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Contributions to Alabama Cretaceous Paleontology

Guest Editors

Jun Ebersole & Takehito Ikejiri

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THE UNIVERSITY OF ALABAMA
TUSCALOOSA, ALABAMA
APRIL 1, 2013

Guest Editors and Cover Art

The Alabama Museum of Natural History is deeply indebted to Jun Ebersole and Takehito Ikejiri, the two guest editors of this two-volume issue of the AMNH Bulletin 31. They undertook the herculean task of encouraging authors to submit the attendant articles and assumed the lion's share of the initial editing in bringing together a wealth of current paleontological research on the Southeast in general and Alabama specifically. The research incorporated here will serve as a significant baseline towards encouraging future generations of researchers to further our knowledge in these areas. We also wish to acknowledge the important contribution and donation of the artwork of Asher Elbein that helps to bring the subject of "long-dead" things to life.

Jun Ebersole is an archaeologist and paleontologist and oversees the natural history department at McWane Science Center in Birmingham, Alabama. In addition to his responsibilities at McWane, Jun is an adjunct instructor in the Department of Anthropology at the University of Alabama at Birmingham where he teaches archaeology, faunal analysis, and museum studies. Jun has varied research interests which include hominid evolution, the history of paleontology, and describing the rich vertebrate fossil diversity in Alabama. This has led him to conduct field work of various sorts such as *Homo erectus* sites in East Africa, Iroquois sites in the northeastern U.S., and paleontological sites in western Kansas and nearly every region of Alabama. Jun holds a degree in anthropology from St. Lawrence University in Canton, NY.

Takehito Ikejiri received an M.S. in geology from Fort Hays State University in Kansas and earned a Ph.D. in geology from The University of Michigan in Ann Arbor. Currently an adjunct instructor in the Department of Geology and a research associate in the Alabama Museum of Natural History at The University of Alabama in Tuscaloosa, Takehito has also worked at the Wyoming Dinosaur Center in Thermopolis, the Museum of Paleontology at The University of Michigan, and the Sternberg Museum of Natural History in Fort Hays, Kansas. Dr. Ikejiri's research interests include describing Alabama's fossil mosasaurs, dinosaurs, and fishes, as well as studies involving vertebrate skeletal fusion, ontogeny, and evolution. Takehito has published numerous papers on recent reptiles such as alligators as well as fossil reptiles such as sauropods and mosasaurs.

The outstanding detailed artwork attempting to bring to life some of Alabama's fossil creatures on the front and rear covers of the two-volume Bulletin 31 was produced by Mr. Asher Elbein. Asher is currently a student artist at The University of Alabama in Tuscaloosa. Asher specializes in paleontological art, creature design, and creative writing of various kinds. More of Asher's artwork can be seen on his website ashere.deviantart.com.

The History of Late Cretaceous Vertebrate Research in Alabama

JUN A. EBERSOLE*[1] and LEWIS S. DEAN[2]
[1]McWane Science Center, 200 19th Street North, Birmingham, AL 35203, jebersole@mcwane.org;
[2]Geological Survey of Alabama, P.O. Box 869999, Tuscaloosa, AL 35486,
ldean@gsa.state.al.us

*Corresponding author

ABSTRACT

Late Cretaceous vertebrate research in Alabama has a long and storied history which is intimately intertwined with the rise of geological and paleontological research in America. This history can be divided into six chronological periods: the *Early Exploration Period* (1540 to 1814), the *Early Settler Period* (1814 to 1842), the *Pioneer Scientific Period* (1830 to 1846), the *Tuomey Period* (1847 to 1865), the *Smith Period* (1865 to 1927), and the *Modern Period* (1927 to present). The history of vertebrate paleontology in Alabama began with geological observations made by early explorers, fur traders, and settlers, which led to visits to the state by many of America's early scientific elite including Thomas Nuttall, Timothy A. Conrad, Charles Lyell, and Robert W. Gibbes. Many of Alabama's early vertebrate discoveries were shipped to the likes of Samuel Morton, Richard Harland, Joseph Leidy, and Edward Drinker Cope. Michael Tuomey and Eugene Allen Smith made their own significant contributions to Cretaceous research while employed at the State Geological Survey. Significant events which shaped this history included the burning of the University of Alabama campus near the end of the Civil War and the establishment of the state's largest Cretaceous vertebrate collections at the Alabama Museum of Natural History, Auburn University Museum of Paleontology, and Red Mountain Museum (now McWane Science Center). This history of research has played a significant role in advancing our understanding of the Late Cretaceous systems in the United States and around the world.

INTRODUCTION

The purpose of this paper is to provide a brief chronological history of Late Cretaceous vertebrate research in Alabama while highlighting the key individuals, institutions, specimens, publications, and historical events that helped shape Cretaceous vertebrate research in the state as we know it today. This history begins with early explorers and settlers writing general observations on the landscape and geology of central Alabama. Their observations attracted the attention of the early paleontological community in the United States, leading to the first descriptions of Cretaceous units and invertebrates found within the state. These descriptions later served as the foundation for studying Late Cretaceous vertebrates in Alabama.

The history of Cretaceous vertebrate research in Alabama can be divided into six chronological periods. These periods are as follows:

1). The *Early Exploration Period* (1540 to 1814) begins with Hernando De Soto's expedition through Alabama in 1540 and ends with the Battle of Horseshoe Bend in 1814. During this time, general observations of the landscape and geology of central Alabama were made by early European explorers and fur traders.

2). The *Early Settler Period* (1814 to 1842) begins with the signing of the Treaty of Fort Jackson in 1814, allowing the open settlement of former Creek lands in what would soon become Alabama. During this period, early settlers began to record detailed observations on the fossils, soil fertility, geology, and landscape of the Cretaceous region in Alabama. This period ends with the publication of Robert W. Wither's 1842 letter

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detailing his observations on the geology and fossils of Greene County.

3). The *Pioneer Scientific Period* (1830 to 1846) begins with Thomas Nuttall's visit to Alabama in 1830. This period overlaps with the end of the *Early Settler Period* but differs as the first systematic studies of the stratigraphy and paleontology of Alabama are carried out by early scientists as opposed to planters. During this period the state was visited by several renowned natural scientists, including Timothy A. Conrad and Charles Lyell. This period ends with the conclusion of Lyell's visit to the state in 1846.

4). The *Tuomey Period* (1847 to 1865) begins with the 1847 appointment of Michael Tuomey to the faculty at the University of Alabama. Later appointed Alabama's first State Geologist, this period is marked by Tuomey's intensive geology survey of the state, which intimately involved personnel and resources from the University. The vertebrate research contributions of Robert W. Gibbes are also made during this time. This period ends in tragedy with the death of Tuomey in 1857 and the burning of the University of Alabama campus by Union Troops in 1865.

5). The *Smith Period* (1865 to 1927) begins with the end of the Civil War and the start of Reconstruction in 1865. This period is highlighted by Eugene Allen Smith's lengthy tenure as State Geologist and the systematic descriptions of many of Alabama's Cretaceous vertebrates by notable figures such as Joseph Leidy, Edward Drinker Cope, and Charles W. Gilmore. This period ends with Smith's death in 1927.

6). The *Modern Period* (1927 to present) begins with the death of Eugene Allen Smith and encompasses nearly all early 20th century and contemporary Cretaceous vertebrate research. Significant events occurring during this period include the Field Museum expeditions to the Black Belt in the 1940s and 1950s, the split of the Geological Survey from the Alabama Museum of Natural History, and the establishment of the Auburn University Museum of Paleontology, the Red Mountain Museum, and McWane Science Center.

Institutional Abbreviations—ANSP: Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania; **AUMP**: Auburn University Museum of Paleontology, Auburn, Alabama; **FMNH**: Field Museum of Natural History, Chicago, Illinois; **GSA**: Geological Survey of Alabama, Tuscaloosa, Alabama; **MSC**: McWane Science Center, Birmingham, Alabama; **RMM**: Red Mountain Museum, Birmingham, Alabama (now McWane Science Center); **UAM**: University of Alabama Museum of Natural History, Tuscaloosa, Alabama; **USGS**: United States Geological Survey, Washington, D.C.; **USNM**: United States National Museum, Washington, D.C.

The Alabama Black Belt

The Cretaceous rocks exposed in Alabama make up a nearly time-continuous series of Upper Cretaceous strata ranging from the Cenomanian to the upper boundary of the Maastrichtian. Nearly all of these Late Cretaceous units lie within the Black Prairie physiographic district referred to locally as the "Black Belt," referencing the dark, fertile soils that blanket the area. The Black Belt is a 275-mile crescent stretching across the central portion of Alabama and extending northwestward into Mississippi (Adams et al., 1926) (Fig. 1). The Black Belt ranges from 50 to 75 miles wide and contains Cretaceous exposures that lie directly on top of Paleozoic strata. In Alabama, the Black Belt stretches across parts of 28 counties, 20 of

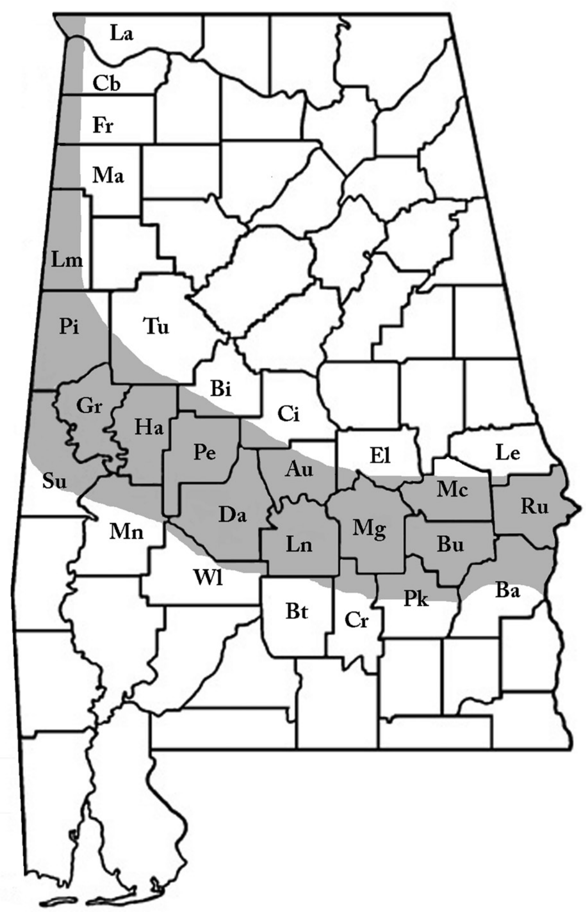


Figure 1. Generalized map of the Alabama Black Belt. The shaded area represents the general extent of the Black Belt and Cretaceous exposures in Alabama. County abbreviations: Au: **Autauga;** Ba: **Barbour; Bi: Bibb;** Bt: **Butler;** Bu**: Bullock;** Cb: **Colbert;** Ci: **Chilton;** Cr: **Crenshaw;** Da: **Dallas;** El: **Elmore;** Fr: **Franklin;** Gr: **Greene;** Ha: **Hale;** La: **Lauderdale;** Le: **Lee;** Lm: **Lamar;** Ln: **Lowndes;** Ma: **Marion;** Mc: **Macon;** Mg: **Montgomery;** Mn: **Marengo;** Pe: **Perry;** Pi: **Pickens;** Pk: **Pike;** Ru: **Russell;** Su: **Sumter;** Tu: **Tuscaloosa;** Wl: **Wilcox.**

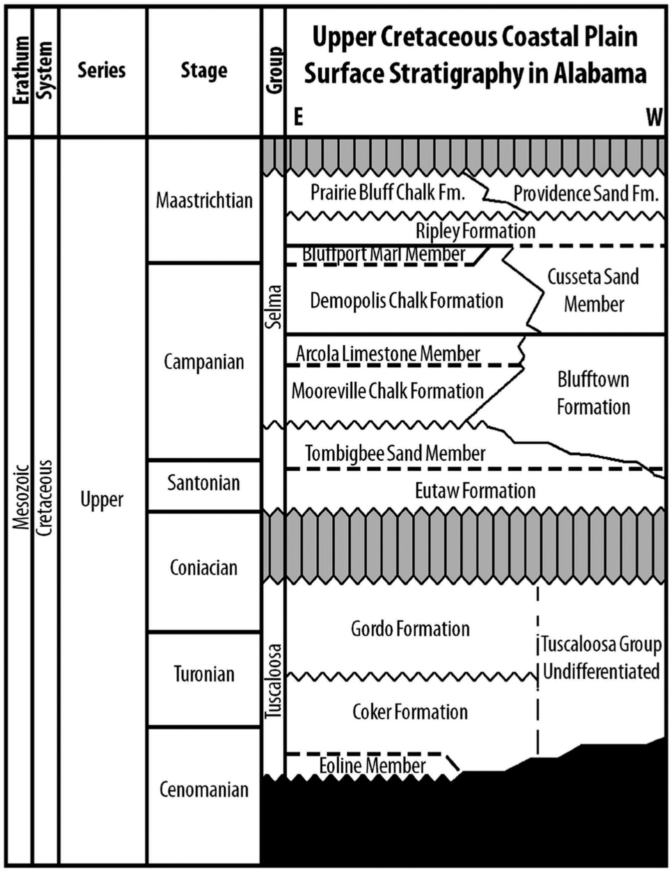


Figure 2. Upper Cretaceous stratigraphic units exposed in Alabama. Grey shaded areas represent unconformities. Areas shaded black are not exposed on the surface in Alabama. Stratigraphic chart modified from Raymond et al. (1988).

which have produced Late Cretaceous vertebrate fossils (Ikejiri et al., this volume). In ascending order, the Upper Cretaceous strata within the Alabama Black Belt are: the Tuscaloosa Group (which includes the Coker Formation, the Eoline Member of the Coker Formation, and the Gordo Formation); the Eutaw Formation (which includes the Tombigbee Sand Member); and the Selma Group which includes the Mooreville Chalk (with Arcola Limestone Member), Blufftown Formation, Demopolis Chalk (with Bluffport Marl Member), Ripley Formation (with Cusseta Sand Member), Prairie Bluff Chalk, and Providence Sand (Raymond et al., 1988) (Fig. 2). Few Cretaceous vertebrates have been recovered from pre-Tombigbee Sand exposures (Kiernan, 2002) whereas the Selma Group units represent some of the most productive for the discovery of Cretaceous marine vertebrates in the United States (see Nicholls and Russell, 1990).

THE *EARLY EXPLORATION PERIOD* (1540 TO 1814)

Archaeological evidence suggests that Native Americans have been in Alabama for nearly 10,000 years, and a large population resided within the Black Belt region during pre-European times (see Walthall, 1980). The earliest written records of the region are the four surviving accounts of the Hernando De Soto expedition from the 16th century which record their travels through the present day Black Belt counties of Montgomery, Lowndes, Dallas, Marengo, Hale, Greene, and Pickens (Rostlund, 1957; Barone, 2005). Rostlund (1957), and later Barone (2005), compiled additional 16th, 17th, and 18th century accounts of the Black Belt, including Tristan De Luna's journey to central Alabama in 1559, Juan Pardo's 1566 expedition to the region, and Marcos Delgado's 1686 journey into Alabama from Florida. While most of these early accounts refer only to the general landscape of the Black Belt, two 18th century accounts make particular reference to the geology. In describing the Black Belt in northern Mississippi, James Adair, who traded with southern Native Americans in the 1730s and 1740s, described the soil as consisting of a "loose rich mould to a considerable depth, and either a kind of chalk or marl underneath" (Adair, 1775:462). As part of his four-year journey to visit the Southern colonies, American naturalist William Bartram wrote the following description of the soils in what would become Montgomery and Lowndes Counties:

> The upper stratum or vegetative mould of these plains is perfectly black, soapy and rich, especially after rains, and renders the road very slippery; it lies on a deep bed of white testaceous, limestone rock, which in some places resembles chalk, and in other places are strata or subterrene banks of various kinds of sea shells, as ostrea, &c. (Bartram, 1958 [1791]:399).

These passages are of interest as they represent two of the earliest documented accounts of chalk, and in the case of Bartram, fossils, in the Black Belt.

THE *EARLY SETTLER PERIOD* (1814 TO 1842)

During the early parts of the 19th century, four main Native American confederations were prevalent in the region: the Cherokee, Chickasaw, Choctaw, and Creek (Walthall, 1980; Rogers et al., 1994). The Creek Confederacy was the largest of these groups and over three-fifths of the land area in present-day Alabama was seen as Creek territory. However, at the conclusion of the Creek (or Red Stick) War of 1813–14, ending with the decisive Battle of Horseshoe Bend (fought near the present-day town of Dadeville in Tallapoosa County; Rogers et al., 1994), the Creek Confederacy was forced to cede much of its land to the United

States government for settlement (Greene, 1985). In April 1814, the signing of the Treaty of Fort Jackson opened the way for thousands of immigrants from the older southern states to settle in the Alabama Territory.

During the *Early Settler Period,* the population of white settlers in the Black Belt grew exponentially (see Rogers et al., 1994). Coinciding with this population growth was a notable increase in written accounts on the geology and fossils of the region. These observations often took the form of letters written by local planters to the editors of magazines and journals such as *Southern Agriculturalist, Farmers' Register,* and *American Journal of Science and Arts* (Rindsberg, 1989). These letters were largely nontechnical and generally focused on the quality of Black Belt soils in respect to their ability to sustain various crops (Anonymous, 1835; Deas, 1835b; Ruffin, 1835; Anonymous, 1838; Lewis, 1838). These planters often discussed how the chalk and fossil shells in the Black Belt provided a source of agricultural lime, a necessary additive for productive plant growth (Heustis, 1831; Deas, 1833, 1835a, 1835b; Elmore, 1835; Magoffin, 1839).

Although true scientific studies of the geology, stratigraphy, and paleontology of the Cretaceous deposits in Alabama would not take place until the 1830s, local planters often described the landscape of the Black Belt in their correspondence. Many planters referenced the "bald prairies" (see Heustis, 1831:76; Deas, 1833:532; Elmore, 1835:716–717), and "rotten limestone" in the region (see McGuire, 1834:94; Elmore, 1835:717; Magoffin, 1839:617; Withers, 1833, 1835a, 1835b, 1842). James T. Deas, for example, who often signed his letters under the pseudonym "A Planter" (Ruffin, 1957), wrote the following about the Black Belt prairies in 1833:

> The Prairies mean the lime lands, and cover a large portion of the surface of the middle parts of that State, and are divided into the wooded and bald, (or unwooded Prairie) which are so interspersed, that in one thousand acres together of the most wooded, there will be from one-third to one-fifth of bald Prairie, and in the most bald, a similar proportion of wooded Prairie (Deas, 1833:467).

The "rotten limestone," as the locals called it, referred to the chalk formations in the Black Belt and got its name to differentiate it from the "hard blue limestone rock" found to the north (Withers, 1833:188). In 1829, W. W. McGuire, the gentleman who established the Tuscaloosa newspaper, *Alabama State Intelligencer* (Smith, 1889), wrote the following about the Black Belt chalks:

> This rock, is generally known by the name *rotten limestone*; when removed for several feet on the top, and exposed to the action of the atmosphere for some time, it assumes a beautiful white color. In its soft state it is easily quarried, and blocks of almost any dimensions can be procured. It had been dressed by planes and other instruments, and used in building chimneys; some of which have stood twelve or fifteen years without injury or decay (McGuire, 1834:94).

McGuire went on to describe how this chalk would "adhere so strongly to the legs of horses and to the wheels of carriages as to remain several days in traveling, unless washed or beaten off" (McGuire, 1834:95).

In addition to making observations on the Black Belt's geology and landscape, some planters also discussed fossils in their letters. Deas, for example, wrote of his discovery of "oyster shells of immense size" and the "petrified remains of salt water fish" (Deas, 1833:468; 1835a:357). McGuire described how shells, such as "oysters, muscle, periwinkle, and some other kinds, are found in great quantities" in the area (McGuire, 1834:93). McGuire also detailed his encounter with a gentleman who had "*Shark's teeth*, from an inch to an inch and a half in length, slender and very sharp" as well as "pieces of the vertebrae of fishes" (McGuire, 1834:98). Another local resident, William S. Porter, boasted of a collection of shells he discovered and shipped to Benjamin Silliman of Yale University and the editor of the *American Journal of Science and Arts*. Porter described one of these shells as being made of "limestone" and collected "from the prairies nearly west from Cahawba" (Porter, 1828:78).

The presence of marine fossils in the Black Belt led some planters to speculate on the origins of the "rotten limestone" prairies. In 1834, for example, McGuire (1834:96) wrote:

> That the prairies were once the boundary of the Atlantic is evident 1. From the fact, that on both sides, they exhibit the indented and irregular appearances of a coast, uniformly stretching up the large water courses; and in general, the sandy low country stretches in a corresponding degree up the rivers into the prairies; but except where it is more or less alluvial, it is unlike the prairies. 2. They are nearly or quite parallel to the present shore. 3. The great quantities of sea shells, found scattered on so large a tract of country, very little of which is within one hundred miles of the coast, support the opinion now advanced. The idea of their having been carried there by the action of winds, tides, is precluded by the fact that in that case they must have been raised three or four hundred feet and I presume in no place less than one hundred feet above the level of the Gulf of Mexico.

Around the same time, James T. Deas speculated that the presence of marine fossils meant the region was "once covered by the ocean" (Deas, 1833:468) or was "once at the bottom of the sea" (Deas, 1835a:357).

Although these letters were intended to lend agricultural advice to immigrant planters considering settlement in Alabama, they also promoted the state's geology and paleontology to scientists in other parts of the United States. While these letters served as the main scientific contribution during the *Early Settler Period,* one Alabama resident in particular, Robert W. Withers, would play an even larger role in the history of Cretaceous research in the state.

Robert W. Withers (1798–1854)

Although not a geologist or paleontologist, Robert W. Withers published – on at least four different occasions in 1833, 1835, and 1842 – short letters on the geology of the Black Belt in Greene County (which, until 1867, included present day Hale County). Withers, a plantation owner in the former river port of Erie (now in Hale County), described the Black Belt as a prairie belt that stretched across the state some "30 to 40 miles wide" that lies "principally between latitudes 32 and 33 degrees north" (Withers, 1833, 1842). Within these four letters, Withers made several references to the fossils he observed in Greene County. Withers wrote on how the soils in the region were often mixed with fragments of shells consisting mostly of "scallop, cockle, and oyster shells, though not of the same species we now find in Mobile" (Withers, 1835a, 1835b, 1842). Furthermore, in 1833, Withers wrote of the discovery of fossilized fish vertebrae and a "vertebra of an animal as large as the elephant" (Withers, 1833:188).

In 1842 Withers' final letter was published, marking the end of the *Early Settler Period*. Withers, however, made one additional contribution to Cretaceous research in the state. On at least three different occasions in 1833, Withers hosted paleontologist Timothy A. Conrad at his Erie home, and introduced Conrad to several Cretaceous outcrops in the area (Wheeler, 1935). This act of generosity ultimately allowed Conrad to play a major role in deciphering the Tertiary and Cretaceous sequences not only in Alabama, but along the entire Gulf and Atlantic Coasts (Harris, 1893). The arrival of Conrad in Alabama, and of Thomas Nuttall two years prior, ushered in a golden age of Cretaceous research in Alabama, known here as the *Pioneer Scientific Period.*

THE *PIONEER SCIENTIFIC PERIOD* (1830 TO 1846)

The *Pioneer Scientific Period* represents one of the most important periods in the history of Alabama Cretaceous research and begins with the arrival of early American scientists to the state. This period overlaps with the end of the *Early Settler Period*, but is differentiated as the first systematic studies of the state's Cretaceous stratigraphy and paleontology took place at this time. During this period, Alabama was visited by several early American natural scientists such as Thomas Nuttall, Timothy A. Conrad, Henry Darwin Rogers, and Charles Upham Shepard. This period also saw fossil material from Alabama shipped to and examined by the likes of Samuel G. Morton, Isaac Lea, Gideon Mantell, Louis Agassiz, Richard Harlan, and Richard Owen. The most notable event during this period was the visit of geologist Charles Lyell to Alabama and much Cretaceous vertebrate research would revolve around two fossil taxa, *Ptychodus mortoni* and *Basilosaurus cetoides*, with personnel of the Academy of Natural Sciences of Philadelphia playing a central role.

The Academy of Natural Sciences of Philadelphia

The Academy of Natural Sciences of Philadelphia (ANSP) was founded in 1812, when Philadelphia was acknowledged as the center of scientific studies in North America (Noland, 1909). During the early 19th century, many of the noted stratigraphers and paleontologists in America could be traced to Philadelphia and, in particular, to the ANSP (Schuchert, 1918). In these early years, scientists such as Thomas Say, John Finch, Lardner Vanuxem, Isaac Lea, Samuel G. Morton, Thomas Nuttall, Constantine Samuel Rafinesque, Charles Lesueur, Gerard Troost, Richard Harlan, and Timothy A. Conrad were filling the pages of the Academy's journal with reports and papers on a wide variety of zoological, geological, and paleontological topics (Youmans, 1896a; Schuchert, 1918). Of this group of early natural scientists, English botanist and zoologist Thomas Nuttall was the first to explore and collect Cretaceous fossils in Alabama.

Thomas Nuttall (1786–1859)

Thomas Nuttall (Fig. 3), an English-born naturalist, emigrated to Philadelphia in 1808 to explore the natural history of North America. In 1811, Nuttall was a part of the Astoria party, the first group to cross the country after the Lewis and Clark expedition, and later made substantial contributions to the understanding of American botany, ornithology, geology, and ecology. Elected to the ANSP in 1817, Nuttall had close associations with celebrities such as Daniel Boone, John James Audubon, and Ralph Waldo Emerson (Graustein, 1967). In 1830, Nuttall travelled to the southeastern United States to study the plants and birds of Georgia, Alabama, and West Florida (Nuttall, 1833, 1859). While paleontology was not his main focus, during his visit to Alabama Nuttall collected a small number of Cretaceous invertebrates at Cahawba in Dallas County (Anonymous, 1829; Morton, 1834). Records indicate that Nuttall donated fossil oyster specimens of *Exogyra costata* and *Gryphaea* (now *Pycnodonte*) *mutabilis* to the ANSP (Anonymous, 1829). Nuttall also sent two specimens, a *Baculites asper* and *Ostrea* (now *Agerostrea*) *falcata*, to fellow ANSP member Samuel G. Morton. Morton described these four species in two separate publications (Morton, 1832, 1834), representing two of the earliest scientific descriptions of Cretaceous fossils from Alabama.

Figure 3. Thomas Nuttall (1808–1841). Reproduced from Graustein (1967).

Timothy Abbott Conrad (1803–1877)

The same year as Morton's 1832 publication, another paleontologist at the ANSP, Timothy A. Conrad (Fig. 4), received his introduction to Alabama fossils. Conrad was an American-born paleontologist who is arguably best known for his systematic studies of the Tertiary formations along the Atlantic and Gulf Coasts of North America (Harris, 1893; Wheeler, 1935). Described by geologist Charles Lyell as "the best-informed paleontologist on this side of the Atlantic" (Arden, 1982), Conrad was a skilled illustrator who not only produced lithographs for his own publications, but also for the works of others (Youmans, 1896a). For example, in John James Audubon's most famous work, *Birds of America,* several of Conrad's illustrations depicting shells, seaweed, and other small objects can be seen in the backgrounds of some of Audubon's illustrations of birds (Youmans, 1896a).

In 1832, Conrad was given the task of describing a number of fossil shells collected by a fellow ANSP member, Dr. Hezekiah Gates. Gates had recently returned from an extensive visit to Tertiary localities along the Atlantic seaboard – the most notable of which was Claiborne, Alabama – where he collected a large number of Eocene invertebrates (Wheeler, 1935). The same year, Conrad described and illustrated many of these specimens in *Fossil Shells of the Tertiary Formation of North America.* Conrad went on to publish three additional parts of this work along with a handful of revisions that were later reprinted by Gilbert D. Harris in 1893. The first part was dated October 1, 1832 and not only brought the Tertiary formations of Alabama to the attention of geologists, but also marked the beginning of systematic research into the Tertiary history of North America (Harris, 1893). Part 2 appeared in December 1832 and announced Conrad's intention to visit Tertiary localities in the southern United States which, in his mind, had been only superficially examined (Harris, 1893). True to his word, Conrad began his journey south in December 1832 and did not return to Philadelphia for over two years.

Conrad started his journey in North Carolina, and then continued to South Carolina, Georgia, and eventually Alabama. From February 28, 1833 to February 20, 1834, Conrad toured through Alabama beginning at Claiborne in Monroe County, where he stayed at the residence of Judge Charles Tait, who had been Alabama's first district court judge (Moffat, 1948). Using Claiborne as his base, Conrad traveled as widely as Tuscumbia and Mobile (Fig. 5) and spent much of his time dredging and collecting fossil and extant shells. Along the way he wrote letters to colleagues at the ANSP, including Samuel G. Morton. In these letters, Conrad detailed his travels across the state, often alluding to the richness of the fossil material as well

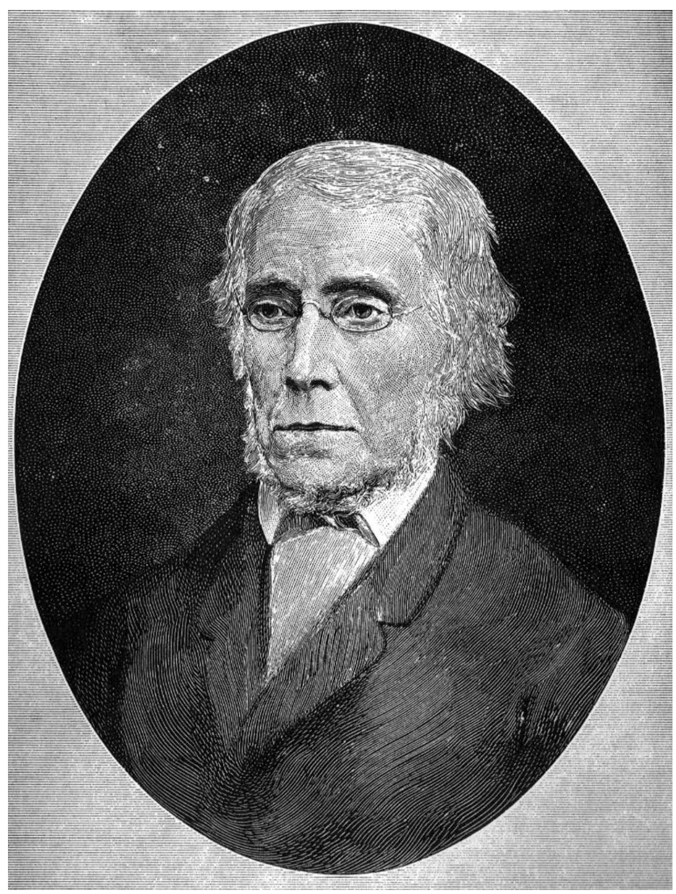


Figure 4. Timothy Abbott Conrad (1803–1877). Reproduced from Wheeler (1935).

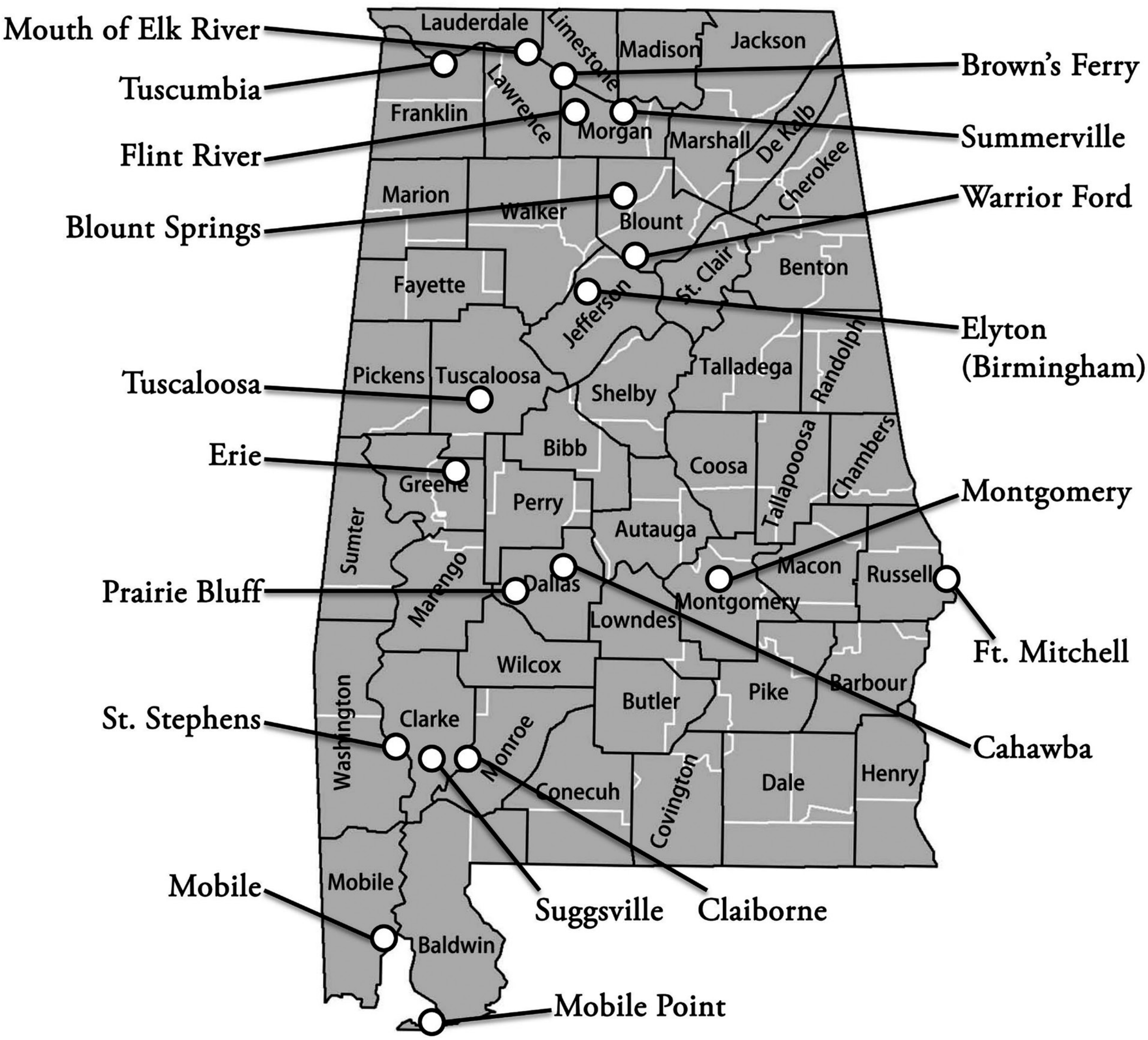


Figure 5. Alabama localities Timothy Abbott Conrad is known to have visited and/or collected specimens. Black lines indicate county boundaries in the late 1830s. White lines indicate current county boundaries. Names in parenthesis represent current location names. Historical county map modified from Remington (1999).

as the thinning of his pocketbook. Conrad's travels were also partly documented by letters written by Tait to another noted paleontologist at the ANSP, Isaac Lea (Wheeler, 1935).

Late in life, Tait was an avid fossil collector who had accumulated, at the time, perhaps the largest collection of Eocene fossils in North America (Moffat, 1948). Ironically, in 1829, Tait sent a box of Claiborne fossils to Lea at the ANSP. Lea took great interest in these fossils and asked Tait to send him additional specimens from upper and lower stratigraphic units of the site (Lea, 1833). For reasons unknown, Lea, who never seemed to turn down an opportunity to introduce new species to science, left these specimens unattended for four years despite the knowledge that many of them would undoubtedly be type specimens. It was not until Lea learned of Conrad's research at Claiborne that his competitive nature drove him to publish on the Tait material in 1833 (Lea, 1833; Wheeler, 1935).

In May 1833, Conrad was introduced to Robert W. Withers from Erie, Alabama, whom Conrad befriended and stayed with on at least three separate occasions during his year-long visit (Wheeler, 1935). Withers introduced Conrad to the Cretaceous exposures at Erie where he collected at least one fossil invertebrate. In addition to Erie, Conrad collected fossil material from two other Cretaceous localities: Prairie Bluff in Wilcox County, and an undisclosed locality in Greene County (Morton, 1834). The Cretaceous fossils that Conrad collected included ammonites, *Baculites*, worm shells, and at least one vertebrate tooth, all of which were shipped back to Morton at the ANSP (Morton, 1834, 1835). This same year, Conrad published two additional parts of his work "Fossil Shells." Part 3, dated August 1833, described 40 Eocene fossils collected from Claiborne. Dated October 1833, part 4 described a total of 77 Eocene fossils from the site. Two years later, Conrad revised the third and fourth parts of his work and republished them with a small geologic map of Alabama (Harris, 1893) (Fig. 6). Published March 1, 1835, this map highlighted the different geological formations of the state, including what was thought to be the northern and southern boundaries of the Cretaceous belt. Conrad's 1835 map was the first geologic map of Alabama.

In 1838, while back in Philadelphia, Conrad was introduced to Philip Henry Gosse (1810–1888). Gosse, a budding naturalist and zoologist, was convinced by Conrad that he could pursue his scientific interests and "seek his fortune" in Alabama (Wheeler, 1935:63). Following Conrad's advice, Gosse spent the next eight months teaching at a plantation and studying the local flora and fauna in Dallas County, Alabama. During this time, Gosse produced an unpublished sketchbook of Alabama wildflowers and insects he called *Entomologia Alabamensis*, and in 1859, he published a work detailing his stay titled *Letters from Alabama*. Of the prairies in Dallas County, Gosse (1859:75) wrote:

> There are in the neighbourhood, many prairies, – not the boundless prairies of the West, resembling an ocean solidified and changed to land, but little ones, varying in extent from an acre to a square mile . . . . Multitudes of fossil shells are scattered over and imbedded in these prairies, but I know nothing of their characters or names.

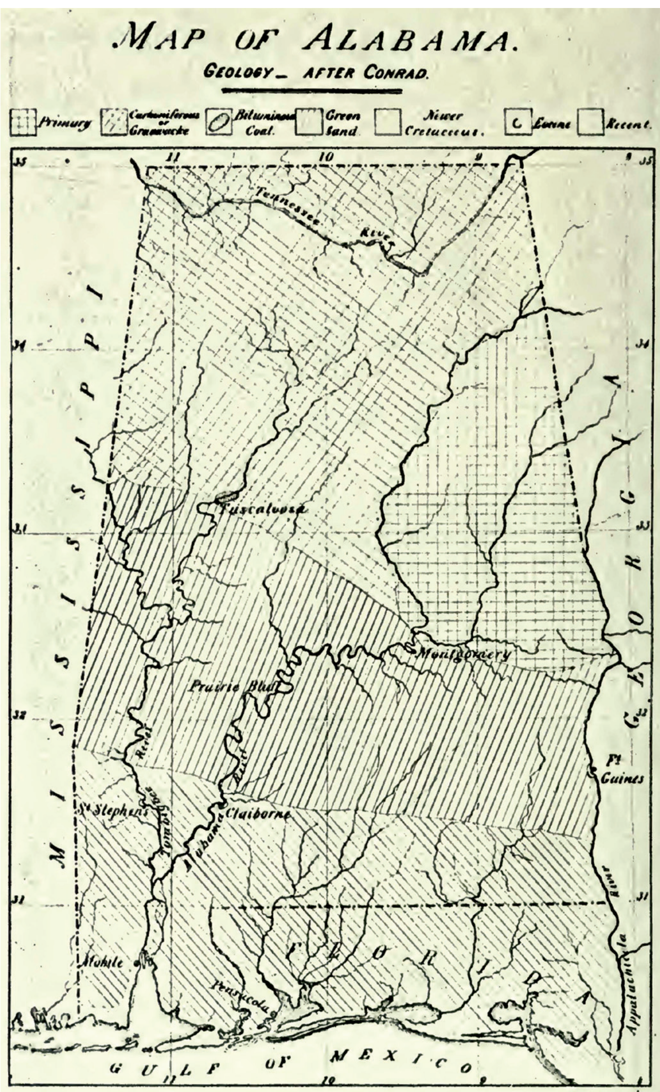


Figure 6. Timothy Abbott Conrad's 1835 geologic map of Alabama. Reproduced from Harris (1893).

Samuel George Morton (1799–1851)

A former president of the ANSP, Samuel G. Morton (Fig. 7) was a Philadelphia-born scientist with a variety of research interests (Lewis et al., 2011). Not only was Morton a practicing physician and geologist, but he was also the first American to practice invertebrate paleontology (Stanton, 1960). Best known for his 1839 work *Crania Americana* (which detailed his controversial studies on skulls of human races), Morton is also credited as the first to determine the Cretaceous sequence along the Atlantic and Gulf Coasts of North America (Schuchert, 1918). Although he never visited Alabama, Morton pieced together the Gulf Coast Cretaceous sequence by communicating with, and examining fossils collected by, fellow ANSP members Nuttall and Conrad (Morton, 1832, 1834). Morton gave credit to Nuttall for detecting the presence of Cretaceous strata in Alabama, and for determining the extent of these units to be at least a thousand miles wide (Morton, 1832). Morton later gave credit to Conrad for determining the strata in Pickens, Bibb, Greene, Perry, Dallas, Marengo, Lowndes, Montgomery, and incorrectly, parts of Clarke, Monroe, and Conecuh counties to be Cretaceous in age (Morton, 1834). Morton estimated the Cretaceous deposits in Alabama to be equivalent in age to those he observed in the northeastern United States as the *Exogyra costata* and *Agerostrea falcata* specimens collected by Nuttall were, in his mind, "specifically identical with those from New Jersey" (Morton, 1832:94). Morton also credited fellow ANSP member Lardner Vanuxem with determining that the Cretaceous strata in the United States were equivalent to those in Europe (Morton, 1834).

Morton divided the Cretaceous strata in the United States into three divisions: the upper, medial, and lower. Of these, Morton believed that both the lower and upper divisions of the Cretaceous were present in Alabama. Morton credited the detection of the upper division exclusively to Conrad, who reported it in South Carolina, west Florida, and the southern section of Alabama between Claiborne and St. Stephens. Based upon the geological observations of Conrad, Morton reported the upper division of the Cretaceous in Alabama was present in the form

Figure 7. Samuel G. Morton (1799–1851). Reproduced from Nott and Gliddon (1854).

of a "nummulite limestone" with the characteristic fossil-being *Nummulites mantelli* (Conrad, 1834; Morton, 1834, 1835). This taxon is known today as *Lepidocyclina mantelli*, a large fossil foraminifer. The upper division, as described by Morton, would later be recognized as late Eocene by renowned geologist Charles Lyell, who visited Alabama over a decade later (Wilson, 1998).

Ptychodus mortoni—In his 1834 work, *Synopsis of the Organic Remains of the Cretaceous Group of the United States*, Morton presented two figures of a tooth he described as "Palate bones of a fish?" (Morton, 1834, explanation of plate 18, figs. 1, 2) (Fig. 8). Morton (1834) mentioned nothing more of this tooth until 1842, when he wrote: "The palates of a Fish belonging to the genus *Ptychodus*, were found by Mr. Conrad in the older cretaceous strata at Prairie Bluff, Alabama, and are figured without a name in my Synopsis, pl. 18, fig. 1, 2" (Morton, 1842:215). The "Mr. Conrad" Morton refers to was none other than his good friend Timothy A. Conrad, who collected the tooth during his stay at Prairie Bluff in 1833 (Wheeler, 1935). After its discovery, Conrad shipped the specimen to Morton at the ANSP, who in turn sent it to his friend and colleague in London, geologist and paleontologist Gideon Mantell (Morton, 1842; Everhart, this volume). After his examination of the tooth, Mantell (1836) declared it to be a new species, naming it *Ptychodus mortoni* after his friend Morton.

Although he credited Mantell with the naming of *P. mortoni*, Morton wrote that Mantell had "not yet informed me in what work the description is published" (Morton, 1842:215). As it turns out, Mantell never published a detailed description of the tooth, he simply erected the name and made brief mention of it in his report (Mantell, 1836). The tooth was instead described by another 19th century paleontologist, Louis Agassiz. After examining the *Ptychodus* tooth in Mantell's collection, Agassiz (1839) published a formal description and illustration of the specimen in the third volume of his work, *Recherches sur les Poissons Fossiles*. Agassiz confirmed Mantell's conclusion that the tooth belonged to a new species of *Ptychodus* and retained Mantell's suggested name, *P. mortoni*. This *P. mortoni* tooth remains the first Late Cretaceous vertebrate fossil and holotype described from Alabama (Ikejiri et al., this volume).

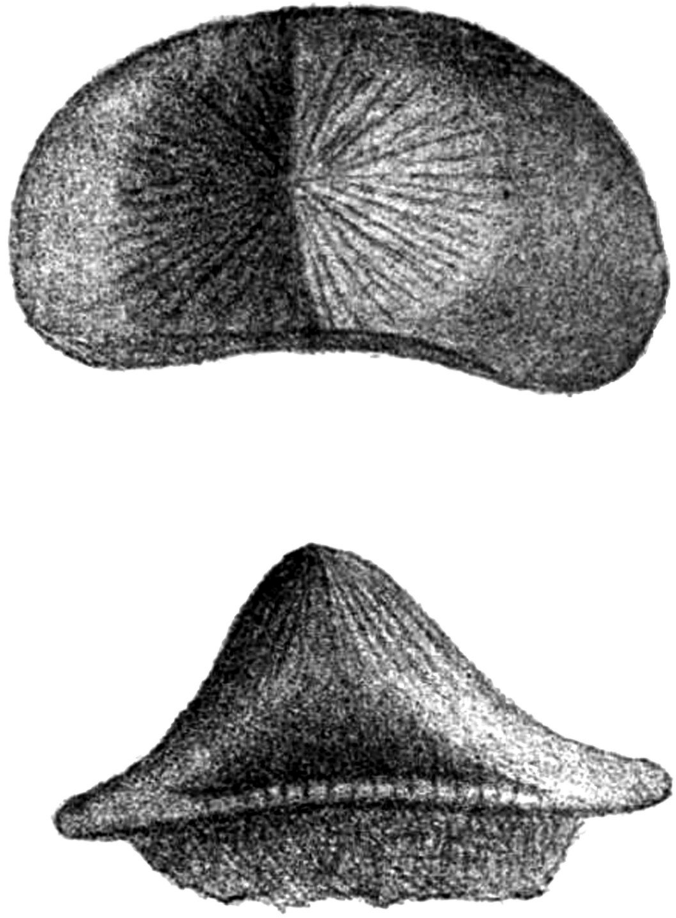


Figure 8. Morton's 1834 illustration of *Ptychodus mortoni*. Top: Occlusal view; Bottom: side view. Reproduced from Morton (1834:pl. 18, figs. 1, 2).

Henry Darwin Rogers (1808–1866)

American-born Henry Darwin Rogers (Fig. 9) was an ANSP member and one of the first professional geologists in the United States. Rogers, best known for his theory on the elevation of American mountain chains, also led two of the earliest state geological surveys in New Jersey and Pennsylvania (Gerstner, 1994). In his 1834 "Synopsis,"

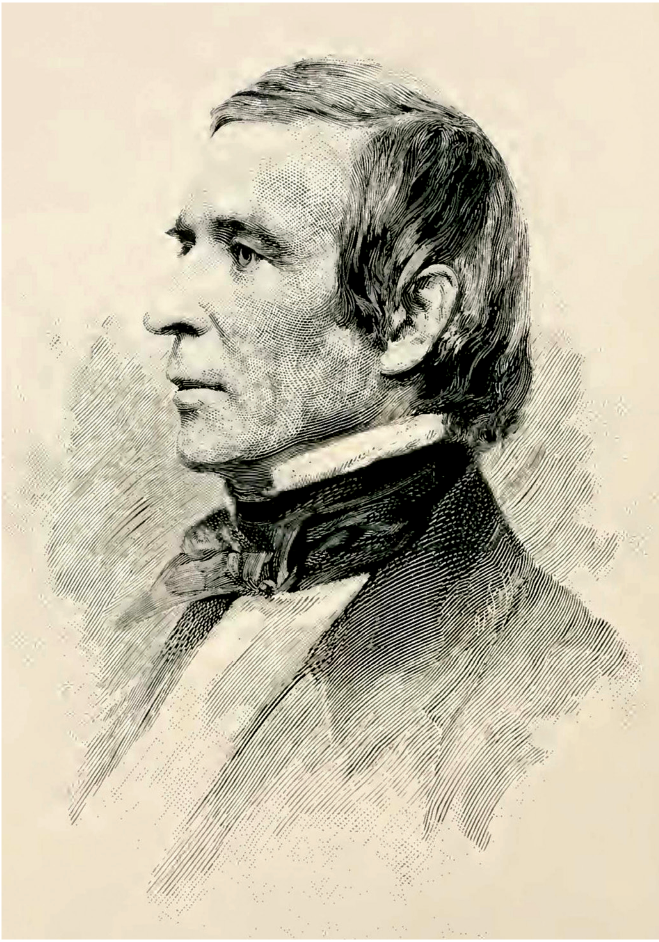


Figure 9. Henry Darwin Rogers (1808–1866). Reproduced from Youmans (1896b).

Morton cited an ANSP journal article written by Rogers documenting a single "Saurian" vertebra "from the lower limestone of Alabama" (Morton, 1834:28–29). While Rogers' paper could not be found for inclusion in this study, he presented the same information in an 1835 report on the geology of North America given at the fourth meeting of the British Association for the Advancement of Science (Rogers, 1835). In this report Rogers wrote "I have recently described two vertebrae from New Jersey, and another from Alabama, which I regard as either identical with, or very closely allied to, bones figured by Cuvier from Honfleur, which he considers to approach nearer to the *Plesiosaurus* than to any other genus" (Rogers, 1835:61). The "Cuvier" Rogers refers to was French paleontologist and naturalist Georges Cuvier who had, just a few years earlier, described the remains of several plesiosaurs discovered in Honfleur, France (see Cuvier et al., 1830).

In this same report, Rogers compiled a list of all Cretaceous vertebrates known from New Jersey, Delaware, and Alabama. Along with the aforementioned "Saurian," Rogers listed the taxon "Squalus," and wrote: "Teeth and vertebrae of several species of shark are abundant in New Jersey and Alabama" (Rogers, 1835:61). Rogers credited Morton for providing this information however, it is unclear whether these reports were based on personal observations or collected specimens. In either case, Rogers' accounts represent two of the earliest of plesiosaurs and sharks from Cretaceous strata in Alabama mentioned in the scientific literature.

Charles Upham Shepard (1804–1886)

Charles Upham Shepard (Fig. 10) was an American chemist, botanist, and mineralogist (Hemphill, 1907). Shepard graduated from Amherst College in Massachusetts in 1824 and, for a year after, studied botany and mineralogy under Thomas Nuttall at Cambridge. Shepard later held appointments at Yale, the South Carolina Medical College at Charleston, the Geological Survey of Connecticut, and served as an assistant to Benjamin Silliman, the editor of the *American Journal of Science and Arts* (Youmans, 1896a). Well known for his 1832 work *Treatise on Mineralogy*, Shepard accumulated a private collection of minerals that was so large it "surpassed all others on the continent" (Anonymous, 1886:536).

During his appointment with Silliman, Shepard spent

Figure 10. Charles Upham Shepard (1804–1886). Reproduced from Youmans (1895).

the winter of 1832–33 investigating the culture and manufacture of sugar cane in the southern states – in particular Georgia, Louisiana, and Alabama (Anonymous, 1886; Youmans, 1896a). While in Alabama, Shepard studied three Cretaceous outcrops along the Alabama River at Prairie Bluff, Campbell's Landing, and an unnamed bluff near Montgomery (Shepard, 1834). At these localities, Shepard noted the presence of certain invertebrate taxa, which led him to disagree with Morton's (1834) determination that the fossil-bearing strata in the area were Cretaceous in age. Convinced that the units instead belonged to the Tertiary, Shepard would ultimately be proven wrong by his own observations as he noted the presence of *Exogyra costata* at both Prairie Bluff and Campbell's Landing (Shepard, 1834). The presence of *E. costata*, now an index fossil for early and middle Maastrichtian formations (Sohl and Kauffman, 1964), confirms Morton's (1834) original assessment of these units being Cretaceous. Six years later, while teaching at the South Carolina Medical College in Charleston (Youmans, 1896a), Shepard published a second paper on the Black Belt, this time on the soil chemistry of the prairie chalks (Shepard, 1841).

Basilosaurus cetoides – the Almost Cretaceous Reptile

In 1829, 28 fossilized vertebrae belonging to a gigantic unknown animal were unearthed near the Ouachita (Washita) River in Louisiana by Judge Henry Bry (Harlan, 1834a). Thinking that the remains might be of scientific interest, Bry shipped a lone vertebra from his find to the president of the American Philosophical Society of Philadelphia, Peter Du Ponceau (Kellogg, 1936). Around this same time, reports of a similar animal began to surface in Alabama. In 1834, for example, a published letter by W. W. McGuire reported:

> A gentleman in Clarke County, Alabama, states that on his plantation, are parts of the back bone of some large animal, from eight to ten inches long, and proportionally large in circumference – some still held together by the cartilaginous ligatures. Many of the early settlers used them instead of andirons. There is not canal for the spinal marrow. An early settler informed him, that he had seen an entire skeleton, on the surface of the earth; it was of enormous dimensions, longer as is reported, than the largest whale (McGuire, 1834:98).

Writing in the *American Journal of Science and Arts*, the editor, Benjamin Silliman, replied: "It is exceedingly desirable that the animal remains described in this page should be collected and examined, and we trust that our intelligent correspondent will not permit it to be neglected" (McGuire, 1834:98). A year later, Robert Withers wrote a similar account:

> There are some fossil remains in Clarke County of an animal whose vertebrae are said to be as large as a dinner plate, and have been used by the inhabitants as fire-dogs. Almost the whole skeleton, I was informed lately, was still lying on the surface of the earth where the animal perished; but I have been unable as yet to procure any specimens of it (Withers, 1835:637).

Perhaps referring the same specimen, discoveries such as these in Alabama soon ignited a global debate over the affinity and age of this mysterious creature. This debate involved many of the world's scientific elite and eventually played out as one of the most bizarre taxonomic histories of any fossil taxon (Kellogg, 1936; Switek, 2010). Sparking this debate was paleontologist and physician, Richard Harlan.

Richard Harlan (1796–1843)

Richard Harlan (Fig. 11) is considered as the first vertebrate paleontologist in America (Simpson, 1942). Like most paleontologists at the time, Harlan was a trained physician and a member of the ANSP, the American Philosophical Society, and the Academy of Medicine in Philadelphia (Simpson, 1859; Simpson, 1942). As the principal authority on fossil vertebrates in the United States, Harlan became the first American to apply Linnaean names to New World vertebrate fossils. Harlan spent much of his professional career publishing descriptions of American

Figure 11. Richard Harlan (1796–1843). Image courtesy of the National Library of Medicine, Bethesda, Maryland.

reptiles, fishes, and mammals, both fossil and extant (see Harlan, 1835). Harlan named 17 fossil vertebrate taxa from the United States, which, at the time, was more than any other American or European scientist. Among the new species Harlan named was the Cretaceous fish *Saurocephalus lanciformis*, the holotype of which is the only surviving vertebrate fossil from the Lewis and Clark expedition (Simpson, 1942).

In 1832, while a member of the American Philosophical Society, Harlan was charged by Du Ponceau to describe the massive vertebra shipped to him by Judge Bry (Kellogg, 1936). After thoroughly examining the massive vertebra, Harlan published the following in 1834:

> The principal fossil which forms the subject of this paper, consists of a vertebra of enormous dimensions, possessing characters which enable us to refer it to an extinct genus of the order "Enalio-Sauri" of Conybeare, which includes numerous extinct genera of marine lizards or crocodiles, generally possessing gigantic proportions, which have hitherto been found only in the sub-cretaceous series, from the *lias* up to the weald clay inclusive, in England, France, and Germany, and in the supposed equivalent formations in North America (Harlan, 1834a:401).

Harlan compared the vertebra to those of "Mosasaurus, Geosaurus, Megalosaurus, Iguanodon, Ichthyosaurus, and Plesiosaurus" and concluded it most closely resembled that of *Plesiosaurus* (Harlan, 1834a:401–402). Admitting that more elements from the same animal would be needed to confirm his conclusions, Harlan provisionally erected the name "*Basilosaurus*" for this new animal (Harlan, 1834a:403), meaning "king of the lizards" (Kellogg, 1936:3; Jones, 1989:12; Uhen, this issue Vol. 2).

In the fall preceding Harlan's 1834 description, additional *Basilosaurus* remains arrived at the ANSP for examination. This time discovered near Claiborne, Alabama, several vertebrae and fragments of a lower jaw were excavated and shipped to Timothy A. Conrad by Judge John Creagh (Harlan, 1834b). At the time, Creagh was a prominent political figure in Alabama who, among his many posts, served as: commissioner and treasurer for the town of Jackson; commissioner and probate court judge for Clarke County; a State Legislator; and an early trustee of the University of Alabama. In addition, in 1819, Creagh founded the town of Suggsville, Alabama (Wood, 1991).

Shortly after examining these new remains, Harlan sent a letter to Creagh asking for additional elements. Creagh obliged and soon shipped a bounty of *Basilosaurus* material to the ANSP. Among these new remains were ribs, portions of a maxilla, a humerus, a tibia, and additional vertebrae. While examining these elements, Harlan observed in *Basilosaurus* what, in his mind, appeared to be both mammalian and reptilian attributes (Harlan, 1834b; Simpson, 1942). Harlan described the lower jaw of *Basilosaurus* as appearing to be hollow, similar to those of reptiles. At the same time, however, Harlan observed that *Basilosaurus* had rooted teeth, a mammalian trait. In the end, Harlan concluded that *Basilosaurus* exhibited more reptilian than mammalian characteristics, thus confirming his original assessment that the animal belonged to the "Saurian order, as a lost genus" (Harlan, 1834b:350).

In 1839, Harlan took portions of his Alabama *Basilosaurus* to London to be examined by some of the leading scientists of the day (Switek, 2010). Richard Owen, arguably the greatest comparative anatomist of the time, was one of the scientists to examine the remains (Simpson, 1942). Owen, who believed in a mammalian affinity for *Basilosaurus*, received permission from Harlan not only to examine the specimen, but to also slice open several of the teeth to see their inner microscopic structure. Owen's subsequent investigation showed *Basilosaurus* to have heterodont teeth (a mammalian trait); a similar morphologic and microscopic tooth structure to cetaceans; and a type of vertebral ossification unlike that of any known reptile, but much like that seen in cetaceans. In the end, Owen proved that *Basilosaurus* was not only a mammal, but a whale. Owen's arguments were so convincing, Harlan granted him permission to propose a new name for the animal, *Zeuglodon*, a name "suggested by the form of the posterior molars, which resemble the two teeth tied or yoked together" (Owen, 1839a:28; Uhen, this Bulletin, Vol. 2).

Albert Koch (1804–1867)—Just as Owen appeared to have solved the mystery over the affinity of *Basilosaurus*, in a strange twist of fate, history would repeat itself a few years later. Just as in 1834 and 1835, reports again began to surface in Alabama of the discovery of a fossil animal of enormous proportions. One such story was told by William Darby to the *National Intelligencer* and was later reprinted in the Boston publication, the *Monthly Chronicle*. Darby, a noted cartographer, historian, college professor, and travel writer (Kennedy, 1981; Gomez, 1993), wrote of the discovery of large extinct "Saurians" from Clarke County (Darby, 1841). The same year, Samuel B. Buckley, an accomplished field naturalist from New York (Dorr, 1992), documented in the *Mobile Commercial Register* how he heard "bones of a large, lizard-like animal, sixty or seventy feet in length, were on the plantation of Judge J. C. Creagh, of Clarke county" (Buckley, 1841:423). Buckley traveled to this site and, with the assistance of Creagh, excavated 44 vertebrae (reported to be in a continuous line), fragments of ribs, and a few leg bones. Of these remains, Buckley explained: "Some idea of the immense size of these bones may be formed from the fact, that they made two heavy wagon loads for two yoke oxen, over a good road." The remains were reassembled and laid out in Creagh's yard "for the inspection of the curious" (Buckley, 1841:424) and were later "shipped to the office of the Geological Survey of New York at Albany, where they were studied and described by Ebenezer Emmons" (Kellogg, 1936:3; Emmons, 1845).

The year 1841 would also see Albert Koch, a "self-taught paleontologist and a commercial exhibitor of natural curiosities," exhibit in his St. Louis museum the remains of a giant fossil skeleton he would call *Missourium theristrocaulodon* (Jones, 1989; Switek, 2010). Koch's *Missourium*, however, was not all it was billed to be. While its size was certainly impressive to the crowds of curious visitors, scientists who examined the specimen noted that the proportions of Koch's *Missourium* were exaggerated by the inclusion of extra bones. In addition, Koch's *Missourium*, while advertised as a new species, was actually that of a known fossil, *Mammut americanum*, the American Mastodon. Although the scientific community was largely critical of the *Missourium*, the British Museum felt strongly enough about the importance of Koch's prize specimen that they purchased it for £1,300 in 1843 (Koch, 1972; Jones, 1989; Switek, 2010). The money earned from this transaction enticed Koch to embark on a North American expedition in search of his next grand fossil attraction. By chance, Koch was close friends with Yale professor and editor of the *American Journal of Science and Arts*, Benjamin Silliman. Obviously aware of the reports of *Basilosaurus* remains coming out of Alabama (at least one of which was reported his own journal; McGuire, 1834), Silliman provided Koch with the necessary information on where he could procure one of these immense "monsters" (Switek, 2010).

Following the advice of Silliman, Koch traveled to Alabama in 1845 to explore the areas around Macon (now Grove Hill), Clarkesville, Coffeeville, St. Stephens, and Washington-Old-Courthouse (Koch, 1972; Jones, 1989). While searching for his next prize specimen, Koch discovered isolated *Basilosaurus* remains in a number of extraordinary locations. For example, in his diary Koch wrote:

> It is really singular in what way the vertebrae of the *Zygodon* were used and destroyed here. As I earlier found several of them instead of the so-called andirons in fireplaces, so one was buried in the ground, near Clarkesville, to be used as a support for a garden gate. Another one I found cemented in as a cornerstone in a chimney. Here at this place where I am just writing one serves a Negro as a pillow. So and in a similar manner were those remains of the prehistoric times snatched from science by ignorance (Koch, 1972:107).

In his diary, Koch referred to these remains as belonging to "*Zygodon*" (Koch, 1972) as opposed to *Zeuglodon*, suggesting he was well aware he was searching for a creature already known to science (Switek, 2010). Nevertheless, after several weeks of searching, Koch discovered what he was looking for as he collected a significant number of *Basilosaurus* remains at three separate locations, "one near Clarksville and two near the old Court House in Washington County, Alabama" (Kellogg, 1936:5). Koch proceeded to crate these remains and shipped them to New York on the *Newark,* a ship that would wreck off the coast of Florida (luckily Koch's crates were among the few that were saved; Switek, 2010).

Once his crates arrived in New York (this time on a different ship, the *Globe*), Koch began to prepare and assemble his huge collection of bones (Switek, 2010). In July 1845, Koch unveiled a 114-foot monster he named "*Hydrargos sillimanii*" meaning "Silliman's sea chief" (Kellogg, 1936; Jones, 1989; Uhen, this Bulletin, Vol. 2) (Fig. 12). Koch named this supposed new species for his good friend Benjamin Silliman, who graciously informed him where to procure one of these enormous creatures (Switek, 2010). Koch's *Hydrargos* became an overnight international sensation and was exhibited in cities such as New York and Boston and later was "shipped to Germany and exhibited in the principal cities of Europe" (Kellogg, 1936:4; Switek, 2010) (Fig. 13). While the general public was enthralled by Koch's new attraction, the scientific community, just as it did with his *Missourium*, criticized the reconstruction (Kellogg, 1936; Jones, 1989; Switek, 2010).

Harvard anatomist Jeffries Wyman, for example, upon viewing the *Hydrargos* in New York noticed the skull of the specimen was too small for the body and the vertebrae exhibited different degrees of ossification (Wyman, 1845; Switek, 2010). This convinced Wyman that Koch's *Hydrargos* was compiled from several different individuals. Wyman also noted that portions of the anterior extremities were made up of cephalopod shells. After further examination, he concluded "that these remains have never belonged to one and the same individual; [and] 2nd, that the anatomical characters of the teeth indicate that they are not those of a reptile, but of a warm-blooded mammal (Wyman, 1845:67). Later that year, George Lister, a doctor from Washington County, published a letter in a Boston journal corroborating Wyman's conclusion that *Hydrargos* was a composite specimen. In this letter, Lister explained how he personally examined the sum of the remains col-

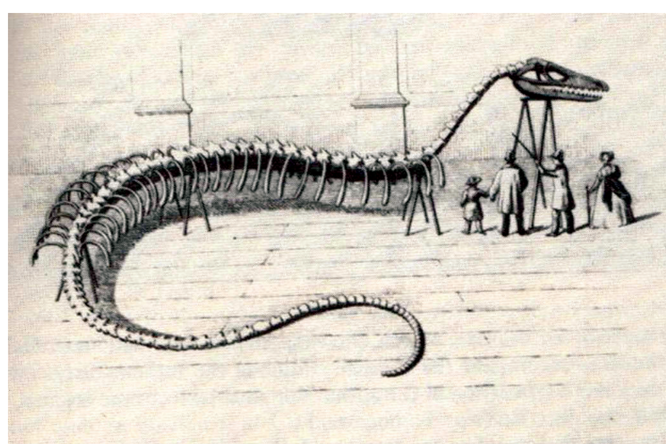
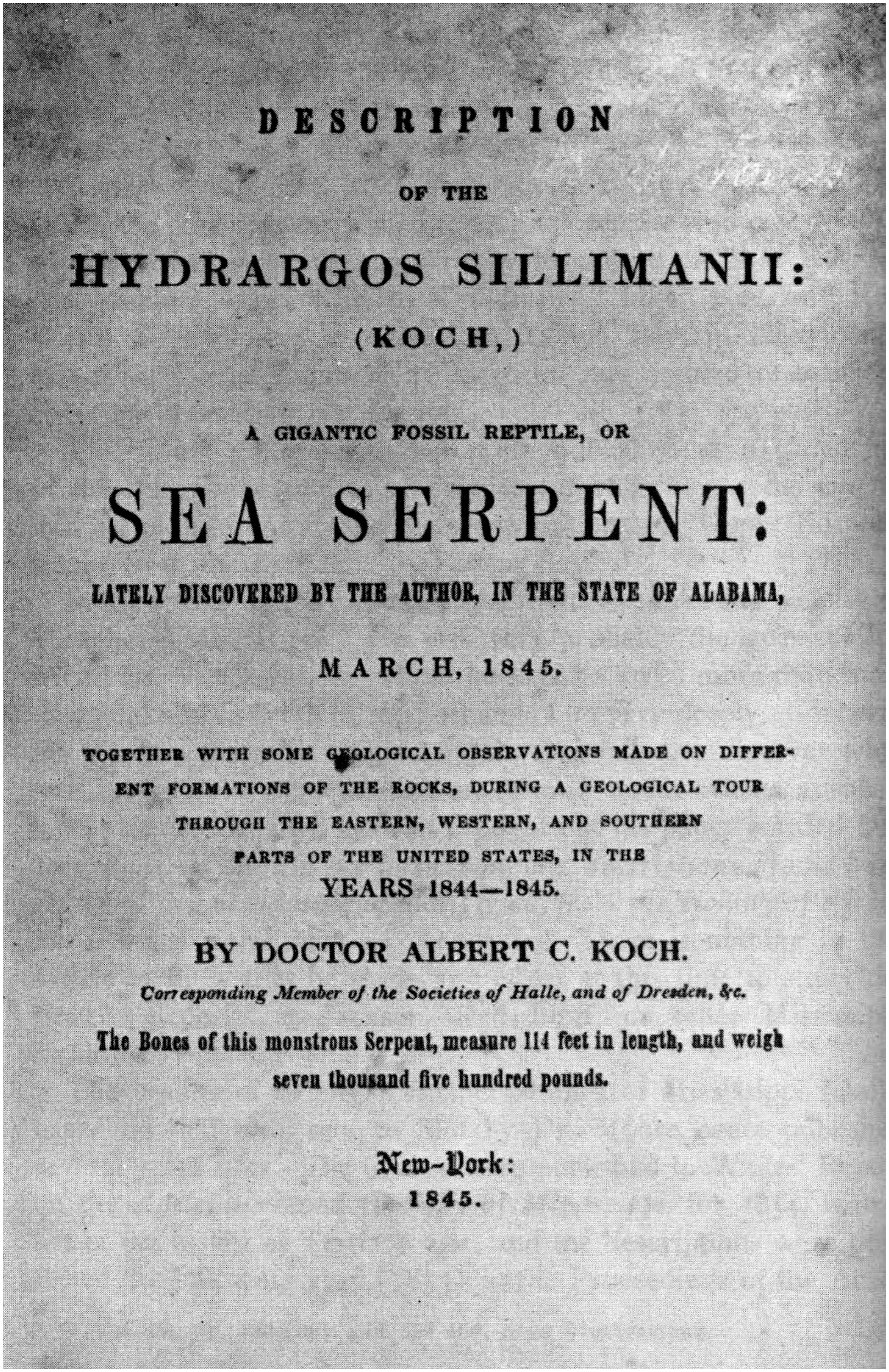


Figure 12. Albert Koch's *Hydrargos* as shown in his diary. Reproduced from Koch (1972).



DESCRIPTION

OF THE

HYDRARGOS SILLIMANII:

(KOCH,)

A GIGANTIC FOSSIL REPTILE, OR

SEA SERPENT:

LATELY DISCOVERED BY THE AUTHOR, IN THE STATE OF ALABAMA,

MARCH, 1845.

TOGETHER WITH SOME GEOLOGICAL OBSERVATIONS MADE ON DIFFERENT FORMATIONS OF THE ROCKS, DURING A GEOLOGICAL TOUR THROUGH THE EASTERN, WESTERN, AND SOUTHERN PARTS OF THE UNITED STATES, IN THE YEARS 1844—1845.

BY DOCTOR ALBERT C. KOCH.

Corresponding Member of the Societies of Halle, and of Dresden, &c.

The Bones of this monstrous Serpent, measure 114 feet in length, and weigh seven thousand five hundred pounds.

New-York:
1845.

Figure 13. Title page of Albert Koch's 1845 pamphlet describing *Hydrargos sillimanii*. Reproduced from Koch (1845).

lected by Koch after their excavation and could attest that they indeed belonged to several individuals (Lister, 1846).

Koch avidly defended his *Hydrargos*, but his dissatisfaction with the scientific criticism led him to take his attraction to Europe (Switek, 2010). Around this time Koch changed the genus name of his creature from *Hydrargos*, "sea chief," to *Hydrarchos*, "sea ruler" (Jones, 1989:16). Koch also changed the species name as Benjamin Silliman apparently had reservations about his name being associated with the sea serpent. Silliman instead suggested Koch rename the specimen *Hydrarchos harlani* after Richard Harlan, the scientist who first described the creature a decade earlier (Switek, 2010).

While on exhibit in Berlin, King Friedrich Wilhelm IV of Prussia acquired the *Hydrarchos* for the Royal Anatomical Museum, and as compensation provided Koch with a yearly pension for life (Jones, 1989; Switek, 2010). With these proceeds, Koch returned to Alabama in 1848 to search for another *Hydrarchos*. Koch did indeed discover another and proceeded to ship the remains to Germany for exhibition (Kellogg, 1936). In 1849, Koch's second monster, this one a modest 96 feet long, was unveiled (Koch, 1972; Jones, 1989). This *Hydrarchos* traveled to New Orleans, was later sold to Koch's old museum in St. Louis (which, by this time, was under new management), and eventually was sold to the Wood's Museum in Chicago where it was destroyed in the great fire of 1871 (Kellogg, 1936).

Koch's first *Hydrarchos*, now property of the Royal Anatomical Museum in Berlin, was finally adequately prepared and studied by Johannes Müller, a German physiologist (Kellogg, 1936; Switek, 2010). Müller went on to confirm the earlier statements of Wyman (1845) and Lister (1846) that this *Hydrarchos* was indeed a composite of several different individuals and determined, as others had done, that the remains belonged to a previously described animal, Harlan's *Basilosaurus*. Müller also proved, as Owen did a decade before, that *Basilosaurus* was not a reptile, but a whale (Müller, 1849). As the story goes, Müller was hosting 50 naturalists at the museum when asked if *Hydrarchos* was a reptile or mammal. To answer this question, Müller pulled out the temporal bone from the skull but accidently dropped it on the floor, shattering the bone to pieces (Switek, 2010). Upon cleaning up the many fragments, Müller noticed how the structure of the inner ear was revealed (Switek, 2010). Closer examination of this inner structure led Müller to conclude that "There was only one other kind of creature with an inner ear that matched: a whale" (Switek, 2010:152). While the conclusions of both Müller (1849) and Owen (1839) finally quieted the debate over the affinity of *Basilosaurus*, during the early parts of the 1840s, there were still questions concerning the age of this extinct cetacean. The answer to this question was finally resolved by the 1845 visit of Charles Lyell to Alabama.

Charles Lyell (1797–1875)—Scottish geologist Charles Lyell (Fig. 14), one of the 19th century's most important scientists, is regarded by many as the founder of modern historical geology (Arden, 1982; Wilson, 1998). Although he graduated from Oxford University with a degree in law, Lyell quickly learned he could make money publishing and lecturing on topics within his rapidly growing interest – geology. Lyell wrote two landmark works, *Principles of Geology,* which was published in three volumes from 1830–33, and *Elements of Geology* in 1838, both of which were reprinted in numerous editions. Lyell's *Principles of Geology* greatly influenced his friend Charles Darwin and his 1859 work *On the Origin of Species,* while *Elements of Geology* became a standard text for those studying stratigraphy and stratigraphic paleontology (Arden, 1982; Wilson, 1998).

Lyell and his wife Mary visited America on four occasions between 1841 and 1853, living on the money Lyell made from lecturing in cities in the northeastern United States (Dott, 1998). During his trips to America, Ly-

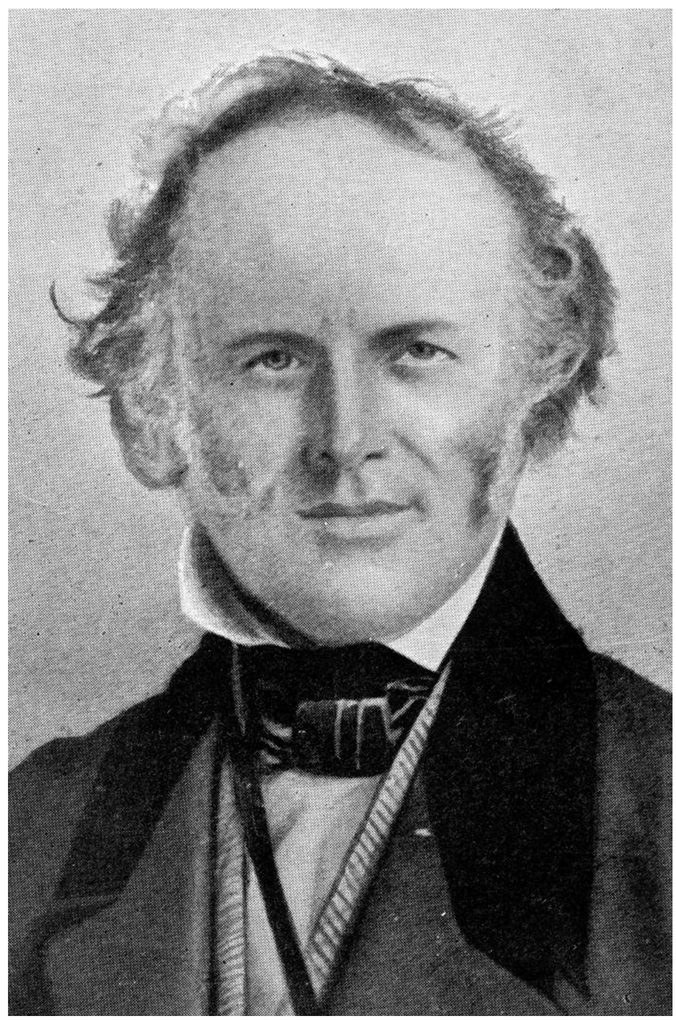


Figure 14. Charles Lyell (1797–1875). Reproduced from Shuster and Shipley (1917:310).

ell took the opportunity to accomplish several tasks that were of interest to him. For one, Lyell was interested in comparing the Cretaceous and Tertiary formations of the Atlantic and Gulf Coasts of America (and their fossils) to their European counterparts to confirm his belief in the uniformity of geologic history. Later, Lyell became interested in determining the age of *Basilosaurus* and the nummulite limestone beds of Alabama (Wilson, 1998).

Lyell's interest in *Basilosaurus* began during his 1845 visit to Boston, which coincided with the exhibition of Koch's *Hydrarchos* (Switek, 2010). After viewing the specimen, Lyell agreed with Owen's assessment of it being an extinct cetacean and stated the vertebrae were "ingeniously arranged by Mr. Koch" to appear as if they were a serpent (Lyell, 1849:107). Of Koch, Lyell described him as "a mixture of an enthusiast and an impostor, but more of the former, and amusingly ignorant" (Arden, 1982:130). Apparently annoyed by the billing of this cetacean as "a colossal and terrible lizard" and "the leviathan of the Book of Job," Lyell set out to not only determine the age of this extinct mammal, but also to prove that Koch's *Hydrarchos* was not what it was said to be (Lyell, 1849:107).

Prior to Lyell's 1845 visit to Alabama, several researchers had attempted to assign an age to the nummulite beds, the strata containing the known *Basilosaurus* remains. During this time, the prevailing thought considered the nummulite beds as either Cretaceous in age or possibly intermediate between the Cretaceous and Eocene (Wilson, 1998). The first to make this determination was Timothy A. Conrad who, after his nearly two years in Alabama, was quite familiar with the geology of the central and southern parts of the state (Wheeler, 1935).

Confused by the undulations of the Tertiary and Cretaceous strata in the Gulf Coastal Plain in Alabama – especially in areas of disturbance such as the Hatchetigbee Anticline in Clarke County – Conrad misinterpreted the nummulite beds to be "more recent than the true chalk of Europe, and even as occupying a place anterior to the Maestricht beds" (Harlan, 1834b:351), referring to them as the "newest secondary limestone" (Conrad,1835:35). In other words, Conrad viewed the beds as intermediary between the Cretaceous and Eocene. Interestingly, in regard to the Ouachita River site in Louisiana – the site that produced the holotype of *Basilosaurus* – Conrad interpreted the beds to be Eocene in age. At the same time, however, Conrad felt the corresponding beds in Alabama were older (Conrad, 1835). Obviously convinced by Harlan's interpretation of *Basilosaurus* being a reptile, Conrad (1835:36) stated the following about the Ouachita River site: "This locality is of great interest to a geologist, as it will, when investigated, solve a problem of great importance, whether or not remains of the Saurian family exist in the tertiary."

Conrad based his conclusions on the work of Lyell, who two years earlier divided the Tertiary into three epochs: the Eocene, Miocene, and Pliocene (Lyell, 1833). Lyell's descriptions of these new Tertiary divisions ultimately changed the minds of some scientists who had previously assigned an age to the nummulite beds in Alabama. In his 1834 "*Synopsis*," for example, Morton assigned the nummulite beds to the upper division of the Cretaceous. Later, however, Morton (1842), crediting Lyell, published the following addendum to his paper:

> The Upper Division embraces the Nummulite limestone of Alabama, which has been traced by Mr. Conrad from a point six miles west of Claiborne, to St. Stephen's, on the Tombecbee river, being especially characterized by the presence of Plagiostoma dumosum, and Nummulites Mantelli. I formerly included in this series the friable white limestone west of the city of Charleston, in South Carolina; but the recent researches of Mr. Lyell prove that this deposit belongs to the Eocene period (Morton, 1842:216–217).

From this, one could argue that Morton (1842) was the first to determine the age of the nummulite beds in Alabama. However, since Morton never visited Alabama, nor did he ever personally examine the nummulite beds, it was Lyell who ultimately confirmed their correct geologic age.

In February 1846, Lyell visited various sites in southern Alabama to view the nummulite beds (Fig. 15). After examining these units, Lyell detailed his conclusions in a letter to Silliman in the *American Journal of Science and Arts* (Lyell, 1846). In this letter Lyell wrote:

> I have visited some of the principal localities where the bones of the gigantic Cetacean (the Zeuglodon) have been discovered in Clarke County, Ala., in the fork of the rivers Alabama and Tombeckbee, and find the geological position of the bones to be everywhere the same, namely, in the white tertiary limestone of the Eocene period, corresponding in age to that of the Santee River, in South Carolina, or of Burke County, in Georgia, or that of the upper part of the celebrated bluff of Claiborne, in Alabama (Lyell, 1846b:313).

In this same letter, Lyell also explained how he met William Pickett, a gentleman who helped Koch excavate multiple *Basilosaurus* remains. Pickett and other individuals took Lyell to the sites of Koch's excavations, where he quickly confirmed that the bones that made up Koch's *Hydrarchos* did indeed come from several different specimens (Lyell, 1846b:313). Thus, in one letter, Lyell was able to show the "fraudulent character" of Koch's *Hydrarchos* (Wilson, 1998:212) and confirm the true age of the nummulite beds (Lyell, 1846). As a result, *Basilosaurus,* once considered a Cretaceous reptile and sea serpent, was finally recognized for what it was – an extinct Eocene whale.

Aside from solving the mystery surrounding the age of *Basilosaurus,* Lyell spent time visiting various Cretaceous sites in the Black Belt (Fig. 15). Lyell and his wife began their tour through the state in 1845 at Chehaw, and traveled by train to Montgomery (Lyell, 1849; Arden, 1982;

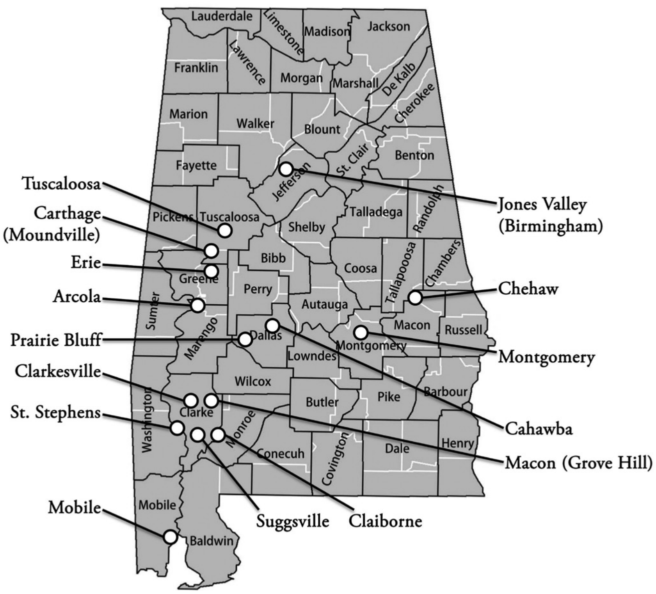


Figure 15. Alabama localities Charles Lyell is known to have visited and/or collected specimens. Black lines indicate county boundaries in the 1840s. White lines indicate current county boundaries. Names in parenthesis represent current location names. Historical county map modified from Remington (1999).

Wilson, 1998). At Montgomery, Lyell immediately headed to Jackson's Ferry along the Alabama River to examine the geology. At this locality, Lyell observed beds of loose gravel and red clay and sand containing fossil shells (known today as the Eutaw Formation) that Lyell interpreted to be Cretaceous in age. After a brief stay in Montgomery, Lyell went by steamboat down the Alabama River to Mobile, and then travelled north up the Tombigbee River to Tuscaloosa (Lyell, 1849; Wilson, 1998). Traveling by steamboat turned out to be advantageous for Lyell, as it allowed him to collect fossils at a number of different river bluffs (Lyell, 1849; Arden, 1982). The captain of the steamboat, Captain Bragdon, was an amateur geologist who graciously allowed Lyell the time to collect fossils at various bluffs and even advised him on the locations of good collecting sites. On occasion, Bragdon also helped Lyell collect samples (Lyell, 1849; Wilson, 1998).

Below the former Alabama capital of Cahawba, Lyell observed bluffs containing Cretaceous fossils that he interpreted as equivalent to those in England. Lyell observed similar Cretaceous exposures at Selma and at Prairie Bluff, and at this latter site he assembled an excellent collection of fossils (Lyell, 1849; Arden, 1982; Wilson, 1998). In Tuscaloosa, Lyell explored the rapids on the Black Warrior River which, in his mind, "marked the boundary between the horizontal Cretaceous strata and the older, harder, more inclined Carboniferous rocks" (Wilson, 1998:212). Around this time, Lyell was introduced to Richard Brumby, professor of chemistry, mineralogy, and geology at the University of Alabama, who went on to tour Lyell through various coal fields in the state (Wilson, 1998). Of Brumby, Lyell stated:

> It would have been impossible for me, during my short visit, to form more than a conjectural opinion respecting the structure of this coal field, still less to determine its geographical area, had not these subjects been studied with great care and scientific ability by Mr. Brumby (Clark, 1889:64).

Upon touring the coal deposits in the Jones Valley area, Lyell expressed his opinion that the iron, limestone, and coal of the region would ultimately "be a source of great mineral wealth to Alabama" (Lyell, 1846).

After visiting Cretaceous beds at Carthage (now known as Moundville), Erie, and Arcola, Lyell travelled back to Mobile and boarded a steamboat to New Orleans (Lyell, 1849; Wilson, 1998). This concluded Lyell's visit to Alabama and also marked the end of the *Pioneer Scientific Period*.

THE *TUOMEY PERIOD* (1847 TO 1865)

In contrast to the research of the previous period, geologic studies during the *Tuomey Period* were largely conducted by resident scientists from the University of Alabama and the Geological Survey of Alabama. This period begins with the appointment of Michael Tuomey as Alabama's first State Geologist. An act that would inaugurate the Geological Survey of Alabama, Tuomey was tasked with carrying out the first systematic study of the state's geology. This period is also marked by the Cretaceous research of Robert W. Gibbes, who described the state's first mosasaurs. The *Tuomey Period* ended in tragedy with Tuomey's death in 1857 and the burning of the University of Alabama campus by Union troops near the end of the Civil War.

The University of Alabama

In 1818 and 1819, as part of Alabama statehood, the Federal Government set aside 46,080 acres of land in Alabama to be rented, leased, or sold, for the sole purpose of funding a much needed "Seminary of Learning." As a result of this gift, in 1820 the Alabama Senate and House of Representatives passed an act to establish "The University of the State of Alabama" (Sellers, 1953:8). Construction of this new university began a few years later and on April 18, 1831, the University of Alabama was open for the admission of students (Sellers, 1953).

The original University campus, designed by State Architect William Nichols, consisted of seven buildings, including two faculty houses, two dormitories, a hotel, the Rotunda, and the Lyceum (Wolfe, 1983). The Rotunda, located in the center of campus, housed the University's library, while the Lyceum contained the principal lecture rooms and laboratories (Wilson, 1998). By 1859, two more dormitories, the President's mansion, two additional faculty houses, a guardhouse, and an observatory were added to the early campus (Wolfe, 1983). Freshmen at the University studied "Latin, Greek, geography, English grammar, history, and mathematics" and, as advanced students, topics such as natural history, botany, natural philosophy, chemistry, geology, and mineralogy (Kushner, 2010:5). The early faculty at the University included Reverend Alva Woods, the first president and professor of moral and mental philosophy; Henry Tutwiler, professor of ancient languages; Gurdon Saltonstall, professor of mathematics and natural philosophy; William M. McMillan, librarian and collector of specimens in natural history; and John Fielding Wallis, professor of chemistry and natural history (Anonymous, 1831). Among the topics Wallis taught included botany, zoology, mineralogy, chemistry, and geology (Sellers, 1953).

In 1834, Wallis left the University and was replaced by Richard T. Brumby, who served as professor of mineralogy and geology from 1834–47, and professor of chemistry and natural history from 1847–49 (Clark, 1889). During his appointment, Brumby made several important contributions to the early geological studies of the state. Not only did Brumby tour Lyell through the coal fields in Alabama in 1846, but he also presented a series of papers, letters, and public talks to the Alabama Legislature from 1839–45 stressing the importance of a geological survey of the state. Recognizing the wealth of natural resources in Alabama, Brumby explained how the study of such resources would "put Alabama in the forefront of industrial progress" (Owen, 1921:647). Brumby's persistence did not go unnoticed, as on January 2, 1848, the Alabama Legislature authorized a geological survey of the state for the purpose of "developing its agriculture and mineral resources and its water power" (Richardson, 1965:152).

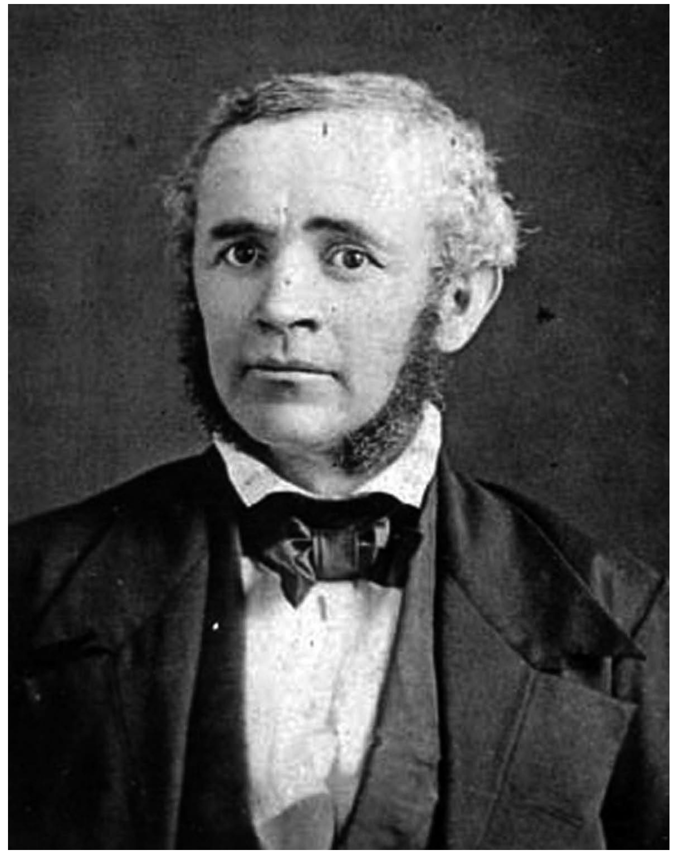


Figure 16. Michael Tuomey (1805–1857). Image courtesy of the W. S. Hoole Special Collections Library, The University of Alabama, Tuscaloosa, Alabama.

Michael Tuomey (1805–1857) and the Geological Survey of Alabama

A graduate of the Rensselaer Institute (now the Rensselaer Polytechnic Institute) in Troy, New York, the Irish-born Michael Tuomey (Fig. 16) served as State Geologist of South Carolina from 1844–47. Tuomey joined the faculty of the University of Alabama at the start of the 1847 fall term (Wilson, 1985) and taught mineralogy, geology, and agricultural chemistry (Tuomey, 1850a). The University took full advantage of having such a distinguished geologist on the faculty as they appointed him department chair, created a geology degree program for him to oversee, and stipulated in Tuomey's contract that he "spend such portions of his time, not exceeding four months in each year, exploring and reporting on the geology of the State" (Tuomey, 1850a:vii; Owen, 1921; Wilson, 1985). Immediately upon his appointment, Tuomey began conducting his geologic explorations and frequently published his findings in the local Tuscaloosa newspapers. In part due to the influence of Brumby, in 1848 the Alabama Legislature authorized a geological survey of the state. Taking notice of Tuomey's geologic reports, the Legislature felt it logical to appoint him the first official State Geologist. The appointment of Tuomey established the Geological Survey of Alabama and, with this office, Tuomey was required to explore and report on "the mineral and other natural resources of this State" (Tuomey, 1850a:vii–viii; Dean, 2001).

Although he now had added responsibilities, Tuomey did not receive any additional compensation from the state other than his University salary (Wilson, 1985). Nevertheless, Tuomey conducted his preliminary survey of the state and in 1850 published his *First Biennial Report on the Geology of Alabama*. Covering everything from coal fields to artesian wells, Tuomey dedicated an entire section of this report to the Cretaceous system of Alabama. Spending considerable time describing the superposition of the strata in Alabama, Tuomey admitted he had some difficulty determining the southern boundary of the Cretaceous system due to the "blending" of Cretaceous and Tertiary beds (Tuomey, 1850a:116). Of the strata at sites such as St. Stephens and Claiborne, localities that were interpreted by previous researchers to be Cretaceous in age, Tuomey wrote:

> The bluff at St. Stephens, like that at Claiborne, has been long known to geologists, and the identity of its rocks with the white limestone of the Santee, in South Carolina, was established by Mr. Conrad, who, misled by some of the embedded fossils, referred the whole to the upper part of the cretaceous system, supposing, as I have said in another place, that the Claiborne bed was newer, instead of being, as we now know it to be, older than the white limestone (Tuomey, 1850a:156–157).

Tuomey explained that this error was "corrected by Sir Charles Lyell during his last visit to this country; and these beds are now known to belong to the upper part of the eocene" (Tuomey, 1850a:143). After determining the extent of the Cretaceous strata in Alabama, Tuomey created a geologic map of the state. Although intended to be included in his 1850 report, Tuomey's geologic map failed to arrive at the printer in time and instead had to be published separately a year later.

After the publication of his "First Biennial Report," Tuomey balanced the geological survey field time with his teaching schedule. As part of his studies, Tuomey corresponded with many of the most prominent geologists and paleontologists of the time including Samuel Morton, Lewis Gibbes, Louis Agassiz, James Dana, Joseph Leidy, and Isaac Lea. Tuomey also exchanged literature with these individuals and, at times, sent them specimens in search of opinions (Dean, 2001). Mostly collected during his investigations, Tuomey (1850a) began to accumulate an extensive fossil collection that contained a number of Cretaceous vertebrates including: *Ptychodus mortoni* teeth from Montgomery (p. 120); vertebrae of "mosasauroids" from Athens (p. 126) and from near Choctaw Bluff in Greene County (p. 120); "numerous remains of fishes" from Erie (from the property of Robert Withers; p. 124); "teeth of *Lamna*, and vertebrae of osseous fishes" in a channel of Big Prairie Creek (p. 125); and mosasauroid vertebrae, a *Testudo* carapace, and teeth from *Lamna, Otodus*, and *Corax* from between Gainesville and Jamestown (p. 130).

Tuomey's collection was enlarged by donations of vertebrate fossils by Mrs. Bagshaw of Greensboro, Robert Withers of Greene County (now Hale County), Dr. Bonner of Dallas County, and Dr. Adams of Pickens County. Tuomey also received fossils from Samuel S. Sherman, President of Howard College (now Samford University), who sent him organic remains found near Marion that were "most valuable" (Tuomey, 1850a:xiii). In March of that year, Tuomey presented these remains – which turned out to be that of a mosasaur – at the meeting of the American Association for the Advancement of Science in Charleston, South Carolina. At this meeting, it was reported that "Prof. Tuomey laid before the Association a specimen of a fossil lacertain reptile, belonging to the genus *Leiodon*, from the cretaceous of Alabama." Upon viewing the remains at this meeting, French paleontologist Louis Agassiz proclaimed it as "one of the most splendid additions to the Paleontology of the United States ever made, and that although several parts are yet wanting, it enables us to construct the animal completely" (Tuomey, 1850b:74).

In 1854 the Alabama Legislature appropriated a sum of $10,000 towards the geologic survey and an annual salary of $2,500 for Tuomey as State Geologist (Tuomey, 1858, xiii). With this newly funded scientific appointment, Tuomey resigned his faculty position at the University to work full time on the survey. Tuomey kept a loose affiliation with the University, retaining an office on campus and occasionally lecturing to students. Furthermore, the University trustees, knowing Tuomey would have difficulty completing the survey with the modest funds appropriated by the Legislature, granted Tuomey the use of the University's laboratories, equipment, and natural history collection (Clark, 1889). This modest funding, however, did allow Tuomey to recruit and hire faculty members from the University to assist in his survey. Among these was Edward Q. Thornton, who served as Tuomey's assistant, and later, John W. Mallet, who was appointed as chemist to the survey (Dean, 2001).

Student-turned-professor Edward Q. Thornton graduated from the University in 1853 (Clark, 1889). A former student of Tuomey's, Thornton was trained as a geologist and assisted Tuomey with the survey from 1854–55. Thornton later became professor of chemistry, natural history, and modern languages at Howard College, a position he left in order to serve the Confederacy in the Civil War. After the war, Thornton returned to Howard College where, from 1868–69, he served as the school's president (Garrett, 1927). Beginning in spring 1854, Tuomey and Thornton spent the better part of the next two years in the field. Early on, Tuomey instructed Thornton to map the northern and southern limits of the Alabama Cretaceous belt (Tuomey, 1858:xvi). Taking the remaining part of the year, Thornton completed this task in such detail that his colleague John W. Mallet wrote:

> [Thornton] not only defined the limits of the formation as a whole, enabling its position to be laid down upon the map with greater exactness than was before possible, but also examined the space occupied by the various beds of which the formation is composed, determined the relative position of these beds, and collected specimens of fossils, rocks, and soils characteristic of the districts passed over (Tuomey, 1858:225).

At the time, Mallet (Fig. 17) was professor of chemistry at the University (Clark, 1889). However, like Tuomey, Mallet resigned his University appointment to serve full-time as the survey's chemist (Owen, 1921). With the assistance of Thornton, Mallet, and others, Tuomey's 1854–55 geolog-

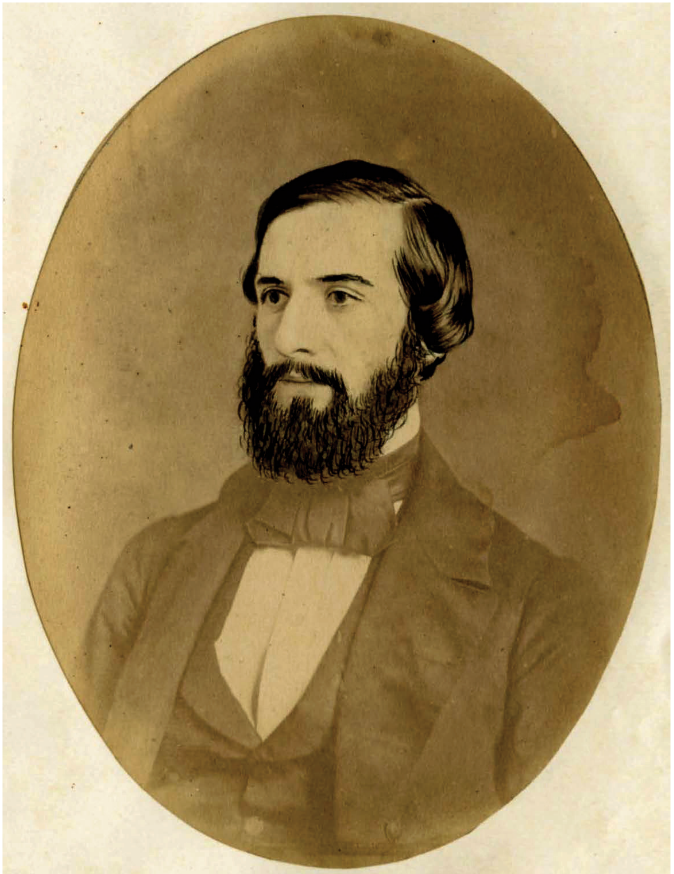


Figure 17. John Mallett (1832–1912). Image courtesy of the W. S. Hoole Special Collections Library, The University of Alabama, Tuscaloosa, Alabama.

ical survey of Alabama would be the most comprehensive and systematic of any yet undertaken of the state.

Unfortunately, by 1856, the State Legislature's appropriation was exhausted and Tuomey returned to teaching fulltime at the University. However, fully intending to complete his second geological report for submission to the state, Tuomey devoted much of his leisure time elaborating his survey field notes (Owen, 1921). Unfortunately, Tuomey did not live to see his work completed. On March 30, 1857, Tuomey fell ill and died from a heart condition and pneumonia, leading to the discontinuation of the Geological Survey and leaving the state with an incomplete draft of his report. Knowing the significance of this work, Governor John Winston tasked Mallet with completing and publishing Tuomey's manuscript (Tuomey, 1858; Dean, 2001).

Completing this second report was not an easy task, as not only was Tuomey's manuscript incomplete, but his detailed section on the Cretaceous units was missing (Owen, 1921). To complete this missing section, Mallet decided to append a report with Thornton's notes on various Cretaceous localities. Of this appendix, Mallet explained how it did "not fully supply the missing matter, or completely represent Mr. Thornton's work, as he had not considered it necessary to describe several localities visited by him and afterwards by Prof. Tuomey himself" (Tuomey, 1858:225). Also included in this appendix were Thornton's notes on the discovery of numerous Cretaceous vertebrate remains. These vertebrates included "sharks' teeth" from near Montgomery (p. 228); House Bluff near the Mulberry Post Office (p. 229); south of Burnsville (p. 232); Collirene in Lowndes County (p. 234); and Eufaula (p. 242). Thornton also mentioned the remains of "mosasaurus" from near Benton (p. 230); from Cunningham's Landing (p. 232); and from Centre Port (p. 236), all located along the Alabama River.

Beyond Thornton's notes on the Cretaceous, Mallet added two additional appendices regarding the state's Cretaceous System. The first included the results of his study on the soil chemistry of various Cretaceous localities. In the other, Mallet included a list of known taxa from the Cretaceous and Tertiary formations of the state (Tuomey, 1858:253–276). Compiled originally by Tuomey, Mallet expanded this list by recording the labels of specimens found in the Survey's collection (p. 255). As a preface to this list of fossils, Mallet explained:

> These lists are not to be looked upon as by any means complete – many Alabama species described by other authorities are not included here, and many of those collected during the Survey, which are new and as yet undescribed, are of course unnoticed. Some of the new species which are mentioned have been described, but some others have been merely named by Professor Tuomey, and their description has never been published (Tuomey, 1858:255).

The Cretaceous vertebrates listed by Mallet included *Corax falcatus* (now *Squalicorax falcatus*), *Galeus pristodontus* (now *Squalicorax pristodontus*), *Lamna elegans* (now *Odontaspis macrota*), *Ptychodus mortoni*, and an undescribed species of *Ptychodus* (Tuomey, 1858).

After dealing with repeated mishaps by the state printer, ultimately forcing him to change printers altogether, Mallet finally saw Tuomey's *Second Biennial Report on the Geology of Alabama* through to publication in 1858. In addition to Mallet's appendices, the report included Tuomey's detailed descriptions of the metamorphic rocks in east Alabama, the Cambrian to Silurian rocks in north-central Alabama, the Cretaceous and Tertiary rocks of southeast Alabama, and an overview of economic materials in the northern half of the state. This report also included a geologic map of Alabama (Tuomey, 1858). More detailed than his first attempt in 1850, Tuomey's new map showed, with great accuracy, the full extent of the Cretaceous belt in Alabama (Tuomey, 1858).

The Antebellum Collection at the University of Alabama

Before the University of Alabama opened its doors in

Figure 18. The Rotunda at the University of Alabama. Taken about 1859, this is the only known photograph of the Rotunda and the early University of Alabama. Image courtesy of the W. S. Hoole Special Collections Library, The University of Alabama, Tuscaloosa, Alabama.

1831, the Trustees had no plans for the institution to have a collection. Local naturalist William McMillan, however, had different ideas. Although not a member of the faculty, McMillan considered it "obvious that the institution must have a museum" and set upon himself the task of collecting specimens of "birds, animals, and other natural history exhibits" for the University (Sellers, 1953:52). Despite McMillan's efforts, the University Trustees were slow to warm to the idea of forming a museum. In fact, at committee meetings in January and July 1830, the Trustees flatly rejected the notion. However, McMillan's persistence was soon rewarded as by January 1831, the Trustees decided to hire McMillan as the University's librarian and collector of natural history specimens (Sellers, 1953). The University provided McMillan with a modest yearly stipend of $200, but also paid him $50 for work he had already done in collecting specimens. Later that year, McMillan was given a $200 raise provided he give over "title to all specimens he had collected or should collect in the future" (Sellers, 1953:93).

The library and early natural history collection were both housed in the University's Rotunda which served as the center of the antebellum campus (Fig. 18). The Rotunda was a two-story, domed building that had both a height and diameter of seventy feet. The first floor housed an auditorium that was used for commencements and chapel services, and the library and natural history collection occupied the second floor (Wolfe, 1983). With his new paid appointment, McMillan acquired specimens at a feverish pace, and by the end of his first year, he amassed a collection of "300 specimens of quadrupeds, birds, insects, reptiles, fish, crustacea, shells, minerals, fossils, and three Indian artifacts." The new curator also acquired a large number of specimens through exchanges with European museums and universities (Howard, 1982:85). However, apparently dissatisfied with his employment at the University, McMillan submitted his resignation in January 1832. In need of someone to oversee the library and natural history collection, the faculty (and for a short while, the Trustees) delegated this responsibility to its fellow members. One of the faculty members elected to this position was Richard Brumby in 1842 (Sellers, 1953).

Brumby was an avid collector of geological specimens who built a sizable personal collection for teaching purposes. Unlike McMillan, who kept his specimens in the Rotunda, Brumby stored his collection in the Lyceum where his laboratory was reported to be full of minerals and fossils (Wilson, 1998). In building this collection, Brumby acquired specimens by purchase and field work, and also solicited donations from private citizens. In 1841, for example, Brumby wrote a letter in a Tuscaloosa newspaper asking “spirited and intelligent men” to help him gather specimens such as ”rocks, minerals, shells, and fossils of the state” for his teaching collection (Sellers, 1953:163). Also housed in Brumby’s laboratory was the “Nuttall Cabinet,” a collection of minerals and fossils collected by Thomas Nuttall that was purchased by the University in 1831 for $1,500 (Sellers, 1953; La Borde, 1859).

Today it is unclear how many of Brumby’s specimens still reside at the University as he took a majority of his collection with him when he accepted a position at South Carolina College (now the University of South Carolina) in 1849. Despite the loss of these specimens, the University’s collection grew substantially with the appointment of Tuomey to the faculty in 1847. Tuomey, Thornton, and others contributed, over several years, countless numbers of fossils and geological samples collected during the state’s geological survey (see Tuomey, 1858). It is unclear exactly how many specimens Tuomey and his team collected, however lists provided by Mallet as part of Tuomey’s second report give an indication to the number of different taxa once housed in the collection. According to these lists, the collection once consisted of over 100 different Cretaceous taxa and over 200 different taxa from Tertiary deposits (see Tuomey, 1858:257–275). As for specimens from older deposits in the state, Mallet wrote, “It is to be wished that lists of fossils, like the above, could be presented for the silurian and carboniferous rocks – for such, however, no materials are to be found” (Tuomey, 1858:275).

Shortly after Tuomey’s death in 1857, his long-time friend and colleague, Francis S. Holmes of Charleston, visited Tuscaloosa and inspected the University’s collections. In a letter to University President Landon C. Garland, Holmes wrote that the collection consisted of three parts: the State Geological Survey collection, the University’s collection, and “the private cabinet of Professor Tuomey” (Dean, 2001:320). The State Geological Survey collection consisted of the fossil material collected by Tuomey, Thornton, and others during the geological survey (see Tuomey, 1850a, 1858). The University’s collection was made up of the specimens acquired by William McMillan and specimens collected or acquired by the University and its faculty members (such as the Nuttall Collection). According to Holmes, Tuomey’s private collection included duplicate specimens collected during the survey, specimens he purchased for his own use, and comparative specimens he acquired during his years in South Carolina. Of these collections, Holmes wrote “in my opinion the science of the country would be greatly advanced by retaining this collection at the University of Tuscaloosa” (Dean, 2001:321). While hesitant to provide an accurate number, Holmes tentatively appraised the value of the collection to be $3,000 (Dean, 2001:322), more than $80,000 today. While Tuomey’s private cabinet and the University’s collection were likely housed in the Rotunda (with teaching collections within the laboratories in the Lyceum), Mallet reported that the Geological Survey collection was kept in a small building located near the Lyceum (Owen, 1901).

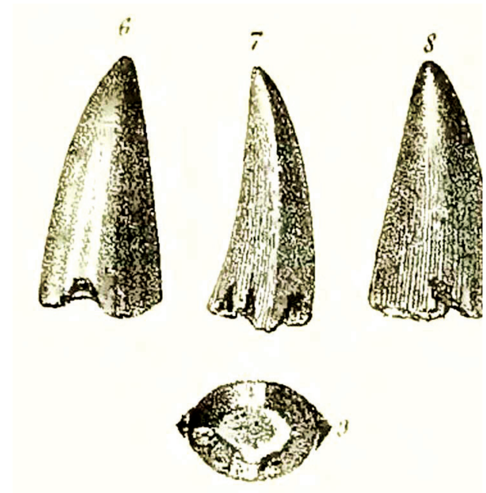


Figure 19. Robert Gibbes’ illustration of the holotype of *Holcodus acutidens*, based upon a single tooth from Alabama given to him by Joseph Jones. Reproduced from Gibbes (1849:pl. 3, figs. 6–9).

Robert W. Gibbes (1808–1866)

A native of Charleston, Robert W. Gibbes was a physician and naturalist who served as assistant professor of chemistry and mineralogy at South Carolina College and, among his many affiliations, was a member of the ANSP and the American Association for the Advancement of Science (Anonymous, 1866). In 1846, Gibbes turned down an offer for the professorship of geology and mineralogy at the University of Alabama, and instead recommended Michael Tuomey, then the State Geologist of South Carolina (Jellison and Swartz, 1965). While working mostly in South Carolina, Gibbes spent considerable time examining fossil vertebrates from both the Cretaceous and Eocene of Alabama. In 1846, Gibbes travelled to Alabama to carry out his own research on the hotly debated *Zeuglodon* (Jellison and Swartz, 1965). A year later, Gibbes (1847) published a paper summarizing all the known facts about *Zeuglodon* and suggested the use of *Basilosaurus* as the name that should supersede all others previously used for this extinct cetacean.

In 1848 Gibbes published a monograph on the fossil sharks of the United States. A work suggested by Agassiz, this monograph was based mostly on specimens from Gibbes’ personal collection (Jellison and Swartz, 1965). Gibbes’ (1848) monograph included descriptions of six new North American shark species as well as descriptions of three sharks from the Cretaceous of Alabama: *Galeocerdo pristodontus* (now *Squalicorax pristodontus*), *Otodus crassus*, and *Oxyrhina mantellii* (now *Cretoxyrhina mantelli*). A year later, at the annual meeting for the American Association of the Advancement of Science, Gibbes read a paper reporting a *Ptychodus polygyrus* tooth from the Cretaceous of Alabama. Of this taxon, Gibbes claimed it "had not been previously noticed" from the state (Gibbes, 1850b:193) and later published his findings in the *Journal of the Academy of Sciences* (Gibbes, 1850c).

At the same 1849 meeting, Gibbes read a second paper reporting three new mosasaur taxa from Alabama (Gibbes, 1850a). In this paper, Gibbes described three vertebrae and two teeth belonging to a small species of mosasaur found at an unspecified locality in Alabama (Gibbes, 1849; 1850a). Gibbes named this new species *Mosasaurus minor*. Gibbes also described a single mosasaur tooth given to him by Joseph Jones of Columbia, South Carolina, collected from another unspecified locality in Alabama. Gibbes described this tooth as having a shape unlike that of any known mosasaur, leading him to erect a new genus and species for the specimen, *Holcodus acutidens* (Gibbes, 1849:9) (Fig. 19). Finally, Gibbes described two large mosasaur vertebrae collected from a third unspecified locality in Alabama. Gibbes again erected a new genus and species for these remains, *Amphorosteus brumbyi*, named for their collector, Richard Brumby. Although these three specimens represent the first descriptions of new species of mosasaurs from Alabama, Russell (1967) later considered all three as *nomina dubia*.

Figure 20. Alexander Winchell (1833–1891). Reproduced from Youmans (1892).

Alexander Winchell (1824–1891)

The New York-born Alexander Winchell (Fig. 20) was a geologist and paleontologist who, among his many posts, served as: President of Masonic University in Selma; Chancellor at Syracuse University; and chair of geology, zoology, and botany at the University of Michigan (Anonymous, 1892). From 1850–53, Winchell taught successively at three Alabama schools: Newbern Academy in Newbern, Mesopotamia Female Seminary in Eutaw, and Masonic University in Selma (Anonymous, 1892). During his three years in Alabama, Winchell studied Cretaceous and Tertiary rocks in Pickens, Sumter, Greene, Perry, Dallas, Wilcox, Marengo, Clarke, Washington, and Monroe counties and visited all the known fossil localities along the Alabama, Tombigbee, Black Warrior, and Cahaba rivers (Winchell, 1857a). During his stay, Winchell befriended Tuomey, who allowed Winchell use of the facilities at the University of Alabama for his geological studies.

In 1857, while on the faculty at the University of Michigan, Winchell published two papers on his geological observations in Alabama (Winchell 1857a, 1857b). One of these papers discussed the presence of artesian wells in Alabama (of which many could be found underneath the "rotten limestone" in the Black Belt; Winchell, 1857b:94), the other described the geology of the southern and middle parts of the state, including the Cretaceous belt. While exploring Cretaceous outcrops in the Black Belt, Winchell (1857a) noted his discovery of "teeth of placoid fishes" from Prairie Bluff (p. 90) and "fish teeth" from Choctaw Bluff (p. 92). Of the Cretaceous strata in Alabama, Winchell went on to divide them into two sequences, the upper and lower. Later known as the Early and Late Cretaceous, Charles White (1891) subsequently referred the entire series to the Upper Cretaceous.

The Burning of the University of Alabama

Landon C. Garland, professor of English and history at the University of Alabama, was elected as the University's third president in 1855. Garland, who previously held the same post at Randolph-Macon College in Ashland, Virginia, worked diligently his first few years to increase the level of discipline on campus (Sellers, 1953; Wolfe, 1983). Student discipline at the time was seen as an issue, not only on campus, but in the nearby town of Tuscaloosa where many local citizens saw the students as "drunkards, gamblers and ruffians" (Wolfe, 1983:38). In an attempt to solve this problem, Garland lobbied to have the University converted to a military academy, a change the University's Board of Trustees adopted in July 1860 (Sellers, 1953;

Wolfe, 1983). The conversion to military discipline had immediate and positive effects on the atmosphere of the campus. Alongside the usual academic curriculum, students took courses in military tactics, wore uniforms, and performed regular drills (Kushner, 2010). Garland, still the University's president, became the superintendent of what was known as the "Alabama Corps of Cadets." New structures were built on the campus to support its new military functions, including temporary barracks and the "Guard House," constructed about 1859 as a shelter for students as they stood watch at night (Wolfe, 1983).

One year after the University converted to a military academy, growing tensions between northern and southern states led to the 1861 outbreak of the Civil War. As early as 1863, Union Lieutenant General Ulysses S. Grant designated the University of Alabama campus as a military target because the school had produced a large number of high-ranking Confederate officers. In the spring of 1865, Major General James Harrison Wilson marched 13,500 Union soldiers into Confederate territory with the goal of wiping out any vestiges of resistance (Kushner, 2010). During their march through Alabama, Union soldiers destroyed miles of railroad tracks, put 16 of 17 blast furnaces out of production (Rogers et al., 1994), and destroyed several factories and arsenals. By late March 1865, Wilson's forces reached the town of Elyton, now known as the city of Birmingham. At this time, General John T. Croxton of Kentucky marched a faction of 800 soldiers towards Tuscaloosa with the intent of destroying the University of Alabama (Kushner, 2010).

In the end, Garland's 300 student cadets were no match for the invading Union battalion and were forced to retreat, leaving both the University and the city of Tuscaloosa unprotected. In the early morning hours of April 4, 1865, Croxton succeeded in his mission as Union troops set fire to the University (Wolfe, 1983). By that afternoon, only a few buildings remained standing on the campus. These buildings included the Gorgas House, the observatory, the President's mansion, three faculty houses, and the Guard House (Wolfe, 1983; Rogers et al., 1994). Among the casualties were two faculty houses, all four dormitories (one of which housed meeting rooms and the mess hall), the temporary barracks, the Rotunda, and the Lyceum. The University of Alabama, left with no dormitories or classrooms, was forced to close. The construction of new buildings on campus began shortly after, but classes did not officially resume until the Fall term of 1871–72 (Wolfe, 1983; Rogers et al., 1994). Just four days after the burning of the campus, Confederate General Robert E. Lee surrendered to Grant marking the end of the Civil War (Kushner, 2010).

The conclusion of the Civil War marked the beginning of years of hardship for the state of Alabama. Railroads and factories were destroyed, as were the economic and financial systems of the state (Rogers et al., 1994). Cotton agriculture, which was built on slave labor, collapsed with the abolishment of slavery (Rodgers et al., 1994). The results of the war also had its effects on Cretaceous vertebrate research in Alabama. With the collapse of the cotton industry, the population of the Black Belt drastically declined (Rogers et al., 1994). As a result, the once plentiful letters written by planters on the agriculture and geology of the Black Belt ceased. The untimely death of Tuomey in 1857 abolished the Geological Survey of Alabama, the closing of the University put an end to any Cretaceous research by its faculty members, and the fire destroyed much of the University's collection. This dark time in Alabama's history marked the end of the *Tuomey Period*.

THE *SMITH PERIOD* (1865 TO 1927)

During the years following the Civil War, studies of the state's Cretaceous fossils continued thanks to three prominent scientists from Philadelphia: Joseph Leidy, Edward Drinker Cope, and Charles W. Gilmore. By the early 1870s, newly appointed State Geologist Eugene Allen Smith began to make strides towards reviving geological research in Alabama. Over his 54-year tenure, Smith reestablished the University of Alabama and the Geological Survey of Alabama as centers for geological research and is credited with rebuilding the University's collection and establishing the Alabama Museum of Natural History.

Joseph Leidy (1823–1891)

Joseph Leidy (Fig. 21), one of the most influential natural scientists in the history of the ANSP (Spencer, 1997), is considered to be the founder of American vertebrate paleontology as well as father of American protozoology and parasitology (Warren, 1998). During his lengthy career, Leidy published over 600 scientific papers (Spencer, 1997) and described numerous extinct vertebrates, including the first dinosaur in America (Warren, 1998). A professor at both the University of Pennsylvania and Swarthmore College (Chapman, 1891), Leidy mentored a number of students who would eventually go on to have distinguished careers of their own. Among Leidy's notable apprentices were Harrison Allen, Edward Drinker Cope, and Joseph Jones (Spencer, 1997). During his career, Leidy described two vertebrate holotypes from the Cretaceous of Alabama, the first of which he received from his future pupil, Joseph Jones (Leidy, 1851).

The Georgia-born Jones attended the University of South Carolina and Princeton before enrolling in medical school at the University of Pennsylvania in 1853 (Breeden, 1975). Graduating with a medical degree in 1856, Jones became an American pioneer in the fields of paleopathology and epidemiology (Spencer, 1997). Before he enrolled at the University of Pennsylvania, Jones possessed a collection of Cretaceous fossils from Alabama (Anonymous,

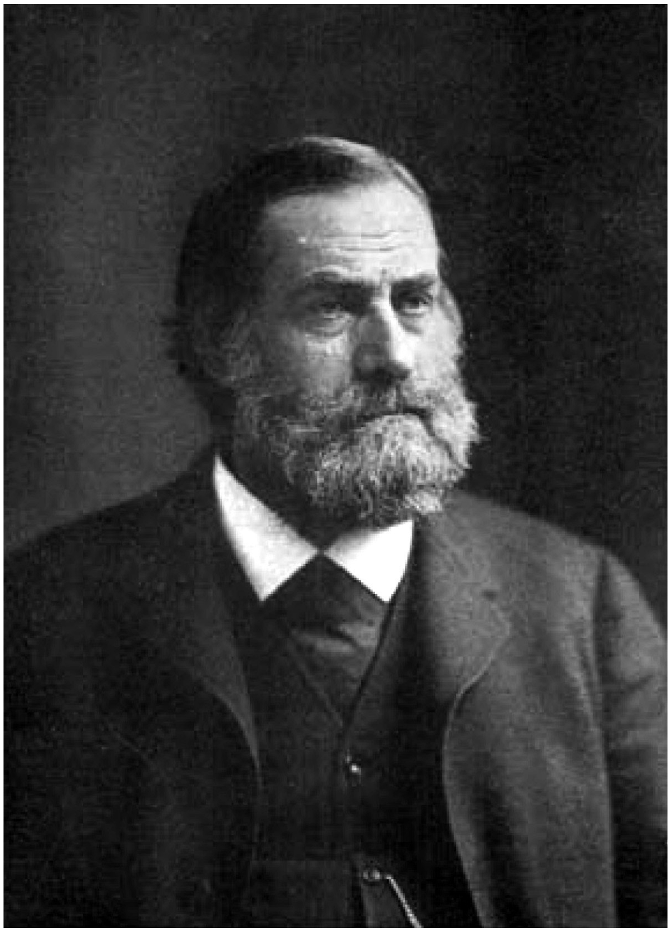


Figure 21. Joseph Leidy (1823–1891). Reproduced from Osborn (1913).

1854), although it remains unclear if Jones collected these fossils or if they were given to him. Nevertheless, at some point before 1851, Jones shipped a single caudal vertebra from his collection to the ANSP for study (Spamer et al., 1995). On December 9, 1851, at a meeting of the Academy of Natural Sciences, Leidy exhibited a "number of fossil reptilian and mammalian remains" (Leidy, 1851:325), one of which was Jones' vertebra (Leidy, 1851:326). Leidy reported this element as a new genus and species of plesiosaur, giving it the name *Discosaurus vetustus* (Leidy, 1851).

In August 1854, nearly three years after Leidy's description of *D. vetustus*, Jones donated a number of additional fossils to the ANSP museum, including "A collection of Cretaceous Fossils from Alabama" (Anonymous, 1854:xi). Among these fossils was a second *D. vetustus* caudal vertebra from Alabama that Leidy later described in his 1865 work, *Cretaceous Reptiles of the United States* (Leidy, 1865). Leidy (1865) described these two vertebrae as being "mutilated bodies" (p. 22) that were "almost identical in size" (p. 23). This later led to confusion as to which of the two vertebrae was actually the holotype. Even though Leidy provided measurements of the type in his 1851 report, the measurements cannot be used to differentiate the two as they are nearly identical in size (Spamer et al., 1995). In addition, although Leidy provided figures of both vertebrae in 1865 (Fig. 22), he failed to distinguish which of the two was the holotype (Leidy, 1865:pl. 5, figs. 4–6).

Leidy (1865) also described two isolated *D. vetustus* vertebrae discovered by Michael Tuomey. In the years prior to Tuomey's death, he and Leidy corresponded on many geological matters, with Tuomey occasionally sending Alabama fossils to Leidy for identification (Dean, 2001). Of the vertebrae sent by Tuomey, Leidy described the first as a "much mutilated body of a vertebra from Choctaw Bluff, Clarke Co., Alabama" with the second as being discovered from the "lower Cretaceous of Mississippi" (Leidy, 1865:24). Leidy, however, was likely confused on the locality of the first specimen as two different Choctaw Bluffs exist in Alabama. While there is a Choctaw Bluff in Clarke County, the exposed strata at this locality are Oligocene. The specimen cited by Leidy (1865) was more likely from the Cretaceous chalks exposed at Choctaw Bluff in Greene County.

Also in his 1865 work, Leidy reviewed all the mosasaurs known to him from the Cretaceous of Alabama. Of the

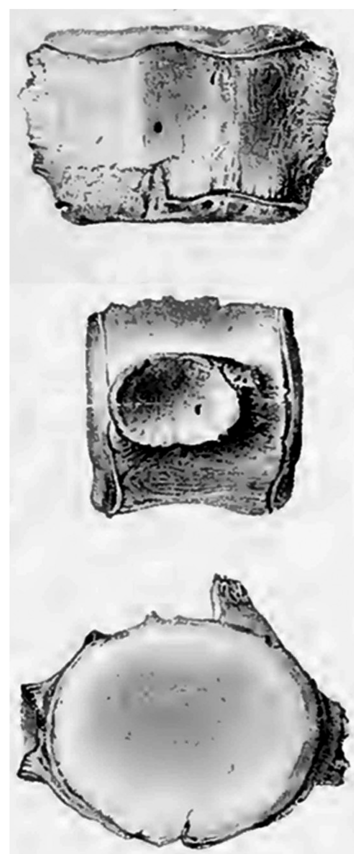


Figure 22. Joseph Leidy's 1865 figures of the caudal vertebra of *Discosaurus vetustus*. The top two figures are the lateral and inferior views of the same specimen. The bottom figure is the end view of a second vertebra. Figures reproduced from Leidy (1865:pl. 5, figs. 4–6).

mosasaur genera previously described by Gibbes (1849, 1850a), Leidy (1865) suspected that both *Holcodus* and *Amphorosteus* belonged to the genus *Mosasaurus*. Leidy also reported on his examination of an upper jaw of a mosasaur found near Marion, Alabama. On loan to him from the Smithsonian Institution, Leidy noted that the jaw "agrees in form with those ascribed to *Leiodon*" (Leidy, 1865:72).

In 1868, Leidy published a paper on the occurrence of the genus *Ptychodus* in America, based largely on specimens discovered in Alabama. Leidy (1868) described 12 Alabama *Ptychodus mortoni* teeth that were housed in the Yale Peabody Museum, all collected by William M. Gabb. Leidy described one in particular from Perry County as being "larger than any on record" (p. 206). Leidy also discussed 19 Alabama *P. mortoni* teeth from Uniontown and Greene County – all collected by Joseph Jones – and also reexamined the two Alabama *Ptychodus polygyrus* teeth first described by Gibbes. In regards to these *P. polygyrus* teeth, Leidy agreed they indeed resembled those previously described from Europe (Leidy, 1868).

In 1870 Leidy described the remains of a mosasaur given to him by Mobile physician Josiah C. Nott, who discovered the specimen in Pickens County. This specimen, ANSP 9032–4, 9029, and 9092–4, consists of a partial dentary and maxilla and several vertebrae. Leidy described the specimen as being intermediate in size between *Clidastes propython* and *Clidastes iguanavus*, and thus assigned it to a new species, *Clidastes intermedius* (Leidy, 1870a). Currently considered as a nomen dubium, Russell (1967) tentatively placed this taxon within the genus *Platecarpus* while Kiernan (2002) suggested that it compared favorably with *Globidens alabamaensis* and is perhaps a sub-adult of this taxon.

Edward Drinker Cope (1840–1897)

Three early American paleontologists are recognized as having raised the level of American paleontology to that of the Old World: Leidy, Othniel Charles Marsh, and Edward Drinker Cope (Schuchert, 1918). A former student of Leidy's, the Philadelphia-born Cope (Fig. 23) enjoyed a long and illustrious professional career, publishing over 1,400 scientific papers. Perhaps best known today for his scientific competition with Marsh, dubbed the "bone wars," Cope dedicated a part of his early career towards describing two new species of mosasaurs discovered in Alabama (Cope, 1869b; Jaffe, 2000).

In 1869, while a member of the ANSP, Cope published a description of a nearly complete mosasaur skeleton collected from Uniontown, Alabama (Cope, 1869a, 1869b). Cope erected a new species for this find, *Clidastes propython*, and figured the specimen in its entirety in his publication *Synopsis of the extinct Batrachia and Reptilia of North America* (Cope, 1869b). A juvenile mosasaur, likely collected from the Mooreville Chalk, this specimen stands as one of the most complete mosasaurs ever discovered in

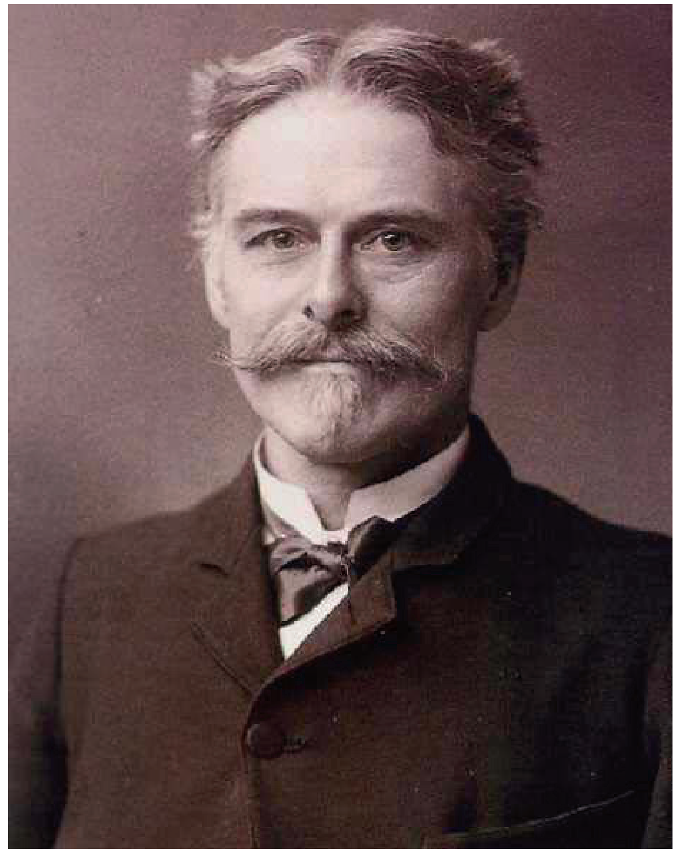


Figure 23. Edward Drinker Cope (1840–1897). Reproduced from Ballou (1897:215).

the state and was later used to replace *Clidastes iguanavus* as the generic holotype of *Clidastes* (Kiernan, 1992). Also in his "*Synopsis,*" Cope erected a second new species of Alabama mosasaur, *Liodon congrops*. This specimen, based upon a posterior cervical vertebra, was collected from an unnamed locality in the "Rotten Limestone of Alabama" (Cope, 1869b, 1871). Considered as a nomen dubium today (Russell, 1967), it is likely this vertebra belongs to a species of *Clidastes* (Kiernan, 2002).

Interestingly, the type specimens of *Clidastes propython* and *Liodon congrops* were both collected and shipped to Cope by the same individual, Dr. Emanuel R. Schowalter (also spelled as the variant "Showalter"). A physician and surgeon who settled in Uniontown in Perry County, Schowalter gained distinction by becoming a highly specialized field naturalist. Over the course of several decades, Schowalter collected hundreds of thousands of fossils and recent freshwater invertebrates, many from waterways such as the Cahaba, Alabama, and Coosa rivers. Schowalter collected these Alabama specimens for eminent conchologists and paleontologists across the country, and also built an enormous personal collection of his own (Smith, 1909; Moore, 1927). Many of the recent invertebrates Schowalter collected turned out to be type specimens, and as a result, several prominent scientists (one being Isaac Lea) named a number of new species in his honor (see Burch, 1982). Of fossil material, museum records indicate Schowalter collected thousands of specimens from various Cretaceous and Eocene localities in Alabama such as Uniontown, Prairie Bluff, Eutaw, and Claiborne. Schowalter also sent at least one additional Cretaceous vertebrate specimen to Cope's arch rival, Marsh at Yale. This specimen, a hyoplastron of the giant turtle, *Protostega gigas*, was discovered in Dallas County along the Cahaba River (Zangerl, 1953b) and may represent the first of this taxon reported from the state.

Throughout the course of his work on mosasaurs, Cope recognized the following six taxa from Alabama: *Mosasaurus minor, Holcodus acutidens, Liodon congrops, Liodon peraltus, Clidastes propython*, and *Clidastes intermedius* (Cope, 1869b, 1871). As Leidy did before him, Cope (1869b) synonymized Gibbes' *Amphorosteus brumbyi* into the genus *Mosasaurus*, only to later combine *Mosasaurus brumbyi* with *Liodon peraltus* (1870). With the exception of *C. propython*, all of these taxa are now considered as *nomina dubia* (Russell, 1967; Kiernan, 2002).

In his 1869 "*Synopsis*," Cope reassigned Leidy's *Discosaurus vetustus* to the genus *Cimoliasaurus*. Leidy (Leidy, 1851, 1865, 1870b) based this taxon on several vertebrae he examined from Alabama, Mississippi, and New Jersey. Later, however, Leidy voiced his uncertainty as to whether all these vertebrae actually belonged to his newly described genus. Cope re-examined the material and agreed they were morphologically different from *Cimoliasaurus magnus*, but similar enough to reside within the same genus (Cope, 1869b).

Figure 24. Eugene Allen Smith (1841–1927). Reproduced from Ballou (1897:219).

Eugene Allen Smith (1841 – 1927)

In terms of contributions to our knowledge of Alabama geology, perhaps no one has provided more than State Geologist Eugene Allen Smith (Fig. 24). Over his 54 years serving as State Geologist and professor of geology at the University of Alabama, Smith helped the state pull itself out of the ashes of the Civil War and transform it from an "aimless and poverty-stricken agricultural state to an industrial giant" (Henderson, 2011:xii). Smith dedicated much of his career toward the identification of the state's rich natural resources, ultimately helping Alabama build an economy that is today seen as one of the most diverse in the South (Henderson, 2011).

Born in Autauga County, Alabama in 1841, Smith attended private school in Prattville and later, at the age of 15, was enrolled in Central High School in Philadelphia. In 1860, at the age of 19, Smith enrolled at the University of Alabama as a junior and graduated with a bachelor's degree two years later. After graduation, Smith served briefly as a private for the Confederacy which led to an appointment as drillmaster and instructor of military tactics at the University, a position he held until the burning of the campus in 1865. With the University shut down, Smith moved to Europe where he attended several universities in Germany, receiving a Ph.D, summa cum laude, from the University of Heidelberg in 1868. Afterwards, Smith returned to the United States and accepted the position of assistant professor of chemistry at the University of Mississippi. At the same time, Smith was hired as an assistant to the State Geologist of Mississippi, Eugene W. Hilgard. In 1871, the year the University of Alabama reopened, Smith accepted a position at his *alma mater* as professor of chemistry and mineralogy (Butts, 1928; Henderson, 2011).

Much like his predecessor Michael Tuomey, this new position required Smith to "spend as much of his time as could be spared from teaching in the investigation of the natural resources of the State" (Butts, 1928:52; Wilson, 1985). For the first years in this appointment, Smith devoted his summer vacations to exploring the state's geology but also worked to convince the Alabama Legislature to reinstate the State Geologist position, abandoned since the death of Tuomey. Smith succeeded in this endeavor as in 1873, the Legislature appointed him the second State Geologist of Alabama, providing him with $500 annually for travel and incidental expenses and $3,000 for the purchase of equipment, laboratory chemicals, and a camp wagon. With this mule-drawn wagon, Smith spent years conducting his survey, along the way exploring the geology in every county in the state. In addition to being State Geologist, Smith taught chemistry, geology, and mineralogy at the University for over 50 years and filled the position of chair of geology until 1913 (Butts, 1928; Henderson, 2011). Aside from being an eminent geologist, Smith took great interest in the fields of zoology, pedology, and botany. These topics often appeared in his field notes, and over the years, Smith compiled an extensive collection of plants – two of which were new to science (Butts, 1928; Henderson, 2011).

Beginning in the 1880s, Smith focused most of his research toward the Coastal Plain of Alabama while turning over the investigation of other parts of the state to his assistants (Butts, 1928). In 1883, Smith and Laurence C. Johnson took a two-week steam boat trip down the Black Warrior, Tombigbee, and Alabama rivers, traveling south from Tuscaloosa to Mobile Bay then back north to Prairie Bluff. Jointly funded by the Alabama and United States Geological Survey's, this investigation became the most detailed study of the Cretaceous and Tertiary stratigraphy of the Gulf Coastal Plain region yet undertaken. This study later culminated with one of Smith's most noted works, *Report on the Geology of the Gulf Coastal Plain of Alabama*, co-authored with Johnson and Smith's assistant, Daniel W. Langdon, Jr. (Smith et al., 1894).

Johnson, who spent considerable time assisting Smith with his Coastal Plain studies, was an employee of the United States Geological Survey (USGS) and was associated with the United States National Museum in Washington, D.C. (USNM). Johnson returned to Alabama in 1890 and 1891 to conduct further fieldwork in the southern part of the state (Smith et al., 1894). During their investigations, both Smith and Johnson collected numerous fossils. While Smith deposited his specimens in the collections at the University of Alabama, Johnson shipped his finds back to the USNM. Today, 35 of Johnson's Alabama Cretaceous vertebrate specimens still reside in the USNM collection. These specimens include various sharks, fishes, and elements of a mosasaur. The mosasaur (USNM 6527), collected by Johnson in Dallas County, consists of a maxilla with teeth, a partial lower jaw, and a cervical vertebra. This specimen was later designated the holotype of *Globidens alabamaensis* by the USNM assistant curator of fossil reptiles, Charles W. Gilmore (1912).

Although Smith himself described no new species of Cretaceous vertebrates, his contributions to Cretaceous vertebrate research in Alabama were substantial. Smith ultimately published 116 works on the geology of Alabama and the southeastern United States, many of which helped increase our understanding of the Cretaceous geology in Alabama. Smith also secured permanent funding for the Geological Survey of Alabama, ensuring that the research started by Tuomey would continue. Finally, Smith is credited with rebuilding the University's collection after its near destruction by fire in 1865 (Butts, 1928; Henderson, 2011).

The Post-Civil War Collection at the University of Alabama

When Smith accepted the appointment as State Geologist, he had little to build on as nearly all of the work of his predecessor, Michael Tuomey, was destroyed during the burning of the campus. Lost during this fire were nearly all of Tuomey's scientific papers, the Geological Survey collection, and a majority of the books from the University's library – which, at the time, was considered to be one of the best in the southeastern United States. In writing of this loss, Tuomey's assistant John W. Mallet wrote:

> All the papers used in my editorial work on the 2nd Geological Report of the Alabama Survey by Prof. Tuomey were placed in a building not far from that known as the "Lyceum" of the University of Alabama, which building also contained the most important lithological and paleontological collections of the Survey. It was, with its contents, destroyed by fire, set by the U. S. cavalry force under Gen. Croxton, just before the close of the Civil War. I saw its ashes soon after my return from service in the Confederate army in 1865 (Owen, 1901:187–188).

Although the Geological Survey's collection was destroyed (which unfortunately contained the most important scientific specimens), large portions of the collection housed in the Rotunda survived the fire. These specimens included those from the University's collection and Tuomey's private cabinet.

Smith himself witnessed the 1865 burning of the campus (in fact, he made sketches of many of the ruins; see Wolfe, 1983), and later wrote of how specimens from Tuomey's private cabinet did indeed survive. For several years beginning in 1869, Smith wrote about these specimens in the University's Course Catalogues while promoting the geology curriculum. In 1869, for example, Smith wrote of "extensive and well selected cabinets" that are available for study by students containing specimens pertaining to "Mineralogy, Geology and Conchology" (Anonymous, 1869:40). In the same catalogue Smith wrote:

> The cabinet of minerals, &c, contains a suit of specimens, illustrative of the Geology of Alabama. This collection, when completed, will present at a glance the mineral resources of the State (Anonymous, 1869:40).

Smith also wrote that "the extensive collections made by Prof. Tuomey, having been saved from destruction in 1865, are by law given to the University" (Anonymous, 1869:36). The same year Smith explained that the collection was "considerably damaged at the time of the burning of the College" but it would be "speedily put in good condition" (Anonymous, 1870:8). In 1871, Smith wrote that his courses on geology and mineralogy were to involve lectures illustrated by natural specimens and that students would be required to spend at least two hours per week "devoted to the Cabinet," thus giving them "a practical acquaintance with the crystals, minerals, rocks, and fossils" (Anonymous, 1871:22).

Of the specimens that reportedly survived the fire, many unfortunately fell victim to a different fate. After the destruction of the campus, Smith reported that many of the specimen labels were lost while being moved by untrained personnel. In a letter to Angelo Helprin at American Academy of Science, Smith wrote: "Prof. Tuomey's collections after the destruction of the University during the war, were moved several times by inexperienced persons, who had no idea of the value of a label, and the consequences is that not one-tenth of the specimens can be labeled as to locality" (Henderson, 2011:33). Later, as part of the effort to prepare the collection for teaching, many of the specimens were relabeled. A number of these specimens still survive today in the Geological Survey and Alabama Museum of Natural History collections and are apparent as their labels are not written in Tuomey's handwriting and often misspell his name as "Toumey" (Fig. 25). Furthermore, according to Andrew K. Rindsberg (pers. comm., 2012), former curator of the Geological Survey collection, these specimens have unique labels and some of the names can be matched with those listed by Mallet in Tuomey's second report. While the most valuable specimens collected by Tuomey were destroyed in the fire (the original Geological Survey collection), countless numbers of other specimens undoubtedly fell victim to attrition as they were either lost, separated from their labels, broken, or stolen as a result of years of teaching and handling by students. Although a number of Tuomey's original specimens still reside in the collections at the State Geological Survey and Alabama Museum of Natural History, the exact number of these specimens is at present unknown.

By chance, however, a subset of Tuomey's collection is intact and is currently housed in London. In 1859, two years after Tuomey's death (and six years before the destruction of the campus), John W. Mallet shipped a collection of fossils to London that was accessioned into the collections at the British Museum in 1882. This collection included a number of Eocene fish fossils and *Basilosaurus* teeth that were mistakenly assumed to have been collected and labeled by Mallet. In truth, these specimens were collected by Tuomey, but fell under the care of Mallet after his death. Collected largely from Clarke County, these specimens were described in 1956 by Errol White who named seven new species and subspecies of sharks from the material (White, 1956).

With a large part destroyed in the fire, Smith took it upon himself to rebuild the University's collection (Butts, 1928; Henderson, 2011). Immediately upon accepting his professorship at the University, Smith sent for his small collection of geological samples and books, which were stored at his Prattville home (Henderson, 2011). In addition to making his private collection available for study, Smith wrote that "Collections from other States, and from abroad, are added, and from time to time by exchange, to the [geology] Cabinet" (Anonymous, 1869:36). By 1872,

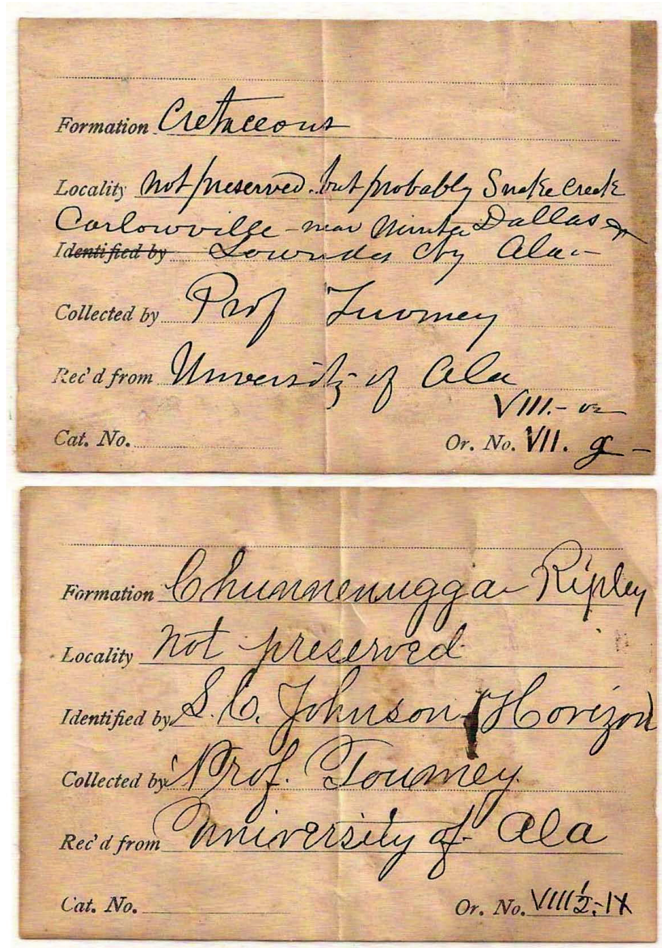


Figure 25. Fossil labels from specimens that are attributed to Michael Tuomey's collections at the Alabama Museum of Natural History. These are likely from the 1870s when scattered specimens were recovered and relabeled. Neither label is written in Tuomey's handwriting and the bottom label misspells his name. Photograph courtesy of the University of Alabama Museums, Tuscaloosa, Alabama.

Smith began requesting donations of specimens from the general public. In the University course catalogues, for example, Smith wrote:

> All persons interested in the development of the mineral wealth of the State are requested to forward to the State Geologist, at Tuscaloosa, specimens of minerals, ores, well preserved fossils, etc. A circular setting forth the particulars necessary to be observed in collecting and labeling specimens may be had on application to the State Geologist (Anonymous, 1872:36-37).

With this serving as the beginning of a new collection, Smith added thousands of geological and paleontological specimens to the collection throughout the course of the geological survey. Originally housed in Smith's office, this rapidly growing collection was later allocated classroom space in Woods Hall, which once served as the men's dormitory and mess hall. Soon outgrowing this space, in 1889 Smith's collection was again relocated, this time to the ground floor of the newly constructed Garland Hall. This new museum space consisted of 2,500 square feet of storage and an exhibition gallery. In 1898, J. A. Anderson became the collection's first curator and, by 1900, the collection consisted of some "25,000 specimens plus 350 drawers and 2,000 cigar and pasteboard boxes of uncataloged material" (Howard, 1982:86; Wilson, 1985).

Around the turn of the 19th century, plans emerged for a "Greater University," which resulted in a master plan for the expansion of the University. As it turned out, the first phase of this plan was to design an appropriate building to house Smith's growing collection. The first cornerstone of this new building was laid on May 28, 1907, and on May 5, 1910, a ceremony dedicated the newly constructed building as "Smith Hall" (named for Eugene Allen Smith despite his protests). Smith Hall was designed to house the University's museum, the Geological Survey, a natural sciences library, and classrooms for biology and geology. Eventually designated by Smith as the "Alabama Museum of Natural History," this new museum served as an adjunct to the Geological Survey with Smith appointing Herbert H. Smith its curator in 1910 (Howard, 1982; Wolfe, 1983; Wilson, 1985; Sartwell, 1994). Of the relationship between the Geological Survey and this new museum, H. H. Smith, wrote: "By law, the collections of the Geological Survey become the property of the University of Alabama: therefore the Museum, a result and monument of the Survey work, is an integral part of the University, and it should be educational" (Smith, 1910:1).

Before his death in 1927, E. A. Smith donated his private library to the museum, which consisted of "three thousand bound volumes, eight hundred unbound volumes, and many thousands of pamphlets" (Sartwell, 1994). Many citizens in Alabama also donated objects and collections to the new museum. The most notable of these acquisitions was the collection of Emanuel Schowalter. Before his death in 1889, Schowalter reportedly donated 100,000 of his specimens to Smith and the Geological Survey. After his death, his heirs donated the remaining one million specimens (Moore, 1927). This collection contained fossils and recent freshwater, land, and marine shells not only from Alabama, but also from around the world (Owen, 1921). Museum curator H. H. Smith recounted the history of this important collection and how it narrowly escaped destruction:

> After Showalter's death the shells were stored for years under his house at Point Clear. Like most southern houses, this is supported by corner pillars, the space beneath being open to the winds and often to driving rains. Some of the boxes rotted, specimens fell out and labels decayed; what at length the collection became the property of the Alabama Geological Survey, portions of it had literally to be scooped up with a shovel . . . . . No doubt some specimens and labels were irretrievably lost, but by far the greater part of the collection was saved intact, and for this we must thank the able director of the Geological Survey, Dr. Eugene A. Smith (Smith, 1909:117–118).

By 1921, the Alabama Museum of Natural History acquired several other important collections. Notable acquisitions included the "Mohr herbarium, which forms the basis for Dr. Charles Mohr's 'Plant life of Alabama'; the Peters collection of fungi; the Aldrich collection of shells and fossils; the Lommel collection of European fossils and rocks; . . . the Dr. H. H. Smith collection of Alabama land and freshwater shells; the Loding collection of Alabama coleoptera; the Tuomey collection of Alabama reptiles [which was misidentified by Owen as this collection was not assembled by Tuomey]; and the Avery bird collection" (Owen, 1921:649).

After the dedication of Smith Hall in 1910, Smith spent his remaining years as professor emeritus at the University and carrying out his duties as State Geologist. On September 7, 1927, Smith passed away at the age of 86. Despite his passing, Smith left Cretaceous research in Alabama in a good place by not only establishing the Alabama Museum of Natural History, but also by reestablishing the University and Geological Survey as the center of geological and paleontological studies in the state. The death of Smith marked both the end of the *Smith Period* and the beginning of the *Modern Period*.

THE MODERN PERIOD (1927 TO PRESENT)

The *Modern Period* of Cretaceous vertebrate research in the state revolves around three Alabama institutions: the Alabama Museum of Natural History, the Auburn University Museum of Paleontology (AUMP), and McWane Science Center (MSC). During the early parts of this period, two significant events took place that shaped the path for contemporary research in the state: the Field Museum of Natural History (Chicago) expeditions to the state in the 1940s and 1950s, and the splitting of the Geological Survey from the University and the Alabama Museum of Natural History. This period also saw the establishment and closing of the Red Mountain Museum and the transfer of its collections to McWane Science Center in Birmingham, Alabama. Continuing today, the *Modern Period* has seen more Cretaceous vertebrate type specimens described from the state than all other periods in Alabama's history combined.

Walter B. Jones and the Modern Era of the Geological Survey and Alabama Museum of Natural History

After Smith's death in 1927, the role of State Geologist and director of the Alabama Museum of Natural History

Figure 26. Walter B. Jones (1895–1977). Photograph courtesy of the Geological Survey of Alabama Library, Tuscaloosa, Alabama.

fell to Smith's handpicked successor, Walter B. Jones (Fig. 26). Jones was a graduate of the University of Alabama and Johns Hopkins University, and served as State Geologist until his retirement in 1961. During his tenure at the Geological Survey, Jones continued Smith's research on the state's natural resources and was later appointed as the first Director of the State Oil and Gas Board. Jones also worked diligently to enrich the collections at the Alabama Museum of Natural History, especially in the field of archaeology. Jones supervised the Survey's acquisition of Moundville in Hale County, a renowned Mississippian-culture mound complex, and donated to the Alabama Museum of Natural History a fine collection of South Pacific artifacts he acquired while briefly serving in the area during World War II (Wolfe, 1983; Wilson, 1985). Jones also took an active interest in paleontology and organized several expeditions to the Black Belt region in search of vertebrate remains (Renger, 1934a).

In 1933, Jones sent one of his students, J. J. Renger, to the Eutaw region in Greene County to secure permission from Mr. Byrd, the postmaster at Eutaw, to set up a field camp on his property. The original purpose of this expedition was to search for fossil remains at Choctaw Bluff on the Tombigbee River. However, Jones' plans quickly changed once Byrd told the story of the discovery of a large fossil creature on his property in 1931. Byrd recounted how a Mr. Grover of Eutaw ran his car off the road and onto his property. While seeking assistance, Grover apparently stumbled across an outcrop containing a number of fossil bones. Thinking the fossils were the remains of a large mule, Grover apparently broke a piece off of one of the fossils and later discarded it about 100 feet away. Intrigued by this story, Renger, with the assistance of Byrd, located this outcrop and over the course of the summer, he, Jones, and a field crew, excavated about three dozen complete bones and countless fragments from a huge fossil sea turtle. Using E. A. Smith's 1883 field notes, Renger was able to determine that the specimen was excavated from the "rotten limestone" of the Selma Chalk, known today as the Mooreville Chalk. Although far from complete, the reassembled specimen's right flipper measured over four feet in length (Renger, 1934a, 1934b, 1935) (Fig. 27). This specimen, still on permanent exhibit at the Alabama Museum of Natural History, was later identified as the Cretaceous turtle *Protostega gigas,* and remains the largest and most complete of this taxon ever discovered from the state.

After the excavation of the *Protostega*, Renger followed

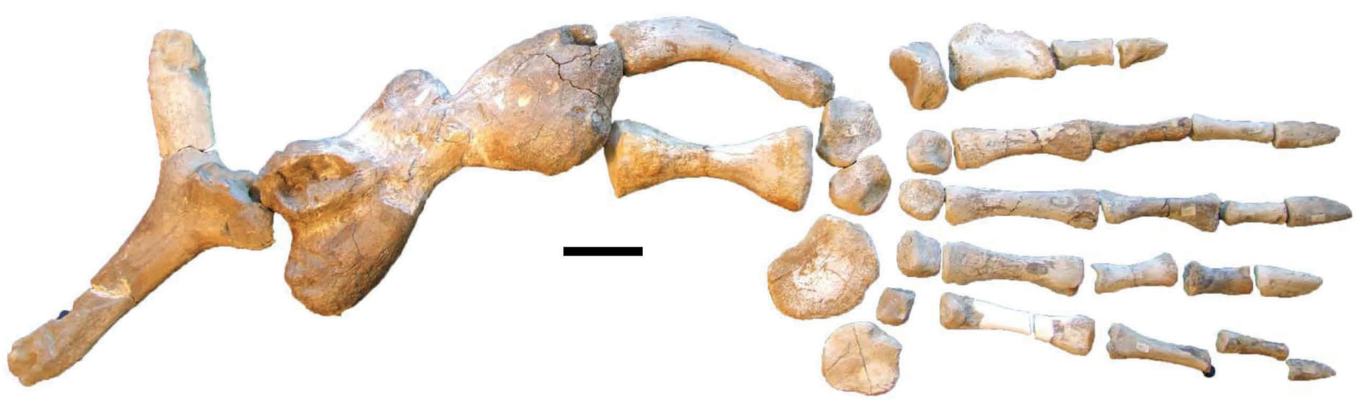


Figure 27. Photograph of the forelimb of J. J. Renger's *Protostega gigas,* (UAP PV 985.10), on display at the Alabama Museum of Natural History. Scale equals 10 cm. Photograph courtesy of Takehito Ikejiri.

up on a second lead regarding the discovery of a vertebrate fossil in nearby West Greene in Greene County. Renger overheard a story of the 1923 discovery of six fossil vertebrae by Reginald Jones while he was on the property of Quillan Hale. Jones was reported to have placed the vertebrae under an ash tree on the property, prompting Renger not only to attempt to locate this tree, but also to find the original outcrop. Renger had no trouble finding the ash tree but only one of the reported six vertebrae was present. With some work, however, Renger located a second of the six vertebrae in a garage on the property where it was being used to "keep the car from rolling off the boards" (Renger, 1934a:12). Renger and his crew later located Jones' original outcrop and discovered the remains of a large mosasaur. Renger reported the skull of this mosasaur to be almost five feet in length and, though only 17 feet of the specimen was recovered in 1933, he expressed his desire to excavate the rest in the very near future (Renger, 1934a, 1934b, 1935). Later determined to belong to the large mosasaur *Tylosaurus proriger*, these remains represented the first known occurrence of this taxon from the state (Kiernan, 2002).

Just a few years later, fellow University of Alabama student Herndon Dowling discovered the remains of a second mosasaur from an outcrop near Eutaw. Dowling published a non-technical description of this specimen in 1941 and provided a photograph showing it consisted of a complete disarticulated skull and a large majority of the post-cranial elements (Dowling, 1941) (Fig. 28). This specimen, likely a *Platecarpus*, was exhibited for years at the Alabama Museum of Natural History. Reportedly taken off exhibit in the 1960s, the present whereabouts of this specimen is unknown (Kiernan, 2002).

By 1961, Walter B. Jones, still the State Geologist, began to receive criticism from the State Legislature for not only operating Moundville without legislative permission, but for doing so at the same time as overseeing the Geological Survey of Alabama and the Alabama Museum of Natural History. In order to ensure that the Alabama Museum of Natural History and Moundville would continue to receive public funding, Jones, along with his successor Philip LaMoreaux, separated the two institutions from the Geological Survey, formally transferring them to the University (Wilson, 1985). This transfer split the University's collection. The majority of the specimens collected by the Geological Survey, including the reference set of identified invertebrates, were separated from the remaining collections and are currently housed in Walter Bryan Jones Hall on the University campus. Constructed in 1961, this new building was named for the recently retired Jones and was built as the permanent home for the Geological Survey (Wolfe, 1983). The remaining University collections remained in Smith Hall until 1997, when they were relocated to the newly constructed Mary Harmon Bryant Hall, where they currently reside today. This new storage facility houses the state's largest natural history collection and the largest collection of cataloged Cretaceous vertebrate specimens collected from Alabama. In 2005, under curator Andrew K. Rindsberg, the vertebrate material housed in the Geological Survey collection was officially transferred to the Alabama Museum of Natural History while the Survey continues to retain what is perhaps the largest collection of fossil invertebrates from the state. Currently, Smith Hall still houses the Alabama Museum of Natural History's exhibits as well as classrooms for the natural sciences.

In 1979, the Alabama Museum of Natural History inaugurated their annual Summer Expedition program, designed to engage members of the general public in archaeology, paleontology, and ecology, while working with

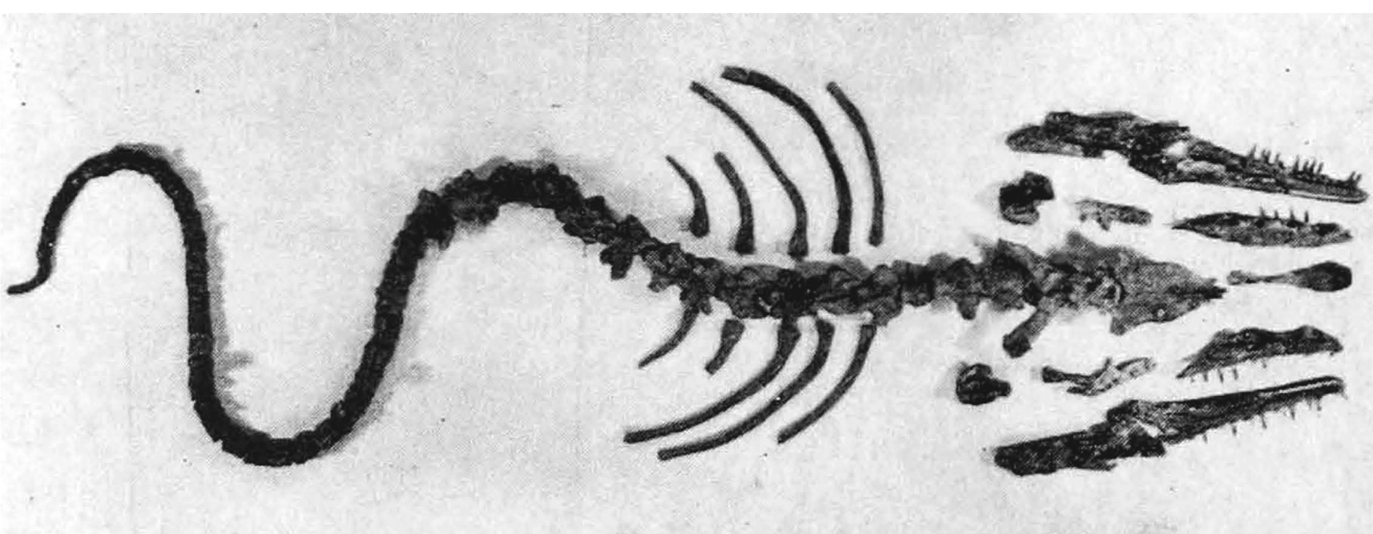


Figure 28. 1941 photograph of Herndon Dowling's mosasaur. Reproduced from Dowling (1941:48).

credentialed scientists in the field. Still in operation today, the museum organized expeditions to Cretaceous localities in the summers of 1981–83, 1988, 1993–94, 2005, and 2011. These public expeditions added hundreds of valuable fossil vertebrate specimens into the museum's collection.

In the late 1970s, Douglas E. Jones, son of Walter B. Jones, began working on the manuscript for *Fossil Vertebrates of Alabama.* Jones, then the Dean of Arts and Sciences and professor of geology at the University, later served as the Director of the Alabama Museum of Natural History. Co-authored with John T. Thurmond of the University of Arkansas in Little Rock, *Fossil Vertebrates of Alabama* still stands as a landmark study of vertebrate paleontology in the state. This book reviewed all fossil vertebrate taxa known from Alabama and reported many of the state's Cretaceous taxa for the first time. As an appendix to later editions of this book, Thurmond and Sam Shannon co-authored an update to the known Cretaceous reptiles from the state (Thurmond and Jones, 1981).

Shannon, a graduate of the University, had recently completed his Master's thesis entitled *Selected Alabama Mosasaurs* (Shannon, 1975). This work included the first records of mosasaurs from the Tombigbee Sand Member of the Eutaw Formation and post-Mooreville Chalk units of the Selma Group, as well the first accounts of *Platecarpus* cf. *P. somenensus* (now *P. tympaniticus*), and *Mosasaurus* cf. *M. missouriensis* within the state. Shannon (1975) also recognized a new subspecies of mosasaur from Alabama, *Clidastes liodontus moorevillensis.* This taxon is at present considered as a nomen dubium while it awaits a formal description. Around this same time, Shannon completed two additional works on Alabama Cretaceous vertebrates. The first discussed the occurrence of plesiosaurs in Alabama; the second, the stratigraphic distribution of mosasaurs in the state (Shannon, 1974, 1977). Later, Shannon, along with Kenneth Wright, described a new genus and species of Alabama mosasaur, *Selmasaurus russelli,* based on material housed at the Alabama Museum of Natural History (Wright and Shannon, 1988). Because the holotype had no locality data, Caitlín Kiernan (2002) extracted matrix from the specimen with the calcareous nannoplankton showing it was collected from the Mooreville Chalk.

In 1991 the Alabama Museum of Natural History purchased a 130-acre plot near Harrell Station in Dallas County (Hawkins, 1993). Preserved by the museum as a research site, this significant stretch of exposed Mooreville Chalk and Demopolis Chalk has produced one of the largest assemblages of Cretaceous vertebrate fossils in Alabama (Ikejiri et al., this volume). The discovery of this site is credited to personnel from the Field Museum of Natural History in Chicago, who led a series of fossil collecting expeditions to the area beginning in 1945.

The Field Museum of Natural History Expeditions

In the summer of 1945, C. M. Barber of the Field Museum of Natural History in Chicago (FMNH) travelled to the southeastern United States in search of Cretaceous fossils. Barber's initial intent was to explore Cretaceous outcrops in Georgia. However, when few were to be found, he turned his attention to Alabama. Barber soon discovered a number of Cretaceous exposures near Eutaw where he collected a handful of fragmentary turtle and fish remains. Upon his return to Chicago, Barber, quite proud of his discoveries, presented these remains to colleagues in an attempt to convince the museum to mount an additional expedition to the area. Rainer Zangerl, the FMNH curator of fossil reptiles, agreed that the Cretaceous formations in Alabama warranted further investigation, and accompanied Barber back to the Eutaw region later that summer. During this return trip, Barber and Zangerl searched for additional fossil-bearing localities in the Black Belt and discovered the expansive erosional gullies in the Harrell Station area of Dallas County. Although the expedition was cut short by heavy rains, Zangerl was pleased by the productivity of the trip, commenting that "Many highly interesting vertebrates were discovered" (Zangerl, 1948a:3).

With the discovery of such a large quantity of well-preserved and scientifically valuable vertebrate specimens, the FMNH organized a total of 10 additional expeditions to the Harrell Station area and other Black Belt localities. The FMNH led as many as two collecting expeditions to the region every year from 1945 to 1950, with an additional trip in 1958 (Zangerl, 1953a; Applegate, 1970). In total, the parties collected nearly 600 cataloged vertebrate specimens prompting an eight-part publication on the material. Titled *The Vertebrate Fauna of the Selma Formation*, this FMNH series described the various turtles, fishes, dinosaurs, and mosasaurs discovered from the Alabama Mooreville Chalk – many of which would be new genera and species. The first five parts of this volume were written by Zangerl (1948a, 1948b, 1953a, 1953b, 1960).

Zangerl's contribution included an introduction to the geology and geography of the Harrell Station area as well as four papers on the numerous fossil turtles collected. Representing the first systematic study of Cretaceous turtles from Alabama, Zangerl described the following type specimens: *Podocnemus alabamae* (1948b); *Protostega dixie* (1953a); *Calcarichelys gemma* (1953a); *Toxochelys moorevillensis* (1953b); *Thinochelys lapisossea* (1953b); *Lophochelys venatrix* (1953b); *Ctenochelys tenuitesta* (1953b), *Ctenochelys acris* (1953b); *Prionochelys nauta* (1953b); *Prionochelys matutina* (1953b); and *Corsochelys haliniches* (1960). With the exception of *Protostega dixie,* which was later reassigned as a junior synonym of *Protostega gigas* (Hooks, 1998), the remaining nine new turtle taxa erected by Zangerl are still considered valid.

In 1960, Wann Langston, Jr., then curator of vertebrate paleontology at the National Museum of Canada,

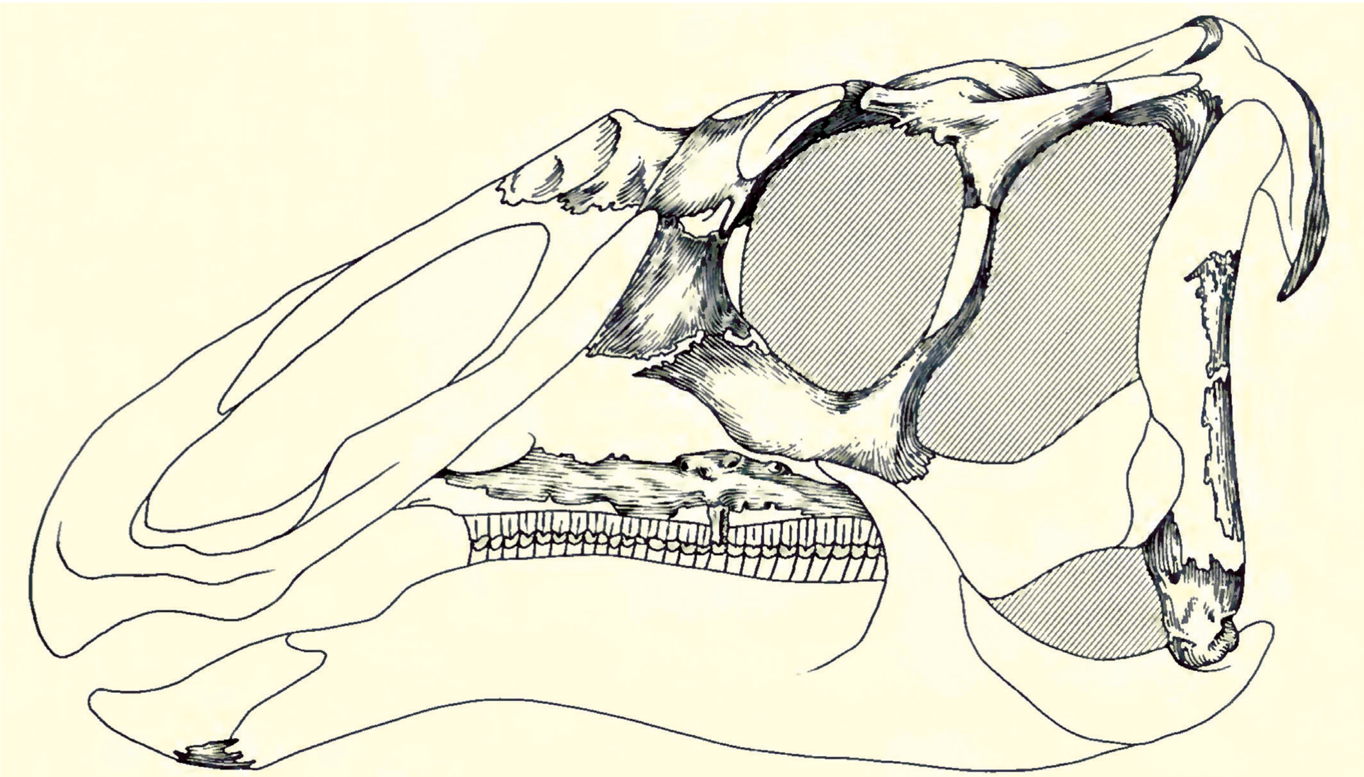


Figure 29. Wann Langston's 1960 reconstruction of the cranium of the holotype of *Lophorhothon atopis* (FMNH P27383). Reproduced from Langston (1960:23).

published part six of this volume on the Mooreville Chalk dinosaurs discovered during the FMNH expeditions. In an examination of these specimens, Langston identified three higher taxonomic groups of dinosaurs from Alabama: Nodosauridae, Theropoda, and Hadrosauridae. While the nodosaurid and theropod remains were too incomplete to assign to any lower taxonomic ranking, the hadrosaur remains were a different story. One specimen in particular, FMNH P27383, consisted of a partial skeleton which included much of a disarticulated skull (Fig. 29), 44 vertebrae, numerous ribs, both lower legs, a femur, parts of the front hands, and a partial ischium. Exhibiting morphological characteristics unlike any previously described hadrosaur, Langston (1960) erected a new genus and species for this specimen, *Lophorhothon atopis*. Langston's descriptions of these specimens represent the first published occurrences of these three dinosaur taxa from the state as well as the first dinosaur holotype ever described from the southeastern United States.

The final two parts of the "Selma Formation" volume were published in 1970 by Dale Russell and Sheldon Applegate, respectively. Russell, then a student at Yale University, visited the FMNH in 1963 after being invited to examine the museum's collection of Alabama mosasaurs. Russell's preceding descriptions of this material were unfortunately not ready in time to be included in his 1967 monograph, *Systematics and Morphology of American Mosasaurs*. His study of this material, however, did culminate as part seven of the "Selma Formation" volume, representing the first systematic study of Alabama mosasaurs since Cope (1869b). Russell recognized eight unique mosasaur taxa from the Mooreville Chalk with the genus *Clidastes* as the most abundant. The examination of so many new *Clidastes* specimens led Russell to the determination that the Kansas taxa, *Clidastes sternbergi*, was conspecific with *Halisaurus* and should therefore be referred to the latter genus. In regard to Leidy's *Platecarpus intermedius*, Russell published the genus name in parentheses noting that, while the morphology of the dentaries of the holotype resembled those of known *Platecarpus*, the examination of additional material would likely place the species within a distinct genus. Russell also recognized a new species of Alabama mosasaur, *Tylosaurus zangerli*, named for Rainer Zangerl (Russell, 1970). The holotype, FMNH P27443, a humerus and femur collected by C. M. Barber, was later shown to belong to a juvenile *Tylosaurus proriger* (Kiernan, 2002). In addition to the aforementioned species, Russell (1970) recognized the following mosasaur taxa from Alabama: *Globidens alabamaensis*; *Clidastes propython*; and indeterminate species of *Prognathodon*, *Tylosaurus,* and *Platecarpus*.

The final part of the "Selma Formation" volume was published by Sheldon Applegate (1970), of the Los Angeles County Museum of Natural History in California. Applegate studied the Cretaceous fishes collected during the FMNH expeditions and took a trip of his own to Alabama in 1958 in order to collect additional material. In what became the first systematic study of Cretaceous fishes from the state, Applegate recognized over 40 distinct fish taxa from the Mooreville Chalk. While most were previously known from other Cretaceous units in the United States, Applegate described four new species: *Propenser hewletti, Palelops eutawensis*, *Bananogmius crieleyi*, and *Moorevillia hardi*, the latter taxon representing a new genus (Applegate, 1970).

While collecting additional fossil material in Alabama in 1958, Applegate discovered a small broken humerus in an outcrop near Boligee in Greene County. This specimen ended up in the collections at the USNM where it was eventually described by Alexander Wetmore (1962). Then a research associate at the museum, Wetmore described this specimen (USNM 22820) as new genus and species of Cretaceous bird, *Plegadornis antecessor* (Wetmore, 1962). Wetmore's proposed genus, *Plegadornis,* was later referred to *Ichthyornis* by Storrs Olsen (1975) and his proposed species was later synonomized with *Ichthyornis dispar* by Julia Clarke (2004). Nevertheless, this specimen represents the first described Cretaceous bird from the state.

The Auburn University Museum of Paleontology

Beginning in the late 1960s, personnel from Auburn University began a concerted effort to acquire Cretaceous vertebrate material from the state. These efforts were largely due to herpetologist James L. Dobie, whose research interests began with extant turtles. Starting in 1966, Dobie initiated a series of collecting trips to the Harrell Station area and other nearby localities in search of Cretaceous turtles and other vertebrate remains. In 1967, Dobie began to receive donations of Cretaceous vertebrate material from three teen-aged amateur collectors: David Phillips, Marc Harvey, and Prescott Atkinson. Over the course of several years, the three collectors donated hundreds of vertebrate specimens to the Auburn museum, collected largely from Dallas and Montgomery counties. In 1970, one of these collectors, Prescott Atkinson, discovered a nearly complete amniote egg from the Mooreville Chalk at Harrell Station. Dobie described this egg in 1978; however, because it possessed morphological characteristics unlike any known dinosaur, crocodile, or turtle egg, Dobie was unable to determine what type of taxa produced it. While the affinity of this racket ball-sized egg still remains a mystery, this specimen (AUMP 1235) remains the only Cretaceous egg known from the southeastern United States (Dobie, 1978).

Beginning in the mid-1970s, Dobie led a series of expeditions to Cretaceous localities in the eastern part of the Alabama Black Belt; particularly in the counties of Russell, Bullock, and Barbour. These collecting efforts eventually produced the state's largest collection of vertebrate remains from the Upper Cretaceous Blufftown Formation. David Schwimmer of Columbus State University in Georgia later described the fishes and dinosaurs discovered within this formation from both Alabama and Georgia (Case and Schwimmer, 1988; Schwimmer et al., 1993). Schwimmer made other significant contributions to Cretaceous vertebrate research in Alabama, authoring numerous papers on the fishes and dinosaurs from the state (Schwimmer, 1997; Schwimmer et al., 1994, 1997a, 1997b, 2002).

In 1995, Dobie served as chair on the Master's committee of student George Edward Hooks III. For his thesis, Hooks (1995) redescribed the turtle *Calcarichelys gemma* (RMM 3216) from a nearly complete specimen, prompting a revision of the Protostegidae. Hooks later wrote a revised version of his thesis for the *Journal of Vertebrate Paleontology* (Hooks, 1998).

In 2003, a small mudstone lens was discovered within the Eutaw Formation in Russell County containing an abundance of well-preserved Cretaceous leaves, fish scales, and surprisingly, feathers. Terrell K. Knight, a Master's student at Auburn University, described the biota discovered within this lens for his thesis (Knight, 2007). Overall, 14 well preserved Cretaceous feathers were discovered at this site which are thought to belong to a number of different theropod species. The largest of these feathers measured nearly 17 cm in length and is thought to be a tail feather from a dromaeosaurid dinosaur or a hesperornithid. A description of these feathers was later published in 2011, with this cache representing the largest collection of Mesozoic feathers known from North America (Knight et al., 2011).

Museum records indicate that Dobie continued collecting Cretaceous vertebrate material for the Auburn collection until 1994. Known as the Auburn University Museum of Paleontology, this collection consists of roughly 950 cataloged Cretaceous vertebrate specimens from the state and is currently housed under the care of the Auburn University College of Veterinary Medicine.

The Red Mountain Museum and McWane Science Center

In 1971, the Council of the City of Birmingham adopted an ordinance to establish the Red Mountain Museum (RMM), which was to serve as the city's center for the interpretation of geology, natural history, science, and local history. The RMM was located on top of the eastern slope of the Red Mountain road cut which overlooked a walking trail that interpreted a rock face that exposed more than 190 million years of Paleozoic history. Between 1971 and 1994, the RMM was very active in local paleontology with personnel including Gorden L. Bell, Jr.; Winston Lancaster; James P. Lamb; Caitlín Kiernan; and Amy Sheldon, spending as much as six months out of the year in the field. Over the course of nearly two decades of intensive collecting across the state, the RMM pieced together what

Figure 30. A nearly complete pycnodont fish, RMM 1950, at McWane Science Center. Scale bar = 15 cm.

is now the world's second largest collection of Alabama vertebrate fossils (second only to the Alabama Museum of Natural History).

In the early 1980s, Gorden L. Bell, Jr. discovered a nearly complete *Clidastes* "*moorevillensis*" specimen in a chalk gully in Greene County. Known as the "Greene County Mosasaur," this specimen represents one of the most complete of this undescribed taxon yet known. Bell also published several papers describing various aspects surrounding Alabama mosasaurs (Bell, 1985; Bell and Sheldon, 1986; and Dobie et al., 1986) and later wrote his thesis on the subject while attending the University of Texas at Austin (Bell, 1993). This thesis, *A Phylogenetic Revision of Mosasauridae (Squamata),* was later revised and submitted as a chapter in the book *Ancient Marine Reptiles* (Bell, 1997). Bell also published an important paper describing a nearly complete pycnodont fish collected from Greene County. His study of this specimen, RMM 1950 (Fig. 30), resulted in the synonymy of several known taxa including *Gryoidus*, *Ancistrodon*, *Hadrodus*, and *Propenser* (Bell, 1986).

In 1981, while collecting in the Harrell Station area, Bell discovered several elements belonging to a plesiosaur. Excavated from the same location as a FMNH expedition several decades earlier, it was determined that bones collected by Bell were actually part of a plesiosaur in the FMNH collection. This determination was made as a neural arch collected by Bell actually matched a previously excavated dorsal vertebral centrum in the FMNH collection. Bell donated the elements he discovered to the FMNH, where they were assigned by Robin O'Keefe to *Polycotylus latpinnis*, the first occurrence of this taxon known from Alabama (O'Keefe, 2004).

In 1982, the wife of Auburn University geologist David T. King discovered the remains of a theropod dinosaur in Montgomery County. In conjunction with personnel from the RMM, the specimen was excavated, jacketed, and prepared at the RMM facilities (King et al., 1988). Composed of two complete hind limbs, a partial cranium, a humerus, a few vertebrae, and a partial pelvis, Thomas Carr, Thomas Williamson, and David Schwimmer described the specimen (RMM 6670) as a new genus and species of basal tyrannosauroid, *Appalachiosaurus montgomeriensis.* This specimen represents one of only two genera of tyrannosaur known from the eastern third of North America and still stands as the most complete tyrannosauroid ever discovered in the southeastern United States (Carr et al., 2005; Ebersole and King, 2011). In 2001, a second theropod was discovered in Alabama by a former RMM employee, Caitlín Kiernan. While wet-screening matrix from the excavation of a toxochelyid turtle in the Mooreville Chalk in Greene County, Kiernan discovered a single dromaeosaurid tooth. This lone tooth represents the only record of this taxon yet described from the state (Kiernan and Schwimmer, 2004).

In 1992, James P. Lamb led an expedition to Greene County, where the party discovered the remains of a small enantiornithine bird. In 2002, these fragmentary remains were described as a new genus and species, *Halimornis thompsoni* representing only the second species of Cretaceous bird known from Alabama (Chiappe et al., 2002).

In 1984, RMM employees Bell and Lamb started the Birmingham Paleontological Society (BPS), a group that encouraged members of the general public to participate in paleontological excavations and laboratory activities. Meeting monthly at the museum, this group of fossil enthusiasts arranged guest lectures on various paleontological topics and participated in museum-sponsored fossil expeditions. In 2002, membership of the BPS split, with some members leaving to form the Alabama Paleontological Society. Today both groups exist as stand-alone, incorporated, non-profit groups that serve not only to involve the general public in paleontology, but also to assist in professional paleontological research and the preservation of fossil sites. The ongoing activities of these groups have added hundreds of valuable specimens to museum collections in the state and have helped bridge the gap that often exists between amateur collectors and the professional research community.

In 1994, the City of Birmingham-owned RMM and a neighboring science center, Discovery Place, were merged with a newly formed private institution, Discovery 2000, Inc. Later renamed McWane Science Center (MSC), this new institution was opened in downtown Birmingham. In 1994, MSC signed a legal agreement of sale with the City of Birmingham, leasing the RMM collection for a term of 75 years. Signed to ensure the RMM collection would remain intact, be properly cared for, be available for research, and remain within the state, the collection is slated to become legal property of MSC at the end of the 75 year lease. From 1994 to 1998, the RMM collection was packed up and relocated to the new MSC collections storage facility while the RMM building remained open for visitors for a few more years. During this time of transition and legal transfer, professional research on the collection ceased until MSC opened its doors to the general public in July 1998. Today, MSC has grown to be the largest institution of its kind in the southeastern United States, combining an IMAX Dome theater with a science center, children's museum, aquarium, and natural history museum with the RMM collection being stored and exhibited on the center's second floor.

In recent years, field expeditions by MSC personnel have continued to add to the RMM collection which, in terms of cataloged specimens, is the second largest collection of Cretaceous vertebrates from the state. Made up of nearly 3,000 cataloged mosasaurs, dinosaurs, turtles, and other marine reptiles (as well as countless uncataloged specimens), MSC houses the largest collection of vertebrate specimens from under-collected units such as the Tombigbee Sand Member of the Eutaw Formation and the Demopolis Chalk (Kiernan, 2002).

THE FUTURE OF CRETACEOUS VERTEBRATE RESEARCH IN THE STATE

Timothy Abbott Conrad's 1833 discovery of a lone *Ptychodus mortoni* tooth from near Prairie Bluff is significant for several reasons. Not only was this the first Late Cretaceous vertebrate fossil and holotype described from Alabama, but this specimen also symbolized the beginning of Cretaceous vertebrate research in the state. The long history of research combined with the exceptional preservation of specimens in Alabama has produced a diversity of Late Cretaceous vertebrate marine forms that rivals that of any other state in the United States (Russell, 1988; Nicholls and Russell, 1990).

Today, significant collections of Cretaceous vertebrate fossils from Alabama can be found in over 12 institutions around the world. Over 90% of these vertebrate specimens are housed within the state and reside in the collections of the Alabama Museum of Natural History, Auburn University Museum of Paleontology, and McWane Science Center (Ikejiri et al., this volume). With thousands of additional specimens at these three institutions still awaiting preparation, identification, and cataloging, there is little doubt these museums will continue to serve as the centers for the study of Alabama Late Cretaceous vertebrates for years to come. The collection of Cretaceous vertebrates in Alabama will also continue to be prosperous. Many of the Cretaceous units in the state have been under-collected and thus under-represented in collections and studies, and countless other Cretaceous exposures have yet to be explored. Furthermore, the sheer number of well-preserved taxa still being recovered from localities in the Black Belt will continue to support new Cretaceous vertebrate studies for the foreseeable future. With more type specimens being described from Alabama in the *Modern Period* than all the other periods combined, it is logical to suggest that many more new species still await discovery.

Building on the nearly 180 years of research in the state, the future of Cretaceous vertebrate studies in Alabama will undoubtedly add to our knowledge of Cretaceous taxa in Alabama as well as aid in our understanding of global Late Cretaceous vertebrate diversity, paleobiology, paleobiogeography, and biostratigraphy.

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An Overview of Late Cretaceous Vertebrates from Alabama

TAKEHITO IKEJIRI*,[1], JUN A. EBERSOLE[2], HARRY LYON BLEWITT[1], and SANDY M. EBERSOLE[3]

[1]Alabama Museum of Natural History and the Department of Geological Sciences, University of Alabama, Tuscaloosa, AL 35487, kejiri1859@gmail.com;
[2]McWane Science Center, 200 19th Street North, Birmingham, AL 35203, jebersole@mcwane.org;
[3]Geological Survey in Alabama, P.O. Box 86999, Tuscaloosa, AL 35486-6999, sebersole@gsa.state.al.us
*Corresponding author.

ABSTRACT

Presented here is an overview of fossil vertebrate specimens collected from Upper Cretaceous strata (Early Santonian–Upper Maastrichtian) in Alabama. In total, 8,275 vertebrate specimens housed in 12 institutions are summarized here by geologic age, locality, year collected, institution, and taxon, using numbers of identified specimens (NISP). A total of 76 genera and 92 species of vertebrates are identified in this study. Taxa identified include Chondrichthyes (21 gen. and 30 spp.; NISP = 2,150), Actinopterygii (23 gen. and 25 spp.; NISP = 2,607), and Reptilia (32 gen. and 37 spp.; NISP = 3,174), and 344 specimens not identifiable to a higher taxonomic level. All Cretaceous vertebrate specimens have been collected from the following five stratigraphic units in Alabama: Unit 1, the Eutaw Formation; Unit 2, the Mooreville Chalk and Blufftown Formations; Unit 3, the Demopolis Chalk and Cusseta Sand Member of the Ripley Formation; Unit 4, the Ripley Formation (excluding the Cusseta Sand Member); and Unit 5, the Prairie Bluff Chalk and Providence Sand. Of these stratigraphic units, Unit 2 has the largest NISP (6,363), and Unit 4 has the smallest NISP (139). Of the 20 counties that have produced Cretaceous specimens, nearly 70% of the vertebrate fossils are from Dallas and Greene counties. Although preservation and collecting biases have a strong influence on the data presented herein, this study does provide a new perspective of the Cretaceous vertebrate diversity as well as the geographic and stratigraphic distributions of these taxa in Alabama.

INTRODUCTION

A tremendous number of vertebrate fossils have been collected from Upper Cretaceous strata in Alabama. Beginning in the early 1830s, these fossil-rich exposures, which represent roughly 11% of the state's surface geology, attracted many of the world's early paleontologists and geologists including Charles Lyell, Thomas Nuttall, Timothy Abbott Conrad, Samuel Morton, and Joseph Leidy (see Ebersole and Dean, this volume). Beginning with these early researchers, the nearly 200 years of paleontological studies in Alabama has resulted in the collection of a large number of Cretaceous vertebrate taxa including numerous holotypes of new taxa (Table 1). The rich marine and terrestrial vertebrate faunas of Alabama have served as a significant addition to our overall understanding of the diversity of Late Cretaceous vertebrates in North America.

Late Cretaceous vertebrates in Alabama include fully aquatic forms (e.g., sharks, rays, bony fish, marine reptiles) from the Cretaceous Gulf of Mexico and terrestrial taxa (e.g., pterosaurs, crocodilians, non-avian dinosaurs, birds) from the southern Appalachia landmass. The Cretaceous fossils from Alabama are representative of the vertebrate fauna from the Cretaceous Gulf of Mexico, a region once physically connected to the southern Western Interior Seaway and the southern Atlantic Seaboard during the Late Cretaceous (Fig. 1). In previous studies, the Late Cretaceous taxa from Alabama have been compared with

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Table 1. Type specimens of Cretaceous vertebrates from Alabama.

Taxon	Status	Specimens	Remarks
CHONDRICHTHYES			
*Edaphodon barberi**	Valid	FMNH PF290	Applegate, 1970
Ptychodus mortoni	Valid	NHMUK PV OR 28394	Agassiz, 1839; Morton, 1842; Everhart, this volume
ACTINOPTERYGII			
*Albula dunklei**	Valid	FMNH P 27494	Applegate, 1970
Megalocoelacanthus dobiei	Valid	CCK-88-2-1; AUMP 3834 (paratype)	Schwimmer, et al., 1994
*Propenser hewletti**	Synonymized as *Hadrodus hewletti*	?	Thurmond and Jones, 1981; Bell, 1986; Applegate, 1970
*Bananogmius crieleyi**	Valid	FMNH PF 3608	Applegate, 1970
*Moorevillia hardi**	Valid	FMNH PF 3567	Applegate, 1970
*Palelops eutawensis**	Valid	FMNH PF 3559	only scales; Applegate, 1970
REPTILIA			
*Clidastes intermedius**	Nomen dubium?	ANSP 9023, 9024, 9029 + 9092-9094	Leidy, 1870; See also Spamer et al., 1995:131
*Clidastes propython**	Valid	ANSP 10193	Cope, 1869; See also Spamer et al., 1995:149
*Tylosaurus perlatus**	Nomen dubium	AMNH FR 2391	Cope, 1870; original material lost (Carl Mehling pers. comm. 2011)
*Tylosaurus zangerli**	Nomen vanum (or nomen vetitum?)	FMNH P 27443	Russell, 1970
*Selmasaurus russelli**	Valid	UAM PV2005.0006.0009 (formerly GSATC 221)	Wright and Shannon, 1988
Globidens alabamaensis	Valid	USNM 6527	Gilmore, 1912
*Discosaurus ventustus**	Valid	ANSP9258 or 9282	Leidy, 1851; See also Spamer et al., 1995:156
Podocnemis alabamae	Synonymized as *Chedighaii barberi*	FMNH P 27370	Zangerl 1948b; Gaffney et al., 2006, 2009
Lophochelys venatrix	Valid	FMNH P 27355	Zangerl, 1953b
Protostega dixie	Synonymized as *P. gigas*	FMNH P 27314	Zangerl, 1953a; Thurmond and Jones, 1981, Hooks, 1998
*Calcarichelys gemma**	Valid	FMNH PR 129	Zangerl, 1953
*Toxochelys moorevillensis**	Valid	FMNH P 27330	Zangerl, 1953
*Corsochelys haliniches**	Valid (or *species inquirenda?*)	FMNH PR 249	Zangerl, 1960
*Ctenochelys acris**	Valid	FMNH P 27354	Zangerl, 1953a
Ctenochelys tenuitesta	Valid	FMNH P 27361	Zangerl, 1953b
*Prionochelys matutina**	Valid	FMNH P 27561	Zangerl, 1953b
Prionochelys nauta	Valid		Zangerl, 1953b
*Thinochelys lapisossea**	Valid	FMNH P 27453	Zangerl, 1953b
*Lophorhothon atopus**	Valid	FMNH P 27383	Langston, 1960
Appalachiosaurus montgomeriensis	Valid	RMM 6670	Carr et al., 2005
*Halimornis thompsoni**	Valid	UAM PV996.1.1	Chiappe et al., 2002
Plegadornis antecessor	Synonymized as *Ichthyornis dispar*		See Thurmond and Jones, 1981 (p. 164); Synonymized by Padian, 2004; Clarke, 2004

*The asterisk (*) next to taxonomic names indicates specimens which are only known from Alabama.

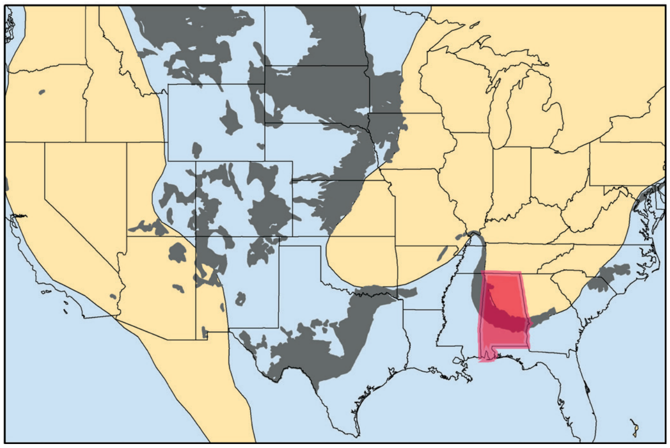

Figure 1. Upper Cretaceous landmass and seas in North America. The gray color indicates outcrops of Upper Cretaceous strata (Cenomanian to Maastrichtian in age). Light tan indicates the Cretaceous land mass. Alabama is indicated by light red.

vertebrate assemblages from other paleogeographic regions of North America such as the central Western Interior Seaway (e.g., the Niobrara Chalk and Pierre Shale of the central U.S.), the northern Western Interior Seaway (e.g., the Mason River Formation in northern Canada), and the Atlantic Seaboard (e.g., the Navesink Group in the northeastern U.S.) (Russell, 1988, 1993; Nicholls and Russell, 1990).

To date, the most comprehensive overview of the Cretaceous vertebrate taxa from the state was *Fossil Vertebrates of Alabama*, published in 1981 by John T. Thurmond and Douglas E. Jones. While still the only study reviewing all of the state's vertebrate fossils, this work has shortcomings with respect to its taxonomic list of Cretaceous vertebrates. Since this book was first published, a significant number of Cretaceous vertebrate specimens have been collected by numerous institutions (most notably the Red Mountain Museum) and the systematics of many taxa have been revised. As a result, this study represents the most comprehensive overview of Alabama Cretaceous vertebrates yet undertaken.

In order to illustrate the taxonomic diversity of vertebrates from Upper Cretaceous marine and coastal strata across North America, previous studies compared and contrasted the quantity and types of genera and species based on stratigraphic units and/or paleogeographic regions (e.g., Russell, 1988, 1993; Everhart, 2005a; Shimada and Fielitz, 2006; Cumbaa et al., 2010). In this study, numbers of identified specimens (NISP) is utilized to quantify relative abundance and diversity of faunal assemblages. NISP is commonly used to quantify relative abundance of Late Cenozoic mammals from archeological sites (e.g. Grayson and Frey, 2004; Davis and Pyenson, 2007). Few studies, however, have used NISP for Cretaceous vertebrates from marine and coastal strata of North America.

The main purpose of this study is to review the occurrences the Cretaceous vertebrates from Alabama based on numbers of vertebrate specimens in museum collections. Using NISP, Alabama Cretaceous vertebrate fossils housed at various institutions are quantified by 1) taxon, 2) institution, 3) year collected, 4) stratigraphic unit, and 5) locality (county). Using these data as an example, the potential uses of NISP are discussed for future studies of Late Cretaceous vertebrate diversity, paleobiogeography, and evolution.

Institutional abbreviations—AMNH, American Museum of Natural History, New York, NY; **ANSP**, Academy of Natural Sciences of Philadelphia, PA; **AUMP**, Auburn University Museum of Paleontology, Auburn, AL; **CCK**, Cretaceous research collections at Columbus State University, Columbus, GA; **FMNH**, Field Museum of Natural History, Chicago, IL; **GSA**, Geological Survey of Alabama, Tuscaloosa, AL (vertebrate fossil collection currently housed at UAM); **MMNS**, Mississippi Museum of Natural Science, Jackson, MS; **MSC**, McWane Science Center, Birmingham, AL; **NHMUK**, Natural History Museum in London, United Kingdom; **RMM**, Red Mountain Museum, Birmingham, AL (fossil collection currently housed at MSC); **UAM**, Alabama Museum of Natural History, University of Alabama, Tuscaloosa, AL; **UWA**, University of West Alabama, Livington, AL; **USNM**, United States National Museum, Washington D.C.; **YPM**, Yale Peabody Museum, New Haven, CT.

Abbreviations for counties in Alabama—Au, Autauga; **Ba**, Barbour; **Bu**, Bullock; **Bt**, Butler; **Cr**, Crenshaw; **Da**, Dallas; **El**, Elmore; **Gr**, Greene; **Hl**, Hale, **Hr**, Henry; **Le**, Lee; **Ln**, Lowndes; **Ma**, Marengo; **Mg**, Montgomery; **Pe**, Perry; **Pk**, Pike; **Pn**, Pickens; **Ru**, Russell; **Su**, Sumter; **Wi**, Wilcox.

Abbreviations for Cretaceous geologic units in Alabama—Kb, Blufftown Formation; **Kd**, Demopolis Chalk; **Ke**, Eutaw Formation; **Km**, Mooreville Chalk; **Kp**, Providence Sand; **Kpb**, Prairie Bluff Chalk; **Kr**, Ripley Formation; **Krc**, Cusseta Sand Member (of the Ripley Formation); **Kt**, Tuscaloosa Group.

MATERIAL AND METHODS

Geologic Setting

Geography—Of the Mesozoic strata in Alabama, only Upper Cretaceous units have surface exposure. Abbreviations for exposed Cretaceous units (listed above) follow the convention employed by the GSA on the Geologic Map of Alabama (Szabo et al., 1988). Cretaceous strata are exposed in 28 counties (Fig. 2) and lie within the Gulf Coastal Plain Physiographic Province. Only counties which have produced Cretaceous vertebrate specimens are recorded in this study. The abbreviations for counties (listed above) follow the system currently employed by the

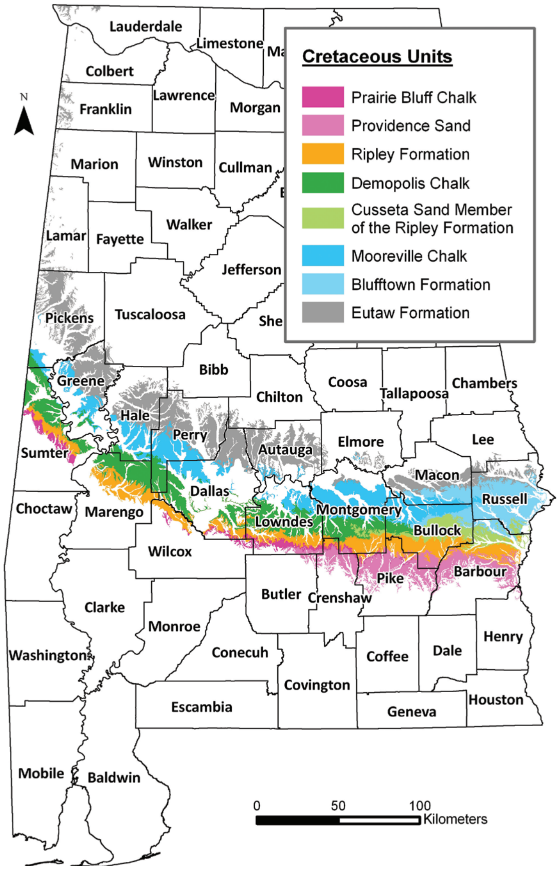

Figure 2. Distribution of Upper Cretaceous surface geology in Alabama based on the 1:250,000-scale digital state geology (GSA, 2006).

UAM and MSC museum catalogues. Detailed information regarding specific fossil localities (e.g., towns, quarries, GPS coordinates) is not provided here but is available to qualified researchers by contacting the UAM or MSC.

All maps in this study were created by one of the authors (SE) using ArcGIS 9.3 software. For the geologic map of Upper Cretaceous units in Alabama, data were derived from the GSA Digital Geological Map (1:250,000 scale) of 2006, which was originally adapted from Szabo et al. (1988). The area of surface geology for each geologic unit was calculated in ArcGIS. Whether or not areas of surface geology (i.e., map area) are strongly correlated with actual exposure has been debated (e.g., Crampton et al., 2003; Dunhill, 2012) and is known to be scale-dependent. In this study, we used the calculated exposure of outcrops as approximate parameters to estimate relative fossil richness (i.e., numbers of specimens per area).

Age—Vertebrate fossils are known from various Upper Cretaceous units (formations and members) in Alabama (Fig. 3). Some of these units are age-equivalent, but geographically separate (Raymond et al., 1988). In this study, five representative stratigraphic units were established: Unit 1, the Eutaw Formation (including the Tombigbee Sand Member); Unit 2, the Mooreville Chalk (including the Arcola Limeston Member) and the Blufftown Formation; Unit 3, the Demopolis Chalk (including the Bluffport Marl Member) and the Cusseta Sand Member (of the Ripley Formation); Unit 4, the Ripley Formation (excluding the Cusseta Sand Member); and Unit 5, the Prairie Bluff Chalk and the Providence Sand. A few formations consist of subdivided members (e.g., the Tombigbee Sand Member in the Eutaw Formation; unnamed upper and lower members of the Mooreville Chalk), but these were not separately investigated in this study mainly due to the lack of specific stratigraphic information associated with most catalogued specimens.

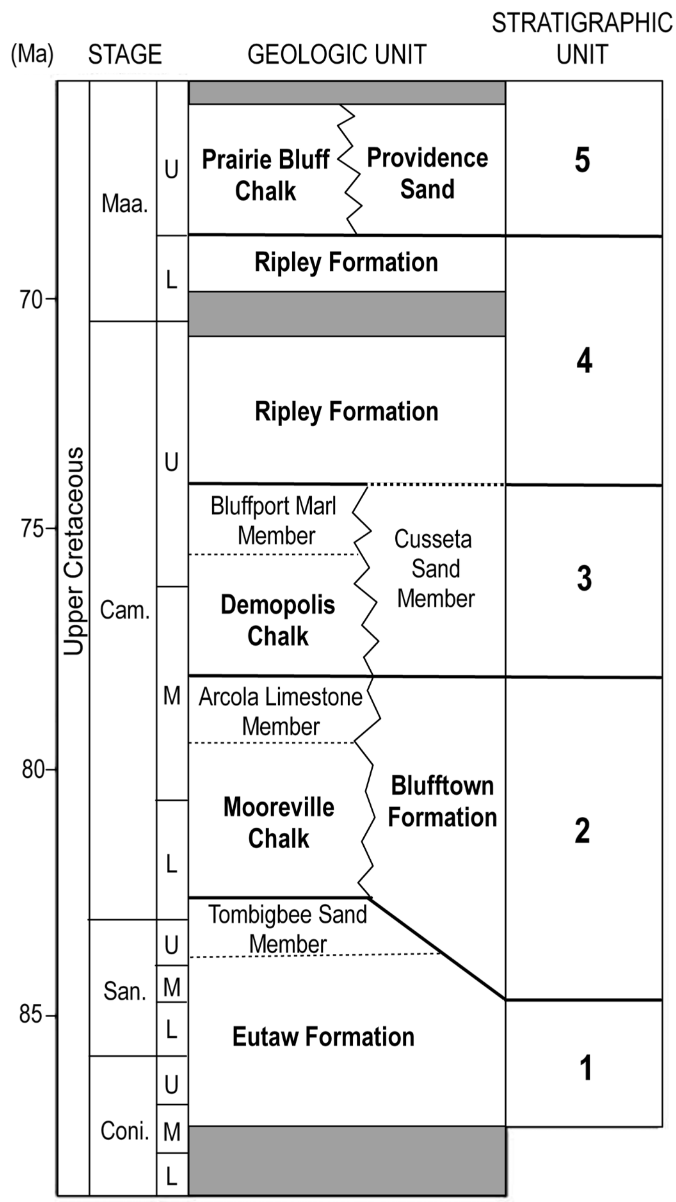

Figure 3. The five Upper Cretaceous Alabama stratigraphic units used in this study.

The terms “Selma Chalk”, “Selma Limestone”, and “Rotten Limestone” have often appeared historical and recent literature. These informal names refer to the Selma Group, which was originally named by Smith et al. (1894), which consists of the Mooreville Chalk, Blufftown Formation, Demopolis Chalk, Ripley Formation, Prairie Bluff Chalk, and Providence Sand (Stephenson and Monroe, 1938; Monroe, 1941; Belt and Anonymous, 1945). “Selma” is not used as a separate stratigraphic name in this study.

Samples

Only body fossils were used in this study. Casts were not included, with the exception of special cases when the original material is missing and only the cast was available. Only specimens catalogued or curated before December 2011 were included. No private collections or uncatalogued museum specimens were incorporated into the dataset. Electronic databases and specimen catalogues (e.g., log books) provided by the following institutions were used in this study: AMNH, AUMP, FMNH, MSC (including the former RMM specimens), MMNS, UAM (including the transferred GSA vertebrate collection), USNM, and YPM.

Whenever possible, specimens were directly examined to verify taxonomic identifications and so additional information (e.g., elements present), which was often missing in original catalogues, could be included. When comprehensive catalogues were not available for a collection, such was the case with the ANSP, CCK, and UWA, published reports and personal communications were used.

In this study, every number in the NISP represents an individual specimen. In the event catalogued specimens contained a group of mixed fossils, the different taxa were counted separately following the methods outlined by Grayson and Frey (2004) and Lyman (2008) for the calculation of NISP. If articulated or associated elements from the same individual were present, they were counted as a single individual. On several occasions, a number of elements of the same taxon, collected from the same locality, were stored together and catalogued under one specimen number (a box of shark teeth, for example). Since there was no way to determine whether or not these teeth belonged to one or multiple individuals, these specimens were counted as a single individual when calculating the overall NISP.

Taxonomic Identification

Three levels of taxonomic identifications were recorded for the Cretaceous vertebrate specimens used in this study. The highest level included the following: Chondrichthyes (chimaeras, sharks and rays), Actinopterygii (bony fishes), and Reptilia (turtles, sauropterygians, squamates, and archosaurs). The intermediate level (30 sub-taxonomic groups) and the lowest level (genus and species) were recorded whenever possible for each individual specimen. Over the past few decades, many taxonomic names of Cretaceous vertebrates, as well as phylogenetic relationships, have been revised, synonymized, and/or newly established. Because a number of these names could be seen as questionable, controversial, or ambiguous, only taxonomic names which have appeared in peer reviewed studies were used (e.g., Russell 1993, Shimada and Fielitz, 2006; Cumbaa et al., 2010). Non peer reviewed literature, such as field guides, abstracts for conferences, and dissertations and theses, were mostly excluded from this study (with the exception of a few instances which are cited herein). Furthermore, personal notes, such as identifications left with specimens by visiting researchers, were not used without verification.

During the course of this study, much of the data recorded in museum catalogues and on specimen labels were found to be outdated or unreliable. Therefore, taxonomic identifications of all specimens were confirmed by the authors whenever possible (with the exception of the specimens housed in distant collections such as the AMNH, ANSP, FMNH, and USNM collections). Specimens with questionable taxonomic assignments are noted herein and listed in Table 5. We recognize that various researchers are engaged in projects establishing new taxa and/or revising taxonomic assignments of various groups of Cretaceous vertebrates. Out of respect for these researchers and their studies, potential new taxa which have not appeared in the literature are not included.

Data Entry and Summary

For this study, a master data set was created in Microsoft Excel that includes: 1) specimen number; 2) taxon (genus, species, and higher taxonomic groups); 3) locality (county); 4) stratigraphic unit (Units 1–5); 5) institution, and 6) year collected. This information was derived from a number of sources including museum catalogs, specimen labels, field logs, and at times the matrix associated with a specimen. In the event key information was missing, the term ‘Unknown’ was entered in the field. For questionable information, a ‘?’ was entered. Once this master data set was completed, the NISP was tabulated for each data field for comparison and analysis.

RESULTS

Summary of Vertebrate Fossil Collections from the Late Cretaceous of Alabama

A total of 8,275 vertebrate specimens from Upper Cretaceous strata of Alabama were recorded from 12 institutions. Of these specimens, 77.9% are housed at two Alabama institutions, UAM (NISP=3,710) and MSC (NISP=2,739) (Table 2). The size of these collections is

Table 2. Numbers of identified specimens (NISP) of Alabama Cretaceous vertebrates from museum collections. Data were based on specimens in museum collections cataloged before August 2011.

Collections	NISP	per total
UAM (including GSA)	3,710	44.84%
MSC (including RMM)	2,739	33.10%
AUMP	1,018	12.30%
FMNH	581	7.02%
USNM	132	1.60%
MMNS	60	0.73%
CCK*	18	0.22%
AMNH	8	0.10%
ANSP**	4	0.05%
TMM***	2	0.02%
YPM	2	0.02%
NHMUK	1	0.01%

*Data from Case and Schwimmer (1988) and Ebersole and King (2011).
**Data from Spamer et al., (1995).
***Data from Wann Langston Jr. (pers. comm., 2012).

due in part to the UAM acquisition of the former Geological Survey of Alabama fossil vertebrate collection and the merger of the former Red Mountain Museum (RMM) with MSC (see Ebersole and Dean, this volume). The third largest collection of Alabama Cretaceous vertebrates is housed at the AUMP (NISP=1,018). This shows that 90.2 % of the Cretaceous vertebrate specimens collected from Alabama are physically located within the state. The FMNH in Illinois and the USNM in Washington house the fourth and fifth largest collections of Alabama Cretaceous vertebrate material, respectively. Other institutions included in this study that are known to house Alabama Cretaceous vertebrate material are shown in Table 2.

Cretaceous vertebrate fossils were first collected in Alabama in the early 19th century (Fig. 4). In the early 1830s, Timothy Abbott Conrad of the ANSP collected a large number of fossils from various Cretaceous localities in Greene, Dallas, and Montgomery counties (Ebersole and Dean, this volume). Among the specimens collected by Conrad was the holotype of *Ptychodus mortoni* which was later figured and described by Mantell (1836), Morton (1842), and Agassiz (1833–1843). Aside from the holotype of *P. mortoni*, the oldest Cretaceous vertebrate specimen from Alabama confirmed in a museum collection (with respect to collection date) is UAM PV 2005.0006.0374 (bone fragments of an indeterminate bony fish: possibly, *Enchodus* sp.), collected in 1850 by Alabama's first State Geologist, Michael Tuomey. Before his death in 1857, Tuomey had accumulated a rather large collection of Cretaceous vertebrate fossils (Tuomey, 1858), but most were destroyed near the end of the Civil War in 1865 when Union troops set fire to the University of Alabama campus (Howard, 1982). According to the UAM catalogue, only three of Tuomey's specimens are recorded as being in the museum today. There is a strong possibility, however, that others exist as well (see Ebersole and Dean, this volume).

Of the Cretaceous vertebrate specimens from Alabama, the USNM (now the National Museum of Natural History) had the largest number of specimens (26 specimens) collected in Alabama during the 19th century. Nearly all of these early USNM specimens were collected by Lawrence C. Johnson, including the holotype of *Globidens*

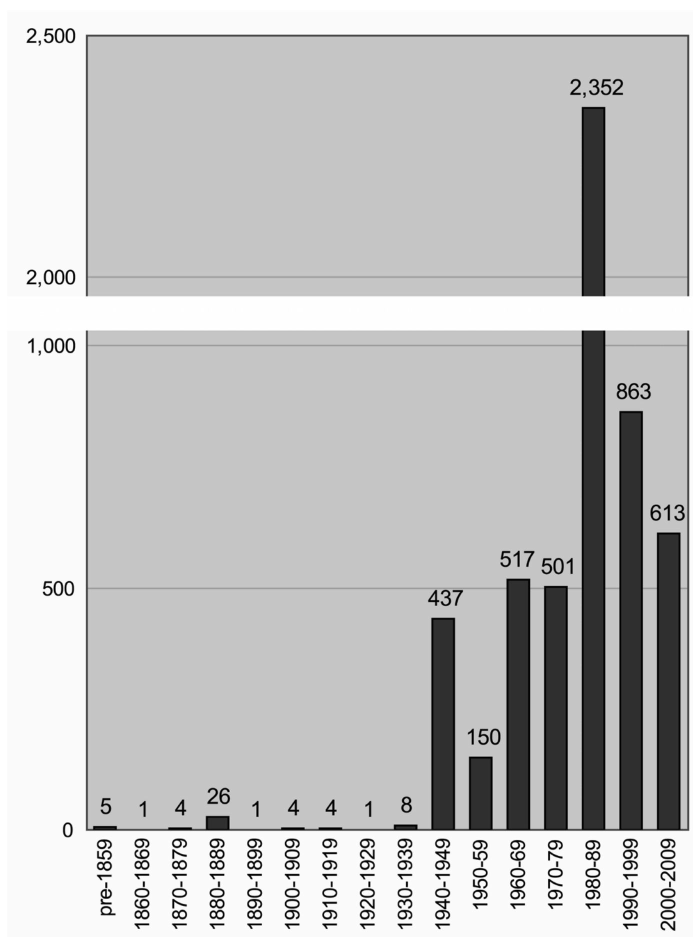

Figure 4. Numbers of vertebrate specimens collected in Alabama since 1850. Note: only specimens catalogued in institutions are included in this figure (see further explanation in the text). Vertical scale represents number of specimens.

alabamaensis (Gilmore, 1912) (Table 1), while employed at the United States Geological Survey (see more information on L. C. Johnson in Ebersole and Dean, this volume).

In the early 20th century, only a handful of Cretaceous vertebrate fossils were collected in Alabama (Fig. 4). Of these, most are housed at the UAM while two are in the AUMP collection. During 1940s to 1950s, the Chicago Museum of Natural History (now the FMNH) organized a number of expeditions to central Alabama for the purpose of collecting Cretaceous vertebrate fossils (Zangerl, 1948a; Applegate, 1970). Starting in 1945, these FMNH expeditions produced a total of 581 catalogued Cretaceous vertebrate specimens, which represents the fourth largest collection from Alabama. During the 1960s and 1970s, there was a noticeable increase in the number of Cretaceous vertebrates collected, a direct result of renewed collecting efforts by the UAM, GSA, and AUMP. In the early 1970s, the RMM was established and later began a series of systematic collecting efforts across the state. The 1980s to early 1990s has been the most productive period for the collection of Cretaceous vertebrate fossils in Alabama (Fig. 4), highlighted by intense collecting by the UAM, RMM, and AUMP. Beginning in the early 2000s, the UAM has conducted a series of fossil expeditions to the Harrell Station area in Dallas County, thus continuing to add large numbers of vertebrate specimens into the collection.

Late Cretaceous Vertebrate Taxa from Alabama

Higher taxonomic groups—Of the total number of vertebrate specimens recorded in this study, 95.8% are assigned to either Chondrichthyes, Actinopterygii, or Reptilia, with 4.1% (NISP = 339) not identifiable to any

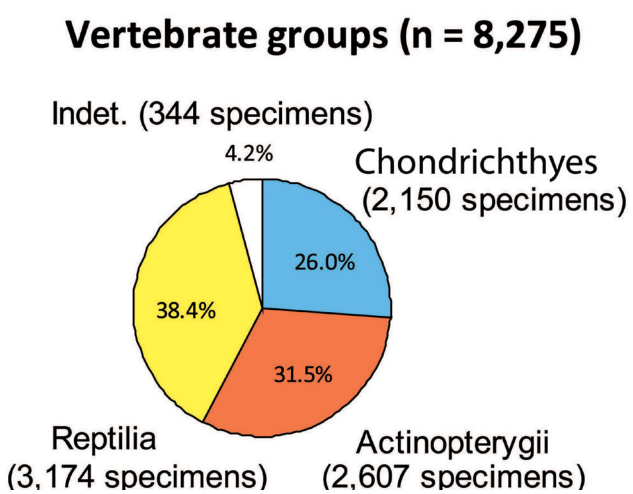

Figure 5. Numbers of Cretaceous specimens in major vertebrate groups from Alabama. 'Indet.' is assigned to specimens not identifiable at any particular taxonomic level.

Table 3. Summary of higher taxonomic groups and number of Cretaceous vertebrate specimens from Alabama. A list of vertebrate genera and species is shown in Table 4.

Taxon	Taxa* (#s)		Specimens	
	Genera	Species**	NISP	per total
CHONDRICHTHYES				
Chimaeriformes	2	2	26	0.3 %
Heterodontiformes	1	?	1	0.01 %
Hybodontidae	2	5	151	1.8 %
Lamniformes	9	13	1,243	15.0 %
Myliobatiformes	2	3	55	0.7 %
Orectolobiformes	3	2	15	0.2 %
Rajiformes	?	?	24	0.3 %
Sclerorhynchiformes?	1	4	169	2.0 %
Squatiniformes	1	1	7	0.1 %
ACTINOPTERYGII				
Pycnodontiformes	3	5	78	1.0 %
Aspidorhynchiformes	1	?	2	0.02 %
Pachycormiformes	2	2	103	1.3 %
Lepisosteiformes (and Semionotiformes)	2	1	16	0.2 %
Tselfatiiformes	4	3	59	0.7 %
Ichthyodectiformes	4	3	244	3.0 %
Crossognathiformes	1	3	153	1.9 %
Albuliformes	1	1	35	0.4 %
Aulopiformes	3	6	857	10.4 %
Beryciformes	1	?	4	0.05 %
Coelacanthiformes	1	1	18	0.2 %
REPTILIA				
Testudines	11	12	1,250	15.1 %
Plesiosauria	2	2	56	0.7 %
Mosasauridae	11	18	1,563	18.9 %
Pterosauria	1	?	27	0.3 %
Crocodylia	2	1	54	0.7 %
Dinosauria	2	2	63	0.8 %
Aves	3	2	79	1.0 %
Total	76	92	6,352	76.8 %

*Ambiguous taxa are not included and are listed in Table 5.
**Only identified species are counted (excluding "sp.")

higher taxonomic group due to their fragmentary state of preservation. To date, no Cretaceous mammals or amphibians have been confirmed from the state. Of all specimens, the largest NISP, 3,168 (38.3% of the total), is referred to reptiles and birds; 2,605 specimens (31.5%) to actinopterygian bony fishes; and 2,163 (26.2%) to chondrichthyan fishes (Fig. 5).

Each of the three higher taxonomic groups of vertebrates were further subgrouped. Of the 30 subgroups identified (Table 3), Mosasauridae (mosasaurs) contains the largest number of specimens (1,563). Turtles (Testudines) and lamniform sharks (Lamniformes) follows with 1,250 and 1,243 specimens, respectively. These three groups make up nearly 49.0% of the total NISP. Relatively rare taxa in Alabama consisting of fewer than 10 specimens were recorded in: Heterodontiformes (one specimen), Sclerorhynchiformes? (four specimens), Squatiniformes (seven specimens), Beryciformes (four specimens), and Semionotiformes (two specimens).

Genera and species—All of the Cretaceous vertebrate genera and species confirmed in this study are listed in Table 4. Numerous miscellaneous or questionable taxa found in museum collections are listed in Table 5; these specimens include those with uncertain phylogenetic position, specimens that cannot at this time be assigned to any known taxon, and/or those with problematic taxo-

Table 4. Late Cretaceous vertebrate taxa from Alabama. Listed references have information on taxonomy, systematics, and/or occurrences from Alabama. Key references are used to confirm phylogenetic positions, taxonomic identifications and/or occurrences in Alabama. Recorded taxa sorted by each stratigraphic unit are listed in Appendix 1.

CHONDRICHTHYES	*Key references
Chimaeriformes	
Edaphodon barberi, *Edaphodon mirificus*, *Ischyodus* sp.	a, b,c,d,e,f,g
Heterodontiformes	
Heterodontus(?) sp.	h
Hybodontiformes	
Hybodus sp., *Lissodus* (=*Lonchidion*?) *babulski*, *Ptychodus marginalis*, *Ptychodus mortoni*, *Ptychodus polygyrus*, *Ptychodus rugosus*	a,i,j,ao, cz
Orectolobiformes	
Cantioscyllium decipiens (=*C. meyeri* or *C. saginatus*?), *Chiloscyllium greeni*, *Ginglymostoma* sp.	a,h,j,k,cz
Lamniformes	
Carcharias sp., *Cretalamna appendiculata*, *Cretodus crassidens*, *Cretodus semiplicatus*(?), *Cretoxyrhina mantelli*, *Paranomotodon angustidens*, *Pseudocorax affinis*, *Pseudocorax laevis*, *Scapanorhynchus raphiodon*, *Scapanorhynchus rapax*, *Scapanorhynchus texanus*, *Serratolamna serrata*, *Squalicorax falcatus*, *Squalicorax kaupi*, *Squalicorax pristodontus*	a,b,k,l,m,n,o,p,q,r,s,u,v,w,x
Squatiniformes	
Squatina hassei	i,j,k
Myliobatiformes	
Brachyrhizodus mcnultyi, *Brachyrhizodus wichitaensis*, *Pseudohypolophus* (=*Brachyrhizodus*?) *mcnultyi*	j,k,q,cz
?Rajiformes	
gen. indet.	i,j,k
?Sclerorhynchiformes	j,q,y,z,aa,ab,cp
Borodinopristis schwimmeri, *Ischyrhiza mira*, *Ptychotrygon triangularis* (= *P. vermiculata* and/or *P. chattahoochiensis*?), *Ptychotrygon vermiculata*, *Sclerorhynchus* sp.	a,i,j,k,q,ac,cp,cz
ACTINOPTERYGII	
Pycnodontiformes	aa
Anomoeodus latidens, *Anomoeodus phaseolus*, *Coelodus* sp., *Hadrodus hewletti*(?), *Hadrodus priscus*, *Phacodus punctatus*	b,j,ac,ad,ae,af,ag,ah
?Aspidorhynchiformes	ah
Belonostomus sp.	ac,cw
Pachycormiformes	
Bonnerichthys gladius, *Protosphyraena nitida*	a,b,ac,ai,aj,ak

Table 4. *continued*

Lepisosteiformes (or Semionotiformes)	al
Atractosteus sp, *Lepisosteus* sp.	ac,am,an,ao
Tselfatiiformes	
Bananogmius crieleyi(?), *Moorevillia hardi*, *Palelops eutawensis*, *Plethodus* sp.	a,b,ac,aj,ak
Ichthyodectiformes	
Ichthyodectes sp. (*I. ctenodon*?), *Saurocephalus lanciformis*, *Saurodon leanus*, *Xiphactinus audax*	a,b,j,ac,ao,ap,aq,as,at,cx
Crossognathiformes	
Pachyrhizodus caninus, *Pachyrhizodus kingi*, *Pachyrhizodus minimus*	a,b,ac
Albuliformes	
Albula dunklei	a,b,ac
Aulopiformes	
Cimolichthys nepaholica, *Enchodus ferox*, *Enchodus gladiolus*, *Enchodus petrosus*, *Enchodus shumardi*, *Stratodus apicalis*	a,b,ac,ac,ao,au,av
Beryciformes	
Hoplopteryx sp.	b,ac
Coelacanthiformes	
Megalocoelacanthus dobiei	av
REPTILIA	
Testudines	
Calcarichelys gemma, *Chedighaii barberi*, *Chelosphargis advena*, *Corsochelys haliniches*, *Ctenochelys acris*, *Ctenochelys tenuitesta*, *Lophochelys venatrix*, *Prionochelys matutina*, *Protostega gigas*, *Thinochelys lapisossea*, *Toxochelys moorevillensis*, trionychid (gen. indet.)	a,aw,ax,ay,az,ba,bb,bc, bd,be,cr,cs,da
Plesiosauria	ct
Discosaurus vetustus, *Polycotylus latipinnis*, elasmosaurid (gen. indet.)	a,bf,bg,bh,bi,bj
Mosasauridae	a,t,bk,bl,bm,co
Clidastes liodontus, *Clidastes "moorevillensis"*, *Clidastes propython*, *Eonatator sternbergi*, *Globidens alabamaensis*, *Halisaurus*(?) sp., *Mosasaurus conodon*, *Mosasaurus maximus*, *Mosasaurus missouriensis*(?), *Platecarpus ictericus*(?), *Platecarpus somenensis*, *Platecarpus tympaniticus*, *Plioplatecarpus* sp., *Prognathodon* sp., *Selmasaurus russelli*, *Tylosaurus nepaeolicus*(?), *Tylosaurus proriger*	a,t,bk,bm,bn,bo,bp,bq, br,bs,bt,bu,bv,bw,bx, co,cu,cx,cy
Pterosauria	
Pteranodon sp.	by
Crocodylia	
Borealosuchus sp.; *Deinosuchus rugosus*	bz,ca,cb,cc,cd,ce
Dinosauria	a,cd,ce
Appalachiosaurus montgomeriensis; dromaeosaurid (gen. indet.); *Lophorhothon atopus*; nodosaur (gen. indet.)	a,cf,cg,ch,ci,cj
Aves	
Ichthyornis dispar; *Halimornis thompsoni*	ck,cl,cm,cn

*__References:__ **a** (Thurmond and Jones, 1981); **b** (Applegate, 1970); **c** (Leidy, 1856); **d** (Case and Schwimmer, 1992); **e** (Egerton, 1843); **f** (Patterson, 1965); **g** (Case, 1978); **h** (Welton and Farish, 1993); **i** (Cappetta and Case, 1975); **j** (Case and Schwimmer, 1988); **k** (Cappetta, 1973); l (Shimada, 2005); **m** (Shimada, 1996); **n** (Shimada, 2007); **o** (Schwimmer et al., 2002); **p** (Shimada, 1997); **q** (Cappetta, 1987); **r** (Shimada, 2009); **s** (Case, 1979); **t** (Kiernan, 2002); **u** (Hamm and Shimada, 2007); **v** (Shimada and Brereton, 2007); **w** (Shimada and Cicimurri 2005), **x** (Schwimmer, 2007); **y** (Case et al., 2001); **z** (Schwimmer et al., 1997a); **aa** (Kriwet, 2004); **ab** (Kriwet et al., 2009); **ac** (Schein and Lewis, 2007); **ad** (Bell, 1986); **ae** (Poyato-Ariza and Wenz, 2002); **af** (Becker et al., 2010); **ag** (Hooks et al., 1999); **ah** (Forey et al., 2003); **ai** (Friedman et al., 2010); **aj** (Friedman et al., 2013); **ak** (Stewart, 1988); **al** (López-Arbarello, 2012); **am** (Wiley, 1976); **an** (Peng et al., 2001); **ao** (Shimada and Fielitz, 2006); **ap** (Cumbaa et al., 2010); **aq** (Harlan, 1824); **ar** (Stewart, 1898a); **as** (Leidy 1870); **at** (Schwimmer et al., 1997b); **au** (Cope, 1872); **av** (Schwimmer et al., 1994); **aw** (Zangerl, 1948a); **ax** (Gaffney et al., 2006); **ay** (Gaffney et al., 2009); **az** (Zangerl, 1953a); **ba** (Hooks, 1998); **bb** (Zangerl, 1953b); **bc** (Zangerl, 1960); **bd** (Zangerl, 1948b); **be** (Zangerl, 1980); **bf** (Welles, 1962); **bg** (Spamer et al., 1995); **bh** (O'Keefe and Street, 2009); **bi** (Carpenter, 1996); **bj** (O'Keefe, 2004); **bk** (Russell, 1967); **bl** (Russell, 1970); **bm** (Bell, 1997); **bn** (Cope, 1869); **bo** (Michael Polcyn, pers. comm., 2012: Clidastes "moorevillensis", Eonatator instead of Halisaurus); **bp** (Bardet et al., 2005); **bq** (Polcyn and Lamb, 2012); **br** (Polcyn et al., 2012); **bs** (Konishi and Caldwell, 2011); **bt** (Wright and Shannon, 1988); **bu** (Konishi, 2008); **bv** (Polcyn and Everhart, 2008); **bw** (Renger, 1935); **bx** (Everhart, 2005b); **by** (Unwin, 2003); **bz** (Chris Brochu, pers. comm., 2012: Borealosuchus); **ca** (Brochu, 1999); **cb** (Schwimmer, 2002); **cc** (Wann Langston Jr., pers. comm.., 2012; Deinosuchus); **cd** (Schwimmer et al., 1993); **ce** (Ebersole and King, 2011); **cf** (Carr et al., 2005); **cg** (Kiernan and Schwimmer, 2004); **ch** (Langston, 1960); **ci** (Horner et al., 2004); **cj** (Vickaryous et al., 2004); **ck** (Olson, 1975); **cl** (Padian, 2004); **cm** (Clarke, 2004); **cn** (Chiappe et al., 2002); **co** (Shannon, 1975); **cp** (Suarez and Cappetta, 2004); **cq** (Case, 1987); **cr** (Hirayama, 1997); **cs** (Nicholls, 1988); **ct** (Shannon, 1974); **cu** (Wright, 1988); **cv** (Gilmore, 1912); **cw** (Whetstone, 1978); **cx** (Stewart, 1898b); **cy** (Bell and Sheldon, 1986); **cz** (Ciccimuri, pers. comm. 2012); **da** (Jasinski, this Bulletin, Vol. 2).

Table 5. Miscellaneous and/or doubtful vertebrate taxa from Upper Cretaceous strata of Alabama.

Higher taxonomic unit	Genus	Species	Geologic unit*	County*
CHONDRICHTHYES				
Lamniformes	*Odontaspis*	*macrota*	Kr	Ba
Lamniformes	*Scapanorhynchus*	*elegans*	Kb	Ru
Lamniformes	*Archaeolamna*	*kopingensis*	Ke	Gr
Lamniformes	*Odontaspis*	*macrota*	Kr	Ba
Lamniformes	*Rhombodus*	*laevis*	Kb	Bu
Myliobatiformes	*Myliobatis*	sp.	Unknown	Unknown
Orectolobiformes	*Cantioscyllium*	*globidens*	Kb	Bu
Orectolobiformes	*Cantioscyllium*	*globidens*	Ke	Mg
Rajiformes	*Pristis*	sp.	Unknown	Unknown
Rhinobatiformes	*Rhinobatus*	*casieri*	Kpb	Ln
ACTINOPTERYGII				
Pycnodontiformes	*Anomoeodus*	*latidens*	Kb	Bu
Pycnodontiformes	*Coelodus*	sp.	Kr	Wi
Ichthyodectiformes	*Ichthyodectes*	cf. *ctenodon*	Km	Gr
Ichthyodectiformes	*Gillicus*	sp.	Km	Gr
Albuliformes	*Albula*	*casei*	Kb	Bu
Aulopiformes	*Stratodus*	*caninus*	Km	Da
Aulopiformes	*Enchodus*	*saevus*	Km	Gr
Aulopiformes	*Enchodus*	*nepaholica*	Km	Gr
Elopiformes, Dussurmieriidae(?)	indet.	indet.	Unknown	Unknown
Myctophiformes, Myctophidae(?)	indet.	indet.	Unknown	Unknown
Perciformes	*Cylindracanthus*	*ornatus*(?)	Unknown	Unknown
Beryciformes, Trachichthyidae	indet.	indet.	Km	Gr
Coelacanthiformes	*Mawsonia*	sp.	Ke	Mg
REPTILIA				
Testudines	*Ctenochelys*	*procax*	Unknown	Su
Testudines	*Peritresius*	*ornatus*	Kr?	Ln
Testudines	*Protostega*	*dixie*		
Mosasauridae	*Clidastes*	*iguanavus*	Kd	Su
Mosasauridae	*Clidastes*	*intermedius*	Unknown	Pn
Mosasauridae	*Liodon*	cf. *sectorius*	Kr	Wi
Mosasauridae	*Mosasaurus*	*missouriensis*	Kd	Ln
Mosasauridae	*Platecarpus*	*ictericus*	Unknown	Unknown
Mosasauridae	*Tylosaurus*	*kansasensis*		
Mosasauridae	*Tylosaurus?*	*perlatus*	Unknown	Unknown
Mosasauridae	*Tylosaurus*	*zangerli*	Km	Da
Crocodylia	*Bottosaurus*	*harlani*	Kb	Bu
Crocodylia	*Leidyo*suchus	sp.	Kb, Ke, Km	Bu, Da, Mg, Pe

*Abbreviations for geologic units and counties are listed in the text.

nomic assignments. Further study of these specimens is recommended.

Of all vertebrate specimens in this study, 4,516 (54.6%) can be identified to at least the generic level, and from these specimens, 76 genera were confirmed (Table 3 and 4). In addition, rajiforms, elasmosaurids, dromaeosaurids, and nodosaurids were identified, but could not be assigned to the generic level. The uncertain generic assignment of these specimens is the result of one or more of the following: 1) the fragmentary condition of a specimen; 2) the current uncertainty of a specimen's phylogenetic position; 3) the lack of reliable diagnostic characteristics for determination to the generic level; and/or 4) the possibility a specimen represents a new genus or species. Based on NISP, the most common genus is that of the aulopiform bony fish, *Enchodus* (765 specimens). The abundance of this taxon is partially due to the relative ease of identification of its palatine teeth (as compared to other fishes), which are often preserved well in the Cretaceous chalks of Alabama. The second and third most abundant genera are the mosasaur *Clidastes* (495 specimens) and the lamniform shark *Scapanorhynchus* (352 specimens). The high number of identified specimens of *Scapanorhynchus*, nearly all isolated teeth, is explainable as these teeth have a distinct morphology allowing them to be easily assigned to the generic level.

Of the specimens identified to the generic level, 3,062 specimens (37% per total) can be assigned to the species level (92 species; Table 4). Single species with a large NISP appear in lamniform sharks such *Scapanorhynchus texanus* (201 specimens), *Cretalamna appendiculata* (176 specimens), *Squalicorax kaupi* (129 specimens), and the bony fish *Enchodus petrosus* (210 specimens) (Table 6). In reptiles, two turtle species, *Protostega gigas* (112 specimens) and *Toxochelys moorevillensis* (105 specimens), are present in relatively large numbers. The abundance of *P. gigas* is likely a result of the size of their elements (which aid in their preservation and make them easy to identify).

Table 6. Selected Cretaceous vertebrate genera and species with high numbers of identified specimens (NISP) from Alabama.

A. Genera.

VERTEBRATA	NISP	per subtotal
Enchodus	765	36.37%
Clidastes	495	23.23%
Scapanorhynchus	352	16.52%
Cretalamna	285	13.37%
Ptychodus	149	6.95%
Xiphactinus	76	3.57%
SUBTOTAL (6 genera)	2,131	

B. Species.

CHONDRICHTHYES	NISP	per subtotal
Scapanorhynchus texanus	201	14.58%
Cretalamna appendiculata	176	12.76%
Squalicorax kaupi	129	9.35%
Ptychodus mortoni	70	5.08%
Cretoxyrhina mantelli	80	5.80%
ACTINOPTERYGII		
Enchodus petrosus	210	15.23%
Saurodon leanus	83	6.02%
Stratodus apicalis	46	3.34%
Enchodus ferox	24	1.74%
REPTILIA		
Protostega gigas	112	8.12%
Toxochelys moorevillensis	105	7.61%
Clidastes propython	76	5.51%
Ctenochelys tenuitesta	39	2.83%
Chegadaii barberi	28	2.03%
SUBTOTAL (14 spp.)	1,379	

Cretaceous Vertebrates by Stratigraphic Unit

Overall, 95.1% of the specimens (NISP = 7,871) had at least some level of stratigraphic information recorded such as formation and/or member (Table 7). Cretaceous vertebrate fossils are known from the five stratigraphic units in Alabama ranging from the lower Santonian to the very upper Maastrichtian (see Appendix 1 for the distribution of vertebrate taxa within each stratigraphic unit). No definitive vertebrate remains are reported from the Tuscaloosa Group (upper Cenomanian–lower Coniacian) which underlies the Eutaw Formation (Santonian) with an unconformity.

A total of 76.9% of the vertebrate fossils are from Unit 2, the Mooreville Chalk and Blufftown Formation (Table 7, Fig. 6). In fact, the Mooreville Chalk alone produced 74.3% of vertebrate specimens recorded in museum collections (6,147 total). The second most vertebrate fossil-bearing unit was Unit 1, the Eutaw Formation, with 943 specimens (11.4%). Based on the 1:250,000 state geologic map, this unit has the largest area of surface geology among any Cretaceous formations in Alabama (Table 7). Within Unit 3, the Cusseta Sand Member of the Ripley Formation, only nine vertebrate specimens (<1%) were collected, probably a result of this unit having a relative-

Table 7. Numbers of vertebrate specimens in Upper Cretaceous strata of Alabama. Ratios of numbers of specimens-to-surface geology areas (#s/km²) are shown in the far right column.

Stratigraphic Unit	Geologic unit	NISP	per total	surface area (km²)	#s/(km²)
Unit 1	Eutaw Fm	943	11.40%	4,359	0.2179
Unit 2	Mooreville Chalk Fm	6,147	74.29%	2,642	2.3255
	(Arcola Mbr)	(21)		NA	
Unit 2	Blufftown Fm	216	2.61%	1,336	0.1624
Unit 3	Demopolis Chalk Fm	211	2.55%	2,476	0.0852
	(Bluffport Marl Mbr)	(40)			
Unit 3	Cusseta Sand Member (of Ripley Fm)	9	0.11%	692	0.0116
Unit 4	Ripley Fm (except for Cusseta Sand Member)	139	1.68%	2,045	0.0680
Unit 5	Prairie Bluff Chalk Fm	203	2.45%	412	0.4830
Unit 5	Providence Sand Fm	3	0.04%	1,472	0.0020
Unknown		404	4.87%		
Total		8,275	100%	15,434	

*Based on a 1:250,000 state map.

ly restricted surface exposure. In contrast, 211 specimens (2.5%) are recorded from the Demopolis Chalk of this unit. Unit 4, the Ripley Formation, includes the smallest number of vertebrate specimens (139 specimens, 1.7%). In Unit 5, 203 specimens (2.5%) are recorded from the Prairie Bluff Chalk, while only three specimens are from the Providence Sand Formation, although fairly large outcrops are exposed (1,472 km²; Table 7).

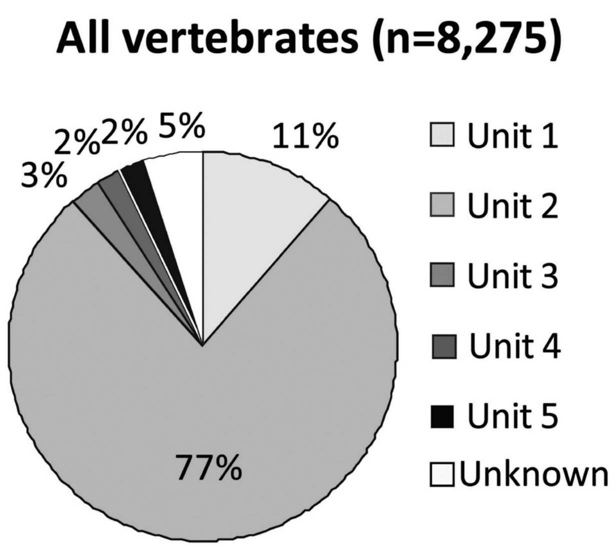

Figure 6. Numbers of vertebrate specimens from five Cretaceous stratigraphic units in Alabama. Geologic units (Fm/Mbr) of the five units are listed in Table 7.

Cretaceous Vertebrates by County

Upper Cretaceous strata are exposed in 28 counties in Alabama, covering roughly 11% of the state's surface area (Fig. 2). From our numbers, 95.8% of the specimens possess locality information at least to the county-level and show these specimens were collected from 20 counties in the state (Fig. 8). Of these 20 counties, Dallas and Greene are the most productive in terms of Cretaceous vertebrates collected. Among the 3,224 specimens from Dallas County, 3,023 were collected from the Mooreville Chalk (93.7%), 76 from the Eutaw Formation (2.3%), 62 from the Demopolis Chalk (1.9%), two from Prairie Bluff Chalk (<1%), and 61 (1.8%) had no associated stratigraphic data. Of the Dallas County specimens, 2,543 (78.9%) were collected from the Harrell Station area near Marion Junction which has sizable exposures of the Mooreville Chalk. At this location, dozens of individual fossil sites are located within a 0.5 mi² (ca 1.29 km²) area, which was purchased by the University of Alabama in 1991. This locality has turned out to be one of the most productive sites for the discovery of Cretaceous vertebrate fossils in Alabama.

According to our dataset, Greene County is the second most productive for the collection of fossil vertebrates in Alabama (Table 8). From this county, 2,885 vertebrate specimens are recorded from the Eutaw Formation, Mooreville Chalk (including the Arcola Limestone Member), Demopolis Chalk, and Ripley Formation. These fossils were collected from over 50 localities with the most productive being AGr-43, a site located along a creek which produced at least 198 specimens. Thousands of additional elements from site AGr-43 remain uncatalogued in muse-

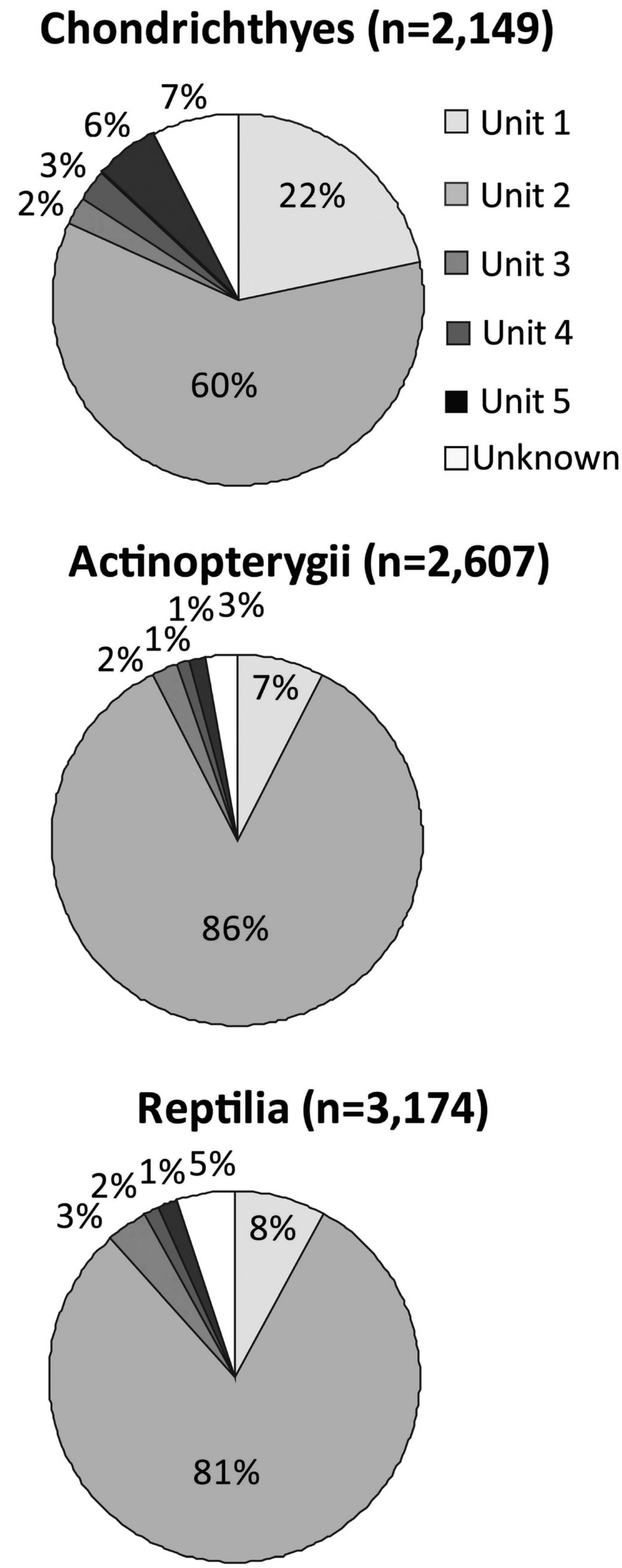

Table 7. Percentage of Chondrichthyes, Actinopterygii, and Reptilia specimens identified from five Upper Cretaceous stratigraphic units in Alabama.

um collections (see also Ciampaglio et al., this volume), indicating this site (AGr-43) may be one of the more productive Cretaceous vertebrate localities in the state.

Vertebrate fossils from the Blufftown Formation are recorded only in three eastern Alabama counties, Barbour, Bullock, and Russell, even though outcrops are exposed in several other neighboring counties. Although exposures of the Prairie Bluff Chalk are small (Table 7, Fig. 2), six counties (Butler, Dallas, Lowndes, Montgomery, Sumter, and Wilcox), located in the eastern to central parts of the state, have produced vertebrate fossils.

In total, only 19 Cretaceous vertebrate specimens are recorded from Autauga, Crenshaw, Elmore, Henry, Lee, and Pike counties combined (Table 8). To date, no Cretaceous vertebrate fossils from these counties have been previously reported in the literature. In Autauga County, all nine recorded specimens were collected from relatively extensive outcrops of the Eutaw Formation. Elmore County, which also has extensive exposures of the Eutaw, recorded only two vertebrate specimens, one of which (an indeterminate plesiosaur) was collected from the Mooreville Chalk. One mosasaur specimen (i.e., fragmentary cranial bones and tooth) was discovered in the Providence Sand in Henry County, the only Cretaceous strata exposed in that county. Three reptilian specimens (two mosasaurs and a turtle; genera indeterminate) from Lee County are from the Mooreville Chalk. Although Pickens County has extensive outcrops of the productive Eutaw Formation, all four known specimens were collected from the Ripley Formation.

DISCUSSION

Few studies have utilized NISP as a tool to illustrate the diversity of catalogued Late Cretaceous vertebrates in museum collections (in contrast to studies of Cenozoic mammals; e.g., Grayson and Frey, 2004; Davis and Pyenson, 2007; Lyman, 2008). Among Western Interior Seaway studies, Shimada and Fielitz (2006) reported 113 chondrichthyan and 510 actinopterygian specimens while Russell (1993) reviewed 7,416 vertebrate specimens, including 4,222 fishes, 1,823 mosasaurs, 878 pterosaurs, 225 birds, and 58 plesiosaurs. The 8,275 specimens reported in this study provides additional data to aid in our understanding of Cretaceous vertebrate paleobiogeography, biostratigraphic distribution, and taxonomic diversity, although there are both advantages and disadvantages in utilizing NISP in this manner. In the following section we discuss potential uses of NISP for stratigraphic and geographic occurrences of vertebrate fauna, as well as biases.

Table 8. Counties in Alabama that have produced Late Cretaceous vertebrate fossils. Abbreviations for counties and geologic units are listed in the text.

County	Abbreviations	Specimen #s	Per total	Geologic unit
Autauga	Au	9	0.11%	Ke
Barbour	Ba	83	1.00%	Kb, Km(?), Kr
Bullock	Bu	111	1.34%	Kb, Kr
Butler	Bt	1	0.01%	Kpb
Crenshaw	Cr	1	0.01%	Km
Dallas	Da	3,224	38.97%	Kd, Ke, Km, Kpb
Elmore	El	2	0.02%	Km
Greene	Gr	2,885	34.87%	Kd, KE, Km
Hale	Hl	255	3.08%	Ke, Km
Henry	Hr	1	0.01%	Kp(?)
Lee	Le	3	0.04%	Km
Lowndes	Ln	247	2.99%	Kd, Ke, Km, Kpb, Kr
Marengo	Ma	17	0.21%	Kd, Ke, Km, Kpb, Kr
Montgomery	Mg	393	4.75%	Kd, Ke, Km, Kp
Perry	Pe	180	2.18%	Kd, Ke, Km
Pike	Pk	4	0.05%	Kr
Pickens	Pn	191	2.31%	Ke, Km
Russell	Ru	80	0.97%	Kb, Ke
Sumter	Su	175	2.12%	Kd, Ke, Km, Kpb, Kr
Wilcox	Wi	67	0.81%	Ke, Kpb, Kr
Unknown		346	4.17%	

Stratigraphic Distribution of Cretaceous Vertebrate Specimens in Alabama

Comparisons of the NISP in each Cretaceous stratigraphic unit provides data for quantifying which units are more or less productive for the collecting of vertebrate fossils. Units 3, 4, and 5, for example, have a smaller NISP than Units 1 and 2 (Table 7). While this find may indicate that Units 3, 4, and 5 are more productive in terms of numbers of vertebrate specimens, this may also be influenced by area of surface exposure (e.g., the large surface exposures of Eutaw Formation as opposed to the smaller exposures of Prairie Bluff Chalk). The difference in NISP may also reflect concentrated efforts to collect more frequently within certain units.

When comparing the ratios of NISP to the surface area of formation, the most fossil-abundant (i.e., the highest value of the ratio) is the Mooreville Chalk (2.3255 NISP/km^2) of Unit 2, with the least fossiliferous being the Providence Sand (0.0020 NISP/km^2) of Unit 5 (Table 7). Because the Providence Sand has a relatively large area of exposure in Alabama (1,472 km^2), this formation can be interpreted as not very productive for the collection of fossil vertebrates. On the other hand, the Prairie Bluff Chalk ranks second in terms of fossil abundance even though the exposed surface area is relatively small. This could indicate that a high concentration of vertebrate fossils can be found within this formation, or there has been a more concentrated effort to collect in this unit as opposed to formations with a lower ratio.

The NISP within each stratigraphic unit can likely be attributed to one or more of the following: 1) preservation bias – vertebrate remains may preserve better in some sedimentary settings than others; 2) collecting bias – some formations have been collected more frequently than others (and/or may be more accessible than others); and/or 3) some paleoenvironments being more suitable for

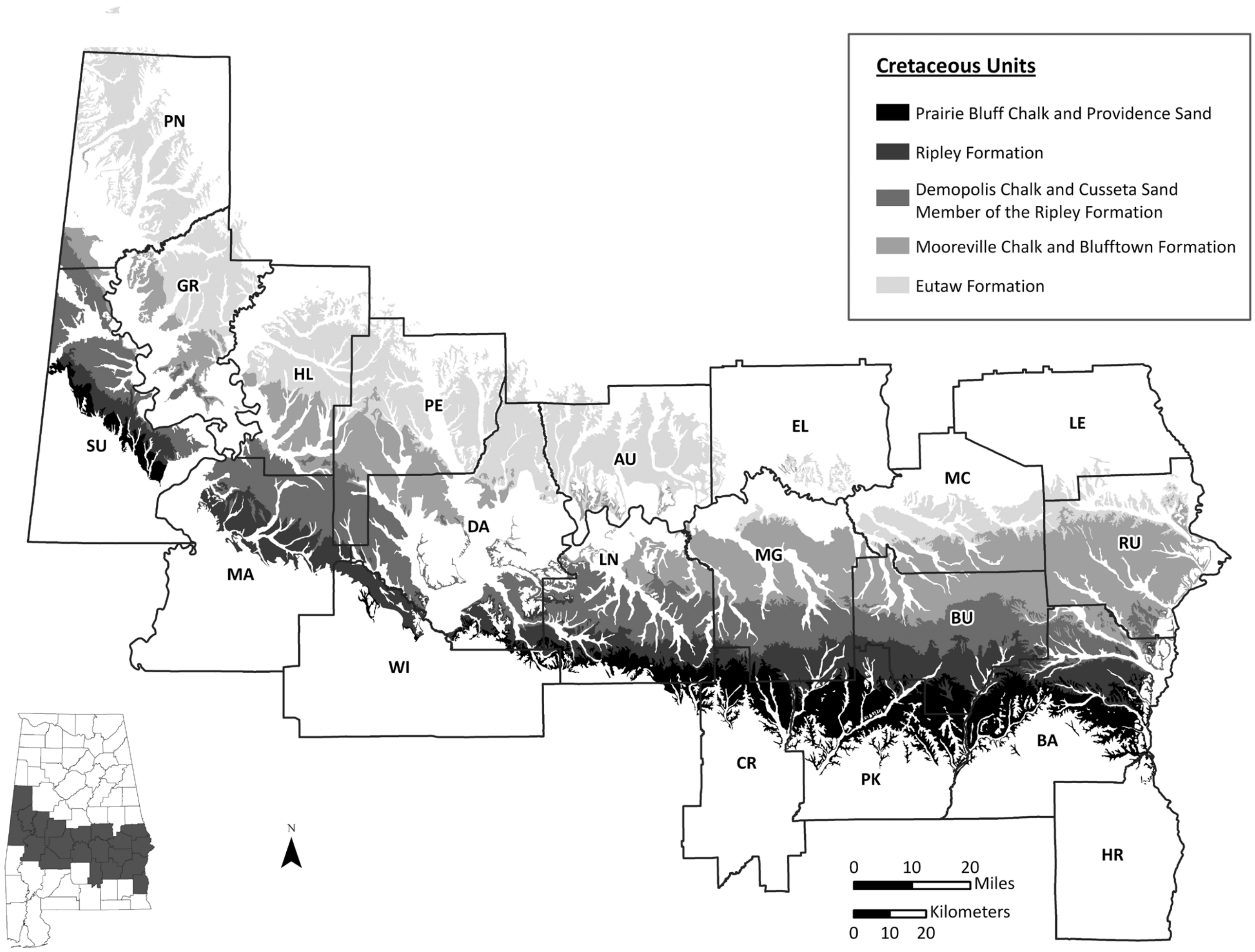

Figure 8. Counties in Alabama producing vertebrate fossils within the five Cretaceous stratigraphic units used in this study. Abbreviations of counties are listed in the text.

vertebrates than others. To further investigate this matter, systematic collecting would need to be undertaken at regular intervals at Units 1–5 and more detailed studies would need to be conducted of the sedimentology and taphonomy of specific fossil sites. Because the validity of correlations between fossil richness and surface geology area has been debated (e.g., Crampton et al., 2003; Dunhill, 2012), further studies are needed that combine the types of landscapes (e.g., creek sites vs. gullies) and actual areas of outcrops with the use of detailed aerial photography, GPS, and field observations.

Geographic Distribution of Cretaceous Vertebrate Specimens in Alabama

The NISP sorted by county may show unique patterns of geographic distributions for Cretaceous vertebrate specimens in Alabama. However, caution is advised when using NISP in this manner as collecting and preservation biases can strongly influence the NISP, thus skewing any paleogeographic reconstructions. For example, in Alabama, Dallas County has produced the largest number of specimens (Table 8). A majority of these specimens, however, were collected from a single area near the Harrell Station Paleontological Site which consists of a large number of concentrated and expansive gullies. In this case, the NISP for Dallas County is directly influenced by the amount of exposed outcrop in the area (i.e., over 0.2 square miles), the fact that a large portion of the site is not a university research site, and the ease of accessibility for collecting. We suggest that in order to reconstruct a better paleobiogeographic distribution of vertebrates in Alabama, further data collection is needed such as the NISP from individual fossil sites and additional collecting within counties where the NISP appears low. A comparison of these data to the amount of surface geology of each formation in each county will provide further insights to reconstruct paleobiogeographic occurrences of certain taxa. Gathering additional data from cataloged specimens, such as the relative completeness of specimens (isolated bones vs. partial or complete skeletons), and the type of collection site (i.e., gully vs. creek), can be useful as well.

Overview of Vertebrate Taxa

When compared to other Cretaceous paleogeographic regions in North America (such as the Western Interior Seaway), the NISP of vertebrate taxa in Alabama can be useful to highlight some patterns of taxonomic diversity in the Cretaceous Gulf of Mexico and the Mississippi Embayment. Previous studies of taxonomic diversity of Cretaceous marine vertebrates from marine and coastal strata focused on the number of vertebrate taxa (species, genus, and higher taxonomic groups) from the northern, central, and southern regions of the Western Interior Seaway, as well as the Gulf of Mexico, the Atlantic Seaboard, and the Pacific Coast (Russell, 1988; Nicholls and Russell, 1990; Everhart, 2005a; Cumbaa et al., 2010). In addition to comparing the types and numbers of vertebrate taxa, the use of NISP can provide additional insights into the taxonomic diversity. For example, Nicholls and Russell (1990) suggested the Cretaceous Gulf of Mexico region near Alabama produced a relatively high number of turtle taxa (10 genera) when compared to other regions of North America such as the Anderson River in northern Canada (0 genera), Pembina (one genus), Sharon Springs (one genus), and Niobrara (nine genera). Similarly, our data shows a higher concentration of turtles (NISP=1,250; Table 3) along the Cretaceous coast lines of the southern-most Appalachia landmass, as opposed to the central Western Interior Seaway (210 specimens: Russell, 1988 and Nicholls and Russell, 1990).

Lyman (2008) argued that NISP was perhaps the most powerful parameter (and perhaps the only parameter) to quantify taxonomic abundances among vertebrate fauna. It is possible for NISP to be used to reconstruct populations of predator and prey taxa among Late Cretaceous vertebrates in North America (e.g., smaller fishes being more common than larger top-level predatory fishes and marine reptiles in the food chain; see Table 6). The comparison of NISP of terrestrial vertebrates may demonstrate other unique taxonomic compositions near paleo-shoreline environments. In addition, NISP of various aquatic and terrestrial tetrapods exhibiting ectothermic or endothermic metabolisms may reflect a restriction to lower-latitudinal warm climates. However, various types of preservation and collecting biases can limit the effectiveness of using NISP in this manner (Nicholls and Russell, 1990).

Within our dataset of 8,275 vertebrate specimens, various types of biases are clearly involved. For example, the presence of the higher number of the marine reptiles, mosasaurs, in museum collections (Table 3; Fig. 5), as opposed to cartilaginous and bony fishes which would be much more abundant in a natural setting. This may reflect a collection, sampling, or preservation bias. Our personal observations suggest that reptilian specimens, even those with small or fragmentary remains, tend to be collected and added to museum collections more often than the remains of fish. Larger, and more dense, reptilian bones also tend to preserve better than small fish elements, presenting a possible preservation bias. Moreover, the collection of microscopic-size remains has largely been neglected in Alabama, representing a sampling bias (see Ciampaglio et al., this volume).

To reduce the risk of misinterpretation, comparisons of intra-taxonomic groups (e.g., reptiles vs. birds) are used here instead of those of inter-taxonomic groups (e.g., Actinopterygii vs. Chondrichthyes). This approach can offer at least a small view of the relative taxonomic abundances of Cretaceous vertebrates from Alabama. In a comparison between 1,234 lamniform sharks and 1,563 mosasaurs (Table 9), for example, most sharks (i.e., 94.9%) were identified at least to the generic level, in contrast to only 47.5% for mosasaurs. This contrast is even more noticeable when viewed at the specific level (72.0% for sharks; only 11.3% for mosasaurs). This is a result of an identification bias as, for most lamniform sharks, even a single, isolated tooth can often be assigned to species (e.g., Welton and Farish, 1993). A better understanding of key elements, diagnostic characteristics, and alpha taxonomy will certainly aid in future studies utilizing NISP in this manner.

CONCLUSIONS

The Cretaceous exposures in Alabama represent one of the southern-most regions of Upper Cretaceous marine and coastal strata in North America. Many of the Cretaceous units in Alabama are fossiliferous and have produced a diverse range of marine and terrestrial vertebrate taxa. Through the use of NISP, this preliminary investigation provides the following data and insights:

1. At least 8,275 vertebrate specimens from Upper Cretaceous marine and coastal strata of Alabama are currently housed at 12 different institutions (Table 2). These vertebrates include Chondrichthyes (25 gen. and 30 spp.; NISP = 2,150), Actinopterygii (23 gen. and 25 spp.; NISP = 2,607), Reptilia (32 gen. and 37 spp.; NISP = 3,174), and 339 specimens of uncertain taxonomic identification (Tables 3 and 4). Vertebrate taxa recorded from each stratigraphic unit are listed in Appendix 1.

2. Among the five units defined in this study (Table 7; Fig. 3), the most abundant in terms of fossil vertebrates collected is Unit 2 (the Mooreville Chalk and Blufftown Formation: lower to mid-Campanian) with 6,363 specimens (Table 7). The Eutaw Formation (Unit 1: Cenomanian–Santonian), which is the largest surface geology area, is represented by the second largest number of Cretaceous vertebrate specimens. Relative to surface exposures, Units 3 and 4 (the Demopolis Chalk and Ripley Formation) are the least fossiliferous in terms of vertebrates.

Table 9. Numbers of specimens with generic-level and indeterminate identifications in lamniform sharks and mosasaurs from Alabama.

	Lamniform sharks		Mosasaurs	
	number of specimens	per total	number of specimens	per total
Total	1234	100.00%	1561	100.00%
Genus identified	1171	94.89%	741	47.47%
Genus unidentified	63	5.11%	820	52.53%
Species identified	889	72.04%	176	11.27%
Species unidentified	345	27.96%	1385	88.73%

3. Reptilians (reptiles and birds) are the most abundant among the vertebrates (38.4% of all specimens) (Fig. 5). This number probably indicates a strong collecting, sampling, and/or preservation biases towards reptilian material. However, among 76 identified vertebrate genera found in this study (and 92 species), the small aulopiform bony fish, *Enchodus*, has the largest value of NISP (n = 770). This is likely the result of the ease of identifying the often well preserved palatine teeth of this taxon.

4. The phylogenetic relationships and taxonomic assignments of some species are ambiguous (Table 5) and many need to be clarified. New taxa are also being described and hundreds of specimens are still waiting to be prepared and catalogued at many of the institutions reviewed in this study. Better understanding of alpha taxonomy of Cretaceous vertebrates can increase the total number of recognized genera and species from Alabama (e.g., Ciampaglio et al., Hamm and Harrell, Jasinski, Schein et al., and Shimada in this *Bulletin*, Vol. 1 and 2).

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Appendix 1. Occurrences of vertebrates in Upper Cretaceous strata from Alabama. References used to confirm taxonomic identifications and stratigraphic occurrences are listed in Table 4. Ambiguous taxa listed in Table 5 are not included.

UNIT 1	
Eutaw Formation	
CHONDRICHTHYES	
Chimaeriformes	*Edaphodon* sp.
Heterodontiformes	*Heterodontus*(?) sp.
Hybodontidae	*Hybodus* sp., *Lissodus* (=*Lonchidion*?) sp., *Ptychodus mortoni*, *Ptychodus polygyrus*, *Ptychodus rugosus*
Orectolobiformes	*Cantioscyllium decipiens* (=*C. meyeri* or *C. saginatus*?)
	Chiloscyllium greeni
Lamniformes	*Carcharias* sp., *Cretodus semiplicatus*, *Cretalamna appendiculata*, *Cretalamna serrata*(?), *Cretoxyrhina mantelli*, *Paranomotodon angustidens*, *Pseudocorax laevis*, *Scapanorhynchus raphiodon*, *Scapanorhynchus texanus*, *Squalicorax falcatus*, *Squalicorax kaupi*, *Squalicorax pristodontus*
Squatiniformes	*Squatina hassei*
Myliobatiformes	*Brachyrhizodus mcnultyi*, *Brachyrhizodus wichitaensis* *Pseudohypolophus* (=*Brachyrhizodus*?) *mcnultyi*
Rajiformes	gen. indet.
Sclerorhynchiformes	*Borodinopristis schwimmeri*, *Ischyrhiza mira*, *Ptychotrygon triangularis* (= *P. vermiculata* and/or *P. chattahoochiensis*?), *Sclerorhynchus?* sp.
ACTINOPTERYGII	
Pycnodontiformes	*Anomoeodus phaseolus*, *Hadrodus priscus*, *Phacodus puncatatus*
Aspidorhynchiformes	*Belonostomus* sp.
Pachycormiformes	*Protosphyraena* sp.
Semionotiformes (or Lepisosteiformes?)	*Atractosteus* sp(?), *Lepisosteus* sp.
Tselfatiiformes	*Bananogmius* sp., *Plethodus* sp.
Ichthyodectiformes	*Xiphactinus audax*
Crossognathiformes	*Pachyrhizodus* sp.
Albuliformes	*Albula dunklei*
Aulopiformes	*Enchodus petrosus*, *Stratodus apicalis*
Coelacanthiformes	gen. indet.
REPTILIA	
Testudines	*Chedighaii barberi*, *Protostega gigas*, *Thinochelys* sp., *Toxochelys* sp., trionychid (gen. indet.)
Plesiosauria	*Discosaurus vetustus*, elasmosaurid (gen. indet.)
Mosasauridae	*Clidastes* sp., *Globidens alabamaensis*, *Halisaurus sternbergi*, *Platecarpus tympaniticus*, *Plioplatecarpus* sp., *Selmasaurus russelli*(?), *Tylosaurus nepaeolicus*, *Tylosaurus proriger*

Appendix 1. ***continued.***

	Crocodylia	*Borealosuchus* sp., *Deinosuchus rugosus*(?)
	Dinosauria	*Lophorhothon atopus*, hadrosaur (gen. indet.), nodosaur (gen. indet.)
UNIT 2		
Blufftown Formation		
CHONDRICHTHYES		
	Chimaeriformes	gen. indet.
	Hybodontiformes	*Hybodus* sp., *Lissodus* (=*Lonchidion*?) *babulski*
	Orectolobiformes	*Cantioscyllium* sp., *Chiloscyllium greeni*
	Lamniformes	*Cretalamna appendiculata*, *Cretoxyrhina mantelli*, *Scapanorhynchus raphiodon*, *Scapanorhynchus texanus*, *Squalicorax texanus*, *Squalicorax kaupi*, *Squalicorax pristodontus*
	Squatiniformes	*Squatina hassei*
	Myliobatiformes	*Brachyrhizodus mcnultyi*, *Brachyrhizodus wichitaensis*
	Rajiformes	gen. indet.
	Sclerorhynchiformes	*Borodinopristis schwimmeri*, *Ischyrhiza mira*, *Ptychotrygon vermiculata*
ACTINOPTERYGII		
	Pycnodontiformes	*Anomaeodus latidens*
	Pycnodontiformes	*Hadrodus priscus*
	Pachycormiformes	*Protosphyraena nitida*
	Semionotiformes (or Lepisosteiformes?)	*Lepisosteus* sp.
	Ichthyodectiformes	*Xiphactinus audax*
	Albuliformes	*Albula* sp.
	Aulopiformes	*Enchodus petrosus*
	Coelacanthiformes	*Megalocoelacanthus dobiei*
REPTILIA		
	Testudines	*Chedighaii barberi*
	Testudines	trionychid (gen. indet.)
	Plesiosauria	elasmosaurid (gen. indet.)
	Mosasauridae	*Clidastes propython*, *Globidens alabamaensis*, *Halisaurus sternbergi*, *Platecarpus* sp., *Tylosaurus* sp.
	Crocodylia	*Borealosuchus* sp., *Deinosuchus rugosus*
	Dinosauria	*Appalachiosaurus montgomeriensis*, hadrosaur (gen. indet.)
Mooreville Chalk		
CHONDRICHTHYES		
	Chimaeriformes	*Edaphodon barberi*, *Edaphodon mirificus*, *Ischyodus* sp.
	Hybodontiformes	*Ptychodus mortoni*, *Ptychodus polygyrus*, *Ptychodus rugosus*

Appendix 1. ***continued.***

	Lamniformes	*Cretalamna appendiculata*, *Cretoxyrhina mantelli*, *Cretoxyrhina* sp., *Paranomotodon angustidens*, *Pseudocorax affinis*, *Pseudocorax laevis*, *Scapanorhynchus rapax*, *Scapanorhynchus raphiodon*, *Scapanorhynchus texanus*, *Serratolamna serrata*, *Squalicorax falcatus*, *Squalicorax kaupi*, *Squalicorax pristodontus*
	Myliobatiformes	*Brachyrhizodus wichitaensis*, *Brachyrhizodus mcnultyi*
	Sclerorhynchiformes	*Ischyrhiza mira*, *Sclerorhynchus* sp.
ACTINOPTERYGII		
	Pycnodontiformes	*Anomoeodus phaseolus*, *Hadrodus priscus*, *Phacodus punctatus*
	Pachycormiformes	*Bonnerichthys gladius*, *Protosphyraena nitida*
	Semionotiformes (or Lepisosteiformes?)	*Lepisosteus* sp.
	Tselfatiiformes	*Bananogmius crieleyi*, *Moorevillia hardi*, *Palelops eutawensis*, *Plethodus* sp.
	Ichthyodectiformes	*Ichthyodectes* sp., *Saurocephalus* sp., *Saurodon leanus*, *Xiphactinus audax*
	Crossognathiformes	*Pachyrhizodus caninus*, *Pachyrhizodus kingi*, *Pachyrhizodus minimus*
	Albuliformes	*Albula dunklei*
	Aulopiformes	*Cimolichthys nepaholica*, *Enchodus ferox*, *Enchodus gladiolus*, *Enchodus petrosus*, *Enchodus shumardi*, *Stratodus apicalis*
	Beryciformes	*Hoplopteryx* sp.
	Coelacanthiformes	*Megalocoelacanthus dobiei*
REPTILIA		
	Testudines	*Chedighaii barberi*, *Calcarichelys gemma*, *Chedighaii* sp., *Chelosphargis advena*, *Corsochelys haliniches*, *Ctenochelys acris*, *Ctenochelys tenuitesta*, *Ctenochelys* sp., *Lophochelys venatrix*, *Prionochelys matutina*, *Prionochelys natua*, *Protostega gigas*, *Thinochelys lapisossea*, *Toxochelys moorevillensis*
	Plesiosauria	elasmosaurid (gen. indet), polycotylid (gen. indet.)
	Mosasauridae	*Clidastes liodontus*, *Clidastes moorevillensis*, *Clidastes propython*, *Eonatator sternbergi*, *Globidens alabamaensis*, *Halisaurus sternbergi*, *Mosasaurus*(?) sp., *Platecarpus tympaniticus*, *Plioplatecarpus* sp., *Prognathodon* sp., *Selmasaurus russelli*, *Tylosaurus proriger*, *Tylosaurus nepaeolicus*(?),
	Pterosauria	*Pteranodon* sp.
	Crocodylia	*Deinosuchus rugosus*
		Borealosuchus sp.
	Dinosauria	*Lophorhothon atopus*, hadrosaur (gen. inet.), nodosaur (gen. indet.), tyrannosaurid (gen. indet.), dromaeosaurid (gen. indet.)
	Aves	*Ichthyornis* sp., *Halimornis thompsoni*

Appendix 1. *continued.*

UNIT 3	
Demopolis Chalk (including the Bluffport Marl Member)	
CHONDRICHTHYES	
Chimaeriformes	
Lamniformes	*Cretalamna appendiculata*, *Scapanorhynchus texanus*, *Serratolamna serrata*(?), *Squalicorax kaupi*, *Squalicorax pristodontus*, *Squalicorax* sp.
Sclerorhynchiformes	*Ischyrhiza mira*
ACTINOPTERYGII	
Pachycormiformes	*Protosphyraena* sp.
Ichthyodectiformes	*Saurodon* sp., *Xiphactinus* sp.
Aulopiformes	*Enchodus ferox*, *Enchodus gladiolus*, *Enchodus petrosus*, *Stratodus* sp.
REPTILIA	
Testudines	*Chedighaii barberi*, *Ctenochelys* cf. *tennuitesta*, *Prionochelys matutina*(?), *Protostega gigas*
Mosasauridae	*Clidastes propython*, *Halisaurus* sp., *Mosasaurus conodon*, *Mosasaurus* cf. *missouriensis*, *Platecarpus* cf. *somenensis*, *Plioplatecarpus* sp., *Tylosaurus* sp.
Crocodylia	*Borealosuchus* sp.
Dinosauria	*Appalachiosaurus*(?) sp., hadrosaur (gen. inet.)
Cusseta Sand Member (of the Ripley Formation)	
CHONDRICHTHYES	
Hybodontiformes	*Ptychodus mortoni*
Lamniformes	*Cretalamna* sp., *Scapanorhynchus texanus*
REPTILIA	
Dinosauria	gen. indet.
UNIT 4	
Ripley Formation (excluding the Cusseta Sand Member)	
CHONDRICHTHYES	
Rajiformes	gen. indet.
Orectolobiformes	*Ginglymostoma*
Lamniformes	*Cretalamna appendiculata*, *Pseudocorax laevis*, *Scapanorhynchus raphiodon*, *Scapanorhynchus texanus*, *Squalicorax pristiodontus*
Myliobatiformes	*Brachyrhizodus* cf. *witchitaensis*
Sclerorhynchiformes	*Ischyrhiza mira*
ACTINOPTERYGII	
Pycnodontiformes	*Anomoeodus phaseolus*
Ichthyodectiformes	*Xiphactinus* sp.

Appendix 1. ***continued.***

Aulopiformes	*Enchodus ferox*, *Enchodus petrosus*
REPTILIA	
Testudines	*Ctenochelys* sp., *Protostega gigas*
Mosasauridae	*Mosasaurus maximus*, *Plioplatecarpus* sp., *Tylosaurus*(?) sp.
Crocodylia	*Deinosuchus rugosus*
Dinosauria	nodosaur (gen. indet.), hadrosaur (gen. indet.)
UNIT 5	
Prairie Bluff Chalk	
CHONDRICHTHYES	
Hybodontidae	*Hybodus* sp., *Ptychodus mortoni*
Lamniformes	*Cretalamna appendiculata*, *Cretodus* sp., *Paranomotodon angustidens*, *Scapanorhynchus texanus*, *Serratolamna serrata*, *Squalicorax kaupi*, *Squalicorax pristodontus*
Myliobatiformes	*Pseudohypolophus* (=*Brachyrhizodus*?) *mcnultyi*
Orectolobiformes	*Ginglymostoma* sp.
Rajiformes	gen. indet.
Sclerorhynchiformes	*Ischyrhiza mira*, *Sclerorhynchus* sp.
ACTINOPTERYGII	
Pycnodontiformes	*Anomoeodus phaseolus*
Aulopiformes	*Enchodus ferox*
REPTILIA	
Plesiosauria	elasmosaurid (gen. indet.; *Cimoliasaurus*?)
Testudines	gen. indet.
Mosasauridae	*Mosasaurus conodon*, *Mosasaurus maximus*, *Plioplatecarpus* sp.
Aves	gen. indet.
Providence Sand	
CHONDRICHTHYES	
Lamniformes	gen. indet.
OSTEICHTHYES	
indet.	gen. indet.
REPTILIA	
Mosasauridae	gen. indet.

Chondrichthyan Origin for the Fossil Record of the Tselfatiiform Osteichthyan Fish, *Thryptodus zitteli* Loomis, from the Upper Cretaceous Mooreville Chalk of Alabama

KENSHU SHIMADA

Department of Environmental Science and Studies and Department of Biological Sciences, DePaul University, 2325 North Clifton Avenue, Chicago, Illinois 60614, U.S.A.; and Sternberg Museum of Natural History, Fort Hays State University, Hays, Kansas 67601, U.S.A., kshimada@depaul.edu

ABSTRACT

The geologically youngest record of *Thryptodus* Loomis, a Late Cretaceous bony fish genus (Tselfatiiformes), is from the Campanian portion of the Mooreville Chalk of Alabama. A re-examination of the sole material representing this youngest record reveals that the specimen consists of calcified cartilage prisms, indicating that it belongs to a chondrichthyan fish rather than to an osteichthyan. The re-identification made here thus concomitantly eliminates the only Campanian record for *Thryptodus* and emends its chronostratigraphic range to late middle Cenomanian through late Coniacian. The specimen closely resembles a skeletal part of a putative anacoracid shark (genus and species indeterminate) from the Mooreville Chalk of Alabama, suggesting that it may belong to Anacoracidae.

INTRODUCTION

Thryptodus Loomis, 1900 (Tselfatiiformes: Plethodidae) is an uncommon Late Cretaceous bony fish genus, which is characterized by a broad, blunt rostrum consisting of fused left and right premaxillae (Taverne, 2003; Shimada and Schumacher, 2003). The genus was first described by Loomis (1900) on the basis of two species, *T. rotundus* and *T. zitteli*, each represented only by the holotype from the Niobrara Chalk of western Kansas. The type specimens for both species were later destroyed during World War II in Germany, but *T. rotundus* is now interpreted to belong to another plethodid genus, *Plethodus* Dixon, 1850 (Dixon 1850; Taverne, 2000; Taverne and Gayet, 2005). Therefore, although the holotype that is represented by an articulated partial skull (Loomis, 1900) is no longer in existence, the only known species of *Thryptodus* to date is *T. zitteli*, and five more recently found rostral specimens support the occurrence of the species from the Niobrara Chalk of western Kansas (Taverne, 2000, 2003; Everhart, 2005:96; Shimada and Fielitz, 2006).

The occurrence of *Thryptodus* is not limited to the Niobrara Chalk or to Kansas. Shimada and Schumacher (2003) described a rostrum of "*Thryptodus* cf. *T. zitteli*" from near the base of the Greenhorn Limestone (upper Cenomanian) of Kansas that represents the geologically oldest record for *Thryptodus*. Although referable materials remain to be properly described, *Thryptodus* is purportedly known to occur in Cenomanian–Turonian deposits of Texas (McKinzie, 2002). In his review of fossil fishes from the Mooreville Chalk (upper Santonian – lower Campanian) of Alabama, Applegate (1970) described a specimen as "*Bananogmius* cf. *zitteli*." This specimen was subsequently referred to *T. zitteli* and has marked the geologically youngest record for the genus (Taverne and Gayet, 2005).

The only description that Applegate (1970:416) gave of the specimen from the Mooreville Chalk was: "This large pitted snout is too fragmentary for positive identification; however, it resembles closely the rostrum of the fish described by Loomis (1900:229–234, Pl.XXI)." This

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Figure 1. FMNH PF 3609 A), reported by Applegate (1970) and previously known as the sole rostral specimen of *Thryptodus zitteli* Loomis from Mooreville Chalk of Alabama (Taverne and Gayet, 2005) compared with KUVP 459; B), rostrum of *T. zitteli* from the Niobrara Chalk of Kansas (orientations: dorsal, ventral, anterior, posterior, and right lateral views from top to bottom).

specimen (Fig. 1A) is housed in the Field Museum of Natural History (FMNH), Chicago, Illinois. Recently, it was re-examined by the author, and it was revealed that the specimen does not belong to *Thryptodus*, but to a cartilaginous fish—possibly an anacoracid shark. The aim of this paper is to document this reinterpretation, and to revise the temporal range of *Thryptodus*. In addition to the FMNH specimen, one comparative specimen in each of the following two institutions is referred to in this paper: Auburn University Museum of Paleontology (AUMP), Auburn, Alabama; and the vertebrate paleontology collection of the University of Kansas Museum of Natural History (KUVP), Lawrence.

SYSTEMATIC PALEONTOLOGY

Class CHONDRICHTHYES Huxley, 1880
Subclass ELASMOBRANCHII Bonaparte, 1838
Cohort EUSELACHII Hay, 1902
Subcohort NEOSELACHII Compagno, 1977
Order LAMNIFORMES(?) Berg, 1958
Family ANACORACIDAE(?) Casier, 1947
Genus and species indeterminate
(Fig. 1A)

Material—FMNH PF 3609, rostral portion of neurocranium, initially described as "snout" of *Bananogmius* cf. *zitteli* Loomis by Applegate (1970), housed in Field Museum of Natural History, Chicago, Illinois.

Occurrence—Middle part (presumably lowest Campanian portion) of Mooreville Chalk (for stratigraphy, see Puckett, 1994; Mancini et al., 1995), Dallas County, Alabama.

Description—The specimen (Fig. 1A) is symmetrical overall and measures 115 mm in maximum preserved width and 53 mm in maximum preserved anteroposterior length. The presumed anterior end, which is gently arched when viewed dorsally or ventrally, is flat and relatively smooth. The presumed dorsal and ventral surfaces are also relatively flat but are ornamented by many faint, shallow depressions that are randomly distributed. The posterior side of the specimen represents broken surfaces, revealing that the specimen consists of one outer layer of 4-mm-thick, polygonal blocks encircling another layer of the same type of blocks that is folded to form two layers (more evident on the right half of the specimen). These blocks are not bony but rather crystalline, and are identified as calcified cartilage prisms.

RESULTS AND DISCUSSION

Externally, the specimen (FMNH PF 3609: Fig. 1A) resembles the rostrum of *Thryptodus zitteli* reported primarily from the Niobrara Chalk of western Kansas (e.g., Fig. 1B). However, the composition of the entire specimen as calcified cartilage prisms (i.e., not bony) is unequivocal evidence that it does not come from an osteichthyan fish, but rather from a chondrichthyan. Although the variation in texture of calcified cartilage prisms has not been adequately surveyed in extant and extinct chondrichthyans (cf. Applegate, 1967), I note that the morphology of the calcified cartilage prisms that make up FMNH PF 3609 (at least on the basis of broken surfaces exposed posteriorly) is consistent at least with that of Late Cretaceous neoselachian sharks, such as anacoracids and cretoxyrhinids, found in Upper Cretaceous marine deposits in North America (e.g., Shimada, 1997, 2007; Shimada and Cicimurri, 2005).

Besides the compositional difference (i.e., calcified cartilage vs. bone), there are also differences between FMNH PF 3609 and the rostrum of *Thryptodus zitteli* in the texture of exterior surfaces. The dorsal and ventral surfaces in both FMNH PF 3609 and the rostrum of *T. zitteli* show many depressions. However, the depressions in *T. zitteli* are characterized by densely-distributed, fine, well-defined pits (Fig. 1B), whereas those in FMNH PF 3609 are represented by sparsely-distributed, shallow, faint pits (Fig. 1A). In addition, the fine pits of the rostrum of *T. zitteli* are locally aligned to form a linear pattern that gives a bony appearance, whereas the shallow pits in FMNH PF 3609 are overall randomly distributed.

The occurrence of a *Thryptodus* specimen from near the base of the Greenhorn Limestone in Kansas (Shimada and Schumacher, 2003) demonstrates that the genus was already in existence by the late middle Cenomanian (ca. 95 Ma: Kauffman et al., 1993), and materials from Texas substantiate the existence of *Thryptodus* through the Turonian (McKinzie, 2002). In the Niobrara Chalk of Kansas, Stewart (1990:29) listed *T. zitteli* (identified as "*Bananogmius zitteli*" in his paper) to occur only in his biostratigraphical zone of *Protosphyraena perniciosa* (Cope). This zone ranges the lowest part of the Smoky Hill Chalk Member in the formation, and is considered late Coniacian in age (Stewart, 1988). "*Bananogmius* cf. *zitteli*" from the Mooreville Chalk (presumably from the lowest Campanian portion) of Alabama on the basis of FMNH PF 3609 (Applegate, 1970) previously marked the geologically youngest occurrence for *Thryptodus* (Taverne and Gayet, 2005). However, the re-identification of the specimen made in this present paper eliminates the Campanian record for the genus. Therefore, the emended chronostratigraphic range for *Thryptodus* is from late middle Cenomanian through late Coniacian based on the present fossil record.

Based on Applegate (1970), Meyer (1974), and Thurmond and Jones' (1981) work, Russell (1988) listed the following chondrichthyan genera from the Mooreville Chalk of Alabama: *Edaphodon* (Chimaeridae), *Ptychodus* (Ptychodontidae), *Chiloscyllium* (Hemiscyllidae), *Cantioscyllium*

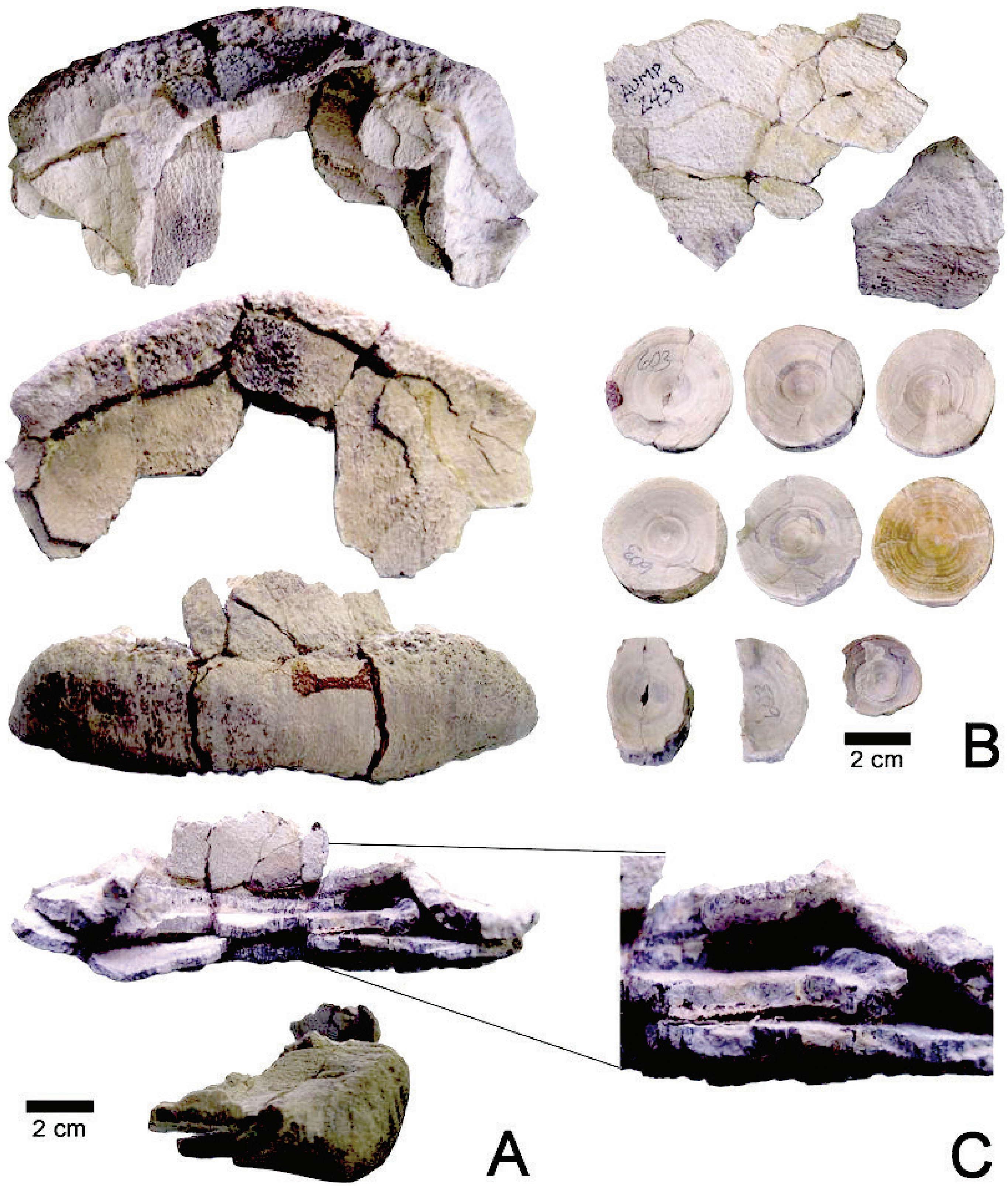

Figure 2. AUMP 2438, skeletal elements of a shark (Anacoracidae?) from the Mooreville Chalk of Alabama. A), rostrum (orientations: dorsal, ventral, anterior, posterior, and right lateral views from top to bottom); B), rest of specimen (two fragments of calcified cartilage sheets and nine vertebrae); C), close-up view of part of rostrum in posterior view.

(Ginglymostomatidae), *Rhincodon* (Rhincodontidae), *Scapanorhynchus* (Mitsukurinidae), cf. *Odontaspis* (Odontaspididae), *Anomotodon* (Alopiidae), *Pseudocorax*, *Squalicorax* (Anacoracidae), *Cretoxyrhina* (Cretoxyrhinidae), *Cretalamna* (Otodontidae?), cf. *Mustelus* and/or *Triakis* sp. (Triakidae), *Rhinobatos* (Rhinobatidae), *Pseudohypolophus* (Rhinobatoidei), *Ptychotrygon*, *Sclerorhynchus* (Sclerorhynchidae), and *Hypolophus* (Dasyatidae). Whether or not the exact taxonomic identity of FMNH PF 3609 lies within these listed taxa is uncertain. However, I here assign FMNH PF 3609 tentatively to Anacoracidae. The justification comes from my observation on AUMP 2438, a skeletal specimen of a probable anacoracid shark (Fig. 2) from the Mooreville Chalk in Dallas County, Alabama. Although AUMP 2438 does not preserve any teeth (that could have decisively allowed its taxonomic identification at least to the genus-level), it is identified as an anacoracid shark based on the similarity of its preserved vertebrae (Fig. 2B) to those of the anacoracid genus *Squalicorax* in size and morphology (e.g., see Applegate, 1970:fig. 179B; Welton and Farish, 1993:figs. 25A, 25D, 26B; Shimada and Cicimurri, 2005). Among the skeletal parts preserved in AUMP 2438 (Fig. 2A) is a nearly identical element to FMNH PF 3609 (cf. Fig. 1A). Like FMNH PF 3609, the posterior view of AUMP 2438 (Fig. 1C) exhibits one outer layer of calcified cartilage prisms encircling another layer of calcified cartilage prisms that is folded to form two layers. Whereas such a skeletal element has not been recognized in *Squalicorax* (see Shimada and Cicimurri, 2005), the only skeletal part which the element may represent is the rostral end of the neurocranium. Although *Squalicorax* is generally identified as a lamniform shark, the taxon may belong to Carcharhiniformes (Shimada and Cicimurri, 2005). Regardless, one can interpret the inner layer of calcified cartilage prisms, which is folded to form a circular pattern, as the anterior extremity of the tripodal rostrum typically observed in Lamniformes and Carcharhiniformes (Compagno, 1988). If so, the outer layer of calcified cartilage prisms could represent 'hypercalcification' that commonly occurs in a number of extant lamniform and carcharhiniform species (see Compagno, 1988). Regardless of the anatomical identity of the skeletal element, its association with anacoracid-type vertebrae warrants the likelihood that AUMP 2438 comes from an anacoracid shark. Given the structural similarity to AUMP 2438, FMNH PF 3609 is taxonomically assigned to Anacoracidae.

CONCLUSIONS

The geologically youngest rostral specimen of *Thryptodus* is found to consist of calcified cartilage prisms, suggesting that it belongs to a chondrichthyan fish rather than to an osteichthyan. As a result, the only Campanian record for *Thryptodus* is eliminated, emending its chronostratigraphic range to late middle Cenomanian through late Coniacian. The specimen closely resembles a putative rostral cartilage of an anacoracid shark from the Mooreville Chalk of Alabama, indicating that it may belong to Anacoracidae.

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A Nearly Complete Skull of *Enchodus ferox* (Actinopterygii, Aulopiformes) from the Upper Cretaceous Ripley Formation of Lowndes County, Alabama

JASON P. SCHEIN*,[1], DAVID C. PARRIS[1], JASON C. POOLE[2], and KENNETH J. LACOVARA[3]

[1]Bureau of Natural History, New Jersey State Museum, 205 West State Street,
Trenton, New Jersey, 08625, Jason.Schein@sos.state.nj.us, David.Parris@sos.state.nj.us;

[2]Academy of Natural Sciences of Drexel University, 1900 Benjamin Franklin Parkway,
Philadelphia, Pennsylvania, 19103, jpoole@ansp.org,

[3]Department of Biodiversity, Earth & Environmental Science, Drexel University,
3141 Chestnut Street, Philadelphia, Pennsylvania, 19104, lacovara@drexel.edu;

*Corresponding author.

ABSTRACT

Remains of the aulopiform bony fish *Enchodus* are very often the most common vertebrate fossils recovered from Late Cretaceous marine deposits around the world, especially in North America. Yet, those remains rarely consist of anything other than isolated dermopalatine bones and teeth. Here we report the discovery of an exceptionally well-preserved *Enchodus ferox* skull in a phosphatic concretion from the lower Ripley Formation (lower Maastrichtian) of Alabama. The specimen is significant because it preserves most of the cranial elements in their original, articulated positions. The specimen reveals characteristics that appear to be common to the genus including a robust skull with massive preoperculars and maxillae, large metapterygoids, fusion of the dentaries to the articulars, and paired sclerotic rings. The enlarged dermopalatine bones and "fangs" are not visible, but are likely preserved within the concretion, suggesting that they may be positioned more medially and posteriorly in the oral cavity than is sometimes depicted. The morphology suggests a specialized feeding behavior and prey, with the enlarged dermopalatine and mandible teeth being well adapted for piercing, holding, and aligning straight cephalopods for most efficient ingestion.

INTRODUCTION

Enchodus Agassiz, 1835 is an elongate, fusiform, laterally compressed teleost genus (Aulopiformes: Enchodontidae) that reached 1 m in length (Goody, 1976). The genus has been found in Late Cretaceous marine sediments on every continent except Antarctica and Australia (Williston, 1900; Woodward, 1902; Fowler, 1911; Raab, 1967; Goody, 1968, 1969, 1976; Thurmond and Jones, 1981; Raab and Chalifa, 1987; Chalifa, 1989, 1996; Fielitz, 1996, 1997; Cavin, 1999; Parris et al., 2007), although recent discoveries may have placed its earliest occurrence in the Albian (Fielitz and González-Rodríguez, 2010). The genus is particularly common in North America (e.g., Williston, 1900; Hay, 1903; McNulty and Kienzlen, 1969; Goody, 1976; Case and Schwimmer, 1988; Chalifa, 1989; Williamson and Lucas, 1990; Fishman et al., 1995), where its remains are found regularly in marine strata, and are often the most common vertebrate remains in those stratigraphic units (Hay, 1903; Applegate, 1970; Thurmond and Jones, 1981; Case and Schwimmer, 1988; Williamson and Lucas, 1990; Schein, 2004; Schein and Lewis, 2007). It is characterized by greatly enlarged, tumid, and dense dermopalatine bones each with a single, straight palatine tooth that is directed ventrally (Williston, 1900; Hay, 1903; Fowler, 1911; Goody, 1976; Fielitz, 2002). The durability of the

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dermopalatine bone and tooth largely accounts for the fish's abundance and makes the remains useful as guide fossils (Grandstaff et al., 1990; Schein, 2004; Schein and Lewis, 2007). Non-tooth bearing elements of *Enchodus* are not common or are often misidentified (Schein, 2004, Schein and Lewis, 2007).

A nearly complete skull identified as an *Enchodus ferox* Leidy, 1855 was recovered from the lower Ripley Formation in Alabama. The specimen (MSC 9514) is significant because it includes the majority of an articulated skull, well-preserved within a phosphatic concretion. Here we describe the specimen and discuss the paleoecological implications of its morphology, including potential prey preference and feeding behavior.

Institutional Abbreviations—MSC, McWane Science Center, Birmingham, Alabama.

Anatomical Abbreviations—dpt, dermopalatine tooth; **fr,** frontal; **hyo,** hyomandibular; **ma,** mandible; **mpt,** metapterygoid; **msc,** mandibular sensory canal; **mx,** maxilla; **na,** nasal; **op,** opercle; **par,** parasphenoid; **pmx,** premaxilla; **pop,** preopercle; **scr,** sclerotic ring; **sop;** subopercle.

SYSTEMATIC PALEONTOLOGY

Class OSTEICHTHYES
Subclass ACTINOPTERYGII
Subdivision TELEOSTEI Müller, 1846
Order AULOPIFORMES Woodward, 1901
Suborder ALEPISAUROIDEI Rosen, 1973
Superfamily ALEPISAUROIDEA Rosen, 1973
Family ENCHODONTIDAE Woodward, 1901; *sedis mutabilis*
Subfamily ENCHODONTINAE Fielitz, 1999
Genus ENCHODUS Agassiz, 1835
ENCHODUS FEROX Leidy, 1855
(Figs. 1–4, Table 1)

Enchodus ferox Leidy, 1855, p. 397
Enchodus pressidens Cope, 1869, p. 241
Enchodus serrulatus Fowler, 1911, p. 162, fig. 98

Referred Material—MSC 9514, a partial skull, laterally compressed and preserved within a phosphatic concretion, including portions of the neurocranium, opercle, preopercle, metapterygoid, hyomandibular, frontals, nasals, sclerotic rings, premaxilla, and the jaws (note: this specimen was previously identified as *Enchodus* sp. cf. *E. ferox* in Schein, 2004).

Locality—Dry Cedar Creek, Lowndes County, Alabama, U.S.A.

Horizon—Ripley Formation (Campanian-Maastrichtian), from a concretion-bearing mudstone horizon within the lower portions of the unit (Hall and Savrda, 2008).

Diagnosis—Following Parris et al. (2007), this specimen is referable to *Enchodus ferox* based on its lack of maxillary teeth and by its possession of a deep, longitudinal mandibular sensory canal near the occlusal margin of the dentary.

DESCRIPTION

MSC 9514 measures 15.9 cm in greatest length and 13.65 cm in greatest depth (Figures 1–4). The specimen is taphonomically laterally compressed, measuring approximately 4.08 cm in its greatest width. It is also slightly sheared, with some elements on the left side of the skull, including the dentary and premaxilla, being displaced ventrally approximately 1 cm relative to their counterparts on the right side. An estimated 1.5 cm of the anterior-most portions of the mandibles, including the symphysis, and 25% of the posterior portion of the skull, are missing based on published illustrations of *Enchodus* specimens (e.g., Goody, 1976, Willimon, 1973; Fielitz and González-Rodríguez, 2010). In general, only the external bones of the skull are visible, with more medial elements either preserved within the concretion or completely replaced by it. All of the visible bone material is articulated or nearly so.

The neurocranium is substantially compressed and ornamentation in the form of radiating ridges is present locally. The suture between the frontals and nasals is difficult to distinguish, but may be subequal with the anterior margins of the orbits. The frontals are crushed and their posterior margins cannot be identified. A short portion (approximately 3.0 cm) of the parasphenoid is visible within the left orbit, and extends slightly posterior to the posterior sclerotic ring. The premaxilla bears a row of small (< 2 mm) marginal teeth along its lateral edge and larger teeth more medially. It is longer than high, with the posterior process extending approximately one half of the distance of the gape. The maxilla is straight, toothless, has a deep groove along its entire length, and extends anterodorsally approximately 75% of the length of the gape from its intersection with the mandible. The suture between the dentary and articular is difficult to discern and the elements may be fused, forming a single mandibular element bearing both large (> 0.5 cm) primary and small (< 0.2 cm) marginal teeth. The mandibular sensory canal is a deep, open, longitudinal groove near the dorsal margins of the mandibles. Primary teeth are slender, straight, and placed more medially than the marginal teeth. Marginal teeth are located on the lateral edge of the mandibles and are more uniform in size, shape, and spacing than the primary teeth. All teeth are acrodont. The orbital bones are fused into a pair of subequal and semicircular sclerotic rings, and the metapterygoid covers most of the area between the sclerotic ring and the preopercle. The hyomandibular is visible on the right side of the skull but is mostly overlain posteriorly by the preoper-

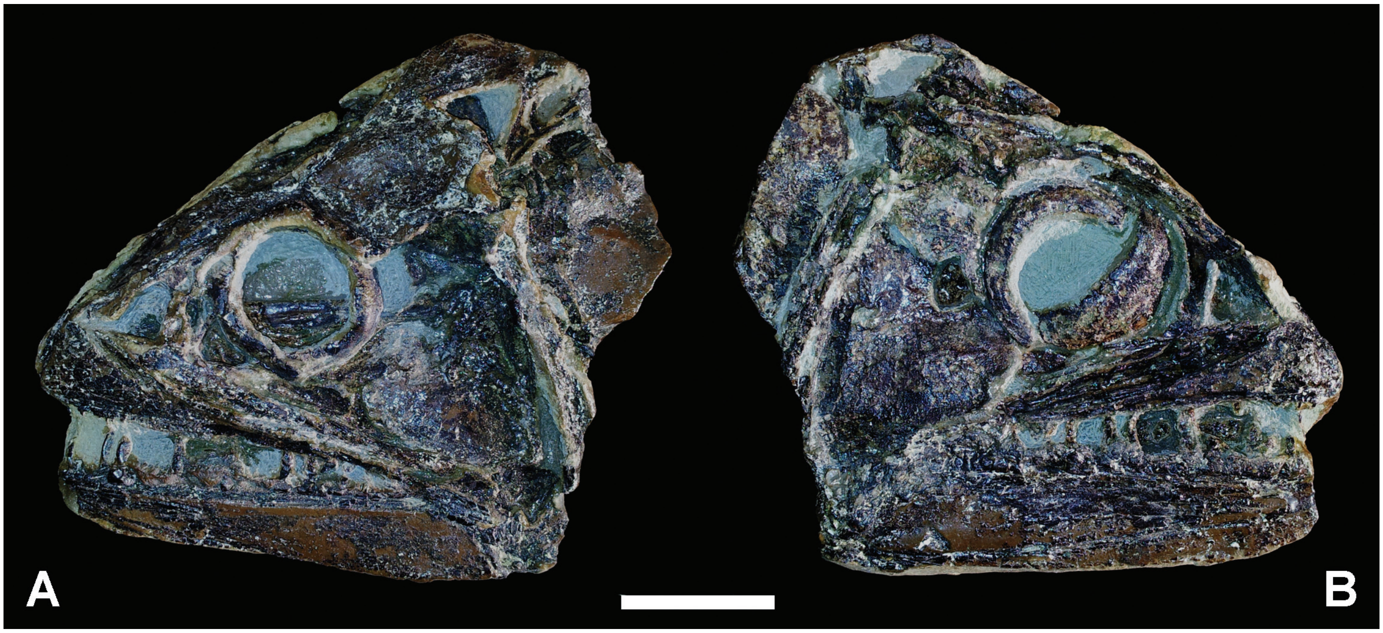

Figure 1. Photograph of MSC 9514, a skull of *Enchodus ferox* from the lower Ripley Formation of Lowndes County, Alabama. A, left-lateral view; B, right-lateral view. Scale equals 3 cm.

cle. Sutures separating the hyomandibular and the symplectic are not visible. The preopercle is uniform in thickness and forms a prominent ridge projecting dorsally to the same level as the dorsal edge of the sclerotic ring. An estimated 33% of the ventral portion of the left preopercle is missing, and approximately 50% is missing from the right preopercle, based on published illustrations of complete *Enchodus* skulls. There appears to be little overlap between skull elements, and no interfingering of adjacent elements.

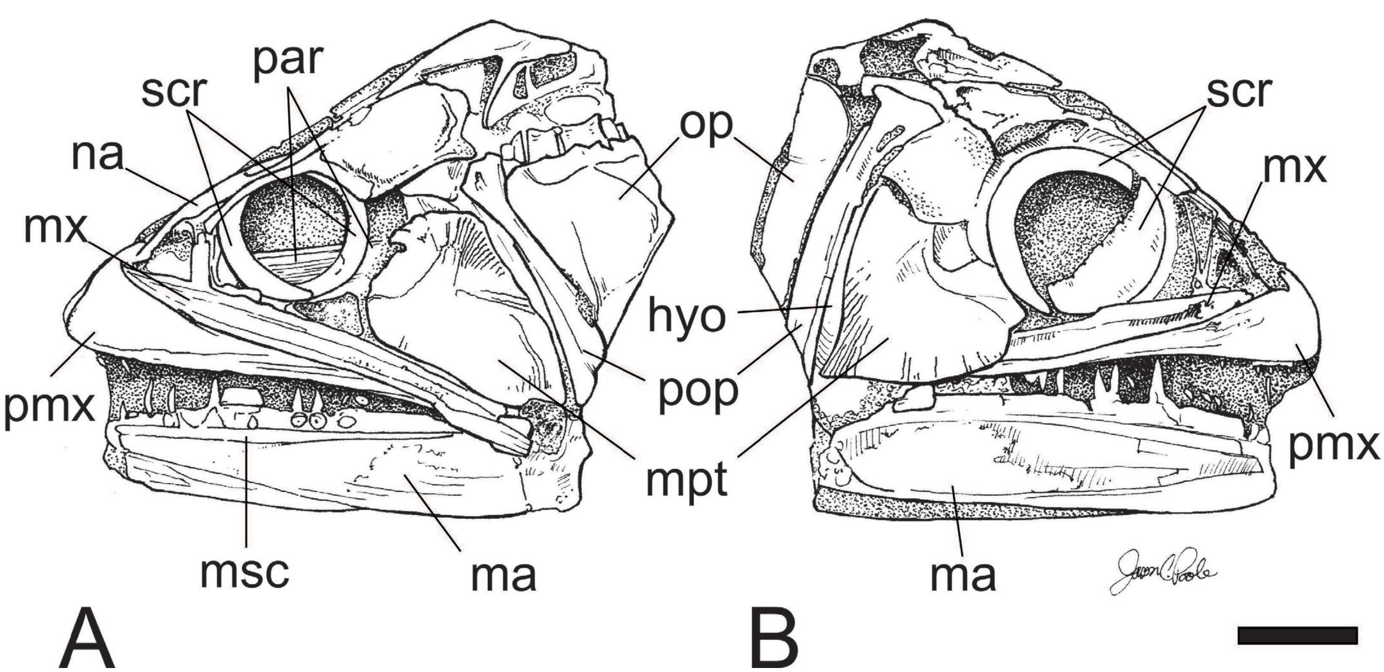

Figure 2. Line drawings of MSC 9514. A, left-lateral view; B, right-lateral view. Scale equals 3 cm.

DISCUSSION

With its exceptional state of preservation, MSC 9514 provides the most complete picture of *Enchodus ferox* skull morphology known to date. The skull of *E. ferox* is composed of numerous robust elements. Orbital bones are fused into paired sclerotic rings and the metapterygoid covers most of the region between the sclerotic rings and the preopercular (Fig. 2). The preopercular is thick and positioned posterior to the very large metapterygoid, providing an expansive area for jaw musculature; specifically, the adductor mandibulae (Eaton, 1935). The maxilla is straight and stout, and the dentary is fused to the articular. All teeth are fused to their respective elements. These features, in addition to the characteristically dense and durable dermopalatine bones and teeth that are diagnostic of the genus, produce a skull that is very robust.

This specimen also provides a number of insights for the genus. For example, MSC 9514 clearly shows the thick, paired, bipartite, nature of the sclerotic rings. The only other *Enchodus* specimen known to preserve these elements is described by Fielitz and González-Rodríguez (2010). Paired sclerotic rings appear to be common among the genus and are not a specific character.

The dermopalatine bones and teeth are not visible in this specimen. Considering the exceptional state of preservation, with most or all of the skull elements being present and articulated, it is likely that these large, dense, durable elements are preserved within the concretion. This suggests that their position in life is completely within the mouth, positioned sufficiently medially and posteriorly so that the teeth do not extend outside of the mandibles. This arrangement is at odds with that proposed by Goody (1976), in which he illustrated the dermopalatine bone and tooth as being located at the anterior ends of the mouth. That illustration has helped to perpetuate the common view of *Enchodus* as being the "saber-toothed salmon." The more medial and posterior placement of the dermopalatine elements, as suggested by MSC 9514, agrees more with the position illustrated by other authors (e.g., Willimon, 1973; Chalifa, 1989; Cavin, 1999; Fielitz and González-Rodríguez, 2010).

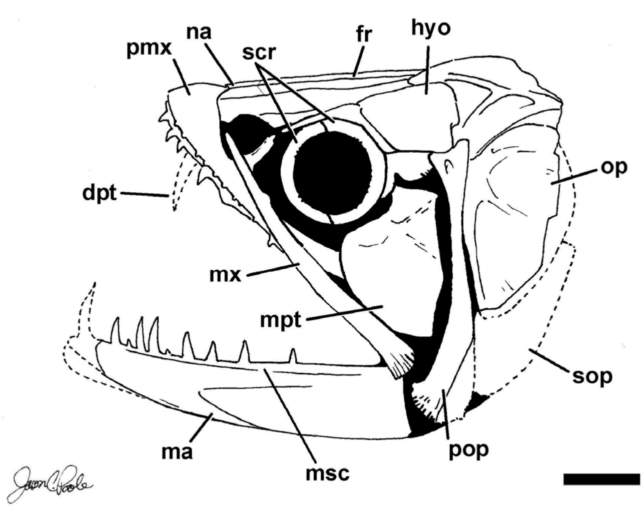

Figure 3. *Enchodus ferox*. Restoration of the skull in left-lateral view, based on MSC 9514. Scale equals 3 cm.

Figure 4. Artistic interpretation of *Enchodus ferox*.

The highly stout nature of *Enchodus* skulls suggests the prey that they pursued was at least somewhat resistant to bite forces. Goody (1976) surmised that the elongated body form and enlarged, interlocking teeth of *Enchodus* spp. indicate that it was an open water pelagic predator. Grandstaff et al. (1990) took this interpretation a step further, suggesting that the sturdiness of certain skull elements and abrasions on the dermopalatine teeth of some specimens is evidence of predation on fast-swimming cephalopods. We believe robust skull elements present in MSC 9514 support this hypothesis. The dermopalatine teeth were sufficiently sturdy for piercing cephalopod shells, yet sufficiently knife-like to be well adapted for seizing and holding struggling, soft-bodied prey. The placement of the dermopalatine teeth near the midline of the mouth, in conjunction with the more anteriorly-positioned enlarged dentary teeth, may have been useful for destroying the living chamber of straight cephalopods, separating its body from the shell, and holding the struggling prey in the proper orientation for ingestion. Furthermore, the autapomorphies used to differentiate *Enchodus* spp., including the presence or absence of postapical barbs on the palatine teeth, tooth serrations, and tooth symmetry may indicate niche separation in terms of the cephalopod species pursued and/or feeding strategies.

CONCLUSIONS

Despite very often being the most common vertebrate fossil in Upper Cretaceous marine strata around the world, and being known for over 150 years, there is still much to be learned about the morphology and paleoecology of *Enchodus*. MSC 9514 provides an unprecedented look at the cranial morphology of *Enchodus ferox* and provides insights into possible feeding habits of the genus. The massively-constructed skeletal elements reveal a robust skull, presumably adapted for predation on resistant prey. The dermopalatine bones and teeth, which are the most diagnostic features of this fish, are positioned more medially and posteriorly in the oral cavity than was suggested by Goody's (1976) reconstructions of *E. petrosus*. These teeth, along with the enlarged, paired anterior dentary teeth, may have formed a lethal piercing and holding structure for a preferred prey of straight-shelled cephalopods. More relatively complete *Enchodus* specimens are needed to allow us greater insights into the morphology and paleobiology of this ubiquitous teleost.

ACKNOWLEDGMENTS

We thank the McWane Science Center for the loan of MSC 9514 and for the opportunity to study it. We also thank the reviewers of this manuscript, which was undoubtedly improved with their contributions, as well as Jun Ebersole and Takehito Ikejiri for inviting us to submit an article for this volume.

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A Note on Late Cretaceous Fish Taxa Recovered from Stream Gravels at Site AGr-43 in Greene County, Alabama

CHARLES N. CIAMPAGALIO[1]*, DAVID J. CICIMURRI[2], JUN A. EBERSOLE[3], and KATELYN E. RUNYON[1]**

[1]Wright State University, 7600 Lake Campus Drive, Celina, Ohio 45822, *chuck.ciampaglio@wright.edu, **runyon.15@wright.edu;

[2]South Carolina State Museum, 301 Gervais Street, Columbia, South Carolina 29201, dave.cicimurri@scmuseum.org;

[3]McWane Science Center, 200 19th Street North, Birmingham, Alabama 35203, jebersole@mcwane.org.

*Corresponding author.

ABSTRACT

AGr-43 is a fossil site located within a stream in central Greene County, Alabama that is bounded by the Black Warrior River to the east and the Tombigbee River to the west. The stream bed consists of fossil-rich gravel that contains large quantities of Cretaceous elasmobranch and bony fish remains, reptile and invertebrate remains, as well as carbonate and siliciclastic lithic fragments. Much of this material likely originates from the Tombigbee Sand Member of the Eutaw Formation (late Santonian to early Campanian), but some could be derived from the overlying Mooreville Chalk (late Santonian to early Campanian). Stream gravels were collected in bulk and later screened, picked, and sorted in the lab. Thus far, 28 Cretaceous fish taxa have been identified from these gravels, 22 of which are elasmobranchs and the remaining six are osteichthyans. Eleven of the specimens we discuss represent new published records for Alabama. These taxa include: *Archaeolamna kopingensis*, *Anomoeodus barberi*, *Borodinopristis* cf *ackermani*., *Carcharias* sp., *Ischyrhiza* aff. *avonicola*, *Lonchidion* sp., *Meristodonoides* sp., *Micropycnodon* sp.?, "*Pseudohypolophus*" *ellipsis*, *Squalicorax* aff. *yangaensis*, and *Texatrygon* sp. Furthermore, the identification of *Chiloscyllium* sp. and *Ischyrhiza* aff. *mira* represent the first of these taxa reported from the Tombigbee Sand of Alabama. The identification of these 28 taxa from site AGr-43 aids in our understanding of Late Cretaceous paleobiodiversity, biostratigraphy, and paleobiogeography within the Mississippi Embayment and Western Interior Seaway.

INTRODUCTION

Greene County, Alabama is dissected by numerous small creeks and tributaries that are bounded by the Black Warrior River to the east and the Tombigbee River to the west. Within one of these tributaries is a small stretch of creek bed that contains numerous gravel bars that are predominantly exposed during low water. The gravel bars at this locality, identified as site AGr-43 (Fig. 1), contain large quantities of well-preserved Late Cretaceous fossils, including teeth, denticles, scales, and vertebrae of elasmobranchs and bony fish as well as remains from reptiles and invertebrates (for more detailed locality information on site AGr-43, qualified researchers may contact the Alabama Museum of Natural History in Tuscaloosa or McWane Science Center in Birmingham).

The creek in which site AGr-43 is located, cuts through the basal portion of the Mooreville Chalk and the underlying Tombigbee Sand Member of the Eutaw Formation (Fig. 2). In addition to Cretaceous fossils, the gravel bars within the creek consist of quartz pebbles, glauconite-rich sand, carbonate fragments, and silty gray clay clasts that can be traced to the Tombigbee Sand. Other components include lithologic remnants that are consistent with the Mooreville Chalk.

The diversity of elasmobranch and osteichthyan taxa in the gravel bars at AGr-43 are similar to those from the Mooreville Chalk of Alabama (Applegate, 1970; Meyer, 1974; Nicholls and Russell, 1990), and the Eutaw (Case et al., 2001) and Blufftown formations (eastern equivalent

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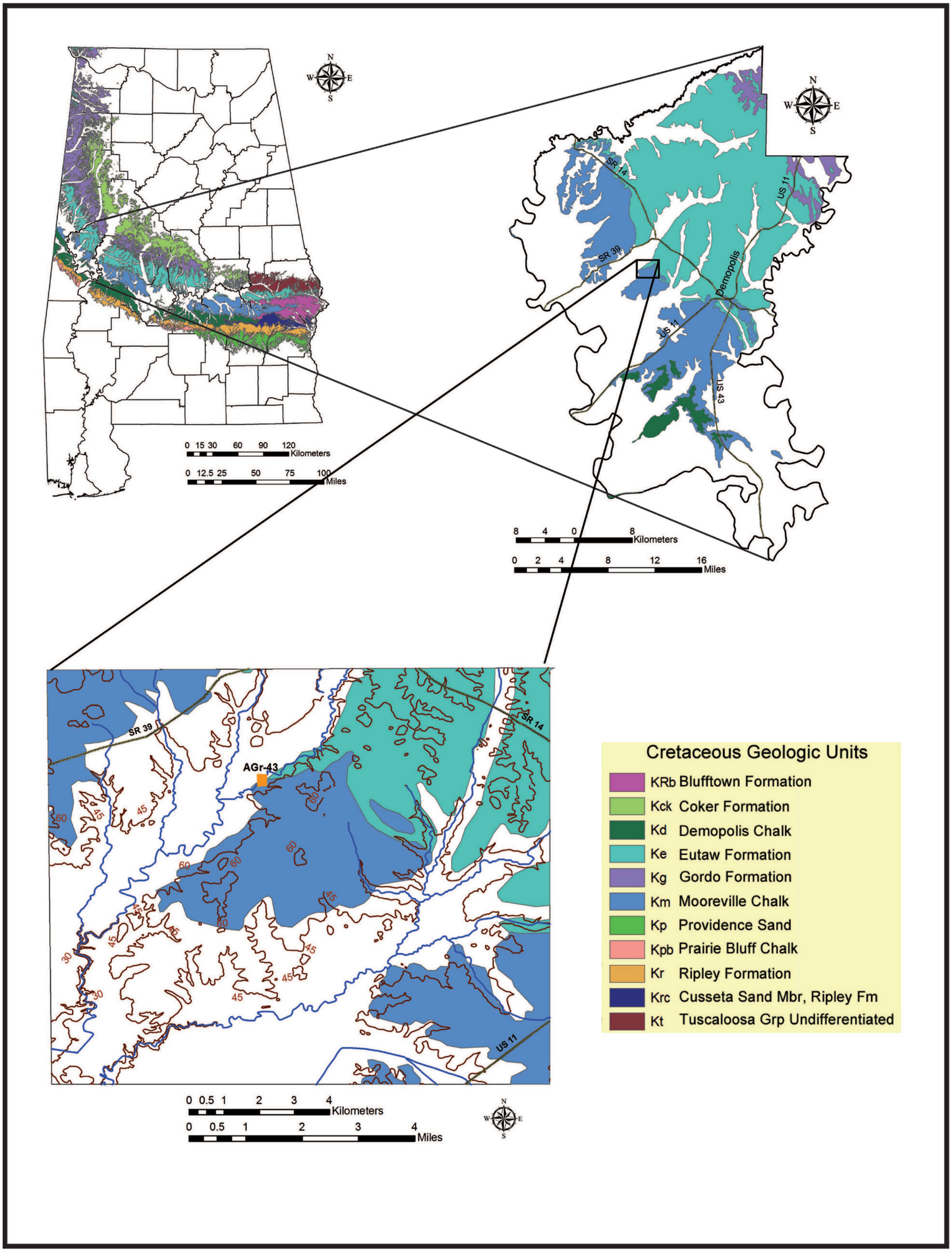

Figure 1: Locality of Cretaceous fossil site, AGr-43 in Alabama. Top left, outline map of Alabama showing outcrop belt of Cretaceous strata. Top right inset showing Cretaceous geology of Greene County, Alabama. Bottom left inset shows detail of Greene County in the region of site AGr-43.

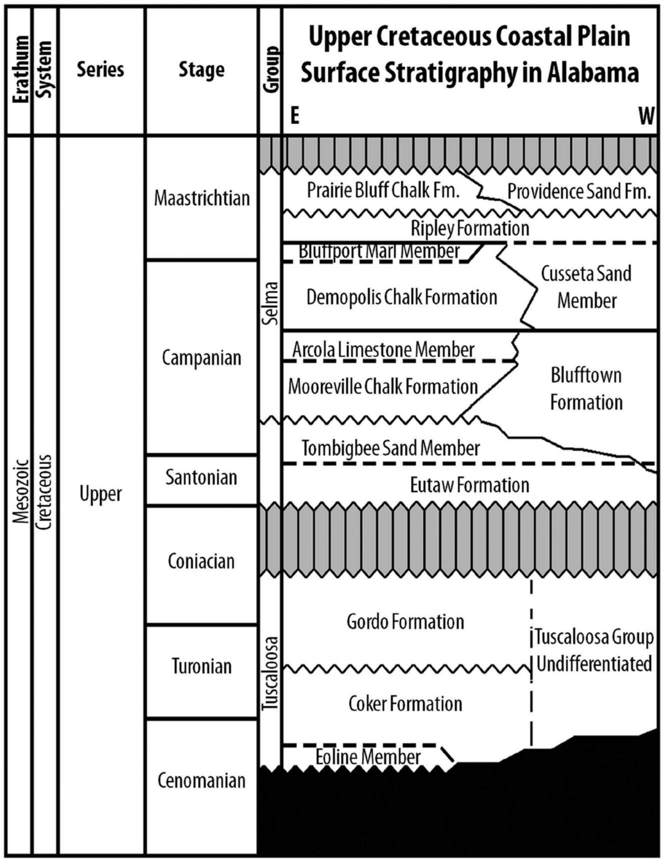

Figure 2: Upper Cretaceous stratigraphy in Alabama. The gray shaded areas represent unconformities. The black shaded area indicates a time interval not represented at the surface in Alabama. Adapted from Raymond et al. (1988).

of the Mooreville Chalk) of Alabama and Georgia (Case, 1987; Case and Schwimmer, 1988). To date, very few of the Cretaceous fish taxa found in the Tombigbee Sand of Alabama have been reported in the literature. Meyer (1974), in his study of Cretaceous elasmobranchs from the Mississippi Embayment, identified a number of shark and ray species he recovered from two sites in Alabama. One sample was obtained from the Tombigbee Sand and the other was taken from the Mooreville Chalk, both in Hale County, Alabama. Although his dissertation was never published, the taxa he identified were later published in the form of a list by Russell (1988) and included 22 taxa from the Tombigbee Sand. Thurmond and Jones (1981) presented a synopsis of the fossil vertebrates of Alabama known to that date, but unfortunately provided little in terms of stratigraphic context. Aside from those listed in Meyer (1974) and Russell (1988), the only additional fish taxa published from the Tombigbee Sand of Alabama include *Megalocoelacanthus dobiei* (Schwimmer et al., 1994), *Cretodus semiplicatus* (Schwimmer et al., 2002), various species of *Enchodus* (Schein and Lewis, 2007), *Ptychodus polygyrus* (Hamm and Harrell, this volume) and *Scapanorhynchus* (Becker et al., 2008). The latter two taxa were reported from site AGr-43. Our recent investigations, however, includes an analysis of the microvertebrates contained within gravel bars at AGr-43, which have yielded a rather diverse assemblage of fish. Elasmobranchii is represented by Hybodontiformes, Heterodontiformes, Squatiniformes, Orectolobiformes, Lamniformes, Rajiformes, Sclerorhynchiformes, and Myliobatiformes, whereas osteichthyans are represented by Lepisosteiformes, Pycnodontiformes, Salmoniformes, and Ichthyodectiformes.

Presented here are a total of 28 Late Cretaceous fish taxa identified from site AGr-43 in Greene County. Included in this list are 11 taxa previously unreported from the state and two that were previously not known from the Tombigbee Sand of Alabama.

MATERIAL AND METHODS

Geologic Setting

The fossils reported herein were collected from gravel deposits at site AGr-43, a stream locality in Greene County, western Alabama (Fig. 1). The exact stratigraphic position of the fossils presented in this study is speculative because they were not collected in situ; incision of the creek near site AGr-43 cuts through the lower Mooreville Chalk and into upper and lower sections of the Tombigbee Sand (Fig. 2). The disconformable contact between these two lithostratigraphic units can be seen within the same creek where site AGr-43 is located. However, closer to the site the Tombigbee Sand disconformably underlies an upper Pleistocene bluish-gray clay-rich silt or Recent alluvium. Although the majority of the fossils are undoubtedly derived from the Tombigbee Sand, some mixing of specimens from the overlying Mooreville Chalk may have occurred.

Lithologically distinct from the underlying Eutaw Formation, the Tombigbee Sand consists of light gray silty mudrock and fine glauconitic tan sand, with rounded quartz pebbles and carbonate contents (Raymond et al., 1988; Mancini and Soens, 1994). The Tombigbee Sand is extremely fossiliferous, and bones and teeth of sharks, bony fish, and marine reptiles can be found along with mollusk steinkerns (i.e., clams and ammonites), echinoderms, foraminifera, and ostracodes. The preservation and ornamentation of the foraminifera and ostracodes occurring in situ indicate that Tombigbee Sand sediments accumulated under low-to-moderate energy, inner-to-middle shelf conditions (Mancini and Soens, 1994).

The Tombigbee Sand is a time-transgressive unit, and deposition spanned the Santonian-Campanian boundary. The base of the Tombigbee Sand exposed in eastern Alabama is latest-most Santonian in age, whereas the top of the member exposed in the central to western portions of the state is early Campanian (Mancini et al., 1995)

(Fig. 2). Index fossils such as ammonites (Kennedy et al., 1997), calcareous nannoplankton, and palynomorphs (King and Skotnicki, 1994), and planktonic foraminifera, and megafossils (Sohl and Smith, 1980; Smith and Mancini, 1983) have been used to establish the relative age of the Tombigbee Sand, with Obradovich (1993) providing a radiometric date of 84.09+/-0.04 Ma (late Santonian) for the base of this member from bentonite sampled in nearby eastern Mississippi. The International Commission on Stratigraphy (ICS, 2012) currently places the Santonian-Campanian boundary at 83.5+/- 0.7 Ma, indicating that the basal portion of this member does indeed extend into the uppermost Santonian.

In contrast, the Mooreville Chalk is composed of grayish chalk and marl. The formation is notable for occurrences of skeletons of large marine reptiles such as mosasaurs and turtles, as well as those of bony fish and isolated shark teeth (Zangerl, 1953a, b; Applegate, 1970; Russell, 1970). Deposition is thought to have accumulated in deeper, less turbid waters with dysoxic bottom conditions (Kiernan, 2002). Like the underlying Tombigbee Sand, the Mooreville Chalk is diachronous with surface exposures ranging in age from the late Santonian to early Campanian (Mancini et al., 1995) (Fig. 2).

Methods

The vertebrate fossils in this study were recovered from stream gravels at site AGr-43 by surface collecting and bulk sampling by a team from Wright State University and McWane Science Center, led by two of the authors (CNC and JAE) in summer 2012. Bulk samples were collected from a small series of gravel bars located within a 50 meter stretch at the site. In all, three five-gallon buckets of material were obtained from random locations within the gravel bars.

Once collected, the bulk material was sieved in the laboratory using #4, #10, #20, and #40 U.S.A. Standard Soil Testing Sieves. All concentrated material was analyzed under magnification. Specimens one centimeter and larger were photographed with a Nikon D7000 with a reversed Nikkor 35 mm prime lens. Material smaller than one centimeter was photographed with the D7000 using a reversed Nikkor 20 mm prime lens. Out of the hundreds of specimens obtained, only those that were complete enough for proper identification were retained. In total, 514 specimens were identified for use in this study and are housed at Wright State University, Celina, Ohio, and McWane Science Center in Birmingham, Alabama. Meyer's (1974) material is available at Southern Methodist University in Dallas, Texas.

Institutional abbreviations—MSC, McWane Science Center, Birmingham, Alabama; **RMM**, Red Mountain Museum (collections now at McWane Science Center), Birmingham, Alabama; **WSU-LC**, Wright State University, Celina, Ohio.

SYSTEMATIC PALEONTOLOGY

A listing of the Cretaceous elasmobranch and osteicthyan species we collected from AGr-43 is presented below. Asterisks denote a first published record for Alabama.

ELASMOBRANCHII Bonaparte, 1838
NEOSELACHII Compagno, 1977
HYBODONTIFORMES Patterson, 1966
HYBODONTIDAE Agassiz, 1843
**Lonchidion* sp. Estes, 1964 (Fig. 3, A) – n = 6
**Meristodonoides* sp. Underwood and Cumbaa, 2010 (Fig. 3, B) – n = 25
PTYCHODONTIDAE Jaekel, 1898
Ptychodus mortoni Mantell, 1836 (Fig. 3, C–D) – n = 10
Ptychodus polygyrus Agassiz, 1839 (see Hamm and Harrell, this volume)
HETERODONTIFORMES Berg, 1940
HETERODONTIDAE Gray, 1851
Heterodontus sp. de Blainville, 1816 (Fig. 3, E–F) – n = 1
SQUATINIFORMES de Buen, 1926
SQUATINIDAE Bonaparte, 1838
Squatina aff. *hassei* Leriche, 1929 (Fig. 3, G–H) – n = 5
ORECTOLOBIFORMES Applegate, 1972
ORECTOLOBIDAE Jordan and Fowler, 1903
Chiloscyllium sp. Müller and Henle, 1837 (Fig. 3, I–J) – n = 1
LAMNIFORMES Berg, 1958
ANACORACIDAE Casier, 1947
**Squalicorax* aff. *yangaensis* Dartevelle and Casier, 1943 (Fig. 3, K–L) – n = 44
Squalicorax cf. *kaupi* Agassiz, 1843 (Fig. 3, M–N) – n = 107
Pseudocorax laevis Leriche, 1906 (Fig. 4, A–B) – n = 3
ARCHAEOLAMNIDAE Underwood and Cumbaa, 2010
**Archaeolamna kopingensis* Davis, 1890 (Fig. 4, C–D) – n = 5
CRETOXYRHINIDAE Glickman, 1958
Cretoxyrhina mantelli Agassiz, 1843 (Fig. 4, E–F) – n = 1
ODONTASPIDIDAE Müller and Henle, 1839
**Carcharias* sp. Rafinesque, 1810 (Fig. 4, G–J) – n = 46
OTODONTIDAE Glickman, 1964
Cretalamna appendiculata Agassiz, 1843 (Fig. 4, K–L) – n = 32
MITSUKURINIDAE Jordan, 1898
Scapanorhynchus texanus Roemer, 1849 (Fig. 4, M–P) – n = 75
BATOIDEI
SCLERORHYNCHIFORMES Kriwet, 2004
SCLERORHYNCHIDAE Cappetta, 1974

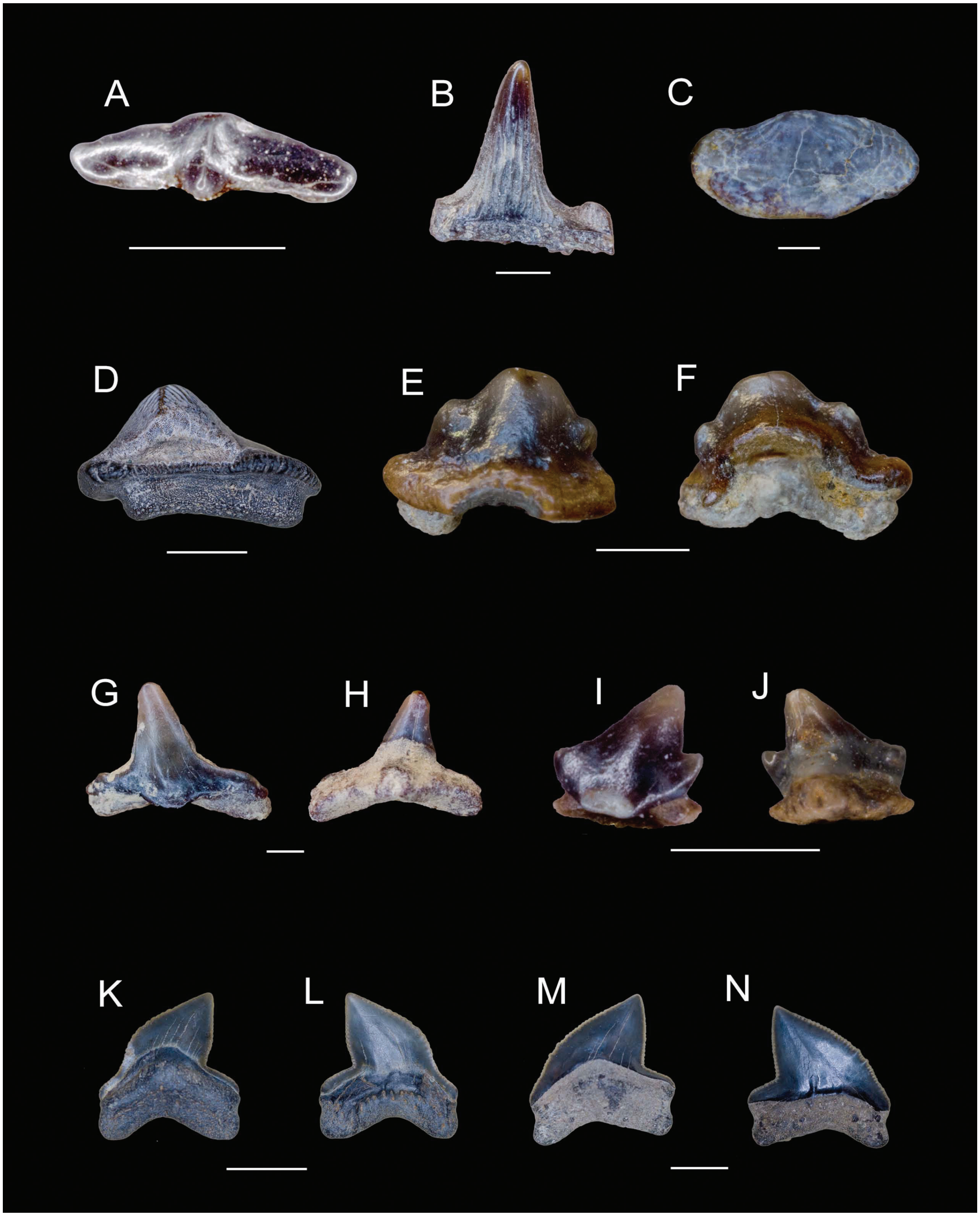

Figure 3: Cretaceous hybodontiform, heterodontiform, squatiniform, orectolobiform, and lamniform sharks recovered from site AGr-43. A, WSU-LC 500, *Lonchidion* sp. in labial view; B, WSU-LC 501, *Meristodonoides* sp. in labial view; C, WSU-LC 502, *Ptychodus mortoni* in labio-occlusal view; D, WSU-LC 502, *P. mortoni* in lingual view; E–F, WSU-LC 503, *Heterodontus* sp. adult anterior tooth in labial (E) and lingual (F) views; G–H, WSU-LC 504, *Squatina* aff. *hassei* antero-lateral tooth in labial (G) and lingual (H) views; I–J, WSU-LC 505, *Chiloscyllium* sp. in labial (I) and lingual (J) views; K–L, WSU-LC 506, *Squalicorax* aff. *yangaensis* in lingual (K) and labial (L); M–N, WSU-LC 507, *Squalicorax* cf. *kaupi* in lingual (M) and labial (N) views. Scale = 5 mm in D and L–O, 1 mm for all others.

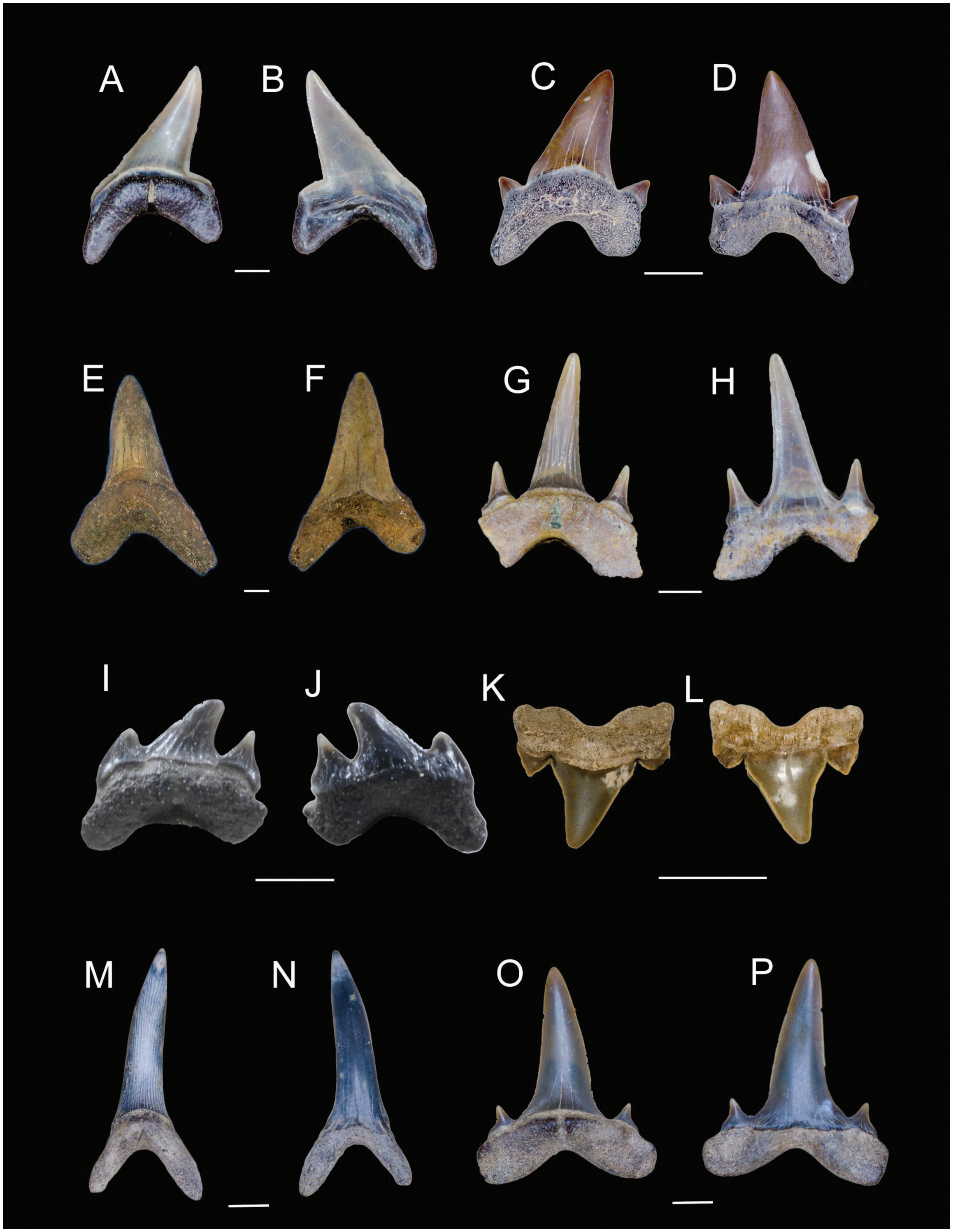

Figure 4: Cretaceous lamniform sharks recovered from site AGr-43. A–B, WSU-LC 508, *Pseudocorax laevis* antero-lateral tooth in lingual (A) and labial (B) views; C–D, WSU-LC 509, *Archaeolamna kopingensis* anterior tooth in lingual (C) and labial (D) views; E–F, MSC 26066, *Cretoxyrhina mantelli* anterior tooth in lingual (E) and labial (F) views; G–H, WSU-LC 510, *Carcharias* sp. anterior tooth in lingual (G) and labial (H) views; I–J, WSU-LC 511, *Carcharias* sp. posterior tooth in lingual (I) and labial (J) views; K–L, WSU-LC 512, *Cretalamna appendiculata* in lingual (K) and labial (L) views; M–N, WSU-LC 513, *Scapanorhynchus texanus* anterior tooth in lingual (M) and labial (N) views; O–P, WSU-LC 514, *S. texanus* lateral tooth in lingual (O) and labial (P) views. Scale = 1 mm in A–B, G–L, 5 mm in C–F, M–P.

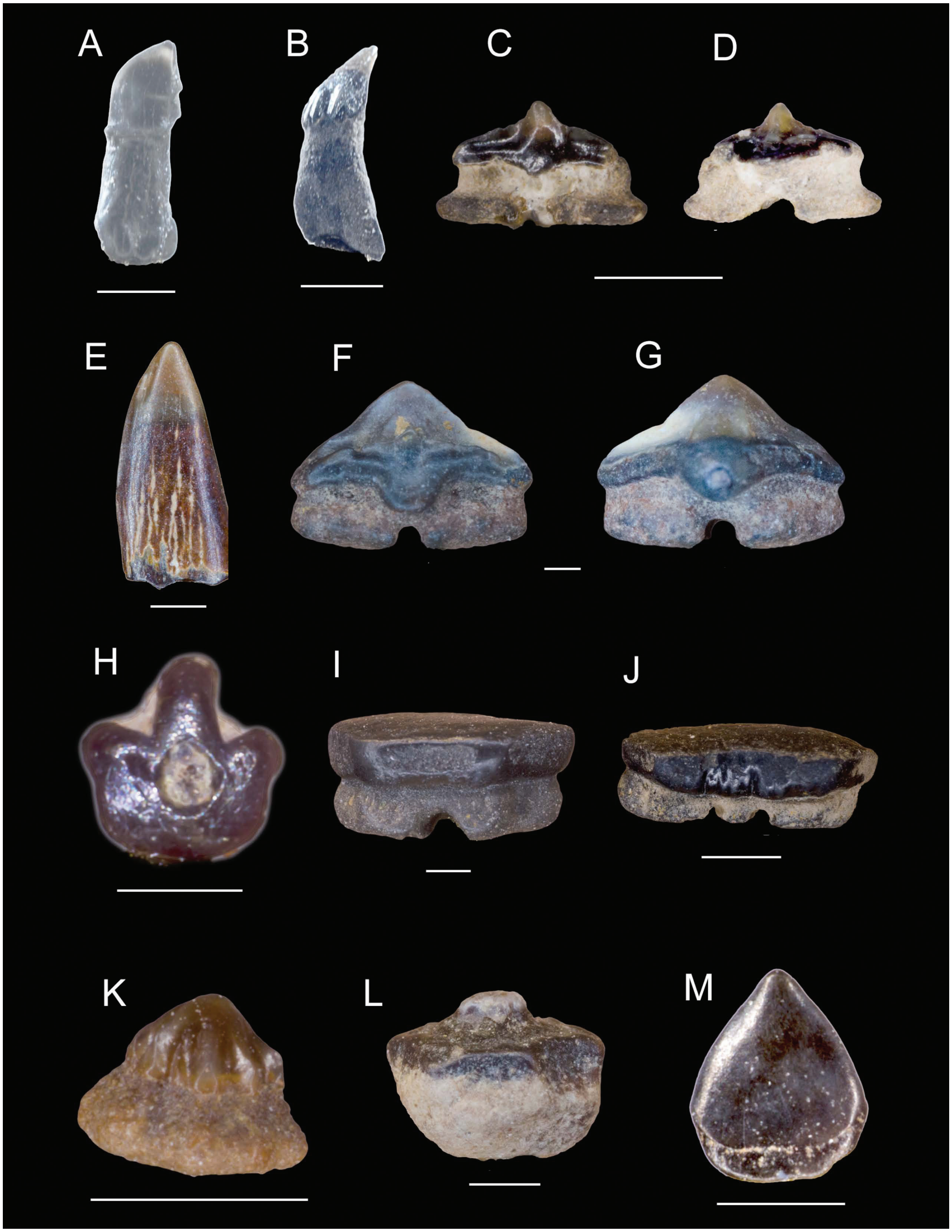

Figure 5: Cretaceous batoids recovered from site AGr-43. A, WSU-LC 515, *Borodinopristis* cf. *ackermani* rostral spine; B, WSU-LC 516, *Ischyrhiza avonicola*-type rostral spine; C–D, WSU-LC 517, *Ischyrhiza* cf. *mira* juvenile tooth in lingual (C) and labial (D) views ; E, WSU-LC 518, *I.* cf. *mira* rostral spine crown; F–G, WSU-LC 519, *Texatrygon* sp. in lingual (F) and labial (G) views; H, WSU-LC 520, *Rhinobatos* sp. in occlusal view; I, WSU-LC 521, "*Pseudohypolophus*" *ellipsis* in lingual view; J, WSU-LC 522, "*P.*" *ellipsis* in lingual view; K, WSU-LC 523, dermal hybodontiform(?) scale in anterior view; L, WSU-LC 524, batoid dermal denticle in lateral view; M, WSU-LC 525, batoid dermal denticle in occlusal view. Scale = 1 mm.

Figure 6: Cretaceous osteichthyes recovered from site AGr-43. A, WSU-LC 526, *Lepisosteus* sp. tooth in profile view; B, WSU-LC 527, *Anomoeodus barberi* prearticular tooth in occlusal view; C, WSU-LC 528, *A. barberi* tooth in occlusal view; D, WSU-LC 529, *Hadrodus priscus* pharyngeal tooth in profile view; E, WSU-LC 530, *H. priscus* tooth in profile view; F, WSU-LC 531, *H. priscus* molariform tooth in lingual view; G, WSU-LC 532, ?*Micropycnodon* sp. tooth in occlusal view; H, WSU-LC 533 *Enchodus* sp. tooth in profile view; I, WSU-LC 534, Saurodontidae tooth in profile view. Scale = 1 mm.

**Borodinopristis* cf. *ackermani* Case et al., 2001 (Fig. 5, A) – n = 2
**Ischyrhiza* aff. *avonicola* Estes, 1964 (Fig. 5, B) – n = 13
Ischyrhiza aff. *mira* Leidy, 1856 (Fig. 5, C–E) – n = 2
**Texatrygon* sp. Cappetta and Case, 1999 (Fig. 5, F–G) – n = 46
Ptychotrygon sp. Jaekel, 1894 (Not figured) – n = 34
RAJIFORMES Berg, 1940
RHINOBATIDAE Müller and Henle, 1837
Rhinobatos sp. Linck, 1790 (Fig. 5, H) – n = 1
FAMILY INDET.
* "*Pseudohypolophus*" *ellipsis* Case et al., 2001 (Fig. 5, I–J) – n = 39
hybodontiform(?) scale morphotype 1 (Fig. 5, K) – n = 2
Batoid dermal denticle morphotype 2 (Fig. 5, L) – n= 3
Batoid dermal denticle morphotype 3 (Fig. 5, M) – n = 1
OSTEICHTHYES Huxley, 1880
LEPISOSTEIFORMES Hay, 1929
LEPISOSTEIDAE Cuvier, 1825
Lepisosteus sp. Lacépède, 1803 (Fig. 6, A) – n = 10
PYCNODONTIFORMES Berg, 1940
PYCNODONTIDAE Owen, 1846
**Anomoeodus barberi* Hussakof, 1947 (Fig. 6, B–C) – n = 2
Hadrodus priscus Leidy, 1857 (Fig. 6, D–F) – n = 3
**?Micropycnodon* sp. Hibbard and Graffham, 1945 (Fig. 6, G) – n = 1
SALMONIFORMES Bleeker, 1859
ENCHODONTIDAE Woodward, 1901
Enchodus sp. Agassiz, 1835 (Fig. 6, H) – n = 1
ICHTHYODECTIFORMES Bardack and Sprinkle, 1969
SAURODONTIDAE Cope, 1871
gen. indet. (Fig. 6, I) – n = 1

DISCUSSION

The vertebrate fossils we collected consist predominantly of isolated shark and bony fish teeth, and a total of 28 taxa have been identified. Teeth of Elasmobranchii are diverse and include 22 species, many representing taxa with teeth measuring less than 1 cm in greatest dimension. Bony fish teeth of varied morphologies were predominately recovered through microscopic sorting. A total of six bony fish taxa were identified, with the majority belonging to pycnodonts. Many of the species we recovered from the stream gravels have been identified in the Eutaw Formation or its temporal equivalents in Alabama, Georgia, Mississippi, and as far to the west as New Mexico, (Leidy, 1873; Meyer, 1974; Williamson et al., 1989; Case et al., 2001; Johnson and Lucas, 2003; Schein and Lewis, 2007; Bourdon et al., 2011). However, taxa including *Ptychodus mortoni, Cretalamna appendiculata, Cretoxyrhina mantelli, Squalicorax cf. kaupi*, and *Hadrodus* sp. have been found in younger deposits of the Mooreville Chalk (see Applegate, 1970; Thurmond and Jones, 1981; Bell 1986). It has already been noted that the gravels at site AGr-43 contain lithologic components of both the Tombigbee Sand Member and the Mooreville Chalk, and it is quite possible that vertebrate remains from these two units have also been mixed together. *Pseudocorax*, for example, represented in our sample by three teeth, occurs within the Mooreville Chalk, but to date the genus has not been identified from the underlying Eutaw Formation. This hypothesis is further supported by our observation of Pleistocene terrestrial fossils in the stream gravels at site AGr-43.

Despite the fact that the fossils discussed herein lack specific stratigraphic context, many of the species we recovered deserve further discussion. Meyer (1974) tentatively identified *Hybodus butleri*, an early Cretaceous taxon (Thurmond, 1971), from Hale County (listed incorrectly by Meyer as Hill County), but his material is conspecific with our single tooth (WSU-LC 501), which appears to be similar to the *Hybodus montanensis* morphology described by Case (1978). *Meristodonoides* (Underwood and Cumbaa, 2010) was recently erected to include several species formerly assigned to *Hybodus* (including those with *H. montanensis* morphology), and the former generic name is utilized here. Meyer (1974) also identified *Lonchidion* from Hale County, but he tentatively assigned his material to the early Cretaceous species *Lonchidion breve* (see Patterson, 1966). However, it appears that Meyer erroneously lumped multiple species into *L. breve*, including a morphology that is conspecific with the specimens we collected. The teeth have a distinctively convex medial occlusal surface and basally sloping lateral shoulders, different from teeth of the Campanian *L. babulskii*. The few teeth in our sample (i.e., WSU-LC 500; Fig. 3A) compare very closely to specimens we have collected from the Eutaw Formation of eastern Mississippi, which may represent a new species. *Heterodontus*, a horn shark, is an uncommon component of Cretaceous strata in North America, but Meyer (1974) identified the genus from Hale County, Alabama. Unfortunately, we cannot make a specific identification for WSU-LC 503 (Fig. 3, E-F), but our tooth likely represents an adult because lateral cusplets are weakly developed. The teeth of *Archaeolamna kopingensis* (WSU-LC 509), distinguished by their lingually curving crowns, have not previously been reported from Alabama, but they could be confused with those of *Cretalamna appendiculata*. The odontaspidid teeth in our sample have a coarsely striated lingual face like *Carcharias holmdelensis*, but the lateral cusplets on the Alabama specimens are larger. It remains to be verified if striated odontaspidid teeth from the Cretaceous of North American are more appropriately identified as *Eostriatolamia* (Glickman and Averianov, 1998). The possibility exists that at least some of these teeth represent juvenile *Scapanorhynchus texanus* (Meyer, 1974).

Three anacoracids were collected during our study, including *Pseudocorax* and two species of *Squalicorax*. *Pseudocorax* is easy to identify based on its smooth cutting edges, gracile crown, and lingual nutritive groove on the root. Hamm and Shimada (2007) recently synonymized *P. granti* (see Applegate, 1970) with *P. laevis*, and this classification is followed here. Of the two *Squalicorax*, one is distinctive in having a long and sinuous mesial cutting edge with large compound serrations at its most convex part (WSU-LC 506; Fig. 3, K–L). These characteristics are consistent with Campanian *S. yangaensis* reported from Africa (see Darteville and Casier, 1943). A very similar species, *S. bassanii*, occurs in Maastrichtian rocks of northern Africa, but teeth appear to be differentiable in having a more convex mesial edge with a distinctive notch near the base, and the root is higher (Gemmellaro, 1920). Although identified from other North American localities, teeth we tentatively identify as *S. yangaensis* have not yet been reported from Alabama (see Wolberg and Bellis, 1989; Schwimmer, 2007, 2008; Bourdon et al., 2011). Other specimens in the sample compare well with some teeth that Agassiz (1833–1843) identified as *Corax kaupii* (= *Squalicorax kaupi*), but a very similar morphology was later named *Corax lindstromi* (= *Squalicorax lindstromi*) by Davis (1890). The latter species name was only recently resurrected, and it remains to be confirmed that it truly represents a species distinct from *S. kaupi*, and that at least some North American teeth identified as *S. kaupi* should be called *S. lindstromi* (see Einarsson et al., 2010). The ability to draw the line between true biological species based on isolated teeth is difficult, as without the aid of numerous associated dentitions it is difficult to simply determine if differences in tooth morphology are related to intraspecific variation and/or heterodonty. That said, the teeth we identify as *S.* cf. *kaupi* (WSU-LC 507; Fig. 3, M–N) have a convex mesial cutting edge that bears finer, simple serrations and lacks a basal notch. Meyer (1974) apparently did not collect *Squalicorax* from either of the two localities he visited, but the specimens identified as *S. falcatus* by Applegate (1970:fig. 178 L and N) appear to be similar to the teeth we herein refer to *S.* cf. *kaupi*.

Rostral spines of the sawfish *Borodinopristis* were collected by Meyer (1974) from Hale County, although he identified them as *Sclerorhynchus*. These spines are unique in that they are typically only 5 mm or less in length and have two or more "collared" posterior barbs. Two species have been erected based on tooth morphology, and the rostral spines are also diagnostic to species within this genus. The genus is known from Santonian and Campanian strata of Georgia (Case, 1987; Case et al., 2001), South Carolina (Cicimurri, 2007), and Mississippi (Meyer, 1974; Manning and Dockery, 1992). Rostral spines like the one shown in Figure 5, B, are similar to Campanian and Maastrichtian material identified as *Ischyrhiza avonicola* (Estes, 1964; Cappetta and Case, 1975), but Case et al. (2001) identified identical spines as a new species, *I. georgiensis*. Similar spines are controversially also assigned to *Ptychotrygon* (Bourdon et al., 2011). An alternative hypothesis that we favor is that the spines represent juvenile individuals or even a different head location within *Ischyrhiza mira* (Meyer, 1974; Cicimurri, 2007). An *I. mira* specimen from Epes in Sumter County, Alabama has previously been reported by Thurmond and Jones (1981), however the authors did not provide any stratigraphic context for the specimen. Likely collected from either the Ripley Formation, Demopolis Chalk, or Prairie Bluff Chalk, the specimen identified in this study as *Ischyrhiza* aff. *mira* represents the first reported from the Tombigbee Sand in Alabama.

Cappetta and Case (1999) erected the generic name *Texatrygon* to include teeth that have a distinctively high central cusp and overall sub-triangular shape in labial/lingual view. At least one species formerly identified as *Ptychotrygon* has been reassigned to *Texatrygon*, *P. hooveri*, teeth of which were tentatively identified by Meyer (1974) from Hale County. Case et al. (2001) identified identical teeth as a new taxon, *Erguitaia benningensis*, but the generic identification is unwarranted because these teeth are morphologically dissimilar to the two species of *Erguitaia* from the Maastrichtian of northern Africa, *E. arganiae* and *E. misrensis* (See Arambourg, 1952; Cappetta, 1991). A new combination, *Texatrygon benningensis*, may be warranted, but a more detailed study remains to be undertaken. The teeth of *Ptychotrygon* have a lower, more rounded medial cusp than those of *Texatrygon* in our sample, and the ornamentation on the labial face consists of multiple transverse ridges. The morphology is consistent with the teeth Meyer (1974) identified as *Ptychotrygon triangularis eutawensis*, but differs from the teeth identified by Case et al. (2001) as *P. eutawensis*. The *Texatrygon* specimens reported in this study represent the first records of this taxon from the state (WSU-LC 519; Fig. 5, F-G).

The guitarfish *Rhinobatos* is virtually unknown from Santonian and Campanian deposits of the Gulf Coastal Plain, but Meyer (1974) questionably referred teeth that he recovered from both the Eutaw Formation and Mooreville Chalk to *R. incertus*, a species reported from Cenomanian and Turonian strata elsewhere (Cappetta, 1973; Cicimurri, 2001). However, a specific identification for WSU-LC 520 (Fig. 5, H) should await the discovery of additional teeth. The apparent rarity of *Rhinobatos* may be due more to a collecting bias as opposed to actual paucity in an ecosystem. Meyer's (1974) *Parahypolophus* is considered a nomen dubium or synonymous with *Pseudohypolophus* (Cappetta and Case, 1975). Meyer (1974) identified *P. mcnultyi* from both the Eutaw Formation and Mooreville Chalk of Alabama, but the teeth we collected from AGr-43 are identified as "*P.*" *ellipsis* (i.e., WSU-LC 521; Fig.

5, I–J). The latter taxon has not been reported from Alabama, and we could not confirm Meyer's identification of his Alabama specimens. The "*P.*" *ellipsis* morphology can be distinguished from *P. mcnultyi* in its larger size, thicker, often six-sided crown and polyaulocorhizous root (presumably within more medial tooth rows). The "*P.*" *ellipsis* morphology is quite similar to Campanian *Brachyrhizodus*, which has larger, wider, six-sided teeth and consistently polyaulocorhizous roots (except for more lateral jaw positions). A histological analysis has not yet been conducted in order to determine any close phylogenetic relationship between the two taxa, or evolutionary convergence. Three dermal denticle morphotypes have been recovered, some of which could be attributed to *Pseudohypolophus*, as denticles shown in Figure 5, L–M occur in Campanian strata along with teeth of this genus (i.e., Robb, 1989). This association cannot be conclusively demonstrated without the aide of a specimen in which teeth and denticles are preserved in situ, and it is equally plausible that the denticles are attributable to another ray like *Ischyrhiza* or *Ptychotrygon*. The specimen in Fig. 5, K appears to represent a hybodontiform scale.

In addition to those already discussed, the following taxa were identified from site AGr-43 and represent first records from the state: *Lonchidion* sp. (Fig. 3, A); *Carcharias* sp. (Fig. 4, G–J); *Ischyrhiza* aff. *avonicola* (Fig. 5, B); *Anomoeodus barberi* (Fig. 6, B–C); and ?*Micropycnodon* sp. (Fig. 6, G). Furthermore, the specimens identified here as *Chiloscyllium* sp. represent the first of this taxon reported from the Tombigbee Sand of Alabama.

CONCLUSIONS

Fossil teeth representing 28 fish species have been collected from stream gravels at site AGr-43 in central Greene County, Alabama. Although the fossils lack stratigraphic context they represent important paleobiogeographic data for species that inhabited the Mississippi Embayment and Western Interior Seaway during the late Santonian to early Campanian. In addition, several of the fossils represent the first published record of that taxon in Alabama, including *Archaeolamna kopingensis*, *Anomoeodus barberi*, *Borodinopristis* cf, *ackermani Carcharias* sp., *Ischyrhiza* aff. *avonicola*, *Lonchidion* sp., *Meristodonoides* sp., ?*Micropycnodon* sp., "*Pseudohypolophus*" *ellipsis*, *Squalicorax* aff. *yangaensis*, and *Texatrygon* sp. Bulk sampling of in situ matrix from the Tombigbee Sand Member and Mooreville Chalk will help better determine the stratigraphic occurrences of the species we collected from the stream gravels, as well as refine interpretations of the paleoenvironments that the fossiliferous strata represent.

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“The Palate Bones of a Fish?” – The First Specimen of *Ptychodus mortoni* (Chondrichthyes; Elasmobranchii) from Alabama

MICHAEL J. EVERHART
Sternberg Museum of Natural History, Fort Hays State University, Hays, Kansas 67601, meverhar@fhsu.edu

ABSTRACT

The crushing teeth of the extinct shark genus *Ptychodus* were initially called “palate bones of fish” or “*dentes tritores*” when encountered in the Late Cretaceous rocks of England. Recognized as teeth organized into opposing jaw plates by Gideon Mantell (1822) and others, the generic name was first coined by Louis Agassiz (1835) in the early portion of his *Recherches sur les Poissons Fossiles*. Agassiz subsequently named five species of *Ptychodus* that had been previously discovered in England. Examples of a unique North American species of *Ptychodus* were also collected in Alabama and Mississippi as early as the 1820s, although they were not recognized at first as being shark teeth. Samuel Morton (1834) figured a specimen from Alabama, having regarded it initially as part of the dermal armor of a dinosaur (e.g. *Hylaeosaurus* Mantell, 1833), and then as “The palate bones of a fish?” Morton had been corresponding with both Mantell and Agassiz for some time on the identification of other species of fossil shark teeth, and may have changed his mind in response to Mantell’s 1833 dinosaur publication. Morton sent the specimen to Mantell who first named it *Ptychodus Mortoni* in 1836. The tooth was eventually transferred to the British Museum of Natural History where it is currently curated as the type specimen of *P. mortoni* (NHMUK PV OR 28394). The naming of *Ptychodus mortoni* provides an interesting window into the pace of scientific discovery during the early part of the 19th century.

INTRODUCTION

Late Cretaceous fossils were collected in Alabama in the early 1800s (Ebersole and Dean, this volume). Many of these first Alabama specimens were sent to private individuals and museums on the East Coast, and even to paleontologists as far as England, but detailed records of these transfers are not generally available in the literature. *Ptychodus mortoni* is one of the Late Cretaceous vertebrate taxa which was first recognized from Alabama.

The distinctive and durable teeth of the Late Cretaceous durophagous shark genus *Ptychodus* were collected as curiosities, and have been recognized as fossils in England for hundreds of years. George Dibley (1911:263) remarked that “among the remains of fishes found in the Chalk, the teeth of *Ptychodus* are so conspicuous and so easily recognized by the quarrymen that they have long been collected in large numbers and distributed to various museums.” Yet it was only during the 1830s that Louis Agassiz described them and coined the genus name.

Although first recognized in England and northern Europe, *Ptychodus* (= rugous or wrinkled tooth) occurs in Late Cretaceous rocks around the world from the Albian through the early Campanian (Shimada et al., 2009). Although many species are shared between Europe and North America, *Ptychodus mortoni* is primarily a North American species. *P. mortoni* occurs from the early Coniacian into the middle Santonian (Shimada et al., 2010) in the Western Interior Seaway over Kansas, although it appears to have persisted longer along the Gulf (Schwimmer and Williams, 1994) and in Africa and Western Europe (Shimada, 2012). Note that Frederick Dixon (1850:pl. 31, figs. 6–7) figured the crown of a “*Ptychodus mortoni*” specimen from Shoreham in England. Subsequent authors have questioned this assignation.

The type specimen of *Ptychodus mortoni* (Fig. 1) was initially figured, but not described or named by Samuel Morton (1834:pl. 18, figs. 1–2). Gideon Mantell (1836:27) briefly mentioned the tooth and gave it the name *Ptychodus mortoni*, but did not provide a description or a figure. Sometime later, Morton (1842:215) received a letter from Mantell which included three figures drawn by Agassiz’s

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Figure 1. The original figures of the type specimen of *Ptychodus mortoni*, adapted from Morton (1834:pl. 18, figs. 1–2), in lingual and occlusal view. No scale.

artist, Joseph Dinkel. Morton noted that Mantell had not told him "in what work the description is published." While the date of this correspondence is uncertain, Mantell's diary (Cooper, 2010) indicates that he wrote to Dr. Morton on February 1, 1836, months before sending the manuscript for his "Descriptive Catalogue" to the publisher in September. Morton (1842:pl. 11, fig. 7) subsequently figured the specimen with the name *Ptychodus mortoni* (Mantell).

Mantell (1854:586) briefly described the tooth sent to him by Morton as "the enameled crown forms a conical projection, traversed by large inosculating ridges, which radiate from the summit towards the margins." In a footnote on the same page, Mantell asserts again that "I have named it *P. mortoni*, in honour of my distinguished friend, the eminent American naturalist and physician, Dr. [Samuel] George Morton, by whom it was discovered." Mantell's figure (1854:lign. 189) of the type specimen in lingual view appears to have been executed or redrawn by someone other than Agassiz's artist, Joseph Dinkel.

Leidy (1868) provided the first detailed description of *Ptychodus* teeth from North America, but did not provide figures, noting that he had seen several specimens from Alabama and Mississippi. Leidy also mentions that he had not seen the species in fossil collections from New Jersey as had been previously reported by Mantell (1836, 1854) and Agassiz (1843). Given that Leidy had many more specimens, including 12 *Ptychodus mortoni* teeth from Alabama, to examine than Agassiz, his description of the teeth is more lengthy and complete. Leidy (1873:pl. 18) published the first figures of *P. mortoni* teeth from Kansas and Mississippi, and additional teeth from Alabama. Cope (1874:48; 1875:294) briefly reported on the occurrence of the genus from Kansas, including *P. mortoni*, and New Mexico, but did not figure any of his specimens.

Joseph Dinkel's drawings of the type specimen (Fig. 2)

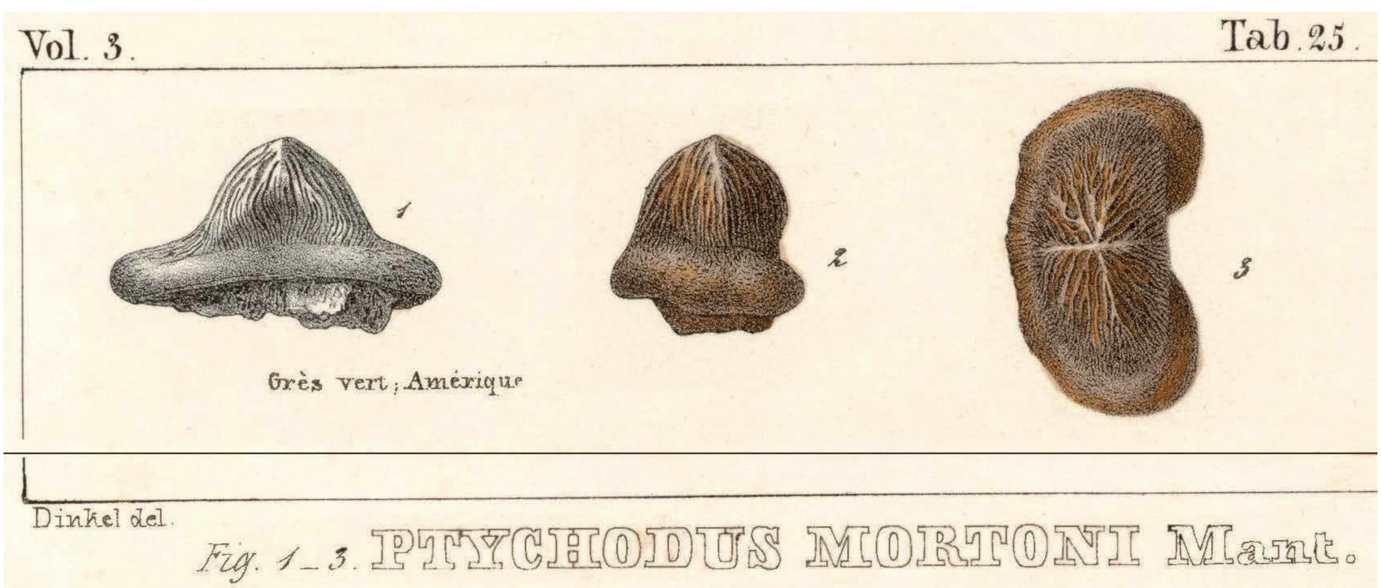

Figure 2. The type specimen of *Ptychodus mortoni* in (L–R) in lingual, left lateral and occlusal views, adapted from Agassiz 1833-1843 (Tome III, Tab. 25, Figs 1–3), and first published in Agassiz's Livraisons for April 1839 from figures drawn by Joseph Dinkel in 1835. No scale.

Figure 3. Type specimen of *Ptychodus mortoni* (NHMUK PV OR 28394) in (L-R) lingual, left lateral and occlusal views. Scale bar = 1 cm. Photo credit: Christopher Duffin, 2012.

were initially published as a separate section (livraison) in April 1839 (Table 1) without a caption, and have been republished over the years by various authors, including Morton (1842) and Dana (1863:477). DeKay (1842:386) simply cites Agassiz's "Vol. 3, Pl. 25" as the source of the figures. Hay (1902:317) listed all of the then available publications regarding *Ptychodus mortoni*, including Jaekel's (1894) attempt to place the American species in a sub-genus ("*Hemiptychodus*").

The type specimen of *Ptychodus mortoni* (NHMUK PV OR 28394) is a single, nearly symmetrical medial tooth of a large durophagous shark (Fig. 3). It measures 3.8 cm in width, 2 cm in total height and about 2.0 cm labiolingually. The crown of the tooth is 1.5 cm in height. Bean shaped in occlusal view, the tooth is dominated by a sub-circular, inflated conical crown, with branching ridges radiating from the apex. There is no apparent wear visible on the crown, such as that observed by Leidy (1873:pl. 18, figs. 11–12) on a *P. mortoni* tooth from Mississippi, but the left side of the root appears to be damaged, possibly by weathering. The photos (Fig. 3) provided by Christopher Duffin (See also Hamm, 2008:pl. 15A) of the type specimen appear almost identical to the original color drawings made by Dinkel and published by Agassiz (1833–1843:tab. 25, figs. 1–3).

Although Mantell (1836, 1839, 1854) reported that the specimen came from the green sand of New Jersey, Morton (1842:215) noted that Timothy A. Conrad had collected the specimen "in the older cretaceous strata at Prairie Bluff, Alabama." Prairie Bluff is now an abandoned townsite originally located on a bluff on the west side of the Alabama River in Wilcox County. While Conrad's original locality is uncertain, Schwimmer and Williams (1994) note the uppermost occurrence of *Ptychodus mortoni* is the early Campanian.

Mantell's confusion regarding the locality and the horizon of the type specimen may be in part due to Morton's (1834:11) early belief that the Cretaceous of the East Coast and Gulf Coast should be included in his "Green Sand or Ferruginous Sand" horizon. In a June 7, 1833 letter to Judge Charles Tait, his host while in Alabama, Conrad wrote "I am now satisfied that the whole region in Mississippi, thro' which the Tombeckbee [Tombigbee River] flows is Morton's 'ferruginous sand'." (Wheeler, 1935:36). Morton (1834:21) noted that "this state presents a vast deposit of both strata, for a knowledge of which I am wholly indebted to Mr. Conrad, who informs me that the counties of Pickens, Bibb, Greene, Perry, Dallas, Marengo, Wilcox, Lownes, Montgomery, and parts of Clarke, Monroe and Conecuth, are chiefly composed of the older Cretaceous strata." Charles Lyell (1848) later noted that exposures in Clarke, Monroe and Conecuh counties were actually Eocene in age.

RESULTS AND DISCUSSION

The term 'fossil palates of fishes' was used as early as Urban (1755:408) to describe several kinds of unusual fish teeth collected from "under the northern cliffs of Shepey Island [Isle of Sheppey]." Bright (1817:200) reported "16. A thin bed of limestone breccia containing rounded pebbles, and organized substances resembling palates of fish." While neither of these early references are in regard to *Ptychodus*, they describe fossil fish teeth with a similar crushing function. Miller, in Hawkins (1819:46), called *Ptychodus* teeth "*dentes tritores*," and Conybeare and Phillips (1822:356) referred to them as "singular palatal tritores." Also called the palate bones of fish, they were observed by Mantell (1822:231) to be "sometimes found in considerable numbers, and of various sizes, forming a tesselated surface of several square inches; and so regularly disposed, the smaller palates being adapted to the intervals between the larger ones, that no doubt can exist of this having been the mode in which they were placed in the original. Hence, instead of each specimen being a distinct palate, like the corresponding teeth of the *Diodon*, they appear to have constituted the covering of the entire roof and base of the mouth." In his book, *Medals of Creation*, Mantell (1854:585) noted that they "occur more or less abundantly in almost every chalk-pit, and are known by the name of "*palates…*"

In the United States, Morton (1834:30, pl. 18, figs. 1–2) was the first to publish figures of a *Ptychodus* tooth from Alabama that he initially thought was a dermal bone from an armor plated dinosaur (e.g. *Hylaeosaurus*) then recently described by Mantell (1833). Morton subsequently changed his mind, in mid-paragraph, and called the specimen a palate bone of "some marine animal." Then, in his "Explanation of the Plates" he described the tooth, with a question mark, as "The palate bones of a fish?" Furthermore, Morton cites his "friend Mr. Mantell" several times in this paper and it is likely he was well aware of Mantell's and others descriptions of similar teeth from the Cretaceous of England. The figures in Morton's Plate XVIII show a *Ptychodus* tooth in occlusal (Fig. 1) and lingual view with a slightly damaged root (Fig. 2). Morton does not provide a scale or give measurements. Plate XVIII, however, is mostly taken up by a very large drawing of *Nautilus alabamensis*, suggesting that the two figures of the *Ptychodus* tooth may have been added after the plate had been largely completed by the artist / engraver (T.A. Conrad), and not coincidentally, the collector of the specimen.

Robert Bakewell (1833:175), a geologist friend of Mantell, reported that "Mr. Mantell has received from Dr. Morton and others, many specimens of American fossils and minerals, and their identity with those of England has been particularly remarked." Morton's respect for Mantell is shown in his description (1833:291) of a new species of fossil foraminiferan from near Claiborne, Alabama; "I have much pleasure in dedicating this only known American species of *Nummulites* [*N. mantelli*], to one of the most zealous and successful cultivators of geological science." Unfortunately, Morton's identification of the genus was in error and the name was corrected to *Orbitolites mantelli* by Lyell (1848).

In the unpaginated Section II of the 'Additional Observations' section following Appendix I in Morton's 1834 book (dated June, 1835), Morton indicated that he had received a note from Agassiz, through Mantell, in reference "to the teeth of Fishes [Cretaceous sharks] figured on Plates XI and XII of this work." Morton (1835:276) stated that "A letter from our distinguished friend G. Mantell, Esq., informs me that my plates of the fossil teeth of Fishes, &c. from the marl of this country, had been carefully examined by M. Agassiz, who thinks he has identified among them the following species:…" While none of the shark teeth figured and subsequently identified by Agassiz included *Ptychodus*, the comment indicates that Morton was in communication with various other scientists of the day in England and on the Continent. In fact, Cooper (2010), in publishing Mantell's journal (1819–1852), notes several instances of letters and packages of fossils being exchanged between Mantell and Morton during the 1830s, including an October 4, 1831 entry regarding the receipt of "my box from Dr. Morton of Philadelphia with very fine American fossils." A review of 16 letters received by Mantell from Benjamin Silliman between 1842 and 1852 showed an average of 20 days from postmark to delivery in England. The westward voyage, with more favorable winds, generally took several days less. In spite of the distance and lengthy travel time across the Atlantic, it is evident that scientific information was being exchanged on a regular basis.

Agassiz published the first section of his five volume book, *Recherches sur les Poissons Fossiles* (1833–1843) in 1833 (Table 1). However, the volumes of the *Recherches* were not stand-alone, finished books. Instead, the volumes and the accompanying plates were published a piece at a time as separate sections (*Livraisons*) over an eleven year period (1833–1843) and sent individually to his subscribers. The volumes were only assembled when completed in 1843 or later. Marcou (1896:62) noted that "New numbers of the "Poissons fossiles" were issued, the text not corresponding with the atlas of plates, which at the time rendered rather difficult and confusing the task of those who wanted to follow him."

From Mantell's journal (Cooper, 2010), it is apparent that Agassiz had visited him at Brighton in October–November, 1834, and again in October, 1835. Agassiz must have discussed the generic and species names of Mantell's specimens with him during these visits. On October 27, 1835, Mantell wrote in his journal at Brighton that "Agassiz was busily engaged in arranging the chalk fishes to figure for his Recherches sur les poissons fossiles." Agassiz's artist, Joseph Dinkel, would then spend three months at Brighton figuring Mantell's fossils (Dean, 1999).

In his Table of Fish Fossils from the Chalk of England, Agassiz (1833–1843: Tome II, 54) mentions the genus name *Ptychodus* for the first time when he lists five species that he observed in the Mantell collection (*P. latissimus*, *P. polygyrus*, *P. mammillaris*, *P. decurrens,* and *P. altior*). He also notes that the teeth had been previously "identified as *Diodons* [Porcupine fish] by the authors" (e.g. Mantell, 1829). In his Table of Contents of the then proposed volumes (1835:68), Agassiz writes that Tome III would be "Devoted to the Placoid order" and that "The text of this volume has not yet been released." Agassiz (1833–1843:Tome III, 150) wrote "Les dents sur lesquelles j'ai basé l'etablissement du genre *Ptychodus,* sont très abondantes dans tous les terrains de la craie, et surtout dans la

Table 1. Publication dates for selected references to *Ptychodus* in the Recherches sur les Poissons Fossiles from Jeannet (1928).

Year	Month	Section	Remarks
1833	July	1st Livraison, Parts of Tome I and II	Initial publication
1835	June	5th Livraison, Part of Tome II, p. 54	First publication of genus name, *Ptychodus* and 5 new species.
1836	March	6th Livraison, Part of Tome II, p. 78	Mention of "*Hybodus, Ptychodus, Acrodus, Psammodus,* etc."
1837	September	8th and 9th Livraisons, Plate 25a	Figures of the teeth of other *Ptychodus* species
1838	November	11th Livraison, Plate 25b	Figures of the teeth of other *Ptychodus* species
1839	April	10th and 12th Livraisons, part of Tome III, caption for Plate 25 on p. 50, pp. 144–156 and Plate 25	Description of other *Ptychodus* species, figures of *Ptychodus mortoni*
1843	March	15th and 16th Livraisons, Part of Tome III, pp. 157–158	Description of *Ptychodus mortoni*, Tome III, p. 157.

craie blanche et dans ses équivalents geologiques" ["The teeth on which I based the establishment of the genus *Ptychodus* are very abundant in all chalk deposits, especially in the white chalk and its geologic equivalents"] (English translation by the author).

While Agassiz and Mantell had apparently agreed on the names for the five species of *Ptychodus* examined in his collection at Brighton, all was not well with many other names that Mantell had already given some specimens in his collection. Dean (1999:144) noted that "when the fourth *livraison* of Agassiz's text reached England, in September 1835, it contained an extensive tabulation of Mantell's Chalk fishes. Unfortunately, Agassiz had changed not only generic designations but specific ones as well – names in which Gideon had commemorated his friends. 'Surely the original discoverer is entitled to the slight privilege of naming his own discoveries,'" Mantell complained in a letter to his friend Benjamin Silliman, Yale professor and editor of the American Journal of Science and Arts.

In a subsequent paper cataloguing his personal collection at Brighton, Mantell (1836:27) lists five species of *Ptychodus* collected from England (*P. latissimus*, *P. polygyrus*, *P. mammillaris*, *P. decurrens* and *P. altior*) without attributing the genus or species names to Agassiz. In a footnote, Mantell (1836:27) writes that "Teeth of a new species have been discovered in the sand at New Jersey, United States, by Dr. Morton, - (*Morton's Synopsis*, pl. 18, fig. 1,2). I have named it *Ptychodus Mortoni*." Mantell (1839:425) repeats the same statement in the first American edition of his "*Wonders of Geology*" lectures. Years later, Mantell (1854) did not mention Agassiz's work on *Ptychodus* in his description of the genus in his *Medals of Creation* while asserting again that he named *P. Mortoni*. He also left off the attribution for *Acrodus nobilis* [Agassiz 1838] in the caption of fig. 4 which accompanied the 1854 *Ptychodus* section. It seems likely that their earlier friendly relationship had deteriorated.

On page 78 of the *Feuilleton Additionnel* for March 1836, Agassiz noted that he sometimes had reason to regret not having published earlier on some of the material, including "*Hybodus*, *Ptychodus*, *Acrodus*, *Psammodus*, etc.," having previously seen specimens of isolated teeth in various collections.

In addition to the publication of sections of the text as separates, Agassiz published the plates individually or in small groups. The three plates that included figures of the various teeth of *Ptychodus* are numbered 25, 25a and 25b. Plate 25b was apparently completed first. On pages 113–114 of the Feuilleton Additionnel for November 1838, Agassiz provides the caption for Plate 25b, figs. 9–26, including figures of *P. decurrens*, *P. altior*, *P. mammillaris*, *P. polygyrus*, and *P. latissimus*, all attributed to himself.

The caption of Plate 25 (Fig. 2) was published in the *Feuilleton Additionnel* for April 1839 on page 124 ("Explication des planches des 10e et 12e livraisons."). Agassiz wrote that Plate 25, figs. 1–3 depicted "*Ptychodus Mortoni* Mant. Green sandstone of America; from the collection of Mr. Mantell," and figs. 4–11 were "*Pt. polygyrus* Agass. White chalk of England; from the collection of Mr. Mantell, except the original figs. 10 and 11 which are in the collection of Mr. Régley, described in Tom. 3, p. 156." It should also be noted here that the inscription at the bottom of Plate 25, prepared by Agassiz's artist (Joseph Dinkel) reads "*Fig. 1-3. PTYCHODUS MORTONI* Mant."

According to the summary provided by W. H. Brown in Woodward and Sherborn (1890), Jeannet (1928), and Quenstedt (1963), text pages 141 to 156 in Tome III, including the then uncompleted Chapter VIII describing *Ptychodus* (including only *P. mammillaris*, *P. decurrens*, *P. altior* and *P. polygyrus*), were published in April 1839.

The final two pages (Agassiz, 1843:157–158) of Chapter VIII on *Ptychodus* are devoted to the descriptions of *P. latissimus* and *P. mortoni*, but were not published until March 1843 when the volume was finally completed (pages 157–390; see also Woodward and Sherborn, 1890; Jeannet, 1928; Quenstedt, 1963; Spamer et al., 1995). Interestingly, Plate 25a was published in September 1837, Plate 25b in November 1838, and Plate 25 in April 1839, each a year or more before their respective species were described.

Thus the type specimen of *Ptychodus mortoni* was actually described by Agassiz for the first time on page 158 of Tome III in March 1843, although it was figured (plate 25, figs. 1–3) nearly four years earlier in April 1839, and an earlier version by Morton (1834:pl. 18, figs. 1–2). Morton (1842:pl. 11, fig. 7) also published what appears to be an early, black and white version of Agassiz's color figures. Note that Morton had actually read the paper at meetings of the Academy of Natural Sciences of Philadelphia on October 12 and November 7, 1841, and January 25, 1842. The figures, possibly copies, may have been given to Mantell while Dinkel, Agassiz's artist, was working on the illustrations at Brighton in late 1835. Morton (1842:215) noted that "my distinguished friend, Dr. Mantell, who returned me three beautiful drawings, (which are accurately copied on the annexed plate) with the name *Ptychodus mortoni* appended. Dr. Mantell, however, has not yet informed me in what work the description is published." In the plate caption, the three views of the type specimen are labeled "*Ptychodus mortoni.* (Mantell.)"

Agassiz (1833–1843:Tome III, 158) noted again that the tooth came from the green sandstone of the United States, and "was provided to Mr. Mantell by Doctor Morton." The mistaken locality (green sand of New Jersey) had been inferred by Mantell (1836) from Morton (1834) comments, and was later repeated again by Mantell (1854). Morton provided the correct locality in his 1842 paper, indicating that the teeth were collected by Mr. Conrad (Morton's artist) "in the older cretaceous strata at Prairie Bluff, Alabama." Wheeler (1935:52) noted that Conrad, a well recognized conchologist and artist of the day, was collecting fossils in Alabama in 1833, and was corresponding with Dr. Samuel Morton. Conrad returned to Philadelphia in early 1834.

CONCLUSIONS

Gideon Mantell (1790–1852) was already well established in the field of paleontology, having written several books, when Louis Agassiz (1807–1873) began his publication of *Poissons Fossils*. Even so, the study of paleontology was relatively new and Mantell welcomed the interest of the young Agassiz in his personal collection. By then, however, Mantell was also in contact with scientists in the United States and was regularly exchanging letters and fossil specimens with Silliman, Morton, Harlan, and others. Fossils from the Late Cretaceous of the southeastern United States including Alabama, were being collected and described during the early part of the 19th Century, decades before the discovery of similar fossil deposits in the Great Plains and far West, and were important contributions to the early science of paleontology.

The discovery, naming and description of *Ptychodus mortoni* provide an interesting window into the pace of science, in general, and paleontology in particular during the early 19th Century. Given the distances and relatively slow pace of transportation both directions across the Atlantic Ocean, scientists on both sides appear to have remained relatively current in regard to new discoveries. As a distinct and unique species, discovered first in Alabama, the history of *P. mortoni* includes the contributions of early paleontologists in the United States, England and Europe.

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I have benefited greatly from discussions, references and corrections provided by Jean-Michel Benoit, Chris Duffin, Jun Ebersole, Alvaro Mones, Markus Moser, Mathieu Richaud, Rudolph Serbet, Kenshu Shimada, and Takehito Ikejiri. I also appreciated the efforts of Chris Duffin to locate and photograph the type specimen in the Natural History Museum, London. The comments of Markus Moser and two anonymous reviewers significantly improved the content of an earlier manuscript.

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A Note on the Occurrence of *Ptychodus polygyrus* (Ptychodontidae) from the Late Cretaceous of Alabama, with Comments on the Stratigraphic and Geographic Distribution of the Species

SHAWN A. HAMM[1*] and T. LYNN HARRELL JR.[2]

[1]8527 Nantucket, Wichita, KS, 67212 U.S.A., shamm821@gmail.com;

[2] Department of Geological Sciences, University of Alabama, Box 870338 Tuscaloosa, AL 35487 tlharrelljr@crimson.ua.edu

*Corresponding author

ABSTRACT

***Ptychodus polygyrus* (Ptychodontidae) is a Late Cretaceous shark that occurs in Santonian and lower Campanian strata within the English Chalk. Herein we describe nine isolated teeth of *P. polygyrus* from the Tombigbee Sand Member (late Santonian-early Campanian) of the Eutaw Formation in Alabama that compare favorably with the type specimen (more than one jaw placement is represented within the dentition). Taxonomically, *P. polygyrus* has erroneously been referred to other low crowned and stratigraphically younger species of *Ptychodus*, but it can be distinguished by a set of distinct characteristics. *Ptychodus polygyrus* is stratigraphically one of the last species of *Ptychodus* in the fossil record and is often found in association with a diverse selachian fauna that includes other high crowned ptychodontids *P. mortoni* and *P. rugosus*, which may be indicative of niche separation.**

INTRODUCTION

The nine Alabama specimens of *Ptychodus polygyrus* described in this study were collected over a period of several years from three or four separate localities that extend across west-central Alabama in a northwest to southeast direction. These localities (Fig. 1) lie within the eastern Gulf Coastal Plain in a region known locally as the Black Belt, due to the rich color of the soil derived from the underlying Cretaceous bedrock. In Alabama, the outcropping Cretaceous marine formations of the Black Belt region range from the Coniacian and Santonian Eutaw Formation to the late Maastrichtian of the Prairie Bluff Chalk (Mancini and Puckett, 2003).

The upper Tombigbee Sand Member of the Eutaw Formation and lower Mooreville Chalk of the Selma Group (Fig. 2) are exposed at all of the Alabama localities presented in this study. The Tombigbee Sand Member in Alabama is composed of micaceous, glauconitic, generally fine-grained, massively bedded sandstone that has an upward-fining trend and represents the start of a regional marine transgression (Mancini and Soens, 1994). Additionally, the amount of carbonate present in the unit increases as the grain size and quantity of sand decrease. Several transgressive lag deposits are found within the member that contain numerous fossils of marine vertebrates (teeth and bone fragments), rarer teeth and bones of vertebrates that would have inhabited fluvial environments, phosphatic wood fragments, and marine invertebrate steinkerns and ichnofossils. The lower portion of the overlying Mooreville Chalk contains very fine calcareous sand and glauconitic marl (Kiernan, 2002) in a continuation of the fining upward sequence observed in the Tombigbee Sand. Although the contact between these two formations is conformable and can be difficult to discern, it is often indicated by a thin layer of sideritic mollusk molds and phosphatic grains (Mancini and Soens, 1994). The Mooreville Chalk is well known for its

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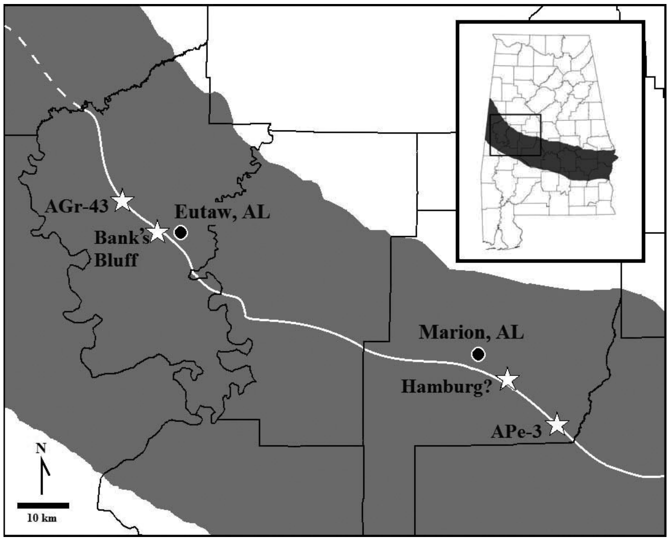

Figure 1. Geographic map of Alabama *P. polygyrus* localities.

articulated and semi-articulated marine vertebrate fossils (Zangerl, 1948, 1953; Russell, 1970) which are indicative of the deeper, quieter, more dysoxic bottom conditions than the Tombigbee Sand. Invertebrate macrofaunal diversity in the Mooreville Chalk is lower than that of the Tombigbee Sand, being mostly comprised of thin shelled oysters and rare ammonite steinkerns (Kiernan, 2002).

The contact between the two formations is interpreted to represent a significant marine flooding event. It is reported to be diachronous with regions in eastern Mississippi near Columbus, and presumably extreme western Alabama, having an age of latest Santonian or earliest Campanian, and regions in central Alabama having an age of late Santonian (Kiernan, 2002; Liu, 2007). This agrees with the reported occurrences of *P. polygyrus* specimens described in this study as the specimens collected from the more western Greene County are from the upper Tombigbee Sand while those from the more eastern Perry County localities were obtained from just below the lower Mooreville Chalk.

The interpreted depositional environments represented at the Alabama localities reflect the fining upward sequence observed in the lithology. Originally, the upper Tombigbee Sand was interpreted as being deposited in a barrier to back barrier island environment whereas the lower portion of the Mooreville Chalk was deposited in a lower-shore face to inner-shelf environment (King and Skotniki, 1990). Current research by Liu (2007) indicates that the Tombigbee Sand Member represents an inner neritic to marginal marine environment that corresponds to a marine transgressive event at the Tombigbee-Mooreville contact. This interpretation is consistent with the overall regional marine transgression that occurred during the late Santonian to early Campanian.

Selachian taxonomy based strictly on isolated teeth is problematic because of the condition of heterodonty (Cook et al., 2011). Because of this, inconsistencies have arisen over the taxonomy of *Ptychodus* species exhibiting similar tooth morphologies (i.e. crown height and ridge patterns) particularly the low crowned species *P. polygyrus* Agassiz, 1839, *P. marginalis* Agassiz, 1839 and *P. martini* Williston, 1900. Comparison of the dental characteristics of the Alabama teeth we studied with the type specimens of *P. polygyrus* (NHMUK 10771) and *P. marginalis* (NHMUK P 10464) from the English Chalk along with *P. martini* (KUVP 55277) from the Smoky Hill Chalk of Kansas (Williston, 1900) indicated a closer morphology with *P. polygyrus.*

The purpose of this communication is to describe the Alabama occurrences of *Ptychodus polygyrus* teeth and discuss its rarity and taxonomic complexity. We correct the taxonomic assignment of North American material previously referred to *P. polygyrus* and document the true stratigraphic and geographic distribution of the species. Also discussed is the variation in tooth morphology within the low-crowned species of *Ptychodus.*

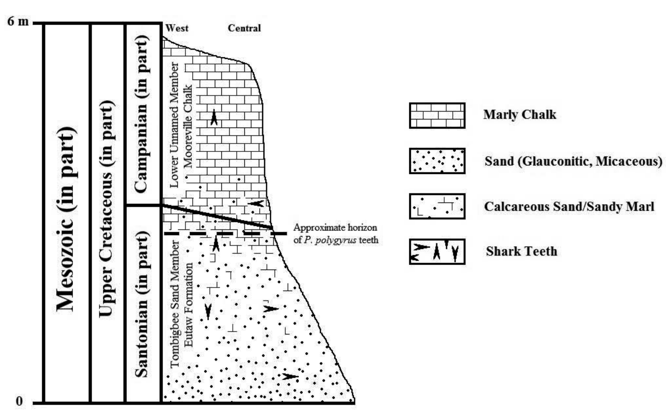

Figure 2. Relevant stratigraphic column for localities for *Ptychodus* from western Alabama. Note diachronous contact between Tombigbee Sand and Mooreville Chalk in west to east direction.

MATERIAL AND METHODS

The nine teeth described herein come from three, perhaps four, different localities in Alabama: two in Greene County and one or possibly two near Hamburg, Perry County. In Greene County, site AGr-43 is well-known to amateur and professional collectors for its diverse marine and non-marine fluvial vertebrate fauna while Bank's Bluff near Eutaw, Alabama is a lesser-known, historical collecting locale that is now submerged under water and no longer accessible. In Perry County, site APe-3 is located near Dry Creek in the southeastern portion of the county. It is unknown whether the Perry County location, labeled as "Hamburg" with UAM PV 1985.0025.0001(a-b) and UAM PV 2005.0006.0293(a-c), is the same as APe-3 or represents another similar exposure in the surrounding area. The "Hamburg" specimens were assimilated into

Table 1. Dental measurements for each specimen of *P. polygyrus*. Abbreviations for measurements: A–B, apex to left posterior tooth edge; A–F, apex to left posterior crown edge; A–C, apex to right posterior tooth edge; A–G, apex to right posterior crown edge; F–G, posterior crown width; B–C, posterior tooth width; B–E, labial tooth length; F–I, labial crown length; C–D, lingual tooth length; E–D, anterior crown width; G–H, lingual crown length; nTR, number of transverse ridges. Except for nTR, all measurements are in millimeters. * Denotes that the tooth root is missing.

Specimen	TH	CH	A-B	A-F	A-C	A-G	F-G	B-C	B-E	F-I	C-D	E-D	G-H	nTR
UAM PV 1985.0025.0001.001	43	29	36.5	26	36	25.5	44	64	36	21	33	64.5	19.5	10
UAM PV 1985.0025.0001.002	19*	15	22	21	21	17	29.5	33	28.5	24	26.5	34	20	9
UAM PV 1993.0002.0164	16	12	20.5	19	19.5	15	26.5	31	26	20	26	31	21	12
UAM PV 2005.0006.0293.001	28	20	26.5	17	27	16	26	43	32	22	N/A	N/A	19	14
UAM PV 2005.0006.0293.002	18*	12.5	21.5	16	19.5	16	29	32	26	20	27	32	18.5	10
UAM PV 2005.0006.0293.003	17*	12	18	9	16.5	14	19	22	26.5	19	26	22	21	8
UAM PV 2011.0002.0058	21	13.5	14	10	14.5	12	17.5	19	19.5	14	20	19	12	6
UAM PV 2011.0002.0059	13	7.00	13	12	13	12	19.0	21	20.0	14	16.5	21	13	8

the UAM collections originally from the Geological Survey of Alabama collections and much of their locality data was lost. The exact locality data for these specimens are on file at the Alabama Museum of Natural History and McWane Science Center in Birmingham. All tooth measurements were taken using digital calipers (Table 1).

All specimens used in this study are housed in museum collections and all information gathered is on file at those institutions including the **NHMUK**, Natural History Museum in UK, London; **FHSM VP**, Fort Hays Museum of Natural History, Hays, Kansas; **FMNH**, Field Museum of Natural History, Chicago, Illinois; **KUVP**, University of Kansas Museum of Natural History, Vertebrate Paleontology Collection, Lawrence, Kansas; and **UAM PV**, University of Alabama Museums Vertebrate Paleontology Collection, University of Alabama, Tuscaloosa, Alabama.

SYSTEMATIC PALEONTOLOGY

Class CHONDRICHTHYES Huxley, 1880
Subclass ELASMOBRANCHII Bonaparte, 1838
Cohort EUSELACHII Hay, 1902
Subcohort NEOSELACHII Compagno, 1977
Order PTYCHODONTIFORMES Hamm, 2008
Family PTYCHODONTIDAE Jaekel, 1898
PTYCHODUS POLYGYRUS Agassiz, 1839
[**Figures 3, 4**]

Holotype- NHMUK P. 10771, associated set of 76 teeth from the *Gonioteuthis quadrata* zone (lower Campanian) of the English Chalk.

Referred Material—UAM PV 1985.0025.0001.001 (one medial tooth); UAM PV 1985.0025.0001.002 (one upper R1 tooth); UAM PV 1993.0002.0164b (one upper medial tooth); UAM PV 2005.0006.0293a (one lateral tooth); UAM PV 2005.0006.0293b (one lateral tooth); UAM PV 2005.0006.0293c (one lateral tooth); UAM 2011.0002.0058 (one lateral tooth); UAM 2011.0002.0059 (one lateral tooth) and FMNH PF 127 (one tooth) from the Tombigbee Sand Member of the Eutaw Formation.

Revised diagnosis of type—Medial teeth low crowned and rectangular in outline, with thick transverse ridges that extend to the distal ends. Transverse ridges on the anterior tooth files extend completely to the mesial and distal tooth edges and curve lingually interconnecting with preceding ridges preventing the formation of a distinct marginal area. Anterolateral and posterior files maintain the same ridge pattern but not always fully extend to the tooth margins. Ridges in the lateral files become finer at their distal ends merging and blending into a proportionally wide marginal area. Marginal area composed of coarse granular enameloid bumps not arranged in a diagnostic pattern.

Description

Until now, the only correctly identified *P. polygyrus* from North America is a single tooth (FMNH-PF 127) from the uppermost Eutaw Formation or lowermost Mooreville Chalk (late Santonian-early Campanian) from Bank's Bluff, Greene County, Alabama (Gibbes, 1848; Applegate, 1970; Thurmond and Jones, 1981). Our specimens (Fig.

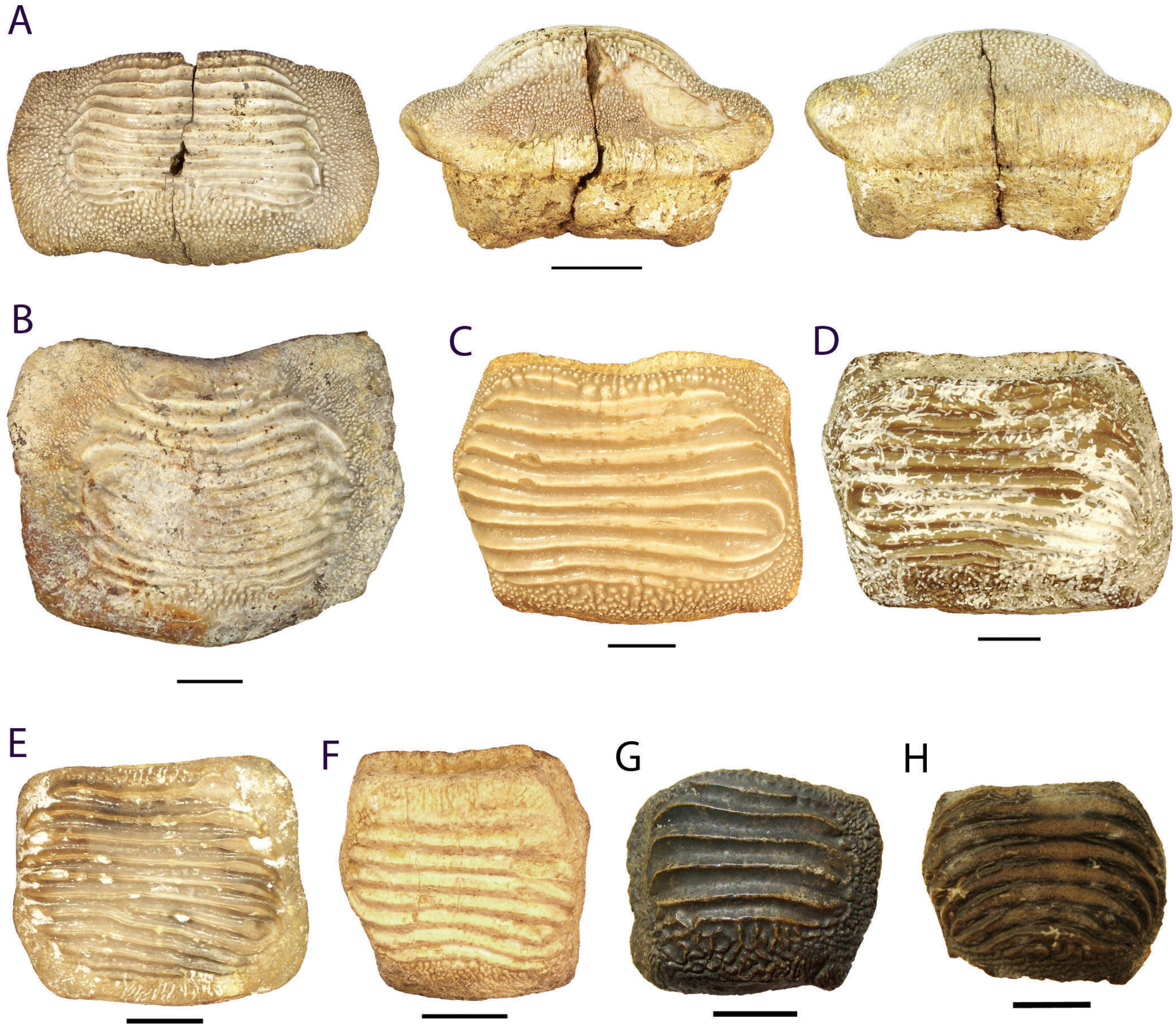

Figure 3. Teeth of *P. polygyrus*, occlusal view. A, UAM PV 1985.0025.0001.001 (one medial tooth); B, UAM PV 2005.0006.0293.001 (one upper medial tooth); C, UAM PV 1985.0025.0001.002 (one upper R1 tooth); D, UAM PV 2005.0006.0293.002 (one lateral tooth); E, UAM PV 1993.0002.0164 (one lateral tooth); F, UAM PV 2005.0006.0293.003 (one lateral tooth); G, UAM 2011.0002.0058 (one lateral tooth); H, UAM 2011.0002.0059 (one lateral tooth). Scale A equals 5 cm; B-H equals 1 cm.

3) are represented by a lower medial file tooth (UAM PV 1985.0025.0001.001; UAM PV 1985.0025.0001.002; FMNH PF 127), an upper medial file tooth (UAM PV 2005.0006.0293a) and five antero-lateral file teeth (UAM PV 2005.0006.0293b; UAM PV 2005.0006.0293c; UAM PV 2011.0002.0058; UAM PV 2011.0002.0059; UAM PV 1993.0002.0164). The medial tooth (UAM PV 1985.0025.0001) measures 64 mm in width and 33 mm in length. The tooth crown is gently raised and flattened at the apex and is 43 mm in tooth height (TH) with a crown height (CH) of 29 mm. There are 10 parallel transverse ridges that curve anteriorly and terminate abruptly at a coarsely granulated marginal area. The granulations on the margin are not concentric and do not bifurcate at the distal edges. Marginal ornamentation on the posterior tooth edge is oriented perpendicular to the last transverse ridge. The anterior protuberance is shelf-like and extends across the apron of the crown. The posterior sulcus is shallow and wide to articulate with the anterior protuberance of the proceeding tooth.

Applegate (1970: 393, fig. 179a) and Thurmond and Jones (1981: 42, fig. 8) described a single tooth, FMNH PF 127, which also possesses the characteristics of lower medial file tooth. It measures 5.5 cm in length and 3.5 cm in width. There are five robust parallel transverse ridges and a weakly developed ridge at the anterior tooth edge. Two sets of raised transverse ridges on the posterior tooth edge appear to be fully developed but are not continuously connected to the lateral tooth edges. None of the ridges extend completely to the marginal area as they terminate abruptly at a coarsely granulated margin. The granulations are not arranged in a discernible pattern (i.e., concentric or radiating).

The four lateral teeth in our sample have a square outline in occlusal view and are identical in morphology to those described in the type specimen. They are short, flat, range in size from 13-15 mm in crown height, and have between 8 and 14 raised transverse ridges.

Morphological Distinctions

Although *Ptychodus polygyrus* teeth are similar to the low crowned species *P. marginalis* and *P. martini,* each taxon can readily be distinguished based on crown width, crown height and occlusal ornamentation.

Hamm (2010) described an associated tooth set of *P. marginalis* (p. 539, fig. 1) and compared it with the type specimen of *P. polygyrus* (p. 540, fig. 2). The anterior teeth of *P. marginalis*, lower medial (LM) and first and second tooth files (R1, R2) are characterized by having low, broad, gently raised, rounded, rectangular and wide occlusal surface crossed by 10 to 14 straight to slightly wavy, parallel and closely spaced transverse ridges. The ridges loop at their distal ends, some interconnecting with one another and terminate at a narrow marginal area. There are small bumps of dentine present between the ridges in the anterior file teeth. Lateral file teeth (L/R 3-5) are more antero-posteriorly shorter and distally elongated than anterior teeth. The central portion of the crown is raised and there are fewer occlusal ridges (7-8), which become more restricted to the center of the crown, and their distal ends curve anteriorly on the mesial tooth edge as they meet at the margin. The ridges are clearly demarcated from the marginal area, which becomes wider and shelf-like and is covered by finely granular enameloid ridges that are arranged concentrically with the occlusal ridges. The posterior teeth (L/R 7-8) have a nearly flat, elongate and rectangular crown with 3 to 5 parallel and wavy transverse ridges that do not loop or curl at the distal ends; no marginal area is present. Depending on the stage of ontogeny, the ridges are distinct and parallel or they have indistinct ridges composed of multiple elongate bumps of enameloid.

Williston (1900, pl. X) described a new species of *Ptychodus* from the Smoky Hill Chalk Member of the Niobrara Formation in Kansas as *P. martini* (KUVP 55271). The lower medial file teeth of *P. martini* are rectangular in outline with an extremely flat occlusal surface crossed by eight to nine parallel and slightly undulating ridges that extend fully to the lateral tooth edges. The ridges are closely spaced, thick at the base and thin at the apex, creating a sharp cutting edge. The ridges curve anteriorly at the mesial and distal edges and do not bifurcate at the lateral tooth margins. The para-medial files (R1/L1) are represented by eight teeth that are nearly rectangular with a gently raised and rounded occlusal surface with seven to eight transverse ridges that terminate at a narrow, shelf-like marginal area. The anterolateral file teeth (R/L 3-4) have seven to eight parallel transverse ridges with a tooth shape that progressively becomes elongate and rectangular. The occlusal surfaces are flat, but are slightly elevated at the distal tooth edge. The posterior files (R/L 5) have completely flat occlusal surfaces with an average of five transverse ridges that extend completely to the mesial and distal tooth margins.

Within each file, the pattern and arrangement of the transverse ridges are consistently parallel and uniform with a slight sinusoidal pattern. The ridges on the anterior files are highly elevated, wider at the base than at the apex creating a sharp edge and increasing the distance between the ridges, presumably for greater crushing ability. The ridges become shallower, narrower at the base, and densely packed in lateral and posterior files. In some of the teeth there are small spheroidal enameloid bumps between the ridges. There is no consistency as to which ridges they occur or among a particular tooth within a file, nor do they consistently occur among all tooth files. The mesial and distal marginal area is coarsely granulated and is not concentric with the crown. The ornamentation on the labial and lingual margins is composed of fine bifurcating ridges oriented perpendicular to the crown.

The presence of small bumps of enameloid between the transverse crown ridges in *P. marginalis*, *P. martini* and *P. polygyrus* may represent another frictional surface that increased the tooth's ability to acquire or process prey more effectively. This characteristic is unique within the Ptychodontidae, as they are not present on teeth of any other species and may be a phylogenetically informative characteristic (Fig. 4).

Stratigraphic and Geographic Distributions

In North America, specimens referred to *P. polygyrus* have been reported from the Kamp Ranch Formation in Texas (Welton and Farish, 1993), the Mooreville Chalk in Alabama (Gibbes, 1848; Leidy, 1868; Applegate, 1970; Thurmond and Jones, 1981), and the Niobrara Chalk in Kansas (Cope, 1874; Williston, 1900; Dibley, 1911; Woodward, 1911; Russell, 1988; Caggiano and Everhart, 2003; Everhart et al., 2003; Shimada and Fielitz, 2006).

When Agassiz originally described *P. polygyrus* he also described three other species, *P. concentricus, P. sulcatus,* and *P. marginalis*, all of which he considered to be related to *P. polygyrus*. Malecki (1980) considered *P. marginalis* to be a sub-species of *P. polygyrus,* and since this observation, reports of *P. marginalis* from Cenomanian and Turonian

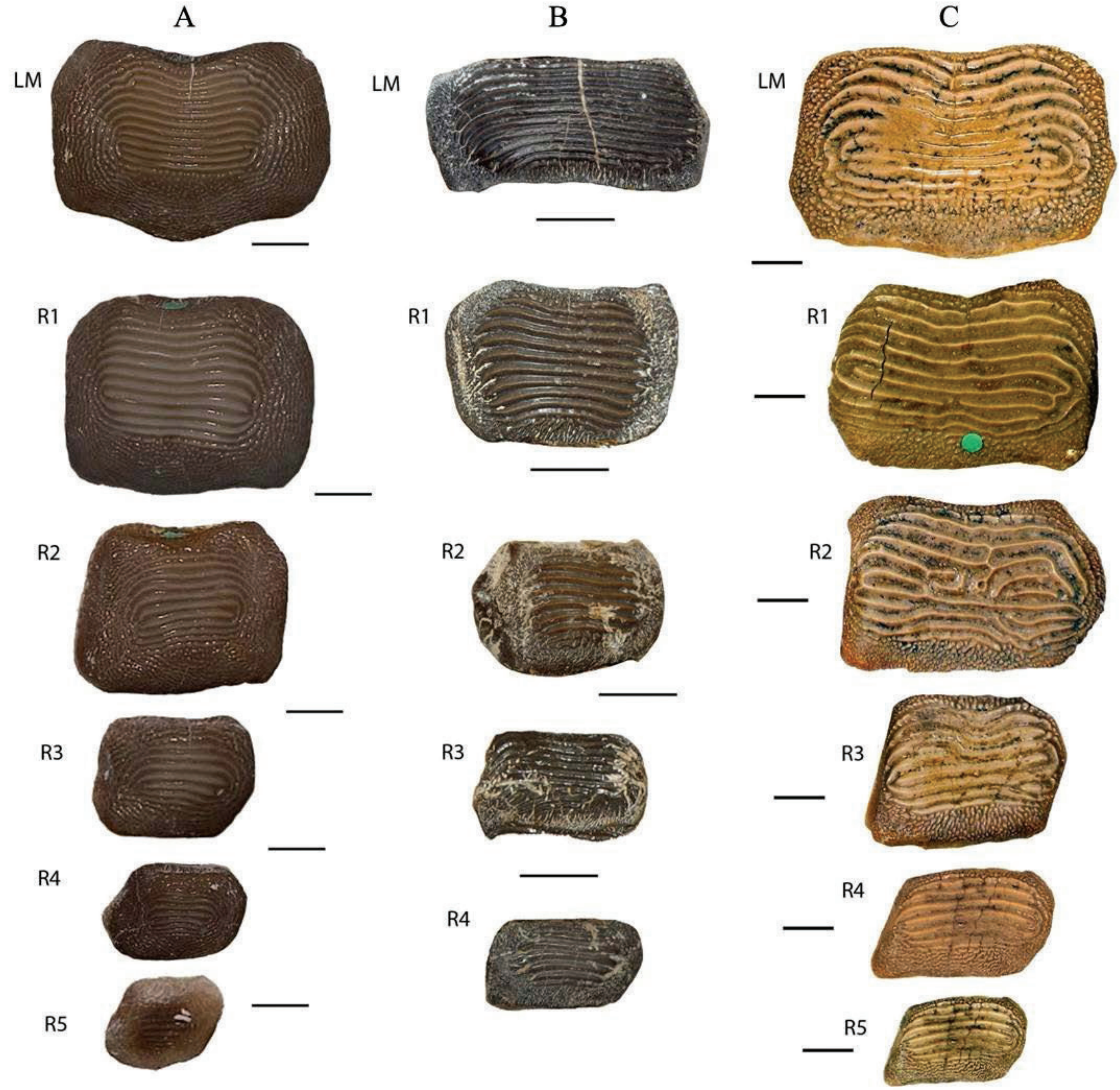

Figure 4. Comparison of tooth morphologies between the type specimens of A, *P. marginalis* (NHMUK P. 10464; B, *P. martini* (KUVP 55271), and C, *P. polygyrus* (NHMUK P. 10771). Scale equals 1 cm.

deposits in North America have been referred to *P. polygyrus* (Welton and Farish, 1993; Cicimurri, 1998, 2004; Hamm, 2003; Everhart et al., 2003; Everhart and Caggiano, 2004; Shimada and Fielitz, 2006). Taxonomic assignment of material from the Cenomanian and Turonian of Europe and North America should be referred to *P. marginalis* (Hamm, 2010).

The first North American occurrence of *P. polygyrus* was reported by Cope (1874: 47) from the Smoky Hill Chalk Member of the Niobrara Chalk and unfortunately cannot be located. Williston (1900: 240, pl. XI, fig. 9) described a large, lower medial file tooth (KUVP 55237) from the "lower beds of the Niobrara Cretaceous of the Smoky Hill River" and "provisionally" referred it to *P. polygyrus,* noting "the resemblances are sufficiently great to render the determination not improbable; at least with some of its varieties". Dibley (1911: 270) briefly stated, "Teeth of the typical form [*P. polygyrus*] from the Niobrara Chalk of Kansas have also been described under the name of *P. martini*". Russell (1988) and Shimada and Fielitz (2006) noted the presence of *P. polygyrus* in the Smoky Hill Chalk but did not illustrate or refer to a specific cataloged specimen. Caggiano and Everhart (2003) ascribed a single tooth (FHSM VP 15008) to *P.* aff. *polygyrus* and Everhart et al. (2003) listed a single tooth of *P.* cf. *P. latissimus* (FHSM VP 14853) as one of five species of *Ptychodus* from the Smoky Hill Chalk. All of these specimens were reviewed by Hamm (2010) and compared with the type specimen of *P. martini* (KUVP 55277) and re-diagnosed as such.

The oldest stratigraphic occurrence of *P. martini* is from the lag deposit at the basal Atco Formation of the Austin Group (early Coniacian) in North Central Texas (Hamm, 2008; Hamm and Cicimurri, 2011). Carpenter (2003) noted that the Last Occurrence Datum (LAD) for *P. martini* within the Niobrara Chalk is within Hattin's (1982) Marker Unit's 1, 2, and 3 (Zone of *Inoceramus grandis*) which includes Stewart (1990) biostratigraphic Zone of *Protosphyraena pernicoisa*, which is late Coniacian in age. *Ptychodus martini* has not been recovered from the underlying early Coniacian Fort Hays Limestone Member of the Niobrara Group. The presence of *P. martini* in basal Atco Formation indicates a northerly distribution of the species from the Gulf Coast into the Western Interior Seaway during the Coniacian.

A single tooth of *P. martini* has also been reported from the Roxton Limestone Member (late early Campanian) of the Gober Chalk in Fannin County, Texas (MacLeod and Slaughter, 1980; Hamm and Shimada, 2004). The current fossil record indicates that the low crowned species of *Ptychodus* from the Coniacian in the Western Interior Seaway should be referred to *P. martini*. It is interesting to note that *P. martini* has not been found in the Santonian units of the Niobrara Chalk and perhaps its reoccurrence in Texas at this time is due to environmental conditions or food sources.

To date, the discoveries of *P. polygyrus* in Alabama represent the only occurrence of this species in North America, with a stratigraphic distribution that mirrors its European occurrences (*Gonioteuthis quadrata* zone) in the English Chalk (Dibley, 1911; Woodward, 1911). The post- Coniacian occurrence of *P. polygyrus* in Alabama coincides with the disappearance of *P. martini* in the Western Interior Seaway indicating a preference for the warmer, shallower waters to the south.

Paleoecology

The distribution of marine vertebrates in the Western Interior Seaway and Gulf Coast is indicative of two faunal sub-provinces, with cool temperate waters in the north and warm temperate, subtropical waters in the south. The boundary zone between these provinces was at the southern border of Kansas to the northern border of Texas (Nicholls and Russell, 1990). The Tombigbee Sand Member of the Eutaw Formation represents an inner neritic to marginal marine environment and corresponds to a marine transgressive event at the Tombigbee-Mooreville contact (Liu, 2007).

Becker et al. (1998) presented a model for the formation of the Tombigbee Sand Member of the Eutaw Formation. In their model, the Tombigbee Sand Member represents a lag deposit containing a mixture of Santonian and Campanian ammonite and chondrichthyan taxa that were reworked from older strata during initial marine transgression, similar to the basal Atco Formation of the Austin Group in Texas (Hamm and Cicimurri, 2011). Ammonites found in the upper part of the Tombigbee Sand Member include *Placenticeras syrtale*, *Texanites lonsdalei*, and *Submortoniceras tequesquitense*, which, along with the inoceramid bivalve *Inoceramus proximus* represent a late Santonian fauna. The ammonites *Pseudoschloenbachia mexicana, Boehmceras arculus, Glyptoxoceras sp.* and *Baculites capensis* from the lower Mooreville Chalk are indicative of an early Campanian age (Kennedy et al., 1997). Other selachian specimens associated with *P. polygyrus* in the UAM VP collections include *Cretoxyrhina mantelli*, *Squalicorax kaupi*, *P. rugosus* and *P. mortoni* and are indicative of late Santonian taxa. Schwimmer et al. (2002) noted the presence of *Cretodus semiplicatus* from the Tombigbee Sand Member and discussed its environmental preferences from nearshore to offshore deposits. The model of Becker et al. (1998) accounts for our material possibly being from differing stratigraphic intervals, and potentially representing different environmental niches mixed together.

Ptychodus marginalis, *P. martini* and *P. polygyrus* illustrate the continuous retention of a low, wide dentition from the middle Cenomanian through the Santonian/early Campanian. Although their general dentition plan is convergent to the myliobatid pavement dentition, their tooth crown morphologies are similar to *Rhina anclystoma*, *Mustelus,* and the posterior teeth of *Heterodontus.* These taxa have dome-like crowns and raised cutting ridges that form a grinding surface as in *Ptychodus.* They are bottom dwellers that inhabit temperate and tropical environments that range from inshore waters to the upper continental slope and feed on a variety of hard-shelled invertebrates including bivalves, gastropods, crustaceans, sea urchins, squid, as well as bony fishes (Compagno, 1999, 2001). Because the dentition of the low crowned species of *Ptychodus* mirrors their crown morphologies in design, it is hypothesized that they lived in a similar environmental conditions having a benthic lifestyle and similar diet. The diverse ammonite fauna described by Kennedy et al. (1997) would have been a readily available food source for not only *P. polygyrus,* but the higher crowned ptychodontids *P. mortoni* and *P. rugosus* as well.

CONCLUSIONS

Although the taxonomic assignment of *P. polygyrus* has been referred to other low crowned and stratigraphically younger species of *Ptychodus*, it has been shown to possess diagnostically differentiated characters. The presence of *P. polygyrus* in the Tombigbee Sand Member in Alabama is significant as it is the only occurrence of the species in North America. Comparison of the dental characteristics with modern taxa having similar tooth crown morphologies and the environments they prefer, with their presence in the Tombigbee Sand suggests that *P. polygyrus* lived a benthic lifestyle. This record documents the southward migration of *Ptychodus* from the Western Interior Seaway into the Gulf Coast, is the last low crowned species and preserves one of the final records of the genus worldwide.

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