer XVII - Djerba: $\chi^2=37.61$, $p<0.001$; Layer XXII

TABLE 1. DESCRIPTIVE STATISTICS FOR TRITIA GIBBOSULA FROM KSÂR 'AKIL (KSA) LAYERS XXII AND XVII (n: number of specimens, SD: standard deviation).

ID	n	min	max	range	mean	SD
<i>Height max</i>						
KSA-XXII	17	15.90	21.43	5.53	18.58	1.35
KSA-XVII	21	15.97	19.87	3.90	17.90	1.12
<i>Max diameter</i>						
KSA-XXII	35	11.60	15.30	3.70	14.01	0.95
KSA-XVII	31	12.41	15.76	3.35	13.55	0.74
<i>Height Aperture</i>						
KSA-XXII	10	10.83	13.96	3.13	12.45	1.30
KSA-XVII	23	10.56	14.36	3.80	12.37	0.92

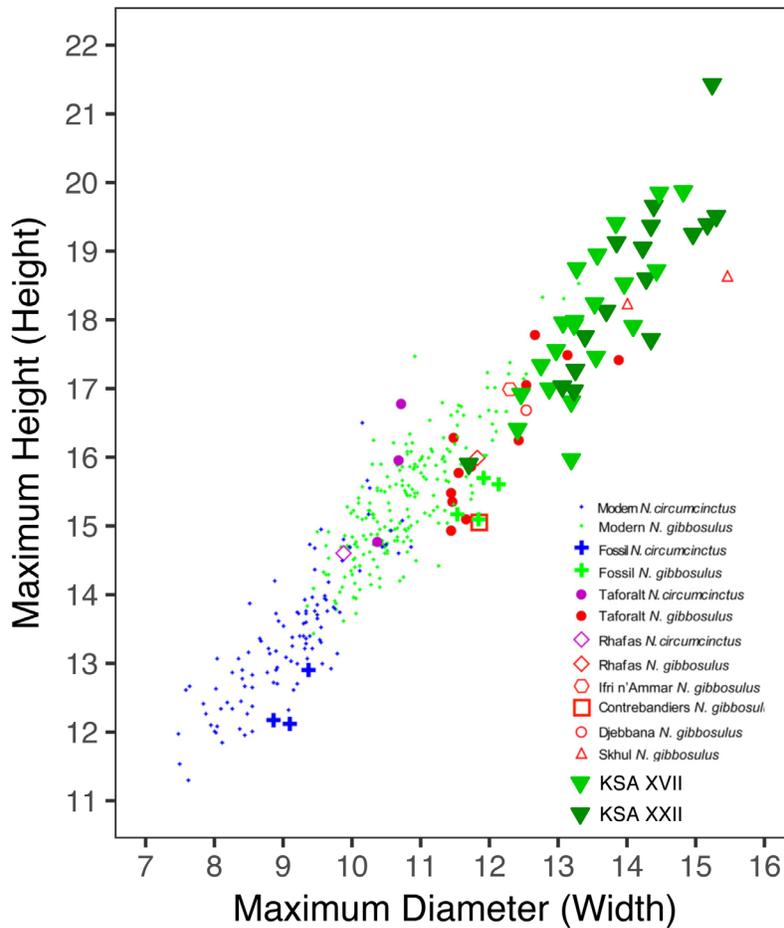


Figure 3. Scatterplot showing the relationship between maximum diameter and aperture height for *Tritia gibbosula*. Ksâr 'Akil Layer XVII (light green inverted triangles) and Ksâr 'Akil Layer XXII (dark green inverted triangles) are plotted onto Figure S2 of d'Errico et al. 2009, showing the Djerba thanatocoenoses assemblages as well as specimens of other Paleolithic North African and Levantine sites.

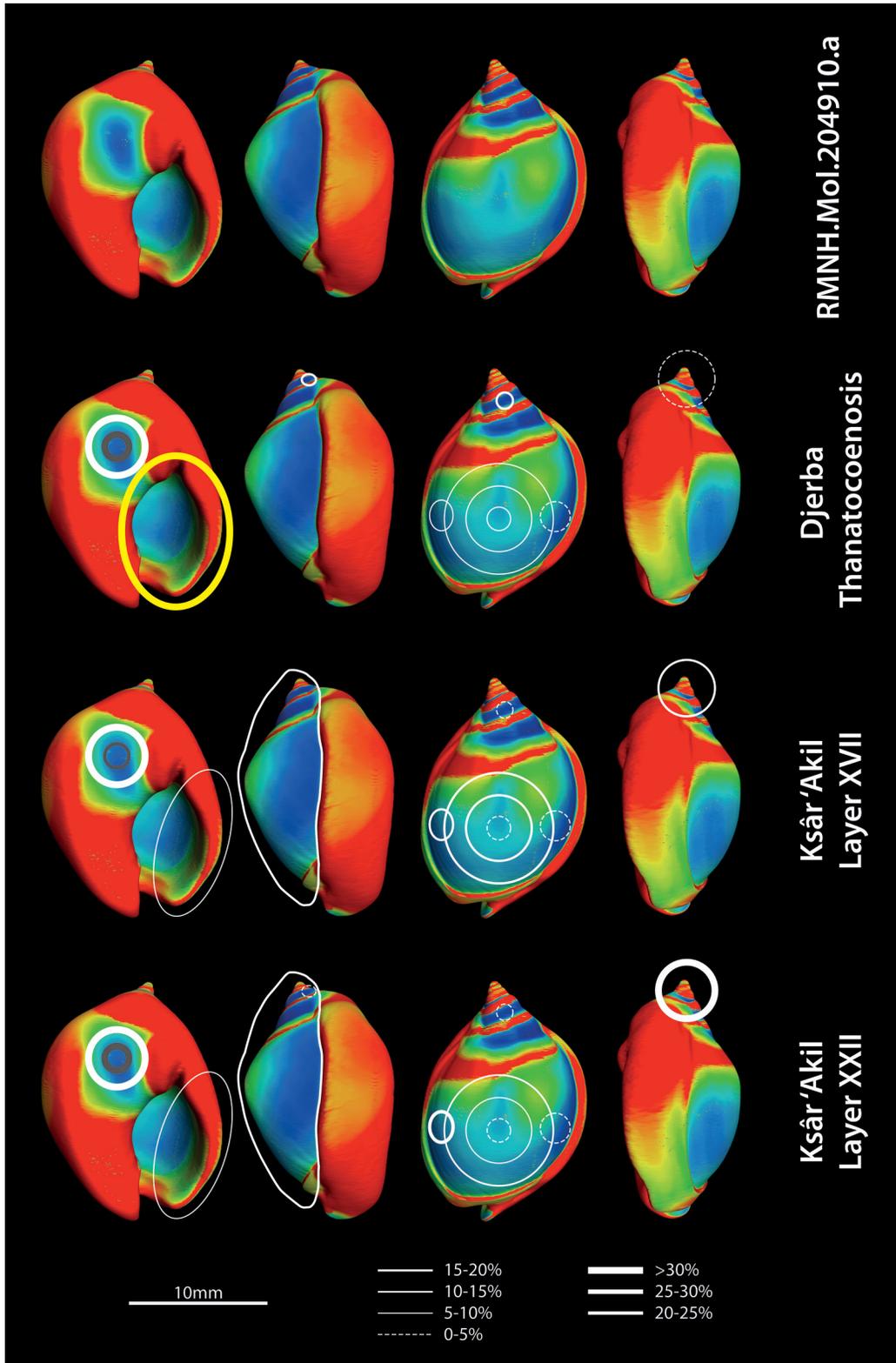


Figure 4. Shell damage in *Tritia gibbosula*, comparing the Djerba modern death assemblage (after Vanhaeren et al. 2006), with Ksâr 'Akil Layers XXII and XVII. White circles: damaged zones, Black circles: perforations by predators, Yellow circles: damage is so extensive that only this zone (i.e., the aperture) was left.



Figure 5. Examples of Ksâr 'Akil specimens from Layer XVII. *Tritia gibbosula*, a) RGM-550225.af, b) RGM-550225.b, c) RGM-550225.av.

- Djerba: $\chi^2=35.404$, $p<0.001$).

Various perforations of the thinnest part of the dorsal shield are distributed evenly in the Djerba modern death assemblage and are in accordance with our above-stated predictions. Interestingly, this is not the case in the assemblages of Ksâr 'Akil Layers XXII and XVII. The locations that facilitate suspension (e.g., on the side of the aperture [dorsal e], or larger central holes [dorsal f, j, and o]) are overrepresented, and others, which do not facilitate suspension (e.g., on the opposite side of the aperture [dorsal h] or smaller holes on the mid-dorsal plain [dorsal d]) are underrepresented (Layer XVII – Djerba: $\chi^2=15.224$, $p<0.001$; Layer XXII – Djerba: $\chi^2=26.644$, $p<0.001$). Ventral damage and perforation patterns do not show any substantial difference between the Djerba and Ksâr 'Akil assemblages. The smaller proportion of predator damage in Layer XVII could be caused by secondary beach-erosion obliterating diagnostic traces of predator activity.

DISCUSSION AND CONCLUSIONS

In this paper, we focus on identifying human decision

making in the shells' prehistoric use-life (i.e., from collection of the shell to its discard). Stiner et al. (2013) argue that if there is evidence for the human modification of some perforated specimens, all specimens of that taxon may be regarded as ornamental on the basis that they were collected with the intent of making them into, or using them as, beads (see also Cristiani et al. 2014). Moreover, it has been argued that the presence of non-perforated shells suggests that bead manufacture took place onsite (e.g., Álvarez Fernández 2008; White 2007). Thus, the presence of unperforated shells is not a distinctive criterion to distinguish natural from anthropogenic assemblages. In addition, it can be difficult to identify traces of human modifications in perforated shell assemblages, especially when they have been smoothed and damaged by exposure to marine environments even before collection, or have been subjected to post-depositional processes obliterating traces of use. For example, perforations made by carnivorous snails are usually recognisable by their distinctive circular circumference and straight perforation edges. Exposure to wave-action however, smooths these edges and thereby erasing its dis-

TABLE 2. DORSAL AND VENTRAL SHELL DAMAGE IN ARCHAEOLOGICAL ASSEMBLAGES FROM KSÂR 'AKIL (KSA) LYERS XXII AND XVII AND THE DJERBA THANATOCOENOSIS (after Bouzouggar et al. [2007; note: ventral damage reported without na]).*

	Djerba		KSA XVII		KSA XXII	
	n	%	n	%	n	%
Beach washed	na	na	99	79.20	113	88.28
Dorsal perforation	n	%	n	%	n	%
not damaged	126	43.60	6	4.80	2	1.56
damaged	163	56.40	119	95.20	126	98.44
damage resulting in hole	81	49.69	102	85.71	106	84.13
b - small hole on apex	28	17.18	1	0.72	2	1.09
c - apex gone	6	3.68	24	17.39	60	32.61
d - small hole mid-dorsal plain	10	6.13	3	2.17	1	0.54
e - dorsal side aperture	12	7.36	26	18.84	37	20.11
f - medium hole mid-dorsal plain	10	6.13	24	17.39	15	8.15
h - lateral opposite aperture	8	4.91	5	3.62	2	1.09
j - large hole dorsal plain	13	7.98	23	16.67	20	10.87
l - aperture broken	12	7.36	7	5.07	15	8.15
m - aperture left	64	39.26	4	2.90	3	1.63
o - hole all dorsal plain incl. apex			21	15.22	29	15.76
Ventral perforation	n	%	n	%	n	%
not damaged	153	67.70	86	68.80	95	74.22
damaged	73	32.30	39	31.20	33	25.78
b - predator hole mid-ventral plain	30	41.10	9	23.08	13	39.39
c - medium hole mid-ventral plain	31	42.47	30	76.92	19	57.58
d - small hole on apex	12	16.44			1	3.03

*Shell damage in bold, perforation locations in normal font.

tinctive appearance. Further, it can be hard to distinguish natural and human-made perforations due to equifinality (d'Errico et al. 1993). Abrasion and percussion damage, for example, may have a natural or an anthropogenic origin, especially when shells are pierced from the outer surface and not internally through the aperture. As a result, the designation 'bead,' is often based on a combination of factors, such as the exclusion of biotic and geologic causes for the presence of perforated shells, evidence for transport of empty shells by humans (i.e., not collected for subsistence purposes), the physical properties or features of perforation edges, perforation location, and traces of use-wear (e.g., Álvarez Fernández 2008; Bar-Yosef Mayer 2005; d'Errico et al. 1993; Taborin 1993; Vanhaeren et al. 2006).

Analyses of the perforation locations in *T. gibbosula* at Ksâr 'Akil suggest that prehistoric humans intentionally collected and/or made perforated shells ideally suited for suspension. In addition, taphonomic investigations have excluded the possibility that transport by animals and geo-

logical processes contributed to the accumulation of these shells, or that they were collected for consumption (Bosch et al. 2015a). Our results show that both the Initial Upper Paleolithic and Early Ahmarian assemblages are significantly different compared to the Djerba thanatocoenosis. The mean shell size of archaeological specimens is significantly larger than their modern counterparts, but fall within the range of the thanatocoenosis. It has been suggested that this is pattern, which has been observed in other Paleolithic, Mesolithic, and Neolithic assemblages, is caused by preferential selection rather than by natural factors as biotic changes in shell size, e.g., due to changing environmental conditions, would result in larger ranges exceeding the maximal dimensions of modern specimens (e.g., Perlès 2016; Vanhaeren et al. 2006).

Regarding breakage patterns, archaeological shells are not only more often broken than the ones collected in thanatocoenoses, shell damage has also more frequently resulted in a perforation. Moreover, dorsal perforation pat-

terns in *T. gibbosula* show a non-random distribution across the weakest parts of the dorsal shield, favouring those that would facilitate suspension.

The perforation patterns in *T. gibbosula* suggests that prehistoric humans specifically selected shells with certain perforations or that they pierced them. In the Ksâr 'Akil specimens, perforation shape is irregular and the edge appearance may be variably irregular or smoothed. Experimental studies suggest that this type of perforation is most likely achieved by direct hard hammer percussion, with or without rotation (e.g., d'Errico et al. 1993; Stiner et al. 2013). The resulting perforations are variably described as medium or large, with an irregular, amorphous, or circular appearance, and an irregular, perpendicular, or 'overhanging' cross-section. Detailed microscopic analysis is needed to identify possible traces of manufacture and use-wear.

Our investigations add to a large body of studies employing thanatocoenoses data, (e.g., Bouzouggar et al. 2007; d'Errico et al. 2009; Stiner et al. 2013; Vanhaeren et al. 2006). The use of three-dimensional shell models contributes to these studies by allowing quantification of shell-damage in relation to species-specific shell structures. Our investigations suggest that in most instances natural shell-damage indeed affects thin zones more frequently than thicker, more robust ones. Evaluation of perforation patterns on this background provides new insights regarding the role of humans in the accumulation of these Initial and Early Upper Paleolithic shell assemblages at Ksâr 'Akil.

Our approach may contribute most in (i) Early Upper Paleolithic and more ancient contexts where a combination of modified and non-modified perforated shells may have been used for suspension; (ii) in cases where abrasion and percussion are the likely means of perforation; (iii) in assemblages which suffered from extensive post-depositional processes that damaged the shells (e.g., crushing, dissolving, compacted with sediment) obliterating any evidence of manufacture and use; and, (iv) in assemblages exhibiting extensive beach-erosion, again obliterating traces of use-wear because the shell surfaces are smooth and polished to begin with.

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APPENDIX I

Video displaying the μ CT-scan data in series of orthoslices through the specimen in three directions and their relation to the virtual 3-D model: <https://www.youtube.com/watch?v=ZB9MmyUbZAg>.