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Feeding ecology of Late Pleistocene *Muntiacus muntjak* in the Padang Highlands (Sumatra)

Écologie alimentaire de Muntiacus muntjak *au Pléistocène Terminal dans les Highlands de Padang (Sumatra)*

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A B S T R A C T

The Dubois Collectie comprises around 1000 isolated fossil teeth of *Muntiacus muntjak* from the Padang Highlands in Sumatra. The majority were retrieved from one of the three fossil cave sites Lida Ajer, Sibrambang or Jambu. Lida Ajer is the only cave, for which exact location, geology as well as the age of the fossiliferous deposits are known. Using the mesowear method, we searched for differences in the dietary signal of *Muntiacus muntjak* and thus in the paleoenvironments of the three caves. *Muntiacus muntjak* from either one of the caves does not differ significantly in the composition of its diet, showing a mixed feeder signal. The samples of Lida Ajer and Sibrambang illustrate an increase of the mixed feeding component, which could be the result of higher seasonality.

Mots clés :
Pléistocène terminal
Muntiacus muntjak
Méthode de denture Mesowear
Paléoalimentation
Paléoécologie
Sumatra

R É S U M É

La collection Dubois comporte environ 1000 dents fossiles isolées de *Muntiacus muntjak*, en provenance des Highlands de Padang à Sumatra. La majorité ont été récoltées dans trois grottes, Lida Ajer, Sibrambang et Jambu. Lida Ajer est la seule grotte dont on connaisse la localisation exacte, la géologie ainsi que l'âge des dépôts fossilifères. En utilisant la méthode de denture « Mesowear », on tente de trouver des différences dans le signal alimentaire de *Muntiacus muntjak*, et ainsi dans les paléoenvironnements des trois grottes. *Muntiacus muntjak* ne se distingue de façon significative d'aucun individu issu des autres grottes dans la composition de sa nourriture, se révélant ainsi un mangeur de nourriture

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mixte. Les échantillons de Lida Ajer et Sibrambang illustrent l'augmentation de composants d'alimentation mixte, qui pourrait résulter d'un plus net caractère saisonnier de la nourriture.

1. Introduction

The environment of Late Pleistocene Sumatra was affected by two mayor events. The youngest Toba eruption (YTE) happened, as well as the transition from Marine Isotope Stage (MIS) 5 to 4. There is ongoing debate when exactly the YTE happened, but estimates range between 75 and 72 ka (Mark et al., 2012; Storey et al., 2012; van der Kaars et al., 2012; Williams, 2012). The transition from MIS 5 to 4 is set to 71 ka (Lisiecki and Raymo, 2005).

Both events are expected to have effects on the fauna and thus should be recognizable in the fossil record. The Dubois Collectie at the Naturalis Biodiversity Center in Leiden (Netherlands) includes over 10,000 specimens collected by Eugène Dubois from the Late Pleistocene of Sumatra. Most of the material from Sumatra stems from the three caves Lida Ajer, Sibrambang, and Jambu (de Vos, 1983; Vu et al., 1996). All three caves are located in the Padang Highlands and cover different periods in the time frame from 80 to 60 ka (Bacon et al., 2015; Westaway et al., 2017).

The fossil assemblages of all three caves contain a large number of molars of *Muntiacus muntjak*, commonly known as the barking deer. This species is still extant today and well observed. It is a forest dweller (Timmins et al., 2016), with a diet that includes a variety of plants and plant parts (e.g., Hoogerwerf, 1970; Kitchener et al., 1990; Oka, 1998). Thus, it can be classified as a mixed feeder, while data from the literature suggests that the diet of the barking deer depends on geographic area and on season (e.g., Barrette, 1977; Hoogerwerf, 1970; Ilyas and Khan, 2003; Oka, 1998; for a detailed discussion on the term mixed feeder, see section 5.3).

Having a large fossil sample of this species from a time frame of big environmental changes creates an excellent opportunity to provide the mesowear method with new insights. This method was developed by Fortelius and Solounias (2000) to assess the abrasiveness of consumed items as a combination of attrition and abrasion. Hence, the mechanical properties of consumed plants or plant parts can be identified, which can be used to reconstruct vegetation to a certain extent (Fortelius and Solounias, 2000). Vegetation, which depends on different abiotic factors, especially climate, is a good indicator for the characteristics of an ecosystem. The shift in climate along with the transition from MIS 5 to 4 should be accompanied by a corresponding shift in vegetation. In mixed feeders, shifts to a rather attrition- or abrasion-dominated diet are more likely to occur than in specialized feeders. Such changes in consumed plants and/or their properties should be accompanied by a corresponding shift in the mesowear signal.

However, there is ongoing debate, which tooth positions should be used for the mesowear method (e.g., Louys et al., 2011). Other questions address the tooth age and the degree of wear sufficient to mask the mesowear signal. The sample of fossil teeth of the barking deer is large enough to study these questions with statistical methods. Thus, it is needed to identify how much wear is appropriate for a tooth to be usable for mesowear analysis and which tooth positions can be used.

In the following, the selected teeth will be used for a mesowear analysis of the barking deer molars for each cave separately. The result will be compared with those from other environmental proxies for coherency.

2. Material

Eugène Dubois excavated in the Padang Highlands in Central Sumatra from 1889 to 1890, where he collected over 10,000 specimens of different mammalian taxa. For the most part his findings stem from the three caves Lida Ajer, Sibrambang and Jambu, which show great diversity (Bacon et al., 2015; de Vos, 1983; Vu et al., 1996). Until recently the exact locations of the three caves were unknown. Therefore, no further information about the geology was available, except the fact that they are located in limestone (Bacon et al., 2015; Vu et al., 1996). Thus, there were only age estimates for the three sites based on biostratigraphic comparisons and amino-acid racemization on bone (Lida Ajer: > 81 ka (de Vos, 1983); Sibrambang: 80–60 ka (Drawhorn, 1994); Jambu: > 70 ka (Skelton, 1985; summary Bacon et al., 2015). Westaway et al. (2017) recently managed to relocate Lida Ajer. Applying luminescence and uranium-series techniques on bone-bearing sediments and speleothems as well as coupled uranium-series and electron-spin-resonance dating on mammalian teeth, the fossil assemblage from Lida Ajer was dated back to an age of 68 ± 5 ka. The fossil- bearing layers are cemented breccias with large allogenic angular clasts buried in clay-rich matrix, overlain and underlain by flowstones (Louys et al., 2017; Westaway et al., 2017).

The collection holds around 1000 isolated fossilized molars of the barking deer. The teeth show chisel marks on the roots, which are typical of porcupine gnawing. In the case of the barking deer, porcupines presumably acted as accumulating agents, actively collecting bones for gnawing on them (Bacon et al., 2015). This taphonomic hypothesis is challenged by Louys et al. (2017), who note that the lack of bone and the abundance of tooth material in the fossil assemblage of Lida Ajer contrasts with observations in recent porcupine dens from South Africa (s.a. O'Regan et al., 2011). Whether the proportion of bones to teeth is caused by a low number of available bones or whether the assemblage has been compiled by further taphonomic processes has to be investigated in future. Because Louys et al. (2017) found bone shafts in a modern porcupine den on Sumatra, they favor the latter hypothesis. Barking deer are small cervids, which were and still are widely spread throughout insular Southeast Asia (Timmins et al., 2016; Tougard, 2001).

Barking deer were chosen as a proxy for environmental change because of two main advantages: the sample is statistically valuable because of its size, they are still extant and thus its diet is well-known.

The sample contains a total number of 972 usable molars with 1610 assessable cusps. The origin of the molars of the barking deer is not in all cases precisely documented. In some cases, the fossil site could only be tracked down to two caves. In other cases, it is known that they are from a cave in the Padang Highlands, but not if they are from one of the three specific caves at all. Which teeth were used to answer the specific questions can be seen in Table 1.

3. Methods

3.1. Recording mesowear signatures

Fortelius and Solounias (2000) introduced the mesowear method to reconstruct the dietary behaviour of fossil herbivores by determining mechanical features of plant parts and their impact on tooth wear of selenodont and selenolophodont herbivores. These features can help, among other, to infer on vegetation structures and hence paleoenvironmental conditions.

Mesowear patterns are the result of a combination of attrition and abrasion, i.e. the relative contributions of tooth-on-tooth and food-on-tooth wear (Fortelius and Solounias, 2000). Attrition occurs when consumed plant parts, e.g., leaves, are soft, because they offer little resistance to teeth, while abrasion is caused by resistive parts of plants, e.g., phyhtoliths of dry grasses but also from external particles eventually consumed along with plant parts (Fortelius and Solounias, 2000; Lucas et al., 2014).

The original mesowear method by Fortelius and Solounias (2000) comprises two variables: the height of the occlusal relief and the shape of the tooth cusps. Treated as separate variables by Fortelius and Solounias (2000), other authors began to combine the variables, because they are correlated. Sharp cusps are present in teeth with high occlusal relief, while high and low occlusal reliefs can feature rounded cusps. Blunt cusps occur in occlusal reliefs with low to no height (e.g., DeMiguel et al., 2010; Kubo and Yamada, 2014; Kubo et al., 2015; Mihlbachler and Solounias, 2006; Mihlbachler et al., 2011; Rivals et al., 2007; Strani et al., 2018). In addition, the data obtained with the original method by Fortelius and Solounias (2000) has a major disadvantage. The same sample can be scored very differently by individual observers and is therefore not observer-independent. A standard that combines the two parameters, i.e. height of the occlusal relief and cusp shape, and defines stages and thus simplifies data analyses, solves these problems (Mihlbachler et al., 2011).

We transfer the classification system developed by Mihlbachler et al. (2011) to ruminants and design a specific mesowear ruler. The virtual ruminant ruler (supplementary material S1) is composed of the outlines of seven exemplary tooth cusps representing characteristic mesowear stages. Each mesowear stage is represented by a number simplifying statistical analysis, increasing the comparability with other data sets and decreasing inter-observational errors. The stages are based on combinations of the variables from the original method: high occlusal relief and sharp cusps (stage 0), high occlusal relief and rounded cusps (stage 2), low occlusal relief and rounded cups (stage 4), and low occlusal relief and blunt cusps (stage 6). Mesowear stages 1, 3, and 5 are intermediate stages improving resolution. The ruler illustrates attrition-dominated wear patterns in the lower stages and abrasion-dominated wear patterns in the higher stages. It is calibrated using the comparative extant database provided by Fortelius and Solounias (2000) to assign the specific mesowear stages to certain diet types (see supplementary material S2).

The ruminant ruler is used on photos. In total, 972 molars are photographed. They are fixated for contrast on dark underground using a small amount of silicon. It is important to take the picture at right angle showing the buccal site in the case of upper molars and the lingual site in case of lower molars (DeMiguel et al., 2008; Kaiser & Solounias, 2003) to avoid parallax. The mesowear stage of each cusp is recorded by applying the mesowear ruler for ruminants. In order to record mesowear stages, the virtual ruler is superimposed on a photo of a molar and adjusted in size to the mesiodistal length of each cusp, using graphics software. All molars with at least one intact cusp are used regardless of tooth position, wear stage, and/or fossil site. Cusps that are completely worn down or damaged cusps are scored as 'indeterminable'. When a cusp is initially scored between two mesowear stages the lower stage +0.5 is recorded.

3.2. Grouping datasets for comparative data evaluation

Before reconstructing the diet of the barking deer, molars providing an interpretable mesowear signal have to be identified. Two aspects are under discussion, namely tooth position (e.g., Fortelius and Solounias, 2000; Franz-Odendaal and Kaiser, 2003; Kaiser and Fortelius, 2003; Kaiser and Solounias, 2003; Louys et al., 2011; Mihlbachler et al., 2011; Rivals et al., 2007) and the stability of the signal throughout life (Rivals et al., 2007). We test the influence of both factors on the mesowear signal.

3.2.1. Tooth age subset (TA & TAe subset)

Tooth age in this context reflects the degree of wear a molar displays and not its individual age in years. We use a standard scale for tooth wear, distinguishing six wear stages. Wear stage 0 represents an unworn tooth, while wear stage 5 represents a tooth with exposed dentin completely worn down (Table 2). Cusps in wear stage 0 are scored, but excluded from the following analyses. The TA subset contains molars of wear stages 1–5 and all positions, even though the tooth position is indeterminable, as long

Table 1
Number of cusps sorted by fossil site, toot position and wear stage.
Tableau 1
Nombre de cuspides triées selon le site fossilifère, la position de la dent et le stade d'usure.

Fossil site	Tooth position	*n* of cusps per wear stage						Sample subset					
		0	1	2	3	4	5						
Lida Ajer	M1 sup	0	8	10	16	6	2	TA	TAe	TP	TPe	CA	IDAS
	M2 sup	2	4	14	22	12	0	TA	TAe	TP	TPe	CA	IDAS
	M3 sup	2	2	8	18	2	0	TA	TAe	TP	TPe		IDAS
	M1 inf	0	0	0	0	0	0	TA	TAe	TP	TPe	CA	IDAS
	M2 inf	0	0	0	0	0	0	TA	TAe	TP	TPe	CA	IDAS
	M3 inf	4	6	16	14	0	0	TA	TAe	TP	TPe		IDAS
	M1/2 sup	0	0	0	0	0	0	TA	TAe			CA	
	M1/2 inf	6	15	26	22	8	0	TA	TAe			CA	
Sibrambang	M1 sup	0	8	18	28	4	2	TA	TAe	TP	TPe	CA	IDAS
	M2 sup	2	8	23	46	15	12	TA	TAe	TP	TPe	CA	IDAS
	M3 sup	2	6	14	14	7	0	TA	TAe	TP	TPe		IDAS
	M1 inf	8	4	9	15	2	4	TA	TAe	TP	TPe	CA	IDAS
	M2 inf	4	6	26	13	11	0	TA	TAe	TP	TPe	CA	IDAS
	M3 inf	2	22	27	13	7	0	TA	TAe	TP	TPe		IDAS
	M1/2 sup	0	0	2	0	0	2	TA	TAe			CA	
	M1/2 inf	2	6	16	7	4	0	TA	TAe			CA	
Jambu	M1 sup	0	0	0	2	0	0	TA	TAe	TP	TPe	CA	IDAS
	M2 sup	0	10	2	4	8	10	TA	TAe	TP	TPe	CA	IDAS
	M3 sup	2	6	4	12	1	0	TA	TAe	TP	TPe		IDAS
	M1 inf	0	0	0	0	0	0	TA	TAe	TP	TPe	CA	IDAS
	M2 inf	0	0	0	0	0	0	TA	TAe	TP	TPe	CA	IDAS
	M3 inf	0	2	12	5	1	0	TA	TAe	TP	TPe		IDAS
	M1/2 sup	0	0	0	0	0	0	TA	TAe			CA	
	M1/2 inf	2	6	15	7	8	0	TA	TAe			CA	
Jambu or Sibrambang (unconfirmed)	M1 sup	0	2	0	4	4	2		TAe		TPe		
	M2 sup	0	8	15	16	9	15		TAe		TPe		
	M3 sup	0	6	20	10	2	1		TAe		TPe		
	M1 inf	0	0	0	0	0	0		TAe		TPe		
	M2 inf	0	0	0	0	0	0		TAe		TPe		
	M3 inf	0	0	0	0	0	0		TAe		TPe		
	M1/2 sup	0	0	0	0	0	0		TAe				
	M1/2 inf	0	0	0	0	0	0		TAe				
Padang Highlands	M1 sup	2	4	11	15	6	10		TAe		TPe		
	M2 sup	6	32	48	69	57	22		TAe		TPe		
	M3 sup	2	10	14	14	7	0		TAe		TPe		
	M1 inf	2	14	13	12	13	6		TAe		TPe		
	M2 inf	3	20	17	17	12	4		TAe		TPe		
	M3 inf	22	43	53	58	32	6		TAe		TPe		
	M1/2 sup	0	0	0	0	0	0		TAe				
	M1/2 inf	2	4	13	8	5	3		TAe				

Table 2
Dental wear stages.
Tableau 2
Stades d'usure définis.

Wear stage	Definition
0	Tooth erupting; enamel bands still closed
1	Enamel bands open at one side
2	Enamel bands opened over entire mesiodistal length of the cusp
3	Enamel bands fused to a single circular band; basal pillar and goat fold (if present) polished and open
4	Enamel bands widely open and dentin polished
5	Central enamel bands completely eroded; dentin exposed

as the origin can be traced back to one specific cave (TA subset in Table 1; wear stages 1–5). This is also done with molars from all locations, i.e., every scorable molar cusp while excluding cusps in wear stage 0 from the study (TAe subset in Table 1; wear stages 1–5). In order to show in which way the mesowear signal changes with increasing wear stage, the sample is further subdivided.

3.2.2. *Tooth position subset (TP and TPe subset)*

For this subset, cusps in wear stages 1–3 are selected, for which tooth position and specific founding location can be identified (TP subset in Table 1; wear stages 1–3). Additionally, we also choose teeth from all locations as long as the tooth position is determinable (TPe subset in Table 1; wear stages 1–3). In order to identify usable tooth positions, the subset is further subdivided.

3.2.3. *Comparing caves (CA subset)*

A change in climate is accompanied by a change in vegetation, which affects the diet of herbivores. To examine this faunal response in the case of the barking deer during different stages of a period of climate change, the reconstructed paleoenvironments are displayed separately. As already mentioned, chronological relationships between the caves are unclear. We therefore correlate the diet signal of the barking deer (CA subset in Table 1; wear stage 1–3) with other climate proxies, i.e. marine isotope stages and palynological data. All compared samples are checked for significance by *t*-tests on a 0.05 significance level.

4. Results

The overall mean mesowear value for the barking deer from the caves in the Padang Highlands, here derived from the TA subset ($n = 747$ cusps; wear stage 1–5; Table 1) displayed in further detail in Fig. 1, amounts to 2.4 (±1.17). This signal corresponds to a mixed feeder diet with grazing component, which is in accordance with the diet of recent representatives of the taxon in the area (Kitchener et al., 1990; Oka, 1998). The high standard deviation, however, illustrates that individual dietary regimes may vary considerably.

4.1. Link between wear stage and mesowear

With the TA subset ($n = 747$ cusps), we examined the link between wear stage and mesowear (Fig. 1). Mesowear stages generally increase by advancing the wear stage. Moreover, the variability of the mesowear signal increases, too.

t-Tests show a significant difference in the mean mesowear value when comparing cusps in wear stages 1–3 to the entire sample (wear stages 1–5) and/or the 'original sample' according to Fortelius and Solounias (2000; wear stages 1–4). Additionally, in a serial comparison of a particular wear stage with the next higher one, the samples always differ significantly, except for the comparison between wear stages 4 and 5.

The sample including all available cusps ($n = 1533$ cusps; TAe subset in Table 1) shows also a significant difference regarding the means of mesowear values, when comparing the cusps in wear stages 1–5 and 1–4. In addition, there is a significant difference between the means of mesowear values, when wear stages 4 and 5 are compared. The aforementioned increase in means of mesowear values from wear stages 3–4 is still clearly visible. We therefore decided to execute further analyses only on a reduced sample of wear stages 1–3.

4.2. Usable tooth positions

With the TP subset ($n = 497$ cusps), we examined the link between tooth position and mesowear. The results are shown in Fig. 2. The box plots of upper molars ('M1 sup', 'M2 sup', 'M3 sup') only differ in the distribution of the dot densities and the length of the whiskers. All boxplots cover the same range, except the upper and lower third molars ('M3 sup', 'M3 inf'). The interquartile ranges differ in the lower first and third molars (M2 inf, M3 inf). The means of mesowear values range from 1.6 to 2.7, with lower third molars ('M3 inf') displaying the lowest mean value, while the lower first molars ('M1 inf') display the highest. Regarding 'M2 sup', the *t*-tests reveal significant differences to 'M3 inf'.

This test was also executed with the subset including tooth cusps ($n = 1042$ cusps) from all sites (TPe). Fig. 2 shows that, in addition to TP, the mean mesowear value of 'M3 sup' differs significantly from that of 'M2 sup'. Consequentially, we decided to continue with a reduced sample including upper and lower molars, but excluding third molars.

4.3. Comparing caves

The remaining CA subset ($n = 418$ cusps) was divided by fossil sites (Fig. 3). The box plots for Lida Ajer and Sibrambang only differ in the distribution of the dot densities. The boxplot of Jambu differs from the other two by showing a shorter range and overall smaller variance. The means of mesowear values of Sibrambang and Jambu are below 2, while the one of Lida Ajer is higher than 2. The *t*-tests show no significant difference between Sibrambang and either of the other caves. There is, however, a significant difference between Lida Ajer and Jambu. The barking deer from all three sites can be classified into the category of mixed feeders. However, the diet of barking deer from Lida Ajer has a grazing component, while the diet of barking deer from Sibrambang and Jambu has a browsing component. When the CA subset is not divided by fossil sites, the overall mesowear signal of the barking deer is 2.02 (±1.39).

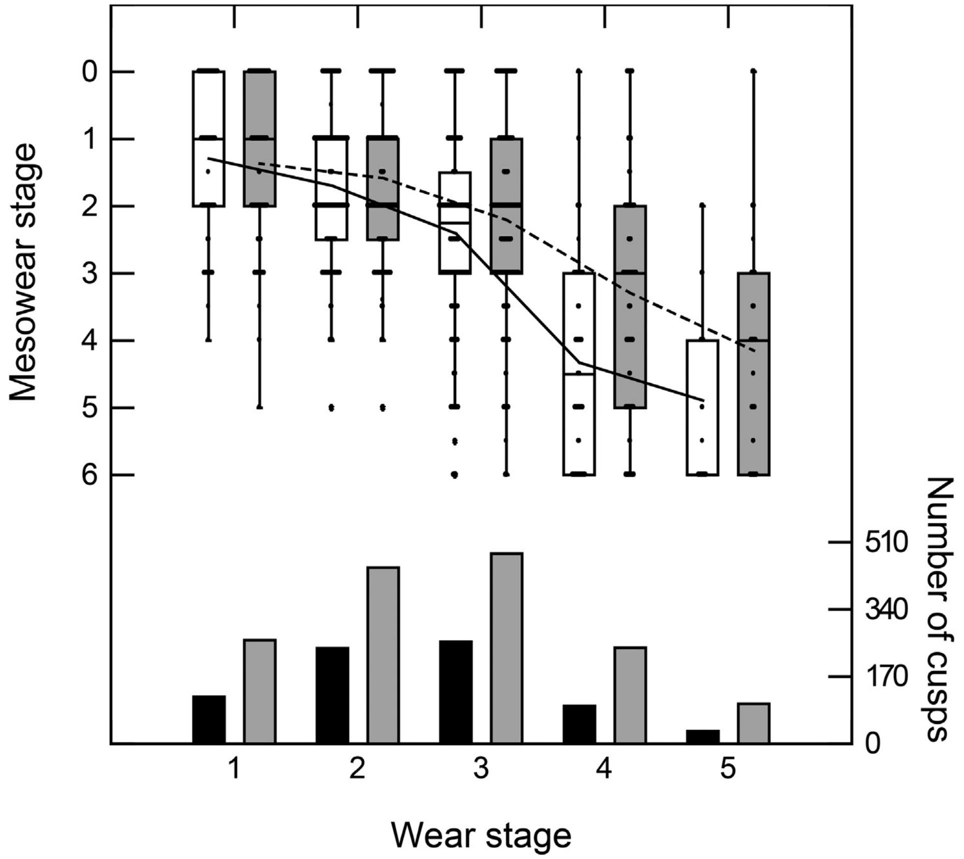
5. Discussion

The paleodiet signal derived from the mesowear study of molars of the barking deer from late Pleistocene caves in the Padang Highlands generally indicates a mixed feeding diet. The variability of the signals, however, increases with the wear stage and displays a considerable variability, even in datasets adjusted for wear stages (Fig. 1). Before we discuss the paleodietary and paleoecological results of our study, we would like to focus on two aspects that are controversially debated in the scientific literature on the mesowear method, i.e. wear stages and tooth positions providing a robust mesowear signal (e.g., Franz-Odendaal and Kaiser, 2003; Kaiser and Fortelius, 2003; Kaiser and Solounias, 2003; Louys et al., 2011).

The number of fossil teeth of barking deer in the Dubois Collectie is big enough for statistical analysis. It is important to use only teeth with a robust mesowear signal. For this, we sorted the teeth by wear stage and examined how the mesowear signal changes with increasing wear stages. The test shows that cusps in wear stages 1–3 display the most consistent mesowear signal. In the next step, the teeth in these wear stages were sorted by tooth position, to test if there are any differences between the mesowear signal of different tooth positions. 'M3 sup' and 'M3 inf' were excluded, because their mesowear signal differs significantly from that of 'M2 sup'. The remaining teeth were then used to reconstruct the properties of the plants eaten by the barking deer. The reconstructions were performed across as well as separated by fossil site.

5.1. Links between wear stages, mesowear stages and individual age

The TA subset in Fig. 1 shows that cusps in wear stages 1–3 should be used for the mesowear method, because the



Wear stages compared	1-5/1-4	1-5/1-3	1-4/1-3	1/2	2/3	3/4	4/5
p-value (TA)	n. s.	$9.26*10^{-8}$	$5.72*10^{-5}$	$1.25*10^{-3}$	$1.59*10^{-9}$	$7.57*10^{-21}$	n. s.
p-value (TAe)	0.01	$1.39*10^{-12}$	$2.97*10^{-6}$	0.01	$1.20*10^{-13}$	$1.58*10^{-15}$	$2.48*10^{-5}$

Fig. 1. Link between wear stage and mesowear. The density of dots shows distribution and the bar charts represent sample size, while the line graph (TA: solid line; TAe: dashed line) shows the arithmetic mean. For exact subset sizes see Table 1: TA subset (black); wear stages 1–5 and TAe subset (grey); wear stages 1–5. Also included are p-values of *t*-tests (threshold value $p = 0.05$).

Fig. 1. Liaison entre usure et *mesowear*. La densité des points montre la distribution et les barres représentent la taille de l'échantillon, tandis que les lignes (TA : ligne continue ; TAe : ligne en pointillé) montrent la moyenne arithmétique. Pour la taille exacte des sous-ensembles, voir Tableau 1 : sous-ensemble TA (noir), stades d'usure 1–5 et sous-ensemble TAE (gris). Les valeurs de *p* des tests *t* sont aussi incluses (valeur seuil de $p = 0{,}05$).

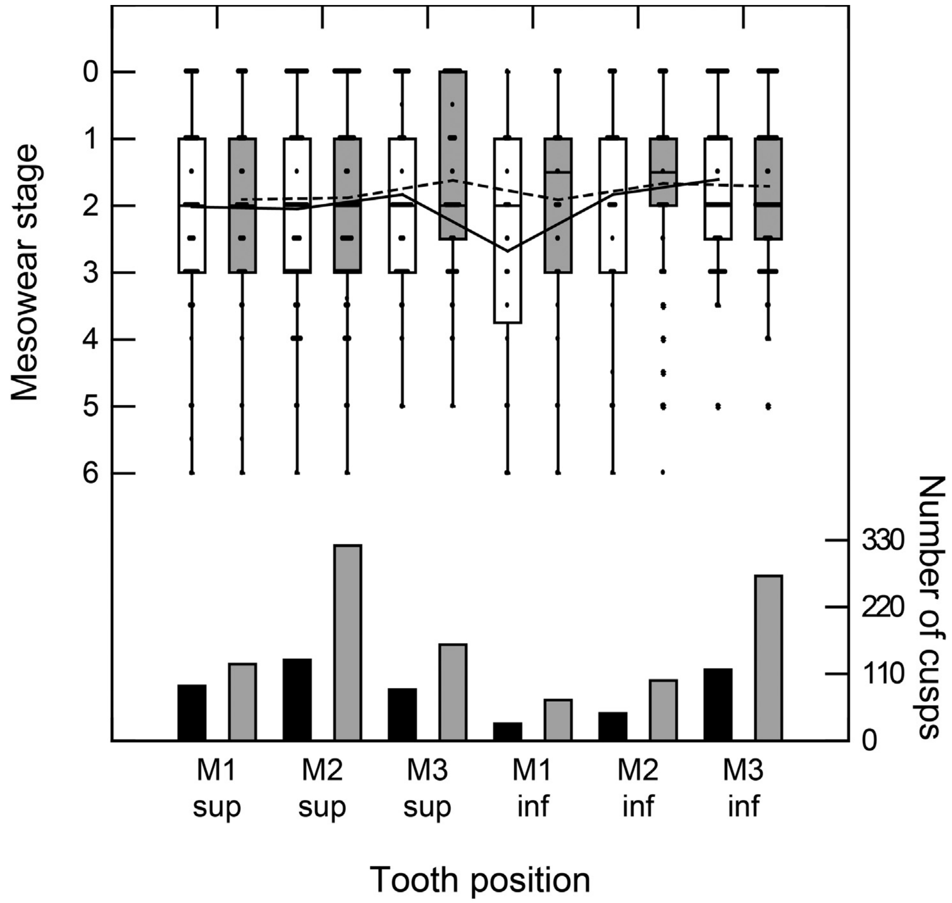
means of mesowear values of cusps in these wear stages fluctuate only marginally. This is also confirmed by *t*-tests. This trend is also visible in the TAe subset, however not as clearly as in the TA subset.

The fluctuations in the mean of the mesowear values between cusps in wear stages 1–3 can be explained using dot densities. With increasing wear stages, the range of mesowear stages increases. Cusps in wear stage 4–5 show an even stronger shift to higher mesowear stages.

The results from the serial comparison of a particular wear stage with the next higher one confirm our decision to exclude wear stage 4, because it is similar to wear stage 5 in terms of mesowear signal. The significant differences between the other wear stages are not surprising, as on the one hand they cover different time intervals and on the other hand it is visible in the distribution of dot densities in Fig. 1. It also shows that they are distinct from each other.

For the original mesowear method, Fortelius and Solounias (2000) suggested to exclude teeth that are either unworn or entirely worn out, corresponding to our wear stages 0 and 5. Unworn teeth cannot display a mesowear signal related to the diet. Teeth that are entirely worn out loose a specific signal as a result of excessive wear. Our results generally confirm the exclusion of higher wear stages, although our studies illustrate that a significant overprint of the mesowear signal begins earlier than expected, i.e. when the dentin is affected by tooth wear, corresponding to our wear stage 4 (Table 2).

The bar charts in Fig. 1 show that most of the cusps are assigned to wear stages 2 and 3. The molars in these stages cover the entire range of mesowear stages between mesowear stages 0 and 6. The wear stages (Table 2) do not necessarily reflect equal periods of time. In order to check correspondences between tooth age and individual



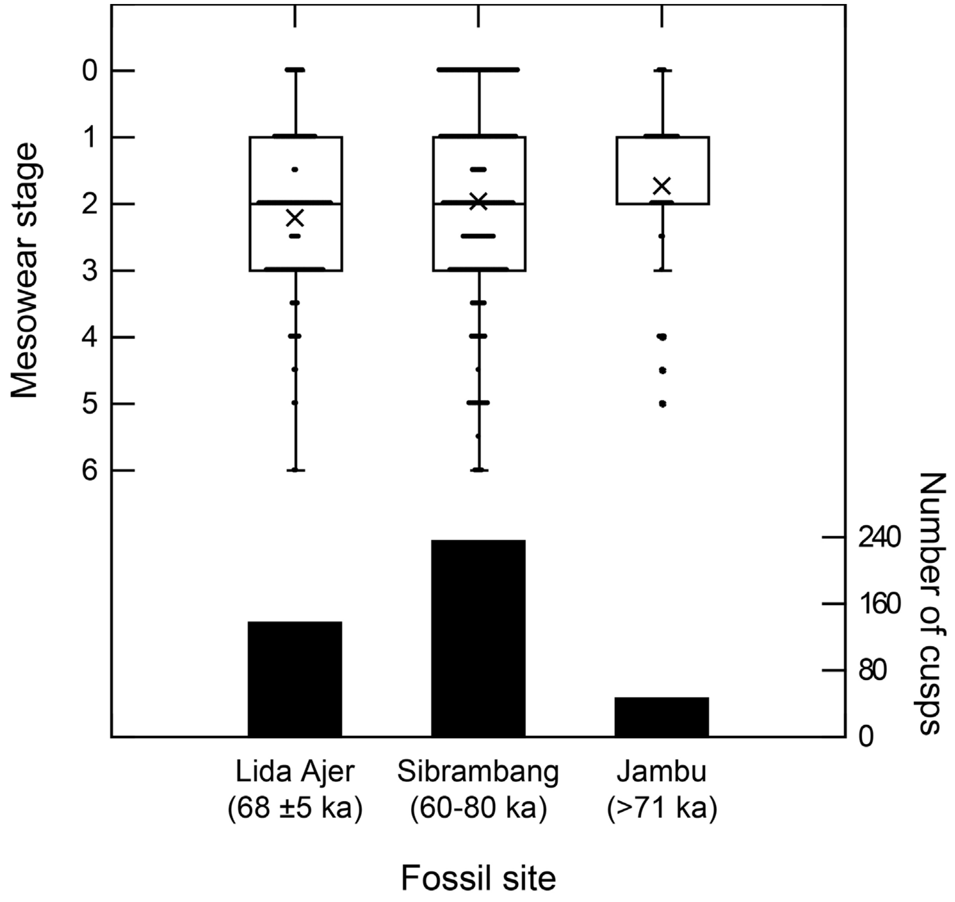
Tooth positions compared	M1 sup	M3 sup	M1 inf	M2 inf	M3 inf
M2 sup (TP)	n. s.	n. s.	n. s.	n. s.	0.01
M2 sup (TPe)	n. s.	0.04	n. s.	n. s.	n. s.

Fig. 2. Comparison between mesowear signals of different tooth positions. The density of dots shows distribution and the bar charts represent sample size, while the line graph (TP: solid line; TPe: dashed line) shows the arithmetic mean. For exact subset sizes see Table 1: TP subset (black); wear stages 1–3 and TPe subset (grey); wear stages 1–3. Also included are p-values of t-tests (threshold value $p = 0.05$).

Fig. 2. Comparaison entre les signaux de *mesowear* de différentes positions des dents. La densité des points montre la distribution et les barres représentent la taille de l'échantillon, tandis que les lignes (TP : ligne continue ; TPe : ligne en pointillé) montrent la moyenne arithmétique. Pour la taille exacte des sous-ensembles, voir Tableau 1 : ensemble TP (noir) ; stades d'usure 1–3 et TPE (gris) ; stades d'usure 1–3. Les valeurs de p des tests t sont aussi incluses (valeur seuil de $p = 0{,}05$).

age, we assigned each of the molars in our sample to a particular age class by a classification system introduced by Anders et al. (2011). Because of the erupting sequence in a tooth row, molars with different tooth positions do not display the same degree of wear (Anders et al., 2011). Anders et al. (2011) introduced six individual dental age stages (IDAS: 'prenatal' (0), 'infant' (1), 'juvenile' (2), 'adult' (3), 'late adult' (4), 'senile' (5). Individuals in IDAS 0 are not usable for the mesowear method. We only have isolated teeth in our sample and no tooth rows, thus only estimates can be made to determine the dental age stage of individuals. We translated the IDAS system in series of wear stages (Table 3). The mesowear method can be used on individuals from IDAS 1–3 on all molars, while individuals of IDAS 4 show only a robust mesowear signal on the third molar. The other molars of individuals of IDAS 4 are in wear stage 4 or higher. Hence individuals from IDAS 5 are not usable for the mesowear method. However, because we excluded the third molar, in fact, only individuals in IDAS 1–3 show robust mesowear signals.

Fig. 4 shows the dental age distribution per cave (TP subset in Table 1 including all wear stages) according to Table 3. It illustrates that the wear stages do not represent equally long periods of time. Recent barking deer enter the weaning period with 61 days (AnAge, 2017; Tacutu et al., 2018). This corresponds to the shift from deciduous to permanent dentition and is reflected in the transition from IDAS 1 to 2. Barking deer reach sexual maturity after a year, which is associated with the onset of an adult life period and IDAS 3. In the wild, barking deer possess a life expectancy



Caves compared	Lida Ajer/Sibrambang	Jambu/Sibrambang	Lida Ajer/Jambu
p-value	n. s.	n. s.	0.02

Fig. 3. Mesowear signal of the barking deer for each fossil site obtained with the ruminant ruler. The density of dots shows distribution and the bar charts represent sample size, while X shows the arithmetic mean. For exact subset sizes see Table 1: CA subset; wear stage 1–3. Also included are the *p*-values of *t*-tests (threshold *p*-value = 0.05).

Fig. 3. Signal *Mesowear* du cerf aboyeur pour chaque site fossilifère, obtenu avec dominance du ruminant. La densité de points montre la distribution et les barres représentent la taille de l'échantillon, tandis que X montre la moyenne arithmétique. Pour la taille exacte des sous-ensembles, voir le Tableau 1 : ensemble CA ; stade d'usure 1–3. Les valeurs de *p* des tests *t* sont aussi incluses (valeur seuil de *p* = 0,05).

Table 3
IDAS stages by Anders et al. (2011) translated into wear stage series.
Tableau 3
Stades IDAS par Anders et al. (2011) traduit en série de stades.

IDAS		Wear stage		
		M1	M2	M3
1	Infant	0–1	Not erupted	Not erupted
2	Juvenile	1–2	0–1	0
3	Adult	3	2–3	1–2
4	Old adult	4–5	4	3–4
5	Senile	5	5	4–5

of less than 17 years. Assuming that late adulthood and senescence would cover a maximum period of 5 years, individuals still spend approximately 11 years in IDAS 3. The cusps in IDAS 3 'adult' represent the longest time interval, reflected by their high numbers (Fig. 4). Moreover, molars can be subjected to mesowear analysis from 'juvenile' to 'adult' life periods covering at least 2/3 of their life span. Because of its small size the sample from Jambu shows a different trend.

5.2. *Usable tooth positions in the barking deer*

According to the original approach of Fortelius and Solounias (2000), a minimum of 20 teeth is required to obtain a robust signal and they only included the sharper cusp of the second upper molar. Fossil samples are normally much smaller than the sample in the Dubois Collectie, so it stands to reason to include as many tooth positions as possible. In the TP subset, we tested all other tooth positions against the 'M2 sup' subset. Fig. 2 shows that all tooth positions can be used, except the lower third molar.

We also tested the entire sample TPe (Fig. 2) and in this case 'M3 sup' provides a significantly different mean value when compared to the one of 'M2 sup'. We

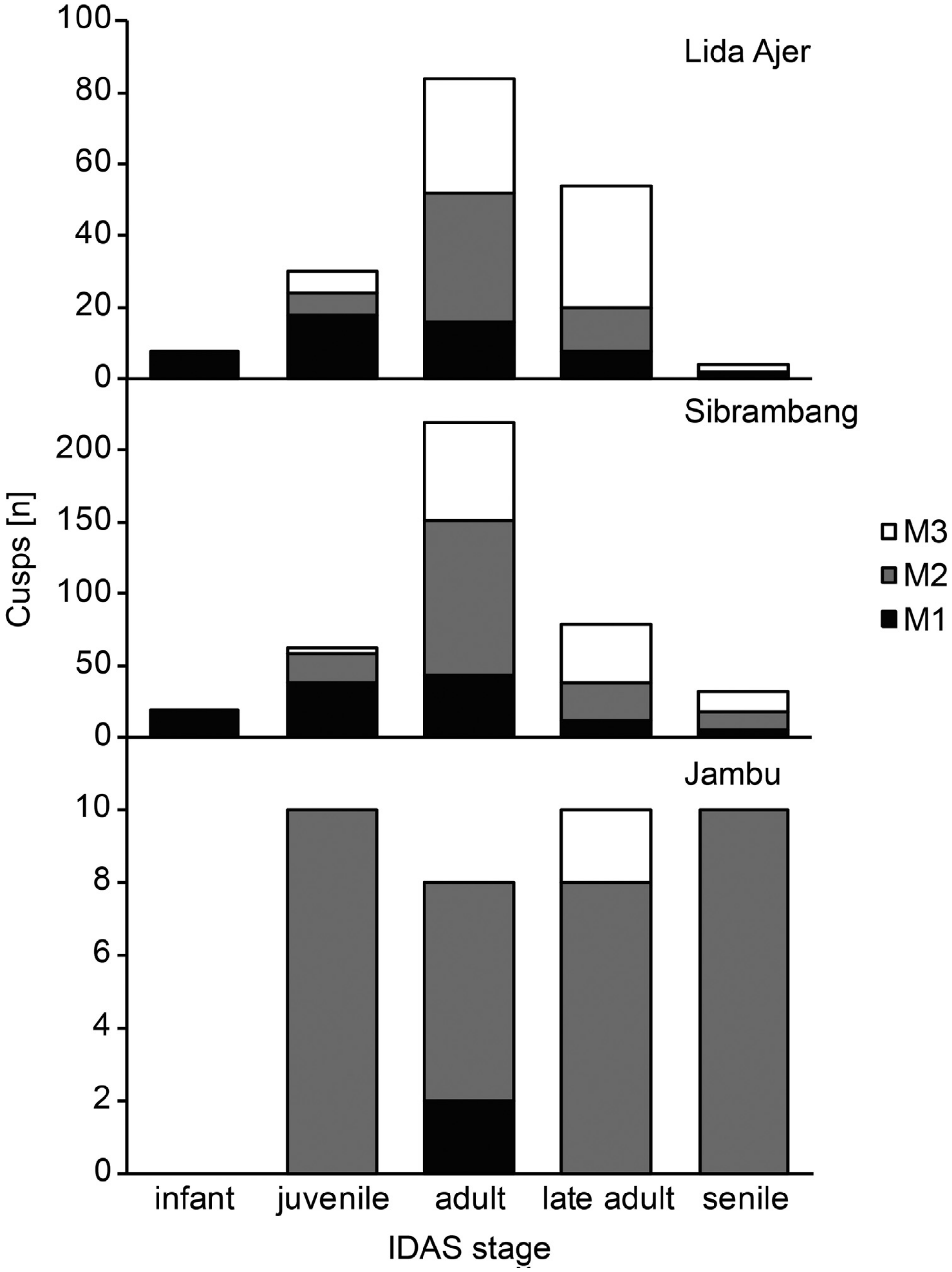


Fig. 4. Number of cusps sorted by tooth position and IDAS stage as well as by cave. Cusps that can be attributed to more than one IDAS stage were counted multiple times (subset IDAS in Table 1, all wear stages).

Fig. 4. Nombre de cuspides triées selon la position de la dent, le stade IDAS et la grotte. Les cuspides qui peuvent être attribuées à plus d'un stade IDAS ont été comptées de nombreuses fois (sous-groupe IDAS dans le Tableau 1, tous stades d'usure confondus).

therefore restricted reconstructions of paleodiet and inferences on the environment on a sample consisting of upper and lower first and second molars only.

Why 'M3 sup' and 'M3 inf' show significantly different mean mesowear values than 'M2 sup' remains to be further investigated. A variety of reasons seems to be conceivable. Firstly, significant differences may be attributed to the marginal position of the third molars in the tooth row, thus supporting a specific involvement in the mastication process that differs from the one of rather central positions. Secondly, the variations may be related to the eruption sequence. M3 erupts later than other molars and is thus not as long in wear.

Several authors tested additional tooth positions. Kaiser and Solounias (2003) included the fourth premolar as well as all molar positions in the upper tooth row for their extended mesowear method. Kaiser and Fortelius (2003) tested additionally the same tooth positions in the lower tooth row. In the latter case, a calibration factor was required, because the mesowear signal obtained from the lower tooth row shifted considerably towards a grazing signal. However, both studies were performed on equids. Premolars are strongly molarized in equids. In contrast to that, molars and premolars are more heterogeneous in Muntjaks. Therefore, we excluded premolars from our sample. Differences between upper and lower tooth row were not as pronounced in our sample as observed by Kaiser and Fortelius.

Franz-Odendaal and Kaiser (2003) tested the extended mesowear method on ruminants and concluded that the method is not applicable to ruminants, because their heterodontia is more distinct than in equids. The authors suggested to restrict mesowear studies of ruminant teeth to upper second and third molars. The dot densities in Fig. 2 show that the sample tested here consists of a higher number of sharp cusps in the upper molars, i.e. mesowear stage 0, than in the lower molars. This is in accordance to the results of Franz-Odendaal and Kaiser (2003). They found that mixed feeders show a tendency to maximise sharpness in upper teeth, whereas this is not the case in more specialised diets. This is also confirmed in our sample, at least by 'M3 sup'.

Louys et al. (2011) examined African antelopes and found a significant difference between 'M3 sup' and 'M2 sup'. They concluded that 'M3 sup' is the most suitable tooth position for mixed feeders. Browsers were reclassified most correctly using 'M3 inf', frugivores using 'M1 inf' and grazers using 'M2 inf'. According to the ruminant ruler, the barking deer can be classified into the category of mixed feeders. The authors used a reclassification approach while we scored directly. The application of different methods may offer an explanation for the different conclusions. Besides, there might be also taxon-specific differences between bovids and cervids.

We moreover found insignificant differences between upper and lower tooth rows. This is in accordance to the results of Louys et al. (2011), who found minor differences in mesowear scores between upper and lower molars across the tooth positions and trophic categories in general.

5.3. Paleodiet of the barking deer

In this study, the barking deer from Lida Ajer, Sibrambang and Jambu are classified as mixed feeders. Up to present, there are no other paleodiet reconstructions for barking deer of this timeframe. Janssen et al. (2016) studied younger barking deer from Wajak (MIS 3 to Holocene interglacial) using δ^{13}C values. They suggest a mixed C3–C4 diet or even a pure C3 open canopy diet. Hence, the reconstructed diet in Janssen et al. (2016) and our study are in accordance with the recent diet of barking deer, which is well known. It consists of tender leaves of trees and shrubs, herbs, forbs, tender shoots, flowers, buds, bark, twigs, mushroom, grass, and fruits (Farida et al., 2003; Hoogerwerf, 1970 and references therein; Ilyas and Khan, 2003 (Kitchener et al., 1990; Nowak, 1999; Oka, 1998). Barrette (1977) reported that fallen fruits represent the staple food component of barking deer. This is, however, challenged by other authors (e.g., Ilyas and Khan, 2003). The observations of Barrette (1977) may be correct for a particular population. Yet, as Ilyas and Khan (2003) report, the diet depends on the seasonal availability of fruits in the habitat. This may also explain why other authors like Odden and Wegge (2007) describe the barking deer as a selective browser.

There is no mesowear signal on the ruminant ruler for frugivore animals. Fortelius and Solounias (2000) suggested "tip crushing wear" as result of biting on pits, which leads to damaged, but eventually rounded or even blunt cusps. In a preliminary study (unpublished data), we tested the ruminant ruler on recent wild *Philantomba monticola* from the Senckenberg Collection in Frankfurt. Its frugivorous diet appeared as a mixed feeder signal on the ruminant ruler. The results obtained with the ruminant ruler are in good accordance with the diet of the recent species, as inferred from field observations.

As Rivals et al. (2011) note, a mixed feeding signal is rather an abrasion index resulting from seasonal shifts in vegetation than a discrete diet type. During rainy seasons attrition dominates, whereas in dry seasons abrasion prevails. Such combination would appear as a mixed feeding mesowear signal. This effect should be more prominent in browsers than in grazers. Molars of grazers are more adapted to abrasive wear than teeth of browsers. Thus the differences between seasons should be less noticeable. While the mesowear signal of a browser is shifted towards the mixed feeder spectrum by consuming dry grass and rather hard food in the dry season, the mesowear signal of a grazer may not change significantly, even though the individual is consuming browse during the rainy season. In the future, this hypothesis should be further investigated with other methods that provide a higher resolution, like microwear, isotopes, or mesowear III (Davis and Pineda-Munoz, 2016; Sánchez-Hernández et al., 2016; Solounias et al., 2014).

5.4. How much changed the environment in the late Pleistocene?

There are noticeable differences between the box plots of Jambu on the one hand and Sibrambang and Lida Ajer on the other one (Fig. 3). Although the barking deer from all three caves can be generally classified into the category of mixed feeders, the diets of barking deer at Sibrambang and Jambu are shifted towards the browsing spectrum, while barking deer from Lid Ajer have a grazing component. The differences between Lida Ajer and Jambu are significant, while Sibrambang is not significantly different from any of the caves.

The significant difference between Lida Ajer and Jambu might be explained by the different sample sizes and resulting variances. Although the size of the sample from Sibrambang is larger than that of the one from Lida Ajer, the difference between Sibrambang and Jambu is statistically not significant. In Sibrambang, the number of cusps in mesowear stages 0–2 is distinctly higher than in Lida Ajer. In this respect, it is more similar to that in Jambu. Overall, the differences between the three samples can be attributed to variable sample sizes and variances.

The sample from Jambu is smaller than those from either Sibrambang or Lida Ajer. Bacon et al. (2015) noted that a selection during excavation for most complete and best preserved teeth should be considered. Bacon and colleagues speculate that the larger portion of fossil teeth from Jambu has been left in the field. Even though they could not be subjected to mesowear studies, comparing the proportions of highly abraded and therefore poorly preserved molars among the samples from the three caves can make a valuable contribution to this discussion. Moreover, other taxa collected from the three caves should show similar effects if the collection protocol at Jambu differs from the one applied at other sites. Despite Lida Ajer being relocated, it is not possible to assign the fossils from the Dubois Collectie to distinct stratigraphic layers. There are several fossil-bearing layers at Lida Ajer (Westaway et al., 2017). The geology and formation of both of the other caves are still unknown. Differences between the samples may result from taphonomic causes as well. One approach would be to compare the percentages of porcupine gnawing marks on the teeth per cave. The impact of porcupines as accumulation agents may not be equal among the three caves. Because we have little (Lida Ajer) to no (Sibrambang and Jambu) information about the geology, except being located in karstic limestone and especially the layers the teeth were found in,the time span covered by the samples remains hidden as well. In case of Lida Ajer, Louys et al. (2017) concluded that the teeth must have been redeposited inside the cave in mass-movement events initiated by rainfall and earthquakes, which further complicate dating.

Taking all this into account, it should be noted that the number of teeth used in the Jambu sample is large enough to provide a robust signal. It is therefore likely that differences in the mesowear signals between the caves result from changes in the environment. Because they were not the aim of this study, we do not discuss ecological parameters like competition by other herbivorous animal. We will focus on the effects of the YTE and by the environmental changes accompanying the transition from MIS 5 to 4.

There are not many studies on the effects of volcanic ash on tooth wear. Spradley et al. (2016) studied how volcanic dust affects tooth wear in howling monkeys (*Alouatta pallita*) and concluded that volcanic ash has an important impact on the tooth wear of anterior teeth but less on molars. Another observation is that heavy wear on the premolars is due to fluorosis as a result of a surge in fluoride caused by volcanic ash. This would affect the premolars in a different way, because molars fully mineralize earlier in life history (Spradley et al., 2016). The sample tested here is restricted to molars. Nevertheless, further studies may look into the wear of premolars in these samples.

Spradley et al. (2016) studied the immediate impact of a volcanic eruption on tooth wear, but it is unrealistic that the barking deer of Lida Ajer or Sibrambang consumed leaves covered with volcanic ash in the first place. In the case of the YTE, the thickness of the initial ash layer is estimated at 10–15 cm, which is deadly for some types of vegetation (Timmreck et al., 2012), resulting in the absence of certain types of plants for a relatively short period of time. Even if the plants were covered by a thick layer of ash, the ash may be directly removed by wind and/or precipitation (Timmreck et al., 2012). However, volcanic ash may have had another important impact worth to be considered. Timmreck et al. (2012) note that the nutrients from the ash fall can induce quick vegetation recovery.

Successions after volcanic events are well studied in two cases: the eruptions of Krakatoa in 1883 (e.g., Bush and Whittaker, 1991) and Mount St. Helens in 1980 (e.g., Dale et al., 2005). However, both case studies are not applicable to the effects of the YTE. Mount St. Helens is located in a different climate zone and on the mainland. Krakatoa is in the same climate zone as Sumatra, but its small size and geographic isolation allowed only for airborne species as pioneers (Bush and Whittaker, 1991). In very contrast, Sumatra is the sixth largest island on the Earth (van der Kaars et al., 2012). Succession started in Sumatra from parts of the island, which were less affected by the immediate effects of the YTE. van der Kaars et al. (2012) recognized an immediate and extensive impact on the vegetation of northern Sumatra. Sumatran pine forests (*Pinus mekusii*) were decimated in the highlands; however, the effect on other forest types appeared to be either rather limited or the effects were compensated by succession and regeneration within a couple of hundred years. Succession and regeneration happen on a time scale that cannot be resolved by the fossil sample in this study (Davis & Pineda-Munoz, 2016). Because of this, the differences in the box plots (Fig. 3) cannot be accounted to the YTE.

The samples of Lida Ajer and Sibrambang show a shift to a mixed feeder diet with a less pronounced browsing component. This could result from episodic shifts towards drier conditions. In fact, a climatic change is likely to have occurred during the relevant period. Large amounts of fossil orangutan and fossil wild boar led Bacon et al. (2015) to reconstruct the environment of the three caves as an aseasonal rainforest. The diet of orangutans consists of about 60% of fruits and leaves. A large population density therefore indicates a regular and abundant fruit source. High atypical densities of modern populations of wild pigs in Asia have been observed in aseasonal lowland dipterocarp rainforests with abundant food resources (Bacon et al., 2015). The authors found no significant differences between the fauna of MIS 5 (Lida Ajer, Sibrambang and Jambu) and MIS 4 (Duoi U'Oi). However, Bacon et al. (2015) treated all three caves as a single fossil site, calling it "Sibrambang", for the purpose of their study, in which they compared different fossil sites in mainland and insular Southeastern Asia. It would be interesting to compare the numbers of orangutan and wild pig specimens from each of the caves to check for variations in abundances.

Van der Kaars et al. (2010) studied the palynological record from deep-sea core BAR94-42 and concluded that the vegetation of Southwest Sumatra consisted of rainforest with open herbaceous swamps along river courses and surrounding lakes during MIS 5. The climate was humid, with short dry seasons. Although vegetation does not fundamentally change in southwestern Sumatra from MIS 5 to 4, van der Kaars et al. (2010) note extended dry periods, increased fire activity, and a weaker monsoon in MIS 4. Kaolinite is a proxy for the availability of water, which was used by van der Kaars et al. (2010) among

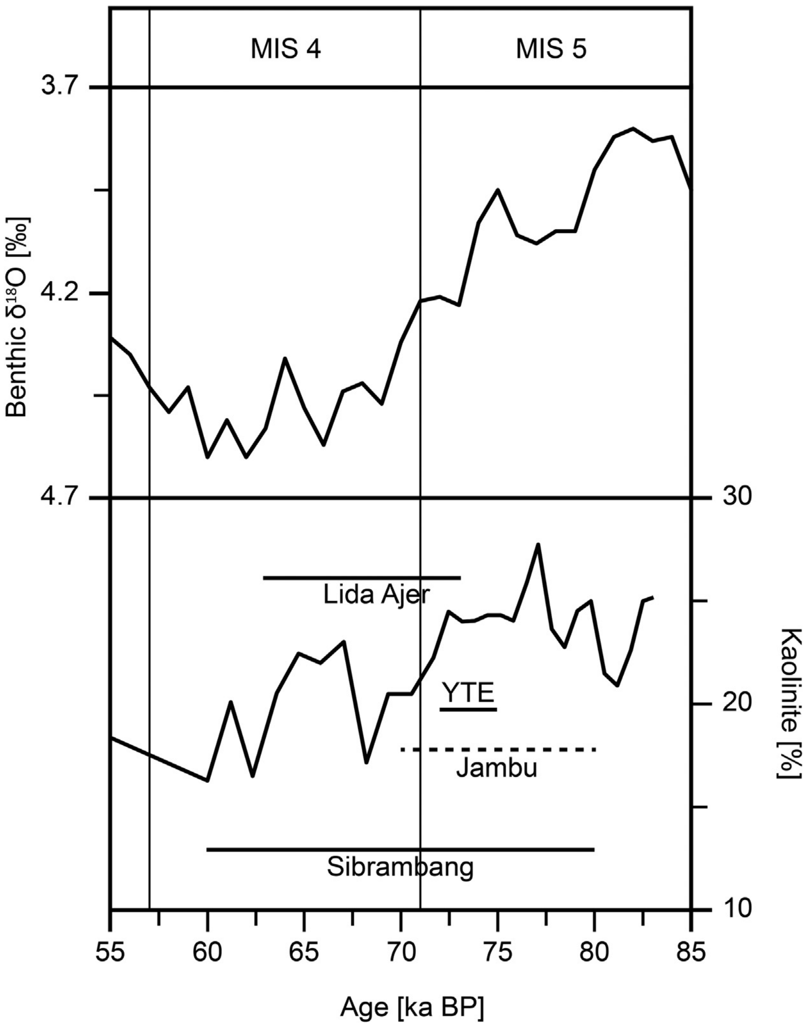


Fig. 5. Kaolinite concentration as a proxy for water availability (van der Kaars et al., 2010) compared to time periods of the caves (Lida Ajer by Westaway et al., 2017; Sibrambang and Jambu by Bacon et al., 2015 and references therein). In addition, the MIS graph with data from Lisiecki and Raymo (2005) is included.

Fig. 5. Concentration en kaolinite en tant que *proxy* pour la disponibilité de l'eau (van der Kaars et al., 2010), comparée à l'âge des grottes (Lida Ajer par Westaway et al., 2017 ; Sibrambang par Bacon et al., 2015 et références incluses). Un graphique des MIS, selon les données de Lisieki et Raymo (2005) a été ajouté.

others. Combining this data with the presumed dates for the caves (Fig. 5) and a potential behavioral response of the barking deer, different options for chronological links between the caves can be discussed.

Fig. 5 shows a match between the wetter conditions and a rather specialized mesowear signal for the barking deer in the time period before 70 ka. The mesowear signals of barking deer of Sibrambang and Lida Ajer show a mesowear signal, which points to a more generalized mixed feeder diet. Combining this information with the kaolinite data and the dating of the caves enables us to narrow down the chronology suggested by Bacon et al. (2015) and Westaway et al. (2017).

Lida Ajer has presumably an age between 63 and 73 ka. The same applies to Sibrambang. As already pointed out, the resolution of the mesowear method is not high enough to illustrate the effects of the YTE; hence certain timelines cannot be ruled out. Sibrambang may be older or younger than Lida Ajer. Also, the dates for Sibrambang and Jambu remain to be confirmed and should be considered with caution. Based on biostratigraphic correlations with the fossil record in Java, Lida Ajer was initially considered to be older than 81 ka years (Bacon et al., 2015 and references therein). Nevertheless, the faunal response of barking deer show that the fauna of Jambu is associated with a period of higher kaolinite availability, hence more humid conditions and less extensive dry periods prior to 71 ka. The faunas of Lida Ajer and Sibrambang should have been active in either one or both of the episodes of lower kaolinite availability between 71 and 63 ka (Fig. 5). Moreover, Sibrambang may predate Jambu. Then again, there is no significant difference between Lida Ajer and Sibrambang in mesowear signals of the barking deer. The climatic conditions should therefore have been similar.

6. Conclusions

The mesowear method enables paleoenvironmental reconstructions by determining the impact of consumed plant parts on tooth wear. However, not every tooth can be used for the mesowear method. The differences between wear stages and tooth positions become only prominent when only cusps, which produce robust mesowear signals, are used. Hence, it is important to know how teeth from different positions and in different wear stages behave, especially when working with small samples.

In the course of this study, molars in wear stages 0, 4, and 5 were excluded. Tooth positions 'M3 sup' and 'M3 inf' behave distinctively different compared to other positions and are therefore excluded from this study. The reason for this still needs to be investigated. The effect may be limited to a particular diet type, by testing ruminants, which are specialized browsers or grazers. It also would be interesting to test teeth of barking deer from other fossil site.

The barking deer was classified into the category of mixed feeders, which is also observed in recent barking deer (e.g., Hoogerwerf, 1970; Kitchener et al., 1990; Oka, 1998). Whether these animals were true mixed feeder or the mixed feeder signal is the result of opportunistic feeding during different seasons, like what was observed in some recent barking deer (e.g., Barrette, 1977; Hoogerwerf, 1970; Ilyas and Khan, 2003; Oka, 1998), cannot be determined with the mesowear method. This should be investigated in future studies, utilizing, e.g., the microwear method, which has a higher resolution to approach than the mesowear method (Davis and Pineda-Munoz, 2016).

If and why there is a change in the paleoenvironment of the Padang Highlands could not be determined in this study with certainty. However, there is a trend of changing environment, reflected in a more abrasion-based diet of barking deer, which implies higher seasonality. This should be further investigated with more precise methods in the future. The impact of the YTE was not big enough to alter the environment to an extent that became visible in the mesowear signal. The changing trend should be attributed to the climatic change accompanying the shift from MIS 5 to 4.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.crpv.2019.03.004.

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