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

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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.

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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; Mihlbachler 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. Mihlbachler 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

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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 (Clauss 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; Mateer 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; NHMBe, 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	*Okapia johnstoni*	11	0.8	1.5	1.3	1.5
Browser	*Giraffa camelopardalis*	16	1.3	1.3	1.6	1.8
Browser	*Alces alces*	14	1.1	1.1	1.3	1.6
Grazer	*Connochaetes taurinus*	14	3.7	3.9	3.9	3.7
Grazer	*Kobus ellipsiprymnus*	12	2.8	3.2	3.3	3.6
Mixed feeder	*Ourebia ourebi*	9	2	3.7	3.6	3.8
Mixed feeder	*Cervus canadensis*	5	1	1.6	1.6	1.4
Mixed feeder	*Gazella granti*	17	2.1	2.3	2.6	2.8