



Invited review article

Multiproxy dietary trait reconstruction in Pleistocene Hippopotamidae from the Mediterranean islands

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ABSTRACT

Geographically isolated insular species face energetic restrictions and commonly evolve adaptations that distinguish them from their mainland ancestors. During the Pleistocene, several Mediterranean islands were inhabited by now extinct Hippopotamidae. They underwent diverse changes in locomotion, dentition and body size. Based on these differences, it is supposed that they occupied different ecological niches depending on their respective faunal complexes and available resources. In this paper, we assess the paleoecology of dwarfed hippopotami from Crete, Malta, Sicily and Cyprus using a novel dental multiproxy approach. We applied dental topography analysis (SAGA-GIS) to measure the mean slope of the dental occlusal surface, mirroring dietary adaptations, as well as 3D surface texture analysis (3DST) to quantify the surface of occlusal wear facets, which correlate with dietary abrasiveness. Low slope values were found in the larger, more hypsodont hippopotami, whilst the smaller *Phanourios minor* displayed the highest occlusal relief with large compression basins. Since *Hippopotamus pentlandi* exhibited lower mean slope values than the larger, more hypsodont *Hippopotamus amphibius*, we conclude that lower occlusal reliefs reflect adaptations to lower diet quality and arid environments, which are characteristic of freshwater-limited island habitats. The 3DST analysis revealed distinct ecological niches for the investigated insular hippos. *Hippopotamus creutzburgi* exhibited enamel surface textures analogous to those of *Hippopotamus amphibius*, a fresh grass grazer, thus confirming a semiaquatic lifestyle at the upland lake at Katharo, Crete. *Hippopotamus pentlandi* was bound to a similar niche to the extant form, probably due to the mainland character of its fauna, but experienced more dust intake. *Hippopotamus melitensis* had to cope with high ingestion of abrasives, seemingly on account of a more generalistic diet in its resource-limited and small habitat. Results point to either *Phanourios minor* broadening its dietary niche in its almost competition-free habitat, or suggest a dietary shift following a climatic change. The adopted multiproxy approach proved to be useful in identifying dental adaptations and individual foraging strategies linked to energetically restricted habitats, and therefore contributes to a better understanding of basic evolutionary and ecological principles.

1. Introduction

Isolated environments, such as islands, are central to the understanding of basic evolutionary and ecological principles. Island species have to constantly cope with energetic limitations in their geographically restricted habitat (Köhler et al., 2008; Raia and Meiri, 2006; Winkler et al., 2013b). As a response, insular species often undergo distinct morphological adaptations and occupy different ecological niches to their mainland ancestors (Boekschoten and Sondaar, 1972; Köhler and Moyà-Solà, 2004; Larramendi and Palombo, 2015; Lomolino,

2005, 1985; Van der Geer et al., 2006; Weston and Lister, 2009; Winkler et al., 2013b, 2013a). Some typical insular adaptations, which develop in mammals over short evolutionary time spans, present as shortened and more stable limbs (Sondaar, 1977), reduced brain and sensor organs (Köhler and Moyà-Solà, 2004; Larramendi and Palombo, 2015; Lyras, 2019; Weston and Lister, 2009), a considerable anatomical reorganisation of the skull morphology (Van der Geer et al., 2018), a change in dental morphology, such as increased hypsodonty (Jordana et al., 2012; Winkler et al., 2013b, 2013a) or the loss of molars (Boekschoten and Sondaar, 1972), and a shift in body size (Lomolino,

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2005, 1985). The last being dubbed the ‘island rule’ by Van Valen, is a noticeable trend in insular populations from gigantism in small mammal species to dwarfism in larger ones. According to Evans et al. (2012), the rapid body mass decrease in insular dwarfs involves 2300 to 120,000 generations over estimated time intervals of 0.006 to 0.8 Myr. In the case of the dwarfed red deer on Jersey in the Last Interglacial, Lister (1989) estimated that it took an, in geologic terms, extremely short time of <6 kyr for a median weight reduction from 200 kg to 36 kg. Such a rapid body size reduction is considered beneficial for larger herbivorous mammals when coping with limited resources on small islands and under unstable environmental conditions (Raia and Meiri, 2006). The difficulties of colonisation can lead to an absence of larger carnivores, rendering the large body size unnecessary as a means of predator avoidance (Lomolino, 2005). Additionally, the presence of other herbivore species competing for resources has a regulating effect, as body size differences reduce competition and thus promote coexistence (Palombo, 2009a, 2009b; Raia and Meiri, 2006).

During the Pleistocene, several Mediterranean islands were inhabited by dwarfed Hippopotamidae (Marra, 2005a) (Fig. 1, Supplement 4). In the course of their evolution, those hippopotami underwent diverse transformations in their locomotor system (Boekschoten and Sondaar, 1972; Sondaar, 1977; Spaan et al., 1994), a decrease in body size compared to their mainland relatives (Lomolino et al., 2013) and morpho-functional changes in their masticatory system (Boekschoten and Sondaar, 1972; Boisserie et al., 2011; von Koenigswald, 2014; von Koenigswald et al., 2013). Because they were present on islands of various sizes, inhabited by different and endemic faunal communities,

these dwarfed hippopotami can help identify selective forces of island habitats which lead to their distinct dietary adaptations.

1.1. Pleistocene Mediterranean hippopotami

From the Middle Pleistocene to the early Late Pleistocene, Sicily was inhabited by *Hippopotamus pentlandi*, which was the largest hippopotamus species among the dwarfed Mediterranean hippopotami with a body mass of approximately 1100 kg (Lomolino et al., 2013). With respect to its ancestor *Hippopotamus amphibius*, living in Europe from the Middle to the Late Pleistocene, *H. pentlandi* underwent a considerable body size reduction of about 10 to 15% (Guglielmo and Marra, 2011; Marra, 2005b). Since lower sea levels regularly produced temporary land bridges, faunal exchange between Sicily and the Italian peninsula was possible at those times, leading to the faunal complex of *H. pentlandi* being very similar to the mainland fauna: impoverished but balanced, featuring a moderate endemism among herbivores (Bonfiglio et al., 2001, 2000). As a consequence, *H. pentlandi* had to deal with rather high predation pressures and competition levels (Palombo, 2009b) (Fig. 1).

During the late Middle Pleistocene, *Hippopotamus melitensis* inhabited Malta, the smallest of Mediterranean islands on which hippopotami were present (Alcover, 2000; Caloi et al., 1986; Herridge, 2010; Marra, 2005a; Savona-Ventura and Mifsud, 1998). Its body mass was approximately 900 kg (Lomolino et al., 2013) and displayed a variation in body size exceeding that of a mainland population (Van der Geer et al., 2010). *Hippopotamus melitensis* was slightly smaller than *Hippopotamus pentlandi*, from which it is supposedly derived (Hunt and

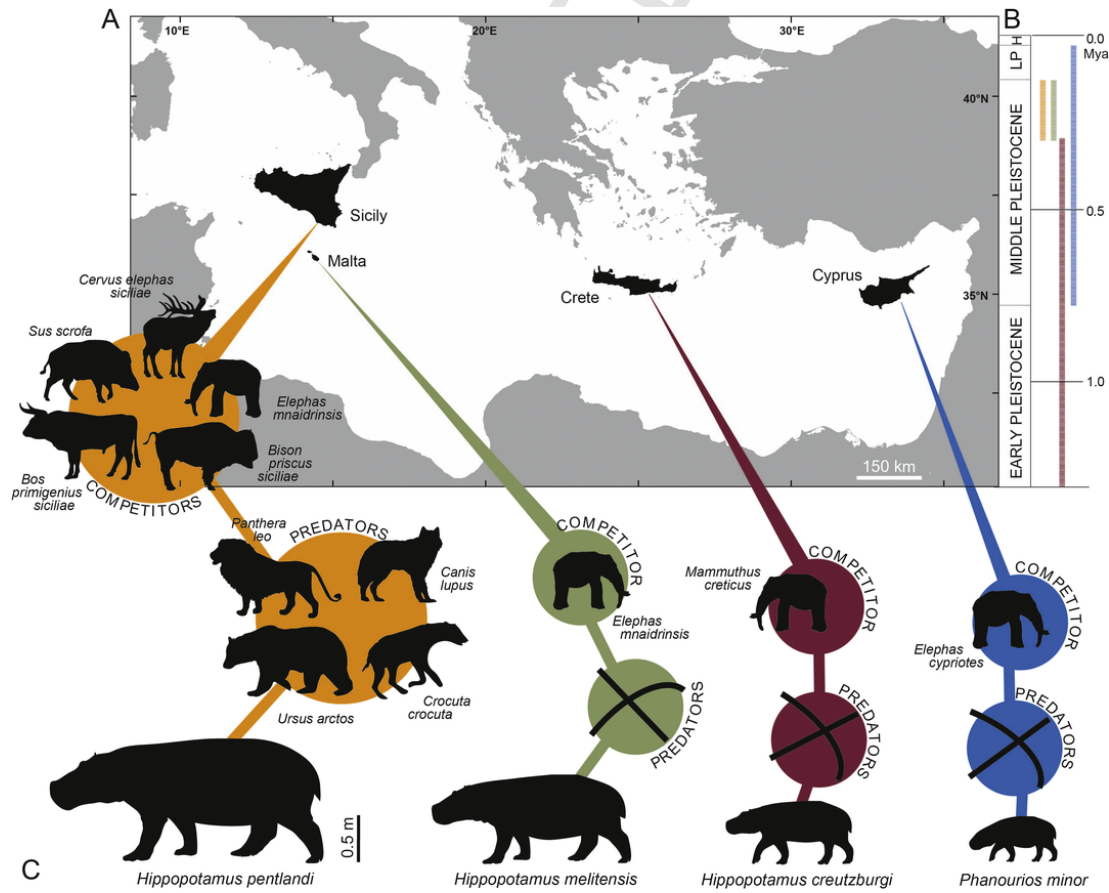


Fig. 1. Mediterranean Islands inhabited by Pleistocene dwarf hippopotami. (A) Map of Mediterranean Sea, showing the location of the study areas of Sicily, Malta, Crete and Cyprus, (B) geochronology of Pleistocene hippopotami from the Mediterranean islands, (C) dwarf hippopotami and their faunal complexes. LP = Late Pleistocene; H = Holocene. Resources for faunal complexes: (Boekschoten and Sondaar, 1972; Bonfiglio et al., 2001; Marra, 2005a; Van der Geer et al., 2010). The map was modified after a file obtained from Wikimedia Commons free media repository licensed under the Attribution-Share Alike 3.0 Unported license, released into the public domain by MapMaster.

Schembri, 1999; Marra, 2005a, 2005b; Van der Geer et al., 2010). The composition of the impoverished and unbalanced Maltese fauna might be the result of a sea level lowering phase, allowing new species to spread from the larger island Sicily (Marra, 2013). However, in the late Middle Pleistocene, connections between Sicily and Malta were occasional and were submitted to a strong filter, leading to the presence of only one other large mammal species (*Elephas mnadriensis*) able to reach the predator free island (Marra, 2013; Savona-Ventura and Mifsud, 1999; Van der Geer et al., 2010; Zammit Maempel, 1989) (Fig. 1).

Remains of *Hippopotamus creutzburgi* have been recorded on Crete (Boekschoten and Sondaar, 1966), a dwarfed *Hippopotamus*, smaller than *Hippopotamus melitensis* weighing approximately 400 kg (Lomolino et al., 2013). *Hippopotamus creutzburgi* time of existence spanned from the Early to the early Middle Pleistocene and it is probably a descendant of *Hippopotamus antiquus* (Marra, 2005b; Sondaar and Van der Geer, 2005). Its faunal complex was endemic and strongly unbalanced since the only other large herbivore of this complex was the endemic dwarf mammoth *Mammuthus creticus*. Large predators were absent (Poulakakis et al., 2002; Sondaar and Van der Geer, 2005) (Fig. 1). *Hippopotamus creutzburgi* showed skeletal modifications, making its locomotion capabilities distinct from larger hippopotami. Its shortened and stable limbs were restricted in lateral movement, resulting in a more unguigrade stance and allowing for a relatively large movability

in the sagittal plane (Pavlakakis et al., 1999; Spaan, 1996). The morphology of its phalanges suggests that *H. creutzburgi* walked on hooves rather than on a footpad (Boekschoten and Sondaar, 1972; Spaan, 1996; Spaan et al., 1994). Those morphological attributes seem to be adaptations to an uneven, rocky terrain and indicate a rather terrestrial, instead of a semiaquatic, lifestyle. Furthermore, *H. creutzburgi* is assumed to have seasonally migrated along the rough stony hillsides (Boekschoten and Sondaar, 1966), indicated by an abundance of specimens at the Katharo basin of Crete, a plateau located at an altitude of 1100 to 1200 m above sea level.

During the Pleistocene, Cyprus was inhabited by *Phanourios minor*, the smallest Mediterranean dwarf hippopotamus known, featuring a body mass of approximately 130 kg (Lomolino et al., 2013). The strongly endemic and impoverished environment of *P. minor* was characterised by few competition and a lack of predation, since larger carnivores were absent (Marra, 2005a). Apart from *P. minor*, the only larger terrestrial herbivorous mammal was the endemic Pleistocene dwarf elephant *Elephas cypriotes* (Boekschoten and Sondaar, 1972; Sondaar and Van der Geer, 2002) (Fig. 1). The limbs of *P. minor* are most similar to those of *Hippopotamus creutzburgi*, being better adapted for walking and climbing on rough terrain rather than a semiaquatic lifestyle (Spaan et al., 1994) (Fig. 2). In addition, the lowered orbits and nostrils of *P. minor* (Hadjisterkotis and Reese, 2008; Houtekamer and Sondaar, 1979) confirm a more terrestrial lifestyle, in contrast to

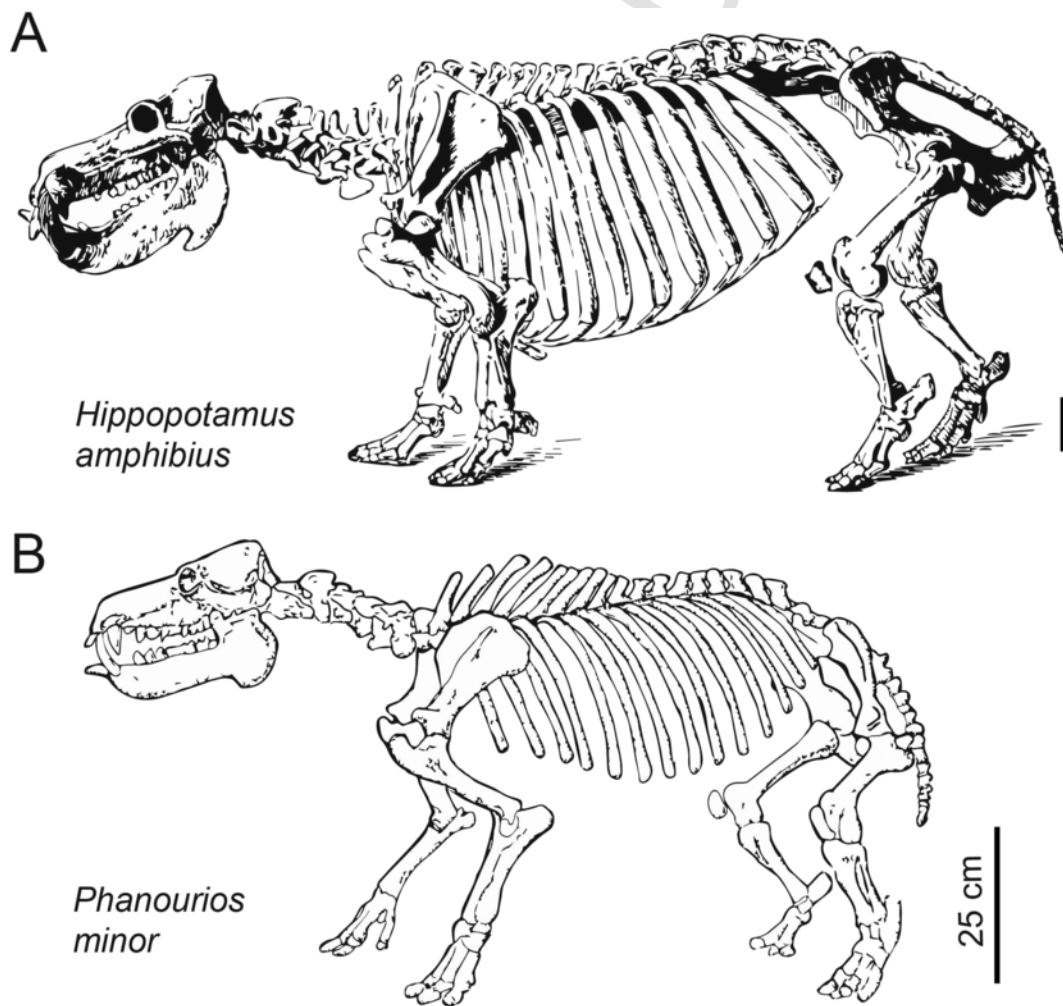


Fig. 2. Skeletal reconstructions of the semiaquatic (A) *Hippopotamus amphibius* modified after Brehm (1883) and the more terrestrial (B) *Phanourios minor* modified after Bate (1906). The orbit of *P. minor* is lowered in contrast to *H. amphibius*. The limb posture of *P. minor* is more unguigrade since only the phalanges carry the weight, whereas in the more digitiportal *H. amphibius* the carpals are involved in carrying. Scale bars = 25 cm.

the elevated orbits and nostrils of semiaquatic forms (Boisserie et al., 2011, 2005; Van der Geer et al., 2014; Wopschall, 2015). The molars of *P. minor* display a shift towards a more lophodont stage, compared to the more complex dental enamel pattern of all other hippopotami (Boekschoten and Sondaar, 1972, 1966). The more brachyodont molars and the shortened and narrow muzzle suggest that this species may have evolved in a closed environment, consisting of trees and shrubs (Wopschall, 2015). In addition, it is hypothesised that transversal jaw movements and the loss of the fourth premolar indicate a dietary shift towards browsing (Boekschoten and Sondaar, 1972; Boisserie et al., 2011; von Koenigswald, 2014; von Koenigswald et al., 2013). As a matter of fact, results of stable carbon isotope analyses on specimens from an archaeological site at the Akrotiri Peninsula support that *P. minor* conformed to a browsing strategy (Wopschall, 2015). However, analyses of stable nitrogen isotopes for the same population indicate an increasing aridity that mirrors the climatic shift of the surrounding mainland, related to the Younger Dryas climatic event (Wopschall, 2015).

1.2. Dietary reconstruction

Based on their specific body size, locomotion mode and occlusion, we can hypothesise, that the four island hippopotami occupied different ecological niches. Depending on faunal complexes and the resource availability on the islands, these hippopotami could have either broadened their dietary niches, becoming generalists, or specialised in more distinct dietary niches. However, more specific pieces of dietary information other than inferences from the general dental morphology and a few isotopic studies are scarce. Therefore, this study aims to reconstruct the paleoecology of the four dwarfed hippopotami using two indirect feeding trait proxies, which are non-invasive and non-destructive: Firstly, a dental topography analysis and secondly, the 3D surface texture analysis (3DST). Dental topography analyses using a system for automated geoscientific analysis have been applied for characterising and comparing occlusal surfaces of phenotypically distinct teeth to infer dietary traits of extant as well as extinct species (Evans and Sanson, 2006; Ungar, 2004; Ungar and Williamson, 2000; Zuccotti et al., 1988). The 2D relief of the ectoloph (mesowear profile) has been shown to be linked to the abrasiveness of the diet (Fortelius and Solounias, 2000). The 3D model of the occlusal surface allows using the slope as measure of change in topography. In analogue to mesowear, an occlusal topography with a low slope and low relief is linked to a harder, more abrasive diet, whereas a steeper slope and a higher relief indicate tougher, more elastic ingesta (Ungar, 2004). In summary, it can be said that the dental topographic approach can be considered a long term dietary proxy, since it strongly encapsulates adaptive traits. 3DST analysis has proven capable in revealing differences in niche occupation and reconstructing diets of extinct and extant species (Calandra et al., 2012; Schulz et al., 2010; Scott et al., 2005; Ungar et al., 2003; Winkler et al., 2013a, 2013b). All in all, 3DST analysis is considered a short term dietary proxy because dental surface textures are partly overprinted by every meal (Schulz et al., 2013b). The combination of both approaches gives us the opportunity to compare dental adaptations with dietary behaviour, and therefore reveal evolutionary forces driving feeding strategies and reconstruct actual dietary niches.

1.3. Research focuses

Because of the aforementioned differences in dental, cranial and postcranial morphology, we propose that the insular hippopotami encountered ecological changes that led to the evolution of distinct dietary traits. By quantifying the dental topography, we aim to identify these adaptations in the topography of the occlusal surface, driven by the following question:

- (1) Does the dental topography differ a) within the group of extinct insular species as well as b) between mainland species and extinct insular species (occlusal adaptation)?

Actual dietary strategies can be incongruent to inherited morphological adaptations. This might be the case when individuals face new environmental conditions. Dealing with limited resources, individuals might deploy different feeding strategies, leading to a broadened or changed dietary niche. Therefore, it is prudent to pose the second question:

- (2) Does 3D enamel surface texture reflect dietary behaviour that is in accordance with dietary niches reconstructed from dental and skeletal adaptations in insular species (dietary behaviour and forage selection)?

2. Methods

Beside the four extinct species of Pleistocene dwarfed hippopotami ($n = 5$, *Hippopotamus pentlandi*; $n = 10$, *Hippopotamus melitensis*; $n = 11$, *Hippopotamus creutzburgi*; $n = 16$, *Phanourios minor*), the extant African *Hippopotamus amphibius* ($n = 10$) is included as reference. The extant dwarf hippopotamus (*Choeropsis liberiensis*) was not considered as a reference species, as it is adapted to living in rainforest environments (Eltringham, 1993), unlike any of the Pleistocene Mediterranean dwarf hippopotami. All analysed specimens and their repositories are listed in Table 1.

2.1. Specimen selection

This study focuses on upper molars, as functional traits are known to be more pronounced in the upper dentition than in lower teeth (Kaiser and Fortelius, 2003). For the dental topography analysis (SAGA-GIS), upper second molars (M2) were analysed, since this tooth position is employed as the standard in other methods of dietary evaluation studying dental characteristics (Archer and Sanson, 2002; Fortelius and Solounias, 2000). To ensure comparison of similar life stages in the sample, only adult individuals with an intermediate wear stage were used. As no comparative wear stages for hippopotami are published, we refer to the IDAS system (Anders et al., 2011), selecting only individuals of IDAS3 stage (covering the period from full eruption of the dentition until the loss of the inner enamel ridges of the first molar). Damaged occlusal surfaces with incomplete enamel were excluded. For the 3DST analysis the M2 was used preferably. Additionally, the first upper molars (M1) of *Hippopotamus creutzburgi* and the third upper molars (M3) of *Phanourios minor* were included in this analysis to increase the sample size. This procedure can be accepted, since no significant differences between the tooth positions could be detected for this analysis and they were similar in wear stage. Because the analyses pose different demands on the examined teeth, some specimens were not suitable for both methods. The suitable specimens for each analysis are included in Table 1.

2.2. Moulding and casting

After cleaning the teeth with acetone, moulds of upper tooth rows or single teeth were made, using high resolution silicone (Provil novo Light C.D.2 regular set; Type 3; Heraeus Kulzer, Dormagen, Germany) following the procedure outlined by Schulz et al. (2010). Positive casts of the silicone moulds were made using epoxy resin (Injektionsharz EP, Reckli-Chemiewerkstoff, Herne, Germany). For the 3DST analysis, the enamel facet localised on the distal lobe of the paracone (Fig. 3) was

Table 1

Specimens used in dental topography and 3D surface texture analyses. SAGA-GIS analysis = dental topography, 3DST analysis = 3D surface texture analysis; M1 = upper first molar, M2 = upper second molar, M3 = upper third molar, l = left jaw, r = right jaw, BP = before present. Museum abbreviations: NHM-PD = Natural History Museum, Department of Palaeontology, London, United Kingdom; NHMC = Natural History Museum Crete, Heraklion, Greece; RGM = Naturalis (Leiden), Rijksmuseum van Geologie en Mineralogie at Naturalis, Nationaal Natuurhistorisch Museum, Leiden, the Netherlands; MHNL = Muséum d'Histoire Naturelle de Lyon, Lyon, France; SMF = Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany; ZMB = Museum für Naturkunde, Humboldt-Universität, Berlin, Germany; ZMH = Zoologisches Museum, Universität Hamburg, Hamburg, Germany.

Species	Specimen	SAGA-GIS analysis	3DST analysis	Tooth	Side	Geography	Site	Epoch/date*	
<i>Hippopotamus amphibius</i>	MHNL-50.002126		x	M2	r	Africa	Cameroon	Recent	
	MHNL-50.002127		x	M2	r	Africa	Sudan	Recent	
	SMF-35488	x		M2	l	Africa	Unknown	Recent	
	ZMB-33787	x	x	M2	l	Africa	Unknown	Recent	
	ZMB-43587	x		M2	l	Africa	Unknown	Recent	
	ZMB-44088	x		M2	l	Africa	Sudan	Recent	
	ZMB-76150	x		M2	l	Africa	Cameroon	Recent	
	ZMB-76152	x		M2	l	Africa	Cameroon	Recent	
	ZMH-8392		x	M2	l	Africa	Unknown	Recent	
	ZMH-8393		x	M2	l	Africa	Unknown	Recent	
<i>Hippopotamus pentlandi</i>	NHM-PD-40995	x	x	M2	l	Sicily	Maccagone Cave	Pleistocene	
	NHM-PD-40996	x	x	M2	r	Sicily	Maccagone Cave	Pleistocene	
	NHM-PD-41000	x	x	M2	l	Sicily	Maccagone Cave	Pleistocene	
	NHM-PD-41001	x		M2	r	Sicily	Maccagone Cave	Pleistocene	
	NHM-PD-M499		x	M2	l	Sicily	San Ciro	Pleistocene	
<i>Hippopotamus melitensis</i>	NHM-PD-M1200-I	x	x	M2	r	Malta	Ghar Dalam	Pleistocene	
	NHM-PD-M1200-III	x		M2	r	Malta	Ghar Dalam	Pleistocene	
	NHM-PD-M1200-IV	x		M2	l	Malta	Ghar Dalam	Pleistocene	
	NHM-PD-M1200-V	x		M2	l	Malta	Ghar Dalam	Pleistocene	
	NHM-PD-M12326	x		M2	r	Malta	Ghar Dalam	Pleistocene	
	NHM-PD-M12327	x		M2	r	Malta	Ghar Dalam	Pleistocene	
	NHM-PD-M12499-I	x		M3	l	Malta	Ghar Dalam	Pleistocene	
	NHM-PD-M12499-II		x	M2	l	Malta	Ghar Dalam	Pleistocene	
	NHM-PD-M12499-III		x	M2	l	Malta	Ghar Dalam	Pleistocene	
	NHM-PD-M12499-VI	x	x	M2	l	Malta	Ghar Dalam	Pleistocene	
	<i>Hippopotamus creutzburgi</i>	NHM-PD-M10286	x	x	M2	l	Crete	Katharo	Pleistocene
		NHM-PD-M10288-I	x		M2	l	Crete	Katharo	Pleistocene
NHM-PD-M10288-II		x		M2	l	Crete	Katharo	Pleistocene	
NHM-PD-M10288-II			x	M1	l	Crete	Katharo	Pleistocene	
NHM-PD-M10288-III		x	x	M2	l	Crete	Katharo	Pleistocene	
NHM-PD-M10288-IV		x	x	M2	l	Crete	Katharo	Pleistocene	
RGM-KTH-175		x		M2	r	Crete	Katharo	850,000–375,000 BP ^a	
RGM-KTHI-89				M3	l	Crete	Katharo	850,000–375,000 BP ^a	
RGM-KTHI-90				M3	l	Crete	Katharo	850,000–375,000 BP ^a	
RGM-KTHIII-163		x		M2	l	Crete	Katharo	850,000–375,000 BP ^a	
RGM-KTHIII-165	x		M2	r	Crete	Katharo	850,000–375,000 BP ^a		
RGM-KTHIII-251			M3	l	Crete	Katharo	850,000–375,000 BP ^a		
<i>Phanourios minor</i>	NHMC-Cyprus-I			M3	r	Cyprus	Ayia Irini	Pleistocene	
	NHM-PD	x	x	M2	r	Cyprus	unknown	Pleistocene	
	RGM-443902	x		M3	r	Cyprus	Kissonerga	21,960–14,640 BP ^b	
	RGM-CAY109			M3	l	Cyprus	Ayia Irini	21,960–14,640 BP ^b	
	RGM-CAY73			M3	l	Cyprus	Ayia Irini	21,960–14,640 BP ^b	
	RGM-H13-CKS			M3	l	Cyprus	Kissonerga	21,960–14,640 BP ^b	
	RGM-H19-CKS			M3	l	Cyprus	Kissonerga	21,960–14,640 BP ^b	
	RGM-H1-cDKM	x		M2	l	Cyprus	Dhikomo	13,104–8736 BP ^b	
	RGM-H1-cDKM		x	M3	r	Cyprus	Dhikomo	13,104–8736 BP ^b	
	RGM-H25-CKS	x		M2	l	Cyprus	Kissonerga	21,960–14,640 BP ^b	
	RGM-h27-CKS		x	M3	r	Cyprus	Kissonerga	21,960–14,640 BP ^b	
	RGM-H29-CKS		x	M3	r	Cyprus	Kissonerga	21,960–14,640 BP ^b	
	RGM-H35-CKS			M3	r	Cyprus	Kissonerga	21,960–14,640 BP ^b	
	RGM-H38-CKS	x		M3	r	Cyprus	Kissonerga	21,960–14,640 BP ^b	
	RGM-H38-CKS		x	M2	r	Cyprus	Kissonerga	21,960–14,640 BP ^b	
	RGM-H39-CKS	x	x	M3	l	Cyprus	Kissonerga	21,960–14,640 BP ^b	
RGM-H80-COSchin	x		M2	l	Cyprus	Oschin	Pleistocene/Holocene		
RGM-H8-CKS	x	x	M2	l	Cyprus	Kissonerga	21,960–14,640 BP ^b		

* Information about age follows the collections' attributions, taken from catalogues and/or label information. Absolute dates were provided by electron spin resonance (ESR) measurements for hippopotamus tooth fragments from Crete^a (Reese et al., 1996) and Cyprus^b (Reese, 1995). Listed epochs are in line with literature (Bonfiglio et al., 2001; Marra, 2005a; Van der Geer et al., 2010).

moulded on the casts of the upper molars by using the high resolution silicone again.

2.3. Dental topography analysis (SAGA-GIS)

The topometric digitisation system (smartSCAN^{3D}, Breuckmann, Meersburg, Germany) was used to generate 3D surface models of the

occlusal surfaces using the positive cast; 3D surface scanning was conducted with an x, y-resolution of 90 µm ().

The industrial design and metrology software PolyWorks v.11 (InnovMetric Software Inc., Québec, Canada) was applied following Nieberg et al. (2009) to extract and analyse the occlusal surface area. A new coordinate system was defined by a plane best fit for spatial orientation and a vector derived from all points of the model. The aligned

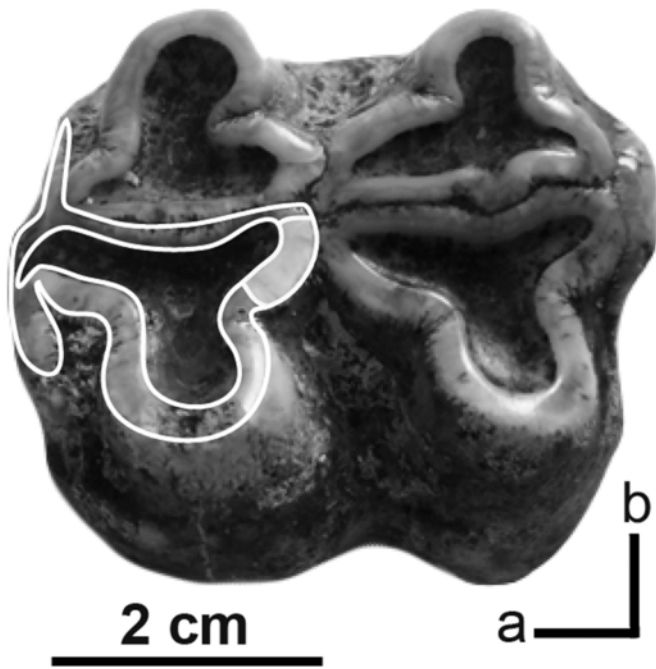


Fig. 3. Occlusal view of an upper second molar of *Hippopotamus melitensis* (NHM-PD-M12499-VI). The position of the measured facet localised on the distal lobe of the paracone is highlighted. Orientation: a = anterior, b = buccal. Museum abbreviation NHM-PD = Natural History Museum, Department of Palaeontology, London, United Kingdom.

Table 2

List of parameters, which return significant differences ($p \leq 0.05$) for statistical tests. Abbreviations for species: see Table 3. Parameters: see Table 4.

Species 1	Species 2	Dental topography analysis	3D surface texture analysis
<i>H. amphibius</i>	<i>H. pentlandi</i>		<i>Sdq, Sdr, S10z, S5p, Sz</i>
<i>H. amphibius</i>	<i>H. melitensis</i>	mean slope	<i>S10z, S5p, S5v, Sdq, Sdr, Sdv, Sp, Sv, Sz</i>
<i>H. amphibius</i>	<i>H. creutzburgi</i>	mean slope	<i>S10z, S5p, S5v, Sdq, Sdr, Spc, Sz</i>
<i>H. amphibius</i>	<i>P. minor</i>	mean slope	<i>S10z, S5p, S5v, Sda, Sdq, Sdr, Sdv, Shv, Sp, Spc, Sv, Sz</i>
<i>H. pentlandi</i>	<i>H. melitensis</i>	mean slope	<i>S5v</i>
<i>H. pentlandi</i>	<i>H. creutzburgi</i>	mean slope	–
<i>H. pentlandi</i>	<i>P. minor</i>	mean slope	<i>Str</i>
<i>H. melitensis</i>	<i>H. creutzburgi</i>	mean slope	<i>S10z, Sz</i>
<i>H. melitensis</i>	<i>P. minor</i>	mean slope	–
<i>H. creutzburgi</i>	<i>P. minor</i>	mean slope	<i>S10z, S5p, Sp, Spc, Spd</i>

occlusal surfaces were exported as stereo lithography format files (STL). This standardised orientation of occlusal surfaces allows for comparative analyses of different mammalian tooth shapes.

The open source software SAGA-GIS v. 2.0.7 (Böhner et al., 2008, 2006) (<http://saga-gis.sourceforge.net/>) was employed to quantify the mean slope according to Nieberg et al. (2009). The digital elevation models of the oriented occlusal surface were imported in SAGA as a raster with a cell size of 0.03 mm. The STL import (Import Stereo Lithography File) was written by Olaf Conrad (Institute of Geography, University of Hamburg). By using a batch tool written by Alexander Czech (Institute of Geography, University of Hamburg), the slope values were calculated as the rate of change of the occlusal surface in an automatic process and exported in txt files. The gained slope data was converted from radiant to degrees. The mean slope per specimen was calculated

by averaging all slope values. Enamel thickness was not considered as a parameter in dental topography analysis.

2.4. 3D surface texture analysis (3DST)

Surface scans of enamel facets were conducted using the high-resolution disc scanning confocal microscope μ surf Custom with a blue LED (470 nm) and a high-speed progressive-scan digital camera (984 × 984 pixels) (NanoFocus AG, Oberhausen, Germany) following Schulz et al. (2010). Where possible, four non-overlapping measurement fields per facet with a square area of 160 μm^2 were collected, using a 100× long distance objective (numerical aperture of 0.8, a resolution in x, y = 0.16 μm and z = 0.06 μm). Measurements with < 95% surface points or a vertical displacement range $\delta z > 40 \mu\text{m}$ were rejected as well as surface areas with defects or adherent dirt. Following Schulz et al. (2010), data were analysed using the 3D industrial areal surface texture standards (Calandra et al., 2012; International Organization for Standardization, 2007; Schulz et al., 2013b, 2013a, 2010). A description of the thirty ISO 3D surface texture parameters used is given in Table 4. The analysis was conducted using μ soft analysis premium v.7.0.6672 software (NanoFocus AG, Oberhausen, Germany; a derivative of Mountains® Analysis software by Digital Surf, Besançon, France).

2.5. Statistics

Statistical analyses were carried out using the open-source software R version 2.13.2 (Development Core Team, 2011) and the procedure of Calandra et al. (2012). All data were trimmed 10% in each tail to compensate for non-normality and heteroscedastic tests were applied due to heterogeneity of variances. The robust Welch-Yuen omnibus test was performed to test for significant differences between species (Wilcox, 2003; Wilcox et al., 2005). Subsequently, the source of significant differences within the arithmetical means was determined using a heteroscedastic pairwise comparison test analogue to Dunnett's T3. The results were accepted if Cliff's ordinal method and the combination of the Welch-Yuen-Test and the Dunnett's T3-test showed a significant output ($p \leq 0.05$).

3. Results

Descriptive statistical values, including the mean and standard derivation (SD) for both the dental topography and the surface texture parameters, are given in Table 3 and raw data in Supplements 1–3.

3.1. Dental topography analysis (SAGA-GIS)

The hippopotami species can be sorted according to an increasing mean slope from lowest to highest value: *Hippopotamus pentlandi*/*Hippopotamus amphibius* < *Hippopotamus melitensis* < *Hippopotamus creutzburgi* < *Phanourios minor* (Fig. 4, A; Fig. 5, Supplement 1 and 3). The examined species can be grouped according to their topography as follows: (1) The more hypsodont, larger hippopotami *H. amphibius* and *H. pentlandi* with the lowest occlusal relief, (2) the medium sized *H. melitensis* and *H. creutzburgi* with an intermediate hypsodonty ($p_D = 0.029$; $p_{WY} < 0.001$; $p_C = 0.024$) and (3) the smallest, brachyodont *P. minor* with the highest occlusal relief ($p_D = 0.001$; $p_{WY} < 0.001$; $p_C = 0.001$).

3.2. 3D surface texture analysis (3DST)

According to the enamel surface texture, the examined species can be assigned to three groups: (1) *Hippopotamus melitensis* and *Phanourios minor* with a rougher surface texture, with steep valleys (*Sdq, Sdr*),

Table 3

Descriptive statistics. n = number per species, SD = standard derivation. Species: *H. amphibius* = *Hippopotamus amphibius*, *H. pentlandi* = *Hippopotamus pentlandi*, *H. melitensis* = *Hippopotamus melitensis*, *H. creutzburgi* = *Hippopotamus creutzburgi*, *P. minor* = *Phanourios minor*. Parameters: see Table 4.

Species		n	mean slope	n	S10z	S5p	S5v	Sa	Sal	Sda	Sdq	Sdr	Sdv	Sha	Shv	Sku	Smc	Smr	n	Sp	Spc	Spd	Sq	Ssk
<i>H. amphibius</i>	Mean	6	23.071	5	0.802	0.420	0.405	0.288	17.002	59.674	0.126	0.793	0.270	68.252	0.514	3.743	0.434	98.633	5	1.280	0.501	0.013	0.365	-0.420
	SD		1.275		0.081	0.076	0.062	0.102	3.912	15.785	0.015	0.181	0.058	17.958	0.197	0.653	0.162	1.648		0.561	0.171	0.004	0.121	0.247
<i>H. pentlandi</i>	Mean	4	19.307	4	2.223	1.175	0.890	0.315	14.343	76.902	0.217	2.311	1.022	80.349	1.321	5.639	0.472	98.271	4	3.606	2.372	0.011	0.409	-0.462
	SD		2.783		1.674	0.840	0.588	0.018	1.492	35.816	0.083	1.564	0.807	35.468	1.111	3.573	0.016	1.006		2.557	2.617	0.005	0.035	0.259
<i>H. melitensis</i>	Mean	8	24.834	4	4.832	1.868	3.017	0.349	14.916	276.332	0.338	4.734	8.106	135.625	3.131	9.805	0.523	97.001	4	6.551	4.465	0.005	0.473	-0.808
	SD		1.354		2.196	1.465	2.582	0.048	2.399	182.358	0.081	1.727	10.031	95.602	2.137	5.648	0.080	0.946		6.864	4.748	0.005	0.078	0.598
<i>H. creutzburgi</i>	Mean	8	28.391	4	1.669	0.693	1.014	0.300	16.284	74.157	0.193	1.783	0.795	68.088	0.758	3.992	0.478	98.818	4	1.705	1.005	0.015	0.386	-0.253
	SD		2.889		0.883	0.247	0.638	0.047	1.907	59.067	0.026	0.447	0.823	32.657	0.430	0.702	0.073	0.945		0.406	0.549	0.008	0.061	0.220
<i>P. minor</i>	Mean	8	37.729	7	5.181	3.113	1.961	0.351	14.006	156.168	0.349	5.449	3.612	92.478	1.542	21.879	0.537	96.809	7	7.034	16.067	0.005	0.481	-0.443
	SD		5.424		3.710	2.710	1.551	0.110	2.623	75.199	0.191	4.871	3.575	46.905	1.551	28.799	0.188	1.792		5.973	20.963	0.004	0.144	0.566

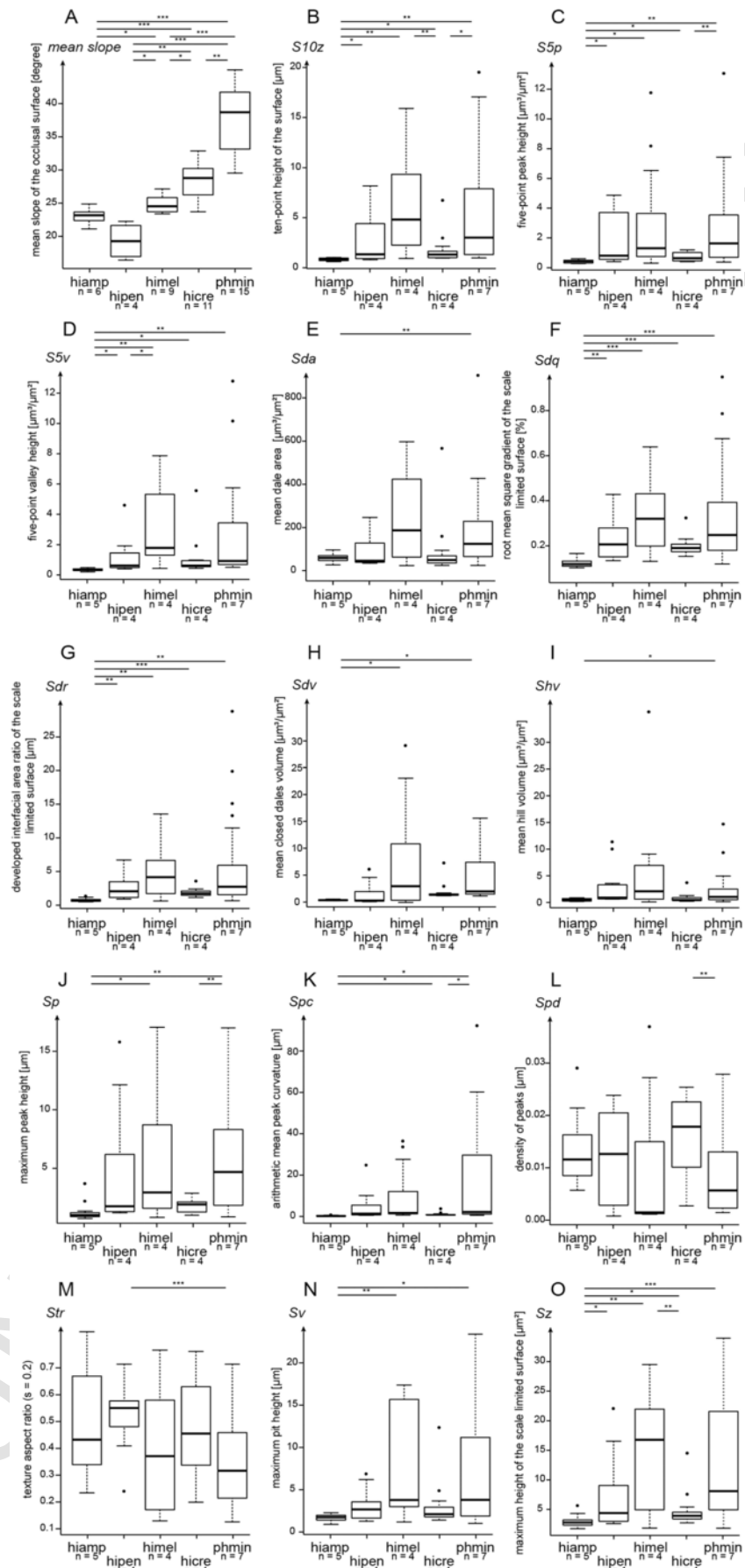


Fig. 4. Box plots of the significant differences between the occlusal surface and the enamel surface texture of the dwarfed hippopotami. The box plots are sorted according to the body size of the hippopotami, from the largest, *Hippopotamus amphibius*, to the smallest, *Phanourios minor*. Box plots indicating the (A) mean slope of the occlusal surface [degree], the ISO 25178 parameters: (B) $S10z$ = ten-point height of the surface [μm], (C) $S5p$ = five-point peak height [$\mu\text{m}^3/\mu\text{m}^2$], (D) $S5v$ = five-point valley height [$\mu\text{m}^3/\mu\text{m}^2$], (E) Sda = mean dales area [$\mu\text{m}^3/\mu\text{m}^2$], (F) Sdq = root mean square gradient of the scale limited surface [%], (G) Sdr = developed interfacial area ratio of the scale limited surface [μm], (H) Sdv = mean closed dales volume [$\mu\text{m}^3/\mu\text{m}^2$], (I) Shv = mean hill volume [$\mu\text{m}^3/\mu\text{m}^2$], (J) Sp = maximum peak height [μm], (K) Spc = arithmetic mean peak curvature [μm], (L) Spd = density of peaks [μm], (M) Str = texture aspect ratio ($s = 0.2$), (N) Sv = maximum pit height [μm], (O) Sz = maximum height of the scale limited surface [μm^2]. * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$, n = number of specimens, hiamp = *Hippopotamus amphibius*, hipen = *Hippopotamus pentlandi*, himel = *Hippopotamus melitensis*, hicre = *Hippopotamus creutzburgi*, phmin = *Phanourios minor*.

higher and rounder peaks ($S10z$, $S5p$, $S5v$, Sp , Sv , Sz , Spc) and with deep and large dales (Sdv , Shv , Sda). (2) *Hippopotamus pentlandi* showing a smoother, less abrasion-dominated surface texture with less steep valleys, smaller and abraded peaks and with narrow, small dales; (3) *Hippopotamus amphibius* and *Hippopotamus creutzburgi* with the smoothest surface texture (Figs. 4, A–O, 6, Supplements 2 and 3). Fourteen ISO parameters individually allow distinction of the investigated hippopotami species (Table 2). The ISO parameters are described in Table 4.

Hippopotamus melitensis and *Phanourios minor* bear the most intraspecific variability in enamel surface texture. In *Hippopotamus pentlandi*, noticeably less variability was measured. *Hippopotamus amphibius* and *Hippopotamus creutzburgi* feature a more consistent, smaller interquartile range as seen in Table 3 (Fig. 4, A–O).

4. Discussion

4.1. Occlusal adaptations

The lower mean slope values in the more hypsodont (high-crowned) hippopotami *Hippopotamus amphibius* and *Hippopotamus pentlandi* reflect their lower occlusal relief. A flat occlusal surface is supposed to be a result of more pronounced horizontal jaw kinematics, associated with efficient shear-cutting action as indicative of grazing traits in ruminants (Kaiser et al., 2010). The multi ridged occlusal morphology in conjunction with a transversal chewing path is effective in processing flat blades of grass without losing any functionality when abrasion is high (Damuth and Janis, 2011; Kaiser et al., 2013; Schulz and Kaiser, 2013). Consequently, the lower occlusal profile, as observed in *H. amphibius* and *H. pentlandi*, can be considered a dental adaptation towards a more abrasive, grass-dominated dietary trait.

High mean slope values, as evident in the smaller, more brachyodont hippopotamus *Phanourios minor*, reflect the higher occlusal relief of this species, which results in voluminous dentin basins between highly protruding enamel shearing blades. Such occlusal traits are commonly found in browsing ruminants, adapted to efficiently extract cell contents by compression (Archer and Sanson, 2002; Damuth and Janis, 2011; Lucas, 2004). Accordingly, we interpret the higher dental profile in *P. minor* to be an adaptation towards a more selective, attrition-dominated, less abrasive feeding.

The investigated species fall into three groups regarding their occlusal topography: (1) *Hippopotamus amphibius* and *Hippopotamus pentlandi* show an occlusal adaptation indicating a grass-dominated diet, (2) *Hippopotamus melitensis* and *Hippopotamus creutzburgi* exhibit dental traits that indicate a mixed diet with a tendency towards grass-dominated feeding and (3) *Phanourios minor* with browse-dominated feeding traits. In the light of these results, it seems that the occlusal profile is lower in the larger and more hypsodont insular hippopotami. This is no surprise, since both, larger body size and a higher hypsodonty index, are associated with more abrasion dominated grass-feeding. Smaller herbivores have to feed more selectively due to their lower gut capacity (Clausen et al., 2003; Jarman, 1974; Owen-Smith, 1989). They have to rely on higher quality diet such as browse, which has a high ratio of cytosol to cell walls (Sanson, 2006). In contrast, larger species with higher energy requirements depend on large amounts of forage and consequently cannot afford to solely rely on selective feeding (Clausen et

al., 2003; Kaiser et al., 2010; Sanson, 2006). Moreover, larger species are able to tolerate a lower minimum dietary quality on account of their longer passage rates and the higher fibre digestibility (Clausen and Hummel, 2005). Therefore, larger herbivores can sustain their higher energetic demands by feeding less selectively on bulk and roughage (Clausen et al., 2003; Codron et al., 2007; Sanson, 2006).

Whilst the body size is related to dietary quality, hypsodonty correlates positively with the percentage of consumed grass as well as the abrasiveness of consumed food and increases with grass intake (Codron et al., 2007). Thus, the evolution of hypsodont teeth in herbivore species is considered an adaptation to a high rate of tooth wear, induced by increased grit ingestion when feeding close to the ground (Damuth and Janis, 2011; Janis, 1988; Kaiser et al., 2013).

Consequently, the recent mainland form *Hippopotamus amphibius*, being the largest and most hypsodont of the investigated hippopotamus species, should exhibit the highest occlusal relief. However, *Hippopotamus pentlandi* showed an even lower occlusal profile. The behaviour of extant *H. amphibius* points out a possible ecological reason for flatter occlusal topographies in *H. pentlandi*. The extant specimens studied here were all collected near large African rivers, whilst extinct island hippopotami had less extensive open freshwater sources available. This relationship is geographically determined. Large rivers need large “hinterlands” and large lakes need large basins. Both basins and hinterlands strictly correlate with island size, but never compete to the mainland. Therefore islands would, compared to the mainland, potentially have fewer and smaller riverine fresh water sources, resulting in a more arid environment.

In consequence, a low occlusal profile might have evolved in *Hippopotamus pentlandi*, suited for feeding from more terrestrial habitat patches. Those would have ultimately featured more external dust and slightly dryer, and therefore more abrasive grass (Winkler et al., 2019). Since the faunal complex *H. pentlandi* lived in had a strong mainland character, the biggest distinction from *Hippopotamus amphibius* seems to be habitat size and consequently freshwater access. The lower occlusal profile in *H. pentlandi* might therefore be a general adaptation to a more arid environment with respect to the mainland. This might also be true for the much smaller insular hippopotami, but due to the large difference in body size with regards to *H. amphibius*, such a response would be masked.

4.2. Dietary behaviour and forage selection

4.2.1. *Hippopotamus amphibius*

The enamel surface texture of extant *Hippopotamus amphibius* is characterised by shallow valleys (Sdq , Sdr), smaller and sharper peaks ($S10z$, $S5p$, $S5v$, Sp , Sv , Sz , Spc) with shallow and small dales (Sdv , Shv , Sda), compared to the investigated insular species. Such a condition is commonly found in extant ungulate browsers (Schulz et al., 2013a, 2010). Stomach content and faecal analyses of *H. amphibius* indicate a diet mostly consisting of C_4 grasses (Field, 1970; Scotcher et al., 1978), but it also consumes more C_3 vegetation (browse) than often noted (Boisserie et al., 2011; Cerling et al., 2008; Scotcher et al., 1978), possibly due to the anatomy of its mouth with its broad jaws (Eltringham, 1999). A recent study (Winkler et al., 2019) demonstrated that fresh grasses with high moisture content result in surface textures of similar roughness as those of browsers. The high abrasiveness of grasses that is

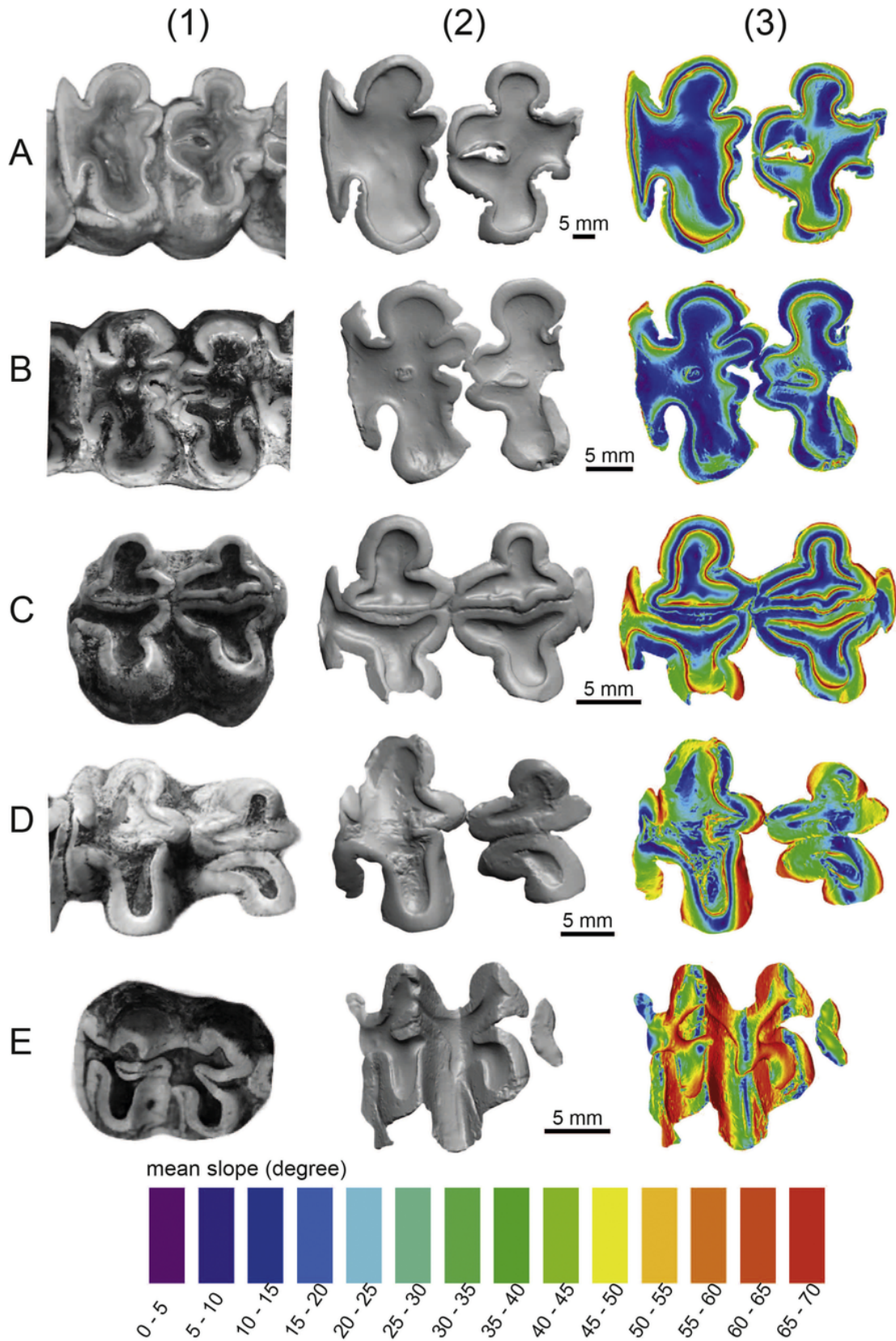


Fig. 5. Dental topography of the second upper molar. (1) Pictures in occlusal view, (2) digital 3D model of the extracted occlusal surface, (3) slope visualisation of the occlusal surface, (A) *Hippopotamus amphibius*, ZMB-76150, (B) *Hippopotamus pentlandi*, NHM-PD-40996, (C) *Hippopotamus melitensis*, NHM-PD-M12499-IV, (D) *Hippopotamus creutzburgi*, NHM-PD-M10288-IV (E), *Phanourios minor*, RGM-80-COSCHIN. Museum abbreviations: ZMB = Museum für Naturkunde, Humboldt-Universität, Berlin, Germany; NHM-PD = Natural History Museum, De-

partment of Palaeontology, London, United Kingdom; RGM = Naturalis (Leiden), Rijksmuseum van Geologie en Mineralogie at Naturalis, Nationaal Natuurhistorisch Museum, Leiden, the Netherlands.

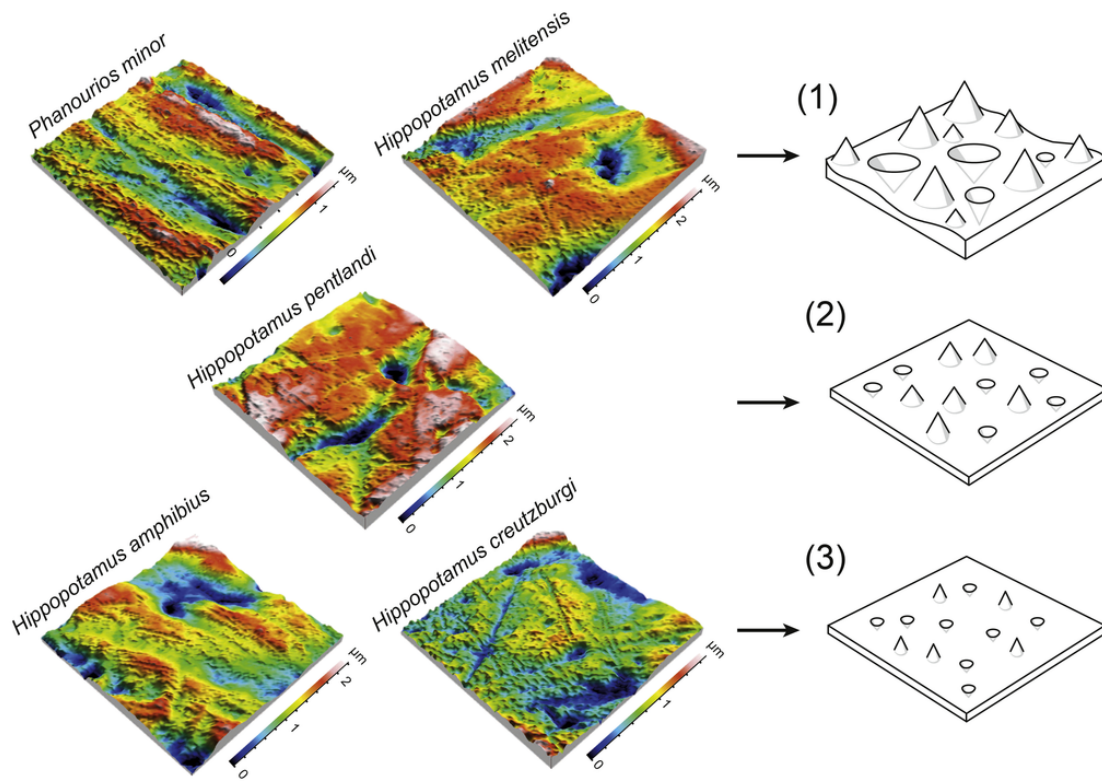


Fig. 6. Meshed axiomatic 3D models ($160 \times 160 \mu\text{m}$) of enamel surfaces and schematic models (1–3). Schematic models for (1) the roughest enamel surfaces of *Phanourios minor* and *Hippopotamus melitensis*, for (2) the more rough enamel surface of *Hippopotamus pentlandi* as well as for (3) the least rough enamel surfaces of *Hippopotamus amphibius* and *Hippopotamus creutzburgi*.

typically associated with increased enamel surface roughness (Schulz et al., 2013b, 2013a) was only found when grasses were fed as hay (Winkler et al., 2019). This observation is in accordance with *H. amphibius* being classified as a fresh grass grazer (Boisserie et al., 2011; Hofmann and Stewart, 1972; Janis, 1988) as they often feed in areas frequently immersed in water (Mendoza et al., 2002). Additional evidence from microwear suggests that extant hippopotami consume less abrasive ingesta than other grazing ungulates, with a preference for short, fresh grasses of low silica content (Boisserie et al., 2005).

4.2.2. *Hippopotamus pentlandi*

According to the surface texture analysis, *Hippopotamus pentlandi* fed on a similar diet as the semiaquatic continental *Hippopotamus amphibius*, with a slightly more abrasion-dominated enamel surface as indicated by steeper valleys (*Sdq*, *Sdr*), higher and rounder peaks (*S10z*, *S5p*, *S5v*, *Sp*, *Sv*, *Sz*, *Spc*) and with deeper and larger dales (*Sdv*, *Shv*, *Sda*). The larger island, Sicily, is characterised by a more constant availability of resources because of its larger area, in comparison to the other investigated islands. In its faunal complex, featuring high predation and competition pressures, *H. pentlandi* had undergone the lowest reduction in body size with respect to the other three Mediterranean hippopotami. It presumably maintained a semiaquatic lifestyle according to its robust limbs (Boisserie et al., 2011). It likely occupied a similar niche as the recent *H. amphibius*. A change to a different niche was probably prevented by the higher inter- and intraspecific competition experienced by *H. pentlandi*. This might have resulted in feeding traits similar to *H. amphibius*: the foraging on fresh grass, yet with slightly more dust intake due to limited water sources and the reliance on dryer, and therefore more abrasive grasses (Winkler et al., 2019).

4.2.3. *Hippopotamus creutzburgi*

Since the vegetation of a terrestrial habitat is prone to dust accumulation, the more terrestrial *Hippopotamus creutzburgi* should have experienced comparatively more abrasive ingesta than the semiaquatic extant *Hippopotamus amphibius*. However, it has to be noted, that the enamel surface textures in *H. creutzburgi* appear smoother and less abrasion-dominated, than one would expect based on the presumed terrestrial trait of the species.

A closer look at habitat conditions on Crete would be needed to approach this problem. All individuals studied derive from localities in the Katharo basin of Crete, located in the Dikti Mountains at 1200 m above sea level. Bate (1905) suggested, that accumulated meltwater might have filled this basin during the Pleistocene resulting in a swamp or lake. In fact, Pleistocene lacustrine deposits in the Katharo basin (Pavlakakis et al., 1999; Poulakakis et al., 2002) including fossil freshwater molluscs (Boeschoten and Sondaar, 1972) strongly suggest a lakeshore environment. Similar conditions can be observed nowadays in the nearby Omalos Plain, which is prone to flooding during summer (Kourgialas and Karatzas, 2017). It seems that *Hippopotamus creutzburgi* used its locomotor adaptations to reach the lake or even seasonally migrate there. During summer times, *H. creutzburgi* was able to access the Katharo basin, which was inundated with meltwater from glaciers (Bate, 1905; Boeschoten and Sondaar, 1966; Pavlakakis et al., 1999; Poulakakis et al., 2002). The resulting large lake environment offered an excellent habitat for fresh grass grazing hippopotami. In winter, the glacier would have occupied the upland basin, forcing *H. creutzburgi* individuals to migrate downhill to coastal caves and cliffs, which probably provided shelter, drinking water and food (Hadjisterkotis and Reese, 2008). Indeed, the possibility of seasonal migration in *H.*

Table 4

Parameters according to 3D industrial areal surface texture standards 6 (ISO 25178). With unit, parameter group and description. Parameters in bold = parameters, which return significant differences ($p \leq 0.05$) for all statistical tests.

Parameter	Unit	Parameter group	Description
S10z	μm	Feature/segmentation	Ten-point height of the surface
S5p	μm	Feature/segmentation	Five-point peak height
S5v	μm	Feature/segmentation	Five-point valley height
Sa	μm	Height	Arithmetical mean height = root mean square roughness (RMS)
Sal ($s = 0.2$)	μm	Spatial	Auto-correlation length
Sda	μm^2	Feature/segmentation	Mean dales area
Sdq	No unit	Hybrid	Root mean square gradient of the scale limited surface
Sdr	%	Hybrid	Developed interfacial area ratio of the scale limited surface
Sdv	μm^3	Feature/segmentation	Mean closed dales volume
Sha	μm^2	Feature/segmentation	Mean hill area
Shv	μm^3	Feature/segmentation	Mean hill volume
Sku	No unit	Height	Kurtosis of the scale limited surface
Smc ($p = 10\%$)	μm	Functions and related	Areal material ratio function of the scale limited surface
Smr ($c = 1 \mu\text{m}$ under the mean plane)	%	Functions and related	Areal material ratio function of the scale limited surface
Sp	μm	Height	Maximum peak height
Spc	$1/\mu\text{m}$	Feature/segmentation	Arithmetic mean peak curvature
Spd	$1/\mu\text{m}^2$	Feature/segmentation	Density of peaks
Sq	μm	Height	Root mean square height of the scale limited surface
Ssk	No unit	Height	Skewness of the scale limited surface
Std	°	Spatial	Texture direction
Str ($s = 0.2$)	No unit	Spatial	Texture aspect ratio
Sv	μm	Height	Maximum pit height
Sxp ($p = 50\%$, $q = 97.5\%$)	μm	Functions and related	Peak extreme height difference in height between p% and q%
Sz	μm	Height	Maximum height of the scale limited surface
Vm ($p = 10\%$)	$\mu\text{m}^3/\mu\text{m}^2$	Functional	Material volume at a given height
Vmc ($p = 10\%$, $q = 80\%$)	$\mu\text{m}^3/\mu\text{m}^2$	Functional	Material volume of the core
Vmp ($p = 10\%$)	$\mu\text{m}^3/\mu\text{m}^2$	Functional	Material volume of peaks
Vv ($p = 10\%$)	$\mu\text{m}^3/\mu\text{m}^2$	Functional	Void volume at a given height
Vvc ($p = 10\%$, $q = 80\%$)	$\mu\text{m}^3/\mu\text{m}^2$	Functional	Void volume of the core
Vvv ($p = 80\%$)	$\mu\text{m}^3/\mu\text{m}^2$	Functional	Void volume of the valley

creutzburgi is a scenario proposed to explain the postcranial adaptations (Boekschoten and Sondaar, 1966) as well as the accumulated remains at both coastal cave sites (Bate, 1905) and the Katharo site.

Since enamel surface textures in *Hippopotamus creutzburgi* and *Hippopotamus amphibius* are alike, a similar feeding trait for both is suggested. This would, at least seasonally, involve extensive feeding on less abrasive forage in a quite similar semiaquatic, more humid envi-

ronment. This favourable habitat would have been accessible through the terrestrial adaptations in the postcranial skeleton of *H. creutzburgi*.

4.2.4. *Hippopotamus melitensis*

Regarding its enamel surface texture, *Hippopotamus melitensis* differs from its more semiaquatic ancestor, *Hippopotamus pentlandi*. Indeed, it displays an abrasion-dominated enamel surface texture as indicated by the steepest valleys measured in this study (*Sdq*, *Sdr*), with the highest and most abraded peaks (*S10z*, *S5p*, *S5v*, *Sp*, *Sv*, *Sz*, *Spc*) and deep and large dales (*Sdv*, *Shv*, *Sda*), more closely resembling that of the terrestrial *Phanourios minor*.

Compared to the other island hippopotami, the high variability in the enamel surface textures of *Hippopotamus melitensis* is striking. This may reflect a strategy of coping with the energetic limitations on the small, predator-free island, by feeding on a more variable diet. The following scenarios might present possible explanations for the high variation.

The high variability in the enamel microtexture of *Hippopotamus melitensis* might mirror an expansion of its dietary niche, resulting in a more generalistic feeding strategy. In fact, smaller islands often feature species with dietary generalism in order to survive seasonal shortages in resource availability (Winkler et al., 2013b, 2013a). Malta certainly offered an extremely limited resource diversity as well as availability. This could have driven *H. melitensis* to broaden its dietary niche. Another explanation is, that the high variability might echo an ecological separation in progress. Such ecological separations might lead to adaptive radiations. This scenario is supported by the size variation within the Maltese hippopotami, which exceeds that of a mainland population (Van der Geer et al., 2010). Such a variation in body size has also been observed in the Cretan deer and seems to be a result of lacking predation pressure and minimal competition on islands (De Vos, 1979).

Since the texture parameters show a steady shift towards less abrasion dominated regimes from *Hippopotamus melitensis*, with smallest habitat, to *Hippopotamus pentlandi*, from larger island Sicily, to the mainland form *Hippopotamus amphibius*, habitat and therefore island size is considered to be a key factor to dietary ecology of island hippopotami.

4.2.5. *Phanourios minor*

The enamel surface texture in *Phanourios minor* is rougher than those in the semiaquatic species *Hippopotamus amphibius* and *Hippopotamus pentlandi*. This is consistent with the postcranial adaptations of *P. minor* to a terrestrial habitat, and therefore higher dust intake.

Its dental adaptations (lophodonty, brachydonty) mark *Phanourios minor* as a terrestrial browser in a closed habitat. Additional stable carbon isotope analyses on specimens from the Akrotiri site on Cyprus showed a narrow browsing strategy, as result of plant availability or specialisation (Wopschall, 2015). The narrow feeding strategy, however, does not seem to be consistent with the highly variable enamel surface texture in *P. minor*.

A possible explanation for the observed variability can be, that the investigated material encapsulates a change in climate. The specimens investigated derive from various, differently dated localities on Cyprus and might therefore differ in geological age. The specimens of *Phanourios minor* are dated to the transition from the Pleistocene to the Holocene (21,960–14,640 BP, Ayia Irini, Kissonerga; 13,104–14,640 BP, Dhikomo). A rapid rise of cold, dry conditions throughout the eastern Mediterranean Sea at the onset of the Younger Dryas might have affected the dietary resources of *P. minor* (Knapp, 2010; Simmons, 2014). This scenario is supported by results from stable isotope analyses on specimens from the Akrotiri site, which show signs of an increasing aridity in the environment *P. minor* individuals, mirroring habitat and climatic shifts of the surrounding mainland (Wopschall, 2015). Consequently, the variability in enamel surface texture of *P. minor* seems to

be linked to a climatic change, which resulted in an alteration of environmental and vegetal conditions from the Pleistocene to the Holocene.

5. Conclusions

Although lower occlusal reliefs are associated with a large body size and a higher hypsodonty index, the insular *Hippopotamus pentlandi* exhibited an even lower occlusal relief than the larger and more hypsodont mainland form, *Hippopotamus amphibius*. We conclude that this reflects an adaptation to a lower diet quality in an arid environment. This would be characteristic for islands because freshwater access and food resources are limited.

Hippopotamus creutzburgi exhibited an enamel surface texture most similar to that of the fresh grass feeding *Hippopotamus amphibius*. The results suggest a semiaquatic lifestyle for *H. creutzburgi* similar to that of *H. amphibius* despite its postcranial adaptations for terrestrial locomotion. This is in accordance with the (presumably seasonal) presence of *H. creutzburgi* at the upland lake of Pleistocene Katharo, from where the material has been sampled. On the large island Sicily, *Hippopotamus pentlandi* seems to have occupied a similar niche as *Hippopotamus amphibius*, confirming the mainland character of its faunal complex. However, the slightly rougher enamel surface textures suggest that *H. pentlandi* consumed more abrasives than the mainland form. In a small habitat and facing extreme resource limitations, *Hippopotamus melitensis* was driven to broaden its dietary niche. The diet probably consisted of a higher amount of dust adherent to dryer plant material, compared to that of the more semiaquatic hippopotami. *Phanourios minor* either broadened its dietary niche as a response to the low competition pressure, or underwent a dietary shift following the Younger Dryas climatic event.

Author's contribution

DEW, ESK and TMK supervised this study and designed the experiments. DEW collected the data, EB performed the experiments, analysed the data and wrote the manuscript. All authors contributed to, read and approved the final manuscript.

Consent for publication

All authors read and approved the final manuscript.

Ethics approval and consent to participate

Not applicable.

Availability of data and materials

All data generated or analysed during this study are included in this published article and its supplementary information files (Supplement 1–4).

Declaration of Competing Interest

The authors declare that they have no competing interests.

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Appendix A. Supplementary data

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