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DIETARY BEHAVIOUR OF THE PLEISTOCENE CRETAN DWARF DEER: PRELIMINARY CLUES FROM MESOWEAR ANALYSIS OF *CANDIACERVUS* EX GR. *CANDIACERVUS ROPALOPHORUS* FROM BATE CAVE

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ABSTRACT: During the Middle and Late Pleistocene Crete was inhabited by endemic dwarf deer. The smallest, *Candiacervus* ex gr. *Candiacervus ropalophorus* (*sensu* Palombo et al., 2008) have been believed to have inhabited rocky environments characterised by typical Mediterranean vegetation. This research aims to investigate dietary behaviour in the sample of the smallest deer found in the Bate Cave late Middle - early Late Pleistocene deposits (152,000±20% to 105,000±20% years).
The molar teeth of *Candiacervus* ex gr. *C. ropalophorus* from Bate Cave mainly show well-defined and high cusps, sometimes also perceptible in teeth in an advanced wear stage. Therefore, it seems rational to suppose that deer had an eating behaviour approaching browsers. In order to substantiate this hypothesis, it was applied the mesowear method proposed by Fortelius & Solounias (2000) to infer the dietary behaviour of herbivores. The method was originally based on facet development on the occlusal surface of the second upper molar tooth, then extended to other molars, although results obtained show some inconsistencies. The number of M^2 specimens of *Candiacervus* ex gr. *C. ropalophorus* from Bate Cave is too low to be statistically valid. Therefore, the analysis was extended to the last two lower and upper molars, divided in group according to their wear stage, with the double aim to check the consistence of results obtained by analysing upper and lower molars and verify to which extent wear may influence the cusp shape. The results obtained by extension of the method are encouraging, in fact all the teeth reveal the same trend suggesting a prevalent mixed-feeder habit for *Candiacervus* ex gr. *C. ropalophorus* from Bate Cave although in some individuals a more marked browsing attitude is observed. A possible diet included leaves, shrubs and other tender and nutritious vegetation.

Key words: *Candiacervus ropalophorus*, Crete, Mesowear, Dietary behaviour, Pleistocene.

1. INTRODUCTION

The study of feeding behaviour in herbivorous mammals (ungulates) is of particular interest to infer habitat preference and behaviour of fossil herbivores and provides some clues about the environment they inhabited. The food preference, indeed, reflects the vegetation cover and availability and partition of resources. According to their feeding behaviour, herbivores are generally classified into three main ecological groups: browser, grazer and mixed feeder.

Cervids are a highly heterogeneous group, most of species are ecologically flexible, some inhabit different environments, and some are opportunistic / mixed feeder, changing seasonality or occasionally their diet depending on resource availability and competition with other herbivores (see inter alios Geist, 1999; Palombo, 2005; Yamada, 2012; De Marinis & Toso, 2015).

The varied dietary habits of herbivores may be inferred by analysing the morphology of the tooth itself. In particular, the method of mesowear analysis, as originally proposed by Fortelius & Solounias (2000), provides information about the prevalent feeding behaviour of a species basing on the observation of occlusal facet of the second upper molar (M^2). The development of this facet is related to the relative ratio of attrition (tooth-to-tooth contact) and abrasion (food-to-tooth contact) that occurs during mastication activities. According to Fortelius & Solounias (2000) the method provides stable trophic classification when at least 20 teeth are investigated. However, in the study of fossil species, sometimes the sample is not large enough to provide firm results. Afterwards, the method has been extended to other teeth including the last two upper molars (two-tooth model - M^2-M^3) (Franz-Odendaal & Kaiser; 2003; Valli & Palombo, 2008), all molars (M^1÷M^3, Kaiser & Croitor, 2004; M^1÷M^3 and M_1÷M_3 Louys et al., 2011) or all the chewing teeth (four-tooth model - P^4÷M^3; P_4÷M_3) (Kaiser & Solounias, 2003; Kaiser, 2003; Kaiser & Fortelius, 2003).

The method has been applied in several studies dealing with the dietary strategy in fossil and extant herbivores, such as Equidae (Kaiser & Solounias, 2003; Kaiser, 2003; Kaiser & Fortelius, 2003; Mihlbachler et al., 2011; Loffredo & DeSantis, 2014), Cervidae (Kaiser & Croitor, 2004; Palombo, 2005; Valli & Palombo 2008; Yamada, 2012) and others (Franz-Odendaal & Kaiser, 2003; Kaiser & Kahlke, 2005; Clauss et al., 2007; Rivals et al., 2011; Louys et al., 2011; Solounias et al., 2014). Furthermore, in order to obtain data comparable with other possible variables (e.g. Hypsodonty, %grass, habitat) (Rivals & Semprebon, 2006; Kaiser et al., 2009; Valli & Palombo, 2008; Loffredo & DeSantis, 2014) the

Fig. 1 - Skulls (a: female specimen 6; b: male specimen 3), jaws (c: sn1-sx; d: 8-dx) and mounted skeletons (e) of *Candiacervus* ex gr. *Candiacervus ropalophorus* from Bate Cave (Paleontological Museum of Sapienza University, Rome).

mesowear qualitative variables (OR and cusps shape) were combined to convert them into mesowear score: high relief and sharp cusps = "0", high relief and rounded cusp = "1", low relief and sharp cusp = "2", low relief and round cusp = "3", low relief and blunt cusp = "4". Indeed, a score of 0 represents the most attrition-dominated mesowear signals, while a score of 4 would represent the most abrasion-dominated signals. (Rivals & Semprebon, 2006; Kaiser et al., 2009; Mihlbachler et al., 2011).

The research aims to infer the dietary behaviour of the Cretan endemic deer, *Candiacervus* ex gr. *Candiacervus ropalophorus* (*sensu* Palombo et al., 2008) (Fig. 1), found in the Bate Cave (Rethymnon) and dated between 150,000±20% and 105,000±20% years (AAR method -Reese et al., 1996).

During the Middle and Late Pleistocene, the Crete island was inhabited by at least five endemic deer which originated from a radiative evolutionary process that led to a niche partition among deer species differing in size, habitat and feeding behaviour (De Vos, 1996, 2000). The *Candiacervus ropalophorus* group includes the smallest among the Cretan endemic deer (*Candiacervus ropalophorus* and *Candiacervus* sp. II in De Vos, 1979, 1984, 1996), *C.* ex gr *C. ropalophorus* is believed to have inhabited rocky environments with a Mediterranean vegetation and to have had a mixed diet mainly consisting of bushes, shrubs, leaves and grass, whose availability and quality were subject to seasonal variations (Caloi & Palombo, 1996; van der Geer et al., 2006; van der Geer et al., 2010; van der Geer et al., 2014; Mujica, 2014; Palombo & Zedda, 2015). To validate such a hypothesis, I applied the mesowear method to the last two upper and lower molars also with the aim of investigating whether results obtained by analysing these chewing teeth are consistent with each other and, therefore, may provide hints to infer dietary behaviour when the M^2 sample is not statistically valid, and the wear variation is particularly high.

2. MATERIALS AND METHODS

The material object of this study is kept at the Paleontological Museum of the La Sapienza University of Rome and consists of 102 molars: 25 M_2, 32 M_3, 24 M^2 and 21 M^3. I chose to analyse the upper and lower penultimate and ultimate molars because results provided by the two-tooth model (M^2-M^3) are similar to those obtained by analysing only M^2 (Franz-Odendaal & Kaiser, 2003), while the analysis of upper and lower M1 and P4 has been demonstrated to be less reliable (as least as ruminants is concerned, conversely to horses) (Kaiser & Solounias, 2003; Kaiser, 2003; Kaiser & Fortelius, 2003) because of the extent of the wear period (see Louys et al., 2011).

Only permanent teeth showing different wear stages have been considered. The sample does not include teeth in very advanced stage of wear. The shape of cusps of molars of deer from Bate Cave ranges from high and sharp in unworn teeth to low and rounded/ sharp in the most worn one. Therefore, prior to performing the mesowear analysis, *C.* ex gr. *C. ropalophorus* molars were grouped according to their degree of wear.

The wear classes were evaluated according the IDAS system (individual dental age stages) based on tooth eruption and tooth wear (Anders et al., 2011) and the progressive decrease of crown height have been used as a guideline to define three wear stages: slightly worn teeth (1° wear stage, W1) (IDAS 2, permanent dentition is fully erupted), average worn teeth (2° wear stage, W2) (IDAS 3, the second molar starts to lose the inner profile), strongly worn teeth (3° wear stage, W3) (IDAS 4, the second molar loses the inner profile) (Anders et al., 2011).

It is well known that in herbivore the height of the tooth crown provides clues as regard to dietary aptitudes, because reflects the resistance of tooth to the abrasive power of food responsible for tooth wear during the masticatory process (i.e. herbivores feeding on fibrous material have a hypsodont dentition) (see inter alios Fortelius, 1985; Janis, 1988; Janis & Fortelius, 1988; Damuth & Janis, 2011; Kaiser et al., 2013). The quantitative measure of hypsodonty, (Hypsodonty Index, HI) can be calculated in different ways: on M^2 by dividing the height of the crown by the occlusal total length of the tooth (Valli & Palombo, 2008), and on M_3 by dividing the height of the crown by width of the tooth (Janis, 1988; Fortelius & Solounias, 2000; Kaiser et al., 2013). Appling both methods the value of the HI measured on unworn teeth is < 1.5 in brachydont, ranges from 1.5 to 3.0 in mesodont, and from 3.0 to 4.5 in hypsodont, and is > 4.5 in highly hypsodont animal.

The HI of *C.* ex gr. *C. ropalophorus* has been evaluated measuring M^2 and M_3 at different wear stage.

As regards to the parameters related to mesowear method (Fortelius & Solounias, 2000), the cusp height (Occlusal Relief-OR) was defined as the difference in height between cusp tips and inter cusp valley as seen in labial projection (M^2, M^3) or in lingual projection (M_2, M_3). The OR values is "high" when the result is greater than 0.1, while "low" when it is less than 0.1. The shape of the cusps was qualitatively evaluated according to three typologies: sharp, rounded, and blunt (Fig. 2). All mesowear results was converted into mesowear score (Kaiser et al., 2009) and plotted *versus* HI in order to verify whether this rating may be regarded as a valid habitat proxy (Kaiser et al., 2013). Data obtained for *C.* ex gr. *C. ropalophorus* have been compared with those of 63 extant species (data from Fortelius & Solounias, 2000; Mendoza & Palmqvist, 2008; Kaiser et al., 2009; Kaiser et al., 2013) (Tab. 1).

To infer the grazer *versus* browser ability of *C.* ex gr. *C. ropalophorus* from Bate cave, a cluster analysis has been performed comparing *C.* ex gr. *C. ropalophorus* with 52 extant artiodactyl species (cervids, bovids, giraffids and camelids, data from Fortelius & Solounias, 2000; Franz-Odendaal & Kaiser, 2003; Louys et al., 2011) (Tab. 2). The species were assigned to dietary categories on the basis of personal observation and comparing results obtained by different authors (Fortelius & Solounias, 2000; Gagnon & Chew, 2000; Louys et al., 2011).

Four extinct species having different trophic and ecological requirement have been added to the cluster analysis (Tab. 2) selected because they show a

Species		DC	MS	HI	Hab
Bison	*bison*	G	3.73	4.87	1
Syncerus	*caffer*	G	1.17	3.82	2
Boselaphus	*tragocamelus*	M	1.27	3.03	2
Tetracerus	*quadricornis*	M	0.90	3.77	2
Taurotragus	*oryx*	M	0.45	2.91	2
Tragelaphus	*strepsiceros*	M	1.00	2.29	2
Tragelaphus	*imberbis*	M	0.42	2.18	2
Tragelaphus	*angasii*	M	0.65	2.52	2
Tragelaphus	*eurycerus*	B	0.64	1.92	3
Tragelaphus	*scriptus*	B	0.54	2.54	2
Cephalophus	*dorsalis*	B	1.07	1.15	3
Cephalophus	*sylvicultor*	B	1.46	2.23	2
Oryx	*gazella*	G	1.00	3.37	1
Hippotragus	*equinus*	G	1.29	4.28	1
Hippotragus	*niger*	G	1.58	3.77	2
Connochaetes	*gnou*	G	2.00	4.75	1
Connochaetes	*taurinus*	G	1.79	4.94	1
Alcelaphus	*buselaphus*	G	1.89	5.23	1
Damaliscus	*lunatus*	G	2.60	5.10	1
Budorcas	*taxicolor*	M	0.71	3.42	1
Ovis	*canadensis*	M	0.72	4.11	1
Capra	*ibex*	M	0.69	4.71	1
Capricornis	*sumatraensis*	M	0.64	3.39	2
Ovibos	*moschatus*	M	0.66	3.69	1
Kobus	*ellipsiprymnus*	G	1.07	3.47	1
Kobus	*leche*	G	1.00	3.63	1
Kobus	*kob*	G	1.00	3.72	1
Redunca	*arundinum*	G	1.00	3.59	2
Redunca	*fulvorufula*	M	1.17	3.79	1
Aepyceros	*melampus*	M	0.98	4.89	1
Ourebia	*ourebi*	M	0.78	3.80	1
Raphicerus	*campestris*	M	1.20	3.44	1
Raphicerus	*melanotis*	M	1.00	2.64	2
Oreotragus	*oreotragus*	M	1.00	3.82	1
Antidorcas	*marsupialis*	M	0.37	4.89	1
Gazella	*granti*	M	0.65	3.45	1
Litocranius	*walleri*	B	0.87	1.32	1
Ammodorcas	*clarkei*	B	0.71	2.23	1
Saiga	*tatarica*	M	1.60	5.29	1
Capreolus	*capreolus*	B	0.55	1.49	3
Alces	*alces*	B	0.98	1.34	3
Rangifer	*tarandus*		1.96	1.52	2
Ozotoceros	*bezoarticus*		0.84	2.12	1
Mazama	*americana*		0.93	1.30	3
Blastocerus	*dichotomus*		0.73	1.49	1
Odocoileus	*hemionus*	B	0.49	1.59	2
Odocoileus	*virginianus*	B	0.60	1.23	2
Axis	*axis*	M	1.45	2.81	1
Axis	*porcinus*	M	1.17	2.53	2
Cervus	*elaphus canadens*	M	0.52	1.96	3
Cervus	*elaphus*		0.83	2.11	2
Cervus	*duvaucelii*	M	1.80	2.85	2
Cervus	*unicolor*	M	0.98	2.20	2
Antilocapra	*americana*	B	0.37	4.61	1
Giraffa	*camelopardalis*	B	0.41	1.20	1
Okapia	*johnstoni*	B	0.11	1.18	3
Hyemoschus	*aquaticus*	B	0.83	1.30	3
Moschiola	*meminna*		0.67	1.72	3
Tragulus	*javanicus*		0.43	1.47	3
Tragulus	*napu*		0.94	1.67	3
Camelus	*dromedarius*	M	0.70	2.52	1
Lama	*guanicoe*		0.66	3.46	1
Vicugna	*vicugna*	M	0.91	3.65	1

Tab. 1 - Date used for the construction of bivariate plot: dietary classification (DC); mesowear score (MS); hypsodonty index (HI); habitat categories (Hab), 1=open, 2=intermediate, 3=closed. (data from Fortelius & Solounias (2000), Kaiser et al., 2009, Kaiser et al. (2013) and references therein).
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mesowear patter similar to that of *C.* ex gr. *C. ropalophorus* (*Duboisia santeng, Metacervoceros rhenanus* and *Croizetoceros ramosus)* and because inhabited on a Mediterranean island environments similar to those of the Cretan deer (*Praemegaceros cazioti)*. Two Pleistocene insular species, *Praemegaceros cazioti* from Dragonara Cave (Sardinia) and *Duboisia santeng* from Java, and two continental Villafranchian cervids *Metacervoceros rhenanus* and *Croizetoceros ramosus* from Saint-Vallier (Drôme, France).

The dwarf megacerine *Preamegaceros cazioti* from Dragonara Cave (Sardinia) was a mixed feeder inhabiting territories characterized by hard and bumpy substrate (Caloi & Palombo, 1991; Mujica, 2014) and a vegetation cover comparable to the Mediterranean scrub (Palombo, 2005). The dwarf bovid *Duboisia santeng* from Java, was a forest dweller, mostly feeding on leaves and only occasionally on harder vegetation (Rozzi et al., 2013). The *Metacervoceros rhenanus* and *Croizetoceros ramosus* Villafranchian deer from Saint-

BROWSER			MIXED FEEDER		
AA	*Alces*	*alces*	**Ap**	*Axis*	*porcinus*
AM	*Antilocapra*	*americana*	**Ax**	*Axis*	*axis*
TE	*Tragelaphus*	*euryceros*	**Bt**	*Budorcas*	*taxicolor*
EI	*Ammodorcas*	*clarkei*	**Ca**	*Capricornis*	*sumatraensis*
GC	*Giraffa*	*camelopardalis*	**Cc**	*Cervus*	*canadensis*
LW	*Litocranius*	*walleri*	**Cd**	*Cervus*	*duvauceli*
NB	*Neotragus*	*batesi*	**Ci**	*Capra*	*ibex*
OH	*Odocoileus*	*hemionus*	**Cl**	*Camelus*	*dromedarius*
OJ	*Okapia*	*johnstoni*	**Cu**	*Cervus*	*unicolor*
OL	*Capreolus*	*capreolus*	**Gg**	*Gazella*	*granti*
OV	*Odocoileus*	*virginianus*	**Gd**	*Gazella*	*dorcas*
SG	*Sylvicapra*	*grimmia*	**Gt**	*Gazella*	*thomsoni*
TC	*Tragelaphus*	*scriptus*	**Gr**	*Gazella*	*rufifrons*
GRAZER			**Gs**	*Gazella*	*soemmerringi*
ab	*Alcelaphus*	*buselaphus*	**Lg**	*Lama*	*glama*
al	*Alcelaphus*	*lichtensteinii*	**Lv**	*Lama*	*vicugna*
ct	*Connochaetes*	*taurinus*	**Ma**	*Antidorcas*	*marsupialis*
he	*Hippotragus*	*equinus*	**Me**	*Aepyceros*	*melampus*
hn	*Hippotragus*	*niger*	**Oc**	*Ovis*	*canadensis*
ke	*Kobus*	*ellipsiprymnus*	**Om**	*Ovibos*	*moschatus*
kk	*Kobus*	*kob*	**Oo**	*Ourebia*	*ourebi*
kl	*Kobus*	*leche*	**Rf**	*Redunca*	*fulvorufula*
ra	*Redunca*	*arundinum*	**Ta**	*Tragelaphus*	*angasi*
rr	*Redunca*	*redunca*	**Ti**	*Tragelaphus*	*imberbis*
sc	*Syncerus*	*cafer*	**To**	*Taurotragus*	*oryx*
FOSSILS			**Tq**	*Tetracerus*	*quadricornis*
pC	*Praemegaceros*	*cazioti*	**Tr**	*Boselaphus*	*tragocamelus*
dS	*Duboisia*	*santeng*	**Tt**	*Tragelaphus*	*strepsiceros*
mR	*Metacervoceros*	*rhenanus*			
crR	*Croizetoceros*	*ramosus*			

Tab. 2 - The extant and fossils species were compared in this study by cluster analysis with *Candiacervus* ex gr. *C. ropalophorus* from Bate Cave.

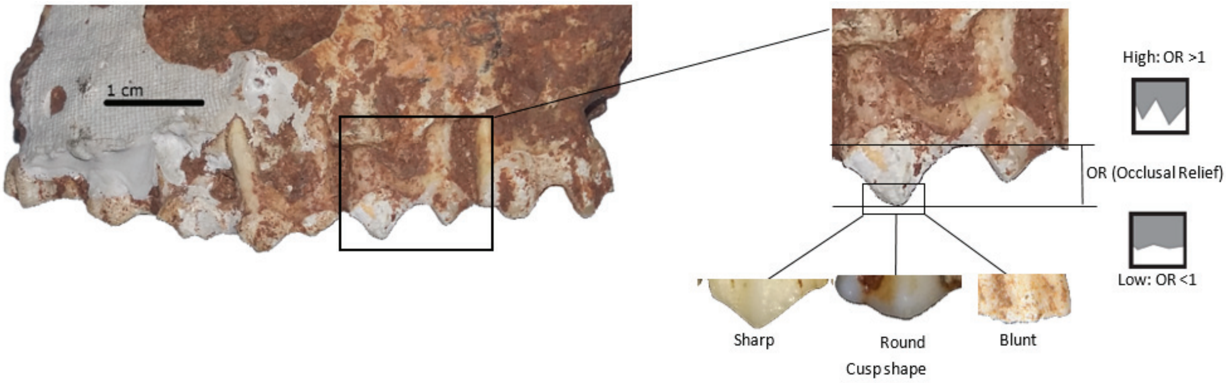

Fig. 2 - *Candiacervus* ex gr. *C. ropalophorus* from Bate Cave (Crete) (Bate 6), fragment of the left maxillary with P^2 - M^3 (on the left). The mesowear variables as in Fortelius and Solounias (2000) (on the right).

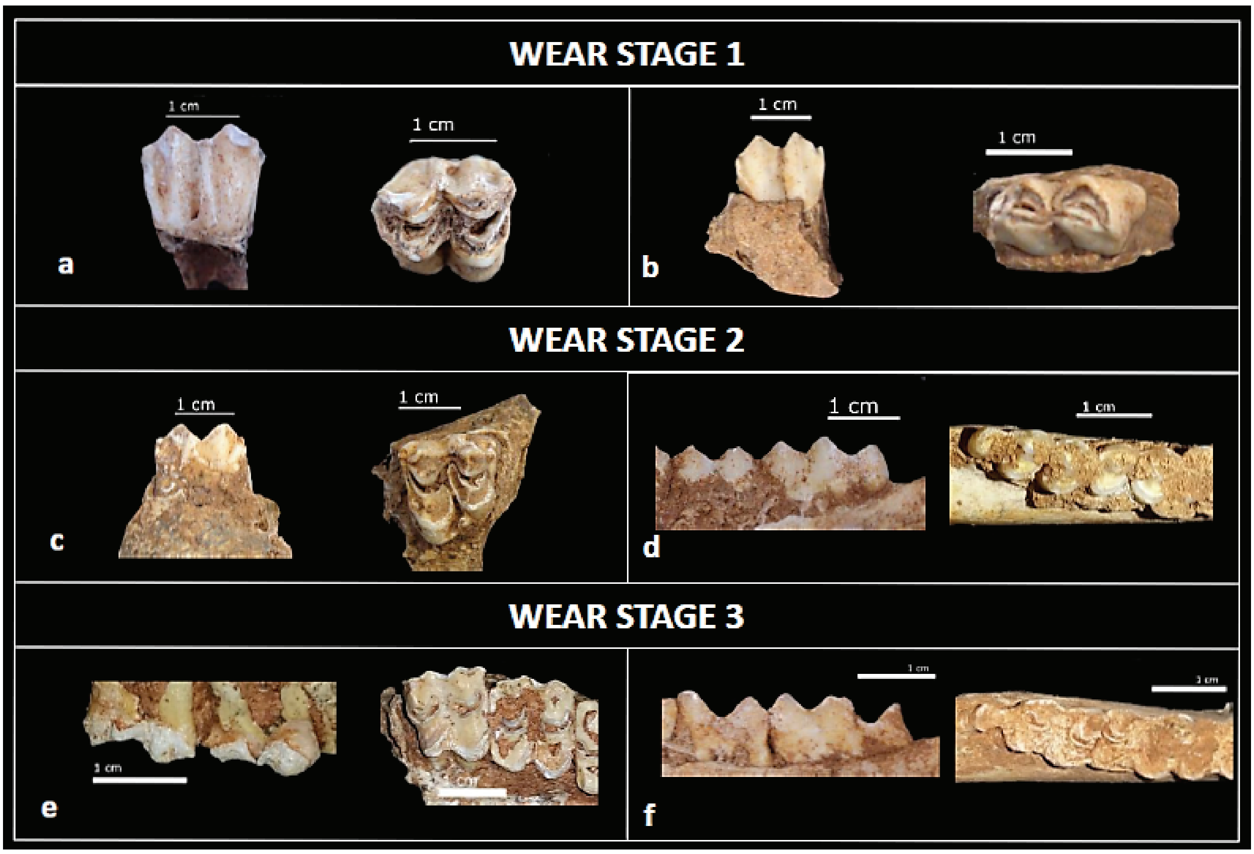

Fig. 3 - Upper and lower molars of *Candiacervus* ex gr. *Candiacervus ropalophorus* from Bate Cave (Crete) grouped according to their wear stages: Wear stage 1: a) third upper molar (labial and occlusal views); b) second lower molar (lingual and occlusal views); Wear stage 2: c) third upper molar (labial and occlusal views); d) second and third lower molar (lingual and occlusal views); Wear stage 3: e) second and third upper molar (labial and occlusal views); f) second and third lower molar (lingual and occlusal views).

Vallier (Drôme, France) were seasonal mixed feeder with a mainly browsing feeding behaviour (Valli & Palombo, 2008).

Hierarchical cluster analysis was performed by means of Past 3.13 software (Hammer et al., 2001) with Euclidean distances and complete linkage, using as variables the percentage of OR and shape cusp resulting from mesowear analysis.

Three clusters analyses have been performed on three samples. In the first, cluster-a, M^2 and the two-tooth model approach were used irrespectively of the wear stage of *C.* ex gr. *C. ropalophorus* teeth. In the second, cluster-b, the last upper and lower molars are individually examined taking into account their wear stage. In the third, cluster-c, the two-tooth model was used, taking into account wear stage of the teeth.

C. ex gr. *C. ropalophorus*	Hypsodonty Index			
	M_3 (Janis, 1988)		M^2 (Valli & Palombo 2008)	
	%	HI	%	HI
Wear Stage 1	23.33	1.23	25.00	0.88
Wear Stage 2	50.00	0.77	37.50	0.57
Wear Stage 3	26.67	0.51	37.50	0.36

Tab. 3 - Hypsodonty Index in the last lower (M_3) and second upper molars (M^2) of *Candiacervus* ex gr. *C. ropalophorus* from Bate Cave (Crete), grouped according to their wear stage.

C. ex gr. *C. ropalophorus*		Occlusal Relief		Cusps Shape		
	n	L%	H%	Sharp %	Round %	Blunt %
All molars	102	13.7	86.3	49.0	48.0	2.9
Wear Stage 1	28	0.00	100.00	82.14	17.86	0.00
Wear Stage 2	42	16.67	83.33	45.24	52.38	2.38
Wear Stage 3	32	21.88	78.13	25.00	68.75	6.25

Tab. 4 - Summary of the percentage of mesowear variables in the molars of *Candiacervus* ex gr. *C. ropalophorus* from Bate Cave (Crete), overall and grouped according to their wear stage.

3. RESULTS

3.1. Wear Stage

In the first wear stage teeth show thin streaks of dentin. The cusps, paracone and metacone, are well defined and the median groove shows a marked "V" shape (Fig. 3.a, 3.b).

At the second wear stage, in the masticatory table the dentine area is wider and shows rhomboidal geometry. The infundibula are evident though reduced with respect to the previous stage, and still connected in the upper molars. The median groove is evident, but the outline is "U-shape". The cusps are still well defined (Fig. 3.c, 3.d). In molars with an advanced wear degree, infundibula are greatly reduced, the dentine is exposed over the whole occlusal surface and the enamel band is thinner than that of previous wear stages. The bottom of the median groove can reach the neck, or even the roots. The cusps are still identifiable, the profile is angled or undulate, though height and shape of cusps show a quite significant variation (Fig. 3.e, 3.f).

3.2. Hypsodonty

The average HI of *C.* ex gr. *C. ropalophorus* M^2 and M_3 shows values roughly consistent with each other, though HI values of M_3 are generally higher than those obtained for M^2. The lower third molar is, indeed, the last tooth to erupt and in extant deer the eruption is completed about 6-12 months (roe deer and red deer respectively) later than that of M^2 (De Marinis & Toso, 2015).

The average HI value in teeth at the first wear stage is < 1.5 confirming that *C.* ex gr. *C. ropalophorus* from Bate Cave has a brachyodont dentition (Tab. 3). As expected HI decreases as the wear augments. As expected, the HI reduction is proportional to the degree of wear. Furthermore, the differences in HI between teeth at the first and the second stage of wear (HI) is slightly greater in M_3 than in M^2, while the differences are almost the same in M_3 and M^2 at the second and third stages of wear.

3.3. Mesowear patterns and dietary behaviour

Results obtained by the mesowear analysis on M^2, M^3, M_2 and M_3 of *C.* ex gr. *C. ropalophorus* from Bate Cave indicate that cusps have generally high (86%) and sharp/rounded (49%/48%) profiles (Tab. 4).

The sharp shape prevails in the second upper molar, while, rounded shapes are more frequent in the second lower molars (Fig. 4).

In teeth at first wear stage, cusps are in upper molars only sharp, while in the lower molars rounded cusps reach the 30%. As the degree of wear augments the shape of cusps changes from sharp towards less-pointed, the percentage of rounded cusps increases and some blunt cusps may be occasionally present. It is worth noting, however, that cusps are still evident even in the worn teeth. Moreover, with the increasing of the wear degree, the percentage of the high cusps slightly decreases, but they are still the most abundant (Fig. 5, Tab. 5).

The HI and MS values of the Cretan small deer are very low.

As regards to the clues about dietary behaviour (Fig. 6) and habitat (Fig. 7) obtained by plotting HI *versus* MS, the *C.* ex gr. *C. ropalophorus* sample fall in the eco-space of browsers and species prevalently inhabiting close environments.

The cluster analysis provides a quite good resolution in splitting extant artiodactyl species according to their dietary adaptation (Figg. 8a, b, c). Three main groups are generally detectable, the first includes a high percentage of browsers, in the second includes mixed feeders and few browsers and grazers, in the third grazers dominate.

In the cluster-a (Fig. 8a), *C.* ex gr *C. ropalophorus* (cRB)'s M^2 falls in the mixed feeder spectrum (B.2) together with *Gazella granti* (Gg), which is a mixed feeder

C. ex gr. *C. ropalophorus*	n	L%	H%	Sharp %	Round %	Blunt %
WEAR STAGE 1						
M_2	8	0.00	100.00	62.50	37.50	0.00
M_3	7	0.00	100.00	71.43	28.57	0.00
M^2	6	0.00	100.00	100.00	0.00	0.00
M^3	7	0.00	100.00	100.00	0.00	0.00
WEAR STAGE 2						
M_2	7	0.00	100.00	28.57	71.43	0.00
M_3	16	12.50	87.50	56.25	43.75	0.00
M^2	9	33.33	66.67	55.56	44.44	0.00
M^3	10	20.00	80.00	30.00	60.00	10.00
WEAR STAGE 3						
M_2	10	20.00	80.00	10.00	90.00	0.00
M_3	9	22.22	77.78	33.33	55.56	11.11
M^2	9	33.33	66.67	33.33	55.56	11.11
M^3	4	0.00	100.00	25.00	75.00	0.00

Tab. 5 - Percentage of mesowear variables in second and third upper and lower molars of *Candiacervus* ex gr. *C. ropalophorus* from Bate Cave (Crete), grouped according to their wear stage.

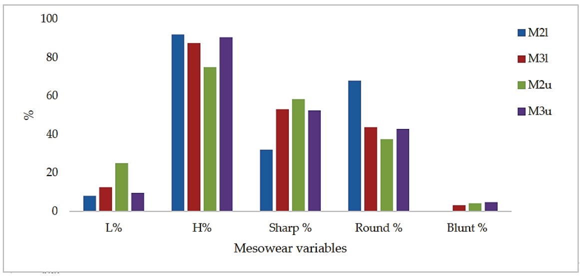

Fig. 4 - Comparison among the percentage of mesowear variables in second (M2u) and third (M3u) upper and lower (M2l-M3l) molars of *Candiacervus* ex gr. *C. ropalophorus* from Bate Cave (Crete).

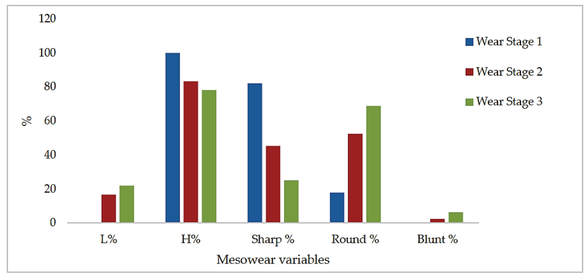

Fig. 5 - Comparison among the percentage of mesowear variables in upper and lower molars of *Candiacervus* ex gr. *C. ropalophorus* from Bate Cave (Crete) grouped according to their wear stage.

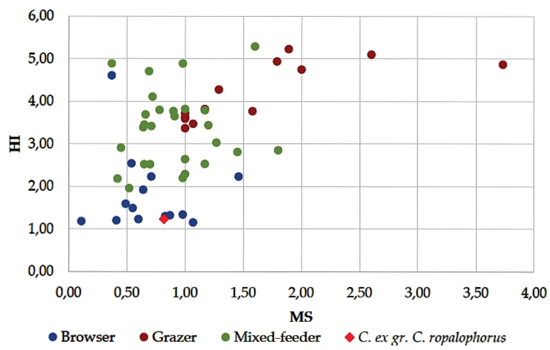

Fig. 6 - Bivariate plot of Mesowear Score (MS) and Hypsodonty Index (HI) of extant artiodactyls and *Candiacervus* ex gr. *C. ropalophorus* from Bate Cave (Crete). Data of extant species from Fortelius & Solounias (2000), Kaiser et al. (2009) and Kaiser et al. (2013) (Tab.3).

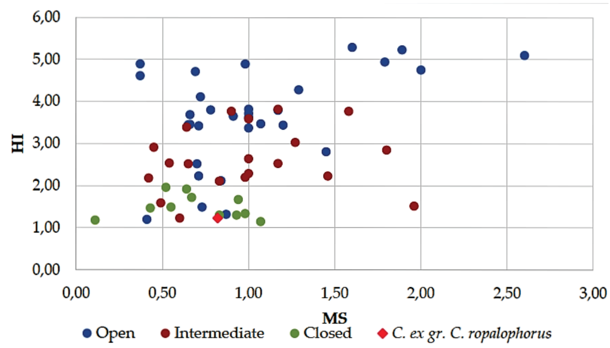

Fig. 7 - Bivariate plot of Mesowear Score (MS) and Hypsodonty Index (HI) with habitat as cofactor of extant artiodactyls and *Candiacervus* ex gr. *C. ropalophorus* from Bate Cave (Crete). Data of extant species from Fortelius & Solounias (2000), Mendoza & Palmqvist (2008), Kaiser et al. (2009) and Kaiser et al. (2013) (Tab.3).

but having a predominant browser behaviour (B.2.2.1.2). When the average value obtained from M^2 and M^3 analysis is considered (two-upper-tooth model), Cretan deer still falls in mixed feeder field (B.2.2.1.2), close to M^2 average value, together with *Ovibos moschatus* (Om) which is an opportunistic specie. When the average value obtained from M_2 and M_3 analysis is considered (two-lower-tooth model), *C.* ex gr *C. ropalophorus* falls between the mixed feeders (B.2.2.1.1) but close to *Antidorcas marsupialis* (Ma), which is an intermediate seasonal browser.

In the cluster-b (Fig. 8b), where the wear stages of *C.* ex gr. *C. ropalophorus* (cRB) have been taken into account, two main groups are identifiable. A small group (A) including browsers, and a large one (B) gathering both mixed feeders (B.1) and grazers (B.2), which, however form two separate sister groups. The *C.* ex gr. *C. ropalophorus* M^2, M^3 (A.2.2) and M_3 (A.1.2), at the first wear stage (W1) fall among browsers (A). In particular, M^2 and M^3 are linked with *Alces alces* (AA), and M_3 with *Odocoileus hemionus* (OH), both typical browsers. Conversely, M_2 teeth fall among the mixed feeders (B.1.2.1.1) possibly because, although the cusps with a sharp shape predominate, the percentage of rounded cusps is not negligible (37.5%). The percentage of rounded cusps considerably increases in M_2 at the third stage of wear, which fall in the grazer range (B.2.1.1.2) although the percentage of high cusps is unusually high (80%) for grazers. Most of the other *C.* ex gr. *C. ropalophorus* molars, showing various degrees of wear, fall in the large group of mixed feeders together with species (e.g. *Gazella granti* (Gg), *G. thomsonii* (Gt), *G. dorcas* (Gd), *Ourebia ourebi* (Oo), *Tragelaphus strepsiceros* (Tt), *T. imberbis* (Ti), but also *Ammodorcas clarkei* (El)) that mainly eat leaves, fruit, or fresh grass, according to the season and the availability of vegetal resources.

In the cluster-c (Fig. 8c), where only the two-tooth model with lower and upper molars of *C.* ex gr. *C. ropalophorus* (cRB) from the first to third stage of wear have been included, the distribution of extant species belonging to the three main trophic groups is similar to that of cluster-b. As regards to Cretan deer, molars at the first stage of wear fall in browser group (A), with *Alces alces* (AA) and *Odocoileus hemionus* (OH), while those at the second and third stage mainly fall among the mixed feeders tree. The sister group of the upper molars at the second and third wear stage and the lower molars at the third wear stage (B.1.1) includes *Gazella soemmerringi* (Gs), which feeds on bush leaves, grasses and herbs and *G. dorcas* (Gd), which eats leaves, pods, fruits and bulbs. The lower molars at the second wear stage has as sister group (B.1.2.2.1) *Ovis canadensis* (Oc), which consumes leaves, grasses, sedges and forbs, but it usually takes some browse during winter, and *Gazella granti* (Gg), its diet consist mainly of leaves and stems.

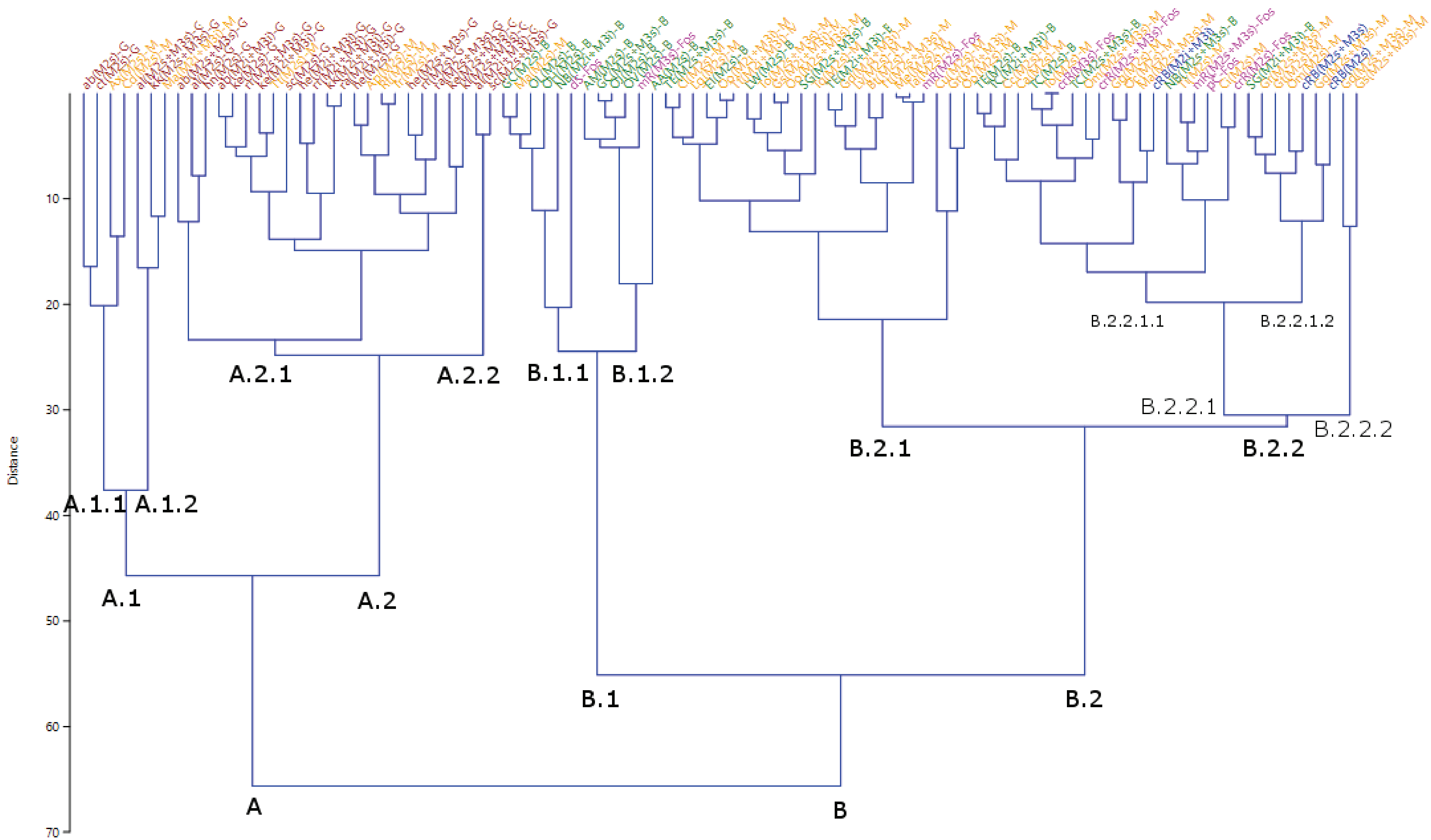

Fig. 8.a - Cluster-a: Hierarchical cluster diagram comparing the one-tooth model using upper second molars only and the upper and lower two-tooth model using second and third molars of *Candiacervus* ex gr. *C. ropalophorus* from Bate Cave, based on a set extant and fossil species (data from Fortelius & Solounias, 2000; Franz-Odendaal & Kaiser, 2003; Louys et al., 2011; Palombo, 2005; Valli & Palombo, 2008; Rozzi et al., 2013). The mesowear variables: percent high occlusal relief, percent shape cusps (sharp, rounded and blunt). Browser=UPPER CASE and green; Grazer=lower case and brown; Mixed feeder=Mixed case and yellow; Fossil species=inverse mixed Case and pink. cRB (blue)= *C.* ex gr *C. ropalophorus* from Bate Cave. “Distance” = Euclidean distance.

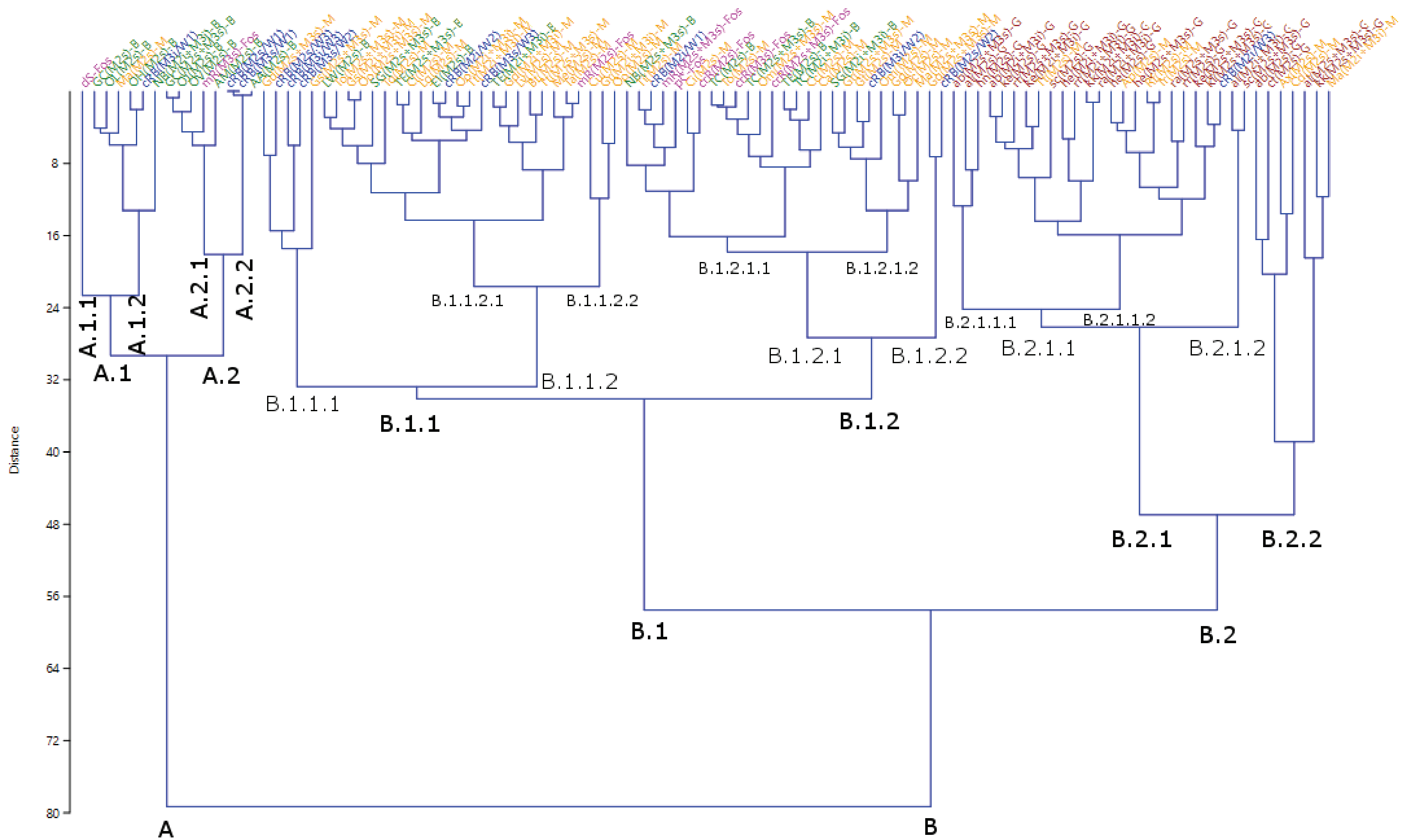

Fig. 8.b - Cluster-b: Hierarchical cluster diagram comparing the one-tooth model using upper and lower second molars and upper and lower third molars grouped according to their wear stage of *Candiacervus* ex gr. *C. ropalophorus* from Bate Cave, based on a set extant and fossil species (data from Fortelius & Solounias, 2000; Franz-Odendaal & Kaiser, 2003; Louys et al., 2011; Palombo, 2005; Valli & Palombo, 2008; Rozzi et al., 2013). The mesowear variables: percent high occlusal relief, percent shape cusps (sharp, rounded and blunt). Browser=UPPER CASE and green; Grazer=lower case and brown; Mixed feeder=Mixed case and yellow; Fossil species=inverse mixed Case and pink. cRB (blue)= *C.* ex gr *C. ropalophorus* from Bate Cave. “Distance” = Euclidean distance.

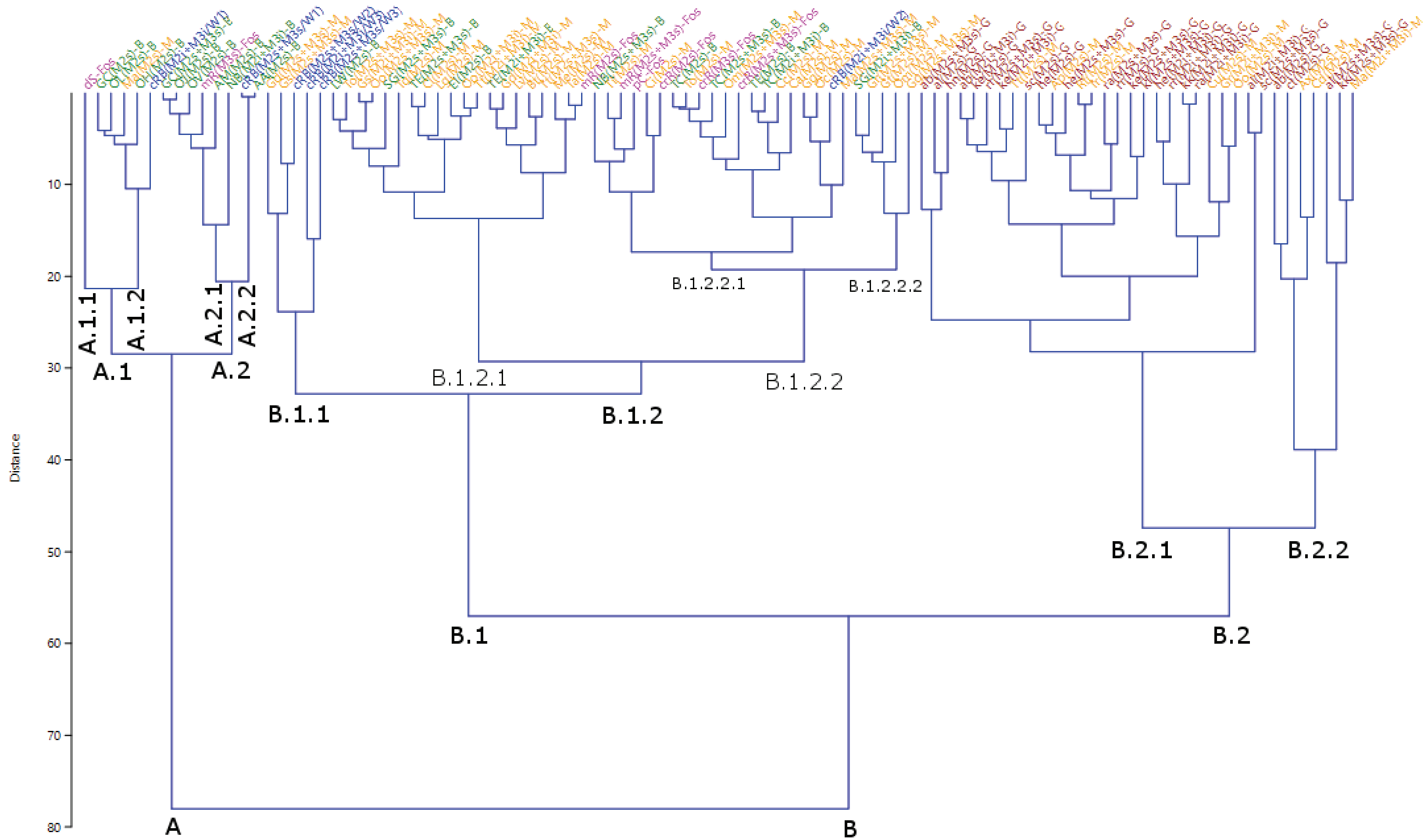

Fig. 8.c - Cluster-c: Hierarchical cluster diagram comparing the upper and lower two-tooth model using second and third molars according to their wear stage of *Candiacervus* ex gr. *C. ropalophorus* from Bate Cave, based on a set extant and fossil species (data from Fortelius & Solounias, 2000; Franz-Odendaal & Kaiser, 2003; Louys et al., 2011; Palombo, 2005; Valli & Palombo, 2008; Rozzi et al., 2013). The mesowear variables: percent high occlusal relief, percent shape cusps (sharp, rounded and blunt). Browser=UPPER CASE and green; Grazer=lower case and brown; Mixed feeder=Mixed case and yellow; Fossil species=inverse mixed Case and pink. cRB (blue)= *C.* ex gr *C. ropalophorus* from Bate Cave. “Distance” = Euclidean distance.

4. DISCUSSION AND CONCLUSION

Results obtained by the mesowear analysis of molars of *C.* ex gr. *C. ropalophorus* from Bate Cave suggest a chewing activity mainly characterised by a friction action associated with a milder abrasive component. The latter becomes more relevant as the degree of wear increases, although, in the cusps are still well delineated (Fig. 3.e, 3.f). Therefore, it is rational to suppose that the chewing process of *C.* ex gr. *C. ropalophorus* may have taken place in two phases. In the first phase a sharing component prevails, while in the second the sharing is progressively lost and the grinding prevails (Janis, 1979; Valli et al., 2012). The abrasive component equals or prevails over the frictional one if the wear is advanced. However, even at the third wear stage sharp cusps are still present (25%), suggesting that *C.* ex gr *C. ropalophorus* likely had an intermediate-browser feeding behaviour.

The variation of HI at different wear stage is not particularly high being the value of HI at the last stage 58% less than at the first. It is worth noting that the typology of food may greatly affect brachyodont teeth, resulting in premature loss of its functionality (Anders et al., 2011). In deer, the extent of the wear stages is not characteristic of a species, conversely intraspecific variation has been observed according to the environmental characteristic and the resources availability. Accordingly, the variation in HI shown by *C.* ex gr. *C. ropalophorus* molars may be regarded as coherent with a diet consisting in no-abrasive food.

This conclusion is supported by cluster analysis. The results obtained indicate that the small deer from Bate Cave had an intermediate-browser feeding strategy (mixed-feeder *versus* browser) and the diet possibly included more leaves and buds than hard grasses. The inferred feeding behaviour is supported by the cranial and mandibular features related to masticatory processes (see Caloi & Palombo, 1996 for a discussion).

In addition, it is interesting to note how mesowear pattern slightly differs in upper and lower molars having similar wear degree (Fig.8b). The cusps of second lower molar, indeed, are generally less sharp then those of last molars (Tab. 5), as indicate by the position of M_2 (W1-W2-W3), which mainly fall among mixed-feeder, at the first and second stage of wear, and among grazers at the third stage. This result confirms for M_2 what observed by Kaiser & Fortelius (2003) and Franz-Odendaal & Kaiser (2003) in some herbivores. Differences in the mesowear pattern shown by upper and lower cheek teeth may depend on the fact that during the masticatory process food frequently is more in contact with the lower teeth than with the upper ones. The degree of functional anisodonty and differences in mesowear pattern seem to be more pronounced in mixed feeders then in specialized feeders, though such differences are less evident when a two-tooth model is applied (Fig. 8c).

All in all, the obtained results indicate that *C.* ex gr. *C. ropalophorus* from Bate Cave had an opportunistic eating habit with a prevalent browser behaviour. These small deer on one hand possibly had a remarkable ability to select the food and change their diet according to the nature and number of competitors, the environmental characteristics and their seasonal changes, on the other they likely did not inhabited environments with a low primary productivity.

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