



An examination of the dietary habits of *Platybelodon grangeri* from the Linxia Basin of China: Evidence from dental microwear of molar teeth and tusks



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ABSTRACT

The paleodiet of shovel-tusked gomphotheres from the upper middle Miocene Hujialiang Formation of the Linxia Basin (Gansu Province, China) was assessed via molar microwear analysis of dental enamel. Both adults and an ontogenetic series of individuals of *Platybelodon grangeri* with assigned dental ages estimated via comparison of eruption and wear to that of extant elephants were analyzed. Mandibular tusks were also examined for microscopic scars to test a long-standing hypothesis that *P. grangeri* used its mandibular tusks to shovel substrate. Results show a consistent browsing signal throughout all of the age classes studied. Evenso, scratch numbers are higher and scratch widths are greater in older individuals indicating that coarser browse was consumed in older versus younger individuals. Results are more similar to those of the extant forest elephant (*Loxodonta cyclotis*) than to other extant forms (*Loxodonta africana* and *Elephas maximus*). Mandibular tusk microwear is very fine and inconsistent with the usage of lower tusks to shovel aquatic or terrestrial substrates and more consistent with stripping vegetation than as shoveling agents.

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1. Introduction

1.1. Background

The Gomphotheriidae represents a diverse family of extinct large proboscideans commonly referred to as gomphotheres. Gomphotheres enjoyed a nearly global distribution during the Miocene, Pliocene, and Pleistocene with the exception of Australia and Antarctica. They migrated from Africa to Eurasia by the early Miocene (Tassy, 1996), reached North America by the middle Miocene (Lambert, 1996), and then migrated into South America during the Great American Interchange (Webb, 1976).

Gomphotheres had two upper and two lower tusks. The upper tusks were curved and oriented in a downward and outward direction while the lower tusks were procumbent and spatulate in appearance and lacked enamel (Fig. 1A). Their facial and nasal bones were retracted which has led to them commonly being reconstructed as having elephant-like trunks (Osborn and Granger, 1932).

Gomphotheres molars are distinctive from modern elephants and more like those of American mastodon. Molar teeth are bunodont and

either trilophont or tetralophont and thus they are generally thought to have been opportunistic browsers (Asevedo et al., 2012; Domingo et al., 2012; Fox and Fisher, 2004). While the systematics and phylogeny of gomphotheres are unclear and the group is generally considered to be paraphyletic (e.g., Shoshani and Tassy, 2005), gomphotheres were a very successful and diversified group. They were also very wide-ranging, making them good biostratigraphic markers for correlation. Gomphotheres enjoyed their peak diversity in the late Miocene and went extinct in the Pleistocene.

The shovel-tusked gomphotheres have long intrigued paleontologists and the general public alike as they are undoubtedly one of the most distinctive of all proboscideans. These bizarre mammals are characterized by their broad and dorso-ventrally flattened mandibular tusks that bear an uncanny resemblance to the head of a shovel. This strange propensity has often earned them a place in popular books on prehistoric life as well as a prominent place in museum wall murals (e.g., Hezheng Paleozoological Museum). Part of this notoriety was certainly fueled by Osborn's report in 1936 on Asian specimens of the genus *Platybelodon* where he depicted the ventral aspect of the lower pair of incisors beside a coal shovel.

The shovel-tuskers include four generally recognized genera: *Amebelodon*, *Platybelodon*, *Torynobelodon* and *Serbelodon* although the latter has sometimes been united with *Amebelodon* (Tobien, 1972).

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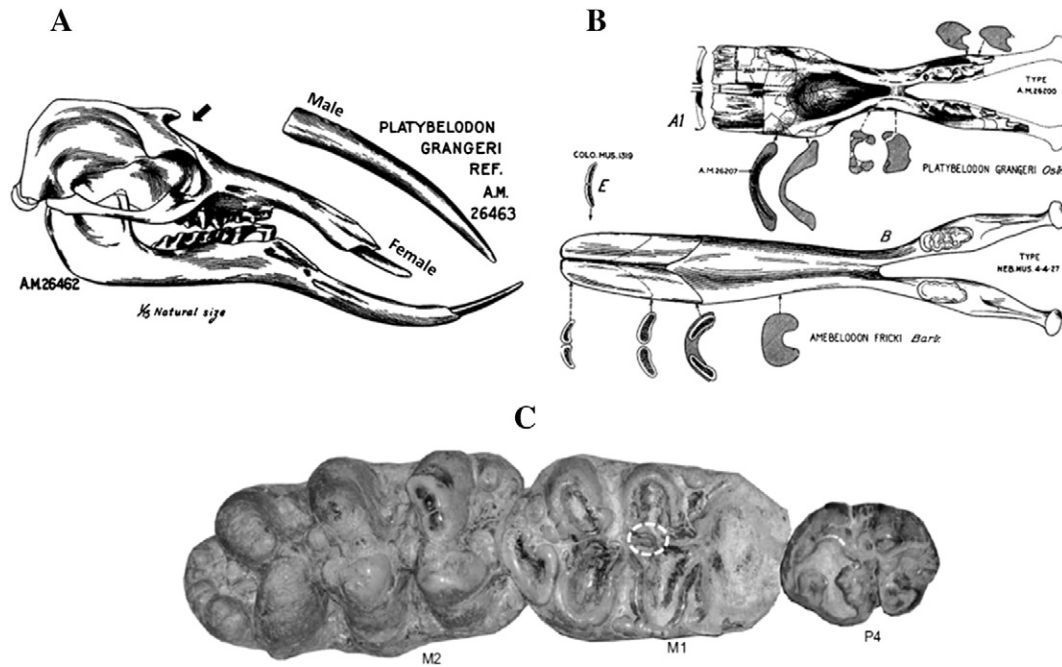


Fig. 1. A. *Platybelodon grangeri* skull from the Tung Gur horizon in China (A.M. 26462) with male upper tusk (A.M. 26463) drawn to the same scale to show the size disparity between male and female tusks (modified from Osborn, 1932). Arrow shows retracted nasals. B. The lower jaws of *Amebelodon* (bottom) and *Platybelodon* (top) compared (from Osborn and Granger, 1931); C. P4, M1, and M2 of *Platybelodon grangeri* (HMV 1828) (modified from Wang et al., 2013). White oval on M1 indicates area sampled on molars (grinding facet); A.M. refers to the American Museum of Natural History.

Platybelodon was first described by the Russian paleontologist Borissiak in 1928 (from the middle Miocene of the Kuban Region to Caucasus Area of Russia). In 1928, the Central Asiatic Expedition by the American Museum of Natural History found a locality near a freshwater well known as Gur Tung Khara Usu in central Inner Mongolia, China (Andrews, 1932; Spock, 1929). This led to the discovery of one of the richest fossil mammal assemblages in the middle Miocene of China (Tunggur Area, Inner Mongolia) that became the basis of the Tunggurian land mammal age in East Asia and is best known from its shovel-tusked gomphotheres — *Platybelodon grangeri* (Wang et al., 2003).

During the past two decades, researchers from the Institute of Vertebrate Paleontology and Paleoanthropology of the Chinese Academy of Sciences (IVPP) and the Hezheng Paleozoological Museum (HPM) have uncovered much new material which is housed in the Hezheng Paleozoological Museum and recently described by Wang et al. (2013). This new material surpasses the material from the Tunggur Area in terms of numbers of specimens and completeness.

The unique dental morphology of the shovel-tuskers has long fueled much speculation about their dietary habits. *Platybelodon* has long been known to be morphologically distinctive from other shovel-tuskers. For example, *Platybelodon* has a relatively short mandibular symphysis and its mandibular tusks are more flattened, shorter and broader than those of *Amebelodon* and much broader than those of *Torynobelodon loomisi* (Osborn and Granger, 1931) but not wider (even narrower) than those of *Torynobelodon barnumbrowni*. In addition, unlike other amebelodontines, all of its intermediate cheek teeth are tetralophodont (Lambert, 1996) (Fig. 1B). In addition, *Platybelodon* upper tusks are notable in being quite reduced, show extreme sexual dimorphism (Fig. 1A), and are vestigial in females (Osborn, 1936; Lambert, 1992).

Of course, there has been a great deal of interest and much speculation regarding the functional significance of the bizarre mandibular tusks of *Platybelodon* and other shovel-tusked gomphotheres. Lambert (1992) pointed out that early and long-lasting speculations regarding the functional significance of shovel-tusker mandibular tusks was based mostly on inference and/or incomplete information rather than on actual direct evidence. For example, Barbour (1927, 1929a) thought at various times that *Amebelodon*'s mandibular tusks were used to dig

and scoop up plants like a shovel (1927), for stripping leaves and/or twigs from trees, or possibly had no specific function at all (1929a). Borissiak (1929) proposed that the mandibular tusks of *Platybelodon danovi* were used for scooping up and feeding on aquatic vegetation from the bottom of freshwater ponds or lakes, a view that was fortified by Osborn and Granger (1932) who observed that the distal edges of the mandibular tusks of *Platybelodon* were sharpened – presumably by abrasive interaction with sediments from lake or pond bottoms. After this reconstruction, a similar mandibular tusk wear and inference of aquatic shoveling was noted by Barbour (1929b, 1931, 1932) for *Torynobelodon loomisi* and *T. barnumbrowni*. Thus, *Platybelodon* has historically and rather consistently been portrayed as having fed in swampy areas of grassy savannas and using its shovel-like incisors to shovel up aquatic and semi-aquatic vegetation. A more recent study (Lambert, 1992) looked at wear patterns on mandibular tusks of shovel-tusked gomphotheres but within the framework of theoretical modeling of upper and lower tusk wear. This study suggested that *Platybelodon* used its lower tusks to strip bark from trees or to cut or strip vegetation (Lambert, 1992).

1.2. The Linxia Basin

The Linxia Basin is located at the junction of the northeastern Tibetan Plateau, the western Qinling Mountains and the Loess Plateau in the Gansu Province of China (Fig. 2). The localities of this basin are notable for their well-preserved and abundant bones of large mammals that are often complete, partially articulated, and tend to occur in dense concentrations (Deng, 2010). The Linxia Basin is particularly well known for its large concentration of *Platybelodon* fossils. *Platybelodon* is an important member of what is known as the middle Miocene “*Platybelodon* Fauna” (Deng, 2004b; Deng, 2004a). These middle Miocene deposits are separated into the upper Hujialiang Formation and the lower Dongxiang Formation (Deng, 2004a). The fossil specimens analyzed in this study were recovered from the upper middle Miocene Hujialiang Formation from which several nearly complete skulls and mandibles have been recovered as well as an ontogenetic series of skulls and mandibles.

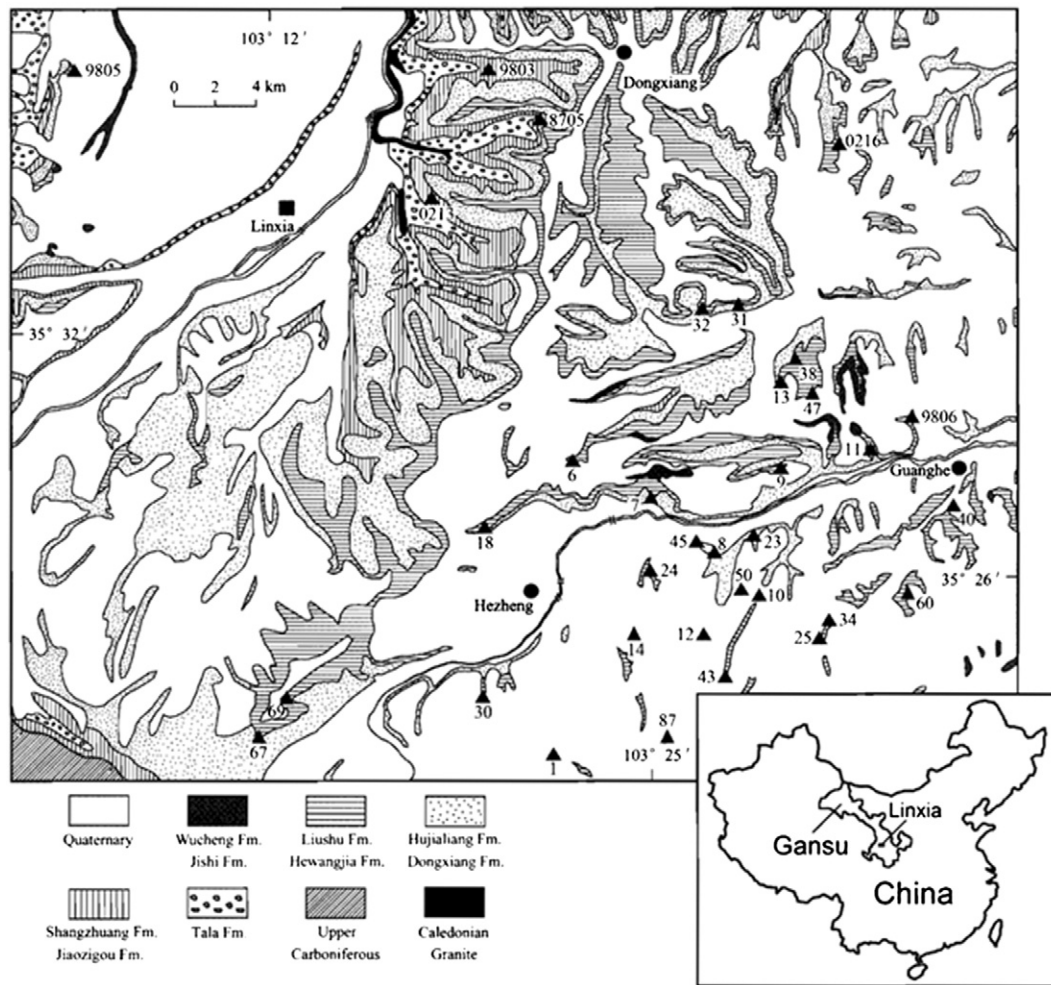


Fig. 2. Geological map of the Linxia Basin in Gansu Province, China showing representative mammal fossil localities (from Deng et al., 2013). The fossil specimens analyzed in this study were recovered from the upper middle Miocene Hujialiang Formation (small stippling) (Locality key may be found in Fig. 9.1, Deng et al., 2013).

A recent study by Wang et al. (2013) has provided a comprehensive revision of the middle Miocene *Platybelodon* material from the Linxia Basin and refers all of the Hujialiang fossils to *Platybelodon grangeri* whereas those from the Dongxiang FM have been assigned to *Platybelodon danovi*.

1.3. Aims of the study

The purpose of this study was threefold: 1) to explore the paleodietary ecology of adult Chinese middle Miocene shovel-tusked gomphotheres (i.e., *Platybelodon grangeri*) from the Linxia Basin (Hujialiang FM, Gansu Province) using stereomicrowear analysis, 2) to examine dietary patterns in an ontogenetic series of *Platybelodon grangeri* molars with assigned dental ages, and 3) to test the long-standing hypothesis that *Platybelodon grangeri* used its mandibular tusks as shovels.

1.4. Microwear

Enamel microwear is a mostly taxon-independent method that gives insight into the dietary behavior of the last days or weeks before an animal's death (Grine, 1986). Therefore, it provides a glimpse into available vegetation and habitat as well as short-term dietary behavior and allows for inferences to be made regarding daily, seasonal, or regional variations in trophic habits that gross tooth morphology generally fails to do. The value of microwear as a *direct* source of dietary

behavior and as a snapshot of dietary behavior often not discerned via gross tooth morphological methods such as mesowear and hypsodonty indices has been demonstrated and discussed by Rivals and Semprebon (2011). Consequently, microwear often gives insight into what a taxon is actually doing despite what it might be optimally adapted to do.

Microwear has been employed for well over three decades as a technique to examine the direct dietary behavior of mammals by visualizing scars etched into dental enamel produced by food items such as plant phytoliths or due to exogenous grit or dust inherent on the surface of the vegetation consumed. Originally, microwear was performed using a scanning electron microscope (e.g., Rensberger, 1978; Walker et al., 1978). More recent methodologies utilize light microscopy such as confocal microscopic techniques (e.g., Scott et al., 2005, 2006; Ungar et al., 2008, 2010) and stereomicroscopic techniques (e.g., Semprebon, 2002; Solounias and Semprebon, 2002; Merceron et al., 2004, 2005; Semprebon et al., 2004). The latter technique (after Semprebon, 2002) was used in this study as it allows for the attainment of relatively larger sample sizes and a very large comparative stereomicrowear database exists which is comprised of extant artiodactyls, perissodactyls, and proboscideans of known diets compiled by a single observer (GMS). All counts on fossil casts were also compiled by a single observer (GMS) to minimize error in the analysis.

The paleodiet of Miocene shovel-tuskers (*Platybelodon grangeri*) was assessed via molar microwear analysis. Both adult and juvenile individuals from an ontogenetic series of molars with assigned dental ages (using stages detailed in Tassy, 2013) and estimated via comparison of

eruption and wear to that of extant elephants were also analyzed. In addition, mandibular tusks were examined with a stereomicroscope to test the hypothesis that *P. grangeri* used its mandibular tusks as shovels.

2. Materials and methods

2.1. Sample

Molar teeth and mandibular tusks of *P. grangeri* from the Hujialiang Formation of the Linxia Basin were sampled from the collections of the Hezheng Paleozoological Museum (HPM) in Hezheng County, Gansu Province, China. The specimens were screened under a stereomicroscope for potential taphonomic alteration of dental surfaces (King et al., 1999). 32 *P. grangeri* adult molar tooth casts, 7 specimens from an ontogenetic series with age estimates based on eruption and toothwear, and 7 mandibular tusks were deemed suitable for analysis and subjected to microwear analysis to reconstruct paleodiet (see Fig. 1C for area analyzed).

2.2. Microwear technique

Tooth surfaces were cleansed, molded, casted and examined at 35 times magnification with a Zeiss Stemi-2000C stereomicroscope. Microscope scar topography was visualized on the grinding facet of a central molar loph (Fig. 1C) by using external oblique illumination. An M1-150 High Intensity fiber optic light source (Dolan-Jenner) was directed across the surface of casts at a shallow angle to the occlusal surface.

On the molar casts, the average number of pits (rounded features) versus average number of scratches (elongated features) per taxon were assessed within a 0.4 mm square area (0.16 mm²). It was also noted if more than four large pits were present or absent per microscope field (within the 0.4 mm square area) and whether gouges were present or absent (after Semprebon, 2002; Solounias and Semprebon, 2002). Results were compared to extant proboscidean and ungulate microwear databases to determine the dietary categories of browser versus grazer. In addition, scratch textures were assessed as being either fine (i.e., narrow scratches that appear relatively shallow and have low refractivity or are relatively dull in appearance), coarse (i.e., wider scratches that are also relatively deep but have high refractivity or are relatively shiny in appearance), hypercoarse (i.e., very wide and deep and non-refractile or dark in appearance), a mixture of fine and coarse, or a mixture of coarse and hypercoarse scratch types per tooth surface. Univariate statistics, ANOVA, and Tukey's post-hoc test for honest significant differences were calculated using PAST software (Hammer et al., 2001). For all statistical tests (ANOVA and Tukey's pairwise comparisons), the significance level was set at $p = 0.05$.

A scratch width score (SWS) was obtained by giving a score of 0 to teeth with predominantly fine scratches per tooth surface, 1 to those with a mixture of fine and coarse types of textures, 2 to those with predominantly coarse scratches, and 3 to those with a mixture of coarse and hypercoarse types of scratches per tooth surface. Individual scores for a sample were then averaged to get the average scratch width score for that taxon.

Because extant seasonal or regional mixed feeders which alternately feed on both browse and grass may overlap the browsing or grazing average scratch/pit morphospaces, raw scratch distributions per taxon were constructed. Browsing taxa have unimodal, low raw scratch distributions, grazers unimodal, high scratch distributions, and mixed feeders show a bimodal split of both high scratch individuals and low scratch individuals.

Mandibular tusks were examined at 35 \times for scratch textures, gouges, large pitting and orientation of scratches to determine the probable functional role of mandibular incisor tusks.

3. Results

3.1. Comparative extant proboscidean microwear

Results of the microwear analysis are shown in Table 1. Fig. 3A shows a bivariate plot of the average number of pits versus average number of scratches for the extant proboscideans analyzed graphed in relation to Gaussian confidence ellipses ($p = 0.95$) on the centroid for extant ungulate browsers (B) and grazers (G) (convex hulls) adjusted by sample size (proboscidean data from Semprebon et al., 2014; ungulate data from Semprebon, 2002 and Solounias and Semprebon, 2002). It is clear from Fig. 3A that extant proboscideans exhibit a fairly flexible dietary behavior – alternating between grass and browse, although the forest elephant, *Loxodonta cyclotis*, exhibits less variability in its diet and is more focused on the browse end of the spectrum than *Loxodonta africana* and *Elephas maximus*.

3.2. Adult *Platybelodon* molar microwear

Fig. 3B shows average scratch and pit results for adult *Platybelodon grangeri* molars plotted in reference to extant ungulates and proboscideans of known diets. Results are more similar to those of the extant forest elephant (*Loxodonta cyclotis*) than to *Loxodonta africana* and *Elephas maximus* and fall within the extant browsing zone. Fig. 3C shows the distributions of raw scratch counts in individual adult molars of *P. grangeri*. The distribution is unimodal and consistently in the low scratch range as is seen in extant leaf – dominated browsers (see Solounias and Semprebon, 2002).

Table 2 reveals that significant differences exist between average scratch and pit numbers between *P. grangeri* and extant elephants (ANOVA; $p \leq 0.001$; Table 2). In particular, average scratch numbers are significantly different between *P. grangeri* and *L. africana* (Tukey's HSD Tests; $p = 0.0057$; Table 2) and between *P. grangeri* and *E. maximus* (Tukey's HSD Tests; $p = 0.0016$) but not significantly different between *P. grangeri* and *L. cyclotis* (Tukey's HSD Tests; $p = 0.5780$). A similar pattern is seen with average pit numbers whereas numbers are significantly different between *P. grangeri* and *L. africana* (Tukey's HSD Tests; $p = 0.0068$) and between *P. grangeri* and *E. maximus* (Tukey's HSD Tests; $p = 0.0004$) but not significantly different between *P. grangeri* and *L. cyclotis* (Tukey's HSD Tests; $p = 1.$).

3.3. *Platybelodon* ontogenetic series

Fig. 3D depicts microwear results for *P. grangeri* individuals with estimated dental age assignments and demonstrates that a consistent browsing signal is seen throughout all of the age classes studied when average scratches are plotted against average pits. Fig. 4 demonstrates that older adults generally have more heavily scratched enamel (Fig. 4A) than younger individuals although scratch numbers are still within the extant browsing range and scratch textures (Fig. 4B) are coarser overall in the oldest individuals. As typical of extant elephants, deeply etched and wide scratches (i.e., hypercoarse scratch textures) are often apparent on molar tooth surfaces (Fig. 5A) (see Solounias and Semprebon, 2002 and Green et al., 2005).

3.3.1. Mandibular tusk microwear

Adult and juvenile *Platybelodon* mandibular tusks were examined for dentinal microwear scars but features were not counted as no extant incisor microwear data is available for comparison. In both the adults and juveniles examined, relatively fine microwear is seen (i.e., relatively few large pits or gouges, and scratches mostly finely textured). In addition, scratches run parallel to the long axis of the tusk in a regular fashion (Fig. 5B).

Table 1Microwear results and statistical test results for differences in pits and scratches for adult molars of *Platybelodon grangeri*.

Species	N	Pit mean	Pit SD	Scratch mean	Scratch SD	%LP	%G	SWS
<i>Loxodonta africana</i>	33	22.9	3.9	17.4	5.3	54.6	36.4	3.1
<i>Loxodonta cyclotis</i>	6	29.8	4.0	12.9	5.1	50	33.3	2.8
<i>Elephas maximus</i>	10	20.9	2.6	18.3	4.3	70	50	3.1
<i>Platybelodon grangeri</i>	26	29.8	6.9	10.2	5.2	19.2	3.9	2.5

ANOVA and Tukey's HSD test results for differences in densities of pits and scratches. Significant differences are indicated in bold.

Number of scratches – ANOVA results:

Source	df	SS	MS	F-ratio	p
Model	3	917.365	305.788	11.5	<0.001
Residual	71	1887.96	26.5909		

Pair-wise comparisons—*q* values below the diagonal (Tukey's method); *p* values above the diagonal (significant comparisons are in bold):

	<i>Platybelodon grangeri</i>	<i>Loxodonta africana</i>	<i>Loxodonta cyclotis</i>	<i>Elephas maximus</i>
<i>Platybelodon grangeri</i>	–	0.0057	0.5780	0.0016
<i>Loxodonta africana</i>	4.83	–	0.1523	0.7580
<i>Loxodonta cyclotis</i>	1.812	3.019	–	0.0611
<i>Elephas maximus</i>	5.417	0.586	3.605	–

Number of pits – ANOVA results:

Source	df	SS	MS	F-ratio	p
Model	3	1038.47	346.155	13.54	<0.001
Residual	71	1815.51	25.5706		

Pair-wise comparisons—*q* values below the diagonal (Tukey's method); *p* values above the diagonal (significant comparisons are in bold):

	<i>Platybelodon grangeri</i>	<i>Loxodonta africana</i>	<i>Loxodonta cyclotis</i>	<i>Elephas maximus</i>
<i>Platybelodon grangeri</i>	–	0.0068	1	0.0004
<i>Loxodonta africana</i>	4.752	–	0.0066	0.7830
<i>Loxodonta cyclotis</i>	0.017	4.770	–	0.0004
<i>Elephas maximus</i>	6.083	1.331	6.101	–

Abbreviations: N = Number of specimens; Pit Mean = Mean number of pits; Pit SD = standard deviation of Pits; Scratch Mean = Mean number of scratches; Scratch SD = standard deviation of scratches; %LP = Percentage of individuals with more than four large pits; %G = Percentage of individuals per taxon with gouges; SWS = Mean Scratch width score from 0–4 (0 = fine scratches only, to 4 = hypercoarse scratches only).

4. Discussion

4.1. Importance of taxon-free analyses

Microwear analysis is now recognized as a vital component of dietary reconstruction for both living and extinct mammals precisely because it is sensitive to what an animal actually ate despite what it might have been optimally adapted to be eating in terms of gross tooth anatomy acquired over deep time. That is, it provides direct evidence of food items actually consumed. For example, Semprebon and Rivals (2007) showed that the highly hypsodont *Antilocapra americana*, while a predominantly browsing form today, evolved from predecessors that apparently regularly consumed grasses. Hence, the modern *A. americana*'s gross tooth morphology was most likely shaped by a more abrasive dietary regime in its evolutionary past but it regularly consumes mostly browse today nonetheless. Rivals and Semprebon (2011) discuss dietary plasticity revealed through microwear analysis in taxa with similar gross dental morphologies.

Also, microwear studies on other gomphotheres (Calandra et al., 2008; Asevedo et al., 2012) with essentially brachydont and bunodont molar morphologies have shown that they may engage in a variety of feeding behaviors even though they are optimally adapted for feeding on soft vegetation (i.e., browse). Isotope studies offer independent confirmation of a variety of behaviors for gomphotheres and mastodons (Domingo et al., 2012). Of course, gomphotheres and mastodons from different localities and time periods most certainly encountered a variety of habitats that would be expected to influence trophic behavior regardless of molar morphology acquired over deep time. Therefore, morphology-independent proxies such as microwear are important techniques to employ to elucidate actual dietary behavior.

4.2. Linxia Basin paleoecology

Our molar microwear results are consistent with what is known about the paleoecology of the middle Miocene Linxia Basin mammals. The fossil *Platybelodon* specimens studied here were recovered from the Hujialiang Formation which is known to consist of a set of fluvial strata composed of grayish–yellow conglomerates and sandstone (Deng, 2004a) suggesting that *P. grangeri* might have lived near freshwater bodies of water which would certainly have supported shrubs and trees (i.e., browse). Several other mostly brachydont fossils also were recovered in the same strata, implying a warm and humid environment (Deng, 2004a) existed at this time. In addition, cenogram studies using body sizes of the late Cenozoic mammalian faunas from the Linxia Basin (Deng, 2009) indicate a probable closed environment for the middle Miocene. Isotope analysis of Linxia Basin sediment reveals a C3 signal with terrestrial C4 grasses either absent or insignificant in the Linxia region prior to 4.3 Ma (Fan et al., 2007). This is in agreement with a $\delta^{13}\text{C}$ record of mammalian tooth enamel from the Linxia basin, which indicates that there were no significant C4 plants in the Linxia basin before 2–3 Ma (Wang and Deng, 2005). These findings are consistent with our results which indicate pervasive browsing on leaves and twigs by both adult and juvenile *P. grangeri*.

4.3. *Platybelodon* mandibular tusks

We tested the hypothesis that *P. grangeri* used its mandibular tusks as shoveling agents by examining microwear scar types and orientations on wear facets of both dorsal and ventral distal surfaces. Our sample size for mandibular tusk microwear is relatively small due to taphonomic alteration of most tusks in the Hezheng collections, rendering most of them unsuitable for microwear analysis. Seven adult tusks

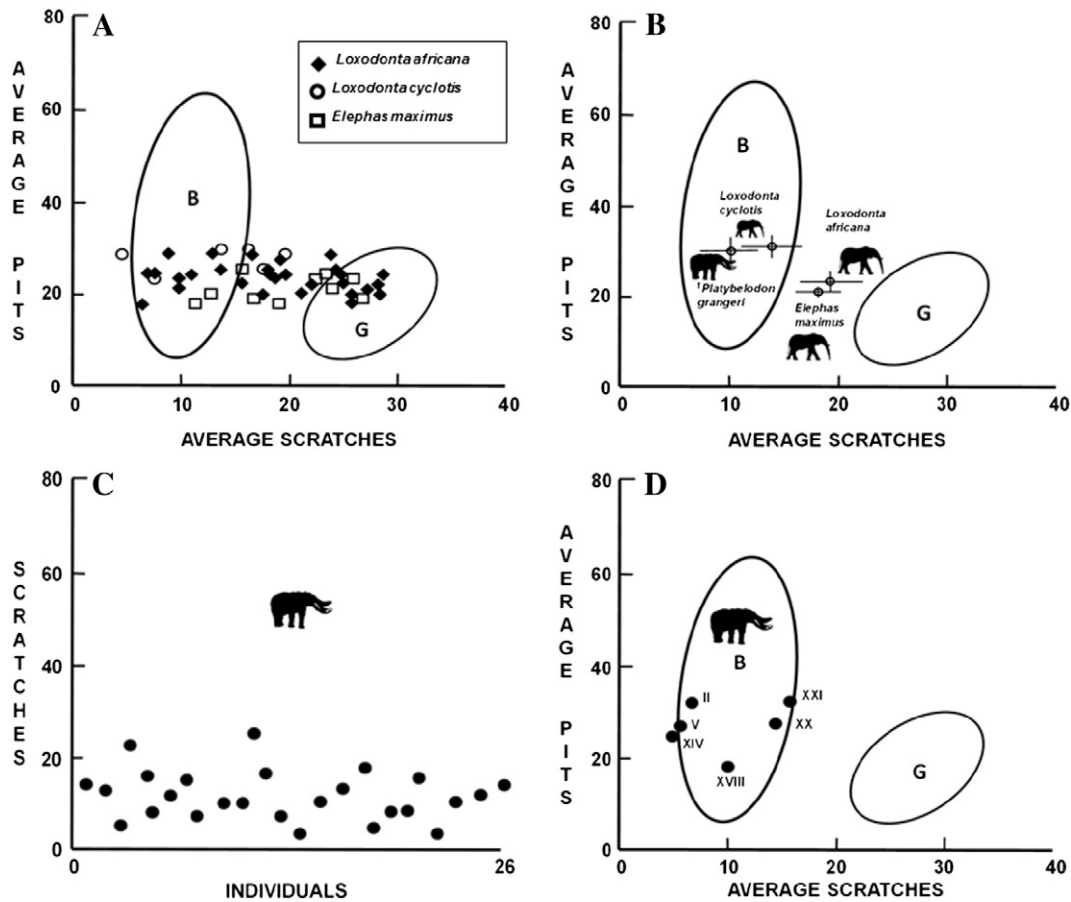


Fig. 3. Microwear scratch and pit results. A. Bivariate plot of the average number of pits versus average number of scratches for the extant proboscideans analyzed. Gaussian confidence ellipses ($p = 0.95$) on the centroid are indicated for the extant browsers (B) and grazers (G) (convex hulls) adjusted by sample size (extant ungulate data from Semprebon, 2002 and Solounias and Semprebon, 2002; extant proboscidean data from Semprebon et al., 2014). B. Bivariate plot of the average scratch versus average pit results of extant elephants and *Platybelodon grangeri*. For the fossil species, error bars represent the standard deviation for each sample. Oval outlines = Gaussian confidence ellipses ($p = 0.95$) on the centroid of the comparative extant grazer (G) and browser (B) samples adjusted by sample size (extant ungulate data from Semprebon, 2002 and Solounias and Semprebon, 2002; extant proboscidean data from Semprebon et al., 2014). C. Raw scratch distribution of *Platybelodon grangeri* adults. D. Bivariate plot of average scratches versus average pits of individuals of *P. grangeri* with assigned dental ages (as per Tassy, 2013) plotted in reference to extant browsing and grazing extant ungulate ecospaces.

were suitable for analysis and results obtained were highly consistent in all tusks analyzed. Mandibular tusk microwear in *P. grangeri* is inconsistent with the usage of lower tusks to shovel aquatic or terrestrial substrates as the type of coarse wear typical of taxa that encounter exogenous grit during feeding is absent. Solounias and Semprebon (2002) reported relatively heavy gouging and pitting, and coarser scratch textures in taxa that encounter exogenous grit along with food items such as extant rooting pigs and camels. Rivals and Semprebon, 2006 and Semprebon and Rivals, 2007 and Semprebon and Rivals, 2010 report the same pattern in open country extant and extinct

pronghorn and camels. Consequently, in order to corroborate a hypothesis of the use of mandibular tusks as shoveling agents in *P. grangeri*, we predicted that the mandibular tusks would exhibit such coarse microwear if used to shovel substrate particularly on the wear facet of their ventral distal end surfaces. Instead, we found relatively fine microwear on both ventral and dorsal facets. Scratches in particular were very finely textured and oriented parallel to the long axis of the tusk.

These results are more consistent with usage of the tusks to strip or cut vegetation and appear to corroborate results from Lambert's (1992) morphological study of *P. grangeri* mandibular tusk wear facets. Lambert proposed that the broad mandibular tusks of *P. grangeri* might have been used in conjunction with a flexible trunk much like a scythe to cut vegetation by sawing the vegetation back and forth against the observed sharp edge of the ventral facet or that they were possibly used to strip bark. Microwear patterns in the seven tusks we examined are consistent with a stripping or cropping function, in that, the microwear observed consists of parallel scratches and lacks the coarse wear expected if frequent shoveling of grit-laden substrate were employed.

Evenso, our results are intriguing given that a defined mechanism for maintaining a sharpened distal edge in *Platybelodon* tusks is not well studied and would seem to be necessary for scythe-like cutting actions of vegetation. A more plausible explanation of our results would seem to be bark stripping behavior as modern elephants are quite

Table 2

Microwear results for an ontogenetic series of *Platybelodon grangeri* molars with assigned ages ($N = 1$ for each assigned age).

Dental Age	Pit	Scratch	%LP	%G	SWS
II	28.5	7	6	0	1
V	26	3.5	0	0	2
XIV	25	2.5	0	0	1
XVIII	16.5	10	0	0	2
XX	25	12	0	0	3
XXI	27.5	12.5	0	0	3

Abbreviations: N = Number of specimens; Pit = number of pits; Scratch = number of scratches; %LP = Percentage of individuals with more than 4 large pits; %G = Percentage of individuals per taxon with gouges; SWS = Mean Scratch width score from 0–4 (0 = fine scratches only, to 4 = hypercoarse scratches only).

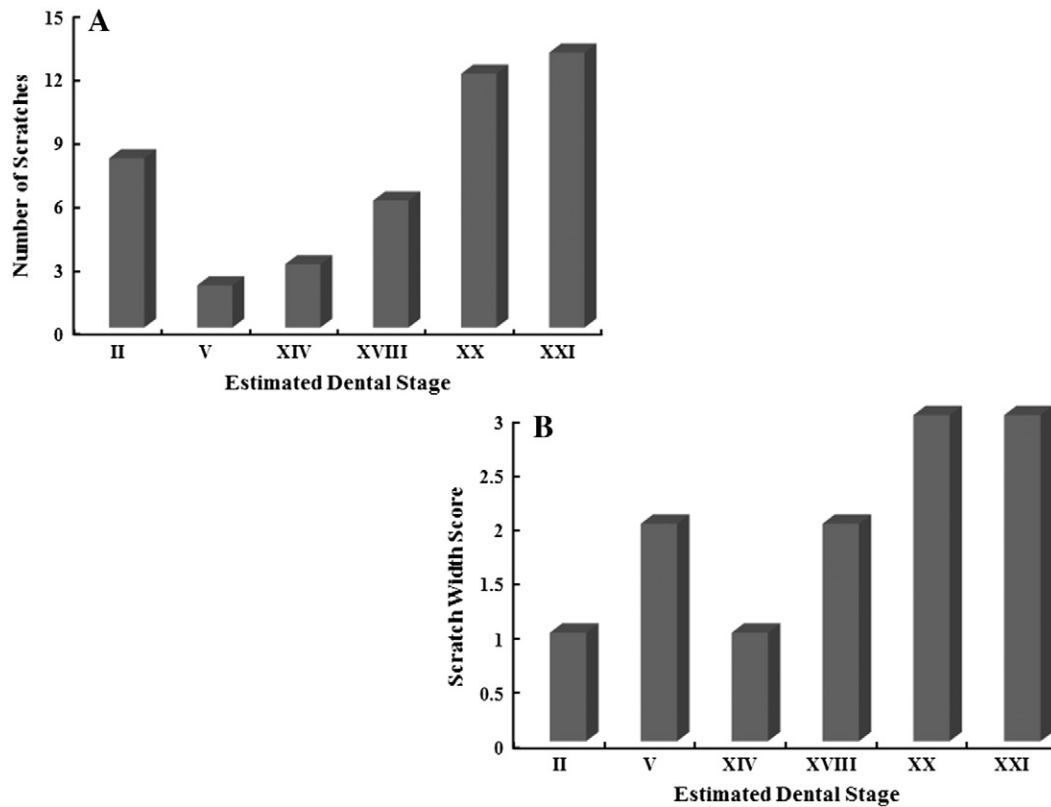


Fig. 4. Bar charts showing scratch numbers (A) and scratch width scores (B) for *P. grangeri* individuals of estimated dental age classes (as per Tassy, 2013).

adept at stripping bark without the need for sharpened distal tusk tips. Also, the hypercoarse scratches observed on molar surfaces are typical of extant bark consumers (Solounias and Semprebon, 2002).

This analysis accomplished four main things: firstly, it provided for the first time direct evidence of feeding behavior (i.e., browsing on leaves and twigs) in *P. grangeri* from the localities of Laogou and Zengjia from the upper Middle Miocene Hujialiang Formation; secondly, it confirmed that *P. grangeri* preferred browse during its juvenile and adult life history stages but then shifted toward a coarser type of leaves and/or twigs in older versus younger individuals; thirdly, mandibular tusks might have been more suitable for stripping actions rather than as shoveling agents; and lastly, it may provide insight into a possible cause for the extinction of *P. grangeri* in the Linxia Basin at the end of the middle Miocene as the climate became cooler and more arid as

available browse would become scarcer as more open grasses encroached on shovel-tusker habitat.

5. Conclusions

1. Adult and juvenile molar teeth of *Platybelodon grangeri* from the Linxia Basin of China have microwear patterns consistent with browsing on leaves and twigs.
2. Results are consistent with paleoenvironmental reconstructions of the middle Miocene Hujialiang Formation of the Linxia Basin as a relatively warm, humid and closed habitat with numerous sources of freshwater.
3. Scratch numbers and scratch widths are greater in older individuals indicating that coarser browse was consumed in older individuals.

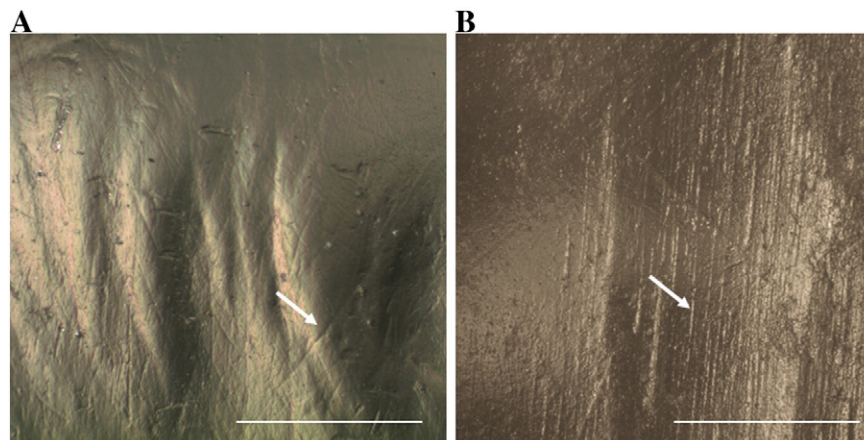


Fig. 5. Photomicrographs of enamel surfaces (@35× magnification) of adult *Platybelodon grangeri* specimens. A. Adult molar (HMV0029). B. Adult mandibular tusk (HMV0049). White arrow in Fig. 5A = hypercoarse scratch. White arrow in Fig. 5B) = Fine scratch (Fig. 5B). Scale bar = 0.4 mm.

4. Mandibular tusk microwear is inconsistent with the usage of lower tusks to shovel aquatic or terrestrial substrates and instead support gross wear studies that hypothesize that mandibular tusks might have been more suitable for stripping vegetation.

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References

- Andrews, R.C., 1932. The new conquest of Central Asia, a narrative of the explorations of the Central Asiatic Expeditions in Mongolia and China, Natural History of Central Asia. American Museum of Natural History 1, pp. 1–678.
- Asevedo, L., Winck, G.R., Mothe, D., Avilla, L.S., 2012. Ancient diet of the Pleistocene gomphotherid *Notiomastodon platensis* (Mammalia, Proboscidea, Gomphotheriidae) from lowland mid-latitudes of South America: stereomicrowear and tooth calculus analyses combined. *Quat. Int.* 255, 42–52.
- Barbour, E.H., 1927. Preliminary notice of a new proboscidean *Amebelodon fricki*, Gen. Et Sp. Nov. Bulletin of the Nebraska State Museum 1, pp. 131–134.
- Barbour, E.H., 1929a. The andibular tusks of *Amebelodon fricki*. Bulletin of the Nebraska State Museum 1, pp. 135–138.
- Barbour, E.H., 1929b. *Tornobelodon loomisi*, gen. et sp. nov. Bulletin of the Nebraska State Museum 1, pp. 147–153.
- Barbour, E.H., 1931. A new amebelodont, *Tornobelodon barnumbrowni* sp. nov., a preliminary report. Bulletin of the Nebraska State Museum 1, pp. 191–197.
- Barbour, E.H., 1932. The mandible of *Platybelodon barnumbrowni*. Bulletin of the Nebraska State Museum 1, pp. 252–258.
- Borissiak, 1928. On a new mastodon from the Chokrak beds (middle Miocene) of the Kuban Region, *Platybelodon danovi* n. gen. n. sp. Ann. Soc. Paleont. Russie, Tom. VII, for the year 1927, pp. 105–120.
- Borissiak, A.A., 1929. On a new direction in the adaptive radiation of mastodonts. *Paleobiologica* 2, 19–33.
- Calandra, I., Göhlich, U.B., Merceron, G., 2008. How could sympatric megaherbivores coexist? Example of niche partitioning within a proboscidean community from the Miocene of Europe. *Naturwissenschaften* 95, 831–838.
- Deng, T., 2004a. A new species of the rhinoceros *Alicornops* from the Middle Miocene of the Linxia Basin, Gansu, China. *Palaeontology* 47, 1427–1439.
- Deng, T., 2004b. Establishment of the middle Miocene Hujialiang Formation in the Linxia Basin of Gansu and its features. *J. Stratigr.* 28, 307–312.
- Deng, T., 2009. Late Cenozoic environmental change in the Linxia Basin (Gansu, China) as indicated by mammalian cenograms. *Vertebrata Palasiatica* 47, 282–298.
- Deng, T., 2010. Linxia Basin: an ancient paradise for late Cenozoic rhinoceroses in north China. *Bull. Chin. Acad. Sci.* 24, 103–106.
- Deng, T., Qiu, Z.X., Wang, B.Y., Wang, X.M., Hour, S.K., 2013. Late Cenozoic biostratigraphy of the Linxia Basin, northwestern China. In: Wang, X.M., Flynn, L.J., Fortelius, M. (Eds.), *Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology*. Columbia University Press, New York, pp. 243–273.
- Domingo, L., Koch, P.L., Grimes, S.T., Morales, J., López-Martínez, N., 2012. Isotopic paleoecology of mammals and the middle Miocene cooling event in the Madrid Basin (Spain). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 339–341, 98–113.
- Fan, M., Dettman, D.L., Song, C., Fang, X., Garzzone, C.N., 2007. Climatic variation in the Linxia basin, NE Tibetan Plateau, from 13.1 to 4.3 Ma: the stable isotope record. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 247, 313–328.
- Fox, D.L., Fisher, D.C., 2004. Dietary reconstruction of Miocene *Gomphotherium* (Mammalia, Proboscidea) from the Great Plains region, USA, based on the carbon isotope composition of tusk and molar enamel. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 206, 311–335.
- Green, J.L., Semprebon, G.M., Solounias, N., 2005. Reconstructing the palaeodiet of Florida *Mammot americanum* via low magnification stereomicroscopy. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 223, 34–48.
- Grine, F.E., 1986. Dental evidence for dietary differences in *Australopithecus* and *Paranthropus*: a quantitative analysis of permanent molar microwear. *J. Hum. Evol.* 15, 783–822.
- Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: paleontological statistics software package for education and data analysis. *Palaeontol. Electron.* 4 (1) (9 pp. http://paleo-electronica.org/2001_1/past/issue1_01.htm).
- King, T., Andrews, P., Boz, B., 1999. Effect of taphonomic processes on dental microwear. *Am. J. Phys. Anthropol.* 108, 359–373.
- Lambert, W.D., 1992. The feeding habits of the shovel-tusked gomphotheres: evidence from tusk wear patterns. *Paleobiology* 18, 132–147.
- Lambert, W.D., 1996. The biogeography of the gomphotheriid proboscideans of North America. In: Shoshani, J., Tassy, P. (Eds.), *The Proboscidea: Evolution and Palaeoecology of Elephants and Their Relatives*. Oxford University Press, Oxford, New York, Tokyo, pp. 143–148.
- Merceron, G., Blondel, C., Brunet, M., Sen, S., Solounias, N., Viriot, L., Heintz, E., 2004. The Late Miocene paleoenvironment of Afghanistan as inferred from dental microwear in artiodactyls. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 207, 143–163.
- Merceron, G., Blondel, C., de Bonis, L., Koufos, G.D., Viriot, L., 2005. A new method of dental microwear: application to extant primates and *Ouranopithecus macedoniensis* (Late Miocene of Greece). *PALAIOS* 20, 551–561.
- Osborn, H.F., 1936. Proboscidea: Volume I Moeritheroidea, Deinotheroidea, Mastodontoidea. The American Museum Press, pp. 463–4732.
- Osborn, H.F., Granger, W., 1931. The shovel-tuskers, Amebelodontinae, of central Asia. *Am. Mus. Novit.* 470, 1–12.
- Osborn, H.F., Granger, W., 1932. *Platybelodon grangeri*, three growth stages, and a new serridentine from Mongolia. *Am. Mus. Novit.* 537, 1–13.
- Rensberger, J.M., 1978. Scanning electron microscopy of wear and occlusal events in some small herbivores. In: Butler, P.M., Joysey, K.A. (Eds.), *Development, Function and Evolution of Teeth*. Academic Press, London, pp. 415–438.
- Rivals, F., Semprebon, G.M., 2006. A comparison of the dietary habits of a large sample of the Pleistocene pronghorn *Stockoceros onusocrogrus* from the Papago Springs Cave in Arizona to the modern *Antilocapra americana*. *J. Vertebr. Paleontol.* 26, 495–500.
- Rivals, F., Semprebon, G.M., 2011. Dietary plasticity in ungulates: insight from tooth microwear analysis. *Quat. Int.* 245, 279–284.
- Scott, R.S., Ungar, P.S., Bergstrom, T.S., Brown, C.A., Grine, F.E., Teaford, M.F., Walker, A., 2005. Dental microwear texture analysis shows within-species diet variability in fossil hominins. *Nature* 436, 693–695.
- Scott, R.S., Ungar, P.S., Bergstrom, T.S., Brown, C.A., Childs, B.E., Teaford, M.F., Walker, A., 2006. Dental microwear texture analysis: technical considerations. *J. Hum. Evol.* 51, 339–349.
- Semprebon, G.M., 2002. Advances in the reconstruction of extant ungulate ecomorphology with applications to fossil ungulates (Ph.D. Dissertation) University of Massachusetts, Amherst.
- Semprebon, G.M., Rivals, F., 2007. Was grass more prevalent in the pronghorn past? An assessment of the dietary adaptations of Miocene to recent Antilocapridae (Mammalia: Artiodactyla). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 253, 332–347.
- Semprebon, G.M., Rivals, F., 2010. Trends in the paleodietary habits of fossil camels from the Tertiary and Quaternary of North America. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 295, 131–145.
- Semprebon, G.M., Godfrey, L.R., Solounias, N., Sutherland, M.R., Jungers, W.L., 2004. Can low-magnification stereomicroscopy reveal diet? *J. Hum. Evol.* 47, 115–144.
- Semprebon, G., Rivals, F., Fahlke, J., Sanders, W., Lister, A., Göhlich, U., 2014. The effect of insular dwarfism on dietary niche occupation in mammoths: what were the pygmy mammoths from Santa Rosa Island of California eating? *Scientific Annals, School of Geology, Aristotle University of Thessaloniki, Greece* 102, pp. 182–183.
- Shoshani, J., Tassy, P., 2005. Advances in proboscidean taxonomy and classification, anatomy and physiology, and ecology and behavior. *Quat. Int.* 126–128C (5–2).
- Solounias, N., Semprebon, G., 2002. Advances in the reconstruction of ungulate ecomorphology with application to early fossil equids. *Am. Mus. Novit.* 3366, 1–49.
- Spock, L.E., 1929. Pliocene beds of the Iren Gobi. *Am. Mus. Novit.* 394, 1–8.
- Tassy, P., 1996. The earliest gomphotheres. In: Shoshani, J., Tassy, P. (Eds.), *The Proboscidea: Evolution and Palaeoecology of Elephants and Their Relatives*. Oxford University Press, Oxford, New York, Tokyo, pp. 89–91.
- Tassy, P., 2013. L'anatomie crano-mandibulaire de *Gomphotherium angustidens* (Cuvier, 1817) (Proboscidea, Mammalia): données issues du gisement d'En Pèjouan (Miocène moyen du Gers, France). *Geodiversitas* 35 (2), 377–445.
- Tobien, H., 1972. Status of the genus *Serridentinus* Osborn 1923 (Proboscidea: Mammalia) and related forms. *Mainz. Geowiss. Mitt.* 1, 143–191.
- Ungar, P.S., Scott, R.S., Scott, J.R., Teaford, M., 2008. Dental microwear analysis: historical perspectives and new approaches. In: Irish, J.D., Nelson, G.C. (Eds.), *Technique and Application in Dental Anthropology*. Cambridge University Press, Cambridge, pp. 389–425.
- Ungar, P.S., Scott, J.R., Schubert, B.W., Stynder, D.D., 2010. Carnivorous dental microwear textures: comparability of carnassial facets and functional differentiation of postcanine teeth. *Mammalia* 74, 219–224.
- Walker, A., Hoek, H.N., Perez, L., 1978. Microwear of mammalian teeth as an indicator of diet. *Science* 201, 908–910.
- Wang, Y., Deng, T., 2005. A 25 m.y. isotopic record of paleodiet and environmental change from fossil mammals and paleosols from the NE margin of the Tibetan Plateau. *Earth Planet. Sci. Lett.* 236, 332–338.
- Wang, X.-M., Qiu, Z.-D., Opdyke, N.D., 2003. Litho-, bio-, and magneto-stratigraphy and paleoenvironment of Tunggur Formation (middle Miocene) in central Inner Mongolia, China. *Am. Mus. Novit.* 3411, 1–31.
- Wang, S., He, W., Chen, S., 2013. The gomphotheriid mammal *Platybelodon* from the Middle Miocene of Linxia Basin, Gansu, China. *Acta Palaeontol. Pol.* 58, 221–240.
- Webb, S.D., 1976. Mammalian faunal dynamics of the great American interchange. *Paleobiology* 2, 220–234.