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The Ksâr 'Akil (Lebanon) mollusc assemblage: Zooarchaeological and taphonomic investigations

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ABSTRACT

Shells of marine molluscs exploited by prehistoric humans constitute archives of palaeoecological and palaeoclimatic data, as well as of human behaviour in coastal settings. Here we present our investigations on the mollusc assemblage from Ksâr 'Akil (Lebanon), a key site in southwestern Asia occupied during the Middle and Upper Palaeolithic. The site plays an important role in understanding modern human dispersals into Eurasia. Taxa from intertidal rocky shore, subtidal soft bottom, and rocky littoral habitats dominate the marine component of the invertebrate assemblage. Terrestrial snails indicate wooded and open half shaded habitats in the vicinity of the site. Species composition suggests that these habitats were present throughout the Upper Palaeolithic. Humans transported marine molluscs to the rockshelter as 'food packages' for dietary purposes (e.g., *Patella caerulea*, *Patella rustica*, *Phorcus turbinatus*) and shells of other taxa to be used as tools (e.g., *Glycymeris* sp.) or possibly for ornamental purposes (e.g., *Nassarius gibbosulus* and *Columbella rustica*). In the Initial Upper Palaeolithic, collection focussed on empty shells as raw material for utilitarian purposes. In the subsequent Early Upper Palaeolithic and later periods, mollusc gathering was performed in an increasing number of habitats and shifted towards collection for human consumption, which was the main reason for the introduction of shells to the site during the Epipalaeolithic. Concurrent size shifts of live collected as well as beached specimens suggests that size changes were linked to environmental change rather than to potential overexploitation of dietary taxa by humans.

1. Introduction

Hominins have consumed marine molluscs at least from the Middle Palaeolithic (Marine Isotope Stage (MIS) 5; roughly 100–115 ka) onwards in the Mediterranean region (e.g., Emiliani et al., 1964; Klein and Scott, 1986; Stiner, 1999; Colonese et al., 2011; Barker et al., 2012) and since the Middle Stone Age (MIS 6; roughly 191–123 ka) at Pinnacle Point in South Africa (Jerardino and Marean, 2010). The oldest use of shell has been documented for *Homo erectus* from Trinil (Java, Indonesia) at ≥400 ka (Joordens et al., 2014). The use of perforated shells for ornamental purposes has been documented throughout Africa and Eurasia at different stages of the Palaeolithic (e.g., Kuhn et al., 2001; Henshilwood et al., 2004; Bar-Yosef Mayer, 2005; d'Errico et al., 2005; Vanhaeren et al., 2006; Bouzouggar et al., 2007; White, 2007; Bar-Yosef Mayer et al., 2009; d'Errico et al., 2009; Stiner et al., 2013; Vanhaeren et al., 2013) and these finds have been of pivotal importance for the debate on behavioural modernity (e.g., Bouzouggar et al., 2007; Zilhão et al., 2010; d'Errico and Stringer, 2011). The earliest evidence for use of shells as ornaments comes from Qafzeh (Israel), where four perforated *Glycymeris nummaria* valves covered in ochre and dating to around 92 ka were found (Bar-Yosef Mayer et al., 2009). Other early evidence includes similarly perforated and coloured *Nassarius gibbosulus* shells from several Aterian and Middle Stone Age sites, dating to around 82 ka, in North Africa (e.g., Vanhaeren et al., 2006; Bouzouggar et al., 2007; d'Errico et al., 2009). In comparable finds of the closely-related species *Nassarius kraussianus* from South Africa (e.g., Henshilwood et al., 2004; Vanhaeren et al., 2013). In the Mediterranean, from the Middle Palaeolithic onwards, humans gathered shells of marine molluscs to be used as tools, such as cutting implements and scrapers (e.g., Stiner, 1994; Douka, 2011; Douka and Spinapolice, 2012; Romagnoli et al., 2014).

Mollusc remains are a potential source of data on past environments, human subsistence practices, and seasonality of site occupation. Reconstructions of past environments have been based on assemblage composition and diversity (e.g., Shackleton and van Andel, 1986). Metric analyses have been undertaken to explore

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human impact on coastal mollusc populations (e.g., Mannino and Thomas, 2001; Klein et al., 2004; Erlandson et al., 2011; Klein and Steele, 2013; Colonese et al., 2014). In addition, oxygen isotope analyses on shell carbonates can be used to obtain data on past sea surface temperatures (e.g., Emiliani et al., 1964; Mook and Vogel, 1968; Schöne et al., 2006; Joordens et al., 2009). These same methods allow us to infer the seasonality of shellfish exploitation, in particular of intertidal marine taxa (e.g., Deith and Shackleton, 1988; Mannino and Thomas, 2003; Mannino et al., 2007; Colonese et al., 2009; Mannino et al., 2011), which, in turn, can be useful to assess the periodicity of site occupation (e.g., Shackleton, 1973; Mannino et al., 2007, 2011; Colonese et al., 2009). Further, shell carbonates have been used as a medium for relative dating (amino acid racemization; e.g., Penkman et al., 2008; Demarchi et al., 2011), as well as numerical dating (radiocarbon; e.g., Benazzi et al., 2011; Douka et al., 2012, 2013).

The archaeological study of mollusc assemblages is informative on many aspects of past human lifeways, as well as the palaeoenvironmental and chronological context of these. Here we present a newly-recovered mollusc collection from Ksâr 'Akil in Lebanon (hereafter named '2015 collection'), a key site in the eastern Mediterranean, and re-evaluate with up-to-date zooarchaeological methods the known and previously-studied (e.g., van Regteren Altena, 1962; Kuhn et al., 2001; Douka, 2011) mollusc collection (hereafter '1962 collection'). We show the potential offered by the Ksâr 'Akil mollusc remains to throw light on past human behaviours, specifically on the interaction of humans with their environment, on mollusc consumption and on the use of shells as raw material for tools and personal ornaments.

2. Ksâr 'Akil: research history and site background

Ksâr 'Akil is a deeply stratified archaeological site in the eastern Mediterranean well-known for its long Initial (IUP) and Early (EUP)

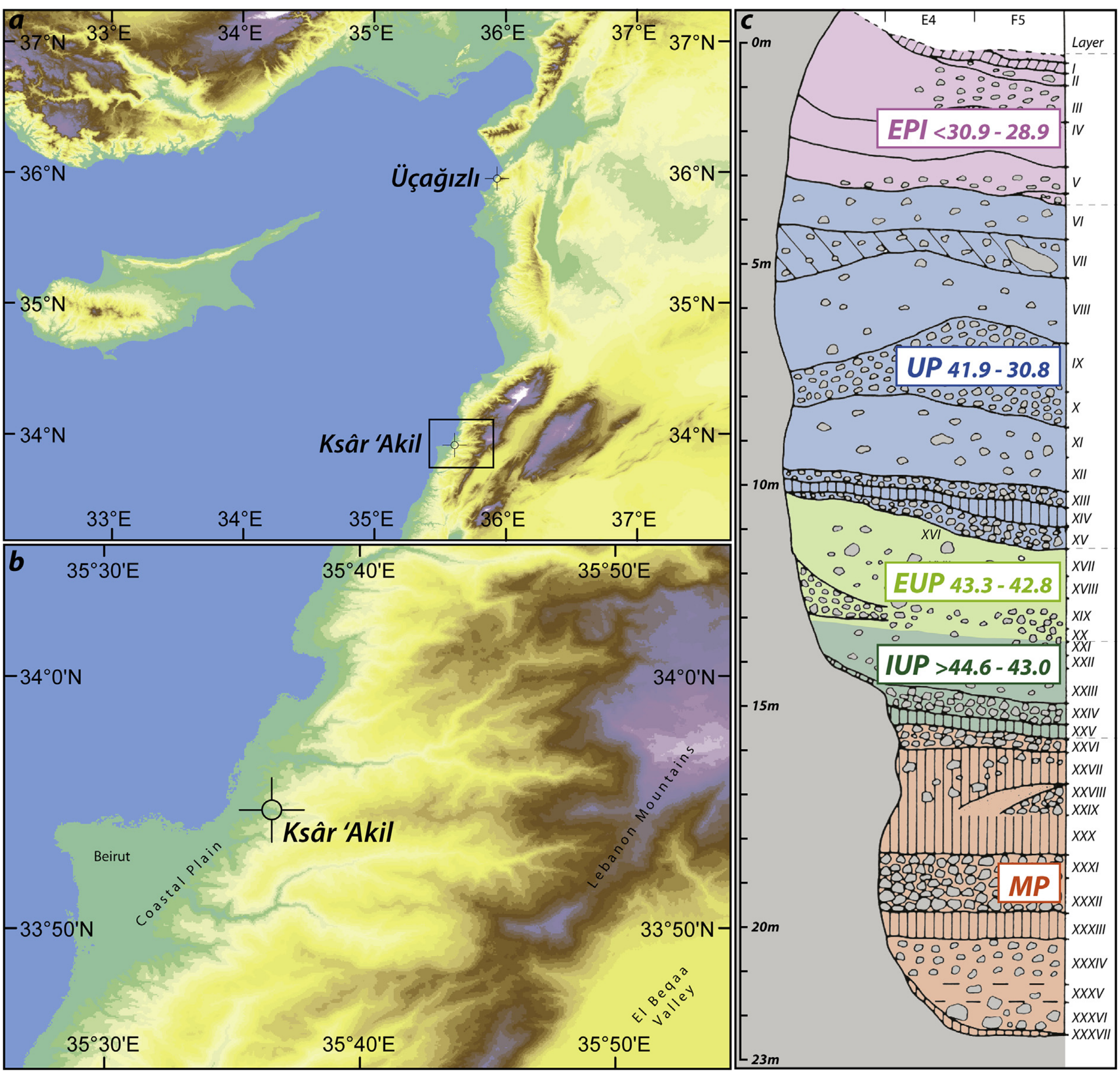

Fig. 1. Ksâr 'Akil site location and stratigraphy. (a) Map of the north-eastern Mediterranean with the location of Ksâr 'Akil (Lebanon) and Üçağızlı I (Turkey; mentioned in the text). (b) Inlet of map a, showing the location of Ksâr 'Akil in relation to the sea, coastal plain, and Lebanon mountains. (c) Stratigraphy of the 23 m thick Ksâr 'Akil sequence comprising from bottom to top Middle Palaeolithic (MP), Initial Upper Palaeolithic (IUP), Early Upper Palaeolithic (EUP), Upper Palaeolithic (UP), and Epipalaeolithic (EPI) layers. Digital elevation data in (a) and (b) originates from the Shuttle Radar Topography Mission (https://lta.cr.usgs.gov/SRTMBasic), downloaded from USGS Earth Resources Observation and Science (EROS) Center (http://eros.usgs.gov). Schematic section drawing in (c) based on Ohnuma and Bergman (1990), age-ranges after Bosch et al. (2015).

Upper Palaeolithic sequences, both of which are associated with human remains. The rockshelter was discovered in 1922 when Professor E. Day was informed of looting activity and was able to obtain some of the uncovered archaeological material (Delcourt, 1927; Ewing, 1949). It was on the recommendation of Abbé H. Breuil, who saw some of the Ksâr 'Akil lithic artefacts and bones, that Reverend J. G. Doherty from Boston College (Massachusetts, USA) and his team started the first scientific excavations in the summer of 1937 (Ewing, 1947). Excavations took place in three seasons (1937, 1938, and 1948–49), the last of which was led by J. F. Ewing who reached the bedrock at 23 m below datum (Ewing, 1949). Between 1969 and 1975, J. Tixier (CNRS, France) carried out additional excavations to a depth of 9 m below datum (Tixier and Inizan, 1981; Mellars and Tixier, 1989).

Ksâr 'Akil is located roughly 10 km northeast of Beirut (Lebanon, Fig. 1a), in the Antelias Valley (Ewing, 1947, 1948; Braidwood et al., 1951; Wright, 1962). The Antelias stream running down the valley terminates in the Bay of St. George. About 2 km inland, on the seaward-facing slopes of the Lebanon Mountains, the valley used to divide into two smaller valleys surrounding a limestone hill with a Semitic 'high place' on top (Ewing, 1947). This is probably the source of the name of the rockshelter (*Qasr* translates to inaccessible or high place and *Akil* meaning wise). The hill has been almost completely destroyed, as quarrying has reduced it almost to the valley floor (Bergman et al., 2012). The rockshelter is situated on the northern slope of the valley (Ewing, 1947; Wright, 1962; Bergman et al., 2012), and in prehistoric times the south-facing opening would have been protected by the hill in the centre of the valley. Freshwater supply would likely have come from the stream on the valley floor. The occupants of Ksâr 'Akil would have had access to a variety of habitats from the mainly rocky littoral to the small coastal plain (sahil) and from the steep and, at least, partly forested slopes of the Lebanon Mountains to the open highlands of the Beqaa Valley (Fig. 1b).

The Ksâr 'Akil sequence is 23 m thick and is subdivided in this study largely according to the archaeological division by Williams and Bergman (2010), as well as by taking into account the geological information provided in Ewing's (1949) and Wright's (in Braidwood et al., 1951; Wright, 1962) original publications. The lowermost 7 m (23–16 m below datum) contain reddish alluvial deposits with evidence of Middle Palaeolithic (MP; Layers XXXVII–XXVI) occupation, followed by very rich IUP (*sensu* Kuhn et al., 1999; Layers XXV–XXI) and EUP or Early Ahmarian (Layers XX–XIV) deposits (roughly 16–13 m and 13–10 m below datum, respectively). The subsequent Upper Palaeolithic (UP; Layers XIII–VI) deposits have been divided in various named and unnamed Upper Palaeolithic phases by different scholars (e.g., Kuhn et al., 2001; Williams and Bergman, 2010; Leder, 2014). Due to the diversity in archaeological attributions these layers, covering 7 m of deposits (approx. 10–3 m below datum), are here grouped in a broader UP. The Epipalaeolithic (EPI; Layers V to I) comprises the uppermost 3 m of the sequence (Fig. 1c) (see also Tixier, 1974; Tixier and Inizan, 1981; Azoury, 1986; Marks and Volkman, 1986; Bergman and Goring-Morris, 1987; Bergman, 1988; Bergman and Stinger, 1989; Mellars and Tixier, 1989; Ohnuma and Bergman, 1990; Williams and Bergman, 2010; Douka et al., 2013; Leder, 2014). Above 16 m, the sediments containing UP artefacts are generally brown-greyish in colour and are intersected by so-called stone complexes at a depth of 17–16 m, 11–10 m, and 2 m below datum. These stone complexes consist of angular limestone blocks, sometimes underlain by red clay bands, and are thought to have coincided with humid climatic conditions, potentially representing pluvial subphases of the last Glaciation (Braidwood et al., 1951; Ewing, 1960; Wright, 1962). The deposits containing Epipalaeolithic layers are blackish.

The material studied here originates from the excavations by Doherty in the 1930s and by Ewing in the 1940s, the only ones to cover the full depth of the sequence. Ewing and Doherty used different datum points, making it difficult to correlate material from both excavations. Lists based on notes from the original excavators that correlate the depths per square of Doherty's excavations to the layers assigned by Ewing thus linking the material from the 1930s and 1940s were kindly provided by A. Kersten (see also Hoojier, 1961; Kersten, 1991).

The envisioned large scale paleontological study of the faunal remains was originally delegated to D. Bate (Natural History Museum, London, UK), but after her death the faunal material was sent to D. Hooijer at the Museum van Natuurlijke Historie (now Naturalis Biodiversity Center) in Leiden, the Netherlands. Hooijer published a study on the vertebrates (Hooijer, 1961; see also Kersten, 1987, 1991, 1992). He also separated the majority of the invertebrate remains, mainly including complete or nearly complete specimens and gave them to C. O. van Regteren Altena for study and curation (van Regteren Altena, 1962). The Ksâr 'Akil faunal assemblages (both vertebrate and invertebrate) are currently curated in the Naturalis Biodiversity Center in Leiden. Molluscs from Tixier's excavations in the late 1960s and early 1970s were studied by Inizan and Gaillard (1978). They were not taken in consideration here, as the main aim of this paper is to compare and reunite the 1962 and 2015 collections, which both originate from Doherty and Ewing's excavations.

3. Material and methods

We conducted zooarchaeological and taphonomic investigations on the mollusc assemblage (n = 3571) consisting of two collections, both originating from the same excavation campaigns, i.e., Doherty's 1937–38 and Ewing's 1947–48 excavations (Tables 1 and 2). The first collection or '1962 collection' (n = 2804) was published by van Regteren Altena (1962) and originates from the entire excavated area. The second or '2015 collection' (n = 767) was recovered during the study of vertebrate skeletal remains of the 2 × 2 meter excavation square F4. Preparation of the square F4 vertebrate material included treatment with acid (i.e., 10% acetic acid solution over 8 h and subsequent exposure to a base, i.e., 10% sodium carbonate solution, to stop any persisting acid reaction) to loosen sediment adhering to the bones. During this process, numerous shells of terrestrial and marine molluscs were recovered. Whenever possible, shells were detached before acid treatment, others had to be loosened using the acid and shell specimens treated in this way have a light glaze on the outer surface. The newly-recovered '2015 collection' is largely fragmentary, but comprises also some intact or nearly intact specimens (n = 82). As a result of the present study, the collection from square F4 was

Table 1
Ksâr 'Akil mollusc collections. 1962: collection studied by van Regteren Altena (1962); 2015: this study. Abbreviations: n: number of specimens, NISP: number of identified specimens, MNI: minimum number of individuals, S: number of taxa, complete: percentage of complete and nearly complete specimens. F4: 2 × 2 m excavation square (see text).

	1962		2015	Total	
	All	F4	F4	F4	All
n	2804	387	767	1154	3571
NISP	2683	387	766	1103	3406
MNI	2259	322	128	436	2370
S	47	22	16	24	49
Complete (%)	76.92	72.35	10.69	31.37	63.19
Burning (%)	16.45	20.16	25.03	23.57	18.68

Table 2
Mollusc NISP per layer (I – XXVIII A) for the Ksâr 'Akil studied shell assemblage (1962 and 2015 collections combined). H: species habitat (1–5 marine, 6 freshwater, 7–9 terrestrial), 1: intertidal rocky shore, 2: estuary/lagoon, 3: subtidal rocky substrate, 4: subtidal soft bottom, 5: deep subtidal bathyal soft bottom, 6: fresh water, 7: woodland, 8: open to half shaded, 9: arid adapted, open to half shaded; MP: Middle Palaeolithic.

Species	H	Epipalaeolithic					Upper Palaeolithic								Early Upper Palaeolithic							Initial Upper Palaeolithic				MP
		I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	XVII	XVIII	XIX	XX	XXI	XXII	XXIII	XXIV	XXVIII A
Marine gastropods																										
Patella caerulea	1		1			1	2	21	6	2	1	1					1	4								
Patella rustica	1	1	1	1		18	7	6	1	3	3						9	19								
Patella ulyssiponensis	1						2	2	2								1	1								
Patella sp.	1				1	1	2	7	1	3		1						11	2		1					
Trochidae	–											1						1								
Phorcus articulatus	1									1		8						2								
Phorcus turbinatus	1			14	5	120	25	34	13	19	21	43	7	7			37	71	6	7	2		1			
Phorcus sp.	1									3		60	3					10		1						
Bolma rugosa	4											3											2			
Cerithium vulgatum	3								1	2			1				10	5		4	5	4	13	2		
Naticarius hebraeus	4																		1				1			
Neverita josephinia	4											1						2		1			1			
Semicassis saburon	4		1																							
Euthria cornea	3																1	2								
Pisania striata	1									1		1														
Columbella rustica	3					3	2	20	16	132	37	5	4		1	1	31	115	4	10	4	2	19	2	1	
Tarantinaea lignarius	3																	2								
Nassarius gibbosulus	4				1	7	9	31	59	145	26	8	10	1			37	125	14	25	10	26	128	10	1	
Nassarius mutabilis	4									1												1				
Nassarius sp.	4																				1		1			
Bolinus brandaris	3																	2								
Hexaplex trunculus	3							2			2						2	5								
Murex sp.	3										1										1					
Mitra cornicula	1										1						1									
Conus ventricosus	3							3		4	1							5	2		3					
Marine gastropod	–										2	13						5			2		1			
Marine bivalves																										
Acanthocardia tuberculata	4		1						4	14	1	2					7	31	2				2	1		
Acanthocardia sp.	4								1			2														
Cerastoderma glaucum	2																	1								
Donax trunculus	4									1																
cf. *Callista chione*	4																	1	1							
Venus verrucosa	4																	1								
Anadara cf. *polii*	4									2																
Arca noae	3																	1								
Barbatia barbata	3																		1							
Glycymeris nummaria	4						1			2			1				10	7		1			1		1	
Glycymeris sp.	4		1		3	1		2	5	26	1	9	1			1	34	78	16	29	7	23	22	6	6	
Lima lima	3									4								2								
Ostrea edulis	3									1												1				2
Spondylus gaederopus	3											1	1											1		
Pinna nobilis	4					1						3														
Marine scaphopods																										
Antalis dentalis	5									10																
Antalis vulgaris	5									13	1															
Antalis sp.	5								2	13																
Freshwater gastropods																										
Theodoxus jordani	6									4										1						
Melanopsis buccinoidea	6							1		2										1						

(*continued on next page*)

Table 2 (*continued*)

Species	H	Epipalaeolithic					Upper Palaeolithic								Early Upper Palaeolithic							Initial Upper Palaeolithic				MP
		I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	XVII	XVIII	XIX	XX	XXI	XXII	XXIII	XXIV	XXVIII A
Freshwater bivalves																										
Unionacea	6						1		2	1																
Potomida littoralis	6									1																
Terrestrial gastropods																										
Pomatias elegans	8																	1			1					
Pomatias olivieri	8					2	1	7	7	6	4	1	2	2			10	10	13	6	1		1			
Buliminus labrosus	7							2	1			1							2							
Pene syriacus	7								1											1						
Cristataria porrecta	7												1													
Oxychilus syriacus	8					3	1	1	4		2							2	1	1						
Helicidae	7											69						3		5	5					
Helix pachya	7	1	1	13	12	80	42	125	64	21	9	21	4	1	2		16	44	2	8		2				
Sphincterochila cariosa	9					1																				
Metafructicola berytensis	8					2	5	5	4	2	3						13	12	4	10	1		2			
Monacha nummus	8																		1			1				
Monacha syriaca	8					2	3	4	1	7	1							6		4			2			
Terrestrial gastropod	–										2	211	16					46		62	2					
Total NISP	–	2	6	28	22	242	103	273	195	446	119	465	51	11	3	2	220	633	72	177	46	60	197	22	9	2

enlarged from 387 to 1154 specimens and from 22 to 24 species (Tables 1 and 2).

The classification of the taxa in the assemblage has been updated, according to the most recent nomenclature, using the online databases WoRMS (Boxshall et al., 2014) for marine species and WMSDB (http://www.bagniliggia.it/WMSD/WMSDhome.htm) for freshwater and terrestrial species. Quantities were recorded in terms of number of shell fragments (n), number of identifiable specimens (NISP, counting refitted shell fragments as one specimen), and minimum number of individuals (MNI) (after Lyman, 2008). MNIs were calculated using landmarks, e.g., presence of apex, aperture, columella and umbo, depending on shell type (i.e., bivalve or gastropod). Scaphopod MNIs were determined by the number of specimens for which >50% of the shell was preserved. Our zooarchaeological investigations further included determination of taphonomic alterations (both pre- and post-depositional), human modifications and metric analysis. Pre-depositional alterations, comprising indicators of peri- and post-mortem exposure to a marine environment (e.g., in active beaches) include bioerosion, epizootic encrustation, seafloors with reductive conditions, surface wear and polish resulting from beach rolling, non-repaired damage of gastropod predation, crab predation, and boring sponges (Table 3). Post-depositional taphonomic alterations include decalcification, erosion, root etching, and sediment encrustations (both local, i.e., originating from the deposits present in the rockshelter, and non-local deposits, which are in essence pre-depositional alterations) (Fig. 2). Observed potential human modifications include impact fractures, retouch, apex detachment of topshells (to facilitate shellfish extraction), edge damage on limpets (congruent with damage from prying the animals off the rocks), perforations, presence of red pigments, and signs of burning. Standard measurements (in mm) comprise maximum length, width, and height for bivalves and conical gastropods, maximum height and basal diameter for scaphopods and coiled shells, and aperture height for coiled shells.

Prior to comparing the mollusc taxa from the different archaeological layers, potential biases that may have affected the assemblage need to be addressed. The Ksâr 'Akil molluscs were recovered long ago and potential loss of material, either through incomplete collection or post-excavation discard of material has to be explored. Although excavation techniques were not up to present-day standards, all sediments were dry sieved (Murphy, 1938) and shell remains were adequately recognised during the fieldwork (Ewing, 1947, 1948, 1960). Murphy (1938) writes that in the 1937 field season both lithics and bones were discarded after initial study, if they were not deemed interesting for further investigation. Regarding the vertebrate fauna, this approach seems to have changed in later seasons as high numbers of small non-identifiable (i.e., "uninteresting") fragments are present in the IUP, EUP, and UP. The majority of the molluscs in the '1962 collection' are intact or almost intact and it is possible that only a sample of the invertebrates was kept. However, species composition of the '2015 collection' includes many small fragments that were found encrusted to bones indicating that mollusc completeness in the '1962 collection' is more likely the result of incomplete separation of the mollusc remains from the vertebrate fauna in the 1960s than of post-excavation discard. Ewing made a very detailed initial account of changes in faunal distribution throughout the sequence. Regarding the invertebrate assemblage, Ewing (1947, 1948) wrote that there were many shells above 12 m depth (which relates to layer XVIII), but none below and that the most common land snail was *Helix* and the most frequent marine species were *Trochus* (now *Phorcus*) and *Patella*. He also stated that the frequency of land snails versus marine species remained the same throughout the occupation, and that three peaks in shell abundance (both terrestrial and marine) were identified at 4 m, 9.3 m, and 11.25 m below datum

Table 3
Pre-depositional taphonomic alterations in marine taxa by phase (MP – EPI) per Layer (I – XXVIII A) and divided in live-collected intertidal rocky shore taxa and beach collected empty shells. Note: as some specimens were subjected to more than one type of pre-depositional alteration the numbers of shells showing marine taphonomic alterations (column: Total MA; row: Total (n)) are lower than the sum of the occurrence of the individual pre-depositional alterations. Abbreviations: EPI: Epipalaeolithic, UP: Upper Palaeolithic, EUP: Early Upper Palaeolithic, IUP: Initial Upper Palaeolithic, MP: Middle Palaeolithic, Bio: bioerosion, Ep. encr.: Epizootic encrustations, Red. con.: exposure to sea floors with reductive conditions, B. wash: beach washed, Gast.: gastropod damage, Crab.: Crab damage, B. sponge: Boring sponge damage, total MA: total Marine Alterations.

Phase	Layer	n	Bio	Ep. encr.	Red. con.	B. wash	gast.	crab.	B. sponge.	Total MA
EPI	I	2	0	0	0	0	0	0	0	**0**
	II	6	0	0	0	0	0	0	0	**0**
	III	28	0	0	0	0	0	0	0	**0**
	IV	22	0	0	0	1	0	0	0	**1**
	V	242	0	0	0	5	0	0	2	**5**
	Total EPI	*300*	*0*	*0*	*0*	*6*	*0*	*0*	*2*	***6***
UP	VI	103	0	0	0	8	0	0	3	**8**
	VII	272	3	0	1	30	0	2	10	**34**
	VIII	195	0	0	2	50	0	8	10	**54**
	IX	448	5	0	7	222	3	30	69	**248**
	X	122	0	0	5	55	5	3	17	**56**
	XI	466	0	0	0	6	0	0	0	**6**
	XII	61	0	0	0	6	4	0	0	**10**
	XIII	11	0	0	0	1	0	0	0	**1**
	Total UP	*1678*	*8*	*0*	*15*	*378*	*12*	*43*	*109*	***417***
EUP	XIV	3	0	0	0	1	0	0	1	**1**
	XV	2	0	0	0	0	0	0	0	**0**
	XVI	220	3	1	5	42	5	0	16	**52**
	XVII	646	14	2	10	215	17	19	79	**233**
	XVIII	72	1	0	0	8	2	0	2	**10**
	XIX	191	0	0	0	27	2	1	8	**28**
	XX	48	4	0	0	10	2	2	6	**18**
	Total EUP	*1182*	*22*	*3*	*15*	*303*	*28*	*22*	*112*	***342***
IUP	XXI	60	0	0	0	18	1	0	2	**18**
	XXII	198	6	1	5	127	8	5	29	**134**
	XXIII	22	1	0	1	10	1	0	1	**12**
	XXIV	9	0	0	0	0	0	0	0	**0**
	Total IUP	*289*	*7*	*1*	*6*	*155*	*10*	*5*	*32*	***272***
MP	XXVIII A	2	0	0	0	0	0	0	0	**0**
Intertidal rocky shore taxa		**684**	**0**	**0**	**0**	**1**	**0**	**1**	**0**	**2**
Other marine taxa		**1676**	**38**	**4**	**36**	**866**	**50**	**71**	**263**	**987**
Total (n)		**2360**	**38**	**4**	**36**	**867**	**50**	**72**	**263**	**989**
Total (%)		**–**	**1.59**	**0.17**	**1.51**	**36.38**	**2.10**	**3.02**	**11.04**	**41.50**

(corresponding to layers V, IX, and XVI – XVII, respectively) (Ewing, 1947).

These observations match the main features of the '1962 collection' almost to the letter. Peaks in mollusc abundance have been detected in layers V, IX, and XVI – XVII, below which the number of shells greatly diminishes. A small additional peak in mollusc numbers corresponds to layer XXII, below which very few shells were recovered. *Helix*, *Phorcus*, and *Patella* are among the most frequent (and largest) taxa and throughout the sequence marine species make up approximately two-thirds and terrestrial molluscs one-third of the assemblage. Further, Ewing (1948) stated that in some parts of the deposits thousands of shells were present, which judging from the general writing style and lack of counts, may be an overestimation. Although it is possible that not all mollusc remains were kept, by comparing the '1962 collection' with the recently-acquired '2015 collection' it can be concluded that both collections combined are a representative sample of what was originally excavated, given that their taxonomic composition matches that of the preliminary observations by Ewing. The 1962, and 2015 collections taken together represent a sizeable mollusc collection ($n = 3571$) for an Upper Palaeolithic site of this antiquity. Overall, it is likely that a representative collection of the original assemblage survives and this is useful to reconstruct the salient aspects of mollusc exploitation by the occupants of Ksâr 'Akil. Moreover, the 1930s and 1940s excavations could successfully be correlated as regards to the layers and find-depths (see above) allowing us to merge the material from the two collections in a combined study.

In addition to potential recovery and curation issues, the taphonomic history may differ between layers and might have resulted in differential faunal preservation. Before comparing layers statistically, it first has to be established if these potential differences could significantly influence the results (e.g., Grayson, 1984). In addition, differences in collection techniques and small sample size could be other sources of bias. The 1962 and the 2015 collections are markedly different, given that the former consists almost completely of intact specimens, while the latter is largely fragmentary. Although the total vertebrate assemblage from the entire sequence in square F4 was subjected to acid treatment, not all layers contained new mollusc material. Therefore, fragmentation rate varies between layers and merging these two datasets might introduce significant differences in completeness between layers rendering them unsuitable for a comparative study. Further, if changes in species abundance and composition are driven by sample size, then these parameters cannot be used to inform us about human behaviour (Grayson, 1984; Lyman, 2008).

To ascertain whether shell completeness and sample size have a significant influence on the Ksâr 'Akil invertebrate assemblage, we carried out best-fit regression analysis (after Lyman, 2008). The interrelatedness between NISP and MNI is assessed by the degree of correlation of the log or lnMNI and lnNISP, as well as between lnNISP and lnS (or lnNTAXA, i.e., the number of species) per layer using Pearson's correlation coefficient (as the values are not ranked). To verify whether sample size is the main factor responsible for the faunal composition of a layer, the relative abundance of several common species (i.e., *Phorcus turbinatus*, *Columbella rustica*,

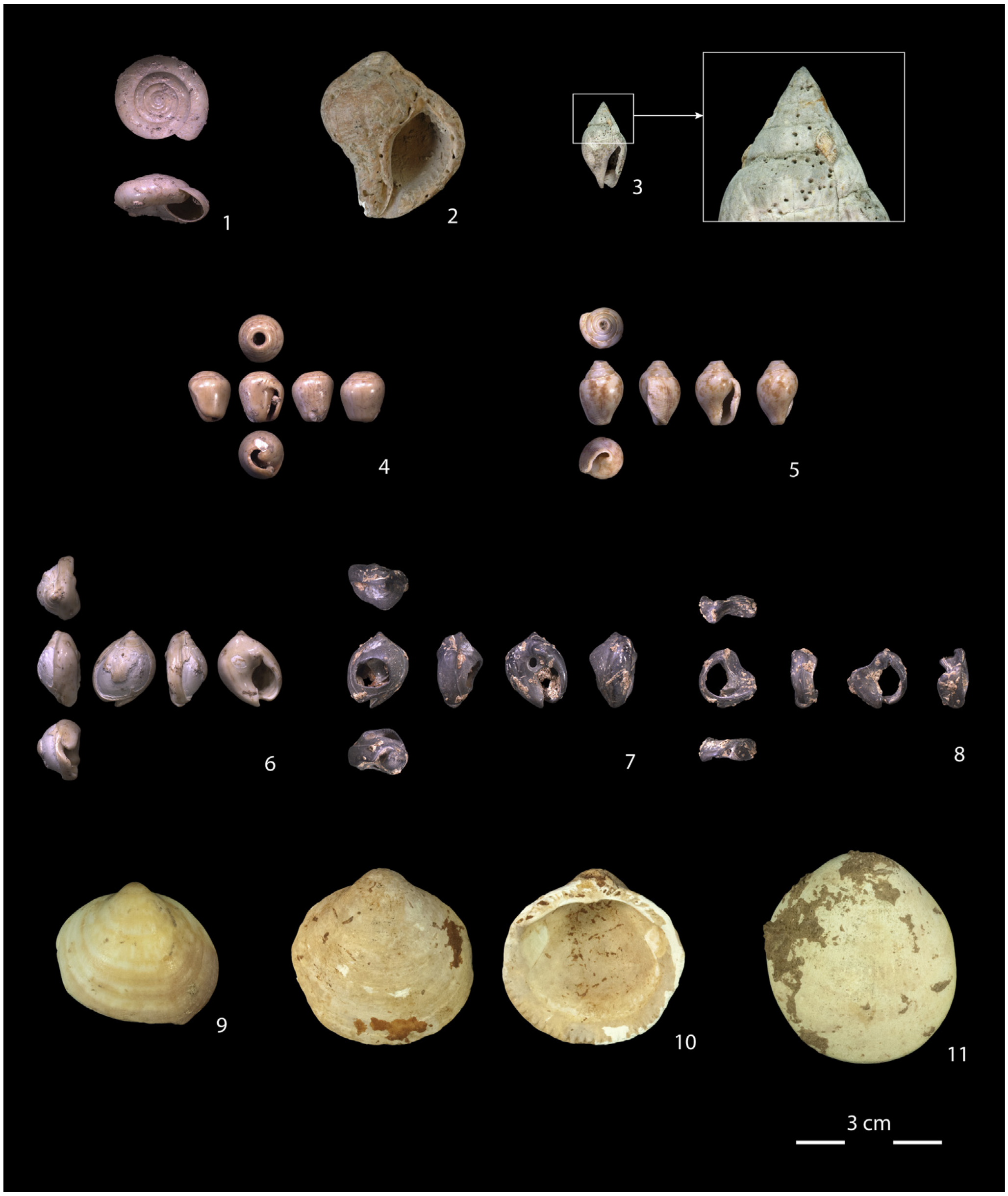

Fig. 2. Examples of taphonomic signatures. 1, 5, 9: Original pigmentation; 2, 4, 5, 8: various stages of beach washing; 2, 3: boring sponge damage (see inlet 3); 3: burning; 6, 10: localized recrystallization; 7, 8: reducing marine atmosphere; 7: gastropod perforation; 7, 10: red pigment stain; 11: fossilized; 1: no traces. Shell species shown: 1: RGM-606482, *Oxychilus syriacus*; 2: RGM-577859, *Bolinus brandaris*; 3: RGM-770824, 5: RGM-550196, *Columbella rustica*; 4: RGM-606214, *Conus ventricosus*, 6: RGM-550222h, 7: RGM-550222a, 8: RGM-550222c, *Nassarius gibbosulus*; 9: RGM-550201, 10: RGM-577852, 11: RGM-550206, *Glycymeris* sp. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

Nassarius gibbosulus and *Helix pachya*) throughout the Ksâr 'Akil assemblage were plotted against the total NISP per layer (following Lyman, 2008). If the NISP per species is not significantly related with the total NISP, this would indicate that sample size is not a driving factor in assemblage composition. We use Spearman's rho (employing a t-distribution) as a significance test because the values are ranked.

Species composition per layer is assessed through the calculation of the taxonomic richness (S), evenness (e), dominance (1/D), and heterogeneity (H) (Lyman, 2008; see also; Stiner et al., 2013). These indices all describe assemblage composition, but with subtle differences. The larger the value of H, the greater is the heterogeneity. Taxonomic evenness values range between 0 and 1, where 1 signifies that all taxa are equally abundant (Lyman, 2008). Inversely, the higher the 1/D value the more evenly species are distributed, whereas low values signify dominance by one or few species (Lyman, 2008). As taxonomic evenness and heterogeneity are calculated on the basis of NISPs, it is possible that the outcomes are driven by sample size. To assess this possibility, both values are plotted against the total NISP per layer and Pearson's correlation coefficient is used to identify significance. This type of regression analysis is also used to discern potential chronological trends in both species composition and average mollusc size (e.g., Grayson, 1984; Lyman, 2008).

4. Results and discussion

The total NISP for which a secure stratigraphic position could be ascertained on the basis of their labels is 3406. The total MNI is 2370 and is attributable to 49 taxa (Table 1). Two valves of *Ostrea edulis*, probably belonging to a single specimen, are the only invertebrate remains found in the MP deposits (Layer XXVIII A).

From the IUP onwards, mollusc remains become more frequent (n = 289) with peaks in the EUP (n = 1182) and subsequent UP layers (n = 1678). The EPI layers have yielded little material culture and faunal remains including molluscs (n = 300) (Table 2).

Overall, the molluscs include species from terrestrial, freshwater, brackish water and fully marine environments and comprise gastropods, bivalves and scaphopods (Table 2). The marine molluscs originate both from hard and soft-bottom habitats. The most common taxa are the intertidal rocky shore *Phorcus turbinatus* (NISP = 431) and *Patella* spp. (NISP = 146), the sublittoral rocky substrate taxon *C. rustica* (NISP = 409), the soft-bottom sublittoral *N. gibbosulus* (NISP = 673) and Glycymeridae (NISP = 295). Brackish and freshwater species are rare (n = 15). Terrestrial species include wooded as well as open and half shaded taxa, of which the woodland species *H. pachya* (NISP = 468) is best represented. From all habitats adult complete or semi-complete specimens dominate the assemblage.

The two collections (i.e., 1962 and 2015) differ mainly in terms of fragmentation and frequency of burning damage (Table 1). A strong significant correlation ($r = 0.97$ $p < 0.001$) exists between lnNISP and lnMNI throughout the sequence, suggesting MNI and NISP of all layers are interrelated. Similarly, lnNISP and lnS are highly negatively correlated ($r = -0.95$, $p < 0.001$). These results warrant merging of the two collections. The relative abundance of several common species, namely *Ph. turbinatus* ($r = -0.03$, $p = 0.89$), *C. rustica* ($r = 0.09$, $p = 0.68$), *N. gibbosulus* ($r = 0.16$, $p = 0.45$), and *H. pachya* ($r = -0.20$, $p = 0.36$) shows no significant correlation with total NISP throughout the sequence, suggesting that sample composition is not driven by sample size. Both, the interrelation and relative abundance analyses, suggest that the taphonomic history per layer did not differ significantly and merit inter-layer comparison.

4.1. Taphonomy

An important question, which needs to be addressed by any study of mollusc remains from archaeological sites, is establishing which agents were responsible for the introduction of the shells to a site. It is essential to distinguish between shell deposits that accumulated naturally or that were accumulated by animals other than humans, from those of anthropogenic origin (Erlandson and Moss, 2001). The Ksâr 'Akil rockshelter lies at an elevation of approximately 80 m (top of the 23 m sequence) above present-day sea level (asl). Several fossil beach deposits have been identified along the Lebanese coast up to a height of 90 m asl. (e.g. Fleisch, 1962; Wright, 1962). However, despite the potential of naturally introduced marine shells in the site, given the presence of fossil beaches at this elevation and the alluvial nature of the lowermost 7 m of the Ksâr 'Akil stratigraphy, these deposits contain virtually no invertebrate remains. The Upper Palaeolithic deposits, rich in both mollusc and archaeological remains, are the result of *in situ* accumulation of sediments (Wright, 1962). This suggests that the marine molluscs were transported to the site by either animals or humans. Many species of birds (e.g., herons and oystercatchers) are known to accumulate mollusc remains, as do many small carnivores (e.g., mustelids, but also wolves) and rodents (Claassen, 1998; Erlandson and Moss, 2001). In general, molluscs gathered by animals show specific taphonomic modifications, such as breakage patterns resulting from dropping shells from great heights on hard surfaces (i.e., birds) or canine punctures on the shell surface, in their efforts to access the mollusc flesh (Claassen, 1998). None of these taphonomic signatures have been encountered on the shells examined for this study. This and the unlikelihood that animals would accumulate hundreds of shells at a site that is relatively distant from the shore suggest that humans introduced the molluscs to the rockshelter (as will also be argued below on the basis of anthropic taphonomic alterations). Moreover, there would have been no apparent reason for birds or other animals to transport beach-rolled shells to the site. It is, therefore, reasonable to assume that at least the marine taxa were introduced to Ksâr 'Akil by humans.

4.1.1. Pre-depositional taphonomy

The taphonomic signatures observed on the shells from the assemblage vary between species. This is especially true for 'pre-depositional taphonomic alterations', which are inflicted on the shells during the time after the death of the mollusc and before final deposition and burial. These alterations are habitat-dependent and are, therefore, described below according to the environment of origin (i.e., marine, freshwater, terrestrial). Post-depositional processes that took place after the shells were incorporated in the Ksâr 'Akil deposits are more uniformly distributed and are thus described for the assemblage as a whole.

4.1.1.1. Marine species. Almost half of the marine shells (41.5%, gastropods, bivalves, and scaphopods) show taphonomic signatures resulting from exposure to marine environments and were, therefore, collected empty from active beaches. Traces of beach weathering (36.4%), staining by exposure to sea floors with reductive conditions (1.5%), boring sponge damage (11.0%), other bioerosion (1.6%), encrustation by epizootic organisms (0.2%), and predator damage from either carnivorous gastropods (2.1%) or crabs (3.0%) were found (Table 3; Fig. 3). The majority of beach-collected taxa are subtidal and live on soft-bottom and hard-bottom substrates. Intertidal and bathyal/low-subtidal soft-bottom taxa (i.e., *Antalis* spp.) are rare. Some bivalves (mainly *Glycymeris* sp., but also *G. nummaria*, *Spondylus gaederopus*, and *O. edulis*) show advanced erosion, decalcification, and fossilization that are consistent with collection from fossil deposits rather than from active beaches. Fossil marine terraces containing *Glycymeris* have been recognised along the Lebanese coast at 45, 35, 15 and 6 m asl (Fleisch, 1962; Wright, 1962).

The majority of the assemblage (58.5%) is composed by rocky shore intertidal gastropods (i.e., *Ph. turbinatus*, *Phorcus articulatus*, *Patella rustica*, *Patella caerulea* and *Patella ulyssiponensis*) that generally show no signs of peri- or post-mortem damage resulting from exposure to destructive marine organisms and/or environments, indicating that they were collected alive by humans for consumption. The frequency of marine taphonomic alterations per layer is mainly linked to the purpose and habitat of gathering. Layers containing mainly shells of molluscs primarily gathered for consumption (e.g., those attributed to the Epipalaeolithic) yielded

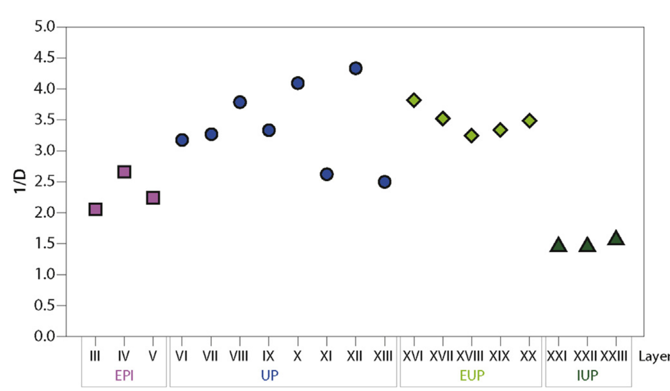

Fig. 3. Taxonomic dominance (1/D) of habitat types per layer (roman numerals). Initial Upper Palaeolithic (IUP): triangles, Early Upper Palaeolithic (EUP): diamonds, Upper Palaeolithic (UP): circles, and Epipalaeolithic (EPI): squares. Note: low sample size in layers I, II, XIV, XV, XXIV, and XXVIII A, prohibit including these layers in this analysis.

only a few specimens with taphonomic signatures compatible with a prolonged exposure to marine taphonomic agents.

4.1.1.2. Freshwater and brackish water species. Freshwater species include: the gastropods *Melanopsis buccinoidea* (n = 4) and *Theodoxus jordani* (n = 5), which are adapted to medium and high energy water regimes (Bößneck, 2011), the bivalve *Potomida littoralis* (n = 1), adapted to low energy regimes, and some unidentified *Unionacea* fragments (n = 4). The absence of taphonomic alterations suggests that all *M. buccinoidea* and the *P. littoralis* specimens were collected fresh, possibly from the Antelias stream, in line with their habitat requirements. The shell structure of the *Unioacea* specimens appears to be well-preserved, but the shells are very fragmentary possibly as a result of post-depositional damage to specimens introduced intact to the site. Preservation of *Th. jordani* varies. Two specimens of this species are fossilised and severely eroded, whilst other two show signatures typical of aquatic alterations and one bears none. Shells of *Th. jordani* could possibly have been collected from different localities (e.g., from a river, from the beach were the stream terminates, and/or from fossil deposits). The only specimen from a brackish water environment is an umbonal fragment of *Cerastoderma glaucum* showing no signs of taphonomic alterations and likely collected from a lagoonal/estuarine environment. In general, fresh and brackish water species are rare and were not an important component of the Ksâr 'Akil assemblage.

4.1.1.3. Terrestrial species. All species of terrestrial gastropods recovered at Ksâr 'Akil live in limestone environments and come from two main habitats. Woodland taxa include *Buliminus labrosus*, *Pene syriacus*, *Cristataria porrecta* and *H. pachya* (Heller, 1974; Bößneck, 2011). The latter species, is adapted to a wide range of habitats and altitudes (Bar and Mienis, 1979). Taxa of open and half-shaded environments are *Pomatias elegans*, *Pomatias olivieri*, *Oxychilus syriacus*, *Sphincterochila cariosa*, *Metafructicola berytensis*, *Monacha nummus* and *Monacha syriaca* (Broza and Nevo, 1996; Bößneck, 2011). There are slight variations in the preferred habitat of the encountered terrestrial species, all of which can be found in the Antelias Valley. The species *M. berytensis* and *O. syriacus* generally live at high elevation (>1000 m), whereas *M. nummus* and *P. elegans* are more frequent in coastal areas (Bößneck, 2011). *Sphincterochila cariosa* is a more arid-adapted species and can be found in semi-desert environments, but is also encountered in scrublands (Broza and Nevo, 1996). *P. olivieri* is a mesic prosobranch more often found in humid areas (Broza and Nevo, 1996). The presence of intact opercula in two *P. olivieri* specimens suggests that the species may have aestivated in Ksâr 'Akil (see also van Regteren Altena, 1962). Most of these species would have lived in the vicinity of Ksâr 'Akil and some specimens may have reached the site alive and died there naturally. One exception might be *H. pachya*, which is twice as numerous as all other terrestrial taxa together (see Table 2). Terrestrial molluscs do not show signs of pre-depositional alterations except perhaps some specimens of *H. pachya* A quarter of *H. pachya* (25.2%; n = 118) were covered in a layer of reddish/brownish fine dust. The red dust was in some cases (n = 14) in turn covered with hard grey encrustations characteristic of the Upper Palaeolithic deposits of the rockshelter. This indicates that the molluscs were in reddish/brownish sediments before their final incorporation into the layer in which they were recovered within the Ksâr 'Akil deposits.

4.1.2. Post-depositional processes

Post-depositional processes include all taphonomic alterations that occurred after the mollusc shells were incorporated into the Ksâr 'Akil sediments. The influence of root etching on the sample is negligible (n = 2).

Diagenetic substitutions of the original shell carbonate structure to secondary calcite generally result in white chalky surfaces (e.g., Kato et al., 2003; Busschers et al., 2014). Chalky surfaces were visible (at the macroscopic level) in 63.2% of the assemblage. This type of diagenetic alteration can have several causes including chemical reaction with acids, fossilization, and exposure to heat (e.g. Claassen, 1998; Kato et al., 2003; see). Twenty-five per cent (n = 193) of these diagenetically altered specimens bear additional damage due to heat exposure (e.g., discolouration in combination with heat cracks and/or potlids). Burning is likely anthropogenic in origin. Finally, some 100 specimens show only localized chalky patches on the shell surface (14.2%) again most likely the result of diagenetic alterations in the carbonate structure. These alterations might have occurred pre- and/or post-depositionally. Encrusting sediments adhere to 64.8% (n = 792) of the shells. They are generally grey and strongly concreted, similar to Wright's (Wright, 1962) and Ewing's (Ewing, 1947, 1948, 1949, 1960) description of the sediments of the Upper Palaeolithic deposits. These encrustations are sometimes accompanied by red stains or small clumps of red sediment either within the adhering sediment or on the shell surface directly. These red stains have not been analysed, but may consist of hematite or iron oxide. They differ in appearance from the reddish/brownish sediment found adhering to *H. pachya* specimens and seem to be incorporated in the grey encrusting sediments rather than forming a separate layer on the shell surfaces. Further investigations are needed to determine their chemical composition.

4.2. Taxonomic composition

Our study of the mollusc assemblage from Ksâr 'Akil confirms that species composition and abundance throughout the sequence are consistent with the preliminary observations made during excavation (e.g., Ewing, 1947, 1948). The nature and composition of the shell assemblages of each archaeological layer is assessed through calculation of taxonomic richness (NISP, MNI), abundance (S), evenness (e), heterogeneity (H), and dominance (1/D) at species level (Table 4). Most of these taxonomic indices are based on NISPs, hence, it is possible that the outcomes are driven by sample size. We tested this and found no significant correlation between lnNISP and 1/D ($r = 0.33$, $p = 0.17$) and between lnNISP and e ($r = -0.44$, $p = 0.06$), suggesting that sample size is not driving these indices, whereas H is significant ($r = 0.56$, $p = 0.01$). Therefore, in the following we discuss only the relation between 1/D and e.

The distribution of molluscs in the IUP (Layers XXIII to XXI) is dominated (1/D) by few species, but the NISP is not evenly distributed (evenness: e) among the taxa that are present. In the EUP (Layers XIV to XX) 1/D increases as does evenness, showing a broader range of taxa per layer and a more even distribution of NISP per taxon than in the IUP. The faunal composition fluctuates during the UP (Layers VI to XIII), but in general 1/D and e are lower than in the EUP, whereas the NISP per taxon is still relatively evenly distributed and dominant species are lacking. The taxonomic composition in the EPI (Layers V to I) is based on low NISPs and number of taxa. Specimens are relatively well distributed between taxa, and the assemblage is dominated by only a few species.

Regrouping of taxa per habitat type, as defined in Table 2, results in a similar pattern as seen in overall taxonomic composition (Fig. 3). In the IUP the majority of specimens came from subtidal soft and rocky substrates as well as terrestrial woodland habitats. In addition, there are individual specimens from intertidal rocky shores and open to half-shaded terrestrial environments. In the EUP a wider range of habitats is represented in the species (i.e., both intertidal and subtidal soft, as well as rocky bottom taxa, freshwater species and woodland and open to half-shaded terres-

Table 4
Taxonomic composition by phase (MP – EPI) and per layer (I – XXVIII A) of the Ksâr 'Akil assemblage. NISP: number of identifiable specimens that could be assigned to species level, MNI: minimum number of specimens identifiable to species level, lnNISP: log NISP, lnMNI: lnMNI, S: taxonomic richness (NTAXA), lnS: log S, H: taxonomic heterogeneity, e: taxonomic evenness, 1/D: inverse of Simpson's index of dominance, EPI: Epipalaeolithic, UP: Upper Palaeolithic, EUP: Early Upper Palaeolithic, IUP: Initial Upper Palaeolithic, MP: Middle Palaeolithic.

Phase	Layer	NISP	MNI	logNISP	logMNI	S	logS	H	e	1/D
EPI	I	2	2	0.69	0.69	2	0.69	–	–	–
	II	5	5	1.61	1.61	5	1.61	–	–	–
	III	28	27	3.33	3.30	3	1.10	0.822	0.748	2.237
	IV	18	18	2.89	2.89	3	1.10	0.787	0.716	2.013
	V	240	234	5.48	5.46	12	2.48	1.308	0.526	2.736
UP	VI	100	96	4.61	4.56	12	2.48	1.742	0.701	4.011
	VII	264	252	5.58	5.53	15	2.71	1.778	0.657	3.760
	VIII	184	169	5.21	5.13	15	2.71	1.808	0.668	4.230
	IX	400	357	5.99	5.88	25	3.22	1.912	0.594	4.042
	X	113	99	4.73	4.60	16	2.77	1.956	0.706	5.149
	XI	99	63	4.60	4.14	14	2.64	1.818	0.689	3.423
	XII	31	26	3.43	3.26	9	2.20	1.849	0.842	5.506
	XIII	11	10	2.40	2.30	4	1.39	1.034	0.746	2.045
EUP	XIV	3	3	1.10	1.10	2	0.69	–	–	–
	XV	1	1	–	–	1	–	–	–	–
	XVI	186	149	5.23	5.00	15	2.71	2.241	0.827	7.863
	XVII	479	376	6.17	5.93	26	3.26	2.200	0.675	5.762
	XVIII	54	47	3.99	3.85	13	2.56	2.127	0.829	6.890
	XIX	80	68	4.38	4.22	14	2.64	1.545	0.586	6.781
	XX	27	24	3.30	3.18	9	2.20	1.857	0.845	5.000
IUP	XXI	37	37	3.61	3.61	7	1.95	1.097	0.564	2.000
	XXII	173	160	5.15	5.08	12	2.48	1.015	0.409	1.775
	XXIII	16	16	2.77	2.77	5	1.61	1.160	0.721	2.553
	XXIV	3	3	1.10	1.10	3	1.10	–	–	–
MP	XXVIIIA	2	1	0.69	–	1	–	–	–	–

trial taxa). The habitats around the site would have been similar in the UP. In the EPI shells mainly originated from intertidal rocky and subtidal soft-bottom shores, as well as from wooded areas, whereas species from open and half-shaded terrestrial and marine subtidal rocky shore habitats were rarely taken back to the site. There is an especially marked change in the mollusc assemblage between the IUP and EUP, which cannot be explained by differences in sample size (see above). Possible reasons for this may be environmental change (e.g., in sea level and coastal morphology) and/or changes in human behaviour and exploitation patterns.

4.3. Metric analysis

Metric analyses were carried out on the four most abundant species, namely the terrestrial woodland gastropod *H. pachya*, the intertidal rocky shore gastropod *Ph. turbinatus*, the subtidal soft-bottom shore gastropod *N. gibbosulus*, and the subtidal rocky shore gastropod *C. rustica*. Shells of the genus *Patella* were measured but not used in the present biometric study, because the number of measurable specimens per species was not high enough for a meaningful analysis. Evaluation of the metric data for these four taxa allows us to compare changes in shell size of species from different habitats. It has been argued that size reduction in taxa that were consumed, might be the result of overexploitation (e.g., Mannino and Thomas, 2001; Klein et al., 2004; Erlandson et al., 2011; Klein and Steele, 2013). However, changes in shell size may also be caused by changing sea-surface temperatures, nutrient availability, and other environmental changes (e.g., Fa, 2008). Here we compare the metric data of live-collected marine taxa with those of which the empty shells were collected from beaches, in an effort to distinguish between potential overharvesting and environmental change. Gathering empty beached shells does not affect shell size in the respective living populations, whereas collecting of live specimens does. The preferential gathering of the largest molluscs by humans should, in fact, result in a decrease in mean shell size and, in more extreme cases, in the local extinction of the species in question (e.g., Klein et al., 2004). We argue that, if size change only occurred in marine molluscs collected for food and not in taxa collected as beached shells, the size change is more likely related to human predation. If, however, similar changes in size are seen for all three marine taxa (i.e., in *Ph. turbinatus*, *N. gibbosulus*, and *C. rustica* alike), these could more likely be ascribable to environmental change rather than to overexploitation by humans. Our results show that trends in shell dimensions (Fig. 4; Table 5) are similar for all three marine species: between the IUP and EUP a significant decrease in size occurs in *N. gibbosulus* (the trend is also present in *C. rustica* but is not significant). From the EUP, which saw the start of a more regular exploitation of *Ph. turbinatus*, to the UP, a significant increase in size is recorded for all three marine taxa. Both the fact that we are dealing with a size increase and that this occurred in species exploited for food and in species introduced for utilitarian purposes as empty shells, suggests that environmental change (e.g., changes in temperature and/or salinity) is the most likely cause for these changes. On the other hand, both *N. gibbosulus* and *Ph. turbinatus* decreased in size between the UP and EPI, but this was not statistically significant. No significant size-change has been observed in *H. pachya*.

4.4. Human mollusc and shell use

Our taphonomic investigations show that humans were likely responsible for introducing marine molluscs, and potentially *H. pachya*, to the Ksâr 'Akil deposits. The analysis of observed human modifications to the shells from Ksâr 'Akil may help to shed light on the purpose for which each taxon was gathered. The evidence suggests that live shellfish were transported to the site probably for subsistence purposes (van Regteren Altena, 1962; Bosch et al., 2013) and that the collection of empty shells served various utilitarian purposes, for instance use as tools (Douka, 2011) or body ornaments (Kuhn et al., 2001; Stiner et al., 2013).

4.4.1. Mollusc consumption

Species collected live include all rocky shore intertidal gastropods, as well as possibly freshwater and intertidal brackish wa-

Table 5
Comparison of size of *Helix pachya*, *Phorcus turbinatus*, *Nassarius gibbosulus* and *Columbella rustica* between technocomplexes (EPI: Epipalaeolithic, UP: Upper Palaeolithic, EUP: Early Upper Palaeolithic, IUP: Initial Upper Palaeolithic) showing trend in size (↑ = increase, ↓ = decrease, – = no difference, – = no data) and p values of pair-wise comparisons (Mann–Whitney U test; significant results in bold). H: maximum height, D: maximum diameter, A: aperture height.

Species	*Helix pachya*				*Phorcus turbinatus*				*Nassarius gibbosulus*				*Columbella rustica*			
Comparison	Trend	H	D	A	Trend	H	D	A	Trend	H	D	A	Trend	H	D	A
EPI-UP	–	0.77	0.67	0.58	↓	0.77	0.13	0.08	↓	0.42	0.27	0.06	–	–	–	–
UP-EUP	↓	0.55	0.68	0.84	↑	–	**<0.0001**	**<0.0001**	↑	**0.0001**	**<0.0001**	**<0.0001**	↑	**0.01**	0.81	**0.001**
EUP-IUP	–	–	–	–	–	–	–	–	↓	**0.001**	**0.001**	0.27	↓	0.37	0.23	0.91

ter taxa (excluding *Th. jordani* that shows signs of pre-depositional post-mortem taphonomic alterations), and the terrestrial gastropod *H. pachya*. Regarding the fresh/brackish water component, the low number of specimens and the absence of any anthropogenic modifications prevent a clear determination of the gathering purpose and, therefore, will not be considered further. Nevertheless, it is unlikely that freshwater and brackish water taxa were important in Upper Palaeolithic human subsistence at Ksâr 'Akil, given that their environments of origin were not common in the vicinity of the site.

Rocky shore intertidal gastropods include the topshells *Ph. turbinatus* and *Ph. articulatus* and the limpets *P. rustica*, *P. caerulea*, and *P. ulyssiponensis*. These molluscs can easily be gathered from rocky shores at low tides. Human collection of these taxa is evident from the overall integrity of their shells, the absence of encrusting organisms that settle on the inner shell surfaces after the death of the mollusc and of any other evidence of bioerosion, as well as from the presence of notches on the edges of *Patella* spp. specimens (n = 73; 50%), which is consistent with damage resulting from prying the animals off the rocks. Other human modifications include the intentional removal of the apex of *Phorcus* snails (n = 89; 16.5%) to facilitate flesh extraction (Fig. 5). This evidence strongly suggests that all these taxa were collected for dietary purposes.

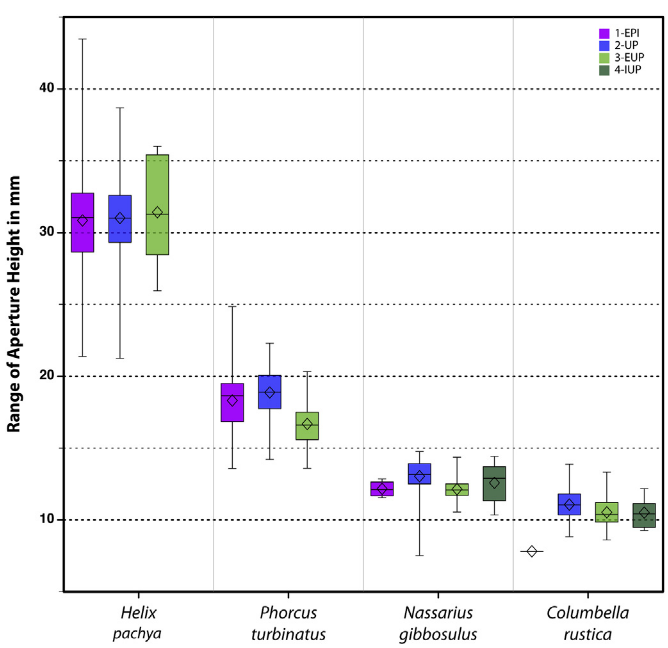

Fig. 4. Range of aperture height of *Helix pachya*, *Phorcus turbinatus*, *Nassarius gibbosulus* and *Columbella rustica* per archaeological technocomplex. The boxes of the boxplots represent 50% of the measurements. The whiskers show the full size range, and the midbar represents the median and the diamond the mean aperture height. EPI: Epipalaeolithic, UP: Upper Palaeolithic, EUP: Early Upper Palaeolithic, IUP: Initial Upper Palaeolithic.

Both van Regteren Altena (1962) and Ewing (1948) proposed the hypothesis that *H. pachya* was exploited as a food source. This assumption was in both cases based on its frequent occurrence in several archaeological layers, but *H. pachya* is adapted to a wider range of habitats and altitudes than any of the other terrestrial species, which might also in part be responsible for its common occurrence. Metric data (Fig. 6) show that *H. pachya* is solely represented by adult specimens. This suggests selective mortality rather than the composition of a natural assemblage (see also Gutiérrez Zugasti, 2011; Fernández-López de Pablo et al., 2014). Taking into account both size and quantity, it is possible that the Upper Palaeolithic occupants took the *H. pachya* specimens back to the site to be consumed. This helicid first occurs in the EUP deposits and is present up to the EPI layers (Table 2), suggesting it may have constituted a foodstuff. Recently, Fernández-López de Pablo et al. (2014) have listed Ksâr 'Akil as a Mediterranean site displaying positive evidence of land snail (undetermined species) exploitation as food source in the EPI based on data from the Tixier excavations (Tixier, 1974; Lubell, 2004).

4.4.2. Marine shells as raw material

Beached shells have been introduced to the site as raw material for tools (e.g., Douka, 2011) and potentially for ornaments (Kuhn et al., 2001; Stiner et al., 2013). Perforated shells, excluding perforations resulting from gastropod and/or crab predation, comprise bivalves (i.e., *Lima lima*, *Anadara* sp., *Acanthocardia tuberculata*, *Acanthocardia* sp., *G. nummaria*, and *Glycymeris* sp.), gastropods (i.e., *Bolinus brandaris*, *Bolma rugosa*, *Ceritium vulgatum*, *C. rustica*, *Conus ventricosus*, *Euthria cornea*, *Hexaplex trunculus*, *Mitra cornicula*, *N. gibbosulus*, *Nassarius mutabilis*, *Nassarius* sp., *Neverita josephinia*, *Pisania striata*, and the fresh water gastropod *Th. jordani*), and the naturally holed scaphopods (i.e., *Antalis dentalis*, *Antalis vulgaris*, and *Antalis* sp.). Marine taphonomic alterations, such as bioerosion caused by beach rolling, are the main factors contributing to these perforations, although some may be anthropogenic in origin. Bouzouggar et al. (2007) and d'Errico et al. (2009) compared perforation frequency and position in archaeological specimens of *Nassarius* with those in shells of the same taxon from modern thanatocoenoses, to evaluate human selectivity in shell gathering and establish whether the holes were anthropogenic or natural. A modern thanatocoenosis from Djerba in Tunisia (Bouzouggar et al., 2007) contained 44.2% of dorsally intact shells. In the Ksâr 'Akil assemblage 1.6% of *N. gibbosulus* shells (n = 11) and 3.2% of *C. rustica* (n = 13) shells were dorsally intact. The high proportion of perforated shells is not congruent with the modern thanatocoenosis data and suggests that *N. gibbosulus*, and possibly *C. rustica*, were either selectively gathered with damage and holes or were possibly perforated by Upper Palaeolithic humans. A more in-depth study of the perforations, including location, use-wear and residue analysis is planned and might provide more information on the nature and extent of human collection preferences and potential bead manufacture.

Some bivalves of *Glycymeris* sp. were collected to be used as tools. The best evidence of anthropogenic modification was found on a *Glycymeris* sp. valve reported by Douka (2011). The shell's

Fig. 5. Species gathered for consumption. 1: RGM-606318a, 2: RGM-606318b, *Phorcus turbinatus*; 3: RGM-606319, *Phorcus articulatus*; 4: RGM-606376, *Patella rustica*; 5: RGM-606532, *Helix pachya*. Anthropogenic modifications are indicated with arrows, 2: cut-off apex to facilitate shellfish extraction and 4: edge notches congruent with damage from prying molluscs off the rocks. Note the reddish dust on the surface of the *H. pachya* shell. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

peripheral rim shows clear retouch and was probably used as a scraper-like tool. Further, our investigations revealed that almost half of the *Glycymeris* valves had breaks resulting in long sharp edges (n = 128; 43%) that were possibly used as cutting implements. Some of these broken shells exhibit impact marks (n = 15), although it is unclear if these edges and impacts are anthropogenic or natural in origin (see Fig. 7). Other specimens show notches at one or both lateral sides of the umbo creating a small channel (e.g., Fig. 7: RGM-577868). Some of them are covered in red sediment. It is, therefore, conceivable that they were possibly used as

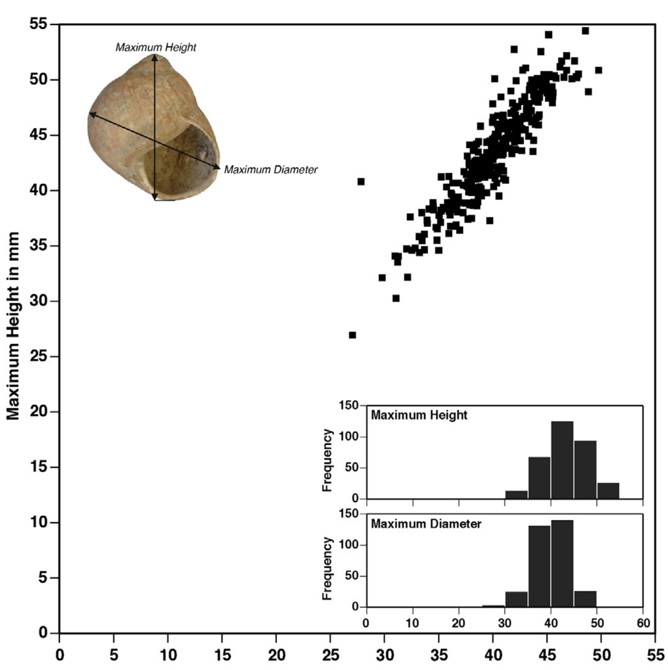

Fig. 6. *Helix pachya* measurements scatterplot: maximum basal diameter versus maximum shell height. Histograms show height (top) and maximum basal diameter (bottom) the number of shells (y-axis) in 5 mm groups (x axis). Measurement locations are shown on specimen RGM-606532 on the top left.

small containers. Clearly, more detailed investigations have to be carried out before the archaeological use of individual specimens can be assigned. Here, marine shells that were collected empty and brought to the site are labelled ‘non-food transported’ specimens.

Changes in human exploitation patterns become evident when grouping molluscs in the following three categories: terrestrial, ‘food’, and ‘non-food transported’ taxa (Fig. 8). The purpose of mollusc and shell gathering changed from the sole collection of empty marine shells for manufacturing tools and ornaments in the IUP, to subsistence-focussed exploitation of selected marine and terrestrial species in the UP and EPI. Food species (including *H. pachya*) first occur in the IUP layers, and start to increase in numbers (both absolute and relative) from the EUP through the later UP and EPI layers, with a marked decrease in layers IX and X. The terrestrial component (excluding *H. pachya*) is small throughout the sequence.

4.5. Burning

Occasional burning (18.7%) resulting in a combination of heat cracks, discolouration (e.g., Stiner, 2005) and decalcification, is observed in the assemblage (Tables 1 and 6). In general, taxa collected by humans (i.e., food species: 14.4%; non-food transported species: 24.9%) show a higher degree of burning than terrestrial species (1.3%). There is a significant difference in burning rate amongst specimens belonging to the 1962 (16.5%) and the 2015 (25.0%) collections (χ^2 199.58, $p < 0.0001$). The higher burning rate in the more fragmentary ‘2015 collection’ might stem from the fact that burned shells are more prone to fragmentation (e.g., Claassen, 1998). However, inclusion of the ‘2015 collection’ does not significantly alter the rate of burning for the whole assemblage (χ^2 3.47, $p = 0.063$). The distribution of burning between food and non-food transported taxa is significantly different (χ^2 21.4, $p < 0.0001$). This burning damage might have resulted from direct or indirect (during deposition) exposure to heat. Direct heat exposure might result from roasting, waste removal practices, or accidental exposure while lying on the surface of the rockshelter after deposition. Indirect exposure to heat might have occurred by lighting a fire on top of deposits containing shell and, therefore, was not necessarily deliberate (Stiner et al., 1995). The frequency of burning in *H. pachya* (n = 25; 5.2%) is intermediate between that

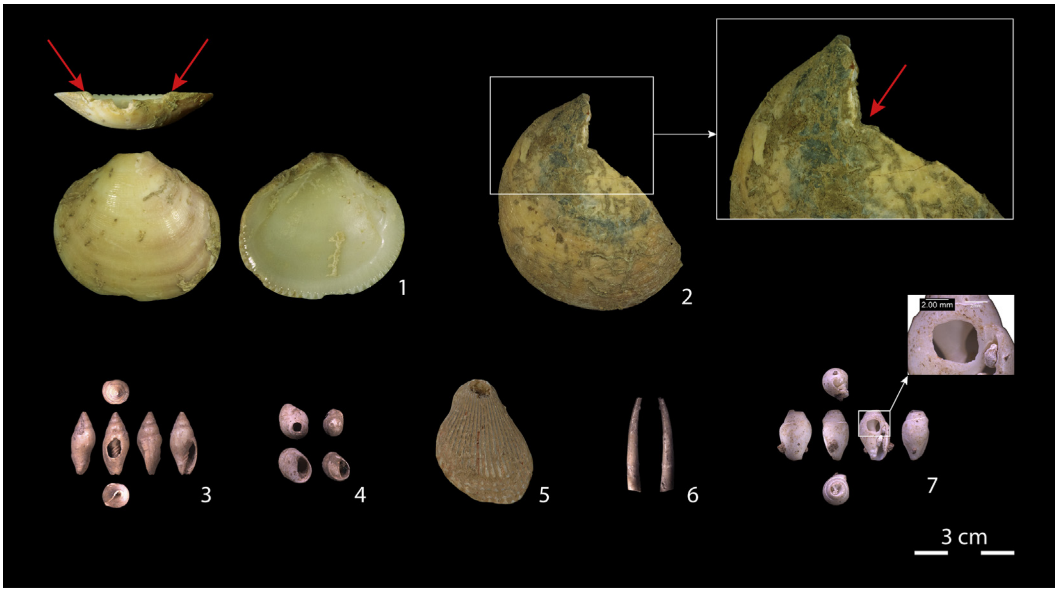

Fig. 7. Non-food transported species. 1: potential container, red arrows indicate impact points on both sides of the umbo; 2: Broken valve with long sharp edges, an impact point is indicated by the arrow in the inlet; 3, 4, 5, 7: Perforated shells. Shell species shown: 1: RGM-577868, 2: RGM-550206 *Glycymeris* sp.; 3: RGM-606218, *Mitra cornicula*; 4: RGM-606459a, b, *Theodoxus jordani*; 5: RGM-577824, *Lima Lima*; 6: *Antalis* sp.; 7: RGM-770825, *Columbella rustica* inlet detail of perforation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

of all marine taxa (i.e. both ‘food’ and ‘non-food’ species) and other terrestrial gastropods. Hutterer et al., (2014) have suggested that cooking was probably necessary to extract mollusc flesh. However, cooking does not always leave recognizable taphonomic signatures, for example, when molluscs are boiled in water. Traces of burning may therefore not be informative in determining if *H. pachya* was gathered for subsistence purposes or not.

4.6. Ksâr ’Akil in its regional context

Few sites containing IUP deposits are known from the region (e.g., Goring-Morris and Belfer-Cohen, 2003), let alone sites with relatively large mollusc assemblages. The site of Üçağızlı I (Turkey) is the only recently excavated site with deeply stratified IUP and EUP deposits containing mollusc remains (e.g., Kuhn et al., 2001, 2009; Stiner et al., 2013). The IUP and EUP lithic technology at Üçağızlı I is very similar to that of Ksâr ’Akil (Kuhn et al., 2001) and a recently published account of the ornamental shells from this site (Stiner et al., 2013) enable us to evaluate our results in a regional context. The IUP and EUP at Üçağızlı I and Ksâr ’Akil largely overlap in age (e.g., Kuhn et al., 2009; Douka, 2013; Douka et al., 2013), although the IUP might start earlier at Ksâr ’Akil (Kuhn et al., 2001; Bosch et al., 2015). The Epipalaeolithic is much later at Üçağızlı I than at Ksâr ’Akil (Mellars and Tixier, 1989; Kuhn et al., 2009; Bosch et al., 2015). We, therefore, focus for our comparison on the IUP and EUP periods, which are very similar in many respects. There is a considerable overlap in species representation, diversity, and exploited habitats. At both sites, molluscs were transported for subsistence purposes and as raw material. The taphonomic signatures observed in the different groups of species (i.e., food species, non-food transported or ornamental species, and terrestrial species) are nearly identical including marine pre-depositional taphonomic alterations, the presence of localised decalcified patches (although in the case of Ksâr ’Akil these are not explained to be the results of root etching, as proposed to Üçağızlı I), as well as traces of burning (Stiner et al., 2013). At Üçağızlı I, marine food species are virtually absent from the IUP, but occur in high quantities in the EUP, the same being true for Ksâr ’Akil. Similarly, at both sites this pattern is also observed for the terrestrial molluscs. *H. pachya* is present at Üçağızlı I, albeit in low frequencies similar to other terrestrial molluscs, and it is hence not thought to have been introduced by the human occu-

Table 6
Burning damage by phase (MP – EPI), per layer (I – XXVIII A), and divided in food, non-food transported, and terrestrial taxa.

Burning					
Phase	Layer	n	Burned	Not burned	na
EPI	I	2		2	
	II	6		6	
	III	28		28	
	IV	22	1	21	
	V	242	8	234	
	Total EPI	*300*	*9*	*291*	
UP	VI	103	6	97	
	VII	272	30	242	
	VIII	195	17	177	1
	IX	448	46	398	4
	X	122	19	103	
	XI	466	139	326	1
	XII	61	12	49	
	XIII	11	2	9	
	Total UP	*1678*	*271*	*1401*	*6*
EUP	XIV	3		3	
	XV	2		2	
	XVI	220	59	161	
	XVII	646	169	476	1
	XVIII	72	15	57	
	XIX	191	21	169	1
	XX	48	8	39	1
	Total EUP	*1182*	*272*	*907*	*3*
IUP	XXI	60	23	37	
	XXII	198	72	126	
	XXIII	22	8	12	2
	XXIV	9	1	5	3
	Total IUP	*289*	*104*	*180*	*5*
MP	XXVIIIA	2		2	
na	na	117	11	106	
Total	**Food**	**1163**	**167**	**992**	**4**
	Non-food	**1690**	**421**	**1260**	**9**
	Terrestrial	**228**	**3**	**225**	
	na	**487**	**76**	**410**	**1**
	n	**3568**	**667**	**2887**	**14**

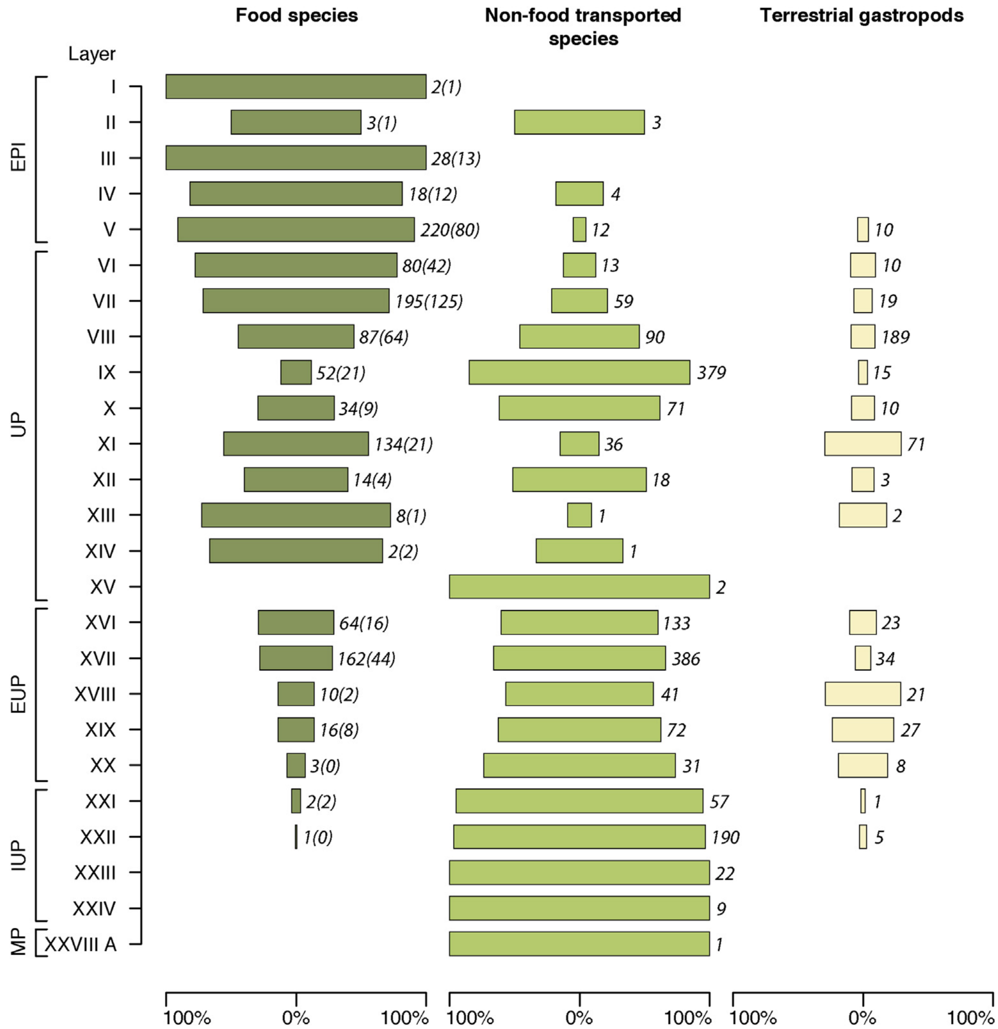

Fig. 8. Frequency and number of identified specimens per mollusc use through time by Layer (I–XXVIII A) and per Phase (MP–EPI). Dark green: food species (*Phorcus turbinatus*, *Phorcus articulatus*, *Patella rustica*, *Patella caerulea*, *Patella ulyssiponensis* and *Helix pachya*), Light green: non-food marine transported species, Yellow: non-food terrestrial species. Note: *Helix pachya* numbers are provided in brackets next to the food-species column. MP: Middle Palaeolithic; IUP: Initial Upper Palaeolithic; EUP: Early Upper Palaeolithic; UP: Upper Palaeolithic; EPI: Epipalaeolithic. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

pants of the cave for consumption. Stiner et al. (2013) see a weak positive correlation in species diversity through time at Üçağızlı I, which is not evident at Ksâr 'Akil. However, although the IUP and EUP deposits are quite similar, the later Palaeolithic sequences are markedly different in composition and age. The Ksâr 'Akil sequence contains a 10 m thick package of UP (roughly 42–31 ka cal BP) and EPI (<31–29 ka cal BP) deposits that cover the time-gap between the EUP and EPI (around 17 ka cal BP) at Üçağızlı I (Kuhn et al., 2009; Bosch et al., 2015). Therefore, trends through time could be a consequence of differences in chronology rather in differences in environmental conditions or human behaviours. Moreover, diversity indices were calculated for the total assemblage at Ksâr 'Akil, whereas they are only based on a single subgroup (i.e., ornamental species) in the study by Stiner et al. (2013). Nevertheless, species as well as habitat diversity are remarkably similar in their marked contrast between low diversity in the IUP and the much higher EUP values.

The comparison of these two Levantine Palaeolithic mollusc assemblages has also exposed some differences. In general, at Ksâr 'Akil, freshwater species, and specifically *Th. jordani*, are present in lower quantities. Scaphopods at both sites occur only sporadically, in the EPI at Üçağızlı I, and in UP Layer IX at Ksâr 'Akil. Additionally, at Üçağizli I tusk shells are fossil and probably collected from fossil marine deposits, whereas at Ksâr 'Akil at least some of them have been collected from active beaches. Bar-Yosef Mayer (2005) mentions *N. gibbosulus*, *Nassarius* sp., *C. rustica*, *Glycymeris* sp., *Mitrella scripta*, *Antalis* (*Dentalium*) sp., and *Theodoxus* sp. as common ornamental taxa, albeit found in varying frequencies in the Levantine Upper Palaeolithic. At Ksâr 'Akil the former four species are abundant, and the latter three are rare or absent. Furthermore, the rare perforation method observed in *N. josephina* and *Naticarius stercusmuscarum* at Üçağızlı I is absent at Ksâr 'Akil. More work on perforated shell (e.g., use-wear analysis, detailed investigation of perforation locations, etc.) is needed before any taxa can be reliably interpreted as being of ornamental use. For now, it suffices to say that the Ksâr 'Akil mollusc assemblage is not unique in its composition and as a source of evidence for Upper Palaeolithic human coastal adaptations. However, it offers great potential to provide a wealth of information on the human behaviour of its occupants and of hunter–gatherers in the Levant. Further studies aimed at the reconstruction of Palaeolithic human subsistence activities linked to the exploitation of marine molluscs are being conducted on the marine shells from Ksâr 'Akil to establish the role of shellfish in hunter–gatherer diets in the Levant, for instance through oxygen isotope analyses aimed at determining whether intertidal gastropods were exploited year-round or seasonally.

5. Conclusions

At Ksâr 'Akil, most mollusc shells discarded after shellfish consumption were gathered from intertidal rocky shores, while shells collected for ornamental purposes originate from subtidal soft and rocky shore habitats. The constant presence of molluscs from these intertidal and subtidal habitats suggests that coastal environments did not change significantly during the different phases of site occupation. Land snail species most frequently originate from open and half-shaded, as well as woodland, habitats suggesting these environments were available in the immediate vicinity of the site throughout the Upper Palaeolithic. Arid or semi-desert taxa as well as freshwater taxa are rare, as are brackish water species and deep marine soft bottom deep subtidal or bathyal taxa (i.e., *Antalis* spp.). Changes in marine mollusc size appear to have been driven by environmental factors (e.g. sea surface temperature, nutrient, and/or salinity fluctuations), rather than by overexploitation by humans. Mean shell size of *Ph. turbinatus* increased significantly between the EUP, when shellfish exploitation was first practised on a larger scale, and the subsequent UP. Moreover, trends in shell size are similar for all three measured species including *N. gibbosulus* and *C. rustica* that were collected dead and, therefore, unaffected by human predation.

Occasionally, shells were additionally gathered from fossil marine terraces. Shells of marine bivalves were collected and potentially used as raw material for a variety of tools (such as scrapers, knives and possible containers). Perforated specimens were probably used as ornaments. Whereas the collection of beached shells started in the IUP, shellfish exploitation was mainly practised from the EUP onward and focussed on the intertidal rocky shore limpets and topshells. The terrestrial taxon *H. pachya* was possibly used as a source of food. The number of molluscs exploited for food increased over time, both in absolute and relative terms. Further, marine taxa introduced to the site by humans show a higher degree of burning than do terrestrial species in which burning damage is nearly absent. Comparisons with the IUP and EUP mollusc assemblages from Üçağızlı I highlight the great similarities in species diversity, habitat exploitation, and human mollusc use. This suggests that the coastal adaptations documented at Ksâr 'Akil were typical of hunter–gatherers across the Levantine region.

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