

## A combined-mesowear analysis of late Miocene giraffids from North Chinese and Greek localities of the Pikermian Biome



Melinda Danowitz<sup>a</sup>, Sukuan Hou<sup>b,\*</sup>, Matthew Mhlbachler<sup>a,c</sup>, Victoria Hastings<sup>a</sup>, Nikos Solounias<sup>a,c</sup>

<sup>a</sup> Department of Anatomy, New York College of Osteopathic Medicine of New York Institute of Technology, Old Westbury, NY 11568-8000, USA

<sup>b</sup> Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China

<sup>c</sup> Department of Paleontology, American Museum of Natural History Central Park West at 79th Street, New York NY 10024

### ARTICLE INFO

#### Article history:

Received 29 November 2015

Received in revised form 23 January 2016

Accepted 9 February 2016

Available online 20 February 2016

#### Keywords:

mesowear

diet

Pikermian Biome

Giraffidae

### ABSTRACT

The family Giraffidae is represented by two extant taxa (*Giraffa camelopardalis* and *Okapia johnstoni*), both of which are committed browsers. During the late Miocene, however, the Pikermian Biome included more than 15 giraffid species with a wider range of dietary ecologies. To examine the diet of these taxa, we apply a novel combined approach using four variables from two methods of dental mesowear. We score the traditional outer mesowear, which evaluates the sharpness and relief of the labial-most paracone enamel band. We also apply inner mesowear, which evaluates the surface morphology of the lingual band of paracone enamel on the mesial and distal ends, as well as the junction point between the two. Using a database of 8 extant species ( $N = 98$ ) of browsing, grazing, and mixed feeding ruminants, we predict the diets 190 extinct giraffid specimens. The discriminant function analysis (DFA) of the extant taxa using all four mesowear variables predicted diet with greater accuracy than any single mesowear variable. We compare the dietary profiles of species found in four Pikermian Biome regions: Samos, Pikermi, North China, and Linxia Basin. We find differences in the giraffid diet throughout the Pikermian Biome: in the localities from Greece, a larger number of giraffids were predicted as browsers, whereas both Chinese regions included a larger number of mixed feeding individuals. Our inner and outer mesowear dietary predictions agree with previously studied ecomorphological paleodietary proxies. Our data supports the hypothesis that the late Miocene giraffids comprised a wider range of dietary habits than the living giraffe and okapi.

© 2016 Elsevier B.V. All rights reserved.

### 1. Introduction

Mesowear is an aspect of dental morphology based on macroscopic wear in ungulate molars caused by relative amounts of attrition and abrasion (Fortelius and Solounias, 2000; Mhlbachler et al., 2011). In contrast to dental microwear, which relates only to the last few meals, mesowear is a macroscopic approach that is a consequence of diet during a time period ranging approximately from weeks to years, depending on the overall rate of dental wear (Rivals et al., 2007; Damuth and Janis, 2014). Therefore, mesowear is a representation of overall diet over an extended period of the individual's life rather than a reflection of its last few meals. Browsing animals with low abrasion diets develop complex occlusion due to attritionally dominated wear, where cusps maintain high relief with sharpened apices. Grazing diets and other abrasive diets, such as those with high concentrations of ingested exogenous grit (e.g. fine silica particles) result in low-relief occlusal surfaces, blunted cusp apices, and less complex occlusal relationships.

The original formulation of a methodology for mesowear analysis involved categorizing the sharpness and degree of relief of the labial-most cutting edge of enamel, either on the paracone or the metacone (Fortelius and Solounias, 2000). Subsequent mesowear analyses, including modifications to the method (e.g. Mhlbachler et al., 2011; Tütken et al., 2013), have focused on the same aspect of morphology. Solounias et al. (2014) expanded mesowear to the lingual band of enamel of the paracone and metacone and its relationship to browsing and grazing diets. Because the portion of the tooth is not on the labial-most edge of the tooth, it is less prone to postmortem damage and more frequently available for sampling in modern and fossil specimens. Here we refer to the traditional approach to scoring the labial most edge of enamel as 'outer mesowear' and the area sampled by Solounias et al. (2014) as 'inner mesowear'.

Traditional outer mesowear evaluates the height and sharpness of the labial-most enamel band, and inner mesowear scores the surface morphology of the lingual enamel band of the paracone and metacone in three areas. While both methods have been successfully utilized to predict the diet of extant ruminants (Fortelius and Solounias, 2000; Solounias et al., 2014), they evaluate different aspects of enamel wear and tooth morphology. The combination inner and outer mesowear

\* Corresponding author.

E-mail address: [housukuan@ivpp.ac.cn](mailto:housukuan@ivpp.ac.cn) (S. Hou).

variables would therefore allow for a more comprehensive analysis of tooth wear, and together could presumably better predict ruminant diet than any single variable. We therefore utilize variables from both outer and inner mesowear to characterize the dietary patterns of the late Miocene giraffids of North China, Samos, and Pikermi, and to evaluate potential ecological differences between these localities.

Giraffes are among the largest-bodied ruminants, and as such, the paleodiets of giraffids are of interest because they provide insights into the evolution of ruminant physiology and its morphophysiological limitations on traits such as body size (Clausen et al., 2003). Moreover, as large animals, giraffids are potential keystone species that were important in forming ancient habitats and ecosystems (Bell, 1971). The giraffe (*Giraffa camelopardalis*) and the okapi (*Okapia johnstoni*), the only extant species of Giraffidae, inhabit sub-Saharan Africa, and have browsing diets (Dagg and Bristol Foster, 1982; Estes, 1991; Dagg, 2014). During the late Miocene, giraffids were taxonomically more diverse than present and inhabited the vast geographic span of the now extinct Pikermian Biome, which stretched from Spain to China and Africa (Crusafont-Pairó, 1952; Kurtén, 1952; Churcher, 1970). Up to 22 species of giraffids have been identified from the middle and late Miocene of Eurasia and Africa (Hamilton, 1978), with new species presently being discovered and described (Harris et al., 2010; Marra et al., 2011).

Approximately 7600 km separated the giraffid faunas in the eastern and western ends of the Pikermian Biome (Kurtén, 1952; Solounias et al., 1999). Some fossil giraffid species had vast geographic ranges that spanned the entire Pikermian Biome. The higher diversity levels of giraffids in the past (Gentry et al., 1999), suggest that they were important components of the Pikermian ecosystem.

Large quantities of dentitions of 18 giraffid species living between 9 and 6 Ma have been recovered in North Chinese localities (Bohlin, 1926; Hou et al., 2014), and from Greek localities such as Samos, and Pikermi (Kostopoulos, 2009). The North China Uppsala collection was assembled from excavations in Shanxi, Shaanxi, Henan and Gansu provinces in the beginning of the 20th century (Bohlin, 1926; Mather and Lucas, 1985). The North China Hezheng collection is derived from more recent excavations around localities of the Linxia Basin in Gansu Province; the Linxia area has produced an abundant mammal fossil collection (Deng, 2005). In this study, we refer to the Uppsala collection as “North China,” and the Hezheng collection as “Linxia Basin.” The Chinese region of the Pikermian Biome has also been termed the “Baodean Biome.” Pikermi is located 20 km east of Athens, and excavations have provided large amounts of late Miocene fossil specimens (Gaudry, 1862; Theodorou and Nicolaides, 1988). Samos bone beds are concentrated in two horizons; an older one at 7.9 Ma and a younger one at 7.2 Ma (Weidmann et al., 1984). Samos is the richest fossil locality for giraffids, with nine species currently identified (Bernor et al., 1996).

Previous microwear and mesowear investigations of giraffid paleodiets from Samos and Pikermi concluded that the majority of Samos and Pikermi giraffids were not browsers, but incorporated grass into their diets (Solounias and Dawson-Saunders, 1988; Solounias et al., 1988, 2000, 2010, 2012). The dietary habits of the giraffids found in North China have never been studied or reported. Thus the present study widens the knowledge of dietary patterns of Pikermian Biome giraffids from the previously studied confined area in Greece to the entire, vast geographic area. Ecological differences between the woodland Greek localities and the steppe Chinese localities are likely reflected in the giraffid dietary patterns (Kurtén, 1952; Quade et al., 1994; Deng, 2005; Velitzelos et al., 2014).

Here we investigate three questions of mesowear analysis and giraffid paleoecology:

- (1) Which if any of the numerous mesowear methods are more related to diet among extant ruminants and are better paleodietary proxies?
- (2) Do giraffids of the Pikermian Biome, which are more diverse than modern giraffids and with a wider geographic range, exhibit a

greater amount of dietary diversity, or were all species of giraffids confined to the browser end of the browser-grazer continuum, as are modern giraffids?

- (3) Do mesowear predictions derived for fossil giraffids agree with other ecomorphological paleodietary proxies such as masseteric area or premaxillary shape?

## 2. Materials and methods

### 2.1. Institutional abbreviations

AMNH, American Museum of Natural History, New York, USA; GMM, Geomuseum of the WWU, Münster, Germany; HLMD, Hessisches Landesmuseum Darmstadt, Germany; HPM, Hezheng Paleozoological Museum, Hezheng, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; MGL, Musée Géologie Lausanne, Switzerland; MNHN, Muséum National d'Histoire Naturelle, Paris, France; NHM, Natural History Museum, London, UK; NHMBa Natural History Museum of Basel, Switzerland; NHMBc, Natural History Museum of Bern, Switzerland; NHMW, Natural History Museum of Vienna, Austria; PIU, Paleontological Institute of Uppsala, Sweden; SMF, Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt, Germany; SMNS, State Museum of Natural History, Stuttgart, Germany; PIUW, Paleontological Institute Vienna, Austria.

### 2.2. Extant database

To establish a relationship of mesowear scoring systems to browsing, grazing, and mixed feeding diets, we scored outer and inner paracone mesowear in extant ruminants (Table 1a) from wild collected specimens from the American Museum of Natural History Mammalogy collection. Three browsing, two grazing, and three mixed feeding species were selected (Table 1). *Okapia johnstoni*, *Giraffa camelopardalis*, and *Alces alces* were selected as representative browsers; *Kobus ellipsiprymnus*, and *Connochaetes taurinus* were selected as representative grazers; *Ourebia ourebi*, *Cervus canadensis*, and *Gazella granti* were selected as representative mixed feeders. Species diets had been previously confirmed by isotope analysis, stomach structure, and animal observation (Cerling et al., 2003; Ambrose and DeNiro, 1986; Hofmann and Steward, 1972; Hörnberg, 2001). Individual teeth that were too young (unworn) or too old (completely worn) were not included in the sample. Each tooth was scored based on the agreement of two observers (M.D. and N.S.); each tooth that had discordant scoring was discussed, and if an agreement could not be made, the specimen was excluded from the sample. The majority of teeth, however, were agreed upon initially, without further discussion. (See Table 1b.)

### 2.3. Scoring of inner mesowear variables

Inner mesowear draws data from the enamel band forming the lingual margin of the metacone from an occlusal view. This lingual enamel band is scored on the mesial and distal sides of the paracone using the

**Table 1a**  
Mean mesowear scores for outer mesowear, mesial, distal, and J, for extant ruminants.

Diet	Species	N	Outer Mesowear	Mesial	Distal	J
Browser	<i>Okapia johnstoni</i>	11	0.8	1.5	1.3	1.5
Browser	<i>Giraffa camelopardalis</i>	16	1.3	1.3	1.6	1.8
Browser	<i>Alces alces</i>	14	1.1	1.1	1.3	1.6
Grazer	<i>Connochaetes taurinus</i>	14	3.7	3.9	3.9	3.7
Grazer	<i>Kobus ellipsiprymnus</i>	12	2.8	3.2	3.3	3.6
Mixed feeder	<i>Ourebia ourebi</i>	9	2	3.7	3.6	3.8
Mixed feeder	<i>Cervus canadensis</i>	5	1	1.6	1.6	1.4
Mixed feeder	<i>Gazella granti</i>	17	2.1	2.3	2.6	2.8

**Table 1b**

Mean mesowear scores for outer mesowear, mesial, distal, and J, for Giraffidae from the late Miocene of China and Greece. LB: Linxia Basin NC: North China.

Location	Species	N	Outer Mesowear	Mesial	Distal	J
LB	<i>Samotherium</i> sp. 1	10	1.9	2.3	2.1	2.3
LB	<i>Samotherium boissieri</i>	1	/	2	4	3
LB	<i>Samotherium sinense</i>	3	4	3.3	3.3	2.7
LB	<i>Alcicephalus neumayri</i>	2	1.5	2	1.5	1.5
LB	<i>Honanotherium schlosseri</i>	10	1.9	2.4	2	2.6
LB	<i>Honanotherium</i> sp. 2	1	/	4	4	4
LB	<i>Honanotherium</i> sp. 3	1	4	3.5	4	4
LB	<i>Palaeotragus coelophrys</i>	12	2.2	2.6	2.7	3
LB	<i>Schansitherium tafeli</i>	10	1.9	2.6	2.2	2.3
NC	<i>Palaeotragus coelophrys</i>	16	1.7	1.9	1.8	2
NC	<i>Palaeotragus rouenii</i>	24	1.9	2.1	2.3	2.4
NC	<i>Samotherium sinense</i>	2	2.8	3.5	3.5	3.5
NC	<i>Samotherium boissieri</i>	2	2	/	/	/
NC	<i>Samotherium</i> sp. 2	2	2.5	3	4	3
NC	<i>Honanotherium schlosseri</i>	10	1.8	2.1	2.5	2.3
NC	<i>Bohlinia</i> sp.	2	2	1.8	2	2
NC	<i>Bramatherium</i> sp.	9	1.9	2.5	2.6	2.5
NC	<i>Schansitherium decipiens</i>	8	2.8	3.5	3.7	3.2
NC	<i>Alcicephalus neumayri</i>	2	/	2.5	3	2.5
Samos	<i>Samotherium major</i>	27	2	2.6	3.1	2.3
Samos	<i>Samotherium boissieri</i>	7	/	2.7	2.8	3.2
Samos	<i>Bohlinia attica</i>	1	1	1	1	1
Samos	<i>Helladotherium duvernoyi</i>	3	1.3	1.7	1.7	1.7
Samos	<i>Palaeotragus rouenii</i>	17	1	1.5	2.1	1.5
Samos	<i>Palaeotragus coelophrys</i>	2	1	2	1	1
Pikermi	<i>Helladotherium duvernoyi</i>	2	2	1	2	1.5
Pikermi	<i>Bohlinia attica</i>	1	3	2	3	2
Pikermi	<i>Honanotherium</i> sp. 1	1	2	1	2	1
Pikermi	<i>Palaeotragus rouenii</i>	21	1.8	1.7	2	1.9

same 4 point scaling system described below (Fig. 1). (1) The occlusal surface of the enamel band is flat and planar and there are no gouges or indentations on the surface of the enamel. (2) The surface of the enamel band is nearly flat and contains several gouges that traverse the surface from either edge. The labial and lingual edges of the enamel band are somewhat rounded. Instead of a single surface as in score 1, several facets are discernible. (3) The enamel surface is similar to score 2, but is more rounded with less defined edges and more gouges. (4) The enamel surface is rounded. The surface is smooth without gouges, and there are no well-defined edges.

This four point scoring system has been experimentally tested using wild adult goats (*Capra hircus*) (Solounias et al., 2014). Before the experiment, the goats were browsing and mixed feeding in the wild. Populations of goats were fed either an exclusively browsing diet, or an exclusively grazing diet for 40 days, and at 10-day intervals, a single individual from each population was sacrificed and the inner mesowear was scored. In the browsing population, the inner mesowear scores reflected incrementally flatter enamel bands. The teeth of the goats that were subjected to grazing became incrementally rounder throughout the experimental period.

The midpoint between the mesial and distal parts of the band surrounding the cusp, termed J (junction), was evaluated as a separate variable using a 4 point scoring system (Solounias et al., 2014). (1) The mesial and distal surfaces join at a sharp, well-defined junction. (2) The midpoint between the mesial and distal surfaces is somewhat sharp, and often contains a gouge. (3) The midpoint on the enamel band is rounded, but the mesial and distal sides appear as distinct, separate surfaces. (4) The J point lacks a discrete apex, and the mesial and distal sides of the enamel band form one continuous surface (Fig. 2).

#### 2.4. Statistical analysis

We conducted Pearson Correlation tests to determine whether the four mesowear variables (outer mesowear, mesial, distal, and J) were

correlated in both the extant and extinct samples. An independent samples Kruskal-Wallis test was performed to analyze the distribution of scores for each mesowear variable. Mann-Whitney U tests were performed to compare the four mesowear variables in the Chinese and Greek localities.

Discriminant function analyses (DFA) were conducted in SAS 9.4 for both the extant ruminants and the extinct giraffids. Because of missing data, due to incomplete specimens, some of the specimens were by necessity excluded from the DFA. Using diet as the grouping variable, DFA was run with the four mesowear variables to evaluate the ability of the mesowear variables to accurately predict diet of individual molars from the extant ruminant sample. The resulting discriminant functions were then used to predict browsing, grazing, or mixed feeding diet in the individual fossil giraffid specimens. With these results, we developed a series of dietary prediction profile histograms for well-represented species (where  $n \geq 5$ ) that could then be compared to the results of the extant species.

Many extinct species were found in several regions. For example, *Palaeotragus coelophrys* comes from North China, Linxia Basin, and Samos. We treated species found in multiple localities as separate samples in the analysis. All available adult fossil giraffid teeth from North China, Linxia Basin, Samos, and Pikermi were scored in this study (Table 2).

### 3. Results

#### 3.1. Relationship of mesowear variables

Pearson Correlation Coefficients (Table 3) were all highly significant in comparing any of the four mesowear variables in both fossil and modern species. In all instances  $P < 0.001$ . Correlation coefficients were higher among the extant data, most likely because the modern sample spanned the entire browser-grazer continuum resulting in high frequencies of mesowear variables at the extreme high and low ends of the scoring spectrum (Fig. 3). Nonetheless, significant correlations between all four mesowear variables suggest they all have a similar ecological signal in both modern ruminants and fossil giraffids. The four individual Kruskal-Wallis tests for each mesowear variable revealed significant differences in the distribution of all inner and outer mesowear variables between extant browsing, grazing, and mixed feeding ruminants. For all tests  $P < 0.001$ . The relationships of the mesowear variables among extant and extinct taxa are the same. In both sets of taxa, comparisons of outer mesowear (OM) with any of the three inner mesowear variables (M, D, J) produce lower correlation coefficients than comparisons of inner mesowear variables with inner mesowear variables.

#### 3.2. Distribution of raw mesowear scores

The distribution of raw mesowear scores (Fig. 4) reveals that extant browsing grazing and mixed feeding species produce distinctive mesowear score profiles. Browsers most frequently produce low mesowear scores for all variables studied (Fig. 4A). Mixed feeders have the widest range of mesowear scores with more intermediate scores on average (Fig. 4B), while grazers produce the highest frequencies of high mesowear scores for all four variables (Fig. 4C).

The fossil giraffids have mesowear score distributions that include frequent instances of mesowear scores exceeding those of browsing ruminants, suggesting a total range of dietary diversity that extends from browsing into mixed feeding and possibly grazing (Fig. 5). This indicates that the total dietary spectrum of these giraffid faunas included individuals that were ingesting a significant amount of grass or grit. However, there are also statistically significant differences between the four localities (see below) suggesting ecological differences in the giraffid faunas in these localities. At Samos, the mesial, distal, and J variables have the lowest scores on average. The majority of individuals scored a 1 in the

**Table 2**

Discriminant function analysis dietary predictions for extant taxa and extinct giraffids, organized by locality. LB: Linxia Basin NC: North China.

Species	Locality	Frequency Browser	Frequency Mixed	Frequency Grazer	Undetermined
<i>Okapia johnstoni</i>		10	1		
<i>Giraffa camelopardalis</i>		14		1	1
<i>Alces alces</i>		13			1
<i>Ourebia ourebi</i>			6	2	1
<i>Cervus canadiensis</i>		4	1		
<i>Gazella granti</i>		2	6	1	8
<i>Kobus ellipsiprymnus</i>		1	6	5	
<i>Connochaetes taurinus</i>			3	11	
<i>Samotherium sp. 1</i>	LB	4	3	1	2
<i>Samotherium boissieri</i>	LB				1
<i>Samotherium sinense</i>	LB			1	2
<i>Alcicephalus neumayri</i>	LB	2			
<i>Honanotherium schlosseri</i>	LB	3	3	1	
<i>Honanotherium sp. 2</i>	LB				1
<i>Honanotherium sp. 3</i>	LB			1	
<i>Palaeotragus coelophrys</i>	LB	2	7	1	
<i>Schansitherium tafeli</i>	LB	3	3		4
<i>Palaeotragus coelophrys</i>	NC	9	5	1	1
<i>Palaeotragus rouenii</i>	NC	13	9	2	
<i>Samotherium sinense</i>	NC		1	1	
<i>Samotherium boissieri</i>	NC		2		
<i>Samotherium sp. 2</i>	NC		1		1
<i>Honanotherium schlosseri</i>	NC	4	5		1
<i>Bohlinia sp. 2</i>	NC	1			
<i>Bohlinia sp. 1</i>	NC				1
<i>Bramatherium sp.</i>	NC	4	3	1	1
<i>Schansitherium decipiens</i>	NC		4	2	1
<i>Alicecephalus neumayri</i>	NC				2
<i>Samotherium major</i>	Samos	8	5	1	9
<i>Samotherium boissieri</i>	Samos		2		4
<i>Bohlinia attica</i>	Samos	1			
<i>Helladotherium duvernoyi</i>	Samos	2	1		
<i>Palaeotragus rouenii</i>	Samos	8			5
<i>Palaeotragus coelophrys</i>	Samos	1			1
<i>Helladotherium duvernoyi</i>	Pikermi	2			
<i>Bohlinia attica</i>	Pikermi		1		
<i>Honanotherium sp. 1</i>	Pikermi	1			
<i>Palaeotragus rouenii</i>	Pikermi	11	3		4

mesial, distal, and J variables (Fig. 5A). Pikermi differs from Samos primarily in having higher mesowear scores for some variables (outer mesowear) and lower mesowear scores for others (distal and J), suggesting that tooth wear patterns were not identical at these localities (Fig. 5B). Chinese giraffids show a high diversity of mesowear scores, like Greek giraffids, suggesting mixed feeding. However they differ from giraffids from Greece mainly in having fewer low mesowear scores among all four variables, suggesting more abrasive diets (Fig. 5C and D).

### 3.3. Comparison of Greek and Chinese giraffid mesowear

Mann Whitney U Tests found significant differences in the distributions of outer mesowear, mesial, and J between the combined Chinese and the combined Greek fossil giraffids, but no significant differences in the distal inner mesowear variable between these two extreme ends of the Pikermian Biome (Table 4). Mann Whitney U tests revealed no significant differences in the four mesowear variables between

giraffids in North China versus Linxia Basin (Table 4), suggesting homogeneous giraffid paleoecology between the two fossiliferous regions of China. However, significant differences in the outer mesowear score were found between giraffids in Pikermi versus Samos (Table 4) perhaps suggesting greater heterogeneity of giraffid paleoecology in Greece. None of the other mesowear variables were significantly different between the two Greek localities, although the mesial and distal variables approached significance, suggesting a larger sample size might reveal significant differences in the inner mesowear of these two Greek faunas.

### 3.4. Dietary predictions based on DFA

DFA's ran separately for the four individual mesowear variables, using diet (browse, grazer, mixed feeder) as the grouping variable, produced significant results. Each individual variable performed similarly and predicted diet for the molars of the extant species with accuracy

**Table 3**

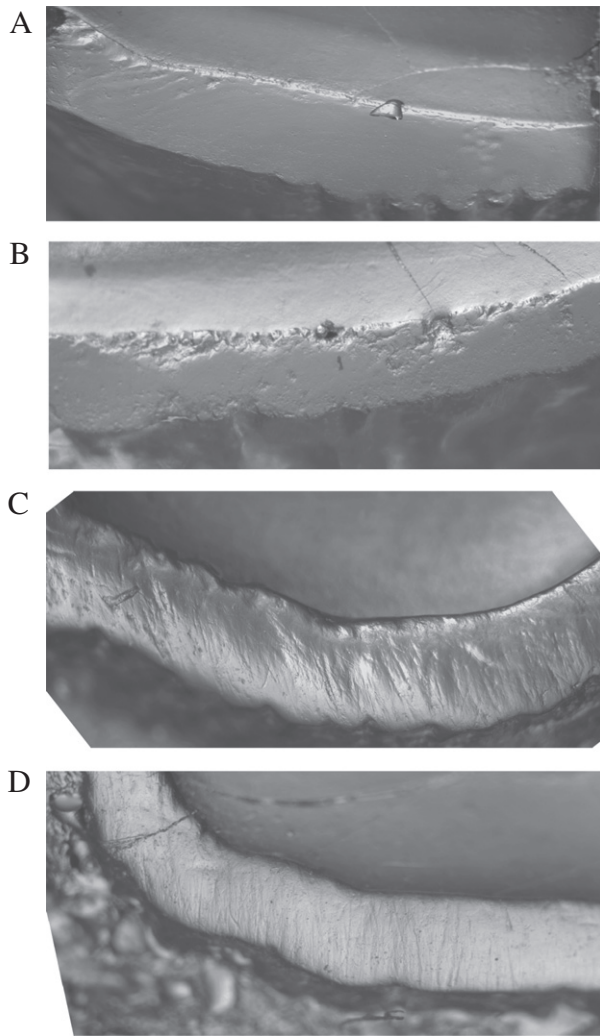
Pearson Correlation of all mesowear variables in extant taxa (bottom left) and in extinct giraffids (top right). All correlation values are significant at the 0.01 level.

	Outer mesowear	Mesial	Distal	J
Outer mesowear		.488	.496	.510
Mesial	.615		.800	.783
Distal	.700	.905		.719
J	.702	.820	.835	

**Table 4**

P-values of Mann Whitney U Tests comparing the inner and outer mesowear variables in the Greek and Chinese localities.

	Greek vs. Chinese faunas	Linxia Basin vs. North China faunas	Pikermi vs. Samos faunas
Outer mesowear	<b>.006</b>	.293	<b>.036</b>
Mesial	<b>.001</b>	.633	.066
Distal	.269	.374	.086
J	<b>.001</b>	.814	.420



**Fig. 1.** The four stages of inner mesowear. This scoring system can be applied separately to the mesial and distal surfaces of the lingual enamel band of the paracone and metacone. (A) Stage 1: The occlusal surface of the enamel band is flat and planar and there are no gouges or indentations on the surface of the enamel. (B) Stage 2: The surface of the enamel band is nearly flat and contains several gouges that traverse the surface from either edge. The labial and lingual edges of the enamel band are somewhat rounded. Instead of a single surface as in score 1, several facets are discernible. (C) Stage 3: The enamel surface is similar to score 2, but is more rounded with less defined edges and more gouges. (D) Stage 4: The enamel surface is rounded. The surface is smooth without gouges, and there are no well-defined edges.

rates ranging from 63.7% – 68.4%. DFA using all four mesowear variables resulted in two significant discriminant functions ( $P < 0.001$  for DF1, and  $P = 0.41$  for DF2) based on the extant taxa with canonical correlations of 0.82 and 0.31. The resultant discriminant model was able to predict diet in the molars of the extant species with 75.9% accuracy.

Using the resultant discriminant functions, the diet of each individual extinct giraffid molar was predicted as a browser, grazer, or mixed feeder (Table 2). We generated dietary prediction profiles (Fig. 6) for the extant and extinct species so that we could compare the pattern of dietary predictions between the two groups, to make inferences about the most likely diets of the fossil giraffid species for which we had appropriate samples. DFA was not always successful at accurately assigning individual teeth to diet among the extant animals, however, the distributions of the predictions created distinctive profiles, represented as histograms (Fig. 3) that could be compared to the profiles of the extinct giraffids.

*Samotherium* was found in both Chinese collections and in Samos. The majority of individuals were predicted as browsing or mixed feeding (Table 2) with higher concentrations of individuals predicted to be mixed feeders and grazers compared to extant browsers. *Samotherium* sp. from Linxia Basin had the largest number of individuals predicted as browsers, followed closely by mixed feeders. *Samotherium major* from Samos had a large number of individuals whose diet was undetermined, followed by browsers (Fig. 6B).

The *Palaeotractus* group had the largest number of individuals in our sample, and was found in all four localities. Most individual specimens of *Palaeotractus* were classified as browsers (Table 2), but also with some specimens classified as mixed feeders and grazers, suggesting that this genus was overall a mixed feeder. *Palaeotractus coelophrys* from Linxia Basin had the greatest number of individuals as mixed feeders, whereas *Palaeotractus coelophrys* from North China, as well as *Palaeotractus rouenii* from North China, Samos, and Pikermi had the majority of individuals as browsers (Fig. 6B).

*Schansitherium* individuals were found in both Chinese localities. The majority of individuals were predicted as mixed feeding (Table 2). *Schansitherium decipiens* had the highest frequency of individuals as mixed feeders (Fig. 6B).

Bohlininae had the largest number of species in our sample, and members have been recovered from all four localities. The largest number of individuals were predicted as browsing, followed closely by mixed feeding (Table 2). *Honanotherium schlosseri* from both Chinese localities had the majority of individuals predicted as browsers or mixed feeders (Fig. 6B).

Sivatheriinae individuals were evaluated from Samos, Pikermi, and North China. The largest number of individuals were predicted as browsing (Table 2). *Bramatherium* sp. had the highest frequency of browsing individuals, followed closely by mixed feeding individuals (Fig. 6B).

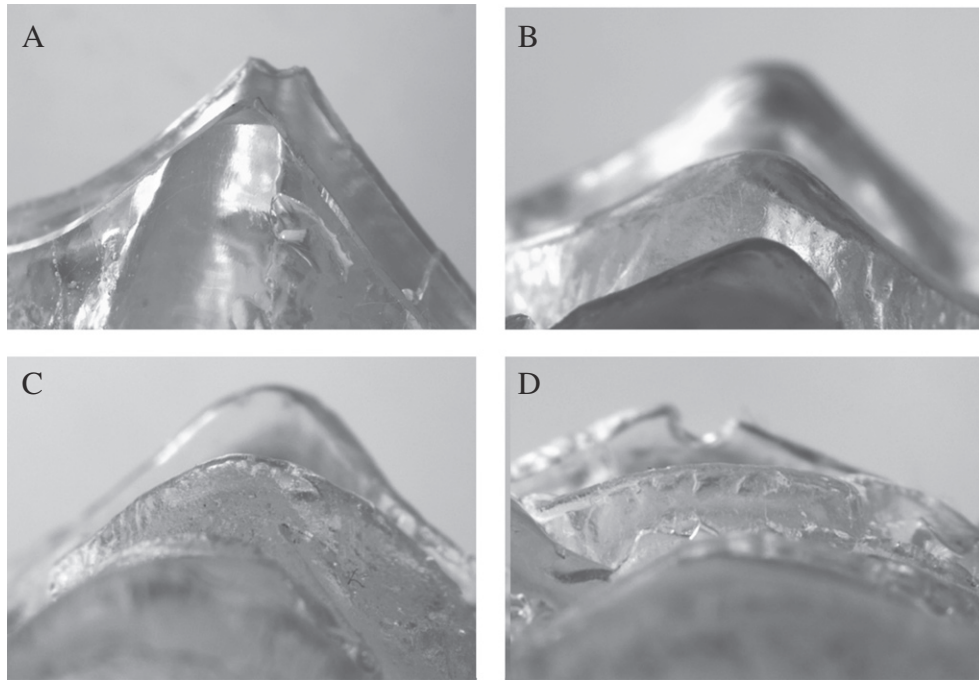
When all of the individual dietary predictions resulting from the DFA are combined into the four faunas, differences between the dietary distributions of the Greek vs. Chinese localities are revealed (Fig. 7). In both Chinese localities, the majority of individuals were predicted as browsers or mixed feeders. In both Greek localities, the dietary predictions were polarized towards browsing (Fig. 7). These results reflect those of the distributions of the raw mesowear scores (Fig. 5).

## 4. Discussion

### 4.1. Dietary analysis using inner and outer mesowear variables

Outer mesowear evaluates the height and relief of the labial-most enamel band (Fortelius and Solounias, 2000; Muhlbachler et al., 2011). Inner mesowear evaluates the surface morphology of the mesial and distal aspects of the lingual band of the paracone and metacone, as well as the height of the central junction, which are scored to predict dietary patterns (Solounias et al., 2014). This is an inherently subjective paleodietary method, as it scores qualitative features of the enamel band. The scoring system clearly differentiates between the extreme stages (1 & 4), however there is overlap between features of the transitional stages (2 & 3), allowing for potential error and bias. The labial aspect of molars is more sensitive to post-mortem damage than inner parts of the teeth. Therefore, inner mesowear data is more frequently available than outer mesowear data (supplemental data).

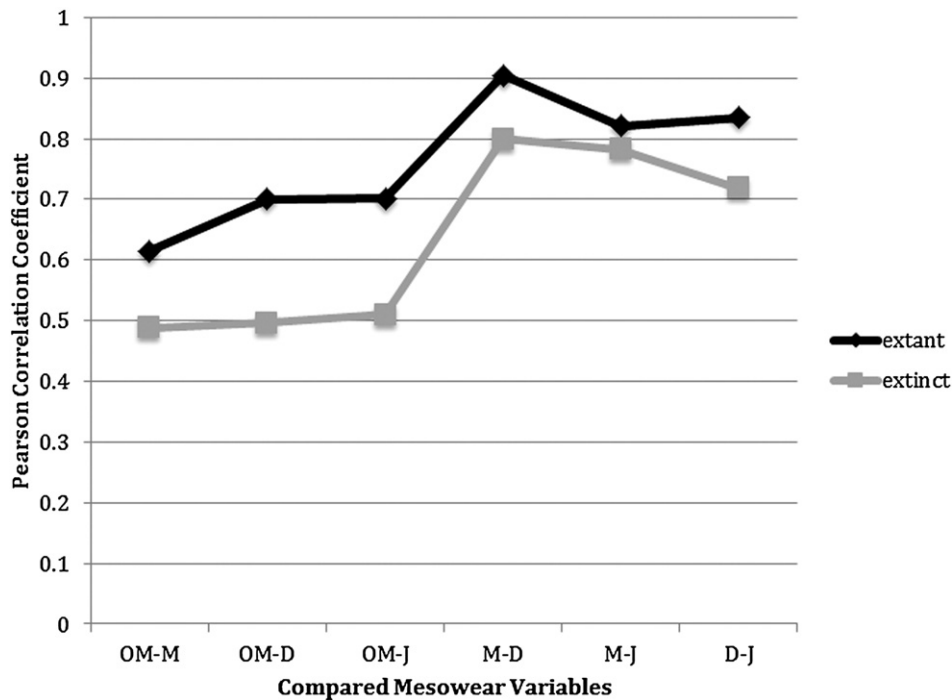
Although inner and outer mesowear characterize dental wear patterns on different parts of the tooth and vary in rate of wear, they both relate to relative amounts of abrasional (food on tooth) and attritional (tooth on tooth) wear and the degree to which these wear processes influence wear rates, occlusal morphologies and occlusal relationships. Browsers have less abrasive diets and correspondingly lower dental wear rates than grazers (Sansom, 2006; Damuth and Janis, 2014). Browsers ingest lower rates of silica phytoliths commonly found in grass and because browsers tend to feed higher off the ground,



**Fig. 2.** The four stages of J. This scoring system applies to the junction point between the mesial and distal surfaces of the lingual enamel band of the paracone and metacone. (A) Stage 1: The mesial and distal surfaces join at a sharp, well-defined junction. (B) Stage 2: The midpoint between the mesial and distal surfaces is somewhat sharp, and often contains a gouge. (C) Stage 3: The midpoint on the enamel band is rounded, but the mesial and distal sides appear as distinct, separate surfaces. (D) Stage 4: The J point lacks a discrete apex, and the mesial and distal sides of the enamel band form one continuous surface.

probably also ingest fewer inorganic particles (e.g. quartz sand and dust) (Baker et al., 1959; Sanson et al., 2007; Damuth and Janis, 2011). Although the causality of mesowear morphology is still poorly understood, there is a clear association of abrasion dominated mesowear patterns with grazing diets.

Outer mesowear records the overall height and shape of a cusp. It involves a macroscopic amount of dental wear and therefore represents the cumulative effects of dental wear, diet, and feeding ecology over a relatively prolonged period of the animals lifetime, perhaps months to a year, depending on the specific rate of dental wear (Mihlbachler



**Fig. 3.** Plotted Pearson Correlation Coefficients between the four inner and outer mesowear variables in the extant (black line) and extinct (gray line) species. OM: Outer mesowear, M: Mesial, D: Distal.

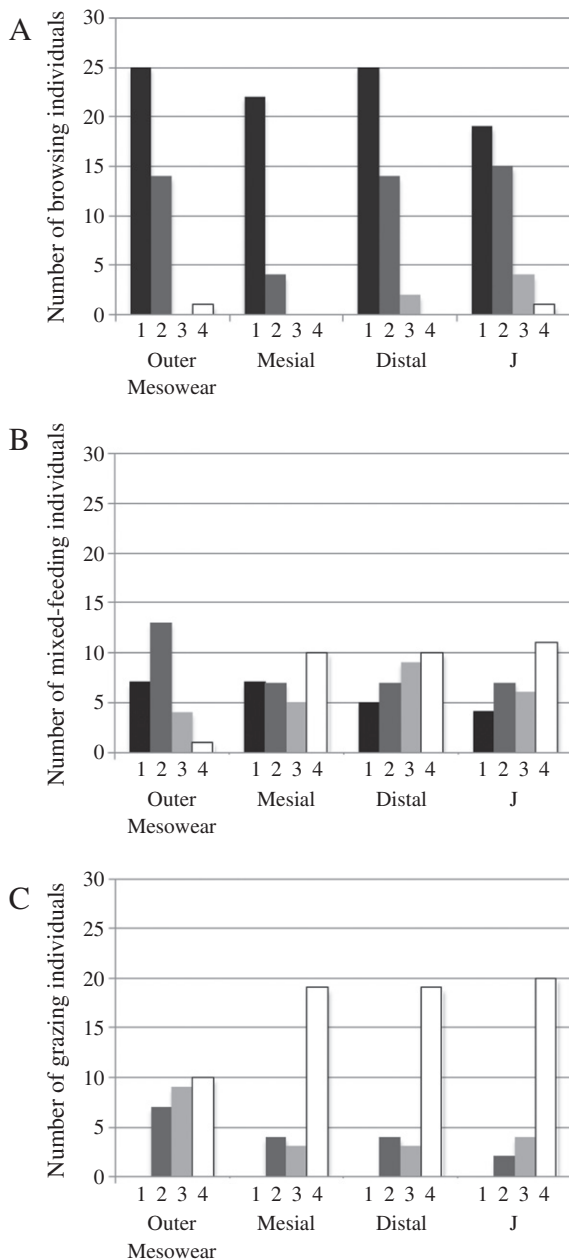


Fig. 4. Collective scores for outer mesowear and the three inner mesowear variables in extant taxa classified as browsers (A), mixed feeders (B), and grazers (C).

et al., 2011). Inner mesowear focuses on the surfaces of the enamel blades and therefore occurs at a smaller scale than outer mesowear. It therefore represents aspects of feeding ecology that are intermediate in time (days to weeks) between outer mesowear and dental microwear, as shown experimentally in Solounias et al. (2014), where the enamel surfaces were incrementally worn over 40 days. Despite this potential difference in time-scale, all mesowear variables are significantly correlated and predict diet similarly suggesting that these dietary variables are robust paleodietary proxies, unlike microwear which is more sensitive to the last-meal phenomenon (Fraser and Theodor, 2013). The Pearson Correlation Coefficients between mesowear variables are lower for fossil giraffids than extant taxa (Fig. 3), for reasons probably relating to a greater disparity of diets among our extant sample which deliberately included specialists from the entire browser-grazer continuum, whereas the fossil sample does not appear to include species that were grazing specialists.

Discriminant function analysis of individual mesowear variables produced similar degrees of accuracy (63.7%–70.1%) when categorizing individual molars of extant species to diet. However, combining inner and outer mesowear variables predicts diet with a better degree of accuracy than any of the four individual mesowear variables alone (75.9%). The combination of inner and outer mesowear variables therefore increases accuracy of dietary prediction.

#### 4.2. Dietary diversity of extinct pikermian giraffids

Our data demonstrates that the giraffid fauna from Greece was mostly browsing with some mixed feeding, while the Chinese faunas included similar amounts of browsing and mixed feeding. The number of teeth classified as grazers in all faunas was low, and it seems unlikely that any of these faunas included committed grazers. The heterogeneity in diets is unlikely due to time differences, as the localities of Greece and China are all Turolian age.

Few giraffid species have been recovered from both the eastern (Chinese) and western (Greek) ends of the Pikermian Biome. Although they are geographically widespread, these wide-ranging giraffids often exhibited homogenous diets. *Palaeotragus rouenii* was abundant in North China, Samos, and Pikermi (Table 1B). This taxon was uniformly predicted to be a browser in both Greek localities, and in North China, the majority of predictions were browsing followed by mixed feeding (Table 2). *Samotherium boissieri* is found in both the most western locality (Pikermi) to the most eastern (North China). The majority of *S. boissieri* individuals appear to have been mixed feeding throughout the Pikermian biome (Table 2). Sivatheriinae giraffids were also found in both North China, and Samos and Pikermi. Although *Bramatherium* sp. and *Helladotherium duvernoyi* are separate species, the morphological differences are minor, notably in the dentition size and frontal sinus size (Matthew, 1929; Colbert, 1935; Lewis, 1939), allowing for effective comparison. *Bramatherium* sp. has individuals predicted for all three dietary categories, with the greatest frequency being browsing (Table 2). Although *Helladotherium duvernoyi* teeth were not abundant in either Greek locality, every individual but one was predicted as a browser on the western end of the biome. While the geographic location of these giraffids is widespread, their dietary patterns appear homogenous.

#### 4.3. Mesowear dietary predictions and ecomorphologic features of the pikermian biome giraffids

Sivatheriinae are the largest of all Miocene ruminants (Kurtén, 1971), but with short necks suggesting that they fed on lower foliage than high-browsing giraffes (Solounias, 2007), although it is unclear if this includes grazing. They are also more hypsodont than other giraffids (Hamilton, 1973). Other dental wear and ecomorphological studies suggest browsing to mixed feeding (Solounias et al., 1999, 2010). Sivatheriinae, *Bramatherium* and *Helladotherium*, are similar in size, skull, and dental morphology (Colbert, 1935). Our data suggests these taxa shared similar dietary habits in both the Chinese and Greek localities. The profile of dietary predictions for *Bramatherium* sp. (Fig. 6B) in comparison to those of extant ruminants (Fig. 6A) suggests a browsing and mixed feeding diet, or a browse-dominated mixed feeding diet.

Palaeotraginae are medium-sized giraffids intermediate in size between okapis and giraffes (Solounias, 2007). They are more hypsodont than extant giraffids suggesting a grazing or mixed feeding diet (Bohlin, 1926; Hamilton, 1978). Our sample contains five species of *Samotherium*. All of these species have very similarly sized and shaped dentitions; their differences are in the size of the masseter and the position of the ossicones (Solounias, 2007). *Samotherium sinense* from North China was more specialized with a larger masseteric area than other species of *Samotherium* (Solounias, 2007) suggesting more grazing habits. The shape of the premaxilla of *Samotherium boissieri* is intermediate between the square-shaped premaxillae of grazers, and the more pointed premaxillary shape of browsers (Solounias et al., 1988).

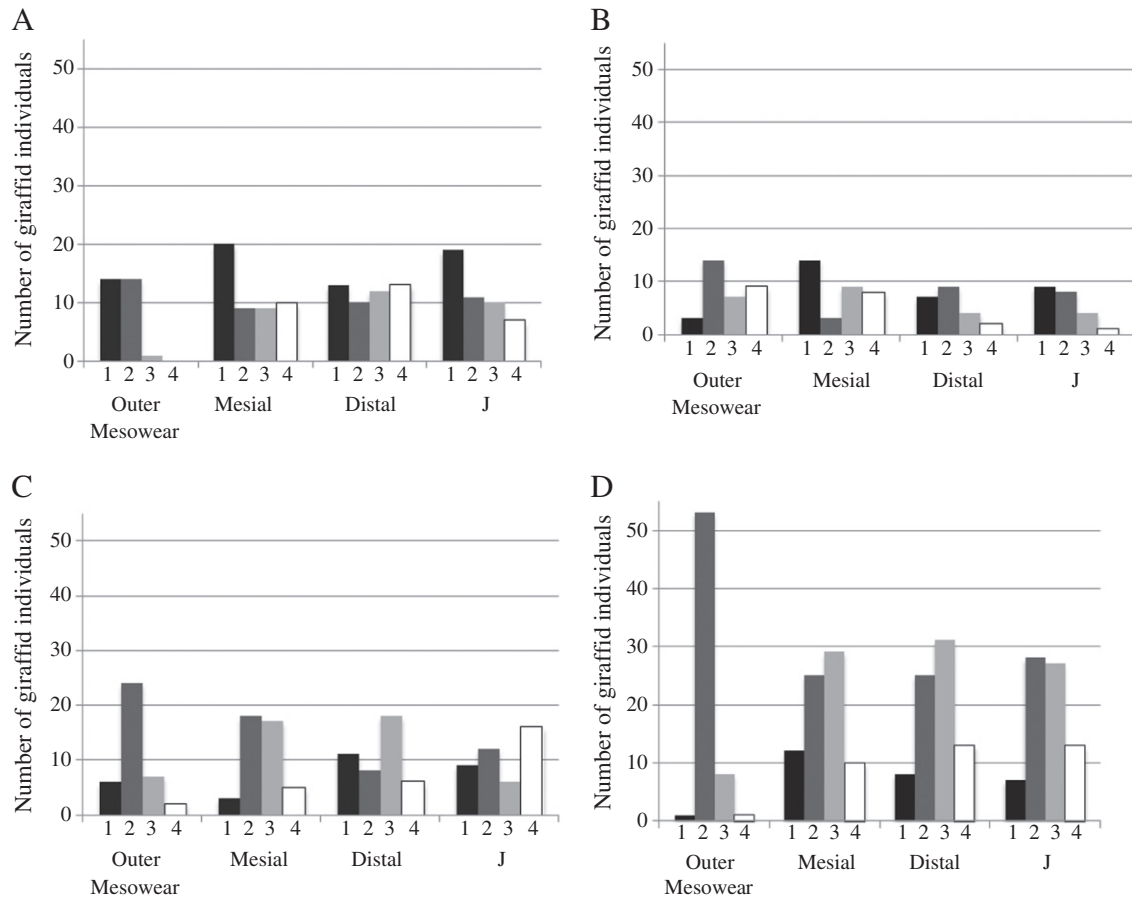


Fig. 5. Collective scores for outer mesowear and the three inner mesowear variables in extinct giraffids from Samos (A), Pikermi (B), Linxia Basin (C), and North China (D).

Consistent with the facial morphology, *S. boissieri* was uniformly mixed feeding throughout the Pikermian Biome.

*Palaeotragus coelophrys* is one of the most abundant species found in both Chinese localities. The largest frequencies of individuals from Linxia Basin were classified as mixed feeders according to the DFA, and from North China were classified as browsers (Fig. 6). On the western end of the biome, *Palaeotragus coelophrys* fossils are scarce. The single tooth from Samos was classified as a browser. *Palaeotragus rouenii*, on the other hand, was abundant in Samos, Pikermi, and North China. These species are morphologically similar, although *Palaeotragus coelophrys* was larger in body size (Bohlin, 1926). *Palaeotragus rouenii* has been described as more apomorphic compared to *Palaeotragus coelophrys*, based on several characters, including their molar absence of accessory crests (Hamilton, 1978), which is congruent with our inner mesowear findings predicting more specialized browsing dietary habits.

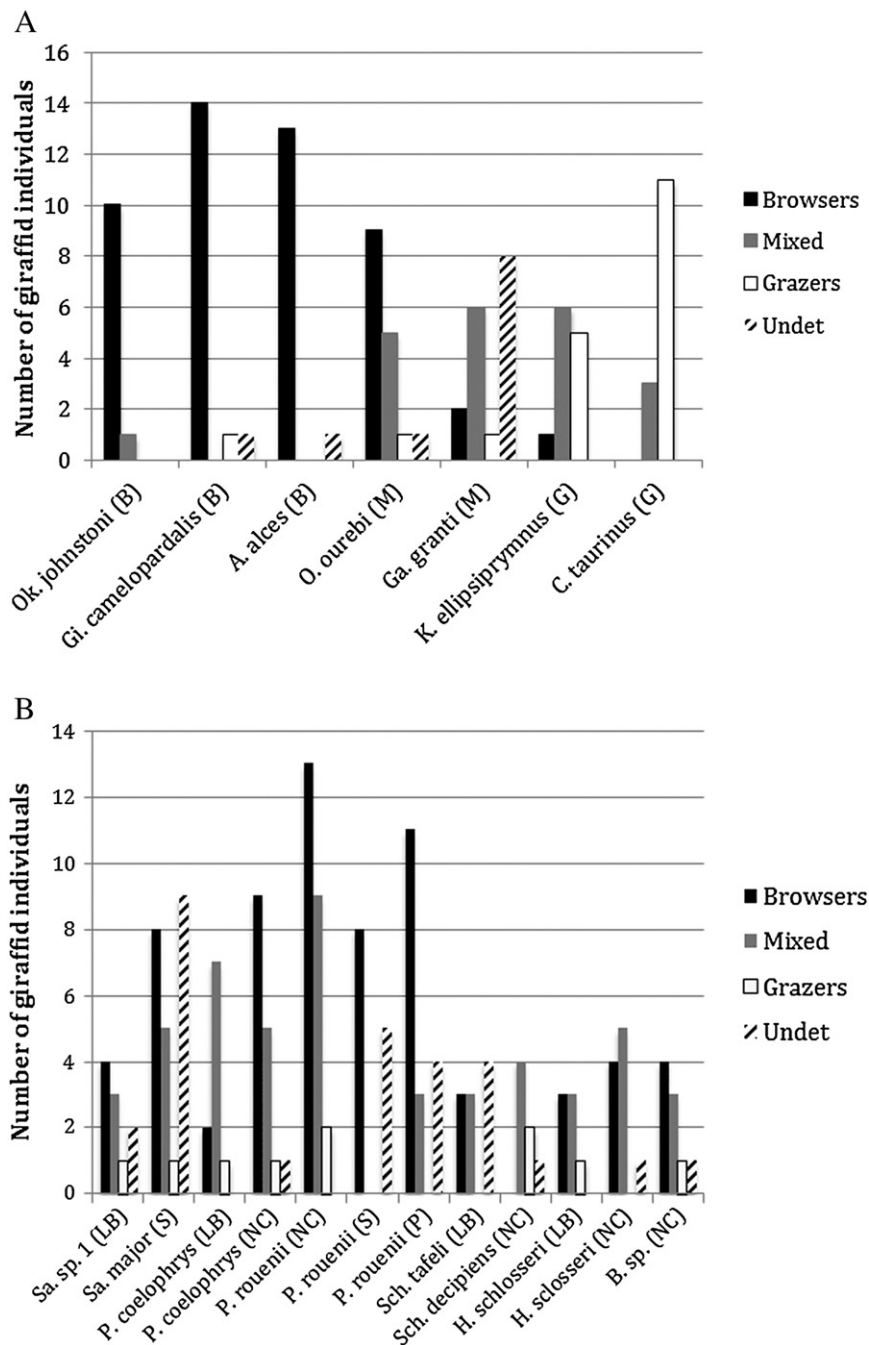
Although there are many fossils of *Schansitherium*, it has yet to be adequately described. Its skull and dentition are similar to that of *Samotherium boissieri*, but detailed descriptions are lacking (Hou et al., 2014). The greatest frequency of *Schansitherium tafeli* individuals were predicted as browsers and mixed feeders (Table 2). The majority of *Schansitherium decipiens* individuals appear to have been mixed feeding, however two individuals are predicted as grazers, which is rare among extinct and extant giraffids (Fig. 6). These species were concentrated only on the eastern end of the biome, which poses the question as to why they were not able to migrate to the western end. There was one skull of *Schansitherium quadricornis* that was found in Samos, however this was destroyed in the bombing of Munich during World War II (Gentry, 1971). Within Palaeotraginae, we have individuals from both

extreme ends of the dietary continuum; however, the majority of the species were categorized as mixed feeding or browsing.

Bohlininae are giraffids that are similarly sized as the modern giraffe, with moderately elongated cervical vertebrae, potentially allowing for a high-browsing diet (Solounias, 2007; Danowitz et al., 2015). They are brachydont, suggesting a browsing diet like the giraffe (Matthew, 1929; Bohlin, 1926). *Honanotherium* is poorly known, but fossils are common in North China and Linxia Basin. Although Bohlininae are close relatives and are likely similarly proportioned to the giraffe (Solounias, 2007), their diet, based on the mesowear-based dietary predictions, may have been mixed feeding. The majority of the specimens were *Honanotherium schlosseri*, but we also have two species from Linxia Basin and one from Pikermi that are yet to be described. Unlike *Honanotherium schlosseri*, which had relatively equal numbers of browsers and mixed feeders in both North Chinese localities, a new species from Linxia Basin is predicted as grazing, although based only upon one specimen, and the small species from Pikermi is predicted as a browser (Table 2). *Bohlinia attica* is not known from China, and is rare in both Greek localities. Mesowear data suggests it was browsing in Samos, and mixed feeding in Pikermi, although only based upon a single specimen in each locality. Although *Bohlinia* is close to *Giraffa* (Hamilton, 1978; Danowitz et al., 2015), the diet appears to have been less exclusively browsing.

The giraffids of the Pikermian Biome exhibit a wider geographic range than that of the modern giraffe and okapi. Unlike the modern giraffids, which are committed browsers, the Miocene giraffids explored a greater dietary diversity. Several taxa were predicted as mixed feeding, including *Honanotherium schlosseri* from both Chinese localities, *Palaeotragus coelophrys* from Linxia Basin, and *Schansitherium decipiens*





**Fig. 6.** Dietary predictions of the extant taxa (A) and extinct giraffids (B) based on the discriminant function analysis. Taxa plotted are those where the model predicted the diet of 5 or more individuals. B: browser, M: mixed feeder, G: grazer, LB: Linxia Basin, NC: North China, S: Samos, P: Pikermi, Ok: *Okapia*, Gi: *Giraffa*, A: *Alces*, O: *Ourebia*, Ga: *Gazella*, K: *Kobus*, C: *Connochaetes*, Sa: *Samotherium*, P: *Palaeotragus*, Sch: *Schansitherium*, H: *Honanotherium*, B: *Bramatherium*.

(Fig. 6b). Mixed feeding was the second most frequent dietary pattern predicted among the extinct giraffids (Table 2). A similar pattern is seen in fossil bovids from the Turkana Basin, where isotopic evidence reveals a polarity towards the mixed feeding diet among the extinct taxa (Cerling et al., 2015). Although the dietary habits of the Miocene giraffid faunas appears polarized towards browse-mixed feeding, the overall mesowear scores suggest a greater diversity than exhibited by giraffids today.

## 5. Conclusion

We find that the utilization of both inner and outer mesowear variables better predicts dietary patterns than individual mesowear

variables alone. Using this novel, combined approach to mesowear analysis, we find that fossil giraffids were exploring diverse dietary adaptations. Unlike the modern giraffe and the okapi, which are committed browsers, the extinct fauna span the dietary continuum, ranging from browsers to mixed feeders. The majority of the browsing giraffids of the late Miocene were concentrated in Samos and Pikermi. This broadens our understanding of the adaptations of Giraffidae. Apparently the diets of the okapi and the giraffe are not representative of the family. The collective mesowear scores of all giraffids shows patterns in the diet in the western versus eastern part of the Pikermian Biome; the giraffids from localities of China appear to be polarized towards both the browsing and mixed feeding category, whereas the giraffids in the Greek localities appear to have been more exclusively browsing. Giraffids were

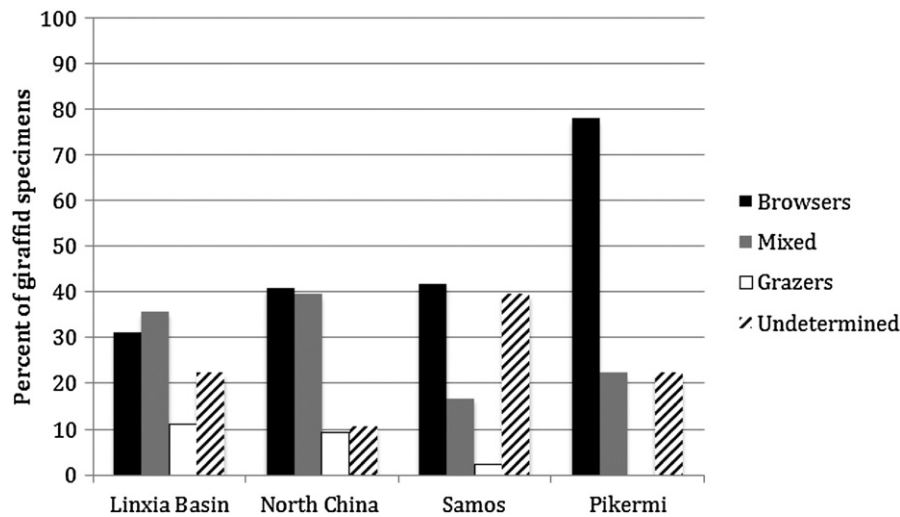


Fig. 7. Percentage of giraffid individuals predicted to each dietary category in the four localities studied.

important components of the mammalian communities of the Miocene, with diets more diverse than the giraffe and okapi today.

### Acknowledgements

We thank the Academic Medicine Scholars Program and Anatomy Department at New York Institute of Technology College of Osteopathic Medicine. We thank the AMNH, GMM, HLMD, HPM, IVPP, MGL, MNHN, NHMUK, NHMBA, NHMBe, NHMW, PIU, SMF, SMNS, and PIUW for access to specimens. We thank Gina Semprebbon, Florent Rivals, Thomas Denk, Mary Harrison, Dimitrios Veltzelos, Deng Tao and Qiu Zhanxiang from IVPP and Chen Shanqin and He Wen from HPM. We thank Bhuma Krishnamachari for assistance with statistical analysis and access to SAS. Funding was covered by N.S (personal funds) and the National Natural Science Foundation of China (41202002) supporting Sukuan Hou.

### Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.palaeo.2016.02.026>.

### References

- Ambrose, S.H., DeNiro, M.J., 1986. The isotopic ecology of East African mammals. *Oecologia* 69, 395–406.
- Baker, G., Jones, L.H.P., Wardrop, L.D., 1959. Cause of wear in sheep's teeth. *Nature* 184, 1583–1584.
- Bell, R.H.V., 1971. A grazing ecosystem in the Serengeti. *Sci. Am.* 225, 86–93.
- Bernor, R.L., Solounias, N., Swisher III, C.C., Van Couvering, J.A., 1996. The Correlation of the Classical "Pikermian" Mammal Faunas—Maragheh, Samos and Pikermi, with the European MN Unit System. In: Bernor, R.L., Fahlbusch, V., Mittmann, H.-W. (Eds.), *The Evolution of the Western Eurasian Neogene Mammal Faunas*. Columbia University Press, New York, pp. 137–154.
- Bohlin, B., 1926. Die familie giraffidae. *Palaeoentol. Sin. Ser. C* 1, 1–178.
- Cerling, T.E., Harris, J.M., Passey, B.H., 2003. Diets of East African bovidae based on stable isotope analysis. *J. Mammal.* 84, 456–470.
- Cerling, T.E., Andanje, S.A., Blumenthal, S.A., Brown, F.H., Chritz, K.L., et al., 2015. Dietary changes of large herbivores in the Turkana Basin, Kenya from 4 to 1 Ma. *PNAS* 112, 11467–11472.
- Churcher, C.S., 1970. Two new Upper Miocene Giraffids from Fort Ternan, Kenya, East Africa. *Paleotragus primaveus* n.sp. and *Samotherium africanum* n.sp. In: Leakey, L.S.B., Savage, J.G. (Eds.), *Fossil Vertebrates of Africa 2*. Academic Press, London, pp. 1–109.
- Clauss, M., Frey, R., Kiefer, B., Lechner-Doll, M., Loehlein, W., Polster, C., Rössner, G.E., Streich, W.J., 2003. The maximum attainable body size of herbivorous mammals: morphophysiological constraints on foregut, and adaptations of hindgut fermenters. *Oecologia* 136, 14–27.
- Colbert, E.H., 1935. Siwalik mammals in the American museum of natural history. *Trans. Am. Philos. Soc.* 26, 1–401.
- Crusafont-Pairó, M., 1952. Los Jiráfidos fósiles de España. disp. provincia Barcelona. Consejo Superior de Investigaciones Científicas, Memorias y Comunicaciones del Instituto Geológico 8, pp. 1–239.
- Dagg, A.I., 2014. Giraffe. Cambridge University Press, New York.
- Dagg, A.I., Bristol Foster, J., 1982. *The Giraffe: its Biology, Behavior and Ecology*. Krieger Publishing Company, Malabar.
- Damuth, J., Janis, C.M., 2011. On the relationship between hypsodonty and feeding ecology in ungulate mammals, and its utility in paleoecology. *Biol. Rev.* 1–26.
- Damuth, J., Janis, C.M., 2014. A comparison of observed molar wear rates in extant herbivorous mammals. *Ann. Zool. Fenn.* 51, 188–200.
- Danowitz, M., Vasilyev, A., Kortlandt, V., Solounias, N., 2015. Fossil evidence and stages of elongation of the *Giraffa camelopardalis* neck. *R Soc Open Sci.* 2, 150393.
- Deng, T., 2005. Character, age and ecology of the hezheng biota from Northwestern China. *Acta Geol. Sin.* 79, 739–750.
- Estes, R., 1991. *The behavior guide to African Mammals (Vol. 64)*. University of California Press, Berkeley.
- Fortelius, M., Solounias, N., 2000. Functional characterization of ungulate molars using the abrasion-attrition wear gradient: a new method for reconstructing palaeodiets. *Am. Mus. Novit.* 3301, 1–36.
- Fraser, D., Theodor, J., 2013. Ungulate Diets Reveal Patterns of Grassland Evolution in North America 369. pp. 409–421.
- Gaudry, A., 1862. *Animaux Fossiles et Géologie de l'Attique*. Martinet Press, Paris.
- Gentry, A.W., 1971. The earliest goats and other antelopes from the Samos Hipparion fauna. *Bulletin of the British Museum (Natural History) Geology* 20, pp. 231–296.
- Gentry, A.W., Rössner, G.E., Heizmann, E.P.J., 1999. Suborder Ruminantia. In: Rössner, G.E., Heizmann, E.P.J. (Eds.), *The Miocene Land Mammals of Europe*. Verlag Dr. Friedrich Pfeil, München, pp. 225–258.
- Hamilton, W.R., 1973. The lower Miocene ruminants of Gebel zelten, Libya. *Bulletin of the British Museum (Natural History) Geology* 24, pp. 73–150.
- Hamilton, W.R., 1978. Fossil giraffes from the Miocene of Africa and a revision of the phylogeny of giraffoidea. *Philos. Trans. R. Soc. B* 283, 165–229.
- Harris, J., Solounias, N., Geraads, D., 2010. African Giraffoidea. In: Sanders, W.J., Werdelin, L. (Eds.), *Cenozoic Mammals of Africa*. University of California Press, Berkeley, pp. 805–819.
- Hofmann, R.R., Steward, D.R.M., 1972. Grazer or browser: a classification based on stomach structure and feeding habits of East African mammals. *Mammalia* 36, 227–240.
- Hörnberg, S., 2001. The relationship between moose (*Alces alces*) browsing utilization and the occurrence of different forage species in Sweden. *For. Ecol. Manag.* 149, 91–102.
- Hou, S., Danowitz, M., Sammis, J., Solounias, N., 2014. Dead ossicones, and other characters describing palaeotraginae (giraffidae; Mammalia) based on new material from Gansu, Central China. *Zitteliana* 32, 91–98.
- Kostopoulos, D.S., 2009. Giraffidae. *Beitr. Paläontol.* 31, 299–343.
- Kürtén, B., 1952. *The Chinese hipparion fauna*. Societas Scientiarum Fennica Commentationes Biologicae 13, pp. 1–82.
- Kürtén, B., 1971. *The Age of Mammals*. Columbia University Press, New York.
- Lewis, G.E., 1939. A new *Bramatherium* skull. *Am. J. Sci.* 237, 275–280.
- Marra, A.C., Solounias, N., Carone, G., Rook, L., 2011. Palaeogeographic significance of the giraffid remains (Mammalia, artiodactyla) from cessaniti (late Miocene, Southern Italy) L'importance paléogéographique des girafes de cessaniti (Miocène Supérieur Italie du sud). *Geobios* 44, 189–197.
- Mateer, N., Lucas, S.G., 1985. Swedish vertebrate palaeontology in China: A history of the lagrelis collection. *Bulletin of the Geological Institution of the University of Uppsala* 11, pp. 1–23.
- Matthew, W.D., 1929. Critical observations upon Siwalik mammals: (exclusive of proboscidea). *Bull. Am. Mus. Nat. Hist.* 56, 437–560.
- Mihlbachler, M., Rivals, F., Solounias, N., Semprebbon, G., 2011. Dietary change and evolution of horses in North America. *Science* 331, 1178–1181.

- Quade, J., Solounias, N., Cerling, T.E., 1994. Stable isotopic evidence from paleosol carbonates and fossil teeth in Greece for forest or woodlands over the past 11 Ma. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 108, 41–53.
- Rivals, F., Muhlbachler, M.C., Solounias, N., 2007. Effect of ontogenetic-age distribution in fossil samples on the interpretation of ungulate paleodiets using the mesowear method. *J. Vertebr. Paleontol.* 27, 763–767.
- Sanson, G., 2006. The biomechanics of browsing and grazing. *Am. J. Bot.* 93, 1531–1545.
- Sanson, G.D., Kerr, S.A., Gross, K.A., 2007. Do silica phytoliths really wear mammalian teeth? *J. Archaeol. Sci.* 34, 526–531.
- Solounias, N., 2007. Family Giraffidae. In: Prothero, D.R., Foss, S.E. (Eds.), *The Evolution of Artiodactyls*. Johns Hopkins University Press, Baltimore, pp. 257–277.
- Solounias, N., Dawson-Saunders, B., 1988. Dietary adaptations and paleoecology of the late Miocene ruminants from pikermi and Samos in Greece. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 65, 149–172.
- Solounias, N., Teaford, M., Walker, A., 1988. Interpreting the diet of extinct ruminants: the case of a non-browsing giraffid. *Paleobiology* 14, 287–300.
- Solounias, N., Plavcan, M., Quade, J., Witmer, L., 1999. The Pikermian Biome and the Savanna Myth. In: Agusti, J., Andrews, P., Rook, L. (Eds.), *Evolution of the Neogene Terrestrial Ecosystems in Europe*. Cambridge University Press, New York, pp. 427–444.
- Solounias, N., McGraw, W.S., Hayek, L.-A.C., Werdelin, L., 2000. The Paleodiets of the Giraffidae. In: Vrba, E.S., Schaller, G.B. (Eds.), *Antelopes, Deer and Relatives*. Yale University Press, New Haven, pp. 84–95.
- Solounias, N., Rivals, F., Semperebon, G.M., 2010. Dietary interpretation and paleoecology of herbivores from pikermi and Samos (late Miocene of Greece). *Paleobiology* 36, 113–136.
- Solounias, N., Semperebon, G., Muhlbachler, M.C., Rivals, F., 2012. Paleodietary Comparisons of Ungulates between the Late Miocene of China, and Pikermi and Samos in Greece. In: Wang, X., Flynn, L.J., Fortelius, M. (Eds.), *Neogene Terrestrial Mammalian Biostratigraphy and Chronology of Asia*. Columbia University Press, New York, pp. 676–692.
- Solounias, N., Tariq, M., Hou, S., Danowitz, M., Harrison, M., 2014. A new method of tooth mesowear and a test of it on domestic goats. *Ann. Zool. Fenn.* 51, 111–118.
- Theodorou, G.E., Nicolaidis, S.N., 1988. Stratigraphic horizons at the classic mammal locality of pikermi, Attica, Greece. *Mod. Geol.* 13, 177–181.
- Tütken, T., Kaiser, T.M., Vennemann, T., Merceron, G., 2013. Opportunistic feeding strategy for the earliest old world hypsodont equids: evidence from stable isotope and dental wear proxies. *PLoS One* 8, e74463.
- Velitzelos, D., Bouchal, J.M., Denk, T., 2014. Review of the Cenozoic floras and vegetation of Greece. *Rev. Palaeobot. Palynol.* 56–117.
- Weidmann, M., Solounias, N., Drake, R.E., Curtis, G.H., 1984. Neogene stratigraphy of the Mytilini Basin, Samos Island, Greece. *Geobios* 17, 477–490.