ANALYSIS OF HADROSAUR TEETH FROM EGG MOUNTAIN QUARRY, A DIFFUSE MICROSITE LOCALITY, UPPER CRETACEOUS, TWO MEDICINE FORMATION, NORTHWEST MONTANA

by

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ABSTRACT

Egg Mountain locality as part of the Willow Creek Anticline in the Upper Cretaceous Two Medicine Formation of northwest Montana has become well known for its preservation of dinosaur eggs, eggshell, nesting traces, insect traces and more recently described mammals and lizards. The diffuse micro-vertebrate locality also turns up an abundance of hadrosaur and theropod teeth. Population dynamics of dinosaurian taxa are known though analysis of long bone material and histology. Here we test the utility of hadrosaur teeth for the same means. Field excavations of a new Egg Mountain Quarry from 2010-2015 resulted in the collection of 564 hadrosaur tooth fragments presumed to belong to *Maiasaura peeblesorum* in addition to a variety of theropod teeth. The most complete *Maiasaura* teeth were measured and compared to *Maiasaura* specimens from museum collections. A subset of the Egg Mt. assemblage was subjected to histological analysis as means to understand tooth formation and shedding rates. Unique factors were developed and applied to the assemblage translating tooth abundance into an abundance of individuals and ultimately mortality and survivorship.

Analysis of museum collections and Egg Mt. hadrosaur teeth revealed high proportions of juvenile individuals as part of the abraded and largely incomplete Egg Mt. specimens. High mortality rates occur within the first year of life followed by a marked decrease until adult age and size is attained. Seasonal nesting grounds and a seasonal and semi-arid environment proposed for the Egg Mt. area is supported by high proportions of young individuals. Individuals gathering at ephemeral ponds and lakes, including identified theropod taxa, promote a concentration of shed and disarticulated teeth in conjunction with autochthonous mammal, lizard, and dinosaur nesting material. Ontogenetic changes in hadrosaur teeth and the conditions of the Egg Mt. assemblage complicate what an individual tooth represents; however, shed and disarticulated hadrosaur teeth appear to show effectiveness in paleoecological population studies. Continued work on abundant dinosaur tooth assemblages would hone these new techniques and potentially provide insight into similar microsite assemblages around the world.

INTRODUCTION

Paleontological analysis goes far beyond simply describing an individual or a group of individuals based on their fossilized remains. Fossil accumulations preserving multiple specimens are an opportunity to understand local ecology and populations of unique species. Models that account for population-scale factors can be used to reconstruct the biology of extinct species. For instance; how did these animals grow (Erickson et al. 2006; Erickson et al. 2009; Horner et al. 2000; Woodward et al. 2015)? Did the species travel in herds (Fiorillo et al. 2014; Funston et al. 2016)? If they did, were the herds partitioned by age (Hone et al. 2014; Varricchio et al. 2008)? Were the species migratory (Fricke et al. 2009)? Did the habitat consist of seasonal nesting or grazing grounds based on age composition or environment (Horner 1982)? These questions and more can be addressed by fitting fossil data to population models.

In this study I will examine shed and/or disarticulated hadrosaur teeth from Egg Mountain locality; a diffuse microsite locality in the Willow Creek Anticline of the Two Medicine Formation, Montana. No hadrosaur long bone material is directly associated with the teeth, however, the dominant taxon in the area during deposition of Egg Mt. was *Maiasaura* and is the only hadrosaur known to the species level within the associated sediments (Horner et al. 2000; Horner et al. 2001; Varricchio and Horner 1993; Varricchio 1995; Woodward et al. 2015). I use these Egg Mt. hadrosaur tooth data to study the population dynamics of Late Cretaceous hadrosaurs, notably *Maiasaura*.

Life tables are a means of studying demography. They allow a glimpse into what affects population structure, such as predation, disease, growth rates, and reproduction strategies, as well as information about sexual and skeletal maturity (Eberth et al. 2007; Shipman 1981, Voorhies 1969). Applying ecological techniques to fossil data can be frought with difficulty as time and geologic process muddle conclusions (Bennett 2012; Erickson et al. 2006; Erickson et al. 2009; Fiorillo et al. 2014; Horner et al. 2000; Robu et al. 2016; Sander 1993; Varricchio et al. 2008; Voorhies 1969; Woodward et al. 2015). Difficulties aside, ecological techniques are our only recourse for understanding the biology, ethology, and ecology of long extinct species.

Careful examination of the taphonomy and sedimentology of the site specimens were collected from affords paleontologists a wealth of information necessary for ecologic interpretation (Behrensmeyer 1975; Behrensmeyer 1978; Blob and Fiorillo 1996; Dodson et al. 1980; Eberth et al. 2007; Eberth et al. 2014; Jinnah and Roberts 2011; Moore et al. in revision; Rogers 1990; Rogers and Brady 2010; Sander 1993; Schmitt et al. 2014; Varricchio and Horner 1993; Varricchio 1995; Varricchio et al. 2008; Voorhies 1969). The individual specimens that compose a fossil assemblage can be separated in time by seconds or millennia and potentially transported over long distances before deposition and preservation (Brinkman et al. 2007; Rogers and Brady 2010; Schmitt et al. 2014; Shipman 1981). Reconstructing population utilizing fossil accumulations is complicated by taphonomic process, and interpretations are limited to the nature of the specimens and their surrounding sediments. Extracting ecologic and population data from a fossil assemblage requires paleontologists to accurately interpret how the accumulation formed. Attritional assemblages may represent a natural mortality pattern where higher percentage of both young and old individuals are represented.

Catastrophic assemblages, where death is temporally concentrated, may reflect the living population more closely by essentially creating a demographic snapshot (Shipman 1981). Population reconstruction thus requires an understanding of mortality and how the specimens in question were taphonomically assembled.

The Western Interior Foreland Basin (WIFB) is a spectacular example of the peak of dinosaurian diversity in the Late Cretaceous (Campione and Evans 2011; Chapman and Brett-Surman 1990; Gates et al. 2012; Horner et al. 2004; Larson et al. 2010; Prieto-Marquez 2010; Prieto-Marquez and Gutarra 2016). High sedimentation rates coupled with the proximity to the Western Interior Cretaceous Seaway (WIKS) provided a variety of environments for dinosaur populations to grow and potentially be preserved (Horner et al. 1992; Lageson et al. 2001). Abundance and preservation of dinosaurian fauna in the WIFB facilitates paleoecological study and population analysis. Dinosaur population models have largely been constructed using collections of long-bone material collected from bone-beds, another fossil bearing horizon or formation (Bell and Campione 2014; Erickson et al. 2009; Hone et al. 2014; Horner et al. 2000; Larson et al. 2010; Scherzer and Varricchio 2010; Varricchio 2008; Varricchio and Horner 1993; Woodward et al. 2015). Bone bed studies have been successful when a large number of the same species can be extracted (Erickson et al. 2006; Erickson et al. 2009; Funston et al. 2016; Mihlbachler 2003; Robu 2016; Sander 1993; Varricchio et al. 2008; Voorhies 1969; Woodward et al. 2015). Having long bone material from each individual provides consistency in histological examination and ontogenetic analysis of LAGs (lines of arrested growth). LAGs provide a direct line of evidence to infer the age of the individual in question (Padian and Lamm 2013). These techniques replace the use of jaws and teeth for aging individuals in population reconstruction of mammals (Mihlbachler 2003; Robu 2016; Voorhies 1969). Fossil trackways have also been useful in understanding population dynamics including estimates of age and herding behavior (Fiorillo et al. 2014). These age and size estimations come as a result of examining trackway size distributions and their abundance.

Hadrosaurs are one of the most diverse and abundant lineages of dinosaurs in the Late Cretaceous of western North America (Campione et al. 2011; Chapman and Brett-Surman 1990; Gates et al. 2012; Horner et al. 1992; Horner et al. 2004; Prieto-Marquez 2010; Prieto-Marquez and Gutarra 2016). Large collections of hadrosaur material are found in bone beds throughout the Western Interior of the United States and Canada. These large bonebed collections often preserve several individuals of a single taxa or species and lend to their potential as a means of reconstructing population. One of the few analyses of hadrosaurian population in the Western Interior was initially done by Varricchio and Horner (1993). Six large assemblages of hadrosaur and lambeosaur material were analyzed from the Upper Cretaceous Two Medicine Formation of Montana. Multiple elements from the assemblages were used to determine the minimum number of individuals (MNI) as well as to determine relative age with size profiles used as a proxy for age. The assemblages showed evidence in support of high juvenile mortality, herding behavior, and the likelihood of drought related mass mortality as evidenced by proximity to shallow lake deposits. Future studies would corroborate and increase knowledge on hadrosaur populations and the local ecology, particularly within the Two Medicine Formation of western Montana (Foreman et al. 2008; Horner et al. 2000; Martin and Varricchio 2011; Jackson and Varricchio 2010; Roberts et al. 1999; Roberts and Hendrix 2000; Rogers et al. 1993; Shelton 2006; Scherzer and Varricchio 2008; Varricchio 1995; Varricchio et al. 2010; Woodward et al. 2015).

Previous Work/Background

Examples of previous population models for dinosaurs can be seen in Figure 1. One of the largest and most cohesive population studies on hadrosaurs was conducted by Woodward and others (2015). They analyzed material from TM-003, TM-151, and TM-158 localities of the Willow Creek Anticline in the Two Medicine Formation. All analyzed localities are part of a laterally extensive monodominant bonebed of *Maiasaura peeblesorum* likely resulting from a sediment gravity flow and representing a weakly time-averaged assemblage. The monodominant nature and low estimated surface residence time may indicate the assemblage is catastrophic despite age-frequency histograms showing no strong signal toward catastrophic or attritional mortality (Fig. 1A). If the assemblage was truly catastrophic, the mortality event may have been age selective preferentially removing weaker individuals. Histological analysis included 50 *Maiasaura peeblesorum* tibiae from the bonebed, representing the largest cohesive histologic dataset to date for both a single species and a single element of an extinct tetrapod. Tibia growth and development, when coupled with LAG counts makes a reasonable predictor for body size and growth rates. The analysis shows that growth and mortality were highest during the first year of life. Mortality dropped from 89.9% to only

12.7% after the first year and growth rates gradually slowed as the individual approached sexual maturity at approximately three years into development. A slight spike in mortality during the two to three year period is hypothesized to be the result of breeding and competition for mates and therefore the possible attainment of sexual maturity. Skeletal maturity was achieved by six to eight years of age where mortality increased to nearly 50% with the onset of adult age and senescence. The population of 50 *Maiasaura* was normalized to 1,000 and a survivorship curve was developed which required no age estimation or retro calculation. Their age-frequency distribution supported previous analyses made by Varricchio and Horner (1993) and does not support a catastrophic mortality hypothesis, but a sample biased toward juveniles and senescent attrition.

Similarly, Hone et al. (2014) examined a collection of femurs from *Shantungosaurus*, the largest hadrosaur known to date, from a large, monodominant bonebed in Zhouchang, China. Initially described by Hu in 1973, Hone returned to the Longgujian Quarry to analyze the series of femurs. The distribution of body size ultimately provided tentative support for partitioning of young and old individuals in herding dinosaurs. The 100 femurs measured, show a narrow size range and are interpreted as being a population of primarily adult individuals. Interpretations of the fossil site support a catastrophic burial event preserving the biocoenose, and support herd partitioning hypothesis for this species.

Varricchio et al. (2008) applied histological analysis and femoral length studies to a catastrophic assemblage of the ornithomimid *Sinornithomimus dongi* in Mongolia. Not only were the orninthomimid remains in close proximity to one another but they shared a preferred orientation; evidence of herd behavior. Histologic samples were taken to examine LAGs, which were then coupled with femoral length to get at approximate body size and age. All 13 individuals analyzed were identified as juveniles/subadults ranging from hatchling to seven years in age. A size distribution was plotted as femoral length vs. the number of specimens. The catastrophic nature of the assemblage presented by Varricchio et al. (2008) provides a unique snapshot of behavior and population dynamics. The overwhelming signal in support of high juvenile mortality and possible herd partitioning found by Varricchio et al. (2008) is supportive of other studies on dinosaur traces and bonebed accumulations (Erickson et al. 2006; Erickson et al. 2009; Fiorillo et al. 2014; Funston et al. 2016; Hone et al. 2014; Varricchio 2010; Woodward et al. 2015).

Another attempt to understand dinosaur population dynamics was conducted by Erickson et al. (2009). A life table for *Psittacosaurus lujiatunensis* was generated from 80 individuals collected from the Lower Cretaceous Yixian Formation, China. The *Psittacosaurus*' remains were recovered from the same lahar deposit or possibly multiple lahars which occurred within a brief period of time. The population recovered from the lahar deposit was deemed catastrophic and thus represented a reasonable approximation of population demographics. The potential issues of gathering specimens from private collections and from collectors where specimen documentation did not exist seemed minimal when the resulting size-age analysis strongly reflected a "natural and randomly sampled" catastrophic assemblage (Erickson et al. 2009). Body size estimates were generated from femoral length measurements. Age profiles came from 26 specimens selected for histological LAG analysis utilizing fibulae, supplemented by radii and humeri where needed. A life table showed the number of individuals surviving to the next growth stage and normalized to 1000 individuals. Analysis showed a sigmoidal B_1 type survivorship curve characterized by high juvenile mortality followed by a period of low mortality, and eventually senescent attrition. The modern population of Red Deer from the Isle of Rum are a good representative of this type of survivorship. Similar survivorship curves were generated by Erickson et al.'s (2006) analysis of large tyrannosaurids. Rapid growth rates and attainment of threshold body size reduced mortality rates due to predation, however other causes of mortality such as competition for mates and strain on the body during reproduction became the leading cause of death. The importance of this analysis is furthered by gaining an understanding of reproductive maturity and the percentage of the population who reached it.

Trace fossils such as footprints and trackways have also been utilized to understand population behavior. Fiorillo et al. (2014) analyzed an extensive trackway discovered in Denali National Park and Preserve, Alaska. Thousands of vertebrate and invertebrate tracks are preserved at this site with the vast majority of vertebrate tracks being hadrosaurid. Scatter plots generated from length to width ratios of the tracks were tested using cluster analysis. Fiorillo et al. found four statistical groupings in the plotted data which they interpreted as four ontogenetic stages of the hadrosaurid in question. Stage 1 represented the smallest individuals, Stage 2, rapidly growing juveniles, Stage 3 equated to subadults, and Stage 4 adult individuals. Herd structure appears to show a substantial proportion of trackways (85%) were created by larger, presumably adult individuals represented by ontogenetic Stages 3 and 4, whereas the smallest tracks (Stage

1) represented only 13% of total measured trackways. The ontogenetic stages appear to corroborate with histological growth trajectories based on histological analyses (Horner et al. 2000; Erickson et al. 2001; Erickson et al. 2009; Woodward et al. 2015). The size disparity between Stage 2 and 3 in the Fiorillo et al. (2014) data supports the rapid growth documented by Horner et al. (2000), Erickson et al. (2001, 2009), and Woodward et al. (2015). An abundance of individuals identified as subadults-adults (Stages 3-4) also supports increased survivorship of larger individuals. Evidence observed in the Fiorillo et al. study on hadrosaur growth was again corroborated by Holly Woodward's examination of *Maiasaura peeblesorum* published the following year (Woodward et al. 2015).

Lockley (1996) also examined a series of ornithopod and sauropod trackways to understand growth dynamics and population structure. Size -frequency distributions of footprint size were compared to growth curve estimates of *Maiasaura peeblesorum* supporting rapid growth during the first year of life. Footprint length was then used as an arbitrary measure of age and applied to a collection of ornithopod trackways from Texas and Colorado as well as a sauropod trackway from South Korea. Analysis showed the Texas and Colorado ornithopod populations were dominated by subadult and adult individuals with a small portion of tracks belonging to individuals ≤ 1 year of age. Alternatively, the South Korean population of sauropods indicated a higher number of hatchling and juvenile individuals relative to the adult and subadult counterparts. This was interpreted to be young individuals milling about the nearby nesting grounds. Modern trackways are good analogues for population and Lockley concluded based on the former that dinosaur trackways not only represent a living population of individuals but may be less biased than the analysis of body fossils due to the preferential preservation of non-juvenile individuals.

Dinosaur population reconstructions have been done on a handful of occasions using a variety of long bone material (Erickson et al. 2006, Erickson et al. 2009, Funston et al. 2016, Horner et al. 2000, Varricchio and Horner, 1993, Varricchio et al. 2008; Woodward et al. 2015). However, there have been no population models developed for dinosaurian taxa through fossil tooth accumulations. Bir, Morton, and Bakker (2002) touched on the subject dealing with collections of theropod teeth in a qualitative manner. They created an understanding of demography based on their theropod tooth collections, but a population model was not developed. This study is meant to deliver one of the first examinations of hadrosaur teeth for population analysis and expand the view into Egg Mountain Quarry; a Late Cretaceous locality in the Two Medicine Formation of western Montana.

Population analysis based solely on teeth are uncommon and almost always centered on mammals (Mihlbachler 2003; Robu et al. 2016; Voorhies 1969). Typically, the first, second, and third lower permanent molars are utilized in mammal population reconstructions. These molars can tell about the number of individuals and provide relative age (Pacher and Quiles 2013; Voorhies 1969). Voorhies (1969) examined an extensive selection of mammal material from the Vertigre Quarry, earliest Pliocene, Nebraska. Although there was an abundance of bone material associated with *Merycodus* and *Protohippus* specimens, discreet age groups were generated through analysis of tooth eruption and wear stages. A non-selective catastrophic assemblage was discerned from the abundance of juveniles, reproductively aged individuals, and a general lack of intermediate age groups. Mortality is interpreted as part of a winter die-off just prior to seasonal birthing times supported by vertebral growth ring analysis of catfish vertebrae and gar scales.

Robu et al. (2016) recently analyzed an extinct Cave Bear population (*Ursus spelaeus*) by measuring and evaluating tooth size and wear. Evaluation of tooth wear both on disarticulated teeth and intact tooth rows of the lower jaw created mortality profiles in support of a high percentage of juvenile (Stage II and III) individuals in the population. Analysis of growth stage abundance and condition of material suggests a catastrophic assemblage due to the preservation of less robust juvenile mandibular elements. Further analysis and interpretation by Robu however, supports an attritional assemblage biased toward juvenile individuals which developed over a long period of time.

Similar tooth assemblage population structure analyses were conducted by Mihlbachler (2003) on extinct rhinoceros assemblages. Cheek teeth crown height and associated wear stages allowed Mihlbachler to assign growth stages to individuals. Two attritional bonebeds, Mixon’s and Love, showed mortality increased during juvenile and subadult stages. Mortality of the extinct rhinoceroses was interpreted to reflect low juvenile survivorship due to predation and starvation. The increase in mortality during the subadult stage focused around sexual maturity and socially mediated mortality.

Bennett (2012) utilizes the abundance of fossil crocodyliform teeth from the Hell Creek Formation of eastern Montana. Previous work done by Erickson (1996) on modern alligators provided Bennett comparative data on tooth abundance, tooth formation, and shedding rates suitable for examining fossil accumulations of related teeth. Associated age profiles and the amount of teeth estimated to be shed from a certain sized individual could then be developed for the fossil crocodyliform teeth. Fore-aft measurements and basal width ratios less than 1.1 preferentially removed the influence of tooth size variation in the extinct crocodyliforms and the extant alligator. Crown height, fore-aft basal length, and basal width measurements were used to group teeth into equal size categories. Smaller categories would be analogous to newborn or juvenile individuals. Although no mortality or survivorship curve was generated, general size groupings and abundances of shed teeth, calculated from estimated shedding rates, supports larger abundances of young individuals shedding smaller teeth more consistently than presumably older individuals of the larger size classes.

Hadrosaurs are known not only for their diversity but also the characteristic mass of teeth which make up their dental battery. Hadrosaur teeth are a common component of dinosaurian fossil accumulations (Coombs 1988; Eberth et al. 2007; Eberth et al. 2010; Edmund 1960; Fiorillo and Currie 1994; Rogers and Brady 2010) but thus far have not been utilized for population analysis. The immense number of teeth found in the hadrosaur dental battery increases the opportunity for their preservation, however it may complicate the prospect of population analysis. Recent studies done by Erickson et al. (2012) and LeBlanc et al. (2016) have expanded our understanding of dental battery function and structure. Reorganization, addition, and utilization of dental tissues including enamel, dentine, and cementum created an advanced mammal-like dentition unmatched in the realm of dinosaurs. Polyphydont dentition meant hadrosaurs were constantly replacing and replenishing teeth in the dental battery throughout their lifetime. Polyphydonty coupled with homodont dentition means lots of teeth all sharing similar form and cannot be distinguished from one part of the dental battery to another. Traditional tooth measurements and tooth-based age assessments applied to mammalian assemblages (e.g. Robu et al., 2016 and Mihlbachler, 2003) are not applicable due to the lack of unique and permanent teeth in hadrosaur dentition. Useful analysis of hadrosaur teeth then requires direct measurements of intact teeth which can be tied to body size.

Changes in the hadrosaur dentition through ontogeny further complicates tooth analysis. Individual tooth families are defined as a single row of teeth being formed and extruded from a common alveolus (Edmund 1960). The number of tooth families contributing to the dental battery as well as average tooth size increase throughout ontogeny (Edmund 1960). Developing a population model from shed hadrosaur teeth requires associating disarticulated teeth with body size or age. (Horner et al. 2000, Varricchio and Horner 1993). It also requires an understanding of the variation of hadrosaur shedding rates through ontogeny. Erickson (1996) laid the foundations for the latter, demonstrating that the growth and shedding rates of teeth for nestling and juvenile individuals occurred more rapidly than adults, supported by work analyzing *Alligator mississippiensis*. Bennett (2012) applied Erickson's (1996) work to extinct crocodyliforms allowing for a more accurate interpretation of his Hell Creek assemblage regarding the number of teeth produced by a given individual, their associated age or growth stage, and their representation in the fossil record. Modern crocodiles and alligators differ from hadrosaurs by retaining the same number of alveoli throughout ontogeny. The question to ask then becomes how overall shedding rates for individuals are affected by addition of tooth families to the dental battery as well as the overall increase in tooth size through hadrosaur ontogeny. Bi-variate plots accounting for tooth size as well as tooth abundance and shedding rates will be applicable to the Egg Mt. assemblage as a means of normalizing tooth abundance and translating it into an abundance of individuals. Additionally, tooth formation rates derived from histology conducted on shed and/or disarticulated hadrosaur teeth from the Egg Mt. locality will assist in tooth and body size relations as well as relative age constraints. Analysis of the Egg Mt. tooth assemblage from northwest Montana will provide a unique view of hadrosaur ecology and can be tested against previous population studies and growth curves derived from long bone material of hadrosaur species in the WCA and elsewhere in the Two Medicine Formation.

The purpose of this thesis is to gain an understanding of population structure and mortality based solely on a collection of shed and disarticulated hadrosaur teeth. Large populations of hadrosaurs inhabiting the WCA of the Two Medicine Formation during the Campanian (Horner and Makela 1979; Horner 1982; Horner et al. 2000; Varricchio and Horner 1993; Varricchio 1995; Woodward et al. 2015) coupled with the numerous teeth contained within their dental batteries helps to ensure a large sample size. The novel aspect of this thesis is the utilization of presumably shed or disarticulated hadrosaur teeth as a means of population analysis. The polyphydont and homodont nature of the hadrosaur dentition does not allow for mammalian techniques to be applied to them. Analysis of the diffuse micro-vertebrate assemblage being excavated from Egg Mt. Quarry will be unique as no population study has been conducted at the site nor has there been such an extensive examination of hadrosaur teeth for this purpose. Fortunately, some of the most extensive population studies have been done in the Two Medicine Formation and involve *Maiasaura*, the dominant taxon in the area during deposition of Egg Mt. (Horner et al. 2000; Varricchio and Horner 1993; Varricchio 1995; Woodward et al. 2015). Extensive analysis of hadrosaur teeth from Egg Mt. will test previous hypotheses about *Maiasaura* population dynamics based on long bone material in other parts of the WCA (Horner et al. 2000; Varricchio and Horner 1993; Varricchio 1995; Woodward et al. 2015)

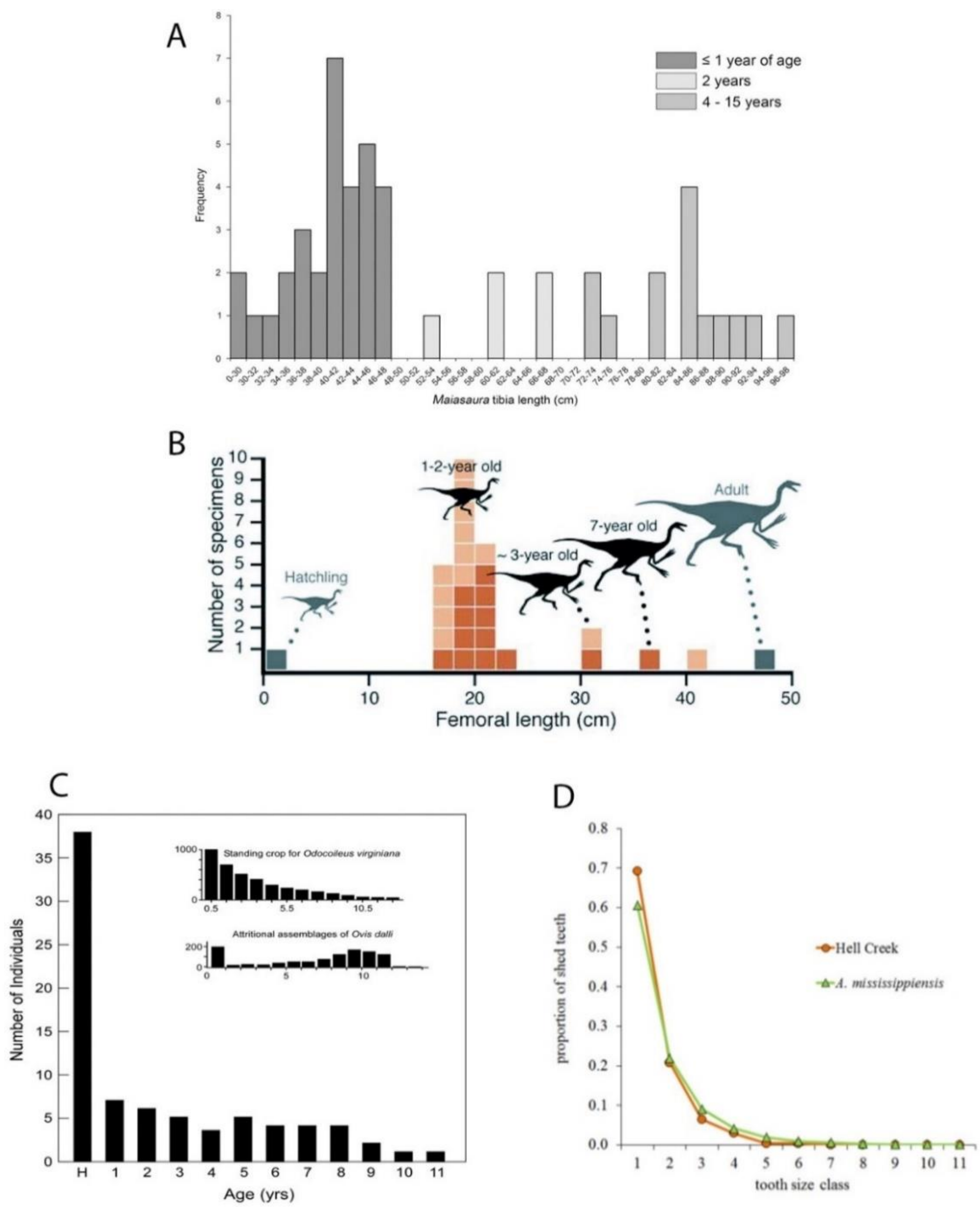


Figure 1—Profiles of death assemblages (A, B) and population distributions (C, D) from previous research which show a dominance of nestling and juvenile individuals. A: Woodward et al. (2015) size-frequency distribution of *Maiasaura* tibial length associated with age estimates based on LAG counts. B: Varricchio et al. (2008) size-frequency distributions of Sinornithomimus dongi and associated age estimates based on LAG counts. C: Erickson et al. (2009) Age-frequency distribution for *Psittacosaurus lujiatunensis* compared to modern population distributions of White-tailed Deer and Mountain Goat. D: Bennett (2012) size-frequency distribution of fossil crocodyliform teeth compared to modern samples of modern *Alligator mississippiensis*.

MATERIALS AND METHODS

Geologic Setting

Two Medicine Formation

The Two Medicine Formation is part of the larger Two Medicine--Judith River clastic wedge which consists of eastwardly thinning non-marine sediments representative of the regressive and progradational cycles of the Western Interior Cretaceous Seaway during Campanian time (Fig. 2) (Lorenz and Gavin 1984; Shelton 2006). Late Cretaceous sediments comprising the Two Medicine Formation were derived from the advancing Sevier Thrust Belt to the west as well as the Adel and Elkhorn Mountain Volcanics (Lageson et al. 2001; Roberts 1999; Roberts and Hendrix 2000; Rogers et al. 1993; Rogers et al. 1995; Rogers 1998; Shelton 2006; Varricchio et al. 2010). Sedimentological analysis by Roberts (1999), Shelton (2006) and others portray the Two Medicine Formation as a fluvial dominated alluvial plain environment which includes fluvial sandstone, overbank mudstones, ephemeral pond carbonates, and volcanic ash layers (bentonites) (Lageson et al. 2001; Roberts 1999; Rogers et al. 1995; Shelton 2006). Active volcanism throughout deposition resulted in a series of ash beds or bentonites allowing for good chronological constraint of the Two Medicine Formation. Dates of the Two Medicine Formation. range from ~80.0 Ma at the base to ~74.0 Ma near the top of the formation (Foreman et al. 2008; Rogers et al. 1993; Varricchio et al. 2010).

Willow Creek Anticline

The Two Medicine Formation near Choteau, MT is more complex than the type section, and subdivided into four "lithofacies" (Lorenz and Gavin 1984). Lithofacies A-D have excellent outcrops in the Willow Creek Anticline and appear as thick successions of lenticular sandstones, grey to red mudstones, carbonaceous lenses, and relatively thin (<1 m) carbonaceous limestones (Lorenz and Gavin 1984). The Upper Two Medicine Formation in the area is characterized by a general lack of laterally extensive sandstones and larger components of mudstones, limestones, and pedogenic carbonates (Lorenz and

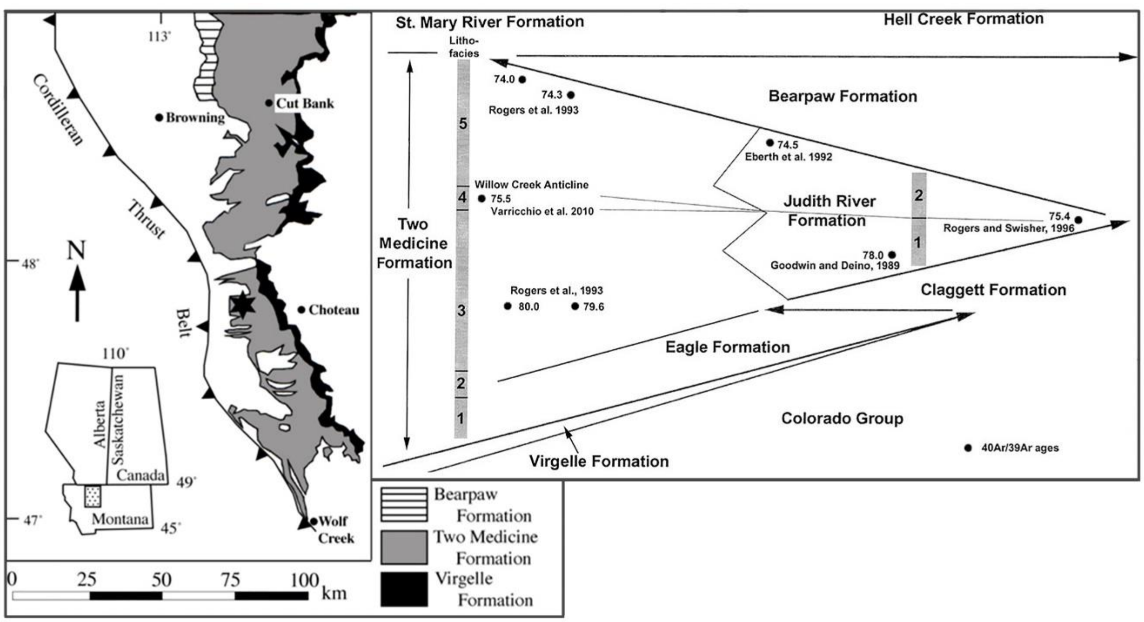


Figure 2— Upper Cretaceous strata from the field area. Egg Mt. is denoted by black star (after Moore et al. in revision) and generic cross-section of the same Upper Cretaceous strata and associated dates (after Jackson et al. 2015).

Gavin 1984). Willow Creek Anticline shows a transition from scattered sandstone lenses and channels to grey-green mudstones with interbedded siltstones and better developed carbonate horizons (Lorenz and Gavin 1984; Shelton 2006). Interest in the area lies in the abundance of hadrosaur bone beds, dinosaur nesting localities, and dinosaur eggs.

Locality

The Egg Mountain locality, the exclusive site of this study (Fig. 2), lies within Teton County NW of Choteau, Montana. Stratigraphically, Egg Mountain exists within the Willow Creek Anticline of the Upper Two Medicine Formation within what Lorenz (1981) deemed "lithofacies D"(Lorenz 1981; Lorenz and Gavin 1984; Rogers et al. 1993; Shelton 2006). Ar/Ar dates by Varricchio et al. (2010) date this part of the Two Medicine Fm. at 75.92 +/- 0.32 Ma. Egg Mt Quarry occurs at the cusp of the upper discontinuity ~345 m above the base of the Two Medicine Formation (Shelton 2006).

"Lithofacies D" as described by Lorenz (1981) and Lorenz and Gavin (1984) is comprised of green to grey-green carbonate mudstones interspersed with carbonate nodules and irregular carbonate horizons. Continued examination of the stratigraphy containing Egg Mt. Quarry by Gavin (1986) produced a more cohesive description of the sediments as well as a paleoenvironmental interpretation. Egg Mt. Quarry exists directly adjacent to charophytiferous limestones which interfinger extensively with calcareous mudstones and is believed to be deposited contemporaneously as a series of raised topographic areas surrounded by shallow carbonate lake deposits (Gavin 1986). The quarry itself is comprised of an extensively bioturbated olive green, well indurated, and resistant series of stacked carbonates consisting of both muddy micrite and calcareous mudstone (Gavin 1986; Lorenz and Gavin 1984; Moore et al. in revision; Rogers et al. 1993 Shelton 2006; Varricchio et al. 1999). Gavin (1986) depicted the paleoenvironment at Egg Mt. to be the result of overall low accumulation rates with a consistently seasonal climate. Most recently Moore et al. (in revision) took a closer look at sedimentology and isotopic signatures found in the fossils and bulk matrix and found the Two Medicine Formation at and around Egg Mt. to contain far less standing water. Instead, the area around Egg Mt. is more representative of proximal deposits of a distributive fluvial system (DFS). Well-drained soils and development of paleosols fit under this DFS model and help to explain the lack of fresh water fossils expected in a shallow carbonate lake environment as previously hypothesized (Gavin 1986; Horner 1984; Lorenz 1981; Lorenz and Gavin 1984; Moore et al. in revision).

Egg Mt. Quarry is a diffuse micro-vertebrate locality well known for dinosaur remains and the accompanying eggs, eggshell, and nesting traces (Horner 1982; Horner 1984; Horner et al. 2009; Horner and Weishampel 1988 & 1996; Oser 2014; Varricchio and Jackson 2004; Varricchio et al. 1997; Varricchio et al. 1999; Varricchio et al. 2002). Continued excavations since the initial discovery at Egg Mt. and most recently since 2010, have turned up associated lizards, mammals, abundant trace fossils, teeth (hadrosaur and theropod), as well as additional nesting material (DeMar et al. 2016; Montellano et al. 2000; Varricchio et al. 1997; Varricchio et al. 1999; Varricchio et al. 2002).

Methods

Generating a life table from shed dinosaur teeth, particularly hadrosaur teeth, is not straight forward. Prominent issues include how tooth size, tooth abundance, and shedding rates vary through ontogeny, and how tooth size changes during development within the dental battery. The following steps were used to process fossil assemblage data into a hadrosaur life table. 1, - preparation of hadrosaur and theropod tooth specimens collected from Egg Mt, 2,- measurement of teeth using a standardized set of dimensions, 3,- generation of size-frequency distributions for the tooth assemblage, 4,- measurement of associated hadrosaur specimens in order to generate a relationship between tooth size and body size as well as tooth size and the number of tooth families through ontogeny, 5,- histological examination of an ontogenetic range of Egg Mt. hadrosaur teeth to assess changes in tooth formation rate through ontogeny, and 6,- development of factors to differenctiate between shed or disarticulated teeth (creation of a "shedding quotient" and a "disarticulation quotient" which reflects ontogenetic changes in the number of tooth size, tooth abundance, and shedding rates by which to compare the relative contribution of different ontogenetic stages to the Egg Mt. tooth assemblage), 7,- conversion, using the shedding quotient and disarticulation quotient, of the size -frequency distribution of the Egg Mt. teeth to a size -frequency distribution of individuals, and 8,- generation of a life tables and survivorship curves based on the Egg Mt. hadrosaur tooth assemblage. Detailed explanations of this process follow.

Collection

Excavation of the new Egg Mt. Quarry consists of a series of jackhammer passes effectively "peeling" away layers of the well indurated, calcitic mudstone. Loosened material is collected and examined for specimens. Depth and position in the quarry is recorded for each specimen and placed in bags which represent portions of the quarry they were taken from. Larger specimens are jacketed however, smaller disarticulated material, including the series of hadrosaur and theropod teeth examined in this study, are given field numbers and bagged as described above. Up to this point a vertical 1.5 m of sediment has been removed with a relatively consistent distribution of fossil material throughout.

Preparation

The assigned museum number given to the Egg Mt. assemblage is MOR 10807 and individual specimens are further delineated by field number. Thin sections of hadrosaur teeth reside in Comparative Histology Collections at the Museum of the Rockies Bozeman, Montana. Excavated hadrosaur and theropod teeth were prepped and catalogued based on the year they were collected in accordance with depth and location in the quarry. Many of the specimens remaining in the rock required extraction with dental picks and pneumatic hand tools. For strength and cohesiveness Vinac was applied to most specimens and superglue was used if any of the specimens broke during extraction. Hadrosaur teeth were largely incomplete and, in many cases, only represented by small fragments and recognizable by retaining enamel or portions of carinae.

Measurement

Prepped and catalogued specimens were then measured. When available, measurements taken on hadrosaur teeth relied on cross-sectional completeness. No hadrosaur teeth in the Egg Mt. collection retained representative longitudinal dimensions. The most commonly preserved dimension consisted of an anterior-posterior or mesial-distal length. This dimension is somewhat analogous to fore-aft basal lengths (FABL) used to measure theropod teeth where the measurement is taken at the widest point at the base of the tooth (Currie et al. 1990; Fiorillo and Currie 1994). The anterior-posterior or mesial-distal dimension will simply be referred to as the AP length (Fig. 3). It was impossible to determine where along the longitudinal axis the tooth was preserved therefore the AP length was recorded as the widest point preserved on the specimen. In instances where AP length was incomplete, a secondary measurement from the most anterior or posterior point of the tooth to the central carinae was made and will be referred to as APC length (Fig. 3). The average ratio between measured AP and APC lengths was used to calculate AP length for teeth lacking this dimension by simply multiplying the average difference to the available APC length. Theropod specimens were measured using established dimensions when preserved. FABL, labial-lingual width, and height were all recorded for collected and prepped theropod teeth where dimensions were preserved. Theropod teeth were then diagnosed down to the family level by analyzing denticle characteristics following descriptions previously made by Currie et al. (1990) as well as Fiorillo and Currie (1994).

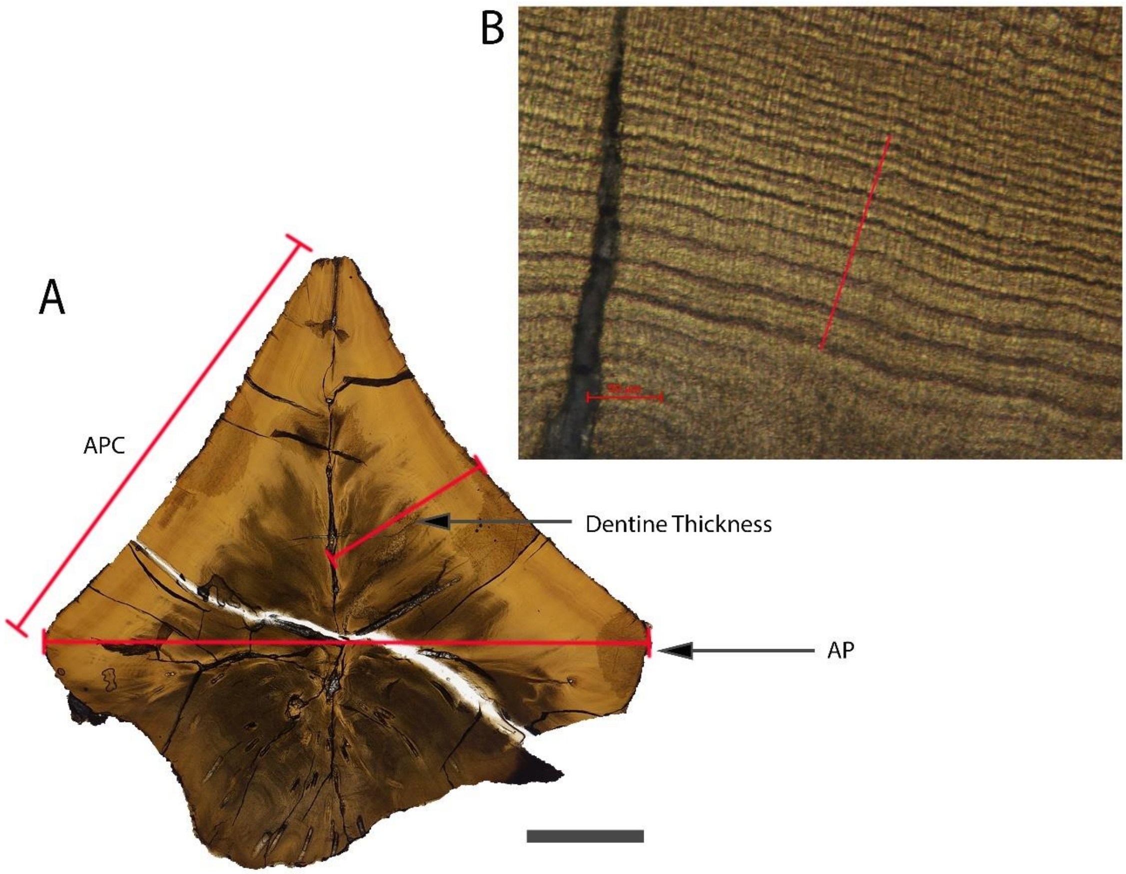


Figure 3—A: Transverse section of a hadrosaur tooth from Egg Mt. Quarry illustrating anterior-posterior measurement and the most anterior or posterior point to tip of central carina. Dentine thickness measured perpendicular to depositional front from pulp cavity to enamel-dentine junction. Scale bar = 1 mm. B: Incremental lines measured perpendicular to deposition. Average von Ebner line thickness in this sample is 15 µm. Scale bar = 50 µm.

Condition and Size-frequency Analysis

General shape and condition of the Egg Mt. tooth assemblage was assessed for completeness and abrasion. Additionally, hadrosaur samples were examined for characteristics indicative of shedding. Shed teeth are typically sourced from the maxillary row and retain their central carina in addition to worn processing surfaces and evidence of root resorption (Erickson pers. comm.). Simple size-frequency analysis was conducted using Microsoft Excel. The size-frequency histogram created for the Egg Mt. hadrosaur teeth utilized AP length including specimens where AP length was estimated from APC, as previously described. Size-frequency distributions for theropod specimens were generated using each measured dimension (FABL, height, and basal width).

Examination of Museum Collections

To better understand the Egg Mt. hadrosaur tooth assemblage as well as ultimately generate mortality and life tables, it was necessary to determine what hadrosaur is likely represented. Relevant information was needed on the ratio of tooth size to body size and how tooth families and size vary through ontogeny. The Egg Mt. hadrosaur tooth assemblage retained no taxonomic identifiers due to their condition and incomplete nature. Genus or species identification therefore relied on previous work conducted within the same area and time frame represented at Egg Mt quarry. The only hadrosaur known at the species level from the Willow Creek Anticline is *Maiasaura peeblesorum*, and Horner et al. (2001) described the stratigraphy containing Egg Mt. Quarry as residing in the *Maiasaura* “biozone”. This is supported by the abundance of fossil material collected and identified from TM-003, TM-067, TM-158, and TM-151 (Horner et al. 2001; Schmitt et al. 2014; Varricchio and Horner 1993; Woodward et al. 2015). The separate localities are part of a laterally continuous bonebed likely generated by a sediment gravity flow (Schmitt et al. 2014; Varricchio et al. 2010). Additionally, the type specimen comes from the Willow Creek Anticline (Horner and Makela 1979; Horner 1983). A recent master’s thesis written by Oser (2014) may also describe some of the first *Maiasaura* eggs and perinates or nestlings found at the Egg Mt. locality. The unfortunate condition of the hadrosaur teeth therefore relies on identifying them through other studies done within the WCA and the Two Medicine Formation. Moving forward, teeth collected and analyzed for this project will be referred to as representative of *Maiasaura* and the resulting population model will be reflective of that. Tooth size distributions say little for the Egg Mt. collection without reference. Several specimens of *Maiasaura* are kept in Museum of the Rockies (MOR) collections. Jaws with intact dental batteries or jaw specimens retaining alveoli from *Maiasaura* provide reference for tooth size and tooth family abundance relative to body size. MOR collections were combed for specimens including bonebed material collected from the Willow Creek Anticline and the Two Medicine Formation. The primary site containing examined material was West Hadrosaur Bonebed (TM-067). Two small specimens from the EMOT site, directly adjacent to Egg Mt. quarry were also examined, as well as a cast of the type specimen (MOR 089) and adult *Maiasaura* specimen (OTM F138) residing at the Two Medicine Dinosaur Center in Bynum, MT. Total length of the jaw element, length of the dental battery, number of tooth families, and average AP tooth size were assessed on all specimens when available.

To ensure the Egg Mt. assemblage of *Maiasaura* teeth were properly represented when being compared to intact museum specimens two paths were taken. Average tooth size on examined museum specimens was measured both at the widest AP length (AP_W) as well as the base of the tooth (AP_B). All tooth measurements were taken from teeth retaining complete AP dimensions and remaining intact to the dental battery. If teeth were shed from the *Maiasaura* dental battery, they should be worn down toward their bases and near the end of their functional life as a contributing part of the dental battery (Edmund 1960; Erickson et al. 2012; LeBlanc et al. 2016). AP length diminishes as you move toward the base of a tooth therefore it was reasonable to analyze tooth size distribution in museum specimens at both the widest AP length and the narrowest (near the base of a given tooth) to accommodate for the possibility that teeth from the Egg Mt. assemblage were shed or worn prior to being disarticulated. The ratio existing between AP_W and AP_B tooth dimensions observed on museum specimens allows for the application of that ratio to the Egg Mt. assemblage of hadrosaur teeth. Applying the tooth size ratio to the assemblage allows for the estimation of AP_W dimensions to be made. This assumes the Egg Mt. teeth all represent shed and worn specimens. As a result, distinct size-frequency distributions will be generated representing face value AP dimensions and estimated AP_W dimensions. Population models generated for the Egg Mt. assemblage through these varied size-frequency distributions will be more representative of variable AP lengths due to shedding or disarticulation.

Previous work by Varricchio and Horner (1993) and Varricchio (1995) on WCA bonebeds linked *Maiasaura* bonebed material to body size. Later analysis on *Maiasaura* growth by Horner et al. (2000) linked femora length to six ontogenetic stages: Small Nestling, Large Nestling, Early Juvenile, Late Juvenile, Subadult, and Adult (Figure 4). Several examined jaw specimens from MOR collections did not have associated body size estimates thereby requiring analysis of associated bonebed material. Femora lengths from MOR 547 (West Hadrosaur Bonebed) were re-examined for this project so associated and examined *Maiasaura* jaw material would have a more accurate constraint on body size and relative age lacking these estimates.

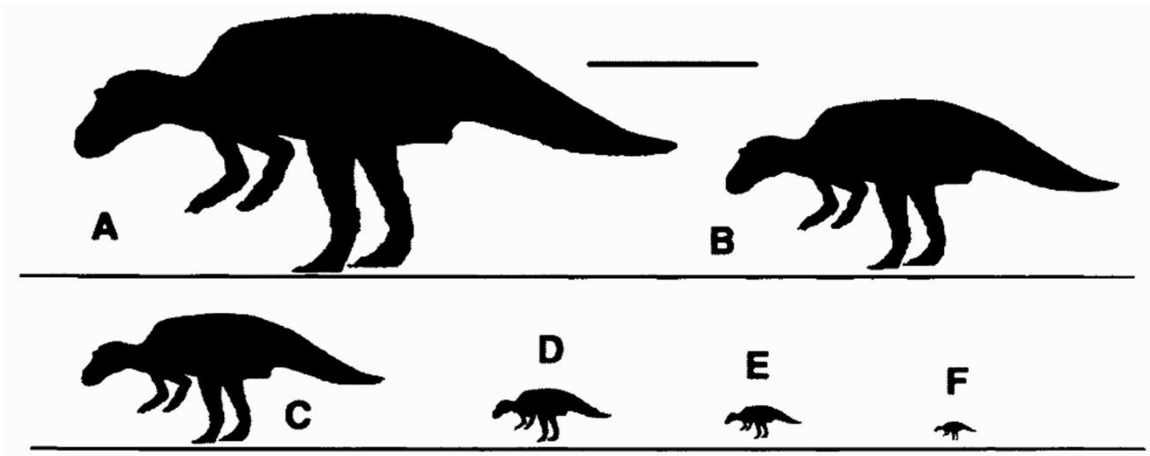


Figure 4—Osteological growth stages as described by Horner et al 2000. A) Adult, B) Subadult, C) Late Juvenile, D) Early Juvenile, E) Large Nestling, F) Small Nestling. Scale bar represents 2 meters.

Histological Examination of Egg Mt. Hadrosaur Teeth

Erickson (1996) calculated hadrosaur tooth shedding rates using histology. Counts of incremental lines of von Ebner on a functional tooth divided by dentine thickness estimates tooth formation rates. When the line count in a functional tooth is subtracted from the incremental line count of the immediate successor (provided by examining intact dental batteries), Erickson's outcome estimated shedding rates. Erickson (1996) found shedding rates in *Maiasaura* decreased from as estimated 46 days as an infant to 58 days in adults. *Maiasaura* teeth represented in the Egg Mt. collection were examined histologically in the same manner to confirm findings made by Erickson (1996) and to generate tooth formation rates for intermediate ontogenetic stages.

Twelve *Maiasaura* teeth were chosen to be thin sectioned and assessed for lines of von Ebner (Table 1). The 12 teeth were chosen to represent the full range of specimen sizes in the AP dimension to see if variations in incremental line spacing and growth rates could be observed. Incremental line spacing taken over dentine thickness allows for tooth formation rates to be generated. Longitudinal sections provide the most accurate identification and record of incremental lines, but lack of unworn and complete teeth in the Egg.Mt. assemblage prohibited their general use. Instead, transverse sections made at the widest part of the tooth would provide the longest record of tooth development but an overall minimum development time (Erickson pers. communication). This phenomenon is caused by the incremental growth of dentine as it progresses from the enamel-dentine junction (EDJ) resulting in a series of stacked “cones” whose edges taper longitudinally toward the base of a tooth (Dean 2000; Hillson 2005). Although still incomplete, two teeth with the largest longitudinal representation had longitudinal sections made.

The 12 *Maiasaura* teeth spanning the AP size range were then sectioned and histologically examined. Molds and casts of the specimens were made prior to embedding in Epothin® Epoxy. Wafers were cut using an Isomet trim saw and a diamond blade. Wafers were mounted to 27X42mm plastic slides and ground down to 50-100 µm using Buehler Ecomet grinders and descending grits of silicon-carbide grinding paper (180-800 grit). Slides were hand polished with 3µm and 1µm aluminum oxide polishing compound. All preparation followed methods as per Standard Small Specimen procedures described in Bone Histology of Fossil Tetrapods (Padian and Lamm 2013).

Table 1—Specimens selected for thin sectioning and histological analysis of lines of von Ebner. To8 was not included as the specimen was found to not be a hadrosaur tooth.

Field Number	**Thin Section Number**	**Anterior-Posterior (AP) Dimension (mm)**	**Anterior/Posterior to Central Carina (APC) (mm)**
2011-B12-H1	To1-1	2	1.5
2012-B1-H3	To2-1	3.5	3
2010-EMQ-045	To3-1	5	4.5
2012-H3-B2	To4-1	4.6	3.2
2015-B5-H5	To5-1	6.5	4
2013-B12-H14	To6-1	7	7
2014-B8-H6	To7-1	1.96	1.55
2012-B5-H9	To8-1	-	-
2012-B7-H3	To9-1	4.11	2.51
2012-B29-H3	To10-1	4.83	4.12
2014-B9-H7	To11-1	5.16	4.52
2014-B5-H3	To12-1	5.21	4.75

Images and scans of the finished slides were taken on a Nikon-Optiphot Pol Microscope fitted with a PRIOR-Optiscan II Automated Stage. Images were taken on a NIKON DS-Fi2 camera using NIKON NIS-ELEMENTS software. Identification of incremental lines was made with polarized microscopy at magnifications of X40-200. Line measurements were made using the linear measurement tool in ImageJ. Images were projected on a high-resolution screen to aid in line demarcation and accurate measurement. Measurement of incremental lines was entered in an Excel spreadsheet and averaged for each specimen. Due to tooth preservation, incremental lines could not be counted across a single plane for each tooth. Instead, several incremental line widths taken throughout the transverse section of each tooth were averaged for each sample. Measurements from the EDJ, perpendicular to von Ebner lines, to the suture where the pulp cavity was closed off with dentine is dentine thickness (Erickson pers. comm.). Ten dentine thickness measurements were taken on each specimen, from various points around the perimeter, and averaged. To determine the amount of time the tooth took to develop, average dentine thickness was divided by the average von Eber line thickness for each specimen. Details on incremental lines and dentine thickness measurements can be seen in Appendix A.

Determination of Shedding Quotient

Shedding rates for teeth derived from an individual or individuals is relatively straight forward when teeth are in association or remain intact to the dental battery of the individual(s) in question. Establishing a baseline of tooth size variation and noting the addition of tooth families to the dental battery by examining MOR collections increased the number of factors to consider when determining how an individual *Maiasaura* contributed teeth to the record. Shedding rates based on Erickson's (1996) work adds a third component to the changes taking place through *Maiasaura* ontogeny. If we try to represent the teeth of the Egg Mt collection as individuals and ultimately a population, shedding rates, addition of teeth to the dental battery, and increase in tooth size must be considered and then applied to the assemblage to effectively normalize the data. Increases in shedding rate, the increase in tooth size, as well as the addition of teeth to the dental battery through ontogeny means potential contribution of teeth to the record varies from individual to individual and should be accounted for. To accomplish this, an equation must be developed resulting in a factor or "shedding quotient" which will translate AP tooth size of *Maiasaura* teeth from Egg Mt. to their representation as individuals and recognizes that the number of teeth shed per time interval (e.g. a year) by an individual depends upon its ontogenetic stage. Development of this "shedding quotient" (SQ) will require tooth size vs. body size, as well as tooth family counts and shedding rates, all of which change through ontogeny.

Linear regression trendline values developed for shedding rate (SR) (Erickson 1996), and the number of tooth families (TF) in relation to growing AP tooth dimensions provide a basis for construction of the SQ. The number of teeth shed by a given individual would be expected to increase through ontogeny and therefore will be included in the development of the SQ. In this study the constant assumption is that one adult tooth is equal to one individual. Variables are labeled to identify these differences: TFa—Tooth families' vs AP width for an adult specimen; SRa—Calculated shedding rate for an adult specimen (Erickson 1996); TFi—Tooth families' vs AP width for the tooth in question; SRi—Calculated shedding rate for the tooth in question. The un-simplified equation looks like this:

Equation 1:

$$SQ = \frac{\left(\frac{TFa}{SRa}\right) * 365}{\left(\frac{TFi}{SRi}\right) * 365}$$

Simplifying the equation prior to introducing variables and AP dimensions results in:

Equation 2:

$$SQ = \frac{\left(\frac{TFa}{SRa}\right)}{\left(\frac{TFi}{SRi}\right)}$$

SQ's must be calculated for each individual tooth size then applied to the size-frequency distribution. This effectively translates tooth abundance data to an estimated number of individuals represented by the teeth. It should be noted the development of this equation is based entirely off AP tooth sizes observed in museum specimens. Application of this equation to AP tooth sizes, in particularly smaller, than observed ranges results in questionable results. Numbers generated from AP dimensions falling below these observed tooth size ranges can be extraordinarily large and/or negative.

Determination of Disarticulation Quotient

Incomplete understanding of shed and disarticulated hadrosaur teeth and how they contribute to the Egg Mt. assemblage required development of the SQ. The SQ assumes the entire collection of *Maiasaura* teeth are derived from shedding but ignores mortality as a determinant of the size frequency distribution. This issue prompted the development of the disarticulation quotient (DQ). The DQ takes into account the number of tooth families relative to changes in tooth size as well as the addition of teeth to each tooth family through ontogeny. If an individual dies and teeth are disarticulated, the number of teeth potentially contributing to the fossil record vary significantly from nestlings to adults and requires appropriate representation if they are to be translated into a population of individuals.

Linear regression trendline values developed for the number of tooth families (TF) in relation to increasing AP tooth size as well as the increase in the number of teeth contributing to each family are the basis for the DQ. Again, one adult sized tooth is assumed to represent one individual. Variables used include TFa—Tooth families' vs AP width for an adult specimen; TFAa—Number of teeth per tooth tooth family; TFi—Tooth families' vs AP width for the tooth in question; TFAi—Number of teeth per tooth family for the tooth size in question. The equation looks like:

Equation 3:

$$DQ = \frac{(TFa)(TFAa)}{(TFi)(TFAi)}$$

DQ's must be calculated for each individual tooth size then applied to the size-frequency distribution in the same manner as the SQ. This effectively translates tooth abundance data to an estimated number of individuals but this time assuming the teeth are generated through disarticulation. It should be noted the development of this equation is premised on AP tooth sizes observed in museum specimens. Application of this equation to AP tooth sizes, in particularly smaller, than observed ranges results in questionable results. Again, numbers generated from AP dimensions falling below these observed tooth size ranges can be extraordinarily large and/or negative.

Due to this problem, which affects the SQ as well as the DQ, size-frequency distributions of the Egg Mt. assemblage presented in this thesis were limited to the minimum observed AP tooth size seen in museum specimens. The raw data generated through the application of the SQ as well as the alternative DQ includes analysis on these small specimens. Further discussion on the limitations of these factors will be discussed later.

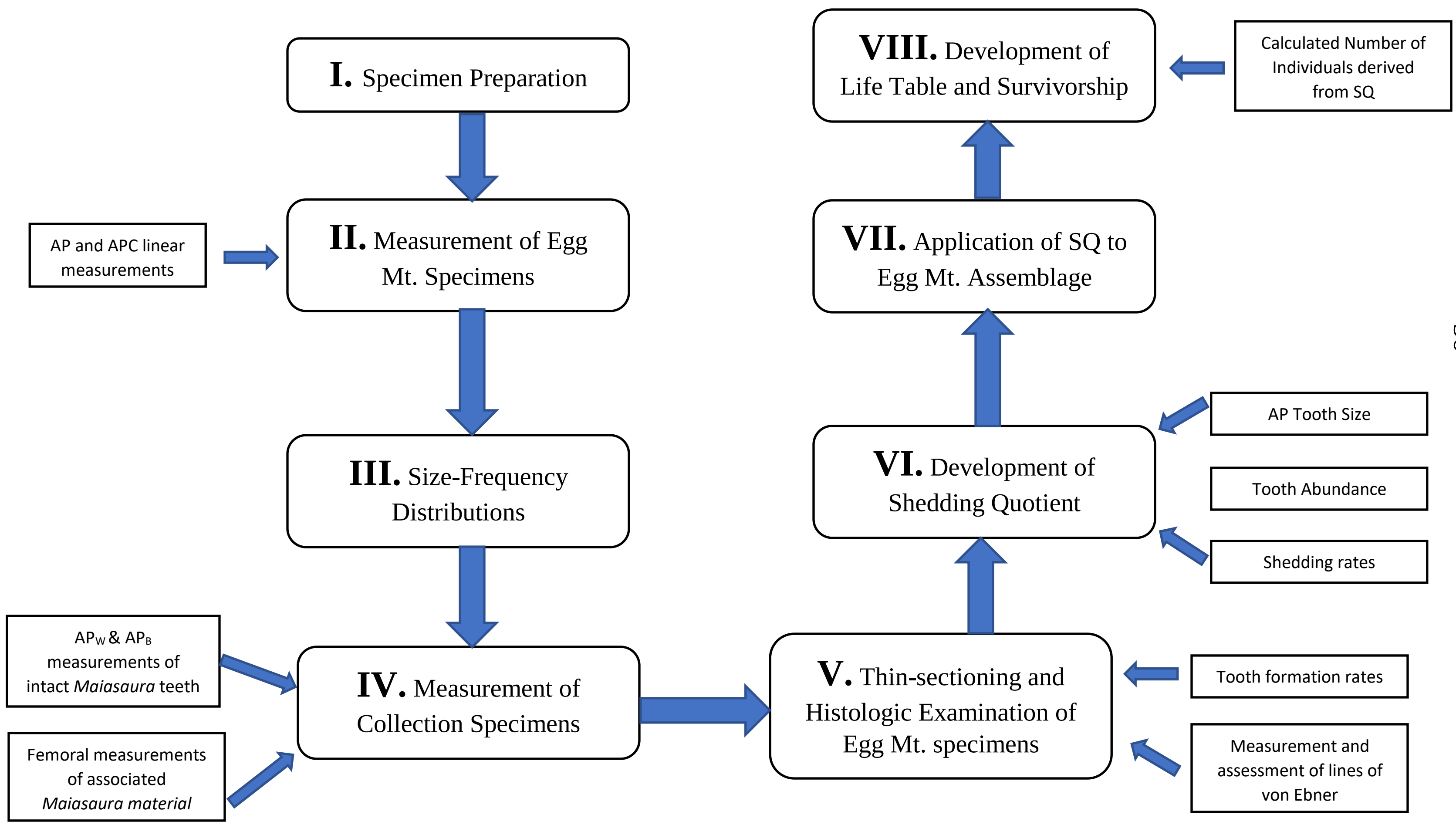
Conversion and Representation of Mortality

Each tooth will have a SQ or DQ factor associated with its AP length, translating the size-frequency of the Egg Mt. hadrosaur teeth into a size-frequency distribution of individuals. The new distribution of individuals represents a hypothetical death assemblage. In addition, tooth size to body size observations recorded from museum specimens can be superimposed over the top of the death assemblage estimating body size for associated AP tooth dimensions and the individuals represented by them.

Life Table and Survivorship

The relatively large sample size also allows for mortality and survivorship to be calculated without normalizing the data to a larger population. The estimated number of individuals resulting from the application of the SQ and DQ factors can then be lumped into relative age brackets based on the ontogenetic stages described by Horner et al. (2000) and continued work on *Maiasaura* growth by Woodward et al. (2015). Numbers of individuals estimated to survive to the next growth stage allows for a simple hypothetical life table and survivorship curve to be generated.

Figure 5—Flowchart illustrating key steps to the examination of the Egg Mt. tooth assemblage. Smaller square boxes are the variables contributing the successful completion of each step. (Following Page)


I. Specimen Preparation
AP and APC linear measurements
II. Measurement of Egg Mt. Specimens
III. Size-Frequency Distributions
APW & APB measurements of intact Maiasaura teeth
Femoral measurements of associated Maiasaura material
IV. Measurement of Collection Specimens
V. Thin-sectioning and Histologic Examination of Egg Mt. specimens
Tooth formation rates
Measurement and assessment of lines of von Ebner
VI. Development of Shedding Quotient
AP Tooth Size
Tooth Abundance
Shedding rates
VII. Application of SQ to Egg Mt. Assemblage
VIII. Development of Life Table and Survivorship
Calculated Number of Individuals derived from SQ

RESULTS

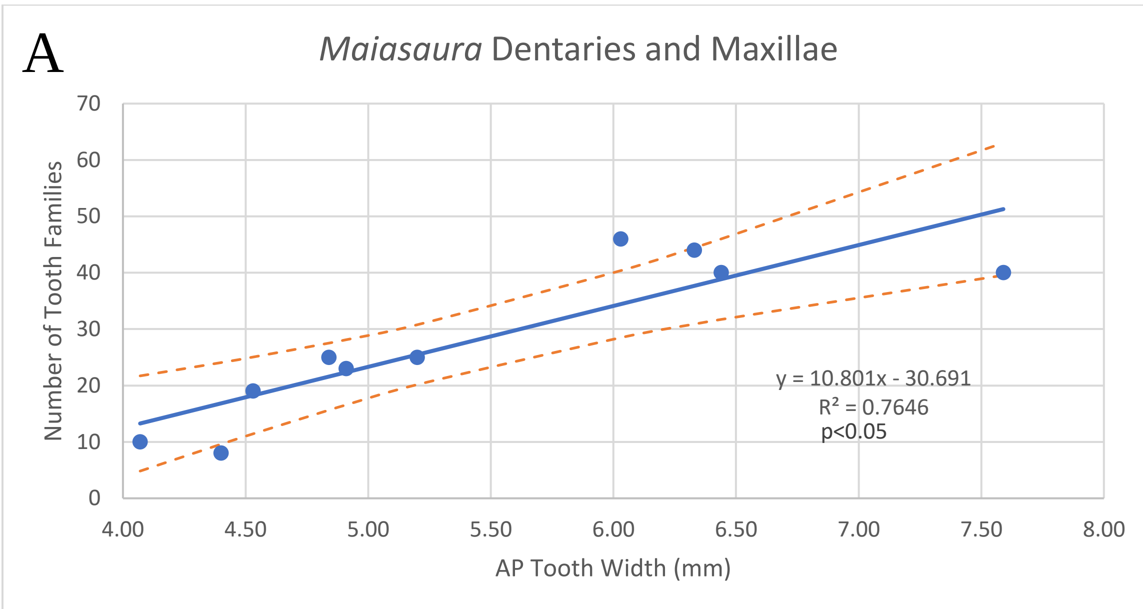
Shedding Considerations and Calculation of Shedding Quotient

As the number of tooth families and tooth size increased through ontogeny so too did shedding rates. Examination of museum specimens with intact dental batteries as well as previous work conducted by Erickson (1996) allowed for the variables necessary to calculate the SQ be put into context. Plotting the number of tooth families against the average AP tooth size observed in museum specimens provided an understanding of how the number of tooth families and tooth size change through ontogeny. The results seen in Figure 6 show a consistent increase in tooth family abundance as AP tooth size increases. A linear regression model inferred from the data provides one of the factors contributing to the SQ. Shed hadrosaur teeth are typically sourced from the maxilla whereas dentary teeth, if identifiable, are primarily generated through disarticulation. It was reasonable to plot *Maiasaura* dentaries and maxillae together but also provide plots of observed dentary or maxillary specimens individually. The best value suited for application in the SQ is the trend line best fit for combined dentary and maxillary specimens. The TF variable will then be represented as:

Equation 4:

$$TF = 10.8x - 30.7 \ (R^2 = 0.76))$$

Development of the SQ also relies on an understanding of shedding rates as they change through ontogeny. Previous work conducted by Erickson (1996) provided the means to do so. Histological analysis conducted on the Egg Mt. assemblage was also used to understand tooth formation and shedding rates which we attempted to compare



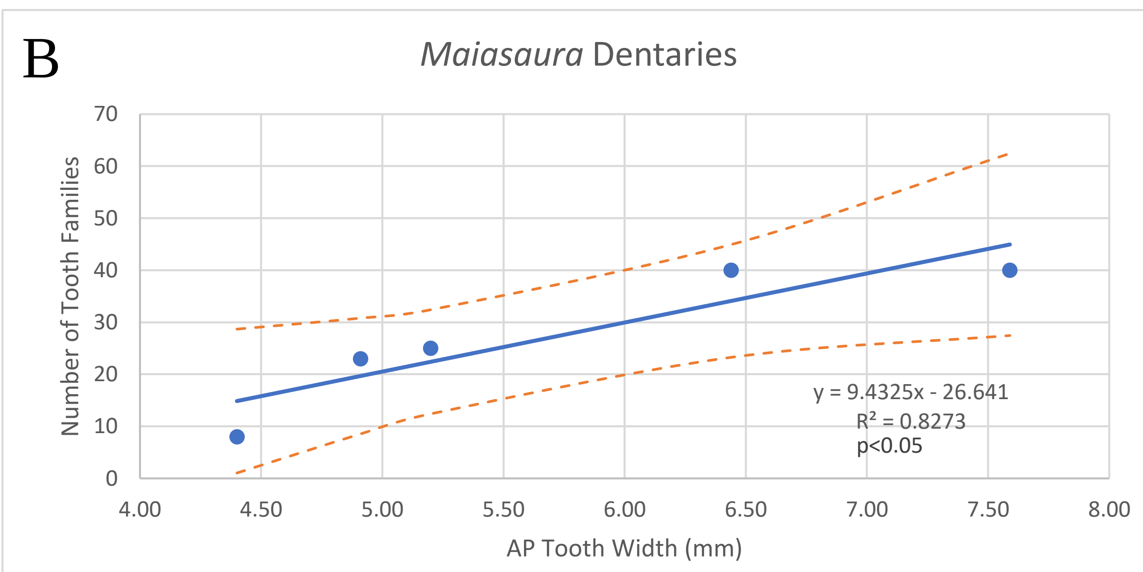


Figure 6—Number of tooth families plotted against average AP tooth width on observed museum specimens. Trendlines bound by 95% confidence interval. $p<0.05$ A: Observed *Maiasaura* dentaries and maxillae. B: Observed *Maiasaura* dentaries.. C: Observed *Maiasaura* maxillae.

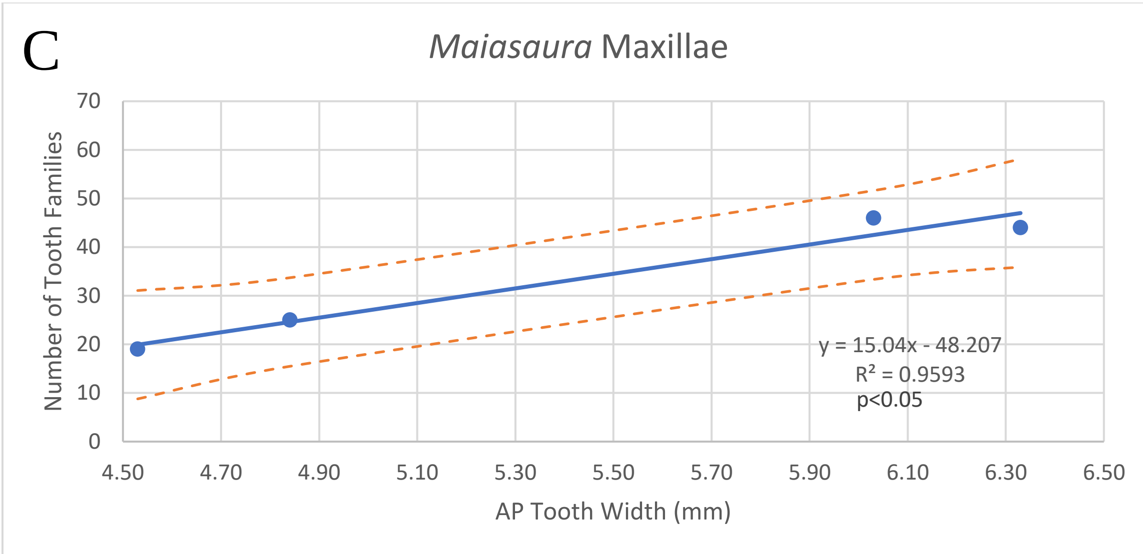


Figure 6—Cont.

with Erickson's findings. The 12 teeth selected from the Egg Mt. assemblage for thin sectioning represented the range of available AP lengths and served as a means to observe possible changes through ontogeny. Thin sections allowed for analysis of incremental growth lines. Lines of von Ebner were examined for this subset of teeth from the Egg Mt. collection to estimate tooth development time which is linked to ontogenetic stage and ultimately the changes in shedding rates which take place over the individuals growth (Erickson 1996). After samples were cut, ground, and polished, polarized microscopy revealed lines of von Ebner in nearly every specimen. Although reminiscent of a tooth on the exterior it was found that To8-1 was in fact a piece of bone showing characteristic osteons and osteocyte lacunae as well as possible LAGs and therefore served no purpose for this study. The remaining 13 sections made and examined allowed for counts of lines of von Ebner as well as dentine thickness average calculations. Dividing the average dentine thickness by the average von Ebner line thickness for each specimen resulted in a mean tooth formation rate. As was expected, the larger specimens took longer to develop. Calculated tooth development ranged from 35-109 (± 20) days all of which fall within or below juvenile stage tooth formation rates (Erickson 1996). The smallest specimens (To1 and To7) had minimum development times of 35 and 60 days respectfully. The largest specimens (To5 and To6) showed minimum development times of 98 and 84 days. To3, representing the middle of the size range shows the longest development time despite its size; 109 days (Figure 7). Specimens selected for longitudinal sectioning (To5 and To12) are decidedly different from each other. The transverse section of To5 unexpectedly records a longer tooth development time than the longitudinal section (98 to 82 respectively). Conversely, To12 displayed a longer tooth development time in the longitudinal section as opposed to the transverse section (165 compared to 93). The longer development time seen in the longitudinal section of To12 was expected based on previous work (Erickson 1996; Erickson pers. comm.; Hillson 2005).

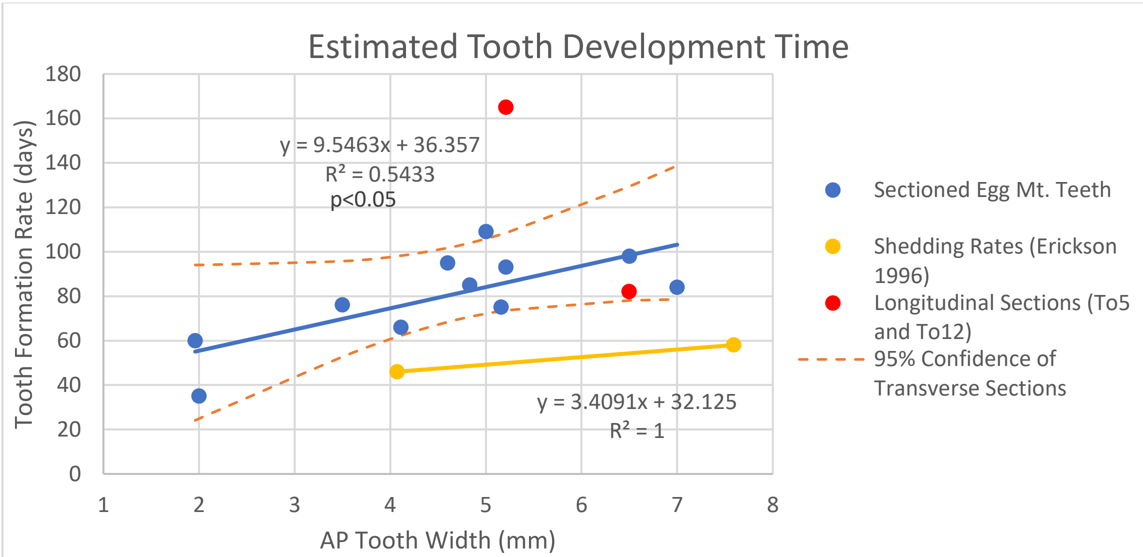


Figure 7—Approximate tooth development time of sectioned Egg Mt. *Maiasaura* teeth. Red markers indicate longitudinal sections but were not included in linear correlation of tooth formation rates. Plot includes shedding rates based on Erickson 1996 and accompanying linear correlation.

Tooth formation rates can tell us about relative age, however, shedding rates are necessary for application of the SQ to the Egg Mt. assemblage. Although tooth formation rates found for the assemblage show consistent increase as AP tooth size increases, the results cannot be directly compared to shedding rates derived by Erickson. Histological analysis of the Egg Mt. assemblage does however tell us about relative age based on von Ebner line spacing and tooth development times. Although, a larger sample size was used to generate tooth formation rates for *Maiasaura* in this study, the result does not reflect shedding rates and therefore does not aid in development of the SQ. Therefore, the best fit trend line fitted to Erickson's shedding rates would result in the most accurate application of the SQ. The resulting variable will play its part in the developed SQ function as:

Equation 5:

$$\mathrm{SQ} = 3.41\mathrm{x} + 32.125 \ (R^2 = 1)$$

Final development of the SQ equation is the result of plugging in the associated variables:

Equation 6:

$$SQ = \frac{\left(\frac{(10.8x - 30.7)}{(3.41x + 32.125)}\right)}{\left(\frac{(10.8x - 30.7)}{(3.41x + 32.125)}\right)}$$

Where x equals the AP dimension of the tooth. If we apply the labels to the x variable as described in the methods, the SQ equation looks like:

Equation 7:

$$SQ = \frac{\left(\frac{(10.8\mathrm{AP}a - 30.7)}{(3.41\mathrm{AP}a + 32.125)}\right)}{\left(\frac{(10.8\mathrm{AP}i - 30.7)}{(3.41\mathrm{AP}i + 32.125)}\right)}$$

Where APa represents the AP tooth length in an adult and APi represents the AP length of the given tooth in question. The sample equation above is derived from tooth size ranges observed in museum specimens (AP_W = 4.07-7.59 mm; AP_B = 1.35-4.53 mm). If one adult tooth equals one individual the numerator then becomes a constant after inserting the largest average AP tooth size observed in adult museum specimens (7.59 ± 1.2 mm). The definitive version of the SQ equation can now be applied to the Egg Mt. assemblage:

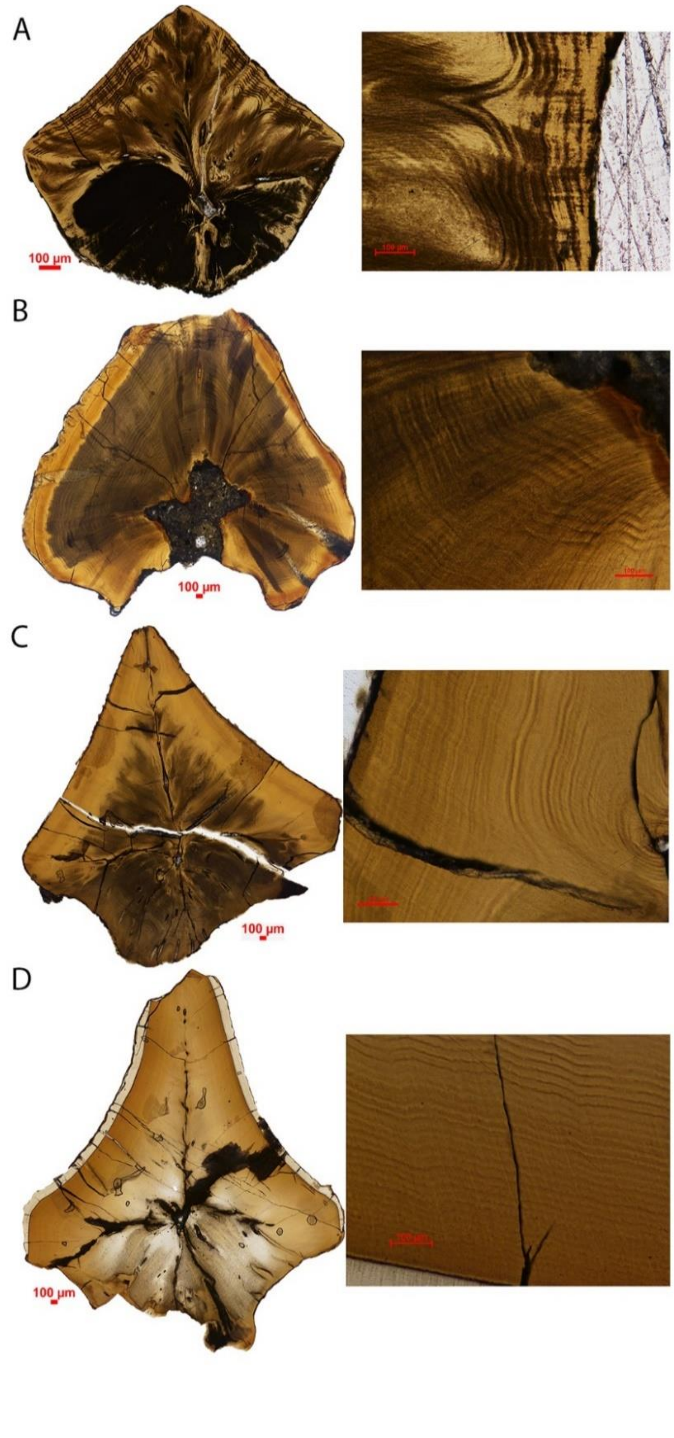


Figure 8—Sectioned Egg Mt. tooth samples whose anterior-posterior tooth measurements fall within size ranges observed in museum specimen ontogentetic stages. A & B: Small Nestling-Late Juvenile C:Large Juvenile-Subadult D: Subadult-Adult.

Equation 8:

$$SQ = \frac{0.88}{\left(\frac{(10.8\text{AP}i - 30.7)}{(3.41\text{AP}i + 32.125)}\right)}$$

Disarticulation Considerations and Calculation of Disarticulation Quotient

Stated variables which change through ontogeny used to develop the shedding quotient can also be used if we assume the Egg Mt. assemblage was derived from disarticulation as opposed to shedding. The DQ utilizes the number of tooth families plotted against AP tooth size similar to the SQ:

Equation 4:

$$TF = 10.8x - 30.7 \ (R^2 = 0.76)$$

However, instead of shedding rates, the DQ takes into account the number of teeth contributing to each tooth family in order to understand the possible contribution of teeth the record through disarticulation (Figure 9). The calculated variable substituted into the TFA position of the DQ equation would be represented as:

Equation 9:

$$TFA = 0.56x + 0.78 \ (R^2 = 1)$$

The resulting DQ equation with x replaced with AP tooth size looks like:

Equation 10:

$$DQ = \left(\frac{(10.8\text{AP}a - 30.7)(0.56\text{AP}a + 0.78)}{(10.8\text{AP}i - 30.7)(0.56\text{AP}i + 0.78)}\right)$$

If we again assume one adult sized tooth (7.59 ± 1.2 mm) equals one individual, the numerator becomes a constant:

Equation 11:

$$DQ = \left(\frac{258}{(10.8\text{AP}i - 30.7)(0.56\text{AP}i + 0.78)}\right)$$

AP dimensions of the Egg Mt. assemblage can be plugged into the DQ equation to represent a population based on disarticulation.

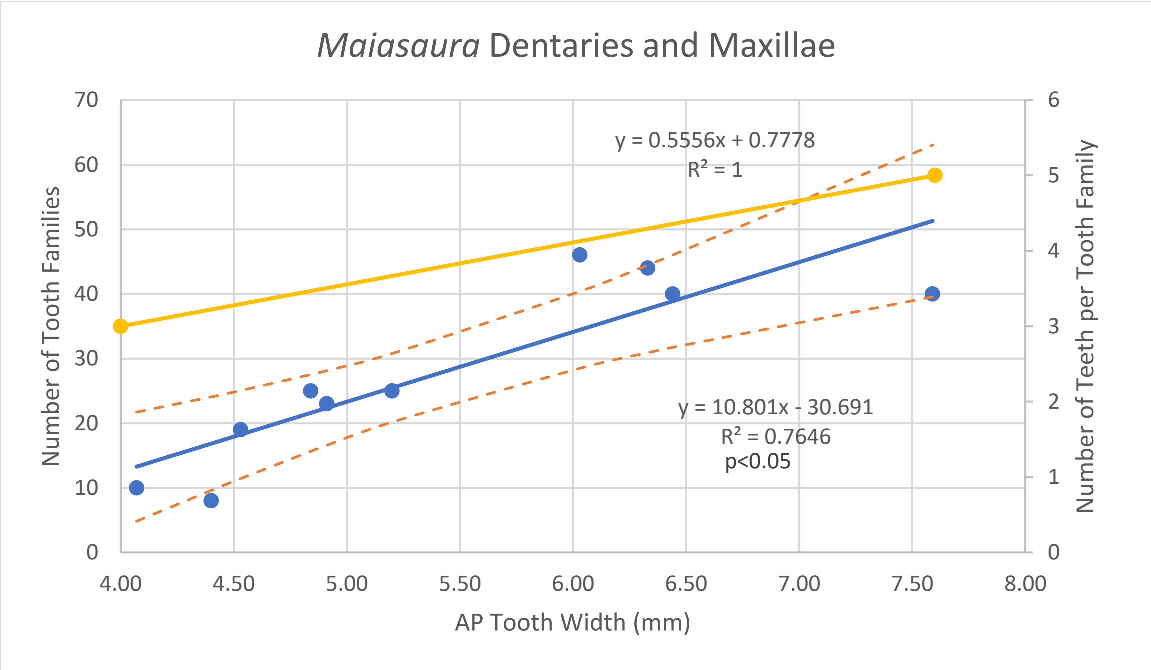


Figure 9—Number of tooth families plotted against AP tooth size based on observed museum specimens (bound by 95% confidence interval) as well as the number of teeth contributing to each tooth family (yellow) based on museum specimens and descriptions of *Maiasaura* neonates (Horner 1999) and an Adult individual (Trexler 1995).

<u>Tooth Size to Body Size Correlations</u>

Body size plotted against observed AP tooth width can be seen Figure 10. The scatter plot depicts body size estimates based on previous descriptions of *Maiasaura* material coupled with AP tooth size observed on the same specimens. Of the 10

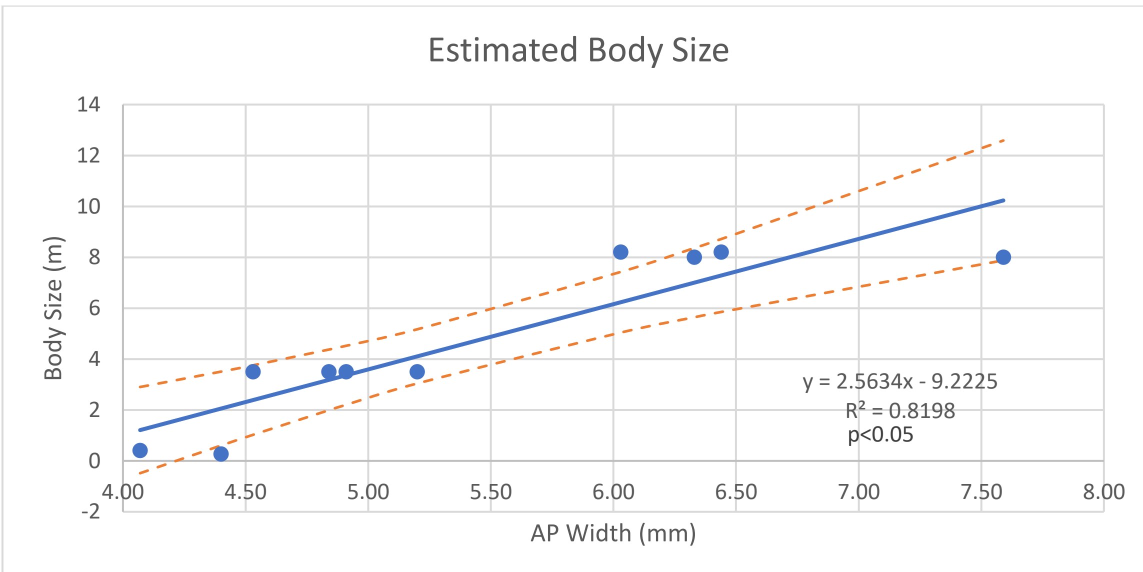


Figure 10—Estimated body size plotted against AP tooth width. Trendline bound by 95% confidence interval.

Maiasaura jaw elements examined, six had previously calculated body size estimates and the remaining four jaw specimens had body estimates based on the measurement of associated femora as well as previous work (Varricchio and Horner 1993; Varricchio 1995). All examined specimens were then applied to the *Maiasaura* ontogenetic series (Horner et al. 2000). Examined specimens and associated measurements can be seen in Appendix C. Several of the museum specimens with intact dental batteries have associated bonebed material or previously estimated ages/body sizes to draw on. MOR 6631 #1 and #2 as well as OTM F138 were the only specimens with previous age or body size estimations (Oser 2014; Trexler 1995). MOR 089, the holotype *Maiasaura peeblesorum* described by Horner (1983), shows similar skull proportions to OTM F138 and can reasonably be assumed to fall within the adult age and size range. Cumulatively, these specimens represent end members of the Horner et al. (2000) age/size classification representing infant/juvenile or adult individuals. Although growth rates are not linear, as indicated by Horner et al. (2000) and Woodward et al. (2015), a linear correlation relating tooth size to body size based on museum specimens was used to maintain simplicity and consistency in this thesis (Figure 10). Plotting the average AP for the Egg Mt. assemblage generates a body size estimate of 3.8 ± 3 m, equating the average tooth size to represent what Horner et al. (2000) would deem Late Juveniles to possibly Subadults.

Variability in the preservation of the Egg Mt. *Maiasaura* tooth assemblage required AP tooth dimensions to be taken in two distinct locations while establishing a baseline through examination of museum specimens. AP dimensions taken at the widest available point on each tooth (AP_W) as well as AP measurements taken at the base of intact teeth (AP_B) would help to account for tooth size variability when examining the shed, disarticulated, and worn Egg Mt. assemblage. Taking variability in AP tooth size into account better serves population representation. Average AP_W tooth size observed in museum *Maiasaura* specimens ranges from 4.07 ± 0.17 mm for the smallest nestling/juveniles all the way up to 7.59 ± 1.2 mm in the largest adult specimens. Average AP_B tooth size range from 1.35 ± 0.15 mm to 4.53 ± 0.5 mm. If we assume the teeth in the Egg Mt. assemblage are only represented by the base of a tooth we can estimate AP_W by determining the average difference between AP_W and AP_B. On average AP_B represented approximately 60% of the maximum tooth width based on museum specimens. We can then apply this ratio to the Egg Mt. assemblage.

Egg Mountain Assemblage

A total of 564 hadrosaur teeth representing field collection between 2010 and 2015 were prepped and catalogued. Teeth are characterized by being largely incomplete in longitudinal dimensions. No roots were present nor were there any noted unworn crowns save sample 2015-B5-H5. Cross-sectional dimensions were largely preserved particularly on the more resilient enameled side of the tooth; labial if from maxilla, lingual if from the dentary. Preservation of the enameled side of the tooth often meant the AP or APC dimension was retained (Refer back to Figure 3). Although the structural integrity of teeth resist abrasion (Hillson, 2005) the hadrosaur samples from Egg Mt. appear to have experienced some transportation due to lack of roots, lack of unworn crowns, somewhat rounded and abraded edges, and the tendency to have a low ratio of longitudinal to fore-aft or labial-lingual dimensions (Peterson et al, 2014). These characteristics may also describe shed hadrosaur teeth. Forty-nine of the 152 teeth used in this analysis, representing 32% of the Egg Mt *Maiasaura* tooth assemblage, retained characteristics which may indicate shedding; i.e. a worn processing surface and “bowled” roots due to resorption (Erickson pers. comm.) The 32 % of teeth showing characteristics indicative of shedding may only be a minimum due to the fractured nature of the remaining specimens. Regardless of shedding or disarticulation, broken teeth show two distinct characteristics. Fresh or clean breaks likely resulted from excavation of the specimens from the quarry, however, other broken or possibly shed teeth show abrasion and rounding of broken edges. The latter indicates some form of exposure and abrasion or possible transportation occurred prior to final burial.

Of the 564 total hadrosaur teeth, 152 of the them were complete enough for measurement using my criteria; i.e. they had complete AP dimensions along a transverse plane, or the cross-sectional area of the specimen retained a measurable distance between the central carina and the most anterior or posterior point (APC). Complete AP measurements were attained from 94 of the measured teeth. The remaining 58 teeth required the AP measurement be extrapolated by using the APC length as described in my methods. Initial analysis of the prepared Egg Mt. Quarry collection spanning 2010-2015 field seasons provided a basic look at the number and distribution of *Maiasaura* tooth size. AP measurement was used as the primary analysis tool. Minimum AP tooth width was 1.96 ± 1.2 mm and a maximum of 8.13 ± 1.2 mm. As can be seen in Figure 11, the tooth collection shows a relatively bi-modal size-frequency distribution with peaks centered around 4.6 mm and 6.2 mm. The largest proportion of teeth fall at approximately 5 mm with an average of 5.08 mm. The Egg Mt. assemblage AP tooth size ranges exceed the observed AP_W and AP_B museum specimen ranges (AP_W = 4.03-7.59 ± 1.2 mm; AP_B = 1.35-4.53 ± 1.1 mm; observed in museum specimens). Twenty-four of the Egg Mt. specimens fall below observed AP_W lengths seen in museum collections. The same collection of small teeth fall within observed AP_B lengths. Tooth size ranges of the Egg Mt. assemblage have implications for the origin and taphonomy of the collection regarding shedding and disarticulation.

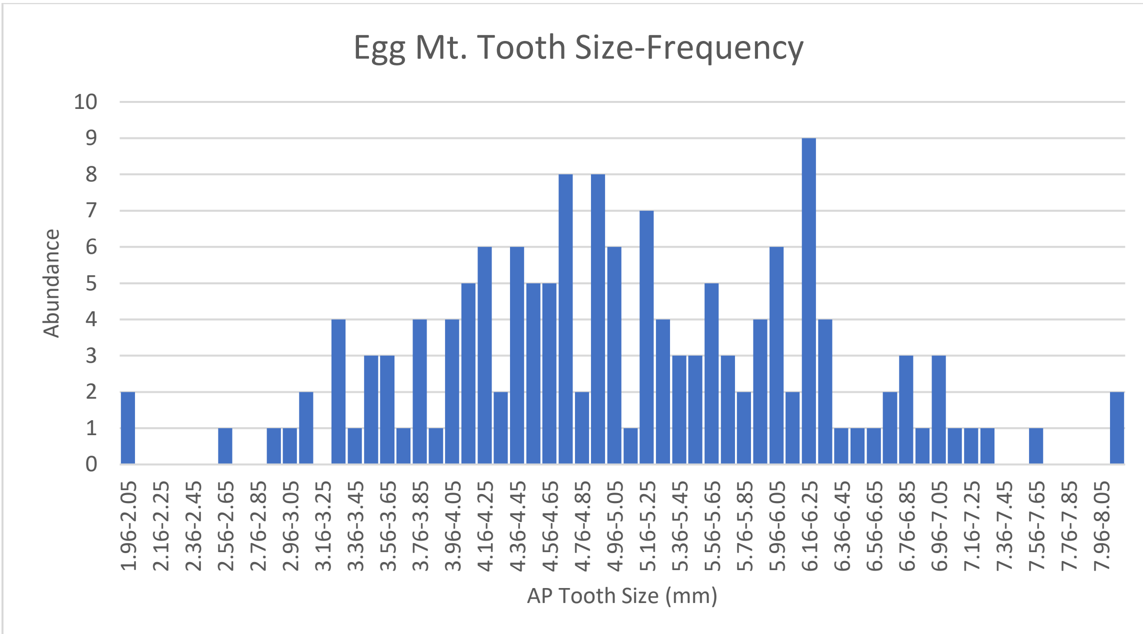


Figure 11—AP tooth size-frequency distribution of measured *Maiasaura* teeth from the Egg Mt. assemblage.

Hadrosaur tooth condition was markedly different from theropod tooth specimens collected from the quarry. Although theropod teeth are less abundant, they are represented by more complete specimens (Figure 13). Where theropod teeth are incomplete, most still retained enamel as well as denticles suitable for diagnosis to the family level (Currie et al. 1990, Fiorillo and Currie 1994). Many the theropod teeth in the quarry demonstrate longitudinal fracturing either buccal-lingually or anterior-

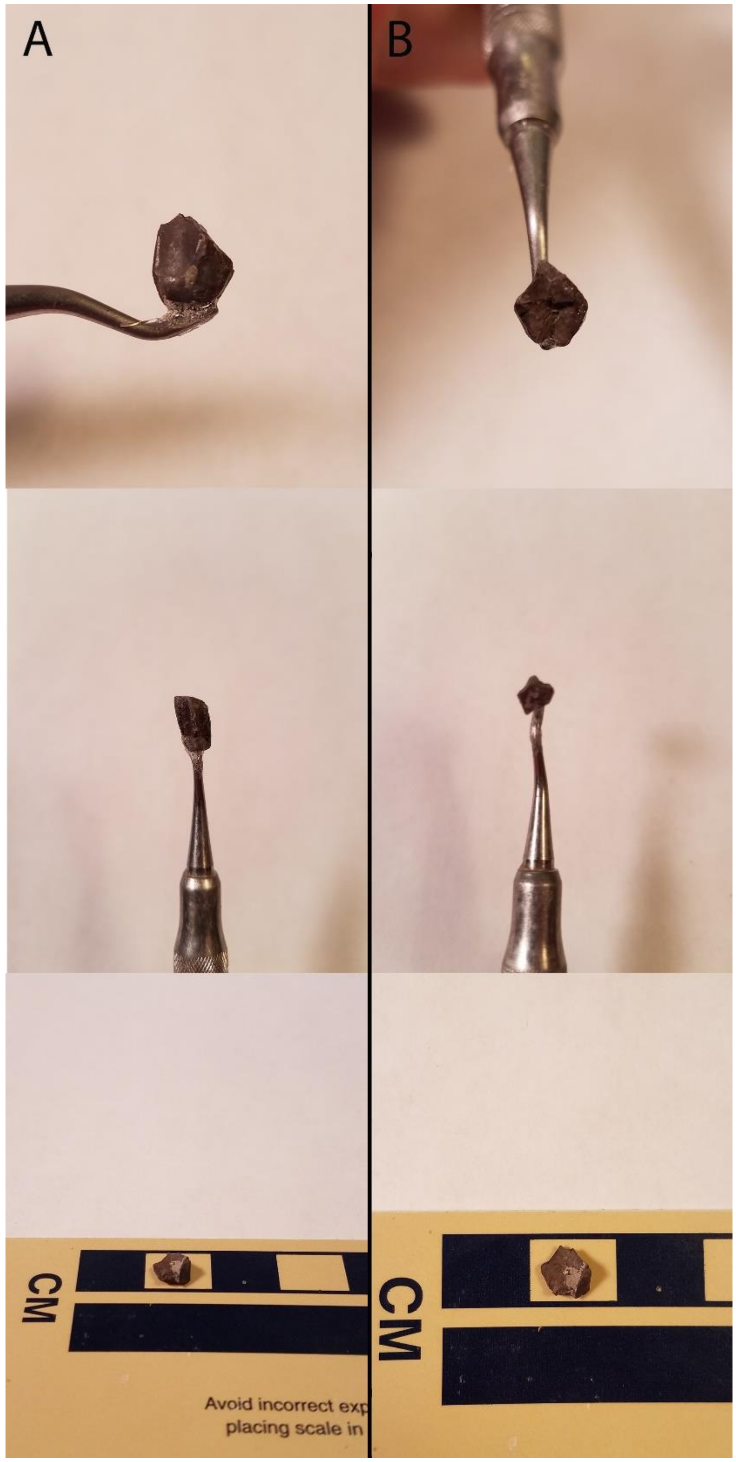


Figure 12—A general selection of the Egg Mt. *Maiasaura* teeth illustrating variation in longitudinal dimension, condition, and overall size. Panel A demonstrates a longitudinal view and the adjacent panel B demonstrates a transverse view of the adjacent specimen.

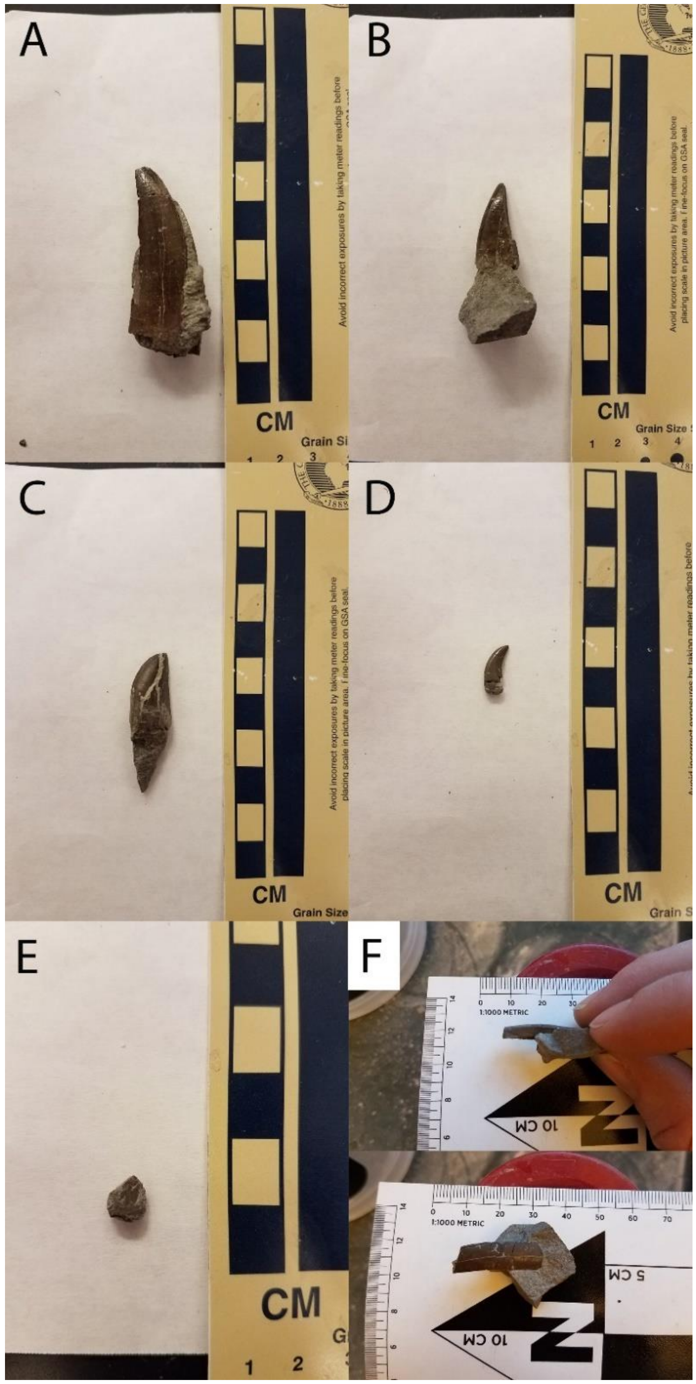


Figure 13—Egg Mt. theropod tooth assemblage. A: Unknown tyrannosaur; similar to "Type A" described by Fiorillo and Currie (1994). B: Unknown tyrannosaur premaxillary tooth. C: Unknown tyrannosaur; similar to "Type B" described by Fiorillo and Currie (1994). D: Dromaeosaur tooth. E: Incomplete Saurnitholestes tooth. F: Example of longitudinal splitting on an unknown tyrannosaur tooth. This splitting generates the characteristic "shards".

posteriorly. The longitudinal splits typically follow the contour of the tooth and edges of the longitudinal fractures appear to show little to no rounding or abrasion compared to the Egg Mt. *Maiasaura* teeth. Fracturing in this manner generates what can be described as "shards" of teeth and can be seen on both complete and incomplete theropod specimens (Figure 13F). This fracturing phenomenon appears to be rather unique to the Egg Mt locality (Moore et al. in review, Varricchio pers. comm.).

A simple abundance and size -frequency analysis was conducted on theropod teeth from the Egg Mt. Quarry for the purpose of better understanding their relationship with *Maiasaura* and the taphonomy of the site. In addition to the *Maiasaura* teeth, 95 theropod teeth were removed from Egg Mt. Quarry within the same volume of rock. The Egg Mt. locality and surrounding areas are well known for specimens of *Troodon formosus,* particularly eggs and nesting traces (Varricchio and Horner, 1993; Varricchio et al, 1997; Varricchio et al, 1999; Varricchio et al, 2002); therefore, it is not surprising their teeth have been found in the quarry. Several other theropod teeth have been collected adding richness to the ecology. Collections are reflective of theropod populations from the Judith River Formation described by Fiorillo and Currie (1994) showing presence of tyrannosaurs, miscellaneous dromaeosaurs, and *Saurnitholestes*. Integrating basic analysis of the theropod teeth with the hadrosaur collection indicates they contributed a large component. Of the 95 theropod teeth, 47 retained one or more of the three dimensions used for measurement. Size -frequency histograms were generated for theropod teeth for each dimension and can be seen in Figure 14. FABL measurements range from 3.2 mm to 21 mm with an average of 8.9 mm (n = 40; SD =

5.7) (Fig. 14A). Theropod teeth heights range from 2.8 mm to 50 mm with an average of 18.6 mm (n = 41; SD = 13.3) (Fig. 14B). Basal widths range from 1 mm to 18.4 mm and average at 5.7 mm (n = 38; SD = 3.9) (Fig. 14C). Theropod tooth abundance was compared to the *Maiasaura* tooth assemblage where the ratio of hadrosaur teeth to theropod teeth is nearly 6:1 or approximately 17% (Table 2). Similar proportions were estimated by Varricchio (1995) when examining Jack's Birthday Site (TM-068) where up to 25% of the representative species in the bonebed consisted of theropods. No theropod teeth were found in association with theropod jaw material therefore in the case of Egg Mt., presence of theropods are only based on teeth with no understanding of the minimum number of individuals (MNI).

Table 2—Total *Maiasaura* and theropod teeth with resulting ratio of the two groups. It should be noted this comparison groups multiple theropod taxa and compares them to only one like hadrosaur (i.e. *Maiasaura*).

Hadrosaur Tooth Total	564
Tyrannosaur Tooth Total	51
Troodon Tooth Total	26
Dromaeosaur Tooth Total	10
Saurnitholestes Tooth Total	4
Unknown Theropod Tooth Total	4
Theropod Tooth Total (w/in Quarry)	95
Hadrosaur/Theropod Ratio (w/out *Troodon* teeth outside main quarry)	5.94

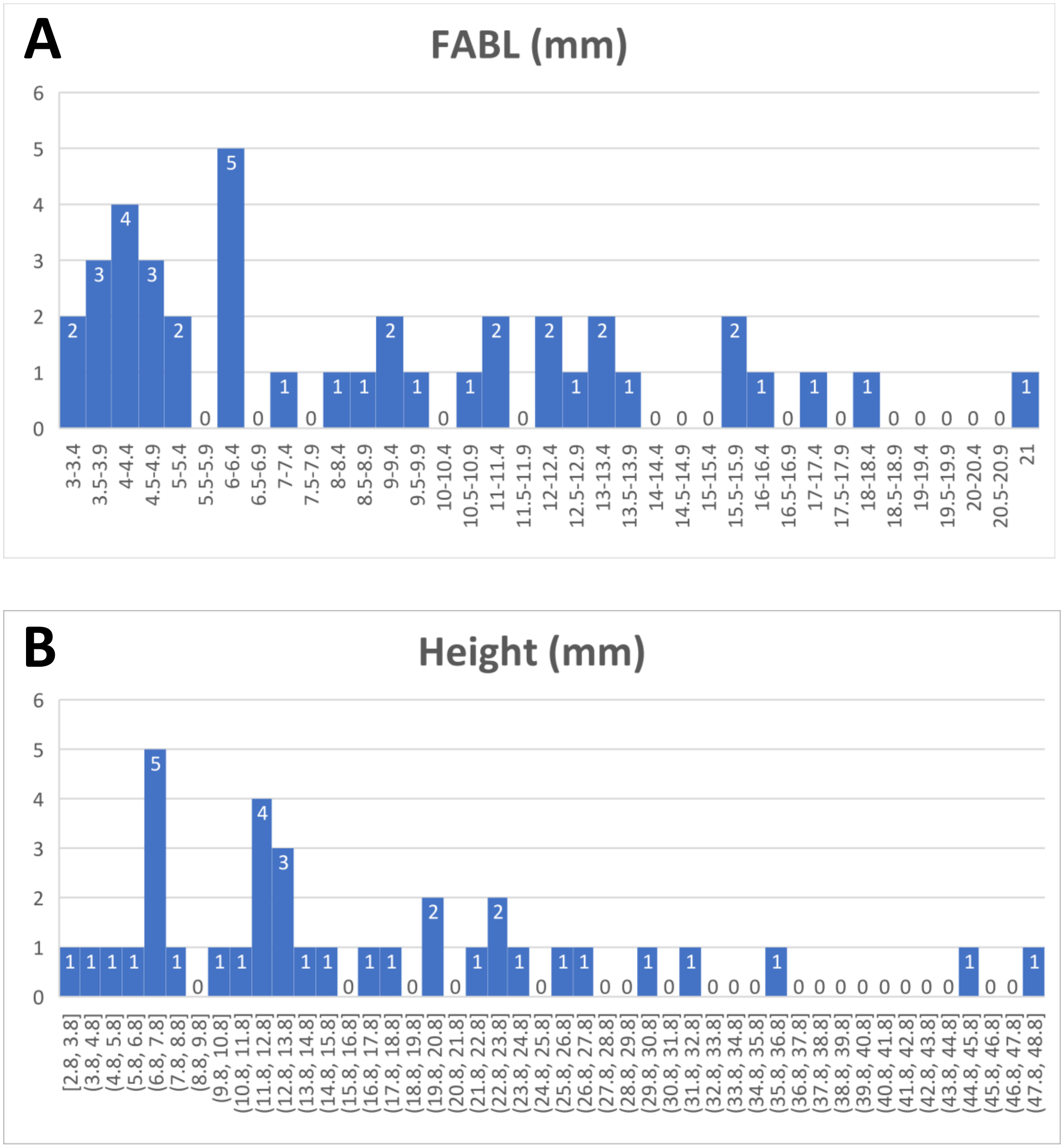


Figure 14—Size -frequency distributions of theropod teeth in all measured dimensions where dimensions were retained. A: Size-frequency of FABL measurements. B: Size-frequency of height measurements. C: Size-frequency distribution of basal width measurements.

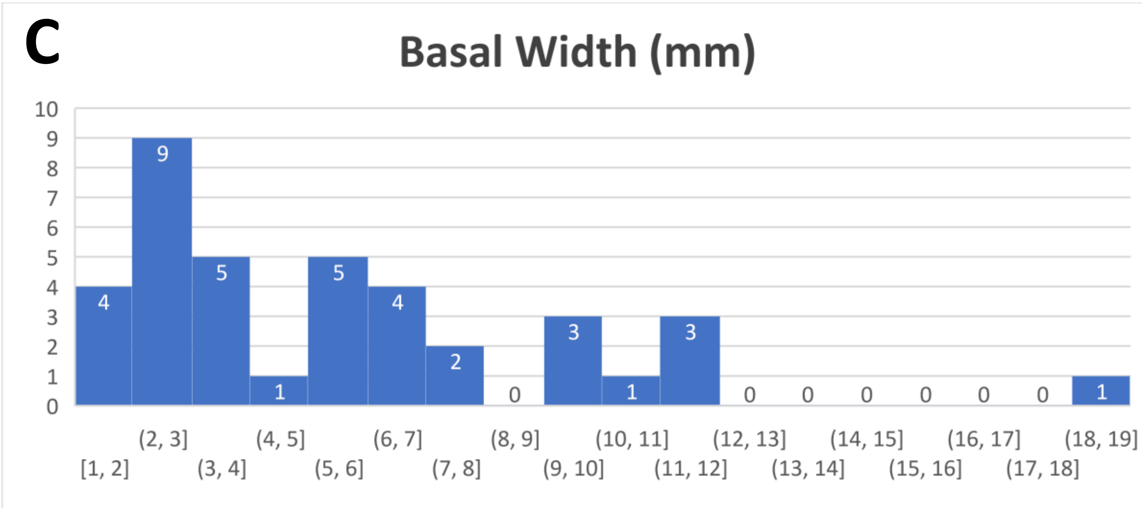
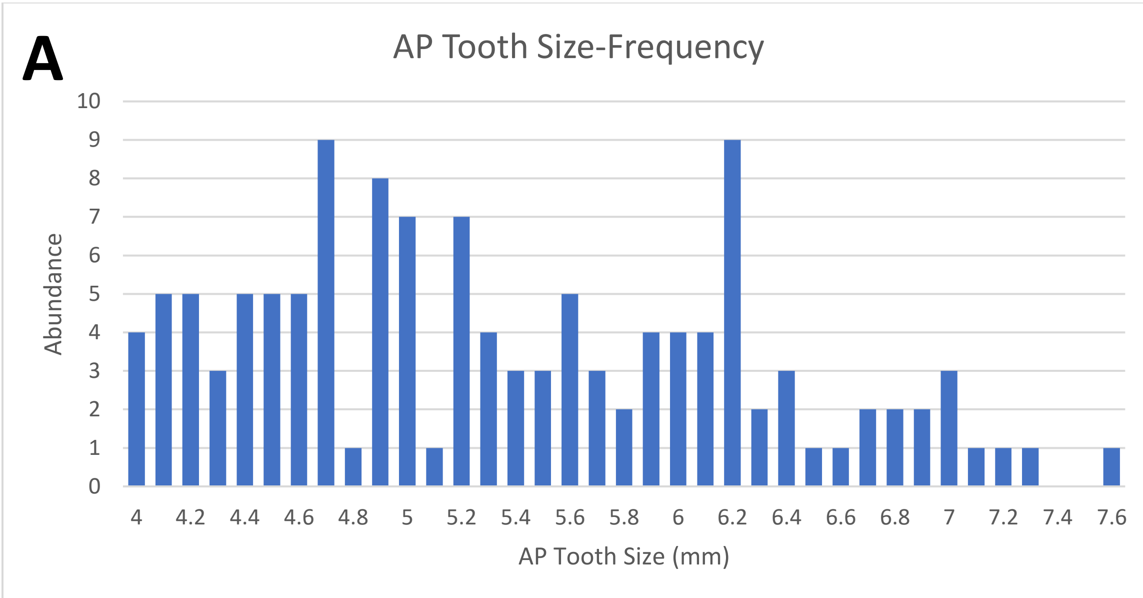


Figure 14—Cont.

Application of the SQ to the Egg Mt. Assemblage

Figure 15A re-visits the size -frequency distribution of the Egg Mt. assemblage, restricted to observed museum tooth dimensions, followed by the same assemblage after SQ values are applied. The size -frequency distribution of the Egg Mt. *Maiasaura* teeth is now represented as a size-frequency distribution of *Maiasaura* individuals (Figure 15B). The same strategy can be applied to the Egg Mt. assemblage but with observed AP_B measurements. The ratio between AP_B lengths and AP_W lengths observed in museum specimens is approximately 60%. Multiplying the Egg Mt. assemblage AP lengths by this ratio we attempt to estimate the full-size or AP_W of the teeth represented by the Egg Mt specimens, this assumes they represent the base of a worn-down tooth. The result is presented in Figure 16. Note the shift in AP tooth size to be representative



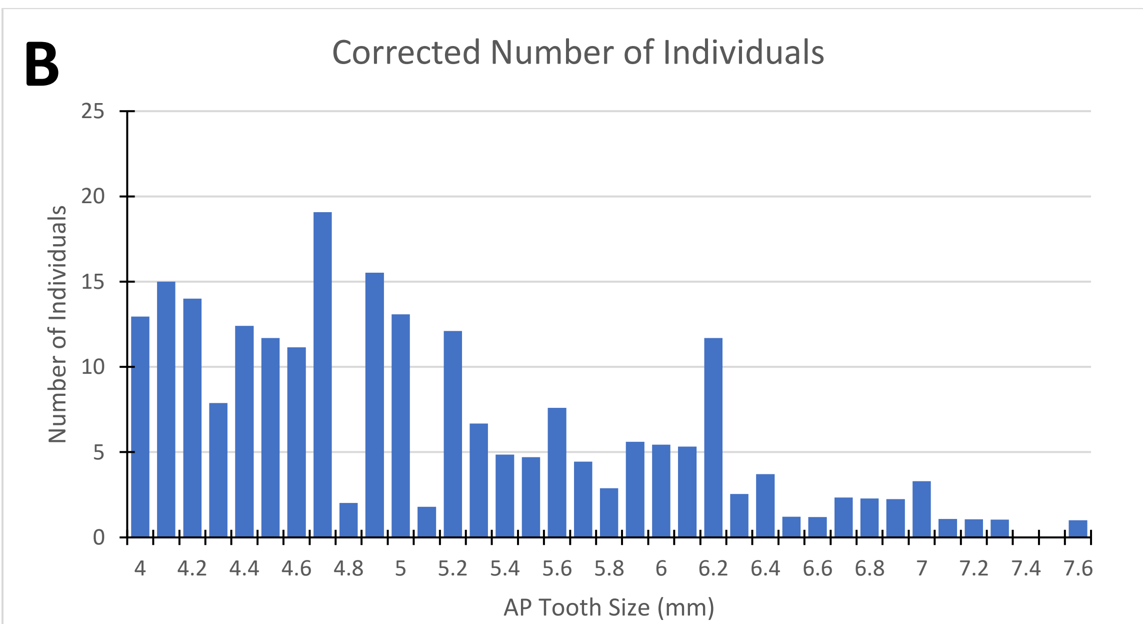


Figure 15—A: AP tooth size-frequency in .1 mm increments. B: Number of individuals represented by the Egg Mt. *Maiasaura* tooth assemblage after applying SQ values to each AP tooth size. Sample limited to observed museum specimen AP ranges.

of an adult population (Observed AP tooth sizes greater than 6 ± 1.2 mm) as opposed to a strongly juvenile population. Application of this scalar also pushes AP tooth sizes from the Egg Mt. assemblage into realms beyond the maximum observed AP tooth size in museum specimens. Applying the linear body size correlation to the new AP tooth sizes results in the same issue, forcing body sizes into far larger realms. In order to determine what may be the best interpretation of the Egg Mt assemblage the same scaling strategy was applied in 10% increments between 0 and 60%. The complete set of results can be seen in Appendix D.

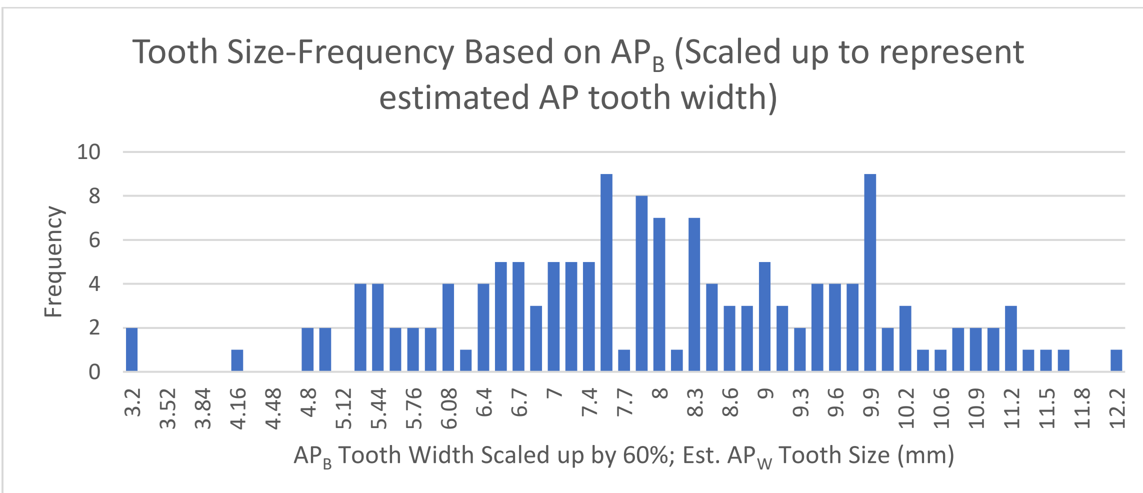


Figure 16—Estimated AP_W tooth size frequency scaled up 60% from observed AP_B lengths. Scale based on AP_B measurements taken on observed museum specimens.

<u>Application of the DQ to the Egg Mt. Assemblage</u>

The DQ was applied to address the possibility the Egg Mt. assemblage was derived from the disarticulation of teeth from the dental battery. Like the SQ, Figure 17 demonstrates the size-frequency distribution of the Egg Mt. assemblage as well as the frequency of individuals based on AP lengths. Egg Mt. teeth identified as shed were scaled up to represent full size teeth (utilizing the 1.6:1 ratio) prior to being input into the DQ. Scaling the shed teeth attempts to render them as a full-sized tooth residing in the dental battery prior to disarticulation.

Maiasaura Mortality and Survivorship

By utilizing the estimated number of *Maiasaura* individuals representing the Egg Mt. assemblage, we can generate life tables and survivorship curves. Different distributions and numbers of individuals were generated by the application of the SQ and DQ factors. Each population derived from these factors will have unique life table and survivorship curves calculated for them.

Raw Tooth Size Represented as Population

If we assume the size-frequency distribution of the Egg Mt. assemblage is a reflection of the population they represent, the 152 teeth illustrated in Figure 18 represent 152 individuals. The first year of life, inclusive of Small Nestlings through Late Juveniles are represented by 93 individuals, 26 within the Subadult AP tooth range, and 33 in the Adult range. The life table and survivorship curve generated from these direct observations (Figure 18) shows high juvenile mortality (84%) followed by a decrease and mortality plateau during the Subadult stage (39%), and ultimately the lowest mortality rates experienced by the time Adult stage is reached (17%).

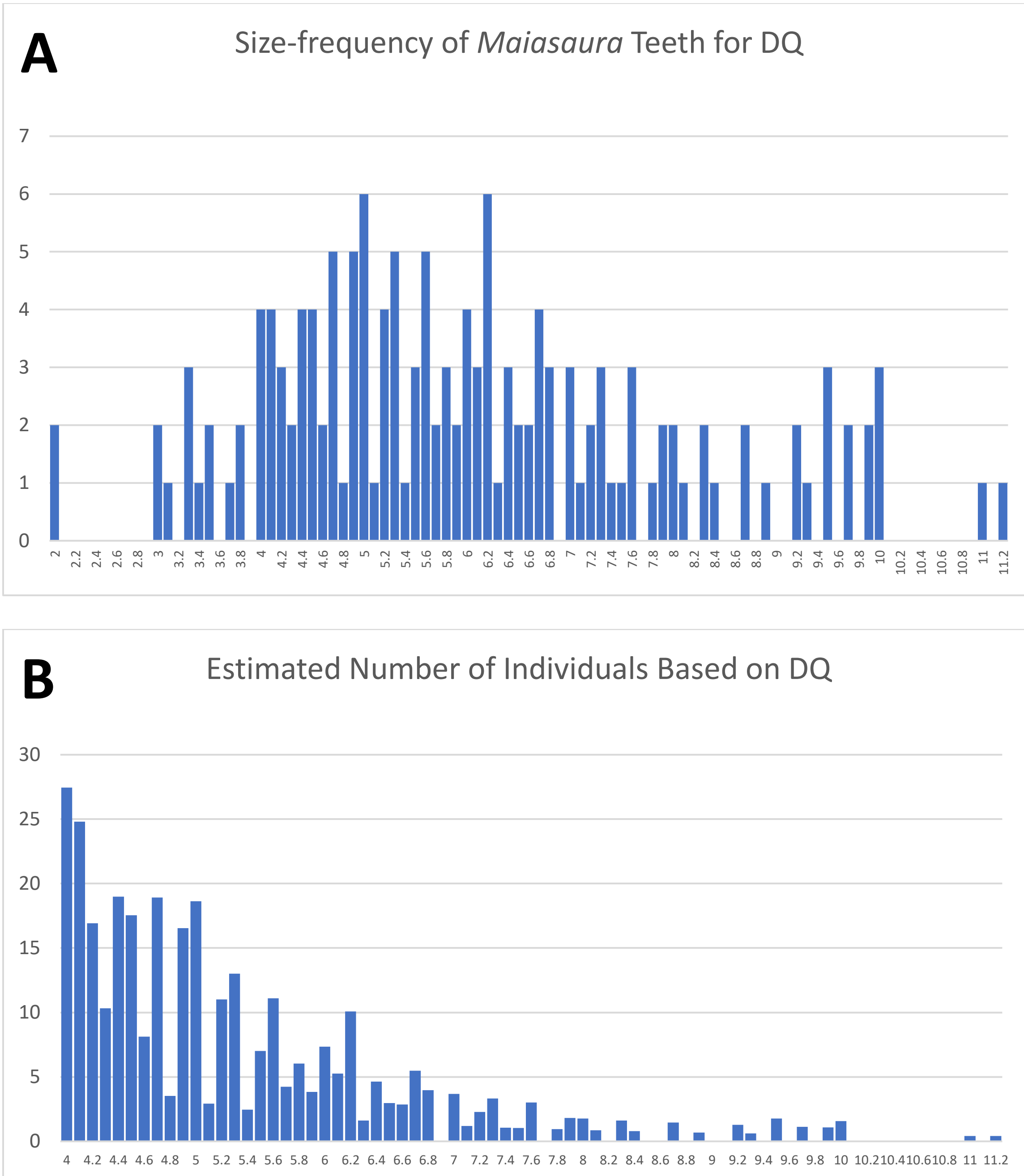


Figure 17—A. Size-frequency distribution of *Maiasaura* teeth from Egg Mt. Quarry derived for application of the DQ. This includes specimens identified as shed teeth, scaled up. B: Number of individuals represented by the Egg Mt. *Maiasaura* tooth assemblage after applying DQ values to each AP tooth size.

Shedding Quotient Population Representation

A total of 152 *Maiasaura* teeth from the Egg Mt. assemblage were analyzed (as stated earlier). The inclusion of 127 of the 152 teeth (restricting size ranges to observed museum ranges) represents 231 ± 5.3 individuals if face value AP lengths are analyzed. Of the 231 individuals 149 ± 5.3 include Small Nestling, Large Nestling, Early Juvenile, and Late Juvenile growth stages. Forty-five fall in the Adult range. The remaining 37 ± 5.3 individuals fall into AP tooth size ranges belonging to Subadults (Figure 19). Survivorship indicates high mortality rates (73%) during the first year of life followed by a mortality plateau (36%) until adult age was reached at approximately 6 years of age and mortality is at a low of 20% (Horner et al. 2000; Woodward et al. 2015).

Disarticulation Quotient Population Representation

The same 152 *Maiasaura* teeth were analyzed producing some estimated 321 ± 6.4 individuals. Two-hundred and eight (± 6.4) fall within Small Nestling-Late Juvenile AP ranges, 42 ± 6.4 in the Subadult range, and the remaining 71 ± 6.4 are Adults. Similar survivorship and mortality rates were estimated for the DQ where mortality was at its highest during the first year of life (64%) followed by a marked reduction during the Subadult stage (35%) eventually dropping to an estimated 22% by the time Adult age is reached (Figure 20).

Relative age brackets placed on the Egg Mt. assemblage are reflected in the life tables and survivorship curves generated for the raw size-frequency data as well as the SQ and DQ (Figures 18,19 and 20). Development of the life tables and survivorship curves assumes zero neonate mortality. Due to the limited ability to discern exact ages from the *Maiasaura* teeth themselves, relative age brackets were generated based on hypothesized growth rates and ages by Horner et al. (2000) and Woodward et al. (2015). Mortality rates after adult age was reached could not be calculated due to the inability to discern different ages between similarly sized teeth interpreted to belong to adult individuals. The survivorship curves generated from this assemblage resemble a sigmoidal Type B1 survivorship curve coined by Pearl and Miner (1935) and is reflective of the curve hypothesized by Woodward et al. (2015) for *Maiasaura peeblesorum* but also reflective of survivorship curves generated for tyrannosaurs (Erickson et al. 2006) and *Psittacosaurus lujiatunensis* (Erickson et al. 2009). Mortality rates indicated by the Egg Mt. assemblage were high during the first year of life followed by a mortality plateau until adult age was reached at approximately six years of age based on previous analyses (Horner et al. 2000; Woodward et al. 2015).

Table 3—Life table representation of *Maiasaura* generated from raw tooth size data. Assumes 0% neonate mortality Mortality rates provided for relative age brackets based on observed AP ranges. Growth stages and relative age based on Horner et al. 2000 and Woodward et al. 2015.

Age (years)	Age Class	Sampled #	Number Dying	Survival Rate
0	Small Nestling	24	152	1
1	Late Juvenile	69	128	0.84
3.5	Unknown	26	59	0.39
6	Adult	33	26	0.17

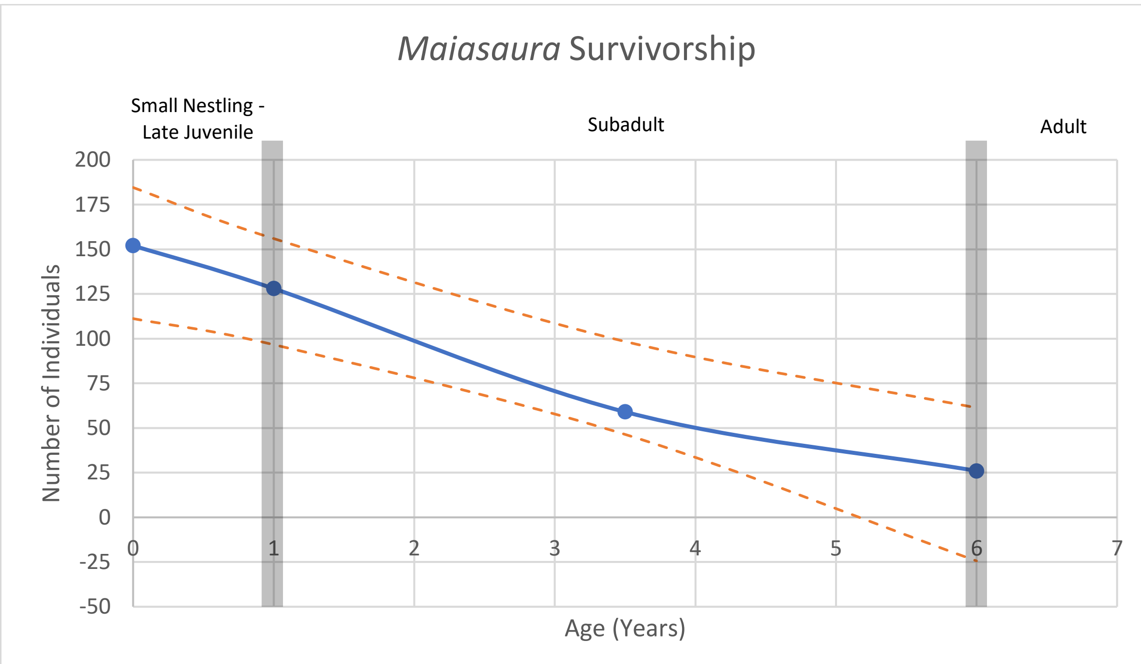


Figure 18—Survivorship curve with 95% confidence interval generated for the Egg Mt. *Maiasaura* tooth assemblage based on the raw AP data. No factor was applied. Assumes 0% neonate mortality. Mortality rates provided for relative age brackets based on observed AP ranges. Growth stages and relative age based on Horner et al. 2000 and Woodward et al. 2015.

Table 4—Life table representation of *Maiasaura* generated from application of the SQ to the Egg Mt. assemblage. Assumes 0% neonate mortality Mortality rates provided for relative age brackets based on observed AP ranges. Growth stages and relative age based on Horner et al. 2000 and Woodward et al. 2015.

Minimum Age (years)	Age Class	Sampled #	Number of Individuals	Survival Rate
0	Small Nestling	62	231	1
1	Late Juvenile	87	169	0.73
~3.5	Unknown	37	82	0.36
6	Adult	45	45	0.2

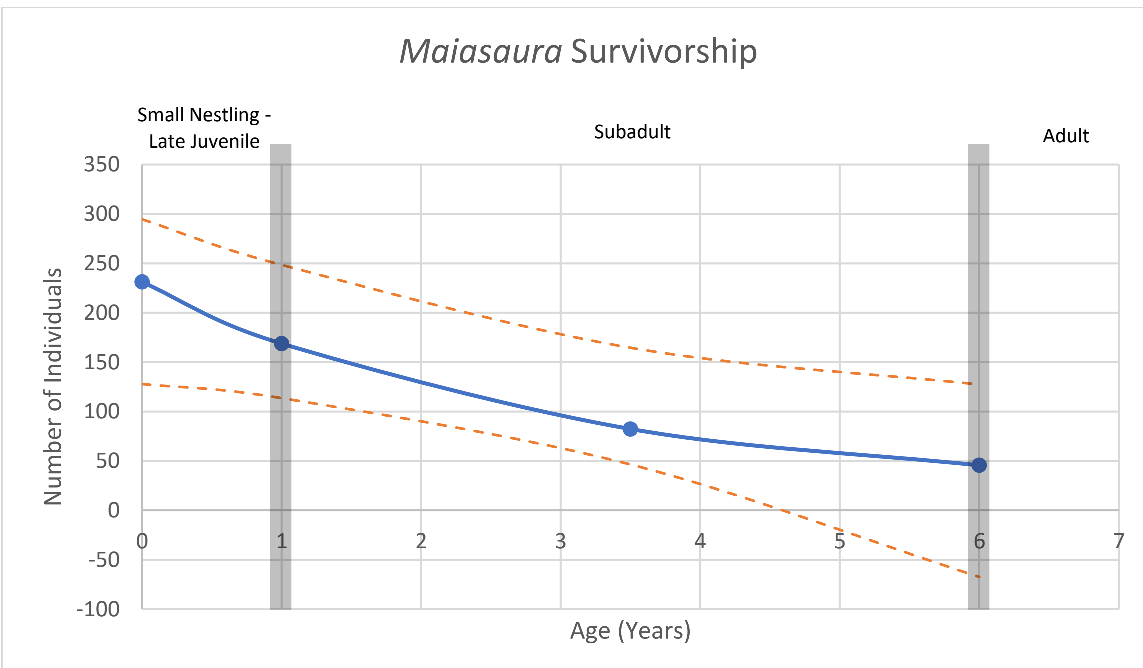


Figure 19—Survivorship curve with 95% confidence interval generated for the Egg Mt. *Maiasaura* tooth assemblage based on application of the SQ. Assumes 0% neonate mortality. Mortality rates provided for relative age brackets based on observed AP ranges. Growth stages and relative age based on Horner et al. 2000 and Woodward et al. 2015.

Table 5—Life table representation of *Maiasaura* generated from application of the DQ to the Egg Mt. assemblage. Assumes 0% neonate mortality Mortality rates provided for relative age brackets based on observed AP ranges. Growth stages and relative age based on Horner et al. 2000 and Woodward et al. 2015.

Age (years)	Age Class	Sampled #	Number Dying	Survival Rate
0	Small Nestling	116	321	1
1	Late Juvenile	93	205	0.64
3.5	Unknown	42	112	0.35
6	Adult	70	70	0.22

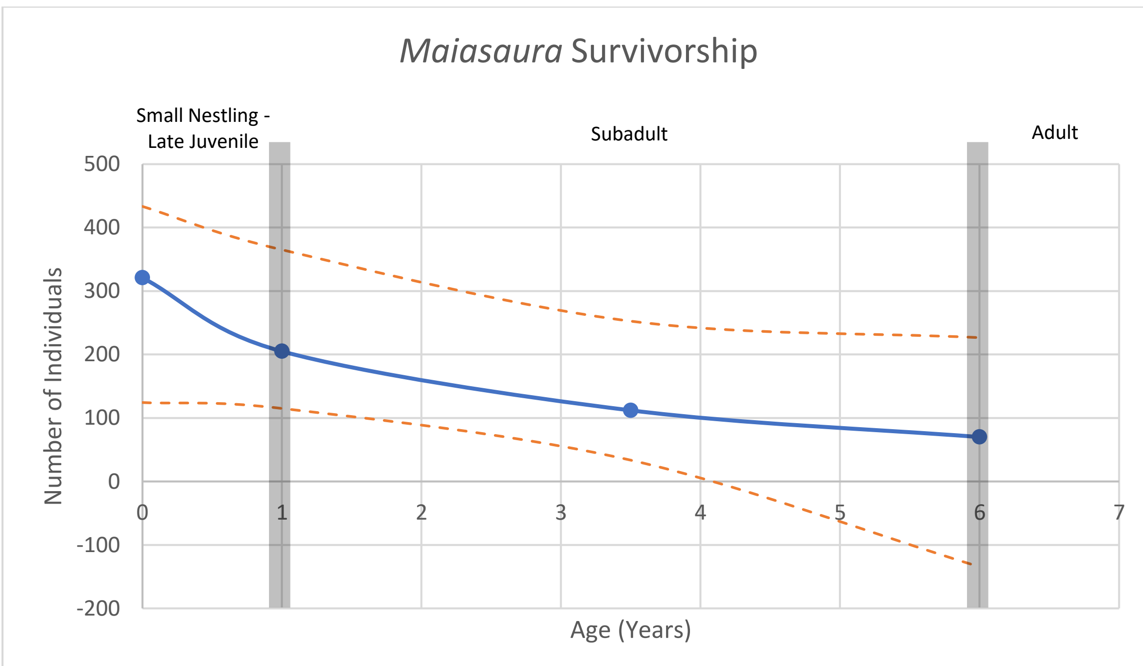


Figure 20—Survivorship curve with 95% confidence interval generated for the Egg Mt. *Maiasaura* tooth assemblage based on application of the DQ. Assumes 0% neonate mortality. Mortality rates provided for relative age brackets based on observed AP ranges. Growth stages and relative age based on Horner et al. 2000 and Woodward et al. 2015.

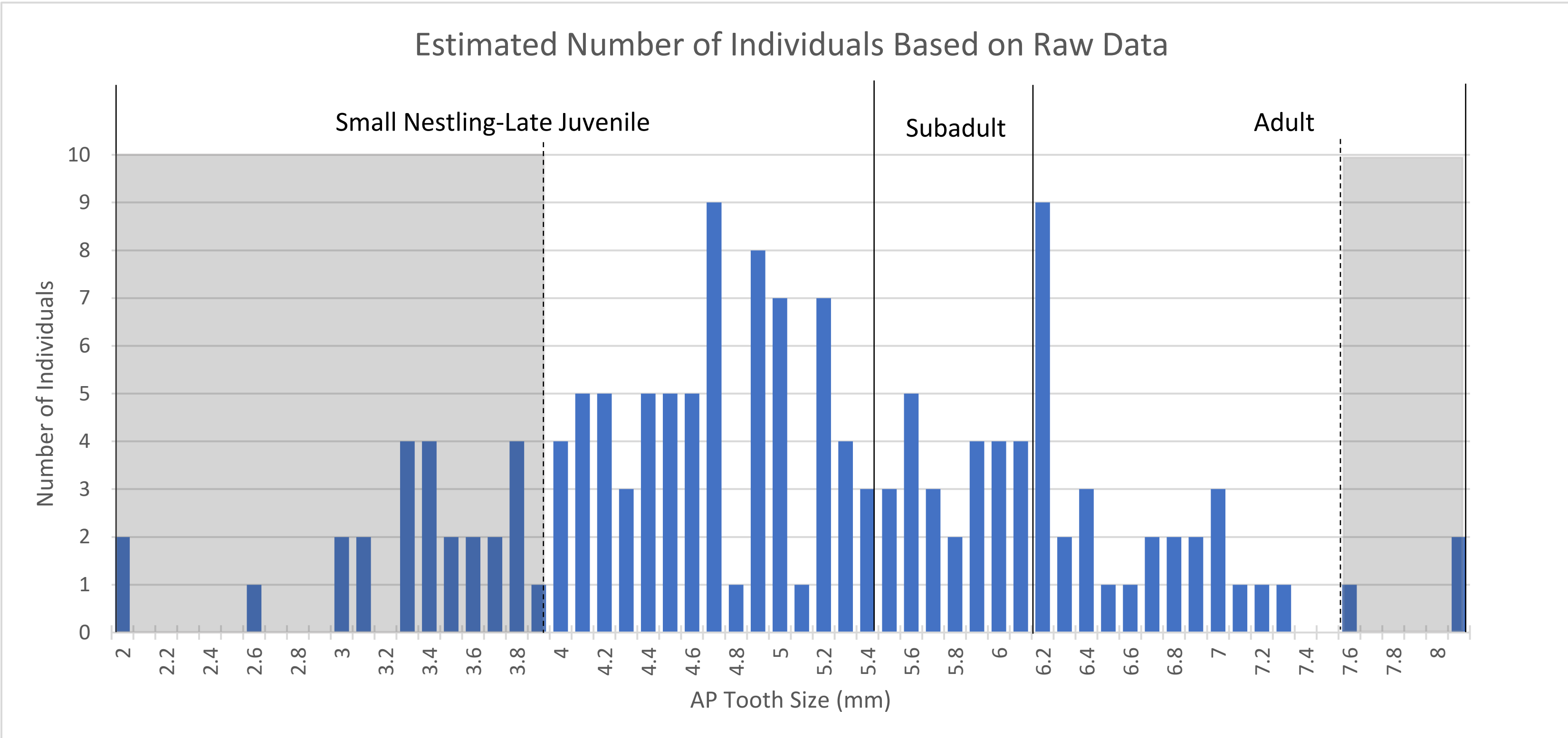


Figure 21—Number of individuals represented by the Egg Mt. *Maiasaura* tooth assemblage based on raw data. No factors were applied to AP tooth size. Shaded areas and dashed lines indicate tooth size ranges falling outside of observed averaged museum specimen ranges. Growth stages described by Horner et al. 2000.

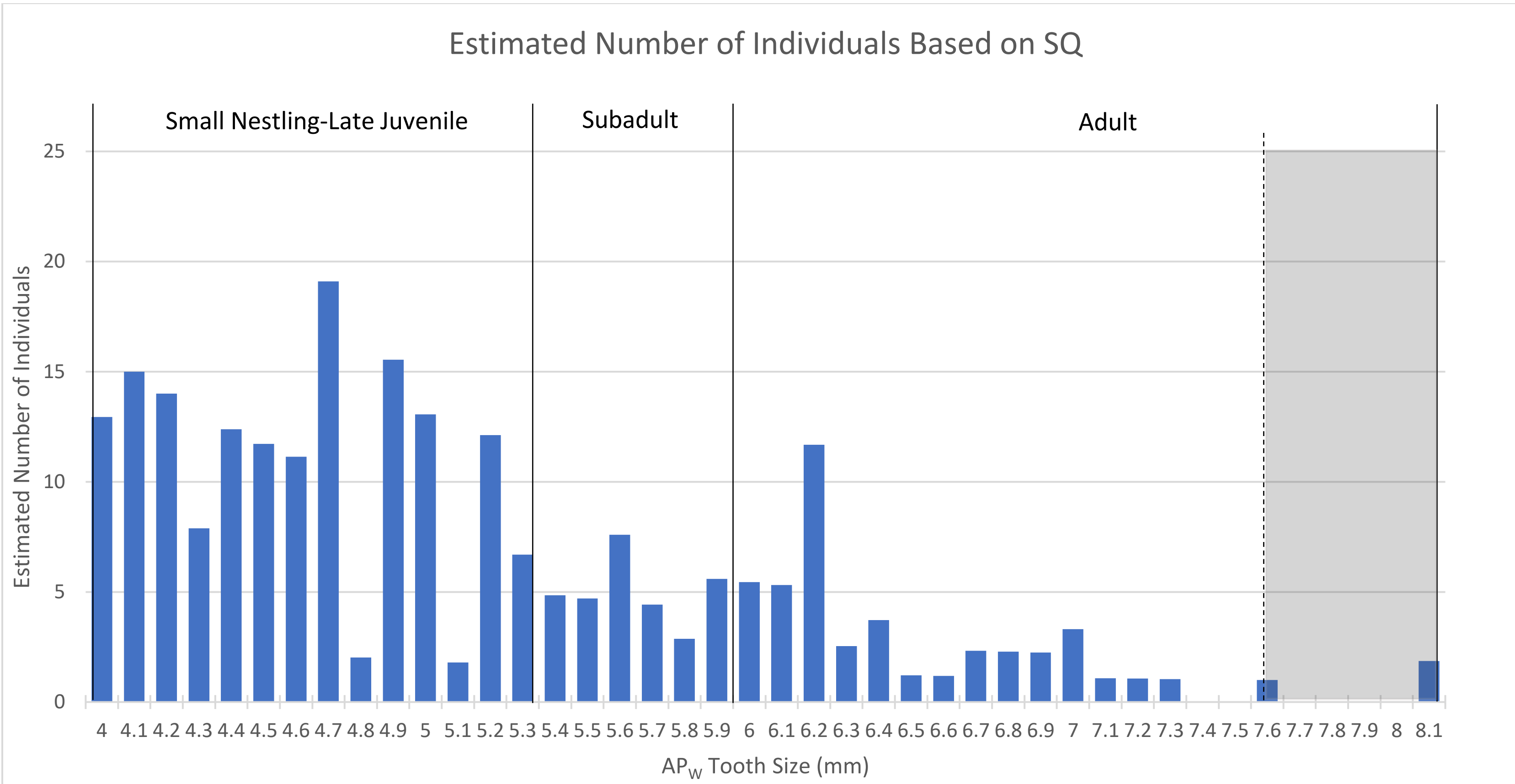


Figure 22—Number of individuals represented by the Egg Mt. *Maiasaura* tooth assemblage as a result of applying SQ factors to AP tooth size. Sample limited to AP tooth size above 4 mm (smallest average AP observed in museum specimens). Growth stages described by Horner et al. 2000.

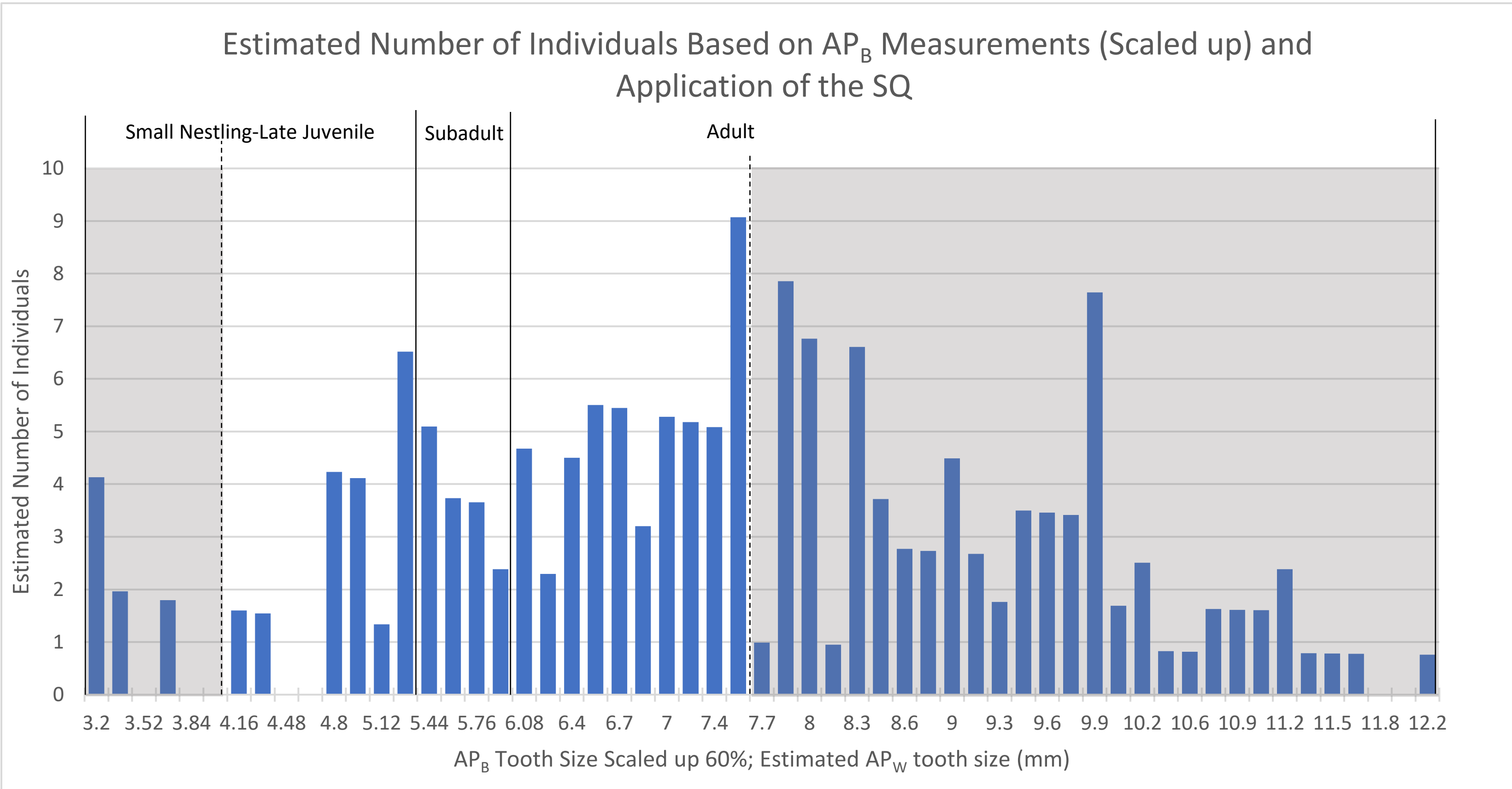


Figure 23—Number of individuals represented by the Egg Mt. *Maiasaura* tooth assemblage as a result of applying SQ factors to scaled AP_W tooth size (160% of AP_B). Shaded area and dashed line indicate tooth size ranges falling outside of observed average museum specimen ranges. Growth stages described by Horner et al. 2000.

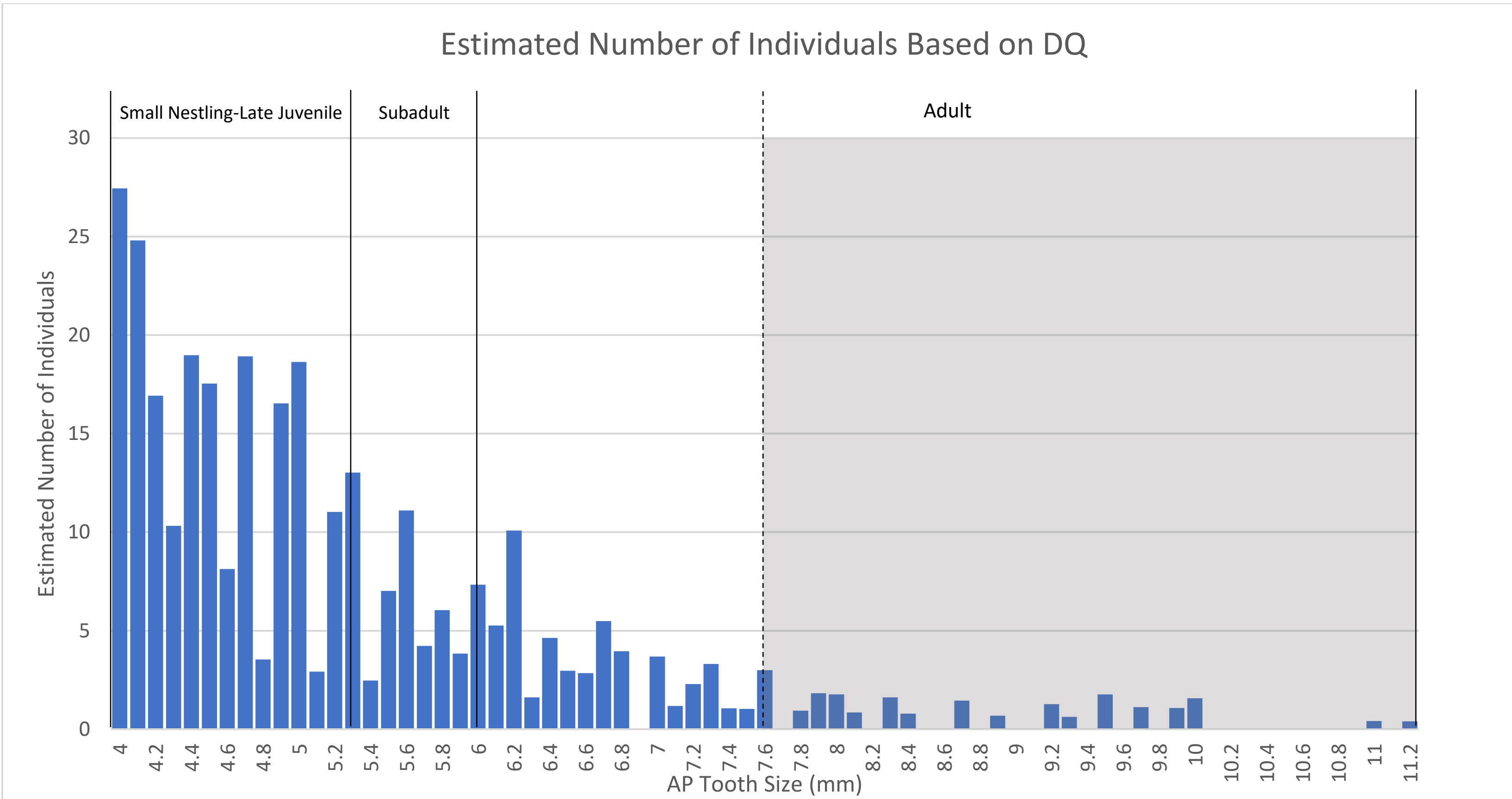


Figure 24—Number of individuals represented by the Egg Mt. *Maiasaura* tooth assemblage as a result of applying DQ factors to scaled AP tooth dimensions. Sample limited to AP tooth size above 4 mm (smallest average AP observed in museum specimens). Shaded area and dashed line indicate tooth size ranges falling above observed museum specimen ranges. Growth stages described by Horner et al. 2000.

DISCUSSION

Taphonomic Interpretation of the Egg Mt. Assemblage

Egg Mt. Quarry has produced a host of body and trace fossils. No agreement has been reached about how all this material became associated. Inspection of the hadrosaur and theropod tooth assemblage from the Egg Mt. locality may help to shed light on Egg Mt. ecology and taphonomy. The Egg Mt. *Maiasaura* teeth have AP tooth sizes ranging from 1.96-8.13 mm, unfractured specimens show abraded edges, and are relatively equidimensional. Contrastingly, theropod teeth have a significantly larger range of sizes (ex. 2.8-50 mm in height), show less abrasion (retaining larger portions of enamel and denticles), and are typically longer than they are wide. A substantial contribution to the Egg Mt. assemblage also includes in-situ eggshell and nesting traces, lizard and mammal material, and terrestrial pupa cases distributed throughout the excavated succession. Co-existence of fossil material within the new quarry have implications for taphonomic interpretation. Here, I describe how microsite formation, shedding/disarticulation of teeth, and models of *Maiasaura* population and growth contribute to the population of teeth analyzed in this study.

The 1.5 m of sediment removed from Egg Mt. quarry since 2010 has not produced any aquatic or semi-aquatic taxa with the exception of one frog element, and one heavily worn turtle carapace fragment – scant evidence for an aquatic hypothesis given the immense amount of terrestrial remains (n > 5,000). A general lack of aquatic taxa coupled with the continuous representation of in-situ nesting material and terrestrial insect pupa cases, throughout the section, support an attritional, time-averaged, and terrestrial origin. Why then is there a significant presence of equidimensional and abraded *Maiasaura* teeth distributed throughout the quarry? Introduction of *Maiasaura* specimens, shed or disarticulated, may have required transportation and concentration occurring on the alluvial plain the Egg Mt. quarry resided on during deposition.

A fossil microsite is a concentration of fossil material defined by Eberth as multi-individual accumulations of disarticulated and dissociated vertebrate hard parts dominated by elements in the millimeter to centimeter size range (≥75% of bioclasts ≤ 5 cm maximum dimension) (Eberth et al. 2007; Rogers et al. 2010). By this definition Egg Mt. Quarry would not be defined as a traditional microsite, not for lack of correctly sized elements but by the diffuse nature of the material. The density of fossils within the Egg Mt. Quarry are low except for pupa cases which occur regularly throughout (Varricchio, pers. comm.). Concentration of material typical of a fossil microsite likely took place around pond and lake environments where distinct species would congregate for food and water (Behrensmeyer 1978; Haynes 1988; Varricchio 1995). Ephemeral pond and lake deposits existed throughout the Two Medicine alluvial plain of the Campanian foreland basin and likely served to concentrate material in a similar way (Lageson et al. 2001; Jackson and Varricchio 2010; Moore et al. in review; Roberts 1999; Rogers et al. 1995; Shelton 2006; Varricchio and Horner 1993). These fossil concentrations are subsequently reworked and redeposited by fluvial systems migrating across the plain (Rogers et al 2010) which may have existed at the Egg Mt. locality based on interpretations by Lorenz (1981), Lorenz and Gavin (1984), Shelton (2006), and Moore et al. (in review). Rogers et al.'s - (2010) interpretation of microsite formation ties together the occurrence of fossil microsites in both floodplain/lake as well as channel hosted sandstone deposits.

Sedimentology of the Willow Creek Anticline shows the evidence of stream channel deposits, overbank fines as well as carbonate muds, and carbonate pond deposits (Gavin 1986; Horner et al. 2001; Jackson and Varricchio 2010; Lageson et al. 2001; Lorenz 1981; Lorenz and Gavin 1984; Shelton 2006; Varricchio 1995). Presence of both streams and pond deposits in the WCA appear to satisfy conditions for microsite formation described by Rogers et al (2010); however, the Egg Mt locality is somewhat of a mystery due to the largely unremarkable and uniform nature of the calcitic mudstone as well as the diffuse nature of the material. Preservation of autochthonous nesting material as well as articulated mammal and lizard specimens found at Egg Mt. appears to contradict its formation by reworking and re-deposition. The hadrosaur and theropod teeth examined in this study however, may lend support for an autochthonous or parautochthonous origin of the Egg Mt. assemblage through a combination of flood plain deposition and contemporaneous nesting behavior.

If the *Maiasaura* or theropod teeth experienced any transportation prior to burial it becomes difficult to distinguish when the matrix containing the specimens does not retain any sedimentological evidence for transportation or contains variation in sedimentary grain size indicating change in flow regime. Transportation of tooth sized material must also accompany sediment grains with similar fluvial transport equivalencies. Behrensmeyer (1975) found that a tooth ~1 cm would be accompanied by quartz grains up to 1.5 mm. All the *Maiasaura* teeth examined fall below 1 cm, indicating sediments accompanying them would be substantially smaller; matching sediment size variation existing throughout the mudstone matrix of Egg Mt. quarry. Although the remaining material found within Egg Mt. Quarry may not show evidence of transportation, the *Maiasaura* specimens may have been equivalent to bed-load of the fluvial process responsible for their deposition. Similar patterns were found by Fiorillo (1991) in regards to analyzing the Careless Creek Quarry and separating out lag deposits from catastrophic deposition of large long-bone material. The relatively small, broken hadrosaur teeth are found alongside larger theropod teeth generally lacking significant abrasion. Nesting material, including an abundance of *in situ* eggshell and nesting traces, would also expect to be disturbed if fluvial processes were strong enough to transport any of the described specimens to or from Egg Mt. although it has been found eggshell fragments can withstand relatively significant flow without transportation occurring if shear stress' are high enough (Imai et al. 2015). An abundance of insect trace fossils interpreted to be cocoons or insect pupation chambers (Freimuth 2017; Martin and Varricchio 2011; Moore et al. in review) indicates the sediments at Egg Mt. were well drained with persistent soil conditions allowing for sufficient colonization between episodes of floodplain inundation and deposition.

The time-averaged collection of *Maiasaura* teeth from Egg Mt. are likely generated through a combination of shedding and disarticulation; however, understanding which process contributed to the Egg Mt. assemblage is muddled by their poor condition. An assemblage completely generated through disarticulation of the dental battery would presumably create specimens with more complete longitudinal dimensions. An assemblage completely generated through shedding would presumably leave out teeth with AP dimensions representing Adult individuals. However, the Egg Mt. assemblage produces *Maiasaura* teeth which appear to demonstrate shedding as well as disarticulation.

If a combination of shedding and disarticulation contributed to the Egg Mt. assemblage, there also remains the possibility the collection is biased toward *Maiasaura* teeth falling within the observed size range. Bias could be the effect of sorting on the hadrosaur teeth transported into the Egg Mt. locality. Complete disarticulation of the dental battery would produce an assortment of tooth sizes including worn and unworn teeth represented by various AP tooth sizes. Sorting through hydrologic processes like Rogers et al.'s (2010) description of microsite formation, may remove the rather worn and equidimensional *Maiasaura* teeth from the sample leaving complete teeth behind and transporting the rest to put them in association with the other in-situ quarry material. Alternatively, a biased selection of smaller, worn teeth could be caused by disarticulation. Several of the museum specimens observed for this study retain both worn and unworn teeth. Partial disarticulation of the dental battery post mortem but prior to burial could potentially involve the selective disarticulation of worn teeth destined for shedding. It was noted by Toots (1965) the presesrvation of mammal teeth would require special conditions particularly in arid environments where teeth tend to weather by cracking and then disintegrating. The semi-arid or seasonally arid environment of the WCA and the Two Medicine Formation would presumably not be suitable for preserving an abundance of teeth unless sufficient sedimentation or burial through fluvial or animal interaction introduced *Maiasaura* teeth to preferential conditions. Extensive exposure or destruction through trampling may be a contributing factor to the poor condition of the Egg Mt. hadrosaur teeth regardless if they are shed or disarticulated.

I address the issues of shedding and disarticulation through application of the SQ and DQ to the Egg Mt. assemblage. By assuming the Egg Mt. assemblage is generated entirely through shedding or entirely through disarticulation limits our vision of the taphonomy of the Egg Mt. quarry. The generation of the assemblage is likely a mixture of shedding and disarticulation influenced by hydrologic processes. We have examined the extremes to which the *Maiasaura* teeth could be introduced and by doing so, effectively limit the scope of possibilities.

Formation of the diffuse micro-vertebrate Egg Mt. quarry is still under investigation, but it does not preclude the selection of teeth examined in this study are primarily young individuals indicated by average size, comparison to individuals of known ontogenetic stages, and tooth formation rates based on histology. If a large component of fast growing, young individuals were living and dying at rates previous hypothesized during seasonal nesting periods, the introduction of teeth, both shed and disarticulated, would be readily available to be introduced to the Egg Mt. sediments (Cooper et al. 2008; Horner 1982; Horner 1984; Horner 1987; Horner et al. 2000; Varricchio 2010; Woodward et al. 2015). Nestlings and juveniles replaced their teeth at a more rapid rate as per Erickson (1996) found, however the number of teeth to replace was significantly smaller. The large component of nestling/juvenile teeth at Egg Mt. could be the result of quicker tooth replacement rates found by previous analysis conducted on *Maiasasura* teeth via Erickson (1996) coupled with a more substantial number of young individuals frequenting the area. The abundance of juvenile individuals may be biased by the seasonal nesting hypothesis, preferentially preserving a selection of small, fast growing teeth. The evidence supporting an attritional, terrestrial assemblage however aids to ensure sampling of a variety of ontogenetic stages would be preserved.

Interpretation of Mortality

Potential contribution of hadrosaur teeth to the fossil record increases through ontogeny because of changes in tooth abundance. Although larger individuals have larger teeth thereby requiring more time to generate replacements, larger individuals have also increased the number of teeth in the dental battery as well as the number of replacement teeth in each tooth family. That said, the evidence presented here shows a larger proportion of teeth from the Egg Mt assemblage belong to juveniles. The large component of nestling/juvenile teeth at Egg Mt. could be the result of quicker tooth replacement rates (Erickson 1996) coupled with a more substantial number of young individuals.

Individual *Maiasaura* did not remain small for long. The contribution of teeth belonging to individuals larger than the Late Juvenile stage are present at Egg Mt., in smaller quantities. The largely juvenile population represented by the Egg Mt. assemblage supports similar interpretations of *Maiasaura* growth and survivorship (Horner et al. 2000; Woodward et al. 2015) where an abundance of young individuals experiencing high mortality rates would be contributing to the fossil record through shedding and mortality (Horner 1982; Horner, 1984; Horner 1987; Varricchio 2010) Increased mortality rates of young individuals, occupying the same nesting grounds on a seasonal basis, increases juvenile representation through shed or disarticulated teeth. We understand survivorship of individuals under one year of age was very low. Based on Woodward et al. (2015) mortality rates peaked at 89.9% during this first year and similar rates were derived for the Egg Mt. population based on application of the SQ, DQ and raw data calculated in this thesis. It is reasonable then to hypothesize that nestling/juvenile abundance (contributing teeth by shedding) and mortality (contribution of teeth through disarticulation) may have contributed a substantial proportion of smaller, faster growing teeth to the record. Abundance of juvenile hadrosaurs in the WCA and elsewhere within the Two Medicine Formation is supported by occurrence of nestling and juvenile dominated bonebeds such as Blacktail Creek North (TM-066), West Hadrosaur Bonebed (TM-067), Sun River Bonebed (TM-260), and the laterally continuous bonebed used in Woodward's (2015) analysis of *Maiasaura* (TM-003, TM-151, and TM-158). Taphonomic studies including sedimentological analysis (Varricchio and Horner 1993; Varricchio 1995; Woodward et al. 2015) indicate these bonebeds are parautochthonous and occurrence of similarly sized individuals is not the result of winnowing. The Egg Mt. locality may have experienced similar conditions where individuals were concentrated, possibly due to nesting behavior (Horner 1984; Horner 1987; Varricchio 2010) as evidenced by the abundance of nesting traces and nesting material throughout. However, the Egg Mt. Quarry represents a terrestrial and attritional succession indicating there was time for hydrologic processes to introduce shed and disarticulated hadrosaur teeth reflecting a large juvenile population.

Method Interpretation

Limitations for a population study of this design are centered around the nature of the *Maiasaura* dental battery. Rapid addition of teeth through ontogeny coupled with the increase in AP tooth width, as well as shedding rate variation casts issues over the resulting population reconstruction of the Egg Mt tooth assemblage. Each of the aforementioned variables were accounted for in this thesis but the methods used to address them have limitations. Dinosaurian teeth have never been used to such an extent for extracting population data. On top of this, there was no consistent measuring method previously developed for hadrosaur teeth and limitations were placed on the Egg Mt. tooth size analysis due to the incomplete nature of the specimens. Not all limitations or variables associated with the Egg Mt. tooth assemblage have been resolved, however effort has been put forth to address them.

Measurement

Initial development of a measuring scheme appropriate for the Egg Mt. assemblage seemed straight forward. Although *Maiasaura* teeth were observed to increase in size through ontogeny, both longitudinally and anterior-posteriorly, condition of the Egg Mt. assemblage meant the former was not useful or in fact possible as a means of analysis. Development of the AP dimension was most appropriate, however effectively translating AP dimension to what it represents as an individual proved to have issues. The technique applied to the measured specimens struggles to accurately deal with variation in AP tooth size in a longitudinal dimension. This is partly due to the largely incomplete nature of the Egg Mt. assemblage where measured specimens come from an unknown section of a *Maiasaura* tooth; i.e. does the specimen represent the tip, middle, or base of a tooth? Although a significant proportion of the Egg Mt. teeth appear to show characteristics indicative of shedding (~32%) (Erickson pers. comm.) and indeed may represent AP dimensions near the base of a tooth, the majority either lack these characteristics or are too incomplete to retain them.

Establishment of tooth size variation required analysis of complete and intact teeth derived from museum specimens. To address variations in individual tooth size along its longitudinal axis required AP measurements on museum specimens to be taken both at the widest and narrowest available points on a given tooth. By doing so we attempt to address the unknown and incomplete nature of the individual Egg Mt. specimens and potentially what variation in tooth size may represent as an individual. If *Maiasaura* were shedding their teeth it is reasonable to assume any shed teeth would not be produced until the life of the tooth as a contributor to the processing surface of the dental battery was at an end (Edmund 1960; Erickson et al. 2012; LeBlanc et al. 2016). Most identifiable shed teeth are sourced from the maxillary tooth row (Erickson pers. comm.). These shed maxillary teeth retain the central carinae as well as the remains of the base of the tooth prompting measurement on museum specimens at the base of intact teeth. Alternatively, teeth generated from *Maiasaura* represented at Egg Mt. could be the result of disarticulation. A recent study by LeBlanc et al. (2016) hypothesized any single hadrosaur tooth was used up through its entirety and living specimens were not regularly shedding teeth but essentially wearing down a constantly growing conveyor-belt. The implications of LeBlanc et al.'s study infers that hadrosaur teeth are primarily generated by the death and disarticulation of individuals. Neither case is definitively supported by the Egg Mt. assemblage based on this study's taphonomic interpretation. A better understanding of what tooth size and condition represents as a hadrosaur individual must first be developed.

<u>Tooth Growth and Shedding Rates</u>

Sectioned Egg Mt. teeth provided information on relative tooth development rates and created speculative links to relative age of the individuals from which the tooth was derived based on von Ebner line spacing (Erickson 1996). Ideally, longitudinal sections would have created the most accurate tooth formation rates (Dean 2000; Erickson pers. comm.; Hilson 2005) by showing full development time. Transverse sections created for the Egg Mt. assemblage may only provide a minimum tooth development time however, von Ebner line spacing can still aid in relative aging of the individual who formed it. The sectioned Egg Mt. teeth provide detailed and accurate insight into *Maiasaura* tooth formation rates; however, without sectioning successive teeth within the jaw, shedding rates could not be determined. Fortunately, the von Ebner line spacing and tooth formation rates are indicative of a largely juvenile population supporting the face value analysis of the Egg Mt. assemblage using AP_W dimensions. Even the largest sectioned specimens have incremental line spacing falling above findings of adult von Ebner spacing made by Erickson (1996). In retrospect, to better develop an understanding of *Maiasaura* tooth formation and shedding rates it would have been beneficial to section an additional series of complete *Maiasaura* teeth from museum collections. Although it was prudent to section teeth from the Egg Mt. assemblage it would have been more beneficial to expand the dataset Greg Erickson started on *Maiasaura* and shedding rates which only included a single infant and adult specimen (Erickson 1996). Von Ebner line spacing in the Egg Mt. assemblage was similar to line spacing observed by Erickson (1996), therefore, the transverse sections do not appear to be biased toward larger line spacing and a false indication of juvenile tooth formation rates. Longitudinal tooth sections of museum specimens from a wider array of *Maiasaura* individuals representing an ontogenetic series would have generated a more accurate representation of tooth formation and shedding rates as they changed through ontogeny and ultimately a more accurate SQ factor when applied to the equation developed for this study. Sectioned Egg Mt teeth did not serve as a hard indication of age but are in support of the overall interpretation of a largely juvenile assemblage.

Species Identification

General tooth size and changes through ontogeny, regarding the dental battery, vary between hadrosaurian taxa based on other specimens observed in museum collections (personal observation). In all cases, application of the method developed for this thesis requires there is a reasonable understanding of the genus or species which generated the tooth assemblage in question. Lack of associated *Maiasaura* material from the Egg Mt. quarry required the assumption the hadrosaur tooth assemblage was in fact generated by *Maiasaura* based entirely off other studies with material loosely associated with the Egg Mt. locality. Although we feel comfortable with this assumption thanks to previous work on the WCA (Horner et al 2001; Schmitt et al 2014; Varricchio and Horner 1993; Woodward et al 2015) making the assumption still means there is a lack of certainty. Shed hadrosaur teeth may encounter issues with regards to identification, however, this study does benefit from the cumulative understanding the Egg Mt. teeth are likely *Maiasaura*. Future population analysis using this method may benefit from sites containing associated bone material even if primary population analysis is conducted on shed and disarticulated tooth specimens.

<u>Shedding and Disarticulation Quotients</u>

Development of the SQ and DQ, necessary for understanding the representation of individuals through their teeth, has limitations as well. One of the primary issues affecting this comes from the nature of the shed and disarticulated *Maiasaura* teeth. What constitutes a shed or disarticulated tooth? How does this affect where measurements are taken? These issues may very well be a problem somewhat unique to the Egg Mt. assemblage whereas more complete hadrosaur teeth from other sites could provide a more meaningful basis on which my methods can be applied with fewer questions. Linear models inferred from the data provide the most basic information in the outcome. As stated earlier, development of the equations providing the SQ and DQ factors were based on observed AP tooth size in museum specimens. Tooth size ranges existing outside of observed museum specimen ranges resulted in erroneous results, particularly AP tooth sizes smaller than 4 mm (the smallest average AP tooth size observed in museum specimens). Extraordinarily large numbers or negative numbers of individuals can be generated from small AP tooth sizes. Application of the SQ and DQ to the Egg Mt. assemblage should effectively balance the proportions of teeth which fall outside of observed museum ranges. Inaccuracies caused by a general lack of understanding regarding tooth size variation are believed to still have a strong influence in application of these factors.

Application of the SQ and the DQ to the Egg Mt. tooth assemblage were made under the assumption that one adult tooth is equal to one individual. This may seem unreasonable given that one hadrosaur dental battery could potentially produce hundreds or thousands of teeth to fossil record over the course of its lifetime. If one tooth is equal to one individual then is could be possible the opposite exists where multiple teeth actually represent an individual. Fortunately, the time-averaged, terrestrial assemblage seen at Egg Mt. may help to ensure a representation of population over time. The *Maiasaura* teeth examined in this study occur throughout the excavated interval which also help to support the assumption I am looking at multiple individuals as opposed to a single individual represented by multiple teeth.

The reconstructed size -frequency distribution generated through AP_B measurements addresses the selection of teeth falling below observed museum tooth size ranges but at the same time pushes teeth already observed to represent adults into much larger and relatively unrealistic realms. Therefore, it appears the Egg Mt. assemblage may constitute a mix of shed and possibly disarticulated teeth. The selection of Egg Mt.

specimens which fall below AP dimensions observed in museum collections are somewhat problematic. These teeth share similar condition to the rest of the Egg Mt. assemblage and made their identification as being shed or disarticulated difficult. There also remains the possibility the small teeth of the Egg Mt. assemblage could represent individuals smaller than observed museum specimens. Although reasonable assumptions have been made regarding species identification for the Egg Mt. hadrosaur tooth assemblage, the possibility remains that the selection of small teeth could also represent an alternative hadrosaur or lambeosaurine taxa. Alternative taxa have been described from the Two Medicine Formation but have not been found in the WCA or the "*Maiasaura* biozone" coined by Horner et al. 2001; these include *Hypacrosaurus stebingeri*, (Horner 1992; Horner and Currie 1994) *Prosaurolophus blackfeetensis,* (Horner 1992) and *Lambeosaurinae sp.* (Trexler, 2001).

Until a better understanding or constraint can be placed on what a shed tooth represents, the SQ and DQ is somewhat constrained by observed tooth size ranges. Future work should include the addition of more accurate tooth formation and shedding rates through the ontogeny of the species under study, a better understanding of hadrosaur tooth replacement in relation to shed or disarticulated specimens, and more complex correlations conducted on these taphonomic and ontogenetic factors to increase the accuracy of the SQ. The model appears to work well when confined to observed tooth size ranges but would benefit from additional observations on *Maiasaura* dental batteries.

Mortality and Survivorship

Survivorship of *Maiasaura* represented by the Egg Mt. assemblage encounters limitations as well. Although the developed life tables and survivorship curves show promising trends when compared to previous studies (Erickson et al. 2006; Erickson et al. 2009; Horner et al. 2000; Woodward et al. 2015; Varricchio and Horner 1993) the teeth once again have their limitations. Long bone analysis allows for ties to age much more accurately. Confidence in the population analysis conducted in this study falls off after adult age/size is reached. This is because even with teeth falling in the adult range, there is no definitive way to determine the precise age the adult in question was, limiting the understanding of mortality after adult size and age was reached.

Abundance of hadrosaur tooth material concentrated in microsite localities allows for required sample sizes needed for proper statistical analysis (Steinsaltz and Orzak 2011). The minimal recommended sample size was 50. The first to achieve this requirement utilizing dinosaurian long bone material was Woodward et al. (2015) and their growth and population analysis of *Maiasaura*. The assemblage of *Maiasaura* teeth used in this thesis are ideal for reaching sufficiently large sample sizes with rare paleontological data. Fortunately, the material used for the comprehensive long bone analysis of *Maiasaura* is from the WCA and works as a good comparative study to the population reconstruction undertaken in this thesis.

The series of analyses run using incremental scaling factors based on AP_B length illustrates the variability tooth size can have on the model. Although the model seems to be a good representation of population without applying the tooth scale ratio, it struggles to accurately represent teeth from the Egg Mt. collection which fall below observed AP widths recorded from museum specimens. By attempting to scale the small specimens up to represent full size teeth we achieve a tooth size distribution and population perhaps more representative of shed and worn teeth. However, application of the scaling factor in this manner then forces larger teeth from the quarry into a similar questionable state befitting the small specimens prior to scaling them up. By alternatively only scaling up the population of teeth tentatively identified as shed, questionably large tooth sizes are more reasonable. Based on body size estimates and previous population analyses, it appears the Egg Mt. *Maiasaura* population is best depicted without applying a scalar to the entire population of teeth. Taking the AP measurements at face value and applying the technique we have, developed a result supported by incremental line spacing, observed tooth size to body size relations taken from museum specimens, and reflective of studies conducted by Woodward et al. (2015) and Varricchio and Horner (1993).

Unfortunately, representation of the Egg Mt. assemblage is not necessarily limited by the shedding quotient but by a poor understanding of what a shed tooth would represent as an unworn tooth and ultimately an individual. If most specimens from the attritional Egg Mt. assemblage are in fact shed teeth, there is a possibility we are simply looking at a collection which shows no significant bias toward a single age group. Fortunately, support from histology and observed tooth size to body size correlation works in cooperation with *Maiasaura* growth and survivorship curves in support of the results.

Previous work on understanding *Maiasaura* mortality and survivorship indicates a significant percentage of the population dying during the first year of life (89-90%) followed by significantly lower mortality rates (12-13%) until after skeletal maturity was reached and death due to senescence was more prevalent (44%) (Woodward et al. 2015). Similar results were obtained from the analysis conducted on the Egg Mt. tooth assemblage. Abundant shedding and/or disarticulation of teeth due to high mortality was again represented by individuals within the first year of life (73%) followed by a decrease between Late Juveniles and Adult growth stages (36%). As stated earlier, mortality is hard to determine after the Adult age/size is reached due to the lack of accurate ages put on the individuals represented by adult sized teeth. The proportion of adult teeth in the measured assemblage does represent a higher number of individuals than the teeth which are presumed to belong to subadult individuals (Refer to Table 3). This is complicated by *Maiasaura* ontogeny where lifespan of an adult individual may be longer than the span of time during sub-adulthood. The inability to directly age an individual based on their teeth means adult individuals are categorized based on their teeth being greater than or equal to a tooth size interpreted to belong to an adult. This indicates mortality may have increased after adult age/size was reached similar to what Woodward et al. (2015). The population analysis undertaken on the Egg Mt. *Maiasaura* tooth assemblage continues to support previous findings on dinosaur survivorship to mimic a sigmoidal B1 Type curve indicating high juvenile mortality followed by a plateau, and finally, increased adult mortality due to senescence (Erickson et al. 2006; Erickson et al. 2009; Pearl and Miner 1935; Woodward et al. 2015).

SUMMARY AND CONCLUSIONS

The Egg Mt. locality of the Willow Creek Anticline in Two Medicine Formation of northwestern Montana has provided a wealth of information on dinosaur ecology, biology, and reproduction (DeMar et al. 2016; Horner 1982; Horner 1987; Horner et al. 2000; Horner and Makela 1979; Horner and Weishampel 1988; Lorenz and Gavin, 1984; Martin and Varricchio, 2011; Moore et al. in revision; Rogers, 1990; Varricchio et al, 1999; Varricchio et al, 2002; Woodward et al, 2015). Excavations within and immediately surrounding Egg Mt. Quarry have also produced abundant trace fossils, small mammals, and lizards. The Upper Cretaceous fossiliferous horizons of the Two Medicine have produced large bonebeds dominated by hadrosaurian taxa accompanied by nearly complete representations of their ontogeny from perinatal and small nestlings associated with nesting material as well as their adult counterparts (Cooper et al. 2008; Horner 1982, Horner 1984; Horner 1987; Jackson and Varricchio 2010; Varricchio and Horner 1993; Varricchio 1995; Woodward et al. 2015). Taphonomic analysis of these bonebeds as well as detailed histological examination of exhumed specimens have generated one of the most comprehensive understandings of hadrosaur growth curves and population dynamics in the world (Horner et al, 2000; Horner and Weishampel; 1988; Varricchio and Horner, 1993; Varricchio, 1995; Woodward et al, 2015). This study utilizes an assemblage of *Maiasaura* teeth collected from the Egg Mt. locality as a novel look at population analysis.

The population analysis of the assemblage of *Maiasaura* teeth required the generation of new measuring techniques as well as examination of intact *Maiasaura* jaw specimens from museum collections. A series of new methods were developed to accommodate ontogenetic changes in tooth size, tooth abundance, and shedding rates.to accurately transform hadrosaur tooth abundance into an abundance of the individuals they represent. Results indicate:

- Anterior-posterior (AP) otherwise known as mesial distal tooth size derived from measured museum specimens show Small Nestling teeth increase from 4 mm to approximately 5.2 mm (n = 12; SD = 0.17) in Late Juveniles. Tooth growth continues to increase until adulthood is reached where AP tooth dimensions can range from 6 -7.59 mm (n = 69; SD = 1.2). The Egg Mt. assemblage ranges from 1.83 mm to 8.13 mm. Size-frequency distribution of the assemblage shows a bi-modal distribution centered around 4.6 mm and 6.2 mm with an average AP tooth size of 5.08 ± 1.2 mm placing the majority of teeth within the Late Juvenile ontogenetic stage.
- Tooth formation and shedding rates derived for *Maiasaura* were necessary to further understand what the tooth assemblage represents as a population. Shedding rates found by Erickson (1996) increase through ontogeny. Histological analysis on the Egg Mt. assemblage revealed tooth formation rates increase as AP tooth size increases. All Egg Mt. samples display relatively fast formation rates which are more representative of juvenile individuals and consistent with the preserved dimensions.
- Development and application of the shedding and disarticulation quotients allowed us to distill tooth growth, tooth abundance, and shedding rates based on

AP tooth size into a representation of population. It was found the 152 teeth utilized in this analysis were $\geq$ 152 individuals. Reconstruction of these individuals into a life table and representative survivorship curves indicate high juvenile mortality rates (64-84%) during the first year of life followed by a mortality plateau of approximately 35-39% decreasing to a minimum estimated mortality rate of 17-22% by the time adulthood was reached at age six. This pattern mimics a sigmoidal B1 Type survivorship curve supportive of other dinosaurian population models derived from long bone material (Erickson et al. 2006; Erickson et al. 2009; Horner et al. 2000; Woodward et al. 2015).

There are limitations to the use of hadrosaur teeth as a means of understanding population. Tooth formation and shedding rates appear to vary between species (Erickson 1996) and therefore caution should be taken when analyzing hadrosaur populations based on teeth without reasonable assumptions about the species and without histological examination of the teeth in question. Fortunately, tooth development analysis does not appear to change between taxa, dinosaurian (Erickson 1996) or otherwise (Hillson 2005), meaning circadian rhythms recorded as lines of von Ebner do not vary. Tooth replacement and shedding rates can be obtained for various species and should be bolstered by histological examinations of multiple teeth, multiple growth stages, and multiple species when available. Additionally, special attention should be paid to the concept of shed and disarticulated teeth and how they are represented in the fossil record. This ultimately affects honing of measuring techniques and how the teeth in question will be represented as individuals. This thesis provides one of the first comprehensive population studies to utilize hadrosaur teeth. The rather homogeneous and abundant hadrosaur tooth, a common component of microsites and micro-vertebrate localities, appears to have utility in understanding basic population structure even without directly associated bone material.

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APPENDICES

APPENDIX A

VON EBNER AND DENTINE MEASUREMENTS

Sectioned Tooth Number	To1-1	To2-1	To3-1	To4-1	To5-1	To5-1L	To5-2L	To6-1	To7-1	To9-1	To10-1	To11-1	To12-1	To12-1L
von Ebner Line Thicknesses	0.015	0.012	0.014	0.019	0.021	0.016	0.02	0.019	0.011	0.016	0.026	0.022	0.016	0.019
	0.014	0.009	0.011	0.018	0.024	0.023	0.026	0.02	0.016	0.019	0.017	0.022	0.014	0.02
	0.014	0.011	0.01	0.011	0.021	0.021	0.032	0.019	0.011	0.02	0.017	0.026	0.017	0.021
	0.016	0.013	0.009	0.01	0.021	0.025	0.028	0.019	0.014	0.02	0.019	0.027	0.019	0.016
	0.018	0.009	0.01	0.012	0.019	0.022	0.028	0.019	0.014	0.022	0.021	0.03	0.014	0.017
	0.021	0.009	0.017	0.014	0.019	0.018	0.025	0.016	0.014	0.022	0.019	0.021	0.017	0.019
	0.02	0.01	0.015	0.012	0.018	0.019	0.023	0.017	0.014	0.019	0.019	0.031	0.018	0.02
	0.014	0.011	0.01	0.01	0.017	0.011	0.017	0.014	0.014	0.017	0.018	0.03	0.016	0.021
	0.016	0.01	0.01	0.013	0.022	0.01	0.023	0.014	0.013	0.02	0.017	0.026	0.014	0.011
	0.012	0.014	0.014	0.013	0.021	0.01	0.026	0.014	0.01	0.017	0.019	0.022	0.013	0.013
	0.018	0.01	0.011	0.012	0.02	0.009	0.023	0.019	0.014	0.019	0.019	0.033	0.015	0.015
	0.017	0.009	0.013	0.013	0.019	0.009	0.024	0.021	0.014	0.019	0.018	0.016	0.015	0.017
	0.014	0.012	0.013	0.013	0.021	0.007	0.022	0.02	0.02	0.023	0.021	0.016	0.017	0.011
	0.014	0.013	0.02	0.013	0.017	0.023	0.022	0.018	0.015	0.022	0.012	0.018	0.017	0.016
	0.015	0.015	0.01	0.017	0.02	0.026	0.022	0.018	0.017	0.02	0.02	0.017	0.021	0.016
	0.018	0.017	0.012	0.016	0.021	0.022	0.027	0.018	0.014	0.017	0.018	0.02	0.02	0.016
	0.015	0.014	0.012	0.013	0.017	0.025	0.029	0.019	0.014	0.018	0.015	0.019	0.015	0.019
	0.015	0.016	0.016	0.014	0.02	0.024	0.029	0.02	0.018	0.017	0.017	0.022	0.019	0.019
	0.016	0.02	0.014	0.012	0.019	0.023	0.027	0.018	0.019	0.018	0.019	0.02	0.018	0.013
	0.022	0.015	0.014	0.013	0.017	0.022	0.028	0.021	0.02	0.022	0.024	0.021	0.016	0.012
	0.017	0.011	0.017		0.017	0.015	0.02	0.02	0.022		0.021	0.027	0.018	0.018
	0.017	0.012	0.021		0.015	0.017	0.025	0.018	0.021		0.023	0.026	0.013	0.022
	0.012	0.014	0.018		0.018	0.011	0.023	0.026	0.019		0.02	0.028	0.012	0.019
	0.011	0.013	0.015		0.016	0.009	0.025	0.023	0.019		0.016	0.021	0.01	0.022
	0.017	0.014	0.021		0.016	0.009	0.03	0.023	0.019		0.018	0.025	0.012	0.021
	0.012	0.018	0.011		0.026	0.009	0.029	0.023	0.02		0.019	0.012	0.016	0.02
	0.013	0.018	0.006		0.028	0.009	0.025	0.022	0.019		0.014	0.013	0.012	0.018

0.011	0.014	0.006	0.032	0.007	0.03	0.02	0.024	0.015	0.012	0.018
0.011	0.01	0.01	0.031	0.009	0.028	0.022	0.024	0.011	0.018	0.018
0.01	0.012	0.015	0.018	0.01	0.016	0.019	0.023	0.01	0.017	
0.011	0.014	0.01	0.028	0.01	0.024	0.015	0.026	0.014	0.023	
0.014	0.016	0.012	0.033	0.01	0.024	0.022	0.028	0.01	0.016	
0.013	0.016	0.009	0.021	0.011	0.02	0.022	0.03	0.015	0.015	
0.016	0.018	0.008	0.02	0.011	0.02	0.02	0.029	0.007	0.019	
0.016	0.016		0.024	0.014	0.017	0.018	0.032	0.01	0.025	
0.015	0.01		0.019	0.017	0.018	0.02	0.028	0.014	0.013	
0.02	0.01		0.022			0.019	0.032	0.021	0.015	
0.018	0.011		0.022			0.02		0.018	0.01	
0.017			0.023			0.02		0.013	0.012	
0.012			0.02			0.018		0.014	0.014	
0.011			0.021			0.018		0.027	0.013	
0.017			0.025			0.015		0.03	0.015	
0.01			0.018			0.015		0.021	0.014	
			0.02			0.017		0.031	0.017	
			0.018			0.016		0.025	0.022	
			0.018					0.031	0.011	
			0.017					0.014	0.014	
			0.016					0.015	0.014	
			0.012					0.015	0.018	
			0.019					0.02	0.014	
			0.018					0.016	0.009	
			0.017					0.017	0.008	
			0.02					0.019	0.012	
			0.017					0.019	0.009	
			0.019					0.02		

					0.018							0.02		
					0.019							0.021		
					0.017							0.018		
von Ebner Thickness Range	0.01-0.022	0.01-0.018	0.008-0.021	0.01-0.019	0.012-0.033		0.016-0.032	0.015-0.026	0.01-0.022	0.017-0.023	0.012-0.032	0.010-0.033	0.008-0.023	0.012-0.022
Average von Ebner width	0.015	0.0130526	0.01276471	0.0134	0.0202069	0.015083	0.02430556	0.01897778	0.01611111	0.01935	0.021135135	0.0195283	0.01524074	0.01748276
Dentine Thicknesses	0.393	1.356	1.64	1.309	2.131	0.842	2.123	1.023	0.925	1.184	1.815	1.938	1.618	2.354
	0.584	0.0922	1.625	1.126	2.046		1.033	1.614	1.308	1.743	2.079	0.723	1.853	3.365
	0.638	1.444	0.934	1.431	2.548		1.522	1.72	1.197	1.678	2.159	0.676	1.342	3.469
	0.988	0.836	1.729	0.805	2.236		1.68	2.261	1.034	1.496	1.584	1.722	2.233	3.397
	0.579	1.604	1.29	1.573	1.159		1.849	1.043	0.881	1.099	1.804	1.793	1.174	3.311
	0.347	0.771	0.982	1.175	2.217		1.298	0.899	0.752	1.687	1.43	1.735	0.674	3.223
	0.527	1.392	1.752	1.526	1.117		3.082	1.256	1.146	0.634	1.8	1.913	1.04	2.719
	0.434	0.714	1.38	1.741	2.016		2.924	2.065	1.013	1.383	1.757	1.94	2.074	2.494
	0.368	1.044	1.485	0.871	2.312		2.545	1.725	0.781	1.02	1.815	1.216	0.902	2.451
	0.511	0.729	1.217	1.174	2.118		1.992	2.474	0.691	1.014	1.758	1.185	1.403	2.227
Dentine Thickness Range	.347-.988	.714-1.604	.934-1.752	.805-1.741	1.117-2.548		1.033-3.082	.899-2.474	.691-1.308	.638-1.743	1.430-2.159	.676-1.940	.674-2.233	2.227-3.469
Average Dentine Thickness (ADT)	0.5369	0.99822	1.4034	1.2731	1.99		2.0048	1.608	0.9728	1.2938	1.8001	1.4841	1.4313	2.901
Tooth Development Time (ADT/Average Von Ebner)	35	76	109	95	98	55	82	84	60	66	85	75	93	165

APPENDIX B

MEASURED TOOTH SPECIMENS

Table 1—Measured hadrosaur teeth from Egg Mt. Quarry listed smallest to largest. Orange fill indicates AP lengths which were estimated from APC ratio.

Field Number	Type	APC (mm)	AP (mm)	Estimated Origin
B8-H6	Hadrosaur	1.55	1.96	?
B12-H1	Hadrosaur	1.50	2.00	?
B8-H2	Hadrosaur	3.05	2.59	Maxillary or disarticulated; shed?
B2-H1	Hadrosaur	1.79	2.95	Maxillary or disarticulated
B16-H3	Hadrosaur	2.18	3.03	Maxillary or disarticulated
B8-H11	Hadrosaur	1.94	3.10	?
B10:2-H11	Hadrosaur	2.34	3.11	Maxillary or disarticulated; shed?
EMQ-027 (8/9/10)	Hadrosaur	2.20	3.26	?
B3-H6	Hadrosaur	2.25	3.31	Maxillary or disarticulated
B8-H5	Hadrosaur	2.25	3.31	Maxillary or disarticulated; shed?
EMQ-009 (7/24/10)	Hadrosaur	2.07	3.34	Disarticulated
B3-H2	Hadrosaur	2.36	3.42	?
B4-H1	Hadrosaur	2.96	3.49	Maxillary or disarticulated; shed?
B1-H3	Hadrosaur	3.00	3.50	?
B5-H9	Hadrosaur		3.50	?
B6-H5	Hadrosaur	1.91	3.56	Maxillary or disarticulated; shed?
B3-H2	Hadrosaur	2.43	3.60	Maxillary or disarticulated; shed?
B19-H2	Hadrosaur	2.59	3.65	Maxillary or disarticulated; shed?
B9-H13	Hadrosaur	2.39	3.71	Maxillary or disarticulated
B6-H11	Hadrosaur	3.15	3.76	Maxillary or disarticulated; shed?
B17-H3	Hadrosaur	2.75	3.81	Maxillary or disarticulated; shed?
B3-H9	Hadrosaur	2.75	3.81	?
B20-H2	Hadrosaur	2.52	3.84	?
B18-H6	Hadrosaur	2.82	3.88	Maxillary or disarticulated; shed?
B12-H4	Hadrosaur	3.73	3.96	Maxillary or disarticulated
B11-H3	Hadrosaur	2.93	3.99	Maxillary or disarticulated
B3-H11	Hadrosaur	3.52	4.01	Maxillary or disarticulated
B5-H6	Hadrosaur	2.98	4.04	Maxillary or disarticulated
B4-H1	Hadrosaur	3.69	4.06	Maxillary or disarticulated
B9-H2	Hadrosaur	2.84	4.09	Maxillary or disarticulated; shed?
B15-H2	Hadrosaur	2.16	4.09	Maxillary or disarticulated
B7-H3	Hadrosaur	2.51	4.11	?
B7-H8	Hadrosaur	2.79	4.11	Maxillary or disarticulated; shed?
B12-H1	Hadrosaur	3.31	4.17	Maxillary or disarticulated
B9-H6	Hadrosaur	3.46	4.18	Maxillary or disarticulated; shed?
B10:1-H3	Hadrosaur	3.41	4.19	Maxillary or disarticulated; shed?

B4-H5	Hadrosaur	3.18	4.24	Maxillary or disarticulated
B8-H10	Hadrosaur	2.23	4.24	Maxillary or disarticulated
B14-H2	Hadrosaur	3.19	4.25	Maxillary or disarticulated
EMQ-005 (7/23/10)	Hadrosaur	2.69	4.26	Maxillary or disarticulated; shed?
B11-H1	Hadrosaur	3.92	4.32	Maxillary or disarticulated
B11-H8	Hadrosaur	3.65	4.37	Maxillary or disarticulated; shed?
B29-H1	Hadrosaur		4.40	?
B12-H2	Hadrosaur	2.27	4.41	?
EMQ-043	Hadrosaur	4.15	4.44	Dentary
B9-H4	Hadrosaur	3.40	4.44	Dentary
EMQ-016	Hadrosaur	3.39	4.45	Maxillary or disarticulated
EMQ-013	Hadrosaur	3.42	4.48	Maxillary or disarticulated
EMQ-037 (7/12/10)	Hadrosaur	3.40	4.50	?
B12-H7	Hadrosaur	3.90	4.50	Maxillary or disarticulated
EMQ-040	Hadrosaur	3.03	4.51	Maxillary or disarticulated; shed?
B4-H2	Hadrosaur	2.97	4.55	Maxillary or disarticulated; shed?
B11-H7	Hadrosaur	3.50	4.56	?
B7-H1	Hadrosaur	4.40	4.58	Maxillary or disarticulated; shed?
B1-H2	Hadrosaur	3.07	4.61	Maxillary or disarticulated; shed?
B2-H1	Hadrosaur	3.58	4.64	?
B12-H2	Hadrosaur	3.81	4.65	Dentary
B12-H5	Hadrosaur	3.83	4.66	Maxillary or disarticulated
B8-H1	Hadrosaur	3.60	4.66	Dentary
B18-H5	Hadrosaur	3.63	4.69	Maxillary or disarticulated
B29-H4	Hadrosaur	3.65	4.71	Maxillary or disarticulated; shed?
B12-H10	Hadrosaur	4.03	4.72	Maxillary or disarticulated; shed?
B15-H6	Hadrosaur	3.67	4.73	?
B10:2-H16	Hadrosaur	3.67	4.73	Maxillary or disarticulated; shed?
B12-H9	Hadrosaur	3.68	4.74	Maxillary or disarticulated; shed?
B29-H3	Hadrosaur	4.12	4.83	?
B7-H6	Hadrosaur	3.79	4.85	Maxillary or disarticulated
EMQ-054	Hadrosaur	3.83	4.89	Dentary
EMQ-032 (8/1/10)	Hadrosaur	3.06	4.89	Maxillary or disarticulated; shed?
B16-H5	Hadrosaur	3.45	4.90	Maxillary or disarticulated
B12-H4	Hadrosaur	5.16	4.91	Maxillary or disarticulated; shed?
B18-H2	Hadrosaur	3.85	4.91	Maxillary or disarticulated
EMQ-041	Hadrosaur	4.79	4.94	Maxillary or disarticulated; shed?
B13-H1	Hadrosaur	3.88	4.94	?
B17-H1	Hadrosaur	3.89	4.95	?
EMQ-033 (8/7/10)	Hadrosaur	3.61	4.97	Maxillary or disarticulated; shed?

B9-H5	Hadrosaur	3.92	4.98	?
EMQ-045	Hadrosaur	4.50	5.00	?
EMQ-023 (7/18/10)	Hadrosaur	3.14	5.00	Maxillary or disarticulated
B11-H2	Hadrosaur	3.50	5.00	Maxillary or disarticulated; shed?
EMQ-025 (7/31/10)	Hadrosaur	3.96	5.02	Maxillary or disarticulated
B20-H3	Hadrosaur	4.71	5.13	Maxillary or disarticulated
EMQ-048 (7/20/10)	Hadrosaur	4.10	5.16	Maxillary or disarticulated
B9-H7	Hadrosaur	4.52	5.16	?
EMQ-044	Hadrosaur	4.04	5.17	Maxillary or disarticulated; shed?
EMQ-010 (7/25/10)	Hadrosaur	4.97	5.18	Maxillary or disarticulated; shed?
B20-H1	Hadrosaur	3.45	5.19	?
B5-H3	Hadrosaur	4.75	5.21	?
B4-H3	Hadrosaur	3.78	5.23	Maxillary or disarticulated; shed?
EMQ-046	Hadrosaur	4.20	5.26	Maxillary or disarticulated
B2-H4	Hadrosaur	4.21	5.27	Maxillary or disarticulated
B6-H5	Hadrosaur	4.27	5.33	Maxillary or disarticulated
B13-H2	Hadrosaur	4.27	5.33	?
EMQ-017 (7/29/10)	Hadrosaur	4.78	5.38	Maxillary or disarticulated
B11-H6	Hadrosaur	3.53	5.41	Maxillary or disarticulated; shed?
B12-H3	Hadrosaur	3.95	5.43	Maxillary or disarticulated; shed?
B2-H2	Hadrosaur	4.24	5.48	Dentary
B7-H5	Hadrosaur	4.47	5.53	Maxillary or disarticulated
B9-H4	Hadrosaur	4.47	5.53	?
B6-H5	Hadrosaur	4.50	5.56	?
B6-H1	Hadrosaur	4.52	5.58	?
B2-H8	Hadrosaur	4.52	5.58	Maxillary or disarticulated; shed?
B1-H3	Hadrosaur	4.46	5.62	Maxillary or disarticulated
B18-H3	Hadrosaur	4.56	5.62	Maxillary or disarticulated
B21-H10	Hadrosaur	4.46	5.72	Maxillary or disarticulated; shed?
B20-H1	Hadrosaur	5.56	5.72	Maxillary or disarticulated; shed?
EMQ-049 (7/20/10)	Hadrosaur	4.52	5.74	Maxillary or disarticulated
EMQ-029 (8/9/10)	Hadrosaur	5.91	5.79	Maxillary or disarticulated; shed?
B13-H5	Hadrosaur	4.17	5.80	?
B8-H1	Hadrosaur	4.50	5.87	Maxillary or disarticulated
EMQ-038 (7/12/10)	Hadrosaur	5.33	5.92	Maxillary or disarticulated
EMQ-034 (8/7/10)	Hadrosaur	5.10	5.93	Maxillary or disarticulated; shed?
B29-H6	Hadrosaur	5.05	5.93	Maxillary or disarticulated; shed?
EMQ-050 (7/27/10)	Hadrosaur	4.48	5.96	Dentary
B2-H1	Hadrosaur	5.40	5.96	Maxillary or disarticulated; shed?
B21-H1	Hadrosaur	5.26	5.98	Dentary

B2-H7	Hadrosaur	4.45	6.00	?
B2-H2	Hadrosaur	5.11	6.05	Maxillary or disarticulated; shed?
B11-H3	Hadrosaur	4.99	6.05	Maxillary or disarticulated
EMQ-030 (7/30/10)	Hadrosaur	5.01	6.07	Maxillary or disarticulated; shed?
B6-H2	Hadrosaur	5.03	6.09	Maxillary or disarticulated
EMQ-036 (7/12/10)	Hadrosaur	5.08	6.18	Maxillary or disarticulated; shed?
B10:2-H7	Hadrosaur	4.84	6.18	Dentary
EMQ-002 (7/22/10)	Hadrosaur	5.28	6.20	Maxillary or disarticulated
B2-H3	Hadrosaur	5.39	6.21	Maxillary or disarticulated; shed?
B6-H12	Hadrosaur	5.16	6.22	Maxillary or disarticulated; shed?
B3-H3	Hadrosaur	5.16	6.22	Maxillary or disarticulated
B6-H9	Hadrosaur	4.93	6.22	Maxillary or disarticulated; shed?
B7-H10	Hadrosaur	5.17	6.23	?
B4-H1	Hadrosaur	5.18	6.24	Maxillary or disarticulated
EMQ-019 (7/15/10)	Hadrosaur	4.47	6.31	Maxillary or disarticulated
B17-H4	Hadrosaur	4.76	6.32	Maxillary or disarticulated; shed?
EMQ-035 (7/6/10)	Hadrosaur	5.19	6.35	Maxillary or disarticulated
B2-H4	Hadrosaur	6.07	6.35	Maxillary or disarticulated
B10-H2	Hadrosaur	5.14	6.37	?
B5-H5	Hadrosaur	4.00	6.50	?
B15-H1	Hadrosaur	5.51	6.57	Maxillary or disarticulated
EMQ-031 (7/30/10)	Hadrosaur	5.66	6.72	Maxillary or disarticulated
B17-H5	Hadrosaur	5.66	6.72	Dentary
EMQ-006 (7/23/10)	Hadrosaur	5.09	6.83	Maxillary or disarticulated
B5-H4	Hadrosaur	5.47	6.83	?
B16-H2	Hadrosaur	5.79	6.85	Maxillary or disarticulated; shed?
B14-H3	Hadrosaur	5.83	6.89	Maxillary or disarticulated; shed?
B8-H11	Hadrosaur	6.50	6.99	Maxillary or disarticulated; shed?
B19-H3	Hadrosaur	5.08	6.99	Dentary
B12-H14	Hadrosaur	7.00	7.00	?
B33-H6	Hadrosaur	6.01	7.07	?
EMQ-026 (8/10/10)	Hadrosaur	5.33	7.18	Maxillary or disarticulated
B19-H1	Hadrosaur	6.26	7.32	Maxillary or disarticulated
B10:2-H9	Hadrosaur	6.51	7.57	Maxillary or disarticulated; shed?
B3-H4	Hadrosaur	7.03	8.09	Maxillary or disarticulated
B10-H4	Hadrosaur	7.75	8.13	Maxillary or disarticulated; shed?

APPENDIX C

MUSEUM SPECIMENS

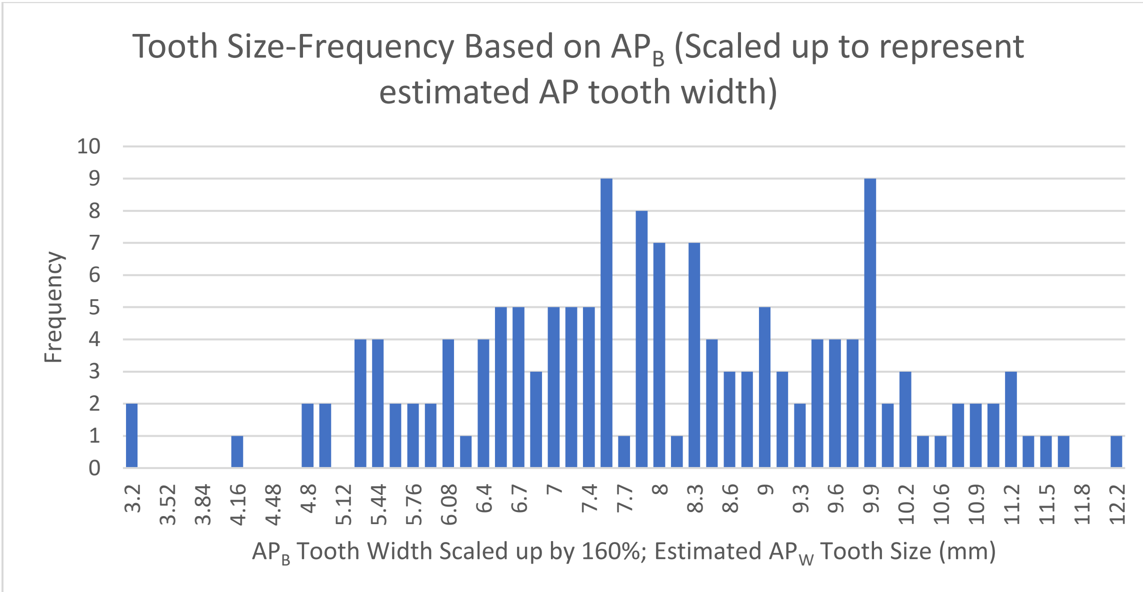
Table 1—Table includes measured AP tooth widths taken on museum specimens. Although *Maiasaura* specimens were the only genera used in the analysis, this table also includes observed AP tooth size ranges and estimated ontogenetic stages for other hadrosaurid and lambeosaurid specimens taken from museum collections. Yellow boxes indicate the growth stage was estimated by femoral length measurements in corroboration with previous bonebed analyses (Varricchio and Horner 1993; Varricchio 1995).

Maiasaur	Bonebed/Site	Relative Age	Relative Age/ Body Size (m)	Average Tooth Size Anterior-Posterior (mm)	Number of tooth families	Overall Length of Specimen (cm)	Length of Dental Battery (cm)	% Contribution of dental battery to overall Jaw component	Jaw Component	Tooth Measurements																															
Bynam Specimen OTM-F138	M1	Adult	8.2	6.44	40	45	25	55.6	Dentary	7	6	5	8	6	7	10	4.5	6	8	4	7	6.5	7	6	7	7	4	6	5.5	6	6	7.5	6	8	7	7	8	6	7	5	5
Bynam Specimen OTM-F138	M1	Adult		6.03	46	35.5	25	70.4	Maxilla	4.98	5.47	6.4	5.59	6.64	4.8	5.62	7	6.81	5.56	5.64	7.05	6.06	5.44	7.4																	
MOR 6631 #1	EMOT	Perinatal	0.27	4.40	8	-	-	-	Dentary																																
MOR 6631 #2	EMOT	Perinatal/Early Nestling	0.4	4.07	10	-	3.3	-	Dentary																																
MOR 547	TM-067 (West Hadrosaur)	Late Juvenile	3.5	4.53	19	-	-	-	Maxilla	4	4.3	4.8	4.2	4	5	5	4.8	5	4.2																						
MOR 547 W-25-6 (no teeth)	TM-067 (West Hadrosaur)	Late Juvenile	3.5	4.91	23	17.8	11.3	63.5	Dentary	-																															
MOR 547 W-20-7 (no teeth)	TM-067 (West Hadrosaur)	Late Juvenile	3.5	5.20	25	20.5	13	63.4	Dentary	-																															
MOR 547 W-28-1 (no teeth)	TM-067 (West Hadrosaur)	Late Juvenile	3.5	4.84	25	12.1	12.1	-	Maxilla																																
MOR 089 Holotype (cast)	N/A	Adult	8	7.59	40	41.5	26.5	63.9	Dentary	7	8	7	8	8	7.5	7.9	8.5	9	6.2	7.5	8	6.7	7																		
MOR 089 Holotype (cast)	N/A	Adult	8	6.33	44	35.4	25.3	71.5	Maxilla	7	5.2	6.1	5.8	6.5	7.2	6.8	6																								
Hypacrosaur	Bonebed/Site	Relative Age	Relative Age/ Body Size (m)	Average Tooth Size Anterior-Posterior (mm)	Number of tooth families	Overall Length of Specimen (cm)	Length of Dental Battery (cm)	% Contribution of dental battery to overall Jaw component	Jaw Component	Tooth Measurements																															
MOR 553S 7-27-2-93B	TM-068 (Jacks B-Day Site)	Juvenile	3	6.55	42	>30.7	27.5	<89.5	Maxilla	-																															
MOR 600 (cast)	TM-081	-	-	6.98	26	>14.2	>13.5	-	Dentary	6.5	7	7.3	6.8	6.5	7	7.2	7.5																								
MOR 600	TM-081	-	-	5.53	32	>16.6	16.6	-	Maxilla	5	6	4.8	5	6	5	5.5	6.5	6																							
MOR 600 Jaw/Tooth Frags	TM-081	-	-	6.14	-	-	-	-	-	6	6	7	5.7	7	5	5	6.5	6.8	6.2	5	7.5																				
MOR 559	TM-066 (Blacktail Cr. North)	Large Nestling	1.5	3.50	8	4.04	2.8	69.3	Dentary																																
MOR 559	TM-066 (Blacktail Cr. North)	Large Nestling	1.5	3.99	11	>4.4	4.4	-	Maxilla	4	3.8	3.5	4.5	4.2	4	3.4	3.8	4	3.3	3.5	4.5	3.9	5	4.5																	
MOR 608 (no teeth) Hypac?	TM-071	-	-	5.86	21	18	12.3	68.3	Dentary																																

Prosaurolophus blackfeetensis	Bonebed/Site	Relative Age	Body Size (m)	Average Tooth Size Anterior-Posterior (mm)	Number of tooth families	Overall Length of Specimen (cm)	Length of Dental Battery (cm)	% Contribution of dental battery to overall Jaw component	Jaw Component	Tooth Measurements																					
MOR 553B 8-6-9-20	TM-068 (Jacks B-Day Site)	Juvenile	3	7.99	51	43	37.5	87.2	Maxilla	8	8	7.2	9	8.8	7.6	8.2	7.3	7.8													
MOR 553 L 7-19-8-37 (No teeth)	TM-068 (Jacks B-Day Site)	Juvenile	3	6.27	33	29.7	20.7	69.7	Dentary																						
MOR 553M 8-21-9-506	TM-068 (Jacks B-Day Site)	Adult	8	11.09	51	65.5	44	67.2	Dentary	11	10.5	11.8	11.5	10	12	9.8	10.8	11.5	10.5	11.2	10	11.6	13								
MOR 447 BF7	TM-041 (Westside Quarry)	Subadult-Adult	6	10.53	50	56.3	37.8	67.1	Dentary	7	8	9.5	10.1	9.8	9.8	10.2	8	11	10	11.2	10	11.5	12	10.8	10.7	12	12.4	11.6	12	12	12
MOR 447 B-11-87-2	TM-041 (Westside Quarry)	Subadult-Adult	6	10.62	40	47.5	32.6	68.7	Dentary	10	9.5	7.5	9.2	11	11.3	11.2	10.5	10	11.2	10.7	11.2	12	11.5	12	12	11.5	11	8.5			
MOR 447 8-7-1-36	TM-041 (Westside Quarry)	Subadult-Adult	6	7.32	49	>36	34	<94	Maxilla	6.5	6	6	7	7	6.5	8	6.8	7.5	8	8	8	8.4	7.2	8	7.5	8					
MOR 447 5-7-1-86	TM-041 (Westside Quarry)	Subadult-Adult	6	7.40	49	>36.2	33.8	<93.4	Maxilla	8	7	6	8.5	9	7.8	6.5	7	7	7.2	8.2	7.5	6	8	8	7.4	6.7					
MOR 454 SSQ-J-2 Holotype (no teeth)	TM-041 (Westside Quarry)	Subadult-Adult	6	7.75	41	44.4	31.8	72	Dentary																						
MOR 454 SSQ 6-24-6-2	TM-041 (Westside Quarry)	Subadult-Adult	6	8.09	46	36	31	86	Maxilla	8	8.8	9	7.5	9.8	8	8.5	7.2	8.5	8	8	8.7	6.5	8.2	8.2	7.5	8	8.2	7.6	7.5		
Unknown Lambeosaur)	Bonebed/Site	Relative Age	Body Size (m)	Average Tooth Size Anterior-Posterior (mm)	Number of tooth families	Overall Length of Specimen (cm)	Length of Dental Battery (cm)	% Contribution of dental battery to overall Jaw component	Jaw Component	Tooth Measurements																					
MOR 548F (no teeth)	TM-067 (West Hadrosaur BB)	Large Juvenile	3.5	4.90	20	13	9.8	75.4	Dentary																						
MOR 548	TM-066 (Blacktail Cr. North)	Late Nestling-Early Juvenile	1	4.36	19	10	8	80	Dentary	3	4.2	5	4.8	5.2	4	4.5	4.5	4	4.8	4											
MOR 548	TM-066 (Blacktail Cr. North)	Late Nestling-Early Juvenile	1	4.77	17	9.7	7.7	79.4	Dentary	5.2	4.5	4.6																			
MOR 548	TM-066 (Blacktail Cr. North)	Late Nestling-Early Juvenile	1	3.83	18	8	6.1	76.3	Maxilla	4	3.8	4	3.5																		
MOR 548 D	TM-066 (Blacktail Cr. North)	Late Nestling-Early Juvenile	1	4.38	19	9.6	7.7	80.2	Maxilla	4	5.5	4.8	4.5	4	3.5																
MOR 548 Q	TM-066 (Blacktail Cr. North)	Late Nestling-Early Juvenile	1	4.32	18	9.5	7.9	83.1	Maxilla	5.5	5	4.8	5	4.5	4.2	4	3.2	4	3												

APPENDIX D

SCALED TOOTH SIZE AND POPULATION DISTRIBUTIONS



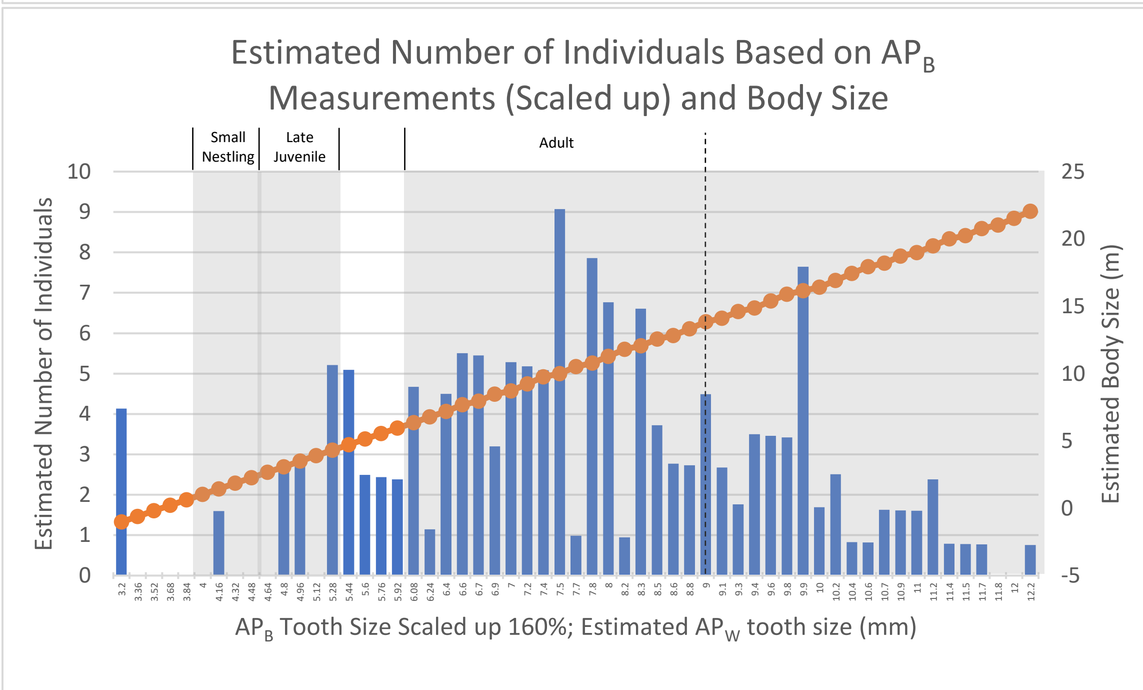


Figure D1-Number of individuals represented by the Egg Mt. *Maiasaura* tooth assemblage as a result of applying SQ factors to scaled AP_W tooth size (160% of AP_B). Estimated body size (orange) in meters is overlain with corresponding ontogenetic stages and their tooth size range based on museum specimens. Small specimens with calculated negative abundance or body size values were excluded. The dashed line indicates the largest (AP) observed adult *Maiasaura* tooth from museum specimens (9 mm). Growth stages described by Horner et al. 2000.

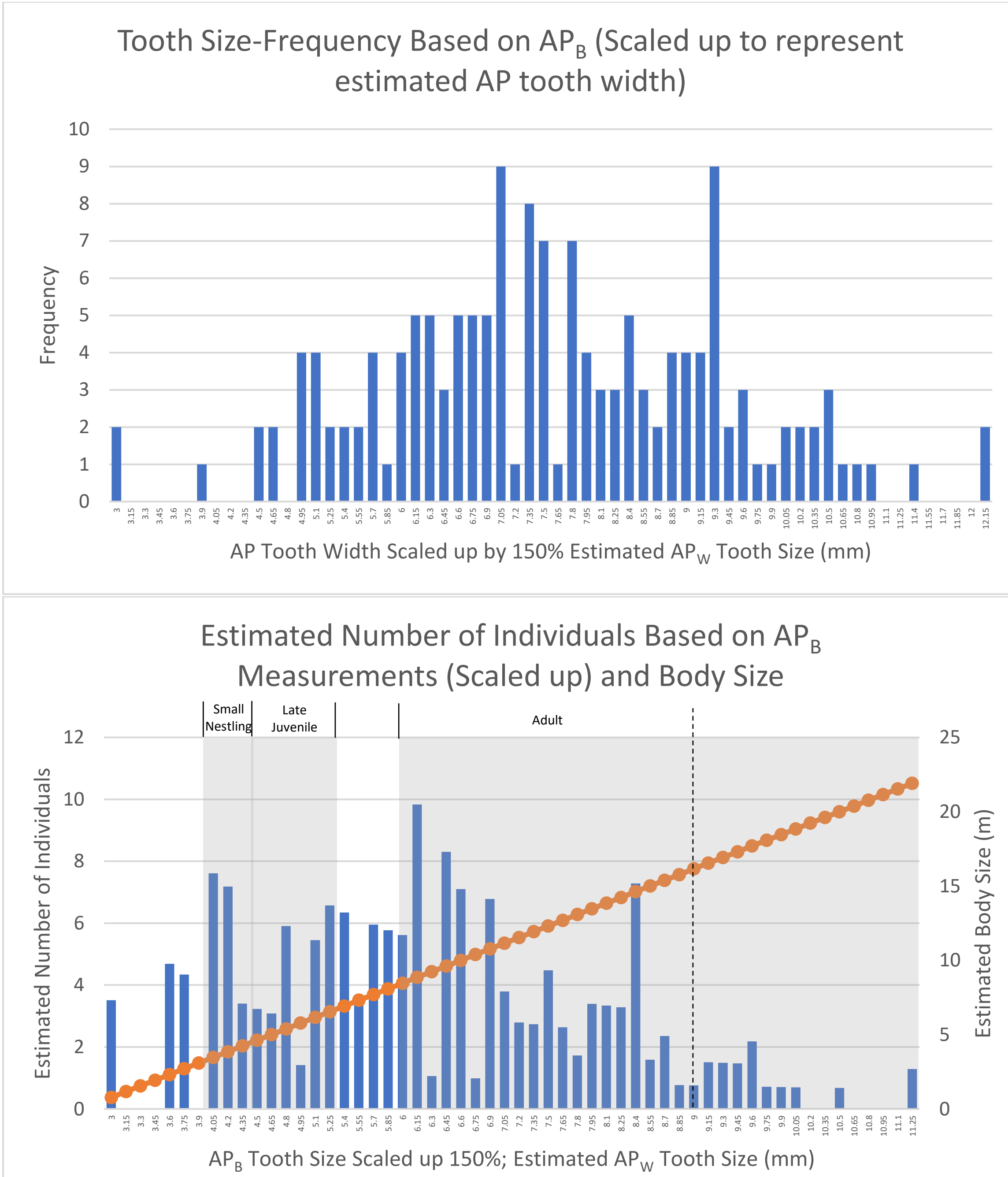
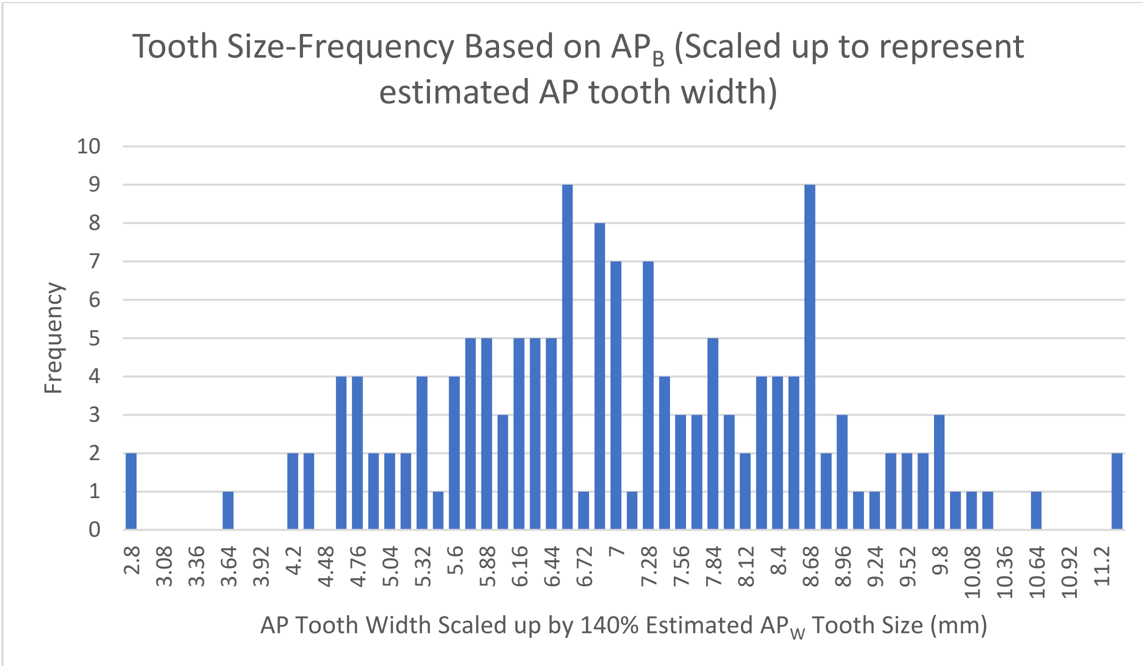


Figure D2-Number of individuals represented by the Egg Mt. *Maiasaura* tooth assemblage as a result of applying SQ factors to scaled AP_W tooth size (150% of AP_B). Estimated body size (orange) in meters is overlain with corresponding ontogenetic stages and their tooth size range based on museum specimens. Small specimens with calculated negative abundance or body size values were excluded. The dashed line indicates the largest (AP) observed adult *Maiasaura* tooth from museum specimens (9 mm). Growth stages described by Horner et al. 2000.



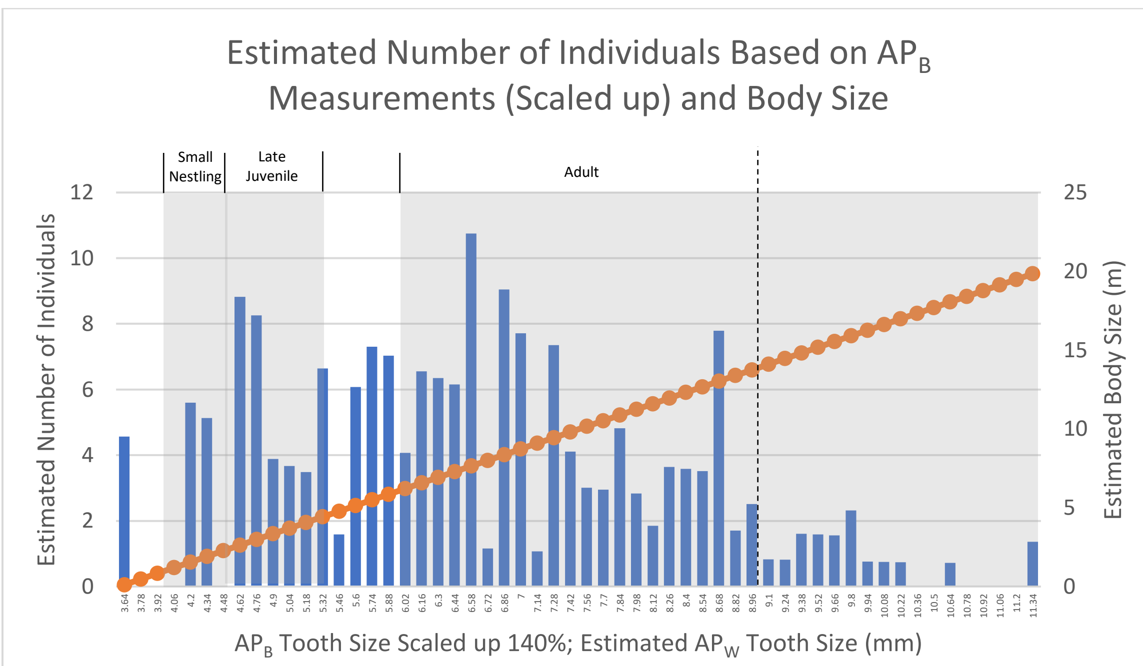
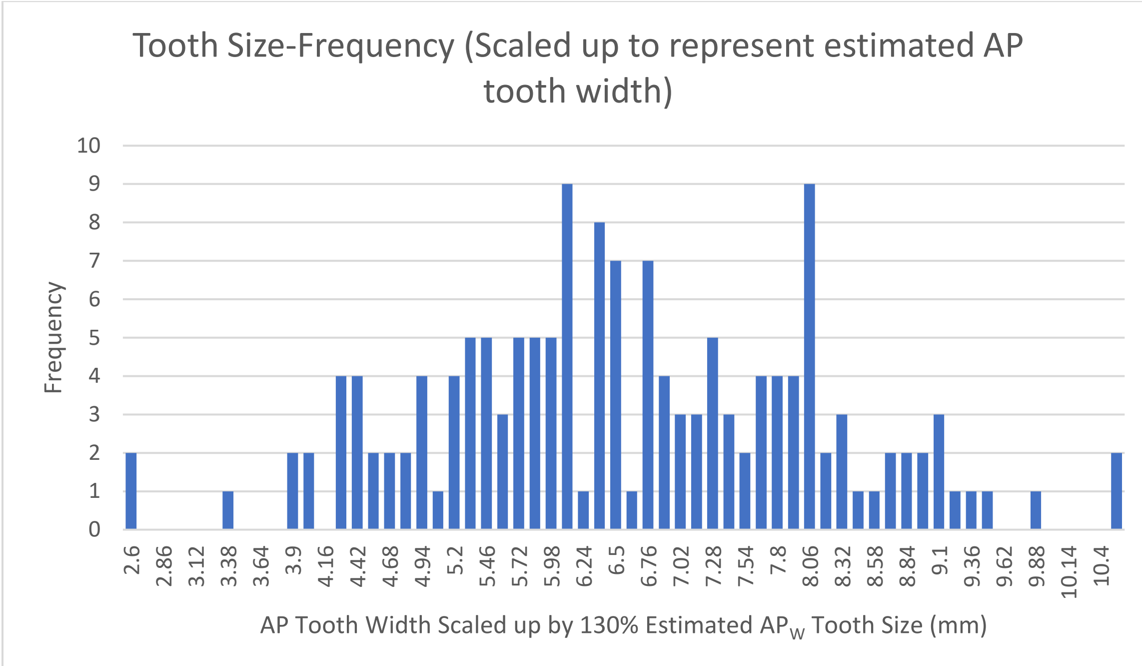


Figure D3-Number of individuals represented by the Egg Mt. *Maiasaura* tooth assemblage as a result of applying SQ factors to scaled AP_W tooth size (140% of AP_B). Estimated body size (orange) in meters is overlain with corresponding ontogenetic stages and their tooth size range based on museum specimens. Small specimens with calculated negative abundance or body size values were excluded. The dashed line indicates the largest (AP) observed adult *Maiasaura* tooth from museum specimens (9 mm). Growth stages described by Horner et al. 2000.



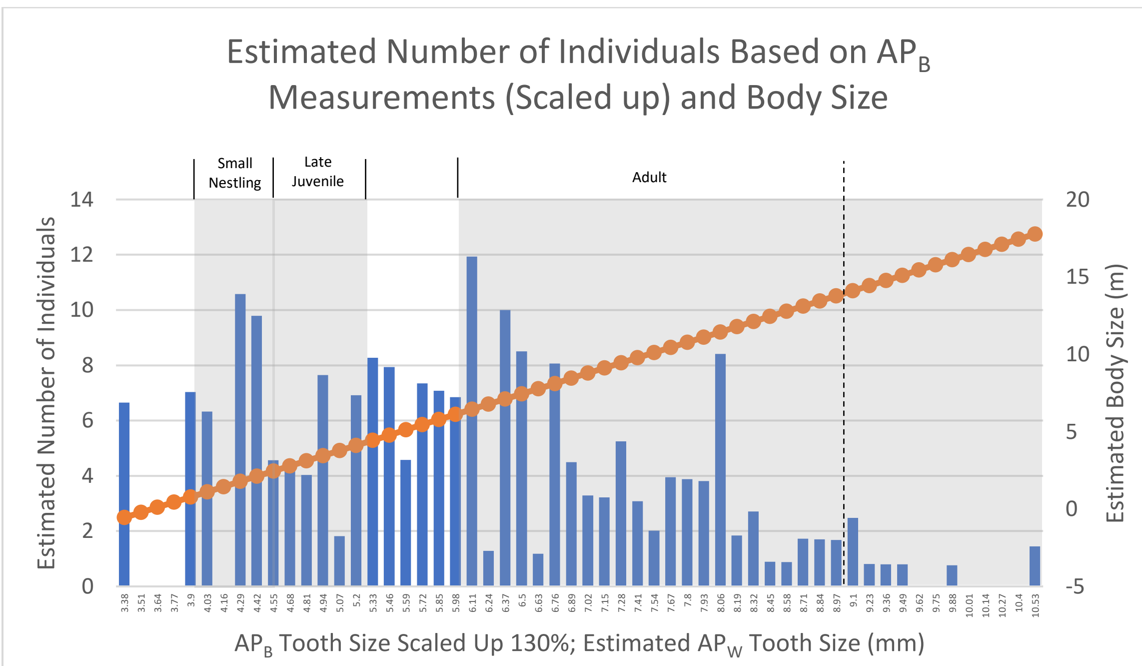
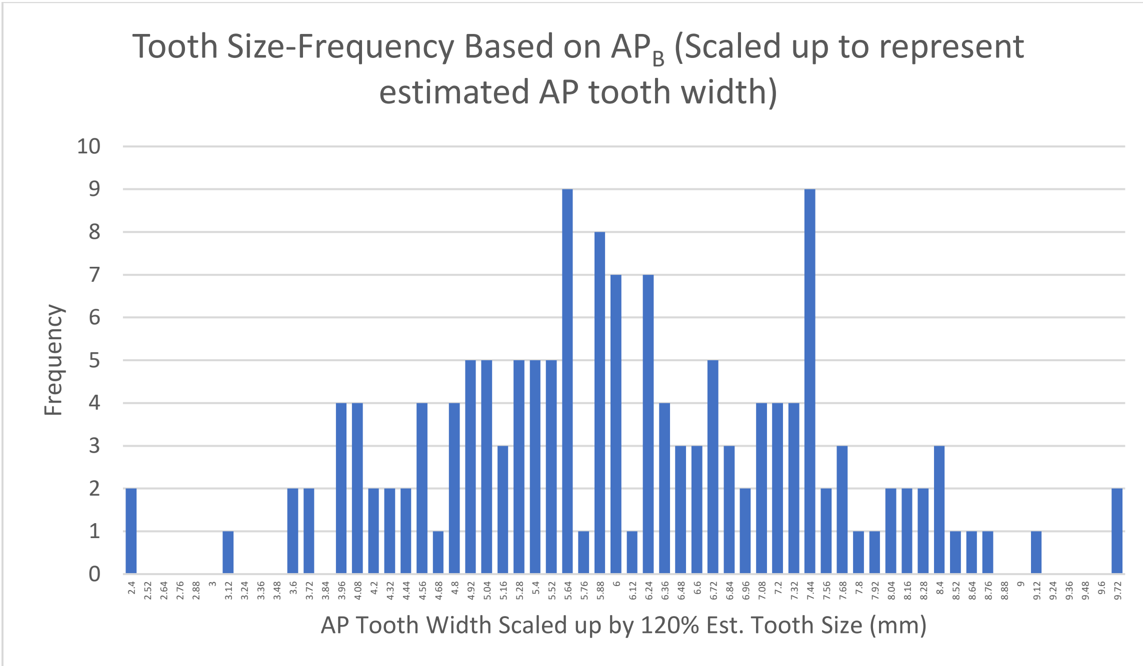


Figure D4- Number of individuals represented by the Egg Mt. *Maiasaura* tooth assemblage as a result of applying SQ factors to scaled AP_W tooth size (130% of AP_B). Estimated body size (orange) in meters is overlain with corresponding ontogenetic stages and their tooth size range based on museum specimens. Small specimens with calculated negative abundance or body size values were excluded. The dashed line indicates the largest (AP) observed adult *Maiasaura* tooth from museum specimens (9 mm). Growth stages described by Horner et al. 2000.



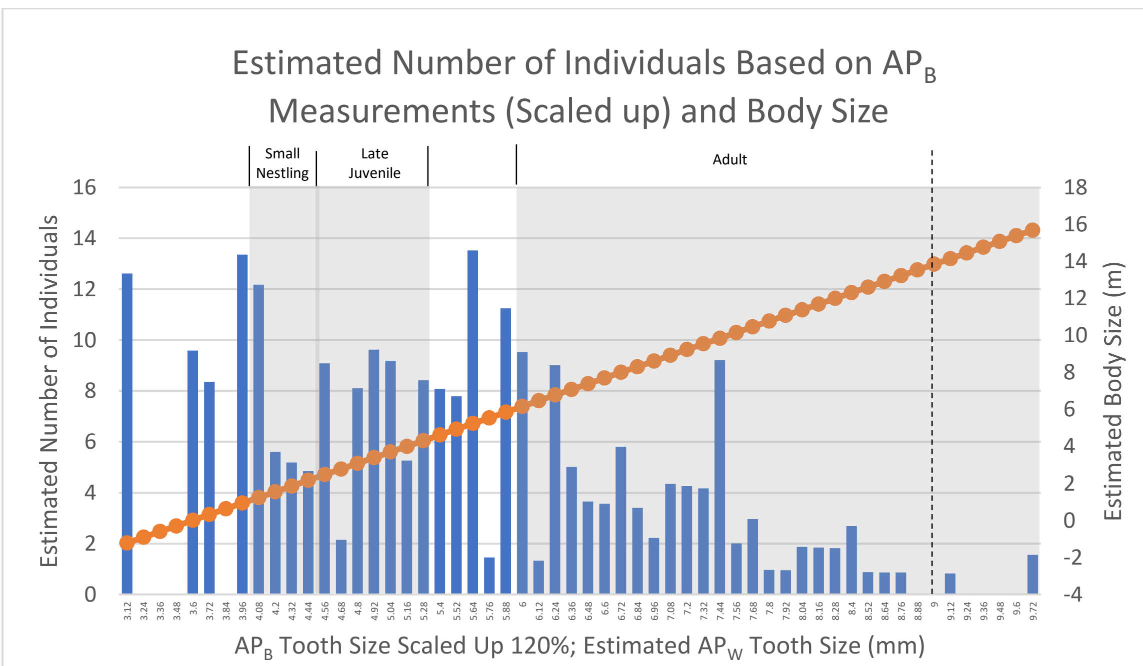
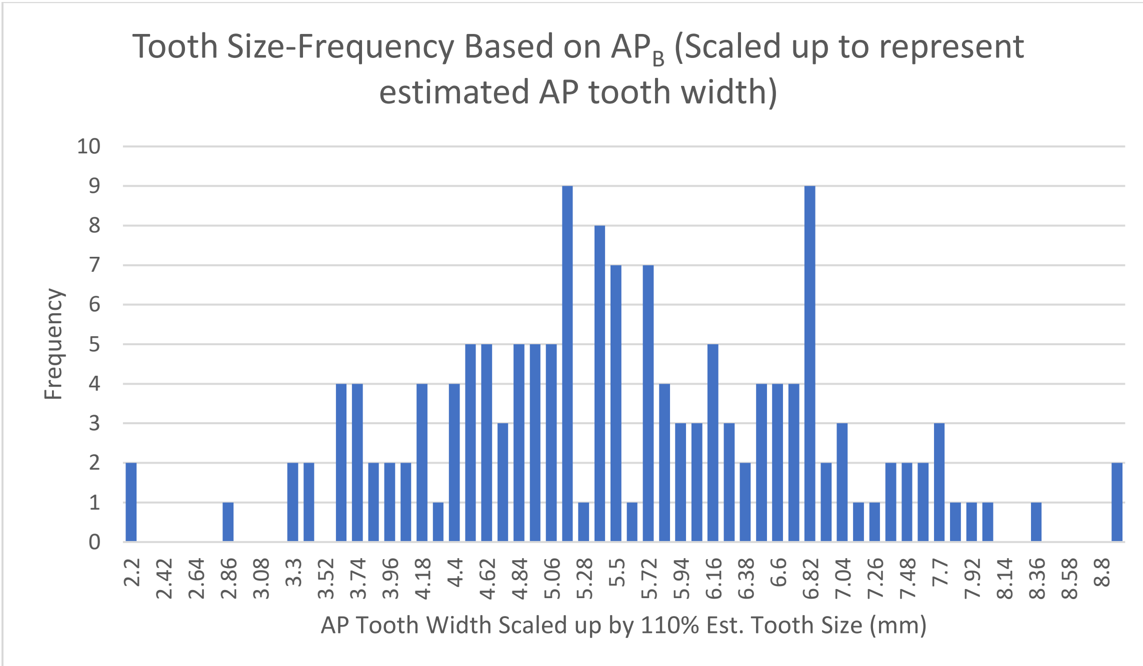


Figure D5- Number of individuals represented by the Egg Mt. *Maiasaura* tooth assemblage as a result of applying SQ factors to scaled AP$_W$ tooth size (120% of AP$_B$). Estimated body size (orange) in meters is overlain with corresponding ontogenetic stages and their tooth size range based on museum specimens. Small specimens with calculated negative abundance or body size values were excluded. The dashed line indicates the largest (AP) observed adult *Maiasaura* tooth from museum specimens (9 mm). Growth stages described by Horner et al. 2000.



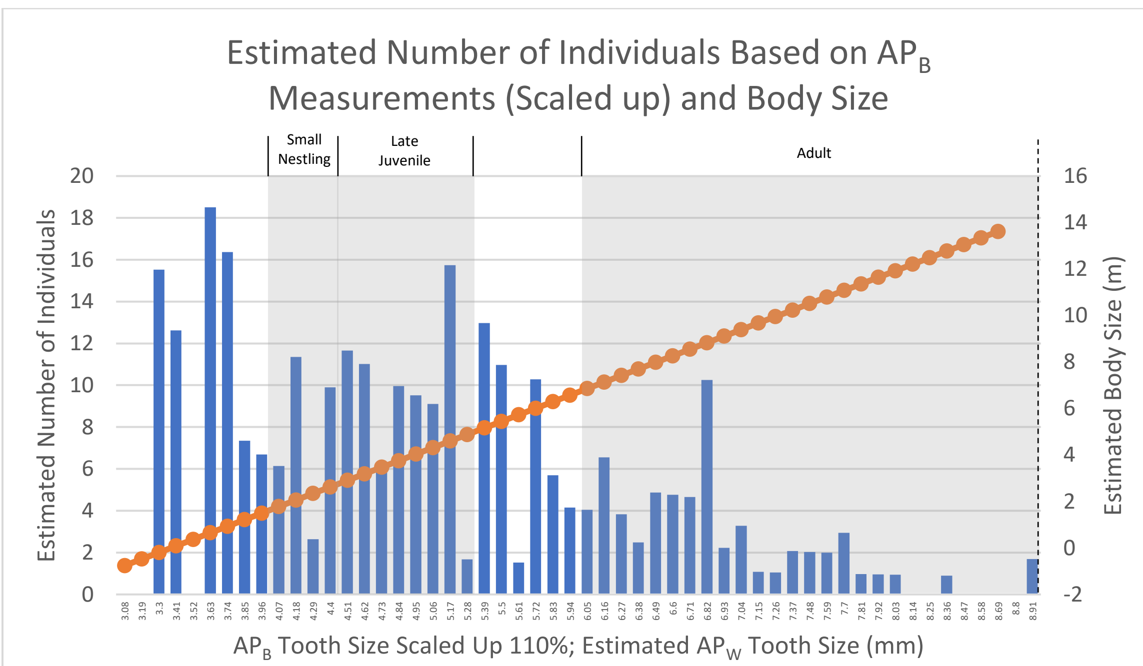
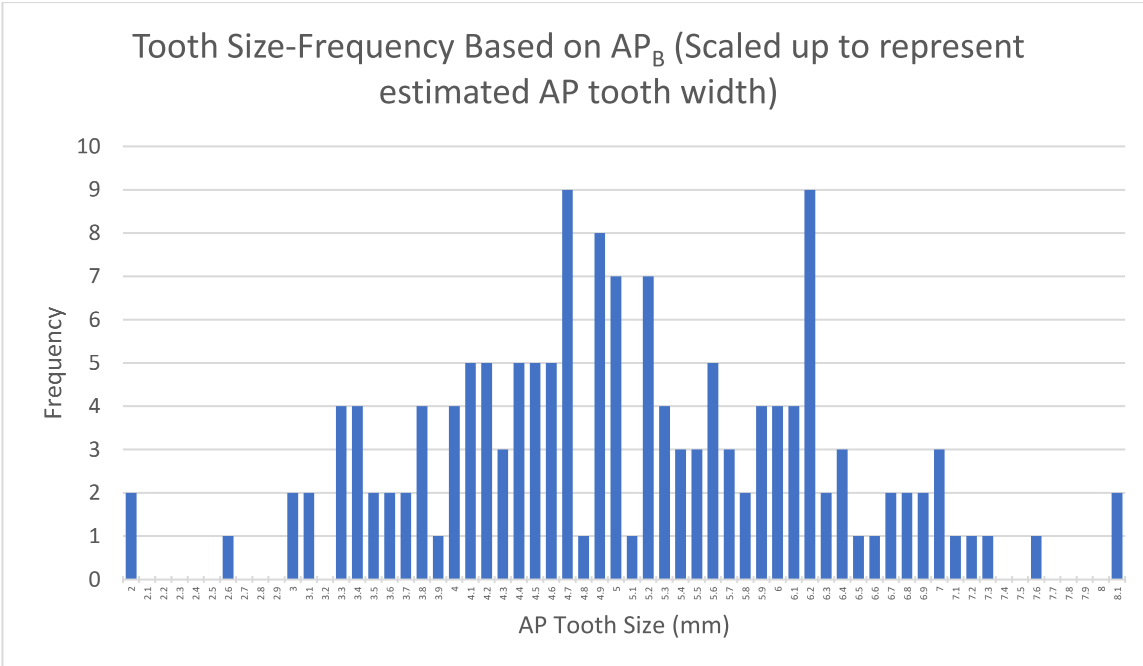


Figure D6- Number of individuals represented by the Egg Mt. *Maiasaura* tooth assemblage as a result of applying SQ factors to scaled AP_W tooth size (110% of AP_B). Estimated body size (orange) in meters is overlain with corresponding ontogenetic stages and their tooth size range based on museum specimens. Small specimens with calculated negative abundance or body size values were excluded. The dashed line indicates the largest (AP) observed adult *Maiasaura* tooth from museum specimens (9 mm). Growth stages described by Horner et al. 2000.



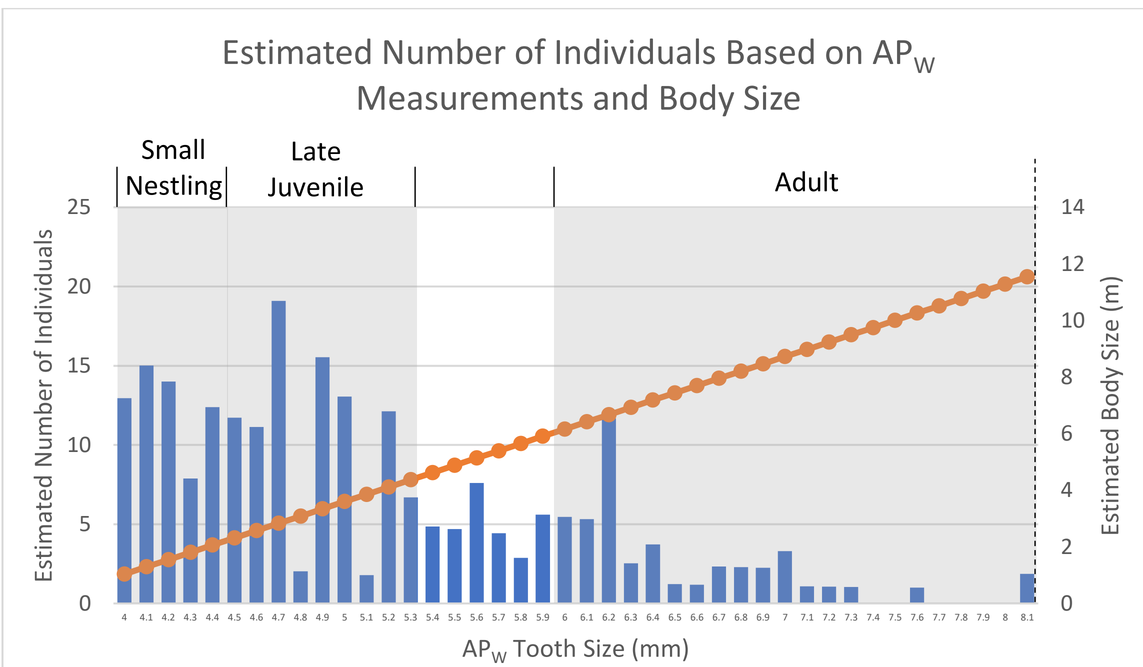
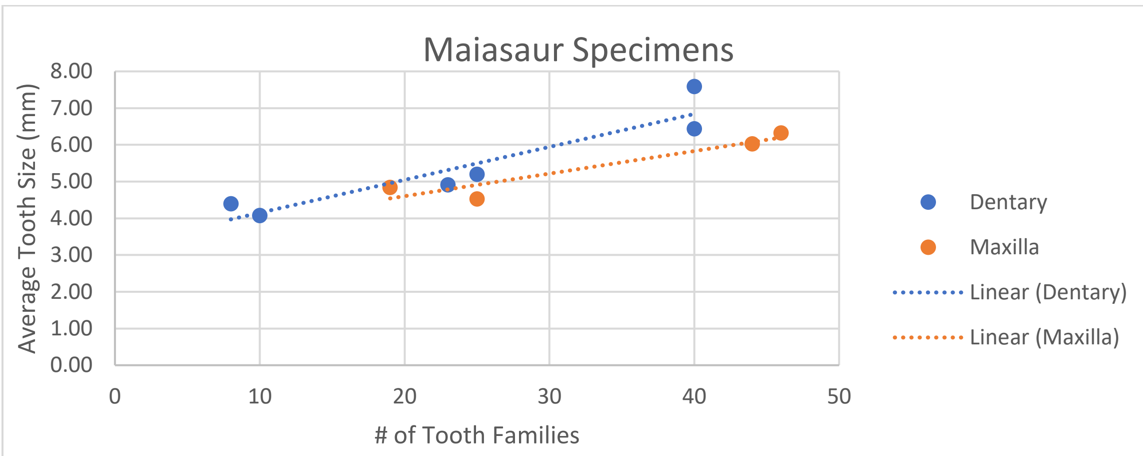


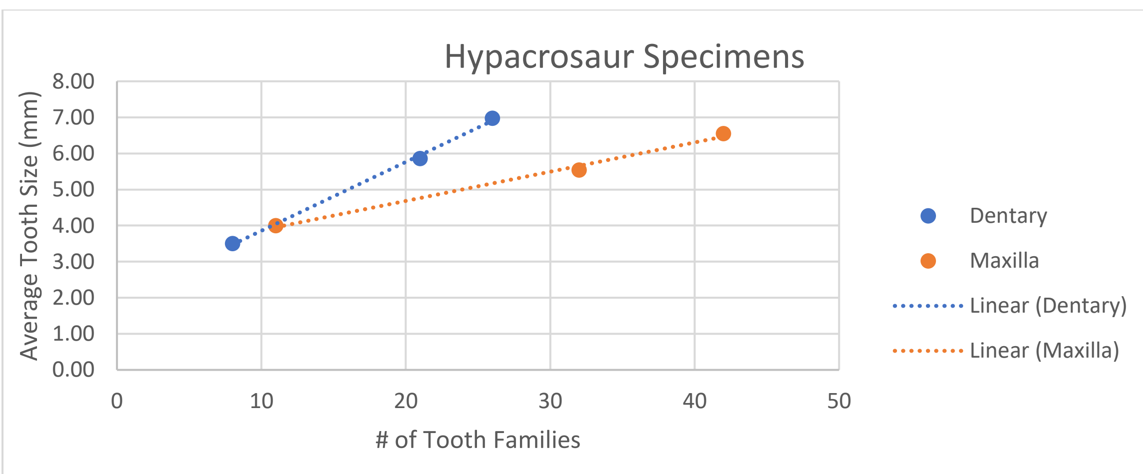
Figure D7- Number of individuals represented by the Egg Mt. *Maiasaura* tooth assemblage as a result of applying SQ factors to observed AP_W tooth size. Estimated body size (orange) in meters is overlain with corresponding ontogenetic stages and their tooth size range based on museum specimens. Small specimens with calculated negative abundance or body size values were excluded. The dashed line indicates the largest (AP) observed adult *Maiasaura* tooth from museum specimens (9 mm). Growth stages described by Horner et al. 2000.

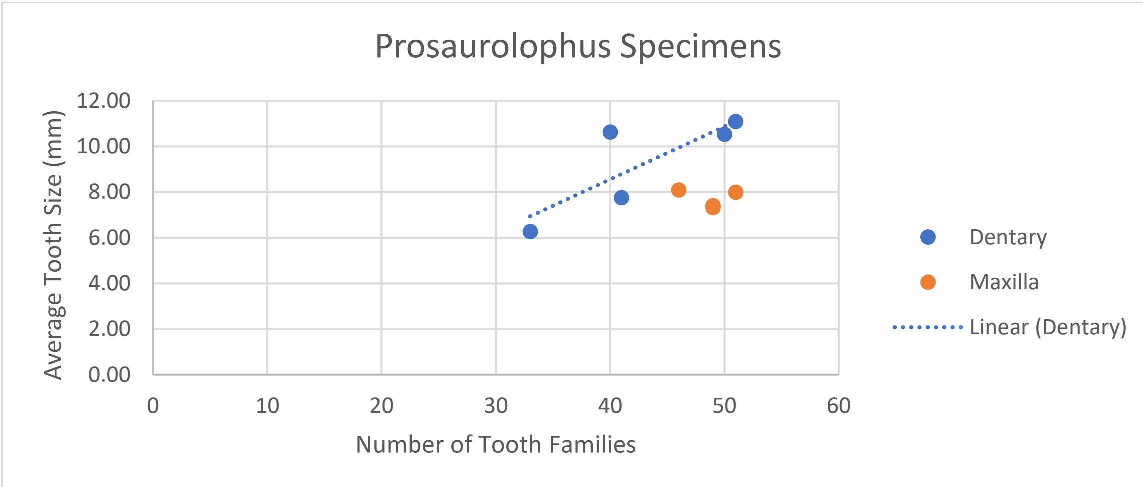
APPENDIX E

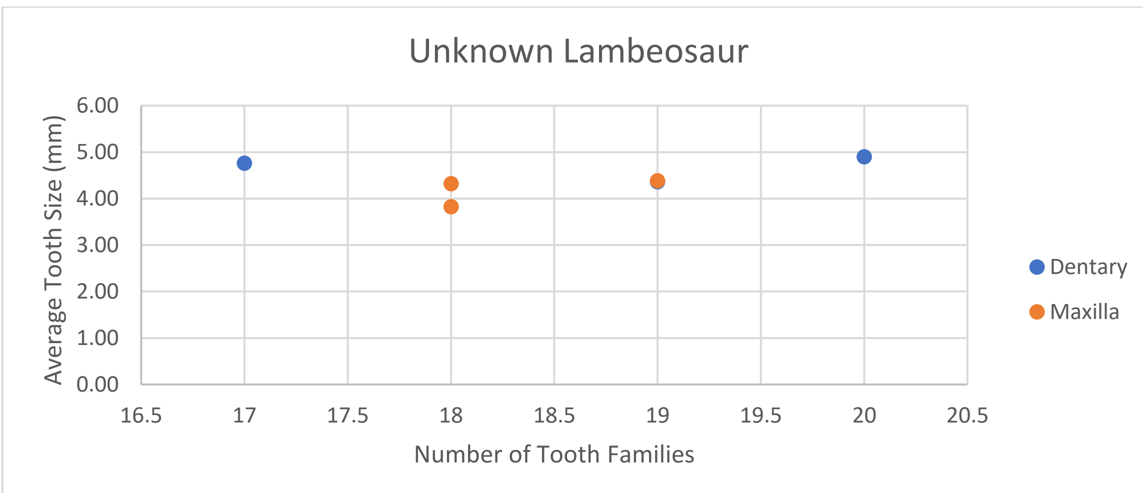
ADDITIONAL GRAPHS OF MUSEUEM SPECIMENS

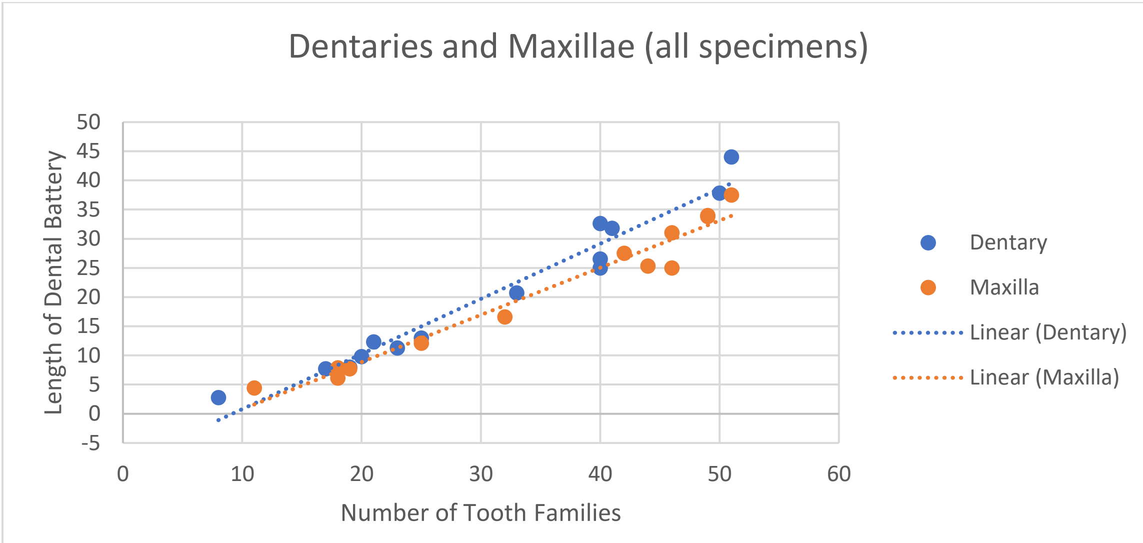
Measurements were taken on additional hadrosaurids from MOR collections which were included in Appendix C. It was ultimately decided to limit the study to *Maiasaura* specimens as was described in the text. Nonetheless, similar graphs plotting average AP tooth size was plotted against the number of tooth families present in each specimen. Similar tends can be noticed regarding the increase in tooth size and the addition of teeth to the dental battery. Although not prudent to this population study, the additional observations and measurements on other hadrosaur species could be beneficial to future work on the topic.

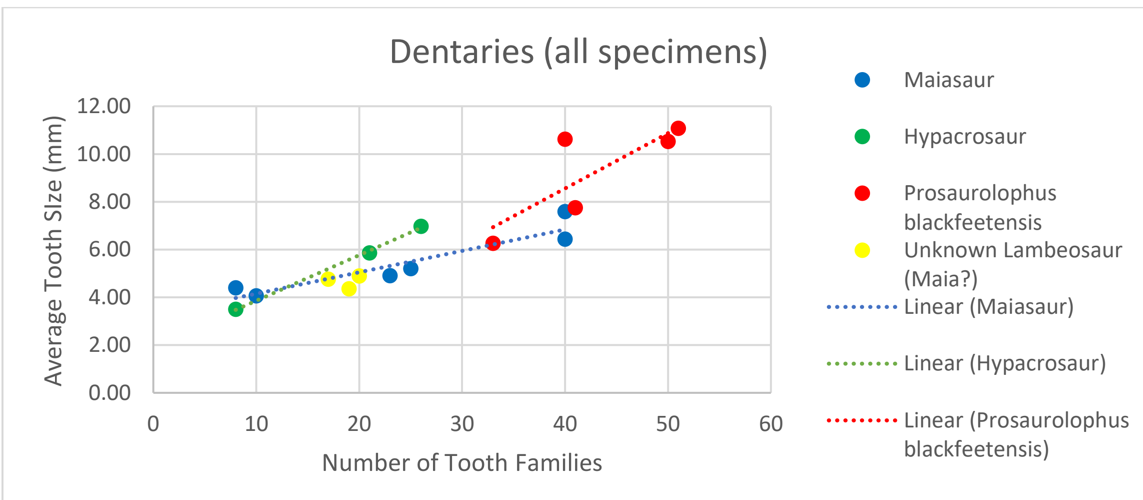


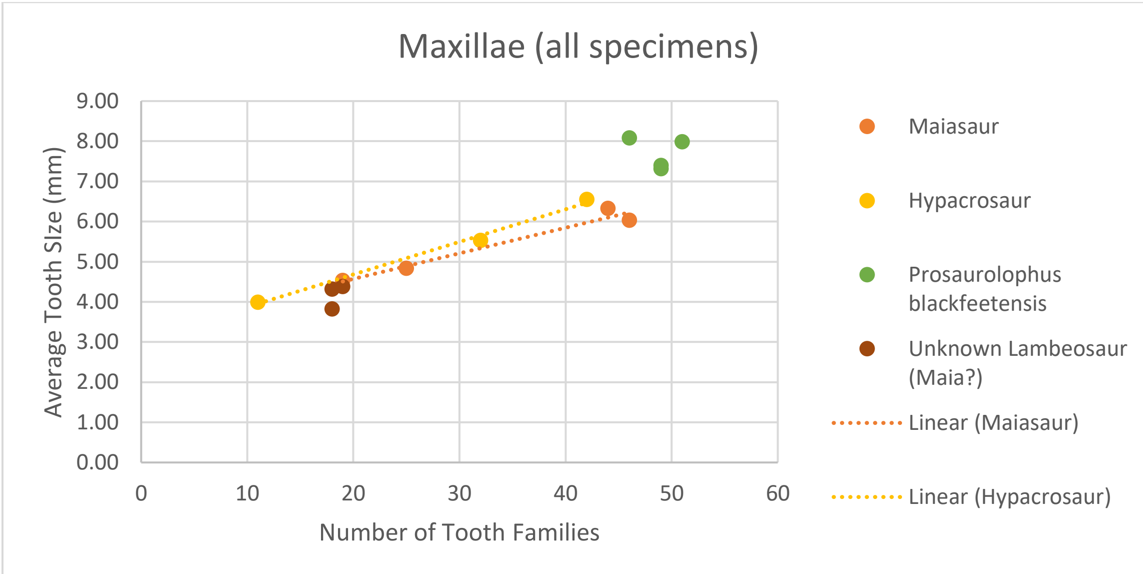



Prosaurolophus Specimens
Average Tooth Size (mm)
12.00
10.00
8.00
6.00
4.00
2.00
0.00
0
10
20
30
40
50
60
Number of Tooth Families
Dentary
Maxilla
Linear (Dentary)


Unknown Lambeosaur
Average Tooth Size (mm)
6.00
5.00
4.00
3.00
2.00
1.00
0.00
16.5
17
17.5
18
18.5
19
19.5
20
20.5
Number of Tooth Families
Dentary
Maxilla


Dentaries and Maxillae (all specimens)
Length of Dental Battery
50
45
40
35
30
25
20
15
10
5
0
-5
0
10
20
30
40
50
60
Number of Tooth Families
Dentary
Maxilla
Linear (Dentary)
Linear (Maxilla)


Dentaries (all specimens)
Average Tooth SIze (mm)
12.00
10.00
8.00
6.00
4.00
2.00
0.00
0
10
20
30
40
50
60
Number of Tooth Families
Maiasaur
Hypacrosaur
Prosaurolophus blackfeetensis
Unknown Lambeosaur (Maia?)
Linear (Maiasaur)
Linear (Hypacrosaur)
Linear (Prosaurolophus blackfeetensis)


Maxillae (all specimens)
Average Tooth SIze (mm)
9.00
8.00
7.00
6.00
5.00
4.00
3.00
2.00
1.00
0.00
0
10
20
30
40
50
60
Number of Tooth Families
Maiasaur
Hypacrosaur
Prosaurolophus blackfeetensis
Unknown Lambeosaur (Maia?)
Linear (Maiasaur)
Linear (Hypacrosaur)