AN ONTOGENETIC SERIES AND POPULATION HISTOLOGY OF THE CERATOPSID DINOSAUR *EINIOSAURUS PROCURVICORNIS*

by

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Julie Ann Reizner

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ABSTRACT

Histologic studies have been utilized in paleontology to determine rates of growth for several dinosaur taxa, but members of the otherwise relatively well-known family Ceratopsidae have largely been excluded. A monodominant bonebed containing remains of the centrosaurine ceratopsid *Einiosaurus procurvicornis* Sampson 1995, ranging from juveniles to putative adults, has been found in the Upper Cretaceous Two Medicine Formation of northwestern Montana. This bonebed represents a drought-induced assemblage, and is hypothesized to represent a single population. The full available range of sizes of tibiae (N = 16) were sectioned and bone histology examined. Tissue types and degrees of remodeling are discussed, and growth lines are used to determine ages at time of death of the individuals.

The rate of growth for *Einiosaurus* peaks at about 3-5 years of age, at which time growth slows, suggesting that this may be the age that reproductive maturity is reached. The nature of the bone tissue suggests that growth in *Einiosaurus* is still relatively rapid in even the largest specimens, indicating that a fully adult tibia has not been recovered from the studied bonebed, and this bonebed is biased toward juveniles and subadults. Since the bonebed is a snapshot of a standing herd, population dynamics of *Einiosaurus*, such as survivorship and behavior, are assessed. This information on growth dynamics and life histories of a species has implications for future taxonomic resolution and morphometric studies of ceratopsid dinosaurs, and marks the first study on population histology of a large-bodied herbivorous dinosaur.

INTRODUCTION

Focus of Study

Dinosaur paleohistology has been utilized as a tool to resolve taxonomic validity (Cubo *et al.* 2005, Sander *et al.* 2006, Knoll *et al.* 2009), interpret metabolic rates (Ricqles 1974 and 1980, Bouvier 1977, Reid 1985, Chinsamy 1990, Reid 1997b, Ricqles *et al.* 2006,) find ages of individuals at their time of death as a means to determine the growth rate of a species, age at sexual maturity and potential species longevity (Chinsamy 1990b and 1993, Varricchio 1993, Curry 1999, Erickson and Tumanova 2000, Horner *et al.* 1999 and 2000, Sander 2000, Horner and Padian 2004, Bybee *et al.* 2006, Lee 2007a, Lee and Werning 2008), and construct life tables and behavior (Horner *et al.* 2000, Erickson *et al.* 2004, 2006, 2009, Redelstorff and Sander 2009). The focus of this study is to determine growth rates, life tables, and behavior of a species of ceratopsid dinosaur – a group that has largely been excluded from previous histologic studies - in order to gain insight on ontogeny, population dynamics, and behavior of this species.

Paleohistologic work on growth rates has involved several species of dinosaur, such as several members of the saurischians: prosauropods and sauropods (Chinsamy 1993, Curry 1999, Sander 2000, Company 2005), and theropods (Chinsamy 1990, Varricchio 1993, Erickson *et al.* 2004, Horner and Padian 2004, Bybee *et al.* 2006). Several groups of ornithischians have been excluded, but those represented by histologic studies on the growth rate of a species include the thyreophorans *Scutellosaurus* (Padian *et al.* 2004) and *Stegosaurus* (Redelstorff and Sander 2009), the ornithopods *Orodromeus*

makelai, Dryosaurus altus, Dryosaurus lettowvorbecki, Maiasaura peeblesorum, Hypacrosaurus stebingeri, and *Tenontosaurus tillettii* (Chinsamy 1995, Horner *et al.* 1999 and 2000, Lee and Werning 2008, Horner *et al.* 2009), *Psittacosaurus mongoliensis* (Erickson and Tumanova 2000), a basal ceratopsian, and some work on *Centrosaurus apertus* (Lee 2006, 2007a, 2007b), a centrosaurine ceratopsid. However, no study using skeletochronology - the process of determining age from the bone itself - of ceratopsids in order to determine age and growth dynamics of the once-living population (population histology), has yet been published.

Skeletochronology is utilized in this study because it is a powerful tool that can closely estimate the age of an animal by directly inferring the animal's own biology, with little assumption from the worker (Brinkman *et al.* 2007, see Ontogenetic Changes in Dinosaur Bone below). Many previous studies have instead compared relative sizes of individuals in order to estimate age at time of death (Dodson 1975, Lehman 2006, Qi *et al.* 2007, Mathews *et al.* 2009), however, somatic size does not always correlate closely to age. In these cases, the presumed rate of growth must be modeled from taxa with known growth rates, often extant reptiles (Case 1978, Lehman 2006), which introduces error and ignores patterns of ontogeny implicit in dinosaurian bone tissue, one of which is that fibrolamellar bone unequivocally records a rapid, generally non-reptilian, rate of growth (Reid 1990).

In addition to bone histology, juvenile features, such as proportionally large heads and shorter faces, and large orbits, can be recognized and are sometimes used in ontogenetic studies (Horner *et al.* 1999, Knoll *et al.* 2009), but in absence of well-

preserved, young cranial material, juvenile features are much more difficult to resolve within a species. Skull anatomy of ceratopsians certainly exhibit notable ontogenetic changes (*e.g.* Horner and Goodwin 2006), however, if sexual dimorphism occurs in ceratopsians, it can be difficult to discern the juveniles from the adults based on cranial material alone (Tanke 1988). Therefore, bone histology is a valuable tool to assist in determining the age of an individual, independent of the size of the animal and despite how much its morphology may change throughout life or between sexes.

This study utilizes material referable to the Late Cretaceous ceratopsid *Einiosaurus procurvicornis* reported from a low-diversity, or monodominant (*sensu* Ryan and Evans 2005) bonebed in northwestern Montana (see Canyon Bone Bed, below). This bonebed is a mass death assemblage and therefore can provide census-like data of a species, and because the individuals are of several different ages, can provide information on growth (Ricqles *et al.* 1997) that complete, isolated skeletons cannot (Sampson 1995b, Sampson and Ryan 1997). A drought-induced mortality has been proposed for Canyon Bone Bed (Rogers 1990), and so represents a population of animals that died together within a short time span and is interpreted to be a possible herd. The current study utilizes bone histology in order to assess life histories and behavior of *Einiosaurus.*

Objectives

This study 1) analyzes and describes the bone tissues of *Einiosaurus* and compares these to other species of dinosaur, 2) assesses ages of the individuals at time of death, 3) reports an ontogenetic series of this species, 4) relates implications of results to

other areas of ontogenetic research, and 5) hypothesizes population dynamics of *Einiosaurus*, such as survivorship and life history, and behavior.

BACKGROUND

Dinosaur Bone Histology

Bone Tissue

Bone is a highly vascular, living tissue that experiences constant remodeling throughout the life of an organism, and like all other connective tissues, consists of cells (osteocytes) and an intercellular matrix. This matrix is composed of both organic materials such as collagen fibers, and inorganic salts rich in calcium and phosphate (Williams, 1995). Within this matrix, vascular canals run throughout the bone, providing its cells with metabolic support and supplying access for other cells, such as osteoclasts, which remove bone, and osteoblasts, which can then deposit bone. Because the orientation and type of vascular canals is a major factor in determining the age of dinosaurs (de Ricqles, 1976 and 1980) they will be discussed in more detail below.

Collagen fibers and mineralized matrix together form tiny cylinders, or osteons, which concentrically encapsulate the blood vessels. Most bone tissues are originally laid down by soft tissues called the periosteum which coats the external bone surface, and the endosteum which coats the internal surface (Francillon-Vieillot *et al.* 1990, Reid 1997c). Mature bone also contains both dense, or compact bone, and spongy or cancellous bone (Williams 1995). As the cancellous portions of dinosaur bones are often damaged by the processes of fossilization, paleohistologists are most concerned with vascularization occurring in the compact bone.

Ontogenetic Changes in Dinosaur Bone

Early in ontogeny, tetrapods exhibit woven bone, which is quickly laid down and therefore is not layered. Primary osteons then occur around blood vessels, and exhibit circumferential lamellae which are layers that are parallel to both the periosteal and endosteal surfaces (Williams 1995). Since the young, growing bone is experiencing circumferential growth, any period of non-deposition may result in an obvious resting line that parallels the periosteum, sometimes followed by a layer of low-vascularity zonal growth (Varricchio 1997). In humans and many other mammals, these resting lines may only occur in young that have experienced successive illnesses (Williams 1995), but in animals that experience physiological stress due to seasonal, climate fluctuations, including some extinct and extant mammals (Frylestam and von Schantz 1977, Chinsamy *et al.* 1998, Horner *et al.* 1999, Sander and Andrassy 2006), many reptiles (Enlow 1969, de Ricqles 1976 and 1980, Castanet and Cheylan 1979, Hutton 1986), and Mesozoic and more recent (though not extant) birds (Chinsamy *et al.* 1994, Turvey *et al.* 2005), these non-vascular resting lines may indicate the age of the individual. These are termed "lines of arrested growth" (LAGs), and the ability to create them is plesiomorphic for tetrapods (Horner *et al.* 1999).

Despite initial controversy over the frequency of LAG formations, in extant non-avian diapsids, including crocodilians, LAGs indicate annual fluctuations in growth and allow for the aging of individuals. Therefore, LAGs have many implications in histological studies of extinct organisms, since the fact that they are annual and are deposited during the non-favorable season has been backed by many studies (*e.g.*,

Castanet and Cheylan 1979, Hutton 1986) and is now considered non-controversial (Chinsamy 1993 and 1994, de Ricqles *et al.* 2006). Not all growth lines are LAGs, however, but may indicate simply a change in the orientation of fibers with growth, or cortical drift – remodeling of bone according to the stresses placed on it which can cause a bone to grow more on one side than another, for instance (Padian 1997). Growth lines are considered to represent true LAGs if they can be followed along the entire circumference of the bone, which is why this study utilizes complete transverse sections of bone rather than core samples.

Throughout ontogeny, remodeling, which is continuous reshaping of a bone, occurs in the primary tissue. Remodeling can also be related to mechanical constraints and physiological demands later in life, as well as somatic growth (Enlow *et al.* 1963). Adult bone construction mostly consists of lamellae arranged in concentric cylinders around blood vessels – the secondary osteons, or Haversian systems (Francillon-Vieillot *et al.* 1990), which are delimited from the surrounding bone by a cement line. In compact bone, the secondary osteons can be so tightly packed together that several are overlapping, and this is known as dense Haversian tissue, in which successive generations of Haversian systems may be superimposed *in situ* (Francillon-Vieillot *et al.* 1990). Remodeling in this case is so extensive that all growth lines that occurred in primary bone are likely to be lost. However, in "loose" Haversian bone tissue, or bone that is undergoing earlier stages of remodeling, primary bone can remain between secondary osteons and is called interstitial tissue. When this occurs, the initial tissue type, as well as any growth lines, can readily be recognized (Francillon-Vieillot *et al.*

1990). Therefore, despite some remodeling, LAGs can be either counted or extrapolated (see METHODS AND MATERIALS), and age can be estimated.

Einiosaurus procurvicornis

Einiosaurus procurvicornis is a centrosaurine ceratopsid found exclusively in Montana, and was named and described in Sampson, 1995a. This material is from the Upper Cretaceous (middle to late Campanian) Two Medicine Formation of northwestern Montana, in bonebeds referred to as Canyon Bone Bed and Dino Ridge Quarry (Rogers 1990). Both of these beds, located in the Landslide Butte Field Area in the Blackfeet Indian Reservation, were originally thought to contain a new species of *Styracosaurus*, and are referred to as such in the taphonomic study by Rogers (1990). Horner *et al.* (1992) refer to the then-unnamed *Einiosaurus* as "transitional taxon B," indicating its hypothesized phylogenetic position between *Styracosaurus* and *Pachyrhinosaurus*.

The placement of *Einiosaurus procurvicornis* within the centrosaurine ceratopsids is problematic and it is uncertain as to whether it forms a sister to the *Pachyrhinosaurus-Achelousaurus* clade or the *Styracosaurus-Centrosaurus* clade (Dodson *et al.* 2004).

Locality of Specimens

The Two Medicine Formation

The Two Medicine Formation is a classic dinosaur-bearing formation that contains many monodominant bone beds for several dinosaur genera, as well as localities with individual specimens. Taxa include the whole spectrum of clades typical for the Late Cretaceous of western North America. Theropods are represented by a variety of

taxa, most notably *Troodon formosus* (Varricchio *et al.* 1997) and *Daspletosaurus* (Varricchio 2001). Hadrosaurs include *Maiasaura* (Horner and Makela 1979), *Hypacrosaurus stebingeri*, *Prosaurolophus*, and *Gryposaurus* (Horner and Currie 1994, Horner *et al.* 1992, Varricchio and Horner 1993, Varricchio 1995). Ceratopsians include *Achelousaurus horneri* and *Einiosaurus procurvicornis* (Sampson 1995a), as well as *Brachyceratops montanensis nom. dub.* (Gilmore 1917, Sampson *et al.* 2001). The Two Medicine Formation is especially notable for its preservation of dinosaur nesting horizons (Horner and Makela 1979) and eggs (Horner and Makela 1979, Hirsch and Quinn 1990, Varricchio *et al.* 1997, Varricchio and Jackson 2004), and some 80% of all dinosaur skeletal remains in this formation represent juveniles of less than half adult size (Horner and Makela 1979).

The Two Medicine Formation is exposed in northwestern Montana east of the Rocky Mountain Overthrust Belt where it is folded and faulted and approximately 600 m thick, and extends eastward into the relatively undeformed plains where it pinches out against the Sweetgrass Arch (Rogers 1990). These strata were deposited beginning approximately 83 million years ago with the regression of the Colorado Sea, and culminating about 74 million years ago with maximum transgression of the Bearpaw Sea, during the Late Campanian (Horner *et al.* 2001, Foreman *et al.* 2007). The sediments represent non-marine depositional systems that occurred in the Two Medicine alluvial plain, with relatively straight stream channels flowing from the Cordilleran highlands in the west toward the western, oscillating shore of the Cretaceous Interior Seaway (Horner *et al.* 2001). Near the study area, the Two Medicine Formation conformably overlies the

nearshore Virgelle Sandstone and is conformably overlain by the marine Bearpaw Shale (Rogers 1990). Explosive volcanism occurred repeatedly in the Elkhorn Mountains to the west, and provide bentonite ash layers with which to accurately date the Two Medicine Formation (Foreman *et al.* 2007).

Abundant caliche horizons and nodules, red oxidized paleosols, mud drapes in sand bodies and mud rip-ups in channel lag deposits, an impoverished aquatic fauna, and scarce lacustrine deposits are evidence that the Two Medicine Formation was deposited in a seasonal, semi-arid climate with a long dry season, warm temperatures, and predominant winds from the west (Lorenz 1981, Gavin 1986, Rogers 1990) with possible rainshadows from the Cordilleran highlands (Carpenter 1987). Plant fossils (Crabtree 1987) and palynological studies (Jerzykiewicz and Sweet 1988) support these conclusions. Additionally, extensive volcanism to the west supplied voluminous volcaniclastic sediment to the coastal plain (Lageson *et al.* 2001), and so the habitats in which dinosaurs in this region lived were subjected to extensive volcanism (Horner *et al.* 2001).

The *Einiosaurus procurvicornis* bone beds occur in the topmost lithofacies of the formation (Lithofacies 5, the *Hypacrosaurus stebingeri* Biozone, Horner *et al.* 2001) which comprises transgressive fluvial sequences deposited during transgression of the Bearpaw Sea. This lithofacies outcrops near Landslide Butte on Blackfeet Nation lands in Glacier and Pondera Counties, and along Badger and Blacktail Creeks (Horner *et al.* 2001). Several paucispecific bone beds have been reported from this horizon, comprising both ceratopsians and hadrosaurs (Horner and Makela 1979, Rogers 1990, Varricchio and

Horner 1993), and two multispecific bonebeds have been found as well (Varricchio and Horner 1993, Varricchio 1995). The Two Medicine Formation is part of the Judith River Group, and is correlative to the Dinosaur Park Formation in Alberta, Canada, which has also produced multiple ceratopsian bone beds (Fiorillo 1987, Wood *et al.* 1988, Eberth 1996, Ryan *et al.* 2001).

Canyon Bone Bed

Canyon Bone Bed (Locality #456) is situated near the middle of the 260-km-wide Two Medicine coastal plain, at a paleolatitude at 48^{o} N (Habicht 1979), occurring in the topmost lithofacies of the formation (Horner *et al.* 2001, Rogers 1990). The other *Einiosaurus* bonebed in the study by Rogers (1990), Dino Ridge Quarry (Locality #373), was omitted from this study since this bonebed has few long bones from which to sample, and likely represents a separate population than that of Canyon Bone Bed, as is evident by stratigraphic data and differential modes of bone preservation (Rogers 1990). The sedimentary matrices of Canyon Bone Bed consist of poorly-sorted and angular clastic grains making up a massive, dark brown, organic-rich sandy siltstone (Sampson 1995a). Clay minerals, organic debris, and calcium carbonate are abundant, and the presence of freshwater bivalves and gastropods implies a shallow lake depositional environment (Rogers 1990).

Original bone histology is generally preserved, having been permineralized with calcium carbonate (Rogers 1990), though some bones are largely infilled by sandy sediment, and possible bacterial infiltration may have occurred. Most bones are flat-lying and fragmentary: dentaries often have no teeth, and limb bones are missing one or both

articular ends. Many bones from Canyon Bone Bed are differentially weathered - one bone surface is rough and the inner cancellous bone is exposed, while the other surface shows little indication of preburial cracking or exfoliation (stage 1 weathering; Behrensmeyer 1978), revealing that these bones experienced episodes of subaerial exposure (Rogers 1990). There is evidence of scavenging (or possibly predation) by the theropod dinosaur *Albertosaurus (Daspletosaurus)* as evidenced by tooth marks on bone as well as shed teeth, and also trampling of bone; however, borings by invertebrates have not been reported from specimens of Canyon Bone Bed (Rogers 1992). Skeletal lag elements are common and suggest that transport of skeletal elements was minimal, though the site is interpreted to be parautochthonous due to conspicuous evidence of reworking, particularly winnowing of the death assemblage by currents (*e.g.*, Voorhies 1969). This results in under-representation of some of the most common bones in a tetrapod skeleton – vertebrae, ribs, and phalanges (Rogers 1990), because these light and porous bones are more easily transported than cranial elements and limbs (Rogers 1990, Aslan and Behrensmeyer 1996).

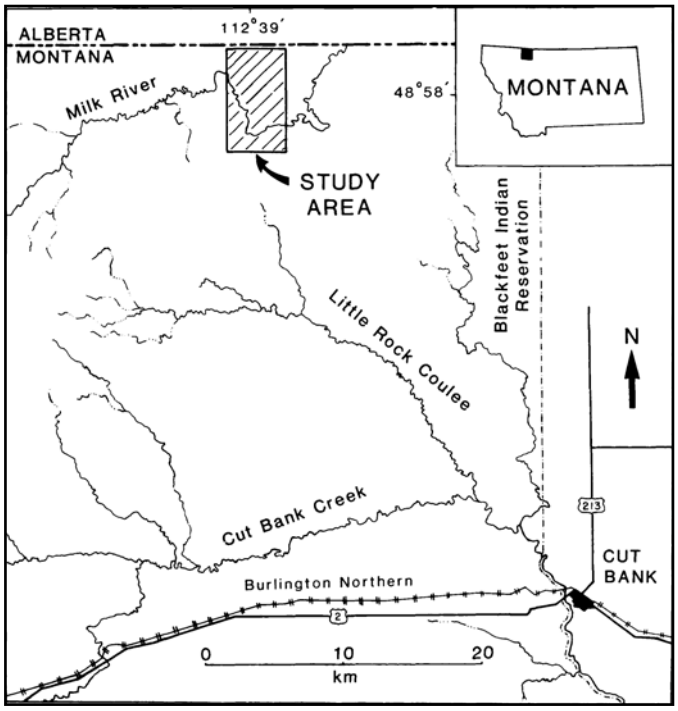

Figure 1: Location of the study area on the Blackfeet Indian Reservation, Glacier County, MT. From Rogers (1990), used with permission.

Canyon Bone Bed contains approximately 300 bones and bone fragments but only two skulls, and represents a MNI of seven specimens of *Einiosaurus* (six subadults and one juvenile, Rogers 1990). Paleoclimatic data, vicinity of the locality near caliche horizons, a "waterhole" and shallow lakes, suggest a drought-induced mortality for Canyon Bone Bed, indicating a population of individuals that lived and died together (Rogers 1990). It is hypothesized that *Einiosaurus* carcasses accumulated in a shallow, vegetated lake occupying an abandoned stream channel (Rogers 1990), after apparently congregating together in herds, family groups, or seasonal aggregates near persistent water sources, much as water-dependent taxa, such as elephants and wildebeest, do today (see DISCUSSION).

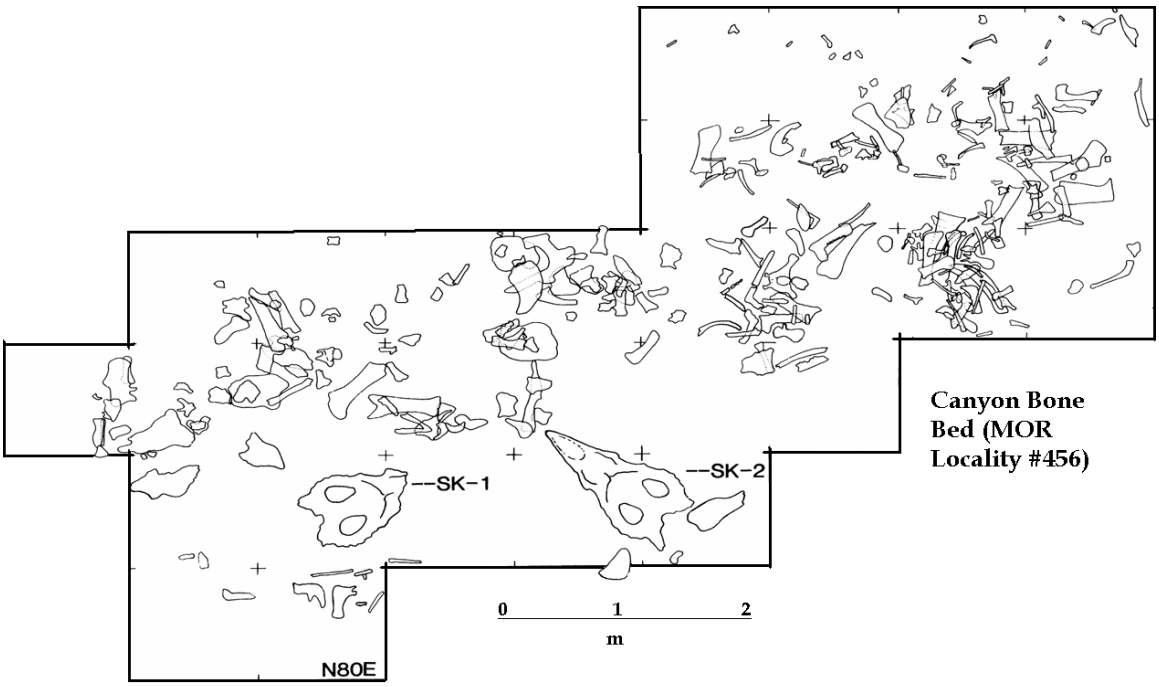

Figure 2: Canyon Bone Bed. Site map taken from Rogers (1990), used with permission.

Mass Mortality of Ceratopsid Dinosaurs

Bone Bed Assemblages

Numerous low-diversity bone beds representing mass death assemblages of ceratopsian dinosaurs occur in many North American Late Cretaceous strata, and have important implications for the behavior, ontogeny, and life history syndromes of animals contained within them. Bonebeds are widely recognized as accumulations of bones from several individuals that are concentrated along a bedding plane or throughout a single bed or facies (Eberth and Getty 2005). Bone bed assemblages are currently known for *Pachyrhinosaurus, Chasmosaurus, Centrosaurus, Styracosaurus, Einiosaurus,* and *Anchiceratops* (Tanke 1988, Ryan *et al.* 2001, Currie and Dodson 1984, Rogers 1990, Rogers and Sampson 1989), as well as *Triceratops* (Mathews *et al.* 2009). Historically,

centrosaurines are found in bonebeds with much more frequency than are chamsosaurines, allowing for interpretations of herd behavior in centrosaurines (Sampson *et al.* 1997, Mathews *et al.* 2009).

Mass mortality appears to have been recurrent in the Two Medicine ecosystem as well as the rest of the Judith River Group, and monodominant bone beds suggest that herds of dinosaurs were repeatedly subject to death by drought (Rogers 1990), volcanic ashfalls (Hooker 1987) or diseases such as botulism (Varricchio 1995). A bonebed in the Two Medicine Formation representing at least 3 *Daspletosaurus* specimens points to herding, and even pack-hunting behavior of these tyrannosaurids, as well as herding of the hadrosaurs on which it appears they were feeding (Currie *et al.* 2005). A monodominant mass death assemblage with a uniform taphonomic signature may be interpreted to be a coherent population of animals that lived and died together at the same time in the same place, and thus can allow for interpretations of dinosaur behavior (Ryan *et al.* 2001). Possible reasons for these aggregations include 1) reproduction (breeding sites and nesting) or parental care, 2) a response to resource availability such as water, particularly during a drought or other stress, and 3) social interaction, as in hunting packs, family groups, or herds (Brinkman *et al.* 2007). Many ceratopsid bone beds are hypothesized, based on taphonomic and paleoclimatic evidence as well as bonebed composition and age structure, to represent actual herds (Currie and Dodson 1984, Tanke 1988, Rogers and Sampson 1989, Rogers 1990, Ryan *et al.* 2001, Mathews *et al.* 2009). As it is understood among mammal biologists, since ungulates and other mammals are

often cited as behavioral comparisons for ceratopsids, “herds” are large, hierarchically organized, socially cohesive units (Geist 1977).

Since at least some species of ceratopsians appear to have lived in herds, evidence may be gathered that supports other herding behavior, such as migration. Ceratopsids apparently lived exclusively in western North America, particularly along the western shores of the Interior Cretaceous Seaway, and Campanian centrosaurines appear to have been geographically highly confined (Ryan *et al.* 2001). Ceratopsids have been found from as far north as the Northwest Territories and the North Slope of Alaska down to Mexico (Dodson *et al.* 2004), and so some have suggested ceratopsians, as well as their hadrosaur counterparts, may have been seasonally migratory (Currie 1983, Parrish *et al.* 1987, Paul 1997), though evidence to test this is largely lacking (Fiorillo and Gangloff 2001, Lehman 2001).

Evidence exists for parental care of some species of dinosaur (Horner and Makela 1979, see Carpenter *et al.* 1994 and Horner 2000 for reviews; Norell *et al.* 1995, Varricchio *et al.* 1997) including the basal ceratopsian *Psittacosaurus* (Meng *et al.* 2004, Qi *et al.* 2007); however, little has been published on to what extent the larger ceratopsids may have cared for their young. Several studies of varying taxa have noted that the association of juveniles and adults in either bonebeds or trackways indicates parental care, or at the very least protection within a herd (Forster 1990, Coria 1994, Lockley 1994, Lockley *et al.* 1994, Currie 1998, Myers and Fiorillo 2009).

Herd Behavior in Ceratopsids

Multiple monodominant ceratopsid bonebeds point toward gregarious behavior in this group of dinosaurs, and assemblages that contain juveniles as well as older animals that share similar taphonomic signatures indicate that the animals died together near the burial site (Brinkman *et al.* 2007). Because of the preponderance of such bonebeds, it is widely accepted that several species of ceratopsid formed mixed-sex, hierarchically structured herds, at least for part of the year (Sampson 2001), similar to many ungulate species (hooved herbivorous mammals) today. It has been suggested that patterns of taphonomy point more toward "infestations" of individuals, as seen today in crocodiles and tortoises (Lehman 1997), however, there is much taphonomic evidence that suggests that ceratopsid individuals indeed form herds. While the existence of a monodominant, mass-mortality assemblage itself should never be the sole evidence for as complex a behavior as herding (Brinkman *et al.* 2007), the fact that centrosaurines are commonly found in bonebeds while chasmosaurines almost never are indicates the possibility of herding in centrosaurines (Hunt and Farke, in press), though depositional environments and taphonomy must also be analyzed in each case. Also, among the centrosaurines, contemporaneous species are often segregated into separate bonebed accumulations which indicates either that these animals occupied taxon-specific habitats, or formed taxon-specific herds (Currie and Dodson 1984).

Aside from taphonomic studies, the most obvious indication that ceratopsids were gregarious is the presence of species-specific horns and frills (Horner 1988, Sampson *et al.* 1997), which suggests complex hierarchical behavior (Farlow and Dodson 1975).

Throughout the evolution of Ceratopsia, these structures become increasingly complex and ornate, indicating that adaptation to their habitat became less important than increasingly complex biological interactions (Lehman 2001). Among extant animals with features such as these, in almost every case these structures function primarily as secondary sexual features (mating signals) (Geist 1966, Farlow and Dodson 1975, Sampson and Ryan 1997, Sampson *et al.* 1997, Sampson 2001, Horner and Goodwin 2006) or cues for species recognition (Padian *et al.* 2004, Goodwin *et al.* 2006). The presence of these visual signals, as well as their postponed growth through ontogeny, indicates interspecific rank recognition in a hierarchical group as seen in extant ungulate herds (Currie and Dodson 1984, Horner 1988).

Sexual dimorphism has been postulated for several species of ceratopsian, and more potential evidence exists for sexual dimorphism in this group than in most other dinosaur groups (Chapman *et al.* 1997) due to the presence of this extravagant cranial ornamentation, correlative to many ungulate species today (Sampson 1995b). Despite the existence of these horns and frills, sexual dimorphism in the large-bodied ceratopsids is difficult to determine and thus far is virtually nonexistent. Dodson (1976) provides a comprehensive quantitative study of sexual dimorphism in the protoceratopsian *Protoceratops andrewsi*, and some cranial evidence may exist for dimorphism in *Pachyrhinosaurus* (Tanke 1988), *Chasmosaurus* (Godfrey and Holmes 1995), and has been suggested, and invalidated, in *Triceratops* (Lehman 1990, Ostrom and Wellnhofer 1990, Forster 1996). Thus far, however, it seems most likely that most ceratopsid species were monomorphic. This may also follow a trend seen among extant ungulates – sexual

dimorphism tends to be most extreme in mid-size taxa, such as *Protoceratops* (Dodson 1976) and somewhat reduced or even nonexistent in the largest species, such as *Triceratops* (Goodwin *et al.* 2006) and *Einiosaurus* (Sampson 2001).

Some statistical evidence suggests that the behavior of the hadrosaurs, often hypothesized along with ceratopsians to have lived in herds (Horner and Makela 1979, Currie 1983, Hooker 1987, Horner 1988, Horner *et al.* 2000) paralleled that of extant ungulates. The sexually monomorphic hadrosaurine hadrosaurs appear to have occupied an open habitat and exhibited gregarious behavior, similar to bison and zebras, while the sexually dimorphic lambeosaurine hadrosaurs lived in more closed habitats and tended to be somewhat solitary, like many deer (Carrano *et al.* 1999). This pattern can be extended to the ecologically-similar centrosaurines, and it may be inferred that monomorphic herbivore taxa frequently found in bonebeds, including *Einiosaurus*, also lived in herds.

In light of the evidence that some centrosaurines, including *Einiosaurus*, formed herds, a study that samples the bone histology across multiple age groups can further determine whether or not this population of *Einiosaurus* lived and died together in a coherent, hierarchically-ranked herd system. Population dynamics of the group can then be assessed, and survivorship of the species hypothesized.

METHODS AND MATERIALS

Specimens

Bones were sectioned from various growth stages include femora, humeri, and neural spines, but only tibiae (N = 16, see APPENDIX A) were used in age calculations because of their relative abundance, large range of sizes, and tendency to be better preserved in Canyon Bone Bed. Ribs, gastralia, and other bones of the axial skeleton have shown extensive remodeling and dense Haversian tissue (secondary osteons), obscuring LAGs (*pace* Erickson *et al.* 2004), and among long bones, tibiae may show even a lesser degree of remodeling (Horner *et al.* 1999 and 2000, Redelstorff and Sander 2009) and so have the best chance of preserving the most LAGs. LAGs, which occur only in primary bone, are an important indicator of age, and so the least amount of remodeling possible is desirable. However, it should be noted that in *Psittacosaurus*, a basal ceratopsian, the fibula has shown the best record of growth (Makovicky *et al.* 2006), but in Canyon Bone Bed, more delicate elements such as fibulae are poorly preserved and uncommon, and so were not sampled.

In Canyon Bone Bed, tibiae are common and have been preserved well enough to obtain an adequate sample size and a large range of sizes; in fact, long bones are over-represented in both *Einiosaurus* bonebeds (Rogers 1990). Periosteal bone growth occurs only in diaphyseal bone tissue, and because the epiphyses and metaphyses of several tibiae from this bonebed are missing, only areas near to or at the mid-diaphysis are studied (*e.g.* Reid 1997a, Padian *et al.* 2001, Rozenblut and Ogielska 2005).

Measurements of the mid-diaphysis circumference and total bone length were also taken, and were used along with LAGs recorded at this location as a method of assigning each bone to an age class, as the mid-diaphysis is least affected by remodeling (Chinsamy 1995). Estimates of individual body mass are not widely acknowledged as superior to length measurements and so were not performed (Ricqles *et al.* 2006, Lee 2007a), and since any error is then tripled in calculations, is avoided here where error due to potentially poor bone condition is imminent. Histological terminology is taken from Francillon-Vieillot *et al.* 1990.

Since no elements in Canyon Bone Bed are articulated and total length of any animal cannot be directly measured, each body length was calculated based on the estimated lengths of the tibiae used in this study. These calculations were derived from measurements and scale drawings of centrosaurine tibiae from several classic manuscripts (Lull 1933, Sternberg 1950, Langston 1975, etc.) and the authors' estimations of total body length, which in many cases, were directly measured from assembled skeletons. Error implicit in this indirect method of obtaining length may result from error in measurement, any anatomical differences between these centrosaurines and *Einiosaurus*, limb proportion changes during ontogeny, individual variation, and the use of measurements from composite skeletons.

The MNI of this study is 14 since it is probable that some similarly-sized tibiae may have belonged to the same animal. However, due to the incompleteness of several of the tibiae, left and right elements were not distinguished, but because very few bones are the same size as well as exhibit similar bone tissues (see RESULTS), the chances of

sampling two tibiae from the same individual is expected to be minimal. This study samples over half of all currently known *Einiosaurus* specimens and represents the full range of sizes available. The sample size is 16 and may indeed represent 16 individual animals.

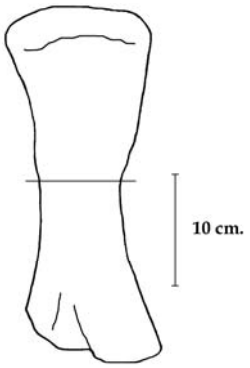

Figure 3: Cranial view of subadult left tibia of *Einiosaurus procurvicornis*.
Horizontal line indicates mid-diaphysis from where slides were taken from each tibia. See Appendix A for images of all whole tibiae.

Identification of Tibiae

This study utilizes 16 putative tibiae of *Einiosaurus procurvicornis* from Canyon Bone Bed. Because virtually all bones are missing articular ends, and some are only represented by the diaphysis (APPENDIX A), accurate identification of these elements is uncertain and is considered a source for potential error and discussed where relevant (see DISCUSSION). All elements in this study are certainly weight-bearing limb bones, and due to obvious, diagnostic features of the centrosaurine humerus and femur near the mid-diaphysis, these potential identifications are rejected as possibilities for the 16 bones used here. Humeri of centrosaurines, including those from Canyon Bone Bed, show a prominent deltopectoral crest that extends into the mid-diaphyseal region, and would be

present in even the partial elements used in this study. The fourth trochanter of centrosaurine femora is small, but occurs on the mid-diaphysis, and would also be visible on these bones, even if broken off as it is in some *Einiosaurus* femora (Reizner, *pers. ob*.). Smaller, thinner elements, such as fibulae and ulnae, exhibit proportions that are not at all similar to those seen in these putative tibiae. *Einiosaurus* tibiae appear to be "twisted" in cranial view, are roughly triangular in cross-section (though lateral compression by overburden is also a possibility), and are quite stout with greatly flaring metaphyses, and the bones used in this study generally fit that diagnosis. Nevertheless, bones that are questionable due to their taphonomic condition include MOR 456 T13, T14, and T15, which may be small enough to be *Einiosaurus* radii. However, histologically, these bones fit conservative expectations of age (*e.g.*, they are not outliers) from similarly-sized tibiae (MOR 456 T1 and T2), and so the influence of any possible misidentification is minimal.

Preparation of Histological Samples

Each bone was first photographed (APPENDIX A) and drawn. The bones were molded, either in their entirety or only the section being removed for thin-sectioning, and then cast so that the surface texture would be preserved. A silicone latex mold was used, covered by a plaster and fiberglass sheeting jacket for stability and protection while casting. The bones were then cut on a water-cooled Felker 41-AR tile saw with Norton diamond blades. A transverse section was taken from the mid-diaphysis of each bone whenever possible, and some sections were also taken from the slightly more proximal or distal ends. These chunks of bone were then cut further to an appropriate size for fitting

onto glass slides, while still retaining the entire cross-section in order to view growth lines in their entirety so as to ensure that they are indeed LAGs, in order to assess age as accurately as possible. The blocks were then embedded in Silmar polyester resin with catalyst, and vacuumed for 5 minutes for infiltration, and allowed to polymerize overnight under refrigeration with no vacuum.

Wafers of bone, approximately 5 mm thick, were then cut on the same tile saw. Penetrant/Stabilizer glue (PALEOBOND^{TM}) was used to coat the mounting side of the wafers, and resin was then used to stabilize this side. The mounting side was then ground to a 600-grit finish using an Ecomet 4 Grinder-Polisher (Buehler Ltd.) with silicon carbide abrasive papers (Buehler Ltd.). Prepared cut sections were then mounted onto frosted glass slides with Devcon^{TM} 5-Minute Epoxy. Mounted cut sections were then ground with silicon carbide papers of decreasing coarseness (60 to 600 grit) on an Ecomet 4 Grinder-Polisher in water. Finally, thin sections were polished using silicon carbide papers (800 and 1200 grit) and Buehler 5.0 micron aluminum oxide powder, until the desired optical contrast, and not a prescribed thickness, is reached (*e.g.* Ricqles and Bolt 1983, Wilson 1994). A Nikon Eclipse E600 POL microscope was used in this study to view the bone tissue (APPENDIX B).

Age Estimation of Remodeled Bone

In the cortex of these tibiae, the lines of slow or ceased growth that alternate between layers of fibrolamellar tissue deposition are called lines of arrested growth or LAGs. These LAGs in *Einiosaurus* exhibit a known, predictable pattern of occurrence where width of the zones between LAGs tends to diminish as the animal ages (*i.e.* LAGs become closer together toward the periosteal surface, see Figure 5). These lines are known to occur on an annual basis, since animals experienced slowed rates of growth as they age, and so are also referred to as annuli (Ricqles *et al.* 2006). One annulus plus one zone of fibrolamellar tissue represents one annual cycle, a hypothesis confirmed by testing of reptilian bones of known age (Castanet and Cheylan 1979, Hutton 1986). This alternating deposition of bone is seen among crocodiles and other ectotherms (Enlow 1969; Ricqles 1976 and 1980; Castanet and Cheylan 1979; Hutton 1986), as well as some endotherms (Horner *et al.* 1999), and shows seasonal cyclicity in bone deposition due to physiological stress caused by environmental fluctuations, such as climate (Varricchio 1997). Paleontological and sedimentological evidence suggests a seasonally wet/dry climate for this part of North America during the Campanian (Dodson 1971; Carpenter 1987; Jerzykiewcz and Sweet 1987; Rogers 1990) so seasonal cyclicity in bone deposition can be expected, however, since LAGs appear to be a plesiomorphic feature of tetrapods (Horner *et al.* 1999), they are frequently deposited in the absence of environmental stressors.

Figure 4 demonstrates how secondary osteons can begin to distort and obliterate LAGs. Secondary osteons are easily distinguishable from primary osteons – the former

having well-defined borders as well as being much larger, on average a diameter of around 0.16 mm in *Einiosaurus.*. In bones that exhibit abundant secondary osteons, it is known that at least one growth line can no longer be seen due to remodeling endosteally, where a growth line is seen in a younger bone that same diameter from the center (Chinsamy 1993, Horner *et al.* 2000, Cooper *et al.* 2008). This enables paleohistologists to determine how many LAGs were present before remodeling took place, and therefore get a more accurate count of LAGs and therefore a more accurate age of the bone.

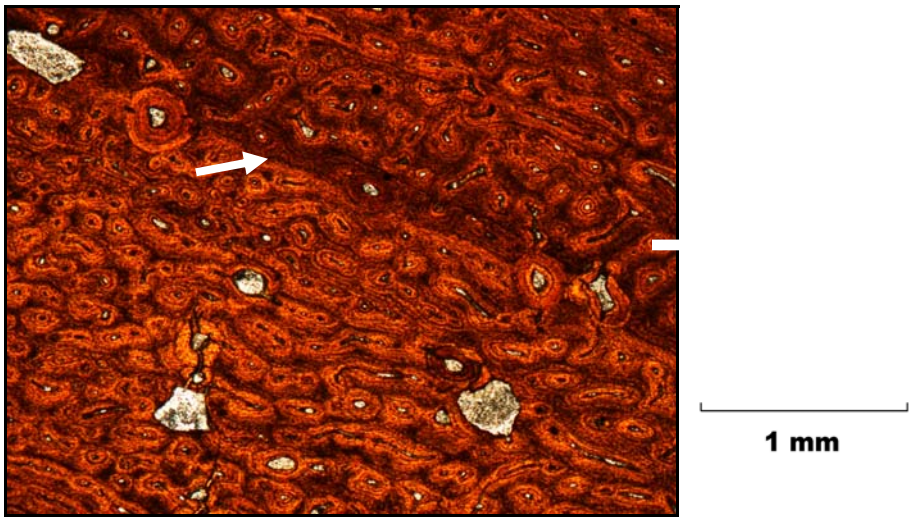

Figure 4: Tibia MOR 456 T9. Innermost LAG is indicated (arrow), and is being obliterated by secondary osteons. Mag. 40x.

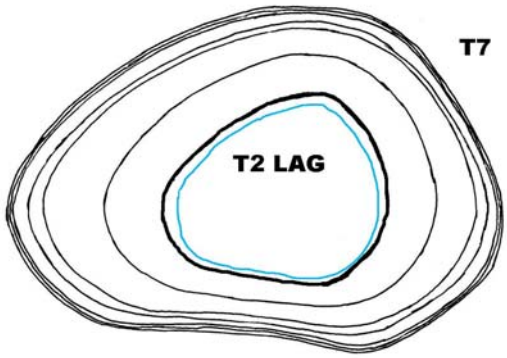

Figure 5: A transverse section of MOR 456 Tibia T2 (outlined in heavy black line) superimposed over MOR 456 T7, showing the diameter of the first (and only) LAG of T2 (blue line).
On T7, there is no LAG at this location, only extensive secondary remodeling that has apparently obscured a LAG (see Figure 4). T7 has 5 visible LAGs (thin lines), and so the total number of LAGs for T7 is 6.

Because some LAGs are obscured by remodeling, retrocalculations must be performed in order to more accurately age each bone by finding how many LAGs were originally in each bone. This was performed on bones that exhibited extensive secondary remodeling - only the largest *Einiosaurus* tibiae. The original number of LAGs, and therefore age, is estimated by using the circumference of smaller bones as they record their earliest LAGs, as a template for obliterated LAGs of large, remodeled bones (Figure 5, *e.g.* Chinsamy 1993). By using a young individual to locate the first LAG, it is then possible to construct an ontogenetic series that includes juveniles, subadults, and adults. This assumes only that all tibiae of *Einiosaurus* grew at relatively similar rates, though the rates of each may change throughout ontogeny. The estimated age for each bone then is the number of evident LAGs, with the addition of any remodeled LAGs.

DESCRIPTION OF HISTOLOGICAL SAMPLES

Bone Tissues

Transverse sections from the mid-diaphyses of *Einiosaurus* tibiae show a central medullary region, mostly infilled with sediment and somewhat damaged during diagenetic alteration, surrounded by a region of compact bone. This cortical tissue is concentrically stratified due to the deposition of zones that contain highly vascularized fibrolamellar tissue (Ricqles 1974) found in virtually all dinosaur species (Padian *et al.* 2001), and zones of somewhat avascular lamellated tissue, showing temporarily slowed or stopped growth, called LAGs (Figures 8, 9, 11, 13, 14; Ricqles 1974, 1980), and occur annually in *Einiosaurus* (see Age Estimation of Remodeled Bone) (Ricqles *et al.* 2006). The number of these LAGs increases with the size of the bone. LAGs are farther apart endosteally, becoming closer together toward the periosteal surface. All bones observed show this highly vascularized fibrolamellar tissue with largely longitudinally-oriented osteons.

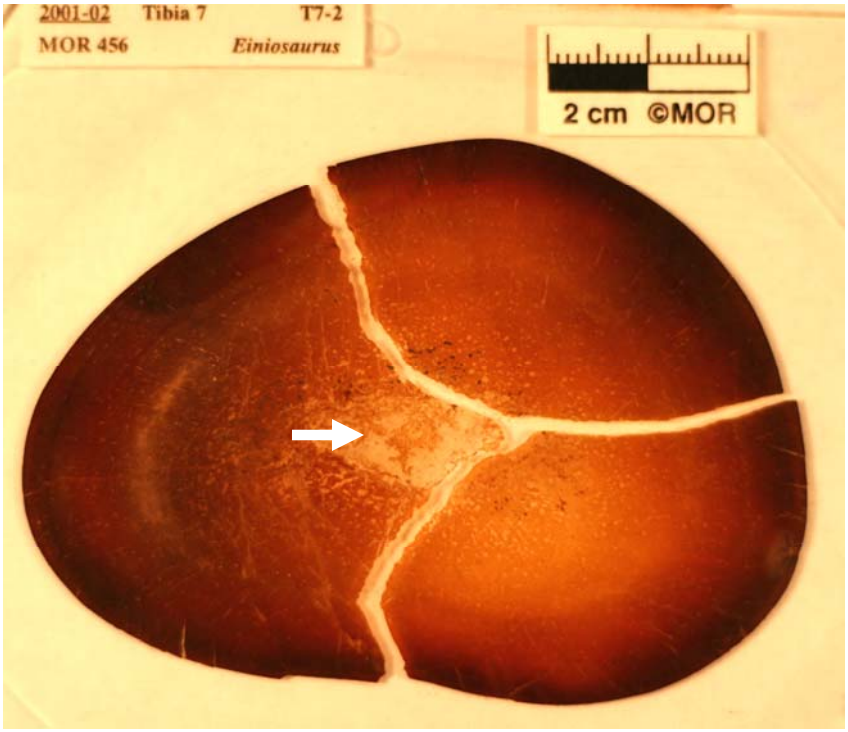

Figure 6: MOR 456 T7. Whole transverse slide of mid-diaphysis.
The medullary cavity, infilled with sediment, is seen (arrow) in this large subadult tibia of *Einiosaurus*. Large, radially-oriented cracks are diagenetic alteration of the bone – several tibiae were crushed or otherwise damaged, but original bone histology is spectacularly preserved. Entire scale bar = 2 cm.

Table 1. MOR 456 (*Einiosaurus procurvicornis*) tibiae.
* indicates that at least one LAG has been obliterated by remodeling and has been added to the visible LAG count (number in parentheses is visible LAG count).

Element	Museum Number	Circumference (cm)	Animal Length (m)	LAGs	Growth Stage
Tibia	MOR 456 – T1	19.0	1.60	0	Juvenile
Tibia	MOR 456 – T6	24.0	2.00	0	Juvenile
Tibia	MOR 456 – T13	26.0	2.30	0	Juvenile
Tibia	MOR 456 – T15	26.5	2.30	0	Juvenile
Tibia	MOR 456 – T2	22.5	1.85	1	Juvenile
Tibia	MOR 456 – T5	29.5	2.50	1	Juvenile
Tibia	MOR 456 – T14	23.5	2.10	1-2	Juvenile
Tibia	MOR 456 – T3	39.5	3.40	2	Subadult
Tibia	MOR 456 – T16	41.5	3.55	2-3	Subadult
Tibia	MOR 456 – T9	42.0	3.60	3	Subadult
Tibia	MOR 456 – T8	41.0	3.30	3-5	Subadult
Tibia	MOR 456 – T10	46.0	4.00	4	Subadult
Tibia	MOR 456 – T4	49.5	4.25	(3)5*	Subadult
Tibia	MOR 456 – T11	53.0	4.40	(3)5*	Subadult
Tibia	MOR 456 – T12	34.5	2.90	(4)6*	Subadult
Tibia	MOR 456 – T7	38.0	3.30	(5)6*	Subadult

Histological Changes Through Ontogeny

Juveniles

The youngest age class is relegated to bones exhibiting either 0 or 1 LAG, and like virtually all dinosaurs, exhibit fast-growing fibrolamellar bone (Figure 7). Some primary vascular canals are oriented longitudinally (Ricqles 1980), though most exhibit a simple reticular pattern, as is seen in juvenile *Psittacosaurus* (Erickson and Tumanova 2000). Some circumferential canals are also exhibited toward the periosteal surface, and a few bones in this class show localized radial canals, previously only seen in older adult ceratopsians and is considered rare (Figure 8; Erickson and Tumanova 2000, Lee 2006). Any radial canals found are not necessarily associated with the beginning of growth cycles, as has been found in *Centrosaurus* (Lee 2006), and only occur in any abundance in the fourth trochanter region of a subadult *Einiosaurus* femur (Reizner, *pers. obs.*). Well-developed primary osteons are arranged in a sub-laminar pattern, and virtually no secondary osteons are present, though some bones begin to show intracortical osteoclastic resorption cavities without lamellar infilling, called erosion rooms (Figure 9). No woven bone (Ricqles 1980) is seen in the juvenile bones, as has been found in *Apatosaurus* (Curry 1999), and one LAG is recorded before any remodeling occurs. This fibrolamellar tissue is highly vascular, and shows no localized zones of low vascularity. This group is represented by 7 individuals – almost half the entire sample, and the average mid-diaphyseal circumference of these tibiae is 24.4 cm, and average body length is 2.1 m (Table 1).

Figure 7: MOR 456 T6, < 1 year old. This bone exhibits no LAGs, and consists of entirely very young fibrolamellar bone made up of reticular and longitudinal osteons. Mag. 10x.

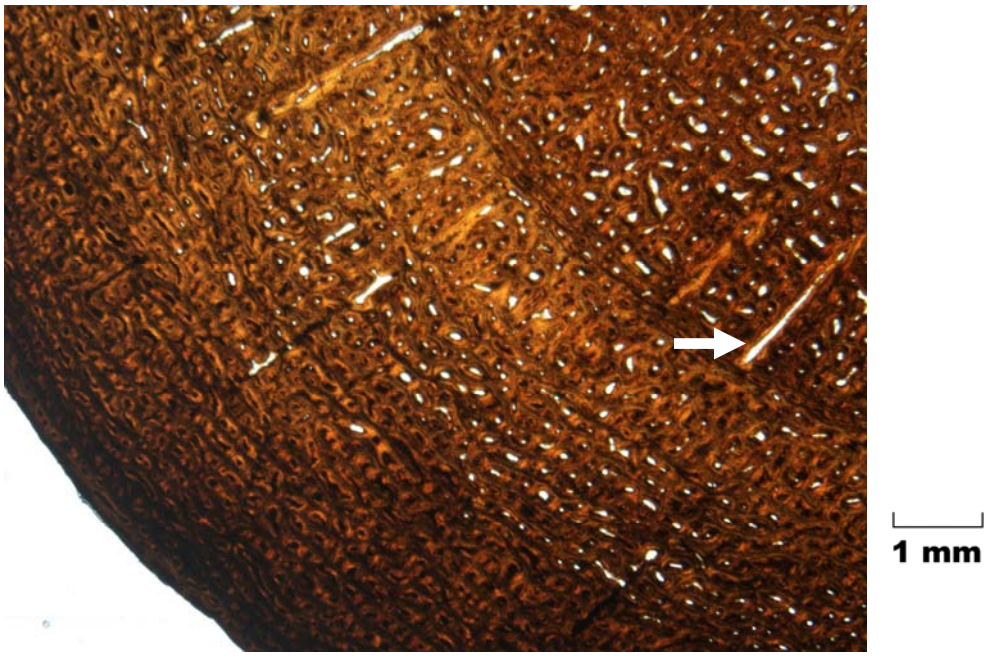

Figure 8: MOR 456 Tibia T2, >1 year old. Primary osteons are mostly reticular and longitudinal but some are radial (arrow). Mag. 10x.

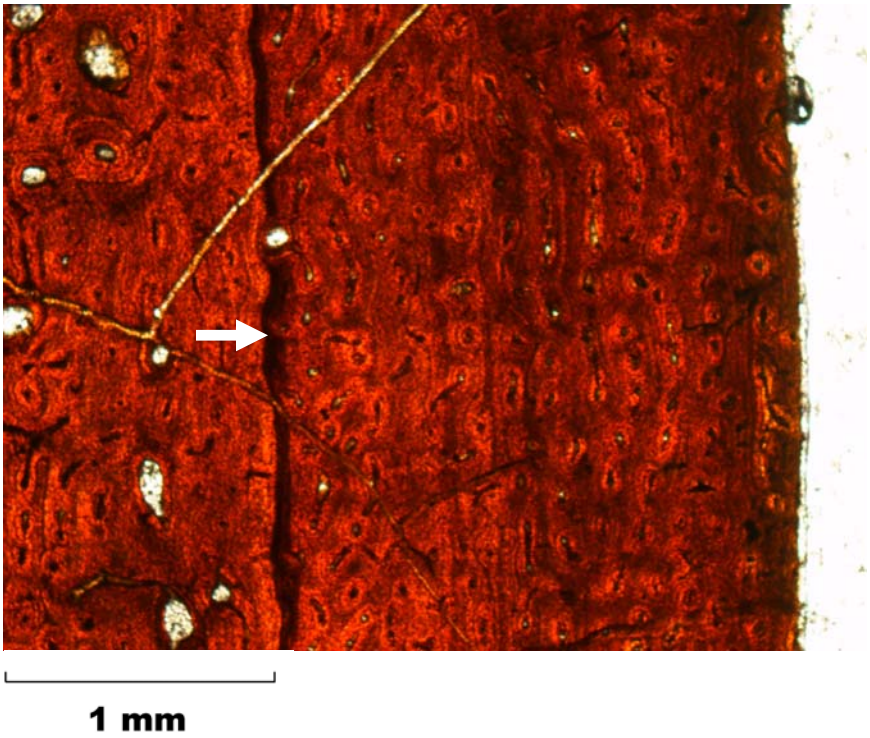

Figure 9: MOR 456 Tibia T14, >1-2 years old. 1 LAG is visible (arrow), as well as some erosion rooms and a few secondary osteons endosteally. Mag. 40x.

Subadults

Subadult tibiae have an average mid-diaphyseal circumference of 42.8 cm, and average body length of individuals is 3.6 m. Young subadult tibiae with 2 - 3 LAGs show some circumferential osteons toward the periosteal surface, as well as the very earliest stages of secondary remodeling, consisting of only a few secondary osteons spaced far apart. Remodeling in younger subadult tibiae (Figure 10) is only beginning to obliterate LAGs, hence none have yet been lost at this growth stage. However, an alternation of zones of differing degrees of vascularity is common toward the periosteum of some subadults, and indicates differing rates of growth as the animal gets closer to the attainment of adulthood (Figures 11 and 12). Secondary remodeling in the oldest tibiae requires the use of retrocalculation in order to locate any lost LAGs (Figure 15, Table 1).

Older subadult tibiae show 4 or more LAGs after retrocalculation, and consist of more circumferential osteons and somewhat more extensive secondary remodeling (Figure 13) and an increasing abundance of reticular vascular canals (Figure 14) (Ricqles 1974). However, there is fundamentally little difference between the bone tissues of "young subadult" versus "older subadult," and so these tibiae are grouped into the same category and will be referred to as "subadult" bones.

The bone tissue of larger subadults contains abundant secondary osteons, which begin to overlap one another but still do not develop the dense Haversian tissue seen in other species of dinosaur (*e.g.* Chinsamy 1995, Curry 1999, Horner *et al.* 1999 and 2000; *see* DISCUSSION). In adult dinosaurs, closely-spaced LAGs in the periphery of the cortex indicate cessation of growth, and is termed the external fundamental system, or EFS (Ricqles 1980). This distinctive tissue has been reported in various species of dinosaur (Chinsamy 1990, Varricchio 1993, Curry 1999, Horner *et al.* 1999 and 2000, Sander 2000, Erickson *et al.* 2004, Horner and Padian 2004, Sander and Klein 2005, Bybee *et al.* 2006, Sander *et al.* 2006, Knoll *et al.* 2009), however, is not seen in *Einiosaurus (see* DISCUSSION). Because these subadults are still rapidly growing, there is no significant change in bone tissue near the periosteum.

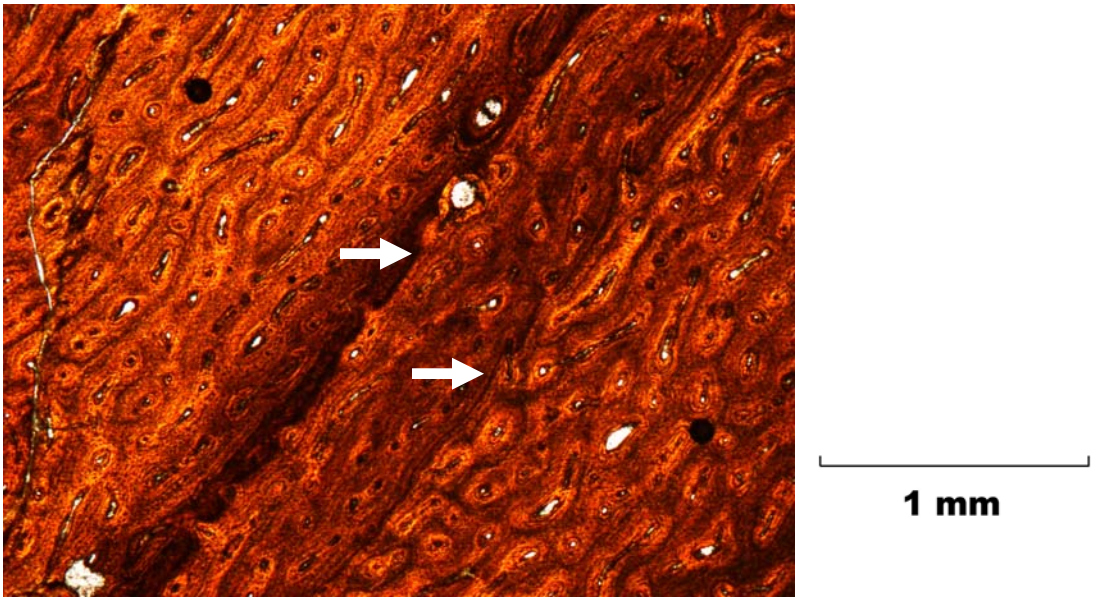

Figure 10: MOR 456 Tibia T9, >3 years old. 2 LAGs (arrows) and early stages of remodeling are seen. Periosteum is toward the right of image. Mag. 40x.

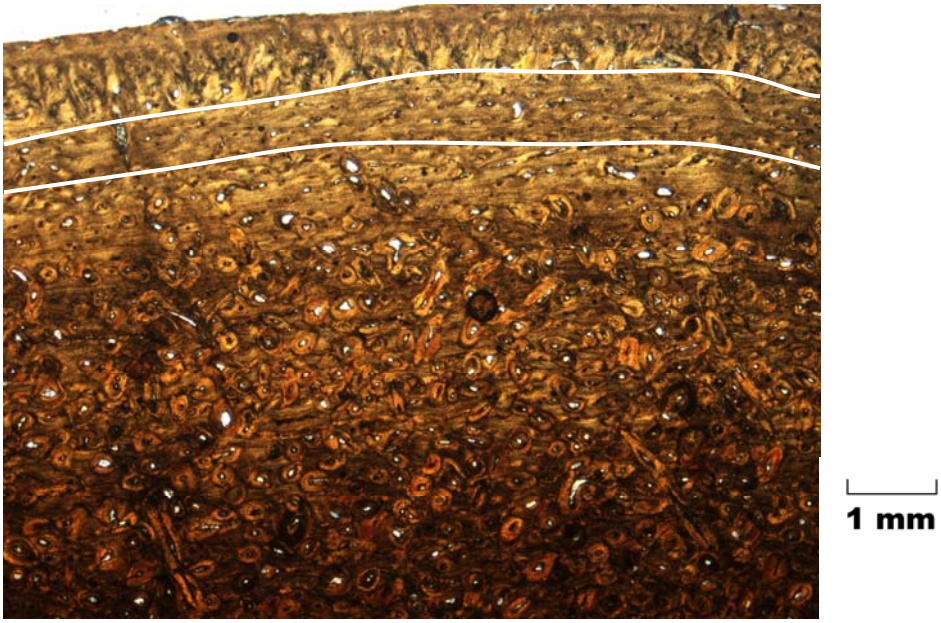

Figure 11: MOR 456 Tibia T16, >2-3 years old. Low vascularity layering is present (between white lines), but still does not resemble an EFS (external fundamental system) since it is followed by a higher vascularity zone periosteally. Mag. 10x.

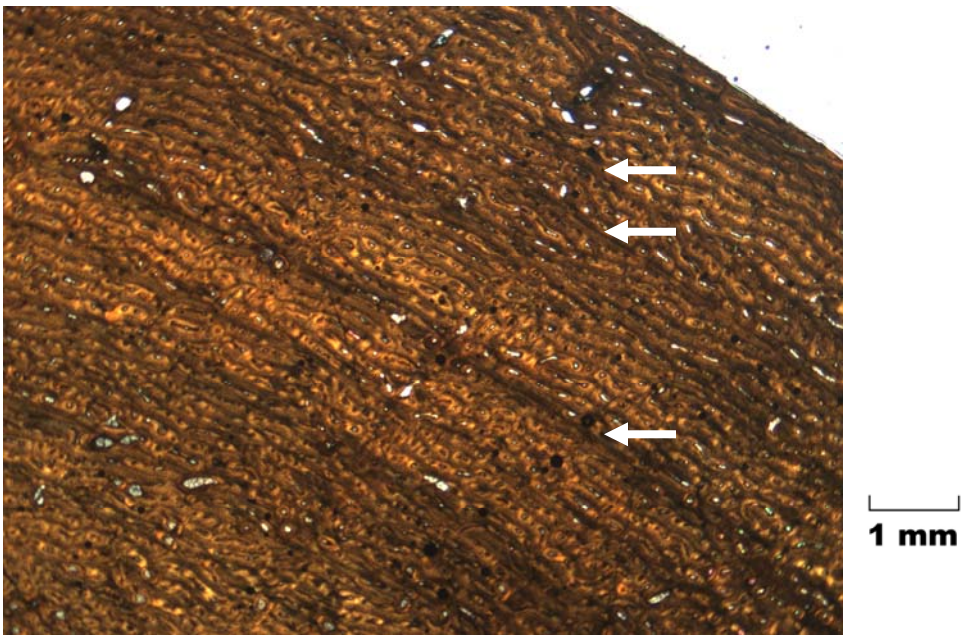

Figure 12: MOR 456 Tibia T10, >4 years old. Zones of somewhat differential growth are visible in this older, laminar bone tissue, and 3 LAGs are marked (arrows). Mag. 10x.

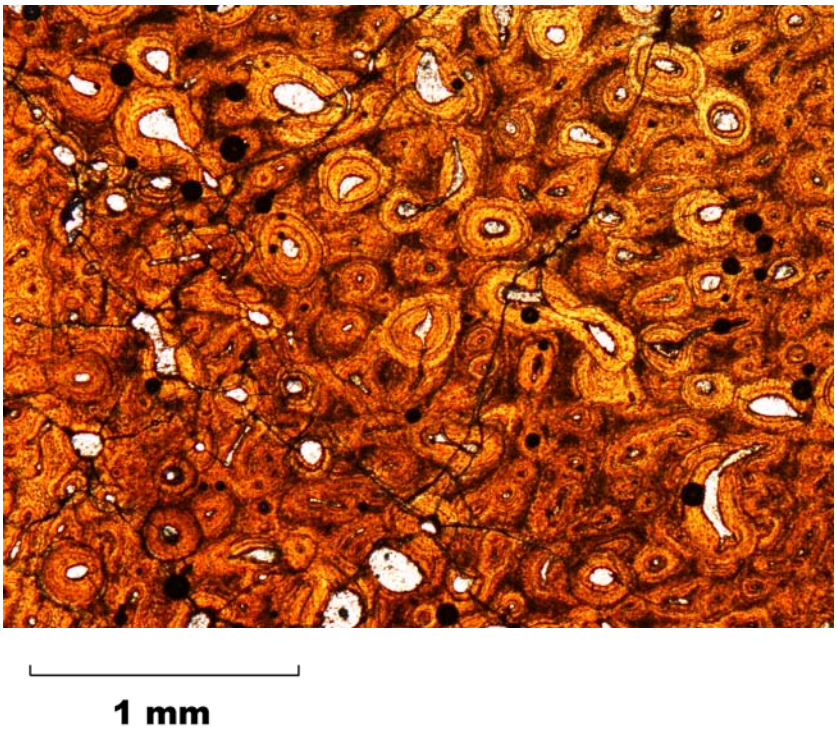

Figure 13: MOR 456 Tibia T10, >4 years old. The deep cortex has abundant secondary osteons and less interstitial tissue, however, few secondary osteons overlap. Mag. 40x.

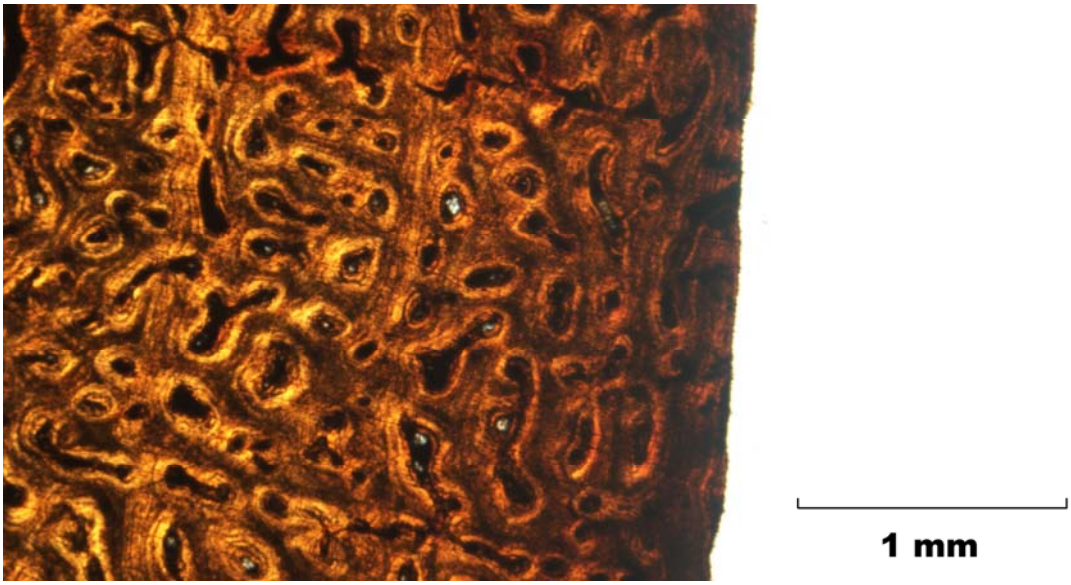

Figure 14: MOR 456 Tibia T12, >6 years old. Several reticular vascular canals are present near the periosteal surface. Mag. 40x.

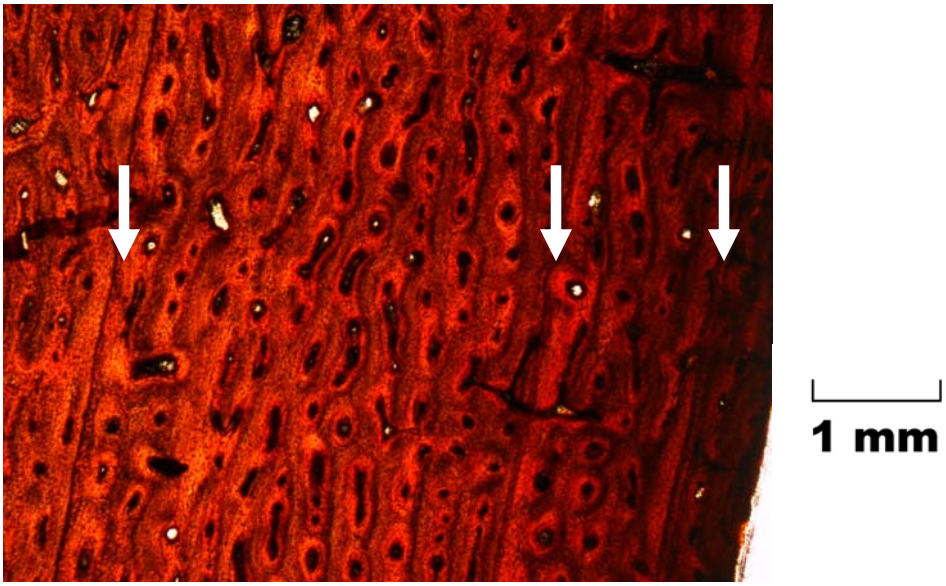

Figure 15: MOR 456 Tibia T7, > 6 years old. Tissue becomes less densely vascularized near the periosteum, though an EFS (External Fundamental System) is not seen. This bone exhibits 6 LAGs, 3 of which are identified by white arrows, but secondary remodeling is largely relegated to the deep cortex. Mag. 10x.

INTERPRETATION OF BONE TISSUES

Rate of Growth of *Einiosaurus*

Growth in *Einiosaurus* is, as expected, very similar to that of *Centrosaurus* (Lee 2007b). At 1 year of age, *Einiosaurus* had tibiae with circumferences of about 25 cm, which translates to an animal that is about 2.0 meters in length and has a mass of roughly 250 kg (Anderson *et al.* 1985, Seebacher 2001). Rate of growth appears to be highest until about 3 years of age. Without a LAG, growth from the time of hatching to 1 year of age can only be guessed, however, it has been suggested that centrosaurs doubled their size within the first year of life (Currie and Dodson 1984). Growth slows at around 2 years and begins to level off at around 3-4 years of age, implying possible reproductive maturity at that age (see DISCUSSION). Like the large theropods *Tyrannosaurus* and *Allosaurus* and ornithopod *Tenontosaurus* (Lee and Werning 2008) but unlike some smaller theropods (Deinonychosauria and Oviraptoridae, Erickson *et al.* 2007), *Einiosaurus* likely reached sexual maturity before full body size was attained. When somatic growth spans several years, as in *Einiosaurus*, reproductive maturity may tend to occur relatively early in life, a pattern seen in some large extant mammals (Lee and Werning 2008).

Some subadult tibiae exhibit zones representing varying growth rates near the periosteum (Figure 10). The low-vascularity zones are not LAGs, but are somewhat narrow (0.25 mm – 0.50 mm), layered zones that are indicative of slowed growth, and are bounded periosteally by a fibrolamellar zone indicative of higher growth rate. Because

low and high vascularity zones alternate, this is not the permanent cessation of growth that occurs with fully-grown animals, but instead indicates that growth may continue, albeit slowly, during seasonal conditions that may otherwise cause a LAG to form in younger individuals. Since this pattern is seen in only a few bones of only average size and age, it may simply be a result of individual variation or of differing growth patterns that are not seasonally influenced.

The oldest tibiae appear to be from animals of about 6 years old, though the specimens are of significantly different sizes (see DISCUSSION). The largest individual in this sample would have been around 4.4 meters in length, or roughly 2000 kg (Seebacher 2001). A power curve fits the growth of *Einiosaurus* most accurately and seems to imply indeterminate growth, and an EFS and other avascular tissue typical of very slow or stopped growth is not seen. Several previous studies have similarly found no evidence of cessation of growth and have interpreted that the species therefore experienced indeterminate growth (Chinsamy 1993 and 1995, Ray *et al.* 2005), however, this assumes that the studied material is indeed representative of all once-living age classes. The present study interprets the lack of fully adult material as evidence that not all age classes are represented, *i.e.* this bonebed does not exhibit full adults (*e.g.* Horner *et al.* 2009).

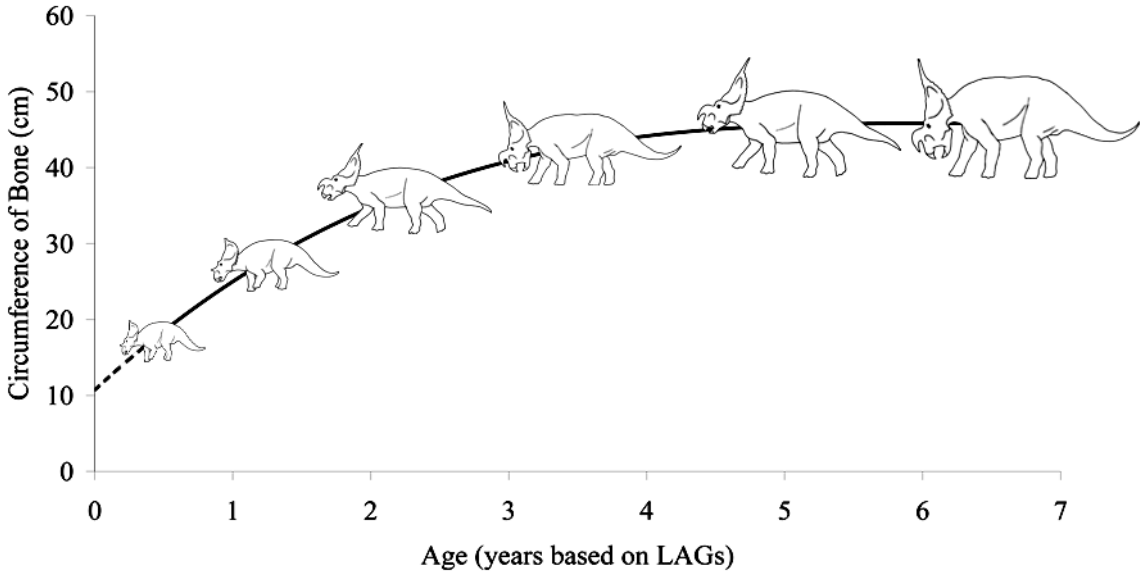

Figure 16: A growth curve of *Einiosaurus*, exhibiting relative somatic sizes correlated to age. Rate of growth is highest until about 2 years of age, and levels out at around 3 – 4 years, reflecting sexual maturity at this age. Rate of growth is unknown for neonates. The 6-year-olds in this population tend to be smaller than some 4- and 5-year-olds, resulting in a graph that actually declines rather than levels out, as this graph suggests, at 6 years of age. It is also possible that growth can continue for 6-year-olds.

Missing Age Classes

With a relatively small sample size (n = 16), it is expected that all age groups may be either underrepresented or overrepresented, or even altogether missing. There are several lines of evidence from the bone histology that reveal that this population of *Einiosaurus* shows taphonomic bias toward younger (but not the youngest) individuals, and it appears that an aged, or even fully mature adult has not yet been found.

First, babies appear to be missing. This bonebed contains four individuals that were less than one year old at their time of death, however, they are already over 1.5 m in length, which is indicative of very rapid growth rates as neonates (Currie and Dodson 1984, Lockley 1994) since newly-hatched ceratopsids were likely much smaller than this.

However, it is also possible that extremely rapid rates of growth may prohibit the formation of a LAG, which requires cessation of growth, during the first year of life. Because this juvenile bone tissue has switched from largely longitudinal osteons to simple reticular osteons, as is seen in post-neonate (2 - 4 years of age) *Psittacosaurus* (Erickson and Tumanova 2000), the neonate stage in *Einiosaurus* has been passed, in these youngest individuals from Canyon Bone Bed. These individuals also have well-ossified articular ends of long bones, and so are not "nestlings," if indeed ceratopsids used nests, and can likely move with the herd (Horner and Currie 1994).

A class between the defined juveniles and subadults is also not present: there is a significant gap between animals of about 1 and 2 years of age. Within this age range, there are no tibiae with mid-diaphyseal circumferences between 29.5 cm and 39.5 cm – a significant gap. (MOR 456 T12 is a subadult tibia of only 34.5 cm in circumference, but since it is evidently 6 years old, it could not exist in this missing age class of 1- to 2-year-olds, and belonged to a particularly small, older individual.) The explanation for this missing class may be taphonomic, however, this could also indicate at least two distinct age classes (see DISCUSSION).

Adults are missing from this sample of *Einiosaurus* specimens. While sexual maturity in this study is determined by the apparent slowing of growth and is expected to precede skeletal maturity (Lee and Werning 2008), a mature adult in this study is designated as one who has experienced almost complete cessation of growth and exhibits bone tissues that reflect this, such as dense Haversian tissue and an external fundamental system (EFS) in the periphery of long bones. Lee (2006) found that the closely-related

Centrosaurus reached skeletal maturity at around 6 years of age, but 6-year-old *Einiosaurus* do not exhibit these bone tissues diagnostic of adults. A very large femur that was also sectioned but not included in age calculations also does not exhibit adult tissue (Reizner, *pers. ob*.).

Dense Haversian tissue is reported from several species of dinosaur (Chinsamy 1995, Curry 1999, Horner *et al.* 1999 and 2000) and is considered an adult characteristic of many tetrapods. In the largest tibiae of *Einiosaurus*, remodeling is much more extensive in the inner cortex (Figure 12), though still does not develop dense Haversian tissue – very few, if any, secondary osteons overlap, indicating that even the oldest individuals were still growing relatively rapidly at the time of their death.

Some reticular vascular canals are noted in the largest *Einiosaurus* tibiae, particularly in the thickest tibia, T12 (Figure 13), toward the periosteal surface, and densely vascularized reticular tissue is associated with relatively rapid growth (Francillon-Vieillot *et al.* 1990, Castanet *et al.* 2000). Erickson and Tumanova (2000) found reticular canals appearing in the outer cortex of rather young *Psittacosaurus mongoliensis*, with older individuals exhibiting almost entirely reticular tissue, however, this predominance of reticular tissue is not seen in *Einiosaurus*. If we expect similar ontogenetic changes in bone structure within Ceratopsia, it can be inferred that the largest *Einiosaurus* tibiae in this study are of similar stage of development as subadult *Psittacosaurus*.

Older specimens of *Troodon formosus* exhibit subperiosteal avascular lamellar tissue, in conjunction with several growth lines (Varricchio 1993); however, no avascular

tissue near the periosteal surface is seen at all in *Einiosaurus*. Also, no external fundamental system, or EFS, as is found in old adults where growth has slowed considerably, (Horner *et al.* 2000) is seen in *Einiosaurus.* The oldest individuals in this study appear to still be growing at their time of death, and the lack of dense Haversian tissue, an EFS, and avascular areas indicates that these specimens may not represent very old individuals (*e.g.* Erickson and Tumanova 2000).

In Chinsamy's (1993) growth study on *Massospondylus*, the apparent continuous growth of *Massospondylus* and the absence of an EFS are interpreted as evidence that this species experienced indeterminate growth (*but see* Lehman 2007) – an admitted peculiarity among dinosaurs. The present study of *Einiosaurus* instead interprets this relatively continuous growth and lack of diagnostic mature bone tissue as evidence that very old individuals simply were not part of the sample, and the bonebed is biased toward younger animals. From this study, it cannot be said whether or not *Einiosaurus* experienced indeterminate growth (*see* Lee 2007a, Horner *et al.* 2009).

By extrapolating the slowed growth rate of 6-year-olds in this sample, it appears as though an EFS would have begun to form when the animal reached 8 years of age, implying full adult status at this age. Due to considerable individual variation among older subadults in this sample (Table 1, see Individual Variation below), potential full adult size is more difficult to obtain but is estimated at between 4.25 – 4.75 m in length, making *Einiosaurus* a relatively small-bodied centrosaurine species even once full-grown. Due to the difficulty in counting LAGs that make up an EFS in dinosaurs that exhibit them, the potential number of LAGs in a hypothetical *Einiosaurus* EFS cannot be

readily estimated, and so any estimate of longevity in this species will contain an unacceptable amount of error.

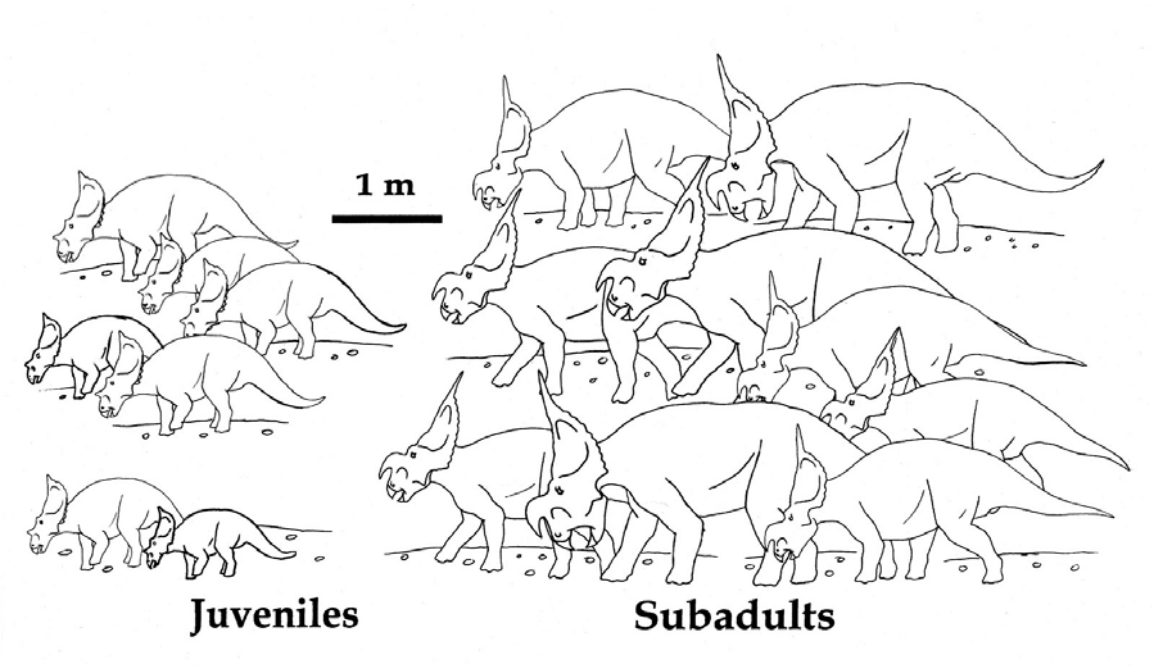

Figure 17: The population of *Einiosaurus* from Canyon Bone Bed, using body length estimates from Table 1. Two relatively distinct age classes are noted between juveniles and subadults, and among subadults of different ages, there is considerable but gradational size variation.

DISCUSSION

Research Implications

Through the study of bone histology, it has been determined that this assemblage of *Einiosaurus* specimens does not represent fully mature individuals. All animals were still growing at a significant rate at the time of their death, and the oldest in this study are still subadults. Whether sexual maturity has been reached at this point is unclear (see below), but skeletal maturity certainly has not. While the absence of an age group is not surprising for a study that utilizes only 16 samples, it has important implications for methods of age determination, as well as species validity of *Einiosaurus procurvicornis* and related, contemporaneous taxa.

Surface texture of *Einiosaurus* limb bones allegedly represents that of adults (Sampson *et al.* 1997), however, the utility of surface texture of dinosaur bone is much more reliable in juveniles than in older individuals (Tumarkin-Deratzian 2009). This study, where the histology indicates that only subadult long bones have been found, lends support to the hypothesis that a diagnostic method has not yet been found for determining adult status from long bone surface texture.

Since material (16 tibiae, and some femora and humeri (Reizner, *pers. obs.*) found thus far in Canyon Bone Bed are those of juveniles and subadults, it may be inferred that the putatively adult skulls of *Einiosaurus* are also only of subadult age. Additionally, sections of parietal spikes of an "adult" *Einiosaurus* skull indeed exhibit metaplastic, immature tissue (JR Horner, *pers. com.* 2010). This leads to questions of taxonomic

validity of *Einiosaurus*, and helps to clarify studies of cranial ontogeny in ceratopsids, and of dinosaurian growth rates in general.

The morphology of cranial structures changes dramatically throughout ontogeny in several species of ceratopsid (Horner and Goodwin 2006, Sampson 1995, Sampson *et al.* 1997), as well as other, putatively gregarious dinosaur taxa, particularly hadrosaurs (Dodson 1975, Gallagher 1995, Evans *et al.* 2005), while also being the primary criterion paleontologists use in naming new taxa. This has historically been problematic and has resulted in several *nomina dubia* as taxonomy is resolved, such as *Brachyceratops montanensis* and *Monoclonius crassus* (Dodson 1990, Sampson *et al.* 1997, Ryan 2006, Tumarkin-Deratzian 2009), both of which were described largely by typically juvenile characters. Because these secondarily sexual characters frequently develop late in ontogeny, particularly in taxa that form hierarchical groups, juveniles and subadults of separate species are often very similar and have generalized, non-ornamented skulls and few diagnostic characters (Sampson *et al.* 1997, Ryan *et al.* 2001). It has therefore been suggested that some centrosaurines may be referable to one another. Since it is difficult to accurately identify species that exhibit many growth-related features (Evans *et al.* 2005), the fact that no fully adult *Einiosaurus procurvicornis* specimens have thus far been reported opens up the possibility of this taxon being referable to another time-equivalent, geographically northern centrosaurine genus (*e.g.* Horner *et al.* 2009), such as *Styracosaurus* or *"Monoclonius."*

It has also been noted that the supraorbital horncores of several centrosaurine species, including *Einiosaurus*, ontogenetically become lower, more rounded, and even

concave as mature adulthood is reached (Sampson *et al.* 1997), though the reasons for this seeming resorption of bone are unknown. The holotype skull of *Einiosaurus* (MOR 456 8-9-6-1) indicates this as well, though *Einiosaurus* generally retains a more juvenile or subadult morph of supraorbital horncore than do other centrosaurine adults (Sampson *et al.* 1997) – this is perhaps because all present *Einiosaurus* specimens are in fact juveniles or subadults; indeed, *Einiosaurus* "adults" exhibit more subadult proportions of the parietal as well (Sampson *et al.* 1997). Study of craniofacial ontogenetic patterns and taxonomy of centrosaurines will have more clarity if relative growth stages of *Einiosaurus* and others are better known through bone histology.

From the bone histology, it is evident that *Einiosaurus* grew at a rate comparable to other relatively large-bodied ornithischians (*Hypacrosaurus*, Horner *et al.* 1999, *Maiasaura*, Horner *et al.* 2000, and *Centrosaurus*, Lee 2007b), reaching sexual maturity at around 3-5 years, and full adult size at upwards of 6 years. This contrasts markedly with Lehman's (2006) report of *Chasmosaurus mariscalensis*, a large ceratopsid, requiring 20 years to reach sexual maturity and 60 years for skeletal maturity. Lehman's study utilizes a model of reptilian growth dynamics using estimated masses of *Chasmosaurus* to achieve these numbers, and not bone histology. Incidentally, Lehman's model elephant growth curve for Chasmosaurus, with sexual maturity at 5 years, fits histological data for *Einiosaurus* (and *Centrosaurus*, Lee 2007a) much better. Since many studies have demonstrated that LAGs are indeed annual (*e.g.*, Castanet and Cheylan 1979), bone histology is presently the best accepted method with which to

generate growth curves of extinct animals, and can allow paleontologists to create better, more taxon-specific models with which to assess growth.

Population Dynamics

Sexual Maturity

Since somatic growth is highest until age 3, and slows greatly at that point, sexual maturity may occur as young as 3 years of age. Though it has not been unequivocally shown that reproductive age can generally be directly observed in the bone histology (Chinsamy-Turan 2005, Erickson 2005), studies on extant tetrapods show that a decrease in growth rate is often correlated to sexual maturity (Ricqles *et al.* 1991, Sander 2000, Erickson *et al.* 2007, Lee and Werning 2008), and is also demonstrated by the rare presence of medullary tissue (Schweitzer *et al.* 2005). Three years to sexual maturity appears comparatively young for a medium-bodied dinosaur (*e.g.* Erickson and Tumanova 2000). The hadrosaurs *Hypacrosaurus* and *Maiasaura* (Horner *et al.* 1999 and 2000) are interpreted to have been among the fastest-growing dinosaurs, requiring only 1-2 years to reach a subadult length of 3.5 m (8 years to reach a full size of 7 m), and *Einiosaurus* grew at a similar rate. However, more closely related and much smaller taxa, *Psittacosaurus mongoliensis* and *Psittacosaurus lujiatunensis*, required 8-10 years to reach somatic maturity of only 20-25 kg (Erickson and Tumanova 2000, Erickson *et al.* 2009), however, comparison with studies that utilize mass rather than length may lead to error in interpretations of *Einiosaurus* growth. While the attainment of sexual maturity in ceratopsians may better be determined from ontogenetic changes in cranial ornamentation (Horner and Goodwin 2006), diminished growth rate indicates that sexual

maturity in *Einiosaurus* occurred at a minimum of 3 years of age, and likely closer to 5 years. As expected from dinosaurs (Lee and Werning 2008), sexual maturity is likely reached before skeletal maturity in *Einiosaurus,* however, reproductive activity in *Einiosaurus* cannot be directly observed and so is unknown. Because an EFS is laid down after attaining sexual maturity (Varricchio 1993), perhaps shortly after, and no *Einiosaurus* specimens exhibit an EFS, age at sexual maturity in *Einiosaurus* may not have occurred until the age of the oldest subadults in this sample, which are 6 years old.

Seasonal Breeding

A reproductive pattern seen in extant ungulates and many other gregarious animals is a specific "breeding season," and even in fossils, seasonal breeding in an extinct taxon is inferred from discrete partitioning of age classes (Kurten 1953, Qi *et al.* 2007, Redelstorff and Sander 2009). This is not seen in a closely-related centrosaurine, *Centrosaurus* (Ryan *et al.* 2001), but it is indicated by this sample of *Einiosaurus*. The division of tibiae into two size-distinct age classes - juveniles and subadults – may indicate a gap in breeding times, as in extant ungulates and other animals that give birth during seasonally optimal conditions for their survival. While there is some overlap among animals less than 2 years old, the largest juvenile (MOR 456 T5, mid-diaphyseal circumference = 29.5 cm) is significantly smaller than the smallest closely-aged subadult (MOR 456 T3, mid-diaphyseal circumference = 39.5 cm). Within subadults of differing ages, there is no significant distinction in size, in fact, in this sample, some of the oldest individuals are smaller than those a year or two younger (Table 1, see caption for Figure

16), implying that individual or gender variation obscures further designation of age classes (*e.g.* Varricchio and Horner 1993).

Individual Variation

Skeletal size of *Einiosaurus* does not correlate precisely with age (Table 1, Figure 16). MOR 456 T7 shows the most LAGs before retrocalculation (5), yet is only 38.0 cm in length – shorter even than T3, which shows only 2 LAGs. T12 is one of the oldest bones and exhibits some of the oldest tissue types of all the specimens (Figure 13), but is the smallest subadult bone. Individuals whose tibiae exhibit 6 LAGs tend to be no larger, on average, than individuals whose tibiae exhibit somewhat fewer LAGs, and this could be due to error implicit in retrocalculation, measurement, bone length estimate (many articular ends of long bones are missing), element misidentification, taphonomic bias, or the biases associated with a single-element study. Other studies have shown animal size to correlate closely to bone histology (Erickson and Tumanova 2000, Erickson *et al.* 2001 and 2004, Bybee *et al.* 2006), however, in *Einiosaurus*, there appears to be some variability (*e.g.* Horner and Padian 2004).

Several dinosaur species are interpreted to exhibit developmental plasticity - the ability to completely stop growth when conditions are not favorable - when a poor correlation between size and age is evident. This pattern is found in the prosauropod *Plateosaurus*, and is considered plesiomorphic for archosaurs (Sander and Klein 2005), occurring in crocodiles and other extant reptiles, and it may also be found in some birds (Starck and Chinsamy 2002). The degree of variation between individuals of the same age in *Einiosaurus* is much less than for *Plateosaurus*, so a similar degree of

developmental plasticity is not here hypothesized for *Einiosaurus*. However, the presence of LAGs themselves may indicate a high degree of developmental plasticity (Starck and Chinsamy 2002).

Sexual dimorphism can be hypothesized to explain this variability in *Einiosaurus*, though sexual dimorphism in any species of ceratopsid has not yet been unequivocally demonstrated (Sampson *et al.* 1997, Dodson *et al.* 2004) and may be limited to facial ornamentation rather than body size (Dodson *et al.* 2004). The nasal horncore of *Einiosaurus* demonstrates dimorphism, having both a small erect form, and a large procurved form (Sampson 1995a), though whether these disassociated elements are sexually dimorphic, based on ontogenetic stages (Sampson *et al.* 1997, Horner and Goodwin 2006, Mathews *et al.* 2009), or even anagenesis (Horner *et al.* 1992), is unknown. Also, any degree of sexual dimorphism would be difficult to determine in *Einiosaurus*, as it is represented by so little cranial material. In closely-related *Centrosaurus*, several intermediate gradations are seen between very different nasal horn orientations (Ryan *et al.* 2001); this gradation would likely not be evident in a sample of only 3 putatively adult skulls, as in *Einiosaurus* (Sampson and Ryan 1997), and so sexually dimorphic forms may erroneously be identified. Without reproductive female-specific medullary tissue (Schweitzer *et al.* 2005) or perimedullary, osteoporotic cavities (Chinsamy 1990), it may be impossible to definitively identify females of a species, and this sample of *Einiosaurus* does not exhibit any of these tissue types. Without a larger sample size, sexual dimorphism in *Einiosaurus* remains speculative and, considering the lack of evidence for dimorphism in its closest relatives, such as *Centrosaurus*, unlikely.

This study concludes that intraspecific variability may be the most parsimonious explanation (*e.g.* Sampson 2001, Redelstorff and Sander 2009) since, to date, there has been no convincing evidence of body size dimorphism in ceratopsids (despite the presence of it in both crocodilians and birds), and the degree of variability seen in *Einiosaurus* is no more than can be expected from normal populational variation.

Patterns of tissue deposition also differ between bones of similar growth stage. In a few individuals growth appears to fluctuate, as evidenced by alternating layers of differing vascularity near the periosteum (MOR 456 Tibia 16, Figure 10). Instead of forming narrow, low vascularity LAGs, a low vascularity "zone" of significant width is laid down instead, and is then followed by higher vascularity tissue. The high-vascularity periosteal tissue may be the very beginnings of radial canals (Lee 2006), but radial canals are not prevalent in other 2- to 3-year-old tibiae of *Einiosaurus*. This pattern of alternating tissue types may reflect the same seasonality that forms LAGs in younger individuals, but indicates that growth during the non-optimal season (*i.e.*, winter), does not always cause growth to temporarily cease. If LAGs are not always formed annually, their utility as accurate age determination indicators may be limited. This may only be relevant in certain paleoclimates – even more seasonally varying environments than that of the Two Medicine Formation may always cause LAG formation in all individuals. This potential trend of variability in skeletochronology may also be limited to taxa or even to individuals (*e.g.*, Horner *et al.* 1999). However, since only some (average-sized and average-aged) bones in this sample exhibit this variation in tissue type, this study hypothesizes it to be a result of individual variation.

Survivorship

The individuals of Canyon Bone Bed died from drought (Rogers 1990), and the bias of this bonebed toward subadults and juveniles is typical of drought-induced mass kills (Shipman 1975, Conybeare and Haynes 1984, Gates 2005). Age-specific (and sex-specific) mortality is often reported from modern drought assemblages, because immature animals are more susceptible to water stress (Voorhies 1969, Hillman and Hillman 1977, Conybeare and Haynes 1984, Rogers 1990). One notable example of extant ungulate-like behavior in *Einiosaurus* is the paucispecific status of Canyon Bone Bed itself. As well as herding behavior, this is evidence for interspecific aggression and territorial behavior around a dwindling water source, which is often seen in extant animals where concomitant use of a waterhole is avoided, and large species frequently drive away smaller species (Farlow and Dodson 1975, Rogers 1990). Dinosaurs of the seasonally arid Two Medicine Formation likely had to engage in effective territorial defense frequently.

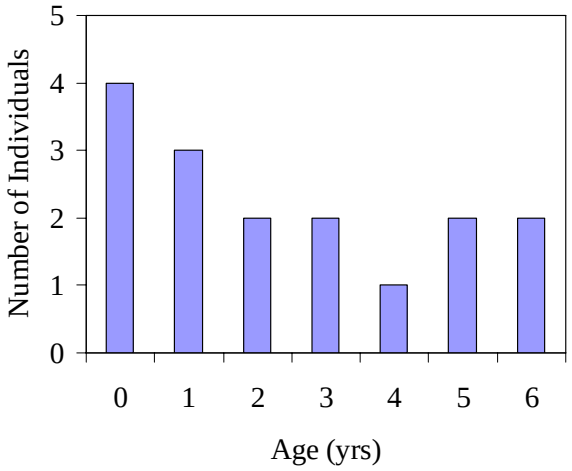

Figure 18: Demography of the Canyon Bone Bed population of *Einiosaurus*.

Therefore, this mass death assemblage of horned dinosaurs is a “snapshot” of a standing crop of animals, representing several age groups. Life tables, the foundation of population analyses in ecology (Deevey 1947), of the species can be deduced (Erickson *et al.* 2006). Reconstructing life tables requires accurately assessing age of individuals from a large, randomly sampled, stable population - rarely does this occur with extinct taxa. This sample of *Einiosaurus* is quite small (n=16), represents a drought assemblage which is a highly selective (non-random) cause of death and is the most likely cause for exclusion of adults from this sample, exhibits a considerable degree of taphonomic bias, and stability of the once-living population is unknown. Despite this, a demographic chart for *Einiosaurus* shares characteristics with that of *Psittacosaurus lujiatunensis*, which is represented by 80 articulated individuals killed by a relatively nonselective event – a lahar (Erickson *et al.* 2009). Since a survivorship curve of this *Einiosaurus* population fits conservative expectations for a medium-large dinosaur (Erickson *et al.* 2006 and 2009), biases may indeed be minimal but are acknowledged and discussed where relevant.

The relatively randomly-sampled population of *Psittacosaurus lujiatunensis* represents the sigmoidal Type B_1 survivorship pattern (a combination of Deevey Type I and III survivorship, Pearl and Miner 1935). This pattern is characterized by very high death rates early in ontogeny, which decrease after the attainment of moderate-large size, and increase again with senescence. However, increased mortality with the onset of sexual maturity may also occur, as breeding competition increases (Spinage 1972, Erickson *et al.* 2006). Birds and mammals of moderate-large size often exhibit Type B_1

survivorship because they experience rapid growth rates and reach a threshold size at which predation pressures diminish.

Table 2: Static life table for *Einiosaurus*. dx = # deaths that occur in each age cohort, lx = # that survives from birth to the next cohort, and S_{1000} = survivorship standardized to a hypothetical population starting with 1000 individuals.

Age (Years)	(d_x)	(l_x)	(S_{1000})	Log_{10} (S_{1000})
0	16	32†	1000	3.00
0.5	4	16	500	2.699
1	3	12	375	2.574
2	2	9	281.25	2.449
3	(2)1.75*	7	218.75	2.340
4	(1)1.75*	5.25	164.06	2.215
5	(2)1.75*	3.5	109.37	2.039
6	(2)1.75*	1.75	54.69	1.738
7	0	0	0	0

† represents original population assuming neonate mortality of 50%
* averaged

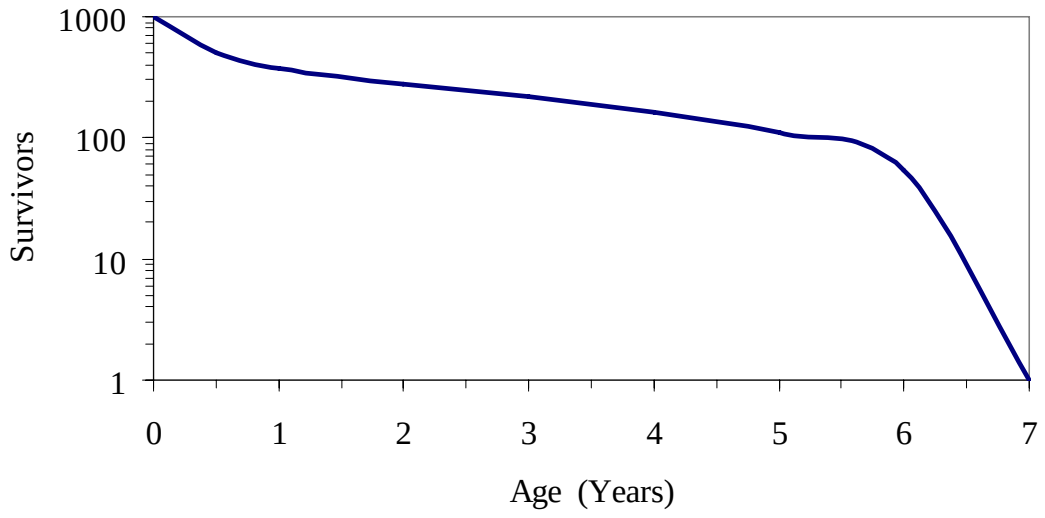

Figure 19: Survivorship curve for *Einiosaurus*.

In *Einiosaurus*, a notable exception to typical Type B_1 survivorship is the apparent low mortality of Neonates – juveniles less than 1 year old. This group should experience the highest degree of mortality, *i.e.* the bonebed should exhibit more of these than any other group (*e.g.* Erickson *et al.* 2009), particularly being representative of a drought assemblage (Voorhies 1969, Rogers 1990). This bias can be expected in Canyon Bone Bed due to either taphonomic or collection bias, or simply a low sample size. Several life table studies of extinct and extant mammals have reported under-representation of the youngest age group (Deevey 1947, Kurten 1953, Caughley 1966, Western 1980), sometimes by as much as 85% (Hulbert 1982). This has been attributed to lower preservation potential of juvenile material, *i.e.* teeth and skulls, in each of these studies. These taphonomic biases are just as real in Canyon Bone Bed, where smaller and more easily transportable elements were winnowed away by currents (Voorhies 1969, Rogers 1990). Also, a mass mortality assemblage in another ceratopsid, *Chasmosaurus mariscalensis* (MNI = 20) tends to be dominated by subadults, while attritional assemblages of the same species exhibit more juveniles and adults (Lehman 2007), so it is expected that this mass death assemblage of *Einiosaurus* also under-represents the very youngest (and very oldest) groups. In general, it has been noted that very young individuals and full-grown adults are relatively uncommon in several dinosaur taxa, a pattern that reportedly should be expected among egg-laying animals (Paul 1994, Lehman 2007).

To accommodate this bias, several ecological studies “fill in” the youngest age class to represent a 50% - 80% mortality rate among neonates (Table 2). Erickson *et al.*

2009 report a nearly 50% mortality among neonate *Psittacosaurus*, and this study does the same with *Einiosaurus,* however, compared to studies of extant mammal populations, this value is conservative. Without this hypothetical neonate mortality, this population of *Einiosaurus* appears to exhibit Type I survivorship, where individuals experience low rates of mortality throughout young life and massive, senescence-driven die-offs toward the end of their lifespan. Type I survivorship is only found in humans from developed countries and their domestic animals, and is therefore rejected as a realistic pattern of survivorship for a large-bodied herbivore such as *Einiosaurus*.

Though the possibility for taphonomic bias is very likely in the *Einiosaurus* bonebeds, and is the most likely explanation for under-representation of the youngest group (Lockley 1994, Lehman 2007), this also suggests that parental care may be involved. The low proportion of the youngest age group (individuals less than 1 year old) indicates parental care, or protection, of the youngest individuals that may have prevented them from entering the fossil record. Perhaps survivorship of *Einiosaurus* decreased dramatically not only with the approach of sexual maturity (see below), but also with the age at which juveniles left the protection of their parent(s). However, it is apparent they remained within the protection of a herd, or nest, as did at least one other ceratopsian, *Psittacosaurus* (Meng *et al.* 2004). Infant survival may have been relatively high until around 1 year of age. Therefore, age at independence (Sander 2000) may possibly be hypothesized for *Einiosaurus*. However, this study concludes that neonates are most likely underrepresented simply due to taphonomic bias (*e.g.* Deevey 1947, Kurten 1953, Caughley 1966, Western 1980, Hulbert 1982, Lockley 1994).

Survivorship increases with the attainment of a threshold size in Type B_1 populations, and that appears to be what happened when *Einiosaurus* reached about 2 years old. A rapid growth rate is a common strategy among large-bodied herbivores - in order to reduce the risk of mortality by predation, it is important that young herbivores outpace the growth of contemporaneous theropods that may prey on them (Horner and Padian 2004, Cooper *et al.* 2008). Large predators reported from the Two Medicine Formation include *Daspletosaurus*, a possible ceratopsian specialist (Rogers 1990), but a 2.5 – 3 m long *Einiosaurus* would have been comparatively safer than it was the year before.

The complete lack of fully-grown adults is most likely a result of the taphonomic bias associated with a drought assemblage, where adults are typically underrepresented. However, missing adults may indicate decreased survival associated with sexual maturity – perhaps relatively few individuals even grow to adult status. In many populations, factors that may cause survivorship to decrease with attainment of reproductive maturity are the physiological demands of egg-laying and fasting, injuries associated with intraspecific combat, and often, heightened exposure to predators. In modern ecosystems, this pattern has been noted among large ungulates (*see* Erickson *et al.* 2006), as well as other extant animals. In hierarchies such as these, few individuals survive to become very old adults. *Albertosaurus sarcophagus* survivorship decreases drastically with sexual maturity (Erickson *et al.* 2006), and is partly explained by evidence of bite wounds by conspecifics. Evidence of agonistic activity in ceratopsians has long been suspected, and evidence now exists to support the hypothesis that some species, namely

Triceratops and *Centrosaurus*, may have engaged in intraspecific combat (Farke 2004, Farke *et al.* 2009, Tanke and Rothschild, in press), likely wrestling or another form of relatively non-fatal encounter (Sampson 2001), though injuries appear to have been sustained (Farke *et al.* 2009, Tanke and Rothschild, in press). It is possible that *Einiosaurus* behaved similarly as its relatives; therefore, perhaps somewhat few individuals ever made it to full adult status due to stress and potential injury from intraspecific combat.

However, the relatively low mortality of all subadult cohorts in this population do not necessarily indicate increased mortality associated with the attainment of sexual maturity. The absence of adults is most likely a result of drought mortality. Also, a trend of high adult mortality has been posited for dinosaurs, since it is seen in many extant animals that tend to reach reproductive age relatively early (Lee and Werning 2008). The present study cannot deduce whether or not *Einiosaurus* experienced increased mortality as a result of older age, as does the Dall sheep (Deevey 1947), since it is apparent that aged adults (who have experienced cessation of growth) are missing from this sample (*see also* Erickson *et al.* 2009).

CONCLUSIONS

Einiosaurus procurvicornis, like virtually all dinosaur species, exhibits fibrolamellar bone tissue indicative of rapid growth. At about one year of age, *Einiosaurus* juveniles were over 2 m in length, and a size gap between 1-year-olds and 2-year-olds implies the possible existence of a breeding season in this species. *Einiosaurus* may have reached sexual maturity and a length of 3.5 – 4.5 m between 3 and 6 years of age, though older animals exhibit considerable individual variation. This rate of growth compares well with other ontogenetic studies utilizing bone histology of large-bodied dinosaur taxa. *Einiosaurus* apparently lived beyond 6 years of age, but longevity cannot be assessed from Canyon Bone Bed from which no adult specimens were identified.

The absence of any adults found of a species raises questions about taxonomic validity of the species itself, especially when diagnostic characters are primarily defined by ontogenetically-variable cranial material, as in ceratopsians. The assessment of individual age through bone histology can also add valuable information to research on ontogenetic changes in cranial morphology and growth rates of ceratopsians.

This study marks one of the earliest studies on population histology of a dinosaur species, utilizing population dynamics - a tool commonly used in ecology to answer questions on individual life histories and patterns of survivorship of a population. After accommodating for realistic neonate mortality, *Einiosaurus* survivorship represents a Type B_1 survivorship trend much like other medium- to large-bodied extant herbivores, including other dinosaur taxa, however, the absence of fully-grown animals is problematic for determining survivorship of a species.

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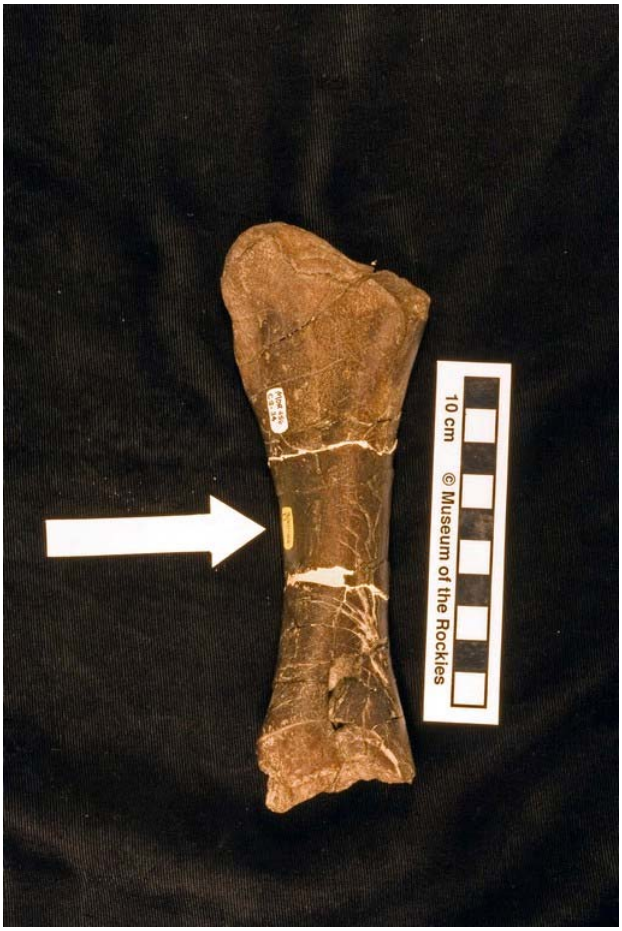
APPENDICES

APPENDIX A

WHOLE *EINIOSAURUS* MOR 456 TIBIAE

Mid-diaphyseal region consists of a painted cast except where indicated, and white arrow shows location from where histological slide was taken. Specimen number is listed for specimens where originally recorded. Due to abrasion and breakage of articular ends, and diagenetic alteration and compression, left and right elements and biological directions are not identified, and were not relevant to this study. Scale bar = 10 cm.

Juveniles

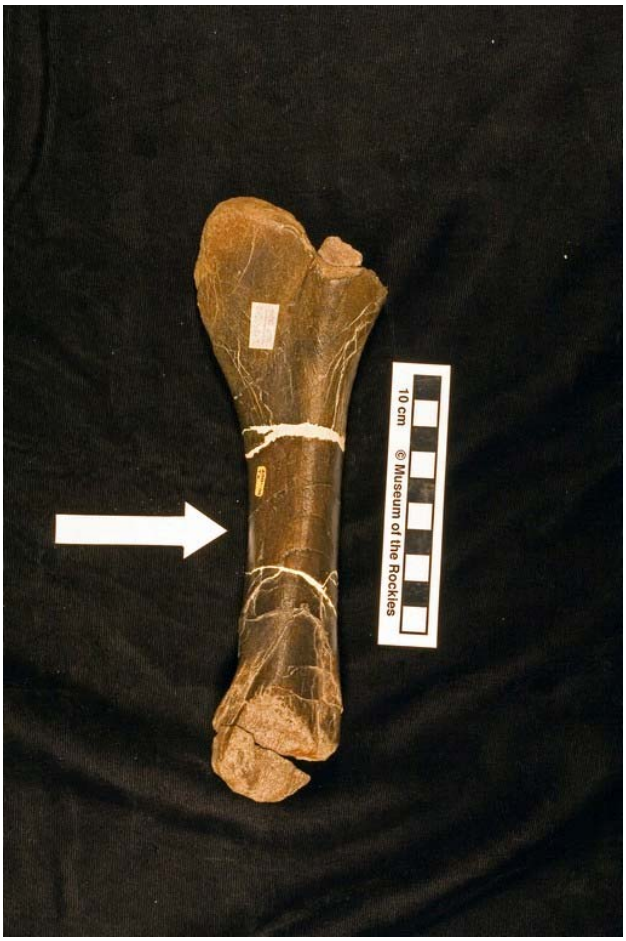


MOR 456 (#C3-34) T1.

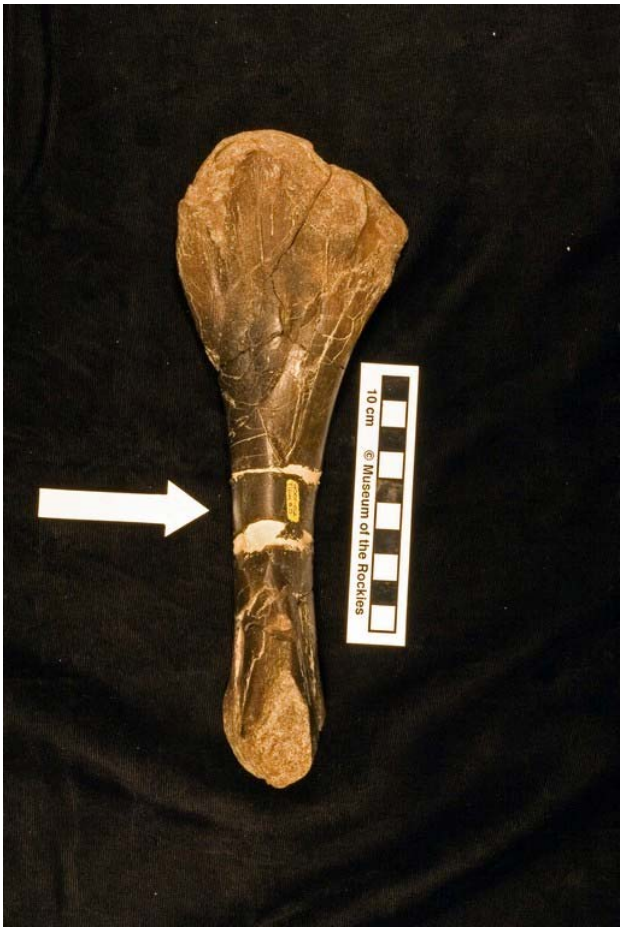
MOR 456 (#8-27-87) T6.

MOR 456 T13. Section has not yet been cut and bone is intact.

MOR 456 (8-29-87) T15. Section has not yet been cut and bone is intact.



MOR 456 (#8-20-7-3) T2

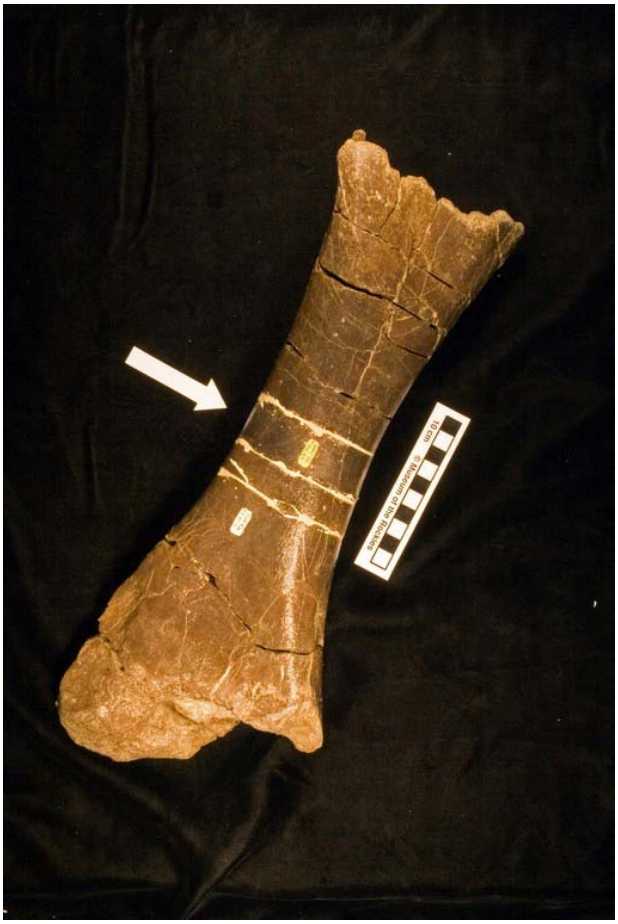


MOR 456 (#8-10-6-1) T5.

MOR 456 (#8-8-87-9) T14. Section has not yet been cut and bone is intact.

Subadults

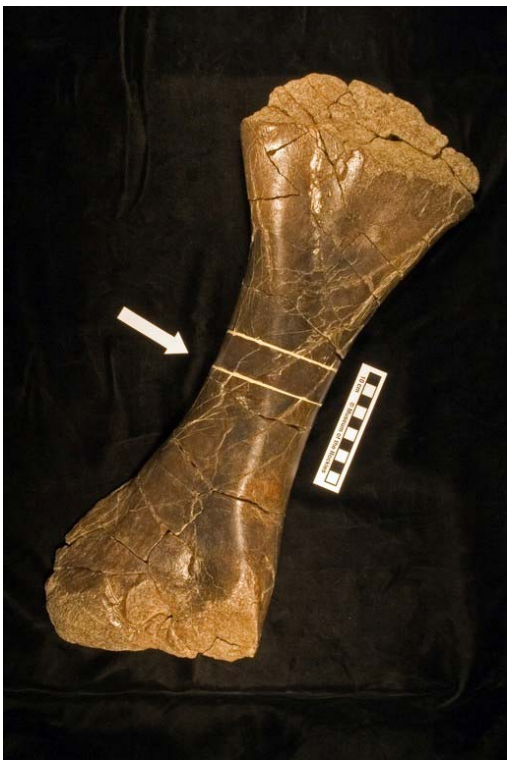
MOR 456 (#A2-126) T16. Section has not yet been cut and bone is intact.



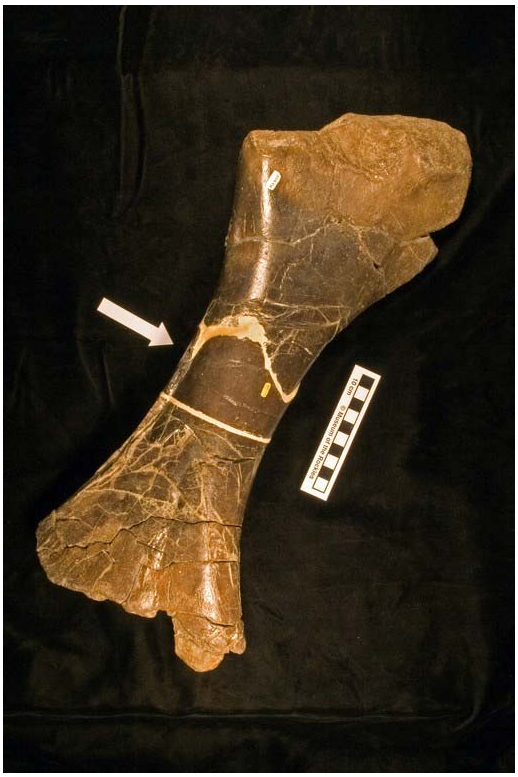
MOR 456 (#8-8-87-15) T9.

MOR 456 (#A2-90) T8.

MOR 456 T10.

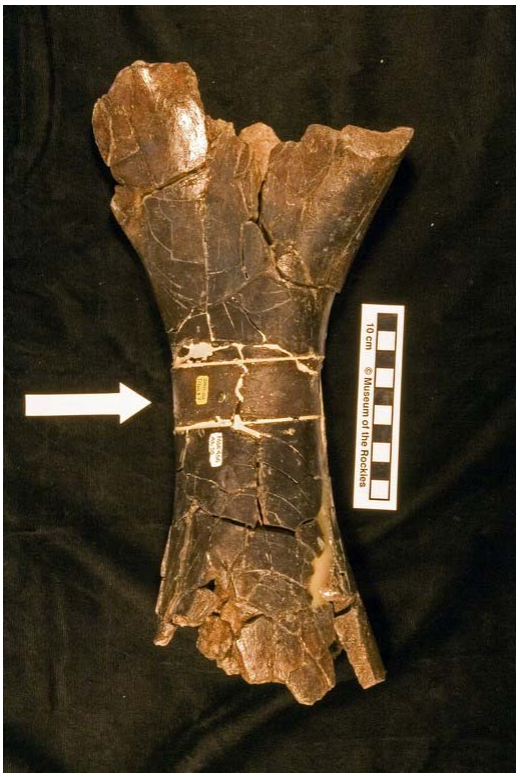


MOR 456 (#B3-124) T11.



MOR 456 T4.

MOR 456 (#8-10-7-16) T12.

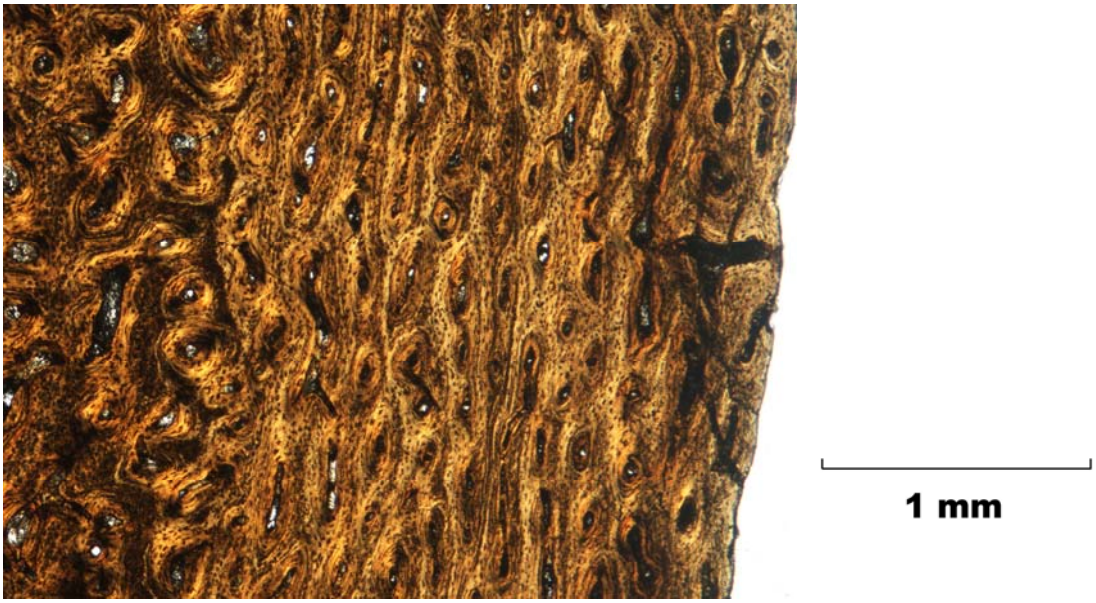


MOR 456 (#A2-55) T7.

APPENDIX B

SLIDES OF *EINIOSAURUS* MOR 456 TIBIAE

Juveniles



MOR 456 T1, 0 LAGs, mag. 40x.

MOR 456 T1, 0 LAGs, mag. 10x.

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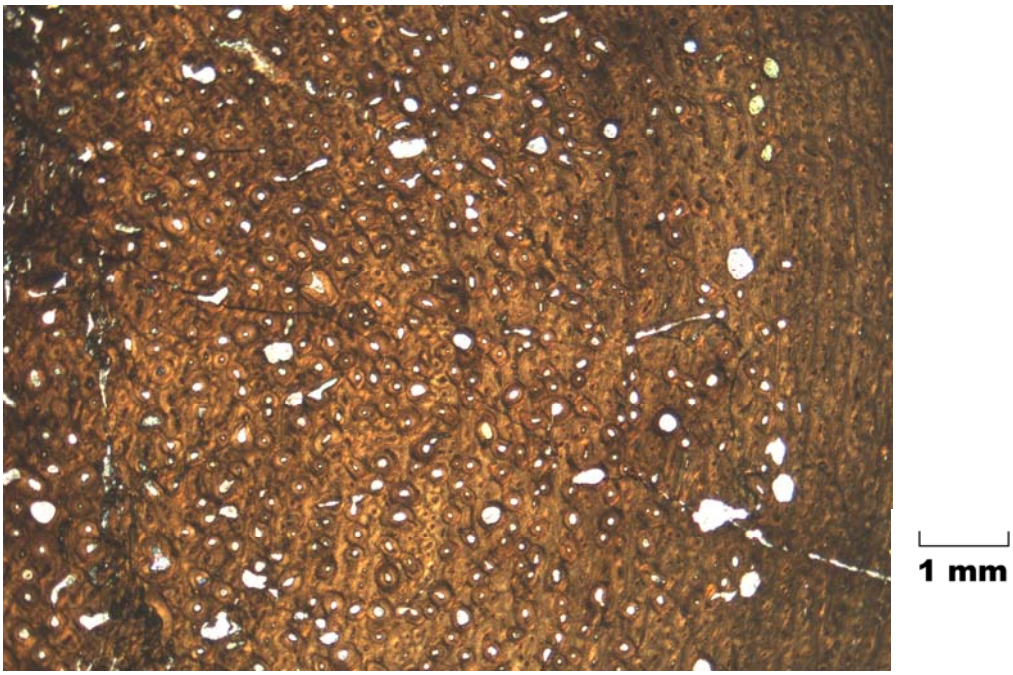
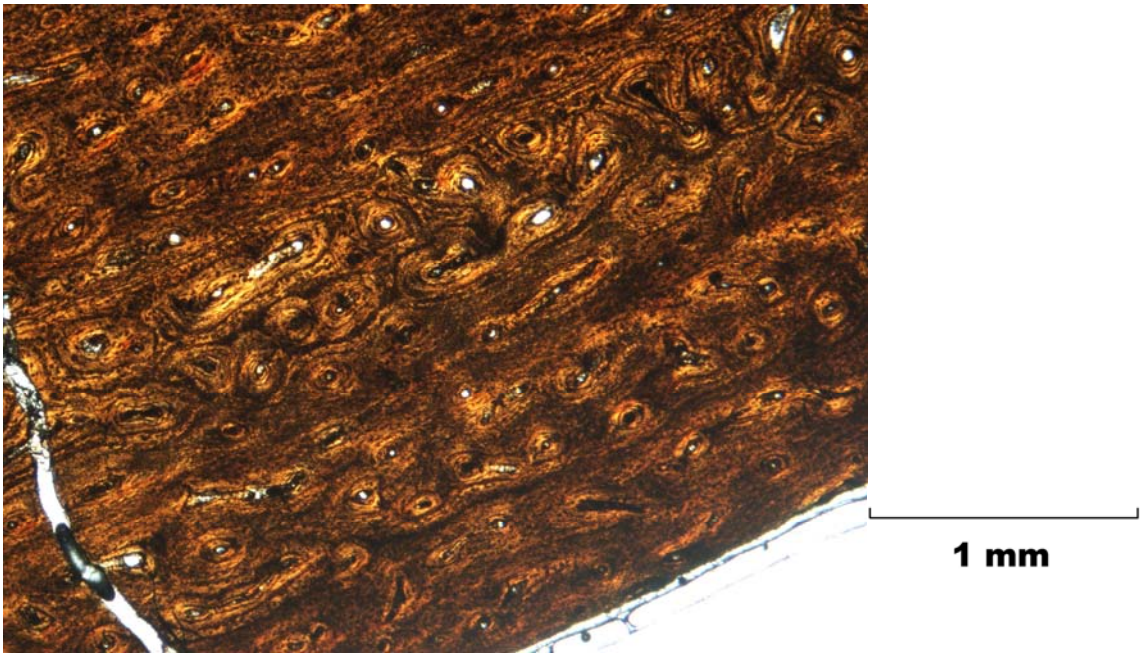
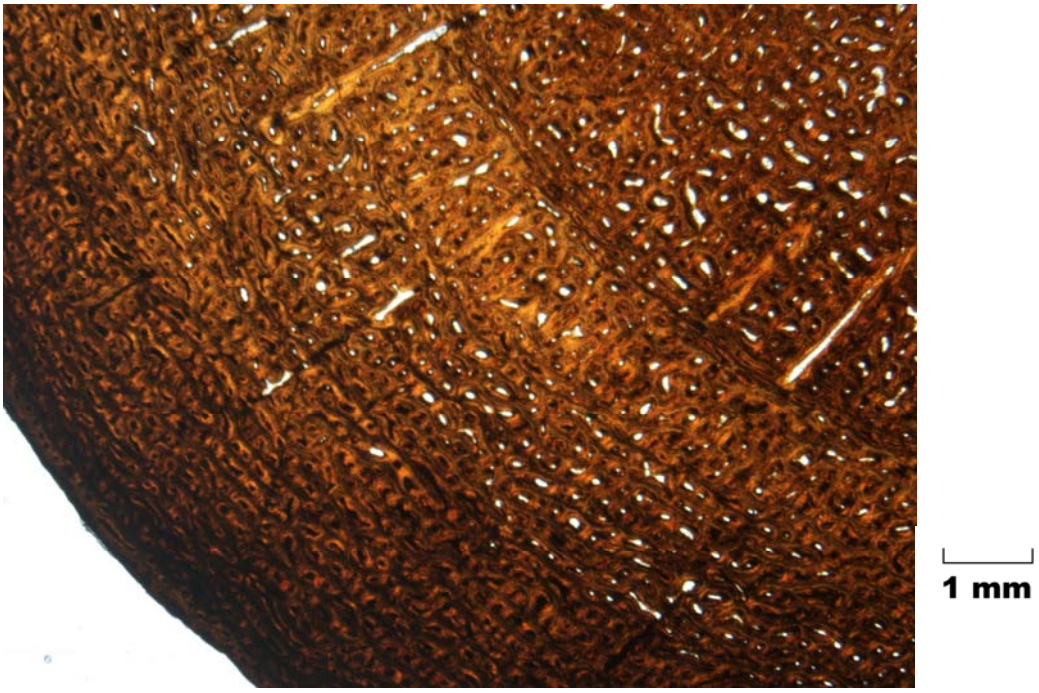
MOR 456 T6, 0 LAGs, mag. 10x



MOR 456 T13, 0 LAGs, mag. 10x.



MOR 456 T15, 0 LAGs, mag. 40x.



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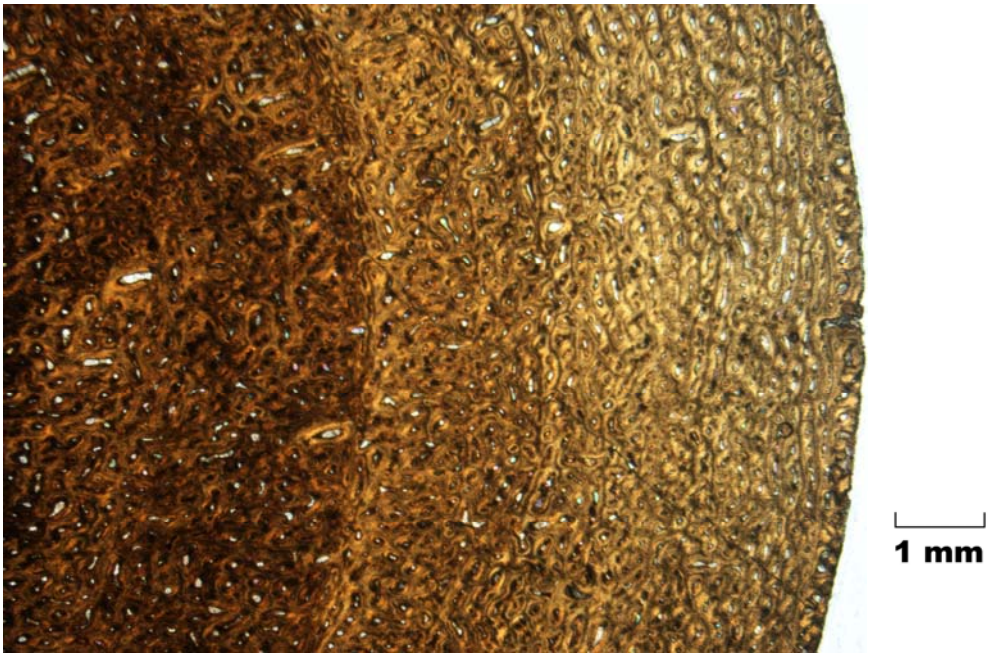

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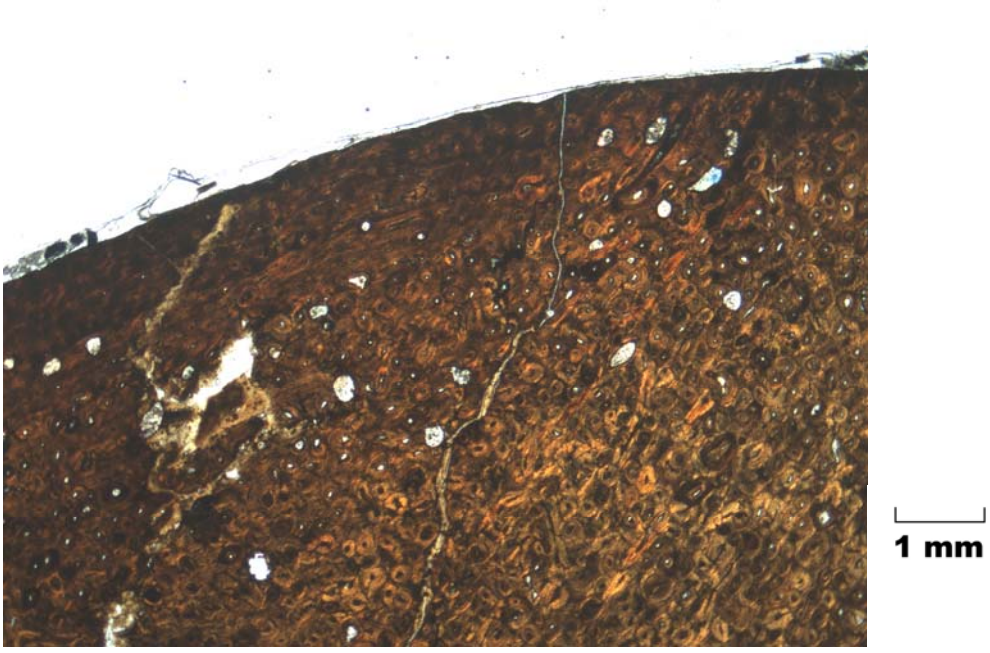
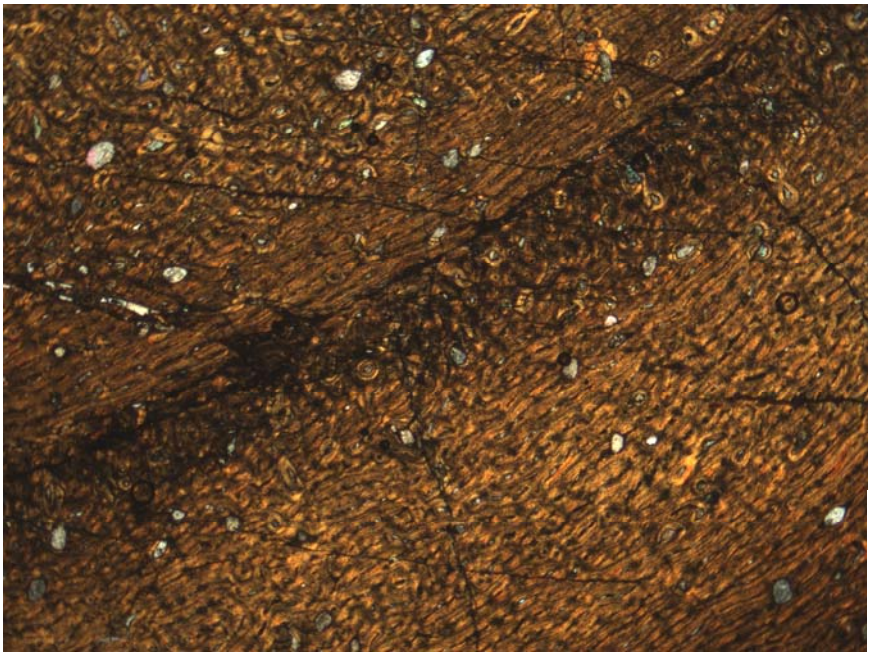


MOR 456 T14, 1 LAG, mag. 10x.

Subadults



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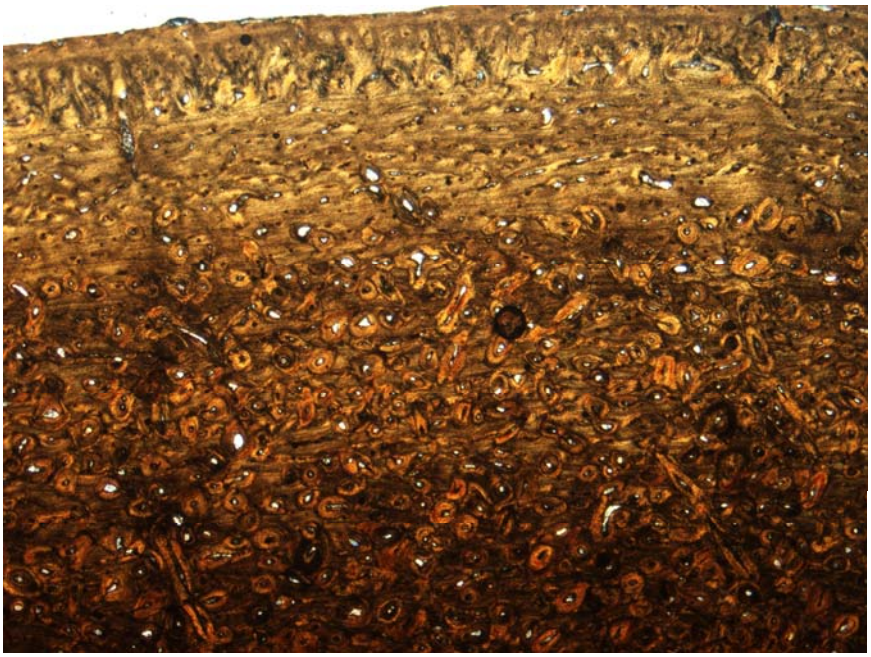

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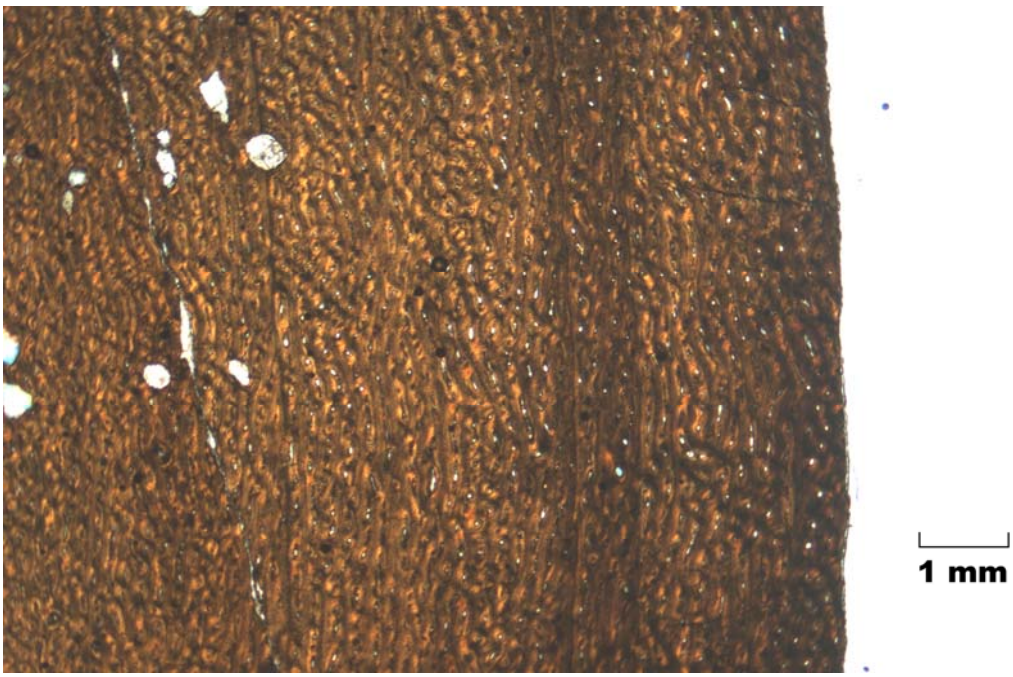

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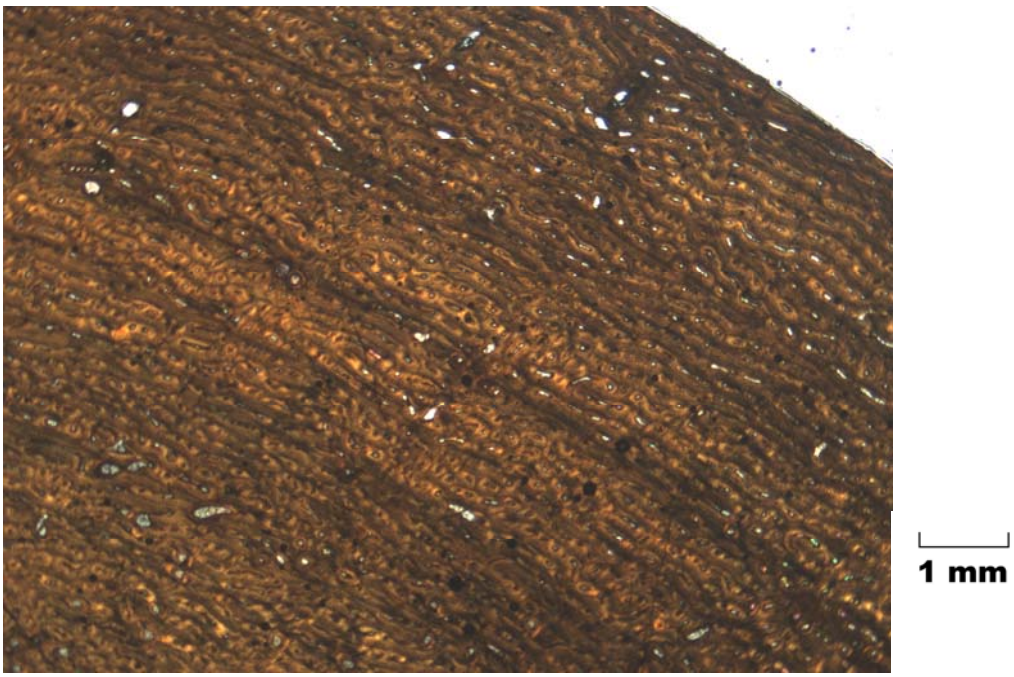
MOR 456 T8, 3 LAGs, mag. 10x.



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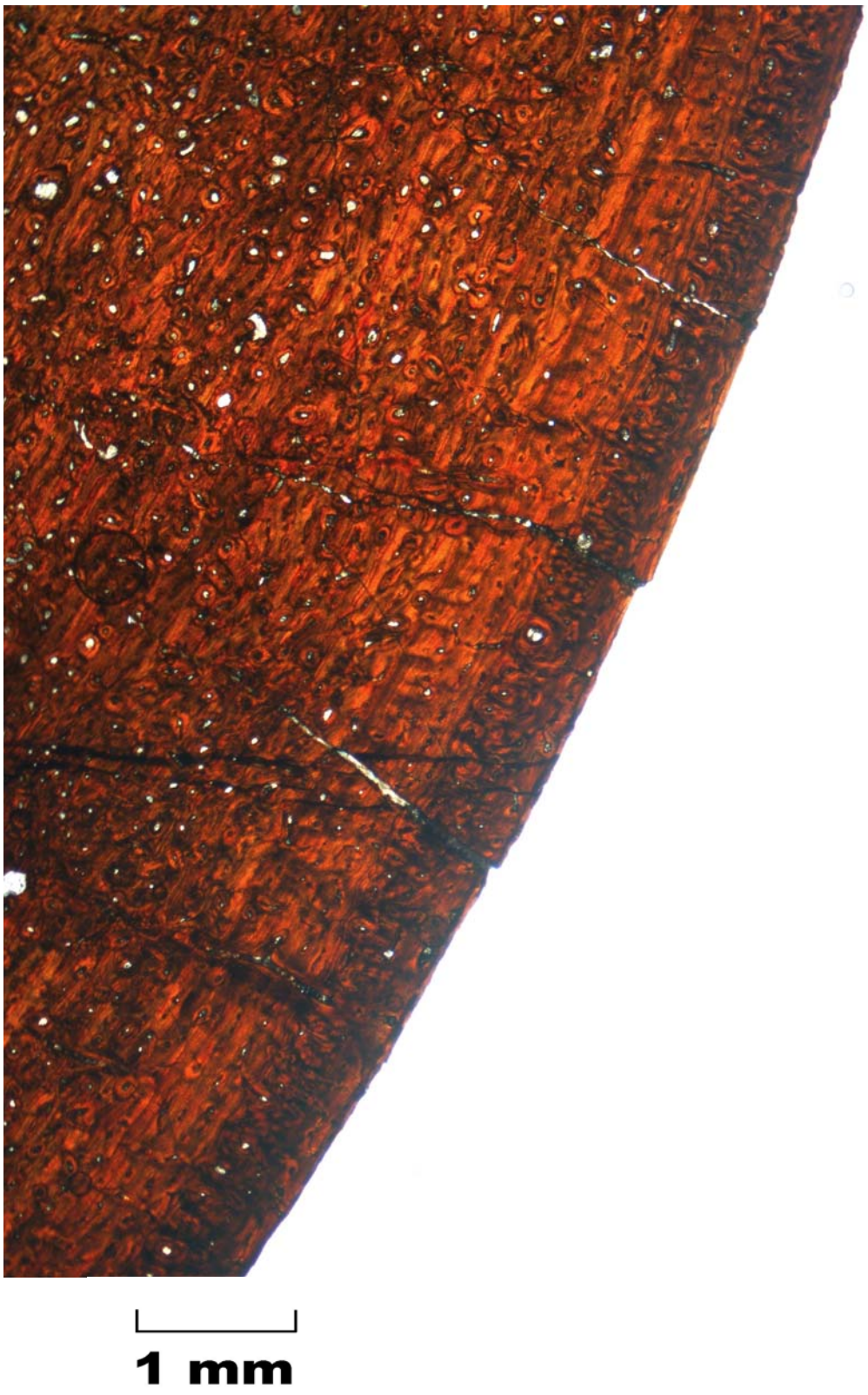

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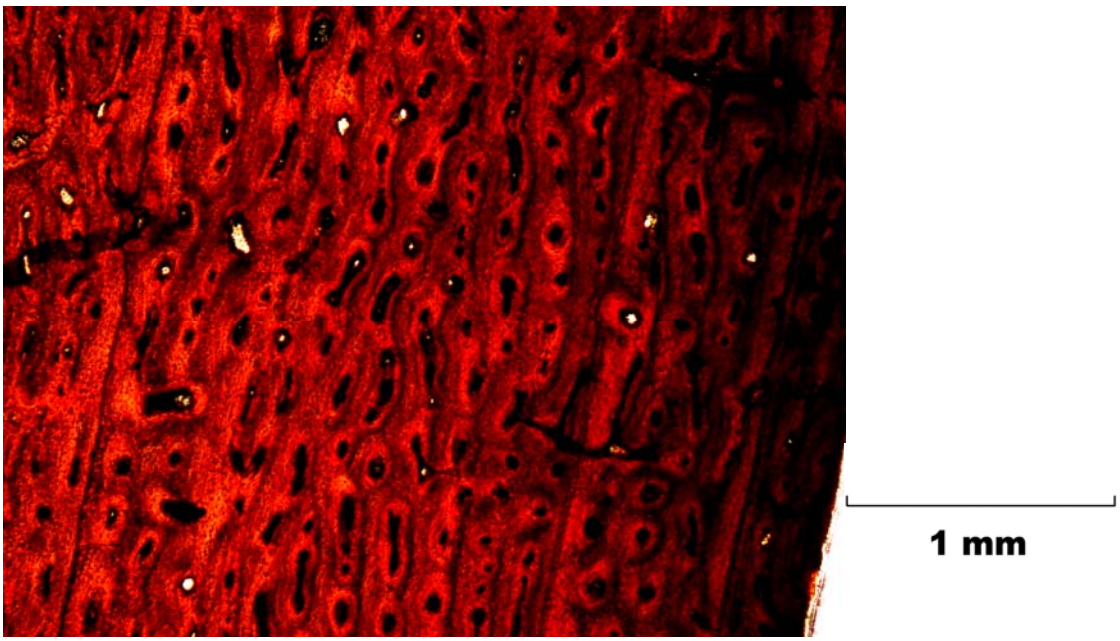

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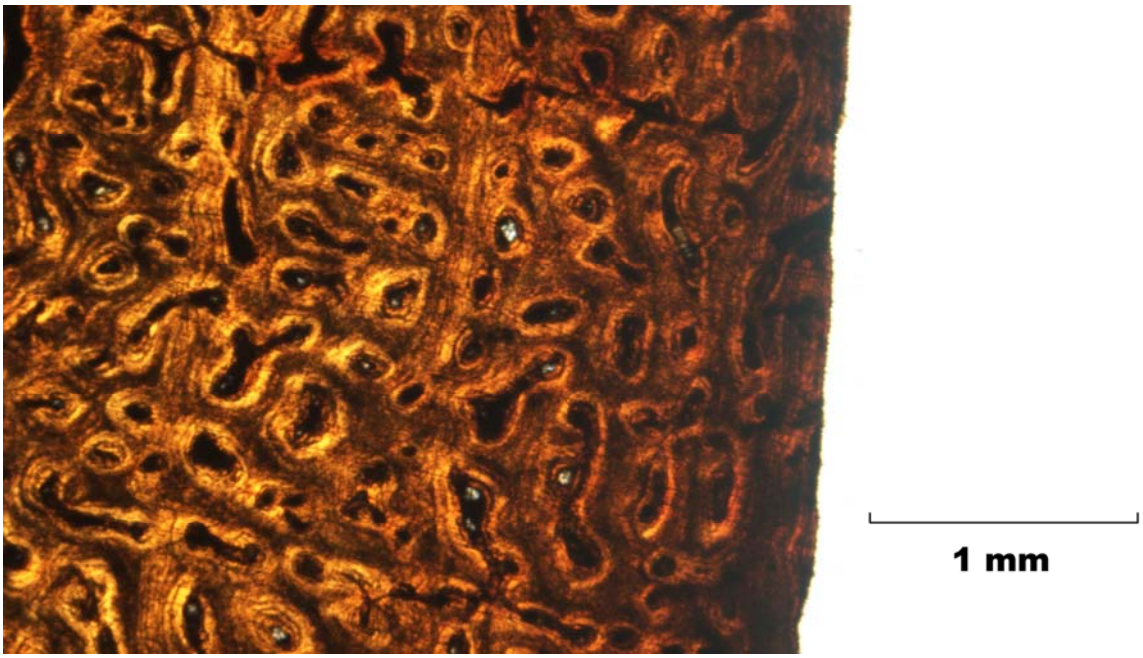

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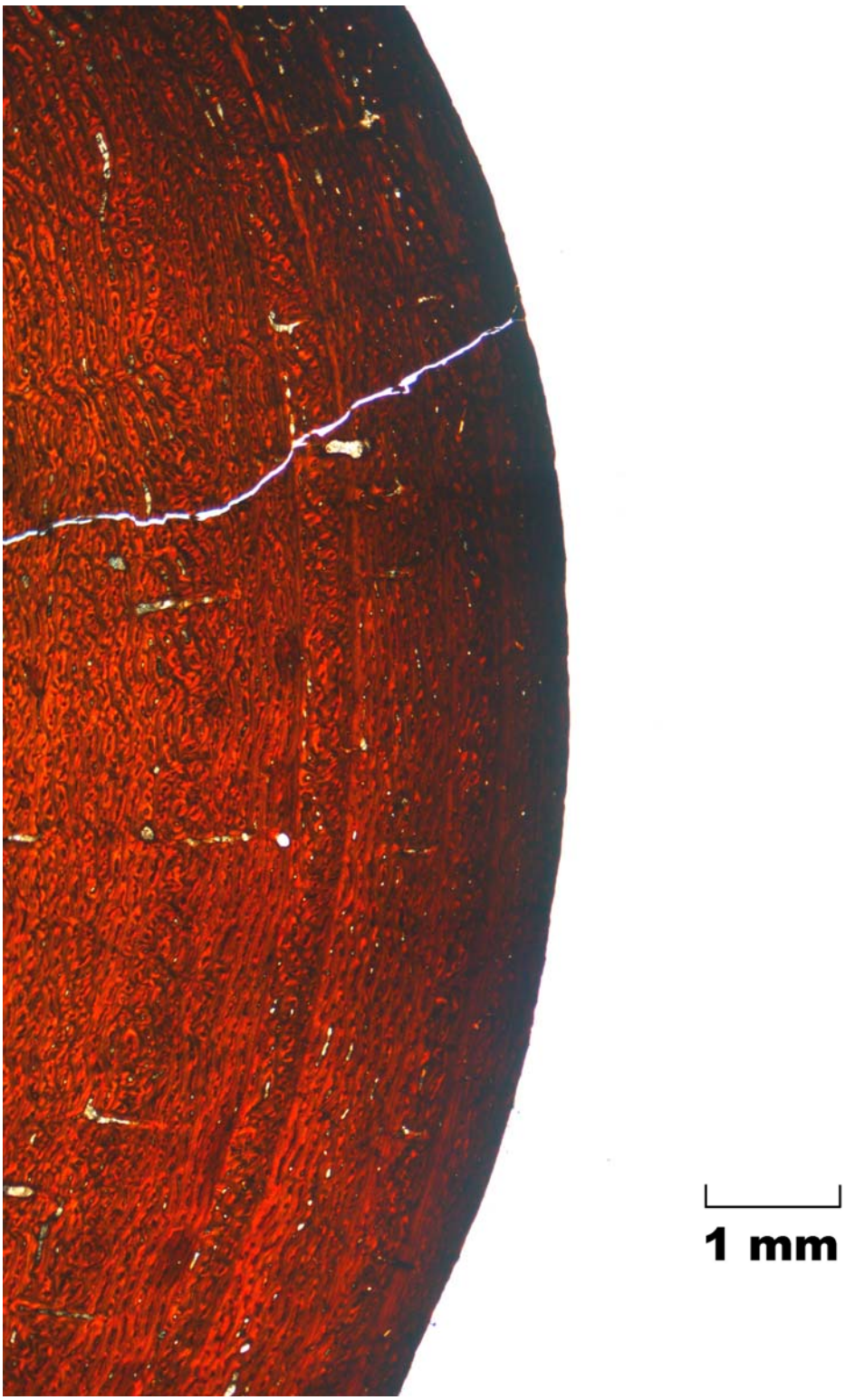

MOR 456 T7, 6 LAGs, mag. 10x.