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Differentiating Black Bears (Ursus americanus) and Brown Bears (U. arctos) using Linear Tooth Measurements and Identification of Ursids from Oregon Caves National Monument

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Differentiating Black Bears (*Ursus americanus*) and Brown Bears (*U. arctos*)

using Linear Tooth Measurements and Identification of

Ursids from Oregon Caves National Monument

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by

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ABSTRACT

Differentiating Black Bears (*Ursus americanus*) and Brown Bears (*U. arctos*)

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North American black bears and brown bears can be difficult to distinguish in the fossil record due to similar dental and skeletal morphologies. Challenges identifying ursid material from Oregon Caves National Monument (ORCA) called for an accurate tool to distinguish the species. This study utilized a large database of lower tooth lengths and ratios in an attempt to differentiate black and brown bears in North America. Further, this project examined how these linear measurements differ in response to ecoregion, latitude, and climate. Analysis of variance (ANOVA) found significant differences between black and brown bears from across North America for every variable studied. Stepwise discriminant analyses (DA) found lengths separated species better than ratios. When sexes were analyzed, ANOVA only found significant differences for lengths while DA found lengths and ratios could not accurately distinguish between sexes. Fossil specimens from across North America, including an ORCA specimen, demonstrated the utility of this study, supporting several identifications and questioning others.

ACKNOWLEDGEMENTS

I would like to thank Dr. Timothy Heaton and Oregon Caves National Monument staff, Mary Merryman, John Roth, and Ivan Yates for providing crucial resources which this thesis is founded on. I am especially grateful for my committee: Drs. Blaine Schubert, Joshua Samuels, and Chris Widga for their guidance and patience throughout the course of this project and the Center of Excellence in Paleontology. Drs. Greg McDonald and Alexis Mychlaw were especially kind for lending specimens from their research. Additionally, thanks to the National Museum of Natural History (Smithsonian) for allowing me to visit and research their collections. Thanks to Dr. Jim Mead for providing background information regarding the collection and treatment of specimens from Oregon Caves, Dr. Andrew Joyner for assistance with the creation of map figures, April Nye and collections staff for making sure I had everything I needed while researching at the Gray Fossil Site, and Keila Bredehoeft for assisting with the cleaning and stabilization of Oregon Caves fossil material. For advice and emotional support I would like to acknowledge Julia Schap and Emily Bruff Simpson.

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CHAPTER 1

INTRODUCTION

This thesis is composed of interlinked components working together to assess the question: can two of the most widespread bears in North American, the black bear (*Ursus americanus*) and brown bear (*U. arctos*), be distinguished by the length of their lower cheek teeth? Further, do these species vary in dental proportions over their extensive ranges? This project began by assessing fossil bear material from Oregon Caves National Monument (ORCA) and recognition of the difficulties in distinguishing if the specimens were *U. americanus* or *U. arctos*. These fossils, consisting of cranial, dental, and postcranial remains, had yet to be described in detail or identified taxonomically. The ORCA fossils and their uncertain identity provided the backdrop of this thesis.

To assess the identification of the bears from ORCA a large database of lower tooth lengths from *U. americanus* and *U. arctos* was analyzed. The primary comparative data set was collected by Dr. Timothy Heaton, is unpublished, and is used here with permission. Additional measurements made by the author capture geographic areas not represented in Heaton's data and the two datasets combined were used in an attempt to statistically separate modern *U. americanus* and *U. arctos*. The first question was whether or not he two species could be separated based on these, and if so, what ursid taxon or taxa are represented at ORCA? Finally, the dataset was used to compare tooth size over the geographic ranges of *U. americanus* and *U. arctos* to assess dental variation in light of ecoregion, latitude, climate, sex, and potential competition.

CHAPTER 2

BACKGROUND

Oregon Caves National Monument

In the paleontological record, caves act as time capsules for speleothems, sediments, and fossils. These non-renewable resources can contain vast amounts of information regarding paleoclimates, paleoecosystems, and establish a sequence of events (Schubert and Mead 2012). Oregon Caves National Monument (ORCA), located in the Siskiyou Mountains of Josephine County, Oregon (Figure 1), represents such a site, and can help fill in gaps of the Pacific Northwest's relatively sparse Pleistocene ursid fossil record. Caves along the Pacific west coast are known to be good repositories for vertebrate fossils (Sinclair 1905; Furlong 1906; Stock 1918; Mead et al. 2006; Feranec et al. 2007); however, these occur south of the Siskiyou mountains where ORCA is located. Thus, any prehistoric record from this region is noteworthy.

Research projects focusing on various aspects of the fauna at ORCA are underway by Drs. Greg McDonald, Kevin Seymour, and Jim Mead, focusing on the descriptions of *Ursus arctos*, jaguar (*Panthera* sp.), and salamander (Caudata) material, respectively; however, none have been formally published. Bears are the most common large mammal fossils recovered throughout ORCA with over 50 elements extracted from the cave between June 1997 and May 2000 (Jim Mead Pers. Comm., 2017). In spite of their abundance, the ursid remains at ORCA have not been fully identified and analyzed. This project focuses, in part, on identifying, describing, and cataloging the bears from ORCA. Descriptions include: skeletal part representation, taphonomy, age and sex demographics, and minimum number of individuals.

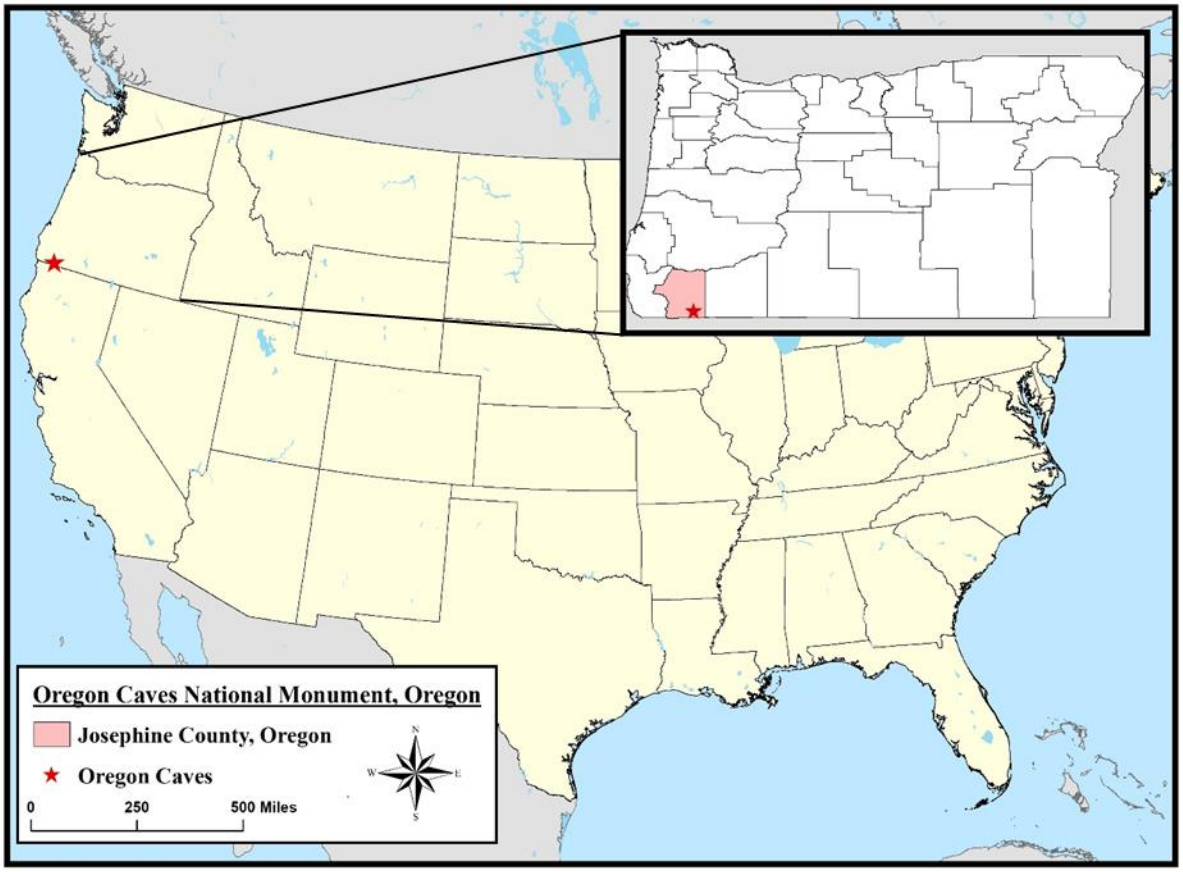


Figure 1. Location of Oregon Caves National Monument in relation to the United States and Josephine County, Oregon.

ORCA contains a diverse array of Quaternary fauna (Figures 2 & 3), including: amphibians, reptiles, birds, small mammals in the form of rodents and bats, and large mammals such as deer, bobcats, jaguars, and bears. At least some of these remains are considered to be Pleistocene, but no radiocarbon dates have been reported yet. According to the Faunmap database (Graham and Lundelius 2010), ORCA is one of four published Pleistocene sites in Oregon, with Fort Rock Cave, Fossil Lake, and La Grande being the others. Five Pleistocene localities are reported for Washington, and 20 for California; however, none of these fossil sites are located in the Siskiyou Mountains, a subunit of the Klamath Mountains, leaving a large gap in Pleistocene biotic community data for this region. The high diversity of both fauna (50,000 species) and flora (3,800 species) in these mountains today is supported by the variety of climatic and geologic conditions (Schubert 2007). Thus, achieving a better understanding of this ecologically diverse area requires a deeper understanding of the Quaternary biotic record.

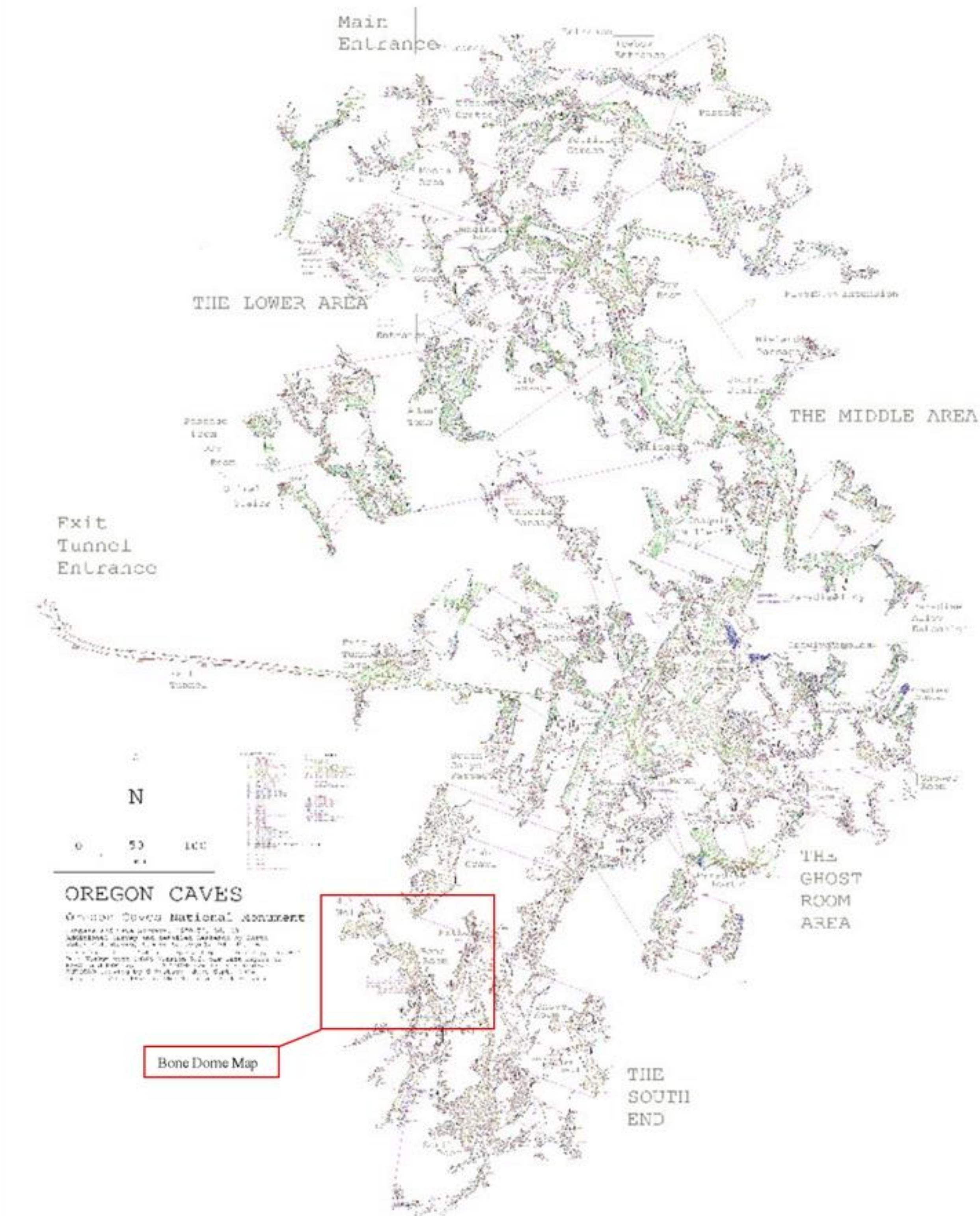


Figure 2. Mapped passageways of Oregon Caves National Monument span over three miles. Highlighted is the 'Bone Dome' where a majority of specimens were recovered. Map courtesy of Oregon Caves National Monument.

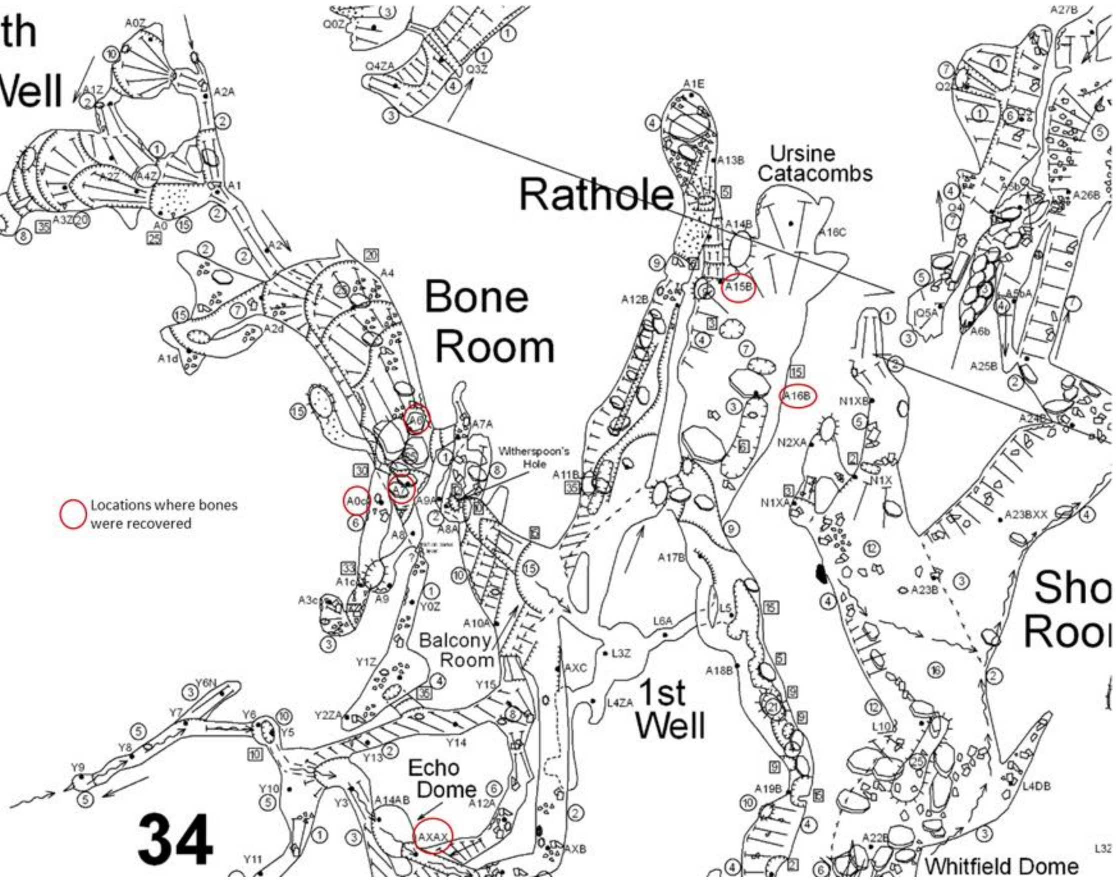


Figure 3. A section of ORCA named the Bone Room where a majority of the fossil ursids were recovered (specific locations circled in red). Map courtesy of Oregon Caves National Monument.

<u>Ursid Family History</u>

The Ursinae subfamily is relatively young, only thought to have diverged from a dog-like ancestor in the early Miocene (~19MA) (Kurtén 1976; Hunt 1998; Krause et al. 2008; Eizerik et al. 2010; Nyakatura and Bininda-Emonds 2012). Early ursids were small, however, a general trend increasing in size for most species continued into the early Holocene (Kurtén 1968; Kurtén and Anderson 1980). While ursids increased in body size their posterior molars became larger as well, leading to a more omnivorous diet (Kurtén 1968; Kurtén and Anderson 1980; Wang et al. 2017).

The genus *Ursus* arose during the early Pliocene, with the oldest fossil dating to ~3.5MA (Kurtén and Anderson 1980; Krause et al. 2008; Nyakatura and Bininda-Emonds 2012). *Ursus minimus*, an early species in the *Ursus* lineage, was small, roughly the size of an Asiatic black bear (*U. thibetanus*) (Kurtén 1968; Krause et al. 2008; Nyakatura and Bininda-Emonds 2012). The general trend towards an increase in body size continued with *U. etruscus*, a slightly younger species in the *Ursus* lineage, and by the time *U. etruscus* went extinct it was roughly the size of *U. arctos* (Kurtén 1968). Throughout *U. etruscus'* reign, the species' dentition became more specialized for omnivory; the M2 and m3 elongated for a larger grinding surface, the carnassials evolved from having a specialized blade to looking more similar in appearance to the posterior molars, and the premolars reduced in size (Kurtén 1968). *Ursus etruscus* is the last bear in the genus *Ursus* to retain all its premolars; during the middle Pleistocene other species began to lose some of their premolars altogether (Kurtén 1968).

The oldest North American fossils attributed to *U. americanus* are from Port Kennedy Cave (Pennsylvania) and date to ~325,000 years ago (Kurtén 1963; Herrero 1971). The *U. americanus* found at Port Kennedy Cave are larger in size compared to earlier forms but still retain somewhat blade-like carnassials and a smaller M2 and m3, similar to earlier forms (Kurtén 1980). It later in the Pleistocene when a gradual reduction in the slicing capability of the carnassials is observed and the cheek teeth expand in size to have a larger grinding surface (Kurtén 1980). *Ursus arctos* is estimated to have diverged around 2MA (Krause et al. 2008) and dispersed into North America ~30,000 years ago at the earliest (Matheus et al. 2004). The oldest fossils of *U. arctos* date to ~500,000 years ago from China (Kurtén 1968; Pasitschniak-Arts 1993)

Historically, *U. americanus* had a large range spanning across North America *and U. arctos* was more widespread in western and central North America than they are found today (Pasitschniak-Arts 1993; Larivière 2001). However, in part due to being two of the largest terrestrial predators (Orr 1971) and the expansion of human civilizations, *U. americanus* and *U. arctos* have recently lost considerable amounts of their previously vast ranges (Ewer 1973). Today, *U. americanus* is the only ursid found in the eastern United States (Hamilton and Whitaker 1979), but are more broadly found across the contiguous United States, Alaska, every province and territory in Canada, and northern parts of Mexico (Ewer 1973; Craighead and Mitchell 1982; Larivière 2001). *Ursus arctos* can be found in the United States west of the Great Plains, Alaska, Alberta, British Columbia, Yukon, and Northwestern territories of Canada (Orr 1971; Ewer 1973; Pasitschniak-Arts 1993).

Ursid Characteristics

All ursids have molars with an enlarged surface area, reduced premolars, are plantigrade, and have five toes on each foot (Kurtén 1980). The Ursinae subfamily have a long and slender skull, elongate molars, and reduced premolars (Kurtén 1980). Two Ursidae subfamilies are present in North America during the Pleistocene, Ursinae and Tremarctinae (Kurtén 1980). Tremarctines can be distinguished from Ursinae by the retention of all premolars and possession of a premasseteric fossa (Kurtén 1980). Additionally, an accessory cusp on the m1 between the trigonid and talonid also separate this subfamily from Ursinae (Kurtén 1980). Ancestral ursids can be distinguished from modern forms by the retention of a specialized carnassial, retention of premolars one through three, no posterior elongation of M2 or m3, short rostrum, flat forehead above the orbit, and high sagittal crest (Hunt 1998; Wang et al. 2017).

Ursids have a wide range of diets, including hypercarnivores, herbivores, insectivores, and omnivores. Because *U. arctos* and *U. americanus* are omnivorous, their carnassials have been secondarily modified to be less blade-like (Elbroch 2006), meaning the carnassials and post carnassials do not differ much in shape (Ungar 2010). Their carnassials instead, are developed for powerful crushing with a broad and relatively flat surface (Hunt 1998; Elbroch 2006). Additionally, *U. americanus* and *U. arctos* have bunodont dentition (Chapman and Feldhamer 1982), highly reduced premolars, and a dental formula of: I3/3, C1/1, P4/4, and M2/3 (Hunt 1998; Ungar 2010). In both species, the premolars are highly reduced, and one or more may be absent in some individuals (Hall and Kelson 1959; Hunt 1998; Ungar 2010). *Ursus americanus* and *U. arctos* differ in the shape of their face; *U. arctos* has a more dished-shaped profile and *U. americanus* has a more concave profile (Pasitschniak-Arts 1993; Larivière 2001). Additionally, *U. arctos* has the presence of a shoulder hump, which *U. americanus* lacks, and longer claws on its forepaws than hindpaws and *U. americanus* has roughly equal length claws on each paw (Pasitschniak-Arts 1993; Larivière 2001). Most commonly observed, *U. arctos* is larger and has a light to dark brown coat while *U. americanus'* color is most commonly black, but can range in shade and variation depending on geographic locality (Pasitschniak-Arts 1993; Larivière 2001).

Variation & Identification

Distinguishing between *U. americanus* and *U. arctos* in the fossil record can be a difficult task (Gordon 1977; Graham 1991; Pasitschniak-Arts 1993; Lariviere 2001). Morphologically, their osteological anatomy is strikingly similar and the features biologists use to identify living ursids are not easily applied in the fossil record. For example, the claws, presence of a shoulder hump, body size, and pelage color are some of the most readily available ways to distinguish between the two species, but are all features which do not readily preserve in the fossil record

(Pasitschniak-Arts 1993; Lariviere 2001). Geographic size and shape variability in *U. arctos* and *U. americanus* can make it especially difficult to differentiate between the two species (Elbroch 2006) and size differentiation alone is not reliable as a means to distinguish between the two species in the fossil record, because during the Pleistocene *U. americanus* is thought to have been comparable in size to *U. arctos* (Kurtén 1963; Kurtén and Anderson 1980; Graham 1991; Wolverton and Lyman 1996).

Sexual size dimorphism is present in all extant North American ursids, with males being larger than females (McDonough and Christ 2012). Size varies throughout ranges, so a large male *U. americanus* can look like small female *U. arctos* and vice versa. According to Rausch (1953), geographic variation is so extreme in *U. arctos* that if there was a skull of a specimen with unknown origin it would be virtually impossible to determine the sex based on cranial measurements. In *U. americanus*, the permanent cheek teeth begin erupting around three months of age (Miller et al. 2009) and sexual size dimorphism is not likely to be observed within the cheek teeth because they form before endocrine factors can take effect (Polly 1998; Miller et al. 2009). *Ursus americanus* teeth that do give indications of sex are the canines, as these teeth do not erupt until 15 months of age, after endocrine factors have started to kick in (Miller et al. 2009).

Dental Variation

It is important to know the extent of variation within a population because that helps differentiate one species from another (Dayan et al. 2002; Wolsan et al. 2015). Wolsan et al. (2015) stated, “No characterization of a taxon, population, organism, or organ can be complete without characterizing its variation.” In large population studies, variation may be evident in the form of extreme variants in one direction or another or bimodal distributions such as sexual dimorphism (Gingerich 1974). Although ursids are one of the most studied carnivoran families (Krause et al. 2008), variation in their tooth size has not been examined extensively (Miller et al. 2009; Wolsan et al. 2015).

In the fossil record, teeth are commonly the most well preserved element, containing critical information allowing for the study of variation within a species (Gingerich 1974; Dayan et al. 1993; Polly 1998; Dayan et al. 2002; Meiri et al. 2005; Wolsan et al. 2015). Variation between two closely related species can often be found in dental morphology (Gingerich 1974; Wolsan et al. 2015). Tooth size is genetic and in mammals without ever-growing teeth, once a permanent tooth is formed it does not grow or remodel thereafter so phenotypic plasticity is limited to prenatal development (Gingerich 1974; Daitch and Guralnick 2007; Miller et al. 2009; McDonough and Christ 2012; Wolsan et al. 2015). Some teeth are less variable in size than others and teeth that erupt earlier in an individual are less variable than teeth that erupt later in life (Gingerich 1974; Polly 1998). For instance, the M1/m1 develop first and are therefore the least variable and most useful teeth when identifying some species (Polly 1998; Wolsan et al. 2015). For example, Gingerich and Winkler (1979) found the carnassials (P4 and m1) of red foxes (*Vulpes vulpes*) showed the least amount of variation. While the M1 and m1 generally have the least amount of variation, the p4 and m2 have higher coefficients of variation (Gingerich 1974). Gingerich (1974) noted that the lengths of the M1 and m1 are the most indicative dental measurements that can be used to distinguish between two sympatric species within the same genus.

Some carnivorans show geographic variation in the size and morphology of their cheek teeth. Miller et al. (2009) stated there is the potential for geographic variability in *U. americanus* molars depending on dietary differences when they are allopatric or sympatric with *U. arctos*. In carnivorans with a specialized diet, there is less intraspecific variation and higher interspecific correlations with tooth size (Miller et al. 2009). Conversely, in animals without a specialized diet, such as the omnivorous *U. americanus* and *U. arctos*, there are higher amounts of intraspecific variability and weaker interspecific correlations with tooth size (Miller et al. 2009). Additionally, teeth in the middle of a tooth row are less variable. And teeth more in the front or back of the row are more variable because they are less constrained (Wolsan et al. 2015).

There is a high degree of dental variation present in bears. In ursids, the P4 is smaller in size compared to M1 and M2 and is triangular, broad, and flat with a posterior-placed protocone (Ungar 2010). The M1 has an enlarged talonid and between the talonid and trigonid there are accessory cusps (Ungar 2010). Most molars are broad and flat with a central valley and tubercular crowns lining the edges (Hall and Kelson 1959; Ungar 2010). According to some researchers, the P4 in *U. americanus* does not have "medial accessory cusps or medial anteroposterior sulcus on posterior part" whereas these features are variably present in *U. arctos* (Hall and Kelson 1959; Elbroch 2006; Gilbert 1980). The m1 in *U. americanus* typically lacks cusps in the valley between the entoconid and metaconid; at least one cusp is present in *U. arctos* (Hall and Kelson 1959). It is important to note that Graham (1991) has found *U. americanus* specimens (ISM 691875) with accessory cusps on the p4 and m1 and *U. arctos* specimens (ISM 69051) without these cusps and various combination of the presence or absence of these cusps are observed in both species (Gordon 1977; Graham 1991). In *U. americanus*, the m2 is typically widest halfway between the anterior and posterior of the tooth while in *U. arctos*, the widest section is at the anterior end (Hall and Kelson 1959; Elbroch 2006; Graham 1991). Because of the similarities and variation between the two species teeth, it can be quite difficult to distinguish between *U. americanus* and *U. arctos* if the teeth are heavily worn or broken (Craighead and Mitchell, 1982).

Ursus americanus and *U. arctos* are common in the North American fossil record and occasionally are found at the same fossil site (Kurtén and Anderson 1980; Graham and Lundelius 2010). Morphologically, the bones of *U. arctos* and *U. americanus* are very similar and diagnostic features to separate the two species are lacking (Gordon 1977; Gilbert 1990; Graham 1991; Pasitschniak-Arts 1993; Larivière 2001). In sum, *U. americanus* and *U. arctos* are often difficult to distinguish in the fossil record, and there is a need for a reliable method to separate the two. Because teeth are the most preserved element at fossil sites, they provide the foundation of this study.

Geographic Variation

Understanding geographic variation of organism traits is important to ecology and evolutionary studies because it demonstrates the adaptive divergence within species (Mayr 1963). Bergmann's Rule is an assessment of morphological and environmental variation (Mayr 1956). The principle concept of Bergmann's Rule states the larger the endothermic vertebrate, the cooler the environment they will be found in. Mayr (1956; 1963) thought Bergmann's Rule represented variation within a species and ecogeographic rules only have validity at the intraspecific level. The majority of studies surrounding Bergmann's Rule rely on correlations of size versus latitude (Ashton et al. 2000). *Ursus americanus* and *Ursus arctos* are two of the most widespread bears across North America; understanding how they differ across their geographic range is important to note for differentiation in the fossil record.

CHAPTER 3

METHODS & MATERIALS

Abbreviations Used

AMNH (American Museum of Natural History), **ANOVA** (Analysis of Variance), **CIT** (California Institute of Technology), **ETSU** (East Tennessee State University), **LACM** (Los Angeles County Museum of Natural History), **MANCOVA** (Multivariate Analysis of Covariance), **OMNH** (Oklahoma Museum of Natural History), **ORCA** (Oregon Caves National Monument), **RBCM** (Royal British Columbia Museum), **DA** (Stepwise Discriminant Analysis), **UCMP** (University of California Museum of Paleontology), **UMNH** (Utah Museum of Natural History), **USNM** (Smithsonian Natural History Museum), **WSC** (Western Science Center). Uppercase is used for upper teeth (e.g., **M1**) and lowercase for lowers (e.g., **m1**).

Specimen Preparation

Ursid material from ORCA was identified to genus and where possible species level, grouped by element (differentiated to the right or left side if applicable), and ORCA catalog numbers were assigned. Some cleaning and preliminary preparation work on the bones was completed by Dr. Jim Mead's lab in the late 1990's and early 2000's, and PaleoBOND™ was applied on some specimens. A majority of the ursid bones have not received final cleaning and preparation work, but have been cleaned and stabilized by Keila Bredehoeft (ETSU) and the author using Butvar 76 and 98.

Specimen Data

For this study, length measurements of p4, m1, m2, and m3 from over 2,000 North American bears (*U. americanus*, n = 1,118; *U. arctos*, n = 959) were included (Figure 4 and 5). Data was collected for each species from the lower 48 states, Alaska, Canadian provinces and territories, and Mexico. For this, Dr. Timothy Heaton shared his ursid dental measurements (n = 1,642) and the author supplemented the data set (n = 431). Thirty individuals, originally measured by Dr. Heaton were measured again by the author to ensure techniques and results would be comparable. Only wild caught specimens with fully erupted dentition were chosen. Fossil specimens (n = 85) were measured by the author (n=1) and Dr. Alexis Mychajliw (n=74) who shared dental measurements for this study (Figure 6). Additional measurements of fossil specimens (n=10) were compiled from literature sources including: Gidley and Gazin (1938), Miller (1949), Kurtén (1963), Graham (1991). Table 1 summarizes the number of individuals used for each analysis. Measurements of extant and extinct specimens were gathered from the following collections: AMNH, CIT, ETSU, LACM, OMNH, ORCA, RBCM, UCMP, UMNH, USNM, WSC.

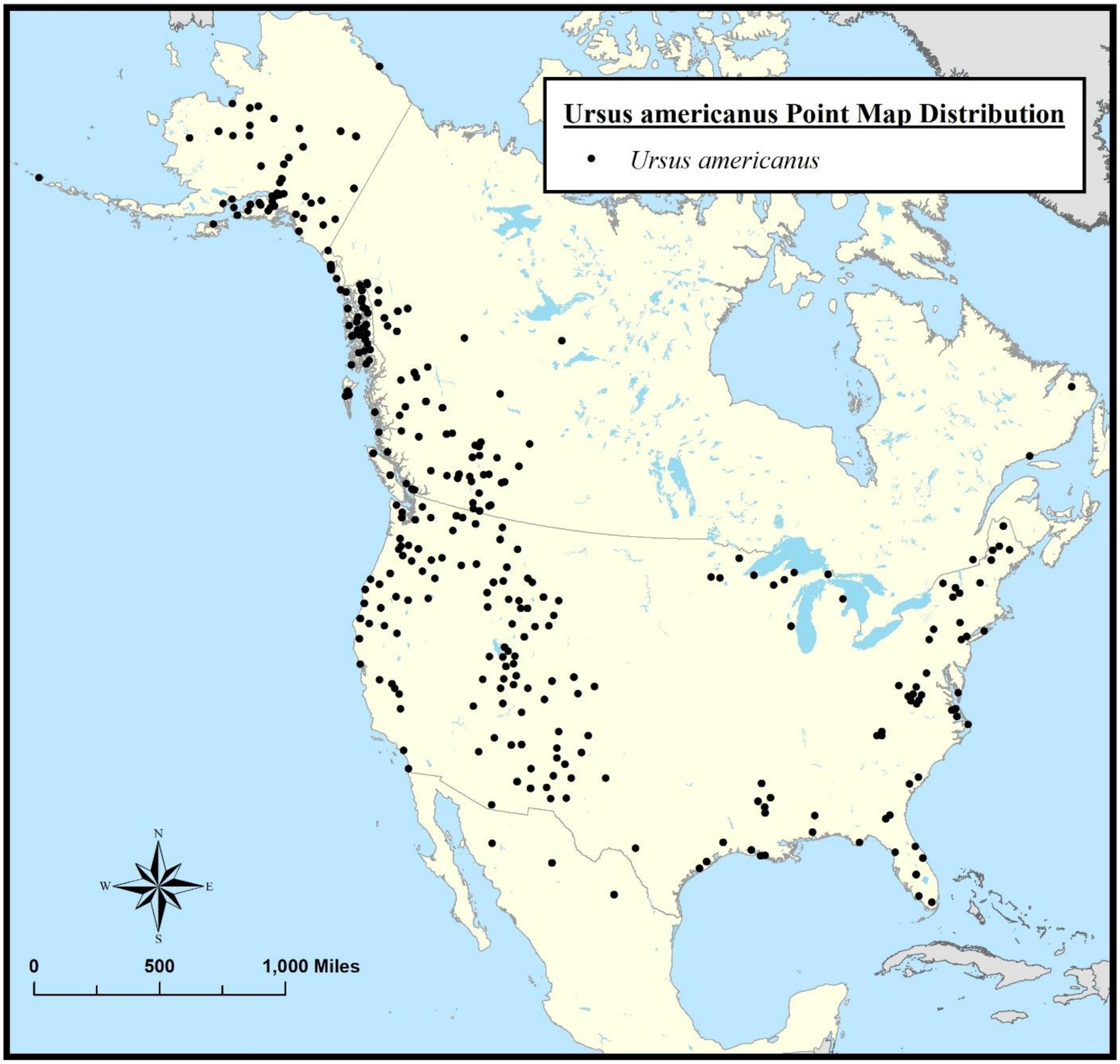


Figure 4. Locations of *Ursus americanus* specimens used in study.

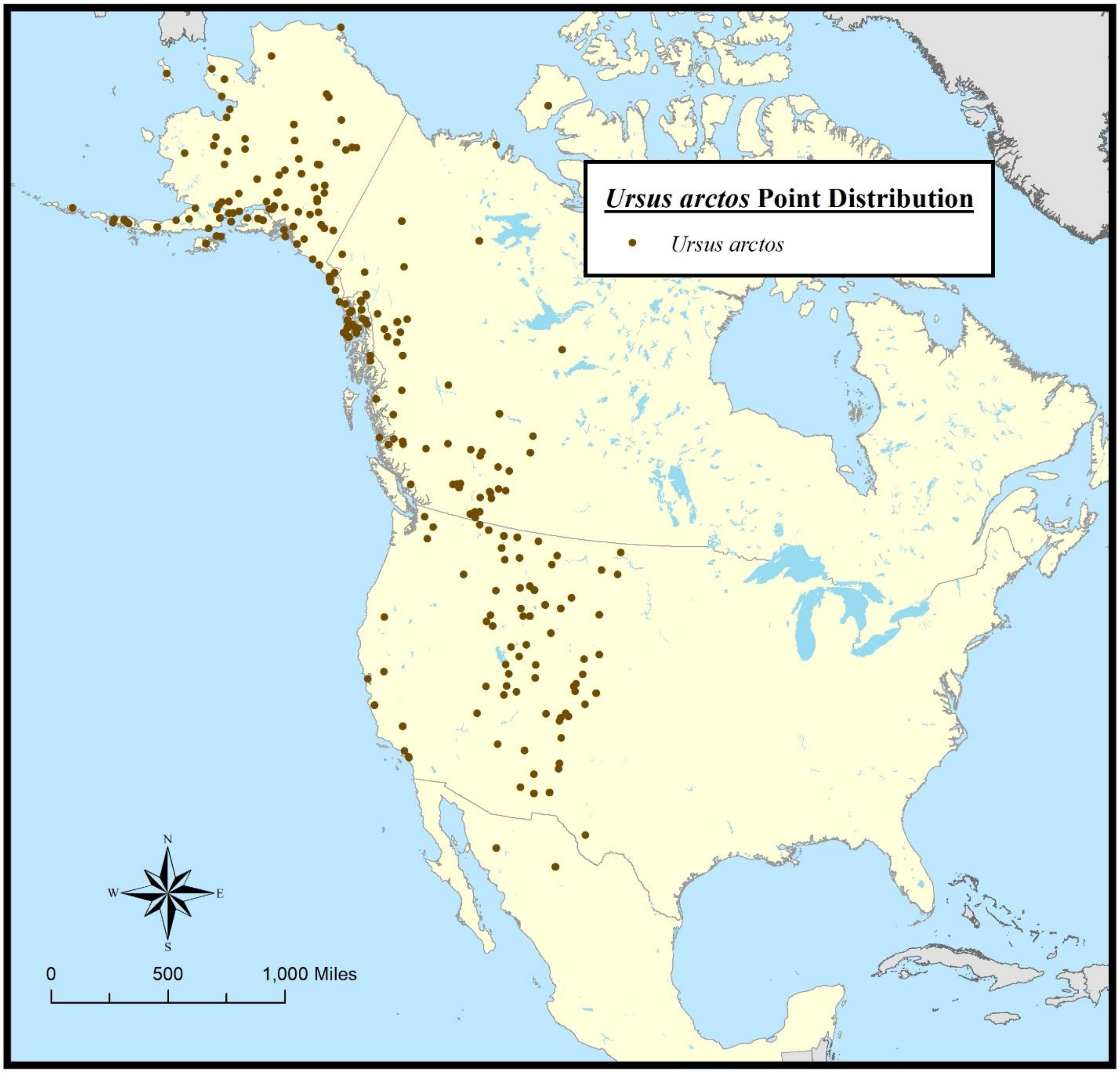


Figure 5. Locations of *Ursus arctos* specimens used in study.

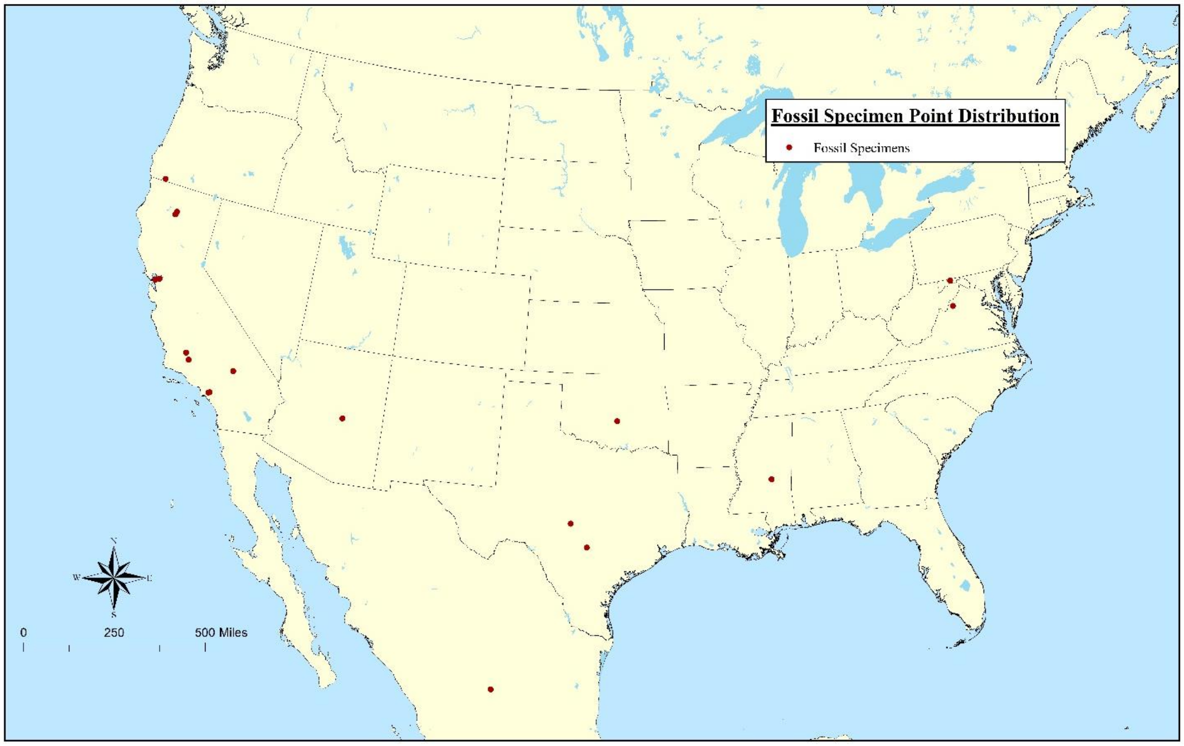


Figure 6. Locations of fossil specimens used in study.

Table 1. Number of individuals used for each study. Groups listed include: BB=Black Bear (*Ursus americanus*), GB=Brown Bear (*Ursus arctos*), FBB=Female Black Bear (*Ursus americanus*), MBB=Male Black Bear (*Ursus americanus*), FGB=Female Brown Bear (*Ursus arctos*), MGB=Male Brown Bear (*Ursus arctos*).

	BB	**GB**	**FBB**	**MBB**	**FGM**	**MGB**
Interspecific	1065	981	-	-	-	-
Intraspecific	-	-	270	422	209	330
Ecoregion 3	34	25	5	15	7	15
Ecoregion 6	354	205	102	68	141	95
Ecoregion 7	383	536	141	95	134	165
Ecoregion 9	24	17	13	5	6	5
Ecoregion 10	67	30	15	9	27	14
Ecoregion 13	38	11	11	4	13	5
Latitude	1065	940	-	-	-	-
Climate	985	809	-	-	-	-
Interspecific	1064	888	-	-	-	-
Intraspecific	-	-	270	422	209	335
Ecoregion 3	-	-	-	-	-	-
Ecoregion 6	354	204	102	67	141	95
Ecoregion 7	383	535	141	95	136	168
Ecoregion 9	23	16	-	-	5	5
Ecoregion 10	67	30	14	8	27	14
Ecoregion 13	38	10	11	4	13	5
Latitude	1062	901	-	-	-	-
Climate	985	802	-	-	-	-

Four dental characteristics were measured to the nearest 0.01 mm using digital calipers and following von den Driesch (1976) (Figure 7). Measurements included lengths of the lower p4, m1, m2, and m3 and were used to examine interspecies and intraspecies differences between ecoregion, latitude, and climate; widths were unavailable in Heaton's dataset. Additionally, ratio data (p4/m1, m2/m1, m3/m1, p4/m3, m2/m3) were calculated for each specimen, where possible, to interpret proportional differences. Statistical analyses were used to examine the relationships between tooth size and ecoregion, latitude, and climate in both *U. americanus* and *U. arctos*.

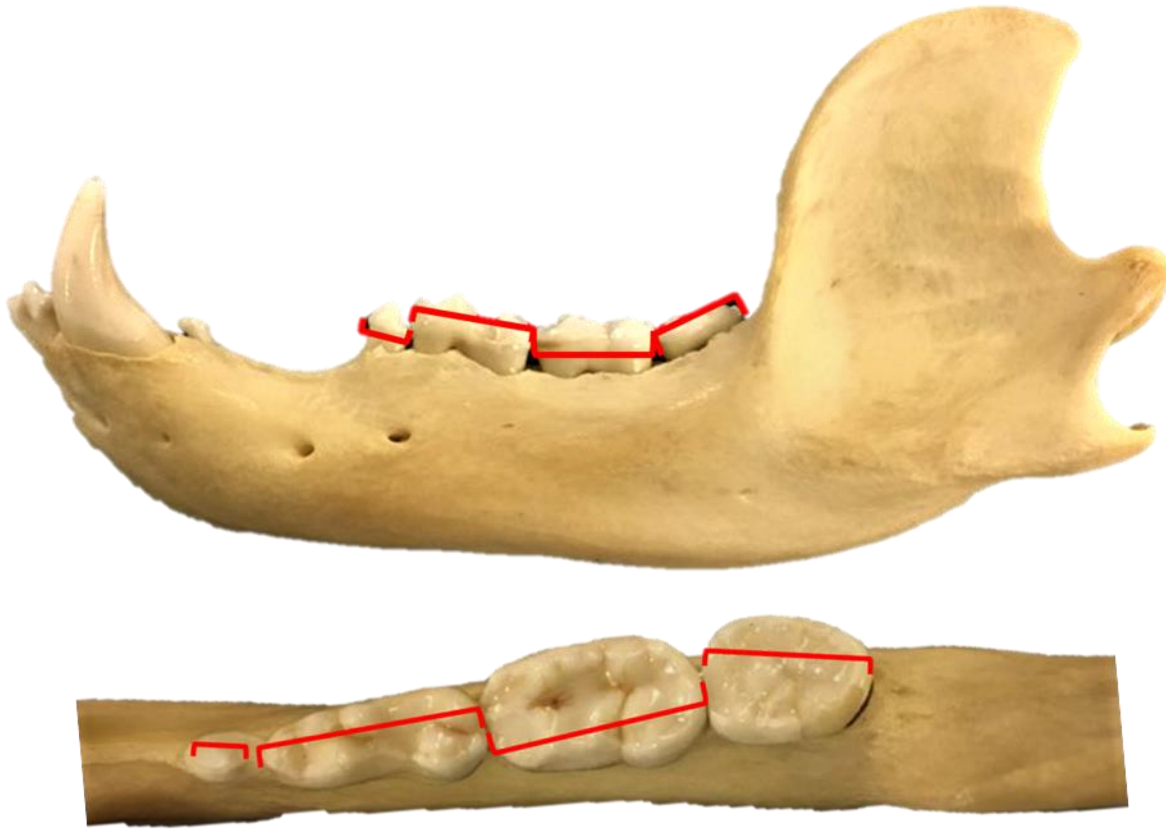


Figure 7. Measurements of lower crown lengths followed von den Driesch (1976).

Analysis of variance (ANOVA) tested for differences in individual variables with Scheffe's F and Tamhane's T2 procedures used for post hoc comparisons. Stepwise discriminant function analysis (DFA) was used to assess the utility of these measurements in classifying species and also to classify extinct fossil specimens. As a selection criterion, the stepwise model included variables with F probability <0.05. To visualize the tooth proportions (ratios) used in the analyses, bivariate plots of log transformed variables were used; these also facilitated the interpretation of fossil specimens, many of which did not have complete dentitions. Sexes of each species were compared to test for intraspecific differences. All analyses were performed using IBM SPSS Statistics 24 and ArcMap version 10.6.1.

Inter/ Intraspecific Comparison

A dataset including *Ursus americanus* and *U. arctos* specimens from across North America, and tooth lengths (p4, m1, m2, and m3) and ratios (p4/m1, m2/m1, m3/m1, p4/m3, m2/m3) was analyzed using ANOVA with tooth lengths and ratios set as dependent variables and the different species, or sexes within each species, set as the independent factor. Contrasts were set to the default, post hoc multiple comparisons utilized Scheffe's F and Tamhane's T2. Missing values for cases were excluded analyses by analysis. Reported results for each analysis include: mean, standard deviation, p-value, and F-value.

To determine which variables best differentiate groups, stepwise discriminant function analysis (DA) was utilized. The range was defined as 1 to 2 because either species or sexes was the input and there were only two variables. Independent variables were tooth length and ratios. The stepwise method was chosen to determine which variables were the most effective at differentiating groups based on Wilks' lambda. Reported results for each analysis include: discriminant function scores (DFA), Wilks' λ, eigenvalue, p-value, % variance explained, and classification results.

Ecoregion

Ecoregion data was sourced from the United States Environmental Protection Agency. Level 1 ecoregions were used for this study because of their broad scale that encompassed sufficient specimen point data to run statistical analyses; if Ecoregion Level 2 or higher had been used there would not have been sufficient point data within each ecoregion to run statistical analyses. Ecoregion Level 1 data was projected into ArcMap with *U. americanus* and *U. arctos* data points layered overtop. In Ecoregion Level 1, North America is divided into 15 different sections based on ecosystems and environmental resources (Figure 9, 10, 11) (EPA). Once specimen data points were projected on the Ecoregion map, points were associated with ecoregions in the dataset. As in prior analyses, for each ecoregion an ANOVA and DA were run testing interspecific and intraspecific variation.

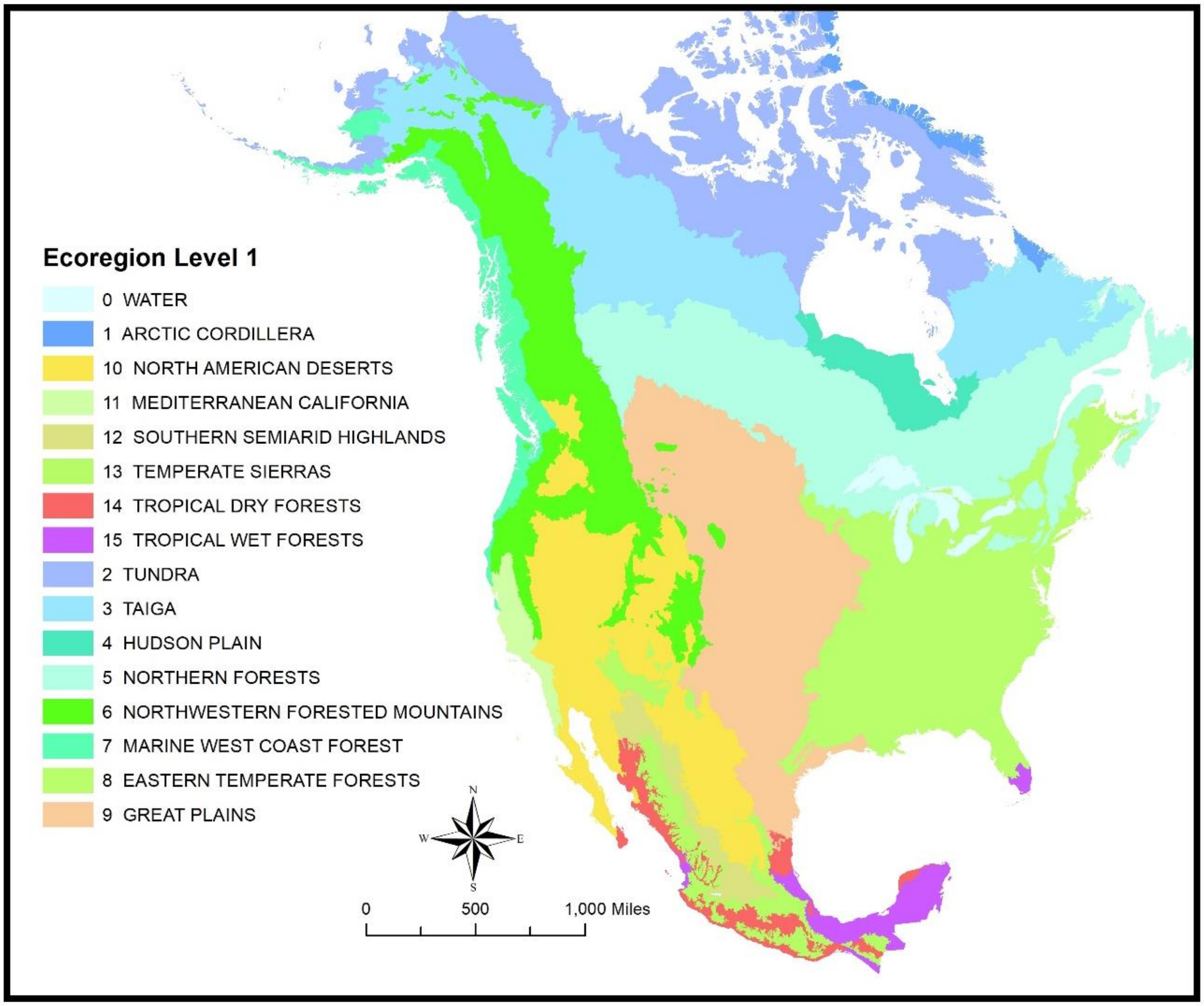


Figure 8. Boundary ranges of ecoregions in level 1. Map sourced from the Environmental Protection Agency.

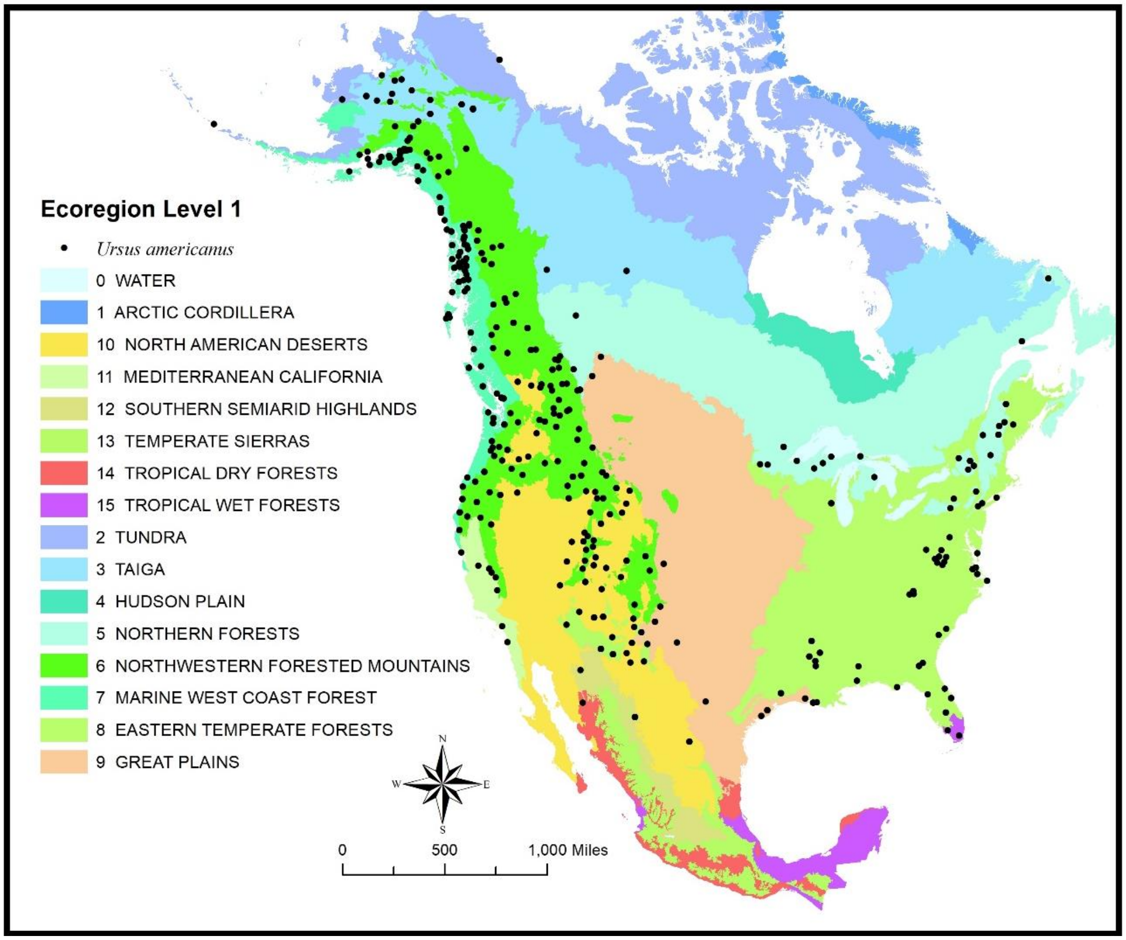


Figure 9. *Ursus americanus* dataset in relation to the ecoregions of Level 1.

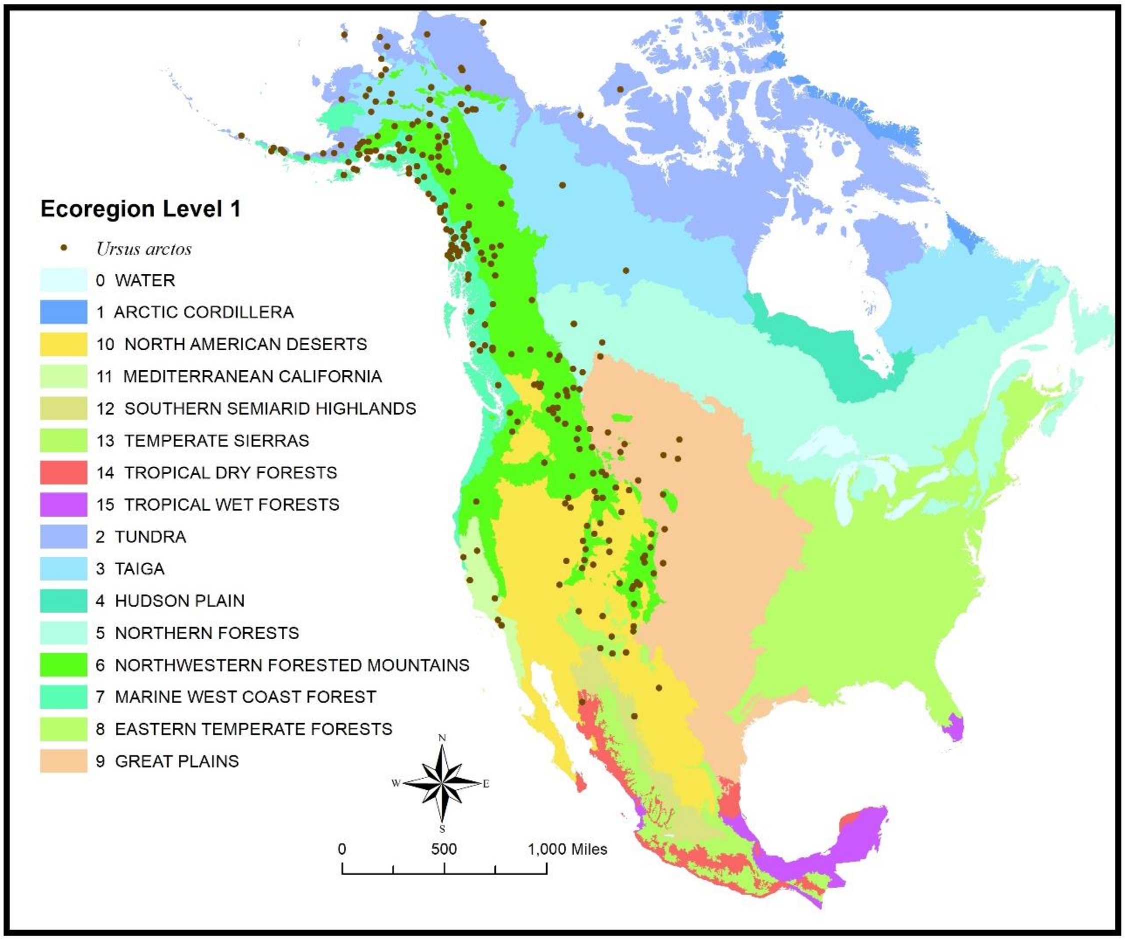


Figure 10. *Ursus arctos* dataset in relation to the ecoregions of Level 1.

Latitude

Ordinary least squares linear regressions were used to test for relationships between latitude and tooth length and ratio data in *U. americanus* and *U. arctos*, and bivariate plots were used to visualize the ratios utilized in the analysis. Linear regressions were run with tooth length and ratio used as the dependent variable and latitude as the independent variable. A Multivariate Analysis of Covariance (MANCOVA) was run with latitude as the covariate, tooth length and ratios as the dependent, and species or sex as the fixed factor. This allowed intra and interspecific differences to be tested while also correcting for latitudinal variation, a proxy for climate. After regressions were run, fossil specimens were plotted on linear regression graphs for *U. americanus* and *U. arctos* for each tooth length and ratio to see how they were classified.

Climate

Modern bioclimatic data was sourced from WorldClim (Fick and Hijmans 2017) at a 10min resolution using version 2.0. Temperature variables were utilized to test if tooth size is correlated to mean annual temperature or minimum temperature of the coldest month. Species location data was accessed on public museum websites from which specimens were originally measured; their latitude and longitude points were transferred into ArcMap and displayed on a map of North America. Once specimen location points were projected onto the map, Bioclimatic variables were also projected and the bioclimatic variable information, in degrees Celsius, at each reference point was extracted into a spreadsheet. Several specimen location points did not include any temperature data and these points were not used in the statistical analyses.

Bioclimatic data recorded for each specimen location point was analyzed using MANCOVA with climate as the covariate, tooth length and ratios as the dependent variables, and species or sex as the fixed factor.

CHAPTER 4

OREGON CAVES URSID MATERIAL

The following is a summary of all Oregon Caves ursid (Carnivora, Ursidae) material on loan to East Tennessee State University (ETSU). Ursid material, containing over 50 cranial and postcranial elements, was collected between May 1997 and June 2000 by Dr. Jim Mead in addition to students and volunteers working with him at the time (including Dr. Blaine W. Schubert). The material was originally loaned to Northern Arizona University, where Dr. Mead was at the time. After Dr. Mead transferred to ETSU, the material and loan moved with him. These descriptions give an account of the previously collected material and assigns each specimen catalogue numbers.

Two additional ORCA specimens, identified as *U. arctos* based on excessive size, were provided by Dr. H. Greg McDonald. Specimens were compared to modern skeletal material of *U. americanus* and *U. arctos* in the ETSU Museum of Natural History modern collection in addition to morphological descriptions by Gilbert (1990) and Smart (2009). It should be noted that most of the ORCA material likely represents *U. americanus* based on size. However, this thesis takes a conservative approach to species assignment, focusing in statistical analyses and morphology.

Specimens from the cave have a variety of preservation states showing differences in density, texture, staining, and coloration, suggesting the specimens could represent multiple ages. Some specimens have been heavily bleached and are chalky and flaking while others have been immaculately preserved. This could be in part due to location in the cave. Some parts of the cave have water running through it and some bones show extreme weathering and water marks. There are also specimens with divots and grooves not related to bite marks but can be associated with water continuously dripping on them. Another taphonomic feature found on numerous bones, is the presence of rodent gnaw marks along the shaft of long bones, or if a specimen was broken along a fragmented edge. Several of the bones are heavily coated in black staining and may be from a fire which in occurred in the cave roughly 1,500 years ago (Jim Mead Pers. Com. 2017). However, it is possible that some of this staining could be manganese oxide. Element identifications are discussed below.

Class MAMMALIA Linnaeus, 1758

Order CARNIVORA Bowdich, 1821

Family URSIDAE Fischer de Waldheim, 1817

Genus *URSUS* Linnaeus, 1758

URSUS AMERICANUS Pallas, 1780

Referred Material – R dentary (ORCA 3039); R and L maxilla, R dentary (ORCA 3040); baculum (ORCA 3052)

Locations – No recorded cave location for ORCA 3039 and 3040; ORCA 3052 was found at station A7 in the cave.

Comments – Ursid mandibles and maxillae can be distinguished from felids, canids, mustelids, and other carnivorans by their relatively unspecialized molars. Two right dentaries with partial permanent dentition are present. ORCA 3039 is disarticulated at the mandibular symphysis; the c1 and m1 are present. Additionally, the condyloid and angular process are present but the coronoid process has been broken off. ORCA 3040 is articulated at the mandibular symphysis, however, the left dentary is broken posterior to the left canine alveolus; the right dentary includes c1, p4, m1, m2, and m3 but is broken just posterior to the m3. The right and left maxillae are present in ORCA 3040 but they are disarticulated along the midline. The right maxilla contains the C1 and M2. The left maxilla contains P4, M1, and M2. ORCA 3039 and 3040 were classified by DA as *U. americanus* based on molar length. Further, the absence of a premasseteric fossa indicated these two are not part of Tremarctinae (Kurtén and Anderson, 1980). See chapter 5 (Results) for statistical results classifying ORCA 3039 and 3040 as *U. americanus*.

Ursus americanus bacula are robust at the proximal end and taper distally. The proximal end is circular in cross section but has a triangular cross section slightly past its mid-point towards the distal end. *Ursus americanus* bacula have a curved ventral surface whereas *U. arctos* bacula are convexly curved on their dorsal surface (Abella et al. 2013). ORCA 3052 indicates male utilization of the cave.

URSUS ARCTOS Linnaeus, 1758

Referred Elements – L partiral humerus and proximal epiphysis (ORCA 3053); R humerus, L ulna (ORCA 3138)

Locations –ORCA 3053 and 3138 are from 8m west of the ghost room in the cave.

Comments – The humerus of ursids have a well-developed lateral epicondylar crest and deltoid tuberosity (Adams and Crabtree 2012). Additionally, ursids have a flanged medial epicondyle and a keeled trochlea. The greater tuberosity is relatively the same size as the head. ORCA 3053 has an associated proximal epiphyses that does not articulate with ORCA 3053 due to the proximal end of the shaft having been broken off; however, it is the same size that would fit on ORCA 3138, but it is a left epiphysis. ORCA 3053 and 3138 were identified as *U. arctos* based on comparative humeral measurements of *U. americanus* and *U. arctos* (Table 2). ORCA 3053 and 3108 are believed to be the same specimen due to size comparisons and morphology.

Table 2. Humeral comparative measurements of *U. americanus* and *U. arctos* (mm) in relation to ORCA 3138. Variables listed include: HAPD=Humerus Anterioposterior Diameter, HMLD=Humerus Mediolateral Diameter, HEB=Humerus Epicondylar Breadth

	HAPD	**HMLD**	**HEB**
U. americanus	30.65	29.51	80.04
U. americanus	34.21	31.88	87.26
U. americanus	29.9	34.03	81.82
U. americanus	25.33	23.73	67.88
U. americanus	31.63	33.23	84.76
U. arctos	43.36	31.39	100.43
U. arctos	46.88	51.81	125.04
U. arctos	28.91	25.95	88.19
U. arctos	45.71	35.35	106.8
U. arctos	30.82	26.62	86.16
ORCA 3138	35.06	40.76	89.4

The ulna in ursids have a well-developed olecranon process, radial notch and coronoid process (Adams and Crabtree 2012). Only the proximal portion of the ulna is preserved in ORCA 3138; however, the well-developed olecranon process indicates this is an ursid and its association with the humerus indicates it is *U. arctos*. ORCA 3108 is believed to be the same specimen as ORCA 3138 due to size comparisons and morphology.

Genus *URSUS* Linnaeus, 1758

Ursus sp.

Elements in this section could not be identified to species level; however, they are found in the presence of *Ursus* material and are in the size range of *U. americanus*, not *U. arctos*. Thus they are most likely *U. americanus*.

Upper Canines

Referred Material – 2 L C1 (ORCA 3035 & 3036)

Locations – ORCA 3035 was found near station A15 and A16, ORCA 3036 was found at station A6 in the cave.

Comments – several indicators were used to identify upper canines. Enamel on the surface of the upper canines extends evenly around the circumference of the tooth. Upper canines have a robust root that does not bend or twist. Left and right C1 can be differentiated by a lengthwise ridge located on the posterior lateral surface that runs from the base of the enamel to the apex of the crown.

Lower Canines

Referred Material – 3 R c1 (ORCA 1475, 3033, & 3034)

Locations – ORCA 1475 was found at station G3D near the 110 entrance, ORCA 3033 was found at station AOC, ORCA 3034 at station C2A near the 110 entrance in the cave.

Comments – Lower canines are identified by several means. On lower canines the enamel extends further back on the posterior surface of the canine and the root bends dorsally and curves laterally. Left and right c1 can be distinguished by a prominent, lengthwise ridge on the lingual surface of the tooth and in older individuals, a wear facet is present on the labial side of the tooth. Additionally, the tooth enamel generally extends lower on the labial side than on the lingual side, reflecting the slightly angled position of these teeth.

An additional canine is present (ORCA 3037), however, it has been warped and fragmented. Only the root remains intact and is therefore indistinguishable. ORCA 3037 was found at station A6 in the cave.

Incisor

Referred Material – R I3 (ORCA 3038)

Locations – ORCA 3038 was at station A7 in the cave.

Comments – The enamel on an ursids I3 is uneven around the circumference of the tooth; medially, the enamel is higher than when observing the lateral surface. Additionally, the enamel extend further on the lingual surface than the labial surface. The I3 are not symmetrical in shape, the enamel of the tooth curves posteriorly and, when viewed from the anterior or posterior, the tooth angles upward medially.

Cranium

Referred Material – Glenoid fossa & parietal (ORCA 3041); temporal bone (ORCA 3219)

Locations – No location was recorded for ORCA 3041, ORCA 3219 was found at station A0C in the cave.

Comments – ORCA 3041 is a portion of the right glenoid fossa with the petrosal and was recovered along with the right parietal, broken along its sutures. ORCA 3219 is a portion of the temporalis bone broken along the cranial sutures.

Humerus

Referred Material – L humerus (ORCA 3054)

Locations – ORCA 3054 was found at station A7 in the cave.

Comments – The humerus of ursids have a well-developed lateral epicondylar crest and deltoid tuberosity (Adams and Crabtree 2012). Additionally, ursids have a flanged medial epicondyle and a keeled trochlea. The greater tuberosity is relatively the same size as the head. ORCA 3054 is broken perpendicular along its shaft and is in two pieces and the epiphyses are not fused. Color differences along the breaks indicate the bone was broken recently.

Radius

Referred Material – 2 R radii (ORCA 3064 & 3065)

Locations – ORCA 3064 and 3065 were found at station A7 in the cave.

Comments – The radius in ursids curves laterally at its distal end and is thicker at the proximal and distal ends but is slimmer in the middle of the shaft. ORCA 3043 has been heavily worn, possibly in an abrasive stream, and is therefore very smooth resulting in a majority of distinguishing features being lost; however, it does retain the defining shape.

Metacarpals

Referred Material – 1 L 1st Metacarpal (ORCA 3024)

Locations – ORCA 3024 was found at station A7 in the cave.

Comments – Ursid metapodials can commonly be mistaken for that of a human (Gilbert 1980). The first metacarpal in ursids is distinct because it is not separated to form an opposable thumb and thus has an articular surface connecting it to the second metacarpal (Gilbert 1980).

Femur

Referred Material – 4 L Femora (ORCA 3055, 3056, 3057, & 3049); R Femur (ORCA 3058)

Locations – ORCA 3055 and 3057 were found at station A6, ORCA 3056 was found in the Echo Dome at station AXAX, ORCA 3058 and 3059 were found at station A7 in the cave.

Comments – The distal condyles in ursids are symmetrical, the shaft is relatively smooth and no major muscle attachment points are present (Adams and Crabtree 2012). The greater and lesser trochanter are not prominent but still present and the trochanteric fossa opens medially and not dorsally. There is no linea aspera present in ursids (Adams and Crabtree 2012). ORCA 3055 has black staining on its posterior surface. None of the femora present have fused proximal or distal epiphyses.

Patella

Referred Material – Patella ORCA 3066

Locations – ORCA 3066 was found at station A0C in the cave.

Comments – The association of a patella with other ursid material, along with the relative size and common morphology as found in bears, ORCA 3066 is referred to *Ursus.*

Tibia

Referred Material – 2 L tibiae (ORCA 3060 & 3061); R tibia (ORCA 3060); L distal epiphysis (ORCA 3060)

Locations – ORCA 3060 was found at station A7 in the cave, ORCA 3061 does not have cave location data.

Comments – Tibiae in ursids have a slight lateral bend at the proximal portion of the shaft, a prominent medial malleolus and tibial tuberosity, and well-developed medial tuberosity. None of the tibiae present have fused proximal or distal epiphyses. ORCA 3060 has an associated left distal epiphyses, however, it is not fused.

Tarsals

Referred Material – R astragalus (ORCA 3027); R calcaneus (ORCA 3028); 2 L calcanea (ORCA 3030 & 3031); R and L navicular (ORCA 3029); L cuboid (ORCA 3032)

Locations – ORCA 3027, 3031, and 3032 were found at station A0C, ORCA 3028 was at station A7, ORCA 3029 and 3030 were found at station A6 in the cave.

Comments – The ursid astragalus has a cube-shaped body, an anteriorly projecting head located on the medial side of the body, and the trochlea is pulley-shaped (Smart 2009). On the ventral surface there are three calcaneal articular facets and a deep sulcus tail (Smart 2009). Ursid calcanea are short and robust with a long calcaneal tuberosity. Additionally, the sustentaculum on the medial surface is well-developed and the lateral projection is well rounded (Smart 2009). ORCA 3027 and ORCA 3028 are an associated astragalus and calcaneus. Only ORCA 3032 has a fused calcaneal tuberosity; ORCA 3028 has an associated calcaneal tuberosity but it has been glued on with PaleoBOND^{TM} (Jim Mead pers. Com. 2017) and is not fused. The ursid navicular is bowl-like in appearance; the posterior surface is concave and the anterior surface in convex. ORCA 3029 are two naviculae that were found at the same location within the cave and are considered associated elements due to size similarities. The ursid cuboid is cube-like in its dorsal view and its anterior view is triangular in form.

Metatarsals

Referred Material – R metatarsals 1 through 5 (ORCA 3023); 1 L 4th metatarsal (ORCA 3025); 1 R 2nd metatarsal (ORCA 3026)

Locations – ORCA 3023 was found at station A0C, ORCA 3025 and 3026 were at station A7 in the cave.

Comments – Ursid metapodials can be mistaken for that of a human (Gilbert 1980). Ursid metatarsals differ from humans in that the fourth metatarsal is the longest (Gilbert 1980) defining ORCA 3023 as being ursid.

Phalanx

Referred Material – 2 medial phalanges (ORCA 3062 and 3063), 2 proximal phalanges (ORCA 1467 and 3215)

Locations – ORCA 1467 and 3215 have no recorded location, ORCA 3062 and 3063 were found at station A6 in the cave.

Comments – The distal end of proximal phalanges are deeply grooved and the proximal end is notched on the ventral surface (Gilbert 1980). Medial phalanges have their proximal surface divided by a medial ridge which extend dorsally to form a convex surface on the dorsal surface of the bone (Gilbert 1980).

Vertebrae

Referred Material – 1 Cervical (ORCA 3042); 3 Thoracic (ORCA 3043, 3044, & 3045); 4 Lumbar (ORCA 3046, 3047, 3048, 3049, and 3214); 2 Caudal (ORCA 3050 & 3051)

Locations – ORCA 3042 was found at station H2, ORCA 3043 was found at station A7, ORCA 3044, 3045, 3046, 3049, and 3051 were found at station A6, ORCA 3047, 3048, 3050, and 3214 were found at station A0C in the cave.

Comments – Cervical vertebrae were identified by the presence of transverse foramina laterally located on either side of the vertebral canal. ORCA 3042 does not have anterior or posterior centrum epiphyses fused. Only the first six cervical vertebrae retain transverse foramina, indicating ORCA 3042 could be cervical three through six.

Thoracic vertebrae were identified by the presence of articular facets on the ventral surface of the transverse process which a rib would articulate to. Additionally, the presence of prezygapophyses, postzygapohyses, demifacets, and lengthy spinous process are all defining features of thoracic vertebrae. ORCA 3043, 3044, and 3045 were able to be identified by the morphological configuration of transverse processes, prezygapophyses, postzygapohyses, and a large spinous process. ORCA 3044 and 3045 do not have the epiphyses on their centrum fused; ORCA 3043 is missing its centrum.

Lumbar vertebrae were identified by the presence of anteriolaterally projecting pleurapophyses and spinous process, mammillary processes, and accessory processes. ORCA

3046, 3047, 3048, and 3049 were identified by their mammillary processes and pleurapophyses. None of the four specimens have their centrum epiphyses fused, however, ORCA 3048 has an associated anterior epiphysis. ORCA 3049 is two articulated lumbar vertebrae connected at the accessory process of the first sequential vertebra and the mammillary processes of the second sequential vertebra.

Caudal vertebrae were identified by the presence of a v-shaped hemal arch on the ventral surface of the centrum. ORCA 3050 does not have any epiphyseal fusion; ORCA 3051 has its posterior epiphysis fused but the anterior remains unfused.

Ribs

Referred Material – 19 ribs (ORCA 3067 – 3071, 3073 – 3083, and 3216 – 3218)

Locations – ORCA 3067 – 3071 were found at station A7, ORCA 3073 – 3083 were found at station A6, ORCA 3216 – 3218 do not have an associated location in the cave.

Comments – The association of ribs with other definable ursid material along with the relative size and common morphology as found in bears, ORCA ribs listed above are referred to as *Ursus*.

Pelvis

Referred Material – ORCA 3207 – 3212

Locations – ORCA 3207 and 3209 were found at A6, ORCA 3208, 3210, 3211, and 3212 were found at A0C in the cave.

Comments – There are no complete pelves in the ORCA collection, but the pelvis fragments presented contain ilium, ischium, and pubic portions. The association of pelvic fragments with other diagnostic ursid material and size and morphological comparisons, these ORCA pelvis specimens are associated with the genus *Ursus*.

CHAPTER 5

RESULTS

Inter/ Intraspecific Comparisons

ANOVA found significant differences between *U. americanus* and *U. arctos* tooth lengths (p4, m1, m2, m3) and ratios (p4/m1, m2/m1, m3/m1, p4/m3, and m2/m3) from across North America (Table 3). *F* test and associated *p* values of <0.001 for all variables indicates the null hypothesis is unlikely. On average, *U. arctos* tooth lengths are longer than *U. americanus*, but *U. americanus* has a longer m2 in relation to m1 and m3.

Table 3. ANOVA results for interspecific comparison. Values listed include mean and standard deviation (SD), along with F values and p values. BB=Black Bear (*Ursus americanus*), GB=Brown Bear (*Ursus arctos*).

	Mean (SD) BB	Mean (SD) GB	*F*	*p*
p4	9.16 (0.94)	13.24 (1.10)	7663.176	<0.001
m1	18.00 (1.11)	23.98 (1.59)	9409.829	<0.001
m2	19.02 (1.26)	24.72 (1.58)	7819.24	<0.001
m3	14.82 (1.33)	20.23 (1.78)	5869.037	<0.001
p4/m1	0.50 (0.04)	0.55 (0.04)	452.999	<0.001
m2/m1	1.05 (0.04)	1.03 (0.04)	143.64	<0.001
m3/m1	0.82 (0.06)	0.84 (0.07)	49.455	<0.001
p4/m3	0.62 (0.06)	0.65 (0.06)	163.167	<0.001
m2/m3	1.28 (0.08)	1.22 (0.09)	236.521	<0.001

Stepwise DFA separated groups fairly well by tooth length; however, ratios were not as successful (Table 4). Specifically, the Wilks' λ values for the ratio DFA was substantially greater, indicating poorer (but significant) separation. The p4/m1 ratio had the strongest correlation with the discriminant function and all other ratios contributed to the model, with the exception of m3/m1 (Table 4). The ability of the discriminant models to separate species was assessed using the classification phase for lengths and ratios (Table 5). Classification was more accurate for *U. americanus* than *U. arctos* (length 99.8% vs 98.2%, ratio 79.5% vs 75%) and ratios were not able to separate groups as well as lengths (99.1% vs 77.5%), most likely due to a substantial amount of overlap that is not seen in lengths.

Table 4. Structure matrix results for interspecific comparison. Values listed include variable contribution to separation, Wilks' λ, eigenvalue, % variance, and *p* value.

	Function 1		Function 1
p4	0.795	**p4/m1**	0.676
m1	0.881	**m2/m1**	-0.381
m2	0.802	**m3/m1**	0.223
m3	0.696	**p4/m3**	0.406
Wilks' λ	0.139	**m2/m3**	-0.488
Eigenvalue	6.219	**Wilks' λ**	0.663
%Variance	100%	**Eigenvalue**	0.509
p	< 0.001	**%Variance**	100%
		p	< 0.001

Table 5. Classification results for interspecific comparison. Values listed indicate how many specimens of each species were correctly classified by DA.

		Species	% Correct	Predicted Group Membership		Total	
				U. americanus	*U. arctos*		
Length	**Original**	*U. americanus*	99.8%	1063	2	1065	
		U. arctos	98.2%	16	875	981	99.1%
	Cross-Validated	*U. americanus*	99.8%	1063	2	1065	
		U. arctos	98.2%	16	875	981	99.1%
Ratio	**Original**	*U. americanus*	79.5%	846	218	1064	
		U. arctos	75%	222	666	888	77.5%
	Cross-Validated	*U. americanus*	79.3%	844	220	1064	
		U. arctos	74.8%	224	664	888	77.3%

ANOVA found significant differences for all tooth length variables studied (p4, m1, m2, and m3) between intraspecific comparison of *U. americanus* and *U. arctos* but only found significant differences in one ratio for *U. americanus* sexes (m2/m1) and none for *U. arctos*. The mean values and standard deviations for each variable studied are summarized in Table 6. In both species, males have slightly larger teeth than females but ratios are strikingly similar and show a substantial amount of overlap, more so than what was observed between species. *F* test and associated *p* values less than 0.001 for all tooth lengths indicate the null hypothesis is unlikely but low *F* values and insignificant *p* values for ratios indicate there is not a substantial difference between groups.

Table 6. ANOVA results for intraspecific comparison of sexes. Values listed include mean and standard deviation (SD), along with *F* values and *p* values. FBB=Female Black Bear (*Ursus americanus*), MBB=Male Black Bear (*Ursus americanus*), FGB=Female Brown Bear (*Ursus arctos*), MGB=Male Brown Bear (*Ursus arctos*).

	Mean (SD) FBB	**Mean (SD) MBB**	***F***	***p***		**Mean (SD) FGB**	**Mean (SD) MGB**	***F***	***p***
p4	8.92 (0.86)	9.36 (0.88)	38.943	<0.001	**p4**	12.71 (1.07)	13.37 (1.09)	47.63	<0.001
m1	17.5 (0.99)	18.34 (0.97)	116.75	<0.001	**m1**	23.36 (1.42)	24.33 (1.60)	50.51	<0.001
m2	18.36 (1.15)	19.45 (1.11)	146.02	<0.001	**m2**	23.94 (1.34)	25.17 (1.51)	90.06	<0.001
m3	14.27 (1.25)	15.13 (1.31)	69.32	<0.001	**m3**	19.44 (1.57)	20.64 (1.72)	65.03	<0.001
p4/m1	0.51 (0.04)	0.51 (0.04)	0.007	0.933	**p4/m1**	0.54 (0.03)	0.55 (0.04)	2.75	0.980
m2/m1	1.04 (0.04)	1.06 (0.04)	10.72	0.001	**m2/m1**	1.02 (0.03)	1.03 (0.5)	5.03	0.250
m3/m1	0.81 (0.06)	0.82 (0.06)	3.23	0.072	**m3/m1**	0.83 (0.07)	0.85 (0.07)	5.81	0.160
p4/m3	0.62 (0.06)	0.62 (0.06)	1.7	0.192	**p4/m3**	0.65 (0.06)	0.65 (0.06)	0.93	0.335
m2/m3	1.29 (0.08)	1.29 (0.09)	0	0.986	**m2/m3**	1.23 (0.09)	1.22 (0.08)	2.62	0.106

The structure matrix for discriminant function 1 revealed lengths and ratios did not significantly contribute to separating sexes of either species (Table 7). The ability of the discriminant model to separate sexes was assessed using the classification phase for *U. americanus* (Table 8) and *U. arctos* (Table 9). Intraspecific classification was more accurate for *U. americanus* than *U. arctos* when using length (72.1% vs 67.9%) but when ratios were utilized, male and female *U. arctos* were separated more accurately than those of *U. americanus* (61.0% vs 62.10%). For both species, males were classified more accurately (*U. americanus* = 83.9%; *U. arctos* = 81.5%) than females (*U. americanus* = 53.7%; *U. arctos* = 46.4%).

Table 7. Structure matrix results for interspecific comparison. Values listed include variable contribution to separation, Wilks' λ, eigenvalue, % variance, and *p* value.

	Function 1 BB	Function 1 GB		Function 1 BB	Function 1 GB
p4	0.493	0.661	**p4/m1**	0.278	0.334
m1	0.873	0.682	**m2/m1**	1	0.582
m2	0.977	0.908	**m3/m1**	0.505	1
m3	0.603	0.772	**p4/m3**	-0.16	-0.623
Wilks' λ	0.812	0.83	**m2/m3**	0.013	-0.814
Eigenvalue	0.232	0.204	**Wilks' λ**	0.984	0.989
% Variance	100%	100%	**Eigenvalue**	0.016	0.011
p	< 0.001	< 0.001	**% Variance**	100%	100%
			p	0.001	0.016

Table 8. Classification results for intraspecific comparison of *Ursus americanus* sexes. Values listed indicate how many specimens of each species were correctly classified by DA.

		Sex	% Correct	Predicted Group Membership		Total	
				Female	Male		
Length	**Original**	Female	53.7	145	125	270	
		Male	83.9	68	354	422	72.10%
	Cross-Validated	Female	53.7	145	125	270	
		Male	83.9	68	354	422	72.10%
Ratio	**Original**	Female	4.1	11	259	270	
		Male	97.4	11	411	422	61.00%
	Cross-Validated	Female	4.1	11	259	270	
		Male	96.9	13	409	422	60.70%

Table 9. Classification results for intraspecific comparison of *Ursus arctos* sexes. Values listed indicate how many specimens of each species were correctly classified by DA.

		Species	% Correct	Predicted Group Membership		Total	
				Female	Male		
Length	**Original**	Female	46.4	97	112	209	
		Male	81.5	61	269	330	67.90%
	Cross-Validated	Female	46.4	97	112	209	
		Male	81.5	61	269	330	67.90%
Ratio	**Original**	Female	1.4	3	206	209	
		Male	100	0	335	335	62.10%
	Cross-Validated	Female	1.4	3	206	209	
		Male	100	0	335	335	62.10%

ANOVA found significant differences for all length and ratio variables interspecific comparison of sexes (Table 10) showing the null hypothesis is unlikely. Wilks' λ results from stepwise DFA found lengths separated sexes better than ratios (Table 11). The m1 contributed the most to interspecific separation of sexes for lengths while the p4/m1 ratio contributed most for ratios. Classification results showed males were more often correctly classified than females (Table 12). When lengths were utilized, there was minimal overlap between male *U. americanus* and female *U. arctos* (Figure 11), but when ratios were utilized there was substantial overlap between all groups (Figure 12).

Table 10. ANOVA results for interspecific comparison of sexes. Values listed include *F* and *p*.

	F	***p***
p4	1684.307	< 0.001
m1	2340.275	< 0.001
m2	2053.484	< 0.001
m3	1390.437	< 0.001
p4/m1	78.834	< 0.001
m2/m1	31.704	< 0.001
m3/m1	14.108	< 0.001
p4/m3	22.748	< 0.001
m2/m3	52.041	< 0.001

Table 11. Structure matrix results for interspecific comparison. Values listed include variable contribution to separation, Wilks' λ, eigenvalue, % variance, and *p* value for functions 1, 2 and 3.

	Function 1	**Function 2**	**Function 3**
p4	0.744	-0.267	0.308
m1	0.87	-0.093	-0.459
m2	0.822	0.535	-0.173
m3	0.679	0.269	0.532
Wilks	0.115	0.969	0.998
Eigenvalue	7.424	0.03	0.002
% Variance	100%	40%	0%
p	< 0.001	< 0.001	0.256

	Function 1	**Function 2**	**Function 3**
p4/m1	0.657	0.489	0.563
m2/m1	-0.394	0.881	0.262
m3/m1	0.238	0.86	-0.451
p4/m3	0.361	-0.31	0.88
m2/m3	-0.529	-0.447	0.712
Wilks	0.686	0.988	1
Eigenvalue	0.439	0.012	<0.001
% Variance	97%	2.8%	0%
p	< 0.001	0.005	0.819

Table 12. Classification results for interspecific comparison of sexes. Values listed indicate how many specimens of each species were correctly classified by DA. For abbreviations, see table 6.

		Species	% Correct	Predicted Group Membership				Total	
				FBB	MBB	FGB	MGB		
Length	Original	FBB	51.4%	132	125	0	0	257	
		MBB	86.2%	56	350	0	0	406	
		FGB	46.9%	0	7	97	103	207	
		MGB	80.2%	0	4	61	264	329	70.3%
	Cross-validated	FBB	51.0%	131	126	0	0	257	
		MBB	86.0%	57	349	0	0	406	
		FGB	46.9%	0	7	97	103	207	
		MGB	79.6%	0	4	63	262	329	70.0%
Ratio	Original	FBB	0.0%	0	201	1	55	257	
		MBB	79.8%	3	324	0	79	406	
		FGB	2.4%	1	53	5	148	207	
		MGB	69.9%	0	93	6	230	329	46.6%
	Cross-validated	FBB	0.0%	0	201	1	55	257	
		MBB	79.8%	3	324	0	79	406	
		FGB	2.4%	1	53	5	148	207	
		MGB	69.9%	0	93	6	230	329	46.6%

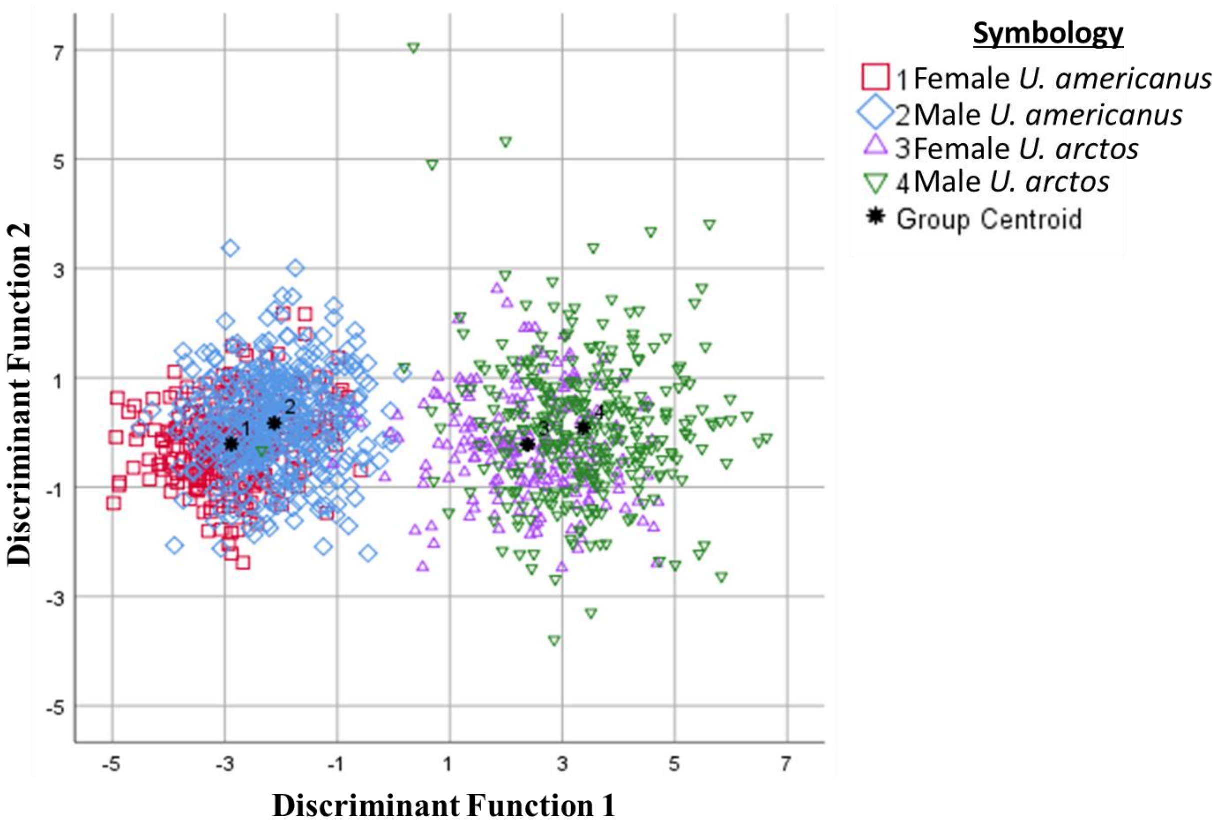


Figure 11. Interspecific comparison of sexes utilizing length measurements.

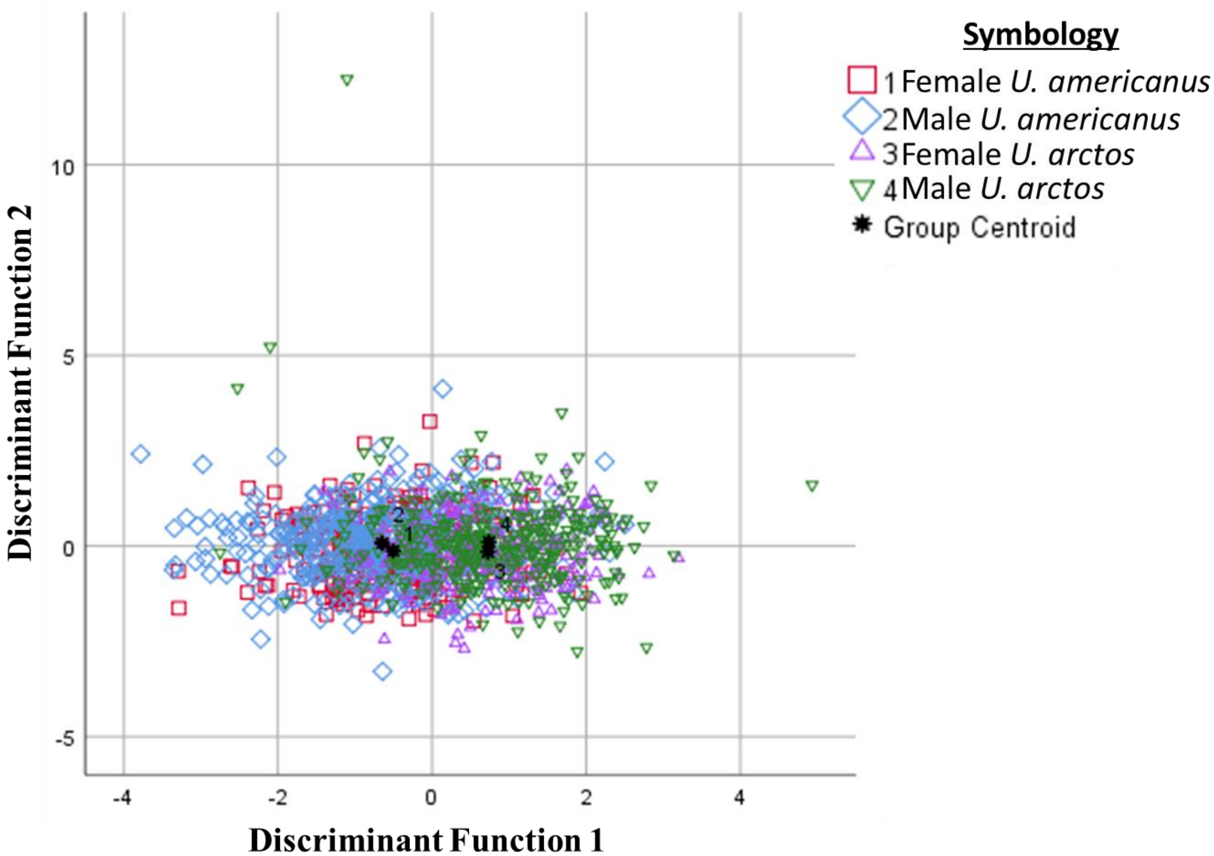


Figure 12. Interspecific comparison of sexes utilizing ratios.

Ecoregion

ANOVA found significant interspecific differences for all length variables of all ecoregions studied (Table 13). No ratios studied showed significant differences between species for ecoregion 3, but all ratios proved to be significant in ecoregion 6. Ecoregions 7 through 13 had varying combinations of significantly different ratios (Table 13); however, when ratios were significant, their accompanying *F* value was low indicating the null hypothesis is likely. Similarly to interspecific differences at the continental level, *U. arctos* has substantially longer teeth than *U. americanus* for every ecoregion.

Table 13. ANOVA results for interspecific comparison. Values listed include mean and standard deviation (SD), along with *F* values and *p* values. See table 3 for abbreviations list.

Ecoregion 3	Mean (SD) BB	Mean (SD) GB	*F*	*p*	Ecoregion 9	Mean (SD) BB	Mean (SD) GB	*F*	*p*
p4	9.34 (0.98)	12.47 (1.08)	133.38	< 0.001	**p4**	8.68 (1.12)	12.29 (0.73)	126.30	<0.001
m1	17.97 (1.32)	24.38 (1.33)	333.83	< 0.001	**m1**	18.15 (1.43)	23.57 (1.14)	156.27	<0.001
m2	18.48 (1.25)	25.06 (1.34)	372.49	< 0.001	**m2**	18.99 (1.57)	25.57 (1.58)	137.43	<0.001
m3	14.72 (1.15)	19.97 (1.58)	217.3	< 0.001	**m3**	15.01(1.36)	20.64 (2.04)	103.76	<0.001
p4/m1	0.51 (0.04)	0.51 (0.04)	0.56	0.457	**p4/m1**	0.47 (0.04)	0.52 (0.02)	12.24	0.001
m2/m1	1.02 (0.04)	1.02 (0.04)	0.006	0.94	**m2/m1**	1.04 (0.03)	1.06 (0.03)	2.04	0.162
m3/m1	0.82 (0.05)	0.81 (0.05)	0.009	0.924	**m3/m1**	0.82 (0.05)	0.87 (0.87)	4.55	0.04
p4/m3	0.63 (0.05)	0.62 (0.05)	0.323	0.572	**p4/m3**	0.57 (0.05)	0.60 (0.05)	1.19	0.281
m2/m3	1.25 (0.07)	1.25 (0.08)	0.003	0.953	**m2/m3**	1.26 (0.07)	1.22 (0.12)	1.90	0.176

Ecoregion 6	Mean (SD) BB	Mean (SD) GB	*F*	*p*	Ecoregion10	Mean (SD) BB	Mean (SD) GB	*F*	*p*
p4	9.07 (0.82)	12.99 (1.19)	2088.33	< 0.001	**p4**	8.88 (0.92)	12.09 (1.12)	211.86	<0.001
m1	17.87 (1.02)	23.82 (1.39)	3336.30	< 0.001	**m1**	17.99 (1.15)	22.98 (1.45)	321.47	<0.001
m2	18.84 (1.14)	24.66 (1.43)	2775.36	< 0.001	**m2**	18.86 (1.34)	24.31 (1.61)	293.12	<0.001
m3	14.44 (1.12)	20.28 (1.72)	2320.99	< 0.001	**m3**	14.44 (1.36)	20.09 (1.80)	284.32	<0.001
p4/m1	0.50 (0.04)	0.54 (0.04)	105.594	< 0.001	**p4/m1**	0.49 (0.04)	0.52 (0.04)	12.24	0.001
m2/m1	1.05 (0.04)	1.03 (0.04)	26.449	< 0.001	**m2/m1**	1.04 (0.03)	1.05 (0.03)	1.379	0.243
m3/m1	0.80 (0.05)	0.85 (0.07)	60.396	< 0.001	**m3/m1**	0.80 (0.05)	0.87 (0.07)	29.87	<0.001
p4/m3	0.63 (0.05)	0.64 (0.06)	6.115	0.014	**p4/m3**	0.61 (0.05)	0.60 (0.05)	1.04	0.309
m2/m3	1.30 (0.08)	1.22 (0.09)	125.691	< 0.001	**m2/m3**	1.31 (0.08)	1.21 (0.07)	28.75	<0.001

Ecoregion 7	Mean (SD) BB	Mean (SD) GB	*F*	*p*	Ecoregion13	Mean (SD) BB	Mean (SD) GB	*F*	*p*
p4	9.60 (0.83)	13.51 (0.98)	3972.06	< 0.001	**p4**	8.08 (0.75)	11.34 (1.33)	99.17	<0.001
m1	17.98 (1.04)	24.07 (1.67)	3980.47	< 0.001	**m1**	17.75 (1.00)	21.46 (1.50)	81.11	<0.001
m2	19.13 (1.18)	24.69 (1.63)	3225.78	< 0.001	**m2**	18.28 (1.14)	23.07 (1.69)	105.26	<0.001
m3	15.13 (1.38)	20.16 (1.74)	2194.41	< 0.001	**m3**	14.06 (1.16)	18.82 (2.45)	75.14	<0.001
p4/m1	0.53 (0.03)	0.56 (0.04)	111.472	< 0.001	**p4/m1**	0.45 (0.03)	0.51 (0.02)	11.24	0.005
m2/m1	1.06 (0.04)	1.02 (.05)	134.896	< 0.001	**m2/m1**	1.02 (0.03)	1.05 (0.02)	2.50	0.137
m3/m1	0.84 (0.06)	0.83 (0.07)	0.324	0.57	**m3/m1**	0.77 (0.03)	0.83 (0.07)	3.81	0.073
p4/m3	0.63 (0.05)	0.67 (0.05)	8.518	< 0.001	**p4/m3**	0.58 (0.03)	0.62 (0.09)	1.57	0.232
m2/m3	1.27 (0.09)	1.22 (0.08)	48.022	< 0.001	**m2/m3**	1.32 (0.06)	1.27 (0.15)	0.72	0.41

Stepwise DFA separated *U. americanus* and *U. arctos* by tooth length for every ecoregion examined; however, ratios did not significantly contribute to separating species (Table

14). The ability of the discriminant model to separate species was assessed using the classification phase and resulted in > 90% correct classification of species for all ecoregions studied when length was utilized; this same percentage held true when cross validated (Tables 15, 16, 17, 18, 19, and 20). Ratios did not contribute to separating species as well as lengths and would not be reliable as a method to distinguish species. There was not sufficient in order for the analysis to interpret ratios from ecoregion 3.

Table 14. Structure matrix results for interspecific comparison from ecoregions 3, 6, 7, 9, 10, and 13. Values listed include variable contribution to separation, Wilks' λ, eigenvalue, % variance, and *p* value.

Ecoregion 3

	Function1		Function 1
p4	0.549	**p4/m1**	N/A
m1	0.796	**m2/m1**	N/A
m2	1	**m3/m1**	N/A
m3	0.602	**p4/m3**	N/A
Wilks' λ	0.133	**m2/m3**	N/A
Eigenvalue	6.535	**Wilks' λ**	N/A
%Variance	100%	**Eigenvalue**	N/A
p	< 0.001	**% Variance**	N/A
		p	N/A

Ecoregion 9

	Function 1		Function 1
p4	0.686	**p4/m1**	1
m1	0.928	**m2/m1**	0.402
m2	0.894	**m3/m1**	0.268
m3	0.756	**p4/m3**	0.53
Wilks' λ	0.165	**m2/m3**	-0.128
Eigenvalue	5.045	**Wilks' λ**	0.746
%Variance	100%	**Eigenvalue**	0.34
p	< 0.001	**% Variance**	100%
		p	0.001

Ecoregion 6

	Function 1		Function 1
p4	0.703	**p4/m1**	0.587
m1	0.889	**m2/m1**	-0.293
m2	0.825	**m3/m1**	0.443
m3	0.741	**p4/m3**	0.141
Wilks' λ	0.116	**m2/m3**	-0.639
Eigenvalue	7.59	**Wilks' λ**	0.644
%Variance	100%	**Eigenvalue**	0.553
p	< 0.001	**% Variance**	100%
		p	< 0.001

Ecoregion 10

	Function 1		Function 1
p4	0.594	**p4/m1**	0.297
m1	0.919	**m2/m1**	0.53
m2	0.893	**m3/m1**	1
m3	0.864	**p4/m3**	-0.511
Wilks' λ	0.198	**m2/m3**	-0.832
Eigenvalue	4.052	**Wilks' λ**	0.759
%Variance	100%	**Eigenvalue**	0.318
p	< 0.001	**% Variance**	100%
		p	< 0.001

Ecoregion 7

	Function 1		Function 1
p4	0.86	**p4/m1**	0.527
m1	0.861	**m2/m1**	-0.577
m2	0.776	**m3/m1**	-0.028
m3	0.639	**p4/m3**	0.459
Wilks' λ	0.146	**m2/m3**	-0.344
Eigenvalue	5.86	**Wilks' λ**	0.693
%Variance	100%	**Eigenvalue**	0.442
p	< 0.001	**% Variance**	100%
		p	< 0.001

Ecoregion 13

	Function 1		Function 1
p4	0.29	**p4/m1**	1
m1	0.38	**m2/m1**	0.033
m2	0.309	**m3/m1**	0.075
m3	1	**p4/m3**	0.699
Wilks' λ	0.186	**m2/m3**	-0.035
Eigenvalue	4.38	**Wilks' λ**	0.536
%Variance	100%	**Eigenvalue**	0.865
p	< 0.001	**% Variance**	100%
		p	0.005

Table 15. Classification results for ecoregion 3 interspecific comparison. Values listed indicate how many specimens of each species were correctly classified by DA.

	Species	% Correct	Predicted Group Membership *U. americanus*	Predicted Group Membership *U. arctos*	Total	
Original	*U. americanus*	97.1	33	1	34	
	U. arctos	100	0	25	25	98.30%
Cross- Validated	*U. americanus*	97.1	33	1	34	
	U. arctos	100	0	25	25	98.30%

Table 16. Classification results for ecoregion 6 interspecific comparison. Values listed indicate how many specimens of each species were correctly classified by DA.

		Species	% Correct	Predicted Group Membership *U. americanus*	Predicted Group Membership *U. arctos*	Total	
Length	Original	*U. americanus*	100	354	0	354	
		U. arctos	99.5	1	204	205	99.80%
	Cross-Validated	*U. americanus*	100	354	0	354	
		U. arctos	99	2	203	205	99.60%
Ratio	Original	*U. americanus*	89	315	39	354	
		U. arctos	64.7	72	132	204	80.1
	Cross-Validated	*U. americanus*	89	315	39	354	
		U. arctos	64.7	72	132	204	80.1

Table 17. Classification results for ecoregion 7 interspecific comparison. Values listed indicate how many specimens of each species were correctly classified by DA.

		Species	% Correct	Predicted Group Membership *U. americanus*	Predicted Group Membership *U. arctos*	Total	
Length	Original	*U. americanus*	100	383	0	383	
		U. arctos	98.7	7	529	536	99.20%
	Cross-Validated	*U. americanus*	100	383	0	383	
		U. arctos	98.7	7	529	536	99.20%
Ratio	Original	*U. americanus*	65.5	251	132	383	
		U. arctos	82.4	94	441	535	75.4
	Cross-Validated	*U. americanus*	65.3	250	133	383	
		U. arctos	82.2	95	440	535	75.2

Table 18. Classification results for ecoregion 9 interspecific comparison. Values listed indicate how many specimens of each species were correctly classified by DA.

		Species	% Correct	Predicted Group Membership		Total	
				U. americanus	*U. arctos*		
Length	**Original**	*U. americanus*	100	24	0	24	
		U. arctos	100	0	17	17	100.00%
	Cross-Validated	*U. americanus*	100	24	0	24	
		U. arctos	100	0	17	17	100.00%
Ratio	**Original**	*U. americanus*	78.3	18	5	23	
		U. arctos	56.3	7	9	16	69.2
	Cross-Validated	*U. americanus*	78.3	18	5	23	
		U. arctos	56.3	7	9	16	69.2

Table 19. Classification results for ecoregion 10 interspecific comparison. Values listed indicate how many specimens of each species were correctly classified by DA.

		Species	% Correct	Predicted Group Membership		Total	
				U. americanus	*U. arctos*		
Length	**Original**	*U. americanus*	98.5	66	1	67	
		U. arctos	96.7	1	29	30	97.90%
	Cross-Validated	*U. americanus*	98.5	66	1	67	
		U. arctos	96.7	1	29	30	97.90%
Ratio	**Original**	*U. americanus*	91	61	6	67	
		U. arctos	43.3	17	13	30	76.3
	Cross-Validated	*U. americanus*	91	61	6	67	
		U. arctos	43.3	17	13	30	76.3

Table 20. Classification results for ecoregion 13 interspecific comparison. Values listed indicate how many specimens of each species were correctly classified by DA.

		Species	% Correct	Predicted Group Membership		Total	
				U. americanus	*U. arctos*		
Length	**Original**	*U. americanus*	100	11	0	11	
		U. arctos	100	0	4	4	100.00%
	Cross-Validated	*U. americanus*	100	11	0	11	
		U. arctos	100	0	4	4	100.00%
Ratio	**Original**	*U. americanus*	100	11	0	11	
		U. arctos	50	2	2	4	86.7
	Cross-Validated	*U. americanus*	90.9	10	1	11	
		U. arctos	50	2	2	4	80

ANOVA found significant intraspecific differences for all tooth lengths studied in every ecoregion except for ecoregion 3 and significant differences for ratios varied in every ecoregion studied (Table 21). Males and females of both species had similar means and standard deviations in ecoregion 3, something that was not observed at the continental level. *F* test values for lengths varied for each ecoregion, but overall indicate the null hypothesis is unlikely for tooth lengths with the exception of ecoregion 3.

Table 21. ANOVA results for intraspecific comparison. Values listed include mean and standard deviation (SD), along with *F* values and *p* values. See table 6 for abbreviations list.

		Ecoregion 3		
	Mean (SD) FBB	**Mean (SD) MBB**	**F**	**P**
p4	9.23 (0.62)	9.23 (0.88)	0	0.999
m1	17.08 (0.34)	18.00 (0.99)	3.92	0.06
m2	17.58 (0.35)	18.69 (1.34)	3.23	0.08
m3	13.71 (1.03)	14.80 (1.03)	4.16	0.05
p4/m1	0.54 (0.03)	0.51 (0.04)	1.31	0.266
m2/m1	1.02 (0.02)	1.03 (0.04)	0.193	0.666
m3/m1	0.80 (0.06)	0.82 (0.05)	0.535	0.474
p4/m3	0.67 (0.03)	0.62 (0.06)	2.57	0.126
m2/m3	1.28 (0.07)	1.26 (0.07)	0.35	0.559
	Mean (SD) FGB	**Mean (SD) MGB**	**F**	**P**
p4	12.22 (1.20)	12.58 (1.12)	0.485	0.494
m1	23.54 (1.25)	24.91 (1.23)	5.86	0.025
m2	24.77 (1.27)	25.36 (1.40)	0.895	0.355
m3	19.20 (1.99)	20.47 (1.36)	3.06	0.096
p4/m1	.51 (0.03)	0.50 (0.04)	0.523	0.478
m2/m1	1.05 (0.03)	1.01 (0.04)	3.27	0.086
m3/m1	0.81 (0.08)	0.82 (0.04)	0.039	0.844
p4/m3	0.63 (0.06)	0.61 (0.05)	0.722	0.406
m2/m3	1.29 (0.09)	1.24 (0.08)	1.9	0.183

		Ecoregion 6		
	Mean (SD) FBB	**Mean (SD) MBB**	**F**	**P**
p4	8.84 (0.75)	12.47 (1.03)	688.414	< 0.001
m1	17.45 (1.05)	23.08 (1.26)	989.002	< 0.001
m2	18.25 (1.07)	23.65 (1.27)	881.678	< 0.001

m3	13.90 (1.03)	19.46 (1.57)	770.815	< 0.001
p4/m1	0.50 (0.04)	0.54 (0.03)	26.863	< 0.001
m2/m1	1.04 (0.04)	1.02 (0.03)	11.523	0.001
m3/m1	0.79 (0.05)	0.84 (0.07)	19.723	< 0.001
p4/m3	0.63 (0.05)	0.64 (0.06)	0.3	0.584
m2/m3	1.31 (0.08)	1.22 (0.10)	44.596	< 0.001
	Mean (SD) FGB	**Mean (SD) MGB**	**F**	**P**
p4	9.23 (0.75)	13.33 (1.21)	1033.157	< 0.001
m1	18.19 (0.87)	24.27 (1.29)	1914.127	< 0.001
m2	19.25 (1.01)	25.24 (1.17)	1808.703	< 0.001
m3	14.72 (1.14)	20.61 (1.67)	1057.367	< 0.001
p4/m1	0.50 (0.03)	0.54 (0.04)	60.228	< 0.001
m2/m1	1.05 (0.04)	1.04 (0.03)	11.462	0.001
m3/m1	0.80 (0.05)	0.85 (0.06)	25.126	< 0.001
p4/m3	0.62 (0.05)	0.64 (0.06)	5.65	0.018
m2/m3	1.31 (0.08)	1.22 (0.08)	54.401	< 0.001

Ecoregion 7

	Mean (SD) FBB	**Mean (SD) MBB**	**F**	**P**
p4	9.38 (0.79)	13.08 (0.95)	759.601	< 0.001
m1	17.61 (1.00)	23.74 (1.44)	1031.475	< 0.001
m2	18.61 (1.17)	24.12 (1.30)	846.384	< 0.001
m3	14.76 (1.38)	19.43 (1.48)	454.999	< 0.001
p4/m1	0.53 (0.03)	0.55 (0.04)	10.014	0.002
m2/m1	1.05 (0.04)	1.01 (0.03)	43.695	< 0.001
m3/m1	0.83 (0.06)	0.82 (0.06)	3.431	0.066
p4/m3	0.63 (0.05)	0.67 (0.05)	18.535	< 0.001
m2/m3	1.26 (0.09)	1.24 (0.08)	2.48	0.117
	Mean (SD) FGB	**Mean (SD) MGB**	**F**	**P**
p4	9.84 (0.84)	13.66 (0.90)	1401.618	< 0.001
m1	18.32 (0.92)	24.35 (1.81)	1222.29	< 0.001

m2	19.51 (1.03)	25.01 (1.69)	1082.38	< 0.001
m3	15.50 (1.40)	20.52 (1.71)	740.129	< 0.001
p4/m1	0.53 (0.03)	0.56 (0.04)	28.477	< 0.001
m2/m1	1.06 (0.04)	1.02 (0.06)	29.299	< 0.001
m3/m1	0.84 (0.07)	0.84 (0.07)	0.037	0.848
p4/m3	0.63 (0.05)	0.66 (0.05)	22.613	< 0.001
m2/m3	1.26 (0.10)	1.22 (0.07)	17.052	< 0.001
		Ecoregion 9		
	Mean (SD) FBB	**Mean (SD) MBB**	**F**	**P**
p4	8.63 (1.12)	11.96 (0.68)	36.907	< 0.001
m1	17.54 (1.26)	22.72 (1.12)	61.336	< 0.001
m2	18.48 (1.48)	23.81 (0.75)	56.311	< 0.001
m3	14.58 (1.51)	19.95 (2.53)	28.534	< 0.001
p4/m1	0.49 (0.04)	0.52 (0.02)	3.168	0.097
m2/m1	1.05 (0.03)	1.04 (0.02)	0.068	0.798
m3/m1	0.83 (0.06)	0.87 (0.10)	1.354	0.264
p4/m3	0.59 (0.06)	0.60 (0.06)	0.104	0.752
m2/m3	1.27 (0.08)	1.20 (0.14)	1.254	0.282
	Mean (SD) FGB	**Mean (SD) MGB**	**F**	**P**
p4	9.02 (0.80)	12.59 (1.00)	37.991	< 0.001
m1	18.98 (1.12)	23.40 (1.06)	41.503	< 0.001
m2	19.94 (1.37)	25.23 (1.73)	28.567	0.001
m3	15.52 (0.73)	21.74 (1.72)	55.144	< 0.001
p4/m1	0.47 (0.03)	0.53 (0.02)	10.767	0.011
m2/m1	1.05 (0.03)	1.07 (0.02)	1.742	0.223
m3/m1	0.81 (0.05)	0.92 (0.06)	7.635	0.025
p4/m3	0.58 (0.03)	0.58 (0.05)	0	0.985
m2/m3	1.28 (0.07)	1.16 (0.09)	5.098	0.054
		Ecoregion 10		
	Mean (SD) FBB	**Mean (SD) MBB**	**F**	**P**
p4	8.69 (0.71)	12.33 (1.01)	96.647	< 0.001
m1	17.42 (0.79)	22.58 (1.03)	171.271	< 0.001
m2	18.04 (1.07)	23.81 (1.37)	119.931	< 0.001

m3	13.93 (1.01)	19.73 (1.90)	100.364	< 0.001
p4/m1	0.49 (0.03)	0.54 (0.03)	8.756	0.008
m2/m1	1.03 (0.03)	1.05 (0.03)	1.359	0.257
m3/m1	0.80 (0.04)	0.87 (0.05)	11.602	0.003
p4/m3	0.62 (0.05)	0.62 (0.03)	0.004	0.95
m2/m3	1.29 (0.04)	1.21 (0.05)	13.519	0.001
	Mean (SD) FGB	**Mean (SD) MGB**	**F**	**P**
p4	9.14 (0.80)	12.23 (1.22)	93.45	< 0.001
m1	18.33 (1.02)	23.53 (1.46)	177.24	< 0.001
m2	19.33 (1.02)	25.04 (1.28)	240.282	< 0.001
m3	14.83 (1.19)	20.62 (1.64)	167.011	< 0.001
p4/m1	0.50 (0.04)	0.52 (0.04)	1.657	0.206
m2/m1	1.05 (0.03)	1.06 (0.04)	0.622	0.435
m3/m1	0.80 (0.05)	0.87 (0.09)	9.412	0.004
p4/m3	0.61 (0.06)	0.59 (0.07)	1.073	0.307
m2/m3	1.30 (0.08)	1.22 (0.09)	8.386	0.006

		Ecoregion 13		
	Mean (SD) FBB	**Mean (SD) MBB**	**F**	**P**
p4	7.66 (0.70)	10.59 (0.99)	41.463	< 0.001
m1	16.94 (0.97)	20.64 (0.85)	44.884	< 0.001
m2	17.35 (1.23)	21.17 (1.33)	34.954	< 0.001
m3	13.14 (0.89)	17.11 (0.90)	56.938	< 0.001
p4/m1	0.45 (0.03)	0.51 (0.02)	11.241	0.005
m2/m1	1.02 (0.03)	1.05 (0.02)	2.509	0.137
m3/m1	0.77 (0.03)	0.83 (0.07)	3.819	0.073
p4/m3	0.58 (0.03)	0.62 (0.09)	1.573	0.232
m2/m3	1.32 (0.06)	1.27 (0.15)	0.726	0.41
	Mean (SD) FGB	**Mean (SD) MGB**	**F**	**P**
p4	8.26 (0.75)	11.94 (1.33)	56.44	< 0.001
m1	18.07 (0.89)	22.12 (1.66)	45.67	< 0.001
m2	18.77 (0.84)	24.17 (1.02)	132.987	< 0.001
m3	13.97 (0.94)	20.20 (2.48)	63.101	< 0.001
p4/m1	0.45 (0.03)	0.53 (0.02)	20.078	< 0.001
m2/m1	1.04 (0.04)	1.09 (0.09)	2.856	0.11

m3/m1	0.77 (0.05)	0.91 (0.12)	11.053	0.004
p4/m3	0.59 (0.05)	0.59 (0.08)	0.019	0.893
m2/m3	1.34 (0.08)	1.20 (0.12)	7.371	0.015

Stepwise DFA produced low Wilks' λ values and significant *p* values for lengths of all ecoregions for both species except ecoregion 3 (Table 22). Discriminant function 1 revealed ratios did not significantly contribute to intraspecific separation of sexes. With the exception of ecoregion 3, every ecoregion had a > 99.0% correct intraspecific classification when lengths were cross validated (Tables 23 - 33). Ecoregion 3 had a relatively high correct classification for distinguishing sexes (*U. americanus* = 80.0%; *U. arctos* = 81.8%), but when cross validated percentages were lower (*U. americanus* = 75.0%; *U. arctos* = 77.3%).

Table 22. Structure matrix results for intraspecific comparison of sexes from ecoregions 3, 6, 7, 9, 10 and 13. Values listed include variable contribution to separation, Wilks' λ, eigenvalue, % variance, and *p* value.

Ecoregion 3

	Function 1 BB	Function 1 GB		Function 1 BB	Function 1 GB
p4	0.365	0.551	**p4/m1**	N/A	N/A
m1	0.417	1	**m2/m1**	N/A	N/A
m2	0.664	0.709	**m3/m1**	N/A	N/A
m3	1	0.504	**p4/m3**	N/A	N/A
Wilks	0.812	0.773	**m2/m3**	N/A	N/A
Eigenvalue	0.231	0.293	**Wilks**	N/A	N/A
% Variance	100%	100%	**Eigenvalue**	N/A	N/A
p	0.05	0.025	**% Variance**	N/A	N/A
			p	N/A	N/A

Ecoregion 9

	Function 1 BB	Function 1 GB		Function 1 BB	Function 1 GB
p4	0.775	0.296	**p4/m1**		1
m1	1	0.33	**m2/m1**		0.613
m2	0.903	0.45	**m3/m1**		0.102
m3	0.566	1	**p4/m3**		0.578
Wilks	0.186	0.127	**m2/m3**		0.099
Eigenvalue	4.381	6.893	**Wilks**		0.426
% Variance	100%	100%	**Eigenvalue**		1.346
p	<0.001	<0.001	**% Variance**		100%
			p		0.011

Ecoregion 6

	Function 1 BB	Function 1 GB		Function 1 BB	- Function 1 GB
p4	0.675	0.666	**p4/m1**	0.468	0.688
m1	0.809	0.896	**m2/m1**	-0.308	-0.306
m2	0.812	0.868	**m3/m1**	0.403	0.451
m3	0.715	0.672	**p4/m3**	0.05	-0.195
Wilks	0.1	0.092	**m2/m3**	-0.606	-0.683
Eigenvalue	9.038	9.817	**Wilks**	0.579	0.647
% Variance	100%	100%	**Eigenvalue**	0.728	0.545
p	< 0.001	<0.001	**% Variance**	100%	100%
			p	<0.001	<0.001

Ecoregion 10

	Function 1 BB	Function 1 GB		Function 1 BB	Function 1 GB
p4	0.554	0.357	**p4/m1**	-0.565	0.28
m1	1	0.67	**m2/m1**	-0.101	0.502
m2	0.819	0.927	**m3/m1**	-0.646	1
m3	0.687	0.773	**p4/m3**	-0.014	-0.507
Wilks	0.105	0.122	**m2/m3**	0.795	-0.861
Eigenvalue	8.564	7.173	**Wilks**	0.483	0.806
% Variance	100%	100%	**Eigenvalue**	1.069	0.241
p	< 0.001	< 0.001	**% Variance**	100%	100%
			p	0.001	0.004

Ecoregion 7

	Function 1 BB	Function 1 GB		Function 1 BB	- Function 1 GB
p4	0.666	0.869	**p4/m1**	0.688	-0.526
m1	0.896	0.812	**m2/m1**	-0.306	0.534
m2	0.868	0.712	**m3/m1**	0.541	0.146
m3	0.672	0.632	**p4/m3**	0.195	-0.598
Wilks	0.092	0.138	**m2/m3**	-0.683	0.24
Eigenvalue	9.817	6.245	**Wilks**	0.647	0.743
% Variance	100%	100%	**Eigenvalue**	0.545	0.346

Ecoregion13

	Function 1 BB	Function 1 GB		Function 1 BB	Function 1 GB
p4	0.29	0.441	**p4/m1**	1	1
m1	0.38	0.294	**m2/m1**	0.033	0.214
m2	0.309	1	**m3/m1**	0.075	0.195
m3	1	0.369	**p4/m3**	0.699	0.519
Wilks	0.186	0.107	**m2/m3**	-0.035	-0.097
Eigenvalue	4.38	8.312	**Wilks**	0.536	0.443
% Variance	100%	100%	**Eigenvalue**	0.865	1.255

p	< 0.001	< 0.001	**% Variance**	100%	100%	***p***	< 0.001	< 0.001	**% Variance**	100%	100%
			p	< 0.001	< 0.001				***p***	0.005	< 0.001

Table 23. Classification results for intraspecific comparison of sexes from ecoregion 3. Values listed indicate how many specimens of each species were correctly classified by DA.

		Species	% Correct	Predicted Group Membership 1	2	Total	
***U. americanus* Length**	Original	*Female*	40%	2	3	5	
		Male	93.3%	1	14	15	80.00%
	Cross-Validated	*Female*	20%	1	4	5	
		Male	93.3%	1	14	15	75.00%
***U. arctos* Length**	Original	*Female*	57.1%	4	3	7	
		Male	93.3%	1	14	15	81.80%
	Cross-Validated	*Female*	42.9%	3	4	7	
		Male	93.3%	1	14	15	77.30%

Table 24. Classification results for intraspecific comparison of *Ursus americanus* sexes from ecoregion 6. Values listed indicate how many specimens of each species were correctly classified by DA.

		Species	% Correct	Predicted Group Membership 1	2	Total	
Length	Original	*Female*	100%	102	0	102	
		Male	98.5%	1	67	68	99.40%
	Cross-Validated	*Female*	100%	102	0	102	
		Male	98.5%	1	67	68	99.40%
Ratio	Original	*Female*	87.3%	89	13	102	
		Male	71.6%	19	48	67	81.1%
	Cross-Validated	*Female*	87.3%	89	13	102	
		Male	70.1%	20	47	67	81.1%

Table 25. Classification results for intraspecific comparison of *Ursus arctos* sexes from ecoregion 6. Values listed indicate how many specimens of each species were correctly classified by DA.

		Species	% Correct	Predicted Group Membership 1	2	Total	
Length	Original	*Female*	100%	141	0	141	
		Male	100%	0	95	95	100.00%
	Cross-Validated	*Female*	100%	141	0	141	
		Male	100%	0	95	95	100.00%
Ratio	Original	*Female*	85.8%	121	20	141	
		Male	73.7%	25	70	95	80.9%
	Cross-Validated	*Female*	85.8%	121	20	141	
		Male	72.6%	26	69	95	80.5%

Table 26. Classification results for intraspecific comparison of *Ursus americanus* sexes from ecoregion 7. Values listed indicate how many specimens of each species were correctly classified by DA.

		Species	% Correct	Predicted Group Membership 1	2	Total	
Length	Original	*Female*	100%	141	0	141	
		Male	100%	0	95	95	100.00%
	Cross-Validated	*Female*	100%	141	0	141	
		Male	100%	0	95	95	100.00%
Ratio	Original	*Female*	85.8%	121	20	141	
		Male	73.7%	25	70	95	80.9%
	Cross-Validated	*Female*	85.8%	121	20	141	
		Male	72.6%	26	69	95	80.5%

Table 27. Classification results for intraspecific comparison of *Ursus arctos* sexes from ecoregion 7. Values listed indicate how many specimens of each species were correctly classified by DA.

		Species	% Correct	Predicted Group Membership 1	2	Total	
Length	Original	*Female*	100%	134	0	134	
		Male	98.2%	3	162	165	99.00%
	Cross-Validated	*Female*	100%	134	0	134	
		Male	98.2%	3	162	165	99.00%
Ratio	Original	*Female*	69.1%	94	42	136	
		Male	78.6%	36	132	168	74.3%
	Cross-Validated	*Female*	69.1%	94	42	136	
		Male	78.6%	36	132	168	74.3%

Table 28. Classification results for intraspecific comparison of *Ursus americanus* sexes from ecoregion 9. Values listed indicate how many specimens of each species were correctly classified by DA.

		Species	% Correct	Predicted Group Membership 1	2	Total	
Length	Original	*Female*	100%	13	0	13	
		Male	100%	0	5	5	100.00%
	Cross-Validated	*Female*	100%	13	0	13	
		Male	100%	0	5	5	100.00%
Ratio	Original	*Female*	N/A	N/A	N/A	N/A	
		Male	N/A	N/A	N/A	N/A	
	Cross-Validated	*Female*	N/A	N/A	N/A	N/A	
		Male	N/A	N/A	N/A	N/A	

Table 29. Classification results for intraspecific comparison of *Ursus arctos* sexes from ecoregion 9. Values listed indicate how many specimens of each species were correctly classified by DA.

		Species	% Correct	Predicted Group Membership 1	Predicted Group Membership 2	Total	
Length	Original	*Female*	100%	6	0	6	
		Male	100%	0	5	5	100.00%
	Cross-Validated	*Female*	100%	6	0	6	
		Male	100%	0	5	5	100.00%
Ratio	Original	*Female*	80%	4	1	5	
		Male	80%	1	4	5	80%
	Cross-Validated	*Female*	80%	4	1	5	
		Male	80%	1	4	5	80%

Table 30. Classification results for intraspecific comparison of *Ursus americanus* sexes from ecoregion 10. Values listed indicate how many specimens of each species were correctly classified by DA.

		Species	% Correct	Predicted Group Membership 1	Predicted Group Membership 2	Total	
Length	Original	*Female*	100%	15	0	15	
		Male	100%	0	9	9	100.00%
	Cross-Validated	*Female*	100%	15	0	15	
		Male	100%	0	9	9	100.00%
Ratio	Original	*Female*	92.9%	13	1	14	
		Male	75%	2	6	8	86.4%
	Cross-Validated	*Female*	92.9%	13	1	14	
		Male	62.5%	3	5	8	81.8%

Table 31. Classification results for intraspecific comparison of *Ursus arctos* sexes from ecoregion 10. Values listed indicate how many specimens of each species were correctly classified by DA.

		Species	% Correct	Predicted Group Membership 1	2	Total	
Length	Original	*Female*	100%	27	0	27	
		Male	100%	0	14	14	100.00%
	Cross-Validated	*Female*	100%	27	0	27	
		Male	100%	0	14	14	100.00%
Ratio	Original	*Female*	96.3%	26	1	27	
		Male	50%	7	7	14	80.5%
	Cross-Validated	*Female*	96.3%	26	1	27	
		Male	50%	7	7	14	80.5%

Table 32. Classification results for intraspecific comparison of *Ursus americanus* sexes from ecoregion 13. Values listed indicate how many specimens of each species were correctly classified by DA.

		Species	% Correct	Predicted Group Membership 1	2	Total	
Length	Original	*Female*	100%	11	0	11	
		Male	100%	0	4	4	100.00%
	Cross-Validated	*Female*	100%	11	0	11	
		Male	100%	0	4	4	100.00%
Ratio	Original	*Female*	100%	11	0	11	
		Male	50%	2	2	4	86.7%
	Cross-Validated	*Female*	90.9%	10	1	11	
		Male	50%	2	2	4	80%

Table 33. Classification results for intraspecific comparison of *Ursus arctos* sexes from ecoregion 13. Values listed indicate how many specimens of each species were correctly classified by DA.

		Species	% Correct	Predicted Group Membership 1	2	Total	
Length	Original	*Female*	100%	13	0	13	
		Male	100%	0	5	5	100.00%
	Cross-Validated	*Female*	100%	13	0	13	
		Male	100%	0	5	5	100.00%
Ratio	Original	*Female*	100%	13	0	13	
		Male	80%	1	4	5	94.4%
	Cross-Validated	*Female*	84.6%	11	2	13	
		Male	80%	1	4	5	83.3%

Latitude

MANCOVA results show varying significance for lengths and ratios (Table 34). When comparing individual tooth lengths and ratios to latitude, all variables studied had an r^2 values < 0.2 indicating there is no strong correlations thought there were significant weak associations for some variables (Tables 35 and 36). r^2 values were lower for *U. arctos* showing less of a correlation than what was observed in *U. americanus*, but still significant.

Table 34. MANCOVA results when comparing latitude to species and sexes. Values listed included *F* values, *p* values, r^2=coefficient of determination, SS=sum of squares.

		F	***p***	**SS**	**r2**
p4	**Latitude**	181.188	< 0.001	161.457	0.161
	Species	142.356	< 0.001	126.854	
	Sex	32.099	< 0.001	85.809	
m1	**Latitude**	6.344	0.012	10.981	0.095
	Species	189.942	< 0.001	328.762	
	Sex	41.778	< 0.001	216.933	
m2	**Latitude**	0.493	0.483	0.888	0.084
	Species	180.828	< 0.001	325.763	
	Sex	70.356	< 0.001	380.241	
m3	**Latitude**	0.473	0.492	1.079	0.073
	Species	118.372	< 0.001	270.159	
	Sex	44.757	< 0.001	306.442	
p4/m1	**Latitude**	181.049	< 0.001	0.367	0.149
	Species	2.916	0.088	0.006	
	Sex	0.607	0.611	0.004	
m2/m1	**Latitude**	3.199	0.174	0.007	0.013
	Species	0.75	0.386	0.002	
	Sex	6.924	< 0.001	0.044	
m3/m1	**Latitude**	3.056	0.081	0.014	< 0.001
	Species	0.983	0.321	0.005	
	Sex	4.725	0.003	0.066	
p4/m3	**Latitude**	209.971	< 0.001	0.583	0.181
	Species	69.191	< 0.001	0.192	
	Sex	1.386	0.245	0.012	
m2/m3	**Latitude**	20.971	< 0.001	0.107	0.11
	Species	309.804	< 0.001	1.611	
	Sex	0.64	0.589	0.01	

Table 35. Parameters for interspecific regressions of lower tooth lengths and ratios against latitude for *U. americanus*. Values listed included a=intercept, b=slope, r^2=coefficient of determination, SE=standard error, %SEE=% standard error of the estimate, *F* values, *p* values.

	a	b	r^2	SE	%SEE	*F*	*p*
p4	7.64	0.03	0.115	0.133	0.87	138.447	<0.001
m1	18.61	-0.01	0.012	0.164	1.09	13.36	<0.001
m2	19.44	0.00805	0.004	0.189	1.25	4.675	0.031
m3	14.77	0.000893	0	0.202	1.33	0.05	0.823
p4/m1	0.41	0.00206	0.171	0.007	0.04	219.166	<0.001
m2/m1	1.05	0.000237	0.003	0.007	0.04	3.276	0.071
m3/m1	0.79	0.00064	0.011	0.01	0.06	11.382	0.001
p4/m3	0.39	0.00186	0.163	0.007	0.04	206.559	<0.001
m2/m3	0.76	0.000421	0.007	0.008	0.05	7.398	0.007

Table 36. Parameters for interspecific regressions of lower tooth lengths and ratios against latitude for *U. arctos*. See table 35 for listed values.

	a	b	r^2	SE	%SEE	*F*	*p*
p4	11.23	0.04	0.064	0.253	1.06	64.013	<0.001
m1	21.14	0.05	0.059	0.371	1.56	59.756	<0.001
m2	23.27	0.03	0.016	0.373	1.57	15.625	<0.001
m3	20.65	-0.00725	0.001	0.435	1.78	0.881	0.348
p4/m1	0.53	0.000422	0.006	0.01	0.04	5.627	0.018
m2/m1	1.09	-0.00108	0.029	0.011	0.04	28.287	<0.001
m3/m1	0.97	-0.00214	0.049	0.018	0.07	46.618	<0.001
p4/m3	0.55	0.00198	0.056	0.015	0.06	53.617	<0.001
m2/m3	1.14	0.00158	0.017	0.022	0.08	16.263	<0.001

Climate

MANCOVA using tooth lengths and ratios in *U. americanus* and *U. arctos* with mean annual temperature and minimum temperature of the coldest month as covariates yielded varying significance values (Table 37). r^2 values less than 0.08 for mean annual temperature (Table 38) and 0.09 for minimum temperature of the coldest month (Table 39) indicate there is minimal correlation, however some were statistically significant. Mean annual temperature has weak, but significant impact on length of the p4 and m3, as well as all ratios including those variables (p4/m1, m3/m1, p4/m3, and m2/m3). Neither m1 nor m2 length significantly associated with annual mean temperature. Minimum temperature of the coldest month is significantly associated with length of the m3 and m3/m1 ratio.

Table 37. MANOVA results for mean annual temperature and minimum temperature of the coldest month. For listed values see table 34.

		F	***p***	**SS**	**r2**
p4	**AMT**	191.072	< 0.001	180.564	0.081
	MINT	153.158	< 0.001	144.735	0.02
	Species	5509.84	< 0.001	5206.819	
	Sex	3.536	0.014	10.026	
m1	**AMT**	0.32	0.572	0.554	0.061
	MINT	0	0.978	0.001	0.024
	Species	7015.63	< 0.001	12162.806	
	Sex	2.115	0.096	10.999	
m2	**AMT**	0.049	0.824	0.096	0.053
	MINT	0.008	0.93	0.015	0.02
	Species	5903.65	< 0.001	11514.72	
	Sex	1.133	0.335	6.628	
m3	**AMT**	1.158	0.282	2.718	0.04
	MINT	4.185	0.041	9.828	0.011
	Species	4493.343	< 0.001	10551.213	
	Sex	2.949	0.032	20.773	
p4/m1	**AMT**	205.279	< 0.001	0.409	0.058
	MINT	162.13	< 0.001	0.323	0.009
	Species	221.909	< 0.001	0.442	
	Sex	2.276	0.078	0.014	
m2/m1	**AMT**	0.025	0.874	< 0.001	0.008
	MINT	0.357	0.55	0.001	0.005
	Species	74.368	< 0.001	0.143	
	Sex	1.155	0.326	0.007	
m3/m1	**AMT**	1.955	0.162	0.009	0
	MINT	7.483	0.006	0.033	0.003
	Species	60.008	< 0.001	0.266	
	Sex	0.988	0.397	0.013	
p4/m3	**AMT**	174.968	< 0.001	0.493	0.097
	MINT	120.857	< 0.001	0.341	0.029
	Species	3329.874	< 0.001	0.9386	
	Sex	1.091	0.352	0.009	
m2/m3	**AMT**	7.731	0.005	0.04	0.073
	MINT	2.933	0.087	0.015	0.029

Species	13712.058	< 0.001	70.257
Sex	1.838	0.138	0.028

Table 38. Parameters for interspecific regressions of lower tooth lengths and ratios against latitude. See table 35 for listed values and abbreviations.

			Mean Annual Temperature BB				
	a	**b**	**r**	**SE**	**%SEE**	**F**	**P**
p4	9.31	-0.01	0.035	0.04	0.927	35.627	<0.001
m1	17.88	0.01	0.024	0.047	1.09	24.876	<0.001
m2	18.89	0.01	0.016	0.054	1.25	16.396	<0.001
m3	14.68	0.00786	0.009	0.058	1.33	8.43	0.004
p4/m1	0.52	0.000939	0.08	0.002	0.04	85.77	<0.001
m2/m1	1.06	0.0000778	0.001	0.002	0.04	0.777	0.378
m3/m1	0.82	-0.0000846	<0.001	0.003	0.06	0.429	0.513
p4/m3	0.49	-0.000856	0.077	0.002	0.04	82.381	<0.001
m2/m3	0.78	0.0000141	<0.001	0.002	0.05	0.018	0.894
			Mean Annual Temperature GB				
p4	**a**	**b**	**r**	**SE**	**%SEE**	**F**	**P**
m1	13.26	-0.00791	0.008	0.044	1.11	6.642	0.01
m2	24.07	-0.03	0.056	0.06	1.51	48.614	<0.001
m3	24.81	-0.02	0.028	0.061	1.55	23.826	<0.001
p4/m1	20.21	0.00175	<0.001	0.07	1.75	0.128	0.721
m2/m1	0.55	0.000321	0.01	0.002	0.04	8.071	0.005
m3/m1	1.03	0.000409	0.013	0.002	0.04	11.059	0.001
p4/m3	0.84	0.00114	0.042	0.003	0.069	33.987	<0.001
m2/m3	0.66	0.000437	0.087	0.003	0.06	5.909	0.015
	1.23	0.00107	0.023	0.004	0.089	18.338	<0.001

Table 39. Parameters for interspecific regressions of lower tooth lengths and ratios against latitude. See table 35 for values listed and abbreviations.

	a	b	r	SE	%SEE	F	P
	Minimum Temperature of the Coldest Month BB						
	a	**b**	**r**	**SE**	**%SEE**	**F**	**P**
p4	9.11	-0.00458	0.01	0.033	0.939	9.763	0.002
m1	18.12	0.00793	0.022	0.038	1.09	22.22	<0.001
m2	19.12	0.00882	0.021	0.044	1.25	20.928	<0.001
m3	14.88	0.00853	0.017	0.047	1.32	17.227	<0.001
p4/m1	0.5	-0.000493	0.038	0.002	0.05	38.89	<0.001
m2/m1	1.06	0.0000165	<0.001	0.002	0.04	0.06	0.807
m3/m1	0.82	0.000102	0.001	0.002	0.06	1.078	0.299
p4/m3	0.48	-0.000472	0.041	0.002	0.04	41.452	<0.001
m2/m3	0.78	0.0000896	0.001	0.002	0.05	1.225	0.269
	Minimum Temperature of the Coldest Month GB						
	a	**b**	**r**	**SE**	**%SEE**	**F**	**P**
p4	13.25	0.0027	0.002	0.051	1.11	1.775	0.183
m1	23.62	-0.02	0.039	0.069	1.59	32.957	<0.001
m2	24.46	-0.01	0.025	0.07	1.55	21.195	<0.001
m3	20.23	-0.000251	<0.001	0.082	1.75	0.006	0.937
p4/m1	0.56	0.000475	0.05	0.002	0.04	42.471	<0.001
m2/m1	1.04	0.000164	0.005	0.002	0.04	4.081	0.044
m3/m1	0.86	0.00059	0.026	0.003	0.07	21.092	<0.001
p4/m3	0.66	0.000127	0.002	0.003	0.06	1.162	0.281
m2/m3	1.21	-0.000621	0.018	0.004	0.08	14.376	<0.001

Fossil

Stepwise DFA was utilized to classify fossil specimens as *U. americanus* or *U. arctos*. Stepwise DFA was not used to classify fossils as male or female within the two species due to its low reliability. Eighty-five fossil specimens were assessed, but only 18 were capable of inclusion in the stepwise DFA analysis for length. Out of these 18 specimens, 15 were classified as *U. americanus* and three were classified as *U. arctos* (Table 40). OCRA 3040 was classified as *U. americanus* with 99.8% confidence.

Table 40. Classification results for fossils. Values listed indicate how many specimens of each species were correctly classified by DA.

	Species	% Correct	Predicted Group Membership		Total	
			1	2		
Original	*U. americnaus*	99.7	1032	3	1035	
	U. arctos	98.1	17	880	897	99.0%
	Fossil		15	3	18	
Cross- Validated	*U. americnaus*	99.7	1032	3	1035	
	U. arctos	98.1	17	880	897	99.0%

The stepwise DFA analysis was able to utilize 17 fossil specimens when utilizing ratio. Of these 17 specimens, 13 were classified as *U. americanus* (Table 41). The ORCA specimen was similarly classified as *U. americanus* with 51.6% confidence by the DFA. Seven of the 17 fossil specimens were originally identified as one species but was classified as another species by this DFA.

Table 41. Classification results for fossils. Values listed indicate how many specimens of each species were correctly classified by DA.

	Species	**% Correct**	**Predicted Group Membership**		**Total**	
			U. americanus	*U. arctos*		
Original	*U. americnaus*	79	817	217	1034	
	U. arctos	76.2	213	681	894	77.7%
	Fossil		13	4	17	
Cross- Validated	*U. americnaus*	78.8	815	219	1034	
	U. arctos	76.2	213	681	894	77.6%

CHAPTER 6

DISCUSSION

Oregon Caves National Monument

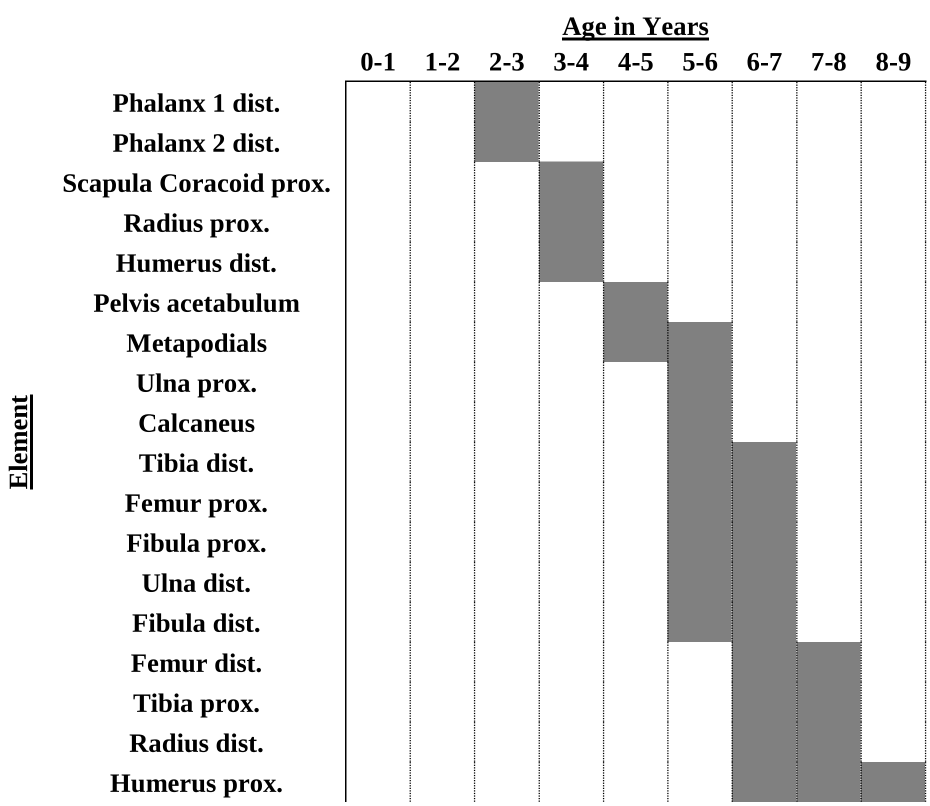
Species – Two species of *Ursus* are represented at ORCA, *U. americanus* and *U. arctos*. Despite the abundance of fossilized remains, only four elements were identified to species level. Distinguishing *U. americanus* and *U. arctos* based on osteological features alone proved difficult and Gilbert (1990) noted a great deal of overlap between potentially defining features. Additionally, most of the distinguishing postcranial features are found in the distal or proximal articular surfaces, which the ORCA specimens lack due to a majority of the epiphyses being unfused. A minimum of five individual ursids are present at ORCA based on lower right canines and the oldest specimen was roughly five years old at the time of death.

Ursus americanus commonly frequent caves for denning and fossil remains are often found in caves (Kurtén 1980). Fossils of Pleistocene *U. americanus* remains have been identified from caves across North America (Kurtén 1980; Graham 2008). Several geographic regions are not represented in the vast representation of *U. americanus* found in caves, including the Siskiyou Mountains of Northern California and Southern Oregon where ORCA is located. Because *U. americanus* is thought to have been larger in the late Pleistocene many of these identifications should be reassessed to confirm species assignments (Kurtén 1980; Wolverton and Lyman 1991; Graham 1991).

Age Demographics – The ursid fossil assemblage at ORCA overall, is dominated by relatively young individuals. The oldest specimens recovered are roughly five to six years of age based on degree of epiphyseal fusion in the calcaneum and proximal ulna (Weinstock 2008). In

2008, Weinstock studied the rates of epiphyseal fusion in *U. arctos*. He studied 86 skeletons of male and female *U. arctos* and came up with an average age range of epiphyseal fusions. Around two years of age, *U. arctos* phalanges begin to fuse; all phalanges at ORCA were fully fused. The last element which Weinstock observed fusion in is the proximal humerus and fusion happens between six and nine years of age; none of the humeri at ORCA had their proximal epiphyses fused. The majority of specimens from ORCA lacked fused distal and proximal epiphyses. Some specimens have epiphyses associated with them, but again, these remained unfused. Different stages of fusion and the associated age of specimens found at ORCA are in Table 42.

Table 42. Age of epiphyseal fusion in *U. arctos*. Modified from Weisnstock (2008) fusion schedule.



Sex Demographics – One baculum was found at ORCA showing male utilization of the cave; male utilization of caves is not uncommon (Kurtén 1968). Wolverton and Lyman (1996) indicated that at least five out of nine bears present at Lawson Cave (Missouri) were male and identified them as *U. americanus*. Ratio of males to females at ORCA is unknown at this time. Some authors have utilized sexual size dimorphism to indicate if remains are male or female (Kurtén 1976), however, due to the abundance of juvenile and immature specimens, this study did not cover that. The ORCA baculum represents an individual between four and six years old (Marks and Erikson 1966).

Inter/ Intraspecific Comparison

Results from ANOVA and DA analyses show a strong separation between *U. americanus* and *U. arctos* when tooth lengths are utilized and indicates this method can be reliably used to separate the two species. Further analysis shows the m1 was the most diagnostic measurement for separating the groups, similar to Gordon (1977) who found the length of the m1 showed 100% success rate in identifying *U. americanus* and *U. arctos.* The first permanent cheek teeth to develop in ursids are the m1 and M1 and in turn have the least amount of variation (Gingerich 1974; Polly 1998; Miller et al. 2009; Wolson et al. 2015). Additionally, Gordon (1977) claimed the m1 in *U. arctos* was no less than 20.4 mm and *U. americanus* m1s were shorter than this cutoff. This rule did not hold true in the current study as multiple examples of *U. arctos* having an m1 shorter than 20.4mm and *U. americanus* having an m1 longer than 20.4 mm were recorded. The shortest *U. arctos* m1 in our database measures 15.99 mm (USNM 075048) and the largest *U. americanus* m1 is 21.60 mm (AMNH 100043). Overall, *U. americanus* tooth lengths are shorter than *U. arctos* on average, however, there is a substantial amount of overlap between both species and there is not a sure cutoff to define *U. americanus* vs *U. arctos.* DA revealed ratios cannot distinguish between groups as well as lengths and overall this method would not be recommended. The most effective ratio at separating *U. americanus* and *U. arctos* was p4/m1.

ANOVA found length measurements were significant for intraspecific separation, however, Wilks' λ values showed minimal separation and classification analyses were only able to correctly distinguish between sexes 72.1% of the time. The m2 was best at distinguishing between sexes. When ratios were used to separate sexes, only the m2/m1 was found significant in *U. americanus*; no ratios were significant in separating *U. arctos* sexes. DA found the m2/m1 was most significant at separating between males and females of *U. americanus* and m3/m1 for *U. arctos*. Miller et al. (2009) found some sexual size dimorphism in *U. americanus* molars from Newfoundland, Alaska, the Adirondacks, and California with differences ranging from 6%, 7.4%, 10%, and 12.1%, respectively. Low rates of successfully separating sexes stems from the eruption timing of molars. Permanent molars begin erupting around three months of age, before estrogen or testosterone hormones develop, so the only factors contributing to molar size are genetics and prenatal development (Gingerich 1974; Daitch and Guralnick 2007; Miller et al. 2009; McDonough and Chrsit 2012; Wolson et al. 2015).

<u>Ecoregion</u>

Results from ANOVA and DA analyses show significant separation of species from all ecoregions studied when tooth lengths are utilized and indicates this method can be used reliably to separate the two species. In contrast to the previous section, when geographically separating *U. americanus* and *U. arctos* by ecoregion, ANOVA and DA distinguished between sexes of both species for every ecoregion except for ecoregion 3. Ratios which had a Wilks' λ less than 0.5 include: *U. arctos*, 9 and 13; *U. americanus* 10 and a correct classification greater than 80%

indicate intraspecific separation is plausible. Ecoregion divisions are determined based on present geologic and biological factors (EPA). Differences in diet by ecoregion may account for the separation of sexes that was not seen when examining the species at a continental level. However, as mentioned in the previous section, Miller et al. (2009) observed minimal sexual dimorphism in *U. americanus* and their study was at a smaller scale, only studying ursids from very specific geographic locations.

Latitude

Results from linear regression show there is no correlation between tooth length or ratio and latitude and indicates this method is not recommended to determine if *U. americanus* or *U. arctos* is present based on specimen latitude. McDonough and Christ (2012) mentioned the further north ursids live the more vegetation they include in their diet, which in turn cause them to hibernate for longer periods. Because tooth size is limited to prenatal development (Daitch and Gurlnick 2007) one might expect to see ursids living at higher latitudes to have smaller teeth due to a less nutritious diet (Sterns 1992; McDonough and Christ 2012). However, this correlation might not be seen because ursids at higher latitude hibernate for longer periods which means cubs have a longer exposure to a nutritious and fat-rich milk source.

Climate

Results from linear regression and MANCOVA analyses show there is no correlation between tooth length or ratio and climate, indicating this method would not be recommended to determine what species of ursid is present based on climate. Bergmann's Rule states body size of endotherms increases with colder climates due to advantages of low surface area to volume (Ashton et al. 2000; Meiri and Dayan 2003; Blackburn and Hawkins 2004; Rodrïguez et al.

2008). Ashton et al. (2000) found a positive correlation between body size and latitude with *U. arctos*. However, as mentioned previously, in ursids, the permanent cheek teeth begin developing around three months of age, but the body does not stop growing until later in life, offering little correlation between body size and tooth size (Miller et al. 2009). Additionally, this rule does not hold true as some of the largest *U. americanus* are found in Florida where temperatures are much warmer than other parts of their geographic range (Millar and Hickling 1990). Because the results reported here did not find any correlation between climate, latitude, and tooth size, there is no reason to suspect tooth sizes of *U. americanus* or *U. arctos* would have been any larger in the Pleistocene.

<u>Fossil</u>

Fossil specimens with the lowest percent correct classification are UCMP 3725 from California with 67.5% and a fossil specimen from Zesch Cave in Texas noted in Graham (1991) with 57.7%. UCMP 3725 has not been formally published but was given the identification *Ursus* and the Zesch Cave fossil was originally noted as *U. americanus*. For UCMP 3725, and the specimen from Zesch Cave, the lengths of all teeth fall within the zone where *U. americanus* and *U. arctos* tooth lengths overlap. Further analyses will need to be carried out to learn the proper identification of these specimens. Additionally, UCMP 35703 and 35704, both from California, should be studied further as they were cataloged at *U. arctos* but both were classified as *U. americanus* in this study.

Table 43. Predicted group membership for fossil specimens utilizing length. BB=Black Bear, GB=Brown Bear.

Fossil ID	Fossil Location	Original Group	Predicted Group	Probability	Predicted Group	Probability
Graham (1991)	Virginia (Bill Neff Cave)	BB	BB	0.967	GB	0.033
Kurten (1963)	Texas (Friesenhahn Cave)	BB	BB	0.869	GB	0.131
ORCA	Oregon (ORCA)	?	BB	0.998	GB	0.002
Gildey (1938)	Maryland (Cumberland Caves)	BB	BB	1.000	GB	0.000
Gildey (1938)	Maryland (Cumberland Caves)	BB	BB	0.981	GB	0.019
Gildey (1938)	Maryland (Cumberland Caves)	BB	BB	0.996	GB	0.004
Graham (1991)	Texas (Zesch Cave)	BB	GB	0.577	BB	0.423
OMNH 73400	Oklahoma	BB	BB	0.997	GB	0.003
UCMP 35709	California	BB	BB	0.674	GB	0.326
UCMP 8851	California	BB	BB	0.998	GB	0.002
UCMP 9502	California	BB	BB	0.989	GB	0.011
Kurten & Kay 1982	Mississippi	BB	BB	1.000	GB	0.000
UCMP 35703	California	GB	BB	0.999	GB	0.001
UCMP 35704	California	GB	BB	0.990	GB	0.010
UCMP 3002	California	Ursus	BB	0.983	GB	0.017
UCMP 3725	California	Ursus	GB	0.675	BB	0.325

A couple specimens which were originally identified as one species were classified by DFA as another. These include a specimen identified by Graham (1991) as *U. americanus* but was classified by the current analysis as *U. arctos* with 57.7% confidence. UCMP 35703 and 35704 are both cataloged as *U. arctos* but were classified as *U. americanus* with 99.0% confidence by this analysis. UCMP 3725 and 3002 were originally identified as *Ursus* but classified as *U. arctos* and *U. americanus,* respectively, by DFA with 67.5% and 98.3% confidence. Two specimens from Cumberland Caves (Gidley and Gazin 1938), one specimen from Zesch Cave (Graham 1991), and UCMP 35709 were originally identified as *U. americanus* but were classified as *U. arctos* with 96.8%, 51.7%, 53.6%, and 77.3% confidence, respectively. UCMP 35703 and 35704 were originally listed as *U. arctos* but were classified as *U. americanus* with 97.7% and 91.8% confidence, respectively. However, the percent correct classification was lower for ratios than lengths (77.7% vs 99.0%).

Table 44. Predicted group membership for fossil specimens utilizing ratios. BB=Black Bear, GB=Brown Bear

Fossil ID	Fossil Location	Original Group	Predicted Group	Probability	Predicted Group	Probability
Graham (1991)	Virginia (Bill Neff Cave)	BB	BB	0.874	GB	0.126
ORCA 3040	Oregon (ORCA)	?	BB	0.516	GB	0.484
Gildey (1938)	Maryland	BB	GB	0.968	BB	0.032
Gildey (1938)	Maryland	BB	GB	0.517	BB	0.483
Gildey (1938)	Maryland	BB	BB	0.505	GB	0.495
Graham (1991)	Texas (Zesch Cave)	BB	GB	0.536	BB	0.464
LACM 17161	California	BB	BB	0.535	GB	0.465
OMNH 73400	Oklahoma	BB	BB	0.979	GB	0.021
UCMP 35709	California	BB	GB	0.773	BB	0.227
UCMP 8851	California	BB	BB	0.830	GB	0.170
UCMP 9502	California	BB	BB	0.618	GB	0.382
Kurten & Kay (1982)	Mississippi	BB	BB	0.663	GB	0.337
UCMP 35703	California	GB	BB	0.977	GB	0.023
UCMP 35704	California	GB	BB	0.918	GB	0.082
UCMP 3002	California	Ursus	BB	0.655	GB	0.345
UCMP 3725	California	Ursus	BB	0.570	GB	0.430

Ursus americanus was thought to have been larger in the late Pleistocene. Body size is sometimes inferred to be as large as *U. arctos*, and their teeth are noted to have been larger than modern specimens (Kurtén 1980; Wolverton and Lyman 1991; Graham 1991). It was not until the Holocene that *U. americanus* is thought to have decreased in size (Kurtén 1963; Kurtén and Anderson 1980; Graham 1991; Wolverton and Lyman 1996); a trend that was not unique to the species but observed in several species of mammalian megafauna (Kurtén 1980). Because it is noted *U. americanus* teeth lengths were possibly larger in the Pleistocene, teeth ratios were included to account for size variation of specimens in the fossil record. However, DA results from the latitude and climate sections denoted there was no correlation between teeth length or ratio and climate and latitude in *U. arctos* or *U. americanus*. These results suggest teeth lengths should not be significantly different in the fossil record versus teeth lengths of modern ursids.

CHAPTER 7

CONCLUSIONS

This project began with an assessment of fossil ursid material from Oregon Caves National Monument and evolved into a project that also incorporated new techniques for separating *U. americanus* and *U. arctos* based on lower teeth measurements. A majority of the specimens from ORCA were not classified to species in part due to a majority of the material being from juveniles and not fully developed in addition to overlapping morphologies. Difficulties identifying ORCA material to species level led to an exploration of new techniques for separation.

A large dataset of dental measurements (p4, m1, m2, and m3) of modern *U. americ*anus and *U. arctos* from across North America allowed for the identification of fossil material, including specimens from ORCA. ANOVA found significant differences (<0.001) in all lengths studied as well as ratios when separating *U. americanus* and *U. arctos*. DA indicated lengths were a more accurate tool than ratios for separation of species and the m1 contributed most to the distinction. Overall, 99.1% of modern specimens from North America were classified correctly when lengths were utilized and 77.5% correctly classified when ratios were utilized.

In addition to species separation, the North American dataset was utilized to determine if intraspecific separation of sexes was possible. All lengths proved to be significant in ANOVA analyses but ratios did not indicate a significant separation of sexes. However, Wilks' λ values from DA showed neither lengths nor ratios could accurately separate sexes and classification results showed minimal correct separation. There was significant overlap between interspecific sexes but intraspecific separation showed males and females have roughly the same sized teeth. It is noted that the osteology of large male *U. americanus* can look like small female *U. arctos*;

this study showed there is minimal overlap between the two and most likely would not result in incorrect classification.

Fossil identification built on the North American dataset and DA classified ORCA material as *U. americanus* when lengths and ratios were utilized. A number of other fossil specimens were assessed and some are clearly misidentified. A separate study will need to re-examine the misidentified material. Because regression results did not find any correlation between climate and latitude and tooth size, there is no reason to suspect tooth sizes of *U. americanus* or *U. arctos* would have been any larger in the Pleistocene and it would not be expected *U. americanus* could potentially be identified as *U. arctos*. The only identified *U. arctos* from ORCA is postcranial material. Measurements of these remains are far outside the range of *U. americanus*, even though the individual was relatively young.

A breakdown of the North American dataset into six separate ecoregions where *U. americanus* and *U. arctos* are sympatric show these species' tooth lengths vary across their geographic range. In some ecoregions, *U. arctos* and *U. americanus* have very similar lengths whereas in other ecoregions there is distinct separation. Additionally, in some ecoregions *U. americanus* teeth are as long as *U. arctos* teeth from a different ecoregion suggesting niche resources could be driving length.

When *U. americanus* and *U. arctos* tooth lengths were compared to latitude to test for Bergmann's Rule there was no significant correlation between either species for length or ratios and r^2 values showed there was minimal correlation. This same result was seen when comparing lengths and ratios to mean annual temperature and minimum temperature of the coldest month. This indicates even though lengths vary across geographic ranges they do not increase or decrease in size linearly. These findings further negate the concept of larger teeth during cooler episodes, like the Pleistocene.

A majority of the ursid specimens from ORCA are juvenile's around the age of sexual maturity. The oldest specimens, indicated by epiphyseal fusion are a baculum and calcaneus, both roughly five years old. A minimum number of individuals was assessed to be five based on lower right canines. At least two species of *Ursus* are represented at ORCA, *U. americanus* and *U. arctos*. While most of the material is likely *U. americanus* based on size, species identifications here are based strictly on morphology, statistical methods, or extreme size (in the case of *U. arctos*).

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