ALABAMA MUSEUM of Natural History

Bulletin

Bulletin 31 Vol. 1 April 1, 2013

Contributions to Alabama Cretaceous Paleontology

Guest Editors

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An Overview of Late Cretaceous Vertebrates from Alabama

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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.

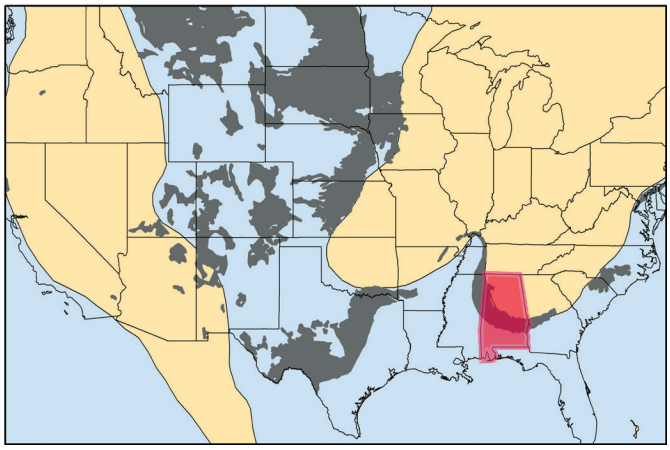

Figure 1. Upper Cretaceous landmass and seas in North America. The gray color indicates outcrops of Upper Cretaceous strata (Cenomanian to Maastrichtian in age). Light tan indicates the Cretaceous land mass. Alabama is indicated by light red.

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

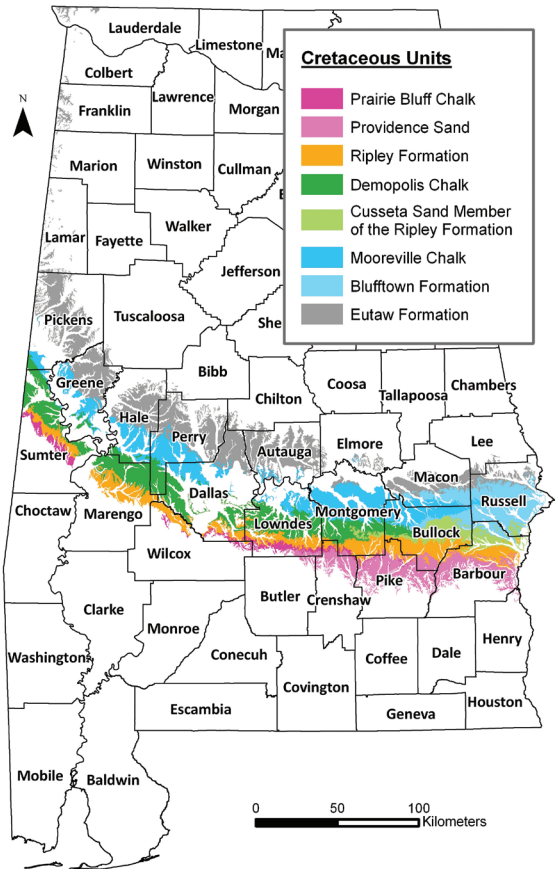

Figure 2. Distribution of Upper Cretaceous surface geology in Alabama based on the 1:250,000-scale digital state geology (GSA, 2006).

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.

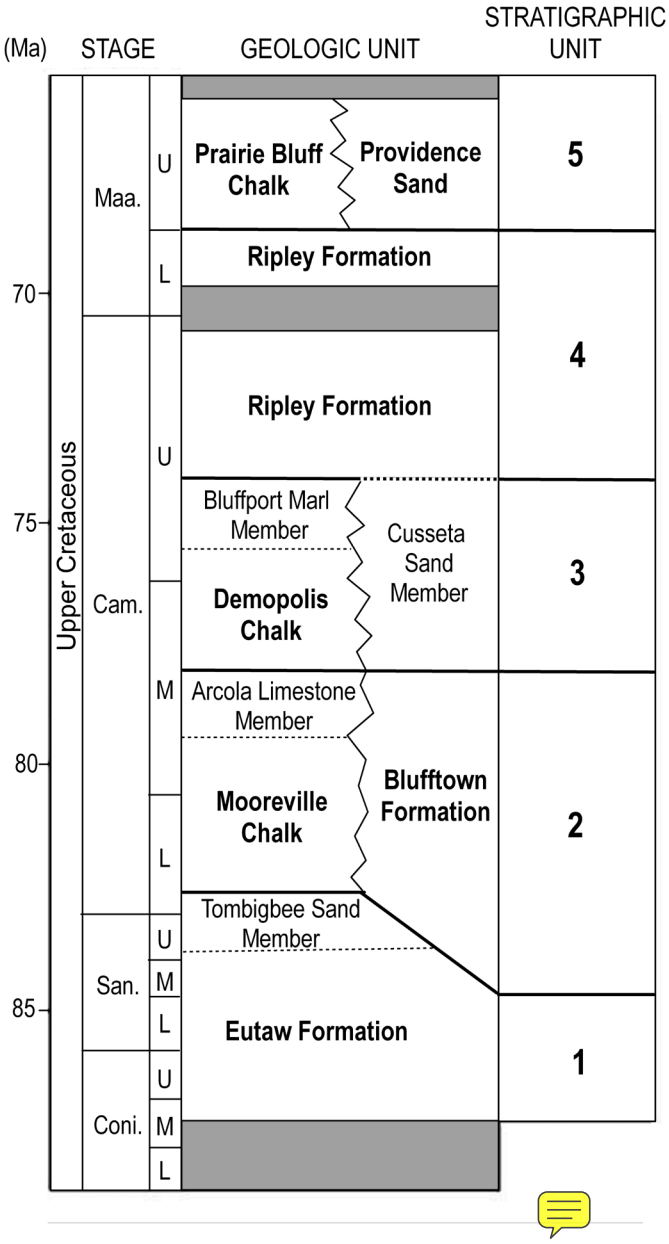

Figure 3. The five Upper Cretaceous Alabama stratigraphic units used in this study.

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*

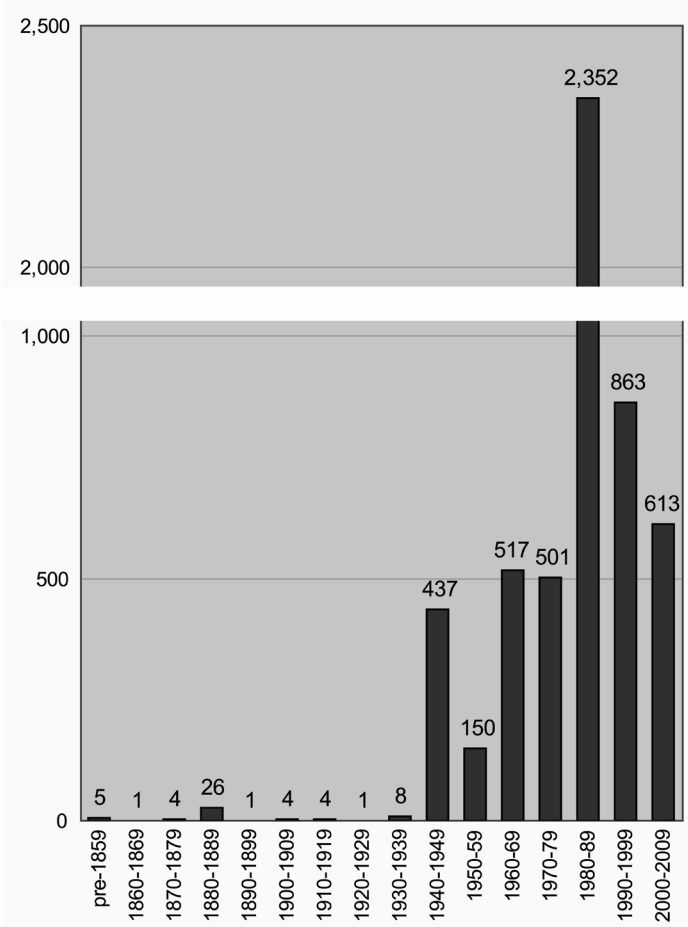

Figure 4. Numbers of vertebrate specimens collected in Alabama since 1850. Note: only specimens catalogued in institutions are included in this figure (see further explanation in the text). Vertical scale represents number of specimens.

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

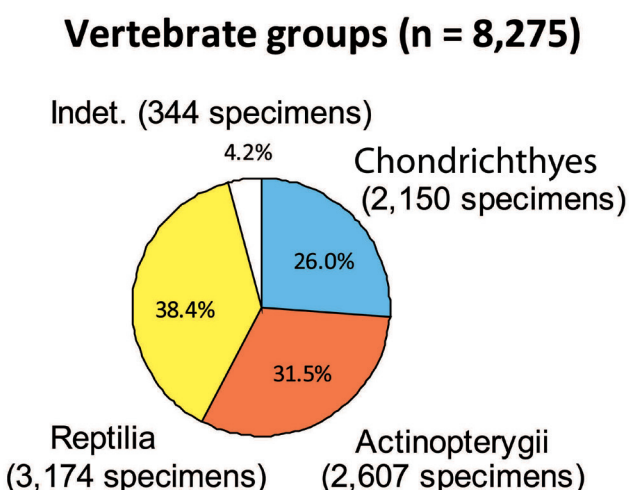

Figure 5. Numbers of Cretaceous specimens in major vertebrate groups from Alabama. 'Indet.' is assigned to specimens not identifiable at any particular taxonomic level.

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).

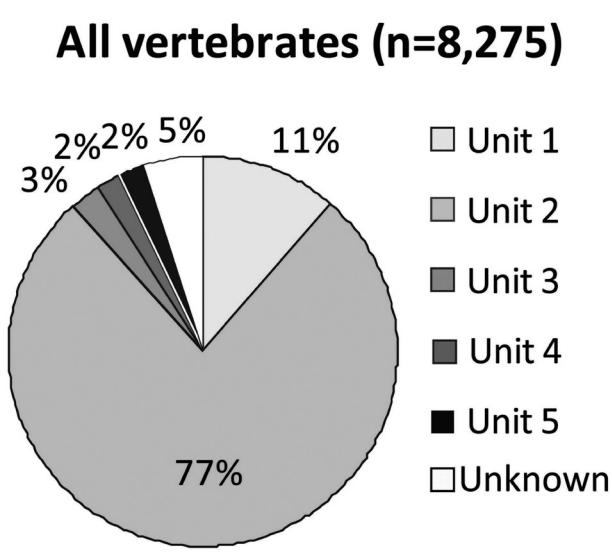

Figure 6. Numbers of vertebrate specimens from five Cretaceous stratigraphic units in Alabama. Geologic units (Fm/Mbr) of the five units are listed in Table 7.

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-

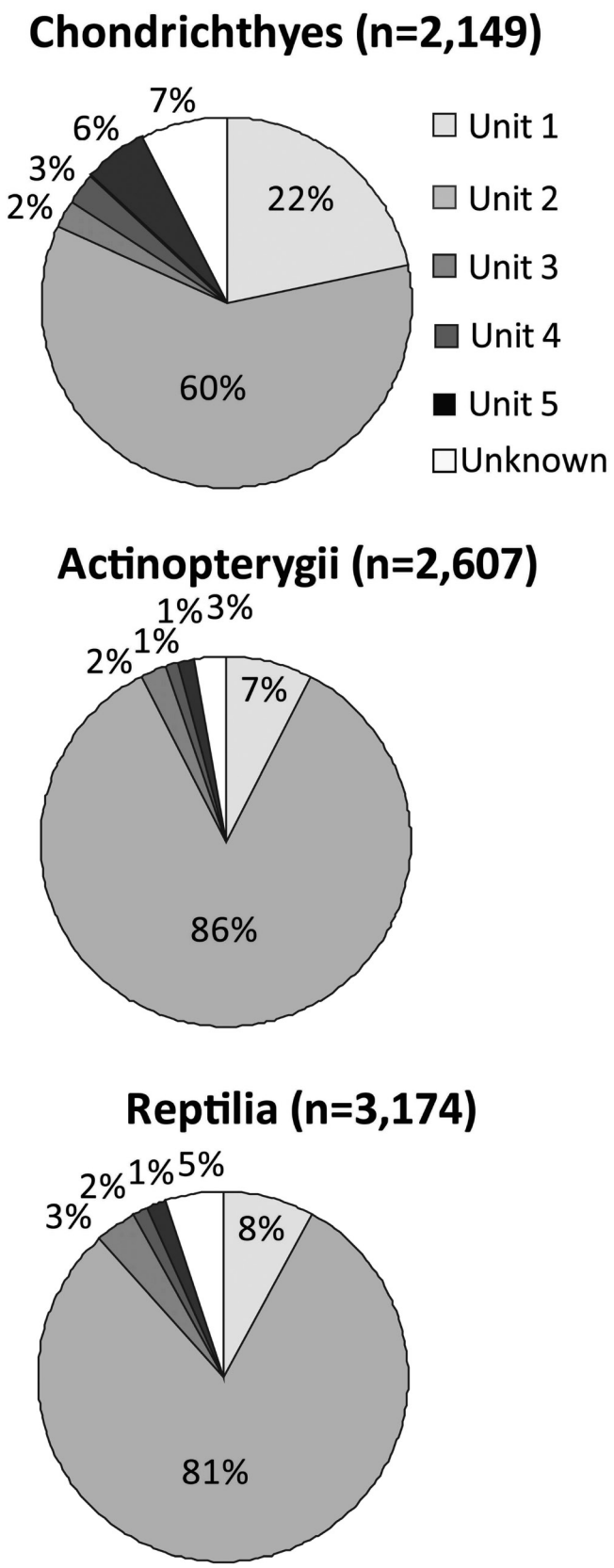

Table 7. Percentage of Chondrichthyes, Actinopterygii, and Reptilia specimens identified from five Upper Cretaceous stratigraphic units in Alabama.

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

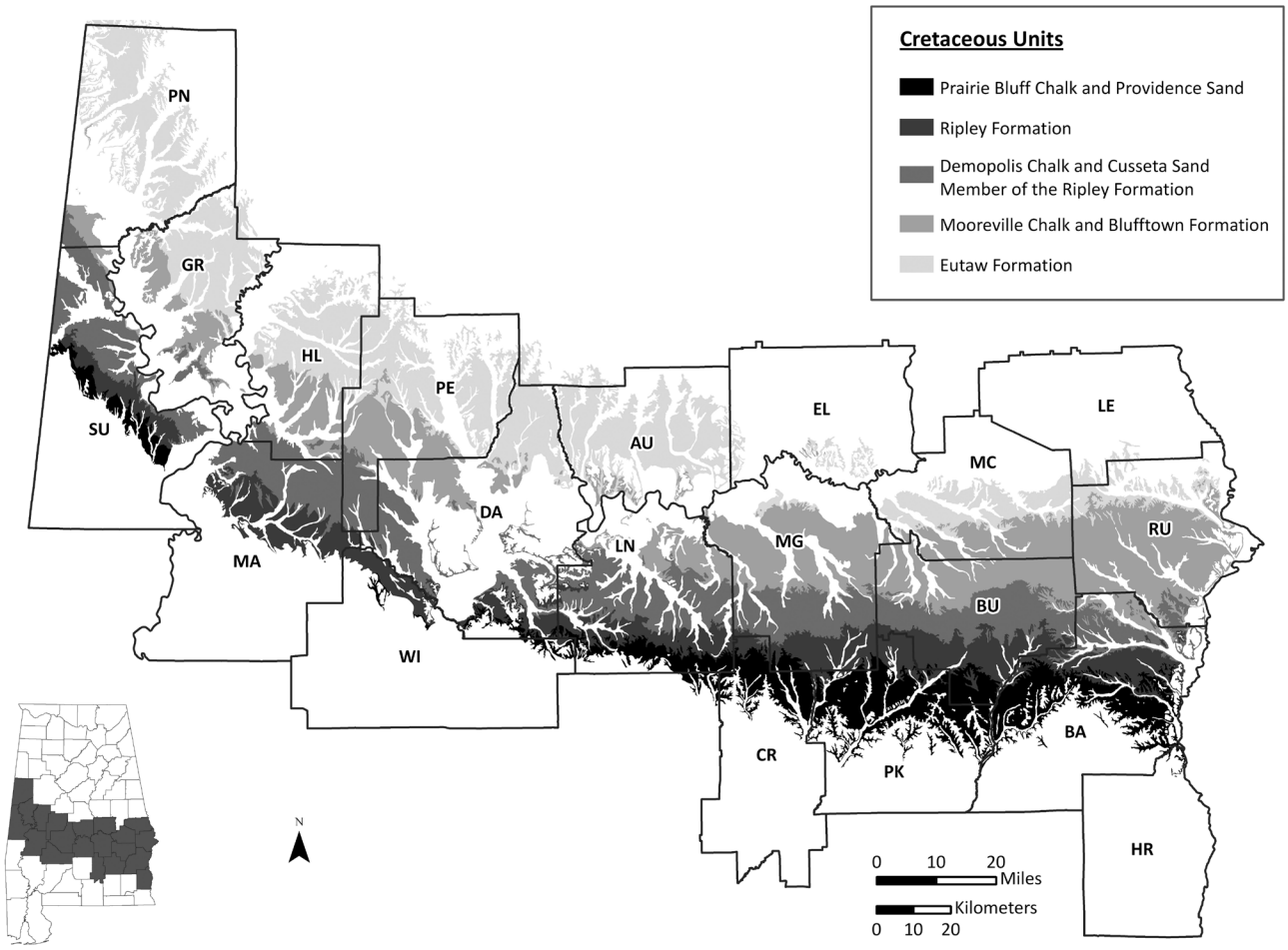

Figure 8. Counties in Alabama producing vertebrate fossils within the five Cretaceous stratigraphic units used in this study. Abbreviations of counties are listed in the text.

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).

ACKNOWLEDGEMENTS

We thank the following curators and/or collection managers who greatly aided in the collection of data throughout the course of this study: Carl Mehling (AMNH), Ted Daeschler (ANSP), Ray Wilhite (AUMP), David Schwimmer (CCK), Bill Simpson (FMNH), George Phillips (MMNS), Mary Bade (UAM), Mike Brett-Surman (USNM), and Dan Brinkman (YPM). We are also indebted to the following researchers for their generous insights surrounding this project: Chris Brochu, Mike Everhart, Lynn Harrell, Ed Hooks, Wann Langston Jr., Mike Polcyn, and Kenshu Shimada. Review comments from Steve Cumbaa and James Parham were also greatly appreciated.

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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.

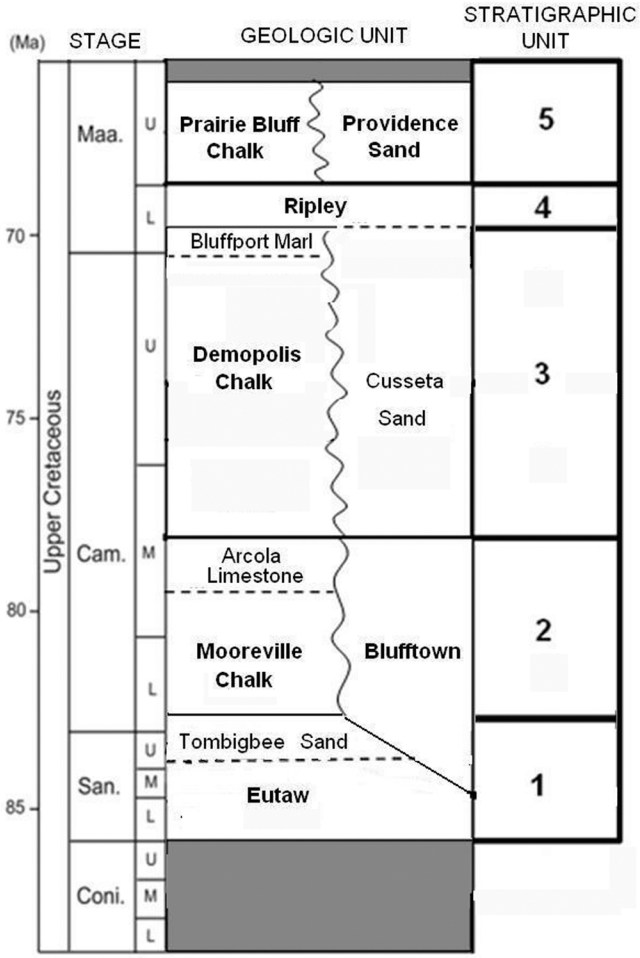

Figure 3 (revised).
The five Upper Cretaceous Alabama stratigraphic stratigraphic units used in this study.

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