USING DENTAL MICROWEAR TEXTURES TO ASSESS FEEDING

ECOLOGY OF EXTINCT AND EXTANT BEARS


By

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To my parents for your endless love and support

and

To my grandfather for getting me where I am today.

# ACKNOWLEDGEMENTS

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# LIST OF ABBREVIATIONS

Ma – Million years ago

SEM – Scanning electron microscope

DMTA – Dental microwear texture analysis

*Asfc* – Complexity

*epLsar* – Anisotropy

*Smc* – Scale of maximal complexity

*Tfv* – Textural fill volume

*HAsfc* – Heterogeneity of complexity

m1 – lower first molar

m2 – lower second molar

AMNH – American Museum of Natural History

FLMNH – Florida Museum of Natural History

LACMHC – Los Angeles County Museum of Natural History, Hancock Collection

NMNH – Smithsonian Institute, National Museum of Natural History

*Ar. simus* – Extinct giant short-faced bear

*A. melanoleuca* – Giant panda

*T. ornatus* – Spectacled bear

*U. malayanus* – Malayan sun bear

*U. americanus* – American black bear

*U. maritimus* – Polar bear

ANOVA – Analysis of variance

MANOVA – Multiple analyses of variance

CHAPTER I


INTRODUCTION



Diet is the closest link an organism has with the environment in which it lives, and is thus a key factor in defining an animal's ecology. Diet has played a central role in mammalian evolutionary history, attested by the extreme disparity in body sizes and dental morphologies exhibited by modern mammals. As such, the ability to infer diet from fossils is critical to determining the ecology and evolutionary history of extinct species. Gaining an understanding of the dietary niches of extinct species is important when considering the fate of modern species facing anthropogenic climatic change and associated habitat fragmentation. Predicting responses of modern species to these changes hinges on making assumptions about their dietary ecology in the past. As dietary niches of species are not necessarily conserved through deep time (DeSantis et al., 2009), and species respond dynamically in the face of climatic and environmental changes (e.g. Walther et al., 2002; Blois et al., 2010), continued studies of the dietary ecology of fossil taxa are critical to making informed decisions regarding the preservation of modern biodiversity.

Of particular interest is the evolutionary history of omnivores, dietary generalists. Did their ability to take advantage of novel food sources during times of food scarcity allow them to persist while more specialized taxa went extinct? Indeed, carnivorous species, considered as specialists relative to omnivores, have the highest extinction rates through deep time, and the modeled rate of transition

into omnivory is higher than any other trophic level transition (Price et al., 2012).

Further, models of mammalian evolution by Price and colleagues (2012) indicate

that biodiversity of omnivorous species is created through a transition from either a

carnivorous or herbivorous lineage, rather than diversification within an omnivorous

lineage.  Studying bears (Ursidae), a family characterized by omnivorous species

that evolved from carnivorous ancestors, can provide direct insight into the evolution

and potential advantages of dietary generalists.

## Evolutionary history and modern ecology of Ursidae

Bears are caniform carnivorans that evolved from a dog-like ancestor about

35 million years ago (Ma) (Krause et al., 2008).  The most notable event in ursid

evolutionary history occurred across the Miocene-Pliocene boundary (5.7 Ma), when

early bears went extinct and a rapid evolutionary radiation of a more modern

community, including short-faced bears, ensued (Figure 1; Krause et al., 2008; Miller

et al., 2012).  This rapid radiation is coincident with major changes in Earth's climate.

Starting in the late Miocene, Earth entered into a long-term trend towards global

cooling and increased seasonality (Zachos et al., 2001). The late Miocene and early

Pliocene are characterized by shorter term warm-cool climatic fluctuations,

particularly with a warming from ~3–5  Ma (Raymo et al., 1996).  These climatic

regimes, combined with a high concentration of atmospheric $CO_2$, drove habitat

changes including the replacement of closed forests with open grassland habitats

(Cerling et al., 1997).  Habitat and food source changes severely affect an animal's

ecology.  In particular, dietary specialists face extinction if they cannot adapt at the same pace as environmental change (Price et al., 2012).  Given that most modern bears are adaptable opportunists in the face of changing seasons and environments (e.g. Raine and Kansas, 1990; Peyton, 1980; Hansen et al., 2010; Wong et al., 2002), dietary versatility may have allowed ursids to persist during the dramatic habitat fluctuations of the Pleistocene and Holocene.  Clarifying the diets of past ursids is key to understanding the evolutionary history of the family and predicting responses to current and future climate change.
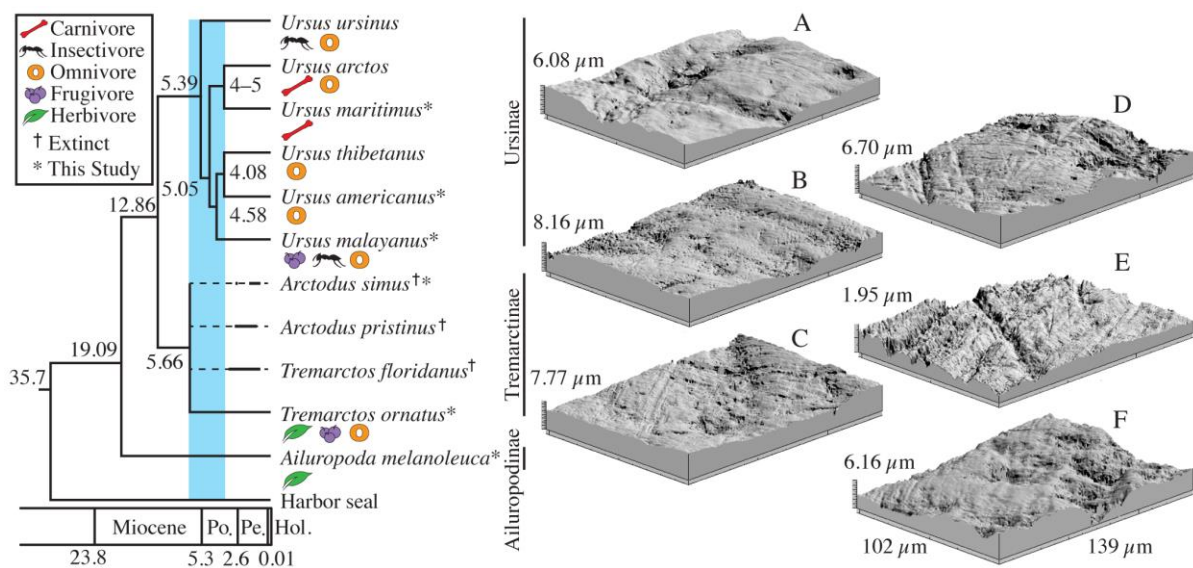


**Figure 1.**  Phylogeny of Ursidae, modified from Krause et al. (2008) with an update to polar bear origination from Miller et al. (2012).  The shaded bar on the phylogeny highlights the rapid evolutionary radiation of bears, which correlates with climatic and environmental changes.  Numbers on phylogeny represent divergence dates (in Ma).  Po., Pliocene; Pl., Pleistocene; Hol., Holocene.  A-F are three-dimensional photosimulations of lower second molars taken at 100x magnification; width and length measurements on F are applicable to all.  **A**.  *Ursus maritimus*, NMNH 512117; **B.**  *Ursus americanus,* UF 28436; **C**.  *Ursus malayanus* NMNH 151866; **D.**  *Tremarctos ornatus*, NMNH 271418; **E**.  *Ailuropoda melanoleuca*, NMNH 259028; **F.**  *Arctodus simus*; LACMHC 1292.

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The eight living bear species encompass a wide diversity of dietary niches and inhabit a variety of habitats across the globe (Figure 2). In this study, I focus on five extant species whose dietary niches characterize the family today.
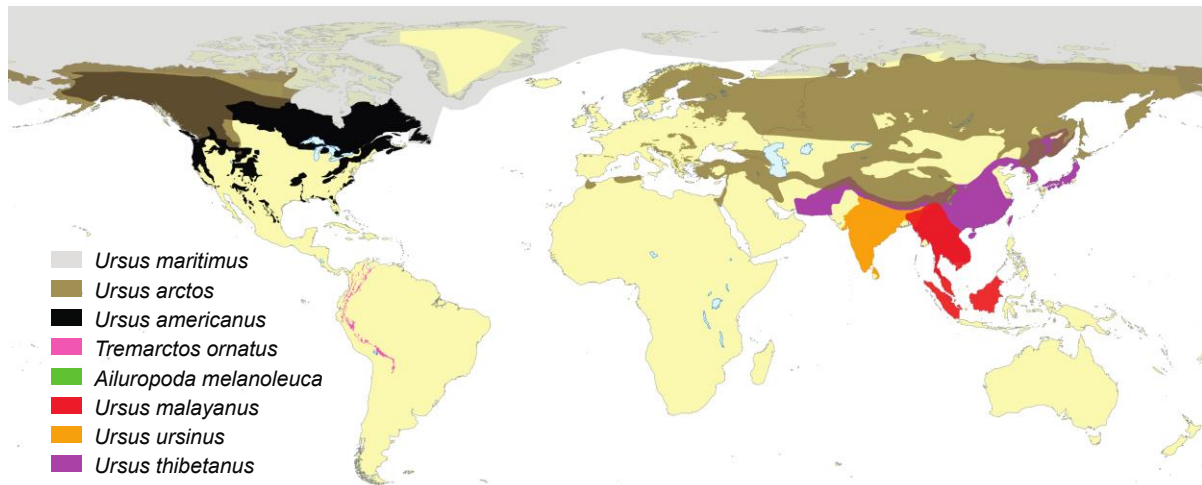


**Figure 2.** Geographic ranges of the eight modern bear species. Antarctica not pictured. Data downloaded from the IUCN Red List of Threatened Species on March 12, 2013.

The carnivorous polar bear, *Ursus maritimus* is considered a hyper-carnivore that actively preys on marine mammals in Arctic waters. The primary food source of polar bears is the ringed seal (*Phoca hispida*), and bears mainly focus on the blubber and flesh of their prey (Theimann et al., 2008). Polar bears also prey upon harbor seals (*P. vitalina*), the larger bearded seals (*Erignathus barbatus*), walruses (*Odobenus rosmarus*), and occasionally narwhal (*Monodon monoceras*) (Theimann et al., 2008; Bentzen et al., 2007). Larger male polar bears are better suited for

hunting bigger prey items than smaller females, who instead focus on smaller bodied seal species, and juveniles.

Polar bears engage in some scavenging of whale carcasses and consume terrestrial food sources to supplement marine prey resources. Scavenging is becoming more frequent with earlier seasonal break up of Arctic sea ice, which polar bears rely on for hunting (Bentzen et al., 2007). Typically, polar bears fast while they are on land during the summer months, and terrestrial food sources and historic observations indicated that terrestrial food sources were negligible in the diet (Theimann et al., 2008). However, rare reports exist of bears hunting large bodied terrestrial herbivores (Thiemann et al., 2008), and Arctic charr (*Salvelinus alpinus,* a fresh water fish in the salmon family) is sometimes consumed (Dyck and Kebreab, 2009). Bears found over ten km inland from northwest Hudson Bay occasionally consume berries, moss, and grasses during the summer months (Derocher et al., 1993). It is hypothesized that as sea ice breaks up earlier, and *U. maritimus* cannot store adequate fat reserves through seal hunting, terrestrial food sources will become increasingly important in the diet (Dyck and Kebreab, 2009).

The American black bear, *Ursus americanus* is an opportunistic omnivore. Its diet is highly variable across seasons and geographic space. Broadly, spring diets include sprouting young vegetation, carrion (i.e. animal carcasses), and insects. In summer, fruits and herbaceous plants are important (e.g. dandelion), and in autumn, berries (soft mast) and nuts (hard mast) are the primary focus (Raine and Kansas, 1990). Animal matter, including carrion, small vertebrates, and insects are consumed opportunistically throughout the year. Rarely, larger vertebrates (e.g.

white-tailed deer, *Odocoileus virginianus*) are hunted (Raine and Kansas, 1990). In Florida, insects play a larger role in the diet, particularly in the fall when beetles and yellow-jackets are consumed in high abundance (Stratman and Pelton, 1999). Saw palmetto hearts (*Serenoa repens*) in Florida are also an important food source year round (Stratman and Pelton, 1999). Because black bears are opportunistic omnivores, their diet is highly adaptable in years of changing food availabilities (Raine and Kansas, 1990; Roof, 1997), which may allow them to survive food-stressed periods.

The insectivorous/frugivorous/omnivorous Malayan sun bear, *Ursus malayanus*, is found in dense forests of Malaysia. Overall, *U. malayanus* relies mainly on insects (termites, ants, beetle larvae, cockroaches, stingless bees), which are the most stable food source in tropical forests (Wong et al., 2002). Other important food sources include figs (*Ficus* sp., present year round), flowers, honey, leafy vegetation and small vertebrates (Wong et al., 2002; Frederiksson et al., 2006).

The vegetation of the Malayan region is strongly influenced by El Niño Southern Oscillations, which prompt mass synchronous fruiting events through a mechanism that is not well understood, but occurs every 2–15 years (Frederiksson et al., 2006). During mass fruiting greater than 15% of tree species produce an overabundance of fruit for a short time period, followed by a fruit scarcity lasting months to years (Frederiksson et al., 2006). The sun bear responds to mass fruiting events by consuming a diet of up to 100% fruit, typically of tree fruits that are fleshy and fibrous. Bears avoid eating large internal fruit pits and consume only those fruits with the highest nutritional value, while avoiding those of lower nutritional content

that are found year-round (e.g., figs) (Frederikkson et al., 2006).  This behavior

allows *U. malayanus* to effectively store fat, which aids in survival during long

periods of fruit scarcity.  The behavioral switch to becoming an

insectivorous/omnivorous bear allows for survival in a habitat where food sources

are both less nutritious and less available.  The evolution of these behavioral

characteristics was likely a critical factor in the persistence of *U. malayanus* through

time, demonstrating the importance of dietary adaptability in the evolutionary history

of this species.

The spectacled bear, *Tremarctos ornatus*, is an herbivorous/omnivorous bear

found in the Andes Mountains of South America.  It is a small bear that is a capable

tree climber, and prefers dense forest cover (Peyton, 1980).  Overall, about 75% of

its diet is composed of plant matter (Peyton, 1980).  The largest plant contributors

are bromeliads (family: Bromeliaceae, up to 22 species consumed).  During the non-

fruiting season, *T.* ornatus almost exclusively consumes tough, succulent bromeliad

hearts, which are eaten following removal of the hard plant exteriors (Peyton, 1980).

Bromeliads are also important because they contain up to one liter of water, which

may be particularly crucial to bears inhabiting coastal desert scrub and steppe

habitats (Peyton, 1980).  During the fruiting season, figs (*Ficus* sp.) and capers

(*Capparis* sp.) are significant food sources, along with numerous other succulent

tree fruits.  Additional vegetation food sources include cactus, palm frond petioles,

shrub berries, and tree wood (Peyton, 1980).  Spectacled bears will also consume

insects and honey in addition to bromeliad hearts during the non-fruiting season

(Peyton, 1980).  Despite *T. ornatus* feeding primarily on plant resources, it will

occasionally feed on animal matter including small vertebrates (e.g. rodents, lizards) and infrequently, larger vertebrates (e.g. goats, cattle, turtles), though larger vertebrates are usually encountered as carrion. Infrequent hunting by *T. ornatus* does occur, and usually involves the bear pursuing cattle up a steep slope, causing them to fall down slope and sustain serious or fatal injuries (Peyton, 1980).

The final ursid included in the baseline study is the giant panda, *Ailuropoda melanoleuca*, the specialist bamboo-consumer. Giant pandas inhabit the Qinling Mountains and Sichuan area of China and will seasonally migrate up and down elevation to track availability of several bamboo species (Long et al., 2004). *Ailuropoda melanoleuca* individuals typically weigh 85-110 kg (Schaller et al., 1985) and have unique features associated with bamboo consumption, including broad, flat, cuspidate premolars and molars, and an enlarged wrist bone (radial sesamoid) which functions similar to an opposable thumb to allow grasping of bamboo (Schaller et al., 1985).

Pandas are highly selective foragers and utilize different parts of bamboo across different seasons. Leaves are present year round, and are the primary focus of *A. melanoleuca* for the majority of the year (Hansen et al., 2012). A panda will strip leaves from a branch by pulling the entire branch through its anterior teeth, and forming a wad of leaves at the corner of its mouth. This wad is then held in the paw and bites are taken as the wad is consumed as a whole (Hansen et al., 2012; Long et al., 2004). In the spring, *A. melanoleuca* switches to consumption of pith (interior layers of the culm, or the major stem), likely due to the higher lignin content of leaves at this time (Long et al., 2004), or perhaps a change in chemical signatures of

the leaves (Hansen et al., 2012).  Consumption of pith occurs following peeling of the hard culm exterior.  An individual holds the bamboo stem with its paw and uses its anterior molars to crack and then strip off the hard outer casing.  Following peeling, the pith is bitten off and chewed (Hansen et al., 2010; Long et al., 2004).  During the season of pith consumption, newly emerged soft shoots are also eaten, likely to supplement pith, which has less nutritional value than leaves (Hansen et al., 2010).  Overall, *A. melanoleuca* has the most specialized diet of all extant bears.

**Table 1.** Review of diet in modern ursids, with predicted microwear based on physical properties of known diet

| Species | Diet Category | Main dietary components | Prediction of Microwear | | Source |
|---|---|---|---|---|---|
| | | | Complexity (*Asfc*) | Anisotropy (*epLsar*) | |
| *Ailuropoda melanoleuca* | Specialist Herbivore | Bamboo leaves, pith, shoots | Low, no consumption of hard/brittle bamboo components | High, silica content of bamboo is high, bamboo chewed thoroughly | Hanson et al., 2012; Long et al., 2004 |
| *Tremarctos ornatus* | Herbivore – Frugivore – Omnivore | Bromeliad hearts, palm fronds, tree wood, tree fruits: e.g. fig, caper | Low, no consumption of hard/brittle plant components | Moderate to high during consumption of tough bromeliad hearts and palm fronds | Peyton, 1980 |
| *Ursus malayanus* | Insectivore – Frugivore – Omnivore | Termites, beetles, larvae, tree fruits, honeycomb, | Low when tree fruits consumed; moderate-high when insects consumed | Low, lack of foods with high silica content, insects not thoroughly chewed | Frederikkson et al., 2006; Wong 2002 |
| *Ursus americanus* | Omnivore | Berries, nuts, insects, herbaceous plants, small vertebrates | High in fall with consumption of nuts, low in spring with consumption of herbaceous plants | High in spring with consumption of herbaceous plants, low other times of year | Raine and Kansas, 1990; Stratman and Pelton, 1999 |
| *Ursus maritimus* | Carnivore | Ringed seals, bearded seals, walruses, carrion, fish, berries | Low, soft seal blubber and flesh; infrequent high values, terrestrial berries and fish | Low to moderate, soft seal blubber and flesh | Theimann et al., 2008; Derocher et al., 1993 |

**Previous work on dietary inferences in bears**

Significant work has furthered our understanding of dietary reconstruction in extinct and extant ursids, yet the dietary niches of extinct ursids are still not well understood.  Studies focusing on cranial and dental morphology such as geometric morphometrics (Sacco and Van Valkenburgh, 2004) and orientation patch count (Evans et al., 2007) provide insight into important evolutionary adaptations of each dietary niche (e.g. an herbivore has complex teeth with large surface area).  These studies provide information on the broad dietary category an ursid was capable of occupying, not what it actually ate.  Previous stable isotope geochemistry studies utilizing nitrogen ($\delta^{15}$N) and carbon ($\delta^{13}$C) help clarify if extinct bears were primary or secondary consumers (Bocherens et al., 1994; 1995) and whether consumed food was from an open or closed habitat (Domingo et al., 2013).  However, isotopic studies can be complicated by hibernation and the influence of "mother's milk" during tooth formation in bears (Bocherens, 1994; Pérez-Rama et al., 2011), and results reveal information about an individual's average diet, rather than what they were eating prior to death.

**Dietary ecology of *Arctodus simus***

The Pleistocene giant-short faced bear, *Arctodus simus,* is the largest bear to traverse North America (Christiansen, 1999), yet its dietary ecology remains a topic of debate (e.g. Schubert and Wallace, 2009; Figuierido et al., 2010).  Fossil occurrences of *Ar. simus* geographically span much of North America and represent a time interval of 2.5–0.3 Ma (Schubert et al., 2010a).  This large range spans a

wide variety of habitats and climatic regimes, including dense forests in Florida,

open plains in Nebraska, coastal lowlands of southern California, and boreal forests

in Alaska (Schubert et al., 2010a).  Tremarctine bears were abundant and diverse in

the Pliocene–Pleistocene of North and South America.  The lesser short-faced bear

(*Ar. pristinus*) is considered ancestral to *Ar. simus*, though the two do not co-occur in

the fossil record (Schubert et al., 2010a).  The Florida cave bear (*Tremarctos

floridanus*) co-occurred with *Ar. simus* in many regions of North America, along with

*Ursus americanus* and *U. arctos* (Schubert et al., 2010a).  As many as six species of

tremarctine bears lived in South America during the Pleistocene (Schubert et al.,

2010a).  The large distribution of *Ar. simus* fossil localities and co-occurrence with

other bear species suggests that the giant short-faced bear had a variable diet

across its range (Schubert and Wallace, 2009), and perhaps through time.

  *Arctodus simus* was initially proposed to be an active predator, running down

prey with its long, gracile limbs (Kurtén and Anderson, 1980), and capturing/killing

victims with large bite forces produced in its short, cat-like muzzle (Kurtén, 1967).

Predatory tendencies of short-faced bears from Alaska and the Canadian Yukon are

consistent with elevated $\delta^{15}N$ values (Bocherens et al., 1995; Matheus et al., 1995;

Barnes et al., 2002), and Fox-Dobbs and colleagues (2010) suggest they specialized

on caribou.  However, others have proposed that the worn teeth and large

mandibular muscle attachments of *Ar. simus* are consistent with substantial

mastication of plant matter (Emslie and Czaplewski, 1985).  Geometric

morphometric studies of the mandible further support this claim (Meloro, 2011).  Yet,

other studies of mandibular biomechanics suggest *Ar. simus* was an omnivore

(Sorkin, 2006; Figuierido et al., 2009; 2010). A final hypothesis suggests *Ar. simus* was an obligate scavenger, given fragile and gracile limbs not well-suited to withstanding erratic forces associated with active prey capture; instead, these features allowed it to efficiently travel long distances to search for and acquire large quantities of carrion (Matheus, 2003). Indeed, the cursorially adapted forelimb morphology of *Ar. simus* (Lynch, 2012) and its large body size (Christiansen, 1999) would have allowed for long-distance travel and defense of carcasses. With such a discrepancy in dietary interpretations, a new proxy is needed to help clarify the diet of this large ursid.

**History of dental microwear**

Dental microwear is a commonly used and effective proxy for dietary reconstruction because it preserves evidence of actual food choice during the last days or weeks of life (Teaford and Oyen, 1989). Microwear studies operate on the basic principle that a high incidence of scratches relative to pits is indicative of consumption of softer or tougher food items, while a greater frequency of pits indicates the consumption of more brittle objects such as seeds, nuts and fruit pits (Walker et al., 1978; Walker, 1981; Teaford and Walker, 1984). While the assessment of microwear in two-dimensions has been commonly used by anthropologists and paleontologists since the late 1970s (e.g. Walker et al., 1978; Grine 1981; Gordon, 1982), the methodologies employed to quantify tooth surfaces are highly variable and still debated among researchers, resulting in data that is not

directly comparable between studies (Grine et al., 2002; Galbany et al., 2005; Ungar et al., 2008; Mihlbachler et al., 2012).

The pioneering microwear studies of the 1970s and 1980s used scanning electron microscopy (SEM) to document the correlation between size, shape, and orientation of wear features and dietary habits of extant taxa (e.g. Walker et al., 1978; Grine, 1981). Standard analyses and subsequent interpretations of microwear features quantified via SEM relied on observers counting individual pits and scratches from two dimensional SEM micrographs (Teaford and Walker, 1984). Similarly, low-magnification microwear studies use simple and low-cost stereo light microscopes to count wear features directly through the microscope lens, or by taking photomicrographs (e.g. Solounias and Semprebon, 2002; Merceron et al., 2004). Regardless of the method employed, identification and quantification of individual wear features by a human participant are prone to high observer biases, particularly between observers of different experience levels (Ungar et al., 2008; Galbany et al., 2005; Mihlbachler et al., 2012). Further, there is a loss of data associated with the analysis of three-dimensional microwear features in two dimensions (Ungar et al., 2003).

**Dental microwear texture analysis**

A relatively new approach to dental microwear, texture analysis (DMTA), alleviates some of the problems surrounding more traditional microwear studies and has been especially valuable for characterizing subtle differences in patterns with higher-level taxa. DMTA combines a scanning white light confocal profiler with scale

sensitive fractal analysis to quantify surface textures using an automated and repeatable method that reduces observer bias (Ungar et al., 2003; Scott et al., 2006). It has been used to successfully differentiate discrete dietary niches within primates (e.g. Ungar et al., 2003; Scott et al., 2005), bovids (e.g. Scott, 2012), marsupials (Prideaux et al., 2009) and carnivores (Schubert et al., 2010b; DeSantis et al., 2012). A confocal profiler scans the tooth surface with light and quantifies it via generation of a three-dimensional point cloud. These data then undergo scale-sensitive fractal analysis through ToothFrax and SFrax softwares (Surfract Corp., http://www.surfract.com/), to produce dental microwear attributes that can be correlated with diet. Scale sensitive fractal analysis operates on the basic principle that surface textures changes with scale. For example, a skydiver may view the earth's surface as smooth upon leaving the plane, but will be surrounded by irregular topography once on the ground.

Several dental microwear attributes were analyzed to infer diet (Figure 3). Area scale fractal complexity (*Asfc*) is a measure of surface roughness across different scales of observation (Figure 3a). Heavy pitting is associated with high *Asfc* scores and is indicative of hard-object feeding. Thus, it is expected that an herbivorous/frugivorous ursid with high *Asfc* values was likely consuming fruits or nuts, similar to the tufted capuchin primate (Scott et al., 2005), while high *Asfc* values in carnivorous ursids indicates consumption of some bone, similar to hyenas (Schubert et al., 2010b). Length scale anisotropy of relief (*epLsar*) quantifies the orientation of microwear surface textures and high values are characterized by numerous parallel scratches, associated with consumption of soft/fibrous foods

(Figure 3b).  High *epLsar* values are expected in bears eating leaves or bamboo, similar to the leaf-eating mantled-howler monkey (Scott et al., 2005), or bears eating flesh, similar to cheetahs (Schubert et al., 2010b).  Texture fill volume (*Tfv*) is a measure of microwear feature volume in the 2 – 10 µm diameter range (Figure 3c), and is calculated by subtracting the volume of smoothed wear from the volume of the entire structure.  Scale of maximum complexity (*Smc*) is a measure of the scale at which roughness increase tails off, and heterogeneity of complexity (*HAsfc*) reflects variation in complexity across a surface by subdividing the sampled area (Figure 3d).  See Scott et al. (2006) for an in depth discussion of each dental attribute.
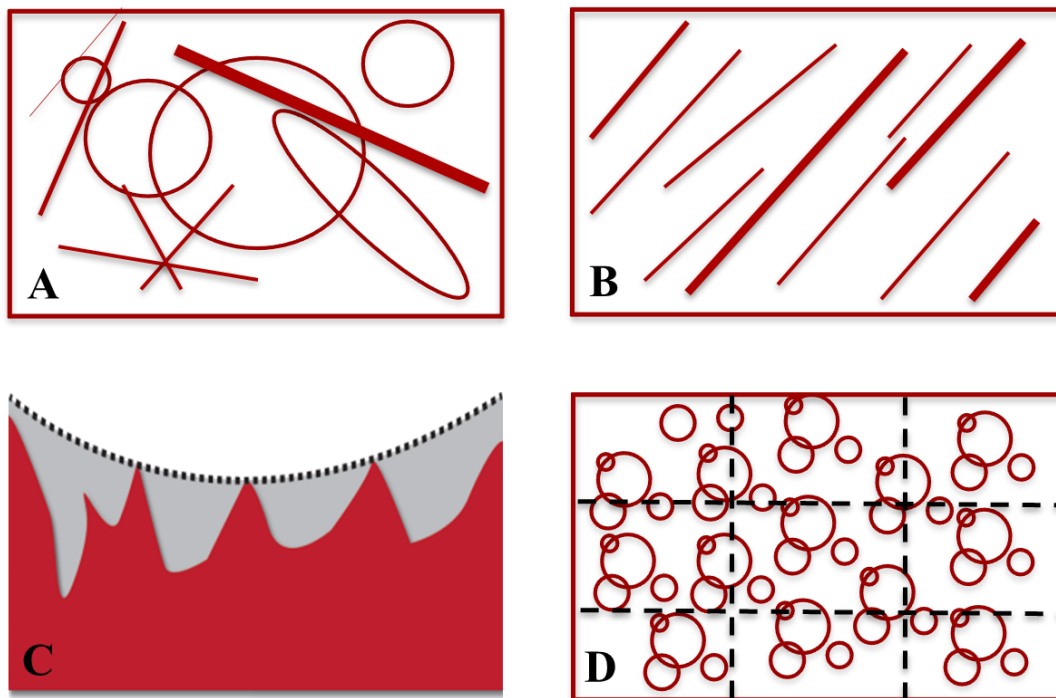


**Figure 3.** Idealized examples of dental microwear attributes.  **A.** Exemplifies high complexity, **B.** high anisotropy.  **C.** diagram of textural fill volume, represented by the gray shaded region.  The black dotted line represents the smoothed tooth surface.  **D.** Exemplifies a homogeneous surface (compared to **A**, which has high heterogeneity).

## Previous microwear work in bears

Low-magnification microwear studies suggest the potential of microwear for retrodicting bear diets (Goillet et al., 2009; Peigné et al., 2009), but the omnivorous brown bear (*Ursus arctos*) and black bears (*U. americanus*, *U. thibetanus*) have not been considered using this approach to date. *Ursus arctos* and extinct European cave bears (*U. spelaeus*) have been studied at 200x by scanning electron microscopy (SEM) to infer both dietary differences and functionality of the first molar (Pinto-Llona, 2013). But as with other microwear studies on bears, the focus was exclusively on lower and upper first molars even though more posterior teeth, which transmit higher bite forces during crushing/grinding, might capture other dietary information especially relevant for omnivorous ursids.

## Goals and Objectives

Here, I report the first application of dental microwear texture analysis (DTMA) to ursids. I analyze five extant species with known feeding behavior to develop a modern baseline to address the following questions: (i) do modern bears with disparate diets have distinct dental microwear textures, and (ii) does dental microwear vary significantly between lower first and second molars given functional differentiation of teeth? I then examine the microwear of *Arctodus simus* to evaluate the hypothesis that the Pleistocene short-faced bear at Rancho La Brea, CA was a bone crushing hyper-scavenger, and discuss the implications of this work.

CHAPTER II

MATERIALS AND METHODS

**Acquisition and preparation of modern samples**

Modern ursid species chosen for analysis occupy a diversity of dietary niches (Figure 1). Extant ursid specimens are adult, wild-caught, have detailed collection data and were collected with an intact skin (inferring that their collection date was on or near their date of death). Because microwear preserves diet during the final days to weeks of life (Teaford and Oyen, 1989), detailed provincial data allows for dietary constraint of specimens based on observational studies. Specimens were chosen to encompass the dietary breadth of each ursid species across different seasons and habitats. Specimens were sampled from the collections of the American Museum of Natural History (AMNH), the Florida Museum of Natural History (FLMNH), and the Smithsonian Institute National Museum of Natural History (NMNH).

Molding and casting procedures followed conventional microwear methods and involved thorough cleaning of tooth facets with an acetone soaked cotton swab (Figure 4a), prior to application of regular body polyvinylsiloxane dental impression material (Figure 4b) (President's Jet, Coltene-Whaledent Corp., Altstätten, Switzerland). Molds were reinforced with polyvinylsiloxane dental putty (Figure 4c) (President's Putty, Coltene-Whaledent Corp., Altstätten, Switzerland) and dental replicas cast using high-resolution epoxy (Epotek 301, Epoxy Technologies Corp., Billerica, MA, USA), consistent with previous work (Ungar et al., 2003; Scott, 2012; DeSantis et al., 2012).
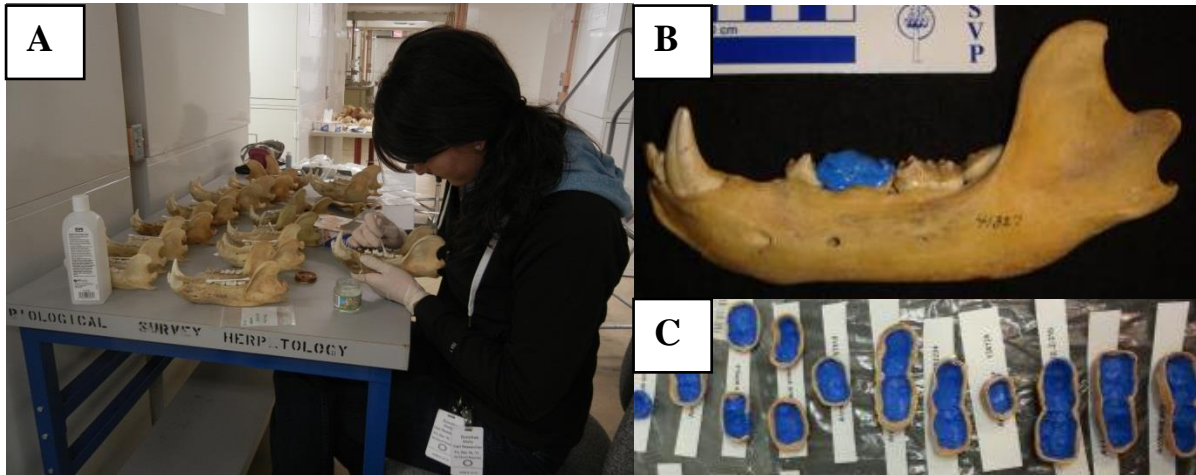
**Figure 4.** Molding and casting procedures. **A.** The author cleaning tooth facets of *Ursus maritimus* at the NMNH. **B.** Mandible of *Ursus americanus* (AMNH 41827) with molding compound applied to the lower left first molar. **C.** Ursid specimen molds with dental putty applied, and laid out for pouring of epoxy at Vanderbilt University.

## Acquisition of fossil samples

Extinct *Arctodus simus* specimens were sampled from the Los Angeles County Museum of Natural History, Page Museum, Hancock Collection (LACMHC). The Rancho La Brea tar pits are a lagerstätte of late Quaternary fossils, dating from the last 50,000 years ago (O'Keefe et al., 2009). Fossil accumulations occur as petroleum percolates upwards into coastal plain sediments, creating cone-shaped pockets of asphalt-impregnated sands that serve as 'sticky animal traps' (Akersten et al., 1983). Petroleum seepage occurs episodically and animal entrapment and preservation on a dynamic alluvial floodplain is highly irregular in time and space (O'Keefe et al., 2009), thus radiocarbon dating is used to assist in age assignment. The high abundance of carnivore fossils relative to those of herbivores is attributed to the luring of carnivores by entrapped prey animals (Spencer et al., 2003).

Continued excavations at Rancho La Brea have resulted in the largest fossil collections of many Pleistocene carnivoran species in North America, including *Ar. simus.* La Brea is further identified as an ideal study locality because of the exceptional preservation of the asphalt-impregnated fossils.

*Arctodus simus* specimens sampled from associated pits at the LACMHC represent a time span of 26,427 (Pit 9) –35,370 (Pit 77) years before present (O'Keefe et al., 2009); however, several specimens lacking pit information were also sampled. Based on the total age estimates of the site, all specimens lived during the end of the Wisconsin glaciation, up to 50,000 years before present (O'Keefe et al., 2009). Sampling protocols are identical to that outlined for modern ursid samples.

## Scanning

Care must be taken when choosing a tooth wear facet to undergo microwear analysis to ensure the chosen facet is recording a true dietary signal. The pioneering studies of microwear by anthropologists provided that Phase II facets in primates, which capture the crushing motion of the mastication cycle, provide the best analog for assessing the physical properties of consumed food (e.g. Kay, 1977). However, in carnivorans, the shearing facet of the m1 carnassial proved to be informative in determing degree of carcass utilization (Schubert et al., 2010b; DeSantis et al., 2012). Ursids have bunodont (short, blunt) teeth that are similar to primates, and the carnassials are reduced, so it is best to assess microwear in both facets in order to determine if they record microwear in a similar way, and if one is more informative than the other. The buccal facet of the m1 protoconid was

analyzed to evaluate shearing functionality, homologous to other carnivorans (Schubert et al., 2010b; DeSantis et al., 2012); the mesial facet of the m2 hypoconulid was analyzed to assess crushing/grinding functionality, analogous to Phase II facets in primates (Kay, 1977; Scott et al., 2005) (Figure 5). Tooth replicas were scanned with a Sensofar Plu white-light scanning confocal microscope (Solarius Development, Inc., Sunnyvale, CA) using a 100x objective lens. Resulting 3D point cloud matrices had horizontal spacing of 0.18μm, and vertical resolution of 0.005μm. Four adjacent scans per facet equaled a total scanned area of 204 x 276 μm. Scanned surfaces were leveled using Solarmap universal software (Solarius Development, Sunnyvale, CA, USA) and small artifacts removed via point deletion editing, identical to DeSantis et al., (2012).
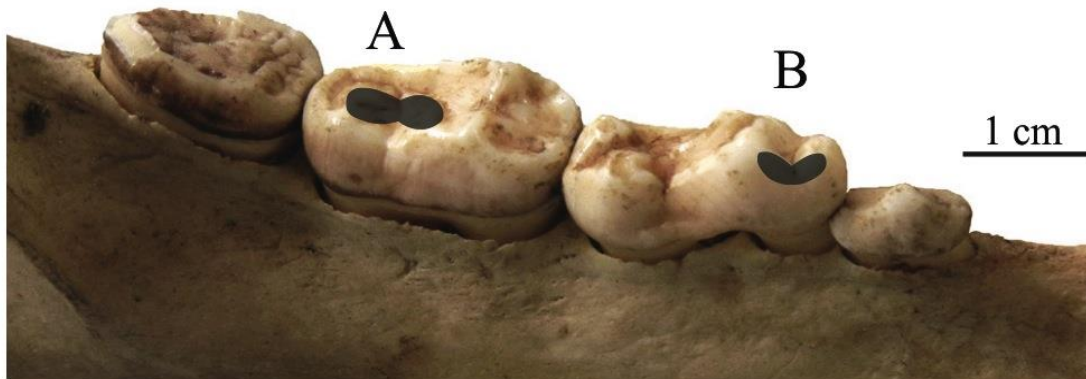


**Figure 5.** *U. americanus* (NMNH 198391), left mandible, buccal view, anterior is to the right. Shading indicates regions of scanning. **A.** Second molar (m2) hypoconulid, mesial facet. **B.** First molar (m1) protoconid, buccal facet.

## Statistical Analyses

Median values were calculated from the four scans run on each specimen, in an effort to reduce the chance of reporting anomalous wear (Scott et al., 2006). DMTA attributes are commonly non-normally distributed (Shapiro Wilk tests, Table 1); thus, nonparametric tests were employed. To assess differential microwear patterning across the tooth row, lower first and second molars from like individuals were compared using a pairwise Wilcoxon signed-rank test (non-parametric), and paired Student's t-test (parametric) where applicable. Character means among species were compared using Kruskal-Wallis tests following Dunn's procedure (Dunn, 1964). In order to account for the possibility of Type I and II errors, multiple analyses of variance (MANOVA) were performed on ranked data (Conover and Iman, 1981), followed by ANOVA's and *post-hoc* Fisher's (LSD) and Tukey's (HSD) tests on individual DMTA attributes to assess sources of variance similar to DeSantis et al., (2012). Differences in variance between taxa were assessed for variables deemed important in dietary reconstruction. Raw data were median-transformed for Levene's test following Plavcan and Cope (2001). A MANOVA, ANOVAs and multiple comparisons tests were run on the transformed data accordingly.

CHAPTER III


RESULTS


Results are presented in Tables 2 − 11.  Significant differences were

exhibited between lower first and second molars of individuals (Table 4).  DMTA

attributes correlating with diet exhibited more differences between disparate dietary

niches in ursid m2's (see discussion).  Significant ($P<0.05$) Kruskal Wallis (Table 5)

and MANOVA (Table 6) results indicate differences in m2 DMTA attributes among

species.  Dunn's procedure indicates that *A. melanoleuca* differs from carnivorous *U.*

*maritimus* by significantly lower *Tfv* values, and from both *U. maritimus* and

omnivorous *U. americanus* by significantly higher *epLsar* values and lower *Asfc*

values.  Complexity values further differentiated diets, as herbivorous *T. ornatus*

exhibited significantly lower values than both *U. maritimus* and *U. americanus,* and

herbivorous/frugivorous *U. malayanus* exhibited significantly lower values than *U.*

*maritimus* (Table 5)*.*  Results from Tukey's (HSD) *post-hoc* tests of ranked data are

consistent with the results from Dunn's procedure, with two exceptions (Table 6).

Fisher's (LSD) test indicates variation in *Asfc* values between *T. ornatus* and *A.*

*melanoleuca*, and *U. americanus* and *U. malayanus.*  These results are considered

suggestive or of marginal significance because Tukey's (HSD) test is more

conservative than Fisher's (LSD) test.

*Arctodus simus* exhibits DMTA attributes with means most similar to *T.*

*ornatus* and *U. americanus* (Table 7), and significant differences ($P<0.05$) in at least

one DMTA attribute distinguishing it from all other taxa.  Specifically, *Ar. simus*

differs from *U. maritimus* with lower *Asfc* and higher *Tfv* values, from *A. melanoleuca*

with higher *Asfc* and *Tfv* and lower *epLsar* values and from *U. malayanus* with lower

*Tfv* values.

Assessment of variability among character distributions in modern ursids

returned significant (*P*<0.05) results for a MANOVA of Levene-transformed *Asfc,*

*epLsar,* and *Tfv* data (Table 8).  Individual ANOVAs on *Asfc* and *epLsar* were

significant (*P*<0.05).  Anisotropy of *A. melanoleuca* is more variable than *T. ornatus,*

*U. americanus* and *Ar. simus* based on Tukey's (HSD) test (*P*<0.05), and marginally

so compared with *U. malayanus* and *U. maritimus* based on Fisher's (LSD) test

(Table 8).  Complexity of *U. americanus* is marginally more variable than all extant

bears (except *U. maritimus*).  Similarly, *Asfc* of *U. maritimus* is significantly more

complex than *T. ornatus,* and marginally more complex than *A. melanoleuca* and *U.*

*malayanus.  Arctodus simus* has significantly and marginally less variable *Asfc*

values than *U. maritimus* and *U. americanus*, respectively, suggesting that it is

overall most similar to *T. ornatus.*

Comparisons of means in lower first molars of ursids are reported in tables 9

– 11.  Significant (*P*<0.05) Kruskal Wallis (Table 9) and MANOVA (Table 10) tests

indicated differences among taxa, but differences do not correlate with known

physical properties of consumed food in modern bears (see discussion).  Table 11

displays results of Kruskall-Wallis tests comparing *Ar. simus* with modern ursids.

Because m1 data does not correlate with diet, variance tests were not performed.

**Table 2.** Descriptive statistics for lower first molars (m1) analyzed in this study

| Species | Tooth | Statistic | $n$ | Asfc | epLsar | Smc | Tfv | Hasfc$_{(3x3)}$ | Hasfc$_{(9x9)}$ |
|---|---|---|---|---|---|---|---|---|---|
| *Ailuropoda Melanoleuca* | m1 | mean | 15 | 5.7047 | 0.0040 | 0.2480 | 3519.72 | 0.3865 | 0.6068 |
| | | SD | | 5.7411 | 0.0051 | 0.1067 | 5431.62 | 0.1054 | 0.1696 |
| | | median | | 2.8400 | 0.0000 | 0.2700 | 111.990 | 0.3898 | 0.6610 |
| | | *P*-value for normality | | **0.0003*** | **< 0.0001*** | **0.003*** | **0.0002*** | 0.562 | 0.287 |
| *Tremarctos ornatus* | m1 | mean | 15 | 4.3480 | 0.0013 | 0.2107 | 8543.40 | 0.4786 | 0.8099 |
| | | SD | | 3.2450 | 0.0035 | 0.0800 | 5247.78 | 0.1155 | 0.1697 |
| | | median | | 3.6600 | 0.0000 | 0.1600 | 7177.10 | 0.4493 | 0.7978 |
| | | *P*-value for normality | | 0.0110 | **< 0.0001*** | **0.001*** | 0.15700 | 0.460 | **0.031*** |
| *Ursus malayanus* | m1 | mean | 7 | 1.4383 | 0.0030 | 0.2726 | 11057.33 | 0.4029 | 0.6278 |
| | | SD | | 0.7195 | 0.0012 | 0.1424 | 3309.30 | 0.0457 | 0.1037 |
| | | median | | 1.5626 | 0.0034 | 0.2665 | 11539.53 | 0.3938 | 0.6473 |
| | | *P*-value for normality | | 0.5790 | 0.7020 | 0.1130 | 0.64100 | 0.877 | 0.347 |
| *Ursus americanus* | m1 | mean | 16 | 4.2075 | 0.0006 | 0.2394 | 9992.03 | 0.5519 | 0.8752 |
| | | SD | | 3.0351 | 0.0025 | 0.0969 | 4232.39 | 0.1303 | 0.3827 |
| | | median | | 2.9050 | 0.0000 | 0.2100 | 10190.29 | 0.5153 | 0.7802 |
| | | *P*-value for normality | | 0.059 | **< 0.0001*** | **0.009*** | 0.65300 | 0.276 | **0.001*** |
| *Ursus maritimus* | m1 | mean | 15 | 4.9133 | 0.0020 | 0.2327 | 10649.85 | 0.4920 | 0.9603 |
| | | SD | | 2.4438 | 0.0041 | 0.1444 | 3812.19 | 0.1890 | 0.4510 |
| | | median | | 4.1600 | 0.0000 | 0.2100 | 11618.49 | 0.4422 | 0.7726 |
| | | *P*-value for normality | | **0.0130*** | **< 0.0001*** | **< 0.0001*** | 0.067 | **0.015*** | **0.028*** |
| *Arctodus simus* | m1 | mean | 15 | 3.3499 | 0.0025 | 2.7714 | 13381.56 | 0.5293 | 1.0416 |
| | | SD | | 1.9620 | 0.0008 | 5.7233 | 2512.69 | 0.1865 | 0.3285 |
| | | median | | 2.7375 | 0.0023 | 0.1512 | 13344.52 | 0.5331 | 0.8740 |
| | | *P*-value for normality | | 0.148 | 0.179 | **< 0.0001*** | 0.352 | 0.233 | **0.036*** |

*Significant values are noted in bold red text (*P*<0.05); *Asfc*, area-scale fractal complexity; *epLsar*, anisotropy; *Tfv*, texture fill volume; *Smc*, scale of maximum complexity; *HAsfc*$_{(3x3)}$, *HAsfc*$_{(9x9)}$ heterogeneity of complexity in a 3x3 and 9x9 grid, respectively.

**Table 3**. Descriptive statistics for lower second molars (m2) of ursids in this study.

| Species | Tooth | Statistic | n | Asfc | epLsar | Smc | Tfv | Hasfc(3x3) | Hasfc(9x9) |
|---|---|---|---|---|---|---|---|---|---|
| *Ailuropoda melanoleuca* | m2 | mean | 11 | 2.0717 | 0.0037 | 0.2031 | 7750.72 | 0.4357 | 0.7976 |
| | | SD | | 0.9980 | 0.0022 | 0.0811 | 5506.47 | 0.1160 | 0.2148 |
| | | median | | 1.9173 | 0.0034 | 0.1541 | 8509.43 | 0.4300 | 0.7189 |
| | | *P*-value for normality | | 0.776 | 0.705 | **0.001*** | 0.055 | 0.800 | 0.083 |
| *Tremarctos ornatus* | m2 | mean | 11 | 4.1717 | 0.0028 | 0.2262 | 12986.93 | 0.4902 | 0.7542 |
| | | SD | | 2.2880 | 0.0009 | 0.1050 | 4409.97 | 0.1482 | 0.2016 |
| | | median | | 3.5384 | 0.0026 | 0.1549 | 13012.03 | 0.4808 | 0.7074 |
| | | *P*-value for normality | | 0.257 | 0.796 | **0.002*** | 0.841 | **0.034*** | 0.570 |
| *Ursus malayanus* | m2 | mean | 6 | 3.9644 | 0.0023 | 0.2020 | 10638.87 | 0.4143 | 0.7945 |
| | | SD | | 2.5193 | 0.0009 | 0.0832 | 3714.54 | 0.1665 | 0.2434 |
| | | median | | 3.9722 | 0.0021 | 0.1511 | 11727.47 | 0.3338 | 0.7403 |
| | | *P*-value for normality | | 0.299 | 0.606 | **0.008*** | 0.191 | **0.024*** | 0.882 |
| *Ursus americanus* | m2 | mean | 15 | 7.8477 | 0.0022 | 0.1720 | 12191.66 | 0.5363 | 0.8695 |
| | | SD | | 4.5757 | 0.0011 | 0.0519 | 4527.92 | 0.1510 | 0.3626 |
| | | median | | 6.7920 | 0.0021 | 0.1514 | 13262.26 | 0.4810 | 0.8318 |
| | | *P*-value for normality | | 0.542 | 0.252 | **< 0.0001*** | 0.082 | 0.628 | 0.123 |
| *Ursus maritimus* | m2 | mean | 16 | 8.4868 | 0.0022 | 0.1889 | 13036.05 | 0.5228 | 1.0190 |
| | | SD | | 3.640 | 0.001 | 0.077 | 2135.50 | 0.174 | 0.454 |
| | | median | | 9.0555 | 0.0019 | 0.1527 | 13358.15 | 0.4820 | 0.8906 |
| | | *P-value for normality* | | 0.761 | **0.023*** | **< 0.0001*** | **0.046*** | **0.028*** | **0.013*** |
| *Arctodus simus* | m2 | mean | 16 | 4.5865 | 0.0022 | 5.0624 | 15027.69 | 0.5866 | 1.0290 |
| | | SD | | 2.2953 | 0.0010 | 13.8352 | 1753.25 | 0.1351 | 0.2309 |
| | | median | | 4.1145 | 0.0020 | 0.1520 | 15394.58 | 0.5809 | 0.9898 |
| | | *P-value for normality* | | 0.218 | 0.216 | **< 0.0001*** | 0.403 | 0.676 | 0.657 |

*Significant values are noted in bold red text (*P*<0.05); *Asfc*, area-scale fractal complexity; *epLsar*, anisotropy; *Tfv*, texture fill volume; *Smc*, scale of maximum complexity; *HAsfc(3x3)*, *HAsfc(9x9)* heterogeneity of complexity in a 3x3 and 9x9 grid, respectively.

**Table 4.** Pairwise comparisons of lower first and second molars in individuals.

| | Asfc | | epLsar | | Smc | Tfv | | Hasfc(3x3) | | Hasfc(9x9) | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | p | np | p | np | np | p | np | p | np | p | np |
| *Ailuropoda Melanoleuca* | -- | 0.563 | -- | 0.197 | 0.398 | -- | 0.100 | 0.273 | 0.266 | 0.093 | 0.197 |
| *Tremarctos ornatus* | 0.586 | 0.824 | -- | 0.307 | 1.000 | **0.075\*** | 0.068 | -- | 0.824 | -- | 0.625 |
| *Ursus malayanus* | **0.030\*** | **0.036\*** | **0.012\*** | 0.529 | 0.402 | 0.839 | 0.834 | -- | 1.000 | **0.041\*** | 0.093 |
| *Ursus americanus* | **0.015\*** | **0.013\*** | -- | **0.011\*** | **0.029\*** | **0.044\*** | **0.050\*** | 0.778 | 0.712 | -- | 0.932 |
| *Ursus maritimus* | -- | **0.005\*** | -- | 0.320 | 0.977 | -- | **0.013\*** | -- | 0.320 | -- | 0.932 |
| *Arctodus simus* | 0.057 | 0.180 | 0.208 | 0.286 | 0.451 | **0.043\*** | 0.060 | 0.260 | 0.315 | -- | 0.851 |

*Significant values are noted in bold red text (*P*<0.05); p indicates parametric Student's t-test; np indicates nonparametric Wilcoxon signed rank test; *Asfc*, area-scale fractal complexity; *epLsar*, anisotropy; *Tfv*, texture fill volume; *Smc*, scale of maximum complexity; *HAsfc*(3x3), *HAsfc*(9x9) heterogeneity of complexity in a 3x3 and 9x9 grid, respectively.

**Table 5.** Pairwise differences for dental microwear attributes of lower second molars of extant ursids in this study (Dunn's procedure).

| | *T. ornatus* | *U. malayanus* | *U. americanus* | *U. maritimus* |
|---|---|---|---|---|
| ***Asfc*** | | | | |
| *A. melanoleuca* | -13.00 | -11.20 | **-26.36\*** | **-29.86\*** |
| *T. ornatus* | | 1.80 | **-13.36\*** | **-16.86\*** |
| *U. malayanus* | | | -15.17 | **-18.67\*** |
| *U. americanus* | | | | -3.5 |
| ***epLsar*** | | | | |
| *A. melanoleuca* | 8.91 | 15.98 | **17.75\*** | **18.51\*** |
| *T. ornatus* | | 7.08 | 8.84 | 9.60 |
| *U. malayanus* | | | 1.77 | 2.52 |
| *U. americanus* | | | | 0.75 |
| ***Tfv*** | | | | |
| *A. melanoleuca* | -14.09 | -3.58 | -12.84 | **-13.47\*** |
| *T. ornatus* | | 10.52 | 1.25 | 0.62 |
| *U. malayanus* | | | -9.27 | -9.90 |
| *U. americanus* | | | | -0.63 |
| ***Smc*** | | | | |
| *A. melanoleuca* | 2.23 | 9.61 | 10.94 | 7.74 |
| *T. ornatus* | | 7.38 | 8.71 | 5.51 |
| *U. malayanus* | | | 1.33 | -1.86 |
| *U. americanus* | | | | -3.20 |
| ***HAsfc*$_{(3x3)}$** | | | | |
| *A. melanoleuca* | -3.55 | 6.85 | -8.95 | -5.82 |
| *T. ornatus* | | 10.39 | -5.41 | -2.27 |
| *U. malayanus* | | | -15.80 | -12.67 |
| *U. americanus* | | | | 3.13 |
| ***HAsfc*$_{(9x9)}$** | | | | |
| *A. melanoleuca* | 3.18 | 0.65 | -1.25 | -5.62 |
| *T. ornatus* | | -2.53 | -4.43 | -8.80 |
| *U. malayanus* | | | -1.90 | -6.27 |
| *U. americanus* | | | | -4.37 |

\*Significant values are noted in bold red text ($P<0.05$) and represent analyses performed absent of the Bonferroni correction; *Asfc*, area-scale fractal complexity; *epLsar*, anisotropy; *Tfv*, texture fill volume; *Smc*, scale of maximum complexity; *HAsfc*$_{(3x3)}$, *HAsfc*$_{(9x9)}$ heterogeneity of complexity in a 3x3 and 9x9 grid, respectively.

**Table 6.** Table of pairwise difference for Fisher's (LSD) and Tukey's (HSD) tests on significant (*P*<0.05) ANOVAs of extant ursid lower second molars.

| | *T. ornatus* | *U. malayanus* | *U. americanus* | *U. maritimus* |
|---|---|---|---|---|
| **Asfc** | | | | |
| *A. melanoleuca* | -13.00* | -11.20 | **-26.36**** | **-29.86**** |
| *T. ornatus* | | 1.80 | -13.36* | **-16.86**** |
| *U. malayanus* | | | -15.17* | **-18.67**** |
| *U. americanus* | | | | -3.50 |
| **epLsar** | | | | |
| *A. melanoleuca* | 8.91 | 15.99 | 17.75* | **18.51**** |
| *T. ornatus* | | 7.08 | 8.84 | 9.60 |
| *U. malayanus* | | | 1.77 | 2.52 |
| *U. americanus* | | | | 0.75 |

*Significant values based on Fisher's LSD test, noted in red text; **significant values (*P*<0.05) based on both Fisher's LSD and Tukey's HSD tests, noted in bold red text; *Asfc*, area-scale fractal complexity; *epLsar*, anisotropy.

**Table 7.** Table of pairwise differences of Dunn's procedure for lower second molar dental microwear attributes of extant ursids and *Arctodus simus.*

| | *T. ornatus* | *U. malayanus* | *U. americanus* | *U. maritimus* | *Ar. simus*[†] |
|---|---|---|---|---|---|
| ***Asfc*** | | | | | |
| *A. melanoleuca* | -18.18 | -15.26 | **-35.29\*** | **-40.47\*** | **-21.15\*** |
| *T. ornatus* | | 2.92 | **-17.11\*** | **-22.28\*** | -2.97 |
| *U. malayanus* | | | **-20.03\*** | **-25.21\*** | -5.90 |
| *U. americanus* | | | | -5.18 | 14.14 |
| *U. maritimus* | | | | | **19.31\*** |
| ***epLsar*** | | | | | |
| *A. melanoleuca* | 10.73 | 19.62 | **22.59\*** | **23.27\*** | **22.64\*** |
| *T. ornatus* | | 8.89 | 11.86 | 12.54 | 11.92 |
| *U. malayanus* | | | 2.97 | 3.65 | 3.02 |
| *U. americanus* | | | | 0.68 | 0.05 |
| *U. maritimus* | | | | | -0.63 |
| ***Tfv*** | | | | | |
| *A. melanoleuca* | **-18.55\*** | -3.97 | **-17.04\*** | -15.45 | **-32.32\*** |
| *T. ornatus* | | 14.58 | 1.51 | 3.10 | -13.78 |
| *U. malayanus* | | | -13.07 | -11.48 | **-28.35\*** |
| *U. americanus* | | | | 1.59 | -15.29 |
| *U. maritimus* | | | | | **-16.88\*** |

\*Significant values are noted in bold red text (*P*<0.05) and represent analyses performed absent of the Bonferroni correction. [†]denotes the extinct taxon; *Asfc*, area-scale fractal complexity; *epLsar*, anisotropy; *Tfv*, texture fill volume.

**Table 8.** Pairwise differences of variance between lower second molars of all extant and extinct bears (using data transformed for Levene's test, X' = │X – median(X) / median(X)│ following Plavcan and Cope (2001).

| | T. ornatus | U. malayanus | U. americanus | U. maritimus | Ar. simus[†] |
|---|---|---|---|---|---|
| *Asfc* | | | | | |
| A. melanoleuca | 0.134 | 0.090 | -0.405* | -0.476* | -0.082 |
| T. ornatus | | -0.044 | -0.538* | **-0.610\*\*** | 0.051 |
| U. malayanus | | | -0.495* | -0.566* | -0.008 |
| U. americanus | | | | -0.072 | -0.487* |
| U. maritimus | | | | | **-0.558\*\*** |
| *epLsar* | | | | | |
| A. melanoleuca | **0.522\*\*** | 0.578* | **0.466\*\*** | 0.411* | **0.510\*\*** |
| T. ornatus | | 0.056 | -0.056 | -0.111 | -0.012 |
| U. malayanus | | | -0.112 | -0.167 | -0.067 |
| U. americanus | | | | -0.055 | 0.044 |
| U. maritimus | | | | | 0.100 |

*Significant values based on Fisher's LSD test, noted in red text; **significant values ($P<0.05$) based on both Fisher's LSD and Tukey's HSD tests, noted in bold red text; *Asfc*, area-scale fractal complexity; *epLsar*, anisotropy. [†] denotes the extinct taxon.

**Table 9**. Table of pairwise differences of Dunn's procedure for dental microwear attributes of lower first molars of extant ursids in this study.

| | *T. ornatus* | *U. malayanus* | *U. americanus* | *U. maritimus* |
|---|---|---|---|---|
| **Asfc** | | | | |
| *A. melanoleuca* | 1.83 | **27.26*** | 3.11 | -7.30 |
| *T. ornatus* | | **25.43*** | 1.28 | -9.13 |
| *U. malayanus* | | | **-24.15*** | **-34.56*** |
| *U. americanus* | | | | -10.41 |
| **epLsar** | | | | |
| *A. melanoleuca* | 10.00 | -13.00 | **12.66*** | 7.50 |
| *T. ornatus* | | **-23.00*** | 2.66 | -2.50 |
| *U. malayanus* | | | **25.66*** | **20.50*** |
| *U. americanus* | | | | -5.16 |
| **Smc** | | | | |
| *A. melanoleuca* | 4.63 | 3.22 | -0.91 | 5.87 |
| *T. ornatus* | | -1.41 | -5.54 | 1.23 |
| *U. malayanus* | | | -4.13 | 2.65 |
| *U. americanus* | | | | 6.78 |
| **Tfv** | | | | |
| *A. melanoleuca* | **-17.20*** | **-24.84*** | **-21.14*** | **-24.67*** |
| *T. ornatus* | | -7.64 | -3.94 | -7.47 |
| *U. malayanus* | | | 3.70 | 0.17 |
| *U. americanus* | | | | -3.53 |
| **HAsfc$_{(3x3)}$** | | | | |
| *A. melanoleuca* | -13.67 | -1.67 | **-24.35*** | -10.20 |
| *T. ornatus* | | 12.00 | -10.69 | 3.47 |
| *U. malayanus* | | | **-22.69*** | -8.53 |
| *U. americanus* | | | | **14.15*** |
| **HAsfc$_{(9x9)}$** | | | | |
| *A. melanoleuca* | **-19.07*** | 0.21 | **-18.06*** | **-18.13*** |
| *T. ornatus* | | **19.28*** | 1.01 | 0.93 |
| *U. malayanus* | | | **-18.27*** | **-18.34*** |
| *U. americanus* | | | | -0.08 |

*Significant values are noted in bold red text ($P<0.05$) and represent analyses performed absent of the Bonferroni correction. *Asfc*, area-scale fractal complexity; *epLsar*, anisotropy; *Smc*, scale of maximum complexity; *Tfv*, texture fill volume; HAsfc$_{(3x3)}$, HAsfc$_{(9x9)}$ heterogeneity of complexity in a 3x3 and 9x9 grid, respectively.

**Table 10**. Table of pairwise difference for Fisher's (LSD) and Tukey's (HSD) tests on significant (*P*<0.05) ANOVAs of extant ursid lower first molars

| | *T. ornatus* | *U. malayanus* | *U. americanus* | *U. maritimus* |
|---|---|---|---|---|
| ***Asfc*** | | | | |
| *A. melanoleuca* | 2.00 | **27.36**\*\* | 3.25 | -7.2 |
| *T. ornatus* | | **25.36**\*\* | 1.25 | -9.2 |
| *U. malayanus* | | | **-24.12**\*\* | **-34.56**\*\* |
| *U. americanus* | | | | -10.45 |
| ***epLsar*** | | | | |
| *A. melanoleuca* | 12.60 | -11.80 | 16.64\* | 5.53 |
| *T. ornatus* | | **-24.40**\*\* | -4.04 | -7.07 |
| *U. malayanus* | | | **28.44**\*\* | 17.33\* |
| *U. americanus* | | | | -11.10 |
| ***Tfv*** | | | | |
| *A. melanoleuca* | -18.20\* | **-25.84**\*\* | **-22.14**\*\* | **-25.67**\*\* |
| *T. ornatus* | | -7.64 | -3.94 | -7.47 |
| *U. malayanus* | | | 3.70 | -0.17 |
| *U. americanus* | | | | -3.53 |
| ***HAsfc*(3x3)** | | | | |
| *A. melanoleuca* | -13.67\* | -1.67 | **-24.35**\*\* | -10.20 |
| *T. ornatus* | | 12.00 | -10.69 | 3.47 |
| *U. malayanus* | | | -22.69\* | -8.53 |
| *U. americanus* | | | | 14.15\* |
| ***HAsfc*(9x9)** | | | | |
| *A. melanoleuca* | **-19.07**\*\* | -0.21 | -18.06\* | -18.13\* |
| *T. ornatus* | | -19.28\* | -1.01\* | -0.93\* |
| *U. malayanus* | | | -18.27 | -18.34 |
| *U. americanus* | | | | -0.08 |

\*Significant values based on Fisher's LSD test, noted in bold red text**;** \*\*significant values (*P*<0.05) based on both Fisher's LSD and Tukey's HSD tests, noted in bold red text; *Asfc*, area-scale fractal complexity; *epLsar*, anisotropy; *Smc*, scale of maximum complexity; *Tfv*, texture fill volume; *HAsfc*(3x3), *HAsfc*(9x9) heterogeneity of complexity in a 3x3 and 9x9 grid, respectively.

**Table 11.** Table of pairwise differences of Dunn's procedure for lower first molar dental microwear attributes of extant ursids and *Arctodus simus*.

| | *T. ornatus* | *U. malayanus* | *U. americanus* | *U. maritimus* | *Ar. simus*[†] |
|---|---|---|---|---|---|
| **Asfc** | | | | | |
| *A. melanoleuca* | 2.30 | **33.98*** | 3.80 | -9.30 | 8.30 |
| *T. ornatus* | | **31.68*** | 1.50 | -11.60 | 6.00 |
| *U. malayanus* | | | **-30.17*** | **-43.28*** | **-25.68*** |
| *U. americanus* | | | | -13.10 | 4.50 |
| *U. maritimus* | | | | | **17.60*** |
| **epLsar** | | | | | |
| *A. melanoleuca* | 14.00 | -16.71 | **17.72*** | 10.50 | -13.47 |
| *T. ornatus* | | **-30.71*** | 3.72 | -3.50 | **-27.47*** |
| *U. malayanus* | | | **34.43*** | **27.21*** | 3.25 |
| *U. americanus* | | | | -7.22 | **-31.19*** |
| *U. maritimus* | | | | | **-23.97*** |
| **Tfv** | | | | | |
| *A. melanoleuca* | **-19.27*** | **-27.43*** | **-23.50*** | **-27.47*** | **-42.67*** |
| *T. ornatus* | | -8.16 | -4.23 | -8.20 | **-23.40*** |
| *U. malayanus* | | | 3.93 | -0.04 | -15.24 |
| *U. americanus* | | | | -3.97 | **-19.17*** |
| *U. maritimus* | | | | | -15.20 |
| **HAsfc(3x3)** | | | | | |
| *A. melanoleuca* | -15.67 | -2.07 | **-28.00*** | -12.47 | **-18.87*** |
| *T. ornatus* | | 13.60 | -12.34 | 3.20 | -3.20 |
| *U. malayanus* | | | **-25.94*** | -10.40 | -16.80 |
| *U. americanus* | | | | 15.54 | 9.14 |
| *U. maritimus* | | | | | -6.40 |

**Table 11, Continued.** Table of pairwise differences of Dunn's procedure for lower first molar dental microwear attributes of extant ursids and *Arctodus simus.*

| | T. ornatus | U. malayanus | U. americanus | U. maritimus | Ar. simus[†] |
|---|---|---|---|---|---|
| **HAsfc(9x9)** | | | | | |
| A. melanoleuca | **-22.13*** | 0.69 | **-21.54*** | **-22.20*** | **-35.93*** |
| T. ornatus | | **22.82*** | 0.60 | -0.07 | -13.80 |
| U. malayanus | | | **-22.22*** | **-22.88*** | **-36.62*** |
| U. americanus | | | | -0.66 | -14.40 |
| U. maritimus | | | | | -13.73 |

*Significant values are noted in bold red text (*P*<0.05) and represent analyses performed absent of the Bonferroni correction. [†] denotes the extinct taxon; *Asfc*, area-scale fractal complexity; *epLsar*, anisotropy; *Smc*, scale of maximum complexity; *Tfv*, texture fill volume; *HAsfc(3x3)*, *HAsfc(9x9)* heterogeneity of complexity in a 3x3 and 9x9 grid, respectively.

Chapter IV


DISCUSSION


**Do lower first and second molars record distinct dental microwear?**

Previous microwear studies of ursids assessed wear on two different locations in the lower first molar (m1): the protoconid shearing facet of the carnassial, and in the carnassial's posterior crushing talonid basin (e.g. Pinto-Llona, 2013).  However, the carnassial experiences lower bite forces, while higher bite forces experienced by more posterior molars may be important in capturing diet of omnivorous bears.  For the foundational study of ursids, I assessed two facets that have previously been documented as important dietary indicators: the shearing carnassial facet (m1) useful in microwear of carnivorans, and the crushing facet (m2) analogous to Phase II facets in primates. These two facets capture different motions of the chewing cycle, and thus likely record microwear differently.

Significant differences between dental microwear attributes of lower first and second molars of individuals are consistent with functional differences along the tooth row. The high *epLsar* values of the m1 carnassial shearing facet relative to the m2 are expected given constrained tooth-tooth contact with the occluding upper fourth premolar (Ungar, 2010).  The higher *Tfv* in the m2 of all taxa, and higher *Asfc* in *U. maritimus* and *U. americanus* are consistent with the crushing of food particles by high bite forces in the m2 talonid basin.  Correlation of wear attributes with

physical properties of diet were assessed in the m1 and m2 separately, in order to evaluate which was the most appropriate dietary indicator.

**Assessment of microwear in lower first molars**

Inferring diet from dental microwear textures of lower first molars of modern bears is complicated by the use of the m1 carnassial during food acquisition and preparation. Ursids often use their forelimbs to stabilize food items while grabbing, tearing, or cracking food with their carnassial teeth (Wong et al., 2002; Peyton, 1980). Thus, it is likely that microwear attributes on the m1 are a reflection of both differences in food acquisition and processing – and it is difficult to parse the two. This is consistent with statistically indistinguishable *Asfc* values between all modern bears analyzed (excluding *U. malayanus*), despite the differences in physical properties of consumed food between species (Table 1, Figure 6). *Ailuropoda melanoleuca*, in particular, uses its anterior teeth (including the m1) during bamboo processing prior to consumption. Higher *Asfc* scores of the m1 reflect peeling and biting of bamboo stalks, while the m2 is used primarily for chewing. In contrast, *U. malayanus* likely avoids using the m1 during food acquisition, as low *Asfc* values do not reflect the high proportion of fruit and insects in its diet (Wong et al., 2002; Fredriksson et al., 2006). Alternatively, low *Asfc* values in *U. malayanus* may indicate either preferential use of the m1 on softer/tougher food items, or are an effect of a small sample size (n=6). Overall, dental microwear attributes of the carnassial shearing facet (m1) do not relate to known dietary differences of modern bears, and thus the m2 is a more appropriate proxy for inferring diet in extinct ursids.
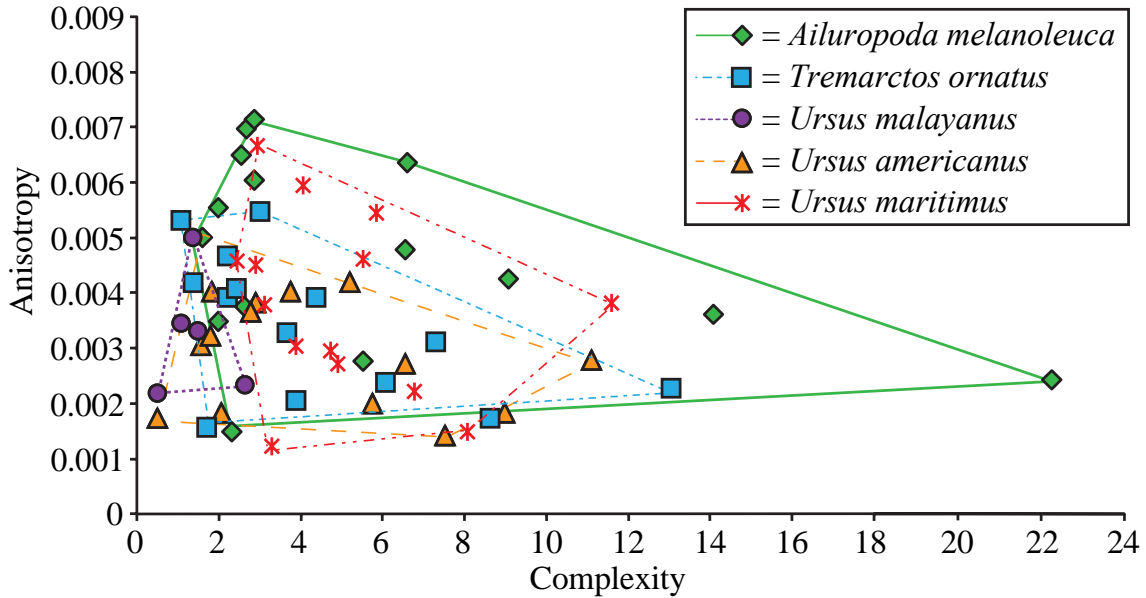
**Figure 6.** Biplot of anisotropy (*epLsar*) vs. complexity (*Asfc*) for lower first molars of extant ursids. Polygons enclose data points.

## Assessment of microwear in lower second molars

Dental microwear differences in m2s correlate well with observed differences in diets of extant bears, suggesting the potential of texture analysis to retrodict diet in extinct bear species (Figure 7, Figure 8). *Ailuropoda melanoleuca* has low *Asfc* values, consistent with oral processing of bamboo leaves, shoots, and peeled stems. Prior to consumption of bamboo stems, the stalk is held by the paw and the hard exterior peeled off using the anterior molars and teeth. The tough peeled stalk is bitten into bite sized pieces and chewed with the more posterior teeth (Long et al., 2004). High *epLsar* values reflect the high silica content of bamboo, and are consistent with previous SEM microwear studies that found high numbers of scratches and infrequent pitting in *A. melanoleuca* (Daegling and Grine, 1994). Consumption of large quantities of plant matter is also reflected in moderate *Asfc* values in *T. ornatus* and *U. malayanus,* who process tough leafy matter, seeded or

pitted fruits, and some insects (Peyton, 1980; Wong et al., 2002). In contrast to more herbivorous bears, the high variance of *Asfc* values exhibited by *U. americanus* (Figure 7) reflects the high degree of dietary adaptability across geographic regions (Alaska vs. Florida, Appendix A) and seasons present in this species. Individuals displaying high *Asfc* values likely consumed brittle or hard food (e.g. nuts or berries with hard seeds) prior to death (Raine and Kansas, 1990; Roof, 1997). *Ursus maritimus* also has highly variable *Asfc* values, similar to *U. americanus,* despite a diet consisting primarily of soft seal flesh and blubber (Theimann et al., 2008). High *Asfc* values are likely the result of bone consumption during scavenging (Theimann et al., 2008; Bentzen et al., 2007) or consumption of terrestrial food sources including coastal and freshwater fish, and berries during summer months (Derocher et al., 1993).
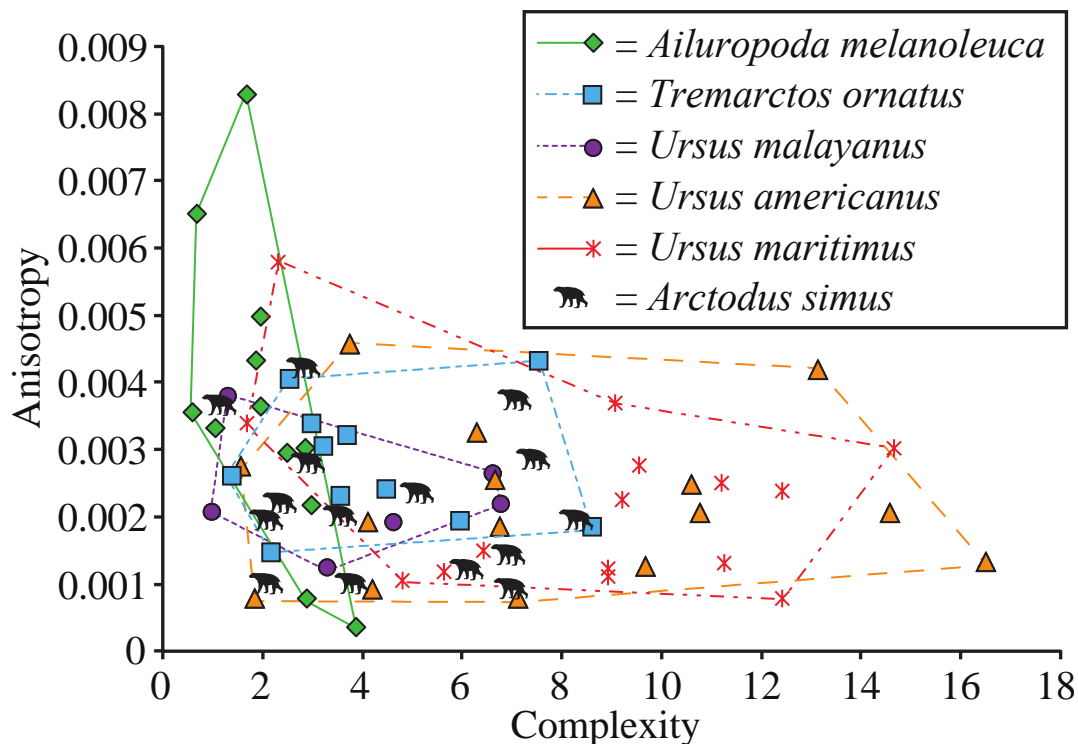


**Figure 7.** Biplot of anisotropy (*epLsar*) vs. complexity (*Asfc*) for lower second molars of extant ursids and extinct *Arctodus simus*. Polygons enclose data points.
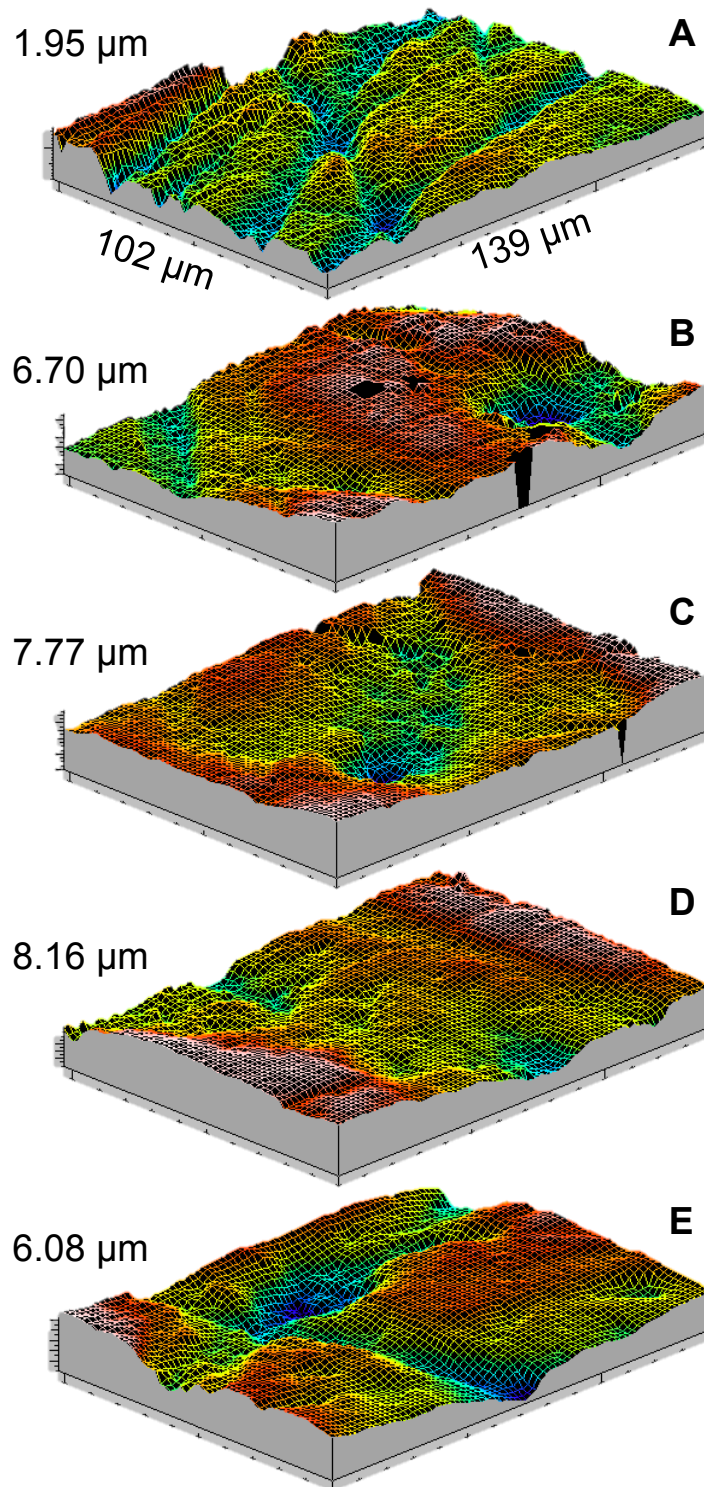
**Figure 8.** Three dimensional colored axiomatic mesh constructions of extant ursid lower second molars. **A**. *Ailuropoda melanoleuca*, NMNH 259028; **B.** *Tremarctos ornatus*, NMNH 271418; **C**. *Ursus malayanus* NMNH 151866; **D.** *Ursus americanus,* UF 28436; **E**. *Ursus maritimus*, NMNH 512117. See Figure 1 for three-dimensional photosimulations.

**Inferring the diet of *Arctodus simus***

Dental microwear texture analysis of lower second molars suggests that *Ar. simus* was not a durophagous hyper-scavenger of carcasses at Rancho La Brea, CA.  It is expected that hyper-scavengers partake in at least some durophagy, and thus would exhibit high *Asfc* values, similar to modern hyenas (*Crocuta crocuta,* mean *Asfc* = 9.315, DeSantis et al., 2012). Significantly lower ($P<0.05$, Wilcoxon signed rank test) *Asfc* values in both the m1 and the m2 of *Ar. simus* in comparison to *C. crocuta* do not support durophagy in this ursid.  Further, *Ar. simus* has significantly lower *Asfc* values ($P<0.05$, Tukey's (HSD) test) than extant *U. maritimus,* which participates in some carcass scavenging of marine mammals on sea ice.  Although microwear differentiates between the physical properties of consumed food, and suggests that *Ar. simus* was not a hard-object feeder at La Brea, it cannot identify the trophic level of the short-faced bear.  Stable carbon and nitrogen isotopes have identified *Ar. simus* from northwestern North America as a carnivore (Bocherens et al., 1995; Matheus et al., 1995; Barnes et al., 2002), but isotopic values have not been reported for mid-lower North America, and the diet of *Ar. simus* likely varied by region (Schubert and Wallace, 2009), as evidenced through the dietary adaptability of modern ursids (e.g. Roof 1997; Peyton 1980, Wong et al., 2002; Hansen et al., 2010).

*Arctodus simus* likely included some plant and animal material in its diet, and seems to have avoided hard/brittle food items at La Brea.  Morphologically, *Ar. simus* exhibits characters common to herbivorous bears, including cheek teeth with high surface area, a deep mandible, and large mandibular muscle attachments

(Figueirido et al., 2009, 2010). Because herbivorous members of the order Carnivora lack a long and efficient digestive tract for breaking down plant matter via microbial action (Dierenfeld et al., 1982), they must break down plant matter via extensive chewing or grinding, and thus possess features to create a high mechanical advantage of the jaw (Sacco and Van Valkenburgh, 2004; Figueirido et al., 2009). While the presence of features indicating herbivory in *Ar. simus* may reflect diet, the close phylogenetic relationship to the herbivorous/omnivorous spectacled bear must also be considered, as these traits may be the ancestral condition of the group. Regardless, highly worn teeth indicate the presence of at least some plant matter in the diet of *Ar. simus* (Emslie and Czaplewski, 1985; Sorkin, 2006). Despite possible inclusion of both plant and animal material in the diet of *Ar. Simus* at La Brea, it was likely less of a generalist than modern *U. americanus*, based on its relatively constrained *Asfc* values.

*Arctodus simus* from La
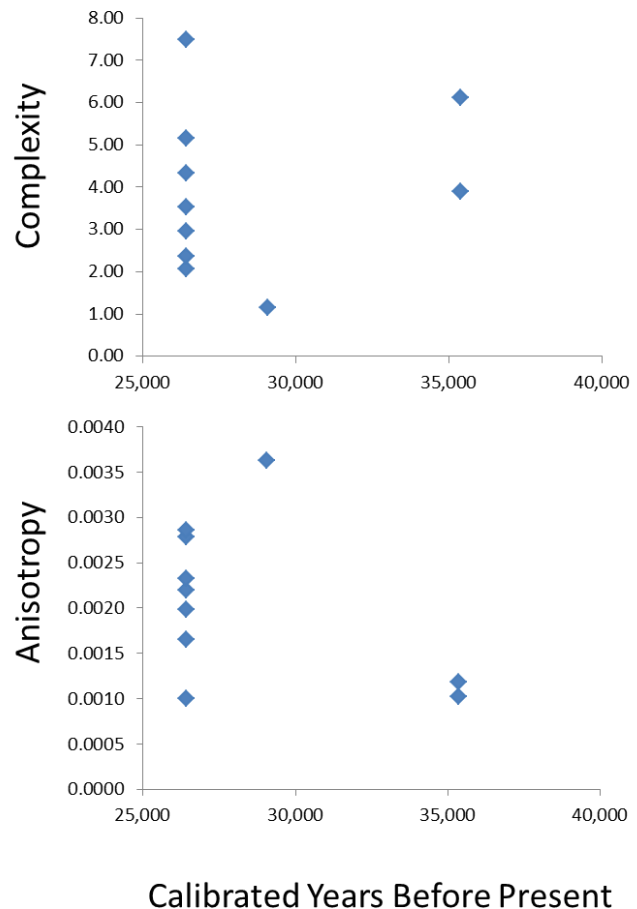


**Figure 9.** Temporal graph of *Arctodus simus* dental microwear. Complexity (top) and anisotropy (bottom)

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Brea may have altered its diet through the late Pleistocene (Figure 9), but our sample size is not large enough to explicitly test this hypothesis. Most *A. simus* specimens come from Pit 9 (26,427 years before present) with only one specimen from Pit 91 (29,068 years before present) and two from Pit 77 (35,370 years before present) (O'Keefe et al. 2009). The seven specimens from Pit 9 have variable *Asfc* and *epLsar* values, which likely captures the dietary breadth of *A. simus*, including seasonal variation. The individual from Pit 91 appears to have been consuming soft/tough food items prior to death and the two individuals from Pit 77 were consuming harder foods. Caution must be exercised when interpreting diet based on so few specimens, as dietary breadth is not fully captured. Further, all specimens lived during the Wisconsin glaciation (O'Keefe et al., 2009) thus assessment of dietary change between glacial – interglacial conditions was not possible.

### Extinction Implications

Previous research concerning the extinction of numerous large-bodied carnivorans at Rancho La Brea examined incidence of tooth breakage, and suggests that times were 'tough' as food shortages led carnivorans to more fully utilize carcasses (Van Valkenburgh and Hertel, 1993). Here, there is no support for durophagous carcass utilization by *Arctodus simus*. Of the 16 specimens examined, not a single bear exhibits evidence of bone consumption through elevated complexity and/or texture fill volume values. While it is possible that *Ar. simus* engaged in scavenging of flesh from recent kills, it is expected that as a scavenger, at least some bone would be consumed. These results are consistent with prior

work assessing dental microwear of carnivorans at La Brea (DeSantis et al., 2012; Schmitt, 2011). Specifically, DeSantis and colleagues (2012) found a lack of evidence for high levels of carcass utilization in the American lion (*Panthera atrox*) and saber-toothed cat (*Smilodon fatalis*). Schmitt (2011) refuted the 'tough times' hypothesis for dire wolves (*Canis dirus*), who exhibited wear less complex than the African wild dog (*Lycaon pictus*), which engages in scavenging behavior and bone consumption. DeSantis and co-authors (2012) suggest that instead, high incidences of broken teeth were inflicted during the acquisition of larger prey abundant on Pleistocene landscapes. Collectively, there is no evidence through dental microwear analyses that *Arctodus simus* engaged in durophagous scavenging behavior, further questioning 'tough times' at Rancho La Brea and the idea that this giant bear was a bone crushing hyper-scavenger throughout its range.

**Implications for future studies**

This foundational work assessing dental microwear textures of Ursidae will allow for future dietary assessment of extinct and extant ursids. Dental microwear can be used to assess dietary patterns and habits of historic and living bear populations, and may offer insight into dietary responses to anthropogenic caused environmental changes. For example, the diet of *Ursus maritimus* is predicted to change as climate warms, since these bears rely on Arctic sea ice to hunt. Because scavenging is associated with high complexity values, it may be possible to assess whether increased scavenging by *U maritimus* is associated with reduction of Arctic ice sheets, as noted by Bentzen and colleagues (2007), or whether terrestrial food sources are accessed during the summer. Dietary assessment can also be made in

numerous extinct ursids, in addition to *Arctodus simus*, including the Pleistocene European cave bear (*Ursus spelaeus*) and the abundant tremarctine short-faced bear species present in North and South America during the Pleistocene.

Dietary assessment of ursids through deep time can offer insights into the adaptive advantages gained through evolving from a dietary specialist to a generalist.  In particular, Ursidae offers a unique opportunity to assess dietary change during an evolutionary radiation event (~4–6 Ma).  Continued research in dietary assessment of past species has the potential to bring further understanding to the complex linkages between diet and evolution in mammals.  This will ultimately aid in better understanding modern biodiversity through more accurate predictions of species responses to current and future climatic and environmental changes.

PART V


CONCLUDING REMARKS


Collectively, this work demonstrates that dental microwear texture analysis can successfully differentiate subtle dietary variations within extinct and extant bear species, and serves as the foundational study for future investigations of dietary ecology in bears.  The lower first and second molars record dental microwear differently.  The m1 records a dietary signal clouded by the use of this tooth as a tool during food acquisition, and the m2 produces an informative dietary signal.  More specifically, the dental microwear attributes of anisotropy and complexity in the m2 serve to best distinguish diet, with texture fill volume being secondarily important. *Ailuropoda melanoleuca*, the specialist bamboo forager, was differentiated from all modern bears based on high and variable *epLsar* values, and low, constrained *Asfc* values. The carnivorous *Ursus maritimus* and omnivorous *U. americanus* have high and variable *Asfc* data relative to *A. melanoleuca*, *Tremarctos ornatus* and *U. malayanus,* bears that consume a higher proportion of soft, tough vegetation.

Arctodus simus exhibits wear most similar to *T. ornatus*, indicating that this large bear was not crunching bone as a hyper-scavenger of carcasses; rather, vegetation served as an important dietary component.  This work further supports the notion that carnivorans at La Brea were not experiencing food-scarcity, at least not until their immediate demise.

APPENDIX A

LIST OF SAMPLED SPECIMENS

| Taxon | Specimen Number | Tooth | Location (extant) or Pit number (extinct[†]) |
|---|---|---|---|
| *Ailuropoda melanoleuca* | NMNH 258423 | m1 | China |
| *Ailuropoda melanoleuca* | NMNH 258425 | m1 | China |
| *Ailuropoda melanoleuca* | NMNH 258834 | m1 | China |
| *Ailuropoda melanoleuca* | NMNH 258835 | m1 | China |
| *Ailuropoda melanoleuca* | NMNH 258836 | m1 | China |
| *Ailuropoda melanoleuca* | NMNH 259027 | m1 | China |
| *Ailuropoda melanoleuca* | NMNH 259028 | m1 | China |
| *Ailuropoda melanoleuca* | NMNH 259029 | m1 | China |
| *Ailuropoda melanoleuca* | NMNH 259074 | m1 | China |
| *Ailuropoda melanoleuca* | NMNH 259075 | m1 | China |
| *Ailuropoda melanoleuca* | NMNH 259076 | m1 | China |
| *Ailuropoda melanoleuca* | NMNH 259400 | m1 | China |
| *Ailuropoda melanoleuca* | NMNH 259401 | m1 | China |
| *Ailuropoda melanoleuca* | NMNH 259402 | m1 | China |
| *Ailuropoda melanoleuca* | NMNH 399447 | m1 | China |
| *Arctodus simus*[†] | LACMHC 1292 | m1 | Pit 77 |
| *Arctodus simus*[†] | LACMHC 401 | m1 | Pit 77 |
| *Arctodus simus*[†] | LACMHC 57520 | m1 | Pit unknown |
| *Arctodus simus*[†] | LACMHC 57521 | m1 | Pit unknown |
| *Arctodus simus*[†] | LACMHC 618 | m1 | Pit 9 |
| *Arctodus simus*[†] | LACMHC 619 | m1 | Pit 9 |
| *Arctodus simus*[†] | LACMHC 626 | m1 | Pit 9 |
| *Arctodus simus*[†] | LACMHC 86 | m1 | Pit 9 |
| *Arctodus simus*[†] | LACMHC 88 | m1 | Pit 9 |
| *Arctodus simus*[†] | LACMHC 90 | m1 | Pit 9 |
| *Arctodus simus*[†] | LACMHC 52234 | m1 | Pit 91 |
| *Arctodus simus*[†] | LACMHC Z-19 | m1 | Pit unknown |
| *Arctodus simus*[†] | LACMHC Z-7 | m1 | Pit unknown |
| *Arctodus simus*[†] | LACMHC Z-8 | m1 | Pit unknown |
| *Arctodus simus*[†] | LACMHC Z-9 | m1 | Pit unknown |
| *Tremarctos ornatus* | AMNH 149032 | m1 | Columbia |
| *Tremarctos ornatus* | AMNH 67732 | m1 | Ecuador |
| *Tremarctos ornatus* | AMNH 99308 | m1 | Peru |
| *Tremarctos ornatus* | NMNH 155575 | m1 | Venezuela |
| *Tremarctos ornatus* | NMNH 168115 | m1 | Venezuela |

| | | | |
|---|---|---|---|
| *Tremarctos ornatus* | NMNH 170656 | m1 | Venezuela |
| *Tremarctos ornatus* | NMNH 170657 | m1 | Venezuela |
| *Tremarctos ornatus* | NMNH 171011 | m1 | Venezuela |
| *Tremarctos ornatus* | NMNH 194309 | m1 | Peru |
| *Tremarctos ornatus* | NMNH 210321 | m1 | Ecuador |
| *Tremarctos ornatus* | NMNH 210322 | m1 | Ecuador |
| *Tremarctos ornatus* | NMNH 210323 | m1 | Ecuador |
| *Tremarctos ornatus* | NMNH 210324 | m1 | Ecuador |
| *Tremarctos ornatus* | NMNH 271418 | m1 | Bolivia |
| *Tremarctos ornatus* | NMNH 582002 | m1 | Unknown |
| *Ursus americanus* | NMNH 176594 | m1 | Alaska |
| *Ursus americanus* | NMNH 177657 | m1 | Alaska |
| *Ursus americanus* | NMNH 177659 | m1 | Alaska |
| *Ursus americanus* | NMNH 180277 | m1 | Alaska |
| *Ursus americanus* | NMNH 231506 | m1 | Alaska |
| *Ursus americanus* | NMNH 231507 | m1 | Alaska |
| *Ursus americanus* | NMNH 231509 | m1 | Alaska |
| *Ursus americanus* | NMNH 231510 | m1 | Alaska |
| *Ursus americanus* | UF 13875 | m1 | Florida |
| *Ursus americanus* | UF 13876 | m1 | Florida |
| *Ursus americanus* | UF 28416 | m1 | Florida |
| *Ursus americanus* | UF 28423 | m1 | Florida |
| *Ursus americanus* | UF 28436 | m1 | Florida |
| *Ursus americanus* | UF 28445 | m1 | Florida |
| *Ursus americanus* | UF 28449 | m1 | Florida |
| *Ursus americanus* | UF 6496 | m1 | Florida |
| *Ursus malayanus* | NMNH 123138 | m1 | Unknown |
| *Ursus malayanus* | NMNH 151866 | m1 | Unknown |
| *Ursus malayanus* | NMNH 197254 | m1 | Malay Peninsula |
| *Ursus malayanus* | NMNH 198713 | m1 | Malay Peninsula |
| *Ursus malayanus* | NMNH 198714 | m1 | Malay Peninsula |
| *Ursus malayanus* | NMNH 198715 | m1 | Malay Peninsula |
| *Ursus malayanus* | NMNH 358645 | m1 | Malay Peninsula |
| *Ursus maritimus* | NMNH 212589 | m1 | Alaska |
| *Ursus maritimus* | NMNH 212590 | m1 | Alaska |
| *Ursus maritimus* | NMNH 215714 | m1 | Alaska |
| *Ursus maritimus* | NMNH 227099 | m1 | Alaska |
| *Ursus maritimus* | NMNH2 27105 | m1 | Alaska |
| *Ursus maritimus* | NMNH 265099 | m1 | Alaska |
| *Ursus maritimus* | NMNH 512111 | m1 | N. Hudson Bay |
| *Ursus maritimus* | NMNH 512113 | m1 | N. Hudson Bay |

| | | | |
|---|---|---|---|
| *Ursus maritimus* | NMNH 512117 | m1 | N. Hudson Bay |
| *Ursus maritimus* | NMNH 512121 | m1 | N. Hudson Bay |
| *Ursus maritimus* | NMNH 512130 | m1 | N. Hudson Bay |
| *Ursus maritimus* | NMNH 512133 | m1 | N. Hudson Bay |
| *Ursus maritimus* | NMNH 512136 | m1 | N. Hudson Bay |
| *Ursus maritimus* | NMNH 512151 | m1 | N. Hudson Bay |
| *Ursus maritimus* | NMNH 512163 | m1 | N. Hudson Bay |
| *Ailuropoda melanoleuca* | NMNH 258423 | m2 | China |
| *Ailuropoda melanoleuca* | NMNH 258425 | m2 | China |
| *Ailuropoda melanoleuca* | NMNH 258834 | m2 | China |
| *Ailuropoda melanoleuca* | NMNH 258836 | m2 | China |
| *Ailuropoda melanoleuca* | NMNH 259027 | m2 | China |
| *Ailuropoda melanoleuca* | NMNH 259028 | m2 | China |
| *Ailuropoda melanoleuca* | NMNH 259074 | m2 | China |
| *Ailuropoda melanoleuca* | NMNH 259076 | m2 | China |
| *Ailuropoda melanoleuca* | NMNH 259401 | m2 | China |
| *Ailuropoda melanoleuca* | NMNH 259402 | m2 | China |
| *Ailuropoda melanoleuca* | NMNH3 99447 | m2 | China |
| *Arctodus simus*[†] | LACMHC 1292 | m2 | Pit 17 |
| *Arctodus simus*[†] | LACMHC 401 | m2 | Pit 77 |
| *Arctodus simus*[†] | LACMHC 57514 | m2 | Pit unknown |
| *Arctodus simus*[†] | LACMHC 57520 | m2 | Pit unknown |
| *Arctodus simus*[†] | LACMHC 57521 | m2 | Pit 9 |
| *Arctodus simus*[†] | LACMHC 618 | m2 | Pit 9 |
| *Arctodus simus*[†] | LACMHC 619 | m2 | Pit 9 |
| *Arctodus simus*[†] | LACMHC 626 | m2 | Pit 9 |
| *Arctodus simus*[†] | LACMHC 86 | m2 | Pit 9 |
| *Arctodus simus*[†] | LACMHC 88 | m2 | Pit 9 |
| *Arctodus simus*[†] | LACMHC 89 | m2 | Pit 9 |
| *Arctodus simus*[†] | LACMHC 90 | m2 | Pit 91 |
| *Arctodus simus*[†] | LACMHC 52234 | m2 | Pit unknown |
| *Arctodus simus*[†] | LACMHC Z-19 | m2 | Pit unknown |
| *Arctodus simus*[†] | LACMHC Z-7 | m2 | Pit unknown |
| *Arctodus simus*[†] | LACMHC Z-9 | m2 | Columbia |
| *Tremarctos ornatus* | AMNH 149302 | m2 | Ecuador |
| *Tremarctos ornatus* | AMNH 67732 | m2 | Peru |
| *Tremarctos ornatus* | AMNH 99308 | m2 | Venezuela |
| *Tremarctos ornatus* | NMNH 155575 | m2 | Venezuela |
| *Tremarctos ornatus* | NMNH 170656 | m2 | Venezuela |
| *Tremarctos ornatus* | NMNH 171011 | m2 | Ecuador |
| *Tremarctos ornatus* | NMNH 210321 | m2 | Ecuador |

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| *Tremarctos ornatus* | NMNH 210323 | m2 | Ecuador |
| *Tremarctos ornatus* | NMNH 210324 | m2 | Bolivia |
| *Tremarctos ornatus* | NMNH 271418 | m2 | Unknown |
| *Tremarctos ornatus* | NMNH 582002 | m2 | Alaska |
| *Ursus americanus* | NMNH 177657 | m2 | Alaska |
| *Ursus americanus* | NMNH 177659 | m2 | Alaska |
| *Ursus americanus* | NMNH 180277 | m2 | Alaska |
| *Ursus americanus* | NMNH 231506 | m2 | Alaska |
| *Ursus americanus* | NMNH 231507 | m2 | Alaska |
| *Ursus americanus* | NMNH 231509 | m2 | Alaska |
| *Ursus americanus* | NMNH 231510 | m2 | Florida |
| *Ursus americanus* | UF 13875 | m2 | Florida |
| *Ursus americanus* | UF 13876 | m2 | Florida |
| *Ursus americanus* | UF 28416 | m2 | Florida |
| *Ursus americanus* | UF 28423 | m2 | Florida |
| *Ursus americanus* | UF 28436 | m2 | Florida |
| *Ursus americanus* | UF 28445 | m2 | Florida |
| *Ursus americanus* | UF 28449 | m2 | Florida |
| *Ursus americanus* | UF 6496 | m2 | Unknown |
| *Ursus malayanus* | NMNH 123138 | m2 | Unknown |
| *Ursus malayanus* | NMNH 151866 | m2 | Malay Peninsula |
| *Ursus malayanus* | NMNH 197254 | m2 | Malay Peninsula |
| *Ursus malayanus* | NMNH 198713 | m2 | Malay Peninsula |
| *Ursus malayanus* | NMNH 198715 | m2 | Malay Peninsula |
| *Ursus malayanus* | NMNH 358645 | m2 | Alaska |
| *Ursus maritimus* | NMNH 212589 | m2 | Alaska |
| *Ursus maritimus* | NMNH 212590 | m2 | Alaska |
| *Ursus maritimus* | NMNH 215714 | m2 | Alaska |
| *Ursus maritimus* | NMNH 227099 | m2 | Alaska |
| *Ursus maritimus* | NMNH 227105 | m2 | Alaska |
| *Ursus maritimus* | NMNH 265099 | m2 | Alaska |
| *Ursus maritimus* | NMNH 336269 | m2 | N. Hudson Bay |
| *Ursus maritimus* | NMNH 512111 | m2 | N. Hudson Bay |
| *Ursus maritimus* | NMNH 512113 | m2 | N. Hudson Bay |
| *Ursus maritimus* | NMNH 512117 | m2 | N. Hudson Bay |
| *Ursus maritimus* | NMNH 512121 | m2 | N. Hudson Bay |
| *Ursus maritimus* | NMNH 512130 | m2 | N. Hudson Bay |
| *Ursus maritimus* | NMNH 512133 | m2 | N. Hudson Bay |
| *Ursus maritimus* | NMNH 512136 | m2 | N. Hudson Bay |
| *Ursus maritimus* | NMNH 512151 | m2 | N. Hudson Bay |
| *Ursus maritimus* | NMNH 512163 | m2 | N. Hudson Bay |

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