

BIOGEOCHEMICAL ANALYSIS OF LATE CRETACEOUS VERTEBRATE  
FOSSILS OF WESTERN ALABAMA, USA

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## ABSTRACT

In the past, vertebrate paleontologists in Alabama focused primarily on classical methods of investigation, for example, by examining the gross anatomy of fossilized skeletal elements. More recently, new methods were developed that enable paleontologists to examine the molecular composition of fossilized bones and teeth, so that they may be used as proxies for determining past environmental and biological conditions. The analyses presented here examine vertebrate fossils from the Late Cretaceous aged marine formations of Alabama, which represent one of the warmest time periods in Earth's history. The first analysis examines the rare earth element (REE) content of biophosphates to determine fossil provenance and relative paleobathymetry of the marine strata in which the fossils were deposited. The second analysis examines the strontium isotope ratios present in fossil shark tooth enameloid to determine numerical ages of the containing geologic formations. The final analysis examines the oxygen isotope content of biophosphates for ambient temperature determination of seawater present during the Late Cretaceous and the body temperatures of a variety of vertebrate organisms including mosasaurs and birds. The data obtained by this study on the greenhouse climate present during the Late Cretaceous may possibly be used to better enhance computer modelling of future climate change, given the current state of global warming, and the biological response to this warming trend.

## DEDICATION

This dissertation is dedicated to the many family members, friends, and colleagues who supported and encouraged me to continue my education. This work would not have been possible without them.

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## 1. INTRODUCTION

Research on the Late Cretaceous marine formations of western Alabama began in the mid-1800s (Gibbes, 1851; Leidy, 1851; Cope 1869; Smith *et al.*, 1894), during which studies focused on the lithology and fossil content using traditional methods of classification, taxonomy, and anatomical description. These types of studies continued through the 20<sup>th</sup> Century, with refinement of the stratigraphic subdivisions of the geologic units and additions to the faunal assemblages (Stephenson and Monroe, 1940; Zangerl, 1948, 1953; Langston, 1960; Russell, 1970; Applegate, 1974, Thurmond and Jones, 1981; Raymond *et al.*, 1988). Near the turn of the millennium researchers developed and refined new biogeochemical methods to potentially learn more about depositional environments and the biology of fossil organisms (Patrick *et al.*, 2007a; Becker *et al.*, 2008; Bernard *et al.*, 2010). Although the geology and paleontology of the Alabama Late Cretaceous marine formations are fairly well understood, these new biogeochemical methods, using trace elements and stable isotopes, have the potential to solve some of the remaining problematic issues. These problematic issues include: i) Determining relative water depth during deposition of Late Cretaceous marine carbonate strata, ii) Precise age-dating of the stratigraphic units, and iii) Measuring seawater temperature during deposition of the Mooreville Chalk and the *in vivo* body temperatures of its fossil vertebrate fauna. As the Late Cretaceous was an age of high sea levels and very warm global temperatures, data obtained concerning this time period may enable better forecasting of future events in relation to global climate change that is currently in progress.

The paleobathymetry of Cretaceous marine formations in Alabama has previously been estimated using microfossils (Florian, 1984), ostracodes (Puckett, 1991), and sequence stratigraphy (Mancini *et al.*, 1996), sometimes resulting in conflicting interpretations. Rare earth elements (REE) have been used to determine relative water depth of siliciclastic marine strata of the Late Cretaceous Western Interior Seaway (Patrick *et al.*, 2007a), and provenance of fossil vertebrates located out of stratigraphic position (Staron *et al.*, 2001; Patrick *et al.*, 2007b). Ratios of heavy rare earths (HREE) to medium (MREE) and light rare earths (LREE) preserved in vertebrate fossils give geologic strata unique REE profiles and allow the interpretation of water depth based on the perceived mixing of oxygenated (shallow) and anoxic (deeper) ocean waters. Whereas these features of REE analysis have been successfully used in the interpretation of siliciclastic deposits, prior to the present study it was uncertain if this type of analysis could be used on the carbonate-rich marine formations present in Alabama (see Chapter 2).

Age determination of the Cretaceous marine formations of Alabama has previously depended primarily upon biostratigraphic correlation using a variety of invertebrate taxa (Hester and Risatti, 1972; Puckett, 1994; Cobban and Kennedy, 1995; Smith, 1997) resulting in conflicting ages depending on the taxa used. This reliance on biostratigraphy has been necessitated by the relative lack of radiometrically dateable strata in these geologic units (Stephenson and Monroe, 1940; Raymond *et al.*, 1988). A potential solution to the need of a more reliable age-dating method is through the use of strontium isotopes. Ratios of stable strontium isotopes ( $^{87}\text{Sr}/^{86}\text{Sr}$ ) dissolved in seawater have been shown to be uniform throughout the oceans and change very slowly over geologic timescales. These strontium isotopes become incorporated in biominerals (biocarbonates and bioapatites) at the same ratios present in seawater at the time of their formation. Well-preserved fossil biominerals have previously been analyzed

for their strontium isotope content and a strontium isotope curve established for the Phanerozoic Eon (McArthur *et al.*, 2012), enabling fossils to be numerically dated. As some biominerals have been shown to lose their original strontium isotope signatures due to diagenetic alteration, bioapatites in diagenetically-resistant fossil shark tooth enameloid (Schmitz *et al.*, 1997) may provide strontium isotope ratios that can be used to numerically age-date the strata in which they are found (Becker *et al.*, 2008). By analyzing the strontium isotope ratios in fossil shark tooth enamel, the numeric ages of the carbonate-rich Cretaceous marine formations of Alabama can be more precisely determined, thus providing a temporal framework across which the rates of Late Cretaceous climate change can be calculated (see Chapter 3).

Global temperatures during the Late Cretaceous are assumed to have been very warm because of tropical to subtropical faunal and floral distributions at high latitudes (Tarduno *et al.*, 1998) but precisely how warm the climate was during this time interval remains uncertain. Stable oxygen isotope ratios preserved in fossil biominerals can be used as a proxy for ambient paleotemperature measurements (Vennemann *et al.*, 2002; Pucéat *et al.*, 2010). The ratio of oxygen isotopes incorporated into biominerals depends primarily upon the temperature at which the minerals form, and the ratio of oxygen isotopes present in the water from which they precipitate. By analyzing the composition of fossil tooth enamel and bone phosphates of cold-blooded (ectothermic) vertebrates from the Mooreville Chalk in Alabama, the ambient paleotemperatures of the sea water in which the Mooreville Chalk was deposited can be determined. These temperature measurements can be compared with paleotemperatures obtained from fossil vertebrates of the contemporaneous, and higher-latitude, Pierre Shale of South Dakota, as well as modern vertebrate analogues. Physiologic temperatures of other extinct fossil

taxa can also be determined using oxygen isotope ratios to gauge their adaptive evolutionary response to the warm climate (see Chapter 4).

By using these advanced biogeochemical analyses on fossils, it is possible to gain a better understanding of global climate change during one of the warmest periods in Earth's history. The rare earth element analysis can assist in measuring changes in relative sea level, the strontium isotope analysis can provide accurate numeric age-dating of stratigraphic units so that we can better calculate the rate of climate change, and the oxygen isotope analysis can provide precise temperature measurements of the marine paleoenvironment and its fauna. The data obtained from these analyses can be used to enhance computer modelling of future climate change as Earth continues to undergo its present warming trend, so that we may be better informed of the consequences of this change.

## 2. RARE EARTH ELEMENT (REE) ANALYSIS OF VERTEBRATE FOSSILS FROM THE UPPER CRETACEOUS CARBONATE MARINE FORMATIONS OF WESTERN AND CENTRAL ALABAMA, USA: TAPHONOMIC AND PALEOENVIRONMENTAL IMPLICATIONS

### ABSTRACT

Rare earth element (REE) analysis of vertebrate fossils has previously been used to answer a number of stratigraphic, taphonomic, and paleoenvironmental questions concerning the depositional environments of Cretaceous siliciclastic marine and freshwater formations. In this study, vertebrate fossils from Upper Cretaceous formations of Alabama were analyzed to determine if REE analyses could be equally effective at resolving taphonomic and paleoenvironmental questions in marine carbonate strata. Results indicate that these fossils possess unique REE signatures, although they are not as distinctive as those of siliciclastic formations. REE data can also be used, with limitations, for stratigraphic assignment of vertebrate fossils as well as indicating relative paleobathymetry. Furthermore, differences in REE signatures between certain taxonomic groups and REE concentrations in different osteological material are observed. In conclusion, findings herein indicate that REE analysis of vertebrate fossils from carbonate deposits can be effective for paleoenvironmental and regional paleogeographic studies.

### INTRODUCTION

In living vertebrates, the combined content of all rare earth elements ( $\Sigma$ REE) present in bones and teeth is approximately 20 ppm or less (Wright *et al.*, 1984; Chenery *et al.*, 1996;

Patrick *et al.*, 2001; Trueman *et al.*, 2004; Trueman *et al.*, 2008). Rare earths are present in food and water that are ingested by living organisms and become incorporated in their tissues (Parker and Toots, 1980; Trueman and Tuross, 2002). The relatively low  $\Sigma$ REE content in living organisms is due to the REE integrated into living bone tissue being mobile, becoming incorporated and later removed from the bone matrix through diffusion and biokinetic processes (Kohn and Moses, 2013). REE are integrated into bone phosphates, both *in vivo* and *post mortem*, through a coupled, or possibly omission, substitution. Trivalent REE<sup>3+</sup> ions, which have similar ionic radii to Ca<sup>2+</sup> ions, can easily substitute into the seven-fold coordination Ca<sup>2+</sup> site 2 when paired with Na<sup>+</sup> [REE<sup>3+</sup> + Na<sup>+</sup> ↔ 2 Ca<sup>2+</sup>] (Reynard *et al.*, 1999; Staron *et al.*, 2001; Skinner and Jahren, 2003; Wopenka and Pasteris, 2005; Kohn and Moses, 2013).

Whereas the bones of living organisms possess relatively low  $\Sigma$ REE concentrations, fossil bones typically contain  $\Sigma$ REE concentrations that are two or more orders of magnitude higher. Most of this substitution occurs *post mortem* shortly after deposition during the recrystallization of biophosphates in early diagenesis, and it is completed within 100,000 years (Millard and Hedges, 1996; Patrick *et al.*, 2001; Trueman and Tuross, 2002; Trueman *et al.*, 2004; Kohn and Law, 2006; Kohn, 2008; Finlay *et al.*, 2013). REE that become concentrated in fossil bone are believed to be present in pore waters surrounding the buried skeletal elements (Trueman, 1996), and may be pre-concentrated from sediments surrounding the fossilizing bone (Reynard *et al.*, 1999; Trueman *et al.*, 2004). Once diagenetically incorporated into the bioapatite in the bone matrix, the REE signature remains stable unless the fossils are subjected to high-grade metamorphism or are dissolved and reprecipitated (Patrick *et al.*, 2004). Herwartz *et al.* (2011), however, have suggested that fossil bones and teeth may remain open systems for long-term REE uptake, based on their observations of lutetium concentrations in fossil specimens of

various ages. Arrhenius *et al.* (1957) first recognized and described the high  $\Sigma$ REE content of fossil bones, between 1,000 and 10,000 ppm, while Grandjean *et al.* (1987) were among the first to test paleoenvironmental interpretations based on the REE content of fossils.

The rare earth element content of vertebrate fossils has been previously used to answer a number of provenance, taphonomic, and paleoenvironmental questions. Patrick *et al.* (2004, 2007a) used REE content of fossils from members of the Upper Cretaceous Pierre Shale in South Dakota (the Pierre Shale Formation was later raised to group status and its subordinate members raised to formation status by Martin *et al.*, 2007) to interpret paleobathymetry and the presence of oxic/anoxic conditions, based on the ratios of light/medium/heavy REE. These authors also analyzed REE profiles to determine the original horizon of vertebrate fossils collected outside their stratigraphic context (Patrick *et al.*, 2007b). Staron *et al.* (2001) described the REE profiles of the Late Cretaceous and Early Paleocene greensands of New Jersey and used them to determine the potential reworking of vertebrate fossils in the Main Fossiliferous Layer of the Hornerstown Formation. In these previous studies, REE data were based on vertebrate fossils collected from terrigenous siliciclastic deposits. Equivalent information for carbonate deposits is scarce, especially for the Cretaceous fossiliferous formations of the Western Interior Seaway of the United States.

In this study, an analysis of Late Cretaceous vertebrate fossils from carbonate-rich formations is conducted to understand the influence of lithology and depositional environments on REE data (specifically, the lanthanide series (La-Lu)) in a comparison with previous observations (Staron *et al.*, 2001; Patrick *et al.*, 2004, 2007a, 2007b). In addition, several

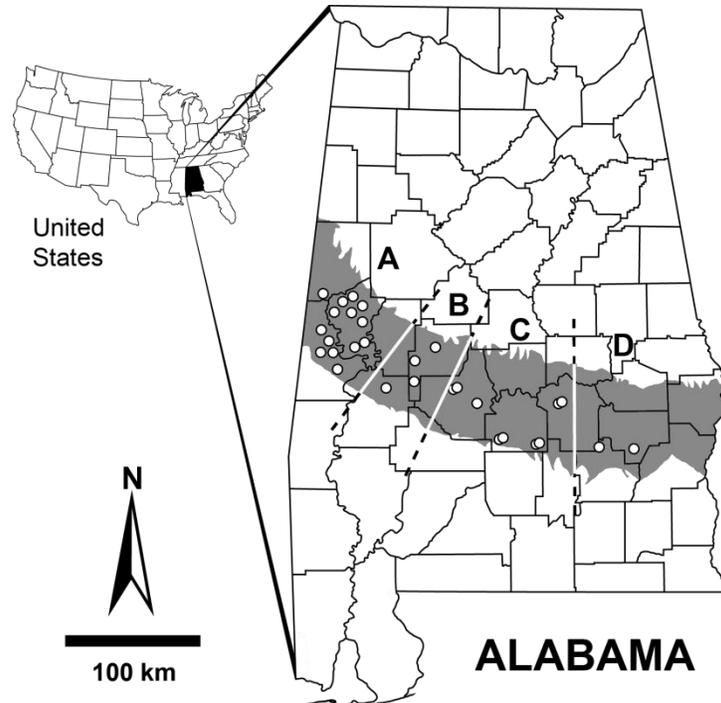


FIGURE 2.1—Areal distribution of outcropping Upper Cretaceous marine formations in Alabama and division of outcropping Upper Cretaceous formations into sub-regions A, B, C, and D of the study area based on locality information from studied specimens. Each dot represents a collection locality.

vertebrate fossil taxonomic groups are examined to test whether different organisms (e.g., mosasaurs) have unique REE “fingerprints”, and to determine that REE signatures are uniform throughout their skeletal anatomy. Finally, ratios of rare earth elements are used to validate previous methodology for paleobathymetric interpretations of Cretaceous deposits, in addition to sedimentological and paleontological (e.g., microfossil assemblages) information (Patrick *et al.*, 2004, 2007a).

## GEOGRAPHICAL AND GEOLOGICAL SETTING

Fossils used in this study were collected by staff members from the Alabama Museum of Natural History over a period of many years from the outcropping Upper Cretaceous marine formations in western and central Alabama, including the following counties: Pickens, Greene,

Sumter, Marengo, Pike, Hale, Perry, Dallas, Lowndes, Montgomery, and Bullock (Fig. 1). The Upper Cretaceous strata of Alabama crop out along the Gulf Coastal Plain as a gently curving arc that originates in eastern Alabama and extends in a westerly direction, before turning to the

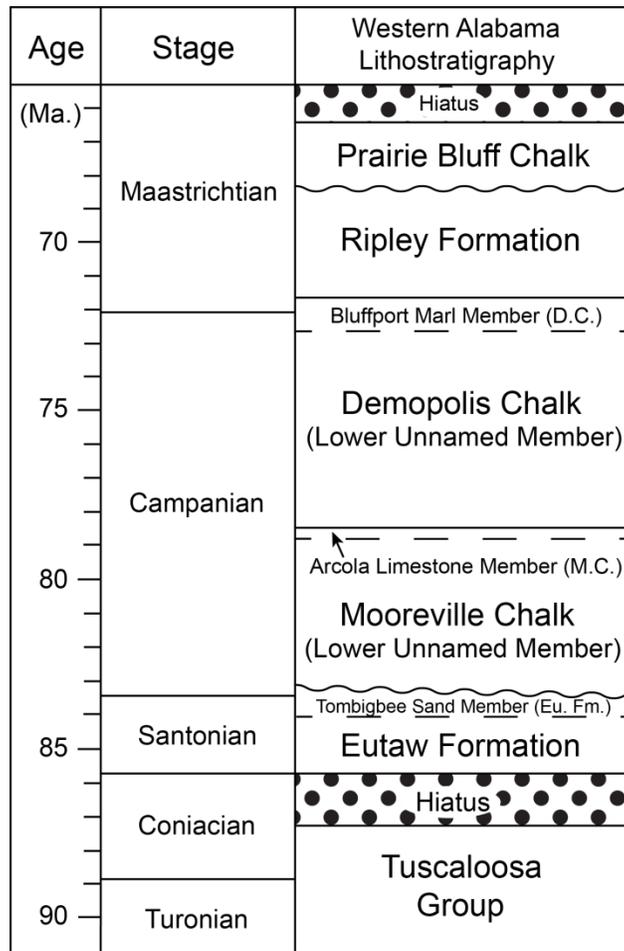


FIGURE 2.2—Stratigraphic column of western and central Alabama reflecting age of surface outcrops reported by Raymond *et al.* (1988).

northwest in the central and western portions of the state. These strata represent the southeastern flank of the Mississippi Embayment region of the Western Interior Seaway that existed during the Late Cretaceous in North America. In the study area of central and western Alabama, these deposits range in age from the late Cenomanian of the Tuscaloosa Formation through the mid to late Maastrichtian of the Prairie Bluff Chalk (Mancini *et al.*, 2008). The sequence of strata is not

continuous as several hiatuses are present throughout the stratigraphic column (Fig. 2). The lower portion of the stratigraphic column can be characterized as an overall fining upward sequence that occurred during a regional marine transgression. This transgression reached its maximum flooding surface in the middle portion of the Demopolis Chalk (Liu, 2007; Mancini *et al.*, 2008). The strata overlying the middle Demopolis Chalk generally coarsen upward, indicating an overall regional marine regression that continued well into the Paleogene Period.

### Sedimentology and Depositional Environments

Eutaw Formation – The Eutaw Formation is divided into the lower unnamed member and the upper Tombigbee Sand Member. The combined members of the Eutaw Formation range in age from the late Coniacian through the late Santonian (Mancini *et al.*, 2008). The lower, unfossiliferous, unnamed member is composed of approximately 52 m of fine to medium-grained, cross-bedded, micaceous and glauconitic sandstone (Mancini and Soens, 1994). The Tombigbee Sand Member disconformably overlies the lower unnamed member and attains a maximum thickness of approximately 6 m in western Alabama (Kiernan, 2002). The Tombigbee Sand Member is comprised of massive fine-grained sandstone to coarse-grained siltstone that is glauconitic, micaceous, calcareous, highly fossiliferous and bioturbated (Raymond *et al.*, 1988; Mancini and Soens, 1994). The environment of deposition for the Eutaw Formation is believed to have ranged from back barrier island to inner shelf environments at the beginning of a marine transgression (King and Skotniki, 1990).

Mooreville Chalk – The Mooreville Chalk is divided into the lower unnamed member and the upper Arcola Limestone Member. The contact of the lower unnamed member of the Mooreville Chalk with the underlying Tombigbee Sand Member of the Eutaw Formation is

gradational but is indicated by a layer of phosphatic pebbles and invertebrate steinkerns (Mancini and Soens, 1994). The age of the contact is diachronous, being earliest Campanian in western Alabama and late Santonian near central Alabama (Kiernan, 2002). The top of the Arcola Limestone Member of the Mooreville Chalk is approximately mid-Campanian in age (Mancini *et al.*, 2008). The lower unnamed member is approximately 79 m thick in western Alabama and increases to 180 m in central Alabama (Raymond *et al.*, 1988). Lithologically, the lower member is comprised of calcareous, glauconitic, and micaceous sandstone near the base that fines upward into clay-rich, chalky marl (Raymond *et al.*, 1988; Kiernan, 2002). The vertebrate fauna of the lower unnamed member of the Mooreville Chalk is well-known and very diverse (Zangerl, 1948; Thurmond and Jones, 1981; Kiernan, 2002). The Arcola Limestone Member is approximately 3 m thick in the study area, and is comprised of two to four beds of impure limestone separated by marl interbeds (Raymond *et al.*, 1988). Whereas invertebrate fossils are comparatively common in this member, vertebrate remains are much rarer. The Mooreville Chalk is interpreted as representing offshore, inner to middle shelf environments for the lower member and a shallow, uplifted carbonate shelf environment for the Arcola Limestone Member (King, 1990; Kiernan, 2002).

Demopolis Chalk – The Demopolis Chalk is divided into the lower unnamed member and the upper Bluffport Marl Member. The age of the Demopolis Chalk ranges from middle Campanian to earliest Maastrichtian (Raymond *et al.*, 1988). The lower unnamed member of the Demopolis Chalk conformably overlies the Arcola Limestone Member of the Mooreville Chalk and it is approximately 132 m in thickness within the present study area (Raymond *et al.*, 1988) (Fig. 1). Near its base in the shallower-water facies, the lower unnamed member is lithologically similar to the Mooreville Chalk that underlies the Arcola Limestone Member, being comprised

of clay-rich marls, but becomes a more pure chalk (Puckett, 1996; Kiernan, 2002; Mancini and Puckett, 2005). This reduction of terrigenous clastics in the deeper-water facies upsection suggests a transgressive maximum of the epic sea during the Late Cretaceous in Alabama (Liu, 2007). The depositional environment for the lower unnamed member of the Demopolis Chalk is interpreted as ranging from middle to outer shelf (Kiernan, 2002). The overlying Bluffport Marl Member ranges from 15 m to 20 m in thickness in western and central Alabama (Raymond *et al.*, 1988), and the depositional environment is still considered to be outer shelf (Cagle, 1985), despite the increase in siliciclastic content. The Demopolis Chalk possesses a relatively rich and diverse vertebrate fauna (Derstler, 1988; Burnham, 1991), although not as fossiliferous as the Mooreville Chalk.

Ripley Formation – The Ripley Formation in western and central Alabama is undifferentiated, unlike that in Mississippi and Tennessee (Stephenson and Monroe, 1940) or eastern Alabama (Raymond *et al.*, 1988). Outcropping exposures of the Ripley Formation in western Alabama are early to mid-Maastrichtian in age (Smith and Mancini, 1983). The Ripley Formation in western Alabama ranges from approximately 11 m near the Mississippi border to 76 m in central and eastern portions of Alabama. Lithologically, the Ripley Formation is comprised of fine glauconitic sandstone, calcareous sand and clay, and thin layers of fossiliferous sandstone (Raymond *et al.*, 1988; Kiernan, 2002). The presence of coarse terrigenous, siliciclastic sediments is indicative of the continued marine regression that was underway at the time of deposition. King and Skotnicki (1990) conclude that the depositional environments of the Ripley Formation consisted of barrier island, lower shoreface, and inner shelf regions. The Ripley Formation contains a diverse, well-preserved invertebrate fauna but also has produced a number of significant vertebrate fossils.

Prairie Bluff Chalk – The Prairie Bluff Chalk disconformably overlies the Ripley Formation in western Alabama. Bryan (1992) suggests that this unconformity represents subaerial exposure and erosion of the upper Ripley Formation. The Prairie Bluff Chalk ranges in age from middle to late Maastrichtian (Moshkovitz and Habib, 1993), and attains a maximum thickness of approximately 34 m in central Alabama. However, it is completely absent in some areas of western Alabama (Raymond *et al.*, 1988). In contrast to the highly siliciclastic lithology of the Ripley Formation, the overlying Prairie Bluff Chalk consists of fine, bluish-gray sand and chalk (Raymond *et al.*, 1988). This formation appears to indicate a brief reversal of the marine regression that occurred at the end of the Cretaceous Period. Depositional environments represented by the Prairie Bluff Chalk are believed to correspond to offshore, shelf environments (King and Skotnicki, 1990; Kiernan, 2002). Fossil content of the Prairie Bluff Chalk includes well-preserved macroinvertebrates (Kiernan, 2002), and a lesser number of vertebrate fossils than underlying strata.

### Taphonomy

The fossil specimens analyzed in this study were all collected from Upper Cretaceous marine geological units contained in the Gulf Coastal Plain Province of western and central Alabama. This province is located on a passive continental margin which has not been subjected any major tectonic event since the opening of the Gulf of Mexico during the Late Jurassic to Early Cretaceous periods (Raymond *et al.*, 1988). Therefore, the outcropping Upper Cretaceous geologic units in Alabama have not been deeply buried and exposed to high temperature and pressure gradients which potentially could have altered the REE signatures in the contained fossils (Armstrong *et al.*, 2001; Patrick *et al.*, 2004).

The marl, chalk, and limestone portions of the Upper Cretaceous sequence in Alabama are largely impermeable to groundwater, while the sandier Tombigbee and Ripley units are used as regional aquifers (Davis, 1987). Regardless of the difference in permeability of the geologic units, it has been suggested that REE uptake of fossilizing bone during early diagenesis ceases when pore spaces in bone become filled with secondary apatite (Trueman *et al.*, 2006). This would imply that the REE content of groundwater in later diagenesis would have no effect on the REE signature of the fossils. Additionally, vertebrate fossils from the sandier Upper Cretaceous units in Alabama show no evidence of dissolution and recrystallization during later diagenesis that could have potentially altered their REE signatures (Patrick *et al.*, 2004).

Most of the samples analyzed in this study were acquired from associated, disarticulated to semi-articulated skeletons (Table 1). A few of the specimens from the carbonate-rich geologic units were recovered as isolated skeletal elements. However, these particular specimens are believed to represent bones dropped from decomposing or scavenged carcasses rather than material reworked from underlying geologic units, as the carbonate-rich units were deposited in relatively deeper or off-shore environments where reworking was unlikely to have occurred (See Sedimentology and Depositional Environments). Furthermore, these isolated skeletal elements lack the fracturing and abrasion typical of material reworked in high-energy environments (Manning and Dockery, 1992). Many of the specimens from the Tombigbee Sand and a few from the Ripley Formation were recovered as isolated skeletal elements. These two geologic units were deposited in higher-energy, nearshore environments (See Sedimentology and Depositional Environments) that contain a higher percentage of coarser siliciclastic material. As many of the isolated skeletal elements from these two geologic units display fracturing and considerable abrasion, reworking of the fossil material from underlying geologic units is a

distinct possibility. For isolated skeletal material of freshwater and terrestrial organisms recovered from these geologic units, the damage observed may also be the result of fluvial transport to the marine environment prior to burial.

## MATERIALS AND METHODS

### Fossil Samples

The vertebrate fossils analyzed in this study were obtained from the collections of the Alabama Museum of Natural History (ALMNH), with permission from the curator of vertebrate paleontology and the collections manager. Fossil specimens were selected on the basis of the relative completeness of their locality and stratigraphic information, as well as the quality of preservation. Museum records were incomplete for some specimens with older dates of collection (prior to 1960) and for some specimens that had been transferred from the Geological Survey of Alabama collections.

Several different taxa of reptiles and sharks, as well as skeletal elements from different parts of their anatomy, were analyzed to reduce potential preservational bias. Although all of the specimens were recovered from primarily carbonate marine deposits, marine, fluvial, and terrestrial vertebrates were included in the analysis to determine if REE content of the fossils was affected by osteological variations in organisms from different taxonomic groups, compared to previous studies of siliciclastic deposits in which there was no variation between taxa (Staron *et al.*, 2001; Patrick *et al.*, 2002, 2004, 2007a, 2007b; Martin *et al.*, 2005). Marine vertebrates included mosasaurs, plesiosaurs, marine turtles, and sharks. Fluvial vertebrates included crocodiles and trionychid turtles, whereas terrestrial vertebrates were represented by several

dinosaur specimens. In total, 49 vertebrate fossil specimens from five different geologic formations were used for this study (Table 1).

### Sample Preparation

Specimens were processed using methods modified from Patrick *et al.* (2004, 2007a) and Staron *et al.* (2001). Approximately 0.5 g of fossil material was removed from larger specimens using a Dremel<sup>®</sup> rotary tool equipped with diamond drill bits. Drill bits were washed with dilute trace metal grade nitric acid (HNO<sub>3</sub>) and rinsed with deionized water between samples to prevent cross contamination. Before sampling, specimens were washed with deionized water in an ultrasonic agitator to remove any adhering matrix and allowed to dry overnight. Sampling was restricted to the cortical region of the bone in an effort to reduce contamination or dilution of REE signatures by infilling matrix located in the trabecular bone. Microscopic examination of sample powders revealed no in-filling carbonate. Where possible, fragments of cortical bone associated with fossil specimens were selected for testing in lieu of damaging better preserved skeletal elements with the drill. Larger shark teeth were separately sampled from the crown and root while smaller shark teeth were entirely crushed and bulk sampled.

Approximately 100 mg of powder per sample were dissolved with 3 ml of trace metal grade nitric acid (10%) and diluted with 7 ml of deionized water. No effervescence was observed during dissolution of the samples that could have indicated the presence of carbonate matrix

Sample	ALMNH Number	Locality	Description
<b>Eutaw Formation, Tombigbee Sand Member</b>			
HA1	PV 1994.0001.0021	Catoma Creek, Montgomery Co.	Tylosaurus premaxilla (isolated)
HA2	PV 1994.0010.0006	Trussells Creek, Greene Co.	Plesiosaur vertebra (isolated)
HA3	PV 1985.0057	Aliceville, Pickens Co.	Plesiosaur partial skeleton
HA4	PV 1993.0002.0132	APE-3, Perry Co.	Platecarpus tympaniticus skull fragments
HA5	PV 2005.0006.0253	Montgomery Co.	Tylosaurus vertebra (isolated)
HA6	PV 2005.0006.0322	Catoma Falls, Montgomery Co.	Mosasaur phalanx fragment (isolated)
HA7	PV 1985.0072.0002	Greene Co.	Dinosaur long bone fragment (isolated)
HA8	PV 1990.0006.0003	Trussells Creek, Greene Co.	Trionychid turtle shell fragment (isolated)
HA9	PV 1990.0006.0011	Trussells Creek, Greene Co.	Crocodile jaw fragment (isolated)
HA10	PV 1991.0028.0013	Pleasant Hill, Greene Co.	Turtle fragmenary skeleton
HA11A	PV 1994.0002.0054.001	Trussells Creek, Greene Co.	Scapanorhynchus tooth (crown)
HA11B	PV 1994.0002.0054.001	Trussells Creek, Greene Co.	Scapanorhynchus tooth (root)
<b>Mooreville Formation, Lower Unnamed Member</b>			
HA12	PV 1985.0019	Newbern, Perry Co.	Tylosaurus partial skeleton
HA13	PV 1985.0022	West Greene, Greene Co.	Tylosaurus proriger partial skeleton
HA14	PV 1985.0048.0001	West Greene, Greene Co.	Clidastes partial skeleton
HA15	PV 2005.0006.0007	Dallas Co.	Clidastes vertebra partial skeleton
HA16	PV 1993.0013.0001	AH1-6, Hale Co.	Platecarpus partial skeleton
HA17	PV 2005.0006.0068	Harrell Station, Dallas Co.	Clidastes partial skeleton
HA18	PV 2005.0005.0072	West Greene, Greene Co.	Clidastes partial skeleton
HA19	PV 1993.0012.0001	Gainesville, Greene Co.	Clidastes partial skeleton
HA20	PV 1985.0010	Eutaw, Greene Co.	Protostegid turtle partial skeleton
HA21	PV 1985.0044	Greene Co.	Turtle carapace
HA22A	PV 1988.0020.0334.001	ADa-3, Dallas Co.	Scapanorhynchus tooth (root)
HA22B	PV 1988.0020.0334.001	ADa-3, Dallas Co.	Scapanorhynchus tooth (crown)
<b>Mooreville Formation, Arcola Limestone Member</b>			
HA23	PV 2005.0006.0058	Bolige, Greene Co.	Clidastes squamosal (isolated)
<b>Demopolis Formation, Lower Unnamed Member</b>			
HA24	PV 2005.0006.0008	Greene, Co.	Platecarpus cf. P.somenensis skeleton
HA25	PV 2005.0006.0074	Greene, Co.	Mosasaurus partial skeleton
HA26	PV 1988.0010	Gainesville, Sumter Co.	Crocodile osteoderm (isolated)
HA27	PV 1994.0001.0036	Harrell Station, Dallas Co.	Peritresius ornatus associated shell frags.
HA28	PV 1988.0004	Gainesville, Sumter Co.	Mosasaur vertebrae (4 associated)
Not Sampled	PV 1988.0020.0025.002	APE-2b, Uniontown, Perry Co.	Scapanorhynchus tooth
<b>Demopolis Formation, Bluffport Marl Member</b>			
HA30	PV 2005.0006.0005	Sumter Co.	Plesiosaur propodial (isolated)
HA31	PV 2005.0006.0069	Marengo, Co.	Mosasaurus partial skeleton
HA32	PV 1991.0017	Old Bluffport, Sumter Co.	Mosasaur vertebra (isolated)
HA33	PV 1991.0019	Type Locality, Bluffport, Sumter Co.	Protostegid turtle skull fragment
HA34	PV 1992.0045.0001	Harrell Station, Dallas Co.	Turtle plastron
Not Sampled	PV1992.0044.0003		Scapanorhynchus tooth
<b>Ripley Formation</b>			
HA36	PV 1990.0003	ALn-3, Sandy Ridge, Lowndes Co.	Mosasaurus hoffmanni skeleton
HA37	PV 1988.0020.0477.001	ALn-11, Braggs, Lowndes Co.	Mosasaur vertebra (isolated)
HA38	PV 2005.0006.0099	ALn-11, Braggs, Lowndes Co.	Mosasaur vertebra (isolated)
HA39	PV 2005.0006.0352	Braggs, Lowndes Co.	Hadrosaur bone fragment (isolated)
Not Sampled	PV 1994.0001.0034	Orion, Pike Co.	Mosasaur atlas intercentrum
HA41	PV 1994.0001.0033	Orion, Pike Co.	Mosasaurus hoffmanni vertebra (isolated)
HA42	PV 2005.0009.0001.001	Mt. Willing, Lowndes Co.	Ctenochelys pelvis
HA43	PV 2005.0009.0001.002	Mt. Willing, Lowndes Co.	Ctenochelys skeleton
HA44	PV 2005.0006.0285	Sumter Co.	Mosasaur partial skeleton
HA45	PV 2005.0006.0287	Bruceville, Bullock Co.	Hadrosaur bones (6 associated)
HA46	PV 1993.0002.0112.001	ALn-11, Braggs, Lowndes Co.	Scapanorhynchus tooth
<b>Prairie Bluff Formation</b>			
HA47	PV 1988.0018	ALn-7, Braggs, Lowndes Co.	Mosasaurus hoffmanni skeleton
HA48	PV 1991.0013.0002	ALn-7, Braggs, Lowndes Co.	Mosasaurus hoffmanni maxilla fragment
HA49	PV 1991.0032.0001	Ft. Deposit, Butler Co.	Plioplatecarpus vertebra (isolated)
HA50	PV 2002.0007.0001	Sumter Co.	Mosasaur partial skeleton
HA51	PV 1988.0021	ALn-7, Braggs, Lowndes Co.	Crocodile limb bone fragment (isolated)
HA52	PV 1991.0013.0019	ALn-7, Braggs, Lowndes Co.	Mosasaur vertebra fragment (isolated)
HA53	PV 1993.0002.0046.002	ALn-11, Braggs, Lowndes Co.	Scapanorhynchus tooth
TEST 1	PV 1988.0018	ALn-7, Braggs, Lowndes Co.	Mosasaurus hoffmanni rib, associated
TEST 2	PV 1988.0018	ALn-7, Braggs, Lowndes Co.	Mosasaurus hoffmanni rib, associated
TEST 3	PV 1988.0018	ALn-7, Braggs, Lowndes Co.	Mosasaurus hoffmanni rib, associated
TEST 4	PV 1988.0018	ALn-7, Braggs, Lowndes Co.	Mosasaurus hoffmanni rib, associated
<b>Unknown Formation</b>			
HA54	PV 1985.0024	Unknown	Turtle Skeleton

TABLE 2.1—Sample numbers, Alabama Museum of Natural History (ALMNH) specimen identification numbers, locality data, and description of fossil material analyzed in this study.

contamination. The solutions were subsequently passed through a Whatman<sup>®</sup> 0.2  $\mu\text{m}$  polyvinylidene fluoride syringe filter prior to chemical analysis to remove any undissolved particles.

### Chemical Analyses

Prepared solutions were diluted by a factor of 100 before analysis with a Perkin Elmer Elan 6000<sup>®</sup> inductively coupled plasma mass spectrometer (ICP-MS). The ICP-MS was calibrated prior to analysis using ICP-MS Multi-element Standard manufactured by High Purity Standards while Claritas PPT Multi-element Standard manufactured by Spex Chemical was used as the quality control standard during testing. Each sample was subjected to 20 runs and automated analytical software was used to process the results. Analytical error for most specimens was within  $\pm 5\%$  of certified values, and results are provided in parts per million (ppm) (Table 2). Resulting values were normalized with the North American Shale Composite (NASC) (Gromet *et al.*, 1984). NASC values used are identical to those used by previous researchers and are listed in Table 2.

### Statistical Analyses

Principal component analysis (Davis, 1986) was conducted using PAST ver. 2.17c (Hammer *et al.*, 2001) to further analyze the normalized results and provide additional graphical representation of the data. REE ratios were used rather than REE concentrations to remove the biasing effects of differing osteological material, differing REE quantities, or other potentially negative effects. Assumption of principle component analysis are: 1) linearity of the data, 2)

large variances have important structure and, 3) principal components are orthogonal (Shlens, 2014).

Sample	Formation/Region	La	Ce	Pr	Nd	Sm	Eu	Gd	Tb	Dy	Ho	Er	Yb	Lu	ΣREE	
HA1	Tombigbee Sand Mbr. / C	76.54	103.91	9.94	37.77	6.42	1.66	6.48	0.98	6.77	1.45	4.60	0.64	4.57	0.71	262.45
HA2	Tombigbee Sand Mbr. / A	583.62	804.63	80.64	310.42	50.64	13.28	66.25	9.90	68.75	15.96	47.71	6.49	39.16	5.88	2,103.33
HA3	Tombigbee Sand Mbr. / A	130.63	165.24	17.19	62.25	10.28	2.41	10.41	1.58	11.04	2.44	7.71	1.14	7.82	1.22	431.37
HA4	Tombigbee Sand Mbr. / B	118.54	194.61	22.30	85.80	15.04	3.61	15.12	2.14	13.86	2.81	8.09	1.02	6.53	0.99	490.47
HA5	Tombigbee Sand Mbr. / C	162.67	226.85	22.63	83.27	14.11	3.73	13.56	2.00	13.36	2.79	8.41	1.18	7.66	1.13	563.36
HA6	Tombigbee Sand Mbr. / C	246.87	362.32	35.57	133.12	21.01	5.41	20.84	3.06	20.32	4.19	12.35	1.67	10.42	1.53	878.67
HA7	Tombigbee Sand Mbr. / A	31.01	35.72	3.39	12.71	2.26	0.68	2.92	0.44	3.49	0.83	2.92	0.43	3.35	0.53	100.69
HA8	Tombigbee Sand Mbr. / A	185.16	338.55	38.85	150.55	29.81	7.34	32.01	4.96	32.80	6.76	19.95	2.82	17.87	2.48	869.90
HA9	Tombigbee Sand Mbr. / A	596.71	707.42	71.39	266.59	42.80	11.71	53.71	8.43	61.44	14.37	46.30	6.77	44.12	6.68	1,938.43
HA10	Tombigbee Sand Mbr. / A	142.68	283.50	31.54	119.19	21.60	5.20	19.24	2.86	18.12	3.49	9.69	1.25	7.57	1.03	666.97
HA11A	Tombigbee Sand Mbr. / A	426.93	778.98	93.46	388.32	78.05	22.61	104.93	16.98	119.41	25.69	73.54	9.72	56.80	7.61	2,203.03
HA11B	Tombigbee Sand Mbr. / A	202.40	369.32	43.38	179.98	36.94	10.33	48.13	7.59	52.82	11.41	33.40	4.52	27.25	3.77	1,031.25
HA12	Mooreville Chalk / C	233.01	216.86	17.40	57.83	6.81	1.35	9.29	1.36	11.04	3.05	11.07	1.69	11.98	1.98	584.73
HA13	Mooreville Chalk / A	338.64	567.47	59.28	223.51	36.25	9.85	39.19	5.65	36.73	7.38	20.30	2.52	14.06	1.93	1,362.76
HA14	Mooreville Chalk / A	54.54	72.92	7.53	28.17	4.71	1.07	5.03	0.73	5.27	1.18	3.86	0.56	4.07	0.67	190.32
HA15	Mooreville Chalk / B	305.34	364.00	36.66	129.69	19.60	4.85	22.19	3.37	23.70	5.38	16.29	2.18	13.21	1.83	948.30
HA16	Mooreville Chalk / A	419.23	676.25	69.40	256.61	41.09	10.43	44.30	6.61	44.11	9.33	27.03	3.53	20.72	2.91	1,631.53
HA17	Mooreville Chalk / B	467.22	726.24	82.73	304.57	50.66	12.00	53.90	8.31	55.88	11.74	33.70	4.30	23.88	3.16	1,838.28
HA18	Mooreville Chalk / A	86.33	171.21	18.39	69.78	12.56	2.98	11.46	1.66	10.50	2.02	5.69	0.72	4.53	0.63	398.49
HA19	Mooreville Chalk / A	507.07	853.55	98.63	366.02	60.65	13.45	58.29	8.80	56.54	11.37	31.79	4.03	22.53	3.03	2,095.75
HA20	Mooreville Chalk / A	53.88	93.30	9.52	36.81	6.82	1.60	6.97	1.03	7.09	1.48	4.62	0.63	4.31	0.63	228.68
HA21	Mooreville Chalk / A	277.02	440.94	45.49	165.80	27.18	7.38	26.35	4.06	26.34	5.53	16.58	2.32	14.70	2.17	1,061.86
HA22A	Mooreville Chalk / B	321.76	470.59	53.24	200.54	31.57	8.23	36.01	5.32	36.46	7.81	22.46	2.87	16.41	2.23	1,215.48
HA22B	Mooreville Chalk / B	123.43	133.76	13.88	51.38	7.78	2.11	10.35	1.62	12.57	3.11	10.48	1.50	9.61	1.42	382.99
HA23	Arcola LS Mbr. / A	29.16	36.12	3.94	14.62	2.44	0.54	2.74	0.41	3.19	0.74	2.55	0.36	2.84	0.43	100.10
HA24	Demopolis Chalk / A2	471.13	846.59	94.45	340.56	55.37	13.20	50.78	7.35	44.82	8.60	23.49	3.04	17.55	2.44	1,979.37
HA25	Demopolis Chalk / A2	146.22	229.07	27.11	106.29	19.49	4.75	19.48	2.81	18.29	3.72	10.95	1.45	8.90	1.27	599.81
HA26	Demopolis Chalk / A1	175.61	296.51	26.15	100.56	15.53	3.61	20.61	3.14	23.34	5.45	16.95	2.34	14.53	2.12	706.43
HA27	Demopolis Chalk / C	732.66	#####	216.08	868.25	159.36	40.88	143.50	20.32	118.22	21.26	53.75	6.41	34.12	4.47	4,378.55
HA28	Demopolis Chalk / A1	94.56	112.80	11.60	42.72	6.84	1.72	8.13	1.25	9.29	2.15	7.21	1.06	7.24	1.09	307.66
HA30	Bluffport Marl Mbr. / A	311.15	494.42	48.73	177.99	28.90	7.20	31.32	4.87	32.16	6.93	19.94	2.64	14.93	2.08	1,183.26
HA31	Bluffport Marl Mbr. / A	128.46	204.65	19.82	73.31	11.50	2.93	13.43	2.05	13.98	3.03	8.75	1.14	6.65	0.92	490.61
HA32	Bluffport Marl Mbr. / A	334.90	474.95	54.62	205.86	35.31	8.28	40.48	6.10	40.61	8.86	25.92	3.46	20.08	2.90	1,262.32
HA33	Bluffport Marl Mbr. / A	445.02	634.55	71.59	265.17	43.91	10.85	47.61	7.09	47.19	10.06	28.46	3.62	20.20	2.76	1,638.08
HA34	Bluffport Marl Mbr. / A	129.75	137.11	13.79	49.62	7.70	1.98	9.51	1.46	10.69	2.60	8.35	1.21	7.59	1.11	382.47
HA36	Ripley Formation / C	77.88	129.64	11.75	44.14	7.06	1.94	7.85	1.18	8.16	1.81	5.50	0.78	5.05	0.77	303.50
HA37	Ripley Formation / C	98.04	184.01	19.19	75.39	14.28	3.66	15.22	2.33	14.98	3.21	9.28	1.30	8.35	1.29	450.52
HA38	Ripley Formation / C	25.68	35.90	3.62	13.75	2.21	0.63	2.63	0.38	2.78	0.66	2.17	0.30	2.24	0.35	93.30
HA39	Ripley Formation / C	12.32	18.49	1.76	6.92	1.12	0.27	1.48	0.20	1.50	0.34	1.11	0.15	1.07	0.17	46.90
HA41	Ripley Formation / D	195.57	193.37	32.14	132.22	24.72	6.91	31.49	4.46	30.09	6.81	20.16	2.79	17.05	2.65	700.43
HA42	Ripley Formation / C	38.29	68.33	7.02	26.19	4.43	1.21	4.64	0.68	4.47	0.95	2.77	0.37	2.41	0.36	162.11
HA43	Ripley Formation / C	82.28	135.79	13.89	53.28	9.23	2.75	10.52	1.61	10.91	2.45	7.54	1.05	6.77	1.03	339.10
HA44	Ripley Formation / A	463.03	917.21	102.73	392.50	66.52	15.50	67.01	9.70	61.36	12.54	34.74	4.43	25.53	3.58	2,176.41
HA45	Ripley Formation / D	12.99	16.75	2.53	10.23	1.86	0.47	1.95	0.26	1.79	0.36	1.09	0.13	0.98	0.14	51.53
HA46	Ripley Formation / C	268.08	473.44	49.73	188.67	30.60	8.29	31.45	4.70	31.04	6.63	18.80	2.46	14.19	1.96	1,130.04
HA47	Prairie Bluff Chalk / C	118.00	208.75	21.53	86.32	13.93	3.79	14.88	2.13	13.84	2.83	7.90	0.99	5.71	0.81	501.41
HA48	Prairie Bluff Chalk / C	29.29	60.81	6.83	27.01	4.79	1.18	4.45	0.66	4.37	0.90	2.63	0.34	2.17	0.30	145.73
HA49	Prairie Bluff Chalk / C	123.91	156.41	15.51	58.90	8.48	2.40	10.12	1.50	10.96	2.64	8.55	1.23	8.11	1.28	410.01
HA50	Prairie Bluff Chalk / A	197.12	365.20	40.55	160.46	26.22	6.42	25.73	3.65	23.58	4.69	12.79	1.58	8.62	1.17	877.79
HA51	Prairie Bluff Chalk / C	34.45	72.18	7.99	31.43	5.45	1.29	5.14	0.73	4.68	0.90	2.58	0.32	2.07	0.28	169.48
HA52	Prairie Bluff Chalk / C	197.15	345.84	36.71	139.64	21.14	5.42	21.22	3.24	21.28	4.61	13.40	1.77	10.41	1.50	823.33
HA53	Prairie Bluff Chalk / C	806.24	#####	224.77	865.09	144.81	36.66	122.69	18.22	107.83	19.55	48.92	5.94	30.68	3.90	4,472.24
Test 1	Prairie Bluff Chalk / C	223.67	452.47	45.60	177.51	30.37	7.78	29.97	4.23	26.51	5.20	14.35	1.81	10.42	1.47	1,031.35
Test 2	Prairie Bluff Chalk / C	236.48	480.08	49.02	190.81	32.23	8.18	31.70	4.48	27.28	5.28	14.32	1.81	10.38	1.44	1,093.47
Test 3	Prairie Bluff Chalk / C	208.61	420.64	43.16	168.16	28.84	7.41	28.91	4.08	25.40	4.99	13.71	1.75	9.95	1.42	967.03
Test 4	Prairie Bluff Chalk / C	226.90	463.80	47.40	185.59	31.63	8.15	31.90	4.52	27.79	5.46	14.91	1.89	10.96	1.53	1,062.43
HA54	Unknown	93.56	147.81	14.59	53.53	8.59	2.12	9.30	1.40	9.30	1.99	5.91	0.83	5.22	0.78	354.91
NASC Values in ppm (Gromet et al.,		31.10	66.70	7.70	27.40	5.59	1.18	4.90	0.85	4.17	1.02	2.84	0.48	3.06	0.46	

TABLE 2.2—Raw results (ppm) of rare earth element (REE) concentrations in analyzed samples. North American Shale Composite (NASC) values of Gromet *et al.* (1984) were used for normalization of data.

## RESULTS

The results of the analysis reveal that vertebrate fossils from the Upper Cretaceous carbonate marine formations in Alabama possess relatively high concentrations of REE ( $\Sigma$ REE range 47 – 4472 ppm, 945 ppm average) that are similar to those reported for the Upper Cretaceous siliciclastic marine formations of the Western Interior Seaway (Patrick *et al.*, 2002, 2004, 2007a) and the Atlantic Coastal Plain (Staron *et al.*, 2001) (Table 2). Overall, NASC normalized results indicate that each of the Upper Cretaceous marine geologic units of western and central Alabama possess unique REE profiles over a relatively wide geographic area.

### Stratigraphy and REE Analyses

The primary focus of this study was to determine if the outcropping Upper Cretaceous marine carbonate formations of western Alabama possessed unique REE profiles. Initially all of the NASC normalized samples from the study area were plotted together on spider diagrams by stratigraphic unit, but offered equivocal results. Spatial relationships among the collecting localities were then considered based on geographical and geological information on record for the fossil specimens at ALMNH. Fossils from individual stratigraphic units display similar REE profiles when restricted to a smaller geographic scale but have different REE profiles from the same stratigraphic units in adjacent areas. As a result, the initial study area in Alabama is subdivided into sub-regions A, B, C and D (Fig. 1). Subsequent spider diagrams for the different stratigraphic units within these sub-regions show an increased consistency in REE profiles based on their more restricted geographic extent.

Sub-region A is the only portion of the study area with samples from all Upper Cretaceous marine stratigraphic units in western Alabama (Fig. 1), and thus, data from this

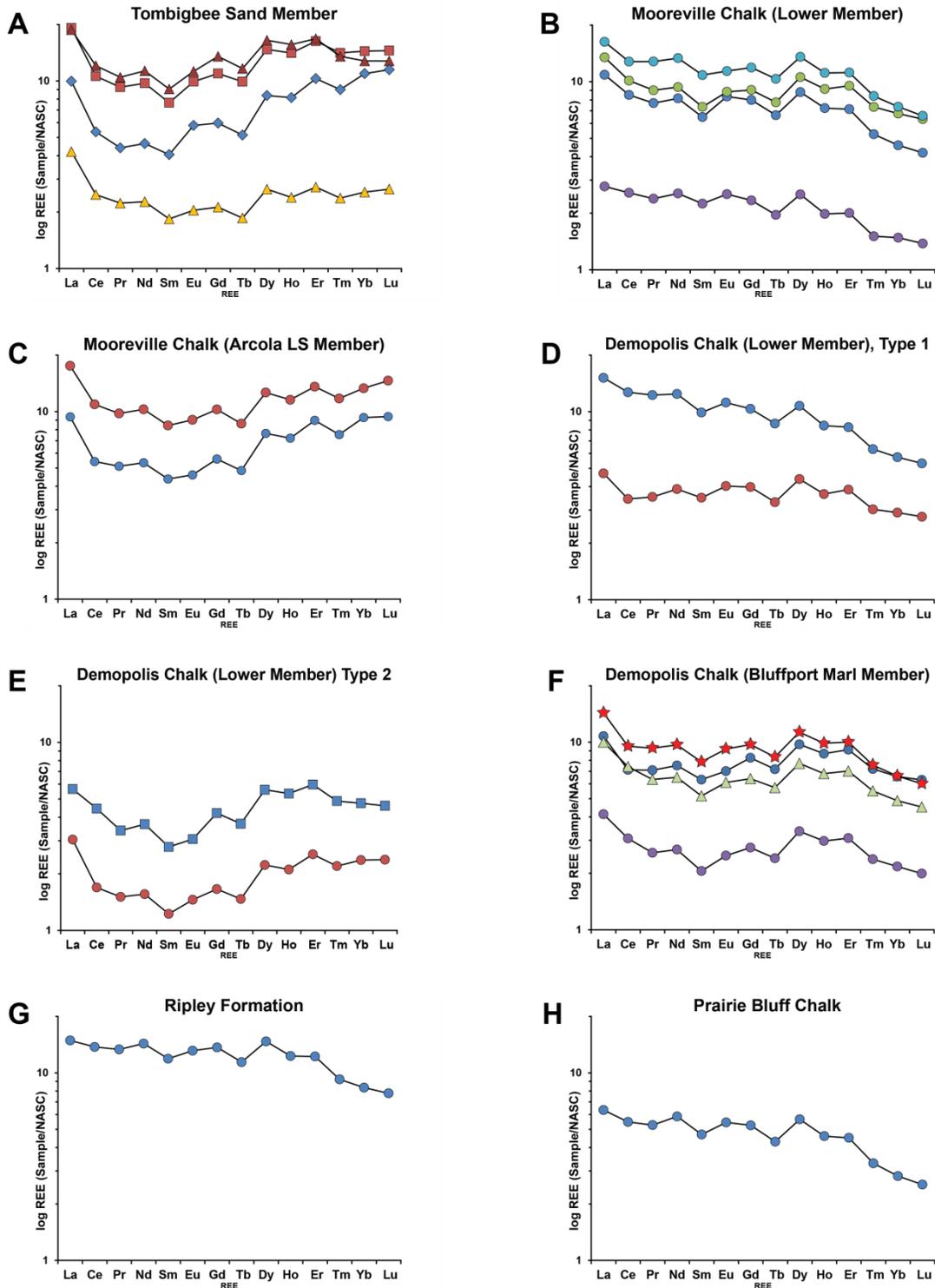


FIGURE 2.3—Spider diagrams of REE profiles for vertebrate fossils from sub-region A of the study area showing representative differences between geologic units. Symbols: Circles = Mosasaurs, Triangles = Plesiosaurs, Squares = Crocodiles, Stars = Marine Turtles, and Diamonds = Dinosaurs. Diagrams A – H are progressively up section, from oldest to youngest.

region is used for further comparison of REE data for different taxonomic groups (Figs. 3, 4, and 5). All spider diagrams were plotted to the same log scale to aid in comparison between geologic units and geographic areas. Therefore, fossil samples with REE concentrations that were too low or too high to fit on the uniformly formatted diagrams were multiplied or divided by a factor of 10.

The seven specimens from the Tombigbee Sand in this region have an average  $\Sigma$ REE of 1,168 ppm (Table 2). Taxonomic groups analyzed from this geologic unit and sub-region include plesiosaurs, marine turtles, sharks, dinosaurs, trionychid (freshwater) turtles, and crocodiles.

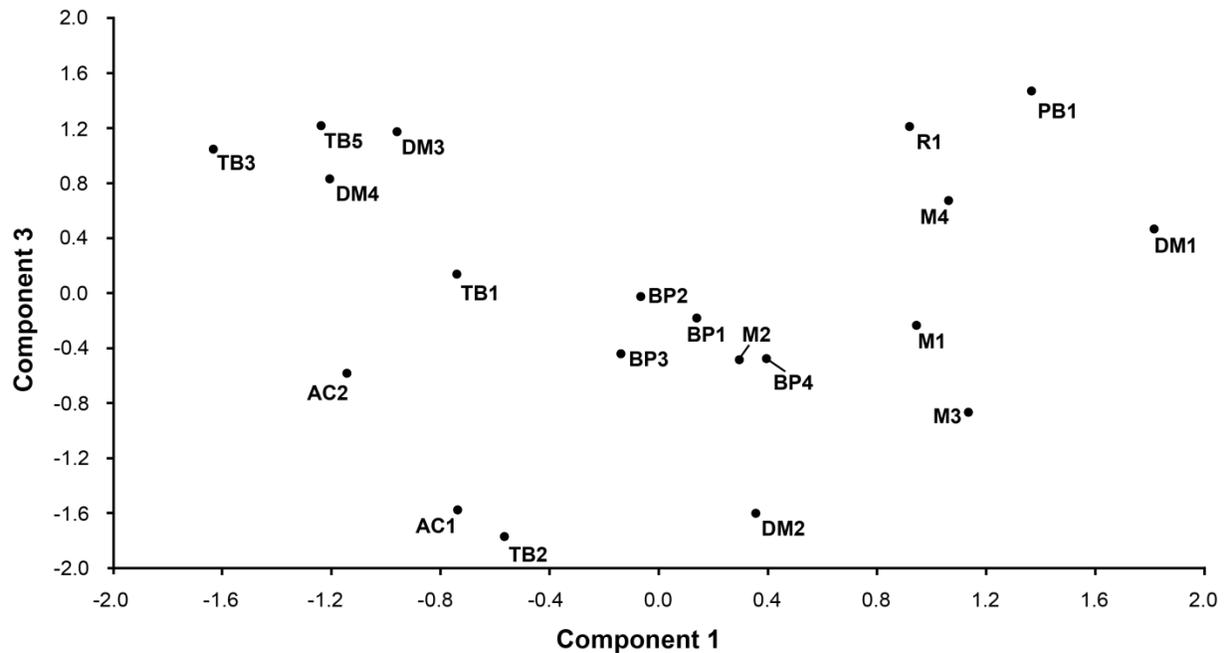


FIGURE 2.4—Results of principal component analysis (PCA) of NASC normalized REE ratios for selected fossil vertebrates from sub-region A. Component 1: Eigenvalue = 0.597233, Variance = 90.627 %; Component 3: Eigenvalue = 0.00437308, Variance = 0.66359 %. Component 2 was not graphed because it provided less visual discrimination than Component 3. TB = Tombigbee Sand, M = Mooreville Chalk, AC = Arcola Limestone, DM = Demopolis Chalk, BP = Bluffport Marl, R = Ripley, PB = Prairie Bluff Chalk.

Of these taxonomic groups, the plesiosaurs, crocodiles, and dinosaurs share a similar REE profile (Fig. 3A) whereas the sharks, marine turtles and freshwater trionychid turtles differ substantially (Fig. 5).

The overlying lower unnamed member of the Mooreville Chalk in sub-region A produces similar results to the Tombigbee Sand, with an average  $\Sigma$ REE of 1,130 ppm. Six specimens from three taxonomic groups were tested from this unit, including mosasaurs,

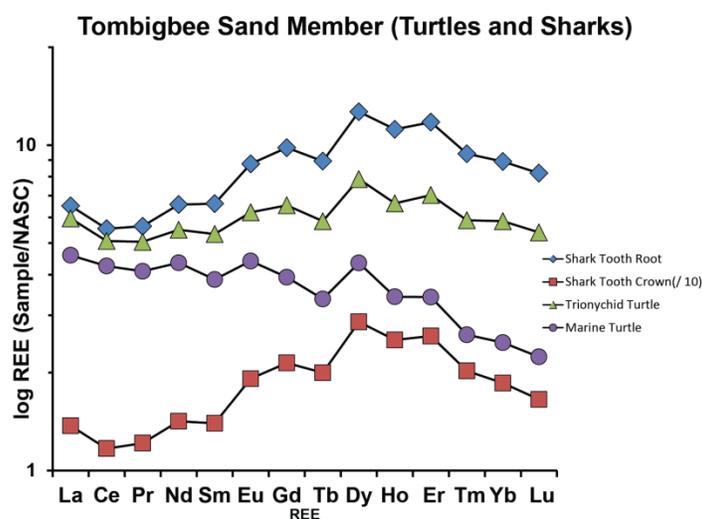


FIGURE 2.5—Taxonomic groups from the Tombigbee Sand Member of the Eutaw Formation in sub-region A with atypical REE profiles. Note differences with typical REE profiles in Figure 3A.

protostegid marine turtles, and toxochelid marine turtles. The mosasaur specimens share a very similar REE profile (Fig. 3B), whereas the turtle groups differ slightly.

Fossil specimens from the Arcola Limestone Member of the Mooreville Chalk are considerably lower in  $\Sigma$ REE than the underlying geologic units, having only about 145 ppm. Vertebrate fossils from the Arcola Limestone are comparatively rare and only two specimens of mosasaur were available for analysis, with both sharing a similar REE profile (Fig. 3C).

Four vertebrate fossil specimens, representing mosasaurs and crocodiles, were analyzed from the lower unnamed member of the Demopolis Chalk, with an average  $\Sigma$ REE of 898 ppm. Two distinct REE profiles are found (Figs. 3D and 3E), which correspond to the two different facies within the member (Mancini and Puckett, 2002).

Five specimens from the overlying Bluffport Marl Member of the Demopolis Chalk in sub-region A have an average  $\Sigma$ REE of 991 ppm, nearly 100 ppm higher than the lower unnamed member. Taxonomic groups analyzed from this geologic unit include mosasaurs, plesiosaurs, protostegid marine turtles, and toxochelid marine turtles. The mosasaurs, plesiosaurs, and protostegid turtles share a similar REE profile (Fig. 3F) whereas the toxochelid turtle differs substantially.

The  $\Sigma$ REE content for the Ripley and Prairie Bluff Chalk specimens are 2,176 ppm and 878 ppm respectively. In each of these geologic units, only one specimen was available in the ALMNH collections from sub-region A, both belonging to the mosasaur taxonomic group. Both of these geologic units share similar REE profiles, but are separated by concentration of  $\Sigma$ REE (Figs. 3G and 3H).

#### REE Profiles in Different Taxonomic Groups

REE profiles from different categories of vertebrates were analyzed to determine if the REE signatures are uniform among taxonomic groups within a given carbonate marine stratigraphic unit and if not, whether differing profiles could be used to classify fragmentary fossil remains whose taxonomic status is unknown. Clear differences in the REE signatures between some groups of taxa are observed, using the Tombigbee Sand in sub-region A as an example (Figs. 3A and 5). Shark teeth are substantially different from other taxa of a given

stratigraphic unit and region in nearly every case. Freshwater turtles and toxochelid marine turtles usually differ considerably from the REE signatures displayed by mosasaurs, plesiosaurs, crocodiles, and dinosaurs but the protostegid turtle (Table 1, HA33) from the Bluffport Marl in sub-region A (Fig. 3F) and the *Ctenochelys* specimen (HA42 – HA43) from the Ripley Formation in sub-region C (Fig. 6) do not differ from the other taxonomic groups in their respective sub-regions. The possible reasons for the REE profile variations observed in sharks and turtles are addressed in the discussion portion of this paper. Most of the statistical analysis in

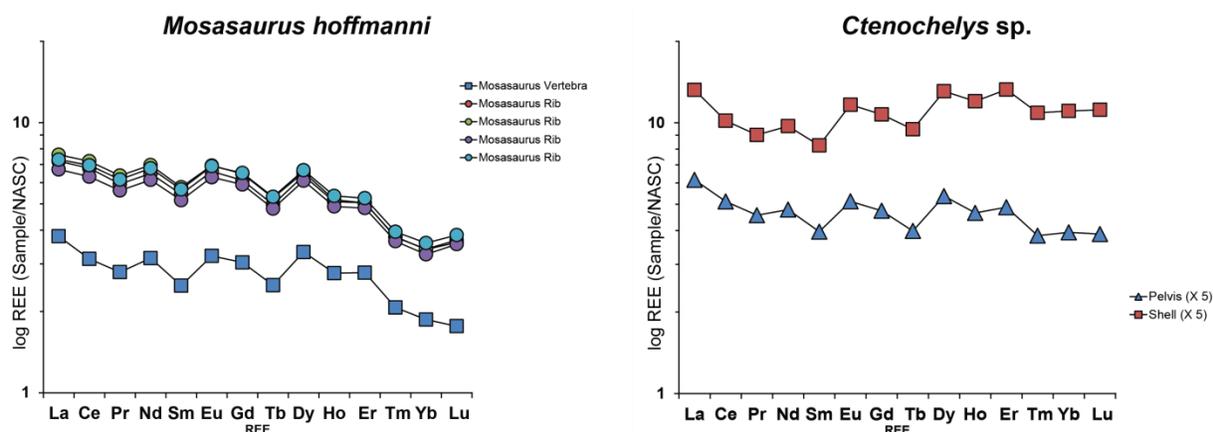


FIGURE 2.6—NASC normalized REE profiles of different skeletal elements in *Mosasaurus hoffmanni* (left), and the marine turtle *Ctenochelys* sp. (right).

this study relies on the REE signatures of mosasaurs and plesiosaurs as they are the most consistent and have the largest sample pool (n = 30).

Dinosaurs analyzed in this study typically have similar REE ratios to the other taxa in a given formation but the total REE content is much lower. For example, samples HA41 (mosasaur) and HA45 (hadrosaur) from the Ripley Formation in sub-region D both produce a similar profile if plotted in a spider diagram, however, the mosasaur has a  $\Sigma$ REE content of 700 ppm whereas the dinosaur specimen has approximately 51 ppm (Table 2).

## Skeletal Element REE Analyses

REE signatures between different skeletal elements within the same individual, collected from the same depositional setting, were analyzed. The first test subject was a partial skeleton of *Mosasaurus hoffmanni* (PV 1988.0018) from the Prairie Bluff Chalk Formation and the second, a nearly complete and well-preserved skeleton of the marine turtle *Ctenochelys* sp. (PV 2005.0009.0001.001) from the Ripley Formation (Table 1).

Two samples of cortical bone were taken from the mosasaur specimen during this study. The first sample was a fragment of a rib that was analyzed in four separate solutions, and the second sample was obtained from the transverse process of a thoracic vertebra (Fig. 6). Results show that although the REE profiles for the two different skeletal elements are nearly identical, the quantities of REE differ greatly, being approximately half as concentrated in the vertebra as they are in the rib.

Two *Ctenochelys* cortical bone samples were further tested (Fig. 6). The first sample was taken from the pelvis, which was located internally within the shell of the living animal, and the second sample was taken from a peripheral bone of the carapace, which is part of the shell located close to the external surface of the living animal. Results show that the profiles are nearly identical but, as in the case of the *M. hoffmanni* analysis, the quantities of REE between the two skeletal elements are considerably different. The amounts of REE in the pelvis bone sample are approximately half of those found in the peripheral bone sample.

## DISCUSSION

### Stratigraphic REE Analysis

The NASC normalized REE concentrations of all the fossil samples were plotted as spider diagrams in order to determine if there were any obvious intraformational similarities and extraformational differences of the geologic units. However, it was clear that the REE signatures had a more limited geographical extent than expected, based on previous work on siliciclastic deposits, and that certain taxonomic groups had inconsistent REE ratios. This revelation led to the division of the results into smaller groups both geographically and taxonomically (Figs. 1 and 3).

Although the majority of the Upper Cretaceous marine strata in western Alabama consist of carbonates, the chalk, marls and limestones in the study area contain subordinate amounts of fine-grained siliciclastic material (King, 1990). This material was likely derived from the Appalachian subcontinent located to the north and northeast of the study area at the time of deposition. It is hypothesized that the observed differences in intraformational REE profiles of fossil specimens over a relatively limited geographic extent may be the result of REE variation in the siliciclastic input from different watersheds draining the nearby Appalachian Mountains during the Late Cretaceous.

Sample HA14 was taken from a *Clidastes* (mosasaur) skeleton with locality information indicating that it was collected from the Mooreville Chalk in sub-region A. However, the REE signature from that particular specimen deviates greatly from the other mosasaur specimens from the Mooreville Chalk in that region. When compared with specimens from adjacent geologic formations, it was determined that sample HA14 is a very close match with the *Clidastes* (HA 23) specimen collected from the Arcola Limestone in the same region. At some outcrops in

western Alabama, it can be difficult to discern the lower unnamed member of the Mooreville Chalk and the marly interbeds of the Arcola Limestone Member. Residual matrix located in the vertebral foramina of HA14 is lithologically similar to the Arcola Limestone, containing a lower percentage of clay. Therefore, this test using mosasaur specimens suggests that REE signatures can be used to place vertebrate fossils within the correct stratigraphic context (provenance) in carbonate settings.

REE profiles for samples from the lower unnamed member of the Demopolis Chalk in sub-region A display a bimodal distribution. Samples HA24 and HA25 have negative slopes that are relatively depleted in HREE (designated as Type 1, Fig. 3D) whereas samples HA26 and HA28 display profiles that are relatively enriched in HREE (designated as Type 2, Fig. 3E). This distribution implies that the two facies types for the lower unnamed member of the Demopolis Chalk, deeper water (Type 1) and shallower water (Type 2), are reflected in the REE profiles for the geologic unit. The deep and shallow facies types of the lower Demopolis Chalk were previously described by Mancini and Puckett (2002) using sedimentology, sequence stratigraphy, and invertebrate fossil content.

Cerium anomalies ( $Ce/Ce^*$ ) for the fossil specimens were calculated ( $Ce/Ce^* = Ce_N / ((La_N + Pr_N) / 2) - 1$ ) using normalized REE data from Table 2. Cerium anomalies are often indicative of redox conditions in marine environments (De Baar *et al.*, 1988) and previously have been used as a proxy for paleoredox conditions (Wright *et al.*, 1987; Holser, 1997; Shields *et al.*, 1997; Patrick *et al.*, 2004). The vast majority of cerium anomalies from the present study are negative, ranging from -0.33 to -0.01. However, a few of the cerium anomalies in specimens from the Prairie Bluff Chalk in sub-region C of the study area (Fig. 1) are slightly positive, ranging from 0.01 to 0.11. Negative cerium anomalies are usually considered to be representative

of oxidizing conditions (Patrick *et al.*, 2004). Paleobathymetry estimates for the carbonate facies in the study area widely vary, ranging from 35 to 90 meters (Puckett, 1991) to possibly as much as 436 to 601 meters (Schein, 2006). The nearshore, siliciclastic-rich Tombigbee Sand Member and Ripley Formation were likely deposited in shallower, well-oxygenated water (King and Skotniki, 1990). The negative cerium anomalies observed in the present data would suggest that the carbonate stratigraphic units in Alabama were deposited at the shallower, more oxic end of the paleobathymetry estimates. This hypothesis is complicated by the tendency for negative cerium anomalies to form in organic-rich alkaline waters in which carbonate and humic acids compete for REE complexing (Pourret *et al.*, 2008). In organic-rich alkaline waters, cerium tends to be adsorbed onto humic acids and removed via colloidal formation, resulting in negative cerium anomalies. In organic-poor waters, cerium preferentially forms complexes with dissolved carbonate, which may result in positive cerium anomalies (Pourret *et al.*, 2008).

Principal component analysis (Davis, 1986) was performed to confirm the result from the spider diagrams that vertebrate fossils from the geologic units in each geographic region possess distinctive REE profiles. This procedure was similar to those performed by Patrick *et al.* (2004, 2007a) and Staron *et al.* (2001). The Pr/Yb, La/Tm, La/Sm, and Nd/Tm ratios were determined to be the most useful for accurate classification of the Alabama geologic units, as these ratios produced the most distinctive clustering during statistical analysis. Principal component analysis (PCA) clustering for the stratigraphic units in sub-region A analyzed in this study are presented in Figure 4.

The statistical analysis did not produce distinctive clusters for all geologic units in sub-region A. However, the analysis did allow for distinction between overlying/underlying stratigraphic units (Fig. 2). For example, the Tombigbee Sand Member of the Eutaw Formation

is statistically distinguishable from the overlying lower member of the Mooreville Chalk (Fig. 4), whereas the Arcola Limestone Member is distinct from the underlying lower unnamed member of the Mooreville Chalk. This pattern of statistical distinction between overlying/underlying geologic units is repeated throughout sub-region A. In the analysis of the Demopolis Chalk, the Type 1, deeper water facies of the lower member (DM1 and DM2) clustered separately from the Type 2, shallower water facies (DM3 and DM4). This characteristic is helpful in distinguishing the lower unnamed member of the Demopolis from the underlying shallow water Arcola Limestone and the overlying deeper water Bluffport Marl Member.

As a further test of the values of REE analysis for stratigraphic applications, a fossil turtle (PV 1985.0024) lacking precise locality data but known to be from the Late Cretaceous of Alabama was analyzed. Based on the results of the discriminant analysis (Fig. 4), it is currently not possible to assign the turtle specimen to a definitive stratigraphic context with any degree of certainty. Furthermore, variation in the REE signature between some fossil vertebrates will require that additional analyses be performed to increase the sample number of the various taxonomic groups in the different geographic regions of Alabama and elsewhere with carbonate strata.

The differences observed in REE signatures of some isolated specimens from the Tombigbee Sand Member of the Eutaw Formation, such as turtles and sharks, may be the result of reworking from the underlying lower unnamed member of the Eutaw Formation. The Tombigbee Sand was deposited in a nearshore marine environment during the beginning of a transgressive phase (Mancini and Soens, 1994; Mancini and Puckett, 2002, 2005). As a result, several transgressive lag deposits with shark teeth and other fossil vertebrate material concentrated from the underlying strata are found within the member (Manning and Dockery,

1992). Many of the isolated skeletal elements from the Tombigbee Sand display evidence of fracture and excessive abrasion typical of reworked fossil material. The comparatively siliciclastic-rich portions of the Ripley Formation were also deposited in shallower nearshore environments (King and Skotnicki, 1990) and REE results may be affected by redeposition of fossil material. Although reworked fossil material is a possibility in the Ripley Formation, many of the specimens analyzed in this study were acquired from disarticulated but associated specimens (Table 1), which suggests that they were not reworked. Furthermore, some of the isolated specimens from the Ripley Formation may have been originally preserved as associated specimens, but became isolated by present-day weathering prior to discovery. Fossils from the remaining stratigraphic units in this study were recovered from deeper, lower energy, offshore deposits (Raymond *et al.*, 1988; King and Skotnicki, 1990) in which reworking of fossils is unlikely.

Although the differences are more subtle than those between the siliciclastic marine formations of the Western Interior Seaway, vertebrate fossils from the Upper Cretaceous carbonate marine formations of western and central Alabama have distinctive REE signatures.

#### REE Profiles in Different Taxonomic Groups

Considerable differences in the REE profiles between some taxonomic groups, such as sharks, freshwater turtles, and some marine turtles are indicated (Fig. 5). Some of these differences could be attributed to reworking of fossil material in certain geologic units, such as the Tombigbee Sand which is known to contain lag deposits (Emry *et al.*, 1981). However, if reworking of the fossils were the cause of REE signature variation in sharks and turtles, one would likely observe differences in other taxonomic groups like mosasaurs and plesiosaurs, or

even variation among individuals within a specific taxonomic group. This would also not explain the differences between turtles and sharks observed in the overlying chalk units where reworking did not occur.

Another possible explanation for the observed differences in REE signatures of shark teeth may lie in the structure of shark tooth enamel. The enamel contains substantial amounts of fluorapatite, which is composed of coarser crystals and is more stable than the carbonate hydroxyapatite found in bone tissue (Vennemann *et al.*, 2001; Trueman *et al.*, 2004; Becker *et al.*, 2008; Kohn, 2008). As a result of this stable structure, the tooth enamel is less likely to recrystallize during fossilization, and resists uptake of REE from the environment in the way that the less stable bone phosphates acquire REE from surrounding pore waters. The method of accumulation of REE in tooth enamel is not fully understood but is likely the result of adsorption or intracrystalline diffusion (Kohn, 2008).

The reason for the REE signature variation in some of the turtle specimens in this study is not certain. It may be due to reworking of isolated skeletal elements in geologic units deposited in nearshore environments such as the Tombigbee Sand, histological differences in the bones of some turtle taxonomic groups (unlikely, based on previous studies), or perhaps it can be attributed to sampling or analytical errors. Although, statistical analysis using cerium anomalies and select REE ratios produce uniform clustering of taxonomic groups by geologic unit, further statistical analysis and an adequate sample size will be necessary to determine if it is possible to distinguish between taxa when dealing with isolated skeletal material.

A more interesting discrepancy among various taxonomic groups is in the quantities of  $\Sigma$ REE that were absorbed during fossilization, particularly in dinosaurs versus other reptiles. The average  $\Sigma$ REE for dinosaurs in this study is 66 ppm, whereas the average  $\Sigma$ REE for other reptiles

in the same stratigraphic units is 777 ppm. However, the REE signatures present in dinosaur fossils are nearly identical to those observed in other reptile groups from the same geologic units and geographic regions (See Fig. 3A for example). If the dinosaur specimens had originally been buried in a terrestrial depositional environment and then became reworked into a marine depositional environment, there should be obvious differences in their REE signatures. Once an REE profile is diagenetically established in a fossil, it is stable unless the specimen is subjected to high-grade metamorphism or experiences dissolution and reprecipitation (Patrick *et al.*, 2004), neither of which are factors in the Cretaceous deposits in Alabama. Herwartz *et al.* (2011) have suggested that fossil bioapatite remains an open system for long-term REE uptake based on their observations of lutetium concentrations in fossil material spanning several geologic ages. However, this slower, long-term REE uptake would likely be of concern in much older material and is not considered to be a significant contributor to the material of Late Cretaceous age analyzed in this study. The reason for the disparity in REE concentration between dinosaurs and the other reptilian taxa is not yet understood. Although dinosaurs were terrestrial and presumably lived inland, *postmortem* REE absorption did not take place until burial and diagenesis in the marine environment (Patrick *et al.*, 2001, 2004, 2007a; Staron *et al.*, 2001; Trueman and Tuross, 2002; Trueman *et al.*, 2004). It would therefore be logical to assume that dinosaurs should have the same  $\Sigma$ REE concentrations as the other reptilian groups in their stratigraphic units. Given that most living vertebrates have  $\Sigma$ REE concentrations in the 20 ppm range or less (Wright *et al.*, 1984; Chenery *et al.*, 1996; Patrick *et al.*, 2001; Staron *et al.*, 2001; Trueman *et al.*, 2004; Trueman *et al.*, 2008), it would seem that the fossil dinosaur material analyzed in this study is comparatively less altered in respect to its *in vivo* REE profile. A potential explanation for the relative absence of REE alteration of the dinosaur fossils may be due to the presence of dense

fibro-lamellar bone in the cortical region that is absent in other non-archosaurian reptiles (Horner *et al.*, 2000; Tumarkin-Deratzian, 2007), which may have affected the flow of REE-bearing pore water through the bone during early diagenesis. However, previous analyses of dinosaur fossils collected from terrestrial environments have reported high  $\Sigma$ REE concentrations of up to 25,000 ppm (Suarez *et al.*, 2007; Koenig *et al.*, 2009), well above the concentrations observed in the present study. Furthermore, mammal bones possess an outer circumferential lamella which is as dense and low-porosity as the fibro-lamellar bone found in archosaurs, yet they have been shown to acquire greater  $\Sigma$ REE concentrations (Drewicz *et al.*, 2011; Drewicz, 2012) than the dinosaur material analyzed in this study. As there are only three dinosaur samples included in the present study, additional analyses will be required to determine if the low  $\Sigma$ REE concentrations observed are consistent within this taxonomic group from the Late Cretaceous marine strata of Alabama, or are a result of random chance.

#### Skeletal Element REE Analysis

Similar REE patterns were expected between different skeletal elements of the same fossil individuals, but there is a substantial difference in the total concentrations of REE (Tables 1 and 2). One possible explanation for the differences observed could be in the location of the skeletal elements within the bodies of the living organisms and the amount of tissue covering them at the time of death. In both the *M. hoffmanni* and *Ctenochelys* specimens, the skeletal elements located closer to the external surface of the body contained higher concentrations of REE, whereas those positioned deeper within the body contained much lower concentrations (Fig. 6). Decomposing body tissues may have either changed the chemical environment in the sediment surrounding the skeletal elements, as occurs in terrestrial ecosystems (Carter *et al.*,

2007), slowing uptake of REE or inhibited the flow of pore water through the bones during the fossilization process. Adipocere is an insoluble, greasy, soap-like substance that is a product of cadaver decomposition in wet, anaerobic environments and develops in portions of the body with a higher percentage of fat (Fiedler *et al.*, 2009). Adipocere is formed by the hydrolysis of triglycerides present in adipose tissue by anaerobic bacteria to produce free fatty acids, which are then hydrogenated to yield saturated fatty acids that are adipocere (Forbes *et al.*, 2005). The presence of Na<sup>+</sup>, K<sup>+</sup>, Ca<sup>2+</sup>, and Mg<sup>2+</sup> ions, which are common in marine environments, can also interact with free fatty acids to enhance adipocere production (Forbes *et al.*, 2004). Adipocere has been observed forming in bodies submerged in marine environments within 11 days from time of death (Anderson and Hobischak, 2004) and is one of the most common *postmortem* alterations of corpses in water (Kahana *et al.*, 1999). Adipocere is stable in wet, low-oxygen environments, having been observed in exceptionally well-preserved archaeological specimens that are 1,600 years old and others that are perhaps 7,000 years old (Fiedler *et al.*, 2009).

Bioapatite in the bones of living organisms is comprised of crystallites of metastable hydroxylapatite that have a large surface area to mass ratio (Trueman and Tuross, 2002). During diagenesis, the small crystallites of hydroxylapatite are recrystallized with substitution of fluorine ions, into larger, more stable crystals of fluorapatite (Wopenka and Pasteris, 2005). Diagenetic bioapatite crystal growth has been observed in modern bones within 10 years of death (Tuross *et al.*, 1989) and complete conversion may occur in 1000 to 100,000 years (Trueman and Tuross, 2002; Trueman *et al.*, 2008, Drewicz, 2012). It is during this process of bioapatite recrystallization that REE are substituted into the crystal matrix. REE uptake of up to an order of magnitude increase in only 15 to 30 years has been observed in mammal bones exposed on the plains of Africa (Trueman *et al.*, 2004). From a long-term diagenetic standpoint, if adipocere

were to form in the fattier regions of a cadaver, and was stable through the early stages of diagenetic transformation of the bioapatite crystals, it would impede the flow of REE-bearing porewater through the bones of that region of the body for hundreds or perhaps thousands of years under ideal conditions, thus reducing REE concentrations in those specific bones. For example, in the *Ctenochelys* turtle specimen analyzed in the present study, the virtually tissue-free portions of the outer shell would have no adipocere formation to impede water flow through the bone during the very early years of diagenesis and would therefore accumulate a higher REE concentration than the fattier, more adipocere-prone internal regions of the body where the pelvic bones are located. Given that significant REE accumulation can occur over a relatively short period of time (Drewicz, 2012), adipocere formation could be one possible explanation for the variation in REE concentration in different parts of the anatomy while maintaining the same REE signature.

Another possible explanation for the difference in REE concentrations is that the bones may have differing degrees of porosity on their outer surface which affected the flow of pore water and delivery of REE into the bones during the fossilization process (Trueman *et al.*, 2004; Kohn and Moses, 2013). The differences in bone porosity may be related to whether the bones are endochondrally or intramembranously derived (Scott and Hightower, 1991).

#### Paleobathymetry Based on LREE/MREE/HREE Ratios

Paleobathymetry estimates of the Upper Cretaceous marine formations in Alabama have previously been determined by analyzing microinvertebrate fossil assemblages, including ostracodes (Puckett, 1991; Puckett, 1996) and foraminifera (Cagle, 1985; Mancini *et al.*, 1996), and by using sequence stratigraphy (King, 1990; Mancini *et al.*, 1995; Liu, 2007). Water depths

for the Upper Cretaceous marine carbonate formations in Alabama have more precisely been estimated at between 65 – 90 meters for purer chalks and approximately 35 meters for marls based on ostracode fossils (Puckett, 1991). Cagle (1985) suggested that the Bluffport Marl Member of the Demopolis Chalk was between 91 and 183 meters based on benthic foraminifera. Schein (2006) calculated water depths of 436 to 601 meters for the carbonate strata of Alabama using a formula developed by Van der Zwaan *et al.* (1990) for paleobathymetry estimates using foraminiferal ratios. Schein rejected these estimates as too extreme and suggested shallower depositional environments using observations of the lithology and foraminiferal assemblages present in these geologic units. The Arcola Limestone Member of the Mooreville Chalk, which is believed to represent a carbonate platform resulting from the uplift of the Monroe-Sharkey Platform to the west of the study area near the conjunction of the Arkansas-Mississippi-Louisiana borders, has been estimated as having a water depth of no more than 6 meters (Florian, 1984; Kiernan, 2002). Several other Upper Cretaceous geologic units in the study area have intraformational subaerial surfaces (Mancini and Puckett, 2005), indicating extremely shallow or emergent conditions.

Recent studies have suggested that ratios of LREE/MREE/HREE (light, medium, and heavy rare earth elements) can be used as an indicator of relative paleobathymetry (Patrick *et al.*, 2004; Patrick *et al.*, 2007a). Patrick *et al.* (2004) collected REE data for modern fluvial, coastal and open marine environments and REE data for anoxic pore and bottom waters and sediment and plotted them on a ternary diagram using NASC normalized neodymium ( $Nd_N$ ), gadolinium ( $Gd_N$ ), and ytterbium ( $Yb_N$ ) percentages as representative light, medium, and heavy REE, respectively. Open ocean, shallow, oxic conditions plotted toward the Yb end of the diagram whereas deeper water, anoxic conditions plotted toward the Nd end of the diagram. Freshwater,

river environments tended to plot toward the Gd end of the diagram, whereas proximity to the Yb vertex appeared to be the most accurate indicator of relative water depth.

Patrick *et al.* (2004, 2007a) provided four primary reasons for the variation of LREE/MREE/HREE content in different natural water environments. The first is that the composition of weathered source rocks providing rare earths to solution varies by region, such that the REE content of marine waters in estuaries may be influenced by influx from nearby rivers, which tend to be LREE and MREE enriched. Also the sorption of LREE by organic matter, clay, hydrous ferric oxides (HFO), and tests of planktonic microinvertebrates is likely. This sorption tends to keep LREE in suspension and away from fossils undergoing early diagenesis in oxic, shallow-water, whereas in deeper, anoxic conditions LREE are released by dissolving tests and other particulates and become enriched in those waters. Thirdly, there is an increased tendency for HREE to form aqueous complexes with carbonate in basic/alkaline waters, which enhances the solubility of HREE and leads to enrichment of these rare earths in open ocean and oxic, shallow-water marine environments. Finally, certain redox reactions in open marine waters result in the sorption and precipitation of oxidized cerium ( $Ce^{4+}$ ), depleting this LREE in the upper portion of the water column and enriching it in the waters of the deeper ocean bottom where the particulates settle and dissolve. These four processes lead to HREE enrichment in shallow, oxic environments and LREE/MREE enrichment in deeper, anoxic environments. Mixing of these two endpoint enrichment zones by ocean currents may lead to gradational changes along the bottom waters between them, allowing for relative paleobathymetric interpretations based on the degree of mixing. These are the primary reasons for LREE/MREE/HREE fractionation in marine waters; however, the process is far more

complex and includes a number of assumptions (see Patrick *et al.*, 2004, 2007a for a detailed discussion on the process of REE fractionation and its assumptions).

In the current study,  $Nd_N$ ,  $Gd_N$ , and  $Yb_N$  percentages obtained from the vertebrate fossil samples from all study regions were plotted by stratigraphic unit on ternary diagrams using TRI-PLOT graphing software (Graham and Midgley, 2000) to determine if these REE ratios could be used as successfully in primarily carbonate marine settings as they are in siliclastic marine settings at indicating relative paleobathymetry (Fig. 7).

Results of the analysis display a good correlation with the paleobathymetry reported in the literature for the Upper Cretaceous carbonate formations in Alabama. For example, the average plot for the Tombigbee Sand Member of the Eutaw Formation (Fig. 7, TB) is slightly closer to the  $Yb_N$  end of the diagram than the overlying Mooreville Chalk (Fig. 7, M), indicating

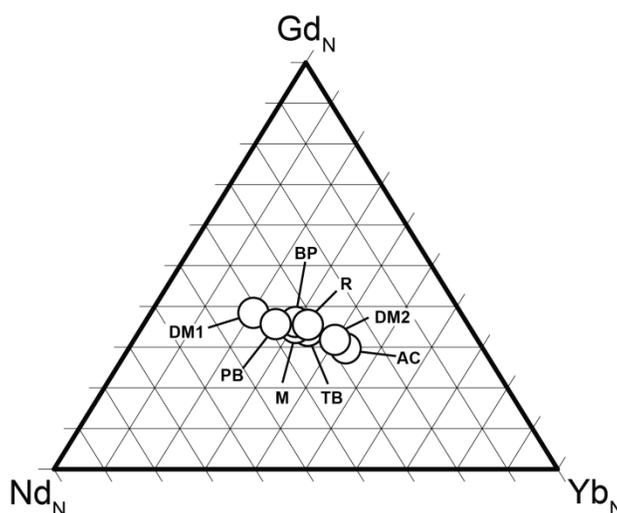


FIGURE 2.7—Ternary diagram of average LREE/MREE/HREE percentages for stratigraphic units in all sub-regions of the study area. AC = Arcola Limestone, BP = Bluffport Marl, DM1 = Demopolis Chalk (deep water facies), DM2 = Demopolis Chalk (shallow water facies), M = Mooreville Chalk (lower member), PB = Prairie Bluff Chalk, R = Ripley Formation, TB = Tombigbee Sand.

a comparatively shallower environment for the Tombigbee Sand. This is in agreement with the previous paleoenvironmental interpretations of inner shelf/back barrier island for the Tombigbee

Sand (King and Skotnicki, 1990) and inner to middle shelf for the Mooreville Chalk (Kiernan, 2002).

Another example can be analyzed in a comparison of the Ripley Formation and the Prairie Bluff Chalk with clear differences in water depth based on sedimentological analyses. The Ripley Formation in Alabama is a less carbonate-rich formation that contains alternating beds of glauconitic, micaceous, and calcareous siliciclastic sands throughout its thickness (Raymond *et al.*, 1988). King and Skotnicki (1990) interpreted this formation as representing an inner shelf to lower shoreface depositional environment. The Nd<sub>N</sub>, Gd<sub>N</sub>, and Yb<sub>N</sub> percentages plotted from the vertebrate fossil samples analyzed in this study are shifted toward the Yb<sub>N</sub> end of the diagram (Fig. 7, R).

The Prairie Bluff Chalk represents a comparatively deeper paleoenvironment (Bryan, 1992) based on the increase in carbonate content in relation to the underlying Ripley Formation in the study area. King and Skotnicki (1990) concluded that the Prairie Bluff Chalk in western Alabama consisted of lower shoreface and shelfal facies. This deepening of the water column in the region during the Late Cretaceous is reflected in the shift of the ternary diagram away from the Yb<sub>N</sub> vertex (Fig. 7, PB) relative to the diagram for the underlying Ripley Formation (Fig. 7, R).

The average LREE/MREE/HREE ratios for all geologic units analyzed in the study area are plotted in Figure 7. The results interpreted from relative LREE/MREE/HREE enrichment in the ternary diagrams suggest that the Arcola Limestone was the shallowest depositional environment of the Late Cretaceous of Alabama. Although the Arcola Limestone appears to be the shallowest depositional environment analyzed in this study, its low siliciclastic content suggests that it was deposited in a region far from shore away from sources of terrigenous

sediment. The deeper water (Type 1) facies of the lower unnamed member of the Demopolis Chalk were indicated as the deepest depositional environment of the Late Cretaceous in Alabama based on the LREE/MREE/HREE ratio. These findings support previous interpretations of both geologic units (Florian, 1984; Mancini and Puckett, 2005). The remaining geologic units of the study area plotted between these end members.

The differences between LREE/MREE/HREE ratios plotted in ternary diagrams of the Upper Cretaceous carbonate marine formations in the study area are modest in comparison with the differences observed in the siliciclastic Pierre Shale Group of South Dakota (Patrick *et al.*, 2002, 2004, 2007a). However, those differences correspond well with the paleoenvironmental interpretations described in the literature for the formations in Alabama. Furthermore, these interpretations reinforce the idea that results from the principal component analysis of REE data reflect changes in water depth (Fig. 4). Geologic units from the deeper water stratigraphic units tend to plot on the left side of the diagram whereas those from the shallower units, with the exception of the single Ripley Formation sample, plot on the right side.

## CONCLUSIONS

1. Rare earth element (REE) signatures in fossil vertebrate material from the Upper Cretaceous carbonate marine deposits of western and central Alabama can be used to determine the provenance of fossils lacking locality data. However, REE signatures from carbonate marine strata are more limited geographically and stratigraphically than those of fossil material recovered from siliciclastic units.
2. REE signatures between some taxonomic groups can vary greatly within a given geologic unit or geographic region although the variances can be inconsistent. Mosasaurs, plesiosaurs,

dinosaurs, crocodiles, and some protostegid marine turtles appear to share similar REE signatures within a given geologic unit, whereas sharks, freshwater turtles, and toxochelid marine turtles typically differ from other taxonomic groups. Statistical analysis using cerium anomalies and select REE ratios produce more uniform clustering and show few differences between taxa.

3. REE signatures from different skeletal elements of the same fossil organism have the same REE profile but total REE concentration ( $\Sigma$ REE) can vary considerably depending on the relative position of the skeletal elements within the body of the living animal.

4. Relative paleobathymetry based on LREE/MREE/HREE ratios of vertebrate fossils from carbonate marine deposits is not as distinctive as that previously reported for siliciclastic deposits of the Western Interior Seaway. However, the inferred differences in water depth based on REE fractionation between the geologic units of western Alabama are in agreement with estimates determined previously using micropaleontology and sedimentological data. These inferred REE differences suggest alternating shallowing and deepening cycles within an overall shallowing upward sequence.

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### 3. STRONTIUM ISOTOPE AGE-DATING OF FOSSIL SHARK TOOTH ENAMELOID FROM THE UPPER CRETACEOUS STRATA OF ALABAMA AND MISSISSIPPI, USA

#### ABSTRACT

Cretaceous strata in Alabama and Mississippi (USA) represent one of the most complete records of shallow marine deposition worldwide for the Upper Cretaceous. The age assignment of these strata in the eastern Gulf Coastal Plain is difficult due to the comparative lack of radiometrically datable beds and sometimes conflicting results of biostratigraphy using different taxonomic groups. Numerical age dating using strontium isotope ratios ( $^{87}\text{Sr}/^{86}\text{Sr}$ ) preserved in diagenetically resistant fossil shark tooth enameloid had been proposed by previous researchers as a solution to dating some geologic units. Here we apply this methodology to the whole Upper Cretaceous, using teeth of two fossil shark genera (*Scapanorhynchus* and *Squalicorax*) collected from variable facies. Shark teeth collected from a bentonite mine in Monroe County, Mississippi, were also analyzed and compared with the radiometric date of the bentonite layer. Results indicate a strong correlation between stratigraphic position of the fossil teeth and numerical age determination based on  $^{87}\text{Sr}/^{86}\text{Sr}$  content. Furthermore, this method is equally effective for both of the fossil shark genera analyzed in the study. Because of the nearly uniform distribution of strontium in ocean water, numerical age dating using strontium isotope ratios preserved in fossil shark tooth enameloid can be a useful method to employ in the correlation of marine geological strata on both regional and global scales.

## INTRODUCTION

The Upper Cretaceous strata of the eastern Gulf Coastal Plain of the United States represent a nearly continuous record of marine depositional cycles, spanning approximately 21 million years in age (Mancini and Puckett, 2003; Liu, 2007). At least three major eustatic transgressive–regressive cycles are recorded in these units, which are important markers for stratigraphic correlation on a regional and global scale (Mancini and Puckett, 2005; Mancini *et al.*, 2008). Precise age dating of these strata in Alabama and Mississippi has primarily depended on biostratigraphic methods using foraminifera (Cushman, 1946; Smith, 1997), coccolithophores (Cepek and Hay, 1969; Hester and Risatti, 1972), ostracodes (Puckett, 1994), bivalves (Stephenson, 1933; Stephenson and Monroe, 1938), or ammonites (Cobban and Kennedy, 1995). Additionally, correlative sequence stratigraphy has been used in conjunction with biostratigraphy for age assignment of these strata (Mancini and Tew, 1997; Mancini and Puckett, 2005; Liu, 2007). In many cases, this dependence on relative dating methods has produced equivocal results leading to considerable variation in the reported age of Cretaceous units in this region (Russell, 1967; Raymond *et al.*, 1988; King and Skotnicki, 1994; Mancini and Soens, 1994; Dockery, 1996; Mancini and Puckett, 2005; Liu, 2007). The variation in reported age is further exacerbated by the lack of radiometrically dateable strata over wide geographic areas in the Mississippi Embayment, although isolated, locally-prominent bentonite beds with suitable minerals do exist (Munyan, 1940; Stephenson and Monroe, 1940; Monroe, 1941; Merrill, 1983). A more definitive method is needed to refine the numerical ages of Upper Cretaceous strata in the region so that age determination is not solely dependent on biostratigraphic relative dating.

A potential solution to the problem of age dating these Cretaceous marine strata in the eastern Mississippi Embayment is through the use of stable strontium isotope ratios ( $^{87}\text{Sr}/^{86}\text{Sr}$ )

preserved in fossil shark teeth (Schmitz *et al.*, 1997; Becker *et al.*, 2008), a dating method that was first proposed by Wickman (1948). Strontium is a trace element dissolved in seawater which has a more or less uniform global distribution due to the long residence time for strontium in seawater of  $\approx 10^6$  years, and the comparatively fast mixing time of seawater by ocean currents of  $\approx 10^3$  years (McArthur *et al.*, 2012). Changes in the  $^{87}\text{Sr}/^{86}\text{Sr}$  ratio occur over long periods of time due to input and removal of strontium in the ocean by geologic processes, and there are two primary pathways through which  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios in seawater are altered: 1) input of weathered silicate continental crust and dissolved marine carbonate deposits via freshwater rivers, and 2) hydrothermal circulation at mid-ocean ridges (McArthur, 1994; Shields, 2007). A portion of  $^{87}\text{Sr}$  is generated by the radioactive decay of  $^{87}\text{Rb}$ , which is often present in potassium-bearing silicate rocks (Faure and Mensing, 2005). Because of this  $^{87}\text{Sr}$  enrichment of silicate rocks, large-scale orogenic events that increase continental crust weathering gradually raise the  $^{87}\text{Sr}/^{86}\text{Sr}$  ratio in seawater, whereas hydrothermal circulation at mid-ocean ridges tends to reduce the ratio through precipitation of anhydrite (McArthur, 1994).

Strontium becomes incorporated in calcium carbonate and apatite crystals through a substitution with calcium, due to their similar ionic radius and oxidation state (Faure and Mensing, 2005). The  $^{87}\text{Sr}/^{86}\text{Sr}$  ratio preserved in calcium-bearing minerals at the time of their formation (both biotic and abiotic) is the same as that present in the surrounding seawater (Veizer, 1989) and, provided there is no diagenetic alteration of the crystals, maintains a record of the oceanic  $^{87}\text{Sr}/^{86}\text{Sr}$  ratio in the geologic past (DePaolo and Ingram, 1985; McArthur, 1994). Preserved  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios have been collected globally (McArthur *et al.*, 1994; Veizer *et al.*, 1997; Veizer *et al.*, 1999; McArthur *et al.*, 2012) and, when combined with the biostratigraphy of containing strata and absolute age dating of appropriate adjacent strata, produce accurate, high-

resolution numeric ages. Databases of  $^{87}\text{Sr}/^{86}\text{Sr}$  numeric ages are combined and the LOWESS (Locally Weighted Scatterplot Smoothing) statistical method (Cleveland, 1981) is applied to produce a continuous strontium isotope curve representing the Phanerozoic Eon that can allow the easy conversion of most  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios into numeric ages (McArthur *et al.*, 2001; McArthur *et al.*, 2012). The peaks and valleys (maxima and minima) of the strontium isotope curve are troublesome in that certain  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios result in two different ages over a narrow span of time. However, the Late Cretaceous portion of the curve relevant to the present study area is represented by a steady increase in the  $^{87}\text{Sr}/^{86}\text{Sr}$  ratio until the Cretaceous/Paleogene (K/Pg) boundary, after which the ratio begins to decrease (Fig. 1) (McArthur *et al.*, 2001).

#### Previous Work

The use of  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios preserved in fossil shark tooth enameloid for numeric age dating in the Mississippi Embayment was first proposed by Schmitz *et al.* (1997) and later by Becker *et al.* (2008), who refined the sampling method. Schmitz *et al.* (1997) analyzed fossil shark teeth from the Paleogene Tuscahoma and Bashi formations in Mississippi, noting that the  $^{87}\text{Sr}/^{86}\text{Sr}$  ratio of the outer enameloid was well-preserved in comparison with the dentine (Osteodentine and orthodentine) found in the tooth interior. Their hypothesis for this difference in ratios was that the dentine had diagenetically recrystallized during fossilization and lost its original  $^{87}\text{Sr}/^{86}\text{Sr}$  signal whereas the enamel, with its larger and coarser bioapatite crystals, was more resistant to diagenetic recrystallization and retained its original  $^{87}\text{Sr}/^{86}\text{Sr}$  ratio.

Becker *et al.* (2008) obtained fossil shark teeth of *Scapanorhynchus texanus* (Roemer 1849) from the Tombigbee Sand Member of the Eutaw Formation in Alabama and a modern

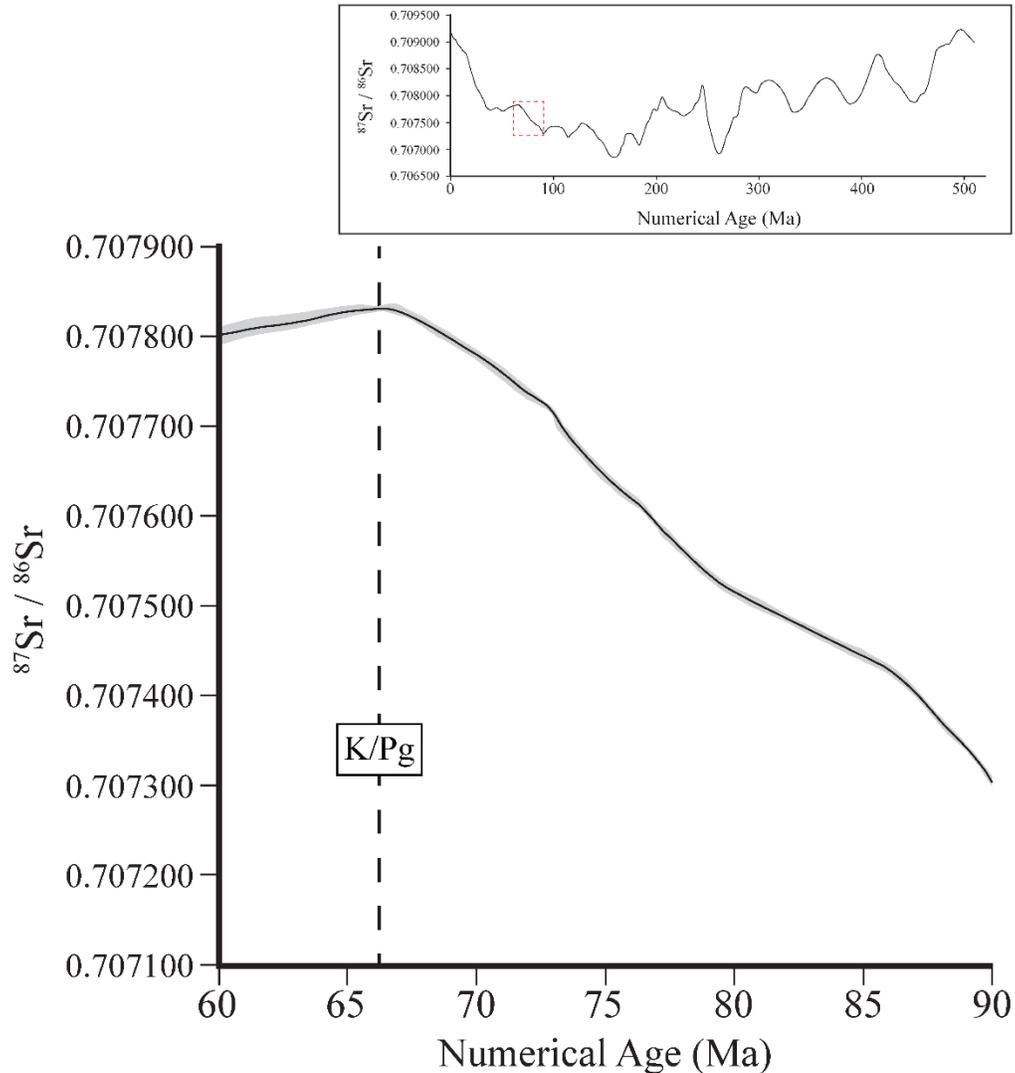


FIGURE 3.1 – LOWESS curve of strontium isotope ratio to numerical age for the Phanerozoic Eon (inset) and Late Cretaceous time period that is the focus of the current study. Gray area in Late Cretaceous graph indicates range of uncertainty in the curve. Figures modified from McArthur *et al.* (2012). K/Pg = Cretaceous/Paleogene boundary.

shark tooth of *Isurus oxyrinchus* to test the hypothesis of Schmitz *et al.* (1997). These authors developed a “scratch” method that restricted sampling to the outermost enameloid portion of the tooth and compared the results with sectioned portions of the tooth that contained osteodentine and/or orthodentine. In the modern shark tooth,  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios of the enamel and dentine portions of the tooth were close to the isotopic composition of present-day seawater. In the fossil shark teeth, the  $^{87}\text{Sr}/^{86}\text{Sr}$  ratio of the dentines was considerably higher than that of the enameloid,

suggesting diagenetic alteration of the interior osteodentine and the resistance of the enameloid. Becker *et al.* (2008) converted the enameloid  $^{87}\text{Sr}/^{86}\text{Sr}$  ratio of the fossil shark teeth to numeric age dates using the LOWESS strontium isotope curve and look-up table (Version 4b) initially developed by McArthur *et al.* (2001). The average age of the fossil shark teeth was  $78.8 \pm 0.4$  Ma, which is within the Late Cretaceous and fits within the known stratigraphic range for *Scapanorhynchus texanus* reported by Becker *et al.* (2008). However, when compared to stratigraphic columns of Upper Cretaceous strata of Alabama, the numeric ages of specimens analyzed by Becker *et al.* (2008) are much too young for the currently accepted age of the Tombigbee Sand of upper Santonian to lowermost Campanian (Fig. 2). When the results of their study are updated to Version 5 of the look-up table (McArthur *et al.*, 2012), which increases the age of the samples, they are still too young for the Tombigbee Sand as well as some of the overlying strata (Fig. 2). Possible reasons for this discrepancy are: 1) that the strontium ratio in the enameloid has been diagenetically altered through long-term leaching by ground water, 2) enameloid contamination by underlying dentine during sampling, or 3) the Tombigbee Sand may be geologically younger than currently accepted.

#### Purpose of Study

The study presented here has three primary objectives: 1) To determine if  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios can be used for accurate numeric age dating of Upper Cretaceous strata in Alabama (AL) and Mississippi (MS); 2) To determine whether Cretaceous fossil sharks other than *Scapanorhynchus texanus* can be used for accurate strontium isotope age dating; and 3) To compare strontium

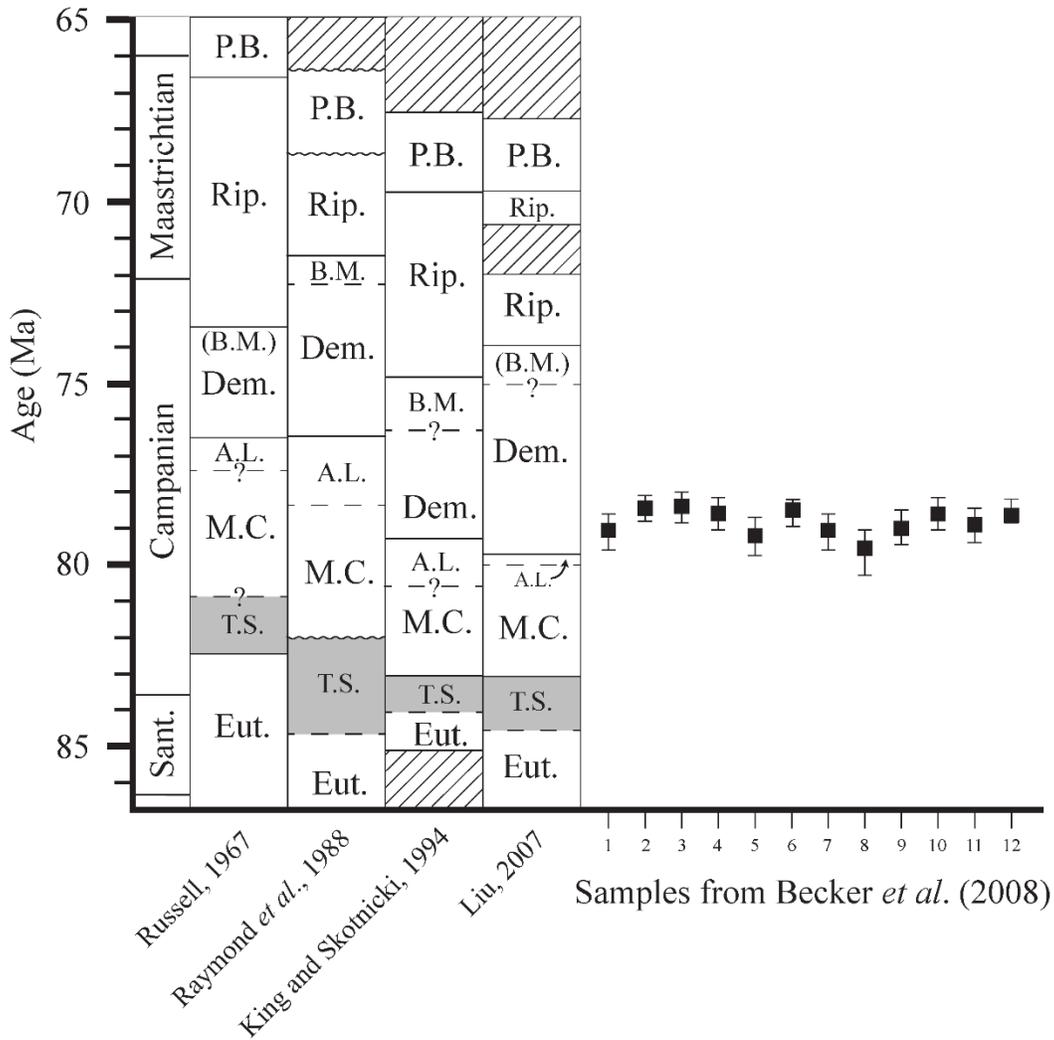


FIGURE 3.2 – Results of Becker *et al.* (2008) updated with look-up table Version 5 (McArthur *et al.*, 2012) plotted against several published stratigraphic columns of Upper Cretaceous formations of Alabama. Note that the numerical ages of the samples are younger than any accepted age of the Tombigbee Sand (Shaded area) in Greene County, Alabama from which the specimens were collected. All Becker *et al.* (2008) samples were from *Scapanorhynchus texanus*. **Eut.** – Eutaw Formation; **T.S.** – Tombigbee Sand Member of Eutaw Formation; **M.C.** – Mooreville Chalk; **A.L.** – Arcola Limestone Member of Mooreville Chalk; **Dem.** – Demopolis Chalk; **B.M.** – Bluffport Marl Member of Demopolis Chalk; **Rip.** – Ripley Formation; **P.B.** – Prairie Bluff Chalk. Dashed lines indicate member divisions of geologic formations analyzed in this study, unnamed members are not indicated. A question mark indicates that the precise division between members was not indicated by the cited authors. Formational divisions are the work of the cited authors.

isotope derived age dates with a radiometric date from the same collection locality to gauge the relative accuracy of this method.

## Geology of Study Area

The fossil shark teeth used in this study (Fig. 3, Table 1) were collected by Alabama Museum of Natural History staff from outcropping Upper Cretaceous marine formations in

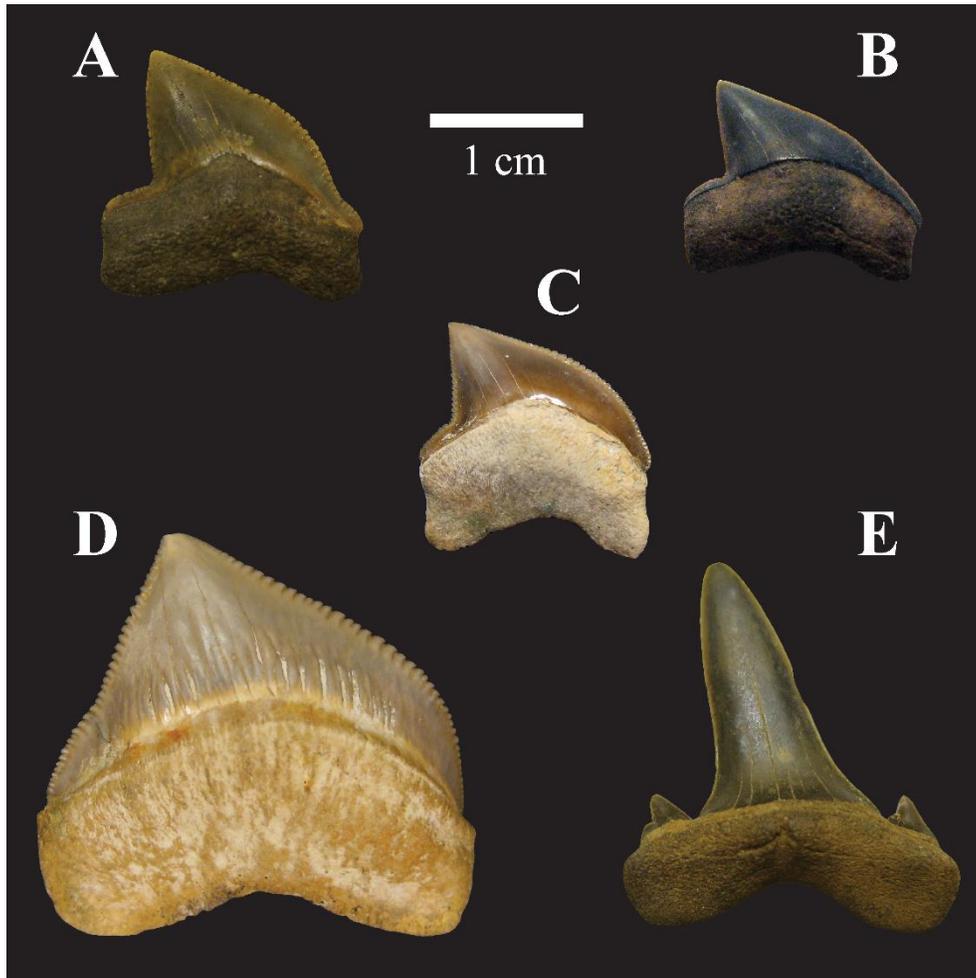


FIGURE 3.3 – Representative teeth of fossil shark taxa analyzed in this study. **A** – *Squalicorax cf. yangaensis* from the Tombigbee Sand Member of the Eutaw Formation in Greene County, AL (AGr-43), **B** – *Squalicorax lindstromi* from the Tombigbee Sand Member of the Eutaw Formation in Greene County, AL (AGr-43), **C** – *Squalicorax kaupi* from the Mooreville Chalk in Dallas County, AL (ADa-3UA), **D** – *Squalicorax pristodontus* from the Prairie Bluff Chalk in Lowndes County, AL (ALn-7), **E** – *Scapanorhynchus texanus* from the Tombigbee Sand Member of the Eutaw Formation in Greene County, AL (AGr-43). All teeth are in lingual view.

Sample #	Museum Specimen #	Taxon	Geologic Unit	Locality #	Site/Town	County	State
MS-1	MMNS RN 8584.3 09-128	<i>Squalicorax lindstromi</i>	Tombigbee Sand	MGS-162	Fowlkes Mine	Monroe	MS
MS-2	MMNS RN 7762 07-168	<i>Squalicorax lindstromi</i>	Tombigbee Sand	MGS-162	Fowlkes Mine	Monroe	MS
MS-3	MMNS RN 7330.1 07-30	<i>Squalicorax lindstromi</i>	Tombigbee Sand	MGS-162	Fowlkes Mine	Monroe	MS
MS-4	MMNS RN 7330.1 07-30	<i>Scapanorhynchus texanus</i>	Tombigbee Sand	MGS-162	Fowlkes Mine	Monroe	MS
MS-5	MMNS RN 8387.2 09-63	<i>Scapanorhynchus texanus</i>	Tombigbee Sand	MGS-162	Fowlkes Mine	Monroe	MS
MS-6	MMNS RN 8387.2 09-63	<i>Scapanorhynchus texanus</i>	Tombigbee Sand	MGS-162	Fowlkes Mine	Monroe	MS
AL-1	ALMNH Unnumbered Specimen	<i>Squalicorax cf. yangaensis</i>	Tombigbee Sand	AGr-43	T russell's Creek	Greene	AL
AL-2	ALMNH Unnumbered Specimen	<i>Squalicorax cf. yangaensis</i>	Tombigbee Sand	AGr-43	T russell's Creek	Greene	AL
AL-3	ALMNH Unnumbered Specimen	<i>Squalicorax lindstromi</i>	Tombigbee Sand	AGr-43	T russell's Creek	Greene	AL
AL-4	ALMNH PV1994.0002.0054.002	<i>Squalicorax cf. yangaensis</i>	Tombigbee Sand	AGr-43	T russell's Creek	Greene	AL
AL-5	ALMNH PV1990.0022	<i>Squalicorax kaupi</i>	Mooreville Chalk	ADa-3UA	Harrell Station	Dallas	AL
AL-6	ALMNH PV2000.0007.0001	<i>Squalicorax kaupi</i>	Mooreville Chalk	ADa-3UA	Harrell Station	Dallas	AL
AL-7	ALMNH PV2001.0005.0003	<i>Squalicorax kaupi</i>	Mooreville Chalk	ADa-3UA	Harrell Station	Dallas	AL
AL-8	ALMNH PV2002.0005.0004	<i>Scapanorhynchus texanus</i>	Mooreville Chalk	ADa-3DW	Harrell Station	Dallas	AL
AL-9	ALMNH PV1988.0020.0324	<i>Squalicorax pristodontus</i>	Demopolis (Lower Mbr.)	ADa-13	Safford	Dallas	AL
AL-10	ALMNH PV2005.0006.0403.001	<i>Squalicorax pristodontus</i>	Demopolis (Lower Mbr.)	Unnumbered	Boligee	Greene	AL
AL-11	ALMNH PV1993.0002.0032.001	<i>Squalicorax pristodontus</i>	Demopolis (Lower Mbr.)	ADa-24	Harrell Station	Dallas	AL
AL-12	ALMNH Unnumbered Specimen	<i>Squalicorax pristodontus</i>	Bluffport Marl	Unnumbered	Belmont	Sumter	AL
AL-13	ALMNH Unnumbered Specimen	<i>Squalicorax pristodontus</i>	Bluffport Marl	Unnumbered	Belmont	Sumter	AL
AL-14	ALMNH Unnumbered Specimen	<i>Squalicorax pristodontus</i>	Bluffport Marl	Unnumbered	Belmont	Sumter	AL
AL-15	ALMNH PV1993.0002.0097.001	<i>Squalicorax pristodontus</i>	Ripley	ALn-11	Braggs	Lowndes	AL
AL-16	ALMNH Unnumbered Specimen	<i>Squalicorax pristodontus</i>	Prairie Bluff Chalk	ALn-7	Braggs	Lowndes	AL
AL-17	ALMNH PV1991.0013.0008	<i>Squalicorax pristodontus</i>	Prairie Bluff Chalk	ALn-7	Braggs	Lowndes	AL
AL-18	ALMNH PV1990.0018.0001	<i>Squalicorax pristodontus</i>	Prairie Bluff Chalk	ALn-7	Braggs	Lowndes	AL

TABLE 3.1—Sample numbers, Alabama Museum of Natural History (ALMNH) and Mississippi Museum of Natural Science (MMNS) specimen identification numbers, taxa, and locality data.

western Alabama, and by the third author (GP) at one additional site in eastern Mississippi (Fig. 4). These formations were deposited along the southeastern portion of the Mississippi Embayment during the Late Cretaceous, in depositional environments ranging from subtidal to outer shelf (Cagle, 1985; King, 1990; King and Skotnicki, 1990; Kiernan, 2002). The reported age of these deposits ranges from late Coniacian for the lower Eutaw Formation through the mid to late Maastrichtian of the Prairie Bluff Chalk (Mancini *et al.*, 2008). Although the sequence of strata is nearly continuous, a few hiatuses are present in the stratigraphic column (Mancini and Puckett, 2005; Liu, 2007) (Fig. 2). Eutaw Formation – The Eutaw Formation is subdivided into the lower unnamed member and the upper Tombigbee Sand Member. The lower unnamed

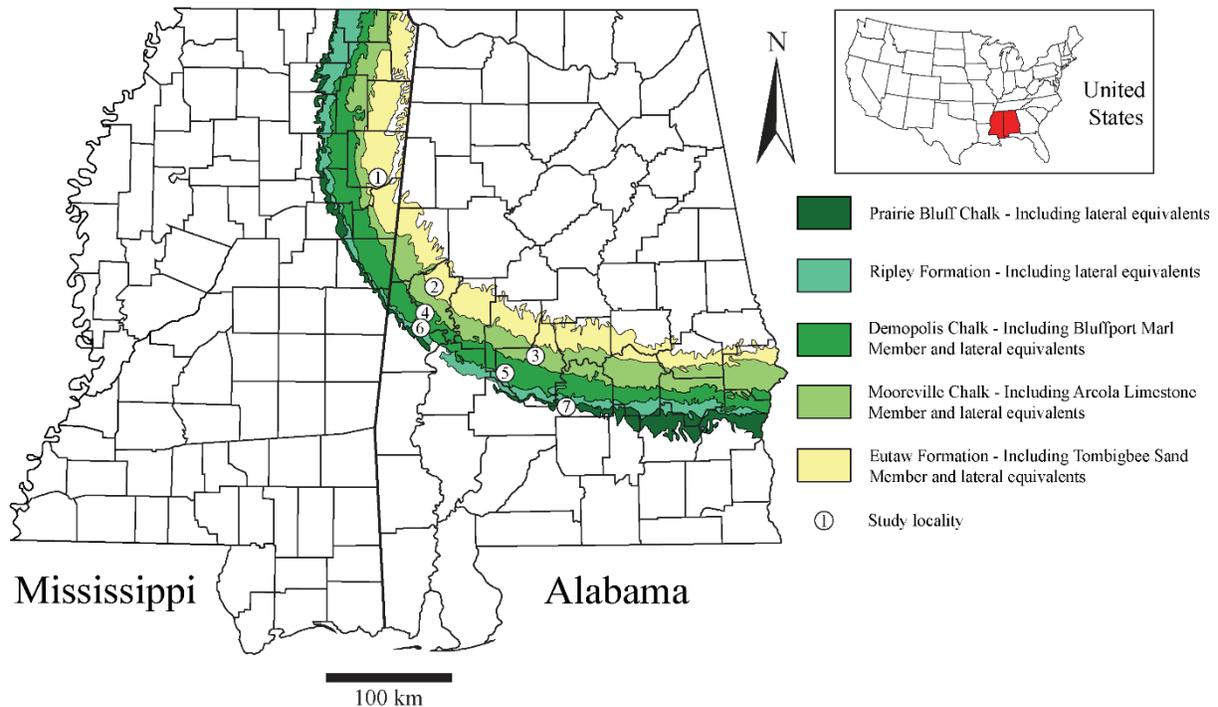


FIGURE 3.4 – Collection localities of specimens sampled in this study and outcropping Upper Cretaceous marine units in Alabama and Mississippi. Localities: **1** – BASF Fowlkes Mine (MGS-162, Tombigbee Sand), Monroe Co., MS; **2** – Trussell’s Creek (AGr-43, Tombigbee Sand), Greene Co., AL; **3** – Harrell’s Station (ADa-3UA and ADa-3DW, Mooreville Chalk; ADa-24, Demopolis Chalk), Dallas Co., AL; **4** – Boligee (Unnumbered site, Demopolis Chalk), Greene Co., AL; **5** – Safford (ADa-13, Demopolis Chalk), Dallas Co., AL; **6** – Belmont (Unnumbered Site, Bluffport Marl), Sumter Co., AL; **7** – Braggs (ALn-11, Ripley Fm; ALn-7, Prairie Bluff Chalk), Lowndes Co., AL.

member is a fine to medium-grained, cross-bedded, largely unfossiliferous, micaceous, glauconitic sandstone approximately 52 m thick (Mancini and Soens, 1994). The Tombigbee Sand Member disconformably overlies the lower unnamed member and attains a maximum thickness of approximately 30 m in western Alabama (Stephenson and Monroe, 1940; Liu, 2007), although other studies report a maximum thickness of approximately 6 m in the same region (Kiernan, 2002). The Tombigbee Sand is composed of massive fine-grained sandstone to coarse-grained siltstone, that is glauconitic, micaceous, calcareous, locally bentonitic, highly fossiliferous, and bioturbated (Raymond *et al.*, 1988; Mancini and Soens, 1994). The macrofaunal assemblage, shark tooth lag deposits, and abrasion evident on many fossils suggest

that reworking of specimens is a possibility in the Tombigbee Sand (Manning, 2006). The Tombigbee Sand is porous and supports an aquifer used locally in the region (Davis, 1987).

Mooreville Chalk – The Mooreville Chalk is divided into the lower unnamed member and the upper Arcola Limestone Member. The contact of the lower unnamed member of the Mooreville Chalk with the underlying Tombigbee Sand Member of the Eutaw Formation is gradational, but it is indicated by a layer of phosphatic pebbles and invertebrate steinkerns (Mancini and Soens, 1994). Other researchers have suggested an arbitrary contact where the sand content reaches 50% (Liu, 2007). The lower unnamed member is approximately 79 m thick in western Alabama and increases to 180 m in central Alabama (Raymond *et al.*, 1988). Lithologically, the lower member is composed of calcareous, glauconitic, and micaceous sandstone near the base that fines upward into clay-rich, chalky marlstone (Raymond *et al.*, 1988; Kiernan, 2002). The vertebrate fauna of the lower unnamed member of the Mooreville Chalk is well-known and very diverse (Zangerl, 1948; Thurmond and Jones, 1981; Kiernan, 2002). The Arcola Limestone Member is approximately 3 m thick in the study area, and it is composed of two to four beds of impure limestone separated by marlstone interbeds (Raymond *et al.*, 1988).

Demopolis Chalk – The Demopolis Chalk is subdivided into the lower unnamed member and the upper Bluffport Marl Member. The lower unnamed member of the Demopolis Chalk conformably overlies the Arcola Limestone Member of the Mooreville Chalk and is approximately 132 m thick within the study area (Raymond *et al.*, 1988). Near its base in the shallower-water facies, the lower unnamed member is lithologically similar to the Mooreville Chalk that underlies the Arcola Limestone Member, being composed of clay-rich marlstones, but upsection becomes a more pure chalk (Puckett, 1996; Kiernan, 2002; Mancini and Puckett,

2005). This reduction of terrigenous clastics in the deeper-water facies suggests a transgressive maximum of the epic sea during the Late Cretaceous in Alabama (Liu, 2007). The overlying Bluffport Marl Member ranges from 15 m to 20 m in thickness in western and central Alabama (Raymond *et al.*, 1988), but the depositional environment is still considered to be outer shelf (Cagle, 1985), despite the increase in siliciclastic content. The Demopolis Chalk possesses a relatively rich and diverse vertebrate fauna (Derstler, 1988), although it is not as fossiliferous as the Mooreville Chalk.

Ripley Formation – The Ripley Formation in western Alabama ranges from approximately 11 m near the Mississippi border to 76 m in central and eastern portions of Alabama. Lithologically, the Ripley Formation is composed of fine glauconitic sandstone, calcareous sand and clay upsection, and thin layers of fossiliferous sandstone (Raymond *et al.*, 1988). The Ripley Formation contains a diverse, well-preserved invertebrate fauna but also has produced a number of significant vertebrate fossils. Like the Tombigbee Sand, sandier portions of the Ripley Formation are used as a regional aquifer (Davis, 1987). Reworking of fossils is a possibility given the nearshore depositional environment for portions of the formation (King and Skotnicki, 1990).

Prairie Bluff Chalk – The Prairie Bluff Chalk disconformably overlies the Ripley Formation in western Alabama. Bryan (1992) suggests that this unconformity represents subaerial exposure and erosion of the upper Ripley Formation. The Prairie Bluff Chalk attains a maximum thickness of approximately 34 m in central Alabama, however, it is completely absent in some areas of western Alabama (Raymond *et al.*, 1988). In contrast to the highly siliciclastic lithology of the Ripley Formation, the overlying Prairie Bluff Chalk consists of fine, bluish-gray sand and chalk (Raymond *et al.*, 1988). Fossil content of the Prairie Bluff Chalk includes well-

preserved macroinvertebrates (Bryan, 1992), and a lesser number of vertebrate fossils than the underlying strata. A disconformity and temporal hiatus represents the upper contact of the Upper Cretaceous (Maastrichtian) Prairie Bluff Chalk with the overlying Paleocene (Danian) Clayton Formation, which has been interpreted as either a subaerial erosional surface resulting from a marine regression (Smith, 1997), or tsunami damage from the Chicxulub impact that occurred far to the south at the K/Pg boundary (Feldl *et al.*, 2002).

## METHODS

Specimens of shark teeth were obtained with permission from the collections of the Alabama Museum of Natural History and the Mississippi Museum of Natural Science (Table 1). The specimens had been previously collected by museum staff over a period of many years. Specimens were selected by their recorded stratigraphic provenance and high-degree of tooth crown preservation. In some geologic units, two genera of sharks (*Squalicorax* Whitley 1939 and *Scapanorhynchus* Woodward 1889) were analyzed to determine if there are any differences in the  $^{87}\text{Sr}/^{86}\text{Sr}$  signatures based on possible habitat preference of taxa. Biostratigraphic limitations of taxa required the use of four species of *Squalicorax* (*S. cf. yangaensis* (Dartevelle and Casier 1943), *S. lindstromi* (Davis 1890), *S. kaupi* (Agassiz 1843), and *S. pristodontus* (Agassiz 1843)) in the analysis (Fig. 3). When possible, three specimens from each geological unit in the study were selected for increased statistical significance of the results. Two *S. pristodontus* teeth (AL-13 and AL-14) from an associated dentition collected from the Bluffport Marl, and a *S. pristodontus* tooth (AL-16) associated with a *Mosasaurus hoffmanni* specimen from the Prairie Bluff Chalk, were analyzed to test the accuracy and precision of this analytical method.

One of the purposes of the study is to analyze  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios of shark teeth collected near a bentonite seam within the Tombigbee Sand in a Monroe County (Mississippi) mine and compare the results with the radiometric (K-Ar) age of the same bentonite layer reported by Obradovich (1993). Access to the high-wall at BASF Fowlkes Mine was restricted because of safety concerns and samples could not be directly acquired *in situ*. However, access was granted to the overburden spoil piles located near the active portion of the quarry and shark tooth samples from the Tombigbee Sand in Mississippi analyzed in the study were collected there.

Specimens were mechanically processed in the Department of Geological Sciences at the University of Alabama (USA). Specimens were first washed in an ultrasonic bath to remove any remaining traces of adhering matrix, rinsed with deionized water, and dried overnight. Each specimen was successively placed in a cleaned and dried agate mortar under a binocular dissecting microscope to collect the sample powders. A Dremel<sup>®</sup> rotary tool equipped with diamond drill bits was used to remove approximately 10 mg of sample powder from the outer tooth enameloid, which collected in the mortar. The sample powder was then transferred to weigh paper and measured on an electronic balance. The sample powders were placed in individually labeled microcentrifuge tubes for transport. Between specimens, the drill bits and mortar were cleaned with dilute trace metal grade nitric acid ( $\text{HNO}_3$ ), rinsed with deionized water, and dried with Kimwipes<sup>®</sup> to prevent cross contamination.

The samples were transported to the Geochronology and Isotope Geochemistry Laboratory at the University of North Carolina-Chapel Hill (USA) for geochemical analysis. Between 2.5 – 5.0 mg of each sample powder was weighed on an electronic balance and transferred to new, individually labeled, microcentrifuge tubes. Approximately 550  $\mu\text{L}$  of 3.5M trace metal grade nitric acid ( $\text{HNO}_3$ ) was added to each microcentrifuge tube to dissolve the

samples. After dissolution, the samples were centrifuged to separate any undissolved particles. The sample solutions were then pipetted into individual separation columns filled with Eichrom<sup>®</sup> SR-B100-S (50 – 100 µm) strontium resin followed by four rinses with 3.5M trace metal grade HNO<sub>3</sub>. In acidic conditions, the strontium atoms in the solution are retained by the resin, while the remaining solution passes out of the column and collects in a waste beaker. The Sr-enriched columns were then transferred to clean, labeled collection cups and rinsed twice with Milli-Q<sup>®</sup> deionized water. The higher pH conditions resulting from the added water causes the resin to release the retained strontium and the solution collects in cups underneath the columns. One drop of 0.1M phosphoric acid (H<sub>3</sub>PO<sub>4</sub>) was added to each of the collected solutions, which were then placed on a hotplate to dry. The end product of chemical processing is a grain-like pellet containing strontium derived from the sample.

Sample pellets were attached to rhenium filaments (99.98% Re) using tantalum pentachloride (TaCl<sub>5</sub>) as an adherent and analyzed in a VG Micromass<sup>®</sup> Sector 54 thermal ionization mass spectrometer (TIMS). Each sample isotope ratio was collected 120 times at 8 second intervals and automated software analyzed the results. The ratios were calibrated against the long-term lab average for strontium standard NIST 987, resulting in an adjustment of  $-2.0 \times 10^{-5}$  to each sample. No correction was made for rubidium content as this element behaves in a manner similar to potassium in vertebrate organisms and is primarily retained in soft tissues rather than hard tissues (Relman, 1956). Additionally, rubidium was not detected in previous strontium analyses of fossil shark teeth conducted in the study area (Becker *et al.*, 2008).

*Squalicorax pristodontus* specimen AL-17 (ALMNH PV1991.0013.008) from the Prairie Bluff Chalk was initially cut in half prior to enameloid sampling, with one half of the tooth crown retained for scanning electron microscopy (SEM), conducted at the University of

Alabama, to determine the quality of fossil preservation. The retained half of the tooth crown was first mounted in cold-setting epoxy resin, which was permitted to set for 24 hours. The labial-lingual axial plane of the tooth was then manually flattened and polished against successively finer aluminum oxide grinding discs and polishing cloths. After polishing, the

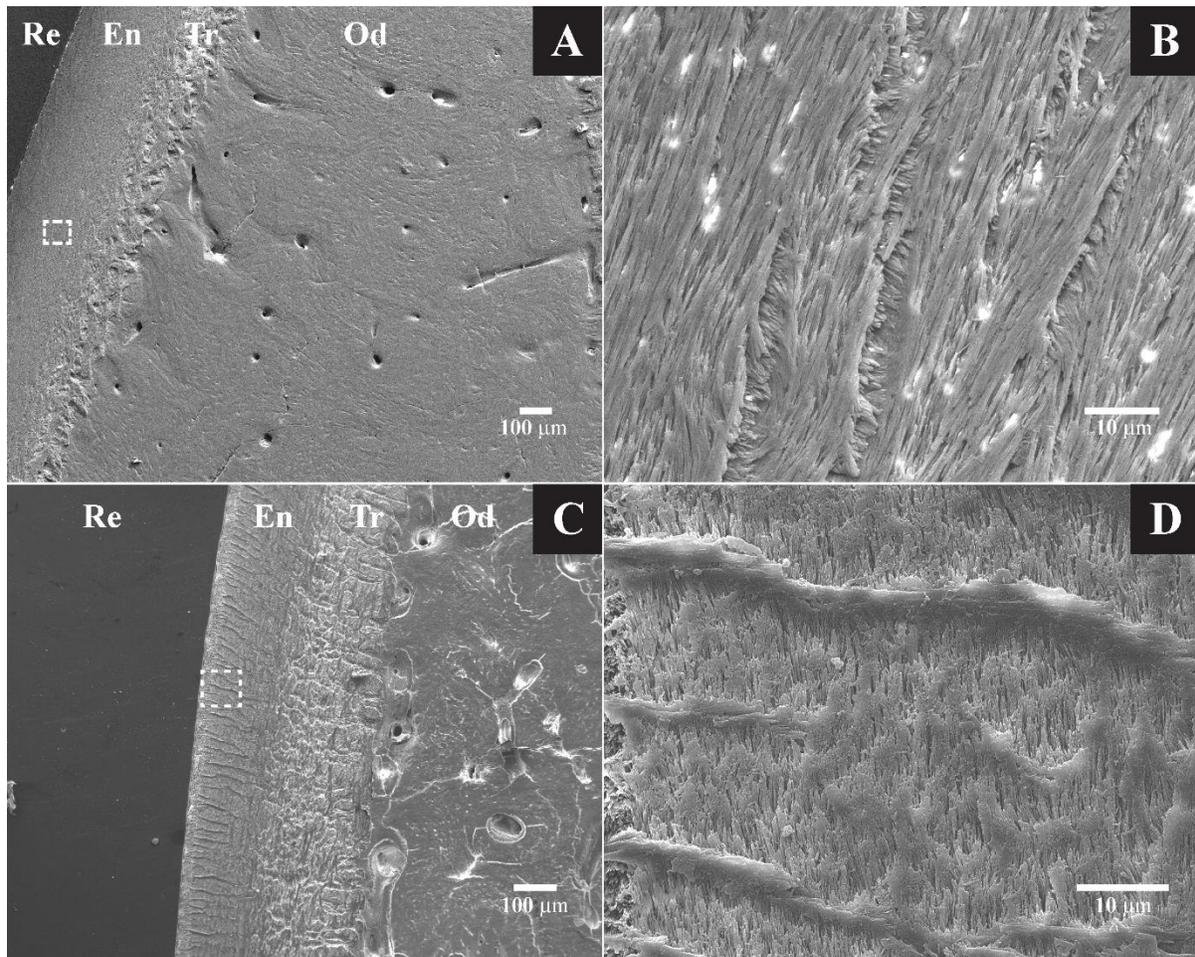


FIGURE 3.5 – Scanning electron micrographs (SEM) of *Squalicorax pristodontus* (A and B, Sample AL-17, Tables 1 and 2) and *Scapanorhynchus texanus* (C and D, unsampled specimen from the Tombigbee Sand in Alabama) in labial–lingual axial cross section showing high quality enameloid preservation. **A** – Low magnification SEM of *Squalicorax pristodontus* showing different regions of internal tooth structure. **B** – Magnified view of enameloid layer. Note relative lack of porosity in enameloid. Cross hatched pattern of bundles containing bioapatite crystals are apparent. **C** – Low magnification SEM of *Scapanorhynchus texanus* showing different regions of internal tooth structure. Dashed line indicates region present in image D. **D** – Magnified view of enameloid layer showing well preserved bioapatite crystals. Note significant structural difference between the two shark genera. Re – Mounting resin; En – Enameloid; Tr – Transition zone; Od – Osteodentine. Dashed line in left image indicates region magnified in right image.

exposed tooth cross-section was etched with 2% trace metal grade hydrochloric acid (HCl) for 20 seconds, rinsed with deionized water, and allowed to dry overnight. The epoxy disc containing the sample was then placed in a vacuum chamber and a thin gold coating applied to help dissipate static charge in the SEM. An aluminum mounting post was applied to the bottom of the epoxy disc using carbon tape, and copper strips were used to cover unimportant areas on top of the epoxy disc to further dissipate charging. The specimen was then placed in a JEOL JSM-7000F<sup>®</sup> field emission scanning electron microscope operated under a  $2.0 \times 10^{-4}$  Pa vacuum, at 15 kV and 8.0 mA of current, using a working distance of between 27 and 29 mm. An unsampled tooth of *Scapanorhynchus texanus* from the Tombigbee Sand in Alabama was also subjected to the same SEM analysis for comparison of genera. Several digital micrographs of the tooth cross sections were recorded at a variety of magnifications and retained for further examination (Fig. 5).

## RESULTS

The results of the analysis are presented in Table 2 and Figures 6 – 7. Numerical ages of the samples were obtained from McArthur *et al.* (2012) using look-up table Version 5. All samples in the analysis collected from the Upper Cretaceous strata yielded  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios that correlate with Late Cretaceous numeric ages (Table 2). Although teeth from some of the lower geologic units vary considerably in age, the general trend in the plotted  $^{87}\text{Sr}/^{86}\text{Sr}$  results shows that overlying strata are progressively younger (Fig. 6).

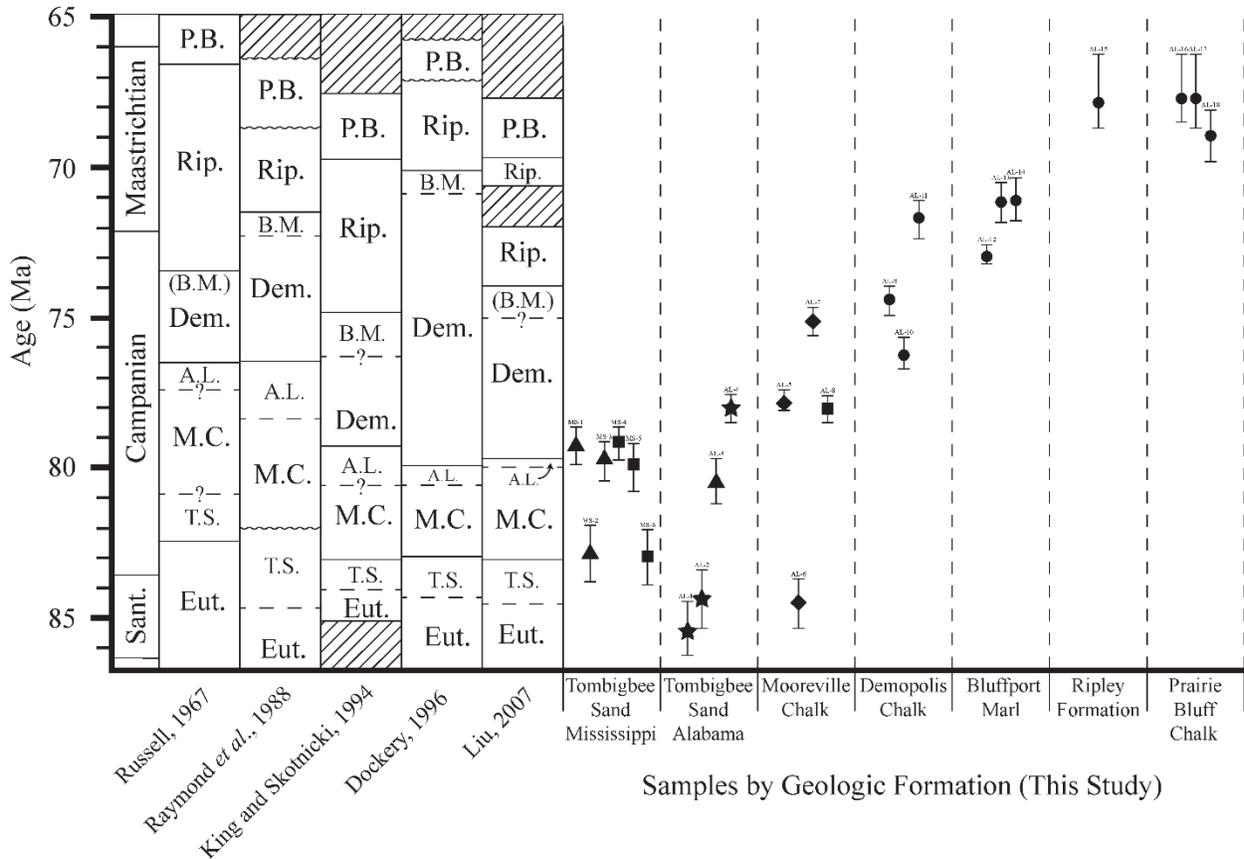


FIGURE 3.6 - Results of the present study plotted against numeric age and published stratigraphic columns of Upper Cretaceous formations of Alabama and Mississippi. Dockery (1996) pertains to Mississippi outcrops only. **Triangles** – *Squalicorax lindstromi*; **Stars** – *Squalicorax cf. yangaensis*; **Diamonds** – *Squalicorax kaupi*; **Circles** – *Squalicorax pristodontus*; **Squares** – *Scapanorhynchus texanus*. Specimens are plotted in order from Table 2. Error bars represent the 2 standard error (95%) confidence range. Geologic time scale is based on Cohen *et al.* (2013; updated to Version 2015/01), however previously published stratigraphic columns are based on time scales available at their time of publication. See Figure 2 for explanation of geologic abbreviations.

Specimens from the Tombigbee Sand in Mississippi produced mixed results (Mean = 80.61 Ma). Four of the six samples analyzed from the BASF Fowlkes Mine produced numeric ages (Mean = 79.48 Ma) that are too young for the Tombigbee Sand or Mooreville Chalk present in the quarry (Fig. 7). Two of the samples yielded dates (Mean = 82.88 Ma) that are younger than the underlying bentonite layer ( $84.09 \pm 0.4$  Ma) at the bottom of the quarry and are comparable to the age of strata exposed in the high wall. Specimens from the Tombigbee Sand in

Sample #	<sup>87</sup> Sr/ <sup>86</sup> Sr Adjusted	2σ abs	Error -	Age Ma	Error +
MS-1	0.707531	0.000010	78.65	<b>79.20</b>	79.90
MS-2	0.707475	0.000010	81.90	<b>82.80</b>	83.80
MS-3	0.707521	0.000008	79.15	<b>79.65</b>	80.45
MS-4	0.707532	0.000008	78.65	<b>79.15</b>	79.75
MS-5	0.707517	0.000010	79.20	<b>79.90</b>	80.80
MS-6	0.707473	0.000010	82.05	<b>82.95</b>	83.90
AL-1	0.707438	0.000010	84.45	<b>85.45</b>	86.25
AL-2	0.707453	0.000010	83.40	<b>84.35</b>	85.35
AL-3	0.707509	0.000008	79.70	<b>80.45</b>	81.20
AL-4	0.707562	0.000009	77.55	<b>78.00</b>	78.50
AL-5	0.707567	0.000008	77.40	<b>77.85</b>	78.10
AL-6	0.707451	0.000008	83.70	<b>84.50</b>	85.35
AL-7	0.707642	0.000009	74.65	<b>75.10</b>	75.60
AL-8	0.707561	0.000009	77.60	<b>78.05</b>	78.50
AL-9	0.707663	0.000011	73.95	<b>74.40</b>	74.90
AL-10	0.707614	0.000010	75.65	<b>76.25</b>	76.70
AL-11	0.707744	0.000010	71.10	<b>71.65</b>	72.35
AL-12	0.707716	0.000008	72.55	<b>72.95</b>	73.20
AL-13	0.707756	0.000011	70.50	<b>71.15</b>	71.80
AL-14	0.707757	0.000011	70.45	<b>71.10</b>	71.75
AL-15	0.707817	0.000010	66.25	<b>67.85</b>	68.70
AL-16	0.707819	0.000008	66.25	<b>67.70</b>	68.50
AL-17	0.707819	0.000011	66.25	<b>67.70</b>	68.70
AL-18	0.707798	0.000010	68.10	<b>68.95</b>	69.80

Table 3.2—Measured strontium isotope ratios (<sup>87</sup>Sr/<sup>86</sup>Sr) in analyzed samples adjusted for laboratory bias (-2.0 x 10<sup>-5</sup>). Numerical ages determined from McArthur *et al.* (2012) using look-up table Version 5.

Alabama produced older results (Mean = 82.06 Ma) although there was less consistency between the samples. The mean age produced by samples from the Mooreville Chalk in Alabama is 78.88 Ma and, similar to the Tombigbee Sand in Alabama, there is considerable variation in the individual results. The lower unnamed member of the Demopolis Chalk (Mean = 74.10 Ma) is more uniform between individual samples than the underlying Mooreville Chalk whereas the Bluffport Marl Member of the Demopolis Chalk (Mean = 71.73 Ma) is even more so. Only one specimen from the Ripley Formation was suitable for sampling, which produced an age of 67.85

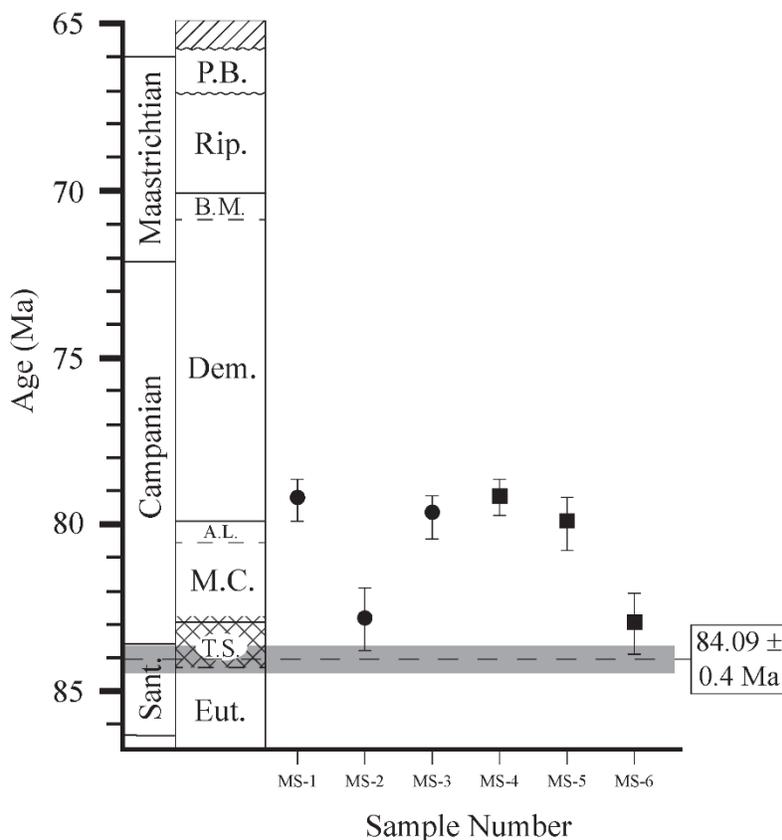


FIGURE 3.7 – Strontium isotope age of specimens collected from BASF Fowlkes Bentonite Mine, Monroe County, Mississippi (MGS-162) compared with radiometric age of bentonite layer ( $84.09 \pm 0.4$  Ma, dashed horizontal line and gray zone) reported by Obradovich (1993). Strata present in the quarry are indicated by the cross-hatched zone in the geologic column. **Circles** – *Squalicorax lindstromi*; **Squares** – *Scapanorhynchus texanus*. See Figure 2 for geologic abbreviations.

Ma. The Prairie Bluff Chalk was uppermost Cretaceous unit analyzed in the study, and yielded a mean age of 68.12 Ma.

## DISCUSSION AND CONCLUSIONS

### Numeric Ages of Stratigraphic Units

Overall, the numeric ages derived from  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios in the samples correlate reasonably well with the currently accepted ages of the Upper Cretaceous strata of the Mississippi Embayment (Fig. 6). A random sampling of previously published stratigraphic

columns from the region is provided in Figure 6 for simple comparison with the strontium isotope derived ages. Although the numeric ages do not correlate precisely with any single previously published stratigraphic column of Alabama, the column produced by Raymond *et al.* (1988) compares best with the strontium isotope derived ages for the younger Cretaceous geologic units. The column published by Dockery (1996) correlates better with the results than Raymond *et al.* (1988); however, that column is only representative of Upper Cretaceous strata in Mississippi as biostratigraphic research and sequence stratigraphy has shown that geologic ages differ between some of the same Cretaceous units in Mississippi and Alabama (Mancini and Puckett, 2005; Liu, 2007).

The strontium isotope numeric ages of shark teeth analyzed from Alabama show a steady trend from older to younger moving upsection in the stratigraphic column (Fig. 6), and the ages of samples become more precise in the younger strata, ranging from the Demopolis Chalk through the Prairie Bluff Chalk. The increased precision may be related to the species of shark sampled from these upper geologic units. *Squalicorax pristodontus* is a large Cretaceous shark (see Shimada and Cicimurri (2005) on size differences in species of *Squalicorax*) whose first occurrence in Alabama, based on material present in the ALMNH collections, is in the lower unnamed member of the Demopolis Chalk (or possibly upper Mooreville Chalk), which then persists to the uppermost portion of the Prairie Bluff Chalk. Adult *S. pristodontus* teeth are comparatively large and are often more than 2 cm across the base of the crown. During specimen sampling, it was noted that the outer enameloid layer appeared relatively thicker than that observed in the older, smaller species *S. kaupi*, *S. lindstromi*, and *S. cf. yangaensis*. This thicker enameloid layer in *S. pristodontus* facilitated obtaining the necessary 10 mg of sample powder, with little risk of contamination from the underlying diagenetically-altered osteodentine. The

thicker enameloid from the larger *S. pristodontus* teeth is therefore the likely cause of the increased precision up section. SEM analysis of the enameloid layers in *S. pristodontus* and *Scapanorhynchus texanus* specimens analyzed in this study shows that it is very well preserved in both genera (Fig. 5), with bioapatite crystallite bundles that are structurally similar to those present in the enameloid of extant shark species (Enax *et al.*, 2012; Enax *et al.*, 2014). The impermeable nature of the chinks, marlstones and clayey sands of the upper strata also likely helped to preserve the original strontium isotope signature in the shark teeth by preventing diagenetic alteration by groundwater flowing through the region (Davis, 1987).

The analysis of shark teeth from the Tombigbee Sand show mixed results in both Mississippi and Alabama (Figs. 6 and 7). Only two shark teeth sampled from the Tombigbee Sand in each state produced strontium isotope ages that are comparable to the generally accepted age of the geologic unit (Table 2). It is interesting to note that the better correlating samples from Alabama (AL-1 and AL-2) are considerably older than the better correlating samples (relative to the radiometric age of the bentonite) from Mississippi (MS-2 and MS-6), where the mean age of the Alabama samples is 84.9 Ma and the Mississippi average is 82.88 Ma. This finding is in agreement with the age difference of the Tombigbee Sand in Mississippi and Alabama based on biostratigraphic methods, in which the upper Tombigbee Sand in Mississippi is younger than the upper Tombigbee in Alabama and the Tombigbee Sand–Mooreville Chalk contact is diachronous (Mancini *et al.*, 1996).

Two separate teeth from the same fossil shark were analyzed during the course of this study to test the precision of fossil shark tooth enameloid strontium analysis. Samples AL-13 and AL-14 (Table 1) were obtained from a partial skeleton of *Squalicorax pristodontus* that included more than 20 teeth and numerous cartilage fragments from the Bluffport Marl in Sumter County,

Alabama. Results of the analysis show that these two samples produced nearly identical  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios, with a separation of only  $1.0 \times 10^{-6}$  (Table 2). The  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios for AL-13 and AL-14 equate to numeric ages of 71.15 Ma and 71.1 Ma respectively, which compare well with the age of the Bluffport Marl reported by Dockery (1996) and Raymond *et al.* (1988). This finding demonstrates that fossil shark tooth enameloid, if carefully sampled, can be utilized for numeric age dating with a high degree of precision and accuracy.

*Squalicorax pristodontus* specimen AL-16 was recovered from a skeleton of *Mosasaurus hoffmanni* skeleton (ALMNH PV 1988.0018), a large marine reptile of the Late Cretaceous, during its preparation. Shark teeth are commonly recovered during the preparation of marine vertebrate fossils at the Alabama Museum of Natural History. Sharks in the Late Cretaceous, as they are now, were often scavengers of carcasses (Schwimmer *et al.*, 1997) and during the course of feeding would shed loose teeth into the tissues of food items. These coeval shark teeth are ideal for age dating fossils where sampling damage to the teeth of the primary specimen is undesirable, or where teeth are non-existent, as in marine turtles. The strontium isotope age of *Squalicorax pristodontus* specimen AL-16 is  $67.70 \pm 0.8$  Ma (the younger error limit is difficult to ascertain in this specimen due to a peak that occurs in the LOWESS curve at the K/Pg boundary, See Fig. 1), meaning that the *M. hoffmanni* specimen from which the shark tooth was recovered is very likely the same age. This strontium isotope age fits well with the known stratigraphic range for *M. hoffmanni* of late Campanian to latest Maastrichtian (Harrell and Martin, 2015), and provides additional evidence as to the accuracy of this dating method.

## Strontium Isotope Age vs. Radiometric Age

The Tombigbee Sand in Monroe County, Mississippi, contains two closely deposited beds of bentonite clay (Stephenson and Monroe, 1940) that are of commercially exploitable thicknesses and have subsequently been exposed by several open pit mining operations in the area. Sanidine crystals obtained from this bentonite couplet were radiometrically dated by Obradovich (1993), who reported an age of  $84.09 \pm 0.40$  Ma for the layer. Fossil shark tooth specimens analyzed in this study were collected from the Fowlkes Bentonite Mine (MMNS locality number: MGS 162), where the Obradovich bentonite samples were obtained. Six specimens (Table 1: MS-1 through MS-6) were collected by the third author (GP) from overburden spoil piles located away from the active high wall. The bentonite couplet in this region of Mississippi is positioned near the base of the Tombigbee Sand, and the approximately 30 m thickness of this geologic unit in eastern Mississippi (Stephenson and Monroe, 1940) is exposed in its entirety in the high wall of the mine. As the contact with the overlying Mooreville Chalk is gradational, and approximately 39 m of strata are present in the mine, it is hypothesized that the lowermost portions of the Mooreville Chalk may also be exposed in the upper reaches of the high wall. The Tombigbee Sand–Mooreville Chalk contact in eastern Mississippi has been reported to be early Campanian in age based on the highest occurrence surface (HOS) of the foraminifera *Dicarinella asymetrica* which is located immediately above the contact (Smith and Mancini, 1983; Dowsett, 1989; Puckett, 1995; Mancini *et al.*, 1996). This means that the Santonian–Campanian boundary in east-central Mississippi is positioned within the upper part of the Tombigbee Sand. The currently accepted age of the Santonian–Campanian boundary is  $83.6 \pm 0.2$  Ma according to the most recent chronostratigraphic chart (ver. 2015/01) published by the International Commission on Stratigraphy (Cohen *et al.*, 2013). Four of the specimens in the

present study (Table 2: MS-1, MS-3 through MS-5) produced strontium isotope numeric ages that are too young for the strata exposed in the mine but are comparable with the ages reported by Becker *et al.* (2008) from the Tombigbee Sand in Alabama (Figs. 2 and 7). However, two specimens (Table 2: MS-2 and MS-6) produced strontium isotope ages of 82.80 Ma and 82.95 Ma respectively that, when their error ranges are included, are comparable with the radiometric age of the bentonite layer in the mine and the age of the Santonian–Campanian boundary (Fig. 7). The reason for the discrepancy between the accurate and inaccurate age dates is not known. As the Tombigbee Sand was deposited in a relatively nearshore environment (Mancini and Soens, 1994), freshwater influx from nearby rivers may have influenced the original strontium isotope signature in individuals with the less accurate age dates, whereas the more accurate samples may have belonged to individuals who migrated in from more offshore areas with normal strontium isotope ratios. Another explanation is that the differences may be due to sampling error as a result of the inclusion of diagenetically altered osteodentine in the enameloid obtained from smaller *Squalicorax cf. yangaensis*, *Squalicorax lindstromi*, and *Scapanorhynchus texanus* teeth (Fig. 3). The observed discrepancies could also be attributed to diagenetic leaching of the strontium content in the shark teeth by groundwater present in the Tombigbee Sand (Davis, 1987), whereas the shark teeth with more accurate age dates may have been deposited in the more calcareous, less-porous layers of the Tombigbee Sand (Stephenson and Monroe, 1940), which protected them from alteration. As the teeth from the mine could only be obtained from overburden spoil piles located away from the highwall, it is uncertain as to the precise lithologic layer from which each was derived.

## $^{87}\text{Sr}/^{86}\text{Sr}$ Ratios in Different Shark Taxa

Samples analyzed in the study were acquired from two genera, *Scapanorhynchus* and *Squalicorax*, to determine if possible habitat preference of either taxon could affect the  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios present in their enameloid. Although the  $^{87}\text{Sr}/^{86}\text{Sr}$  ratio in present day oceans is relatively uniform on a global scale, nearshore regions close to large rivers may have a diluted or  $^{87}\text{Sr}$ -enriched signature (McArthur *et al.*, 2012). If a particular taxon of shark preferred to live in this type of nearshore or brackish water environment, its  $^{87}\text{Sr}/^{86}\text{Sr}$  ratio would likely differ from that of the known coeval marine values of the LOWESS curve (Fig. 1). An equal number of specimens ( $n=3$ ) of each genus were sampled from the Tombigbee Sand exposed in the Fowlkes Mine in Mississippi. Although the sample number is small, results show no discernable difference between taxonomic groups. The mean age of the *Squalicorax lindstromi* specimens from the site is 80.55 Ma whereas the average for *Scapanorhynchus texanus* is 80.67 Ma. Although the average ages of both taxa are significantly younger than the currently accepted age of the Tombigbee Sand, two of the six samples produced ages that are within the range of this geologic unit (Table 2, Fig. 7). Among the Upper Cretaceous strata in the Gulf Coastal Plain, the Eutaw Formation including the Tombigbee Sand Member has the highest level of porosity and permeability (Mancini *et al.*, 2008). Another possible explanation for the unusually young numerical age is that the Tombigbee Sand was deposited in a relatively nearshore environment (King and Skotnicki, 1994), in which the strontium isotope ratio was altered by the influx of freshwater drainage from the nearby Appalachian subcontinent. In any case, this finding suggests that both shark taxa likely inhabited similar marine environments due to their nearly identical analytical results. Three teeth of *Squalicorax kaupi* and one tooth of *Scapanorhynchus texanus* from the Mooreville Chalk near Harrell Station in Dallas County, Alabama were also analyzed in

the present study (Table 1). Two of the *Squalicorax* samples (Table 2: AL-6 and AL-7) produced strontium age dates that are not comparable with any recently reported age of the Mooreville Chalk (Fig. 6). The reason for this discrepancy is not known but may be the result of sampling error in the comparatively small *S. kaupi* teeth (Fig. 4). However, *S. kaupi* sample AL-5 and the lone *Scapanorhynchus texanus* sample (AL-8) resulted in very similar ages that are compatible with the age of the Mooreville Chalk reported in older stratigraphic columns published by Russell (1967) and Raymond *et al.* (1988). This again suggests that the two shark taxa likely inhabited similar marine environments.

In addition to the analysis of two genera of shark, four different species of *Squalicorax* were sampled during the study due to the biostratigraphic limitations of each species. *Squalicorax cf. yangaensis* and *S. lindstromi* are species that are relatively abundant in the upper Santonian Tombigbee Sand of the Mississippi Embayment region. However, the comparatively small adult tooth size of these taxa makes it difficult to obtain the necessary 10 mg enameloid sample without contamination from the underlying dentine tissues. *Squalicorax kaupi* is more common in the lower Campanian Mooreville Chalk and has slightly larger teeth than *S. yangaensis* or *S. lindstromi* that are still somewhat difficult to sample. *Squalicorax pristodontus* is common in strata that are mid-Campanian to Maastrichtian in age, ranging from the Demopolis Chalk through the Prairie Bluff Chalk in Alabama. Teeth of adult *S. pristodontus* are comparatively large and the 10 mg sample of enameloid is easily obtained with little risk of penetrating into the underlying dentine material. The results of the present analysis (Table 2; Fig. 6) show better precision and accuracy in specimens acquired from younger Cretaceous strata, which may simply be the result of less-contaminated enameloid sampling of the larger *S. pristodontus* teeth, or perhaps because they were deposited in a more favorable depositional

environment. A more precise method of sampling such as micro-milling or laser ablation may be necessary to properly analyze enameloid from smaller shark taxa to ensure more reliable results, as it is difficult to obtain the 10 mg of enameloid sample powder required by the current analytical method from smaller teeth. Limited funding and time constraints on the first author (LH) prevented the exploration of these possible alternate sampling techniques although they may be addressed in future analyses.

### Stratigraphic Correlation and Petroleum Production

The Upper Cretaceous marine strata of the eastern Gulf Coastal Plain are significant reservoirs of hydrocarbons in the United States, with approximately 2 billion barrels of oil and 7.4 trillion cubic feet of natural gas recovered as of 2002 (Mancini and Puckett, 2002; Mancini and Puckett, 2003), and possess considerable potential for future production (Mancini *et al.*, 2008). Much of the hydrocarbon potential of these geologic units depends on their stratigraphic position in relation to marine transgressive-regressive cycles, with the majority of hydrocarbons produced by strata deposited during transgressive or back-stepping phases (Mancini and Puckett, 2002). The correlation of these strata with hydrocarbon-rich Cretaceous marine strata in the western Gulf Coastal Plain (Condon and Dyman, 2006) and Western Interior Basin (Higley and Cox, 2007) of the United States largely depends on sequence stratigraphy used in conjunction with biostratigraphy of microfossils. Correlation of stratigraphic units is useful for prospecting geological formations that may have high potential as hydrocarbon sources or reservoirs. Many foraminifera and other microorganisms are dependent on environmental conditions (Tappan, 1951) which unfortunately may not exist on a global scale and therefore may not be widely distributed at a synchronous stratigraphic level, resulting in suboptimal correlation of marine

strata. The use of strontium isotope ratios present in fossil shark tooth enameloid, which appear to be relatively stable in certain geologic conditions, may therefore be of use in constraining the timing of eustatic sea-level changes and age relations of marine strata in areas of conflicting or indeterminate biostratigraphic data. The uniform distribution of strontium isotopes in oceanic water (McArthur *et al.*, 2012), aside from very nearshore environments, suggests that fossil shark tooth enameloid may be used to help correlate marine strata on a global scale regardless of depositional environment, based on the findings of the current study.

### Conclusions

1. Stable strontium age dating of fossil shark tooth enameloid correlates to numerical ages that are relatively precise and accurate in younger Late Cretaceous strata of the Mississippi Embayment region and compare well with some previously published stratigraphic columns. The strontium isotope dates obtained in this study compare best with the stratigraphic column published by Raymond *et al.*, 1988.

2. One-third of the stable strontium isotope ages obtained from specimens from the Fowlkes Bentonite Mine in Monroe County, Mississippi, compare well with the radiometrically derived age of the bentonite layer and the age of the Santonian–Campanian boundary exposed in the strata whereas the remaining specimens produced numeric ages that are younger than the currently accepted age of the strata.

3. Of the specimens that were analyzed in this study, no differences in strontium isotope ratios were observed between the fossil shark genera or species. Larger *Squalicorax pristodontus* teeth, with their thicker enameloid layer, produced more accurate and precise strontium isotope numeric ages relative to their respective geologic units than the smaller *S. cf. yangaensis*, *S.*

*lindstromi* and *S. kaupi*, and *Scapanorhynchus texanus* teeth. Better enameloid sampling methods are needed for analyzing smaller shark teeth to reduce potential contamination from underlying osteodentine material.

4. Non-porous geologic strata that contain high percentages of chalk, marlstone, or clay appear to preserve original strontium isotope ratios in fossil shark teeth better than sandy strata that contain large quantities of ground water. Geologic units deposited in relatively nearshore environments, such as the Tombigbee Sand, produced poorer results than geologic units deposited in deeper, offshore environments.

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#### 4. MOSASAURS: ECTOTHERMS OR ENDOTHERMS?

##### ABSTRACT

The thermoregulatory style of Late Cretaceous mosasaurs has become a highly controversial subject in vertebrate paleontology. These extinct marine reptiles have previously been described as poikilothermic, endothermic, or gigantothermic. Here we analyze three genera of mosasaurs from the Mooreville Chalk in Alabama (USA) of differing body mass and compare their  $\delta^{18}\text{O}_{\text{PO}_4}$  derived body temperatures ( $T_b$ ) with those of coeval poikilothermic fish (*Enchodus*) and endothermic pelagic seabirds (*Ichthyornis*). Results show that all mosasaurs, *Clidastes* ( $T_b = 33.1\text{ }^\circ\text{C}$ ), *Platecarpus* ( $T_b = 36.3\text{ }^\circ\text{C}$ ), and *Tylosaurus* ( $T_b = 34.3\text{ }^\circ\text{C}$ ), had elevated average body temperatures in relation to those of *Enchodus* ( $T_b = 28.3\text{ }^\circ\text{C}$ ) and were closer to those of *Ichthyornis* ( $T_b = 38.6\text{ }^\circ\text{C}$ ), suggesting endothermy in mosasaurs. The temperatures calculated for *Enchodus* compare well with previously reported temperature estimates for the Mooreville Chalk and the  $T_b$  of *Ichthyornis* compares well with temperatures that have been reported for modern seabirds, suggesting that this method provides accurate results. Finally, although there are small differences of body temperature among mosasaur genera, these are independent of size, and thus inferred body mass, suggesting that mosasaurs were not gigantotherms, but rather endotherms.

##### INTRODUCTION

Mosasaurs were a diverse group of highly successful marine reptiles that evolved in the mid-Cretaceous, experienced a rapid adaptive radiation, and died out during the

Cretaceous/Paleogene (K/Pg) extinction event. This sudden evolutionary success is often attributed to the opportunistic exploitation of ecological niches left vacant by the extinction of the ichthyosaurs during the mid-Cretaceous (Sharma, 2005; Everhart, 2007). Prior to the mosasaurs, ichthyosaurs were the dominant marine reptiles for a large portion of the Mesozoic Era (Motani, 2005), using their highly-derived fusiform shape to enhance their capabilities as pursuit predators (Massare, 1988). This advanced dolphin-like or tuna-like shape and a probable active lifestyle led some researchers to suggest the possibility that ichthyosaurs may have also had advanced thermoregulation in order to maintain a high activity level and increase their chances of feeding success (Massare, 1994).

In spite of these derived characteristics, the ichthyosaurs died out during the mid-Cretaceous extinction event and were quickly replaced by the early mosasaurs, which likely evolved from small, near-shore marine squamates (Dutchak, 2005; Reeder *et al.*, 2015). From a morphological standpoint, the evolutionary success of the mosasaurs is often attributed to specialized intracranial mobility and other characters found in the skull, including streptostyly and a flexible mid-mandibular joint, which allowed a better grasp on prey items (Russell, 1967). As mosasaurs further evolved, they began to develop some of the same morphological features of their ichthyosaur predecessors, such as a heterocercal tail (Lindgren *et al.*, 2010). By the time of their extinction, highly-derived mosasaurs such as *Plotosaurus bennisonni* (Camp, 1942) had acquired a number of features present in basal ichthyosaurs, including a heterocercal tail, hyperphalangic paddles, a long slender muzzle with small sharp teeth, and a probable dorsal fin (Russell, 1967; Lindgren *et al.*, 2007, 2008). This trend toward convergent evolution has led some researchers to hypothesize that mosasaurs may have similarly developed elevated thermoregulation (Bernard *et al.*, 2010), which would have helped facilitate the transition from

ambush predation to active, pursuit predation. Endothermy, which is the ability to regulate body temperature via metabolic control versus ambient or passive methods such as sunning, would have also enabled the mosasaurs to exploit cooler water polar environments to expand their potential habitat range (Martin, 2002; Chin *et al.*, 2008).

Bernard *et al.* (2010) assessed the potential thermoregulation in a variety of Mesozoic marine reptiles using the  $\delta^{18}\text{O}$  of biophosphates (teeth) with coeval poikilothermic fish, from the same collection locality as the marine reptiles, as a proxy for ambient seawater temperatures. Poikilothermic animals have internal temperatures that vary considerably, typically fluctuating with the temperature of their surrounding environment. This approach indicated that ichthyosaurs and plesiosaurs were likely endothermic homeotherms, animals with a constant body temperature (homeotherms) that regulate that temperature metabolically (endotherms). Mosasaurs were more difficult to constrain and were thought to be potentially more influenced by ambient sea temperatures, or even that they could be gigantothermic, maintaining a high internal body temperature by virtue of their smaller surface area to volume ratio (Bernard *et al.*, 2010; Motani, 2010). Part of the problem that prevented constraining the potential for thermoregulation in mosasaurs was the absence of an endothermic taxon (e.g. toothed seabird) for comparison. Additionally, the whole range of body sizes in mosasaur genera was not evaluated for its influence in thermoregulation.

In this study, we assess thermoregulation in mosasaurs by comparing  $\delta^{18}\text{O}$  data from tooth enamel, with some additional results from well-preserved cortical bone, of three genera *Clidastes*, *Platecarpus*, and *Tylosaurus*, chosen on the basis of their adult size to provide context for small, medium, and large mosasaurs respectively (Fig. 1). These data were further compared to stable oxygen data from *Enchodus*, as the representative of small poikilothermic fish in the

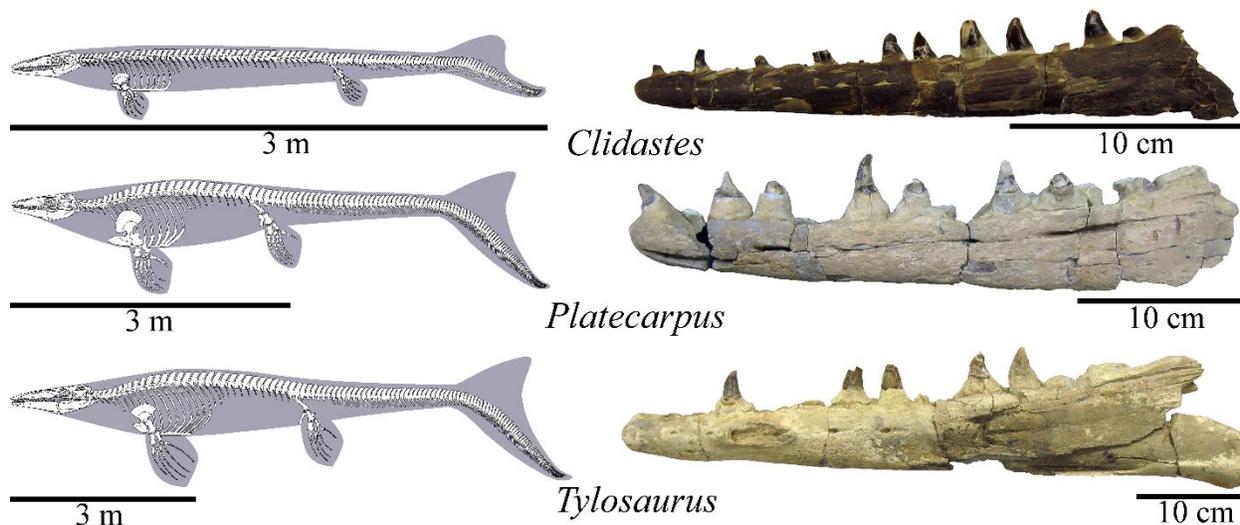


FIGURE 4.1 – Body outlines and skeletons of mosasaur genera analyzed in this study for scale (left) and representative dentaries for each genus (right). Figures redrawn from Russell (1967), Lindgren *et al.* (2010), and Field *et al.* (2015).

Late Cretaceous, *Toxochelys*, a medium-sized marine turtle with a shell typically less than 1 m in length that provided an analog for an atmospheric breathing marine ectotherm, and *Hesperornis* and *Ichthyornis*, which are basal, toothed seabirds and chosen as coeval endothermic analogs.

## MATERIAL AND METHODS

### Samples

Fossils analyzed in this study were either obtained with permission from the Alabama Museum of Natural History (ALMNH) collections from documented localities, or were field collected by the first author (Table 1). Mosasaur material for isotopic analyses ( $\delta^{18}\text{O}$  from the phosphate) was mainly extracted from well-preserved tooth enamel, because the apatite is considered to resistant to diagenesis (Koch, 2007). For further assessment of the preservation, visual and SEM observations of tooth enamel were conducted and rare earth element (REE) data were evaluated from two previous studies (Harrell and Pérez-Huerta, 2015a, 2015b). REE content indicates minimum alteration in mosasaur tooth to the point of using these data to

Sample #	Taxon	Material	ALMNH Number	Sample #	Taxon	Material	ALMNH Number
<b>Mooreville Chalk (Alabama)</b>							
AL-1a	<i>Enchodus</i>	Enamel	PV2004.0003.0010	AL-7d	<i>Clidastes</i>	Bone	PV1994.0004.0004
AL-1b	<i>Enchodus</i>	Enamel	PV2004.0003.0010	AL-8a	<i>Platecarpus</i>	Enamel	PV1993.0007.0307
AL-1c	<i>Enchodus</i>	Enamel	PV2004.0003.0010	AL-8b	<i>Platecarpus</i>	Enamel	PV1993.0007.0307
AL-1d	<i>Enchodus</i>	Bone	PV2004.0003.0010	AL-8c	<i>Platecarpus</i>	Bone	PV1993.0007.0307
AL-2a	<i>Enchodus</i>	Enamel	PV2010.0008.0010	AL-8d	<i>Platecarpus</i>	Bone	PV1993.0007.0307
AL-2b	<i>Enchodus</i>	Enamel	PV2010.0008.0010	AL-9a	<i>Tylosasaurus</i>	Enamel	PV1993.0001.0001
AL-2c	<i>Enchodus</i>	Enamel	PV2010.0008.0010	AL-9b	<i>Tylosasaurus</i>	Enamel	PV1993.0001.0001
AL-2d	<i>Enchodus</i>	Bone	PV2010.0008.0010	AL-9c	<i>Tylosasaurus</i>	Enamel	PV1993.0001.0001
AL-3a	<i>Enchodus</i>	Enamel	Destroyed in Analysis	AL-9d	<i>Tylosasaurus</i>	Bone	PV1993.0001.0001
AL-3b	<i>Enchodus</i>	Bone	Destroyed in Analysis	AL-10a	<i>Tylosasaurus</i>	Enamel	PV1985.0011
AL-4a	<i>Toxochelys</i>	Bone	Destroyed in Analysis	AL-10b	<i>Tylosasaurus</i>	Enamel	PV1985.0011
AL-4b	<i>Toxochelys</i>	Bone	Destroyed in Analysis	AL-10c	<i>Tylosasaurus</i>	Enamel	PV1985.0011
AL-5a	<i>Clidastes</i>	Enamel	PV2001.0002.0001	AL-10d	<i>Tylosasaurus</i>	Bone	PV1985.0011
AL-5b	<i>Clidastes</i>	Enamel	PV2001.0002.0001	AL-11a	<i>Tylosasaurus</i>	Enamel	Destroyed in Analysis
AL-5c	<i>Clidastes</i>	Enamel	PV2001.0002.0001	AL-11b	<i>Tylosasaurus</i>	Enamel	Destroyed in Analysis
AL-5d	<i>Clidastes</i>	Bone	PV2001.0002.0001	AL-11c	<i>Tylosasaurus</i>	Bone	Destroyed in Analysis
AL-6a	<i>Clidastes</i>	Enamel	PV2005.0006.0087	AL-12a	<i>Ichthyornis</i>	Bone	PV2008.0002.0007
AL-6b	<i>Clidastes</i>	Enamel	PV2005.0006.0087	AL-12b	<i>Ichthyornis</i>	Bone	PV2008.0002.0007
AL-6c	<i>Clidastes</i>	Enamel	PV2005.0006.0087	AL-13a	<i>Ichthyornis</i>	Bone	PV2008.0002.0008
AL-6d	<i>Clidastes</i>	Bone	PV2005.0006.0087	AL-13b	<i>Ichthyornis</i>	Bone	PV2008.0002.0008
AL-7a	<i>Clidastes</i>	Enamel	PV1994.0004.0004	AL-14a	<i>Ichthyornis</i>	Bone	PV2014.0001.0362
AL-7b	<i>Clidastes</i>	Enamel	PV1994.0004.0004	AL-14b	<i>Ichthyornis</i>	Bone	PV2014.0001.0362
AL-7c	<i>Clidastes</i>	Enamel	PV1994.0004.0004				
<b>Sharon Springs Formation (South Dakota)</b>							
SD-1a	<i>Enchodus</i>	Bone	PV2014.0001.0365	SD-3a	<i>Hesperornis</i>	Bone	PV2014.0001.0363
SD-1b	<i>Enchodus</i>	Enamel	PV2014.0001.0365	SD-3b	<i>Hesperornis</i>	Bone	PV2014.0001.0363
SD-2a	<i>Platecarpus</i>	Bone	PV2014.0001.0357	SD-3c	<i>Hesperornis</i>	Bone	PV2014.0001.0363

TABLE 4.1 – Specimen data of samples analyzed in this study.

evaluate habitat preference (Harrell and Pérez-Huerta, 2015a). In addition,  $\delta^{18}\text{O}$  data from well-preserved cortical bone were compared to tooth enamel results to determine the possible influence of diagenesis and to evaluate whether  $\delta^{18}\text{O}$ -temperature derived data would reflect body temperatures (Table 1). The same procedure used to evaluate mosasaur samples was also used for *Enchodus* and *Toxochelys*. Finally,  $\delta^{18}\text{O}$  results from mosasaur and fish from the Mooreville Chalk in Alabama, which represent the bulk of data for this study, were compared to

samples from the Sharon Springs Formation in South Dakota, which are known to be partially altered by diagenesis (Cicimurri and Everhart, 2001).

Late Cretaceous birds were used as an analog for an endothermic organism for comparison with contemporaneous mosasaurs, because all modern birds are endotherms and generate a relatively high body temperature (Prinzinger *et al.*, 1991). Well-preserved cortical bone of *Hesperornis* and *Ichthyornis* were used for isotopic analyses as their teeth were too small and fragile for sampling. *Hesperornis* was a fully-marine, flightless seabird that inhabited the Western Interior Seaway, ranging from present-day Arkansas to the Canadian arctic (Wilson and Chin, 2014). *Ichthyornis* was a seabird that superficially resembled a modern seagull and was fully capable of flight, however its fossils are presently known only from offshore marine deposits in Kansas, Alabama, Texas, and New Mexico (Clarke, 2004; Shimada and Fernandes, 2006). *Hesperornis* and probably *Ichthyornis* obtained water from the sea and therefore acquired oxygen isotopes from the same source as marine reptiles.

### Sample Locality Stratigraphy

Fossil specimens sampled in this study were collected from the lower unnamed member of the Mooreville Chalk in Greene and Dallas counties in Alabama, and the Sharon Springs Formation along the southeast flank of the Black Hills in Fall River County, South Dakota. Although many of the Mooreville Chalk specimens were previously collected by the Alabama Museum of Natural History, some were collected by the first author at the Harrell Station locality in Dallas County, a site that is well-known for its rich vertebrate fauna (Zangerl, 1948, 1953; Langston, 1960; Applegate, 1970; Russell, 1970; Thurmond and Jones, 1981; Ikejiri *et al.*, 2013). All of the Sharon Springs Formation specimens analyzed in this study were collected by

the first author from a landfill facility near Buffalo Gap, South Dakota. The numerous outcrops in this area are known for producing a variety of Cretaceous marine vertebrate fossils, as well as pterosaurs (Hargrave, 2007). These two geologic formations were selected for study because of their latitudinal variation and similar temporal occurrence (early Campanian).

The lower unnamed member of the Mooreville Chalk in Alabama consists of beds of yellowish-grey to bluish-grey chalk and chalky marl that typically weather to a lighter white color (Raymond *et al.*, 1988). This relatively complete upper Santonian to lower Campanian geologic section ranges in thickness from 107 – 122 m in western and central Alabama and it is representative of an inner or middle shelf depositional environment (Mancini *et al.*, 1996; Liu, 2009). Water depth at the time of deposition is estimated to have ranged from 35 – 90 m based on the number of “sighted ostracodes” preserved in the chalk and marl beds (Puckett, 1991). The marine vertebrate and invertebrate fauna of the Mooreville Chalk is very diverse (Stephenson and Monroe, 1940; Zangerl, 1953; Thurmond and Jones, 1981; Ikejiri *et al.*, 2013) and well-preserved, with little diagenetic alteration due to the shallow burial depth and impermeability of the chalk (Liu, 2009).

The Sharon Springs Formation is a component of the Pierre Shale Group in South Dakota and consists of 6 – 14 m of dark, thinly bedded, organic-rich shale with numerous bentonite interbeds (Martin *et al.*, 2007). In the Black Hills region of South Dakota, the Sharon Springs Formation ranges from the lower to middle Campanian and represents a comparatively deeper water depositional environment than other formations of the Pierre Shale Group (Patrick *et al.*, 2007). Although the macroinvertebrate fauna is mostly restricted to cephalopods, the vertebrate fauna of the Sharon Springs Formation is relatively diverse, with skeletons often preserved in

articulation. Bone preservation can be poor, especially for weathered specimens at or near the surface, which typically have a veneer of selenite crystals.

### Oxygen Isotope Analysis

Fossil specimens were mechanically processed in the Department of Geological Sciences at the University of Alabama (USA). Specimens were first washed in an ultrasonic bath to remove any remaining traces of matrix, rinsed with deionized water, and dried overnight. Each specimen was successively placed in a cleaned and dried agate mortar under a binocular dissecting microscope to collect the sample powders. A Dremel<sup>®</sup> rotary tool equipped with diamond drill bits was used to obtain approximately 1-2 mg of sample powder, which collected in the mortar. Sampling was restricted to the outer enamel of tooth specimens because of its resistance to diagenetic alteration, and restricted to the outer cortical region of bone specimens to minimize contamination from infilling matrix and secondary minerals. Each sample powder was then transferred to weigh paper and measured on an electronic balance. Sample powders were placed in individually labeled microcentrifuge tubes for transport. Between specimens, the drill bits and mortar were cleaned with dilute trace metal grade nitric acid (HNO<sub>3</sub>), rinsed with deionized water, and dried with Kimwipes<sup>®</sup> to prevent cross contamination.

Powder samples were transported to the Department of Geosciences and the Stable Isotope Lab at the University of Arkansas (USA) for chemical processing and analysis. Methods were adapted from O'Neil *et al.* (1994) and Venneman *et al.* (2002). Approximately 300-500 µg of material from each sample was weighed on a balance, placed in individual microcentrifuge tubes with 1 mL of 4% NaOCl solution and allowed to sit overnight to remove organic material. Samples were rinsed 5 times with nanopure deionized water, using a vortex and centrifuge with

each rinse, and allowed to dry. The samples were then dissolved in 100  $\mu\text{L}$  of 0.5M  $\text{HNO}_3$ . Exactly 75  $\mu\text{L}$  of 0.5M  $\text{KOH}$  was then added to increase pH and decrease solubility of  $\text{CaF}_2$ . Next, 200  $\mu\text{L}$  of 0.17 M  $\text{KF}$  was added to precipitate out  $\text{Ca}^{2+}$  as  $\text{CaF}_2$  for 1-2 hours. Samples were centrifuged and supernatant was transferred to clean, low-binding microcentrifuge tubes using disposable glass pipettes for each sample. 250  $\mu\text{L}$  of silver amine solution was then added to each of the samples, which were then placed in an oven at 46.5  $^\circ\text{C}$  to heat for 20 hours. Yellow  $\text{Ag}_3\text{PO}_4$  crystals precipitated during the heating process, and samples that did not produce  $\text{Ag}_3\text{PO}_4$  crystals were discarded. The samples were then centrifuged and the supernatant decanted and disposed. Samples were rinsed 5 times with deionized water, and allowed to dry overnight.  $\text{Ag}_3\text{PO}_4$  crystals were weighed and then transferred to 3.5 x 5 mm silver capsules. The capsules were loaded into a zero-headspace autosampler attached to a Finnigan<sup>®</sup> MA TC/EA (thermochemical/elemental analyzer) operated at 1400  $^\circ\text{C}$ . The resulting CO was measured on line by a Thermofinnigan<sup>®</sup> DeltaPlus XL gas chromatograph-IRMS. Results (Table 1) were normalized to internal standards (returned values) consisting of USGS 24 ( $-28.1 \pm 0.2$ ), USGS 35 ( $57.1 \pm 0.7$ ), ANU Sucrose ( $37.1 \pm 0.08$ ), and Alpha Aesar  $\text{Ag}_3\text{PO}_4$  ( $8.4 \pm 0.8$ ) and reported in standard delta notation ( $\delta^{18}\text{O}$ ) relative to V-SMOW. NIST 120c was analyzed as a quality control standard rather than a calibration standard and returned an average value of  $22.4 \pm 0.4\%$ . The lab reported external precision is  $\sim 0.3\%$  ( $1\sigma$ ).

## RESULTS

The  $\delta^{18}\text{O}_{\text{PO}_4}$  results for all taxa are summarized in Figure 2 and Table 2. Detailed results of all taxa are presented in Appendix 1. Most of the data is obtained from the analysis of

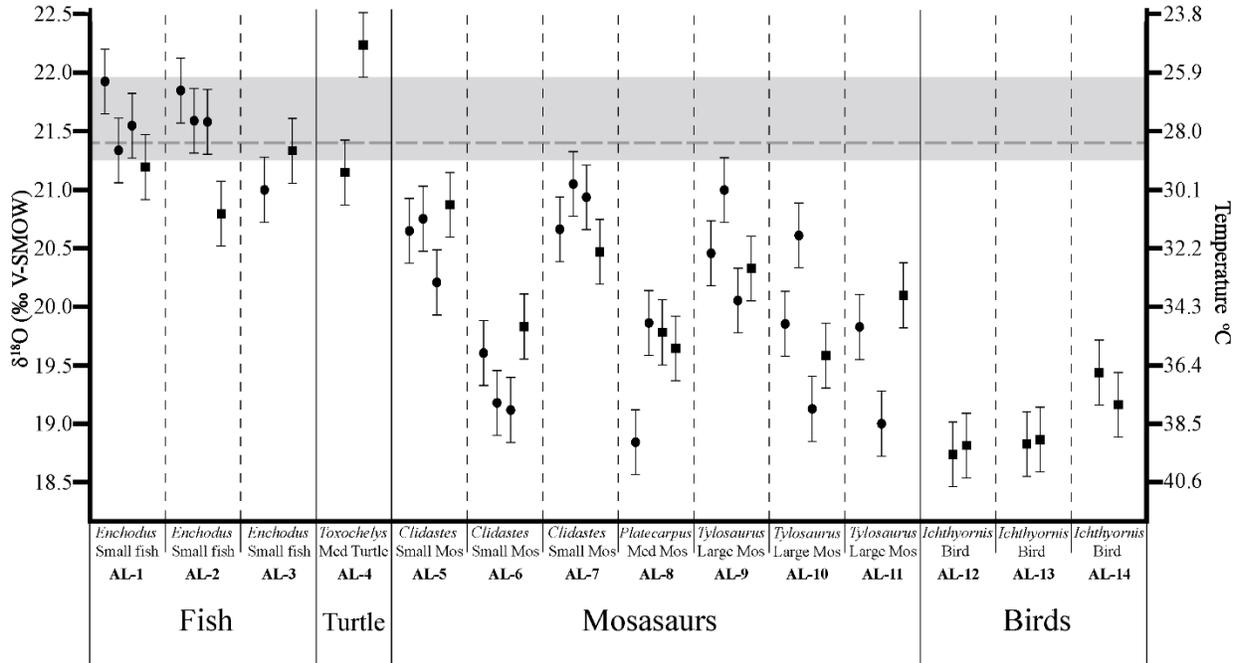


FIGURE 4.2 –  $\delta^{18}\text{O}_{\text{PO}_4}$  and derived temperature results of specimens from the Mooreville Chalk in Alabama. Circles represent tooth enamel samples, squares represent bone samples. Horizontal dashed line is average temperature of fish. Gray region is temperature range calculated for Mooreville Chalk sea using carbonates by Liu (2009). Temperature scale calculated using bioapatite formula of Pucéat *et al.* (2010) and 0‰ for  $\delta^{18}\text{O}_{\text{water}}$ . Med = medium, Mos = mosasaur.

specimens collected from the Mooreville Chalk, since many of the samples from the Sharon Springs Formation did not produce sufficient  $\text{Ag}_3\text{PO}_4$  crystals.  $\delta^{18}\text{O}_{\text{PO}_4}$  values range from a maximum of 22.23‰ for *Toxochelys* (specimen AL-4b), to a minimum of 18.74‰ for *Ichthyornis* (specimen AL-12a). Overall, the  $\delta^{18}\text{O}_{\text{PO}_4}$  values of bone samples correlate well with those of the enamel samples, showing no clearly differing trend. Therefore, the  $\delta^{18}\text{O}_{\text{PO}_4}$  of bone and enamel samples for each specimen were averaged together and body temperatures were calculated using the revised biogenic apatite formula by Pucéat *et al.* (2010;  $T(^{\circ}\text{C}) = 118.7 - 4.22[(\delta^{18}\text{O}_{\text{PO}_4} + (22.6 - \delta^{18}\text{O}_{\text{NBS120C})) - \delta^{18}\text{O}_{\text{water}}]$ ), with  $\delta^{18}\text{O}_{\text{water}}$  values of -1.37‰, -0.36‰, 0‰,

Taxon	$\delta^{18}\text{O}_{\text{PO4}}$	Temperature °C ( $\delta^{18}\text{O}_{\text{Water}}$ )			
		(-1.37‰)	(-0.36‰)	(0.00‰)	(0.23‰)
<b>Mooreville Chalk, Alabama</b>					
<i>Enchodus</i> (n=10)	<b>21.41</b>	22.6	26.8	<b>28.3</b>	29.3
<i>Toxochelys</i> (n=2)	<b>21.69</b>	21.4	25.6	<b>27.2</b>	28.1
<i>Clidastes</i> (n=12)	<b>20.28</b>	27.3	31.6	<b>33.1</b>	34.1
<i>Platecarpus</i> (n=4)	<b>19.53</b>	30.5	34.8	<b>36.3</b>	37.3
<i>Tylosaurus</i> (n=11)	<b>20.00</b>	28.5	32.8	<b>34.3</b>	35.3
<i>Ichthyornis</i> (n=6)	<b>18.98</b>	32.8	37.1	<b>38.6</b>	39.6
<b>Sharon Springs Formation, South Dakota</b>					
<i>Enchodus</i> (n=2)	<b>20.58</b>	26.1	30.3	<b>31.9</b>	32.8
<i>Platecarpus</i> (n=1)	<b>20.24</b>	27.5	31.8	<b>33.3</b>	34.3
<i>Hesperornis</i> (n=3)	<b>19.90</b>	28.9	33.2	<b>34.7</b>	35.7

TABLE 4.2 – Average  $\delta^{18}\text{O}_{\text{PO4}}$  for each taxonomic group and temperature calculations using formula of Puc at *et al.* (2010) with differing values for  $\delta^{18}\text{O}_{\text{water}}$  in parentheses.

and 0.23‰ (Table 2). The  $\delta^{18}\text{O}$  of body water was assumed to be approximate to the  $\delta^{18}\text{O}$  of seawater for marine vertebrates, and likely so for pelagic birds (see Discussion). The  $\delta^{18}\text{O}_{\text{water}}$  values were determined based on the turtle bone analysis of Coulson *et al.* (2011) using clumped isotopes, and the turtle bone results of the present study (see Discussion). The  $\delta^{18}\text{O}_{\text{PO4}}$  of each Mooreville Chalk specimen was averaged and subtracted from the  $\delta^{18}\text{O}_{\text{PO4}}$  of fish and plotted on a line graph to show the relationship of sampled taxa between poikilothermic fish and endothermic birds (Fig. 3).

The mosasaurs analyzed in the present analysis correspond well with the regression line reported by the Bernard *et al.* (2010) study for marine reptiles. The small mosasaur analog, *Clidastes*, produced mean  $\delta^{18}\text{O}_{\text{PO4}}$  values of  $20.28 \pm 0.20\text{‰}$  with a corresponding body temperature ( $T_b$ ) of 33.1 °C. The single medium-sized mosasaur specimen from the Mooreville Chalk, *Platecarpus*, produced the lowest mean  $\delta^{18}\text{O}_{\text{PO4}}$  value and highest body temperature of the mosasaurs in the study ( $\delta^{18}\text{O}_{\text{PO4}} = 19.53 \pm 0.23\text{‰}$ ,  $T_b = 36.3$  °C). The large mosasaur

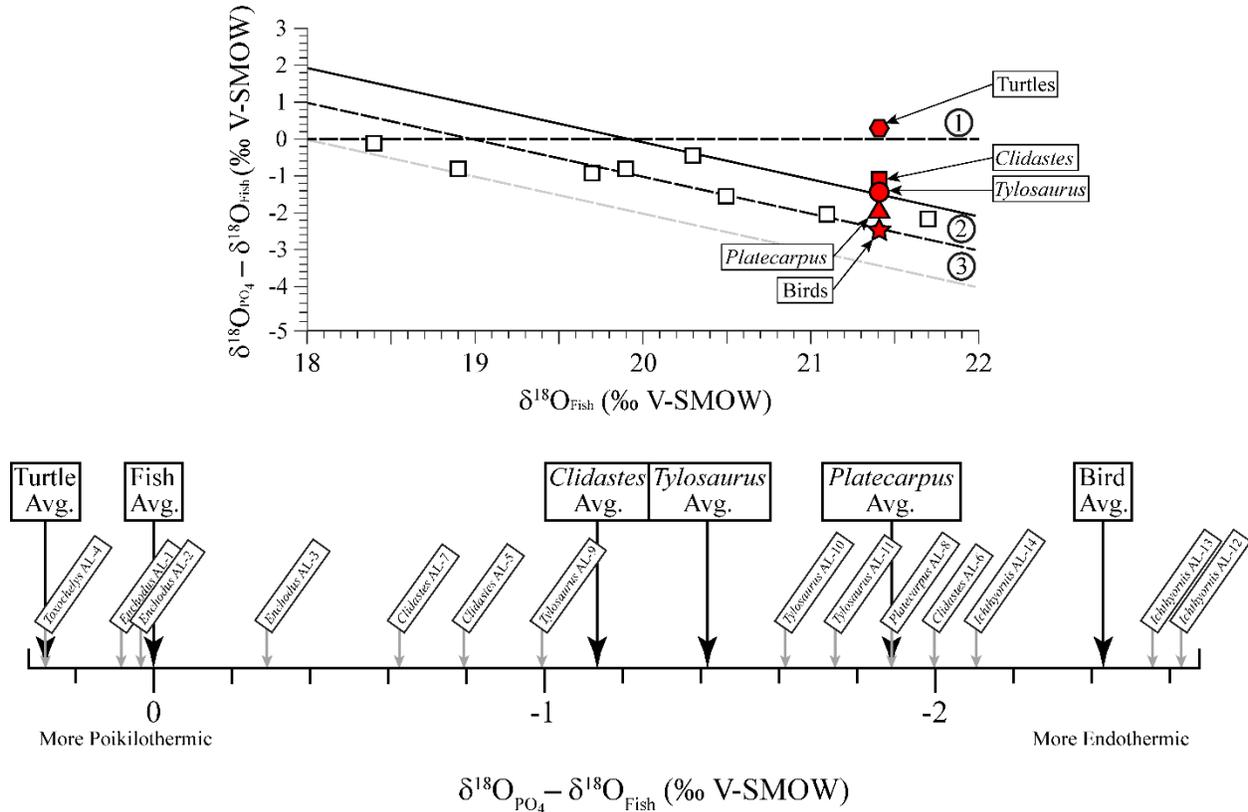


FIGURE 4.3 – (Top)  $\delta^{18}\text{O}_{\text{PO}_4}$  averages of mosasaur genera, birds, and turtle of this study included with mosasaur data (open squares) reported by Bernard *et al.* (2010). Line 1 = poikilothermic fish, Lines 2 and 3 = endothermic organisms. (Bottom)  $\delta^{18}\text{O}_{\text{PO}_4}$  data of Mooreville Chalk specimens relative to fish (left) and birds (right). The 0 position on the line graph indicates the mean  $\delta^{18}\text{O}_{\text{PO}_4}$  of all Mooreville Chalk fish. Figure modified from Bernard *et al.* (2010).

representative, *Tylosaurus*, produced temperature estimates ( $\delta^{18}\text{O}_{\text{PO}_4} = 20.00 \pm 0.18\text{‰}$ ,  $T_b = 34.3$

$^{\circ}\text{C}$ ) that are warmer than *Clidastes*, but cooler than the medium-sized *Platecarpus*. The mean

$\delta^{18}\text{O}_{\text{PO}_4}$  of each Mooreville Chalk specimen was subtracted from the mean  $\delta^{18}\text{O}_{\text{PO}_4}$  of all

*Enchodus* specimens and plotted along a line graph modified from Bernard *et al.* (2010) (Fig. 3).

Specimens plotting closer to the zero region of the graph were considered to be poikilothermic

while those with more negative values were considered to be more endothermic. The *Ichthyornis*

bird specimens produced the most negative values and were designated as the endothermic

endmember of the graph. Four of the mosasaurs (*Tylosaurus* specimens AL-10, AL-11;

*Platecarpus* AL-8; *Clidastes* AL-6) plotted close to the *Ichthyornis* specimens, indicating high

body temperatures comparable to those of probable endotherms. The remaining three mosasaurs (*Clidastes* specimens AL-5, AL-7; *Tylosaurus* AL-9) were less negative but still plotted away from the poikilothermic zero point on the graph. The *Toxochelys* turtle specimen (AL-4) used as an analog for an air-breathing poikilotheric reptile, plotted well within the range of poikilothermic fish (Figs. 2 and 3).

## DISCUSSION

The mosasaur taxa from the Mooreville Chalk analyzed in the present study produced a range of  $\delta^{18}\text{O}_{\text{PO}_4}$  values (Figs. 2 and 3), however the mean of each genus (*Clidastes* =  $20.28 \pm 0.20\text{‰}$ ,  $P = 1.3\text{E}^{-4}$ ; *Platecarpus* =  $19.53 \pm 0.23\text{‰}$ ,  $P = 2.8\text{E}^{-6}$ ; *Tylosaurus* =  $20.00 \pm 0.18\text{‰}$ ,  $P = 3.5\text{E}^{-6}$ ; p-values derived from paired t-tests relative to mean *Enchodus*  $\delta^{18}\text{O}_{\text{PO}_4}$  value) is significantly less than that of poikilothermic fish (*Enchodus* =  $21.41 \pm 0.11\text{‰}$ ). The corresponding temperature calculations for each mosasaur genus (*Clidastes* =  $33.1\text{ °C}$ ; *Platecarpus* =  $36.3\text{ °C}$ ; *Tylosaurus* =  $34.3\text{ °C}$ ) are substantially higher than that of poikilothermic fish and the ambient sea temperature ( $28.3\text{ °C}$ ). As the Mooreville Chalk sea was less than 90 m deep (Puckett 1991) and therefore unlikely to have a significant thermal gradient, the observed differences in body temperatures are not attributable to possible habitat partitioning in the water column. Sea water temperatures in present-day warm, tropical environments are nearly uniform to depths of 100 m (Wallace and Hobbs, 2006).

The present study uses a  $\delta^{18}\text{O}_{\text{water}}$  value of  $0\text{‰}$  for the Mooreville Chalk as a good approximation of the difference between the  $\delta^{18}\text{O}_{\text{water}}$  calculated from the turtle bone average ( $0.23\text{‰}$ ) and the  $\delta^{18}\text{O}_{\text{water}}$  calculated from the presumably more accurate turtle sample ( $-0.36\text{‰}$ , AL-4a). Clementz and Sewall (2011) reported  $\delta^{18}\text{O}_{\text{seawater}}$  for the Eocene ranging from  $0.00\text{‰}$  to

-0.4‰ at latitudes of 30° – 35° N, which are comparable to the geographic position of central and southern Alabama during the Late Cretaceous (Vrielynck and Bouysse, 2003).

For paleotemperature calculations, it is vital to determine the  $\delta^{18}\text{O}$  of body water ( $\delta^{18}\text{O}_{\text{bodywater}}$ ) rather than the  $\delta^{18}\text{O}$  of ambient seawater ( $\delta^{18}\text{O}_{\text{seawater}}$ ). Whereas the  $\delta^{18}\text{O}_{\text{bodywater}}$  of terrestrial organisms will vary based on the  $\delta^{18}\text{O}$  of meteoric water, marine organisms should have  $\delta^{18}\text{O}_{\text{bodywater}}$  that is relatively homogenous with seawater (Schaffner and Swart, 1991; Koch, 2007). The  $\delta^{18}\text{O}_{\text{bodywater}}$  in fish is determined by the  $\delta^{18}\text{O}$  of ingested water rather than the  $\delta^{18}\text{O}$  of ingested phosphates from food items (Kolodny *et al.*, 1983) and so in marine fish body water is in equilibrium with the  $\delta^{18}\text{O}_{\text{seawater}}$ . Little research has been done on the  $\delta^{18}\text{O}_{\text{bodywater}}$  of other aquatic vertebrates. Mosasaurs were large, marine reptiles incapable of traveling onto land (Field *et al.*, 2015), with no modern ectothermic tetrapod analogue. Studies performed on crocodylians, which are relatively large ectothermic aquatic reptiles, showed as much as 2‰ enrichment of  $\delta^{18}\text{O}_{\text{bodywater}}$  relative to environmental water (Amiot *et al.*, 2007). However, crocodylians are only semiaquatic, with the ability to travel onto land and cool themselves through evaporative panting, which would likely enrich their body water in  $^{18}\text{O}$ , and range in habitats from freshwater rivers to coastal marine environments that have a wide range of environmental  $\delta^{18}\text{O}$ . Cetaceans are a possible modern endothermic tetrapod analogue for mosasaurs as they are fully aquatic tetrapods incapable of traveling onto land. Cetaceans ingest water from food items, which have similar  $\delta^{18}\text{O}_{\text{bodywater}}$  to that of  $\delta^{18}\text{O}_{\text{seawater}}$ , and so cetacean  $\delta^{18}\text{O}_{\text{bodywater}}$  is also in isotopic steady state with  $\delta^{18}\text{O}_{\text{seawater}}$  (Luz *et al.*, 1984; Yoshida and Miyazaki, 1991). As mosasaurs were fully marine reptiles incapable of travelling onto land, and ingested food from marine sources (Martin and Bjork, 1987), they are here assumed to have  $\delta^{18}\text{O}_{\text{bodywater}}$  approximately equal to  $\delta^{18}\text{O}_{\text{seawater}}$ .

The  $\delta^{18}\text{O}_{\text{bodywater}}$  of Cretaceous sea birds are more difficult to constrain. Whereas *Hesperornis* was a fully marine bird incapable of flight and could only walk on land with great difficulty (Reynaud, 2006), *Ichthyornis* both flew and had legs that could support it in terrestrial environments (Clarke, 2004). *Ichthyornis* is currently only known from offshore marine deposits (Clarke, 2004; Shimada and Fernandes, 2006) and is superficially similar to a gull or albatross in appearance (Clarke, 2004), so it is therefore assumed to have had a similar pelagic lifestyle. Although no gastric residues have been identified with any described *Ichthyornis* specimen, it likely fed on small fish and/or soft-bodied marine invertebrates based on its small size and tooth morphology. As these marine food items likely had  $\delta^{18}\text{O}_{\text{bodywater}}$  approximate to that of seawater, it is here assumed that *Ichthyornis* had an initial  $\delta^{18}\text{O}_{\text{bodywater}}$  approximate to seawater as well. Although the  $\delta^{18}\text{O}_{\text{bodywater}}$  of modern birds has not been reported extensively, Kerstel *et al.* (2006) report that stable oxygen isotopes in the body water of shorebirds occur at “natural abundances” while Hobson and Koehler (2015) suggested a close association between  $\delta^{18}\text{O}_{\text{bodywater}}$  and meteoric water ingested by migrating terrestrial birds. Schaffner and Swart (1991) report that ingested water is the only source of  $\delta^{18}\text{O}_{\text{bodywater}}$  in terrestrial vertebrates including birds, with only minor short term fluctuations due to respiration and metabolism. Because *Ichthyornis* could potentially cool itself through evaporative panting, unlike the other fully marine tetrapods and fish in this study, the possibility exists that its  $\delta^{18}\text{O}_{\text{bodywater}}$  could have been enriched with  $^{18}\text{O}$  by evaporative fractionation. Modern seagulls sometimes cool by panting when they overheat during nesting but at other times they also cool by immersing their unfeathered legs in water (Ehrlich *et al.*, 1988). Although there is no exchange of oxygen with ambient water vapor during respiration in birds (Hobson and Koehler, 2015), Amiot *et al.* (2007) noted an enrichment of  $\delta^{18}\text{O}_{\text{bodywater}}$  in semiaquatic crocodiles, which are distantly related to birds (archosaurs) and also

use evaporative cooling, of up to 2‰. These  $\delta^{18}\text{O}_{\text{bodywater}}$  enrichments were greatest in crocodiles with higher mass whereas small crocodiles had  $\delta^{18}\text{O}_{\text{bodywater}}$  approximate to their ambient  $\delta^{18}\text{O}_{\text{water}}$ . Amiot *et al.* (2007) concluded that the enrichment was due to metabolic processes related to mass however they also noted that uncertainties of up to  $\pm 2\%$  in determining the  $\delta^{18}\text{O}$  of source waters and in determining the temperature of bone formation, suggesting that crocodile  $\delta^{18}\text{O}_{\text{bodywater}}$  could still be used to determine the  $\delta^{18}\text{O}$  of environmental water. Because of these factors and its small body mass, the  $\delta^{18}\text{O}_{\text{bodywater}}$  of *Ichthyornis* in this study is assumed to be the same as the  $\delta^{18}\text{O}_{\text{seawater}}$  used in this study (0‰), although evaporative cooling may have caused slight enrichment of  $\delta^{18}\text{O}_{\text{bodywater}}$ .

When 0‰  $\delta^{18}\text{O}_{\text{water}}$  is used in the fish paleothermometry equation by Pucéat *et al.* (2010), revised from an earlier equation by Kolodny *et al.* (1983), the average temperature of poikilothermic fish (mean  $\delta^{18}\text{O}_{\text{PO}_4} = 21.41 \pm 0.11\%$ ) from the Mooreville Chalk is 28.3 °C. This temperature is comparable with the temperature range of ~26 – 29 °C (Fig. 2) calculated for the middle Mooreville Chalk by  $\delta^{18}\text{O}_{\text{CO}_3}$  carbonate analysis (Liu, 2009). The average fish temperature reported here is also close to the temperature range of ~27.1 – 27.8 °C calculated for the Mississippi Embayment region using clumped isotope analysis (Coulson *et al.*, 2011). The depositional environment of the Mooreville Chalk sea is estimated to have been between 90 – 35 m deep (Puckett, 1991) so there would have been little thermal gradient between surface and bottom waters affecting the fish. However, seasonal migrations of fish to other geographic regions with different water temperatures or  $\delta^{18}\text{O}_{\text{water}}$  values that might have affected their  $\delta^{18}\text{O}_{\text{PO}_4}$  values cannot be excluded. In contrast to fish data, and using 0‰  $\delta^{18}\text{O}_{\text{water}}$ , *Ichthyornis* specimens, with a mean  $19.0 \pm 0.11\%$   $\delta^{18}\text{O}_{\text{PO}_4}$ , produce an average body temperature of 38.6 °C. This temperature falls within the measured resting and active (r/a) temperature range of modern

birds (38.5 °C / 41 °C), and more specifically of modern Charadriiformes (38.5 °C / 40.9 °C) that include many of the pelagic seabirds (Prinzinger *et al.*, 1991). Enriching the  $\delta^{18}\text{O}_{\text{water}}$  of *Ichthyornis* to 1‰ (unlikely to be greater due to the small mass of *Ichthyornis*) to account for fractionation due to evaporative cooling during overheating produces a higher body temperature ( $T_b = 42.8$  °C) that is still within the high activity temperature range (41.0 – 43.6 °C) of modern Charadriiformes (Prinzinger *et al.*, 1991). As with the fish, the migration of birds to other geographic regions with potentially differing  $\delta^{18}\text{O}_{\text{water}}$  values cannot be discounted. However, as the fish and bird paleotemperatures reported here are consistent with temperatures reported elsewhere, it would suggest that the  $\delta^{18}\text{O}_{\text{PO}_4}$  values acquired from this analysis are relatively accurate and suitable for comparison between different taxa for determining thermoregulation by proxy.

The analysis of other organisms that included both tooth enamel and bone from the same individual showed good correlation between the two biophosphate samples, with no trend of the enamel  $\delta^{18}\text{O}_{\text{PO}_4}$  being greater or lesser than that of the bone (Fig. 2). This is also an indication of the resistance to diagenetic alteration of fossils from the Mooreville Chalk because of the impermeable nature of the clay-rich chalk and the relatively shallow burial depth of the formation (Liu, 2009). Comparisons by Coulson *et al.* (2011) of  $\delta^{18}\text{O}_{\text{PO}_4}$  with  $\delta^{18}\text{O}_{\text{CO}_3}$  values in turtle bone samples from the Mississippi Embayment region (that includes the present study region in Alabama) suggest that there is little diagenetic alteration and that the original  $\delta^{18}\text{O}_{\text{PO}_4}$  values have been retained. The bone phosphates of the *Ichthyornis* specimens from the Mooreville Chalk are therefore believed to be suitable for comparison with other taxa, and serve as the endothermic endmember.

Two samples of turtle bone were analyzed in this study in order to provide an analog for a likely ectothermic reptile for comparison with the mosasaur genera. Turtle bone can also be used to determine the  $\delta^{18}\text{O}_{\text{water}}$  independent of the temperature at which it formed (Coulson, 2008, 2011). Whereas the turtle specimens from the Sharon Springs Formation did not produce any  $\text{Ag}_3\text{PO}_4$  crystals for testing, the samples from the Mooreville Chalk produced  $\delta^{18}\text{O}_{\text{PO}_4}$  values comparable to those of the fish (Fig. 2). The mean  $\delta^{18}\text{O}_{\text{PO}_4}$  turtle values were inserted into the formula of Coulson *et al.* (2008) and produced a  $\delta^{18}\text{O}_{\text{water}}$  value of 0.23‰. This value is slightly greater than the hypothesized  $\delta^{18}\text{O}_{\text{water}}$  value of Late Cretaceous ocean water of between 0 and -1.00‰ (Lécuyer *et al.*, 2003). Of the two turtle samples from the Mooreville Chalk analyzed in the present study, one (AL- 4b) produced a  $\delta^{18}\text{O}_{\text{PO}_4}$  value that is substantially greater than the other turtle sample (AL-4a) and the coeval fish. If this higher sample is omitted, and the lower turtle sample is inserted into the Coulson *et al.* (2008) equation, the  $\delta^{18}\text{O}_{\text{water}}$  is -0.36‰. Coulson *et al.* (2011) determined a  $\delta^{18}\text{O}_{\text{water}}$  value of -1.37‰ for the Mississippi Embayment region using toxochelyid and protostegid turtle fossils. However, their study involved a much wider geographic area and also included fossils from the underlying Tombigbee Sand Member of the Eutaw Formation, a geologic unit that contains transgressive lag deposits with some reworked fossils (Mancini and Soens, 1994). When their  $\delta^{18}\text{O}_{\text{water}}$  value of -1.37‰ for the Mississippi Embayment region is used, the calculated average fish temperature is 22.6 °C (Table 2), which is lower than the temperature reported by Liu (2009) for the middle of the Mooreville Chalk. Using the Coulson *et al.* (2011)  $\delta^{18}\text{O}_{\text{water}}$  value also results in a  $T_b$  for *Ichthyornis* that is lower than any presently known bird. The very warm temperatures and shallow depth of the Mooreville Chalk sea in the Mississippi Embayment likely made the region one of high evaporation potential in the Late Cretaceous, which would have enriched the water in  $^{18}\text{O}$  and potentially produced  $\delta^{18}\text{O}_{\text{water}}$

values close to 0‰. Therefore, the temperature calculations in this analysis were influenced by the  $\delta^{18}\text{O}_{\text{PO}_4}$  present in turtle specimen AL-4 rather than the much more negative value determined by Coulson *et al.* (2011).

To further corroborate whether calculated body temperatures are accurate, data from Late Cretaceous specimens collected from Alabama and South Dakota were compared. Most samples from the Sharon Springs Formation in South Dakota failed to produce  $\text{Ag}_3\text{PO}_4$  crystals or produced an insufficient mass of  $\text{Ag}_3\text{PO}_4$  crystals for reliable analysis. The likely reason for the lack of crystal production is that many of the specimens from the Sharon Springs Formation have poor preservation on their outer surfaces and the original biophosphate has been lost during diagenesis. The diagenetic effect is obvious in the lower average body temperature of *Hesperornis* (34.7 °C) in comparison to *Ichthyornis* data (Table 2). Nevertheless, the relationships between the taxa from the Sharon Springs Formation that did produce sufficient  $\text{Ag}_3\text{PO}_4$  crystals and  $\delta^{18}\text{O}_{\text{PO}_4}$  values are the same as those from the Mooreville Chalk, and overall mosasaur and bird body temperatures are higher than those of fish (Table 2).

## CONCLUSIONS

The findings of the present study indicate that mosasaurs were able to maintain a higher internal temperature independent of the ambient seawater temperature and were likely endotherms, with values closer to contemporaneous fossil and modern birds and higher than fish and turtles. Although there are small differences of body temperature among mosasaur genera, these are independent of size, and thus inferred body mass, suggesting that mosasaurs were not gigantotherms. Mosasaurs high internal body temperatures would enable them to not only adapt a more active lifestyle that complimented their evolutionary shift to a more ichthyosaur-like

morphology, but also to exploit cooler water environments. Mosasaur fossils are presently known from both the Antarctic Peninsula (Martin, 2002) and Devon Island (Chin *et al.*, 2008), which is north of the Canadian coastline and presently within the Arctic Circle. Although the seawater temperatures of these two regions were higher in the Late Cretaceous than they are presently, they were still likely cooler than preferred for poikilothermic marine reptiles.

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APPENDIX TO CHAPTER 4

Sample #	ALMNH Number	Taxon	Material	$\delta^{18}\text{O}_{\text{PO}_4}$	Sample #	ALMNH Number	Taxon	Material	$\delta^{18}\text{O}_{\text{PO}_4}$
<b>Mooreville Chalk (Alabama)</b>									
AL-1a	PV2004.0003.0010	<i>Enchodus</i>	Enamel	<b>21.92</b>	AL-9b	PV1993.0001.0001	<i>Tylosasaurus</i>	Enamel	<b>21.00</b>
AL-1b	PV2004.0003.0010	<i>Enchodus</i>	Enamel	<b>21.33</b>	AL-9c	PV1993.0001.0001	<i>Tylosasaurus</i>	Enamel	<b>20.05</b>
AL-1c	PV2004.0003.0010	<i>Enchodus</i>	Enamel	<b>21.55</b>	AL-9d	PV1993.0001.0001	<i>Tylosasaurus</i>	Bone	<b>20.33</b>
AL-1d	PV2004.0003.0010	<i>Enchodus</i>	Bone	<b>21.19</b>	AL-10a	PV1985.0011	<i>Tylosasaurus</i>	Enamel	<b>19.85</b>
AL-2a	PV2010.0008.0010	<i>Enchodus</i>	Enamel	<b>21.84</b>	AL-10b	PV1985.0011	<i>Tylosasaurus</i>	Enamel	<b>20.61</b>
AL-2b	PV2010.0008.0010	<i>Enchodus</i>	Enamel	<b>21.59</b>	AL-10c	PV1985.0011	<i>Tylosasaurus</i>	Enamel	<b>19.13</b>
AL-2c	PV2010.0008.0010	<i>Enchodus</i>	Enamel	<b>21.58</b>	AL-10d	PV1985.0011	<i>Tylosasaurus</i>	Bone	<b>19.58</b>
AL-2d	PV2010.0008.0010	<i>Enchodus</i>	Bone	<b>20.79</b>	AL-11a	Destroyed in Analysis	<i>Tylosasaurus</i>	Enamel	<b>19.83</b>
AL-3a	Destroyed in Analysis	<i>Enchodus</i>	Enamel	<b>21.00</b>	AL-11b	Destroyed in Analysis	<i>Tylosasaurus</i>	Enamel	<b>19.01</b>
AL-3b	Destroyed in Analysis	<i>Enchodus</i>	Bone	<b>21.33</b>	AL-11c	Destroyed in Analysis	<i>Tylosasaurus</i>	Bone	<b>20.10</b>
AL-4a	Destroyed in Analysis	<i>Toxochelys</i>	Bone	<b>21.15</b>	AL-12a	PV2008.0002.0007	<i>Ichthyornis</i>	Bone	<b>18.74</b>
AL-4b	Destroyed in Analysis	<i>Toxochelys</i>	Bone	<b>22.23</b>	AL-12b	PV2008.0002.0007	<i>Ichthyornis</i>	Bone	<b>18.81</b>
AL-5a	PV2001.0002.0001	<i>Clidastes</i>	Enamel	<b>20.64</b>	AL-13a	PV2008.0002.0008	<i>Ichthyornis</i>	Bone	<b>18.83</b>
AL-5b	PV2001.0002.0001	<i>Clidastes</i>	Enamel	<b>20.75</b>	AL-13b	PV2008.0002.0008	<i>Ichthyornis</i>	Bone	<b>18.87</b>
AL-5c	PV2001.0002.0001	<i>Clidastes</i>	Enamel	<b>20.21</b>	AL-14a	PV2014.0001.0362	<i>Ichthyornis</i>	Bone	<b>19.44</b>
AL-5d	PV2001.0002.0001	<i>Clidastes</i>	Bone	<b>20.87</b>	AL-14b	PV2014.0001.0362	<i>Ichthyornis</i>	Bone	<b>19.17</b>
AL-6a	PV2005.0006.0087	<i>Clidastes</i>	Enamel	<b>19.60</b>	AL-15a	PV 2005.0006.0108	<i>Protosphyraena</i>	Enamel	<b>20.70</b>
AL-6b	PV2005.0006.0087	<i>Clidastes</i>	Enamel	<b>19.18</b>	AL-15b	PV 2005.0006.0108	<i>Protosphyraena</i>	Enamel	<b>21.50</b>
AL-6c	PV2005.0006.0087	<i>Clidastes</i>	Enamel	<b>19.12</b>	AL-15c	PV 2005.0006.0108	<i>Protosphyraena</i>	Enamel	<b>20.96</b>
AL-6d	PV2005.0006.0087	<i>Clidastes</i>	Bone	<b>19.83</b>	AL-15d	PV 2005.0006.0108	<i>Protosphyraena</i>	Bone	<b>20.90</b>
AL-7a	PV1994.0004.0004	<i>Clidastes</i>	Enamel	<b>20.67</b>	AL-16a	PV 2010.0005.0094	<i>Protosphyraena</i>	Enamel	<b>21.06</b>
AL-7b	PV1994.0004.0004	<i>Clidastes</i>	Enamel	<b>21.05</b>	AL-16b	PV 2010.0005.0094	<i>Protosphyraena</i>	Enamel	<b>19.29</b>
AL-7c	PV1994.0004.0004	<i>Clidastes</i>	Enamel	<b>20.94</b>	AL-16c	PV 2010.0005.0094	<i>Protosphyraena</i>	Enamel	<b>21.41</b>
AL-7d	PV1994.0004.0004	<i>Clidastes</i>	Bone	<b>20.47</b>	AL-16d	PV 2010.0005.0094	<i>Protosphyraena</i>	Bone	<b>20.64</b>
AL-8a	PV1993.0007.0307	<i>Platecarpus</i>	Enamel	<b>18.84</b>	AL-17a	PV 2010.0008.0060	<i>Protosphyraena</i>	Enamel	<b>20.84</b>
AL-8b	PV1993.0007.0307	<i>Platecarpus</i>	Enamel	<b>19.86</b>	AL-17b	PV 2010.0008.0060	<i>Protosphyraena</i>	Enamel	<b>21.02</b>
AL-8c	PV1993.0007.0307	<i>Platecarpus</i>	Bone	<b>19.78</b>	AL-17c	PV 2010.0008.0060	<i>Protosphyraena</i>	Enamel	<b>20.86</b>
AL-8d	PV1993.0007.0307	<i>Platecarpus</i>	Bone	<b>19.65</b>	AL-17d	PV 2010.0008.0060	<i>Protosphyraena</i>	Bone	<b>21.03</b>
AL-9a	PV1993.0001.0001	<i>Tylosasaurus</i>	Enamel	<b>20.46</b>					
<b>Sharon Springs Formation (South Dakota)</b>									
SD-1a	PV2014.0001.0365	<i>Enchodus</i>	Bone	<b>20.83</b>					
SD-1b	PV2014.0001.0365	<i>Enchodus</i>	Enamel	<b>20.32</b>					
SD-2	PV2014.0001.0357	<i>Platecarpus</i>	Bone	<b>20.24</b>					
SD-3a	PV2014.0001.0363	<i>Hesperornis</i>	Bone	<b>20.40</b>					
SD-3b	PV2014.0001.0363	<i>Hesperornis</i>	Bone	<b>19.30</b>					
SD-3c	PV2014.0001.0363	<i>Hesperornis</i>	Bone	<b>19.99</b>					

TABLE 4.3. Detailed results of oxygen isotope analysis.

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