Title: Perforations in Columbellidae shells: Using 3D models to differentiate anthropogenic piercing from natural perforations.

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Highlights:
* New approach aids identification of personal ornaments in the archaeological record
* *Columbella rustica* shells were used as beads from the Initial Upper Palaeolithic on
* 3D shell thickness models aid distinction of natural from anthropogenic perforations
* *Columbella rustica* and *C. adansoni* share overall shell-thickness distribution pattern
* Standardisation of perforation size suggests formal bead manufacture at Ksâr 'Akil

Abstract

Perforated shells are often used to study socially mediated behaviour in past hunter-gatherer groups. One of the key issues regarding empty shells from beaches or fossil outcrops is determining human agency in the accumulation and modification of an assemblage. Here we investigate anthropogenic mediation in Initial Upper Palaeolithic and Early Ahmarian assemblages of *Columbella rustica* at Ksâr 'Akil (Lebanon). We compare perforations in the archaeological specimens with data from newly gathered Columbellidae modern death assemblages Tenerife (Spain) using three-dimensional shell-thickness models as templates. This approach, using micro-CT scans of pristine shells to map robust and fragile zones on shell outer-surfaces, allows us to contextualise the two datasets within their natural morphology. Our results show that in natural death assemblages the vast majority of perforations occur in structurally weak zones, and their distribution can be explained by shell morphology in combination with predator activity and other post-mortem damage. In our archaeological dataset we found a higher frequency of perforations in more robust zones and a higher uniformity in their location, size and shape. This suggests human mediation in either the selection or manufacture process and indicates that at Ksâr 'Akil *C. rustica* were used as beads from as early as the Initial Upper Palaeolithic and throughout the Early Ahmarian. Standardisation in perforation shape, size and distribution have been

argued to be indicative of formalised manufacture processes and our results are thus more congruent with intentional bead manufacture than the selection of naturally-holed specimens.

Introduction

Symbolic behaviour is aimed at sharing information including social conventions, personal and group identity within and between groups (e.g., d'Errico and Stringer 2011). These socially-mediated behaviours strengthen internal group coherence and serve to establish and maintain boundaries with neighbouring groups (e.g., Hodder 1977). Symbolic information can be coded in material culture, for example ethnographic studies show that personal ornaments including scarification, body paint and beadwork, are often used to mark self-identity and group affiliation (e.g., Kuhn and Stiner 2007; Rigaud et al. 2018; Vanharen 2009; Vanhaeren and d'Errico 2006; White 1992). Personal ornaments have often been used to study socially mediated behaviour in the past as they are among the few items across the range of archaeological material culture remains the function of which is entirely symbolic (e.g., d'Errico and Stringer 2011; d'Errico and Vanhaeren 2007; Hovers and Belfer-Cohen 2006; Martínez-Moreno et al. 2010; Micheli 2021; White 2007). In this context there has been an emphasis on basket-shaped shells of the genus *Tritia* (e.g., Bosch et al. 2019; Bouzouggar et al. 2007; d'Errico et al. 2005, 2009; Henshilwood et al. 2004; Vanhaeren et al. 2006; Steele et al. 2019) and bivalves of the genus *Glycymeris* (e.g., Bar-Yosef Mayer et al. 2009; 2020; Zilhão et al. 2010). Here we investigate anthropogenic mediation in the Initial Upper Palaeolithic and Early Ahmarian assemblages of dove shells (*Columbella rustica*) at Ksâr 'Akil, Lebanon. Columbellidae are more frequently used for personal adornment in later periods (e.g., Álvarez Fernández 2008, 2016; Álvarez Fernández and Jöris 2008; Bar-Yosef Mayer 1997, 2019a; Cristiani et al. 2014; Kandel et al. 2018; Perles and Vanhaeren 2010; Reese 1982; Rigaud et al. 2015), but are also occasionally recovered in early Upper Palaeolithic European and Levantine contexts (e.g., Bosch et al. 2015a; Bar-Yosef Mayer 2019a,b, 2020; Marder et al. 2013; Shimelmitz et al. 2018; Stiner et al. 2013; Vanhaeren and d'Errico 2006).

In the Mediterranean and the northeastern Atlantic Ocean three morphologically very similar species of *Columbella* Lamarck, 1799 are recognised based on genetic data and a single morphological criterion (Moolenbeek and Hoenselaar 1991; Russini et al. 2017). Genetic research suggests that the Macaronesian *Columbella adansoni* Menke, 1853 and the Mediterranean *Columbella rustica* Linnaeus, 1758 are closely related and together form a sister-clade to the West African *Columbella xiphitella* Duclos, 1840 (Russini et al. 2017). The only morphological feature differentiating *C. rustica* from the other two taxa is that it has a so-called paucispiral protoconch, suggesting direct development without a planktotrophic larval state, whereas *C. adansoni* and *C. xiphitella* share a multispiral protoconch indicating that their ontogeny does involve such a larval state (Moolenbeek and Hoenselaar 1991; Russini et al. 2017). In archaeological specimens the apex on which the protoconch is situated is rarely preserved or has been heavily damaged, rendering the three taxa morphologically indistinguishable. Here we base our taxonomic identifications on the proposed geographic separation and previous malacological assessments (Moolenbeek and Hoenselaar 1991; van Regteren Altena 1962; Russini et al. 2017).

Taphonomic investigations into the Ksâr 'Akil shell assemblage have shown that *Columbella rustica* were collected as empty shells after the mollusc had died (Bosch et al. 2015a). One

of the key issues in dealing with beach-collected shells is determining human agency in the accumulation and modification of an archaeological assemblage. In broad chronological terms, the archaeological record suggests that during the Levantine Middle Palaeolithic and the onset of the Upper Palaeolithic, shells were purposefully collected (Bar-Yosef Mayer et al. 2020). Fully intact shells may have been pierced to be used as ornaments, whereas naturally perforated shells may have been intentionally collected for the same purpose without the need for further modification before use (e.g., Bar-Yosef Mayer 2005, 2015; Bosch et al. 2019; Stiner et al. 2013; Vanhaeren et al. 2006). Within an archaeological assemblage there is usually a mix of fully intact, perforated and just broken shells. Several authors have suggested that if evidence can be found for the intentional use of some shells, we can assume that all specimens of that taxon were collected for the same purpose (e.g., Cristiani et al. 2014; Stiner et al. 2013; see also Haynes and Stanford 1984; Lyman 2013). In fact, White (2007) has argued that the occurrence of fully intact shells is indicative of on-site bead manufacture (see also Álvarez Fernández 2008). Identification of human modification of shells into beads is hampered by two things. First there is considerable overlap or equifinality between human-made and natural perforations (d'Errico et al. 1993). For example, direct or indirect percussion damage may look very similar to shell-damage caused by being twirled around in a rocky-shore environment. Second, damage caused by exposure to an active beach environment prior to collection as well as post-depositional alterations may mask traces of use. Therefore, the classification 'bead' frequently rests on a range of factors such as the exclusion of (a-)biotic actors, collection for subsistence purposes, signs of manufacture and or use-wear (see for recent reviews Bay-Yosef Mayer and Bosch 2019; Steele et al. 2019). Anthropogenic-mediation may be identified in selection and transport of raw materials, manufacture processes, beadwork composition and use (e.g., Álvarez Fernández 2008; Bouzouggar et al. 2007; Bar-Yosef Mayer 2005; d'Errico et al. 1993; Perlès and Vanhaeren 2010; Rigaud et al. 2019; Taborin 1993; Vanhaeren et al. 2006, 2013).

Here we divide shell-life into three stages (Fig 1). Stage 1 presents the phase prior to human collection, including the mollusc's life and the period after its death when the shell is in a beach environment and exposed to various taphonomic agents including bioerosion (e.g., attacks by crabs, boring sponges and carnivorous molluscs), wave action and abrasion. Stage 2 represents the so-called prehistoric use-life, i.e., from human collection to shell discard. During their use-life shells may be preferentially selected based on their appearance, size, and natural perforations, further they may be intentionally perforated and broken during use, lost or discarded. Stage 3 represents the period after discard, i.e., before and after burial in a sedimentary matrix. In stage 3, post-depositional damage may be caused by e.g., sediment reworking, diagenesis, trampling and rock falls and lead to chemical dissolution, polish, scratches and breakage through crushing. Stage 3 also comprises damage during excavation (e.g., during sieving) and curation (White, personal communication, 2017).

We investigate traces of human decision-making in stage 2, namely during collection, manufacture, and/or use of perforated shells (e.g., Claassen 1998; Steele et al. 2019). Frequently used avenues to address these questions include comparing thanatocoenoses with archaeological assemblages, as well as technological and use-wear analyses (e.g., Bar-Yosef Mayer et al. 2009; Bouzouggar et al. 2007; d'Errico et al. 2009; Perlès 2016; Vanhaeren et al. 2006). Here we focus on role of shell structure in the shell-piercing process both in human-made and natural contexts. By using shell thickness as a proxy for structural

resistance we aim to improve our ability to distinguish natural from human-made perforations. A recent study has shown that in *Tritia gibbosula* damage caused by natural taphonomic processes (i.e., those occurring both in stage 1 and 3) are more frequent in thinner and structurally weaker zones, and that within these zones damage is randomly distributed (Bosch et al. 2019). We assume this also to be the case for *Columbella* spp. If proven correct, any deviation between the modern death and archaeological assemblages likely reflects human involvement during stage 2 of the shell-life through e.g., manufacture (perforation) processes or specimen selection.

Material and Methods

Following the approach developed in Bosch et al. (2019) we use μCT (micro computed tomography) data of pristine modern Columbellidae to create virtual models of shell thickness. From these data three-dimensional (3D) virtual models with heat-maps of shell-thickness are derived to better understand the role of shell-structure in relation to shell morphology in both *Columbella rustica* and its sister taxa: *Columbella adansoni*. We show that both taxa display strong similarities in overall morphology and especially in shell-thickness distribution. We then overlie natural perforation damage from two newly collected modern death assemblages stemming from a rocky shore environment (Tenerife, Spain). In this step, we test our predictions regarding the distribution of natural perforations and damage to which shells may be subjected in the above-mentioned stage 1 of the life of the shell. Finally, we compare these data with perforation distributions in archaeological collections from the Initial Upper Palaeolithic and Early Ahmarian of Ksâr 'Akil in an effort to differentiate natural and anthropogenic perforations.

A generalised model of shell thickness.

Columbellidae are known to adapt to external factors such as wave-action, their littoral position and tidal height as well as temperature and acidic changes which lead to morphological variation (e.g., Chatzinikolaou et al. 2021; Moolenbeek and Hoenselaar 1991; Russini et al. 2017). In any given assemblage therefore, we may expect a fair amount of morphological variation. To investigate this variability and its effect on our shell thickness models we μCT-scanned shells from two rocky-shores with drastically different energy regimes, namely the eastern Mediterranean (Tripoli, Lebanon) and the Atlantic (Tenerife, Spain). We chose recent non-archaeological specimens instead of seemingly intact archaeological specimens for two main reasons. First, we needed specimens in pristine condition to obtain the most accurate information about shell-structure and thickness. Second, selecting non-archaeological specimens provides the most accurate representation of the species natural state before human collection (i.e., stage 1). Another option would have been to use more or less intact archaeological specimens in an effort to closely mimic the morphology of the prehistoric shells. However, given scarcity of intact specimens and the extent of intra-species variation it is doubtful that this approach would have captured an accurate representation of the morphological range. Moreover, archaeological specimens although seemingly intact may have endured damage, e.g., polish and abrasion, during archaeological use-life and post-depositionally after discard (stages 2 and 3) which would be impossible to disentangle. Instead we opted for a multi-species approach selecting specimens with different apparent morphology to arrive to a generalised model which can be both applied to our modern-death assemblage (*C. adansoni*) as well as to the Ksâr 'Akil

assemblages (*C. rustica*). Our virtual models are thus aimed at reflecting average shell-density and showing differences between thinner and thicker zones within a shell, rather than highlighting specific morphological differences such as the shape and attachment of the aperture's shoulder and the height of the spire. We assume therefore that our generalised model is a good basis to compare and contextualise the distribution of damage in both the Tenerife and Ksâr 'Akil assemblages.

Micro-CT-scans of recent specimens

Recent Eastern Mediterranean *Columbella rustica* were selected from the collection Mollusca at Naturalis Biodiversity Center (Locality: Tripoli, *RMNH.Mol.203708*). Recent Macarodonesian *Columbella adansoni* were selected from the thanatocoenosis: TF1 (Tenerife, Spain; personal collection of MDB). Prior to μCT-scanning specimens were selected for their pristine preservation and damaged specimens (e.g., showing traces of bioerosion, smoothing and abrasion) were avoided. Several specimens were scanned to detect any specimen-specific abnormalities and ensure the resulting virtual models reflect average shell-density. In addition to scanning intact shells, a sample of *C. rustica* (Locality: Tripoli, *RMNH.Mol.203708*) exhibiting boring sponge damage were selected for μCT-scanning to investigate the effect of this type of damage on shell-robustness. This was done as a high proportion of the archaeological shells from Ksâr 'Akil display boring sponge damage.

The shells were μCT-scanned at the Cambridge Biotomography Centre, University of Cambridge, using a Nikon Metrology XT H 225 ST High Resolution Scanner. Scan parameters were optimised for individual scans (voxel size: 0.01–0.03 mm, isotropic). Segmentation and post-processing were done using Avizo 8.1 (Thermo Fisher Scientific - FEI). For more details on the protocol see Bosch et al. (2019). Shell thickness was computed using a scalar field which was then mapped onto the surface using a colour range from blue (thin) to red (thick) with green representing intermediate thickness. The colour range was adjusted to emphasize thickness variation in the areas of interest and is unique to each shell. The final images were obtained in six standardized views, namely dorsal, ventral, both lateral sides, basal, and apical.

Modern death assemblages

Two modern death assemblages from rocky shores on Tenerife, Canary Islands, Spain – TF 1 and TF 2 - were collected (Fig 2). A survey of multiple rocky shores revealed that *C. adansoni* are most frequent in patches of sandy substrates, which serve as natural traps for (semi-)intact specimens. Sporadically, exceptionally large and intact specimens were recovered from both the sandy patches and rocky substrates at the upper limit of the upper intertidal zone. The most time-effective method was to target patches of sandy substrates in the mid to upper intertidal zone at low tide, from which both the modern death assemblages TF1 (n=258; search time 30 min) and TF2 (n=91; search time 20 min) were collected. Compared to a thanatocoenosis from an Atlantic rocky shore, an Eastern Mediterranean assemblage would presumably show less damage, due to the reduced zonal amplitude and limited wave action of the Mediterranean Sea, especially on its eastern coast. Using modern death assemblages from a high-energy environment, like the Tenerife beach, amplifies the array of damage that could potentially be observed. The Tenerife thanatocoenoses data, therefore, are ideally suited to investigating the extent of natural damage in relation to shell thickness.

Recording perforation damage followed Bouzouggar et al. (2007) which was adapted for Columbellidae.

Archaeological samples

The *Columbella rustica* assemblages of Ksâr 'Akil, Lebanon (Layers XXII and XVII; Fig 3) were used as archaeological datasets. Layer XXII is attributed to the Initial Upper Palaeolithic, which dates to >45.900–43.200 calibrated years before present (cal BP). Layer XVII is attributed to the Early Upper Palaeolithic or Early Ahmarian and dates to 43.300–42.800 cal BP (Bosch et al. 2015b; but see Douka et al. 2015 vs. Bosch et al. 2015c).

Ksâr 'Akil is well-known for its multi-layered Initial and Early Upper Palaeolithic deposits, which are rare in the region and make it, next to Üçağızlı I (Turkey) and Manot (Israel) Caves, one of the key archaeological sites for this period (e.g., Hershkovitz et al. 2015; Kuhn et al. 2001; Stiner et al. 2013). The Ksâr 'Akil rockshelter situated about 3 km from the present-day coast. The excavations in the 1930s and 1940s by Ewing and Doherty recovered exceptionally large mollusc assemblage, making it an ideal case-study. The total mollusc assemblage counts 3571 specimens, twelve percent of which (n=429) are beach-collected *C. rustica* (Bosch et al. 2015a; van Regteren Altena 1962). The excavations by Tixier in the late 1960s and 1970s never reached the Initial and Early Upper Palaeolithic deposits and the recovered mollusc assemblage is therefore not included in this study (Inizan and Gaillard 1978; Tixier and Inizan 1981). The studied material is currently housed in the Department of Fossil Mollusca at the Naturalis Biodiversity Center, Leiden, the Netherlands.

Data recording and statistics

Data recording of archaeological and the natural death or thanatocoenoses assemblages employed E4 (freeware: www.oldstoneage.com) and Microsoft Access software packages. All statistical analyses were done in R (version 3.5.0; R Core Team 2018). Graphics were produced using the R package ggplot2 (Wickham 2009). Pearson's chi-squared tests were used to statistically evaluate categorical data and with small sample sizes Monte Carlo simulations (with 10,000 iterations; Patefield 1981) were caried-out to compute the p-value. For continuous data, the Shapiro-Wilk test was used to test for the normality of the distribution. When appropriate t-tests were used, otherwise Mann-Whitney U tests were employed. For comparison of the multiple modern and archaeological *Columbella* spp. assemblages a Kruskal-Wallis test and Wilcoxon signed rank pairwise tests (with adjusted p-values using the Bonferroni correction) were carried out as not all measurements were normally distributed. In all cases, a p-value < 0.05 was considered significant. Outliers in boxplots are defined as ≥ 1.5x the inter-quartile range above the upper quartile and ≤ 1.5x below the lower quartile.

Results

Figure 4 shows thickness heat-maps of modern pristine *Columbella adansoni* from TF 1 (top) and *Columbella rustica* Tripoli (centre) and a Tripoli specimen that was subject to damage by boring-sponges (bottom). As expected, there is substantial morphological variation between specimens from both localities. Adaptation to a high-energy regime is apparent in the overall squatter appearance of the TF specimen. Also reflected is Russini and colleagues' (2017) diagnosis concerning the length of the body whorl (i.e. ⅔ of the shell in *C. rustica* and ⅔ to ¾ in *C. adansoni*). Further, our TF specimen shows broad layered spiral whorls, a well-

developed aperture and squat shoulder. The Tripoli specimens conversely are more gracile, displaying an elongated spire and siphonal canal. Despite these morphological differences the spatial distribution of shell-thickness appears to follow a more or less identical template. The shells are thickest (coloured red) along the top of the body whorl attaching to the spire, the siphonal canal and the outer lip of the aperture. The spire-whorls are thinner (coloured blue) than the body whorl. The body-whorl gradually gets thinner towards the periphery (widest part) as well as in the direction of growth. Ventrally, this pattern is overlain by a thicker (coloured yellow to orange) patch on the mid-ventral plain.

Descriptive statistics for three size measurements, i.e., maximum height, maximum diameter and aperture height, for the here studied *Columbella* spp. assemblages are provided in Table 1. All three measurements show a similar pattern. For KSA Layer XXII, maximum height and aperture height could only be measured in two specimens. Thus, to maximise the sample, maximum diameter is chosen as a proxy for shell size and compared here between the assemblages (Fig. 5). Shapiro-Wilk normality tests revealed that maximum diameter in TF1 is not normally distributed (W: 0.93012, $p<0.001$). A Kruskal-Wallis test shows strong evidence of a significant difference between the mean ranks of at least one pair of assemblages (Kruskal-Wallis $\chi^2=76.358$, $p<0.001$). Wilcoxon signed rank pairwise tests (p-values adjusted using the Bonferroni correction) show that the modern shell assemblages from Tenerife, TF1 and TF2, are not significantly different ($p=1$), neither are the Ksâr 'Akil assemblages XXII and XVII ($p=1$). However, both Ksâr 'Akil assemblages differ significantly from both TF1 and TF2 (all p-values are <0.001). These differences are mainly caused by the presence of smaller specimens in both Tenerife thanatocoenoses, which are outside the range of the Ksâr 'Akil assemblages. Individual larger specimens, falling in the upper half of the Ksâr 'Akil ranges, are present in the TF1 assemblage and probably cause the non-normal distribution of TF1.

Most natural damage observed in both the modern death and archaeological assemblages, is situated in the thinner parts of the shell (Fig 6). The exception being boring sponge damage, which appears to be randomly distributed on the shell surface. This latter pattern of damage does not usually penetrate the entire shell surface, is evident in all assemblages and visible in the μCT-model (Fig. 4, bottom). Although, this type of damage weakens the shell-wall it does not lead to perforations large enough to be suitable for suspension, neither is there any indication that these pits and holes were used to puncture the shell during bead-manufacture. In other words, boring sponge damage is randomly distributed and not aligned with larger perforations. Further, in the modern death assemblages, shell damage is mainly restricted to structurally weaker zones, the thin apex being most affected. Damage on the body-whorl, the next weakest zone, centres on the mid dorsal surface which is the most exposed surface of the body-whorl. A similar pattern is seen in thanatocoenosis of other taxa like *Tritia gibbosula* (Bouzouggar et al. 2007). This pattern is observed in both the archaeological and the thanatocoenoses datasets.

As expected, there are more types of damage in the modern death assemblages than in the archaeological ones. In part, this could be due to more intense wave action in the Tenerife rocky shore environment or to anthropogenic selection of less damaged shells. Apical damage or loss is frequent in both archaeological and modern specimens. The edges of breaks include both smoothed surfaces, likely caused by water erosion, as well as irregular

breakage, which could have been caused by wave-action or post-depositional crushing (e.g., Claasen 1998). In addition, the lack of smaller (e.g., apical) fragments in the Ksâr 'Akil assemblages may be explained by a size-bias due to recovering techniques (e.g., mesh-size for sieving) during the 1930s and 1940s excavation campaigns. Overall, there is a significant difference in the proportion of damaged versus intact shells between the modern-death and archaeological assemblages (Table 2). Equally, the proportion of damage resulting in a perforation is significantly higher in both archaeological assemblages as is the frequency of dorsal perforations that would facilitate suspension (see e.g., Perlès 2016; Stiner et al. 2013).

The perforation location in both archaeological layers is largely restricted to the mid dorsal (dorsal f and j) and ventral (ventral c) planes. Dorsally, the perforations of all assemblages fall in the thinnest (weakest) part of the body whorl. In the archaeological samples the mid dorsal plane is nearly exclusively affected, whereas in the modern death assemblages damage is more evenly distributed throughout the thinnest part of the body whorl. In addition, there is a marked difference in perforation size relative to shell dimension. In the archaeological assemblages, there is a significant dominance of medium-sized (dorsal f) on the mid dorsal plane compared to both smaller (dorsal d) and larger (dorsal j and o) holes (Table 3). Interestingly, the inter-quartile range of the Ksâr 'Akil maximum perforation diameter is much narrower than in the modern-death assemblages even though the latter shells are overall smaller (Fig. 7). This suggesting standardisation in perforation size in the archaeological specimens.
Ventral damage is much less frequent overall and does not warrant statistical evaluation of the data. However at face value, ventral perforations follow the dorsal pattern in that there is a larger variation in perforation size in the modern death assemblages. Further, perforations situated in the thicker (orange) zone of the ventral plane are more common in the Ksâr 'Akil assemblages. Large perforations on the ventral plane in the TF assemblages are caused by damage on the thinner surrounding of the mid dorsal plane removing the thicker central part in the process. The small holes observed in various ventral locations in the TF1 assemblages are largely caused by boring sponges and other bioeroders.

Discussion and Conclusions

In this study we used three-dimensional models of shell thickness to shed light on human decision making in archaeological shell assemblages. Our goal was to contribute to a better understanding of whether shell perforations in archaeological contexts are the result of natural or anthropogenic processes. We distinguished three stages in shell use-life, in which perforations can occur: 1) before human collection, 2) the prehistoric use-life, and 3) after discard. We predicted that most natural taphonomic processes (in stages 1 and 3) would affect structurally weak zones to a higher degree than more robust zones and that damage in zones of similar thickness should be randomly distributed. For stage 1 these hypotheses were largely met. Shell damage is mainly restricted to structurally weak zones, albeit with the exception of boring sponge damage which is randomly distributed across the entire shell surface and leaves holes too small to be suitable for suspension. The thinnest part of the shell, the apex, is most affected by damage, followed by the thinner parts on the periphery of the body whorl. Damage within the thinnest zone of the body whorl is more or less evenly distributed. To verify whether our predictions are correct for stage 3 of shell use-life, more experimental data is needed to better understand the damage caused by post-

depositional processes and recovery techniques. For example, by burying whole shells and to expose them to trampling, excavation, sieving, and transport.

Regarding stage 2 damage, our results suggest that *C. rustica* with natural perforations were specifically collected and/or specimens were intentionally pierced to be used as beads. Previous taphonomic investigations have excluded that these shells were transported to the site by animals and geological processes or that they were collected for consumption. Instead, these specimens were collected as empty shells from beaches (Bosch et al. 2015a). Our results show that all Ksâr 'Akil assemblages are significantly different compared to the modern death assemblages. Average shell-size is significantly larger, but falls within the range of their modern beach-collected counterparts. This pattern has been observed for multiple taxa in Palaeolithic, Mesolithic and Neolithic assemblages (e.g., Benghiat et al. 2009; Bosch et al. 2019; Perlès 2016; Vanhaeren et al. 2006). For Columbellidae it has been suggested that changes in archaeological shell-size are not caused by natural factors – such as changing sea surface temperatures – but by preferential selection seeing as the archaeological specimens do not exceed the maximal dimensions of modern specimens (e.g., Benghiat et al. 2009; Perlès 2016).

Our results on breakage patterns show that archaeological shells are more commonly broken than beach-collected ones and that shell damage more often results in a perforation. Further, both shell damage and the spatial distribution of holes is less variable in the archaeological shells. Centrally-located perforations both on the mid-dorsal and mid-ventral plain predominate and medium-sized holes (again both dorsally and ventrally) are significantly more frequent. In fact, the medium to large dorsal perforations often observed in archaeological specimens occur in roughly 10% of the TF natural death assemblages versus approximately 70% in the Ksâr 'Akil shells. Perlès (2016) sees a similar pattern in comparing thanatocoenoses data of *C. rustica* from the Eastern Mediterranean with the Upper Palaeolithic to Neolithic assemblages at Franchthi Cave (Greece). Although she reports drastically lower return rates for intact specimens - namely 11 to 80 shells per collector per hour versus 360 and 355 in TF 1 and TF 2 respectively – she reports a low (less than 10%) return rate for specimens with a dorsal perforation suitable for suspension and congruent with the dominant perforation pattern in her archaeological assemblage. Equally, Stiner and colleagues (2013) report a 20% perforation rate for a modern collection of *C. rustica* from the beach below Üçağızlı I Cave (Turkey) of which 10% display medium to large dorsal perforations as seen in the Üçağızlı I Cave specimens. In all three thanatocoenoses overall shell damage and breakage patterns, including perforation rates are very similar. For example, Stiner et al. (2013) report a 75% proportion of (semi)-intact specimens versus 70%–78% in the Tenerife assemblages and 66%–79% reported by Perlès (2016). These data suggest that 1) breakage patterns in both *C. rustica* and *C. adansoni* thanatocoenoses are comparable and that 2) the few available Eastern Mediterranean Palaeolithic assemblages deviate significantly from a natural distribution. In addition, our three-dimensional shell models show that perforations on the shells' ventral surface are situated in a thicker part of the shell than its surrounding areas i.e., in a zone which we assumed would be less frequently affected by natural damage. Indeed, although medium-size perforations in this thicker zone do occur in the natural TF1 and TF2 datasets, damage in the weaker zones is more abundant. In other words, the perforations in the archaeological *C. rustica* are more uniform in their location and size. This pattern of standardisation would, from an etic point

of view, be ideally suited for ornamentation. Not too small to facilitate suspension, not so large that the object loses its original shape and appearance.

The perforation patterns cannot be explained solely by natural processes. Instead, they suggest that prehistoric humans specifically selected shells with certain perforations or that they pierced them. We argue that the standardisation of perforation diameter (shown by the narrow inter-quartile range) in *C. rustica* is indicative of anthropogenic piercing (e.g., Stiner et al. 2013). Indeed, standardisation in bead perforation shape, size and distribution have been argued to signify formalised manufacture processes (e.g., d'Errico et al. 1993; Kuhn and Stiner 2007; White 1999, 2007) and our results are thus more congruent with human manufacture processes than solely selection of naturally-holed specimens.

In the archaeological *C. rustica*, perforation shape is predominantly irregular and the edge appearance may variably be irregular or smoothed. If the Ksâr 'Akil specimens are indeed anthropogenically pierced as our data suggests, experimental studies suggest that this type of perforation is most likely achieved by direct hard hammer percussion, with or without rotation (e.g., Benghiat et al. 2009; Cristiani et al. 2014; d'Errico et al. 1993; Stiner et al. 2013). In relation to the large shell-size, Benghiat et al. (2009) found during their experiments that larger specimens are less likely to shatter during manufacture when using hard hammer percussion. Detailed microscopic analysis of the archaeological assemblage is needed to identify possible traces of manufacture and use-wear, which could confirm or refute the suggestion that direct hard hammer percussion was used to perforate the Ksâr 'Akil shells.

Our study adds to a growing body of data using modern death assemblages (e.g., Bouzouggar et al. 2007; d'Errico et al. 2009; Perlès 2016; Stiner et al. 2013; Vanhaeren et al. 2006). We contribute to these studies by providing data on perforation locations in thanatocoenoses of *C. adansoni*, which to our knowledge has not been published before. In addition, the use of our three-dimensional shell models aids to better quantify shell-damage in relation to species-specific shell structures. This approach using micro-CT scans is perhaps most useful in 1) shell assemblages where (post-depositional) taphonomy has obliterated any evidence of bead manufacture and use 2) in cases where both modified and naturally perforated shells were used, and 3) like with the Ksâr 'Akil *C. rustica*, in instances in which the mode of perforation mimics natural damage processes. In addition, our approach facilitates identification of evidence for standardisation in manufacture processes, which in turn, can help us to better understand socio-economic behaviours underpinning shell bead manufacture and use. Our investigations suggest that in general thin shell-zones are more prone to natural damage than more robust ones. Evaluation of perforation patterns on these templates and especially identifying deviations from the natural patterns provides new insights into human-mediation with *C. rustica* shells during Initial and Early Upper Palaeolithic at Ksâr 'Akil. Such as evidence for formalised bead manufacture using *C. rustica* as early as the Initial and Early Upper Palaeolithic in the eastern Mediterranean.

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664 ## Tables and captions
665
666 Table 1: Descriptive statistics for *Columbella rustica* from Ksâr 'Akil (KSA) Layers XXII and
667 XVII, n: number of specimens, SD: standard deviation.
668

ID	n	min	max	range	mean	SD
Height max						
KSA-XXII	2	13.71	16.73	3.02	15.22	2.14
KSA-XVII	8	13.81	16.61	2.80	15.21	0.97
TF 1	79	9.09	15.53	6.44	11.88	1.04
TF 2	35	10.53	12.95	2.42	11.40	0.65
Max diameter						
KSA-XXII	11	8.21	11.08	2.87	9.58	0.92
KSA-XVII	29	8.10	10.65	2.55	9.26	0.75
TF 1	142	6.64	10.73	4.09	7.82	0.64
TF 2	62	6.69	9.71	3.02	7.77	0.66
Height Aperture						
KSA-XXII	2	11.14	12.18	1.04	11.66	0.74
KSA-XVII	17	9.81	11.81	2.00	10.63	0.70
TF 1	104	7.14	12.87	5.73	8.93	0.89
TF 2	43	7.66	10.54	2.88	8.85	0.73

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670
671 Table 2: Statistical evaluation of shell damage. *= simulated p-values with 10,000 replicates.
672

damaged vs intact shells		
	TF1	TF2
KSAXXII	χ^2=7.4712, p=0.005*	χ^2=7.1646, p=0.013*
KSAXVII	χ2=11.536, p<0.001	χ^2=9.809, p=0.002
damage resulting in a perforation		
	TF1	TF2
KSAXXII	χ^2=7.9722, p=0.005	χ^2=13.654, p<0.001
KSAXVII	χ^2=30.287, p<0.001	χ^2=37.582, p<0.001

dorsal perforation diameter		
	TF1	TF2
KSAXXII	χ^2=18.305, p<0.001*	χ2=15.367, p<0.001*
KSAXVII	χ^2=41.916, p<0.001	χ2=25.07, p<0.001*

673
674
675 Table 3: Dorsal and ventral shell damage in rocky shore thanatocoenoses from Tenerife (TF1
676 and TF2) and archaeological assemblages from Ksâr 'Akil (KSA) Layers XXII and XVII. Shell
677 damage in bold, perforation locations in normal font.
678

	TF1		**TF2**		**KSA XVII**		**KSA XXII**	
	n	**%**	**n**	**%**	**n**	**%**	**n**	**%**
Beach washed	**239**	**92.64**	**89**	**97.80**	**102**	**88.70**	**13**	**68.42**
Dorsal damage	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**
Not damaged	**72**	**27.52**	**27**	**29.67**	**13**	**11.30**	**0**	**0.00**
Damaged	**186**	**72.09**	**64**	**70.33**	**102**	**88.70**	**19**	**100**
Damage results in perforation	**88**	**47.31**	**21**	**32.81**	**83**	**81.37**	**16**	**84.21**
b - small hole on apex	17	6.54	9	10.11	2	1.26	1	4.00
c - apex gone	85	32.69	30	33.71	62	38.99	8	32.00
d - small hole mid dorsal plain	14	5.38	3	3.37	6	3.77		
e - dorsal side aperture					2	1.26		
f - medium hole mid dorsal plain	15	5.77	1	1.12	60	37.74	13	52.00
h - lateral opposite aperture	3	1.15	1	1.12	1	0.63		
j - large hole dorsal plain	15	5.77	6	6.74	13	8.18	2	8.00
l - aperture broken	40	15.38	14	15.73	12	7.55	1	4.00
m - aperture left	2	0.77						
o - hole all dorsal plain incl apex	29	11.15	1	1.12	1	0.63		
ak - apex left	9	3.46	9	10.11				
an - lateral side left	19	7.31	2	2.25				
ap - body whorl fr	2	0.77	2	2.25				
ar - basal part gone	4	1.54	9	10.11				
as - small hole basal plain	1	0.38	2	2.25				
ao - columella left	5	26.32						
Ventral damage	n	%	n	%	n	%	N	%
Not damaged	**258**	**87.21**	**87**	**95.60**	**106**	**92.17**	**18**	**94.74**
Damaged	**33**	**12.79**	**4**	**4.40**	**9**	**7.83**	**1**	**5.26**
b - predator hole mid ventral plain					2	22.22		
c - medium hole mid ventral plain centre	6	18.18			6	66.67	1	100
d - small hole on apex			2	50	1	11.11		
e - small hole mid ventral plain centre	3	9.09						

f - small hole mid ventral aperture side	4	12.12		
g - small hole mid ventral opposite aperture	3	9.09		
h - small hole basal plain	1	3.03		
i - all ventral side gone	2	6.06		
j - large hole mid ventral plain aperture side			1	25
k - medium hole mid ventral plain opposite aperture	3	9.09		
l - basal part gone	2	6.06		
m - large hole mid ventral plain	9	27.27	1	25

679
680

Figure captions

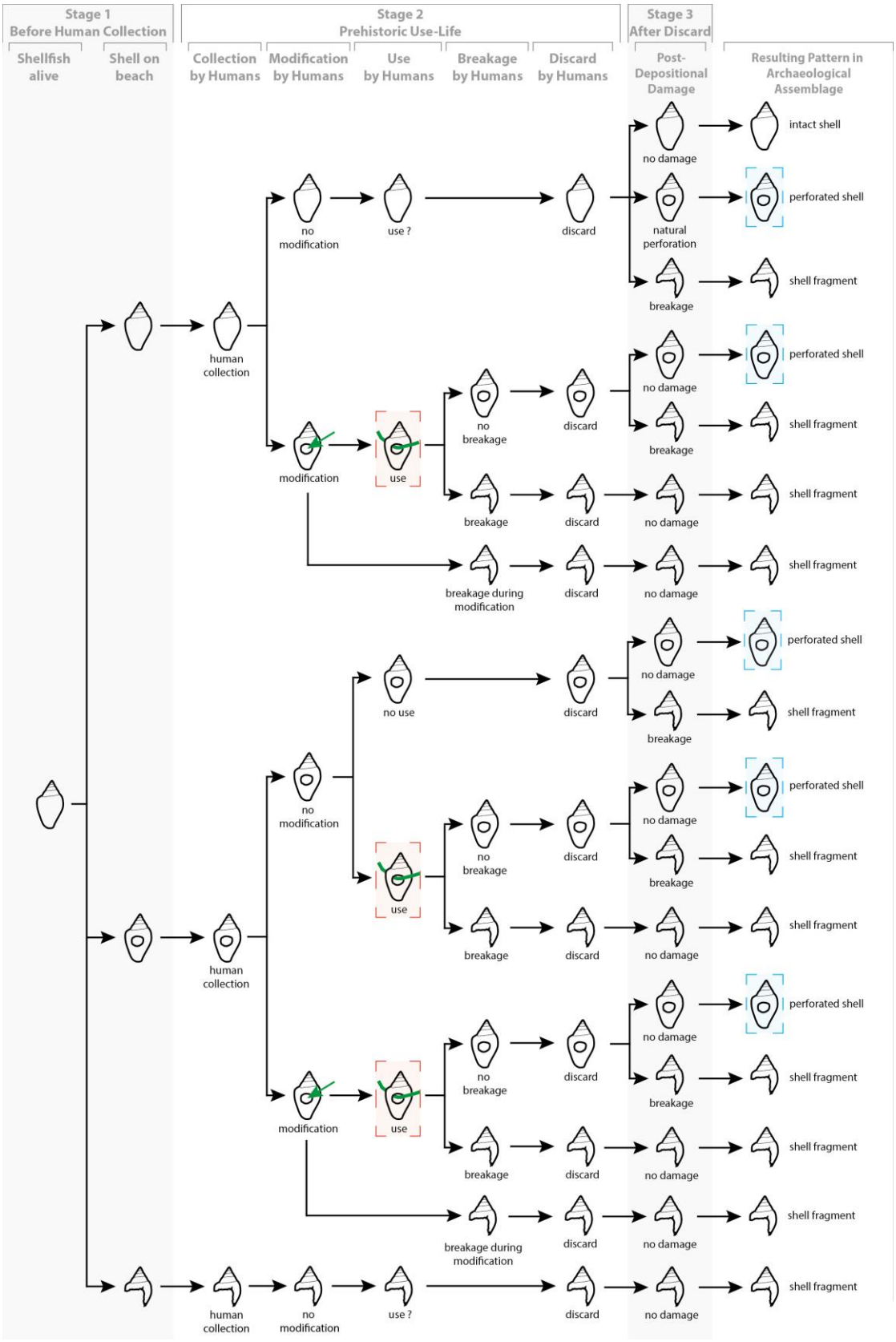


Figure 1. Flow chart showing the use-life of shell specimens found in archaeological assemblages, green arrows: human modifications, red: perforated shells used as beads by prehistoric humans, blue: perforated shells in archaeological record.

Figure 2. Examples of shell damage in *Columbella adansoni* from Tenerife, Spain thanatocoenosis (TF1).

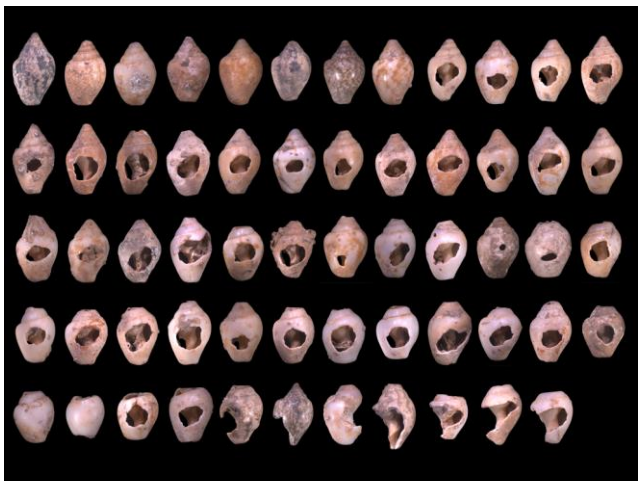


Figure 3. Examples of shell damage in archaeological specimens of *Columbella rustica* from Ksâr 'Akil, Lebanon Layer XVII (Early Ahmarian).

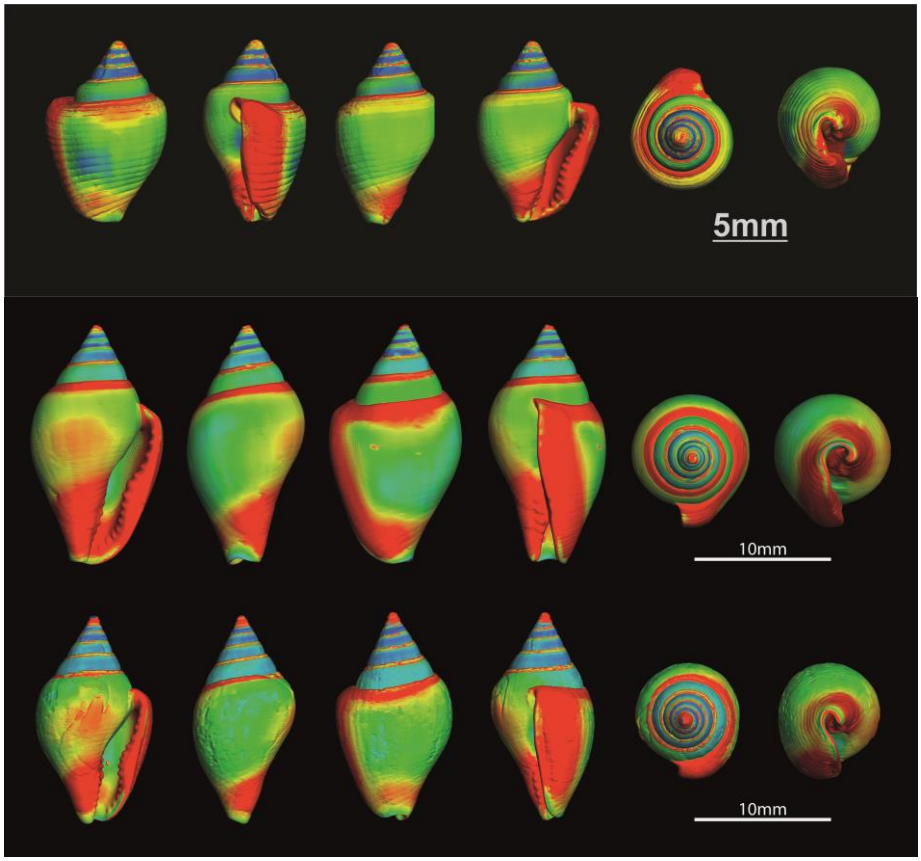
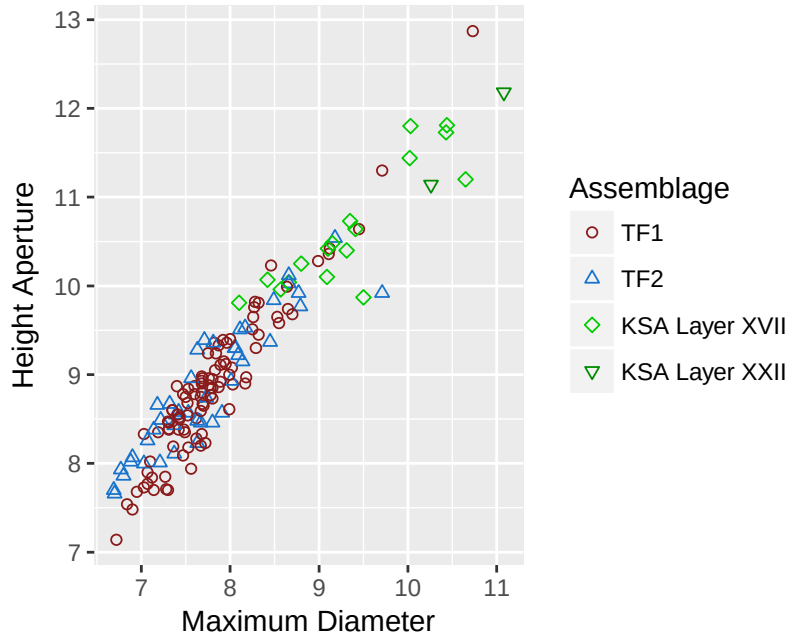


Figure 4. Heat maps of shell thickness in *Columbella* spp. Top: *Columbella adansoni* from thanatocoenosis (TF1), Middle: pristine *Columbella rustica* (RMNH.Mol.203708.a), bottom: *Columbella rustica* showing boring sponge damage (RMNH.Mol.203708.c). Red to blue: thick to thin.



704
705 Figure 5. Scatterplot comparison of the maximum diameter and the aperture height for
706 *Columbella rustica* of each analysed assemblage. Tenerife thanatocenoeses TF1: red circles,
707 TF2: blue triangles, Ksâr 'Akil Layer XVII: light green diamonds, Layer XXII: dark green
708 inverted triangles.

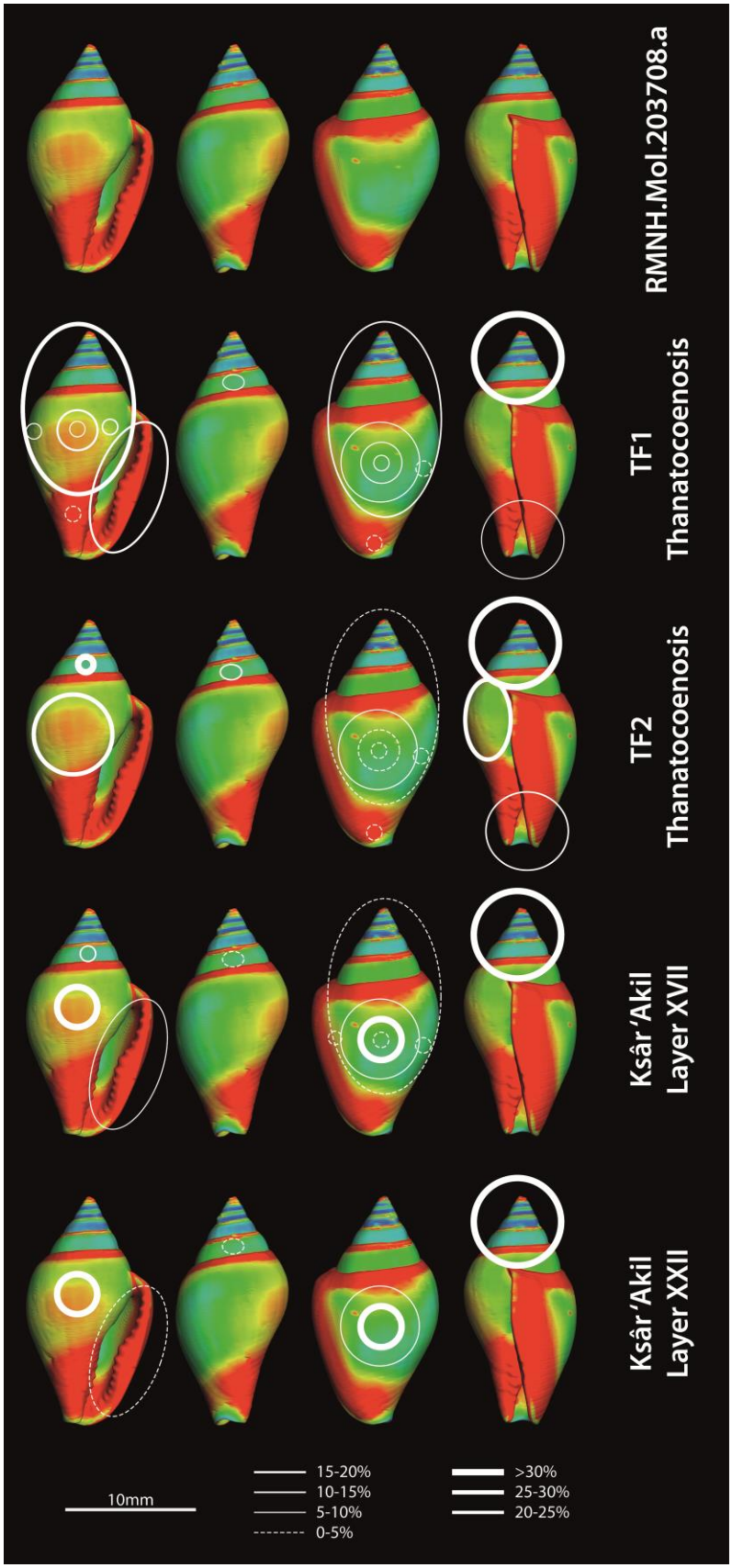


Figure 6. Shell damage in *Columbella rustica*, comparing thanatocoenoses TF1 and TF2 with Ksâr 'Akil Layers XXII and XVII. Red to blue: thick to thin. White circles: damaged zones,

thickness of line indicates percentage shells damaged in this region (see key in figure). Black circles: perforations by predators.

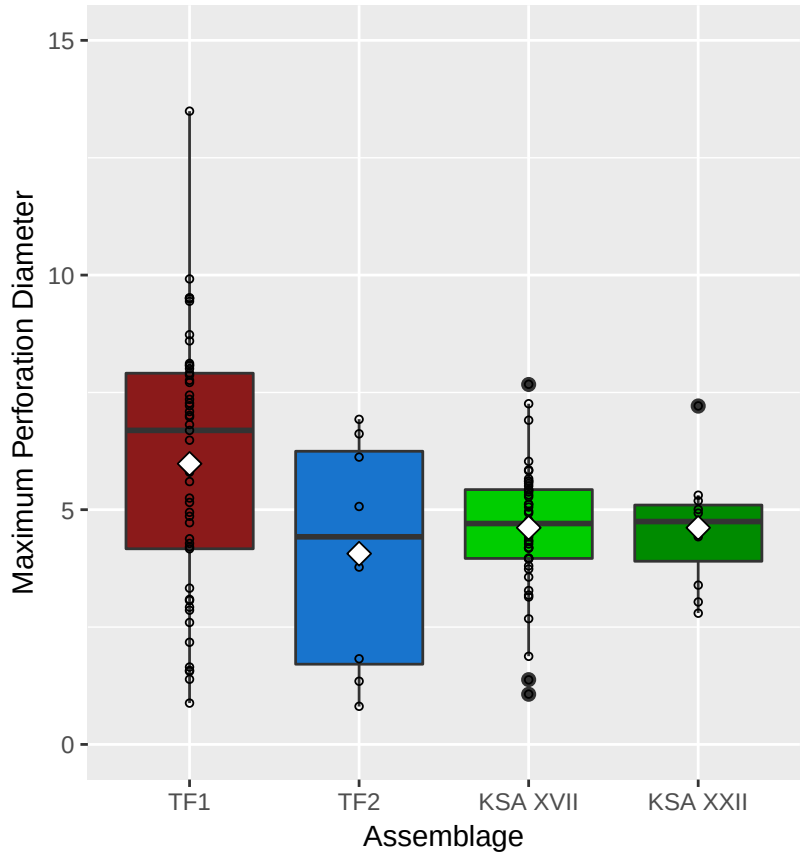


Figure 7. Boxplots comparing the maximum dorsal perforation diameter for *Columbella rustica* between each analysed assemblage. Tenerife thanatocoenoses TF1: red, TF2: blue, Ksâr 'Akil Layer XVII: light green, Layer XXII: dark green. Outliers are shown as solid black circles. Diamonds display the mean.