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Microwear–mesowear congruence and mortality bias in rhinoceros mass-death assemblages

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Abstract.—Although we do not know the cause of death of most fossil animals, mortality is often associated with ecological stress due to seasonality and other stochastic events (droughts, storms, volcanism) that may have caused shifts in feeding ecology preceding death. In these instances, dental microwear, which reflects feeding ecology in a narrow window of time, may provide a biased view of diet. Mesowear, another dental-wear proxy based on the morphology of worn cusps, requires macroscopic amounts of dental wear and reflects diet for a longer interval and may be less prone to bias from near-death ecological stress. We compared congruence between microwear and mesowear of North American, fossil rhinocerotid mass-death assemblages and collections of hunted modern rhinocerotids to test the hypothesis that fossil assemblages yield more incongruous microwear and mesowear data as a result of near-death ecological disturbances. In extant rhinos, both mesowear and microwear are associated with diet and height of the feeding environment. Mesowear and microwear in the modern rhinocerotid collections are statistically correlated, with strong relationships between average mesowear scores and labially distributed dental microwear. In contrast, a relationship between mesowear and microwear was not observed among the fossil rhinocerotid assemblages. Mesowear suggests that the fossil rhinos had low-abrasion diets, suggesting that they fed from clean, possibly tall vegetation. Some, but not all, mass-death assemblages produce microwear data with excessive scratches and/or pits compared with expectations based on mesowear results, suggesting that dental microwear was altered shortly before death in some but not all of the fossil assemblages. The dental-wear proxies available to paleoecologists provide a mosaic of dietary evidence reflecting diet over long (mesowear) and more abbreviated (microwear) periods of time that, together, provide a richer understanding of feeding ecology and its relationship to environment, seasonal change, and other ecological disturbances.

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Introduction

Dental-microwear features are the consequences of occlusal events involving mastication of hard, abrasive, or tough particles that damage enamel surfaces, causing wear (Lucas et al. 2013; Ungar 2015; Xia et al. 2015). As dental wear progresses throughout life, microwear features wear away and are replaced by new microwear features. Consequently, the microwear on the occlusal surface of a tooth is largely a product of the last meal or the last few meals (Mainland 1996; Ungar 2009; Gogarten and Grine 2013). This creates a considerable problem for the field of dental microwear. While some studies recognize that dental microwear is an ephemeral signal of feeding ecology (Rivals et al. 2009, 2014; Merceron et al. 2010a; Gogarten and Grine 2013; Rodríguez-Hidalgo et al. 2016; Sánchez-Hernández et al. 2016), most microwear studies attempt to answer questions about the feeding ecology of species, not individuals, and they do not explicitly consider the possibility that the actual specimens under study may have suffered diet-altering ecological stress shortly before death resulting from drought, parasitism, disease, malnutrition, starvation, or a variety of other ecological phenomena that decrease longevity. In most instances, we have very limited understanding of the cause of death of fossil specimens. However, except in circumstances under which animals died suddenly from predation, drowning, lethal injury,

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or other sudden causes of death, the possibility that dental microwear has been altered by near-mortal ecological stress should be a concern when interpreting dental-microwear results.

Our understanding of the relationship of dental wear and feeding ecology in nature comes from large extant mammal databases derived from modern specimens in mammalogy collections. These collections consist mostly of specimens collected directly from the wild (e.g., hunting, trapping) (Solounias and Semprebon 2002; Merceron et al. 2004, 2005; Fraser and Theodor 2011). However, the fossil record does not sample individuals in an equivalent way. Fossil occurrences are likely to be biased toward particular sedimentological facies that represent localized depositional environments and preserve microwear patterns that reflect localized aspects of feeding ecology rather than the generalized ecology of species. Additionally, mortality rates of species living in seasonal environments fluctuate with the seasons, with higher rates of mortality during the more stressful times of year (Young 1994; Gogarten et al. 2012; Taylor et al. 2016). Therefore, biased dental-microwear data may be more prevalent in the fossil record than has been generally surmised.

Mesowear analysis is another dental-wear proxy applicable to ungulate mammals that relates the relief and sharpness of worn cusp apices to the relative amounts of abrasive (food on tooth) and attritive (tooth on tooth) wear (Fortelius and Solounias 2000; Kaiser et al. 2011; Louys et al. 2011; Mihlbachler et al. 2011). While microwear represents last meals, a more extensive amount of dental wear is required to reshape the gross morphology of a cusp. Therefore, mesowear is the culmination of many successive meals and represents feeding ecology over a period of time that is longer than that represented by microwear. A mesowear-derived dietary interpretation of a sample of individuals that experienced near-death shifts in feeding ecology would very likely be incongruous with conclusions achieved via microwear analysis.

It has become commonplace to publish paleodietary studies that combine microwear and mesowear. Some studies either reported no disagreement between these proxies or did not comment on the extent of congruence (DeMiguel et al. 2008, 2011; Semprebon and Rivals 2007, 2010; Rivals et al. 2009, 2013; Merceron et al. 2010b; Rivals and Semprebon 2012; Tütken et al. 2013). However, many studies report some amount of disagreement between mesowear and microwear (Franz-Odendaal and Solounias 2004; Rivals et al. 2007, 2008, 2010, 2011; Schulz et al. 2007; Wolf et al. 2010; Semprebon et al. 2016). Incongruence between these dental-wear proxies does not indicate that either method is flawed. Mesowear and microwear have both been amply demonstrated to accurately predict dietary ecology in modern ungulates (Fortelius and Solounias 2000; Fraser and Theodor 2011; Louys et al. 2012; Mihlbachler et al. 2016). More likely, ecological pressure, proximate to the time of death, may frequently disassociate these two wear proxies. Contrast between these two dental-wear proxies could be informative of both short-term dietary fluctuations due to seasonal mixed feeding and episodes of ecological stress in the fossil record.

If the feeding ecology of a species fluctuated seasonally and/or spatially over the home range, sampling biases in the fossil record would dictate the degree of congruence between microwear and mesowear results. If a fossil sample consisted of individuals sampled from a population over an extended period of time over an extended area, the microwear data would reflect the total range of that population's feeding activities, which could include feeding in a variety of seasons and feeding environments (Rivals et al. 2015; Rodríguez-Hidalgo et al. 2016; Sánchez-Hernández et al. 2016). Conclusions reached about general aspects of feeding ecology from microwear data would be congruent with mesowear. A sample of the same population taken at one locality during a temporally constrained period of ecological stress would result in greater incongruence between mesowear and microwear. Microwear would relate more strongly to the spatially and temporally localized conditions, while mesowear would more strongly relate to generalized aspects of diet.

Bone beds often contain evidence of mass deaths due to ecological stress (Lyman 1994; Rogers et al. 2007). Such assemblages provide opportunities to test for dental-wear bias in the fossil record. Rhinocerotids and other large megaherbivorous species are commonly found in mass-death assemblages and other bone-bed deposits. Rhinocerotid mass-death assemblages range from time-averaged mortality, to drought-induced seasonal die-offs, to other haphazard events, including volcanic ashfall. In mass-death assemblages, we might expect a higher frequency of microwear–mesowear incongruence due to near-death dietary shifts related to ingestion of more abrasive, tougher, or less nutritious food items and/or increased ingestion of food contaminants (dust, sand, soil, ash).

We sampled microwear and mesowear from 13 modern and fossil rhino assemblages. Rhinocerotids, among all megaherbivorous ungulate clades, are suited to address these concerns with dental-wear methods. Fossil rhinocerotids commonly occur in concentrated bone-bed deposits in North America, and there are many fossilized mass-death assemblages whose dental-wear patterns can be compared with hunted collections of extant species. Extant rhinocerotids are the only living family of megaherbivores whose diets span the browser–grazer spectrum with both specialized browsing and grazing species (Owen-Smith 1988). This study includes all five extant rhinocerotid species, all wild-collected over different times of year from African and Asian localities. The modern rhino assemblages were mostly collected during expeditions in the early twentieth century (Heller 1913). The rhinos represented in the modern rhino assemblages were hunted over a period of years and during several seasons. Documentation of some of these hunting exploits (Heller 1913; Roosevelt and Heller 1914) suggest the hunted animals were not exposed to extreme ecological events prior to death. If that is the case, both mesowear and microwear in these modern assemblages should correspond closely to the feeding ecology of these species as reported in the literature.

Because the mortalities of the modern specimens are not associated with exposure to extreme ecological events, we hypothesize a high degree of congruence between microwear and mesowear. The dental microwear on the labial edge of perissodactyl molars is strongly predictive of feeding ecology among browsing and grazing rhinos, while the dental microwear from the lingual edge is not (Mihlbachler et al. 2016). Therefore, we hypothesize a stronger relationship between mesowear and labially distributed microwear among extant rhinos. Because the fossil assemblages, whose causes of death are described below and summarized in Table 1, are associated with taphonomic evidence for mass-death events, we hypothesize the fossil assemblages will be characterized by less microwear–mesowear congruence than the largely hunted modern samples.

Feeding Ecology of Extant Rhinos

There are significant phylogenetic biases in how dental-microwear features are distributed on the molars of different ungulate groups (Mihlbachler et al. 2016). Therefore, we depart here from the general approach of comparing dental wear of fossil species with taxonomically diverse extant mammal dental-wear data sets (Solounias and Semprebon 2002; Merceron et al. 2004, 2005; Semprebon et al. 2004) and confine our analysis to comparisons of extant and extinct rhinocerotids. It is important to review the feeding ecology of the extant species of rhinos before discussing the results of the mesowear and microwear data.

All dietary studies of *Ceratotherium simum* (CS) indicate a nearly pure grass diet. Stable isotopes of fecal material suggest 90% of its diet consists of C_4 grasses (Codron et al. 2007). It preferentially grazes on short grass, which it crops with a square upper lip (Player and Feely 1960; Groves 1972; Owen-Smith 1975, 1988; Pienaar 1994; Shrader and Perrin 2006; Shrader et al. 2006; Waldram et al. 2008; Pedersen 2009). CS acts as a keystone species, maintaining short grassy lawns (Waldram et al. 2008; Arsenault and Owen-Smith 2011; Kleynhans et al. 2011; Rookmaaker 2013). Heller (1913) examined the stomach contents of hunted specimens that are used in this study and found them to contain only grass.

Diceros bicornis (DB) is a browser that feeds extensively on shrubs, herbs, legumes, woody plants, and other succulent plants using a

TABLE 1. Summary of rhinocerotid modern and mass-death fossil-assemblage data and cause-of-death hypotheses. *Dicerorhinus sumatrensis* and *Rhinoceros sondiacus* are combined in this study as Asian browsing rhinos (ABR). Museum collections: AMNH, American Museum of Natural History, New York; F:AM, Frick Collection at the American Museum of Natural History, New York; FLMNH, Florida Museum of Natural History, Gainesville, FL; NMNH, National Museum of Natural History, Washington, D.C.; UNSM, University of Nebraska State Museum, Lincoln, NE. *N* refers to the number of observations.

Species	Locality	Abbreviation	Museum collection	Age	Probable cause of death	Microwear (*N*)	Mesowear (*N*)
Ceratotherium simum	Africa	CS	AMNH, NMNH	Recent	Hunted	40	38
Diceros bicornis	Africa	DB	AMNH, NMNH	Recent	Hunted	52	58
Dicerorhinus sumatrensis	Asia	ABR	AMNH, NMNH	Recent	Hunted	4	4
Rhinoceros sondiacus	Asia	ABR	AMNH, NMNH	Recent	Hunted	3	3
Rhinoceros unicornis	Asia	RU	AMNH, NMNH	Recent	Hunted	8	7
Aphelops malacorhinus	Love Bone Bed, FL	ALBB	FLMNH	Clarendonian (Cl3) 10.1—9.0 Ma	Seasonal drought	21	9
Aphelops malacorhinus	Mixson's Bone Bed, FL	AMBB	F:AM	Hemphillian (Hh1) 9.0—7.5 Ma	Localized attritional mortality	15	5
Teleoceras proterum	Love Bone Bed, FL	TLBB	FLMNH	Clarendonian (Cl3) 10.1—9.0 Ma	Seasonal drought	23	13
Teleoceras proterum	Mixson's Bone Bed, FL	TMBB	F:AM	Hemphillian (Hh1) 9.0—7.5 Ma	Localized attritional mortality	31	48
Teleoceras major	Ashfall Fossil Bed, NE	TASH	UNSM	Clarendonian (CL2) 12.1—10.1 Ma	Catastrophic ashfall	23	32
Teleoceras fossiger	Long Island Rhino Quarry, KS	TLIRQ	NMNH	Hemphillian (Hh1) 9.0—7.5 Ma	Seasonal droughts	46	27
Menoceras arikarense	Agate Springs, NE	MAGS	UNSM	Arikareean (Ar4) 19.4—18.8 Ma	Seasonal drought	22	16
Diceratherium annectens	77 Hill Quarry, WY	D77H	F:AM	Arikareean (Ar3) 23.0—19.4 Ma	Seasonal drought	22	25

prehensile upper lip (Ritchie 1963; Goddard 1968, 1970; Schenkel and Schenkel-Hulliger 1969a; Joubert and Eloff 1971; Mukinya 1977; Hall-Martin et al. 1982; Loutit et al. 1987; Owen-Smith 1988; Oloo et al. 1994; Dudley 1997; Muya and Oguge 2000; Brown et al. 2003; Lieverloo et al. 2009; Luske et al. 2009; Buk and Knight 2010). DB can break branches up to 17 cm in diameter (Goddard 1968; Owen-Smith 1988), although most browsed twigs are less than 3.5 mm in diameter (Owen-Smith 1988; Lieverloo et al. 2009). Stable isotopic analyses of feces suggest about 9% of its diet is C_4 grass, suggesting that DB may eat more grass than other studies indicate (Codron et al. 2007), but confirm that it is overwhelmingly a browser.

Two of the three species of Asian rhino, *Rhinoceros sondiacus* (RS) and *Dicerorhinus sumatrensis* (DS) (combined in this study as ABR: Asian browsing rhinos) are browsers. RS eats leaves, shoots, and twigs of woody species, which it grabs with a prehensile upper lip. It consumes little to no grass and few herbaceous species (Schenkel and Schenkel-Hulliger 1969b; Hoogerwerf 1970; Amman 1985; Owen-Smith 1988; Groves and Leslie 2011). DS ingests stems and leaves of broadleaf herbs, shrubs, and trees and fruits (Strickland 1967; Groves and Kurt 1972; Groves 1982; van Strien 1986; Owen-Smith 1988).

Rhinoceros unicornis (RU) is the only extant mixed-feeding rhinoceros (Owen-Smith 1988; Dinerstein 2003). Its diet consists of tall and short grasses, shrubs, herbs, leaves, twigs, bark, aquatic plants, and fruits (Laurie 1982; Laurie et al. 1983; Dinerstein and Wemmer 1988; Dinerstein and Price 1991; Fjellstad and Steinheim 1996; Mary et al. 1998; Deka et al. 2003; Bhatta 2011; Sarma et al. 2012). Its spends the majority of its time in wet alluvial grasslands dominated by a tall floodplain grass, *Saccharum spontaneum*, which is the most abundant plant in its diet at all times of year and in all populations (Laurie 1982; Laurie et al. 1983; Dinerstein and Price 1991; Jnawali and Wegge 1991; Dinerstein 1992, 2003; Fjellstad and Steinheim 1996; Mary et al. 1998; Deka et al. 2003; Steinheim et al. 2005; Wegge et al. 2006; Kandel and Jhala 2008; Pradham et al. 2008; Sarma et al. 2012; Tripathi 2012). The amount of grass reported in its diet ranges from 60% to 90%. In the warm/wet season, grass is the most dominant component (86–92%) of its diet and in the cool/dry season, grass consumption is reportedly as low as 57–42% (Jnawali 1995; Wegge et al. 2006; Tripathi 2012).

Rhino Assemblages and Cause-of-Death Scenarios

The fossil assemblages studied here represent four rhinocerotid genera, *Diceratherium*, *Menoceras*, *Aphelops*, and *Teleoceras*, all prominent members of North American Miocene land mammal faunas (Prothero 2005). *Diceratherium* and *Menoceras* are early Miocene rhinocerotids that lived before grasslands were widespread in North America (Strömberg 2005, 2011; Edwards et al. 2010; McInerney et al. 2011; Feranec and Pagnac 2013). Based on their brachydont molars, it would be uncontroversial to hypothesize that they were browsers. *Aphelops* and *Teleoceras* were abundant in the middle and late Miocene of North America, a time period during which open grasslands were spreading in North America. *Aphelops* is classically considered a browser and *Teleoceras* a grazer (Cerdeno 1998; Prothero 1998; Janis 2008). *Aphelops* had comparatively low-crowned molars, a larger body size, and a posteriorly retracted nasal bone, possibly suggesting a short proboscis or some other type of highly mobile upper lip. These traits suggest a browsing diet. *Teleoceras*, on the other hand, evolved high-crowned molars and shortened limbs, suggesting grazing habits. Results of a prior dental-microwear study of *Teleoceras fossiger* and *Aphelops mutilis* suggest either browsing or mixed feeding (Fraser and Theodor 2013). Stable isotope studies suggest *Teleoceras* diets ranged from pure C_3 to mixed C_3 and C_4 diets (Clementz et al. 2008; DeSantis and Wallace 2008). Following the expansion of C_4 grass in Florida after 7 Ma (MacFadden and Cerling 1996; MacFadden 1998), where grazing and browsing diets are isotopically widely differentiated, *Teleoceras* was a mixed feeder with a range of carbon isotopic values suggesting about 60% C_4 grass, while *Aphelops* was a C_3 browser (MacFadden 1998).

Bone beds containing these extinct rhino species have varied taphonomic histories that provide important clues about the causes and durations of the death events. The North American fossil rhino assemblages used in this study were sampled from six densely concentrated bone beds from the continental interior (Nebraska, Kansas, Wyoming) and Florida. Evidence supporting the probable causes of death for each fossil assemblage (Table 1) is summarized below.

Agate Springs.—Volcaniclastic sediments of the early Miocene Arikaree group include tuffaceous waterhole muds that accumulated in abandoned stream channels that are the locus for major mammalian bone beds, including the famous Agate Springs bone bed in Nebraska and the lesser known 77 Hill Quarry of Wyoming (Hunt 1990). Agate Springs contains a death assemblage consisting of disarticulated skeletons of the small horned rhinocerotid *Menoceras arikarense*. Deaths occurred in an abandoned stream channel, and the skeletons were buried by renewed aggradation of fine volcaniclastics due to subsequent heavy rains. Hunt (1990) suggested the assemblage was caused by a drought-induced death event in a seasonally dry climate. Mortality profiles of *Menoceras* collected from more attritional interchannel sites of the Arikaree group are reportedly different from that of Agate Springs, suggesting a strong catastrophic mortality component to the Agate Springs assemblage (Hunt 1990). Although the assemblage has a balanced sex ratio, the age structure of the assemblage contains different male and female mortality profiles (Mihlbachler 2007). The males, identified via prominent tusk and horn sexual dimorphism, more commonly died as young adults, and the females were frequently older adults. This aspect of the demographic structure resembles the natural age structure of living rhino populations (Mihlbachler 2007). The total evidence suggests a semicatastrophic mass death event (catastrophic mortalities mixed with some background attritional mortality) that disrupted a demographically normally structured rhinocerotid population (Mihlbachler 2007).

The 77 Hill Quarry.—The 77 Hill Quarry bone bed of Wyoming contains a dense accumulation of another small early rhinocerotid, *Diceratherium annectens*. The taphonomy of this assemblage is not as thoroughly studied but represents a shallow-waterhole setting nearly identical to that of Agate Springs. Mortality profiles of the two assemblages are similar (Hunt 1990), suggesting that the 77 Hill assemblage is also a similar kind of mass-death event.

Ashfall Bone Bed.—The Ashfall Bone Bed of Nebraska contains a large catastrophic death assemblage of articulated *Teleoceras major* skeletons buried in pure volcanic ash within an abandoned fluvial channel (Voorhies 1985). The carcasses were deposited above the level of the primary air-fall layer within the ash bed. Rhinos exhibit bone pathologies associated with ash inhalation and asphyxiation, suggesting that the animals died after surviving the initial ashfall and were quickly buried by reworked ash after death (Tucker et al. 2014). The age and sex structure of the Ashfall rhino assemblage, consisting mostly of juveniles and adult females with fewer numbers of adult males (Mead 2000), is a demographic pattern that resembles a snapshot of a standing population of living rhinos rather than an attritional death assemblage (Mihlbachler 2003) and is therefore congruent with taphonomic evidence suggesting a localized mass-death event occurring over a short interval of time following prolonged exposure to what would have been an extremely unusual and stressful ecological event.

Long Island Rhino Quarry.—From 1884 to 1886 Charles Sternberg and John Bell Hatcher made extensive collections of *Teleoceras fossiger* from the Long Island Rhino Quarry in Phillips County, Kansas (Osborn 1898a,b). Hatcher's (1885) field notes describe a dense rhinoceros bone bed contained in a horizontal stratum of loose sand overlying a more compact layer of clay and calcareous sandstone some 2 or 3 feet in thickness. There are two fossil-bearing strata containing dense concentrations of rhinoceros bone, separated by 1 to 3 feet of unfossiliferous strata that may possibly represent two discrete death events. If there were two separate death events, the fossils from each event have been hopelessly mixed. The state of preservation of the material and Hatcher's drawings of excavation units suggest disarticulation, although the absence of strong weathering and fine degree of preservation indicate rapid burial without transportation or winnowing (Osborn 1898a,b). The state of preservation and the demographic structure of the sample, which is composed primarily of young individuals and females with few males (Mead 2000), resembles the catastrophic Ashfall sample and suggests a mass-death event or two mass-death events followed by reworking and, finally, rapid burial by subsequent depositional events in a fluvial channel.

Love Bone Bed.—The Love Bone Bed from Florida is a large multispecific bone bed originating from yet another fluvial depositional (cut and fill) event (Webb et al. 1981). The deposit contains large assemblages of both *Teleoceras proterum* and *Aphelops malacorhinus*, although *Teleoceras* is more abundant (Mihlbachler 2003, 2005). Age clusters in the *Teleoceras* assemblage suggest births and localized deaths were seasonal (Mihlbachler 2003). The clustering could be due to a single seasonally constrained die-off event or a series of seasonally coordinated die-off events due to annual droughts or because the animals migrated seasonally and were only present at the locality during a small portion of the year. Either scenario suggests a highly seasonal environment and that rhinos preserved in the bone bed died in a particular season. The *Teleoceras* assemblage has a supernumerary abundance of young adult and subadult males, suggesting that some mortalities may have been socially mediated (due to fighting, territoriality) rather than purely drought induced (Mihlbachler 2003). Therefore, the Love Bone Bed assemblages may contain mixtures of seasonally constrained attritional and catastrophic deaths.

Mixson's Bone Bed.—The final bone bed, Mixson's Bone Bed in Florida, most closely resembles an ideal attritional death assemblage. Rhinos are the most abundant animals in the bone bed, although other large mammals are represented (Leidy and Lucas 1896). The most abundant rhino is *Teleoceras proterum*, but *Aphelops malacorhinus* is common (Harrison and Manning 1983; Mihlbachler 2003, 2005). The fossils were contained in clay deposited in a shallow sinkhole resulting from karstification of the underlying Eocene Ocala Limestone, which experienced active deposition for a brief interval (Harrison and Manning 1983). The large *Teleoceras* assemblage contains excessive numbers of subadult and young adult males; this demographic bias is strongest at Mixson's (Mihlbachler 2003) suggesting that the vast majority of the deaths were socially mediated and less likely related to drought or other types of ecological distress. Discrete age clusters were not found in the *Teleoceras* assemblage, indicating that deaths were aseasonal, births were aseasonal, or possibly both. This locality appears to contain an attritional record of localized mortality, with deaths occurring over a prolonged interval of time (Mihlbachler 2003), and among all the fossil assemblages may have a degree of microwear–mesowear congruence resembling the modern assemblages.

Materials and Methods

Specimen Selection.—Specimens used in this study are housed in public museum collections and available for additional study. Individual specimen numbers, localities, and raw data are provided in Supplementary Material 1. For both microwear and mesowear, upper second molars (M2) were prioritized for sampling. Adjacent molars (M1 or M3) were selected in instances where the M2 could not be sampled due to extensive wear, nonpreservation, or postmortem damage. The included specimens conform to wear stages 6–7 (Taylor et al. 2013). Following common practice, young individuals with poorly developed wear facets and dentally senescent individuals were excluded from all dental-wear analyses. For microwear analysis, specimens showing signs of chemical weathering, postmortem abrasion, contamination with chemical residues, or other macroscopic postmortem damage were rejected (King et al. 1999; El-Zaatari 2010). Specimens were also excluded when irregularities in the shape of the transparent cast undermined the desired lighting effects needed to bring a satisfactory amount of contrast on the cast wear surfaces. Incomplete and partially weathered teeth were included when at least one of the two sampling areas (A1 or A4) (Fig. 1) met the inclusion criteria. The entire microwear study comprises 536 photographs of wear surfaces on 310 specimens.

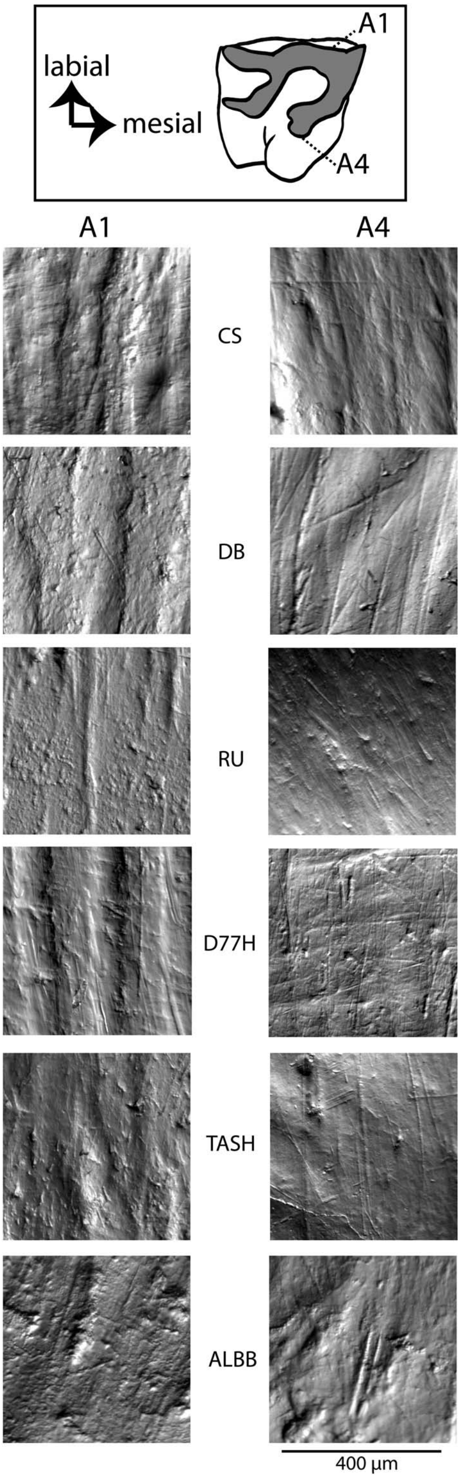

FIGURE 1. Labial (A1) and lingual (A4) areas of occlusal enamel surfaces sampled for microwear analysis of rhinocerotids (Mihlbachler et al. 2016), and examples of microwear photomicrographs used in the study. Abbreviations for species identification are given in Table 1.

Because of their extreme rarity, few specimens of the two Asian browsing rhinos (*Dicerorhinus sumatrensis* and *Rhinoceros sondiacus*) are available. These were combined into a single Asian browsing rhino sample (ABR), as they have similar feeding ecologies.

Because mesowear examines macroscopic aspects of cusp shape, it is less sensitive than microwear to small amounts of weathering, postmortem abrasion, or chemical contamination. Mesowear is more sensitive to macroscopic forms of damage (e.g., cracking, broken cusp apices). Therefore, inclusion criteria for mesowear were nonidentical to the microwear inclusion criteria. Inclusion for mesowear analysis required complete preservation of the paracone cusp and the surrounding part of the ectoloph. Postmortem damage to rhinoceros cusp apices is common due to their size and weight; therefore, the mesowear study consisted of fewer ($N = 285$) specimens compared with the microwear study.

Microwear Analysis.—Methods of observer blind microwear analysis follow Mihlbachler et al. (2012b) with modifications to digital resolution following Mihlbachler and Beatty (2012). We provide a brief summary here so the reader can understand basic aspects of the method, but molding, casting, photographic methods, and digital manipulations made to the images are described more completely in those references. Data produced using this method are capable of correctly predicting diets from individual molars of grazing and browsing ruminants with 91% accuracy (Mihlbachler et al. 2016). This success rate is a good indication of the efficacy of the method for identifying dental-wear patterns that are known to be associated with diets.

Grayscale photomicrographs were taken on clear epoxy casts under a stereomicroscope with a Spot 4 megapixel camera, using white light reflected from a white surface positioned below the specimen. The original digital resolution of the images, in which each pixel represents 0.74^2 µm of tooth surface, was reduced to 20% of the original pixel density, with each pixel representing 3.70^2 µm of tooth surface, a resolution found to yield the lowest levels of observer error (Mihlbachler and Beatty 2012). Microwear variables were traced and labeled on the images in a 400 µm × 400 µm ($1.6 \times 10^5\,\mu m^2$) area using Adobe Illustrator. The four largest microwear variables defined by Mihlbachler et al. (2012b) were considered: wide scratches (width: ≥5 µm to ≤20 µm), very wide scratches (width: > 20 µm), large pits (maximal diameter: ≥20 µm to ≤50 µm), and very large pits (maximal diameter: >50 µm). Smaller microwear features were ignored, because observer repeatability for these features was found to be low at all resolutions possible with this methodology (Mihlbachler and Beatty 2012). Data for these four variables are provided in the Supplementary Material. To reduce the number and complexity of statistical tests, the data were combined into a single scratch variable and a single pit variable. Earlier investigations with this same methodology (Mihlbachler and Beatty 2012; Mihlbachler et al. 2012b) found that a basic bivariate (scratches vs. pit) approach sufficiently identified major differences in microwear patterns associated with diet (Fig. 2).

The images used in this study were randomized, so the single observer (M.C.M.) was blind to the taxon and the area of the tooth being sampled. Microwear was sampled in two areas of the occlusal enamel surface (Mihlbachler et al. 2016), including the labial band of enamel of the paracone (A1) and the enamel surrounding the lingual margin of the protocone (A4) (Fig. 1). The series of images was examined three times, saving the superimposed tracings of pits and scratches each time. These additive examinations eliminate the diminishing effects of observer error by allowing the observer to identify features that were missed in earlier passes. By the third pass, very few additional microwear features were identified, suggesting that further passes would not substantially improve the data.

Mesowear Analysis.—Rhinoceros mesowear has been studied with a variety of scoring methods (Kahlke and Kaiser 2011), some involving multiple cusps (Taylor et al. 2013) and photographic and morphometric techniques (Hernesniemi et al. 2011). The comparatively simple univariate mesowear method adopted here, developed for Equidae (Mihlbachler et al. 2011), was chosen to maximize sample size and to simplify statistical comparison with microwear results. The "ruler" method is a reasonably robust and simple mesowear proxy that relies on use of a single homologous cusp. It is a way to collect simple mesowear data with minimal observer error (Mihlbachler et al. 2011; Loffredo and DeSantis 2014). Using the mesowear ruler composed of casts of seven equid cusps (Mihlbachler et al. 2011), we assigned the paracones to seven mesowear stages ranging from 0 (sharp with high relief) to 6 (zero relief) (Fig. 3). Although the mesowear ruler was designed for use with equid teeth, it was relatively easy to adapt its use to rhinocerotids, as rhinos and horses show similar ranges of overall cusp relief and sharpness. Rhino teeth are larger than equid teeth, and so it is important to point out that cusps were scored according to cusp shape rather than absolute relief, since the latter is influenced by size. Data were scored by a single observer (M.C.M.).

Statistical Analysis.—A parallel series of parametric and nonparametric analyses of the dental-microwear data were run, and no differences were found with regard to the results and conclusions of this paper. For brevity, we report only the parametric results. For examining the distributions of microwear features on rhino molars, the numbers of pits and scratches occurring on the labial (A1) and lingual (A4) sides of each molar were compared with paired t-tests. For testing for differences in the numbers of microwear features between different assemblages, analysis of variance (ANOVA) was run for each microwear variable. Tukey's post hoc measures were used to determine which rhino assemblages more likely had significantly different microwear patterns.

Because mesowear data are categorical, nonparametric Mann-Whitney U-tests were used to test for differences in mesowear scores among the rhino assemblages. In comparing all 13 rhino assemblages, 66 Mann-Whitney U-tests were run.

Running large numbers of tests increases the chance of type I error (falsely rejecting the null hypothesis). A Bonferonni correction ($p = 0.001$) can be used to minimize type I error, but at the cost of greatly increasing the probability of a type II error (incorrectly retaining the null hypothesis) (Perneger 1998). We report both the uncorrected and corrected results. However, due to the possibility of error in any individual test, we caution than patterns in the distribution of significant results among the data are more important than the results of any individual test.

Finally, we used a nonparametric Spearman's rho test for correlation of mesowear scores and microwear variables. Because of different types of taphonomic damage, mesowear and microwear could not always be collected from the same specimens. These tests are based on a subset of 206 specimens (83 modern, 123 fossil) for which both mesowear and microwear were available.

Results

Distribution of Dental-Microwear Features.— Extant perissodactyl microwear features have a distinct distribution, with more pits on the labial occlusal margin (A1) and more scratches on the lingual occlusal margin (A4) (Mihlbachler et al. 2016). We found the same pattern in the majority of the rhino assemblages (Fig. 2A,B). For most assemblages, there were significant differences in the number of labially and lingually distributed scratches or pits, or significant differences among both types of microwear features (Table 2). The strength of these labiolingual trends in numbers of microwear features varies considerably for both scratches

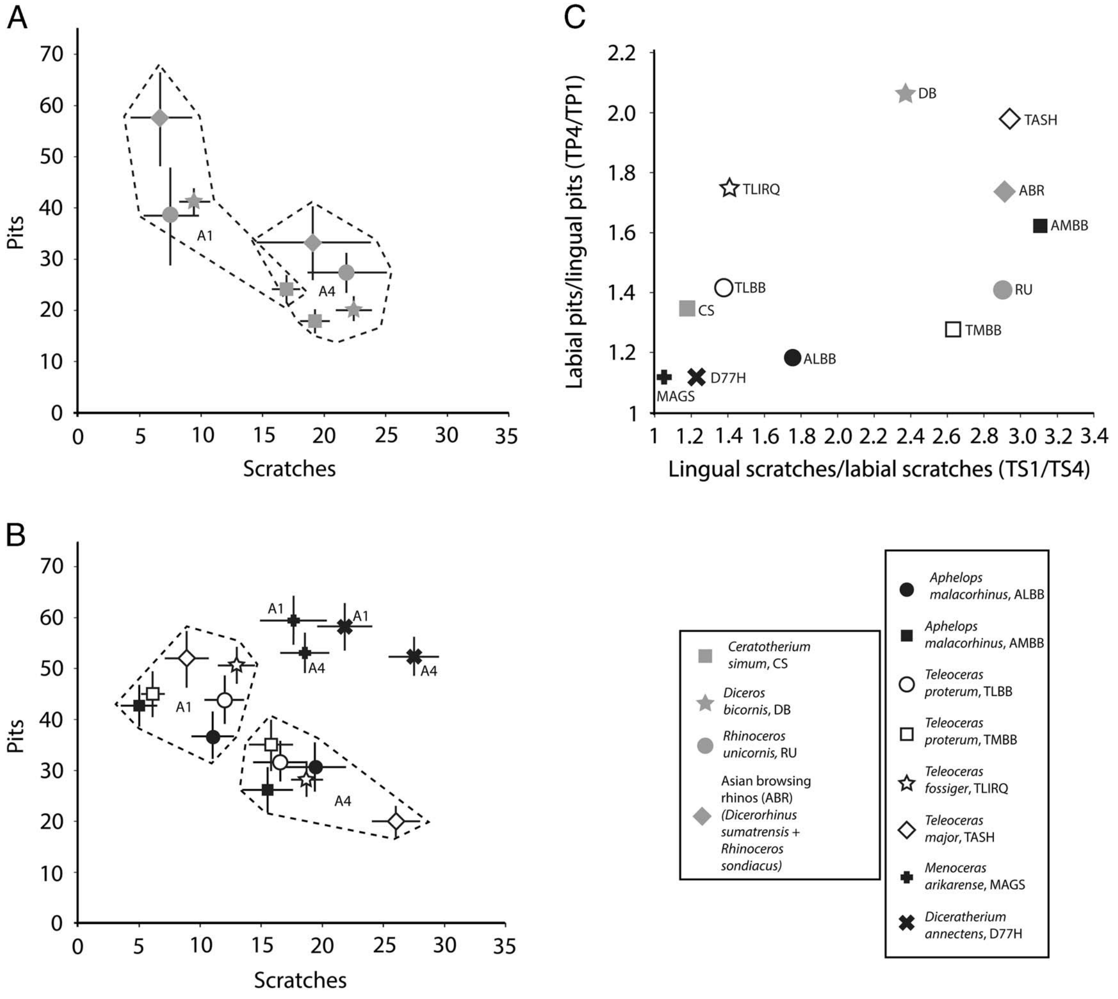

FIGURE 2. Means and SEs of labial (A1) and lingual (A4) dental microwear data for (A) extant species and (B) North American Miocene species. The dashed outlines in A and B surround labial and lingual microwear data. Figure C plots ratios of labially and lingually distributed pits and scratches and demonstrates the varying degrees of asymmetry in the distribution of pits and scratches on the labial and lingual sides of teeth. See Table 1 for abbreviations.

TABLE 2. The p-values resulting from paired t-tests comparing the frequencies of scratches and pits from the labial (A1) and lingual (A4) aspects of rhino molars. Bold values indicate significant differences in the numbers of labially and lingually distributed dental-microwear features. Species and assemblage abbreviations given in Table 1.

Assemblage	Scratches	Pits
CS	0.100	**0.004**
DB	**<0.001**	**<0.001**
RU	**<0.001**	0.177
ABR	**0.050**	**0.014**
ALBB	**0.019**	0.058
AMBB	**0.007**	**0.007**
TLBB	0.417	0.230
TMBB	**0.012**	0.081
TLIRQ	0.148	**0.010**
TASH	**<0.001**	**<0.001**
MAGS	0.738	0.245
D77H	0.129	0.473

and pits (Fig. 2C). These trends are strongest among browsers (DB and ABR) and the mixed feeder (RU), and weaker for grazers (CS).

The two assemblages of early Miocene rhinos (D77H and MAGS) had more homogenously distributed microwear than any other assemblage. The statistical results for *Teleoceras* and *Aphelops* are mixed. The TASH assemblage has significant labiolingual microwear trends for both scratches and pits, while the TLIRQ assemblage only shows a significant trend for pits. Results are equally mixed in the Florida assemblages. Both *Teleoceras* and *Aphelops* from Mixson's Bone Bed (TMBB and AMBB) have significant labiolingual trends, while the same species from the Love Bone Bed (TLBB and ALBB) do not.

Microwear Differences between Rhino Assemblages.—All ANOVAs testing for differences in scratch and pit frequency between rhino assemblages were significant ($p = 0.00$), indicating strong differences in the frequencies of scratches and pits between the molars of the different rhino assemblages in both the A1 (labial) and A4 (lingual) sampling sites.

Tukey's honest significant difference post hoc tests, showing the significance of individual assemblage–assemblage comparisons, are shown in Table 3 for labially distributed microwear (A1) and Table 4 for lingually distributed microwear (A4). Significant microwear differences among extant rhinos are only found on the labial edge (A1). This is consistent with more

TABLE 3. The p-values for Tukey's honestly significant difference post hoc tests from ANOVAs comparing the frequencies of scratches (shaded results) and pits (unshaded results) for the labial sampling region (A1). Bold values indicate significant differences in microwear-feature frequency. Species and assemblage abbreviations given in Table 1.

	CS	ABR	DB	RU	ALBB	AMBB	TLBB	TMBB	TLIRQ	TASH	MAGS	D77H
CS		**0.002**	**0.008**	0.750	0.613	0.153	0.052	**0.009**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
ABR	**0.048**		0.605	0.753	0.390	0.860	0.912	0.929	0.999	1.000	1.000	1.000
DB	**0.002**	0.997		1.000	1.000	1.000	1.000	1.000	0.581	0.684	**0.030**	0.051
RU	0.078	1.000	1.000		1.000	1.000	1.000	1.000	0.919	0.910	0.321	0.380
ALBB	0.305	0.976	1.000	0.996		1.000	0.997	0.982	0.404	0.461	**0.027**	**0.040**
AMBB	**<0.001**	1.000	0.767	1.000	0.620		1.000	1.000	0.975	0.970	0.367	0.443
TLBB	0.637	0.910	0.996	0.972	1.000	0.398		1.000	0.992	0.989	0.447	0.531
TMBB	**<0.001**	1.000	0.857	1.000	0.725	1.000	0.480		0.995	0.994	0.430	0.522
TLIRQ	0.579	0.645	0.730	0.801	0.999	0.064	1.000	0.057		1.000	0.908	0.949
TASH	**0.010**	1.000	1.000	1.000	1.000	0.960	0.988	0.990	0.742		0.984	0.993
MAGS	1.000	**0.042**	**0.006**	0.068	0.277	**0.000**	0.562	**<0.001**	0.545	**0.016**		1.000
D77H	0.389	**<0.001**	**<0.001**	**0.001**	**0.002**	**<0.001**	**0.009**	**<0.001**	**0.002**	**<0.001**	0.816	

Table 4. The *p*-values for Tukey's honestly significant difference post hoc tests from ANOVAs comparing the frequencies of scratches (shaded results) and pits (unshaded results) for the lingual sampling region (A4). Bold values indicate significant differences in microwear-feature frequency. Species and assemblage abbreviations given in Table 1.

	CS	ABR	DB	RU	ALBB	AMBB	TLBB	TMBB	TLIRQ	TASH	MAGS	D77H
CS		0.504	1.000	0.943	0.248	0.957	0.156	**0.002**	0.165	1.000	**<0.001**	**<0.001**
ABR	1.000		0.669	1.000	1.000	0.998	1.000	1.000	1.000	0.764	0.208	0.244
DB	0.915	0.998		0.986	0.428	0.993	0.295	**0.006**	0.329	1.000	**<0.001**	**<0.001**
RU	1.000	1.000	1.000		1.000	1.000	1.000	0.993	1.000	0.993	**0.012**	**0.016**
ALBB	1.000	1.000	0.991	1.000		1.000	1.000	0.999	1.000	0.655	**0.001**	**0.002**
AMBB	0.987	1.000	0.480	0.947	0.993		0.999	0.896	1.000	0.998	**<0.001**	**0.001**
TLBB	0.997	1.000	0.446	0.975	0.999	1.000		1.000	1.000	0.540	**0.001**	**0.002**
TMBB	0.941	1.000	0.113	0.908	0.981	1.000	1.000		0.950	0.054	**0.009**	**0.014**
TLIRQ	1.000	1.000	0.854	1.000	1.000	0.996	0.999	0.980		0.659	**<0.001**	**<0.001**
TASH	0.191	0.802	0.915	0.993	0.497	0.069	**0.046**	**0.006**	0.150		**<0.001**	**<0.001**
MAGS	1.000	1.000	0.906	1.000	1.000	0.999	1.000	0.997	1.000	0.229		1.000
D77H	**0.050**	0.571	0.590	0.941	0.220	**0.021**	**0.011**	**0.001**	**0.038**	1.000	0.073	

generalized findings for browsing and grazing perissodactyls, wherein only dental microwear from the labial edge of the tooth is found to be associated with diet (Mihlbachler et al. 2016). The grazer (CS) has significantly more scratches and fewer pits than browsers (DB, ABR). Neither browsing nor grazing rhinos were significantly different from the single mixed feeder (RU). RU clusters more closely with browsers.

Early Miocene rhinos (D77H, MAGS) have microwear patterns that differ from all other rhinos. TASH has a higher number of lingual scratches, but otherwise, *Aphelops* and *Teleoceras* microwear patterns were found to be undifferentiated. In comparison with extant rhinos with known diets, both *Teleoceras* and *Aphelops* have microwear that is indistinguishable from browsers (DB and ABR) and the mixed feeder (RU) but in many cases is statistically different from the grazing rhino (CS). Most of these significant differences occur on the labial sampling region (A1), the portion of the tooth that in extant rhinos is most strongly correlated with feeding ecology.

Mesowear.—There are many more significant differences between the mesowear scores of the rhino assemblages than there are microwear differences (Table 5). Out of 66 possible two-way nonparametric comparisons, 42 are significant. Thirty-two of these comparisons are still significant after Bonferonni corrections. CS has significantly blunter cusps than all other extant or extinct rhinos examined here (Figs. 3, 4). Mesowear scores varied significantly among extant browsing rhinos; DB cusps were blunter than ABR cusps. The mixed feeder (RU) has mesowear values that are significantly different from CS but fall within the range of browsing rhinos.

All of the fossil rhinos examined have significantly lower mesowear scores than the grazer CS and the browser DB, with average mesowear values that are similar to Asian rhinos (ABR and RU) or lower. Early Miocene rhinos (MAGS and D77H) have average mesowear scores and mesowear distributions similar to ABR. The mesowear scores of the four assemblages of *Teleoceras* all differ significantly from one another, suggesting different populations of *Teleoceras* may have had significant variation in overall dietary

TABLE 5. The *p*-values for Mann-Whitney *U*-tests comparing mesowear scores of extant and extinct rhino samples. Bold values indicate significant mesowear scores. Asterisk (*) indicates significant result after Bonferroni correction. Species and assemblage abbreviations given in Table 1.

	CS	DB	ABR	RU	ALBB	AMBB	TLBB	TMBB	TLIRQ	TASH	MAGS
DB	**<0.001***										
ABR	**<0.001***	**0.001***									
RU	**<0.001***	0.182	0.128								
ALBB	**<0.001***	**<0.001***	**0.001***	**0.001***							
AMBB	**<0.001***	**0.003**	0.639	0.106	**0.042**						
TLBB	**<0.001***	**<0.001***	**<0.001***	**<0.001***	0.342	0.059					
TMBB	**<0.001***	**<0.001***	0.116	**0.011**	**<0.001***	0.871	**<0.001***				
TLIRQ	**<0.001***	**0.002**	0.617	0.504	**<0.001***	0.285	**<0.001***	**0.019**			
TASH	**<0.001***	**<0.001***	0.226	**0.014**	**0.001***	0.914	**0.001***	0.774	**0.025**		
MAGS	**<0.001***	**<0.001***	0.671	0.118	**<0.001***	0.398	**<0.001***	**0.010**	0.643	**0.041**	
D77H	**<0.001***	**<0.001***	0.624	0.030	**<0.001***	0.787	**<0.001***	**0.070**	0.191	**0.180**	0.217

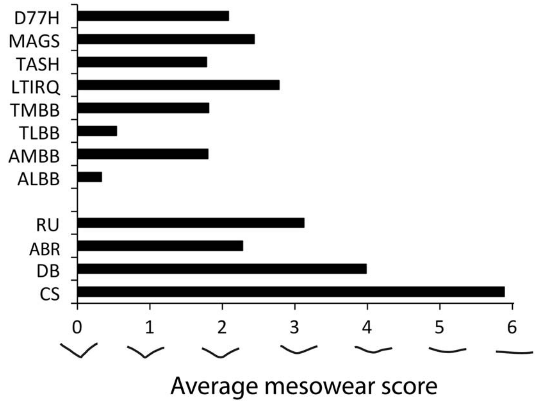

FIGURE 3. Average mesowear scores for M2 paracones. Species and assemblage abbreviations are given in Table 1.

abrasion. In the two localities where *Teleoceras* and *Aphelops* co-occur (Love Bone Bed and Mixson's Bone Bed), the average mesowear scores between these rhinos are virtually the same; however, the mesowear scores between these localities differ considerably. At Mixson's, *Teleoceras* and *Aphelops* have average mesowear scores that are only slightly lower than ABR, but these same species at the Love Bone Bed have average mesowear scores that are well below any other rhino assemblage.

Mesowear and Microwear Compared.—Figure 5 shows Spearmen's rho correlation coefficients for the mesowear scores and associated microwear data collected from those teeth for which both types of data were available. In the extant rhino data, significant microwear–mesowear correlations were found between mesowear scores and labially distributed microwear data (A1 scratches, A1 pits) (Fig. 5). In plots of average values for each rhino assemblage, A1 scratches and A1 pits strongly trend with average mesowear scores (Fig. 6A,B), with more scratches and fewer pits associated with higher average mesowear scores. No significant correlation was found between mesowear and lingually distributed microwear data (A4 scratches, A4 pits).

In contrast to the extant rhinos, no significant microwear–mesowear correlation was found among the extinct rhino assemblages (Fig. 5). Some of the fossil rhino assemblages (ALBB, TLBB, MAGS, D77H) appear to have excessive numbers of labially distributed scratches (A1 scratches) in comparison to their

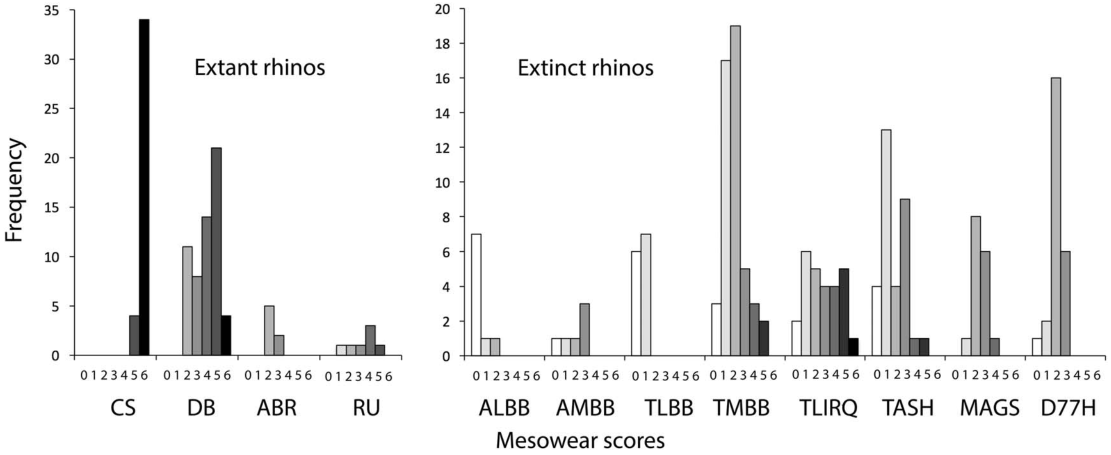

FIGURE 4. Distributions of mesowear scores for M2 paracones along the mesowear "ruler" (Mihlbachler et al. 2011), where the sharpest cusps with high relief are scored (0) and the bluntest cusps are scored (6).

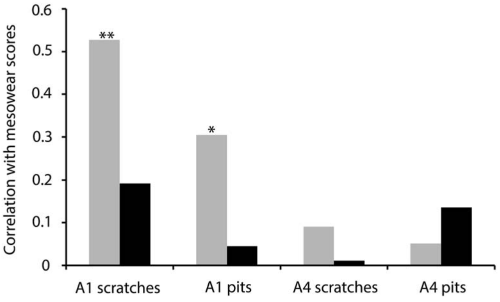

FIGURE 5. Nonparametric Spearman's rho correlation coefficients for mesowear and microwear variables for extant (gray bars) and extinct (black bars) rhinocerotid assemblages. Significant correlations are marked as follows: $^{**}p < 0.001$; $^{*}p = 0.007$.

comparatively low mesowear scores (Fig. 6A). Some of these assemblages (MAGS, D77H) also seem to have fewer numbers of labially distributed pits (A1 pits) (Fig. 6B). Other assemblages (TASH, TLIRQ, AMBB, TMBB) plot more closely to the microwear–mesowear trend lines suggested by extant rhinos (Fig. 6A,B).

Discussion

Premortem and Postmortem Microwear.—Rhinocerotids show labiolingual trends in the distribution of dental-microwear features, with more pits distributed labially and more scratches distributed lingually (Mihlbachler et al. 2016). The cause of this pattern is unclear but may be phylogenetically linked (Mihlbachler et al. 2016), as ruminant molars show a more homogenous pattern of dental microwear distribution. This same heterogeneous pattern of microwear distribution was found in the fossil rhino data (Fig. 2) and is strong evidence that dental microwear on the fossil rhino specimens is of premortem origin. Postmortem taphonomic alteration would tend to homogenize the appearance of surface wear. Only two fossil assemblages (MAGS and D77H) have statistically undifferentiated labial and lingual microwear. However, as noted in the "Materials and Methods," specimens showing signs of chemical weathering, postmortem abrasion, contamination with chemical residues, or other macroscopic postmortem damage were rejected in agreement with criteria applied in other microwear studies (King et al. 1999; El-Zaatari 2010). In addition, other evidence suggests the microwear of these specimens is premortem. For example scratches on occlusal surfaces have strong labiolingual orientations in the direction of mastication (Fig. 1). Furthermore, the microwear features are largely confined to occlusal surfaces. The nonocclusal enamel surfaces of these specimens have fewer microwear features and have markedly different surface textures. Therefore, we consider it unlikely that postmortem processes have severely altered microwear of any of the specimens included in the study.

Dental Wear and Diet in Extant Rhinos.—Blunted cusps (i.e., high mesowear scores), a high frequency of scratches, and a lower

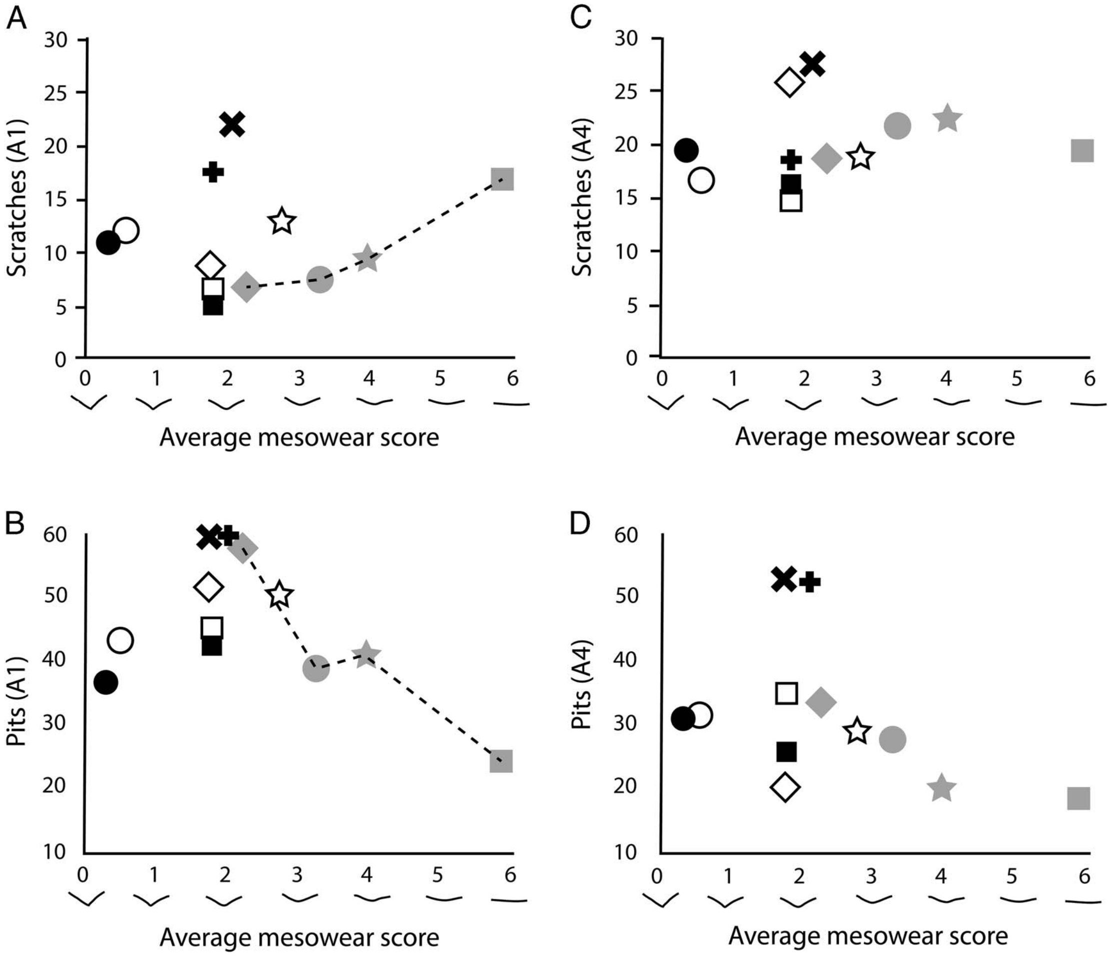

FIGURE 6. Plots of average mesowear scores against mean values for microwear variables. Key to symbols is given in Fig. 2. The gray symbols represent extant species, with dotted lines connecting them when mesowear and microwear are significantly correlated.

frequency of pits are associated with grazing diets (Fraser and Theodor 2011; Mihlbachler et al. 2016). There are significant differences between the dental-wear patterns of the grazing (CS) and browsing species (DB, ABR) that are consistent with typical grazer and browser dental-wear patterns. Given the association of these dental-wear patterns with browsing and grazing, the dental wear of RU, a grass-dominated mixed feeder, should either resemble CS or be intermediate between that of CS and browsing species. However, the mesowear and microwear of RU are like those of browsing rhinos (Figs. 2, 3). Similar results were found in another analysis of extant rhinocerotid mesowear (Taylor et al. 2013), in which differences associated with abrasive and attritive dental wear were observed between browsing and grazing species, but RU mesowear patterns were more attritive in nature and similar to those of browsers. These results lend credence to the suggestion that phytoliths may not be the only factor in driving rhinocerotid dental wear.

High rates of abrasive dental wear in herbivorous mammals have been attributed to both ingestion of phytolith-rich grasses and non-dietary abrasives (sand, dust, soil), and this had led to debate on weather dental wear in mammals is more of an indicator of diet or of feeding environment (Lucas et al. 2013, 2014; Erickson 2014; Kubo and Yamada 2014; Rabenold and Pearson 2014; Xia et al. 2015). Recent studies suggest phytoliths are generally softer than mammalian enamel (Sanson et al. 2007; Erickson 2014). Although it has been recently demonstrated that phytoliths are capable of wearing teeth despite being softer (Xia et al. 2015), rhinocerotid enamel is harder than that of other ungulates (Hager et al. 2014) and has a highly derived vertical Hunter-Schreger band orientation that enhances resistance to mechanical abrasion (Rensberger and Koenigswald 1980; Rensberger et al. 1984; Boyde and Fortelius 1986; Koenigswald et al. 2011). While rhino enamel could be more resistant to abrasion by phytoliths, it would still be more susceptible to abrasion from abiotic abrasives such as quartz, which is many times harder than enamel.

Further examination of the feeding habits of modern rhinos suggests environmental variables that influence the cleanliness of the feeding environment and the proximity of food to abiotic abrasives (sand, soil, dust) may play a dominant role in dental wear. There is a strong relationship between feeding height and dental wear patterns. Among the five extant species, CS feeds lowest to the ground and has the highest abrasion signal in its dental wear. In a study of tooth-blade sharpness in a variety of browsing and grazing mammals, CS was an outlier, with extremely rounded blade tips for which the authors also concluded the degree of abrasion must be very high (Popowics and Fortelius 1997). CS rarely feeds on grasses more than 0.5 m tall (Foster 1967; Groves 1972; Kleynhans et al. 2011; Rookmaaker 2013), and more than 50% of grasses eaten are reportedly under 5 cm tall. Using a square upper lip, CS crops grasses nearly down to ground level (Owen-Smith 1988; Arsenault and Owen-Smith 2008, 2011).

As noted above, if a grassy diet were the primary agent of abrasive tooth wear, RU would have dental-wear patterns most similar to CS, although its mesowear and microwear fall in the range of browsers. Its grazing strategy is quite different from CS. While CS feeds in short grassy lawns with a square lip, RU pushes grasses that are 4–8 m tall between its front legs and grazes the tips using a prehensile upper lip (Laurie 1982; Laurie et al. 1983; Mary et al. 1998; Hazarika and Saikia 2010).

A lower feeding height increases opportunities to ingest soil, sand, or other abrasive food contaminants. Large mammal molars commonly accumulate ingesta particles that become impacted in the infundibula of molars. CS molar infundibula contain very high concentrations of impacted quartz sand, whereas those of other rhino species contain mostly plant material (Mihlbachler et al. 2012a). The differences in feeding height and the greater quantity of quartz sand and dust impacted in CS molars suggest that CS ingests more nondietary abrasives than RU. A cleaner diet, mostly taken from several meters above the ground, may explain why RU has more browser-like dental wear despite its predominantly grassy diet. These findings suggest feeding height and probably other factors that impact the cleanliness of the immediate feeding environment may influence dental wear in rhinocerotids.

Variation in dental-wear patterns among browsing rhinos may also be related to feeding height. DB has higher frequencies of scratches and blunter cusps with lower relief (higher mesowear scores) than other browsing or mixed-feeding rhinos, suggesting a level of dietary abrasion that is intermediate between CS and other rhinos. It also feeds relatively low to the ground. DB has been observed extensively feeding on small herbs and shrubs (Goddard 1970; Mukinya 1977; Birkett 2002) and taller woody material (Goddard 1968, 1970; Oloo et al. 1994; Birkett 2002). About 30–60% of biomass consumed by DB is reportedly under 0.5 m tall (Owen-Smith 1988; Lieverloo et al. 2009). Most studies indicate that DB preferentially browses at a height of 0.5–1.5 m (Joubert and Eloff 1971; Owen-Smith 1988; Emslie and Adcock 1994; Baggallay et al. 1995; Hennig and Gindrig 2002; Ganqa et al. 2005; Makaure and Caston 2013). ABR feed from higher levels and in more forested environments than DB and have dental-wear patterns suggesting less-abrasive diets. Both Asian species use chest, shoulders, neck, and chin to bring foliage from saplings into reach (Hoogerwerf 1970; Owen-Smith 1988). They push over young trees up to 6–7 cm in diameter. Young trees make up the largest portion of their diet (Strickland 1967; van Strien 1986; Owen-Smith 1988; Pratiknyo 1991).

Microwear–Mesowear Congruence.—Our hypothesis that congruence between mesowear and labially distributed microwear will occur in the modern rhino assemblages is borne out by the results. The dental microwear on the labial edge of perissodactyl molars (A1) is strongly predictive of diet in browsers and grazers (Mihlbachler et al. 2016) and is also statistically correlated to mesowear scores in extant rhinos. Our second hypothesis, that mesowear and microwear are not as strongly correlated in mass-death assemblages is also supported, as we did not find a statistical correlation between these two dental-wear proxies among the fossil rhino assemblages. The possibility that some of the fossil assemblages sustained changes in feeding environment or diet before the mass-death events occurred, leading to disassociations between mesowear and microwear, is supported. Short-term shifts in microwear could be caused by changes in diet or changes in the rate of ingestion of abiotic abrasives due to excessive aridity, cropping vegetation lower to the ground, or contaminated food.

Although there is a difference in the degree of microwear–mesowear congruence between the modern and fossil assemblages, it is difficult to find deeper associations with the hypothesized cause-of-death scenarios for the individual fossil bone-bed assemblages. We hypothesized the time-averaged attritional assemblages from the Mixson's Bone Bed locality (AMBB, TMBB) would show microwear–mesowear congruence. Indeed, the average mesowear and microwear values of the AMBB and TMBB assemblages plot in close proximity to the microwear–mesowear trend lines for extant rhinos for labial microwear variables, suggesting strong microwear–mesowear congruence (Fig. 6A,B). However, although one might hypothesize less congruence among the catastrophic and semicatastrophic assemblages, these assemblages show a mixture of congruent and incongruent patterns. Two *Teleoceras* assemblages (TASH and TLIRQ) have relatively congruent mesowear and labially distributed microwear (Fig. 6A,B). Others show more incongruence. The Love Bone Bed rhinos (ALBB, TLBB) have more labially distributed scratches than mesowear would predict, and the early Miocene assemblages (MAGS, D77H) have more labial scratches and fewer labial pits than mesowear would predict (Fig. 6A,B). These four assemblages (D77H, MAGS, ALBB, TLBB) appear to be responsible for the lack of statistically significant correlation of mesowear and microwear among the fossil rhinos.

Unfortunately, in most instances it is difficult to predict from taphonomic evidence the duration of ecologically stressful periods that precede mass deaths. In instances in which catastrophic mortality occurs, variation in the duration of exposure to the events leading to the mortality may influence the degree to which microwear shifts out of alignment with mesowear. At the onset of ecological pressure, such as a drought, microwear should become altered at a faster rate than mesowear. If the ecologically stressful event were sufficiently prolonged, many of the animals would have been exposed for an extended period of time before finally succumbing. Longer exposure would tend to bring microwear and mesowear into alignment in the dentitions of the eventual victims. For instance, at the Ashfall locality, rhinos exhibit bone pathologies associated with ash inhalation and asphyxiation, suggesting that the animals succumbed over weeks or months (Tucker et al. 2014). The evidence for prolonged exposure could explain the more congruent nature of mesowear and microwear in this assemblage. Those assemblages that show greater microwear–mesowear incongruence may have been events of shorter duration. We conclude that while the data provide evidence for greater frequency of microwear–mesowear incongruence in fossil bone beds in comparison with modern hunted assemblages, probably due to ecological disturbance proximate to the time of death, it remains difficult to understand details of the individual death events that would allow for more specific predictions about mesowear and microwear agreement.

If further studies show that the degree of microwear–mesowear incongruence in mass death assemblages relates to the duration and severity of ecological pressure associated with the mortality event, this adds an additional dimension of ecological evidence that these proxies can offer. We endeavor to demonstrate this possibility in the following section, but caution that studies of the dental-wear rates and turnover rates of mesowear and microwear signals in nature (Solounias et al. 1994; Damuth and Janis 2014) and in experimental settings (Schulz et al. 2013; Hoffman et al. 2015) are needed to better establish the time duration represented by these different dental-wear proxies.

Miocene Rhino Dental Wear and Feeding Ecology.—Bearing in mind the results presented earlier, we attempt to derive conclusions about the feeding ecologies of Miocene North American rhinocerotids. In cases in which mesowear and microwear show incongruence, we suggest mesowear is more appropriate for drawing conclusions about generalized aspects of diet. The majority of the fossil rhino assemblages have low mesowear scores that resemble Asian rhinos and are significantly different from African rhinos, suggesting these rhinocerotids typically adopted low-abrasion browsing or mixed-feeding diets, possibly from tall vegetation or other relatively clean feeding environments.

While mesowear is consistent with a hypothesis of browsing diets for *Diceratherium* and *Menoceras*, the microwear of these early Miocene rhinos is unique, with excessive quantities of both scratches and pits. The specific diets associated with these microwear patterns are unclear and may be consequences of some localized aspect of diet and or feeding environment during these mass-death events, possibly associated with ecological stress.

The only fossil assemblage examined here for which there is direct evidence of diet is the Ashfall locality. Fossil grass anthoecia of the genus *Berriochloa* are found in the oral and abdominal cavities of Ashfall *Teleoceras* skeletons (Voorhies and Thomasson 1979), indicating *Teleoceras* consumed siliceous grasses shortly before the mortality event caused by prolonged exposure to an ash-contaminated environment. However, neither the mesowear nor the microwear offer compelling evidence of an excessively abrasive diet caused by short-grass grazing or ingestion of volcanic ash. Such extreme ecological disturbance may not always have predictable effects on feeding behavior. For example, if *Teleoceras* had a feeding ecology similar to RU and fed from taller vegetation, including browse and taller riparian grasses, its feeding environment might not have been heavily contaminated by ash.

Both *Aphelops* and *Teleoceras* are abundant in the Love Bone Bed and Mixson's localities from Florida, and these localities provide insights into the ecology of these two sympatric rhinos. At each locality, the mesowear and microwear of *Aphelops* and *Teleoceras* are undifferentiated. This finding is peculiar considering their differing ecomorphologies and considering evidence indicating their diets were isotopically differentiated at times with *Teleoceras* consuming higher amounts of C_4 grass (MacFadden 1998). However, the mesowear and microwear patterns of both rhinos differ significantly between Mixson's and Love Bone Bed, suggesting the feeding ecology of these rhinos differed between localities. A stronger relationship of dental wear with feeding environment rather than diet better explains how *Aphelops* and *Teleoceras*, two rhinos with ecomorphologically dissimilar morphologies and isotopically differentiated diets (MacFadden 1998), have similar dental patterns that covary with fossil localities. Both mesowear and microwear proxies suggest feeding ecologies similar to ABR at Mixson's. The Love Bone Bed results for both rhinos (TLBB and ALBB) are more anomalous; both *Teleoceras* and *Aphelops* have exceptionally low and outlying mesowear scores that are significantly different from all other rhinos, with many sharpened, tall cusp apices. The Love Bone Bed was a pure C_3 ecosystem that existed prior to the spread of C_4 grasses in Florida (MacFadden and Cerling 1996; MacFadden 1998). *Teleoceras* and *Aphelops* have statistically undifferentiated isotopic signals from this locality and are among the species with the most negative $\Delta^{13}C$ values of the entire fauna along with a tapir *Tapirus simpsonii*, suggesting habitation of closed environments (Feranec and MacFadden 2006). The clean and minimally abrasive diets suggested by mesowear could be a reflection of these isotopic results. The Love Bone Bed assemblages of *Aphelops* and *Teleoceras* have microwear patterns that imply more abrasive diets than their mesowear scores would indicate, again suggesting seasonal fluctuation in feeding environments and possibly associated seasonal dietary shifts (e.g., seasonal mixed feeding) or some form of short-term ecological disturbance (e.g., drought) near the time of death that increased the abrasiveness of the diets of both rhinos.

Conclusions

This study offers conclusions on patterns of incongruence between mesowear and microwear in death assemblages and conclusions on the relationship of dental wear and ecology in living and extinct rhinocerotids. Most studies of ungulates and other strictly herbivorous mammals attempt to relate dental wear to diet in terms of browse/graze. As a consequence of their larger size, megaherbivores feed less selectively than smaller herbivores (Owen-Smith 1988) and are more likely to ingest abiotic abrasives (dust, sand, silt) if food (e.g., short grass) is in close proximity to such material. Because minerals such as quartz are much harder than enamel, frequent ingestion of such particles may strongly influence dental wear. Mesowear and microwear of extant rhinos is strongly associated with diet and feeding height. Dental-wear patterns in rhinos may be more closely related to the rate of ingestion of abiotic minerals than intake of phytoliths. Therefore, dental-wear patterns of rhinos (and possibly other megaherbivores) may tell us less about diet and more about the conditions of the feeding environment.

A high degree of congruence between mesowear and microwear was encountered in collections of modern rhino material, which mostly consists of specimens that were hunted. In contrast, microwear–mesowear incongruence was more often found among the fossil mass-death assemblages. Mesowear suggests North American Miocene rhinocerotids had diets either less abrasive than all extant rhinos or similar to that of Asian browsing and mixed-feeding rhinos that feed on tall vegetation. However, about half of the fossil assemblages show microwear patterns that suggest altered diets near the time of death. These results are consistent with our hypothesis that near-death changes in feeding ecology related to ecological stress may commonly bias microwear data in fossil assemblages. However, this conclusion is not a negative reflection of the value of dental microwear. The three main paleodiet proxies for ungulates in the paleoecologist's tool kit include stable isotopes, mesowear, and microwear. All three of these proxies relate to diet at different life-history intervals, including growth and development (stable isotopes), an extended period of time before death (mesowear), and a brief interval of time before death (microwear). We recommend that paleoecological studies recognize the limitation of each proxy and that integration of these methods provides a more richly textured view about not only paleodiet, but how diets drift throughout the lives of the organisms with ontogeny, seasonal change, and stochastic ecological disturbances.

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Literature Cited

Amman, H. 1985. Contributions to the ecology and sociology of the Javan Rhinoceros. Ph.D. dissertation. Universität Basel, Basel.

Arsenault, R., and N. Owen-Smith. 2008. Resource partitioning by grass height among grazing ungulates does not follow body size relation. Oikos 117:1111–1717.

——. 2011. Competition and coexistence among short-grass grazers in the Hluhluwe-Imfolozi Park, South Africa. Canadian Journal of Zoology 89:900–907.

Baggallay, T., N. Owen-Smith, and R. R. Swaisgood. 1995. Black rhinoceros browsing facilitates resource availability: implications for donor population management. Nineteenth Annual Meeting of the Society for Conservation Biology, Abstracts of papers, pp. 11–12.

Bhatta, R. 2011. Ecology and conservation of great one-horned rhino (*Rhinoceros unicornis*) in Pobitora Wildlife Sanctuary, Assam, India. Ph.D. dissertation. University of Gauhati, Guwahati, India.

Birkett, A. 2002. The impact of giraffe, rhino and elephant on the habitat of a black rhino sanctuary in Kenya. African Journal of Ecology 40:276–282.

Boyde, A., and M. Fortelius. 1986. Development, structure and function of rhinoceros enamel. Zoological Journal of the Linnean Society 87:181–214.

Brown, D. H., P. C. Lent, W. S. W. Trollope, and A. R. Palmer. 2003. Browse selection of black rhinoceros (*Diceros bicornis*) in two vegetation types of the eastern Cape Province, South Africa, with particular reference to Euphorbiaceae. Pp. 509–512. *in* N. Allsopp, A. R. Palmer, S. J. Milton, K. P. Kirkman, G. I. H. Kerley, C. R. Hurt, and C. J. Brown, eds. Proceedings of the Seventh International Rangelands Congress, 26 July–1 August, Durban, South Africa. Document Transformation Technologies, Johannesburg, South Africa.

Buk, K. G., and M. H. Knight. 2010. Seasonal diet preferences of black rhinoceros in three arid South African National Parks. African Journal of Ecology 48:1064–1075.

Cerdeno, E. 1998. Diversity and evolutionary trends of the Family Rhinocerotidae (Perissodactyla). Palaeogeography, Palaeoclimatology, Palaeoecology 141:13–34.

Clementz, M. T., P. A. Holroyd, and P. L. Koch. 2008. Identifying aquatic habits of herbivorous mammals through stable isotope analysis. Palaios 23:574–585.

Codron, D., J. Codron, J. A. Lee-Thorp, M. Sponheimer, D. De Ruiter, J. Sealy, R. Grant, and N. Fourie. 2007. Diets of savanna ungulates from stable carbon isotopes composition of faeces. Journal of Zoology 273:21–29.

Damuth, J., and C. M. Janis. 2014. A comparison of observed molar wear rates in extant herbivorous mammals. Annales Zoologici Fennici 51:188–200.

Deka, R. J., N. K. Sarma, and K. K. Baruah. 2003. Nutritional evaluation of the principal forages/feed consumed by Indian rhino (*Rhinoceros unicornis*) in Pobitora Wildlife Sanctuary and Assam State Zoo-Cum-Botanical Garden, Assam. Zoos' Print. Journal 18:1043–1045.

DeMiguel, D., M. Fortelius, B. Azanza, and J. Morales. 2008. Ancestral feeding state of ruminants reconsidered: earliest grazing adaptation claims a mixed condition for Cervidae. BMC Evolutionary Biology 8:13.

DeMiguel, D., B. Azanza, and J. Morales. 2011. Paleoenvironments and paleoclimate of the middle Miocene of central Spain: a reconstruction from dental wear of ruminants. Palaeogeography, Palaeoclimatology, Palaeoecology 302:452–463.

DeSantis, L. R. G., and S. C. Wallace. 2008. Neogene forests from the Appalachians of Tennessee, USA: geochemical evidence from fossil mammal teeth. Palaeogeography, Palaeoclimatology, Palaeoecology 266:59–68.

Dinerstein, E. 1992. Effects of *Rhinoceros unicornis* on riverine forest structure in lowland Nepal. Ecology 73:701–704.

——. 2003. The return of the unicorns: the natural history and conservation of the greater one-horned rhinoceros. Columbia University Press, New York.

Dinerstein, E., and L. Price. 1991. Demography and habitat use by greater one-horned rhinoceros in Nepal. Journal of Wildlife Management 55:401–411.

Dinerstein, E., and C. M. Wemmer. 1988. Fruits *Rhinoceros* eat: dispersal of *Trewia nudiflora* (Euphorbiaceae) in lowland Nepal. Ecology 69:1768–1774.

Dudley, C. O. 1997. The candelabra tree (*Euphorbia ingens*): a source of water for black rhinoceros in Liwonde National Park, Malawi. Koedoe 40:57–62.

Edwards, E. J., C. P. Osborne, C. A. E. Strömberg, S. A. Smith, and C_4 Grasses Consortium 2010. The origins of C_4 grassland: integrating evolutionary and ecosystem science. Science 328:587–591.

El-Zaatari, S. 2010. Occlusal microwear texture analysis and the diets of historical/prehistoric hunter-gatherers. International Journal of Osteoarchaeology 20:67–87.

Emslie, R. H., and K. Adcock. 1994. Feeding ecology of black rhinos. Pp. 65–81 *in* B. L. Penzhorn and N. P. J. Kriek, eds. Proceedings of a symposium on rhinos as game ranch animals, 9–10 September, Onderstepoort, South Africa.

Erickson, K. L. 2014. Prairie grass phytolith hardness and the evolution of ungulate hypsodonty. Historical Biology 26: 737–744.

Feranec, R. S., and B. J. MacFadden. 2006. Isotopic discrimination of resource partitioning among ungulates in C_3-dominated communities from the Miocene of Florida and California. Paleobiology 32:191–205.

Feranec, R. S., and D. Pagnac. 2013. Stable carbon isotope evidence for the abundance of C_4 plants in the middle Miocene of southern California. Palaeogeography, Palaeoclimatology, Palaeoecology 388:42–47.

Fjellstad, J. I., and G. Steinheim. 1996. Diet and habitat use of greater Indian one-horned rhinoceros (*Rhinoceros unicornis*) and Asian elephant (*Elephas maximus*) during the dry season in Babai Valley, Royal Bardia National Park, Nepal. M.S. thesis, Agricultural University of Norway, Ås, Norway.

Fortelius, M., and N. Solounias. 2000. Functional characterization of ungulate molars using the abrasion-attrition wear gradient: a new method for reconstructing paleodiets. American Museum Novitates 3301:1–36.

Foster, J. B. 1967. The square-lipped rhino (*Ceratotherium simum cotton*) in Uganda. East African Wildlife Journal 5:167–171.

Franz-Odendaal, T. A., and N. Solounias. 2004. Comparative dietary evaluations of an extinct giraffid (*Sivatherium hendeyi*) (Mammalia, Giraffidae, Sivatheriinae) from Langebaanweg, South Africa (early Pliocene). Geodiversitas 26:675–685.

Fraser, D., and J. M. Theodor. 2011. Comparing ungulate dietary proxies using discriminant function analysis. Journal of Morphology 272:1513–1526.

——. 2013. Ungulate diets reveal patterns of grassland evolution in North America. Palaeogeography, Palaeoclimatology, Palaeoecology 369:409–421.

Ganqa, N. M., P. F. Scogings, and J. G. Raats. 2005. Diet selection and forage quality factors affecting woody plant selection by black rhinoceros in the Great Fish River Reserve, South Africa. South African Journal of Wildlife Research 35:77–83.

Goddard, J. 1968. Food preferences of two black rhinoceros populations. East African Wildlife Journal 6:1–18.

——. 1970. Food preferences of black rhinoceros in the Tsavo National Park. East African Wildlife Journal 8:14–161.

Gogarten, J. F., and F. E. Grine. 2013. Seasonal mortality patterns in primates: implications for interpretation of dental microwear. Evolutionary Anthropology 22:9–19.

Gogarten, J. F., L. M. Brown, C. A. Chapman, M. Cords, D. Doran-Sheehy, L. M. Fedigan, F. E. Grine, S. Perry, A. E. Pusey, E. H. M. Sterck, S. A. Wich, and P. C. Wright. 2012. Seasonal mortality patterns in non-human primates: implications for variation in selection pressures across environments. Evolution 66: 3252–3266.

Groves, C. P. 1972. *Ceratotherium simum*. Mammalian Species 8:1–6.

——. 1982. Asian rhinoceroses: down but not out. Malayan Naturalist 36:11–22.

Groves, C. P., and F. Kurt. 1972. Dicerorhinus sumatrensis. Mammalian Species 21:1–6.

Groves, C. P., and D. M. J. Leslie. 2011. *Rhinoceros sondiacus* (Perissodactyla: Rhinocerotidae). Mammalian Species 43:190–208.

Hager, S., M. C. Mihlbachler, and B. L. Beatty. 2014. Indentation hardness of tooth enamel of multiple mammalian species and the role of enamel microstructure on dental wear mechanics. Journal of Vertebrate Paleontology, 74th Annual Meeting, Abstracts of Papers, p. 143.

Hall-Martin, A. J., T. Erasmus, and B. P. Botha. 1982. Seasonal variation of diet and faeces composition of black rhinoceros *Diceros bicornis* in the Addo Elephant National Park. Koedoe 25:63–82.

Harrison, J. A., and E. M. Manning. 1983. Extreme carpal variability in *Teleoceras* (Rhinocerotidae, Mammalia). Journal of Vertebrate Paleontology 3:58–64.

Hatcher, J. B. 1885. Information as to occurrence of bones in Kansas. Field records on file in the archives of the Department of Paleobiology. National Museum of Natural History, Washington, D.C.

Hazarika, B. C., and P. K. Saikia. 2010. A study of the behaviour of great Indian one-horned rhino (*Rhinoceros unicornis*) in the Rajiv Gandhi Orang National Park, Assam, India. NeBIO 1(2):62–74.

Heller, E. 1913. The white rhinoceros. Smithsonian Miscellaneous. Collections 61:1–77.

Hennig, J., and T. Gindrig. 2002. Feeding habits of desert dwelling black rhinoceros (*Diceros bicornis*), in Kunene Region northwest of Namibia. Pp. 311–312 *in* H. M. Schwammer, T. J. Foose, M. Fouraker, and D. Olson, eds. Proceedings of the International Elephant and Rhino Research Symposium. Schuling, Muenster.

Hernesniemi, E., K. Blomstedt, and M. Fortelius. 2011. Multi-view stereo three-dimensional reconstruction of lower molars of recent and Pleistocene rhinoceroses for mesowear analysis. Palaeontologia Electronica 14:palaeo-electronica.org/2011_2/246/index.html.

Hoffman, J. M., D. Fraser, and M. T. Clementz. 2015. Controlled feeding trials with ungulates: a new application of *in vivo* dental molding to assess the abrasive factors of microwear. Journal of Experimental Biology 218:1538–1547.

Hoogerwerf, A. 1970. Udung Kulon: the land of the last Javan rhinoceros. Brill, Leiden, Netherlands.

Hunt, R. M. 1990. Taphonomy and sedimentology of Arikaree (lower Miocene) fluvial, eolian, and lacustrine paleoenvironments, Nebraska and Wyoming; a paleobiota entombed in fine-grained volcaniclastic rocks. *In* M. G. Lockley, and A. Rice, eds. Volcanisms and fossil biotas. Geological Society of America Special Paper 244:69–111. Boulder, Colo.

Janis, C. M. 2008. An evolutionary history of browsing and grazing ungulates. Pp. 21–45 *in* I. J. Gordon, and H. H. T. Prins, eds. The ecology of browsing and grazing. Springer, Berlin.

Jnawali, S. R. 1995. Population ecology of greater one-horned rhinoceros (*Rhinoceros unicornis*) with particular emphasis on habitat preference, food ecology and ranging behavior of a reintroduced population in Royal Bardia National Park in lowland Nepal. Ph.D. dissertation. Agricultural University of Norway, Ås, Norway.

Jnawali, S. R., and P. Wegge. 1991. Space and habitat use by a small re-introduced population of greater one-horned rhinoceros (*Rhinoceros unicornis*) in Royal Bardia National Park in Nepal. A preliminary report. Pp. 208–227 *in* O. A. Ryder, ed. Rhinoceros biology and conservation. Zoological Society of San Diego, San Diego.

Joubert, E., and F. C. Eloff. 1971. Notes on the ecology and behaviour of the black rhinoceros *Diceros bicornis* Linn. 1758 in South West Africa. Madoqua 1:5–53.

Kahlke, R.-D., and T. M. Kaiser. 2011. Generalism as a subsistence strategy: advantages and limitations of the highly flexible traits of Pleistocene *Staphanorhinus hundsheimensis* (Rhinocerotidae, Mammalia). Quaternary Science Reviews 30:2250–2261.

Kaiser, T. M., D. W. H. Müller, M. Fortelius, E. Schulz, D. Codron, and M. Clauss. 2011. Hypsodonty and tooth facet development in relation to diet and habitat in herbivorous ungulates: implications for understanding tooth wear. Mammal Review 43:34–46.

Kandel, R. C., and Y. V. Jhala. 2008. Demographic structure, activity patterns, habitat use and food habits of *Rhinoceros unicornis* in Chitwan National Park, Nepal. Journal of Bombay Natural History Society 105:5–13.

King, T., P. Andrews, and B. Boz. 1999. Effect of taphonomic processes on dental microwear. American Journal of Physical Anthropology 108:359–373.

Kleynhans, E. J., A. E. Jolles, M. R. E. Bos, and H. Olff. 2011. Resource partitioning along multiple niche dimension in differently sized African savanna grazers. Oikos 120:591–600.

Koenigswald, W. v., L. Holbrook, and K. D. Rose. 2011. Diversity and evolution of Hunter-Schreger band configuration in tooth enamel of perissodactyl mammals. Acta Palaeontologica Polonica 56:11–32.

Kubo, M. O., and E. Yamada. 2014. The inter-relationship between dietary and environmental properties and tooth wear: comparisons of mesowear, molar wear rate, and hypsodonty index of extant sika deer populations. PLoS ONE 9:e90745.

Laurie, W. A. 1982. Behavioural ecology of the greater one-horned rhinoceros (*Rhinoceros unicornis*). Journal of Zoology 196:307–341.

Laurie, W. A., E. M. Lang, and C. P. Groves. 1983. Rhinoceros unicornis. Mammalian Species 211:1–6.

Leidy, J., and F. A. Lucas. 1896. Fossil vertebrates from the Alachua Clays of Florida. Transactions of the Wagner Free Institute of Science of Philadelphia 4:7–61.

Lieverloo, R. J. v., B. F. Schuiling, W. F. d. Boer, D. Brown, and H. H. T. Prins. 2009. A comparison of faecal analysis with backtracking to determine the diet compositions and species preference of the black rhinoceros (*Diceros bicornis minor*). European Journal of Wildlife Research 55:505–515.

Loffredo, L. F., and L. R. G. DeSantis. 2014. Cautionary lessons from assessing dental mesowear observer variability and integrating paleoecological proxies of an extreme generalist *Cormohipparion emsliei*. Palaeogeography, Palaeoclimatology, Palaeoecology 395:42–52.

Loutit, B. D., G. N. Louw, and M. K. Seely. 1987. First approximation of food preferences and the chemical composition of the diet of the desert-dwelling black rhinoceros, *Diceros bicornis* L. Madoqua 15:35–54.

Louys, J., C. Meloro, S. Elton, P. Ditchfield, and L. Bishop. 2011. Mesowear as a means of determining diets in African antelopes. Journal of Archaeological Science 38:1485–1495.

Louys, J., P. Ditchfield, C. Meloro, S. Elton, and L. Bishop. 2012. Stable isotopes provide independent support for the use of mesowear variables for inferring diets in African antelopes. Proceedings of the Royal Society B 279:4441–4446.

Lucas, P. W., R. Omar, K. Al-Fadhalah, A. S. Almusallam, A. G. Henry, S. Michael, L. A. Thai, J. Watzke, D. S. Strait, and A. Atkins. 2013. Mechanisms and causes of wear in tooth enamel: implications for hominin diets. Journal of the Royal Society Interface 10:1–9.

Lucas, P. W., A. van Casteren, and K. Al-Fadhalah. 2014. The role of dust, grit, and phytoliths in tooth wear. Annales Zoologici Fennici 51:143–152.

Luske, B. L., T. Mertens, P. C. Lent, W. F. de Boer, and H. H. T. Prins. 2009. Impact of the black rhinoceros (*Diceros bicornis minor*) on a local population of *Eurphorbia bothae* in the Great Fish River Reserve, South Africa. African Journal of Ecology 47:509–517.

Lyman, R. L. 1994. Vertebrate taphonomy. Cambridge University Press, Cambridge.

MacFadden, B. J. 1998. Tale of two rhinos: isotopic ecology, paleodiet, and niche differentiation of *Aphelops* and *Teleoceras* from the Florida Neogene. Paleobiology 24:274–286.

MacFadden, B. J., and T. E. Cerling. 1996. Mammalian herbivore communities, ancient feeding ecology, and carbon isotopes: a 10 million-year sequence from the Neogene of Florida. Journal of Vertebrate Paleontology 16:103–115.

Mainland, I. L. 1996. The lamb's last supper: the role of dental microwear analysis in reconstructing livestock diet in the past. Environmental Archaeology 1:55–62.

Makaure, J., and M. Caston. 2013. Dry season browse preference for the black rhinoceros (*Diceros bicornis*): the case of the Midlands Black Rhino Conservancy (MBRC), Zimbabwe. Greener Journal of Biological Sciences 3:31–47.

Mary, P. O., G. S. Solanki, D. Limboo, and K. Upadhaya. 1998. Observations on feeding and territorial behaviour of Indian rhino (*Rhinoceros unicornis*) in Kaziranga National Park, Assam, India. Tiger Paper 25:25–28.

McInerney, F. A., C. A. E. Strömberg, and W. C. White. 2011. The Neogene transition from C_3 to C_4 grasslands in North America: stable carbon isotope ratios of fossil phytoliths. Paleobiology 37:23–49.

Mead, A. J. 2000. Sexual dimorphism and paleoecology in *Teleoceras*, a North American Miocene rhinoceros. Paleobiology 26:689–706.

Merceron, G., C. Blondel, M. Brunet, S. Sen, N. Solounias, L. Viriot, and E. Heintz. 2004. The Late Miocene paleoenvironment of Afghanistan as inferred from dental microwear in artiodactyls. Palaeogeography, Palaeoclimatology, Palaeoecology 207: 143–163.

Merceron, G., C. Blondel, L. De Bonis, G. D. Koufos, and L. Viriot. 2005. A new method of dental microwear analysis: application to extant primates and *Ouranopithecus macedoniensis* (late Miocene of Greece). Palaios 20:551–561.

Merceron, G., G. Escarguel, J.-M. Angibault, and H. Verheyden-Tixier. 2010a. Can dental microwear textures record inter-individual dietary variations? PLoS ONE 5:e9542.

Merceron, G., T. M. Kaiser, D. S. Kostopoulos, and E. Schulz. 2010b. Ruminant diets and the Miocene extinction of European great apes. Proceedings of the Royal Society B 277:3105–3112.

Mihlbachler, M. C. 2003. Demography of late Miocene rhinoceroses (*Teleoceras proterum* and *Aphelops malacorhinus*) from Florida: linking mortality and sociality in fossil assemblages. Paleobiology 29:412–428.

——. 2005. Linking sexual dimorphism and sociality in rhinoceroses: insights from *Teleoceras proterum* and *Aphelops malacorhinus* from the late Miocene of Florida. Bulletin of the Florida Museum of Natural History 45:495–520.

——. 2007. Sexual dimorphism and mortality bias in a small Miocene North American Rhino, *Menoceras arikarense*: insights into the coevolution of sexual dimorphism and sociality in rhinos. Journal of Mammalian Evolution 14:217–238.

Mihlbachler, M. C., and B. L. Beatty. 2012. Magnification and resolution in dental microwear analysis using light microscopy. Palaeontologia Electronica 15:14.

Mihlbachler, M. C., F. Rivals, N. Solounias, and G. M. Semprebon. 2011. Dietary change and evolution of horses in North America. Science 331:1178–1181.

Mihlbachler, M. C., B. L. Beatty, and M. Ayoub. 2012a. Extraction and analysis of ingesta impacted in the dentitions of modern ungulates: new evidence for linking dental wear and feeding ecology. Journal of Vertebrate Paleontology, 72nd Annual Meeting, Abstracts of Papers, p. 141.

Mihlbachler, M. C., B. L. Beatty, A. Caldera-Siu, D. Chan, and R. Lee. 2012b. Error rates in dental microwear analysis using light microscopy. Palaeontologia Electronica 15:22.

Mihlbachler, M. C., D. Campbell, M. Ayoub, C. Chen, and I. Ghani. 2016. Comparative dental microwear of ruminant and perissodactyl molars: implications for paleodietary analysis of rare and extinct ungulate clades. Paleobiology 42:98–116.

Mukinya, J. G. 1977. Feeding and drinking habits of the black rhinoceros in Masai Mara Game Reserve. East African Wildlife Journal 15:125–138.

Muya, S. M., and N. O. Oguge. 2000. Effects of browse availability and quality on black rhino (*Diceros bicornis michaeli* Groves 1967) diet in Nairobi National Park, Kenya. African Journal of Ecology 38:62–71.

Oloo, T. W., R. Brett, and T. P. Young. 1994. Seasonal variation in the feeding ecology of black rhinoceros (*Diceros bicornis* L.) in Laikipia, Kenya. African Journal of Ecology 32:142–157.

Osborn, H. F. 1898a. A complete skeleton of *Teleoceras fossiger*. Notes upon the growth and sexual characteristics of the species. Bulletin of the American Museum of Natural History 10:51–59.

——. 1898b. A complete skeleton of *Teleoceras* the true rhinoceros from the upper Miocene of Kansas. Science 7:554–557.

Owen-Smith, R. N. 1975. The social ethology of the white rhinoceros *Ceratotherium simum* (Burchell 1817). Zeitschrift für Tierpsychologie 38:337–384.

——. 1988. Megaherbivores: the influence of very large body size on ecology. Cambridge University Press, Cambridge.

Pedersen, G. 2009. Habitat use and diet selection of reintroduced white rhinoceros (*Ceratotherium simum*) in Pafuri, Kruger National Park. M.S. thesis. Stellenbosch University, Stellenbosch, South Africa.

Perneger, T. 1998. What's wrong with Bonferroni adjustments? British Medical Journal 316:1236–1238.

Pienaar, D. J. 1994. Habitat preference of the white rhino in Kruger National Park. Pp. 59–64 *in* B. L. Penzhorn and N. P. J. Kriek, eds. Proceedings of a symposium on rhinos as game ranch animals, 9–10 September, Onderstepoort, South Africa.

Player, I. C., and J. M. Feely. 1960. A preliminary report on the square-lipped rhinoceros. Lammergeyer (Natal) 1:3–23.

Popowics, T. E., and M. Fortelius. 1997. On the cutting edge: tooth blade sharpness in herbivorous and faunivorous mammals. Annales Zoologici Fennici 34:73–88.

Pradham, N. M. B., P. Wegge, S. R. Moe, and A. K. Shrestha. 2008. Feeding ecology of two endangered sympatric megaherbivores: Asian elephant *Elephas maximus* and greater one-horned rhinoceros *Rhinoceros unicornis* in lowland Nepal. Wildlife Biology 14:147–154.

Pratiknyo, H. 1991. The diet of the Javan rhino. Voice of Nature. 93:12–13.

Prothero, D. R. 1998. Rhinocerotidae. Pp. 595–605 *in* C. M. Janis, K. M. Scott, and L. L. Jacobs, eds. Evolution of tertiary mammals of North America Vol. 1. Terrestrial carnivores, ungulates, and ungulatelike mammals Cambridge University Press, Cambridge.

——. 2005. The evolution of the North American rhinoceros. Cambridge University Press, Cambridge.

Rabenold, D., and A. Pearson. 2014. Scratching the surface: a critique of Lucas et al. (2013)'s conclusion that phytoliths do not abrade enamel. Journal of Human Evolution 74: 130–133.

Rensberger, J. M., and W. v. Koenigswald. 1980. Functional and phylogenetic interpretation of enamel microstructure in rhinoceroses. Paleobiology 6:477–495.

Rensberger, J. M., A. Forsten, and M. Fortelius. 1984. Functional evolution of the cheek tooth pattern and chewing direction in Tertiary horses. Paleobiology 10:439–452.

Ritchie, A. T. A. 1963. The black rhinoceros (*Diceros bicornis* L.). East African Wildlife Journal 1:54–62.

Rivals, F., and G. M. Semprebon. 2012. Paleoindian subsistence strategies and late Pleistocene paleoenvironments in the northeastern and southwestern United States: a tooth wear analysis. Journal of Archaeological Science 39:1608–1617.

Rivals, F., N. Solounias, and M. C. Mihlbachler. 2007. Evidence for geographic variation in the diets of late Pleistocene and early Holocene *Bison* in North America, and differences from the diets of recent *Bison*. Quaternary Research 68:338–346.

Rivals, F., E. Schulz, and T. M. Kaiser. 2008. Climate-related dietary diversity of the ungulate faunas from the middle Pleistocene succession (OIS 14–12) at the Caune de l'Argo (France). Paleobiology 34:117–127.

——. 2009. A new application of dental wear analyses: estimation of duration of hominid occupations in archaeological localities. Journal of Human Evolution 56:329–339.

Rivals, F., M. C. Mihlbachler, N. Solounias, D. Mol, G. M. Semprebon, and J. de Vos. 2010. Palaeoecology of the mammoth steppe fauna from the late Pleistocene of the North Sea and Alaska: separating species preference from geographic influence in paleocological dental wear analysis. Palaeogeography, Palaeoclimatology, Palaeoecology 286:42–54.

Rivals, F., N. Solounias, and G. B. Schaller. 2011. Diet of Mongolian gazelles and Tibetan antelopes from steppe habitats using premaxillary shape, tooth mesowear and microwear analysis. Mammalian Biology 76:358–364.

Rivals, F., D. Rindel, and J. B. Belardi. 2013. Dietary ecology of extant guanaco (*Lama guanicoe*) from Southern Patagonia: seasonal leaf browsing and its archaeological implications. Journal of Archaeological Science 40:2971–2980.

Rivals, F., S. Takatsuki, R. M. Albert, and L. Maciá. 2014. Bamboo feeding and tooth wear of three sika deer (*Cervus nippon*) populations from northern Japan. Journal of Mammalogy 95:1043–1053.

Rivals, F., L. Prignano, G. M. Semprebon, and S. Lozano. 2015. A tool for determining duration of mortality events in archaeological assemblages using extant ungulate microwear. Scientific Reports 5:17330.

Rodríguez-Hidalgo, A., F. Rivals, P. Saladie, and E. Carbonell. 2016. Season of bison mortality in TD10.2 bone bed at Gran Dolina site (Atapuerca): integrating tooth eruption. wear, and microwear methods. Journal of Archaeological Science: Reports 6:780–789.

Rogers, R.R., R., D. A. Eberth, and A. R. Fiorillo. 2007. Bonebeds: genesis, analysis, and paleobiological significance. University of Chicago Press, Chicago.

Rookmaaker, K. 2013. *Ceratotherium simum*: white rhinoceros (grass rhinoceros, square-lipped rhinoceros). Pp. 446–454 *in* J. Kingdon, and H. M. Hoffmann, eds. Mammals of Africa Vol. 5. Carnivores, pangolins, equids and rhinoceroses. Bloomsbury, London.

Roosevelt, T., and E. Heller. 1914. Life Histories of African game animals, Vol. 1. Scribner, New York.

Sánchez-Hernández, C., F. Rivals, R. Blasco, and J. Rosell. 2016. Tale of two timescales: combining tooth wear methods with different temporal resolutions to detect seasonality of Palaeolithic hominin occupational patterns. Journal of Archaeological Science: Reports 6:790–797.

Sanson, G. D., S. A. Kerr, and K. A. Gross. 2007. Do silica phytoliths really wear mammalian teeth? Journal of Archaeological Science 34:526–531.

Sarma, P. K., B. S. Mipun, B. K. Talukdar, H. Singha, A. K. Basumatary, A. K. Das, A. Sarkar, and B. C. Hazarika. 2012. Assessment of habitat utilization pattern of rhinos (*Rhinoceros unicornis*) in Orang National Park, Assam, India. Pachyderm 51:38–44.

Schenkel, R., and L. Schenkel-Hulliger. 1969a. Ecology and behavior of the black rhinoceros. Parey, Hamburg.

——. 1969b. The Javan rhinoceros (*Rh. sondaicus* Desm.) in Udjung Kulon Nature reserve. Its ecology and behaviour. Acta Tropica 26:97–135.

Schulz, E., J. M. Fahlke, G. Merceron, and T. M. Kaiser. 2007. Feeding ecology of the Chalicotheriidae (Mammalia, Perissodactyla, Ancylopoda). Results from dental micro- and mesowear analyses. Verhandlungen des Naturwissenschaftlichen Vereins zu Hamburg 43:5–31.

Schulz, E., V. Piotrowski, M. Clauss, M. Mau, G. Merceron, and T. M. Kaiser. 2013. Dietary abrasiveness is associated with variability of microwear and dental surface texture in rabbits. PLoS ONE 8:e56167.

Semprebon, G. M., and F. Rivals. 2007. Was grass more prevalent in the pronghorn past? An assessment of the dietary adaptations of Miocene to recent Antilocapridae (Mammalia: Artiodactyla). Palaeogeography, Palaeoclimatology, Palaeoecology 253: 332–3347.

——. 2010. Trends in the paleodietary habits of fossil camels from the Tertiary and Quaternary of North America. Palaeogeography, Palaeoclimatology, Palaeoecology 295:131–145.

Semprebon, G., L. Godfrey, N. Solounias, M. R. Sutherland, and W. L. Jungers. 2004. Can low-magnification stereomicroscopy reveal diet? Journal of Human Evolution 47:115–144.

Semprebon, G. M., F. Rivals, N. Solounias, and R. C. J. Hulbert. 2016. Paleodietary reconstruction of fossil horses from Eocene through Pleistocene of North America. Palaeogeography, Palaeoclimatology, Palaeoecology 442:110–127.

Shrader, A. M., and M. R. Perrin. 2006. Influence of density on the seasonal utilization of broad grassland types by white rhinoceroses. African Zoology 41:312–315.

Shrader, A. M., N. Owen-Smith, and J. O. Ogutu. 2006. How a mega-grazer copes with the dry season: food and nutrient intake rates by white rhinoceros in the wild. Functional Ecology 20: 376–384.

Solounias, N., and G. Semprebon. 2002. Advances in reconstruction of ungulate ecomorphology with applications to early fossil equids. American Museum Novitates 3366:1–49.

Solounias, N., M. Fortelius, and P. Freeman. 1994. Molar wear rates in ruminants: a new approach. Annales Zoologici Fennici 31:219–227.

Steinheim, G., P. Wegge, J. I. Fjellstad, S. R. Jnawali, and R. B. Weladji. 2005. Dry season diets and habitat use of sympatric Asian elephants (*Elephas maximus*) and greater one-horned rhinoceros (*Rhinoceros unicornis*) in Nepal. Journal of Zoology 265:377–385.

Strickland, D. L. 1967. Ecology of the rhinoceros in Malaya. Malayan Nature. Journal 20:1–17.

Strömberg, C. A. E. 2005. Decoupled taxonomic radiation and ecological expansion of open-habitat grasses in the Cenozoic of North America. Proceedings of the National Academy of Sciences USA 102:11980–11984.

——. 2011. Evolution of grasses and grassland ecosystems. Annual Review of Earth and Planetary Science 39:517–544.

Taylor, L. A., T. M. Kaiser, C. Schwitzer, D. W. H. Müller, D. Codron, M. Clauss, and E. Schulz. 2013. Detecting inter-cusp and inter-tooth wear patterns in rhinocerotids. PLoS ONE 8:1–12.

Taylor, K. L., J. L. Beck, and S.V. Huzurbazar. 2016. Factors influencing winter mortality risk for pronghorn exposed to wind energy development. Rangeland Ecology and Management 69:108–116.

Tripathi, A. K. 2012. Habitat and population ecology of *Rhinoceros unicornis* in Dudhwa National Park, Uttar Pradesh. International Journal of Pharmacology and Life Sciences 3:2090–2097.

Tucker, S. T., R. E. Otto, R. M. Joeckel, and M. R. Voorhies. 2014. The geology and paleontology of Ashfall Fossil Beds, a late Miocene (Clarendonian) mass-death assemblage, Antelope County and adjacent Knox County, Nebraska, USA. Geological Society of America Field Guide 36:1–20.

Tütken, T., T. M. Kaiser, T. Vennemann, and G. Merceron. 2013. Opportunistic feeding strategy for the earliest Old World hypsodont equids: evidence from stable isotope and dental wear proxies. PLoS ONE 8:e74463.

Ungar, P. S. 2009. Teeth form and function: insights into adaptation through the analysis of dental microwear. Frontiers of Oral Biology 13:38–43.

——. 2015. Mammalian dental function and wear: a review. Biosurface and Biotribology 1:25–41.

van Strien, N. J. 1986. The Sumatran rhinoceros *Dicerorhinus sumatrensis* (Fischer, 1814) in the Gunung Leuser National Park Sumatra, Indonesia. Parey, Hamburg.

Voorhies, M. R. 1985. A Miocene rhinoceros herd buried in volcanic ash. National Geographic Society Research Reports 19:671–688.

Voorhies, M. R., and J. R. Thomasson. 1979. Fossil grass anthoecia within Miocene rhinoceros skeletons: diet in an extinct species. Science 206:331–333.

Waldram, M. S., W. J. Bond, and W. D. Stock. 2008. Ecological engineering by a mega-grazer: white Rhino impacts on a South African savanna. Ecosystems 11:101–112.

Webb, S. D., B. J. MacFadden, and J. A. Baskin. 1981. Geology and paleontology of the Love Bone Bed from the late Miocene of Florida. American Journal of Science 281:513–544.

Wegge, P., A. K. Shrestha, and S. R. Moe. 2006. Dry season diets of sympatric ungulates in lowland Nepal: competition and facilitation in alluvial tall grasslands. Ecological Research 21:698–706.

Wolf, D., S. V. Nelson, H. L. Schwartz, G. M. Semprebon, T. M. Kaiser, and R. L. Bernor. 2010. Taxonomy and paleoecology of the Pleistocene Equidae from Makuyuni, Northern Tanzania. Palaeodiversity 3:249–269.

Xia, J., J. Zheng, D. Huang, Z. R. Tian, L. Chen, Z. Zhou, and P. S. Ungar. 2015. New model to explain tooth wear with implications for microwear formation and diet reconstruction. Proceedings of the National Academy of Sciences USA 112: 10669–10672.

Young, T. P. 1994. Natural die-offs of large mammals: implications for conservation. Conservation Biology 8:410–418.