RESEARCH PAPER

Feeding preferences of *Gomphotherium subtapiroideum* (Proboscidea, Mammalia) from the Miocene of Sandelzhausen (Northern Alpine Foreland Basin, southern Germany) through life and geological time: evidence from dental microwear analysis

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Abstract The objective of this study is to estimate changes in feeding preferences of the proboscidean species *Gomphotherium subtapiroideum* (Schlesinger 1917) by means of dental microwear analyses. The dietary changes are first evaluated through the ontogeny of this species, between juveniles and adults, and are then studied through geological time, from early Middle Miocene (MN5) to middle Late Miocene (MN8–9) localities of the German Molasse Basin. The microwear patterns of juvenile and adult individuals of *G. subtapiroideum* from Sandelzhausen (MN5) differ merely by the variable "length of scratches", emphasizing longer jaw movements during mastication in adults. The microwear signatures of *G. subtapiroideum* do not vary significantly between the two geological time periods studied, but reflect mixed feeding preferences in both cases. These results imply that, despite an important environmental change at that time (drying and opening), the ecology of *G. subtapiroideum* and, especially, its feeding habits were not affected. Its dental microwear pattern is then compared with those of other species of Proboscidea from the Middle-Late Miocene of Germany, namely *Deinotherium giganteum* and *Gomphotherium steinheimense*.

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Kurzfassung Die vorliegende Untersuchung hat das Ziel anhand von „Microwear"-Analysen an Backenzähnen eventuelle Veränderungen von Futterpräferenzen der Rüsseltierart *Gomphotherium subtapiroideum* (Schlesinger 1917) abzuklären. Hierbei werden eventuelle innerartliche Veränderungen zum einen im Laufe der Ontogenie, also zwischen juvenilen und adulten Tieren, zum anderen im Laufe der Zeit vom frühen Mittel-Miozän (MN5) zum mittleren Ober-Miozän (MN8–9), basierend auf Material von Fundstellen aus dem deutschen Molassebecken, ausgewertet. Das „Microwear"-Muster von *G. subtapiroideum* aus Sandelzhausen (MN5) zeigt keine nennenswerten Unterschiede zwischen juvenilen und adulten Individuen, außer für die Länge der Kratzer, die wohl von längeren Kieferbewegungen bei adulten Tieren herrühren. Die „Mircowear"-Signatur von *G. subtapiroideum* lässt auch keine wesentliche Veränderung zwischen den beiden, untersuchten geologischen Zeiten erkennen; in beiden Fällen ist das Signal typisch für „mixed-feeder". Dieses Ergebnis spricht dafür, dass, obwohl in diesem Zeitraum eine nicht unwesentliche Veränderung zu einer allgemein trockeneren und offeneren Umwelt statt gefunden hat, dies keinen Einfluß auf die Lebensweise und das

Nahrungsverhalten von *G. subtapiroideum* hatte. Des Weiteren wird das „Microwear"-Muster von *G. subtapiroides* mit denen anderer mittel-/obermiozäner Rüsseltiere, nämlich *Deinotherium giganteum* und *Gomphotherium steinheimense*, verglichen.

Schlüsselwörter Nahrung · Umwelt · Europa · Miozän · Proboscidea · Entwöhnung

Introduction

Given that dental microwear patterns reflect abrasion between tooth enamel and the most recent food items consumed (Walker et al. 1978), microwear analyses have improved our knowledge on tooth functionality and ecology of fossil mammalian species. Numerous studies have been performed on fossil primates (Grine 1986; Merceron et al. 2005; Ungar 1996; Walker 1976) and ungulates (Merceron et al. 2004; Merceron et al. 2007a; Solounias et al. 2002; Solounias et al. 1988). Despite all this work, only a few microwear analyses have been attempted to estimate the feeding habits of megaherbivores, and especially proboscideans (Calandra et al. 2008; Green et al. 2005).

The order Proboscidea originated in Africa, but then spread all over the world during Neogene times and represented a diverse group of mammals especially in Europe (Göhlich 1999). Because we know from the extant African elephant (*Loxodonta africana*) that the mere presence of such megaherbivores highly disturbs the structure of the mesoherbivores' guild (mammals ranging from 4 to 450 kg, Fritz et al. 2002), we assume crucial impacts of extinct proboscideans on palaeoecosystems because of their past biodiversity and large body mass.

In this context, our study aims to investigate the feeding preferences of the extinct proboscidean species *Gomphotherium subtapiroideum* from the fossil site Sandelzhausen (Early/Middle Miocene) in the Northern Alpine Foreland Basin (Molasse Basin) of Germany (see Göhlich 2010 this volume) from an ontogenetic and an evolutionary and palaeoecological aspect. First, because of the high abundance of proboscidean materials, the changes in diet through ontogeny are investigated by means of dental microwear comparisons between juveniles with deciduous dentition (dP3-dP4) and adults with molars (M1-M3) in occlusion. Second, the dental microwear pattern of adults of *G. subtapiroideum* from Sandelzhausen is compared to a dataset composed of representatives of the proboscideans families Gomphotheriidae and Deinotheriidae (according to Shoshani and Tassy 2005) from several Middle or Late Miocene localities from the German Molasse Basin, and, especially, a sample of later *G. subtapiroideum* (Appendix: Table 3). This will reveal the role of Miocene

environmental changes in the evolution of specific proboscidean dietary preferences.

Materials and methods

Materials

All studied materials come from the northern autochthonous unfolded Molasse Basin section in southern Germany, filled with limno-fluvial sediments of the Upper Freshwater Molasse, dating from the late Early Miocene (Mammal Neogene Zone 4, MN4) to the early Late Miocene (MN9). This lithostratigraphic formation is well known for its abundance of vertebrate fossils (Dehm 1955; Doppler et al. 2000; Heissig 1989, 1997) and, based on these fossils, divided into three biostratigraphic levels: the "Ältere Serie", the "Mittlere Serie", and the "Jüngere Serie".

Fossil materials from two different biostratigraphic levels of the Upper Freshwater Molasse were analyzed here. Teeth of juveniles and adults of *Gomphotherium subtapiroideum* from Sandelzhausen (biostratigraphic unit "Ältere Serie", MN5, 17.0–15.3 Ma) were investigated in order to infer dietary changes through the ontogeny of this proboscidean species. Most microwear studies have focused on a single tooth, usually the second molar. However, in this study, first, second and third molars of adults and third and fourth deciduous premolars of juveniles were considered for the analysis to increase sample size. This increase in sample size was necessary to reliably discriminate the feeding preferences between these Miocene megaherbivores. Molars from 11 adults and deciduous premolars from 13 juveniles of *G. subtapiroideum* from Sandelzhausen were analyzed (Appendix: Table 3). Because of the horizontal tooth replacement of most proboscidean (including gomphotheres), it can be difficult to assess whether an isolated tooth or tooth row belongs to a juvenile or an adult. To avoid this problem, we chose to use only deciduous premolars, which belong with no doubt to juveniles, and molars, which certainly correspond to adult teeth.

Second, the dataset of dental microwear patterns of adult proboscideans from the fossil site of Massenhausen and nine other localities, all from the biostratigraphic unit "Jüngere Serie" and dated to MN8–9 (12.7–9.7 Ma), from Calandra et al. (2008) was added to the analyses. Molars from six individuals belonging to *G. subtapiroideum*, 13 to *G. steinheimense* (Klähn 1922), and 17 to *Deinotherium giganteum* (Kaup 1829) were included (Appendix: Table 3; Calandra et al. 2008: supplementary electronic material S2).

The crown patterns of the molars of deinotheres and gomphotheres are very different. The molars of *Deinotherium* are markedly lophodont (M_1/M^1 trilophodont, M_2/M^2 and M_3/M^3 bilophodont); the transverse valleys are
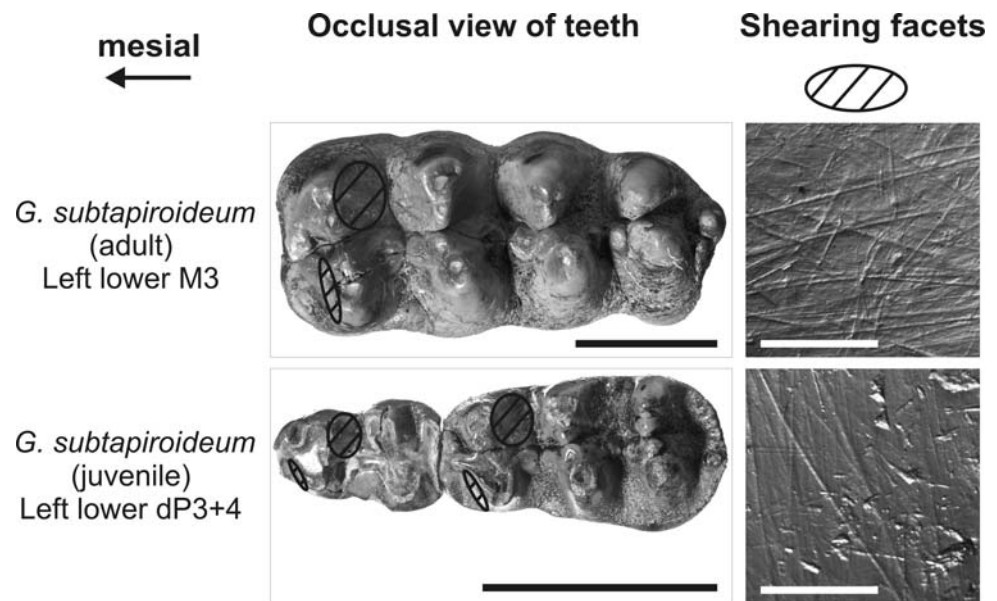
wide and unblocked. *Gomphotherium*, on the other hand, shows a bunodont crown pattern (intermediate molars trilophodont, third molars 3½—5 loph(id)s); each loph(id) is made up of several, more or less bulky cones and is separated by a median sulcus into a pretrite and posttrite halfloph(id); anteriorly and/or posteriorly attached to the pretrite halfloph(id) is mostly an additional central conule, which more or less blocks the valleys (Fig. 1, Appendix: Fig. 4). The differences on the species level between *G. subtapiroideum* and *G. steinheimense* are size-related and morphology-related. In contrast with *G. steinheimense*, the bunodont habitus of the molars of *G. subtapiroideum* is somewhat diminished and the loph(id)s appear slightly more lophodont because of, e.g., more but smaller cones per loph(id), slightly more slender (anteroposteriorly) loph(id)s, and weaker or bulge-like central conules (Fig. 1, Appendix: Fig. 4). The juvenile milk teeth (dP_4/dP^4 trilo-phodont, dP_3/dP^3 bilophodont, and dP_2/dP^2 more or less uni-cuspid) of *G. subtapiroideum* show a very similar morphological pattern to the adults, but the structures are often somewhat more delicate (Fig. 1).

All materials studied are housed at the Bayerische Staatssammlung für Paläontologie und Geologie in Munich, Germany (BSPG).

Methods

Among most mammals, the masticatory process is mainly divided into two phases (Kay 1975; Kay and Hiiemae 1974). The first phase (phase I) corresponds to mandibular movements parallel to the plane of the dental facets, resulting in the shearing of food items and slicing of cell walls of vegetal items in order to extract the cell content.

During the second phase (phase II) movements perpendicular to the dental facets allow the crushing of food items and thus a second phase of extraction of the cell energy (Kay 1975; Kay and Hiiemae 1974). Because dental microwear patterns on shearing molar facets discriminate feeding style for ungulates (Calandra et al. 2008; Merceron et al. 2007a; Solounias et al. 2002), we here consider solely the shearing dental facets, in relation to the masticatory phase I (Fig. 1, Appendix: Fig. 4; see also Calandra et al. 2008). Because the dental microwear signature is not significantly different on occluding dental facets (Semprebon et al. 2004; Teaford and Walker 1984), upper and lower teeth were not differentiated in the analyses.

For the past four decades, many protocols have been developed to quantify the microwear pattern on enamel surfaces. They differ by casting procedures and data acquisition. Here, the protocol of Merceron et al. (2004, 2005) was employed. It combines light stereomicroscopy with reliable analyses of high-resolution digitized images (Merceron et al. 2005; Ungar 1996). This protocol was previously used to study the mastication processes (Charles et al. 2007) and feeding preferences of extinct species (Boisserie et al. 2005; Goillot et al. 2009; Gomes Rodrigues et al. 2009; Koufos et al. 2006; Merceron et al. 2007b; Merceron et al. 2007a). Two digital microphotographs per facet were taken. After quantifying the number of pits (Np, width to length ratio >1/4) and the number of scratches (Ns, width to length ratio <1/4), microwear scars are assigned to a category depending on their size. Numbers of wide scratches (width >15 μm) and of large pits (major axis breadth >15 μm) are then defined. Finally, the total number of microwear scars (Tot = Ns + Np) and the percentage of pits (Pp = Np/Tot) are computed (Table 1).

Table 1 Statistical summary

	N (n)	Mean ± SEM						
		Ns	Ls	Np	Nws	Nlp	Tot	Pp
D. giganteum MN8-9 sites	17 (26)	16.4 ± 1.1	316.4 ± 34.9	73.4 ± 5.7	0.4 ± 0.1	7.1 ± 0.7	89.7 ± 5.4	79.3 ± 3.0
G. steinheimense MN8-9 sites	13 (20)	26.5 ± 2.7	299.6 ± 23.5	69.8 ± 9.2	0.4 ± 0.1	3.9 ± 0.8	96.4 ± 8.0	68.9 ± 4.7
G. subtapiroideum MN8-9 sites	6 (14)	30.2 ± 2.2	300.0 ± 46.6	69.9 ± 7.0	1.3 ± 0.5	2.9 ± 0.9	100.1 ± 5.3	68.7 ± 3.5
G. subtapiroideum Sandelzhausen, adults	11 (12)	40.7 ± 2.9	212.5 ± 11.6	61.7 ± 5.7	1.6 ± 0.3	3.6 ± 0.6	102.4 ± 6.5	59.4 ± 2.8
G. subtapiroideum Sandelzhausen, juveniles	13 (13)	38.7 ± 2.1	151.4 ± 10.4	77.0 ± 5.8	0.7 ± 0.2	5.8 ± 0.7	115.7 ± 5.8	65.5 ± 2.7

Mean and standard error of the mean (SEM) of the dental microwear variables on the shearing facet

N, number of individuals; n, number of specimens studied (for details, see Appendix: Table 3); Ns, number of scratches; Ls, length of scratches (μm); Np, number of pits; Nws, number of wide scratches (width >15 μm); Nlp, number of large pits (major axis breadth >15 μm); Tot, total number of microwear features (Tot = Ns + Np); Pp, percentage of pits (Pp = Np/Tot)

Table 2 Inter group results for pairwise comparisons on the shearing facet

	MN8-9 sites			Sandelzhausen (MN5)	
	D. giganteum	*G. steinheimense*	*G. subtapiroideum*	Adults of *G. subtapiroideum*	Juveniles of *G. subtapiroideum*
MN8-9 sites					
D. giganteum					
G. steinheimense	**Ns, Nlp**, *Pp*				
G. subtapiroideum	**Ns**, *Nws*, **Nlp**, *Pp*	*Nws*			
Sandelzhausen (MN5)					
Adults of *G. subtapiroideum*	**Ns, Nws, Nlp, Pp**	**Ns, Nws**, *Pp*	*Ns*		
Juveniles of *G. subtapiroideum*				**Ls, Nlp, Pp**	

Significance at α < 0.05 is indicated in italic for Fisher's LSD test and in bold for both Fisher's LSD and Tukey's HSD tests

Ns number of scratches, Ls length of scratches (μm), Np number of pits, Nws number of wide scratches (width >15 μm), Nlp number of large pits (breadth >15 μm), Pp percentage of pits [Pp = Np/(Ns + Np)]

These two sets of measurements achieved from the two digital microphotographs per dental facet were first averaged. Measurements of every shearing facet of all available teeth were then averaged for each individual. Two sets of single-classification analyses of variances (ANOVAs hereafter) were performed for testing differences between juveniles and adults of *Gomphotherium subtapiroideum* from Sandelzhausen, and between the different samples of adult proboscideans. By combination of two pairwise tests (Fisher's least significant difference and Tukey's honestly significant difference), the sources of significant variation were determined; the former pairwise test being less conservative than the latter. All variables were rank-transformed before analyses to mitigate possible effects of violating assumptions for parametric analyses (Conover and Iman 1981; Sokal and Rohlf 1995).

Results

A statistical summary is displayed in Table 1. The results of ANOVAs and pairwise comparison tests are displayed in Appendix: Table 4 and Table 2, respectively.

ANOVAs and pairwise tests display significant differences between juveniles and adults of *G. subtapiroideum* from Sandelzhausen. Juveniles have significantly shorter scratches, more large pits, and a higher pit percentage than adult *G. subtapiroideum* from Sandelzhausen (Tables 1 and 2; Fig. 2).

Both groups of adult *G. subtapiroideum* differ from each other by the number of scratches, the one from MN8–9 sites having the lower density of scratches. However, this difference is barely supported by the less conservative test (Tables 1 and 2; Fig. 3).

G. subtapiroideum from Sandelzhausen has a significantly higher density of narrow and wide scratches and, to
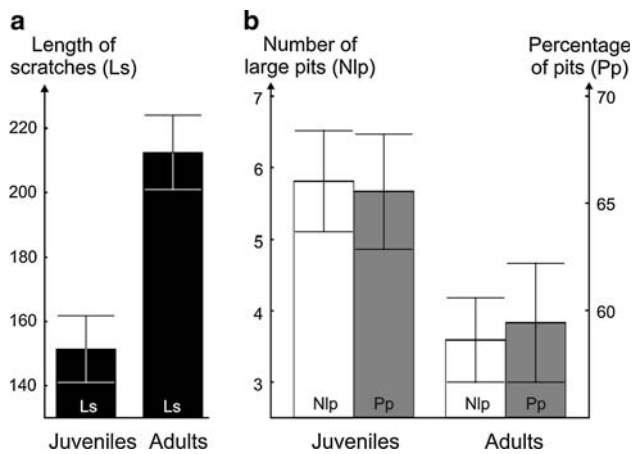
Fig. 2 Mean and standard error of the mean of microwear variables length of scratches in micrometers (*Ls*; **a**, *left*), and number of large pits (*Nlp*) and percentage of pits (*Pp*; **b**, *right*) on the shearing facet for juveniles and adults of *Gomphotherium subtapiroideum* from Sandelzhausen (MN5)

a lesser extent, a lower pit percentage on the shearing facet than *G. steinheimense* (Tables 1 and 2; Fig. 3).

As already demonstrated by Calandra et al. (2008), *D. giganteum* significantly differs from the two species of *Gomphotherium* from MN8–9 sites in having fewer scratches and more large pits, leading to a higher pit percentage, on the shearing facets. *D. giganteum* has a significantly lower density of both narrow and wide scratches, a higher density of large pits, and therefore a higher pit percentage than *G. subtapiroideum* from Sandelzhausen (Tables 1 and 2; Fig. 3).

Discussion

Adults of *Gomphotherium subtapiroideum* from Sandelzhausen have longer scratches on the shearing facet than juveniles (Tables 1 and 2; Fig. 2a). These longer scratches emphasize a larger lateral mandible amplitude during the shearing phase I. Although some significant differences were detected, the dental microwear pattern points out that juvenile individuals with dP3 and dP4 still in occlusion probably had feeding preferences similar to those of adult individuals, having however a larger proportion of browse in their diet (Tables 1 and 2; Fig. 2b). Here it should be noticed that the complete deciduous dentition (dP2-dP4) was probably present and functional from birth as it is for present-day elephants. Our results imply that weaning probably occurs before the dP3 is lost. This is in agreement with what is known for present-day Asian elephants (*Elephas maximus*), because weaning occurs about 18 months after birth and about 6 months before the loss of the more anterior deciduous premolar (dP2) (Shoshani and Eisenberg 1982).
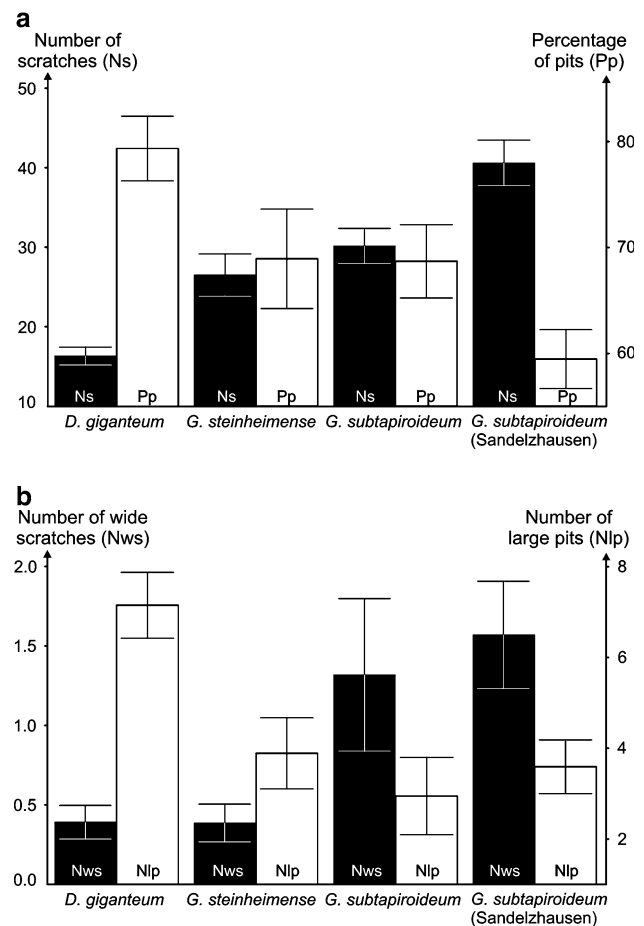

Fig. 3 Mean and standard error of the mean of microwear variables number of scratches (*Ns*) and pit percentage (*Pp*; **a**, *left*), and number of wide scratches (*Nws*) and of large pits (*Nlp*; **b**, *right*) on the shearing facet for the four groups of adult proboscideans

Hofmann and Stewart (1972) recognized three main dietary categories from the gut structures of ruminants: browser, grazer, and mixed feeder. A grazing diet is mainly (>90%) composed of monocots (graminoids: grasses, sedges, and rushes). Browsers feed mainly (>90%) on dicotyledonous plants, that is, herbaceous plants (except graminoids), shrubs, bushes, and trees. Mixed feeders incorporate various amounts of monocots and dicots depending on their preferences and on the availability of the different food resources.

The dental microwear pattern is characteristic of the food items ingested and can therefore be used to discriminate between the three dietary categories. Indeed, several studies conducted on various extant mammals, for example hyraxes, ruminants, and equids, have revealed that intensive consumption of graminoids scratches the shearing molar facets more heavily than other food resources, for example foliage (MacFadden et al. 1999; Merceron et al. 2004; Nelson et al. 2005; Solounias et al. 2002; Walker et al. 1978). In parallel to the gradient of abrasiveness observed on the shearing facets of extant herbivores, Calandra et al.

(2008) concluded that *G. subtapiroideum* and *G. steinheimense* from MN8–9 sites were probably mixed feeders; the former species seems to have ingested more abrasive material than the latter (the difference between the two species of gomphotheres appears mainly on the grinding facet, Calandra et al. 2008: Tables 1 and 2; Fig. 2b).

The present results also point to mixed feeding preferences in all the gomphotheres studied (Tables 1 and 2; Figs. 2 and 3). The higher density of scratches observed in adults of *G. subtapiroideum* from Sandelzhausen compared with *G. steinheimense* from MN8–9 sites implies that the former species ingested more abrasive food than the latter (Tables 1 and 2; Fig. 3). This pattern, although less pronounced, is also found between these two species from MN8–9 sites (Tables 1 and 2; Fig. 3).

G. subtapiroideum from Sandelzhausen differs significantly from its relatives from later sites only by having a few more scratches (Tables 1 and 2; Fig. 3a). It therefore appears that the feeding preferences of *G. subtapiroideum* did not change dramatically during five to seven million years, from MN5 to MN8–9.

In contrast with all the gomphotheres studied, which were probably mixed feeders, the high pit percentage observed in this study on the shearing facets of *D. giganteum* (Tables 1 and 2; Fig. 3) points to a browsing diet composed of dicotyledonous plants (see also Calandra et al. 2008).

Generally, reconstructed feeding preferences of fossil herbivorous species can provide insights into the palaeoenvironments where these species lived. We know from the study of extant species that browsers usually live in closed areas such as forests or woodlands; grazers inhabit more open patches where graminoids are available (grasslands, savannas); and mixed feeders occupy a variety of environments (Estes 1991; Gagnon and Chew 2000; Kingdon 1997). There are some exceptions to this pattern, however. For instance, the giraffe (*Giraffa camelopardalis*) browses in open savanna (Codron et al. 2007; Leuthold and Leuthold 1972; Pellew 1983). *Syncerus caffer* is a grazer, but inhabits both savannas and forested environments where it exploits graminoids available in open patches (Blake 2002).

During the MN5, the German Molasse Basin was characterized as "a wetland with forest and woodland hinterland, abundant water bodies surrounded by riparian vegetation, and floodplains with seasonal grass cover" (Eronen and Rössner 2007, p 488). Starting around the Middle-Late Miocene transition, a major uplift phase of the Alps and the drying of the Paratethys Sea in Central Europe increased the conditions of continentalization, resulting in cooler climate and higher seasonality. The environment therefore changed from wetland forests to drier and more open woodlands in this region (Eronen and Rössner 2007). The mixed diet of the gomphotheres studied is consistent with an environment including both open and closed patches, for example woodlands. In this context, the browser *Deinotherium giganteum* could have fed on the dicots available in the closed, woody areas. However, within either wetland forests or more open woodlands, *Gomphotherium subtapiroideum* does not show a significant shift in its feeding preferences. This therefore indicates that this opening of landscapes did not affect the ecology of this species. Assuming that wetland forests reduced during the Middle-Late Miocene, we suggest that *G. subtapiroideum* was not devoted to dense forested habitats and instead may have favored open woodlands that were not affected as much as dense patches by this environmental change.

Conclusions

This study points out the usefulness of dental microwear analyses for shedding light on the palaeobiology of extinct species. First, these results reveal that the feeding preferences of *Gomphotherium subtapiroideum* did not dramatically change through post-weaning ontogenetic development. These first results clearly support that dental microwear is determined not by tooth morphology but solely by the physical properties of food items. Second, our results indicate that *G. subtapiroideum* probably had a wide but constant spectrum of feeding preferences through geological time (see also Calandra et al. 2008; Fox and Fisher 2004). Finally, this study reveals that the three sympatric species of proboscideans from MN8-9 sites differed in their feeding preferences, as suggested by the diversity of their molar occlusal designs. As already emphasized by Calandra et al. (2008), all these sympatric megaherbivores partitioned the food resources available to avoid direct food competition. This process of avoiding ecological niche overlap feeding is called niche partitioning: *G. subtapiroideum* was a mixed feeder; *G. steinheimense* was a mixed feeder also, but less involved in grazing than the former species; and *D. giganteum* mainly browsed on dicots.

Appendix

Table 3 Material list

Species	Locality	Number[a]	Tooth	Loph[b]	Grinding facet	Shearing facet	Comments
G. subtapiroideum (juveniles)	Sandelzhausen (MN5)	1959-II-392	LdP_4			X	
		1959-II-393	RdP_4			X	
		1959-II-441	LdP^3			X	
		1959-II-443	RdP_4			X	
		1959-II-445	RdP_3			X	
		1959-II-446	LdP_3		X	X	LdP_4 present
		1959-II-11304	LdP^3		X	X	
		1959-II-11305	LdP^3			X	
		1959-II-11310	RdP_3			X	
		1959-II-11311	RdP_3			X	
		1959-II-11312	LdP_3			X	
		1959-II-11314	LdP_3			X	
		1959-II-11322	RdP^4		X	X	
G. subtapiroideum (adults)	Sandelzhausen (MN5)	1959-II-384	LM^2		X	X	M^3 present
		1959-II-438	LM^2		X	X	
		1959-II-3722	LM^3		X	X	Same individual as 4783
		1959-II-3723	LM_3			X	
		1959-II-4783	RM^3		X	X	Same individual as 3722
		1959-II-11353	RM^1			X	
		1959-II-11360	LM_1			X	P_4-M_3
		1959-II-11376	RM_2			X	
		1959-II-11377	LM_2			X	
		1959-II-11381	LM_3		X	X	
		1959-II-11382	RM_3		X	X	M_1 or M_2 present
		1959-II-11384	LM_3			X	
	Massenhausen (MN8-9)	1950-I-24a	RM^3	1	X	X	
				2	X	X	
		1954-I-190	LM_3	1	X	X	
				2	X	X	
				3	X	X	
		1954-I-283	RM_3	1	X	X	
				2		X	
G. subtapiroideum (adults)	Massenhausen (MN 8-9)	1967-I-163	LM_3	1	X	X	Same individual as 1950-I-2c
				2	X	X	
				3	X	X	
		1950-I-2c	LM^3	1	X	X	Same individual as 1967-I-163
				2	X	X	
	Illenberg (MN 8-9)	1951-I-26	LM_2	1		X	
	Isarbett bei Grünwald (MN 8-9)	1990-XVIII-153	RM^3	1	X	X	
G. steinheimense (adults)	Markt Indersdorf (MN 8)	1958-I-315	LM^3	2		X	
	Massenhausen (MN 8-9)	1949-I-13a	LM_3	1	X	X	
				2			
		1950-I-20a	LM_2	2	X	X	Same individual as 1950-I-20b
		1950-I-20b	LM_3		X	X	Same individual as 1950-I-20a
		1950-I-22	LM^3	1	X	X	
				2			
		1950-I-34a	LM_3	1	X	X	
				3			
		1950-I-110	LM_3	2	X	X	
				3			

Table 3 continued

Species	Locality	Number[a]	Tooth	Loph[b]	Grinding facet	Shearing facet	Comments
		1955-I-236	RM^1		X	X	Same individual as 1955-I-237 and 239
		1955-I-237	LM^1		X	X	Same individual as 1955-I-236 and 239
		1955-I-239	RM$_1$	1	X	X	Same individual as 1955-I-236 and 237
				2		X	
		1956-I-400a	RM^3		X	X	Same individual as 1956-I-400b
		1956-I-400b	LM^3	1	X	X	Same individual as 1956-I-400a
		1959-I-432	LM$_2$	1		X	
			LM$_3$	1		X	
	München-Ingolstätter Straße (MN 8-9)	1938-I-36	LM$_3$	2	X	X	
				3			
	Giggenhausen (MN 8-9)	1956-I-408	RM$_3$	3	X	X	
				4			
	Hirschhorn (MN 8-9)	1975-I-110	LM$_3$	1	X	X	
				2		X	
				3			
	Grosslappen (MN 9)	1925-I-49	LM^2	1	X	X	
D. giganteum (adults)	Fraunberg (MN 8)	1953-I-297	LM^1		X	X	
		1963-I-22	M^2		X	X	
	Massenhausen (MN 8-9)	1949-I-13d	RM^1	1	X	X	
		1950-I-16a	LM^3	1	X	X	
		1950-I-17	LM^2	1	X	X	
		1950-I-20c	LM^2	1	X	X	
		1950-I-23b	RM^2	1	X	X	
		1950-I-27b	RM^1	1	X	X	
				2		X	
				3		X	
		1951-I-47D	LM$_2$	1	X	X	Same individual as 1951-I-47G,H,L,Q
		1951-I-47G	LM$_1$	1	X	X	Same individual as 1951-I-47D,H,L,Q
				2	X		
				3			
		1951-I-47H	LM$_3$			X	Same individual as 1951-I-47D,G,L,Q
		1951-I-47L	RM^1	1	X	X	Same individual as 1951-I-47D,G,H,Q
				2	X		
		1951-I-47Q	LM^2		X	X	Same individual as 1951-I-47D,G,H,L
		1953-I-103	LM$_2$		X	X	
			LM$_3$		X	X	
		1953-I-361	RM$_2$		X	X	
			RM$_3$		X	X	
		1954-I-284	LM$_2$		X	X	
		1954-I-503	LM^2	1	X	X	
		1959-I-431	RM^1	1	X	X	
	Hirschhorn (MN 8-9)	1953-I-363	RM^2		X	X	
	N-Ebing Inn. (MN 9)	1970-XII-1	M$_1$ or M$_3$		X	X	
		1970-XII-2d	M^2		X	X	Same individual as 1970-XII-2 h
		1970-XII-2 h	M^3		X	X	Same individual as 1970-XII-2d

d deciduous, *L* left, *M* molar, *P* premolar, *R* right

[a] The inventory numbers are preceded by "BSPG", in reference to the Bayerische Staatssammlung für Paläontologie und Geologie in Munich, Germany

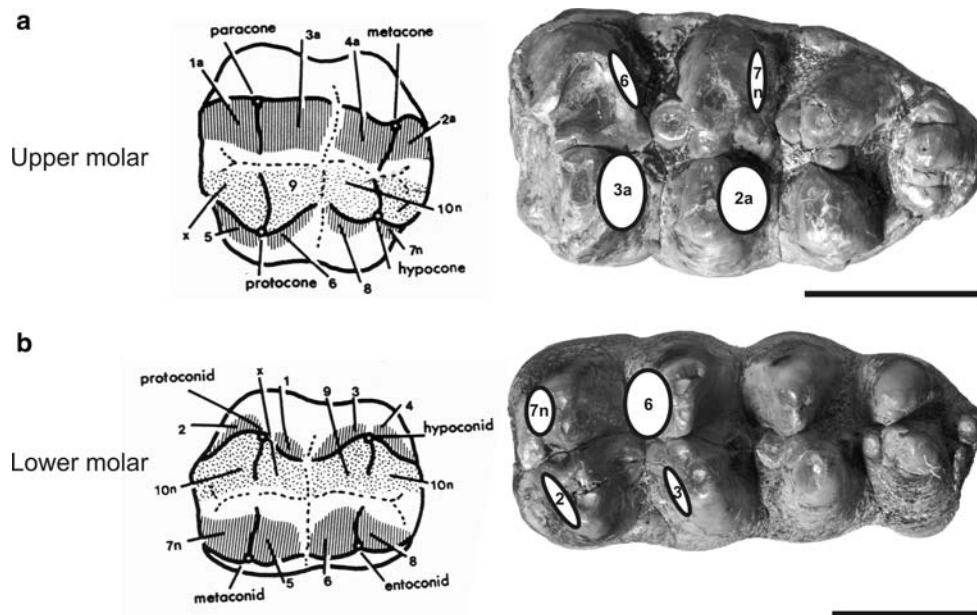[b] Lophs are numbered from mesial to distal

Fig. 4 Dental facet nomenclature. Occlusal views of left M^2 (**a**, *left*) and right M_2 (**b**, *left*) of *Macaca mulatta* with location of each dental facet superimposed (modified after Kay 1977). *Stippled features* symbolize the grinding facets that are involved in phase II of mastication. Shearing facets are *hatched* and are involved in the lingual and buccal chewing phases I. The shearing facets that were investigated in this study are drawn on a right M^3 (BSPG 1959 II 4783; **a**, *right*) and on a left M_3 (1959 II 11381; **b**, *right*) of adult of *Gomphotherium subtapiroideum* from Sandelzhausen. Homologous facets on the posterior loph(id)s of molars are not represented here but were also investigated in this study. *Scale bars* = 50 mm

Table 4 ANOVA summary

		df	Number of scratches (Ns)				Length of scratches (μm)			
			SS	MS	F	p	SS	MS	F	p
Species versus species (adults)	Shearing facet effect	3	5537.02	1845.67	25.53	**<0.001**	1388.58	462.86	2.74	0.055
	Residuals	43	3108.48	72.29			7259.42	168.82		
Juveniles versus adults	*G. subtapiroideum* effect	1	24.17	24.17	0.47	0.499	445.13	445.13	13.89	**0.001**
Sandelzhausen, shearing facet	Residuals	22	1124.33	51.11			704.87	32.04		

		df	Number of pits (Np)				Number of wide scratches (width > 15 μm)			
			SS	MS	F	p	SS	MS	F	p
Species versus species (adults)	Shearing facet effect	3	289.92	96.64	0.50	0.686	2431.52	810.51	5.90	**0.002**
	Residuals	43	8357.08	194.35			5911.98	137.49		
Juveniles versus adults	*G. subtapiroideum* effect	1	131.58	131.58	2.85	0.106	177.27	177.27	4.26	0.051
Sandelzhausen, shearing facet	Residuals	22	1016.92	46.22			914.73	41.58		

		df	Number of large pits (breadth > 15 μm)				Total number of microwear scars (= Np + Ns)			
			SS	MS	F	p	SS	MS	F	p
Species versus species (adults)	Shearing facet effect	3	2720.57	906.86	6.60	**<0.001**	390.10	130.03	0.68	0.571
	Residuals	43	5905.93	137.35			8257.40	192.03		
Juveniles versus adults	*G. subtapiroideum* effect	1	229.76	229.76	5.55	**0.028**	104.90	104.90	2.21	0.151
Sandelzhausen, shearing facet	Residuals	22	910.24	41.37			1044.60	47.48		

		df	Percentage of pits (= Np/[Np + Ns])			
			SS	MS	F	p
Species versus species (adults)	Shearing facet effect	3	2801.30	933.77	6.87	**<0.001**
	Residuals	43	5846.70	135.97		
Juveniles versus adults	*G. subtapiroideum* effect	1	211.51	211.51	4.96	**0.037**
Sandelzhausen, shearing facet	Residuals	22	938.49	42.66		

df, degrees of freedom; *F*, *F*-value; *MS*, mean square; *p*, probability; *SS*, sums of squares
The bold values indicate *p* values lower than 0.05

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