FLORIDA MUSEUM

BULLETIN

of the Florida Museum of Natural History

CENOZOIC VERTEBRATE BIOSTRATIGRAPHY OF SOUTH CAROLINA, U.S.A., AND ADDITIONS TO THE FAUNA

L. Barry Albright III, Albert E. Sanders, Robert E. Weems, David J. Cicimurri, and James L. Knight

Vol. 57, No. 2, pp. 77–236
ISSN 2373-9991

October 31, 2019

UNIVERSITY OF FLORIDA

GAINESVILLE

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ISSN: 2373-9991

Publication Date: October 31, 2019

Send communications about this publication to:

Editor of the Bulletin; Florida Museum of Natural History; University of Florida; P.O. Box 117800;
Gainesville, FL 32611-7800 USA

FAX: 352-846-0287; Email: bulletin@flmnh.ufl.edu
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Cover image. View of the Charleston Museum's 1971 Chandler Bridge excavation pit (see p. 115).

IN MEMORIUM
ALBERT E. SANDERS
(1934-2019)

Just as this volume was being prepared for press, we learned that Albert E. Sanders passed away peacefully in his sleep the morning of 15 October 2019. I first met Al upon his arrival at the Charleston Museum as its new Curator of Natural Sciences in 1968. I was 11 years old at the time, and was involved in a kids group that met at the Museum every Saturday morning. The group, called The Nature Trailers, was active for nearly 40 years and served youngsters from 9 to 13 years old who had an interest in natural history and the outdoors. My fortuitous membership in this group over the same time that Al was hired and was establishing his program quite literally set the course of my career. Noticing my interest in natural history in general, and paleontology in particular, Al tucked me under his wing, further nurtured my interest in paleontology, and this resulted in an association that lasted over 50 years. One of the pivotal moments of my life occurred when I received a phone call from Al one summer day in 1973 asking if I'd be interested in joining a team that would search for and excavate archaeocete whales from one of the Eocene limestone quarries in South Carolina. It was as if I had won the lottery.

Although known primarily for his expertise on fossil whales, particularly early odontocetes and mysticetes, Al was also what we would consider today an "old style" true naturalist. A keen observer and a careful, meticulous scientist, he knew the natural history of the South Carolina Lowcountry as few others do or ever have - the birds, the reptiles and amphibians, the plants, and more – and he was an expert on the history of SC natural history, as well. He was a remarkably gentle and soft-spoken man. It seemed that every sentence he spoke was well thought-out; he was never one to "shoot-from-the-hip." He appeared to be always cheerful; stress apparently was not a factor in his life; he never seemed to be in a rush. In fact, Al had to "talk me off the ledge" a few times when I thought this current volume was falling too far behind the schedule I had envisioned for it. "Behind what schedule" was Al's attitude. And he was right!

Perhaps more important than Al's careful, insightful approach to his science, was his approach to life. He never forgot, nor did he let us forget—as scientists, paleontologists, naturalists—just how exceedingly fortunate we are. He was so right about this. What we do is special and it's wonderful and it makes for such an interesting life; as such, we never really experience the drudgery of "a job"!

I could see from what would become my last visit with Al in early July, 2019, that his health was failing; but I was so hoping that he could hold on long enough to see the publication of this volume, as it represents the culmination of over ten years of work among its authors. But I had a sinking feeling it would be close. Close it was, as I received notification of his death from his wife Randa the very day before editor Richard Hulbert informed me that the page proofs were ready. Al did know, however, that this volume was "in the can," and for that we are grateful. Al's quirky wit, his friendship, and his life lessons will be deeply and affectionately missed.

Barry Albright

Albert E. Sanders (center) in November 2014 at the Mace Brown Museum of Natural History at the College of Charleston with two of his protégés, Barry Albright (left) and Jonathan Geisler (right).

CENOZOIC VERTEBRATE BIOSTRATIGRAPHY OF SOUTH CAROLINA, U.S.A., AND ADDITIONS TO THE FAUNA

L. Barry Albright III[1], Albert E. Sanders[2], Robert E. Weems[3],
David J. Cicimurri[4], and James L. Knight[5]

ABSTRACT

Study of vertebrate fossils from the South Carolina Coastal Plain played a significant role in the early history of vertebrate paleontology as a scientific discipline in North America. However, a clear understanding of the state's vertebrate biostratigraphy has been greatly hindered by the paucity of well-exposed fossil-bearing stratigraphic sections and a complicated subsurface stratigraphy. Most units, particularly those of Neogene and Quaternary age, exist as thin veneers of marine or estuarine sediments that typically occur as infilled topographic lows or erosional remnants as determined primarily from borehole stratigraphy. Hence, lateral continuity can be difficult to confirm over broad geographic areas often resulting in confusion insofar as vertebrate fossil provenance is concerned. The evaluation of vertebrate fossils from the South Carolina Coastal Plain presented here, and of the geologic units from which they originated, or are thought to have originated, results in the first modern biostratigraphic framework for the known Cenozoic record of the state. Results provide (1) updated correlations of many units to the most recent, astronomically-tuned marine oxygen isotope stages; (2) the first viverravid from the Atlantic Coastal Plain, *Didymictis proteus*; (3) new information on the timing of certain Neotropical immigrants into the Southeast during the Great American Biotic Interchange, including the oldest record of *Erethizon* in this region and the oldest records of capybara in the USA; (4) the possible oldest record of the microtine rodent *Allophaiomys pliocaenicus* in the USA; (5) new details on the unit of origin for the type specimen of the archaeocete *Dorudon serratus*; and (6) new details on the ontogeny of the early odontocete *Agorophius pygmaeus*. New taxonomic records from South Carolina include *Glyptotherium texanum*, *Holmesina floridanus*, *Ondatra idahoensis*, *Erethizon* ?*bathygnathum*, *Leopardus amnicola*, *Miracinonyx* ?*trumani*, *Canis lepophagus*, *Canis latrans*, *Phocanella pumila*, *Callophoca obscura*, *Monatherium* sp., *Anchippus texanus*, *Subhyracodon mitis*, *Aphelops* ?*malacorhinus*, *Teleoceras* ?*guymonense*, and *Perchoerus* sp. New specimens of previously recorded taxa are also noted.

Key words: South Carolina, vertebrate paleontology, stratigraphy, biostratigraphy.

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Albright III, L. B., A. E. Sanders, R. E. Weems, D. J. Cicimurri, and J. L. Knight. 2019. Cenozoic vertebrate biostratigraphy of South Carolina, U.S.A., and additions to the fauna. Bulletin of the Florida Museum of Natural History 57(2):77–236.

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INTRODUCTION

Until recently, South Carolina has not often been considered a state yielding a wealth of vertebrate paleontological resources, although the study of its fossils, particularly those from the famous "Ashley River phosphate beds" near Charleston, played an major role in the early history of vertebrate paleontology in North America. Louis Agassiz, Joseph Leidy, and other notable 19th century naturalists recognized the importance of fossils from the state, and collections they studied can be found in such venerable institutions as the American Museum of Natural History, the Academy of Natural Sciences of Drexel University (formerly the Academy of Natural Sciences of Philadelphia), Harvard's Museum of Comparative Zoology, and the United States National Museum of Natural History, in addition, of course, to the oldest established museum in the USA, The Charleston Museum.[1] Missing up to this time, however, has been a clear understanding and representation of the stratigraphic framework for fossil vertebrates from the state, primarily due to the reasons discussed below.

As part of the southeastern USA Atlantic Coastal Plain (Fig. 1), much of the state is low lying with little topographic relief, and its warm temperate climate results in a thick vegetative cover – both factors of which severely limit exposure of fossil-bearing strata. Another factor to consider is the complicated nature of South Carolina's subsurface geology. As generalized by Katuna et al. (1997:182), "the coastal plain of SC is underlain by a thick seaward-dipping wedge of late Cretaceous to Holocene siliciclastic and carbonate strata deposited on Paleozoic and Mesozoic rocks along the eastern, passive continental margin of North America" (also see Gohn, 1988; Idris and Henry, 1995). Additionally, as noted by Ward et al. (1991), the deposition and geographic distribution of strata within the lower coastal plain of SC has been influenced primarily by two structurally positive areas, the Cape Fear Arch to the north and the Yamacraw (aka Beaufort Arch) to the south, between which formed a coastal embayment known as the Charleston Embayment (Fig. 1A). Additional controls on deposition/erosion in this region were those imposed by currents of the Gulf Trough and the

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[1] This point is somewhat arguable. Simpson (1942:158) concluded that "the first American natural history museum definitely organized as such, public and independent, was apparently Peale's Philadelphia Museum, in which vertebrate paleontology and the American Philosophical Society played the leading parts." He noted that Peale's museum was a "cabinet" of "going concern in 1770," thereby predating The Charleston Museum by three years.

ancestral Gulf Stream during the middle Eocene to early Oligocene (Idris and Henry, 1995; Popenoe et al., 1987). Several units deposited in this embayment, particularly those of Neogene age, have been partly to completely removed by erosion (multiple transgressions plus dissection during low stands) leaving, in many cases, only thin veneers of marine, estuarine, or (rarely) fluvial sediments that typically occur as infilled topographic lows or erosional remnants seen only in cores, auger cuttings, very limited outcrops, or seismic reflection and/or resistivity profiles (e.g., Popenoe et al., 1987; Krantz, 1991; Idris and Henry, 1995; Weems and Lewis, 2002; Putney et al., 2004; Williams et al., 2009). As noted by Cronin et al. (1984:26), further limitations arise from the deposition of the same group of lithofacies ("dunes, beach sands, back-barrier muds to shelf sands") over the course of many marine transgressions "… so that distinguishing the same facies from two separate transgressions on lithologic grounds is difficult unless independent dating of the marine facies is available." Correlation of these units is therefore difficult over broad geographic areas and typically relies on mollusc and/or microfossil biostratigraphy, with data provided by ostracods, dinoflagellates, radiolarians, foraminiferans, and/or calcareous nannoplankton (e.g., Abbott and Andrews, 1979; Weems et al., 1982; Bybell, 1990; Ward et al., 1991; Campbell and Campbell, 1995; de Verteuil and Norris, 1996; Ward, 2008). Still further complications arise from the mixing of fossils of very different ages in lag deposits found at the bases of many units, again due to the numerous transgressions and regressions to which the region has been subjected. These limitations result in particular confusion insofar as terrestrial (and sometimes marine) vertebrate fossil provenance is concerned.

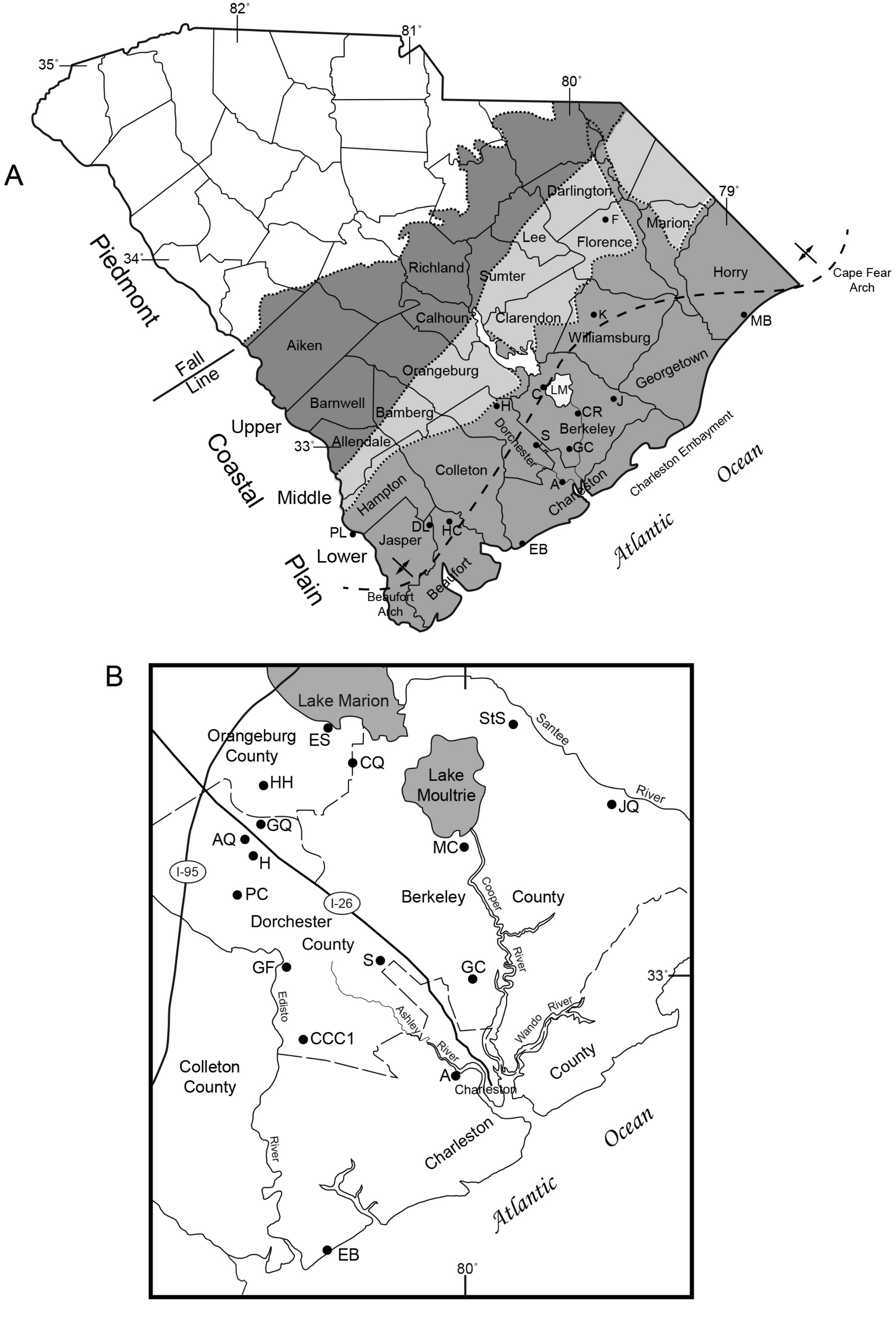
Even when provenance can be determined with a high degree of confidence, an additional problem lies in providing a refined age estimate for the unit of origin. Magnetostratigraphic analysis of formations across the SC Coastal Plain is of only limited utility due to the absence of thick, exposed stratigraphic sections, which might provide a discernable polarity reversal pattern that can be correlated to the global Geomagnetic Polarity Time Scale. The nonexistence of radioisotopically dateable volcanic horizons additionally precludes calibration to the time scale of sites of determinable magnetic polarity. Furthermore, temporally calibrated range zones (plus FADs and LADs) for the biochronologically significant invertebrate groups noted above are constantly being refined as new sections and/or cores are studied, and these changes often outpace the boundaries of these zones as reflected in the most recently published geologic time scales. Thus, for an undertaking such as this one to be relevant at the time of its publication depends heavily on familiarization with the most recent literature and/or results from a variety of geological subdisciplines including paleoceanography, radioisotopic and geochemical geochronology, and invertebrate biostratigraphy/biochronology.

However, despite the above noted shortcomings, some geologic units are relatively well characterized from a paleontological, and to some extent a temporal, perspective. Examples include the Eocene Santee Limestone, Tupelo Bay, and Harleyville formations, plus the Oligocene Ashley and Chandler Bridge formations, with their spectacular records of fossil cetaceans. Pre-Pleistocene terrestrial strata, on the other hand, are essentially non-existent, and as Weems and Lewis (2002) noted, all of the middle Eocene through Pliocene lithologies underlying the Charleston area (and the SC Coastal Plain in general; Figure 2A–C) formed in marine (including coastal) depositional environments. Although rare and isolated land mammal fossils of late Arikareean North American Land Mammal Age (NALMA) provide a limited glimpse into the latest Oligocene-earliest Miocene terrestrial record, and obviously originated from sediments deposited in a coastal plain/fluvial setting, they nevertheless were recovered from much more recent marine to marginal marine sediments, having been reworked from subjacent strata. The Miocene record is particularly sparse, represented by only five formations broadly spaced across the 17.5 myr span of that series (Fig. 2B). The Pliocene is somewhat better represented, with mammal fossils known from the Goose Creek Limestone and the Raysor and Duplin formations (Fig. 2C). Fossils from these units are providing important new information on the timing of Neotropical immigrants, such as capybara, glyptodonts, megalonychid sloths, and porcupines into North America during the Great American Biotic Interchange (e.g., Woodburne, 2010). Pleistocene mammals are relatively well-represented from units such as the Waccamaw, Ladson, and Wando formations, plus the submerged unnamed and geologically uncharacterized units off Edisto and Myrtle beaches (Fig. 1A). The oldest well-dated remains of *Bison* in the lower 48 states were found in the upper Pleistocene Ten Mile Hill Formation, thus providing important implications for the boundary between the Irvingtonian and Rancholabrean NALMAs (Sanders et al., 2009).

The primary purpose of this paper, therefore, is to provide a much needed modern chronostratigraphic and biostratigraphic foundation for the fossil vertebrates (mainly mammals) found in South Carolina. We have attempted to correlate all of the state's lower coastal plain units with the most recent astronomically tuned marine oxygen isotope stages (i.e., those of Lisieki and Raymo, 2005; Raffi et al., 2006; Cramer et al., 2009; and Wade et al., 2011) in order to provide the highest temporal resolution currently available for the fossils found within them (Figures 3A–C). This work is not intended as an exhaustive review of all of South Carolina's Cenozoic vertebrate fossils, although additions to the state's fossil fauna are included, along with an updated faunal list, in Appendices 1 and 2. Appendix 1 provides a list of all known non-marine mammals from SC and the faunas and/or stratigraphic units from which they are known, plus their ages. Appendix 2 provides the same information for the known marine mammal record. Appendix 3 is provided as a quick reference list of the faunas and/or stratigraphic units from which the non-marine taxa are known, plus their ages, but also includes comparably aged faunas and/or sites in Florida that are frequently noted throughout the text.

For relatively recent discussions of fossil vertebrates from South Carolina, the reader is referred to Roth and Laerm (1980), Bentley et al. (1994), Sanders (1998a), Sanders (2002), Geisler et al. (2005, 2014, 2017, 2018), Kohn et al. (2005), Chandler and Knight (2009), Fierstine and Weems (2009), Sanders et al. (2009), Cicimurri and Knight (2009a, b, c; 2019), Knight and Cicimurri (2010), Fields et al. (2012), Weems and Knight (2013), Ksepka (2014), Weems and Sanders (2014), Vélez-Juarbe and Domning (2014a, b), Cicimurri et al. (2016), Weems and Brown (2017), Babiarz et al. (2018), Boessenecker et al. (2018), Domning and Beatty (2019), and others mentioned throughout the text. Important older references include Leidy (1859, 1860, 1869, 1876a, b, c, 1877, 1890), Hay (1923), and Allen (1926). Sloan (1908) is valuable resource for older South Carolina geological literature, as is Cooke (1936).

Figure 1. A, Index map of the South Carolina (SC) Coastal Plain and **B**, Charleston-Berkeley-Dorchester tri-county region, showing counties, towns, and major localities noted in text. **A**, general area where Ashley River Phosphate Beds were mined near Middleton Place; **AQ**, Argos Cement Quarry (formerly called the LaFarge, Blue Circle, or Gifford-Hill & Co. Harleyville quarry); **C**, Cross, SC; **CCC1**, Clubhouse Crossroads Core 1; **CQ**, Cross quarries; **CR**, Cooper River; **DL**, Dawson's Landing; **EB**, Edisto Beach; **ES**, Eutaw Springs; **F**, Florence, SC; **GC**, Goose Creek, SC; **GF**, Givhans Ferry State Park; **GQ**, Giant Cement Quarry; **H**, Harleyville, SC; **HC**, Huspa Creek; **HH**, Holly Hill, SC; **J**, Jamestown, SC; **JQ**, Jamestown Quarry; **K**, Kingstree, SC; **LM**, Lake Moultrie; **MB**, Myrtle Beach; **MC**, Monks Corner, SC; **PC**, Pregnall Core (DOR-208); **PL**, Porters Landing, Georgia; **S**, Summerville, SC; and **StS**, St. Stephen Pit. Note: often mentioned in the text, the Camelot, Crowfield, and Walrus Ditch sites are located near the Giant Cement quarry, Goose Creek, and Summerville, respectively. Dashed line = approximate location of major structural features (Beaufort Arch, Charleston Embayment, and Cape Fear Arch) of SC Coastal Plain after Ward et al. (1991).


A
82˚
81˚
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35˚
34˚
33˚
Piedmont
Fall Line
Upper
Coastal
Middle
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Plain
Darlington
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Marion
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Florence
Horry
Richland
Sumter
Cape Fear Arch
Calhoun
Clarendon
K
MB
Williamsburg
Aiken
Orangeburg
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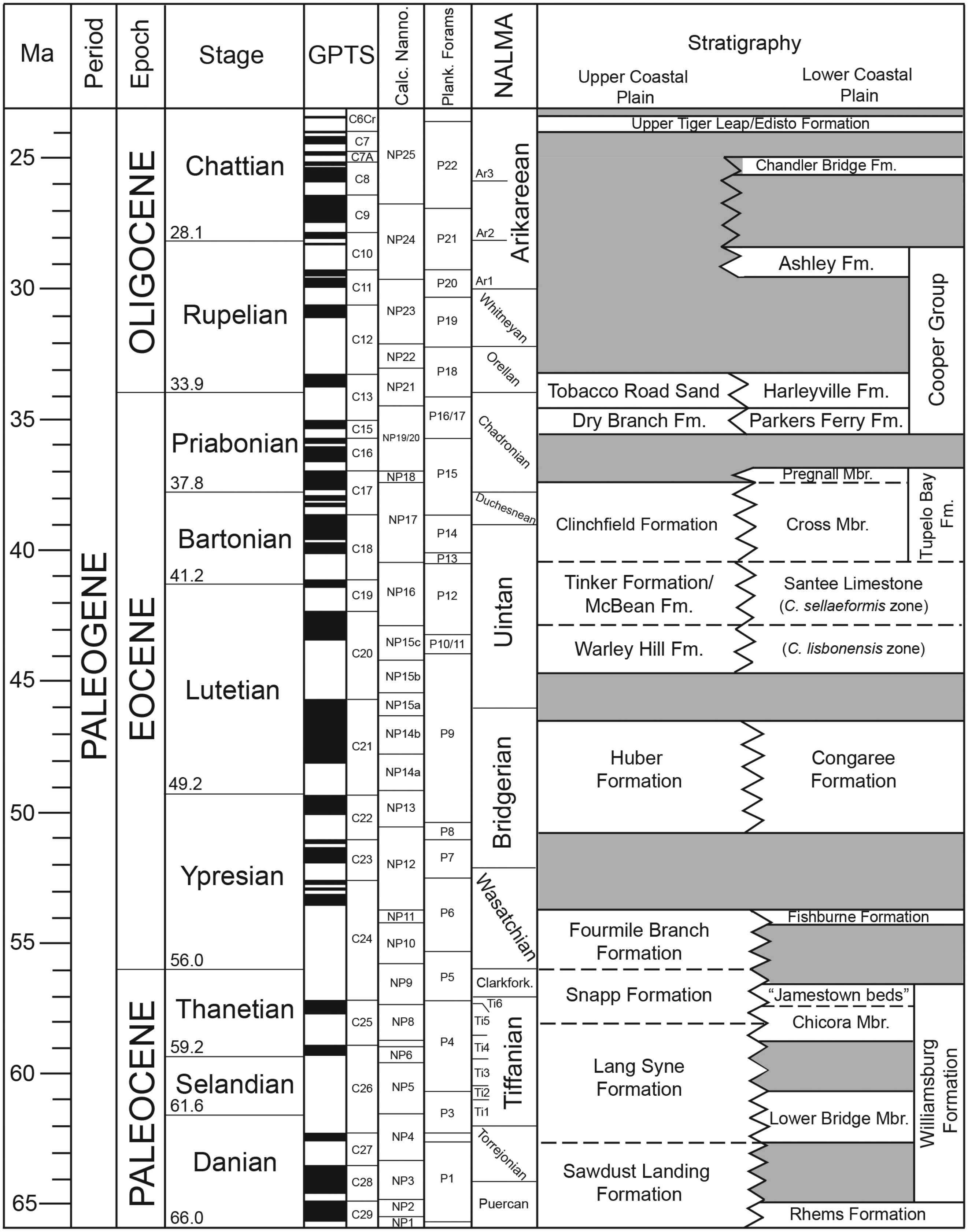
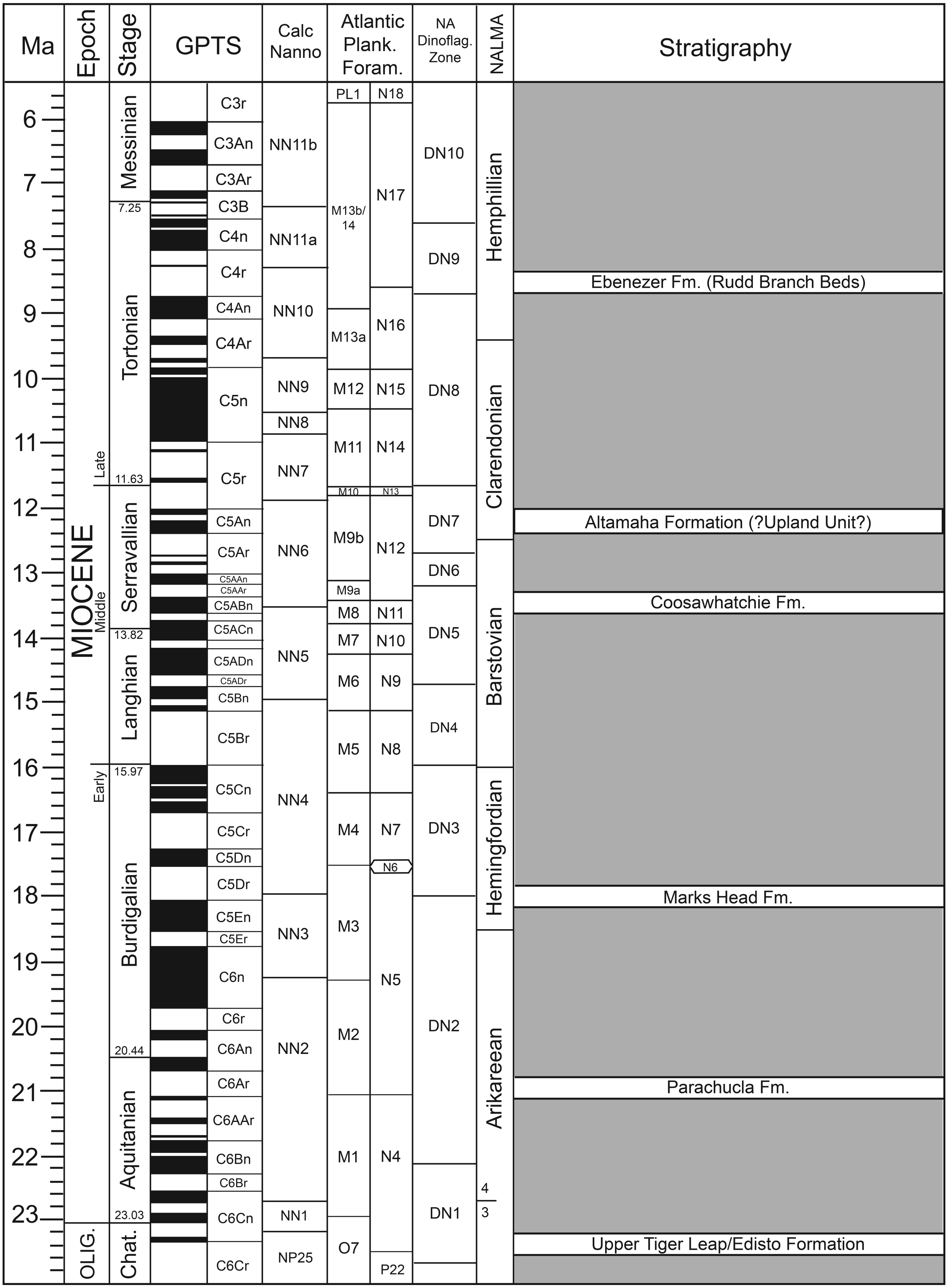


Figure 2A. Caption is located on pp. 86–87.



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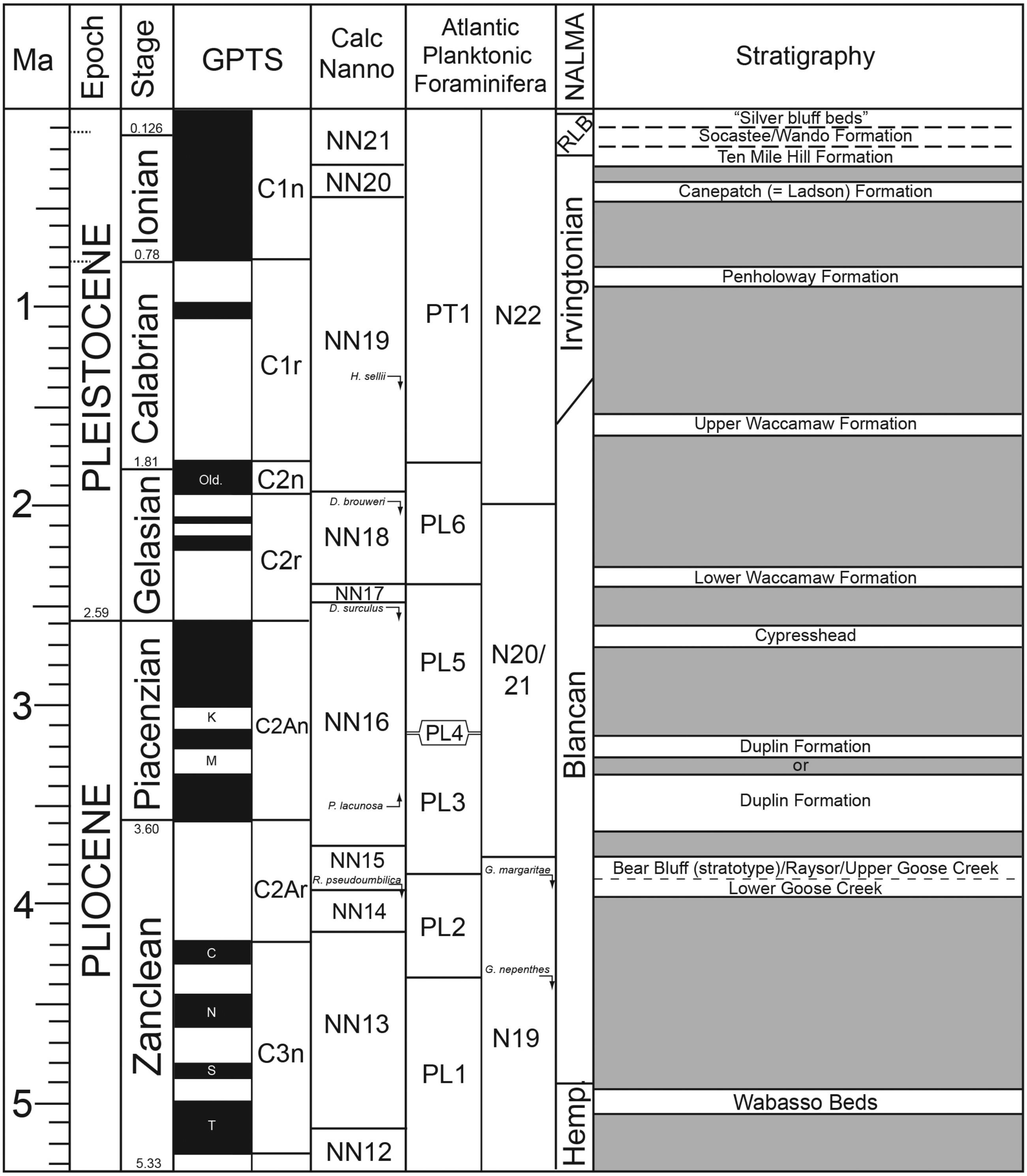


Figure 2C.

Figure 2. Generalized stratigraphic charts for named units of the South Carolina Coastal Plain. Geochronologic framework based primarily on GTS2012; boundaries of calcareous nannoplankton and foraminiferal zones follow Lourens et al. (2004), Mudelsee and Raymo (2005), Raffi et al. (2006), Anthonissen (2008), Coccioni et al. (2008), and Wade et al. (2011); NALMA boundaries follow Woodburne (2004), Flynn et al. (2005), Morgan (2005), Secord et al. (2006), Albright et al. **[caption continues on next page]**

Figure 2. Continued. (2008), Sanders et al. (2009), Tsukui and Clyde (2012), May et al. (2014), and Murphey et al. (2018).**A**, Paleogene stratigraphic units; chronostratigraphic placement of formations based on Nystrom et al. (1991), Fallaw and Price (1995), Edwards et al. (2000), and Weems et al. (2016); boundaries of chrons C21–C23 from Tsukui and Clyde (2012); inclusion of "Jamestown beds" in Chicora Member of Williamsburg Formation from Cicimurri et al. (2016). **B**, Miocene stratigraphic units; DN zones based on recalibration of de Verteuil and Norris (1996) using Dybkjaer and Piasecki (2008); boundaries of chrons C4Ar–C5r from Evans et al. (2007); placement of Upland unit in upper Serravallian follows Nystrom et al. (1991), Huddlestun (1988), and Weems and Edwards (2007a). **C**, Pliocene and Pleistocene stratigraphic units; Pliocene/Pleistocene boundary follows Gibbard et al. (2010); Reunion I and II subchrons follow Kidane et al. (2007); Blancan-Irvingtonian boundary follows Morgan (2005); Hemphillian-Blancan boundary follows May et al. (2014); short dashed lines in PLEISTOCENE column separate Lower, Middle, and Upper Pleistocene; see text for further discussion. **RLB** = Rancholabrean NALMA.

METHODS AND MATERIALS

Institutional Abbreviations

AMNH, American Museum of Natural History, New York; **ANSP**, Academy of Natural Sciences of Drexel University, Philadelphia, Pennsylvania (formerly the Academy of Natural Sciences of Philadelphia); **CCNHM**, College of Charleston Natural History Museum (recently renamed the Mace Brown Museum of Natural History), Charleston, SC; **ChM PV**, vertebrate paleontology collections at The Charleston Museum, Charleston, SC; **CMM-V**, vertebrate paleontology collections at the Calvert Marine Museum, Solomons, Maryland; **FLMNH**, Florida Museum of Natural History, University of Florida, Gainesville; **GSM**, Georgia Southern Museum, Georgia Southern University, Statesboro; **McK**, McKissick Museum, University of South Carolina, Columbia; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; **SCSM**, South Carolina State Museum, Columbia (note: only "**SC**" is used as the prefix in catalogue numbers for specimens at the SCSM); **UF**, vertebrate paleontology collection of the FLMNH; **USGS**, United States Geological Survey; **USNM**, United States National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Anatomical Abbreviations

AP and **TR** refer to antero-posterior (length) and transverse (width) measurements, respectively; **P** or **M**, upper premolars and molars, respectively; **p** or **m**, lower premolars and molars, respectively.

Figure 3. Stratigraphic units of the South Carolina Coastal Plain with correlation to oxygen isotope curves; geochronologic/chronostratigraphic base as in Figure 2. **A**, Paleogene units correlated to generalized oxygen isotope curve of GTS2012, figure 28.11 (derived from Raffi et al. [2006] and Cramer et al. [2009]); **EECO** = Early Eocene Climatic Optimum; **MECO** = Middle Eocene Climatic Optimum; **PETM** = Paleocene-Eocene Thermal Maximum. **B**, Miocene units correlated to generalized oxygen isotope curve of Raffi et al. (2006); DN zones based on recalibration of de Verteuil and Norris (1996) using Dybkjaer and Piasecki (2008); **MMCO** = Middle Miocene Climatic Optimum. **C**, Pliocene and Pleistocene units correlated to generalized oxygen isotope curves of Lisiecki and Raymo (2005) and Raffi et al. (2006); nannoplankton and foraminiferal boundaries follow Lourens et al. (2004), Mudelsee and Raymo (2005), Raffi et al. (2006), Anthonissen (2008), and Wade et al. (2011); Reunion I and II subchrons follow Kidane et al. (2007); Pliocene-Pleistocene boundary follows Gibbard et al. (2009); Blancan-Irvingtonian Boundary follows Morgan (2005); Hemphillian-Blancan boundary follows May et al. (2014); Bridgerian-Uintan boundary follows Murphey et al. (2018); **IRD** = Ice Rafted Debris; **LMGI** = Late Miocene Glacial Interval; **MPWP** (Middle Pliocene Warm Period) from Dowsett et al. (2005) and Robinson et al. (2008); **RLB** = Rancholabrean NALMA. **[images follow on pp. 88–90]**

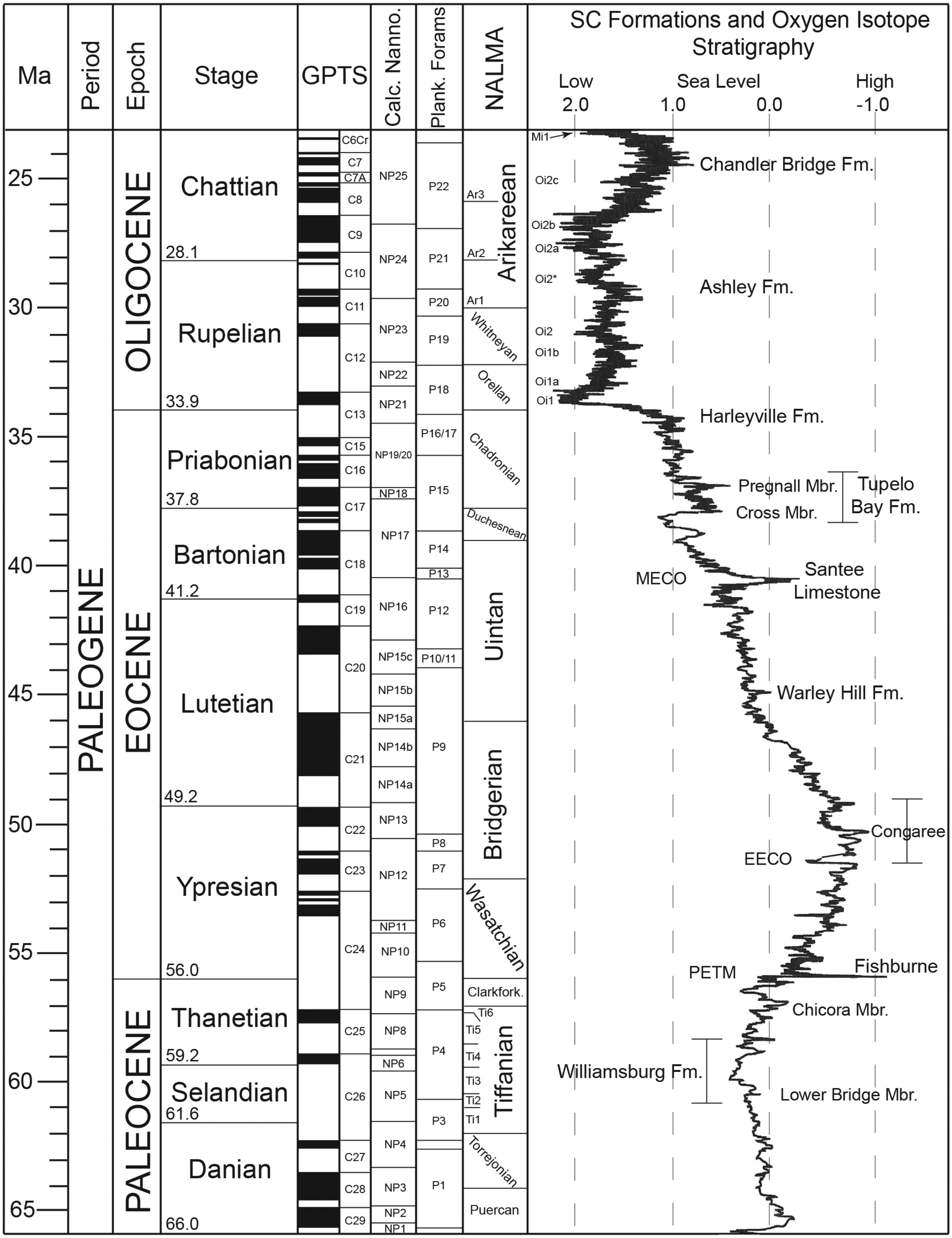
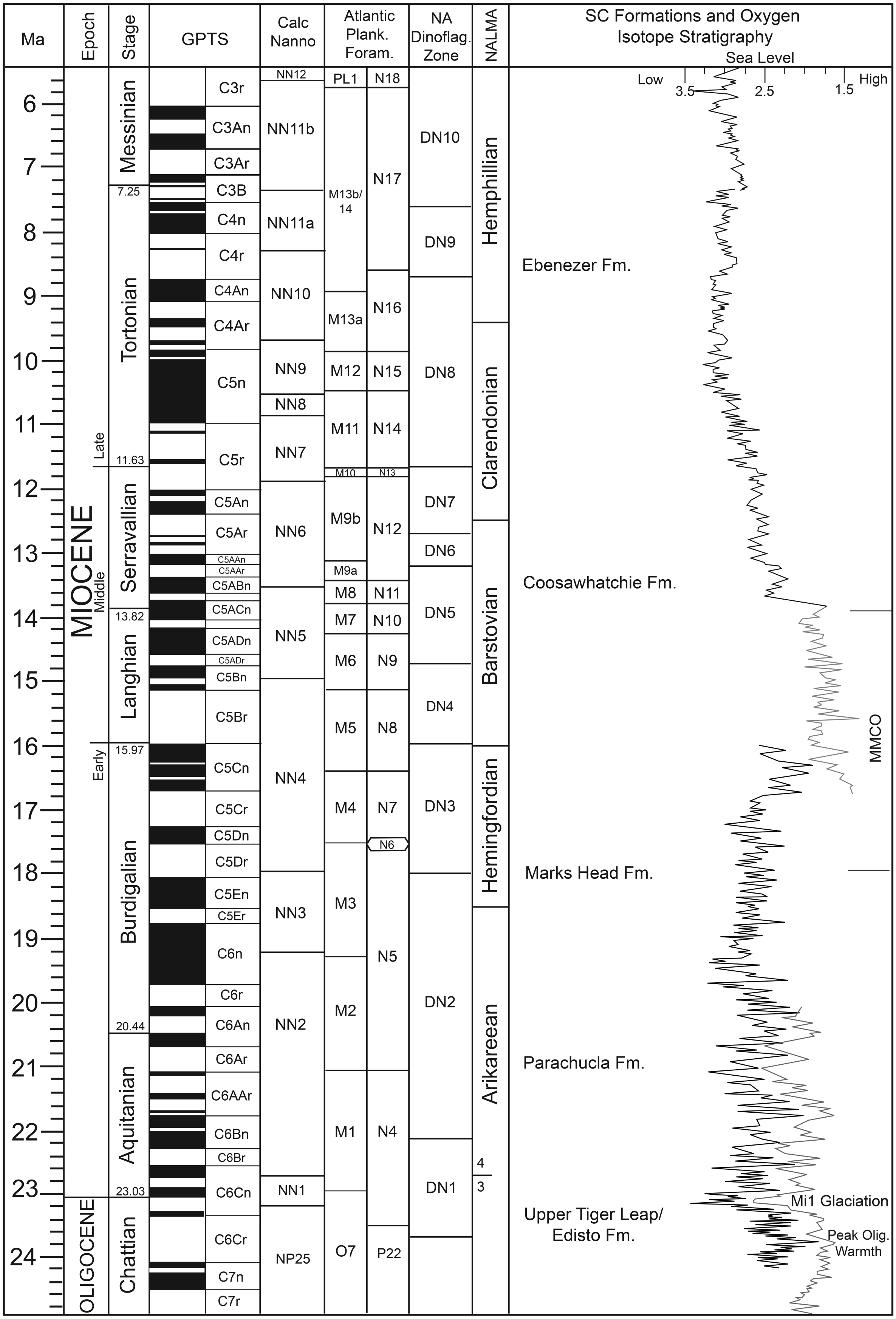


Figure 3A. Caption is located on pp. 87.



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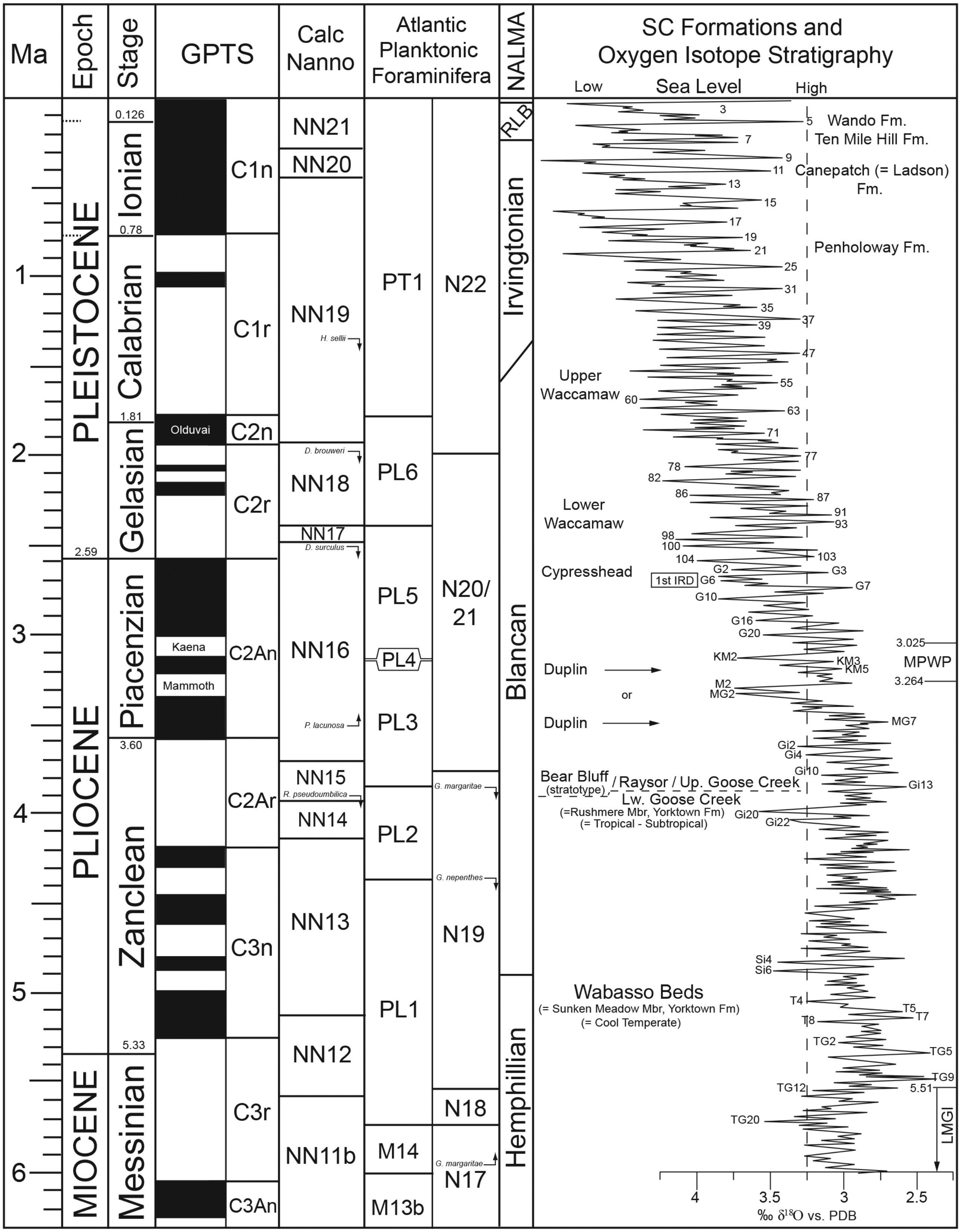

Figure 3C. Caption is located on pp. 87.

GEOCHRONOLOGY/CHRONOSTRATIGRAPHY

The version of the global Geomagnetic Polarity Time Scale (**GPTS**) used for the temporal framework in this contribution is primarily **GTS2012**, i.e., that of Gradstein et al. (2012). Particularly germane to our work are those portions of GTS2012 compiled by Vandenberghe et al. (2012) for the Paleogene and by Hilgen et al. (2012) for the Neogene (the latter similar to Lourens et al., 2004, in **GTS2004**), although the recently re-ratified Pliocene-Pleistocene boundary follows Gibbard et al. (2010) in its placement at the base of the Gelasian Stage at marine isotope stage (**MIS)** 103 at about 2.59 Ma. The terms "**Fauna**" and "**Local Fauna**" (**LF**) follow Tedford (1970) and definitions in Woodburne (1987). Boundaries of North American Land Mammal Ages (**NALMA**s) follow those in Woodburne (2004) with the following exceptions: divisions of the Arikareean follow Albright et al. (2008); Hemphillian-Blancan boundary follows May et al. (2014); Blancan-Irvingtonian boundary follows Morgan (2005); and Irvingtonian-Rancholabrean boundary follows Sanders et al. (2009). For the last glacial stage in North America, "Wisconsian" is used in favor of "Wisconsinan" following Pillans and Gibbard (2012). **FAD**, first appearance datum; **LAD**, last appearance datum; **HO**, highest stratigraphic occurrence; **LO**, lowest stratigraphic occurrence; **Ma**, mega-annum (million years), a radioisotopically calibrated numerical age; **myr**, millions of years, elapsed time or duration; **kyr**, thousands of years, elapsed time or duration.

A NOTE ON "HOBBY COLLECTING" VERTEBRATE FOSSILS IN SOUTH CAROLINA

Over the course of conducting research for this project, it came to the attention of the authors that the "hobby collecting" of vertebrate fossils from SC is, in a word, thriving, although sadly to different ends. There are substantial advantages to these activities, as hobby collectors often have the time and resources required to prospect for new sites and specimens; but there is an alarming downside, as well. The trend started primarily in the 1970s as avocational fossil collectors began finding mainly sharks teeth and remains of early cetaceans in drainage ditches cut through what were then new residential neighborhoods, primarily in the Summerville area, which exposed the highly fossiliferous Oligocene-aged Ashley and Chandler Bridge formations. The trend gained additional traction as land was cleared and excavated for new highways and construction projects in the North Charleston and Summerville areas throughout the 1980s, in turn creating further, more easily accessible exposures of these formations. Although recently emplaced local ordinances, primarily in Dorchester County, together with the dense jungle-like growth of vegetation along the ditches, have hindered collecting activities, it is known as a matter of fact that fossil collecting in these settings continues today.

"Hobby collecting" of SC's fossil resources was significantly compounded by the explosion of scuba diving activities in the coastal rivers as word spread among divers that these rivers were essentially littered with fossils, as well as archaeological artifacts. As a member of the "second wave" of river divers in the state in the early 1970s (see below), the first author can attest to the quantity and quality of paleontological and archaeological resources that were present in the rivers then. In fact, the first author's pursuit of vertebrate paleontology as a career was driven in part by his underwater explorations of the Cooper and Edisto rivers during those times. (Note: the true "first wave" of SC river divers included Drew Ruddy, Jim Batey, Steve Howard, and William Hunt of Charleston. Ruddy and Hunt were older neighbors of the first author's, who, as a child, was fascinated by their "Sea Hunt"-like exploits; see Ruddy, 2013).

The collection of paleontological and archaeological resources from the bottoms of rivers meandering through the SC Coastal Plain began in the mid-1960s to early 1970s by only a very few adventurous divers who decided to explore the inky depths. But by the late 1970s, diving for fossils and artifacts began to rise in popularity due in large part to the early expansion of recreational scuba diving. Scuba class checkout-dives were often conducted in the regional tanic acid-stained "black water" rivers as an alternative to diving in murky offshore waters or driving several hours to

Florida's clear water springs, sinkholes, or keys. As soon as this practice began, divers started bringing up 18th century black glass bottles, Native American artifacts, and what quickly became the most sought after prize of all, giant teeth of the late Miocene shark, *Megaselachus megalodon* (= *Carcharodon megalodon*, *Carcharocles megalodon*, *Procarcharodon megalodon*, *Otodus megalodon*, etc.), along with numerous other fossils. By the early 1980s, an increasing popularity in scuba diving led to an explosion of "hobby-divers" who were quite literally scouring the bottoms of nearly all the state's coastal plain rivers. This practice was eventually regulated by the State of South Carolina because of the wealth of material, both paleontological and archaeological, being recovered that was of significant cultural, historic, and scientific importance. The state had no way of knowing what was being recovered and removed from its waters without imposing certain sanctions on this growing population of enthusiasts. Some method by which an account of the resources being found needed to be maintained. Therefore, to collect any artifact or fossil from the state's waters, divers were required to apply for a "hobby diving" permit. All that was (and still is) required by the diver was the submission of a quarterly report citing the locality of their dives and the material collected. There is no doubt that exceptional and important specimens were never accounted for in these reports for fear that the state would confiscate the items – an action which prior to 2014 never occurred. Fortunately, on the other hand, the SC State Museum, The Charleston Museum, and the College of Charleston's Mace Brown Museum of Natural History have greatly benefitted from the relatively limited cohort of "hobbyists" who, in understanding the scientific importance of their finds, have donated material to these institutions.

The downside, however, has been the commercial exploitation of SC's fossil resources. Starting in the 1990s and continuing at an ever increasing pace through today, a growing web-based fossil market has resulted in many spectacular specimens of what are often undescribed and/or very poorly known taxa effectively being removed from scientific access – the fossils have become "trophies" that now have a bounty ascribed to them rather than specimens of scientific value that can be studied then placed on exhibit for all to share. Particularly frustrating is the sale of specimens known to be new to science, but which cannot be made known to the scientific community, or the public, because of their removal from scientific/public access. Specimens held in private collections cannot be technically described (i.e., published in a peer-reviewed scientific journal); for that to occur the specimens must be curated in an accredited institution dedicated to their storage and safety, and where they can be made available for study in perpetuity by future generations of students and scientists. Exceptions can be made if it is understood that a private collection may be bequeathed to an institution in the future, or if the specimen is so important that it should at least be mentioned in a technical publication so as to provide a written record (as occurs in this report). However, the future of specimens held in private collections is never certain.

As an example, it is known with certainty that virtually complete skulls of xenorophid cetaceans from South Carolina, some of the rarest and most important members of the early odontocete radiation, are currently on display in a Japanese museum, and that they were purchased by that museum, or a representative thereof, from a SC fossil dealer. Another example is a nearly complete skull of what appears to be a new, undescribed species of *Eosqualodon* currently on its way (as this report is being finalized) to be offered for sale at the 2019 Tucson Gem and Mineral show. Why are they not in one of South Carolina's museums where they could be studied in the context of all other cetacean material from the region? Several reasons account for this problem. First, most museums do not have the discretionary funds required to purchase such specimens. Second, most museums do not subscribe to the practice of purchasing specimens due to the "bounty" noted above that this places on the fossils – i.e., it immediately places a somewhat randomly assessed commercial value on an otherwise scientifically important specimen, in turn encouraging further collecting for purely commercial rather than scientific reasons.

Following Section 6 of the Society of Vertebrate Paleontology's Code of Ethics, "the barter, sale, or purchase of *scientifically significant vertebrate fossils* [italics ours] is not condoned, unless it brings them into, or keeps them within, a public trust. Any other trade or commerce in scientifically significant vertebrate fossils is inconsistent with the foregoing [code of ethics] in that it deprives both the public and professionals of important specimens, which are part of our natural heritage." This prompts us to add a quote from the eminent 19th century paleontologist Joseph Leidy (1877:209): "The finder and unscientific owner of fossils, ignorant of their real importance, often retain them as curiosities, with exaggerated notions of their pecuniary value, and no argument is sufficient to induce them to part with the specimen or place them where they may be accessible to the student."

Very fortunately, on the other hand, and as noted above, many of SC's fossil hobbyists have made exceptionally important contributions to our understanding of the state's paleontological resources. These individuals, realizing the scientific importance of so many of their finds, have very generously donated their specimens to both the Charleston and South Carolina State museums, as well as to the Mace Brown Museum of Natural History, understanding that the academic study, technical description, and publication of those specimens in scientific journals is in some cases prohibited unless the specimens are curated in public repositories (accredited museums or universities) where they can be accessed by students and scientists (and the public through exhibits) in perpetuity. In fact, much of what we know about vertebrate paleontology in SC today is a direct result of their dedication, hard work, and generosity, and we hereby acknowledge and thank those who subscribe to this view (and list those of whom we are aware in the "Acknowledgments" section at the end of this report). It should also be noted that there are some local fossil enthusiasts who purchase specimens from dealers in an attempt to keep SC's fossil resources in the state. Some are purchased and then donated to academic institutions, while others are purchased and maintained in private collections. Although we do not condone the practice of purchasing fossils due to the reasons pointed out above, it is comforting to know that many of these purchased specimens, often of exceptional importance, have been deposited into museum collections where they can be studied and held in perpetuity. Whereas those held in private collections are not in a condition immediately conducive to detailed scientific study, some owners do allow access to their material, and we sincerely hope that these private collections will eventually be donated to the state's museums or academic institutions for study and perpetual curation.

HISTORICAL BACKGROUND

In the period between 1750 and 1850, three great centers of learning existed in the colonies of what is now the United States of America: Boston in Massachusetts Colony; Philadelphia, in Pennsylvania; and Charleston, in the colony of South Carolina. In 1773 members of a special committee of the Charles Town Library Society, several of whom were educated in England or Scotland, had the foresight to propose the establishment of a natural history museum, likely inspired by visits to the British Museum (Sanders and Anderson, 1999). Thus was born The Charleston Museum. Unbeknownst to, or under-appreciated by, many of today's paleontologists, however, The Charleston Museum played a pioneering role in the development of paleontology as a scientific discipline in this country. Contributions to (and from) the collection have been made by some of the very founders of the field.

Lardner Vanuxem conducted the first geological survey of South Carolina in 1824, but limited funds restricted his work to five districts in the Piedmont region (Vanuxem, 1826). Later, in 1843, Edmund Ruffin published an agricultural survey of the state, which also included descriptions of the state's then known geological units, as well as a list of invertebrate fossils. It was the geologist Michael Tuomey, however, who, after his 1848 geological survey of South Carolina, stimulated interest in the paleontology of the state (Sanders and Anderson, 1999). Another pioneer was the Charleston native Robert Wilson Gibbes who first published paleontological investigations in SC such as that describing the primitive archaeocete *Dorudon serratus* from

Berkeley County, north of Charleston (Gibbes, 1845). The celebrated 19th century naturalist Louis Agassiz (founder of the Museum of Comparative Zoology at Harvard University) spent considerable time in Charleston and recognized in 1847 after viewing an extensive collection of fossils accumulated by Francis S. Holmes “that the Charleston area contained fossil-bearing beds of major significance” (Sanders and Anderson, 1999:66). As curator of The Charleston Museum from 1851 to 1869, Holmes oversaw the publication of two now classic volumes, *Pleiocene* [sic] *Fossils of South Carolina* (Tuomey and Holmes, 1857) and *Post-Pleiocene* [sic] *Fossils of South Carolina* (Holmes, 1860), to which Joseph Leidy contributed the section on vertebrate fossils. Leidy, considered the “Father of American Vertebrate Paleontology” (Warren, 1998), studied and published on fossils from the Charleston area (e.g., Leidy, 1853, 1859, 1860, 1868a, 1869, 1876a–c, 1877, 1890), and his protégé, E. D. Cope, also published several papers on South Carolina fossils (e.g., Cope, 1867, 1868, 1883). In 1915, O. P. Hay examined specimens in the Charleston Museum and in 1923 he described *Neochoerus pinckneyi,* a new species of capybara, *Alces runnymedensis* (more recently referred to *Cervalces scotti* by Sanders, 2002), and the marine turtle *Carolinochelys wilsoni*.

Major paleontological contributions continue today at The Charleston Museum, the South Carolina State Museum, and the Mace Brown Museum of Natural History. For example, one of the most significant Paleocene faunas from eastern North America was reported in Sanders (1998a, b, c), and Eocene marine units in the state have yielded the best North American glimpses yet into the early evolution of cetaceans, with several taxa of protocetid and basilosaurid archaeocetes having been recovered (Albright, 1996; Uhen and Gingerich, 2001; Geisler et al., 2005; McLeod and Barnes, 2008; Uhen, 2008; Gibson et al., 2019). Similar explorations by AES and colleagues (particularly J. Geisler) in the above noted Ashley and Chandler Bridge formations (together with a host of diligent and concerned avocational collectors) have resulted in an unparalleled assemblage of archaic odontocetes and mysticetes of profound evolutionary significance (e.g., Whitmore and Sanders, 1976; Sanders, 1980; Sanders et al., 1982; Sanders and Barnes, 2002a, b; Geisler et al., 2014; Sanders and Geisler, 2015; Churchill et al., 2016; Godfrey et al., 2016; Boessenecker et al., 2017a, b). Still under study by JLK, DJC, and colleagues at the SCSM and the USNM is the spectacular Camelot Local Fauna, by far the richest and best preserved Irvingtonian flora and fauna in the state, rivaling those from Florida and California (Kohn et al., 2005; Beaty et al., 2007; Fields, 2010). Additional vertebrate assemblages under study at the SCSM include those from the Walrus Ditch, Crowfield, and Rodent Ditch localities (Chandler and Knight, 2009; Knight and Cicimurri, 2010), which are adding several new taxa of Blancan through Rancholabrean age to the state’s list; a newly recognized latest Paleocene fauna has come to light, as well. There have even been exciting new discoveries of Late Cretaceous vertebrates in South Carolina, including dinosaurs (Weishampel and Young, 1996; Schwimmer et al., 2015).

Although long overshadowed by the exceptionally rich Cenozoic record from Florida (e.g., Hulbert, 2001), as well as the impressive collections from Lee Creek Mine, North Carolina (Ray et al., 2008), renewed efforts in South Carolina over the last three to four decades have resulted in a wealth of new data from sites that rival, and in some cases surpass, any others along the USA Atlantic Coastal Plain. Current studies of these sites are resulting in a much greater understanding of paleobiodiversity along the southeastern coastal plain than was available only a few years ago.

CENOZOIC VERTEBRATE FOSSIL-BEARING BEDS OF THE SOUTH CAROLINA COASTAL PLAIN

The stratigraphic foundation presented in this report is based on studies of the SC Coastal Plain by the United States Geological Survey, the South Carolina Geological Survey, and by academic and state geologists across the eastern USA. Sediments representing approximately 40 named formations were deposited on the upper and lower Coastal Plain of the state during Cenozoic time (Figures 2A–C), with others not yet named or fully characterized (e.g., offshore Pleistocene units). Although some are accessible in outcrops along watercourses, road-cuts, or in exposures in commercial quarries or construction sites, many are known only from subsurface encounters in auger holes and cores, such as the Fishburne, Parachucla (although exposed on the Georgia side of the Savannah River), and Ebenezer formations. Others, such as the Marks Head Formation, the Coosawhatchie Formation, and/or the Wabasso beds, may have exposures on river bottoms in the coastal region of Jasper and Beaufort counties, as does the Ashley Formation in, for example, the Cooper and Edisto rivers. (Note: the Marks Head Formation is also exposed on the Georgia side of the Savannah River at Porters Landing).

Vertebrate fossils other than those of fish have been recovered from eight Paleogene formations, three Neogene formations (all Pliocene in age), and eight Pleistocene units including the unnamed terrestrial sediments now offshore, but deposited across the continental shelf during Wisconsian time prior to Holocene inundation (Table 1). The offshore deposits have yielded a rich record of Rancholabrean-aged fossils, specimens of which are regularly washed ashore along the present coasts of Myrtle and Edisto beaches – the latter being one of the best-known localities for Pleistocene mammal remains on the USA Atlantic Coastal Plain (Roth and Laerm, 1980; Sanders, 2002). For that reason these offshore deposits are included among the recognized stratigraphic units even though they are not currently formally named or characterized. All other units of the lower Coastal Plain are marine in origin and formally recognized by the USGS, with the exception of the Ten Mile Hill Beds – an informal name used in USGS literature (e.g., Bybell, 1990; Edwards et al., 2000) for middle to late Pleistocene sediments in the Charleston area, but recently formalized by Sanders et al. (2009) as the Ten Mile Hill Formation.

In this section, we focus primarily on those geological units from which vertebrate fossils (mostly mammals) have been recorded; but we also provide limited discussion of some units that have not yet yielded vertebrates (unequivocally), such as the lower Eocene Fishburne Formation, the middle Eocene Congaree and Warley Hill formations, and the Miocene Parachucla, Marks Head, and Coosawhatchie formations. In addition to these units from the lower Coastal Plain, nearly all of the formations from the upper Coastal Plain (Figs. 1, 2A) lack a vertebrate record with the exception of fish (noted below; see Nystrom et al., 1991; Fallaw and Price, 1995; and Edwards et al., 2001). These include the following:

- the lower Paleocene Sawdust Landing Formation (NP1; updip equivalent of the Rhems Formation; unpublished shark, ray, and fish material is noted from this unit by DJC);
- the middle to upper Paleocene Lang Syne and

Table 1. Formally and informally named geologic units in South Carolina that have produced fossils of tetrapods (oldest to youngest descending; see Figures 2 and 3 for detailed chronology of these units).

Paleogene	Neogene	Quaternary/Pleistocene
Williamsburg Formation	?Marks Head Fm.	Waccamaw Formation
Santee Limestone	Goose Creek Limestone	Penholoway Formation
Tupelo Bay Formation	Raysor Formation	Ladson/Canepatch Formation
Parkers Ferry Formation	Duplin Formation	Ten Mile Hill Formation
Harleyville Formation		Socastee Formation
Ashley Formation		Wando Formation
Chandler Bridge Formation		Unnamed Ardis LF deposits
Tiger Leap/Edisto Formation		Offshore Rancholabrean deposits

Snapp formations (updip equivalents of the Williamsburg Formation);

- the lower Eocene Fourmile Branch Formation (NP11; updip equivalent of the Fishburne Formation);
- the lower to middle Eocene Huber Formation (NP12–14; updip equivalent of the Congaree Formation; shark, ray, and teleost material was noted from the Huber by Kite, 1982, and Nystrom et al., 1991);
- the middle Eocene Warley Hill Formation (NP15/lower 16; updip equivalent of the *Cubitostrea lisbonensis* zone of the Santee Limestone [Harris and Fullagar, 1987]);
- the upper middle Eocene McBean/Tinker Formation (NP16; updip equivalent of the Santee Limestone *Cubitostrea sellaeformis* zone);
- the upper Eocene Clinchfield Formation (NP17(?)–18; likely updip equivalent of the Pregnall Member of the Tupelo Bay Formation based on remains of basilosaurid archaeocetes and a fragment of brontothere tooth reported from Georgia by Westgate (2001); no vertebrate material known from this unit in SC;
- the upper Eocene Dry Branch Formation (NP19–20; updip equivalent of the Parkers Ferry Formation; shark, ray, and fish material was noted from the Dry Branch by Fallaw and Price, 1995; Cicimurri and Knight, 2019);
- the upper-most Eocene Tobacco Road Sand (updip equivalent of the Parkers Ferry and Harleyville formations; shark and ray teeth were noted from the Tobacco Road Sand by Nystrom et al., 1991);
- the middle Miocene (late Serravalian) Upland Unit (equivalent to middle Miocene Altamaha Formation per Nystrom et al., 1991, Huddlestun, 1988, and Weems and Edwards, 2007a; but see alternative interpretation as an updip equivalent of the upper Oligocene Chandler Bridge Formation by Katuna et al., 1997; also see Colquhoun et al., 1993); and
- the “upper Miocene/lower Pliocene” Pinehurst Formation (eolian dune deposits; considered as “probably Pleistocene glacial-age dune deposits” by REW).

Figures 2 and 3 accompany the following discussion and provide our interpretations of the temporal placement of SC’s Cenozoic strata. Figure 3, in particular, is a compilation that includes correlation of refined calcareous nannoplankton zones, Atlantic planktonic foraminiferal zones, dinoflagellate zones, NALMAs, and the $\delta^{18}O$ record to the GTS2012 time scale. Both figures also provide, for the reader’s convenience, the boundary dates associated with each Epoch and Stage following GTS2012. It will be noticed that in some cases our placement of SC’s stratigraphic units differs from traditional interpretations, but this is due in large part to the highly refined, astronomically tuned nature of the marine $\delta^{18}O$ record (Lisiecki and Raymo, 2005; Raffi et al., 2006) and its latest correlation to the most recent GPTS, as well as to our interpretations. This in turn has resulted in revised ages for some of these units. Although this report focuses primarily on the mammalian biostratigraphy of the state, certain biochronologically significant invertebrate taxa are also noted because of their utility in providing refined temporal placement of some of the units from which vertebrate fossils were recovered (e.g., Appendix 4).

Paleocene Series (66.0 –56.0 Ma)

What is known of the Paleocene vertebrate fauna of South Carolina is derived primarily from an enormous pit excavated in 1979 near the town of St. Stephen, Berkeley County, as part of a project to redivert water previously diverted from the Santee River to the Cooper River back into the Santee. The pit, reaching a depth of ~43 m (140 feet), penetrated the Williamsburg Formation of the Black Mingo Group, exposing virtually the entire Chicora Member and the top of the underlying Lower Bridge Member (Weems and Bybell, 1998). At the pit locality the Williamsburg Formation is overlain unconformably by the lower Pleistocene Penholoway Formation.

The geology, paleobotany, and vertebrate fauna sampled from the St. Stephen pit and its extensive spoil piles were analyzed in a volume edited by Sanders (1998a), providing the first glimpses of early Cenozoic paleobiology from the southern Atlantic Coastal Plain. In his summary Sanders (1998b:262) listed 31 genera and 43 species of vertebrates including sharks, rays, a sawfish, bony fishes, turtles, a snake, crocodilians, and mammals from what is thought to be the Chicora Member.

Five reptilian taxa from the Williamsburg Formation, the turtles *Adocus*, *Agomphus*, *Taphrophys*, *Aspideretes*, and possibly *Bothremys* (Hutchison and Weems, 1998), together with two crocodilians from Cretaceous beds in Florence and Darlington counties, *Bottosaurus* and *Thoracosaurus* (Erickson, 1998a), provide the first evidence of a continuum of vertebrate taxa across the Cretaceous-Paleogene (K-Pg) boundary in South Carolina. Pollen and other paleobotanical material indicate a subtropical environment in this region in late Paleocene time (Melchior, 1998).

Another site yielding fossils of Paleocene age is the Clapp Creek locality within the town limits of Kingstree, SC. This locality, first noted by Sanders (1998c:6) and by Weems and Bybell (1998:10–11), consists of two open pits immediately east of the creek that were dug by Ms. A. Baker, an avocational fossil hunter, with mechanized heavy equipment in 1987. Each pit was originally about 10–12 meters long by 4–5 m wide, and the pit nearest the creek is separated from it by about 3 meters. Apparently abandoned for many years, current efforts to recover fossils there are difficult in that only hand tools can be used to remove the years of accumulated slumped overburden. Constant pumping or bailing is required to keep the water level low, but the pit is never dry and an accurate evaluation of the stratigraphy is difficult at best. The fossils originate from a prominent lag deposit in a coarse-grained, non-indurated, muddy quartz sand unit approximately 2–2.5 meters below the ground surface. The fossils are collected by shoveling the muddy sand at the lag level into buckets, and then screen-washing the contents of the buckets in the weakly flowing creek. The most ambitious recent efforts to recover fossils from the site are currently being undertaken by Dr. C. Ciampaglio and students from Wright State University, Celina, Ohio, who are often joined by SC avocational fossil collectors B. Palmer (deceased) and R. Shafto. Websites highlighting South Carolina fossils indicate that others are collecting from the site as well.

The fossils originate from a temporally mixed lag deposit that yields an abundance of crocodilian, turtle, and fish material, plus coprolites, but also includes material of dinosaurs, mosasaurs, plesiosaurs, and Pliocene to Pleistocene mammals such as rodents, horses, tapirs, mastodons (or gomphotheres), elk, and sloth. Although Schwimmer et al. (2015) considered the Clapp Creek dinosaur material as having originated from the upper Campanian Donoho Creek Formation, more recent analysis of the Cretaceous elasmobranchs by DJC concludes that they are Maastrichtian in age, and that there are no taxa strictly indicative of the Campanian. The unit of origin for the dinosaurs, mosasaurs, and plesiosaurs, therefore, is here considered to be the Steel Creek Formation – a Maastrichtian deltaic unit mapped in Georgia and South Carolina (hence the mixture of marine and worn specimens of terrestrial taxa), and correlative with the offshore deposits of the Peedee Formation (Fallaw and Price, 1995) – rather than the Donoho Creek Formation. Regarding the Paleocene, Danian sharks teeth are found at this site, apparently originating from the Rhems Formation (Santana et al., 2011), but mammals have yet to be recovered.

Additional material of Paleocene age was noted by Cicimurri et al. (2016) from sediments immediately underlying the Santee Limestone at the Martin Marietta Materials quarry near Jamestown, northeastern Berkeley County (Fig. 1; detailed discussion below). Previously referred to as the “Jamestown beds” (Cicimurri and Knight, 2009a; Cicimurri, 2010) and thought to be early Eocene in age, the unit yielding the fossils, upon further study (Cicimurri et al., 2016), was found to be latest Paleocene in age and correlated with the Chicora Member of the Williamsburg Formation. In Table 2, vertebrate taxa from this locality have been added to those noted in Sanders (1998b:262) that were recovered from the St. Stephen pit.

Williamsburg Formation, *Lower Bridge Member*. Weems and Bybell (1998) described the Lower Bridge Member at the St. Stephen pit as lithified to semi-lithified silts to fine-grained sands and silty cristobalitic shales. They added that the only unlithified part of this unit was the uppermost two feet. Fossils recovered included "remains of sharks, rays, the bony fish *Phyllodus*, and small ... crocodile teeth" (Weems and Bybell, 1998:13, 25). Silty, lithified matrix adhering to a vertebra of the crocodilian *Hyposaurus* indicated that it, too, originated from this unit.

Edwards (1998), studying dinoflagellates from the Lower Bridge Member exposed in the pit, determined that its age was equivalent to calcareous nannoplankton zones NP3, 4, or 5 (early to middle Paleocene). The age was refined to NP5, and to reversed magnetochron C26r, upon study of a core drilled in Charleston County (Edwards et al., 1999), followed by further revision to zones NP4–5 (approx. 60 Ma, middle Paleocene, Selandian; Figs. 2A, 3A) after study of another core drilled in Dorchester County (Edwards et al., 2000).

Williamsburg Formation, *Chicora Member*. The Chicora Member is composed of medium to coarse-grained sands with an abundantly shelly stratum observable at the stratotype outcrop on the Santee River about 0.8 km (0.5 miles) northeast of Wilson's Landing in northern Berkeley County (Van Nieuwenhuise and Colquhoun, 1982; Sanders, 1998a; Weems and Bybell, 1998). In addition to four gastropod and nine bivalve taxa (including the first Paleocene record of *Pitar ovatus*), the stratotype has also yielded vertebrate remains including ray dental plate segments, sharks teeth, and a crocodilian tooth.

At the St. Stephens pit, Weems and Bybell (1998) noted a prominent lag deposit at the boundary between the Chicora Member and the underlying Lower Bridge Member that included rounded phosphate pebbles and worn bone fragments. Edwards' (1998) study of dinoflagellates from the Chicora Member at the pit resulted in an NP8 or 9 assignment, but, as with the Lower Bridge Member, additional study from the Charleston and Dorchester cores revised the age to NP5-9 (upper middle to upper Paleocene, upper Selandian-Thanetian).

The land mammal fossils from the St. Stephen pit, referred to as the Black Mingo Fauna by Schoch (1985, 1998), were all collected from spoil piles, therefore precluding an exact determination as to their unit of origin. Schoch (1985, 1998), however, concluded that they were likely derived from the Chicora Member. Represented by only five teeth, two were described as new subspecies of the condylarth *Phenacodus grangeri* (*P. grangeri mccollumi*) and the taeniodont *Ectoganus gliriformis* (*E. gliriformis lobdelli*), and a third was referred to an enigmatic new taxon of uncertain ordinal position, *Mingotherium holti*. Another partial tooth was too incomplete to be referred beyond "Tribosphenida incertae sedis," and a large caniniform tooth was thought to be representative of a pantodont, uintathere, or large condylarth (Schoch, 1998:238). *Phenacodus grangeri* is known from Tiffanian 1–5 faunas elsewhere in North America (Thewissen, 1990), and *Ectoganus* occurs in Ti5 through the Clarkforkian (Archibald et al., 1987). Lofgren et al. (2004) assigned the Black Mingo Fauna to Ti5, which is compatible with their derivation from the Chicora Member given the dinoflagellate correlation noted above, although the possibility that they originated from the unlithified upper two feet of the Lower Bridge Member cannot be discounted. In addition to the mammalian component, Erickson (1998b) reported a vertebra of a palaeophid snake from the fauna (Table 2).

"Jamestown beds." From sediments immediately underlying the Santee Limestone at the Martin Marietta Materials quarry near Jamestown, northeastern Berkeley County, Cicimurri and Knight (2009a:24) reported "a highly diverse vertebrate assemblage consisting of elasmobranch, osteichthyan, and reptilian species," which, together with the invertebrates, indicated an Ypresian (early Eocene) age. Included in the osteichthyan assemblage, they noted the perciform fish, *Fisherichthys folmeri*, originally described by Weems (1999) from the basal portion of Bed B of the Potapaco Member of the Nanjemoy Formation of Virginia, and assigned to calcareous nannoplankton zone NP11 by Gibson and Bybell (1991). *Fisherichthys*

Table 2. Summary of taxa from the Williamsburg Formation, including those collected in the pit excavated for the Santee rediversion project near St. Stephen, Berkeley County (summarized from Sanders, 1998b:table 2) and from "Jamestown deposits" (see text).

- Chondrichthyes
  - *Myliobatis* sp.
  - *Rhinoptera* sp.
  - *Meridiania convexa*
  - *Rhinobatos bruxelliensis*
  - *Pristis* sp.
  - *Nebrius* sp.
  - *Carcharius macrotus*
  - *Carcharius hopei*
  - *Odontaspis rutoti*
  - *Otodus obliquus*
  - *Cretolamna appendiculata*
  - *Palaeocarcharodon orientalis*
  - ?*Scyliorhinus* sp.
  - ?*Triakis* sp.
  - *Coupatezia woutersi*
  - *Jacquhermania duponti*
  - *Heterotorpedo fowleri*
  - *Ischyodus* sp.
- Osteichthyes
  - *Lepisosteus* sp.
  - ?*Pycnodus* sp.
  - *Albula oweni*
  - *Egertonia isodonta*
  - *Phyllodus toliapicus*
  - Ostraciidae indet.
  - *Fisherichthys folmeri*
- Osteichthyes (cont.)
  - *Progymnodon hilgendorfi*
- Chelonia
  - Cheloniidae indet.
  - *Osteopygis emarginatus*
  - *Taphrosphys sulcus*
  - ?*Bothremys* sp. indet.
  - *Agomphus pectoralis*
  - "*Agomphus*" sp. aff. "*A.*" *alabamensis*
  - *Adocus* sp. indet.
  - *Aspideretes virginianus*
  - Kinosternoid A
  - Kinosternoid B
- Squamata
  - *Palaeophis* sp.
  - Glyptosaurinae gen. et sp. indet.
- Crocodilia
  - *Hyposaurus* sp.
  - *Bottosaurus* sp.
  - *Thoracosaurus* sp.
  - *Eosuchus* sp.
- Mammalia
  - *Didymictis proteus*
  - *Mingotherium holtae*
  - *Phenacodus grangeri mccollumi*
  - *Ectoganus gliriformis lobdelli*
  - Tribosphenida indet.

folmeri is also known from the upper part of the Tuscahoma Formation in Alabama, considered earliest Wasatchian (Wa0) in age (correlative with calcareous nannoplankton subzone NP9b) on the basis of mammals recovered (Beard and Dawson, 2001, 2009). This species has also been reported from the marine portion of the Bashi Formation of eastern Mississippi (Case, 1994) deposited during the lower half of NP10 (see Cicimurri and Knight, 2009a:25). Another species reported by Cicimurri (2010) from the Jamestown deposits, plus the Bashi and Nanjemoy formations, is the extinct early Eocene ray *Meridiania convexa* Case, 1994.

Taken together, the above noted biochronological data seemed to suggest an early Eocene age. Although Cicimurri and Knight (2009a) noted that these Jamestown sediments were lithologically different than those of the lower Eocene Fishburne Formation (see below), therefore precluding direct correlation, they considered the possibility that the two units were laterally equivalent. In a later study describing the myliobatoid ray *Eorhinoptera grabdai* (here considered a junior synonym of *Meridiania convexa*), Case et al. (2011) assigned these deposits to the Fishburne Formation.

However, more recent analysis of the calcareous nannoplankton from these sediments by Cicimurri et al. (2016) resulted in a refinement of the age of the Jamestown deposits to latest Paleocene subzone NP9a (i.e., uppermost Thanetian). They also determined, on the basis of lithologic and paleontologic similarity, that these beds are correlative with the Chicora Member of the Williamsburg Formation, not with the Fishburne Formation, and therefore assigned the Jamestown deposits to that member (Figs. 2A, 3A).

Supporting the NP9a age of these Jamestown beds is a small partial mammal tooth found in 2007 by Charleston Museum volunteer Bill T. Palmer. The tooth was recovered from the same spoil pile in which the material of Cicimurri and Knight (2009a) and Cicimurri et al. (2016) originated. It consists only of the trigonid, but has been identified as belonging to the late Tiffanian (Ti5) through earliest Wasatchian (Wa0) viverravid *Didymictis proteus* Cope, 1875 (J. Bloch and P. Morse, pers. comm. to LBA, 2015; see "Systematic Paleontology" section below). This specimen (ChM PV7687) represents the first viverravid known from the USA Atlantic Coastal Plain. How close the specimen is in age to the mammals of the Black Mingo Fauna, also considered as originating from the Chicora Member, is undeterminable, but the work of Cicimurri et al. (2016) points toward a late Thanetian rather than Ypresian age (Clarkforkian NALMA, approx. 56 Ma).

Eocene Series (56.0–33.9 Ma)

Fishburne Formation. Gohn et al. (1983) described the Fishburne Formation from the 416–440 ft interval of the Clubhouse Crossroads Corehole No. 1 (CCC1; Fig. 1B) from Dorchester County as a greenish-gray to pale-olive, finely crystalline, nodular, glauconitic, clayey, microfossil-mollusc limestone with apparent lack of bedding due to bioturbation. In the core, the Fishburne sharply underlies the Santee Limestone (NP16); the stratigraphically intervening Warley Hill Formation (NP15) is absent.

Although CCC1 was recovered about 40 km (24 miles) southwest of the Jamestown quarry, a much closer corehole was drilled by the USGS in 1996 on the Santee Coastal Reserve near the Santee River in northeastern Charleston County, about 20 km (12 miles) southeast of the quarry (Edwards et al., 1999). In that core, a 9.5 ft-thick section (2.9 m) of mollusc-bryozoan limestone was encountered above the upper Paleocene Chicora Member of the Williamsburg Formation – a stratigraphic position similar to that of the stratotype Fishburne Formation. Edwards et al. (1999:28) observed that "This poorly recovered limestone is not the same age as the Santee and may consist of two units of different ages. It may be equivalent to the lower Eocene Fishburne Formation (Gohn et al., 1983), or the lower Eocene Congaree Formation (Fallaw and Price, 1995), or parts of both." The best evidence for the age of this unit as determined by Edwards et al. (1999) comes from three samples of the core that yielded calcareous nannofossils indicative of uppermost zone NP9 to NP12 (Ypresian). Enigmatic as this stratum may be for formational interpretation, it does establish the presence of lower Eocene deposits relatively close to the Jamestown quarry at least partly correlative with the Fishburne Formation.

Congaree Formation. Cooke and MacNeil (1952) elevated Sloan's "Congaree phase" to formational rank, and correlated it to the Tallahatta Formation of Alabama and Mississippi on the basis of similar lithology and on the mutual occurrence of the molluscs *Anadontia augustana* and *Ostrea johnsoni*. Fallaw and Price (1995) suggested an NP12–14 (Upper Ypresian-Lower Lutetian) age for the Congaree. No vertebrates are known from this unit.

Warley Hill Formation. Referred to by Sloan (1908:458) as the "Warley Hill phase," as the Warley Hill Marl by Cooke and MacNeil (1952:23), and as the Warley Hill Formation by Pooser (1965), these dominantly glauconitic non-calcareous sediments containing the oyster *Cubitostrea lisbonensis* correlate with the lower Lisbon Formation of Alabama. The unit lies between the Congaree Formation below and the Santee Limestone above (in the currently restricted sense, i.e., the *Cubitostrea sellaeformis* zone; see further discussion in the section on Santee Limestone below and on the McBean and Tinker formations in Kier, 1980, and Fallaw and Price, 1995). Kier (1980) dated the Warley Hill Formation as lower middle Claibornian on the basis of the occurrence of the echinoid *Protoscutella mississippiensis*, and Fallaw and Price (1995) noted an NP15 age (middle Eocene, upper Lutetian). Harris and Fullagar (1987) reported a Rb-Sr glauconitic mica isochron date of 42.0 ± 0.5 Ma for the unit, but later revised this date to 45.1 ± 1.7 Ma (correlative with the NP15 designation) based on a conventional K-Ar date, also from glauconitic micas (Harris and Fullagar, 1991). The only vertebrates known from this unit are some sharks teeth noted by DJC.

Santee Limestone. This often highly indurated, typically gray limestone was named "the Santee white limestone" by Charles Lyell, who, in the company of Edmund Ravenel in 1842, correctly determined that oysters he observed in outcrops near Eutaw Springs along the bank of the Santee River in Orangeburg County (now submerged) were of Eocene age (Lyell, 1845). Referred to as the "Great Carolina beds" by Ruffin (1843), the "Santee beds" by Tuomey (1848), and the "Santee marl" by Sloan (1908), it was Cooke (1936) who designated the exposures at Eutaw Springs as the type section of his Santee Limestone (Banks, 1977). The unit is widespread in the subsurface of the SC Coastal Plain, although normally exposed only in deep commercial quarries, such as those at the Martin Marietta Berkeley and Orangeburg quarries near Cross, SC.[2] These quarries, together with another in Georgetown and a fourth in Jamestown, have yielded over 200 species of Eocene molluscs (Campbell, 1995; Campbell and Campbell, 2003).

Ward et al. (1979) divided the Santee Limestone into a lower Moultrie Member for the highly indurated bryozoan-dominated carbonate facies with abundant *Cubitostrea sellaeformis* and an overlying Cross Member for the much more mollusc-dominated unit, which includes *Crassatella alta*. They designated a measured section within the Martin Marietta Berkeley (Cross) quarry as the stratotype for the Moultrie Member, and equated this unit with lithozones I and II of Banks (1977). However, Ward et al. (1979) did not note *C. lisbonensis* in this section – the taxon that occurs stratigraphically below *C. sellaeformis* and biostratigraphically characterized Banks' (1977) lithozone I, and on which a correlation with the lower Lisbon Formation of Alabama and with the Warley Hill Formation was based (Note: Campbell and Campbell [2003] also did not record *C. lisbonensis* in the Cross quarry). Banks (1977) correlated lithozone II, disconformably overlying zone I, with the upper Lisbon Formation based on the presence of *C. sellaeformis*. Thus, the Moultrie Member as conceived by Ward et al. (1979) was actually a correlate only with Banks' (1977) lithozone II, not with zone I. An intermediate *C. smithvillensis* zone, recognized in the Gulf Coastal Plain, is absent. The Cross quarry was also the location for Ward et al.'s (1979) stratotype of the Cross Member. They correlated this unit with Banks' (1977) lithozones III and IV, and with the Gosport Sand of Alabama, on the basis, in part, of the presence of *Crassatella alta*.

Baum et al. (1980) divided the Santee Limestone into a lower *Cubitostrea lisbonensis* faunal zone (Banks' zone I) and an upper *C. sellaeformis* faunal zone (Banks' zone II; Chapel Branch Member of Powell, 1984), and recommended abandonment of Ward et al.'s (1979) stratigraphically equivalent Moultrie Member. They similarly recommended abandonment of the lithostratigraphic term Warley Hill Formation due to its correlation with their lower Santee, i.e., the *Cubitostrea lisbonensis* zone. Finally, they excluded Ward et al.'s (1979) Cross Member from the Santee Limestone, and elevated it to formational status. Powell and Baum (1982) followed the terminology of Baum et al. (1980:1100–1101), but proposed a Caw Caw Member of the Santee Limestone for "a curious updip equivalent of the typical carbonates of the Santee Limestone …," adding that the term "Caw Caw" had priority over "McBean." Edwards et al. (1997, 2000) followed Ward et al.'s (1979) concept of the Santee Limestone, maintaining usage of the Moultrie and Cross 'member' terminology; they

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[2] Approximately 8.9 km west of Cross, SC, straddling the north-south trending County Line Road, are the Martin Marietta Aggregates Cross quarries (Fig. 1B, "CQ"). Quarries on the east side of the road, now abandoned and flooded, are in Berkeley County, thus "Martin Marietta Berkeley Quarry"; those on the west side are in Orangeburg County, i.e., "Martin Marietta Orangeburg Quarry" (cited as the "Southern Aggregates Orangeburg Quarry" in Campbell, 1995). Unless otherwise noted, reference to the "Cross quarry" implies the Berkeley quarry.

correlated the Moultrie Member to nannoplankton zone NP16 and the Cross Member to zones NP17–18.

More recently Geisler et al. (2005), in proposing their new Tupelo Bay Formation as a replacement for Baum et al.'s (1980) Cross Formation (further discussion below), recommended restriction of the name "Santee Limestone" to the indurated unit of NP16 age previously referred by Ward et al. (1979) to the Moultrie Member (Banks' zone II; *C. sellaeformis* zone; Fig. 2A, 3A) lying disconformably below the Cross Member. Although the above discussion would seem to imply that some level of stability has been finally reached with respect to an understanding of the Eocene stratigraphy of South Carolina, Campbell's (1995:121) note that "Little consensus exists on nomenclature and correlation" still holds true to some extent today, as does a similar sentiment noted by Campbell and Campbell (2003) that "The Eocene stratigraphy of the [SC] region remains debated."

Regarding vertebrate fossils from the Santee Limestone, the first published account of a protocetid archaeocete in South Carolina was Albright's (1996) report of three teeth (ChM PV5037, 5038, 5039) collected in the Cross quarry, presumably from the Santee Limestone (*Cubitostrea sellaeformis* zone). Although the teeth were collected on a spoil pile, their derivation from the Santee Limestone was based on the very similar morphology they share with those of *Georgiacetus vogtlensis* Hulbert et al., 1998. The Georgia type specimen was collected from the informally named Blue Bluff unit of the McBean Formation, which, based on similar molluscs (including *Cubitostrea sellaeformis*) and on nannoplankton indicative of zone NP16, is directly correlative with the Santee Limestone (Fallaw and Price, 1995). (Note: in Appendix I of Janis et al. [2008:736] the teeth are reported from the overlying Cross Formation [currently the Cross Member of the Tupelo Bay Formation; see discussion below]). As noted below, the Cross Member at the Cross quarry has yielded remains of protocetid archaeocetes, but for reasons noted above ChM PV5037, 5038, and 5039 are thought to have originated from the Santee Limestone; however, their derivation from the Cross Member is possible). Albright (1996) chose not to assign the SC teeth to a known taxon, but subsequent authors, noting the similar dental morphology, referred them to *Georgiacetus* cf. *vogtlensis* and to *Georgiacetus*, aff. *G. vogtlensis* (Uhen, 1999, and McLeod and Barnes, 2008, respectively).

Based on the marine $\delta^{18}O$ isotope record (Fig. 3A), it appears that deposition of the Santee Limestone coincided with the Middle Eocene Climatic Optimum (MECO) – a warm, high sea level pulse among the background of general climatic deterioration that was occurring through the middle and late Eocene (e.g., Edgar et al., 2010; Galazzo et al., 2014).

Tupelo Bay Formation. Poorly understood for many years, two of the calcareous Eocene beds above the Santee Limestone – one exposed in the Cross quarry in Berkeley county and the other in the Giant Cement quarry in Dorchester County – have at various times been assigned, together or in part, to the Castle Hayne Formation (Cooke and MacNeil, 1952), the Santee Limestone (Sanders, 1974; Ward et al., 1979), or the Cross Formation (Baum et al., 1980). More recent work, however (Geisler et al., 2005), has shown that none of those arrangements reflected the true chronostratigraphic relationships of these two beds.

Recognizing two lithologic subunits within the Cross Formation (of Baum et al., 1980) in the Pregnall core from Dorchester County (Edwards et al., 1997), Sanders and Katuna (2000) recommended dividing that unit into a lower Berkeley Member and an upper Pregnall Member. In proposing the Tupelo Bay Formation as a replacement for Baum et al.'s (1980) Cross Formation, Geisler et al. (2005) retained the name Cross Member of Ward et al. (1979) rather than "Berkeley Member" for the lower unit and maintained the previously proposed Pregnall Member terminology for the upper member, which comprise the deposits underlying the Harleyville and Parkers Ferry formations in the Giant Cement quarry.

The two units differ biostratigraphically in their nannoplankton and cetacean content; the Cross Member falls within calcareous nannoplankton zone NP17 and contains only the remains of archaeocetes of the primitive family Protocetidae, whereas the Pregnall Member is NP18 in age and has yielded only the remains of archaeocetes of the more derived Basilosauridae (Geisler et al., 2005). As seen in Figure 3A, correlation of the Tupelo Bay Formation to NP17 and NP18 indicates that it too was deposited during another transient warm interval, this time in the late Eocene across the Bartonian-Priabonian boundary.

Tupelo Bay Formation, Cross Member. In 1994, the holotype material (ChM PV5401) of the protocetid *Carolinacetus gingerichi* Geisler et al., 2005, was collected from the base of the Cross Member at the Cross Quarry by a ChM party. This material consists of a partial skull, seven vertebrae, and 15 ribs. As seen in figures 3 and 4 of Geisler et al. (2005; and reproduced herein as Figure 4), the nasal opening is situated above the canine tooth – a plesiomorphic feature previously unrecorded in New World protocetids (e.g., *Georgiacetus*) and more typical of Old World forms such as *Rodhocetus*. On that basis, *Carolinacetus* is currently the most primitive known cetacean from North America (Geisler et al., 2005). Additional protocetid material from the Cross Member includes six partial skulls (ChM PV6850, PV6856, PV6950, PV8002, PV8003, PV8022) at least some of which represent undescribed taxa. Collected for The Charleston Museum by B. Palmer (who passed away in 2018), this material represents the largest body of protocetid material from the Western Hemisphere. ChM PV6950 was recently described by Gibson, et al. (2019) as the new taxon *Tupelocetus palmeri* in

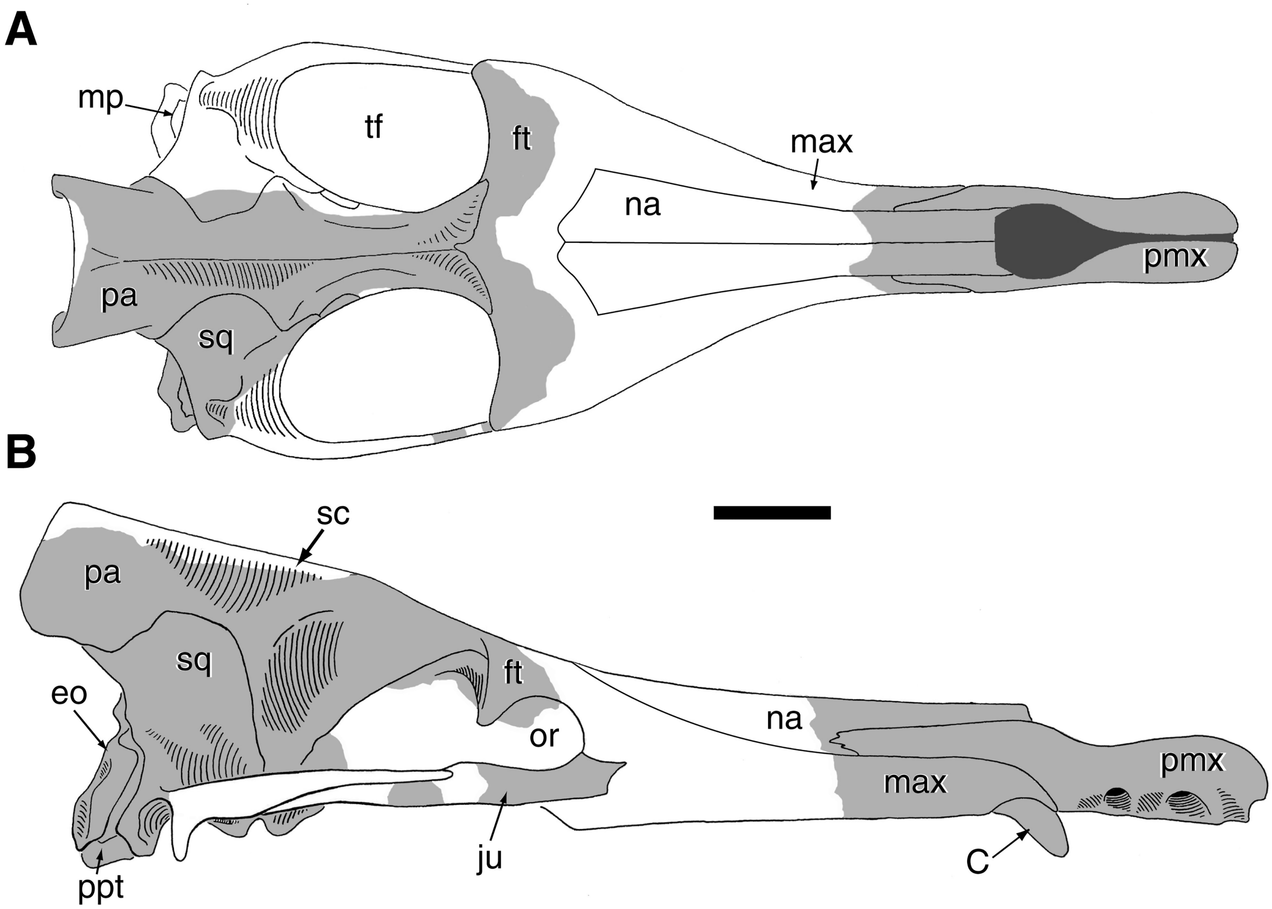

Figure 4. Reconstruction of the holotype skull of *Carolinacetus gingerichi* (ChM PV5401) from the Cross Member of the Tupelo Bay Formation. **A**, dorsal view; **B**, right lateral view. Scale bar = 10 cm. Reproduced from Geisler et al. (2005) with permission of the AMNH.

honor of Palmer's contributions.

The ChM holdings from the Cross Member also include fish remains, small portions of the carapace of an undescribed leatherback sea turtle (ChM PV9102 plus material at the SCSM, the earliest yet known from South Carolina), a vertebra of the large Eocene snake *Pterosphenus schucherti* (ChM PV5766), and a large, diverse assemblage of crabs also collected by Palmer (see Blow and Manning, 1996; Bishop and Palmer, 2006; and Franţescu et al., 2010).

Also from the Cross Member, but from the Martin Marietta Orangeburg quarry, is another specimen collected by Palmer that includes the partial inominate (GSM 1333) of an early sirenian conservatively referred to *Protosiren* sp. by Beatty and Geisler (2010), who noted that it was collected within the basal 30 cm of the member.

Tupelo Bay Formation, Pregnall Member. According to Geisler et al. (2005), it is this member of their Tupelo Bay Formation that is extensively exposed in the Giant Cement quarry and in the nearby Argos Cement Plant quarry (formerly called the LaFarge, Blue Circle, or Gifford-Hill & Co. Harleyville quarry), both near Harleyville (Fig. 1B). In 1973, when quarrying activities were underway in the now-abandoned southwestern portion of the Giant Cement quarry, a paleontological survey of the Eocene beds was conducted by a Charleston Museum party under the direction of AES and of which LBA was a member (Sanders, 1974). Cooke and MacNeil (1952) had assigned the lower beds in the quarry to the Castle Hayne Limestone, but Sanders (1974) provisionally referred them to the Santee Limestone. These are also the beds that Ward et al. (1979) referred to the Cross Member of the Santee Limestone, additionally noting the eroded, irregular nature of the unit's top surface. But it was the recognition by Edwards et al. (1997) in the USGS Pregnall No. 1 core from Dorchester County (Fig. 1B) that the Cross Member spanned two calcareous nannoplankton zones (NP17 and 18) with a subtle change in lithology that prompted Geisler et al. (2005) to propose the NP17-aged Cross Member and the NP18-aged Pregnall Member as subunits of their Tupelo Bay Formation.

During the 1973 Charleston Museum survey, what is now considered the Pregnall Member by Geisler et al. (2005) was measured to a depth of 9.76 m below its upper surface, and eight distinct faunal and/or lithological facies were recorded (Sanders, 1974:6). Cooke and MacNeil (1952:26) had previously separated their "Castle Hayne limestone" in the quarry into two beds. Their Bed 1 equates with the lower-most zone of Sanders (1974), from 5.05 m below the top of the Pregnall to 9.76 m, and their Bed 2 is equivalent to Sander's zones 1–7 above the 5.05 m horizon (Fig. 5). From their Bed 2 they recorded the molluscs *Chlamys cookei*, *Chlamys* n. sp., *Glycymeris staminea*, *Chlamys* n. sp. aff. *C. deshayesii*, *Ostrea trigonalis* (= *Pycnodonte trigonalis*) and the echinoid *Periarchus lyelli*, the latter of which they also found in Bed 1 along with *C. cookei*. To date, 32 taxa of gastropods and bivalves collected during the Charleston Museum survey have been identified by D. C. Campbell (pers. comm. to AES, 2014).

Also revealed by the 1973 survey was the highly fossiliferous nature of the contents of the "solution pits" eroded into the upper surface of the Pregnall Member. These pits are filled with olive-gray phosphatic sediments from the phosphate zone at the base of the unconformably overlying Harleyville Formation, and it was from these pits that all of the archaeocete material (Basilosauridae only) collected over the course of the survey was recovered (Sanders, 1974). However, undescribed material currently housed at the SCSM was collected in situ from the Pregnall Member, including that of basilosaurid archaeocetes and early sirenians.

Regarding such material, a partial basilosaurid skeleton dug by machinery in the Giant Cement quarry and currently housed at the SCSM (SCTC279), includes a small, elongate lumbar vertebra. Although its length/width ratio of 0.55 falls within the range of the *B. cetoides* lumbar vertebrae measured by Kellogg (1936:53), the specimen is considerably smaller than vertebrae of that taxon. From the nearby Argos Cement quarry, the purported Pregnall Member yielded a partial vertebral column of another undescribed basilosaurid archaeocete (ChM PV6761) collected by B. Palmer

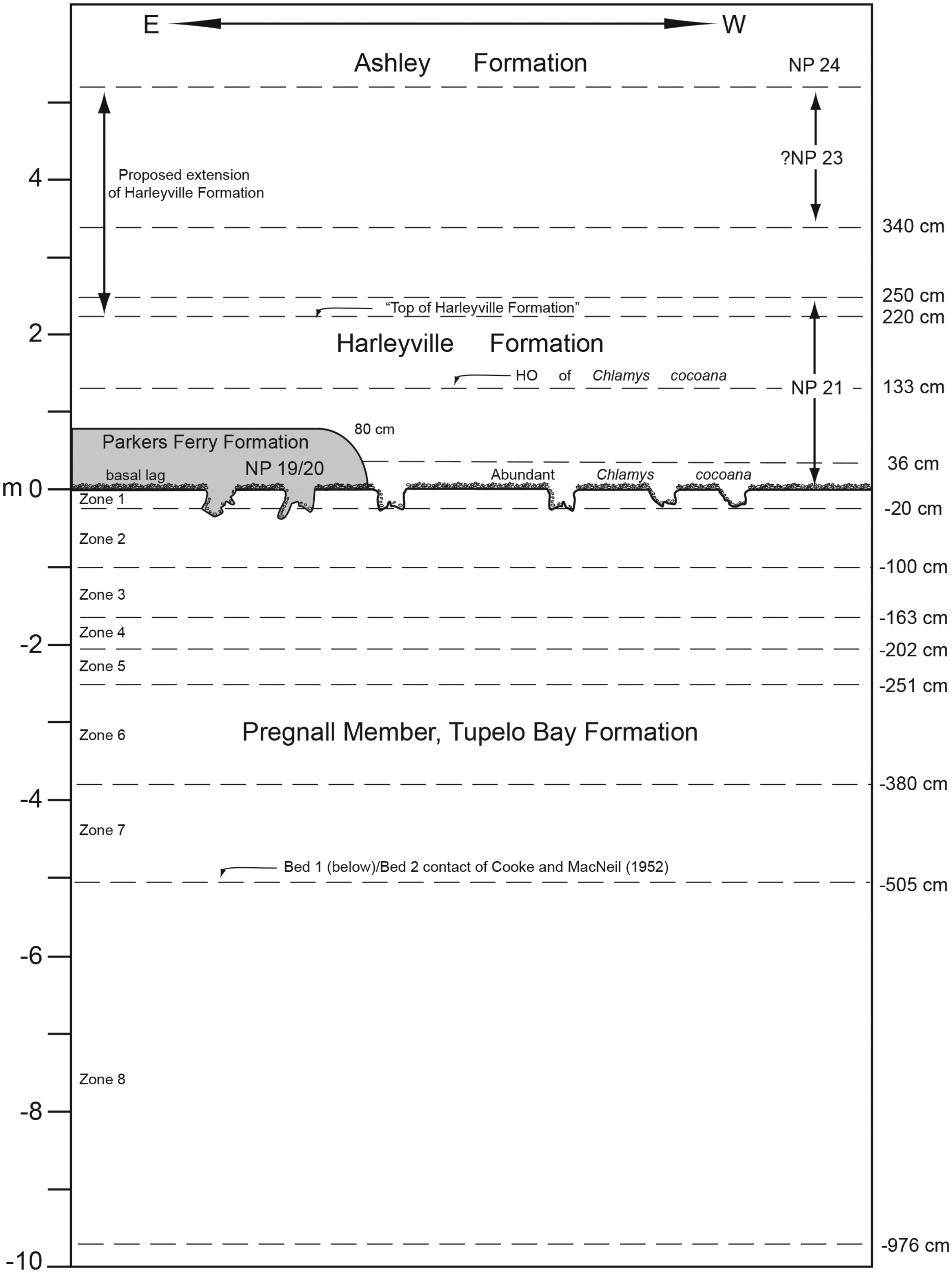

Figure 5. Redraft of Sanders' (1974) figure 2 with updated stratigraphic nomenclature, inclusion of represented calcareous nannoplankton (NP) biostratigraphy, demonstration of Parkers Ferry Formation subjacent to Harleyville Formation vs. previous superjacent interpretations, and proposal to extend Harleyville Formation upward to include beds of potential NP23 age. See text for further discussion.

from near the bottom of the exposure (Geisler et al., 2005). Still another basilosaurid, *Chrysocetus healyorum* (SC87.195), was described from the "Cross Formation" by Uhen and Gingerich (2001) from remains found in the Holcim Inc. Holly Hill quarry (formerly the Santee Portland Cement Company quarry) in Orangeburg County approximately 3.2 km (2 miles) NNE of the Giant Cement quarry (Fig. 1B). Uhen (2013) modified the stratigraphic unit of origin to the Pregnall Member of the Tupelo Bay Formation following Geisler et al.'s (2005) re-evaluation of the stratigraphy of that area.

In addition to the remains of basilosaurid archaeocetes, the record of early sirenians has been expanded beyond the specimen noted above from the Cross Member at the Martin Marietta Orangeburg quarry, with several additional specimens now known from the Pregnall Member at the Giant Cement quarry. This material includes USNM 537206, a skull and partial skeleton of an archaic dugongid found by B. Palmer; SC2006.30.1–15, another skull and partial skeleton found by JLK and V. McCollum that may represent the same taxon; and ChM PV7639, a skull cap of a small, as-yet undetermined species. USNM 537206 and SC2006.30.1–15 are exceptional specimens currently under study by D. P. Domning and I. S. Zalmout, who are provisionally considering them a new species of *Eotheroides* (D. Domning, pers. comm. to LBA, May 2015). *Eotheroides* was previously known only from the middle to late Eocene (Lutetian to early Priabonian) of Egypt, India, and Madagascar (Zalmout and Gingerich, 2012). ChM PV7639 was first mentioned by Sanders (1974), then later reported as lost by Domning et al. (1982); but the specimen was subsequently relocated with archaeocete material in the collections of The Charleston Museum. Although ChM records indicate that it was collected in August of 1973 from the Harleyville Formation (from Harleyville Formation-filled erosional pits at the top of the Pregnall Member), Beatty and Geisler (2010) noted that it may have been derived from the Pregnall Member. Another skull cap, SC2015.65.1, collected by V. McCollum from a spoil pile near the bottom of the Giant Cement quarry is provisionally referred to *Protosiren* (V. McCollum, pers. com., 2016). Additional material, including that of marine reptiles, is represented by a partial carapace of another leatherback sea turtle (ChM PV7808) and two vertebrae of *Pterosphenus schucherti* (ChM PV5765, PV5768).

NOTE ON THE STRATIGRAPHIC POSITION OF THE ARCHAEOCETE *DORUDON SERRATUS*

Upper Eocene beds in Berkeley County (then in the old Charleston District) furnished the holotype partial skull, teeth, and associated vertebrae of *Dorudon serratus* Gibbes, 1845 (MCZ 8763), the second archaeocete taxon made known to science following the description of *Basilosaurus* by Harlan (1834). In its description, Robert W. Gibbes (1845:254), a physician-naturalist of Columbia, SC, and a pioneer investigator of the paleontology of the state, reported that the type material was found "in a bed of Green sand near the Santee Canal….on the plantation of R. W. Mazyck, Esq., about three miles from the entrance of the canal from the head waters of the Cooper river," which was almost directly east of the small crossroads community of Moncks Corner. (Note: on the map of the Charleston District in Mills' Atlas [1825], the Mazyck property was about 5.5 miles north of Moncks Corner). A cousin of Gibbes, Mazyck had found the bones in a marl pit on his property and reported them to Gibbes.

The stratigraphic unit in which the remains were found has never been positively identified. During the 1930s, C. Wythe Cooke of the U.S. Geological Survey visited the old Mazyck Place (then belonging to E. J. Dennis) and noted that "There are said to be several old marl pits, now overgrown, on the plantation," but he did not actually observe any of them (Cooke, 1936:80). In 1940 the Mazyck property was covered by the waters of the newly-created Lake Moultrie, thus inhibiting further investigation of the stratigraphic units at this important locality.

The most detailed observations of its geological and paleontological features were those of the SC State Geologist Michael Tuomey, who visited the Mazyck property about 1846 and observed that "The green sand stratum is about four feet thick, much indurated towards the lower part, where fossil shells are most abundant" (Tuomey, 1848:156). He further noted that "Below this remarkable deposit is a stratum of white marl, abounding in corals" and that the green sand was exposed only in the excavations of the marl pits.

Tuomey (1848:156) reported several species of molluscs from the green sand, including the bivalve *Pecten perplanus* and the brachiopod *Terebratula harlani*, and stated that specimens from the site were "now in the collection of Dr. Ravenel, of Charleston." Clearly, the reference was to Dr. Edmund Ravenel, a well-known conchologist of his day who had guided Charles Lyell to Eutaw Springs, where Lyell discovered the Santee Limestone. Ravenel's collection of molluscs is in The Charleston Museum today. A search of the Ravenel collection by the second author for some of the molluscan taxa mentioned by Tuomey resulted in a remarkable discovery – a 30 x 24 mm sample of green sand from the Mazyck site containing two single valves of two different pectenids and a brachiopod, evidently *Terebratula harlani* Morton, 1829, the brachiopod mentioned by Tuomey (1848) as occurring in the green sand. The pectenids remain to be identified. Collected in about 1845, when interest in the green sand was at its peak, this small sample is the only remaining evidence of that stratum from the type locality of *Dorudon serratus*.

Despite the diminutive size of the green sand sample, a small portion of it was removed without damage to the remainder and was found to contain calcareous nannoplankton referable to NP zones 16, 17, and 18 (J. Self-Trail, pers. comm. to AES, July 2009). Because the archaeocete cetaceans known to occur in deposits of NP16 (Santee Limestone) and NP17 (Cross Member, Tupelo Bay Formation) age in South Carolina are all members of the primitive family Protocetidae, and because protocetids do not occur in beds of NP18 age in North America, the NP16 and 17 dates for the green sand are here discounted. Moreover, *Dorudon serratus* is a member of the more derived family Basilosauridae, presently known in South Carolina only from the Pregnall Member of the Tupelo Bay Formation of NP18 age and from the overlying (in places) Parkers Ferry Formation of NP19–20 age. Isolated remains of basilosaurid archaeocetes are also known from the Harleyville Formation-filled pits eroded into the upper surface of the Pregnall Member (e.g., Sanders, 1974). Given that the lower Harleyville has recently been determined to be of NP21 age (Cicimurri et al., 2016; Weems et al., 2016), the archaeocete material found within the pits and as part of the prominent lag deposit that rests upon the top surface of the Pregnall Member may have been reworked from the latter unit or from the Parkers Ferry Formation.

However, there is no green sand stratum currently exposed in the Pregnall Member at the Giant Cement quarry. Therefore, the green sand in which the *D. serratus* remains were found (here provisionally assigned the informal name Moncks Corner Greensand) may represent a bed within or immediately above the Pregnall Member, but which was later eroded by the Harleyville (or Parkers Ferry) seas (the base of the Harleyville is NP21 in age and the Parkers Ferry Formation, which also rests immediately above the Tupelo Bay Formation in some areas, is of NP19/20 age; Fig. 5). At present, however, that inference is merely speculation.

Cooper Group. Established by Weems and Lemon (1984a, b), the Cooper Group consists of middle Priabonian through late Rupelian aged sediments that comprise, in ascending order, the upper Eocene Parkers Ferry and Harleyville formations and the middle Oligocene (upper Rupelian) Ashley Formation (Fig. 2B). Also included were the "Drayton Limestone beds" of Weems and Lemon (1996) for a calcarenite known only from core samples to lie stratigraphically between the Parkers Ferry and Ashley formations in Charleston and Dorchester counties. However, because these beds were found to contain a similar suite of calcareous nannofossils to that of the Harleyville Formation (NP21), Weems et al. (2016) proposed the term Drayton Limestone Member of the Harleyville Formation for them.

The base of the Cooper Group lies at the distinct, disconformable contact with what is now considered the top of the Pregnall Member of the Tupelo Bay Formation. This disconformity occurs at the 227 ft level of CCC1 (Hazel et al., 1977), and all sediment from that level up to the 16 ft level, encompassing both the upper Eocene and Oligocene, were termed the "Cooper Formation." Upper Eocene beds were noted as spanning the 227 to 180 ft interval, whereas Oligocene beds extended from that point up to the 16 ft level. Ward et al. (1979) referred the upper Eocene beds between 227 and 186 feet to the Harleyville Member of the Cooper Formation. The beds of this interval are, in turn, correlated with the interval between 255 and 227 feet in the OS-1 core (Ward et al., 1979; Weems et al., 1987) recovered 7.3 miles SE of the CCC1 (Weems et al., 2016).

Parkers Ferry Formation. This "glauconitic, clayey, fine-grained limestone" (Edwards et al., 2000) was assigned to nannoplankton zones NP19/20 and to planktonic foraminiferal zone P17 (Hazel et al., 1977; Ward et al., 1979; Edwards et al., 2000). The stratotype is in CCC1 and it is also known "from the subsurface along the east side of the Edisto River" (Harris and Zullo, 1991), although Weems et al. (2016) noted the existence of a poorly exposed outcrop on the north side of the east branch of the Cooper River based on the earlier work of Weems and Lemon (1989). Long considered to lie stratigraphically between the Harleyville and Ashley formations, recent work by DJC and J. Self-Trail demonstrated that in the eastern region of the Giant Cement quarry (but not everywhere throughout the quarry), the Parkers Ferry Formation lies directly upon the Pregnall Member of the Tupelo Bay Formation (Cicimurri et al., 2016; Weems et al., 2016) and beneath the Harleyville (Fig. 5). This is confirmed on the basis of calcareous nannoplankton representative of zone NP19/20 in the Parkers Ferry Formation. Although the basal-most portion of the Harleyville Formation also appears to be of NP19/20, most of this unit is of NP21 age (further discussion below).

Long thought to be devoid of vertebrate fossils, more recent work by DJC and JLK at the Giant Cement quarry has determined that the Parkers Ferry Formation has a rich chondrichthyan and osteichthyan fauna. Additional vertebrate material from this formation includes a series of associated vertebrae from the marine palaeophid snake *Pterosphenus schucherti* (SC2017.28.1 from the Argos quarry), carapace elements of leatherback sea turtles, and an abundance of material belonging to basilosaurid archaeocetes (e.g., SC76.6 and SC2016.31). None of this material appears to be reworked from the subjacent Pregnall Member of the Tupelo Bay Formation.

Harleyville Formation. These deposits were first described as the Harleyville Member of the then-recognized Cooper Formation by Ward et al. (1979) from a 3 m thick stratotype section in the Giant Cement quarry in Dorchester County on the east side of SC Route 453, approximately 3.2 km (2 miles) NNE of Harleyville (not "3.2 miles" as stated by Ward et al., 1979:12). Weems and Lemon (1984a, b) subsequently elevated this unit to formational status. The Harleyville Formation unconformably overlies what Ward et al. (1979) then considered the Cross Member of the Santee Limestone, but what Geisler et al. (2005) referred to as the Pregnall Member of the Tupelo Bay Formation. Unconformably overlying the Harleyville Formation, Ward et al. (1979) measured nearly 2 m of Ashley "Member" (now Formation, see below).

During the 1973 Charleston Museum survey of the quarry (Sanders, 1974), this unit, then included in deposits known at that time as the Cooper Marl (Cooke and MacNeil, 1952; Sanders, 1974:fig. 2), formed the lower portion of a 5.6 m section in the quarry wall (Fig. 5). The basal 36 cm of that exposure (Zone 1) consisted of olive gray (5Y3/2) clayey phosphatic sediments containing profuse numbers of the small pectenid *Chlamys cocoana* Dall, 1898, reported from this stratum by Cooke and MacNeil (1952) and confirmed as that taxon by D. T. Dockery (pers. comm. to AES, 2009). Above the basal phosphate zone the Harleyville grades into a greenish gray (5GY6/1) calcarenite and *C. cocoana* becomes less numerous; its HO is at a facies change 1.33 m above the contact with the Tupelo Bay Formation (Sanders, 1974:6). *Chlamys cocoana* is known primarily from the Gulf Coast, ranging throughout the Upper Eocene Moodys Branch Formation (NP17) and Yazoo Clay (NP18, NP19/20) into the lower

Oligocene Red Bluff Formation (NP21) (Dockery and Lozouet, 2003). Also known from a number of localities in Georgia, its occurrence in the Harleyville Formation at the Giant quarry appears to be the only record of this mollusc from SC.

From the location of the section measured during the 1973 survey, the blanket of Cooper Group sediments thinned easterly to a thickness of less than 0.6 m, terminating well short of the active portion of the quarry (in 2016). However, a visit to the eastern, actively worked area of the quarry by DJC in August, 2015, resulted in the determination that approximately 80 cm of Parkers Ferry Formation immediately overlies the Pregnall Member of the Tupelo Bay Formation, and is in turn overlain by approximately 2 m of Harleyville Formation at that location. Revision of the stratigraphic relationship between the Pregnall Member of the Tupelo Bay Formation, the Parkers Ferry Formation, and the Harleyville Formation was reported in Weems et al. (2016).

The top of the Harleyville Formation in the section of the quarry surveyed in 1973 was defined by a change in lithology at 2.2 m above the contact with the Pregnall Member (Fig. 5). Above that change, at 2.5 m, nannoplankton were not as informative because of the absence of certain marker species; but present was *Ericsonia formosa*, a form that last appears at the top of NP21. Previously published ages for the Harleyville based on calcareous nannoplankton placed the unit within zones NP18 through NP19/20 (Laws, 1988; Edwards et al., 1997, 2000), but more recent analysis of sediments from the type section at the Giant Cement quarry indicates that the Harleyville lies primarily within NP21, with indicators of NP19/20 in the lowermost part – particularly the calcareous nannofossil *Isthmolithus recurvus* and the coccolithophore *Discoaster barbadiensis* (J. Self-Trail, pers. comm. to AES, 2009; L. Edwards and J. Self-Trail, pers. comm. to LBA, 2012). Weems et al. (2016) placed the entirety of the Harleyville Formation within NP21, noting that the presence of *I. recurvus* in the basal-most portion of the formation did not necessarily indicate an NP19/20 age because that taxon extends up into NP21, and that its presence could be the result of reworking from nearby Parkers Ferry strata, which is of NP19/20 age.

A sample taken 3.4 m above the Pregnall contact in the eastern part of the quarry visited by DJC in 2015 is suggestive of zone NP23 (Fig. 5) based on the absence of *Reticulofenestra umbilicus* (LAD at NP22/23 boundary and present in samples stratigraphically lower), the presence of *Sphenolithus distentis* (FAD in middle NP23), and the absence of marker species for NP24 and NP25 (J. Self-Trail, pers. comm. to AES, July 2009). Based on the measured section of Ward et al. (1979:fig. 5), this level would be within the lower part of their "Ashley Member." As noted by both Ward et al. (1979) and Weems et al. (2016), however, the Ashley Formation includes calcareous nannofossils indicative of NP24, i.e., upper Rupelian. Perhaps these strata between the above noted lithologic change at 2.2 m above the contact with the Pregnall Member and the overlying Ashley Formation, of NP24 age, represent a previously unrecognized upper part of the Harleyville Formation.

Although NP21 straddles the Eocene/Oligocene boundary (uppermost Priabonian to lowest Rupelian; Fig. 3A), several age-diagnostic dinocysts (including *Batiacasphaera baculata*, *B. compta*, *Cordosphaeridium funiculatum*, *Homotryblium plectilum*, *Samlandia chlamydophora*, and *Trigonopyxidia fiscellata*) support a latest Eocene age rather than an early Oligocene age for these sediments (L. Edwards, pers. comm. to LBA, 2012; Weems et al., 2016). An accurate age for the lower portion of the Harleyville Formation, the *C. cocoana* zone, is particularly significant because it is from this zone, primarily from Harleyville-filled solution pits eroded into the top surface of the Pregnall Member, that all known vertebrate fossils from this unit are derived, including the isolated archaeocete elements recovered during the 1973 Charleston Museum survey (Sanders, 1974).

Sanders (1974:8) noted two teeth from the Giant Cement quarry that "had been found out of place prior to the [1973 ChM] survey" that he tentatively referred to *Zygorhiza*. He added, however, that the assignment was tentative because this taxon had not been previously recorded from

SC. More recent work by Uhen (2013) apparently confirmed the limited distribution of *Zygorhiza* to Priabonian aged deposits of the Gulf Coastal Plain only, i.e., this taxon has not yet been found in similar aged deposits of the Atlantic Coastal Plain. Of particular interest among the archaeocete material, however, is another small, elongate, lumbar vertebra (ChM PV7636) similar to the SCSM specimen noted above from the Pregnall Member. Although proportionate in form, Sanders (1974) hesitated to assign the specimen to *Basilosaurus* because its overall dimensions are smaller than those given for the lumbar vertebrae of *B. cetoides* by Kellogg (1936:53). However, its length/width ratio (0.46) is roughly comparable to those of that taxon (0.49-0.55) as determined from Kellogg's (1936:53) measurements of USNM 4675 and 12261. These two specimens from SC (in addition to ChM PV7637, a partial vertebra with similar proportions to ChM PV7636) appears to document the presence of an undescribed diminutive species of *Basilosaurus* in the late Eocene seas of the western North Atlantic.

Another marine mammal element thought to have been reworked from the Pregnall Member and deposited into one of the Harleyville-filled pits is the skull cap of the small sirenian noted above in the section on the Pregnall Member (ChM PV7639 and further discussed in "Systematic Paleontology" section). In addition to the marine mammal material noted from these pits are two exceptionally important fossils representing terrestrial taxa.

During the preparation of this report it came to our attention that an avocational fossil collector, Mr. J. Metts, had in his possession an exceptionally well-preserved upper molar of a large brontothere from the Giant quarry, as well as a palate with teeth of the primarily Chadronian to Orellan rhinoceros *Subhyracodon* collected in the nearby Argos Cement Plant quarry. Although both specimens are currently maintained in Metts' private collection, the first author was allowed to examine, measure, and photograph them. However, because they are privately held, we are unable to give them the detailed treatment in the "Systematic Paleontology" section of this report that they deserve. Efforts to obtain casts of these specimens were unsuccessful, and at this time it is not known if these specimens will ever be catalogued into a public repository.[3]

Both were collected from the Harleyville Formation-filled solution pits at the top of the Pregnall Member, and this was confirmed by a sample of matrix from the *Subhyracodon* site provided to the first author by the collector. The sample included abundant specimens of *Chlamys cocoana*, and a portion was sent to L. Edwards and J. Self-Trail of the USGS for microfossil analysis in early 2012. Results indicated that the matrix was from calcareous nannoplankton zone NP21 (L. Edwards and J. Self-Trail, pers. comm. to LBA, 2012). The presence of the large brontothere in these sediments further supports the data from the above noted microfossils that the lower Harleyville Formation is in the uppermost Eocene part of NP21 rather than in the lowest Oligocene, because brontotheres are not known to persist into the Oligocene of North America (Prothero and Emry, 2004; Lourens et al., 2004:fig. 20.4; M. Mihlbachler, pers. comm. to LBA, 2012). The importance of the rhino and brontothere specimens cannot be overstated, as they represent the only remains of latest Eocene terrestrial mammals (late Chadronian NALMA) yet recovered from the USA Atlantic Coastal Plain (with the exception of a brontothere tooth fragment from the upper Eocene Clinchfield Formation of Georgia [Westgate, 2001]).

As noted above, NP21 straddles the Eocene/Oligocene boundary. The dramatically different lithology of the Parkers Ferry and Harleyville formations compared with the outer shelf limestones on which they rest (Tupelo Bay Formation) reflects the separation of deep water deposition from shallower water deposition purportedly due to activation of the Gulf Trough during this time (Popenoe et al., 1987).

OLIGOCENE SERIES (33.9 – 23.03 Ma)

Ashley Formation. Described as a "homogeneous section of calcareous, microfossiliferous, silty and sandy clays" (Edwards et al., 1997:17),

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[3] While this paper was in review, we learned that Mr. Metts passed away. We are unaware of any plans regarding the future of his extensive collection.

the Ashley Formation underlies most of Charleston, Berkeley, and Dorchester counties, and a portion of southeastern Colleton County; it thickens seaward and is approximately 30 m thick beneath Charleston (Bybell et al., 1998). Referred to as the "Ashley marl" by Tuomey (1848), Sloan (1908) separated the unit in some areas into "Ashley" and "Cooper" marls, based on typical outcrops along these two rivers, whereas in other regions he included the two "phases" together as a single "Ashley-Cooper marl." As Weems et al. (2016) reviewed in detail, the stratigraphic and temporal placement of the Ashley and Cooper "phases" has been long debated, and the reader is referred to that reference for the history of the debate and its clarification (see additional discussion in Whitmore and Sanders, 1976).

The best natural outcrop of the Ashley Formation is exposed along the eastern bank of the Edisto River at Givhans Ferry State Park (Fig. 1B), and it is this section that Ward et al. (1979) designated as the lectostratotype. The unit also crops out in a number of bluffs along the Ashley and Cooper rivers, and is broadly and cleanly exposed in submerged outcrops in the upper reaches of the Cooper and Edisto rivers (LBA, pers. observ.).

Long thought to be of Eocene age (e.g., Ruffin, 1843; Tuomey, 1848), the Ashley Formation is now known to have been deposited during the late Rupelian (late early Oligocene), with calcareous nannofossils indicative of zone NP24 (Hazel et al., 1977; Edwards et al., 1997, 2000). Supporting the late Rupelian age are ^{87}Sr/^{86}Sr dates derived from mollusc shells that average 29.1 Ma (Weems et al., 2016). Beneath Charleston, the Ashley Formation apparently rests unconformably, for the most part, on the upper Eocene Parkers Ferry Formation (NP19/20), as there are no units yielding nannofossils indicative of the intervening upper most Eocene and lower Oligocene zones NP21, 22, or 23 (Weems et al., 2016). The absence of strata harboring microfossils characteristic of those zones is apparently due to strong currents flowing through the Gulf Trough that swept across this region and cut down into upper Eocene units during the Rupelian (Popenoe et al., 1987).

Interesting, however, is the report by Brainard et al. (2009) of a 30-to-40 foot-thick "sand lens" in the Ashley Formation beneath Daniel Island and the Cooper River. This unit was discovered during exploratory drilling for construction of the Daniel Island Extension Tunnel, which extends from the Charleston peninsula beneath the river to the Daniel Island wastewater treatment plant. That stratum was originally encountered beneath Daniel Island at 88 ft below ground surface and subsequently found to slope southwesterly to a depth of 150 ft beneath the edge of the Charleston peninsula (Brainard et al., 2009:fig. 8). However, those depths are greater than those recorded by Weems and Lewis (2002) for the base of the Ashley Formation in that region. Weems et al. (2016:6) interpreted this "sand lens" as "a previously unrecognized subcrop area" perhaps equivalent to their Drayton Limestone Member of the Harleyville Formation, a unit they noted was distinctive in its abundance of medium-grained bryozoan fragments.

Recent work by Weems et al. (2016) has resulted in the recognition that the Ashley Formation can be divided into three members, each separated by quartz and phosphate-rich lag deposits which also produce prominent gamma-ray log signatures. The lower member they designated as the Gettysville Member for the part of CCC1 that ranges from -158 to -63 feet. They noted that the unit consists primarily of foraminiferal sand with a silt-clay fraction considerably less than the overlying members. With foraminifera indicative of zone P20 of Blow (1969) and calcareous nannoplankton of NP24 age, the Gettysville Member is approximately 29.5 myr old.

Overlying the Gettysville Member, in the interval of CCC1 between -63 and -51 feet is the Runnymede Marl Member. The 29.1 Ma strontium date noted above was derived from an oyster shell collected near the base of this member, thus supporting the 29.5 Ma age of the underlying Gettysville Member (Weems et al., 2016). The Runnymede Marl Member, in turn, is overlain by the Givhans Ferry Member, which in CCC1 spans the -51 to -16 foot interval (Weems et al., 2016). The section noted above at Givhans Ferry State Park is designated the stratotype for the Givhans Ferry Member. Foraminifera from this member are indicative of zone P21, and three $^{87}Sr/^{86}Sr$ dates derived from mollusc shells support this, as they range from 28.75 to 28.43 Ma (Weems et al., 2016).

Although the Runnymede Marl and Givhans Ferry members are separated by a distinctive and widely recognizable lag deposit that marks an unconformity between the two units, their appearances are similar and their lithologies are only slightly different; the Givhans Ferry is more quartzose and phosphatic than the Runnymede Marl, which consists primarily of foraminifera. The lag consists of "calcite-quartz-phosphate sand, with a variable content of worn shells, phosphate pebbles, occasional quartz pebbles, and fossilized vertebrate material including sharks teeth, bones and teeth of cetaceans, and marine turtle shell fragments that vary in quality from pristine to worn" (see details in Weems et al., 2016). In the vicinity of Givhans Ferry State Park the lag deposit occurs along the underwater portion of the exposures; on the Ashley River it can be seen above the low-water level during low tide, but is typically draped by an apron of tidal "pluff mud" characteristic of the salt marsh environment along that portion of the river where the unit crops out. Given (1) the nature of this lag deposit as described above, (2) the more quartzose/phosphatic lithology of the Givhans Ferry Member, and (3) the dramatically more nearshore/lagoonal/estuarine lithological nature of the overlying Chandler Bridge Formation (see below), it is our opinion that the lag deposit separating the upper two members of the Ashley Formation represents the point of maximum transgression during the late Rupelian and the beginning of the regression that occurred across the Rupelian-Chattian boundary (Pälike et al., 2006).

Over the last few decades the Ashley Formation has yielded numerous skulls of archaic odontocetes (many still undescribed), as well as the most primitive of mysticetes. But discoveries of vertebrate remains from this unit have been a common occurrence since the first settlement of Charleston in 1670. Specimens were sent back to naturalists in London, such as Sir Hans Sloane and James Petiver, with the earliest mention of vertebrate fossils from SC in Petiver's (1705) brief report of two fossil sharks' teeth and "some Fossil bones, as vertebrae, &c" received from "our ingenious friend Mr Job Lord." Joseph ("Job") Lord was the pastor of the church at the small settlement of Dorchester on the Ashley River northwest of Charleston, now protected as Fort Dorchester State Park. He probably collected the fossils along the banks of the Ashley River and nearby Eagle Creek, where fossils can still be found over 300 years later.

The Ashley Formation also has been determined to be the unit of origin for the holotype of *Agorophius pygmaeus* (Müller, 1849) of the family Agorophiidae Abel, 1914, first thought to be an archaeocete and reported by Tuomey (1847) as a "cranium of the zeuglodon." Collected by Charleston naturalist F. S. Holmes (with additional elements of the holotype subsequently collected by L. R. Gibbes) from what Tuomey (1847:152) referred to as "the Eocene beds of Ashley River" sometime during the mid-1840s, the specimen has not been seen since 1869 and is now considered as irretrievably lost (Fordyce, 1981). Although Whitmore and Sanders (1976) were unable to locate the exact site of collection, it is known to be near "Greer's Landing" near Middleton Place on the Ashley River, northwest of Charleston, according to Tuomey (1848:166), from what is now known to be the Oligocene, not Eocene, aged Ashley Formation. Fortunately, however, additional skulls of *Agorophius* have since been recovered through more recent exploratory efforts, including SC2015.51.1 collected by J. Osborne from the west bank of the Ashley River in the area of the type locality and ChM PV4256 from the bottom of the Edisto River (see Godfrey et al., 2016, and Boessenecker and Geisler, 2018).

These two specimens, together with the beautiful lithograph in True (1907) of the lost cranium, provide important new information on the changes in skull morphology during ontogeny of this early odontocete. Whitmore and Sanders (1976) concluded from study of a series of *Eosqualodon*-like specimens from the Chandler Bridge Formation (see below) that the parietals are exposed dorsally in young individuals, but in later stages of ontogeny they become progressively covered by forward growth of the anterior margin of the supraoccipital toward the vertex of the skull. This progression appears to exist in *Agorophius pygmaeus*, as well. In ChM PV4256, for example, the anterior terminus of the supraoccipital is nearly in contact with the fronto-parietal suture (Fig. 6). In SC2015.51.1, on the other hand, there are approximately 12 mm separating these two morphological landmarks. The now lost holotype shows an even greater degree of separation, about 27 mm ("1 in. 1 l[ine]"), based on measurements in Leidy (1869:423). It should be noted, however, that some measurements of the holotype are difficult to assess because the original figure in Tuomey (1847) is not well scaled, nor is the lithograph in True (1907). Godfrey et al. (2016:fig. 1) also noted the difficulty in accurately scaling the holotype. It is clearly evident, however, that the distance between the anterior terminus of the supraoccipital and the fronto-parietal suture does vary, and that these specimens likely represent three different ontogenetic stages as *A. pygmaeus* transitioned from sub-adult to adult (Fig. 6). Supporting our hypothesis is the interesting observation by Tuomey (1847:153) that the holotype "was evidently a young individual," exactly what would be expected given that it shows the greatest separation.

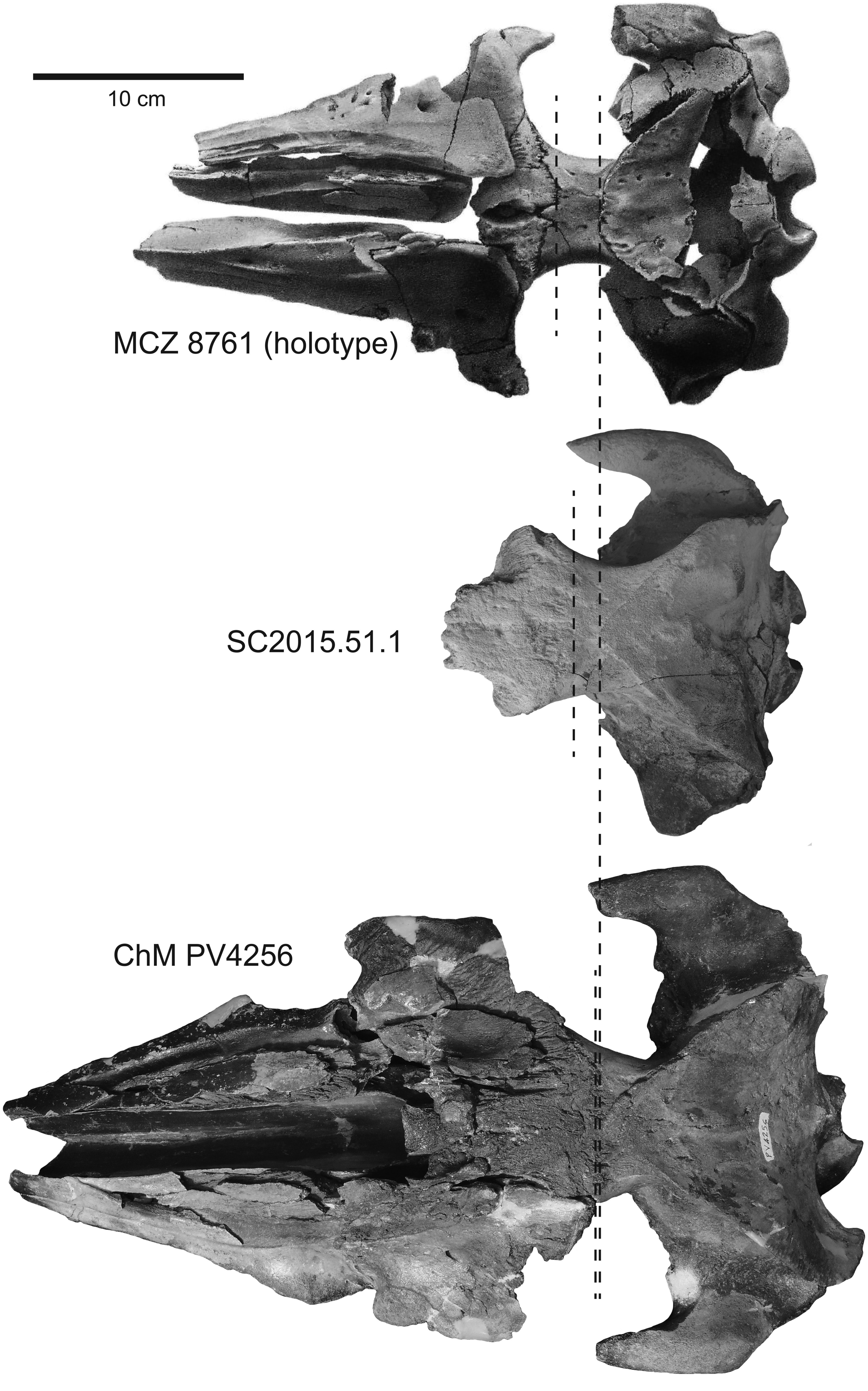
Germane to this discussion is a recently published paper by Boessenecker and Geisler (2018) who described new remains of *Agorophius* from the Chandler Bridge Formation. In this study of material from both the Ashley and Chandler Bridge formations, they concluded that material from the latter unit (including ChM PV4256 noted above) might possibly represent a distinct species from the specimens known from the former, with the shorter exposure of the parietals on the vertex of the cranium serving as one of their diagnostic characters. Rather than naming a new species, they referred the Chandler Bridge material to *Agorophius* sp., "pending further study."

In 1851, Robert Gibbes, who in 1845 described *Dorudon serratus*, described and figured six teeth from "the Eocene of Ashley River, South Carolina" as a new "mosasauroid" to which he applied the name *Conosaurus bowmani* (Gibbes, 1851:pl. 3, figs. 1–9). The "Eocene of Ashley River" is, as noted above, the Ashley Formation, now known to be Oligocene in age, but in either case, it is much too young to have yielded mosasaur teeth. Joseph Leidy (1848) set the matter to rights in concluding that Gibbes' specimens were fish teeth, not mosasaur, and establishing the name *Conosaurops* to replace *Conosaurus*.

Even earlier, Agassiz (1848) applied the name *Saurocetus gibbesii* to a cetacean tooth (MCZ 8760) from the Charleston area that is presently of undetermined familial affinity. Subsequently, Leidy (1853) described a new odontocete, *Colophonodon holmesii*, from a partial tooth and fragments of five others, but that taxon is regarded as a nomen dubium by Fordyce and De Muizon (2001).

The Ashley Formation has also yielded the holotype skull (USNM 11049) of *Xenorophus sloanii* Kellogg, 1923, upon which the family Xenorophidae was established by Uhen (2008). Xenorophids are archaic forms that have a land mammal-like braincase with a prominent sagittal crest (see Whitmore and Sanders, 1976:fig. 1a). Additional species of xenorophids from the Ashley Formation include *Albertocetus meffordorum* Uhen, 2008, (see Boessenecker et al., 2017a) and the apparently suction-feeding *Inermorostrum xenops* Boessenecker et al., 2017b. The early baleen whale *Micromysticetus rothauseni* Sanders and Barnes, 2002a, (ChM PV4844) was also recovered from the Ashley Formation, as were at least three species of toothed mysticetes with archaeocete-like teeth in an archaeocete dental formula, such as the recently described *Coronodon havensteini* Geisler et al., 2017 (with additional material noted by Geisler et al., 2018). Of particular importance is the holotype partial skull of *Ashleycetus planicapitis* Sanders and Geisler, 2015, one the most primitive odontocetes yet reported. Two other skulls (ChM PV4824 and PV7679) represent undescribed taxa that somewhat resemble the holotype skull of the odontocete *Eosqualodon langewieschei* Rothausen, 1968, from the Chattian age Doberg Formation of the North Sea Basin, Germany, and *Eosqualodon*-like skulls from the unit overlying the Ashley Formation, the Chandler Bridge Formation (discussed below).

Another skull (SC2015.33.1) recovered from the Givhans Ferry Member was recently described


10 cm
MCZ 8761 (holotype)
SC2015.51.1
ChM PV4256
PV4256

by Albright et al. (2018). *Ediscetus osbornei* superficially resembles *Waipatia maerewhenua* Fordyce, 1994, from the Oligocene of New Zealand. However, although geologically older than the New Zealand taxon, the SC species differs in having a significantly more advanced degree of telescoping, whereby the posterior frontomaxillary suture (posterior temporal crest) has progressed so far posteriorly that it has been pushed up vertically in its broad contact with the supraoccipital. This has resulted in a complete override of the parietals, a condition much advanced relative to contemporary species found in the same strata such as *Xenorophus*, *Agorophius*, and *Ashleycetus*.

In addition to a diverse cetacean fauna, the Ashley Formation has also yielded an abundance of other vertebrate fossils. Sirenians are represented by *Priscosiren atlantica* Vélez-Juarbe and Domning, 2014a, *Stegosiren macei* Domning and Beatty, 2019, and *Crenatosiren olseni* (Reinhart 1976) (see Domning, 1997;Vélez-Juarbe and Domning, 2014a, b). A single partial tooth (ChM PV9480) from the Ashley Formation may be referable to *Metaxytherium albifontanum* Vélez-Juarbe and Domning, 2014b, but all other known material of this taxon from SC is from the Chandler Bridge Formation (see discussion below on the Chandler Bridge Formation and in the "Systematic Paleontology" section). As noted by Vélez-Juarbe and Domning (2014a:951), "the early Oligocene is an important time period in sirenian evolution, because it is a transitional period between the extinction of prorastomids and protosirenids by the end of the Eocene and the appearance of more derived sirenian lineages in the late Oligocene (Vélez-Juarbe, 2014)."

Koretsky and Sanders (2002:17) reported the recovery of the proximal portion of a femur of a pinniped (ChM PV5713) from the Ashley Formation near Summerville, in Dorchester County, noting that the specimen was "similar in size to those of the modern Harp seal, *Pagophilus groenlandicus*, of the family Phocidae." Although this would appear to be the oldest known record of a true seal in the Atlantic Ocean basin, and one of the oldest records of a seal anywhere, the biogeographic analysis of pinnipeds by Deméré et al. (2003) calls into question this record and suggests that the provenance of the specimen may be suspect.

Four additional specimens, first noted in the 19th century, are also of interest (Fig. 7). In 1856 Joseph Leidy described *Phoca debilis* on the basis of three teeth (now catalogued as ANSP 10322, 10324 and 10325) "from the sands of the Ashley River, South Carolina" (Leidy, 1869:415). Subsequently, Leidy (1869) removed ANSP 10322 from the *P. debilis* type material and combined it with another tooth (now ANSP 10323) also from "the Ashley River deposits, South Carolina" as representative of another new species, *Phoca modesta* (Leidy, 1869:415), evidently because of the greater similarity of the crown morphology of these two teeth to each other rather than to either ANSP 10324 or 10325. Cope (1867:144) assigned *P. debilis* to the odontocete genus *Squalodon*, but Leidy's *debilis* teeth are considerably smaller than those of presently recognized species of *Squalodon* (e.g., *Squalodon calvertensis* Kellogg, 1923). Noting Cope's assignment, Leidy (1869:415) observed that such "may be the case, or perhaps they may belong to a Dolphin." Kellogg (1923:13) question-

Figure 6. Comparison of skulls of *Agorophius pygmaeus* showing inferred ontogenetic change in distance between anteriormost point of supraoccipital and fronto-parietal suture (juvenile to adult from top to bottom). Regarding scale: because the holotype is lost, any scale for the Agassiz lithograph published in True (1907) must necessarily rely on the measurements of that specimen as published in Tuomey (1847), Leidy (1869), and True (1907). Two measurements in particular can be used to provide a reasonable approximation of the size of the type. One of these is Tuomey's (1847:153) "greatest breadth [of skull] 7 ½ in." also reiterated in True (1907:5). But a less ambiguous measurement, and the one used here to scale the holotype, and, in turn, ChM PV4256, is Leidy's (1869:423) "Breadth of skull at postorbitals, 7 in."

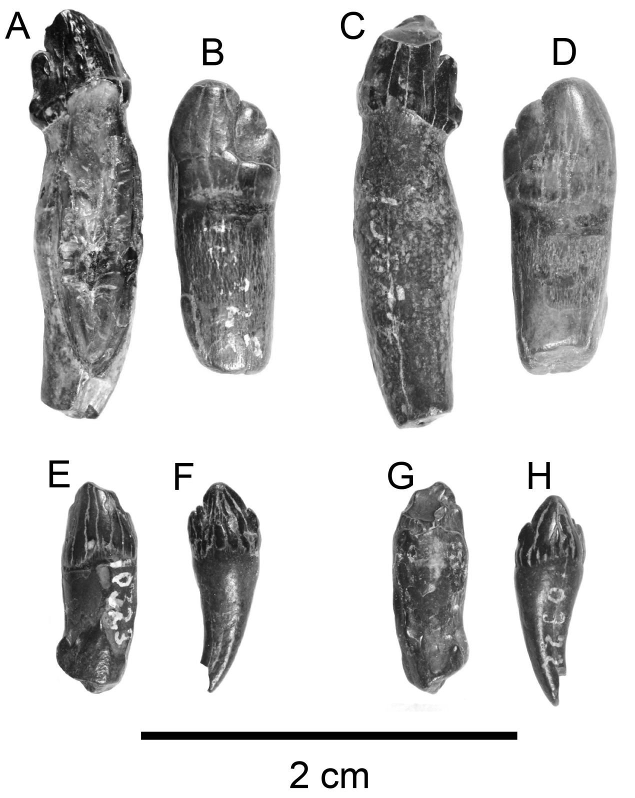


Figure 7. *Phoca debilis* Leidy, 1856: **A**, ANSP 10324 and **B**, ANSP 10325, in lingual view; **C** and **D**, same teeth, respectively, in labial view. *Phoca modesta* Leidy, 1869: **E**, ANSP 10323 and **F**, ANSP 10322, in lingual view; **G** and **H**, same teeth, respectively, in labial view. (ANSP 10324 measures 21.6 mm; ANSP 10322 measures 11.1 mm).

ably referred *P. debilis* to "*Delphinodon*?", a Miocene odontocete genus, cautiously noting that the teeth "do not sufficiently agree with those of *Delphinodon* to be definitely referred to that genus," but that "it seems probable … that they represent some Miocene delphinid." He then gave the stratigraphic origin of the specimens as "Edisto marl or Upper Miocene," though he did not cite the source of that information. Both his systematic and stratigraphic referrals are problematic because upper Miocene deposits are not known from the banks of the Ashley River (e.g., Weems et al., 2016). Doubtful of its validity as a species of phocid, Kellogg (1923:26) also referred Leidy's *Phoca modesta* to *Phoca*? *modesta* (ANSP 10322, 10323). Regarding ANSP 10323, he noted that "It seems more likely, from what is now known concerning the various described species of *Squalodon* and other Miocene cetaceans, that this tooth belongs to some pinniped." In summary, the stratigraphic origin of all four of these teeth is uncertain, there is no evidence that any of them came from the Ashley Formation, they may be representative of more than two different taxa, and they may not be definitively representative of pinnipeds!

The first known representatives of a western North Atlantic Oligocene avifauna are now known from the Ashley Formation, as well. These specimens, in collections at both The Charleston Museum and the SCSM, were first studied by R. Chandler who concluded that several new species are represented. Preliminary results of a more recent study by D. P. Ksepka (pers. comm. to AES, September, 2012) indicate the presence of an albatross (*Plotornis* sp.), an indeterminate genus of petrel (Procellariidae), and two species possibly representing new genera of gannets and boobies (Sulidae).

Crocodilian remains from the Ashley Formation consist of only three specimens, all of which are assigned to *Gavialosuchus carolinensis* Erickson and Sawyer, 1996, the holotype (ChM PV4279) and paratype (SC90.93.1) of which came from the overlying Chandler Bridge Formation. Two are well-preserved associated dentaries excavated from the bottom of Dorchester Creek in Dorchester County (ChM PV4282), and the other specimen is a cranial fragment from Charleston County (ChM PV4280). Sea turtles are represented by (1) *Carolinochelys wilsoni* Hay, 1923, the holotype skull of which is MCZ 1005-A; (2) *Ashleychelys palmeri* Weems and Sanders, 2014, the holotype of which includes a skull, shell, and limb elements (ChM PV7002), another skull (SC90.19), and additional elements of a juvenile (ChM PV6869 and PV7202); (3) *Procolpochelys charlestonensis* Weems and Sanders, 2014, represented by a humerus (MCZ 1005-B) originally referred to *Carolinochelys wilsoni* by Hay (1923), and (4) an undescribed new taxon of leatherback sea turtle (family Dermochelyidae) collected by JLK, DJC, V. McCollum, and several volunteers (SC2007.36.1).

Fierstine and Weems (2009) studied the billfish remains from the Ashley Formation and these include specimens of *Aglyptorhynchus robustus*, *Aglyptorhynchus* sp., the holotype material of *A. palmeri* and *A. alsandersi*, and additional specimens of uncertain specific allocation referred to *Xiphiorhynchus*. They placed both of these genera into a new subfamily, Aglyptorhychinae.

Although this work focuses on the vertebrate biostratigraphy of the state, the biostratigraphic utility of molluscs prompts a discussion of them, as well. Appendix 4, therefore, provides a summary of the molluscs currently known from the Ashley Formation based primarily on recent, extensive, studies conducted by Dr. Matthew Campbell on specimens from the unit in the collections at The Charleston Museum and the SCSM. In his updated assessment he noted that calcitic taxa were preserved as the original shell, but aragonitic taxa are preserved as internal or external molds resulting in identification only to the genus level.

Chandler Bridge Formation. The Chandler Bridge Formation was named by Sanders et al. (1982) for a thin sequence of noncalcareous, arenaceous beds that unconformably overlies the Ashley Formation with a patchy distribution in Charleston, Berkeley, and Dorchester counties. The unit is typically less than 2 m thick, with a maximum known thickness of about 5 m, and it was originally divided into three conformable beds numbered 1–3 in stratigraphically ascending order (Sanders et al., 1982; Weems and Sanders, 1986; Fig. 8A); a fourth bed, 1A, has been additionally recognized since original description of the unit (Fig. 8B; further discussion below). The stratotype section of the formation was described from the east side of a 21 m by 21 m (70 ft x 70 ft) pit excavated in 1970 as part of a study to recover Oligocene marine vertebrates from this highly fossiliferous unit (Sanders, 1980; Sanders et al., 1982; Fig. 9A). The pit has since been filled, but additional exposures have been described (e.g., Katuna et al., 1997; Fig. 9B).

The Charleston Museum excavation was prompted by the recovery of a nearly complete skull of an unknown, albeit obviously Oligocene-aged, odontocete by an avocational fossil collector in 1969. The specimen was recovered from the bank of a ditch on the north side of Ladson Road (County Road S-18-230) near Chandler Bridge Creek in Dorchester County about 23 km northwest of Charleston (Fig. 10) and donated to The Charleston Museum by Mr. R. Lambert of Summerville. It was the scarcity of Oligocene-aged marine vertebrate-bearing strata throughout the world that resulted in the second author's determination to excavate these beds, with funding granted under the auspices of The Charleston Museum by the Charleston Scientific and Cultural Education Fund in 1970 and by the National Geographic Society in 1971 and 1972.

Like the unconformably underlying Ashley Formation, the Chandler Bridge Formation was also found to harbor a highly diverse, well-preserved cetacean fauna. The excavation was highly successful, yielding 17 partial skeletons representing six undescribed odontocete taxa recovered over three summer field seasons by an excellent crew of students from the College of Charleston. An account of the excavation methods, results, and significance of that undertaking was provided by Sanders (1980) and summarized with additional results in Sanders et al. (1982). It should be noted that the "archaeocetes" mentioned in Sanders (1980:620) and in Sanders et al. (1982:118) as having come from the Chandler Bridge Formation have since been found to be toothed mysticetes, which have an archaeocete-like dentition.

Weems and Sanders (1986) considered the Chandler Bridge Formation as representing a shallow marine transgressive sequence, with basal Bed 1 considered indicative of an estuarine/lagoonal environment and the uppermost Bed 3 representative of a beach face/shallow water marine environment. The abundance of well-preserved cetacean skeletons in Bed 3 at the excavation pit, due possibly to stranding events, supported their beach face environmental characterization. Additional support was provided by the identification of marine mollusc taxa from numerous internal casts that point toward a similar environment. These include the gastropods *Xenophora* sp. and *Apiocypraea* sp., plus the bivalves *Glycymeris* sp., *Chlamys* sp., *Astarte* sp., *Nemocardium* sp., *Gastrochaena* sp.,

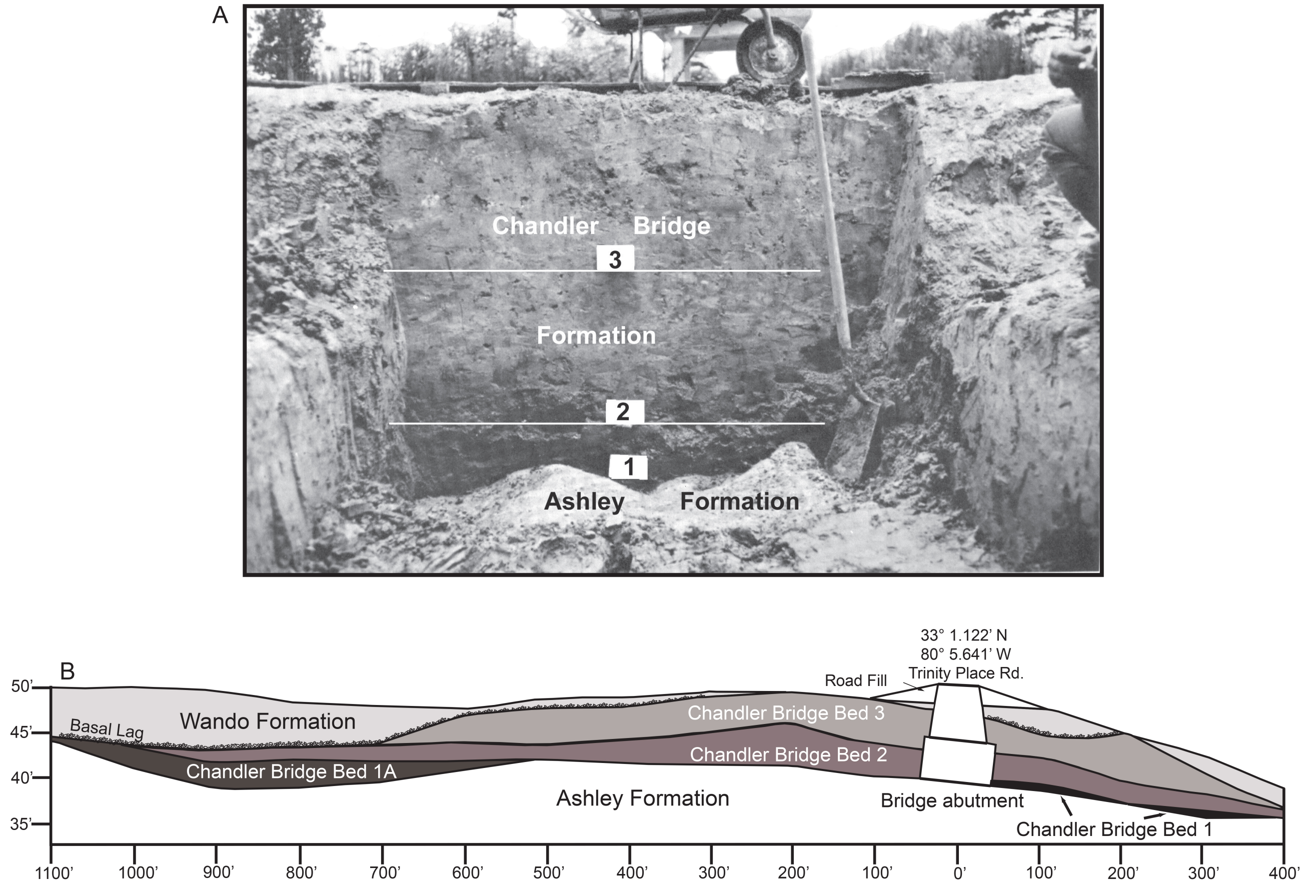


Figure 8. A, Type section of the Chandler Bridge Formation resting disconformably on the Ashley Formation. Bottom of each "Zone" card marks the base of that bed. Described and measured on the east wall of a paleontological excavation pit (Fig. 9A) opened by The Charleston Museum in 1970 adjacent to Chandler Bridge Creek, 0.7 km NW of the confluence with Eagle Creek, in the NE quarter of the Stallsville 7.5' USGS quadrangle, Dorchester County (see Fig. 10); reproduced from Sanders et al. (1982:fig. 26). **B**, Diagrammatic cross-section of the Chandler Bridge Formation as exposed along a drainage ditch (Limehouse Branch) in College Park development (between Goose Creek and Summerville), Berkeley County (see LAT, LON in figure), showing stratigraphic relationship of Bed 1 and 1A.

Eburneopecten calvatus, and three species of Veneridae (M. Campbell, pers. comm. to AES, July 2015). Only Bed 3 was excavated over the entire 441 sq-m study area. Bed 2 also yielded an odontocete skull and postcranial material, but the presence of *Callianassa*-like burrows suggests a lagoonal depositional environment for this unit. Additional molluscs from the Chandler Bridge Formation include the bivalves *Barbatia* sp., *Pecten* sp., *Cyclocardia* sp., *Cardium* sp., and the gastropod *Epitonium chamberlaini* (M. Campbell, pers. comm. to LBA, August 2019)

Bed 1A, as noted above, was not included in the original description of the formation. This bed was first encountered in 1981 when a skull and partial skeleton of the primitive odontocete *Agorophius pygmaeus* (ChM PV4256 noted above) was collected by three scuba divers from sandy, grayish-green sediments at the bottom of the Edisto River, the recovery at which AES was present. At a different site in the Edisto River an undescribed species of another archaic odontocete, *Xenorophus* (ChM PV4823), was recovered from similar sediments. Both *Agorophius* and *Xenorophus* were known previously only from the Ashley Formation; but the sediments at the bottom of the Edisto

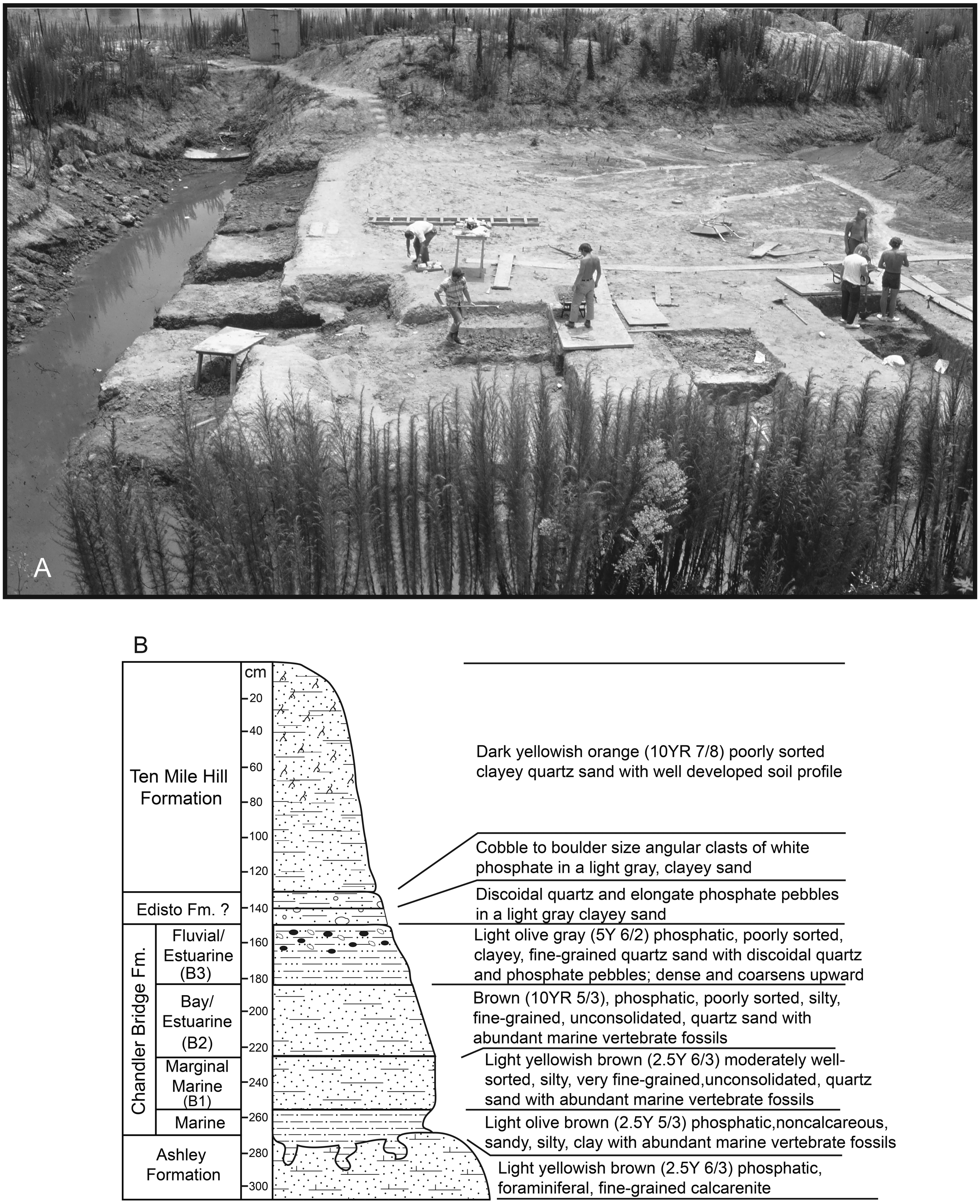


Figure 9. A, View of Charleston Museum's 1971 Chandler Bridge excavation pit. **B**, Redraft of section of the Chandler Bridge Formation measured and described by Katuna et al. (1997:fig. 7) reported at 32°59.57' N, 80°03.18' W (their site CH2). According to the Geologic Map of the Ladson Quadrangle (Weems and Lemon, 1988), the Chandler Bridge Formation crops out near this locality along the NNW-SSE trending border between Charleston and Berkeley counties. This site is approximately 4.36 km SE of the College Park cross-section locality of Figure 8B; B1, B2, and B3 refer to Beds 1, 2, and 3 of Weems and Sanders (1986).

River from which these two specimens were recovered were not of typical Ashley lithology, in turn suggesting the probability that they were from an undescribed facies of the Chandler Bridge Formation, as they did not resemble the latest Oligocene Edisto Formation either.

That suspicion was subsequently verified with the discovery of an outcrop of the greenish sediments in the banks of Limehouse Branch in the College Park subdivision of North Charleston, Berkeley County, approximately 32 km (20 miles) northeast of the Edisto River locality where it was first encountered. One of the College Park localities is about 240 m north of the Trinity Place Street bridge (33º 1.122'N, 80º 5.641'W), where the greenish stratum, Bed 1A, unconformably overlies the Ashley Formation and fills an Oligocene channel eroded into the Ashley (Fig. 8B). Bed 1A is overlain by Bed 2, which in turn is overlain by upper Pleistocene sediments of the Wando Formation; Bed 3 was apparently scoured away. Immediately south of the bridge are two short, thin deposits of Bed 1 in the same stratigraphic relationship as is Bed 1A, between the Ashley Formation and Bed 2 (Fig. 8B); but whether Beds 1 and 1A are directly correlative has not yet been demonstrated unequivocally. Another exposure of Bed 1A was found in the bank of a small tributary of Limehouse Branch near the Sangaree Middle School, about 1.35 km WNW of the Trinity Place bridge. Bed 1A at this locality yielded the holotype of the xenorophid *Echovenator sandersi* Churchill et al., 2016. Another xenorophid skull identified as *Albertocetus* sp. (ChM PV8680; M. Gibson, pers. comm. to LBA, June 2019) was collected at this locality, but from the underlying Ashley Formation. Billfish material is also known from Bed 1A, as are molluscs including the gastropods *Epitonium charlestonensis* and *E. cooperensis*, and the bivalves *Pycnodonte* sp. cf. *P. paroxis*, *Gastrochaena* sp., and apparently three representatives of the pectinid genus *Chlamys* (these molluscs were collected by R. Patterson in July 2012, and identified by M. Campbell).

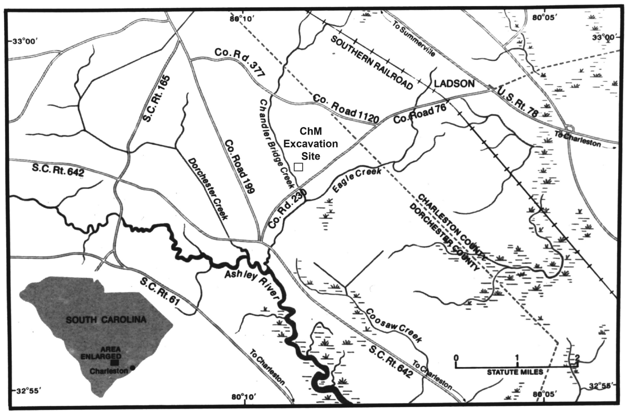


Figure 10. Map of area in Dorchester County showing location of Charleston Museum excavation site and spatial relationship of Chandler Bridge Creek and Eagle Creek with the Ashley River.

In contrast to the transgressive interpretation of the unit by Weems and Sanders (1986), Katuna et al. (1997) concluded that the overall trend within the unit was that of a shallowing upward, and coarsening-upward, regressive sequence with sediment provided from fluvial systems to the west. As summarized by Cicimurri and Knight (2009b), Katuna et al. (1997) recognized four sedimentary facies within the formation (Fig. 9B): (1) a basal marine facies rich in sharks teeth and well-preserved neritic nearshore marine dinoflagellates below Bed 1 of Weems and Sanders (1986) and possibly equivalent to Bed 1A (but yet to be confirmed); (2) a marginal marine facies equivalent to Bed 1 of Weems and Sanders (1986) within which acorns and hickory nuts were noted (Sanders et al., 1982); (3) a bay/estuarine facies indicative of a restricted brackish bay or lagoonal environment with access to open ocean from which cetacean and sea turtle remains were recovered, equivalent to Bed 2 of Weems and Sanders (1986); and (4) an upper fluvial/estuarine facies lacking dinoflagellates but containing freshwater pollen, discoidal quartz and phosphate clasts, angular quartz sand grains, and a concentration of fine grained sediments ("40% silt and clay by weight" Katuna et al., 1997:191), but also abundant cetacean remains, equivalent to Bed 3 of Weems and Sanders (1986). Further support for the regressive interpretation are the findings of Cicimurri and Knight (2009b:644) who concluded on the basis of the species of sharks, rays, ostracods, foraminifera, and corals collected from the lower marine facies that it was deposited in a "shallow inner to middle neritic environment where surface water temperatures were between 20° and 25° C."

Added to this is the generally regressive nature of the Chattian (GTS2012:fig. 28.1). Subsequent to opening of the Drake Passage and development of the Antarctic Circum-Polar Current around the time of the Eocene-Oligocene boundary (e.g., Miller et al., 1991, 2005; Vandenberghe et al., 2012), the Oligocene experienced several globally recognized cooling events related to eccentricity and obliquity cycles (Pälike et al., 2006). The Oi2* cooling event at 29.16 Ma prior to the Rupelian-Chattian boundary, as well as Oi2a shortly after at 27.91 Ma and Oi2b at 26.76 Ma (Fig. 3A), are associated with sea level falls estimated to be on the order of 50 to 65 meters (Wade and Pälike, 2004). However, starting at about 26 Ma there is a middle to late Chattian warming trend (Raffi et al., 2006:fig. 5). Although still punctuated by cooling events such as Oi2c in magnetochron C7 and ending with the Mi1 glaciation event at the Oligocene-Miocene boundary, it is within this warm interval that the Chandler Bridge Formation was likely deposited. We investigate this further below.

The sediments that would eventually be described as the Chandler Bridge Formation by Sanders et al. (1982) were originally inferred to be Oligocene in age by Whitmore and Sanders (1976) on the basis of a skull from the ChM excavation first thought to be referable to *Xenorophus sloanii*, the holotype of which is from the Ashley Formation, then regarded as upper Oligocene. This suggested that the Chandler Bridge Formation was not much younger than the Ashley Formation. But upon preparation of that skull, it proved to be an undescribed relative of *X. sloanii*. Subsequent estimates, as noted in Weems et al. (2006, 2016), resulted in an early Chattian age based on the similarity of some of the cetaceans from the Chandler Bridge to one from the lower Chattian sequence ("Chattian A") in the Doberg Formation of northwestern Germany. This was based primarily on comparisons by AES of three undescribed odontocete skulls from the Chandler Bridge excavation (ChM PV2753, 2754, 2755) with the holotype skull of *Eosqualodon langewieschei*. One of those skulls (PV2753), informally designated as "Genus X" by Whitmore and Sanders (1976), displays the same morphology of the skull roof as that of *Eosqualodon*, i.e., the parietals are still present in the skull roof but are concealed medially by a forward thrust of the supraoccipital and are exposed only as small triangular-shaped remnants at the outer margins of the intertemporal constriction of the skull roof. That morphology represents a grade of odontocete evolution that had not been recognized previously. Noted, however, was the much smaller size of the Chandler Bridge skulls, clearly representing different taxa than *Eosqualodon* from the Doberg Formation.

Supporting the original Chandler Bridge-Chattian A correlation was the work of De Man et al. (2010) who reported $^{87}Sr/^{86}Sr$ dates from benthic foraminifera (27.2 ± 0.7, 27.5 ± 0.7 Ma) and a K/Ar radioisotopic date from glauconite (27.0 ± 0.3 Ma) that placed the age of their lower Chattian (= Chattian A) of the Doberg Formation at ~27 Ma. Additionally, the Chattian A sequence lies within a correlate of calcareous nannoplankton zone NP24 (De Man et al., 2010; also see Anderson, 1961; Anderson et al., 1971; and Curry et al., 1978). Those determinations provided a time frame for the occurrence of the evolutionary grade represented by *Eosqualodon* and the morphologically similar specimens from South Carolina. Accordingly, the age of the Chandler Bridge was placed at approximately 28 Ma (Sanders et al., 1982; Weems and Lemon, 1984a, b; Sanders and Barnes, 2002b).

Recently, however, calcareous nannoplankton from the Chandler Bridge Formation definitively place the unit within zone NP25. Jean Self-Trail (pers. comm. to REW, 2014; also see Weems et al., 2016) noted the presence of *Sphenolithus ciperoensis* and *Triquetrorhabdulus carinatus* in samples from the formation. The former's LAD occurs at the top of NP25, and the latter's FAD occurs at the base of NP25. Further support for an NP25 assignment includes the absence in these samples of *S. distentus*, which last occurs at the top of NP24. These data securely bracket the age of the Chandler Bridge Formation to between 26.84 and

23.13 Ma (GTS2012), i.e., slightly younger than "Chattian A" of the Doberg Formation in Germany. De Man et al.'s (2010) middle and upper Chattian sequences (Chattian B and C) correlate with NP25. Additional data bearing on the age of the Chandler Bridge Formation include ^{87}Sr/^{86}Sr dates provided by W. B. Harris from oyster shells, reported herein as *Pycnodonte* sp. cf. *P. paroxis*, collected from the same locality as were the calcareous nannoplankton samples (Weems et al., 2016). Analysis of these specimens yielded an average date of 24.7 ± 0.2 Ma, which falls within the ages bracketing NP25 noted above.

Together these data provide an age for the Chandler Bridge Formation younger than that implied by the evolutionary grade of the cetacean fauna, and correlative with the Chattian B and C sequence at Doberg rather than Chattian A. This indicates that the unconformity between the Ashley and Chandler Bridge formations is apparently longer than originally considered. Based on all of the data above we revise the age of the Chandler Bridge Formation to about 25 Ma (Figs. 2A, 3A; also see following discussion on biostratigraphic utility of fossil cetaceans).

Katuna et al. (1997) placed the Chandler Bridge Formation in the uppermost Chattian adjoining the boundary of the Aquitanian Stage of the lower Miocene, and as a lateral equivalent of the Upper SC Coastal Plain Upland Unit. At the time of their publication the Chattian/Aquitanian boundary was placed at about 23.8 Ma (following the time scale of Berggren et al., 1995). The revised estimate of this boundary at 23.03 Ma (GTS2012) maintains a middle-to-late Chattian age for the formation, but positions it well below the Chattian/Aquitanian Stage boundary. Additionally, the Upland Unit has since been shown to be no older than late middle Miocene in age by Weems and Edwards (2007a), and therefore not a stratigraphic correlative of the Chandler Bridge Formation (also see Nystrom et al., 1991).

In addition to those cetaceans noted above, the Chandler Bridge Formation has also yielded two toothed mysticetes, ChM PV2778 and PV5720, both from Bed 3 at sites in Charleston and Berkeley counties, respectively. The smaller of the two, ChM PV2778, apparently belongs to the same taxon as a toothed mysticete from the Ashley Formation represented by ChM PV4745, thought to be a juvenile of *Coronodon havensteini* (see Sanders and Geisler, 2015:fig. 15; Geisler et al., 2017; and Hocking et al., 2017; NOTE: Hocking et al., 2017, incorrectly noted this specimen as ChM PV4645). Though not yet described, ChM PV5720 was found to share a sister taxon relationship with *Coronodon* by Geisler et al. (2017). In addition to having archaeocete-like teeth and dental formula, they all have other characters that define them as basal mysticetes comprising a previously unknown family, which appears to support the hypothesis that the suborder Mysticeti (the baleen whales) evolved from the basilosaurid subfamily Dorudontinae (Barnes and Sanders, 1996). The nearly 2 m-long skull suggests an overall length that may have approached 7.5 m, the largest of any cetacean yet recovered from the Chandler Bridge and/or Ashley formations.

The Chandler Bridge Formation is also the source of the holotypes of the most primitive known baleen-bearing whales, *Eomysticetus whitmorei* and *E. carolinensis* Sanders and Barnes, 2002b, for which those authors erected the new family Eomysticetidae and the superfamily Eomysticetoidea. The former was recovered from Bed 3 and the latter from Bed 2 at separate sites in Dorchester County.

The most common odontocetes from the formation are members of the family Xenorophidae. In a detailed examination of xenorophid skulls in the collections of the Charleston Museum, J. Geisler and AES found several that appear representative of taxa other than *Xenorophus*. For example, one yet-to-be described skull, ChM PV2775, represents a grade similar to that of *Albertocetus meffordorum* described from a partial skull (USNM 525001) from the upper Oligocene Belgrade Formation at Onslow Beach, NC (Uhen, 2008). In this taxon the anterior wall of the braincase is situated farther forward than in *Xenorophus* such that it extends beyond and below the level of the posterior margin of the supraoccipital processes of the frontals

(Sanders, 1996). Strontium isotope analysis by W. B. Harris from mollusc shells adhering to the NC specimen yielded a date of about 26.5 Ma (Uhen, 2008). Two additional xenorophids from the Chandler Bridge include the early echo-locating *Cotylocara macei* Geisler et al., 2014, from Bed 2, and the above noted *Echovenator sandersi* from Bed 1A.

Another grade of odontocete evolution is exemplified in *Agorophius pygmaeus*. The holotype of this taxon was collected from the Ashley Formation, as noted above in the discussion of that unit, but it disappeared from collector F. S. Holmes' private collection sometime during the late 19th century and has never been relocated (see Fordyce, 1981). In this evolutionary grade, the braincase is separated from the rostrum by a narrow, tabular intertemporal constriction formed by the parietals. Additional specimens from the Chandler Bridge Formation support what Boessenecker and Geisler (2018) considered to be a second species of the genus, described and referred to as *Agorophius* sp.

Also from the Chandler Bridge is ChM PV4753, a small skull about 350 mm in length that represents the first North American specimen of the family Patriocetidae Abel, 1913. Only two species have been described, *Patriocetus ehrlichi* (Van Beneden, 1865) from upper Oligocene sands on the south side of the Danube River at Linz, Austria, and *Patriocetus kazakhstanicus* Dubrovo and Sanders, 2000, from the Karaginskaya Formation of Kazakhstan. A third species, from the upper Oligocene Grafenberg Formation near Dusseldorf, Germany, is currently under description by K. Rothausen and AES. In these taxa the parietals are exposed as a narrow band across the skull roof and the zygomatic processes are "pistol-shaped" (Dubrovo and Sanders, 2000). A similar cranial morphology, excluding the "pistol-shaped" zygomatic process, is seen in skulls (e.g., ChM PV4755) that resemble *Waipatia*, originally described from the upper Oligocene of New Zealand (Fordyce, 1994), and which are currently being referred to as "waipatiids" until detailed study more accurately reveals their relationships.

More derived cetaceans also appear to have been relatively common in coastal Chandler Bridge seas, including "Genus X" of Whitmore and Sanders (1976:figs. 5-8), exemplified by ChM PV2753 and discussed above as apparent relatives of *Eosqualodon* from the Doberg Formation of Germany. As in *Patriocetus*, the parietals in these taxa form a narrow rectangle in the skull roof, but are covered medially by the apex of the supraoccipital and are visible dorsally only as small triangles at the outer margins of the intertemporal constriction.

The same morphology occurs in the much larger "Genus Y" (e.g., ChM PV2757) of Whitmore and Sanders (1976:figs. 4a, b), the largest odontocete yet known from either the Chandler Bridge or Ashley formations. Recovered during the 1970 ChM excavation, the axial skeleton consists of a complete skull and vertebral column, missing only the last two caudal vertebrae, with a total length of about 5.5 m. A mounted cast of ChM PV2757 is on display at The Charleston Museum, and additional specimens considered representative of "Genus Y" are housed in collections at the Mace Brown Museum of Natural History (see Boessenecker et al., 2018). Dooley (2003, 2005), who recognized only two (possibly four) valid North American species of the genus *Squalodon*, including *S. calvertensis* Kellogg, 1923, *S. whitmorei* Dooley, 2005, and possibly "*Squalodon*" *atlanticus* (Leidy, 1856) and "*Squalodon*" *tiedemani* Allen, 1887, concluded that "Genus Y" closely resembles "*Squalodon" tiedemani*, but that neither likely represent that genus (i.e., that "Genus Y" and "*Squalodon" tiedemani* are likely not squalodontids; Boessenecker et al. [2018] referred to "Genus Y" as an unnamed "*Agorophius*-like giant dolphin"). Recovered during phosphate dredging operations in the Wando River, the type specimen of "*S." tiedemani* has matrix adhering to it that resembles Ashley Formation, although the indurated nature of this material suggests to some (REW) that it may possibly represent Edisto Formation. Additional material of "Genus Y" from the Ashley Formation, however, further supports derivation of the type from the Ashley (Boessenecker et al., 2018).

Regarding *Squalodon*, a specimen much smaller than "Genus Y" but with teeth closely resembling those of "*Squalodon"atlanticus* was collected by the first author in 1973 from a spoil pile of Chandler Bridge sediment during dredging operations of the NW-SE trending canal 1.15 km NE of the intersection of SC Highway 17 and Bees Ferry Road (State Road S-10-57), Charleston County. Further study of this specimen (ChM GPV3) is required to determine more accurately its taxonomic affinity, particularly considering that the genus *Squalodon* is primarily an early to middle Miocene, rather than Oligocene, form.

Another grade of odontocete cranial evolution is represented in ChM PV4802, a well-preserved skull missing most of the rostrum, from Bed 2 in Berkeley County. Although in general appearance it resembles members of the long-snouted odontocete family Eurhinodelphinidae, such as "*Rhabdosteus latiradix*"[4] from the lower and middle Miocene of Virginia and Maryland (and possibly Georgia and SC; see section below on Marks Head Formation), Geisler et al. (2011) found no relationship of this specimen with this family. Their analysis placed ChM PV4802 near the base of crown group Odontoceti.

From the above discussion, it is obvious that the morphological and taxonomic diversity of whales from the Chandler Bridge Formation is truly astounding, with new specimens representing even more taxa being regularly added to collections as the cohort of avocational collectors in the region explore previously and newly exposed outcrops. Whereas The Charleston Museum and the Mace Brown Museum of Natural History house the bulk of the cetacean material from the Chandler Bridge Formation, the collections at the South Carolina State Museum include a number of specimens, as well.

In addition to the great diversity of cetaceans, however, are other marine mammals from this unit, one of which may be another very early record of a pinniped. In their description of the purportedly oldest known record of a true seal from the Ashley Formation, Koretsky and Sanders (2002) also included a proximal femur from the Chandler Bridge Formation (ChM PV5712). Although this specimen, like that noted above from the Ashley Formation, is at odds with the biogeographic findings of Deméré et al. (2003), thus calling into question the accuracy of the stated provenance, the collector of the specimen, Mr. V. McCollum, vividly recalls the precise circumstances of its recovery from the Chandler Bridge Formation (V. McCollum, pers. comm. to LBA, January 2017).

Sirenians are somewhat better represented. Several specimens in the ChM and SCSM collections represent *Crenatosiren olseni*, *Dioplotherium manigaulti* Cope, 1883, and the oldest known species of the genus *Metaxytherium*, *M. albifontanum* Vélez-Juarbe and Domning, 2014b (Domning, 1989a, b, 1997; Vélez-Juarbe et al., 2012; Vélez-Juarbe and Domning, 2014a, b; *M. albifontanum* may also occur in the Ashley Formation [see discussion in "Systematic Paleontology" section]).

Knowledge of marine bird life along the Atlantic Coastal Plain during Oligocene time comes not only from the Ashley Formation, as noted above, but also from specimens recovered from the Chandler Bridge Formation. These, like those from the Ashley, are currently under study by D. P. Ksepka and include four new species within the family Sulidae (boobies and gannets) and two new species within Procellariidae (petrels). The most impressive specimen in the entire avian assemblage from this unit is the holotype partial skeleton (ChM PV4768) of the enormous pseudodontorn *Pelagornis sandersi* Ksepka, 2014, a spectacular albatross-like bird with bony tooth-like projections and a wingspan of about 6.4 m. A life-size replica of the specimen, collected from Bed 2 near the Charleston Airport by AES and avocational fossil collector J. Malcolm in February, 1983, is on display at The Charleston Museum (Fig. 11) together with the partial remains of another smaller specimen (ChM PV4801) that may represent a new, but not-yet-described species.

Reptilian taxa from the Chandler Bridge con-

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[4] De Muizon (1988) considered *Rhabdosteus latiradix* Cope, 1868, as incertae sedis because of the incomplete nature of the type specimen. He also considered specimens from the Calvert Formation of Maryland referred to *Rhabdosteus* by Myrick (1979) congeneric with the holotype of *Schizodelphis sulcatus* Gervais, 1853, from France. Hence, the quotation marks, "*Rhabdosteus latiradix*" (see Lambert, 2004, for additional discussion).

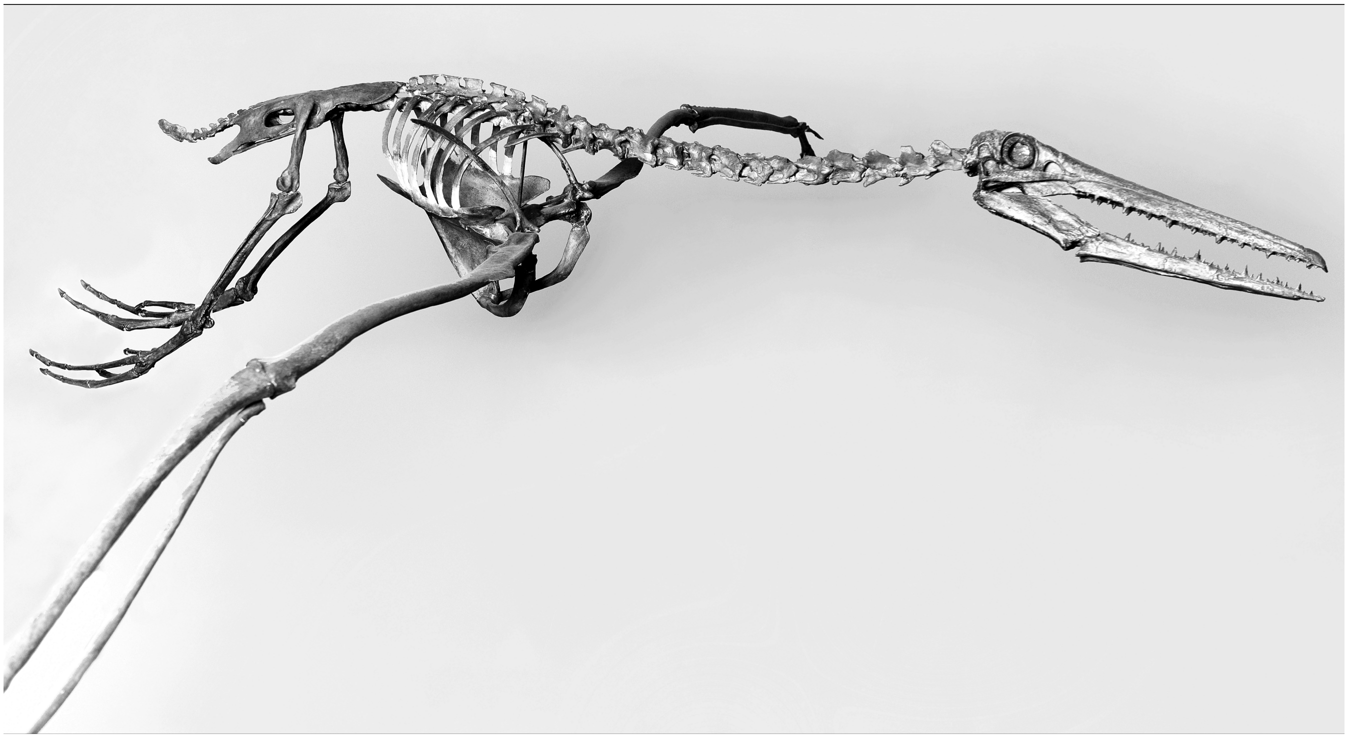


Figure 11. Life-size replica of the holotype partial skeleton of *Pelagornis sandersi* (ChM PV4768) on display at The Charleston Museum; a spectacular albatross-like bird with bony tooth-like projections and a wingspan of about 6.4 m. Collected from Chandler Bridge Formation near the Charleston Airport by AES and avocational fossil collector J. Malcolm in February, 1983.

sists of only one crocodilian, but several taxa of turtles. Specimens of *Gavialosuchus carolinensis* were noted above in the section on the Ashley Formation, but the holotype skull and skeleton, ChM PV4279, was recovered in 1978 from the Chandler Bridge Formation in what is now the Trailwood subdivision off Dorchester Road in Charleston County. A mounted cast of the specimen measuring about 5.4 m long is on display at The Charleston Museum, and an isolated femur (ChM PV4281) from the ChM excavation is from an even larger individual. The paratype skull and partial skeleton, SC90.93.1, was also recovered from exposures of the Chandler Bridge Formation at the bottom of a lake that was being excavated in the Crowfield Plantation subdivision of Berkeley County. Additional material of *G. carolinensis* is known from Dorchester County and includes two associated vertebrae (ChM PV4283) and three dissociated vertebrae (ChM PV4284, 4285, 4286).

Turtle remains include the anterior half of a carapace (ChM PV7180) of *Gopherus* sp., the only terrestrial taxon yet recovered from the Chandler Bridge Formation (Franz, 2014), plus the first North American occurrence of an Oligocene side-necked turtle (family Podocnemididae), the fluvial to estuarine *Bairdemys healeyorum* (Weems and Knight, 2013). The latter is represented by two specimens, both from Dorchester County: SC90.16, the holotype which includes skull, shell, and skeletal elements, and ChM PV4794, a referred specimen consisting of a partial carapace from Bed 2. Weems and Knight (2013) also mentioned a specimen of soft-shelled turtle (ChM PV4882), probably *Apalone*. In the collections of The Charleston Museum is a partial carapace of a chicken turtle (Subfamily Deirocheylinae, family Emydidae) found along the bank of Eagle Creek near its junction with the Ashley River in Dorchester County (Fig. 10). It was originally thought to have come from the Chandler Bridge Formation, which crops out in the vicinity, but chicken turtles are known almost exclusively from Pliocene and Pleistocene localities in the southeastern USA – not from the Oligocene (Jackson, 1978). That this specimen was found together with a humerus of the extant star-nosed mole *Condylura* (see "Systematic Paleontology" section below) supports its origination from Pleistocene sediments overlying the Chandler Bridge at this locality, not from within the latter.

Three species of cheloniid sea turtles are known and are most commonly represented by carapacial elements. An exceptional specimen is the first complete carapace (ChM PV4792) of *Carolinochelys wilsoni*, which was originally described from a nearly complete skull and humerus from the Ashley Formation (Weems and Sanders, 2014; also, see above). The humerus has since been referred to *Procolpochelys charlestonensis*, the holotype of which (ChM PV6056) is from also the Chandler Bridge Formation (Weems and Sanders, 2014). Additional, much more complete material of *Procolpochelys charlestonensis* (CCNHM 893 and 300.1) was recently reported by Weems and Brown (2017). *Ashleychelys palmeri* was also originally described from the Ashley Formation, but appears to be more abundantly represented in the Chandler Bridge Formation. Remains of subadults of *P. charlestonensis* have not yet been encountered. Leatherback sea turtles (family Dermochelyidae) are represented in the Chandler Bridge Formation by several carapace fragments in collections at both The Charleston Museum and the SCSM and by a virtually complete carapace over 2 m in length, with the vertebral column and ribs preserved (ChM PV4893). Collected near the Charleston Airport by AES and a ChM party in 1984, the partially prepared carapace has seven low and narrow longitudinal ridges, and appears to represent a new genus. Several additional specimens of sea turtles from the Chandler Bridge Formation await study at the Mace Brown Museum of Natural History.

Fish remains are particularly abundant in the Chandler Bridge Formation, especially the dental elements of sharks, skates, and rays. Cicimurri and Knight (2009b) reported 29 different species, including the oldest known record of the whale shark, *Rhincodon*, and a new skate, *Raja mccollumi*. Scombroid bony fish were reported by Fierstine and Weems (2009), with specimens referred to *Xiphiorhynchus rotundus*, *Xiphiorhynchus* sp., *Aglyptorhynchus robustus*, *Aglyptorhynchus* sp., and to Istiophoridae gen. and sp. indet.

Notably absent from the formation are remains of freshwater fish and turtles (with the exception of a few carapace elements of softshell turtle, as noted above), amphibians, alligators, aquatic freshwater mammals, and terrestrial mammals (Weems and Knight, 2013), although a single isolated peccary tooth (ChM PV5025) here referred to *Perchoerus* sp. was recovered and is discussed later in this report.

Tiger Leap Formation/Edisto Formation. Huddlestun (1988) divided the Parachucla Formation in Georgia into a lower Tiger Leap Member and an overlying Porters Landing Member. Weems and Edwards (2001) raised the Tiger Leap Member to formational status (dividing it into four informal members) and restricted the Parachucla Formation to Huddlestun's Porters Landing Member. In Georgia the Tiger Leap Formation consists of a "quartzose calcarenite to calcareous quartz sand" (Weems and Edwards, 2001:11) and in the Charleston area it is described as a "very quartzose and phosphatic, often shelly calcarenite" (Weems and Lewis, 2002:28). On the basis of dinoflagellate assemblages, the lower members were found to be of latest Oligocene age (dinoflagellate cyst zone DN1 of de Verteuil and Norris, 1996); but Weems and Edwards (2001:11) correlated the upper member with South Carolina's Edisto Formation, or "above the highest occurrence of the genus *Chiropteridium*," which they considered lower Miocene (also see Weems et al., 2006).

Originally named the "Edisto marl" by Sloan (1908), the Edisto Formation was later formalized by Ward et al. (1979:26) for the "lower Miocene sandy limestones unconformably overlying the Cooper Formation and unconformably overlain by the Raysor Formation (lower Pliocene) as exposed in the vicinity of Givhans Ferry on the Edisto River." In contrast to the generally accepted early Miocene age, more recent work has refined that age estimate. $^{87}Sr/^{86}Sr$ isotopic analysis on samples of molluscs (*Ostrea haitiensis*) from exposures of the Edisto Formation at Givhans Ferry yielded a date of 23.4 to 23.5 Ma, entirely within the late Chattian (Weems et al., 2006; Weems and Harris, 2008; Weems et al., 2016).

Based on oxygen isotope curves (Fig. 3B), the upper Tiger Leap/Edisto formations could not have been deposited immediately preceding nor across the Oligocene/Miocene boundary, as there was a major lowstand, the Mi1 glaciation, during that interval (e.g., Miller et al., 1991; Naish et al., 2001; and Zachos et al., 1997, 2001). Therefore, they were likely deposited during high sea level associated with peak Oligocene warmth during chron C6Cr (Pälike et al., 2006) between about 23.6 to 23.2 Ma, which again is consistent with the ^{87}Sr/^{86}Sr dates noted above.

Currently the only known terrestrial vertebrate fossils that may have originated from the Tiger Leap/Edisto Formation are the type specimen of the giant entelodont *Daeodon mento* (Allen, 1926), a massive mandibular symphysis (see "Systematic Paleontology" section below), and a fragment of maxilla with teeth from the horse *Anchippus texanus* Leidy, 1868b. Interestingly, both of these specimens are recorded from the "Ashley River phosphate beds," now known to be within the Wando Formation, which dates to around 100 kyr, but which is well understood to harbor reworked fossils of much greater age (e.g., Leidy, 1877; Domning, 1989b). Recent study of the entelodont specimen revealed an indurated sandy calcarenite still adhering to portions of the bone, examination of which suggests it as Edisto Formation. Although there are no known outcrops of Edisto Formation along the Ashley River in the vicinity of the old phosphate mining region, it is the detached, worn boulders of this phosphatized unit reworked into the Wando Formation there that were the focus of mining operations (Sloan, 1908; Sanders, 2002). Alternatively, that the adhering matrix may be recrystallized Givhans Ferry Member of the Ashley Formation rather than Edisto cannot be discounted given its somewhat quartzose lithology. Considered an immigrant from Asia, *Daeodon* first appeared in North America in the early Arikareean, then became widespread across the continent until its demise in the early Hemingfordian (Brunet, 1979; Lucas et al., 1998). *Anchippus texanus* is a "medial" to late Arikareean taxon morphologically transitional between early Arikareean *Miohippus* and early Hemingfordian *Parahippus* (e.g., *Parahippus leonensis*). A latest Chattian age for the Edisto Formation correlates with the late Arikareean NALMA (Figs. 2A, 3B), consistent with the temporal range of *A. texanus*, but the matrix within vugs of the latter specimen is not as diagnostic as that still adhering to the specimen of *Daeodon*.

Note on biostratigraphic correlations of Paleogene cetaceans from South Carolina

Although terrestrial mammal taxa have long been utilized as biostratigraphic markers to establish the framework for North American Land Mammal Ages (e.g., Wood et al., 1941; Woodburne, 1987, 2004), marine mammals have seldom been employed as aids in determining the age of marine stratigraphic units. Marine biostratigraphy has traditionally relied upon molluscs, foraminifera, dinocysts, and calcareous nannoplankton for that purpose (e.g., Berggren et al., 1995). There is mounting evidence, however, that Paleogene fossil cetaceans can be effectively utilized in chronostratigraphic correlations.

Because Paleogene cetaceans were rapidly evolving forms with distinctive evolutionary grades that occurred within a limited temporal span and range of chronostratigraphic units, the presence of one of those forms in a marine formation is *generally* a good indication of the age of that unit (to the extent that we can currently determine based on limited samples sizes). For example, archaeocetes of the family Protocetidae, among the most primitive known cetaceans, are not known to occur in strata younger than middle Eocene (e.g., Gingerich et al., 1997), and members of the family Basilosauridae, in North America, are known only from the late Eocene. Those distinctions enabled Geisler et al. (2005) to use protocetid and basilosaurid archaeocete cetaceans to support the respective ages of two marine stratigraphic units in the Eocene of South Carolina, protocetids being restricted to beds of NP16–17 age (Santee Limestone and Cross Member of the Tupelo Bay Formation) and basilosaurids to NP18 (Pregnall Member of the Tupelo Bay Formation).

Some of the most salient skeletal changes in the evolutionary history of cetaceans have been 1) the loss of hind limbs, still present in the earliest cetaceans (e.g., Protocetidae); 2) replacement of the rotational elbow, present in all archaeocetes, with the non-rotational structure present in all known post-archaeocete cetaceans; and 3) the posterior movement of the nasal opening from the anterior end of the rostrum in the most primitive cetaceans to a position near the top of the skull in modern odontocetes (toothed whales) and mysticetes (baleen whales). The latter process, traditionally called "telescoping," involved the elongation of the maxillary bones posteriorly until they covered most of the frontals, the reduction of the length of the frontals, the elimination of the parietal bones from the skull roof, and a forward thrust of the supraoccipital toward the vertex of the skull (Miller, 1923; Churchill et al., 2018). During the Oligocene, various grades of telescoping can be seen between earlier and later forms, the position of the nasal opening and the degree of reduction of the parietals being especially important evolutionary landmarks (e.g., Whitmore and Sanders, 1976:fig.3).

Among the Oligocene cetacean taxa of Europe, two species are known only from the lower Chattian (Chattian A) Doberg Formation in the famous Doberg quarry two kilometers south of Bünde (Westfalen) in the North Sea Basin of northwestern Germany. Both are odontocetes, viz., *Eosqualodon langewieschei* Rothausen, 1968, and *Microcetus ambiguous* (Meyer, 1840), the latter known only from teeth. As discussed above in the section on the Chandler Bridge Formation, *Eosqualodon* is now considered to have relatives in the Oligocene beds near Charleston and in marine deposits at Linz, Austria. As demonstrated by Whitmore and Sanders (1976:figs. 3b, 5), several undescribed Charleston Museum specimens from the upper Oligocene Chandler Bridge Formation represent the same evolutionary grade as *Eosqualodon*, share similar cranial features with *E. langewieschei*, and belong in the same as yet to be described family. The Charleston Museum specimens, together with specimens at the Mace Brown Museum of Natural History, appear to represent at least two genera and three species. Two other undescribed genera possibly related to *Eosqualodon* are known from two specimens from the Ashley Formation. They are slightly more primitive than *Eosqualodon* and the other *Eosqualodon*-like forms from the overlying Chandler Bridge Formation in that the parietals are exposed across the entire skull roof in adults, although much narrower than in *Patriocetus.* It is important to point out, however, as noted above, that the so called "waipatiids" share a similar morphological "grade," thus complicating the relationships between the *Eosqualodon*-like and waipatiid-like forms from the Chandler Bridge. The teeth of these small relatives of *Eosqualodon* from the Chandler Bridge and Ashley formations are also similar to the teeth from Doberg to which the name *Microcetus ambiguous* was applied (Sanders et al., 1982), suggesting that *M. ambiguous* may be familially related to these forms from South Carolina, as well.

A similar pattern also exists between the mysticetes *Micromysticetus tobieni* Rothausen (1971) from the lower Chattian (upper Chattian A) Meeresand near Dusseldorf, Germany, and *Micromysticetus rothauseni* Sanders and Barnes, 2002a, the holotype partial skull (ChM PV4844) of which was found in the Ashley Formation near Charleston. Both of those stratigraphic units are of NP24 age (Rothausen, 1971; Sanders and Barnes, 2002a). A second paratype partial skull (ChM PV5933) and an isolated periotic (ChM PV7225) are also known from the Ashley Formation. Originally described as *Cetotheriopsis tobieni* by Rothausen (1971), the holotype skull of that taxon was found to have diagnostic characters that ally it congenerically with *M. rothauseni* (Sanders and Barnes, 2002a). The occurrence of *Micromysticetus* in upper Rupelian sediments in South Carolina suggests that this genus may have originated in the Western North Atlantic.

A periotic of *Micromysticetus* (CMM-V-5011) is also known from New Kent County, Virginia. Collected in 2004 by REW on the beach at the foot of a bluff on the south bank of the Pamunkey River near the mutual boundary of Hanover, New Kent, and King William counties, the specimen was almost certainly washed out of the Old Church Formation at this locality, which ^{87}Sr/^{86}Sr dates noted elsewhere in this report place at an age very similar to that of ^{87}Sr/^{86}Sr dates acquired for the Ashley Formation (Weems et al., 2006). At the collection site, the Old Church Formation is underlain at beach level by the middle Eocene Piney Point Formation, which is far too old to contain mysticete remains. The Old Church Formation is overlain by the lower Burdigalian (Lower Miocene) Popes Creek Sand Member of the Calvert Formation, which is assignable to dinoflagellate zone DN2b/c and is placed at 19-19.5 Ma (Weems and Edwards, 2007b:fig. 1). Because the only known specimens of *Micromysticetus* from North America are from the Ashley Formation (~29.1 Ma), it is highly unlikely that the Virginia specimen was eroded from the lower Burdigalian sediments at this locality. Thus, the Virginia specimen strongly supports the ^{87}Sr/^{86}Sr date of 29.15 Ma for the Old Church Formation at the Pamunkey River locality, and provides additional evidence that the Ashley and Old Church formations are correlative. CMM-V-5011 also extends the known geographic range of *Micromysticetus* northward from Charleston to Virginia along the Atlantic Coastal Plain. The periotic from Virginia is somewhat smaller than that from South Carolina, inferring that it may represent a different species. In addition to the periotic is an axis vertebra (CMM-V-5010) indistinguishable from that of the type material of *M. rothauseni* found by J. Osborne while diving the Pamunkey River. This specimen provides further evidence of *Micromysticetus* in Virginia.

Recent discoveries in North Carolina provide additional correlations with Oligocene cetacean taxa in South Carolina. Uhen (2008) described a partial odontocete skull, USNM 525001, from a block of indurated matrix of the Belgrade Formation washed ashore at Onslow Beach, Onslow County, as the new taxon *Albertocetus meffordorum*, and erected the family Xenorophidae, the type of which is *Xenorophus sloanii*, described by Kellogg (1923b) from a partial skull from the Ashley Formation near Charleston. Uhen (2008) referred two other partial skulls from Onslow Beach, USNM 529238 and 529241, to *A. meffordorum*, as well. Apparently two additional partial skulls from Onslow Beach, USNM 529239 and 533993, also represent the Xenorophidae. Remains of this family had previously been found only in the vicinity of Charleston, where they occur abundantly in the Ashley and Chandler Bridge formations (Sanders, 1996; Boessenecker et al., 2017a).

In connection with this study, samples of mollusc shells from Belgrade matrix in which the North Carolina skulls were found yielded ^{87}Sr/^{86}Sr dates ranging from 26.5 to 27.5 Ma. As noted above, the Chandler Bridge Formation is now known to correlate with nannoplankton zone NP25, with an age range of between 26.84 and 23.13 Ma. Although the lithology of the Belgrade samples from Onslow Beach differs considerably from that of the Chandler Bridge Formation, which is a fine- to medium-grained non-calcareous quartz-phosphate sand (Sanders et al., 1982), the slight overlap in ages of the Chandler Bridge and Belgrade formations, together with the abundance of relatives of the archaic odontocete *Xenorophus* from both areas, suggests that the Onslow Beach sediments currently referred to the Belgrade Formation may be time equivalent with the Chandler Bridge Formation.

Additional evidence of the value of Paleogene cetaceans as chronostratigraphic markers is indicated by examination of an apparent conflict between the dating of the Linz Sands at Linz, Austria, and the evolutionary grades of cetacean skulls found during the 19th century in a sand mine on the south side of the Donau (Danube) River at Linz. Conserved at the Oberöseterreichesches Landesmuseum in Linz, those specimens were assumed to have come from the Linz Sands, a marine deposit at Linz (Rothausen, 1968). Rabeder and Steininger (1975) placed the age of the Linz Sands as latest Oligocene (uppermost NP25) based on the presence of the foraminifera *Myogypsina formosensis*, which is restricted to the uppermost Oligocene. Three taxa have been described from the Linz specimens: the odontocetes *Agriocetus incertus* Brandt 1874, and *Patriocetus ehrlichi* (van Beneden, 1865), and the mysticete *Cetotheriopsis lintianus* von Meyer, 1849. As noted by Sanders et al. (1982), *Agriocetus* is familially related to *Eosqualodon* from Chattian A at Doberg and its allied forms from South Carolina. Of the two odontocetes, *Patriocetus* is the more primitive, the parietal bones still being visible dorsally as a narrow band across the skull roof. By the early Miocene, if not by latest Oligocene time, the telescoping process had eliminated those bones from the skull roof in most odontocetes (but see further discussion below).

Two other species of *Patriocetus* are now known: *Patriocetus kazakhstanicus* Dubrovo and Sanders, 2000, from the "fish bed" of the Karaginskaya Formation of Kazakhstan (upper Chattian A, upper NP24,) and a new species currently under description by K. Rothausen and AES from the similarly aged Grafenberg Formation in the Lower Rhine Embayment near Krefeld, Germany. Sediment from the holotype skull of the new species contained the nassariid gastropod *Hinia* (*Tritonella*) *pygmaea* (Schlotheim, 1920), form *bispirallis* Koch and Weichmann, 1872, a transitional form toward *H.* (*T.*) *schlotheimi* (Betrich, 1854) that is common in the *Palliolum decussatum* zone of upper Chattian A. Sediment from the type locality of the new species of *Patriocetus* contained the foraminifer *Cribononion subnodosum,* which is typically confined to shallow marine sediments of upper Chattian A in this region (K. Rothausen, pers. comm. to AES, 2004). Thus, since two of the three known species of *Patriocetus* were found in lower Chattian (Chattian A) sediments, it seems highly unlikely that the nominal species, *P. ehrlichi* from Linz, is of latest Oligocene age. There is also an undescribed ChM specimen from the Chandler Bridge Formation that is familially related to *Patriocetus* (Dubrovo and Sanders, 2000).

The mysticete *Cetotheriopsis linitanus* from Linz is also an archaic form and was formerly a member of the subfamily Cetotheriopsinae of the Cetotheriidae, to which Sanders and Barnes (2002a) referred *Micromysticetus*. Because these taxa were more primitive than the other members of the Cetotheriidae, most of which are Neogene forms, Geisler and Sanders (2003) removed the Cetotheriopsinae from the Cetotheriidae and elevated Cetotheriopsinae to familial rank (Cetotheriopsidae).

The three cetacean taxa from Linz – *Agriocetus, Patriocetus,* and *Cetotheriopsis* – appear too primitive to have been members of the cetacean fauna of the latest Oligocene, and are more characteristic of earlier Chattian evolutionary grades. If the beds on the south side of the Danube were of latest Oligocene age they would have yielded specimens more closely related to the cetaceans of the Aquitanian (lower Miocene) rather than to those lower in the Chattian. A possible explanation for the conflict between the lower Chattian evolutionary grades of the cetaceans and the latest Chattian date of the Linz Sands is indicated by the presence of the foraminifer *Miogypsina formosensis* as reported by Rabeder and Steininger (1975). In recent correspondence between F. Steininger and AES about this biostratigraphic incongruity, Steininger related that the sample of the Linz Sands that furnished the *Miogypsina* specimen that he and Rabeder used to date that unit was taken on the north side of the Danube, not on the south side in the region where the cetacean specimens were found. Steininger further stated that "there is no direct geological evidence that the Linz Sands with *Miogypsina* [on the northern side of the river] are the same formation of sands as the sandy deposits from which the whales are coming on the southern bank of the Danube" (F. Steininger, pers. comm. to AES, October, 2005). Consequently, we suggest that the sediments that furnished the cetacean skulls on the south side of the Danube at Linz comprise an undetermined formation of lower or middle Chattian age, and that specimens from this unit should no longer be regarded as having come from the Linz Sands until the stratigraphic relationships between these two units on opposite sides of the Danube can be determined.

The preceding examples provide evidence that correctly identified cetacean cranial elements can aid in determining the age of Eocene and Oligocene stratigraphic units and subunits, and when combined with $^{87}Sr/^{86}Sr$ dates, radioisotopic dates, or planktonic and/or dinocyst age analyses, can, in *some* cases, provide dependable biostratigraphic correlations. It is important to point out, however, that there are certainly examples which prompt a degree of caution if relying solely on cetacean skulls for biostratigraphic purposes. The example above concerning the cetacean fossils from the Linz sands provides a good case in point.

Another example involves the hiatus between the Ashley and Chandler Bridge formations. Originally, on the basis of the evolutionary "grade" of their cetacean faunas and on certain taxa found in both formations, it was thought that little time was represented by the unconformity separating them, and both formations were thought to be early Chattian in age (e.g., Sanders, 1980; Sanders et al., 1982). Not until microfossils indicated that the Ashley Formation was of NP24 age (upper Rupelian) and that the Chandler Bridge Formation was of NP25 age ("middle" to upper Chattian) was it realized that the hiatus between the two units was much greater than that indicated by the apparent similarities of their respective cetacean faunas. Another example is provided by the recently described odontocete *Ediscetus osbornei* Albright et al., 2018. Although *E. osbornei* is currently known only from the Ashley Formation (base of Givhans Ferry Member), it shows an unexpectedly derived stage of telescoping much advanced relative to contemporary species found in the same unit such as *Xenorophus*, *Agorophius*, and *Ashleycetus*, as well as significantly younger species from the Chandler Bridge Formation. In this species the parietals have been completely overridden by the anterior migration of the supraoccipital, and the posterior progression of the posterior frontomaxillary suture (posterior temporal crest) has progressed so far posteriorly that it has been pushed up vertically due to contact with the supraoccipital. Additional examples include the primitive archaeocete-like morphology of the various toothed mysticetes, such as *Coronodon havensteini*, from the Chandler Bridge Formation – a "grade" much more typical of significantly older units.

Miocene Series (23.03 – 5.33 Ma)

Long and apparently frequent episodes of erosion during much of the Miocene along coastal South Carolina have resulted in a poor stratigraphic record for this interval of time, with a consequent paucity of non-marine vertebrate fossils. As Weems and Lewis (2002:36) noted for the Charleston area, "preserved patches of Miocene units lie directly on the Oligocene Ashley Formation and not on each other," a pattern indicating "that each Miocene unit either was only deposited in isolated patches or was mostly eroded from the Charleston area before each subsequent Miocene unit was deposited." They further noted that despite abundant evidence for repeated marine submergence of the Charleston region since deposition of the Ashley Formation in the late early Oligocene, no evidence for accumulation of any unit of great thickness exists. The few Miocene units that are known consist primarily of small, sparsely distributed subcrops characterized on the basis of comparisons with lithologically and biostratigraphically similar strata much better represented in Georgia (e.g., Huddlestun, 1988, and Weems and Edwards, 2001). In ascending order these include the Parachucla, Marks Head, Coosawhatchie, and Ebenezer formations (Figs. 2B, 3B). As noted above, the upper members of the Tiger Leap (equivalent to the Edisto Formation) historically have been considered earliest Miocene, but new data indicates a latest Oligocene age. In North Carolina, Virginia, and Maryland the Miocene is much better represented and known primarily from the Pungo River, Calvert, Choptank, St. Marys, and Eastover formations.

It is important to note, however, that over the last couple of years (2015–2019) occasional photographs of specimens circulating among avocational fossil collectors (and seen by LBA) indicate that late Miocene fossils of both terrestrial and marine mammals are being recovered from a borrow pit or quarry of some sort in Jasper County, as well as from the bottoms of rivers in that region. This is certainly tenable, as sediments of this age would potentially be in the shallow subsurface of that region due to uplift of the "Beaufort Arch," and fossils from nearby Brays Island support this. The authors of the current volume hope to learn more about this important development pending availability of additional information.

Parachucla Formation. Originally named by Sloan (1908) for marls and shales that crop out along the Savannah River in the vicinity of Porters Landing in Effingham County, Georgia, the Parachucla Formation of Weems and Edwards (2001) is, as noted above, equivalent to the Porters Landing Member of the Parachucla Formation of Huddlestun (1988). These "weakly lithified shales and mudstones" that Weems and Edwards (2001:11) noted are "thin or missing in the vicinity of Savannah on the crest of the Beaufort Arch," occur in "very limited subcrop ... in the far western part of the Charleston area" (Weems and Lewis, 2002:29). Disconformably overlying the Tiger Leap Formation, the Parachucla Formation harbors a foraminiferal assemblage indicative of late zone N4 to N5 and dinoflagellates indicative of dinoflagellate zone DN2, i.e., late Aquitanian in age (Huddlestun, 1988; Weems and Edwards, 2001; Fig. 3B).

Although no vertebrate fossils are known from the Parachucla Formation in South Carolina, the White Springs Local Fauna of northern Florida is thought to derive from what is considered an extension of the Porters Landing Member into the White Springs region (Morgan, 1989). The N4 to N5 correlation results in an age of about 21 Ma, and Jones et al. (1993) reported a ^{87}Sr/^{86}Sr date of 20.2 Ma for the Porters Landing Member at its type section in Georgia, thus supporting the upper Aquitanian correlation. Although a date of 20.2 Ma places the White Springs LF in the late Arikareean (Ar4) NALMA, the mammalian fauna is more indicative of the early Arikareean (Morgan, 1989, 1993; Albright, 1998; MacFadden and Morgan, 2003). Supporting this is another ^{87}Sr/^{86}Sr date reported by Jones et al. (1993) of 24.4 Ma on mollusc shells from the White Springs locality, and even more compelling is the mutual occurrence of the dugongid *Crenatosiren olseni* from the White Springs LF (type locality) and from the Chattian-age Chandler Bridge Formation in the Charleston area (Domning, 1997). Thus, and as also concluded by Domning (1997), what is considered the Porters Landing Member of the Parachucla Formation in the vicinity of White Springs, Florida, is significantly older (Chattian) than the same member in its type area along the Savannah River in Georgia (upper Aquitanian).

Another dugongid originally described from the "Ashley phosphate beds," *Dioplotherium manigaulti*, is also known from the White Springs LF. It was this exceptional specimen (UF 95615) that finally shed light on the unit of origin for the Charleston holotype (ChM PV2896) and referred specimen (ChM PV2894), namely the Chandler Bridge Formation (see Domning, 1989a, b, for further discussion). Again, the Parachucla Formation in SC, of late Aquitanian age, is not age equivalent with the formation given the same name in northern Florida; the latter is Chattian in age and equivalent with the Charleston area's Chandler Bridge Formation.

Marks Head Formation. Like the Parachucla, the "Marks Head marl" was also named by Sloan (1908) for medium to coarse grained, clayey, phosphatic and calcareous sands that crop out along the Savannah River. Although the term "Hawthorne Formation" has also been applied to these sediments, Huddlestun (1988:50) used the term "Marks Head Formation." Harboring a dinoflagellate assemblage indicative of DN2, Weems and Edwards (2001:12) noted that "the highest [informal] member probably can be assigned to dinoflagellate zone DN3." The probable DN3 correlation is supported by a terrestrial mammalian fauna from this unit at Porters Landing, Georgia, which includes taxa indicative of the early Hemingfordian (Pratt and Petkewich, 1989). Deposition of sediments with a DN2-DN3 dinoflagellate assemblage together with mammals indicative of the early Hemingfordian provide a date for this unit of around 18 Ma (Figs. 2B, 3B). Additional support for this age is provided by very fragmentary material of what was thought to be the lower to middle Miocene long-snouted odontocete "*Rhabdosteus latiradix*," collected by AES and REW along the Georgia bank of the Savannah River near Porters Landing from "the basal couple of feet of the Marks Head … directly above the Parachucla" (REW, pers. observ., ca. 1978). However, a recent search for this material at The Charleston Museum, where it was taken after it was collected, failed to relocate it.

Although Weems and Lewis (2002:29) noted that the Marks Head Formation "is the most widespread unit above the Ashley [Formation] in the Charleston region," no vertebrate fossils are known unequivocally from this unit in South Carolina. There is, however, a fragmentary cranium of "*Rhabdosteus latiradix*" in the collections of the SCSM labeled as having been recovered from the "Salkahatchie ooze" (see Sloan, 1908:472), but with no additional accompanying data. It is thought to have originated from the Marks Head Formation, or perhaps the underlying Parachucla, given the recovery of this taxon from the Porters Landing section, as noted above; but its origin will likely remain a mystery.

Coosawhatchie Formation. The Coosawhatchie clay of Heron et al. (1965), or the Coosawhatchie Clay Member of the Hawthorn Formation of Abbott and Andrews (1979), was raised to formational status by Huddlestun (1988) for a diatomaceous clay unit that, in SC, crops out near Dawson's Landing (southeast of Coosawhatchie), Jasper County (Fig. 1A). This unit is also well exposed at low tide in a small tidal creek that runs beneath US Highway 17, 1.44 km west of Gardens Corner (west of the intersection of US 17 and US 21) in Beaufort County, where it crops out as a chert-like lithology. This is the locality referred to by Sloan (1908:346) and Cooke (1936:111) as Huspa Creek (Fig. 1A), although they referred these silicified deposits to the "Parachucla shale."

Weems and Edwards (2001) slightly revised Huddlestun's (1988) stratigraphy of the Coosawhatchie Formation, and it is only the lower Berryville Clay Member that correlates to that part of the section at Dawson's Landing (as also noted by Huddlestun, 1988). They noted dinoflagellates from the lower Berryville indicative of DN5. Ernissee et al. (1977) placed the unit in upper N11 to lower N12 foraminiferal zones (about 13.5 Ma following GTS2012; Figs. 2B, 3B), and Abbott and Andrews (1979) correlated the Coosawhatchie with the Choptank Formation of Maryland on the basis of diatom assemblages. In turn, the Choptank Formation was correlated with nannofossil zone NN6 (see text-figure 3 of Abbott and Andrews, 1979), and de Verteuil and Norris (1996) correlated the lower Choptank with dinoflagellate zone DN6. Palmer (1988) studied radiolarians from the Dawson's Landing section and determined that it fell within the lower part of the *Dorcadospyris alata* zone (approx. 13.5-15 Ma).

In addition to their correlation of the Coosawhatchie with the Choptank Formation, Abbott and Andrews (1979:228) also concluded that the unit must have formed under cool conditions. Although they suggested that this cool signal may have been due to localized coastal upwelling "rather than a general cooling of the Northern Hemisphere," we now know that there was an abrupt global cooling event that terminated the middle Miocene Climatic Optimum (MMCO) at about 14 to 13.8 Ma (see, e.g., Cronin, 2009:107). Consideration of all these data supports our placement of the Coosawhatchie Formation in SC in the early Serravallian at about 13.4 Ma, slightly after termination of the MMCO (Fig. 3B).

Although no vertebrate fossils are known unequivocally from the Coosawhatchie Formation, a single upper molar of the middle to late Miocene rhinoceros, *Aphelops*, currently housed in a private collection, may have originated from this unit. The tooth is reported to have been found by scuba divers in coastal Jasper County (see discussion of *Aphelops* in "Systematic Paleontology" section).

Ebenezer Formation. The only other formation of Miocene age currently recognized along the SC Coastal Plain that would have the potential to harbor vertebrate fossils is the Ebenezer Formation, a unit in the Charleston area known only from two small patches informally referred to as the Rudd Branch beds by Weems et al. (1987, 1997; also see Weems and Lewis, 2002). Originally considered a member of the Coosawhatchie Formation by Huddlestun (1988), Weems and Edwards (2001) raised this unit to formational rank on the basis of its late, rather than middle Miocene age and on lithological grounds as well (more sand-rich than clay-rich).

In southern Georgia, Weems and Edwards (2001) divided the Ebenezer into five unconformity-bounded members, four of which they correlated to dinoflagellate zone DN8. In the vicinity of Savannah they noted only the upper two members, the uppermost of which they considered to be the unit that Huddlestun (1988) referred to the Wabasso beds. In their assessment, the Wabasso beds do not occur in the Savannah area, because the type Wabasso beds in central Florida contain an early Pliocene foraminiferal assemblage (zone PL1), whereas those beds in the Savannah area referred to the Wabasso beds by Huddlestun (1988) contain, according to Weems and Edwards (2001), late Miocene dinoflagellates indicative of zone DN9 (late Tortonian; Fig. 2B). On the other hand, Weems and Edwards (2001:13, 14) also noted calcareous nannoplankton from a core taken in the vicinity of Savannah that yielded taxa indicative of "the late Miocene *and (or) early Pliocene* time interval" (italics ours) in addition to shells of the mollusc *Amusium mortoni* in "the youngest Ebenezer member."

Contrary to Weems' and Edwards' (2001) note that *A. mortoni* has a late Miocene to Pliocene range, a Pliocene to lower Pleistocene range is more accurate, and this taxon is particularly diagnostic of the upper Zanclean ("middle" Pliocene) Goose Creek Limestone (L. Campbell, pers. comm. to LBA, February, 2011). It is highly doubtful that *A. mortoni* occurs in sediments indicative of dinoflagellate zone DN9, as that zone spans the late Tortonian interval from about 8.7 to 7.6 Ma (Figs. 2B, 3B) – nearly 4 million years prior to its common occurrence in the Goose Creek Limestone at about 3.8 Ma. Therefore, in this report we recognize an upper Ebenezer Formation member in SC of late Miocene age (DN9; late Tortonian), and place it at about 8.5 Ma, as well as the early Pliocene Wabasso beds (Figs. 2C, 3C). Further discussion of the Wabasso follows.

Pliocene Series (5.33 – 2.59 Ma)

The Pliocene Epoch represents a nearly 3 myr long interval of Earth history characterized by dramatic variations in temperature and precipitation as global climate deteriorated toward the high-magnitude variability associated with Pleistocene glacial/interglacial cycles. There were intervals of the Pliocene that were relatively warmer than present, as well as short, significantly cooler intervals that marked the early stages of Northern Hemisphere glaciation (NHG; e.g., Sosdian and Rosenthal, 2009). Several reasons for this variability are summarized by Haywood et al. (2009) and therefore will not be reiterated here. Germane to the goals of this report, however, is the fact that these climatic variations impacted sea level, which is, in turn, important with respect to the preservation of continental shelf successions along the Atlantic Coastal Plain. As Williams et al. (2009:86) noted, "shelf successions tend to be preserved during global highstands," thus recording warm climatic intervals, but lowstands induced by cooler climates "are often reflected in unconformities." Also affecting depositional patterns of the sedimentary units in this region over this interval were minor tectonic adjustments which "altered the elevation of the continental shelf relative to sea level and realigned basin configurations" (Ward et al., 1991:274). More recently Rowley et al. (2013) and Rovere et al. (2014, 2015) have concluded that the present surface topographic architecture of the Atlantic Coastal Plain is due in large part to mantle flow influences (so called "DT" or dynamic topography influences) and to a lesser extent to glacial isostatic adjustments (GIA). They noted that these factors confound "attempts to use regional stratigraphic relations as references for longer term sea-level determinations" (Rowley et al., 2013:1560). Such factors provide additional complications when attempting to evaluate and understand the late Neogene stratigraphy of the SC Coastal Plain.

To gain an understanding of the Pliocene stratigraphy of the Atlantic Coastal Plain, much work has focused on the highly fossiliferous units that underlie Maryland, Virginia, North Carolina, Georgia, and Florida (e.g., Cronin et al., 1984; Huddlestun, 1988; Scott and Allmon, 1992; Campbell, 1993; Petuch, 2003; Ward, 2008; Ward and Andrews, 2008). The limitations and difficulties of South Carolina's Neogene stratigraphy have been noted previously, but there is a long history of attempts to correlate this stratigraphy, based primarily on molluscan faunas, with that of those states noted above where the record is more easily observed and studied and, hence, better understood. Maryland, Virginia, and North Carolina have much better, more laterally extensive exposures of these fossiliferous units in stream and river banks/bluffs than does South Carolina, but the long term geological and paleontological studies of the Lee Creek Mine in North Carolina (e.g., Campbell, 1993; Ray, 1983, 1987, 2001; Ray et al., 2008), as well as the spectacular record of marine invertebrates from commercial shell pits in Florida (e.g., Petuch, 2003; Petuch and Roberts, 2007; Portell et al., 2012), have greatly added to that understanding.

Krantz (1991) attempted to correlate Pliocene-Pleistocene marine sedimentary units of the USA Atlantic Coastal Plain to the more continuous deep ocean record “on evidence of sea-level highstands inferred from high-resolution δ^{18}O records” (Krantz, 1991:163). This early work was successful as a first approximation, but since then the marine δ^{18}O isotope record has been refined significantly and it also has been astronomically calibrated (e.g., Lisiecki and Raymo, 2005; Raffi et al., 2006) to the more recent GPTS of Gradstein et al. (2012). In this section we update the work of Krantz (1991), as well as that of others who have more recently used his 1991 model in a similar manner, i.e., to refine the temporal placement of South Carolina’s Plio-Pleistocene stratigraphy through correlation to sea level curves (e.g., Campbell, 1993; Campbell and Campbell, 1995). Additional, more recent papers germane to this discussion include those by Doar and Kendall (2014), Rovere et al. (2014, 2015), and references within those publications.

Wabasso Beds. With the exception of limited subcrops of uppermost Ebenezer Formation noted above, upper Miocene sediments appear to be entirely missing from the SC stratigraphic record. The lower Pliocene, on the other hand, appears to be represented in the southeastern-most part of the state by what Huddlestun (1988) referred to as the Wabasso beds. Known only from the subsurface of coastal Florida, Georgia, and apparently southern South Carolina, Huddlestun (1988:98) described this informally named unit as a “phosphatic, calcareous and microfossiliferous, variably argillaceous, silty, fine-grained to very fine-grained sand . . .” Although he reported no macrofossils from the Wabasso beds, vertebrate or invertebrate, Campbell (1993) and Campbell and Campbell (1995) reported that large specimens of the scallop *Chesapecten jeffersonius* were collected by scuba divers from a unit exposed on the bottom of the Savannah River, which the Campbells interpreted to be the Wabasso beds. Indeed, Huddlestun’s (1988:plate 2) stratigraphic cross-section along the Savannah River indicates the presence of Wabasso beds in the subsurface of that region, and he also noted the occurrence of this unit in the shallow subsurface near Beaufort, SC, about 25 km northeast of the Savannah River. To the contrary, however, and as discussed above, Weems and Edwards (2001:13) did not recognize Wabasso beds in the Savannah region, instead referring Huddlestun’s unit to the upper member of the upper Miocene Ebenezer Formation (“Ebenezer member #5”).

Campbell and Campbell (1995) correlated the Wabasso beds to Zone 1, or the Sunken Meadow Member, of the Yorktown Formation in NC based primarily on the characterization of those beds by *Chesapecten jeffersonius*; Ward (2008) also shows these units as equivalent in his figure 3. Campbell (1993) and Campbell and Campbell (1995) additionally considered these units equivalent on the basis of planktonic foraminifera found in both that are indicative of zone N18. Although Ward and Blackwelder (1980:D31) noted a personal communication from Joe Hazel confirming the occurrence of N18 foraminifera in the Sunken Meadow Member, Huddlestun (1988) did not indicate the presence of N18 foraminifera in the Wabasso beds – he assigned the unit to the upper part of Atlantic planktonic foraminiferal zone PL1 (Huddlestun, 1988:100), a zone much less temporally restrictive than N18. In fact, few if any of the species listed by Huddlestun are restricted to N18 and several, particularly the more ubiquitous and biochronologically significant forms such as *Globoturborotalia* (= *Globigerina*) *nepenthes*, *Globorotalia margaritae*, and *Dentoglobigerina* (= *Globoquadrina*) *altispira*, are more indicative of N19. Ward (2008:352) provided a long list of planktonic foraminifera from the Sunken Meadow Member, many of which are also indicative of N19. Together, these two lines of evidence suggest an N19 age for the Wabasso beds rather than N18, if indeed the Wabasso beds and the Sunken Meadow Member are equivalent. There is one additional line of evidence supporting an N19 age, as well.

Recovered from the Sunken Meadow Member is a mammalian assemblage originally described by Tedford and Hunter (1984), but later revised by Eshelman and Whitmore (2008), known as the Lee Creek Local Fauna. On the basis of several mammalian species, Morgan (1994) and Eshelman and Whitmore (2008) concluded that this fauna correlated with the latest Hemphillian (Hh4, 4.7–5.0 Ma) Palmetto Fauna of Florida (also see Morgan, 2005; Webb et al., 2008). If all the temporal data are considered, including a PL1 plus an N19 planktic foraminifera designation, together with a *latest* Hemphillian land mammal fauna, the marine highstands over which the Wabasso beds and the Sunken Meadow Member of the Yorktown Formation were likely deposited (again – *if the Wabasso beds and the Sunken Meadow Member are equivalent*) are those spanning marine $\delta^{18}O$ isotope stages T5–T7, or perhaps the interval of high sea-level bracketed by the Si6 and T4 lowstands (Fig. 3C). This provides a refined age for these units of between 4.9 and 5.15 Ma. If the Wabasso beds fell within N18, this would place the unit in the uppermost Miocene rather than lower Pliocene, and within the early late Hemphillian (Hh3), rather than the latest Hemphillian (Hh4) NALMA (Figs. 2C, 3C).

Although not a mammal, some of the most common and highly sought after vertebrate fossils from the southeastern Atlantic Coastal Plain (by avocational fossil collectors) are the impressively large teeth of the shark *Megaselachus megalodon*. As Ward (2008:275–276) noted, this taxon last occurs in the Sunken Meadow Member of the Yorktown Formation and "is common in middle to upper Miocene beds from Florida to Maryland." Its distribution throughout a number of lag deposits typically found at the bases of various Pliocene and Pleistocene units in the SC Coastal Plain supports Ward's (2008:276) conclusion that "the Sunken Meadow Member [and equivalent units] may have been more broadly distributed than its present preserved limit" (see further discussion of Wabasso beds in the "Systematic Paleontology" section on *Phocanella pumila* below). Although Boessenecker et al. (2019:30) did not consider specimens of *Megaselachus megalodon* (their *Otodus megalodon*) from South Carolina in their analysis of its extinction, they did consider this taxon's absence from the members of the Yorktown Formation overlying the Sunken Meadow Member as "biochronologically real" thus reflecting the "genuine absence of this taxon." They concluded that this largest of all sharks likely went extinct around the Zanclean/Piacenzian boundary at 3.6 Ma. Teeth of *Megaselachus megalodon* are also known from the Bee Ridge Fauna, Florida, of similar age (Morgan, 1994).

Goose Creek Limestone. Originally named the "Goose Creek phase" by Sloan (1908), this "medium- to coarse-grained, quartzose and phosphatic, sparsely shelly, pale-buff (wet) to chalk white (dry) calcarenite" was "revived, formalized, and renamed" the Goose Creek Limestone by Weems et al. (1982:H137, H140). Obviously of Pliocene age based on its fossil content, its position within SC Coastal Plain stratigraphy, as Weems et al. (1982) noted, has been controversial and the reader is referred to that publication, and also to Campbell and Campbell (1995), for details and clarification. The extent of the Goose Creek Limestone is based mainly on data from auger holes, but a few isolated outcrops are known in the Charleston area, and Weems et al. (1982) noted its extensive occurrence along the axis of the Cooper River. This has been confirmed through the efforts of scuba divers (including the first author) who have observed limited, but highly distinctive, outcrops of this unit submerged, but in shallow depths, resting unconformably on the Ashley Formation within the Cooper River. These outcrops harbor exceptionally large specimens of *Amusium mortoni* and *Encope* sp. (pers. observ., LBA). Additionally, several vertebrate fossils from the Cooper River have matrix trapped in vugs, voids, alveoli, etc., closely matching the lithology of the Goose Creek. In March 2010, LBA, AES, REW, and J. Osborne visited the type locality of this unit on the banks of Goose Creek in Berkeley County and observed several specimens of *Amusium mortoni* and *Euvola hemicyclicus* (Ravenel, 1834). Sediment samples were collected from this locality for paleomagnetic analysis.

Adding significantly to an understanding of the Goose Creek Limestone and its stratigraphic relationships is the work of Campbell (1993) and Campbell and Campbell (1995) who provided detailed studies of the unit's molluscan fauna, as well as that of Bybell (1990) who reported on the calcareous nannofossils. The Campbells' studies resulted in a biostratigraphic subdivision of the Goose Creek into lower and upper units. Those exposures at the stratotype section on Goose Creek in Berkeley County, at the Martin Marietta Berkeley quarry near Cross, and at Givhans Ferry along the Edisto River (the latter of which the first author searched for unsuccessfully on numerous occasions) comprise the lower unit, whereas the upper unit was determined to be equivalent to the Raysor Formation at Canady's Bridge on the Edisto River (see discussion below), at the Martin Marietta quarry (see Blackwelder and Ward, 1979, and Ward and Huddlestun, 1988), and to the stratotype section of the Bear Bluff Formation at Bear Bluff on the Waccamaw River, north of Conway, SC. It is important to note, however, that the lithology of the Raysor Formation at the above cited localities is a shelly quartz sand, in stark contrast to the calcarenite typical of the Goose Creek Limestone in the Charleston area (Weems et al., 1982). Additional correlations include that of the upper unit to the Buckingham Limestone of south Florida and to strata at Rice's Pit in North Carolina; and of the lower unit to the stratotype of the Tamiami Formation in south Florida and to the Aurora beds in North Carolina (Campbell, 1993). On the basis of the shared occurrence of *Chesapecten septenarius*, *Euvola hemicyclicus*, *Amusium mortoni*, *Ecphora quadricostata*, and several other invertebrate taxa, the Goose Creek Limestone is typically considered essentially equivalent to the Rushmere Member of the Yorktown Formation. It does not correlate to the older Sunken Meadow Member as implied by Petuch (2003:141, 144).

From a vertebrate paleontological perspective, the importance of an accurate age for the Goose Creek Limestone cannot be understated due to the fact that some of the mammalian remains from the unit belong to Neotropical taxa involved in the Great American Biotic Interchange (GABI). Depending on the age of the unit, remains of these taxa may represent their oldest records in North America.

One example is the capybara *Neochoerus pinckneyi* (see discussion of capybara nomenclature/taxonomy in "Systematic Paleontology" section). Teeth referred to this species by Sanders (2002) from the Charles Pinckney collection at The Charleston Museum, including the holotype (ChM PV2506), were dredged from the Ashley River during phosphate mining operations at Runnymede Plantation around 1900. That they were derived from the Goose Creek Limestone is based on matrix of this unit still adhering to the specimens (Sanders, 2002:101). Additional confirmation was provided in 1979 when Doris Holt, an avocational fossil collector, recovered a capybara tooth from a borrow pit excavated on the west bank of the Ashley River about 8 km downstream from Runnymede Plantation during construction of the Mark Clark Expressway in Charleston within which were exposures of the Goose Creek Limestone. Campbell and Campbell (1995:59, 64) determined that these exposures belonged to the upper unit.

The presence in the Goose Creek Limestone of the calcareous nannofossils *Reticulofenestra pseudoumbilica* and *Sphenolithus abies*, noted by Weems et al. (1982), helps refine the age of this unit, as does the presence of *Pseudoemiliania lacunosa* reported by Bybell (1990). According to Raffi et al. (2006:fig. 3; also see Mudelsee and Raymo, 2005), *R. pseudoumbilica* ranges from approximately 3.8 to 4.9 Ma, and the HO of *S. abies* is at about 3.55 Ma. Bybell (1990) placed the FAD of *P. lacunosa* in South Carolina in lower NN15, which, following the time scale of Lourens et al. (2004), occurs at approximately 3.9 Ma (late Zanclean). That the formation can be no younger than 3.8 Ma is additionally supported by an N19 foraminiferal zone designation for Rice's Pit (Weems et al., 1982; Akers, 1972, as noted in Campbell, 1993:13), as well as the PL3 foraminiferal zone and NN15 to middle NN14 calcareous nannofossil designation for the section of lower Goose Creek Limestone at Givhans Ferry State Park (Ward and Huddlestun, 1988; Bybell, 1990). These lines of evidence imply an age for the Goose Creek of between 3.8 and 4.0 Ma. To satisfy these biochronologic criteria, we correlate the upper and lower units of the Goose Creek Limestone (and their equivalents; see Fig. 2C) to that part of the marine oxygen isotope curve bracketed by Gi20 below (a major lowstand) and Gi10 above (the HO of *Reticulofenestra pseudoumbilica*). Supporting this correlation, which places the Goose Creek Limestone within magnetochron C2Ar, is the recent paleomagnetic analysis by LBA suggesting reversed polarity (but not definitive) for this unit. Together these data imply that capybaras were present along the southeastern Atlantic Coastal Plain before 3.8 Ma – a conclusion similarly reached by Woodburne (2010), but supported here with additional evidence (see further discussion in "Systematic Paleontology" section).

Additional vertebrate remains from the Goose Creek Limestone include those of a Minke whale and a gannet (Weems et al., 1982), as well as the possible presence of three pinnipeds – the walrus *Ontocetus emmonsi* Leidy, 1859, and the seals *Phocanella pumila* Van Beneden, 1877, and *Callophoca obscura* Van Beneden, 1877 (see "Systematic Paleontology" section). Cicimurri and Knight (2009c) described a partial skeleton, including the skull (SC79.65.20), of another possible Minke whale recovered by scuba divers from the Goose Creek Limestone in the Cooper River that showed evidence of scavenging by sharks. Campbell and Campbell (1995) noted "deer antler, Artiodactyl genus uncertain, porpoise, ... sperm whale," and teeth of various sharks.

Leidy (1877; also see Allen, 1926) described several species of ziphiid (beaked) whales from the Ashley River phosphate beds, nearly all specimens of which are heavily permineralized and highly water worn. It has been speculated that some of these may have been reworked from the Goose Creek Limestone, but no adhering matrix remains to confirm this and specimens from these "beds" range in age from late Eocene to Pleistocene (see Domning, 1989b, and discussion on Wando Formation below). On the other hand, one of the cetacean specimens that Leidy (1877:231) described, *Ceterhinops longifrons* (although not a ziphiid), included matrix still adhering to the partial skull. Personal examination of this specimen in collections at the Academy of Natural Sciences, Philadelphia, by AES resulted in the determination that the matrix belonged to the Goose Creek Limestone. A second specimen referred to *Tusciziphius crispus*, originally described from the lower Pliocene of Italy, but reported by Post et al. (2008) from the Morgan River of Beaufort County, is also noted as having been recovered from the Goose Creek Limestone. Further discussion of these beaked whales is provided below in the section on the Wando Formation.

Although the marine vertebrates of the Goose Creek suggest deposition under cool to temperate conditions, the Rushmere Member of the Yorktown Formation is typically considered to have been deposited under somewhat warmer conditions (e.g., Ward et al., 1991) not unlike those off North Carolina today (Snyder et al., 2001). If these units are indeed correlative, which the evidence supports, perhaps the Goose Creek Limestone was deposited under conditions of localized dynamic upwelling similar to those hypothesized by Snyder et al. (2001) for deposition of the Sunken Meadow Member of the Yorktown Formation. The presence of phosphate nodules in the Goose Creek lends additional support.

Raysor Formation. Like the Goose Creek Limestone, the status of the Raysor Formation has a similarly confusing and complicated history, which was summarized and somewhat clarified in Weems et al. (1982), but also discussed in several other works on Coastal Plain stratigraphy, principally Huddlestun (1988), Ward and Huddlestun (1988), Ward et al. (1991), and Campbell and Campbell (1995). To briefly summarize, the Raysor Formation was originally named the "Raysor marl" by Cooke (1936) for exposures of Sloan's 1908 "Upper Pee Dee Phase" along the west bank of the Edisto River near what Sloan (1908) mistakenly believed was Raysor's Bridge. The location has more recently been determined to have been where Canady's Bridge crosses the river, as the physical attributes there very closely match those described by Sloan – a bluff 1200 feet below the bridge. At the Raysor's Bridge locality, there is no bluff (see details in Huddlestun, 1988:114). The bluff below Canady's Bridge is now referred to as Serenity Bluff as determined from the name of the road that provides access to the private property currently encompassing the bluff, i.e., Serenity Bluff Road. Furthermore, the distance from Givhans Ferry to Raysor's Bridge according to Sloan (1908:471) was about 12 miles; this is the distance from Givhans Ferry to Canady's Bridge. The distance from Givhans Ferry to the location of Raysor's Bridge, based on the locality given by Huddlestun (1988:113, fig. 45), is about 16 miles. Because the original "type" locality (at the bluff below Canady's Bridge) has long been inaccessible (overgrown and on private property), Blackwelder and Ward (1979) assigned a neostratotype section on the east bank of the Edisto River near Givhans Ferry State Park and updated the term Raysor Marl to Raysor Formation. However, as Weems et al. (1982:H144–H146) and Campbell and Campbell (1995) noted, the lithology at Givhans Ferry referred to the Raysor Formation by Blackwelder and Ward (1979) contrasts with that at the Canady's Bridge locality and "matches well with the Goose Creek Limestone (to which Sloan, 1908 referred this locality) ..." (see above discussion under Goose Creek section). Weems et al. (1982) recommended abandonment of the Givhans Ferry section as a neostratotype for the Raysor Formation, noting the "striking" contrast between it, which they generalized as a biocalcarenite with a quartzose matrix, and the Goose Creek Limestone, which they referred to as a biocalcarenite with a calcareous matrix. In what we perceive to be a glaring omission, neither Ward and Huddlestun (1988) nor Ward et al. (1991) referenced the findings of Weems et al. (1982) regarding the inadequacy of the Givhans Ferry site as a neostratotype for the Raysor Formation. Ward and Huddlestun (1988:fig. 2), in fact, placed the Goose Creek Limestone stratigraphically *above* the Raysor Formation, a likely result of Blackwelder's and Ward's (1979) assignment of Goose Creek exposures at Givhans Ferry to the Raysor, thus perpetuating the erroneous stratigraphic relationship deeper into the technical literature.

Although Weems et al. (1982) and Bybell (1990) noted the problematic stratigraphic relationship between the Raysor Formation and Goose Creek Limestone, Campbell and Campbell (1995) were able to shed light on this problem based on exposures of these units in the Martin Marietta Aggregates Berkeley ("Cross") quarry. Exposures of the Raysor at this quarry had been previously noted by Ward et al. (1979). Determining that the Goose Creek Limestone is biostratigraphically divisible into upper and lower units, Campbell and Campbell (1995) found the Raysor Formation resting disconformably above the lower Goose Creek unit in the quarry exposures. On the basis of mutually occurring biochronologically significant invertebrate taxa (e.g., *Chesapecten septenarius*, *Carolinapecten eboreus* var. *walkerensis*, *Ecphora quadricostata*, *E. bradleyae*, *Encope macrophora*, and others), they also determined that the Raysor was 1) laterally equivalent to the upper unit of the Goose Creek (the former an inshore, more siliciclastic facies than the latter, which is an offshore calcareous facies); 2) that both of these units, in turn, are equivalent to the stratotype section of the Bear Bluff Formation ("bed A" of DuBar, 1987) in Horry County; and 3) that these units pre-date the Duplin Formation (in the restricted sense, i.e., at the Natural Well, NC, stratotype; see further discussion below). Supporting the latter correlation, Campbell and Campbell (1995) noted that *Chesapecten septenarius* went extinct prior to deposition of the Duplin, in turn implying a post-Rushmere Member (Yorktown Formation) age for that formation.

The concept of equivalent Goose Creek and Raysor formations and a post-Raysor (= post-Rushmere) aged Duplin Formation contrasts with the more traditional stratigraphic model (e.g., that of Cooke, 1945; Blackwelder and Ward, 1979; Cronin et al., 1984; Ward and Huddlestun, 1988; Ward et al., 1991; Ward, 2008) whereby the Raysor and Duplin formations, plus the Rushmere and Morgarts Beach members of the Yorktown Formation, are considered correlative. Although Ward and Huddlestun (1988) also noted the absence of *C. septenarius* in units above the Rushmere, Ward et al. (1991:277) cited the presence of this taxon in Duplin strata at Tarheel, NC.

Mansfield (1935) and Cooke (1936) originally considered the Raysor Marl equivalent with strata now referred to the Sunken Meadow Member of the Yorktown Formation. After recommending abandonment of the term "Duplin Marl or Formation," Blackwelder and Ward (1979:36) introduced the term "Raysor Formation" for calcarenite beds in southern South Carolina and southeastern Georgia that they considered to be biostratigraphically equivalent to "most of the Yorktown, although perhaps not the lowermost part." Refining this correlation, Ward and Huddlestun (1988) correlated the Raysor to the Rushmere and Morgarts Beach members, and upon reinstating the Duplin Formation as a formal lithostratigraphic unit, Ward et al. (1991) considered it an updip lithofacies of the Raysor. Noting that *Chesapecten septenarius* was absent in units above the Rushmere Member, and considering the Rushmere and Morgarts Beach members as "lithofacies of the same transgressive event," Ward and Huddlestun (1988:72) attributed this pecten's absence in the latter member to different substrate conditions. Ward (2008:360) interpreted the Rushmere Member as the "very shelly, poorly-sorted sands of a transgression," and the Morgarts Beach Member as "the quiet-water, fine, well-sorted sands of the high-stand that followed that transgression." On the basis of ostracod assemblages, mollusc δ^{18}O profiles, and benthic foraminiferal assemblages, Snyder et al. (2001:259) additionally noted that the two members were essentially indistinguishable from one another with respect to paleotemperature estimates. Based on comparisons with modern faunas, however, they concluded that the Morgarts Beach Member may have been deposited under slightly cooler temperatures, and under shoaling or middle neritic conditions, than the conformably underlying Rushmere Member.

In contrast, Campbell (1993:7) contested the view that the Rushmere and Morgarts Beach members were deposited during a single transgression, which he supported through an attempt to correlate statistically determined biostratigraphic intervals to Krantz's (1991) δ^{18}O model of sea level fluctuations. Although Campbell (1993:11) noted that the marine isotope curves used by Krantz were "extremely well supported" and that they could "be expected to withstand significant revision for the foreseeable future," these curves have in recent years been further refined and recalibrated to the updated GPTS of, primarily, Lourens et al. (2004). Consequently, it is now difficult to correlate parts of Krantz's (1991) curve, such as the segment in his figure 6 between the two major lowstands at 4.8 and 3.1 Ma, to the more refined curves of, e.g., Raffi et al. (2006). It is relatively obvious that the two aforementioned lowstands correlate to isotope stages Si4–6 and M2–MG2, respectively, in the more recent and refined δ^{18}O curves (Fig. 3C). However, it is quite difficult to accurately discern to which isotope stages between those two events the "Krantz events" referred to by Campbell and Campbell (1995) as K2–K11 correlate, and on which Campbell (1993) based his model of refined Yorktown/Chowan River depositional patterns.

Regarding fossil vertebrates, the only specimen of a borophagine canid known from SC was found in what was likely the Raysor Formation in the Martin Marietta Orangeburg quarry. This specimen, a single lower premolar (p4), has been identified by Tseng and Geisler (2016) as belonging to *Borophagus hilli* (see "Systematic Paleontology" section), previously known from the latest Hemphillian of Kansas, Texas, and Florida and the early Blancan of Idaho, Washington, New Mexico, and Mexico (Wang et al., 1999).

Duplin Formation. The traditional view of the Duplin Formation holds that this unit includes those beds south of the Neuse River in North Carolina, and across the Cape Fear Arch into northern South Carolina, that are correlative with the Rushmere and Morgarts Beach members of the Yorktown Formation. The Duplin Formation also has been considered the updip, siliciclastic facies of the more calcareous Raysor Formation in South

Carolina (Blackwelder and Ward, 1979; Cronin et al., 1984; Huddlestun, 1988; Ward and Huddlestun, 1988; Dowsett and Cronin, 1990; Ward et al., 1991; Ward, 2008).

An alternative interpretation espoused by Campbell (1993) and Campbell and Campbell (1995), who subscribe to a more restricted view of the Duplin Formation, suggests that this unit is younger than the Raysor/upper Goose Creek/Rushmere complex. They base this on a comparison of molluscs from these and equivalent sites considered "pre-Duplin" with species derived specifically from the Duplin Formation's Natural Well, NC, stratotype and from the Tearcoat Branch and Muldrow Place localities in Sumter County, SC, which they consider equivalent to the stratotype. As noted above, *Chesapecten septenarius* is not found stratigraphically above the Rushmere Member of the Yorktown, and in contrast to other workers who include this taxon in the Duplin fauna (see Ward et al., 1991:277), Campbell and Campbell (1995) noted its extinction prior to deposition of their concept of the Duplin Formation. They explain this discrepancy by noting (p. 58) that "the majority of species noted by Dall (1903) from 'Natural well and vicinity of Magnolia' came from the Strickland Farm rather than from Natural Well ... ." Campbell (1993:9) does, however, note the presence of *C. septenarius* in the type section of the Raysor, as do Ward and Huddlestun (1988). If *C. septenarius* is indeed absent from the highly fossiliferous Natural Well stratotype, then this would lend support to a post- Raysor/upper Goose Creek/Rushmere aged Duplin Formation, as well as to a possible Morgarts Beach Member correlation; the age of the Duplin is further investigated below.

The Duplin Formation has long been considered extremely fossiliferous; Campbell and Campbell (1995) noted over 450 molluscan species from this unit. Traditionally it has been considered to have been deposited during the same major transgression as that under which the Rushmere-Morgarts Beach members of the Yorktown Formation were deposited. The geomorphic expression of this middle Pliocene shoreline has resulted in a long, nearly continuous feature, which extends from North Carolina to Florida (e.g., Dowsett and Cronin, 1990; Rovere et al., 2015). In South Carolina this feature is known as the Orangeburg Scarp; in Virginia as the Chippenham-Thornburg Scarp. Ward et al. (1991:276) noted that these deposits "overlapped the entire Coastal Plain and portions of the eastern Piedmont," and that "[a]long the western margin of the outcrop belt, Rushmere strata rest directly on crystalline rocks ... ." On the basis of planktonic foraminiferans, calcareous nannofossils, and ostracods collected from two sites, one each in SC and NC near the Orangeburg Scarp, Dowsett and Cronin (1990:436) determined that this major transgression ranged from 3.5 to 3.0 Ma. They additionally noted a correlation of the Duplin and its equivalents "to the uppermost part of zone N19 and part of zone N20 of Blow (1969) and to zone PL3 of Berggren (1973)," which closely matches Ward and Huddlestun's (1988) designation of the Raysor Formation to N20/PL3.

Since Dowsett's and Cronin's (1990) publication, not only has the GPTS been significantly refined, but so have LADs of several biochronologically significant foraminiferans and calcareous nannofossils (e.g., Lourens et al., 2004; Mudelsee and Raymo, 2005). GTS2012, in which marine oxygen isotope stratigraphy has been astronomically tuned over the Pliocene, allows for a reassessment of the age of this transgression. A correlation to upper N19, lower N20, and PL3 would indicate an age of about 3.5 to 3.8 Ma (Fig. 3C). Importantly, however, and as seen in Figure 3C, if the Duplin is younger than the upper Goose Creek/Raysor/Rushmere, then it cannot have been deposited prior to 3.66 to 3.63 Ma, as those points in time correspond to what Lawrence et al. (2009:8) referred to as "precursor glaciations" at marine isotope stages Gi4 and Gi2, respectively (i.e., precursors to intensification of large scale Northern Hemisphere glaciation [NHG] at ~2.7 Ma; see Fig. 3C). Similarly, the Duplin cannot have been deposited from 3.340 to 3.295 Ma either (marine isotope stages MG2–M2), as these also represent significant (and early) events of NHG with estimates of sea level approximately 65 m below present (Lisiecki and Raymo, 2005; Mudelsee and Raymo, 2005; Dwyer and

Chandler, 2009; Lawrence et al., 2009). This constrains the age of the Duplin to between 3.34 and 3.63 Ma; hence our placement of the Duplin during the early Piacenzian highstand at MIS MG7 at 3.5 Ma (Fig. 3C).

On the other hand, there were significant events of sea-level rise within the PRISM interval, or Middle Piacenzian Warm Period (MPWP), centered at about 3.2 Ma (e.g., Dowsett and Cronin, 1990; Dowsett, 2007; Dowsett et al., 2005, 2009, 2010, 2011, 2016) during which the Duplin could have been deposited, and it is in this window that L. Campbell (pers. comm. to AES and LBA, 2009) suggests the unit was formed (Fig. 3C). These high sea-level events, particularly MIS KM5 and KM3 estimated at about 25-30 m above present, followed the dramatic sea-level lowering at MIS M2, and they, in turn, were followed by another major lowstand at KM2 (40 m below present) at about 3.15 Ma (Dwyer and Chandler, 2009).

In summary, the age of the Duplin remains somewhat equivocal. If it is indeed younger than the Goose Creek/Raysor/Rushmere, then it was either deposited during the MG7 sea level highstand at about 3.5 Ma, or within the MPWP during marine isotope stages KM3 or KM5 at about 3.2 Ma. Based on the above, and keeping in mind that there are few places, if any, in SC where the stratigraphic relationships of these units are exposed in outcrop, it should be obvious that the determination of whether a fragmentary vertebrate fossil originated from the Raysor or the Duplin formations is a challenging exercise. However, on the basis of the more siliciclastic nature of the Duplin Formation inasmuch as it represents a more shoreward facies than the Raysor (regardless of age), the fossilized remains of terrestrial mammals are more likely to have derived from the former than the latter in those areas of SC where mammals are being recovered from distinctively sandy/shelly units of appropriate age. These include the remains of *Phugatherium* and *Glyptotherium* from Florence and Dorchester counties, respectively.

In the Charleston area, Ward et al. (1991:277) noted that the Duplin Formation grades laterally into a “calcarenite that is relatively free of siliciclastics” which they further noted was mapped as the Raysor Formation following the recommendation of Blackwelder and Ward (1979). This description prompts the question as to whether the *siliciclastic-free* calcarenite might more accurately be the Goose Creek Limestone, and if their Duplin is actually the Raysor, particularly considering Blackwelder’s and Ward’s (1979) mistaken assignment of Goose Creek exposures at Givhans Ferry to the Raysor Formation, and Weems et al.’s (1982) assessment of the Raysor in the Charleston area as a biocalcarenite with a *quartzose* matrix (and the Goose Creek as a biocalcarenite with a calcareous matrix). The interpretation that the Raysor Formation is the down-dip facies of the Duplin Formation is certainly tenable between Charleston and the NC border given the more calcareous nature of the former relative to the more siliciclastic nature of the latter; but it is our opinion that Ward et al. (1991) erred in their concept of a relatively clastic-free Raysor Formation in the Charleston area. This siliciclastic-free unit is likely the Goose Creek Limestone.

Cypresshead Formation. Although described and characterized primarily in Wayne and Effingham counties, Georgia, Huddlestun (1988:122) also noted that the Cypresshead Formation extends “at least as far north as the vicinity of Summerville in Dorchester County, South Carolina ....” These burrowed, bioturbated, non-phosphatic, horizontal and cross-bedded sands are considered to have been deposited in a coastal beach/sound environment. Stratigraphic and limited paleontological data indicate a late Piacenzian (late Pliocene, PL5/N21) age (Huddlestun, 1988). No vertebrate fossils are known from this unit.

Pleistocene Series (2.59 – 0.0117 Ma)

In the most recent synthesis of Pleistocene mammalian faunas of SC, Sanders (2002) added taxa previously unknown from the state, updated the identification of some known specimens, and also included discussions and clarifications of the geologic units from which many of the specimens were recovered. Of particular importance are his discussions on the “Ashley River phosphate beds,” from which so many of Charleston’s fossils were recovered, and which he determined were derived from the middle portion of the Wando Formation of McCartan et al. (1980). The following discussion reiterates information provided in Sanders (2002), but also provides further details on discoveries that were just coming to light as that work was being published, such as the spectacular assemblage of beautifully preserved mammals that constitute the Camelot Local Fauna, the rich and highly diverse Walrus Ditch Local Fauna, and the equally important Crowfield Local Fauna. The fossils from these three assemblages are curated at the SCSM.

Waccamaw Formation (Lower Pleistocene). Originally named the "Waccamaw beds" by Dall (1892) for shelly sands exposed along the Waccamaw River in Horry County, it was Blackwelder (1979) who formalized the term "Waccamaw Formation." Ward et al. (1991:282) noted the unit's limited distribution as occupying "an area on the southeastern flank of the Cape Fear arch." They also noted that the Waccamaw sites along the Intracoastal Waterway in Horry County had a "somewhat different" molluscan fauna than the sites in Columbus and Brunswick counties, NC, thus concluding that the two beds were deposited during separate transgressions. This, in turn, led to the concept of an upper and lower Waccamaw. According to Ward et al. (1991) the upper Waccamaw is represented by those beds at Calabash, NC, and along the Intracoastal Waterway in Horry County, SC, whereas the lower Waccamaw is represented by sites in Columbus and Brunswick counties, NC, such as the Old Dock, Shallotte, and Walkers Bluff localities. Campbell and Campbell (1995) recognized both the upper and lower units at Calabash noting their separation by an unconformity. (Also see abstracts by Graybill et al., 2009; Kelley et al., 2010a, b; Badyrka et al., 2010).

Several attempts have been conducted to accurately date the Waccamaw Formation, including the use of calcareous nannoplankton, planktic foraminiferans, molluscs, ostracods, ^{87}Sr/^{86}Sr analysis, amino acid racemization, uranium series dating, and magnetostratigraphy (e.g., McCartan et al., 1982; Cronin et al., 1984, Bybell, 1990; Ward et al., 1991; Campbell and Campbell, 1995; Graybill et al., 2009; Appleby et al., 2010; Badyrka et al., 2010). Most of these have resulted in a generalized "late Pliocene-early Pleistocene" age assignment for the unit. Note, however, that the recent establishment of the Pliocene-Pleistocene boundary at the base of the Gelasian Stage (Gibbard et al., 2010) results in placement of the unit wholly within the lower Pleistocene.

According to Campbell and Campbell (1995:66), "the lower Waccamaw dates from 2.4 Ma based on the planktonic foraminifera, and from 2.53 Ma by U-He coral dates from correlative deposits in southern Florida (Bender, 1973)." They added that the molluscan fauna was dominated by mid-shelf species, many of which Ward et al. (1991:288) noted grew to large size "suggesting optimal [subtropical to tropical] conditions..." Between 2.42 and 2.52 Ma are three significant events of sea level lowering at marine isotope stages 96, 98, and 100 (Lisiecki and Raymo, 2005), therefore precluding deposition of the lower Waccamaw over that interval. Preceding those events are two highstands at stages 101 and 103 (2.57 Ma and 2.59 Ma, respectively), but more significant are the intervals of high sea level at stages 93 and 91, at about 2.38 and 2.34 Ma, respectively; it is to these stages that we correlate deposition of the lower Waccamaw Formation (Fig. 3C).

Edwards et al. (2000) determined that the Waccamaw Formation extends farther south into SC (into Dorchester County) than previously considered, although separation into upper and lower units is not as easily determinable as in its more typical area to the north. Bearing on the age of this unit is the Walrus Ditch Local Fauna, also from Dorchester County (Downing and White, 1995; Fields et al., 2012). Although the sediments from which the fauna was recovered yielded both marine and terrestrial species, their gravelly, poorly sorted, coarse-grained nature failed to yield microfossils that might help refine its age. However, referral of these beds to the Waccamaw Formation is supported by the nearly identical description of that unit by Edwards et al. (2000) from several cores drilled in Dorchester County, who noted that the unit weathers to a dark-yellowish-orange to reddish-brown color – exactly that seen at the Walrus Ditch locality.

Table 3. Mammalian taxa of the Walrus Ditch Local Fauna and their known ranges.

Megalonyx leptostomus	early to late Blancan
Eremotherium eomigrans	early late Blancan – early Irvingtonian
Pachyarmatherium leiseyi	early late Blancan – early Irvingtonian
Holmesina floridanus	early late Blancan – early Irvingtonian
Dasypus bellus	early late Blancan – Rancholabrean
Sylvilagus webbi	late Blancan – earliest Irvingtonian
Castoridae indet.	
Peromyscus sp.	Barstovian – Recent
Allophaiomys pliocaenicus	latest Blancan – middle Irvingtonian
Erethizon ?bathygnathum	late middle Blancan – late Blancan
Phugatherium? sp.	early late Blancan -- Rancholabrean
Smilodon gracilis	late Blancan – middle Irvingtonian
Canis lepophagus	middle Blancan – late Blancan
Arctodus pristinus	late Blancan – late Irvingtonian
Procyon sp.	late Hemphillian – Recent
Nannippus sp.	late Clarendonian – late Blancan
Equus sp.	Blancan – late Rancholabrean
Tapirus haysii	late Blancan – middle Irvingtonian
Mylohyus sp.	latest Hemphillian – Irvingtonian
Hemiauchenia macrocephala	late Blancan – Rancholabrean
Odocoileus virginiana	late Blancan – Recent
Rhynchotherium falconeri	late Hemphillian – late Blancan

The terrestrial species include several indicative of a late Blancan to early Irvingtonian age, some of which have long ranges, but others of which are biochronologically significant (Table 3). The presence of the porcupine *Erethizon* limits the maximum age of the fauna to about 2.6 Ma, whereas the presence of *Nannippus* places a youngest limit on the fauna of about 2.1 Ma (Bell, 2004). The occurrence of *Allophaiomys* represents one of the oldest records of this taxon in North America. These records provide a late Blancan age for the fauna (also see Fields et al., 2012), again compatible with our correlation to marine isotope stages 93 and 91.

Correlation of the Walrus Ditch LF to the late Blancan also supports placement of the lower Waccamaw Formation in chron C2r2r, the lowermost reversed interval of the Matuyama Chron, spanning 2.2-2.58 Ma. Although Liddicoat et al. (1981) reported a reversed polarity for the Waccamaw beds in the Charleston area, which would provide further support for our correlation, later interpretation of those beds by Weems and Lemon (1988) resulted in a Penholoway Formation assignment (the unit overlying the Waccamaw). Nevertheless, the variety of data from the lower Waccamaw converges on a date of about 2.3-2.4 Ma (Figs. 2C, 3C). In addition to the terrestrial mammals listed in Table 3, the fauna also includes cetaceans representative of four families (Delphinidae, Kogiidae, Pontoporiidae, and Mysticeti), a dugongid, an undescribed taxon of walrus (the fauna's namesake), and several species of marine birds and marine/estuarine fish.

Blancan aged mammals from the highly mixed assemblage recovered from the earlier noted Clapp Creek locality in Kingstree, SC, may also be derived from the lower Waccamaw, as these are represented by teeth of *Ondatra idahoensis*, *Holmesina floridanus*, capybara, *Nannippus pen-*

insulatus, and *Cormohipparion* sp. (SC2012.10.2). (In addition to these Blancan species and to the dinosaurs, plesiosaurs, and mosasaurs recovered there, the Clapp Creek site has also yielded evidence of later Pleistocene mammals including a tooth fragment of *Megalonyx* sp., a lower molar of *Tapirus veroensis* [SC2012.10.1], several teeth and tooth fragments from *Equus* sp., a partial lower molar of *Cervus* sp., and several fragments of ivory and enamel from proboscidean teeth [mammutid and/or gomphotheriid, not *Mammuthus*]).

The upper Waccamaw, which is present at Blackwelder's (1979:A54) lectostratotype locality ("180 m downstream from Tilly Lake on the Waccamaw River, Horry County") and at sites along the intracoastal waterway near Myrtle Beach in Horry County, has a reversed magnetic polarity (Cronin et al., 1984; also see Liddicoat and Opdyke, 1981). Together with Bybell's (1990) determination that these sediments were deposited during the lower part of nannoplankton zone NN19, these data support referral of the upper Waccamaw to chron C1r2r (Figs. 2C, 3C). The upper Waccamaw, therefore must be younger than the 1.77 Ma top of the Olduvai normal chron, but older than the 1.34 Ma LAD of the nannofossil *Helicosphaera sellii* noted from this unit by Cronin et al. (1984) and by Bybell (1990). McCartan et al. (1982:339) noted a 1977 personal communication from M. L. Bender that "corals from the Waccamaw Formation have 1.1–1.4 my dates by the He/U method." Campbell and Campbell (1995:66), noting the dominance of littoral and shallow sublittoral species in the upper Waccamaw, considered it a direct correlate of the upper Caloosahatchee of southern Florida, "which unconformably underlies the 1.5 Ma Bermont beds." We place the upper Waccamaw Formation at 1.6 Ma, coincident with marine isotope stage 55 (Fig. 3C). Mammals noted from the "upper bed" of the Waccamaw by Sanders (2002:131) include *Neofiber* cf. *N. diluvianus* (referred in this report to *Ondatra idahoensis*; see discussion in "Systematic Paleontology" section), *Cuvieronius* sp., *Miracinonyx inexpectatus*, *Hydrochoerus holmesi*, and *Tapirus haysii*.

Another locality in Dorchester County that may occur in the upper Waccamaw Formation consists of a series of closely situated sites collectively referred to as the Austin Sand Pits. Located near Ridgeville, SC, the fossil mammals collected there constitute the Ridgeville Local Fauna of Boessenecker et al. (2018), who consider it somewhat younger than the Walrus Ditch LF, i.e., latest Blancan to earliest Irvingtonian. A faunal list provided in Boessenecker et al. (2018) includes material referred to the cetotheriid mysticete *Herpetocetus* sp., the Gray Whale *Eschrichtius* sp., cf. *E. robustus*, the Bowhead whale *Balaena* sp., cf. *B. mysticetus*, the extinct mysticete *Balaenula* sp., the Humpback whale *Megaptera* sp., the large rorqual *Balaenoptera*, the delphinid *Astadelphis*, and the early Sperm whale *Physeterula* sp. M. Gibson of The Charleston Museum (pers. commun. to LBA, March, 2017) notes that material of another early sperm whale, *Scaldicetus* sp., is also known from the Austin Pit. Boessenecker et al. (2018) also reported the presence of the walrus *Ontocetus emmonsi* in the Ridgeville Local Fauna, as well as the terrestrial mammals *Equus* sp., *Tapirus* sp., cf. *Cuvieronius* (more likely *Rhynchotherium* based on age; see discussion of *Rhynchotherium* in "Systematic Paleontology" section), *Castoroides* sp. (perhaps *Procastoroides* based on age), *Neochoerus pinckneyi*, *Eremotherium* sp. (likely *E. eomigrans* based on age), and cf. *Holmesina* (likely *H. floridanus* based on age). They concluded that the Austin Pit Site occurs in sediments stratigraphically above those that yield the Walrus Ditch LF and suggest that it may lie within the upper Waccamaw Formation.

Penholoway Formation (Uppermost Lower Pleistocene). The term Penholoway, in the geological sense, was originally applied by Cooke (1925) as a name for a marine terrace, the type area of which is in Wayne County, Georgia. Later, Cooke (1936, 1943, 1945) applied the name Penholoway Formation for the deposits underlying the terrace. Huddlestun (1988) abandoned "the lithostratigraphic context of the Penholoway," retaining the name for its original intent, the terrace. Edwards et al. (2000) maintained lithostratigraphic use of the term for the "coastal complex of estuarine, lagoonal, barrier island, and shallow marine shelf deposits" that crop out in Wayne County, and also for correlative strata that occur across the SC Coastal Plain (unit Q5 of McCartan et al., 1990). Bybell (1990) suggested a date for the unit of between 700 and 925 kyr based on calcareous nannoplankton and uranium series dating of corals (Szabo, 1985), and this appears to have been refined by Edwards et al. (2000), who reported an age spanning the interval from 730 to 900 kyr. Weems et al. (1997) noted a 1984 personal communication from L. Bybell who considered the age of the Penholoway Formation as no older than the upper part of Quaternary Zone NN19. The upper part of NN19 falls within the uppermost reversed portion of the Matuyama chron (C1r1r), and supporting this correlation is the reversed magnetic polarity of the Penholoway (see discussion above regarding polarity of "Waccamaw" beds in the Charleston area). Given, therefore, that the unit must be between 0.78 and 0.99 Ma based on magnetostratigraphy, and that it was apparently deposited during a major transgression (Weems et al., 1997), we suggest that deposition occurred during the significant sea level high at marine isotope stage 21, or about 850 kyr (Fig. 3C).

The molluscan fauna of the Penholoway Formation appears to be correlative with that of the stratotype James City Formation of DuBar and Solliday (1963), which is located on the south bank of the Neuse River in southeastern North Carolina. The James City Formation is a later name for the older of two "very different and unrelated lithic units" earlier referred to the "Croatan beds" of Dall (1890, 1892; see discussion in Blackwelder, 1981:B2–B3, B11–B12, and in Ward et al., 1991:281). The Penholoway and James City formations both contain nearly identical taxa, including many extant forms, and both also include the exceptionally rare gastropod *Calliostoma erosa* Dall, 1892, a taxon known only from its unique Croatan holotype until a Penholoway specimen was discovered in SC. The stratotype James City Formation is not the same as the "James City Formation" of Ward and Blackwelder (1987). Dated to approximately 2.4 Ma, the latter strata are located at Aurora, NC (McCartan et al., 1982), and they contain a fauna that is largely extinct.

Sanders (2002) noted the following mammals from the Penholoway Formation: *Dasypus bellus* (early late Blancan to Rancholabrean), *Eremotherium* sp., *Miracinonyx inexpectatus*, *Equus* sp., and *Cervus elaphus*. More recent analysis of the *Eremotherium* material by Fields et al. (2012) provided an updated referral to *E. laurillardi*, thus extending the Rancholabrean range of this taxon into the middle Irvingtonian. The stratigraphic context of a specimen of *E. laurillardi* from the Penholoway Formation (ChM PV4748, see Fields et al., 2012:6) is provided in Figure 12.

Ladson/Canepatch Formation (Middle Pleistocene). The Ladson Formation was named by Malde (1959) for deposits near Ladson (Summerville area) that represent a coastal complex similar to that noted above for the Penholoway Formation. Edwards et al. (2000) noted the possible correlation of the Ladson with the Canepatch Formation of the Myrtle Beach area, and the unit is also correlative with unit Q4 of McCartan et al. (1990). Liddicoat and Opdyke (1981) noted a normal polarity (i.e., C1n) for the Canepatch Formation and, as noted in Bybell (1990), Szabo (1985) reported uranium-series ages from corals for the unit that clustered around 460 kyr. Szabo (1985:403, 405) further noted that the Canepatch Formation represented deposition during an interglacial high sea level stand, which he correlated to MIS 11 rather than 13 "because oxygen isotope values suggest that the interglacial represented by oxygen stage 11 was warmer and of longer duration than was stage 13." This has since been confirmed, with estimates of sea level at ~6 to 13 meters above present (see Raymo and Mitrovica, 2012; Candy et al., 2014; and references within). The more recent astronomically tuned correlations (e.g., Lisiecki and Raymo, 2005) place MIS 11 at 410 kyr, and it is MIS 13 that is closer to 460 kyr. With error bars of ±100,000 yr on the coral dates, MIS 11 remains our favored correlation due to its greater magnitude than MIS 13 (Fig. 3C).

The late Irvingtonian aspect of the mammals known from the Ladson Formation provides additional support for a correlation to MIS 11. Sanders

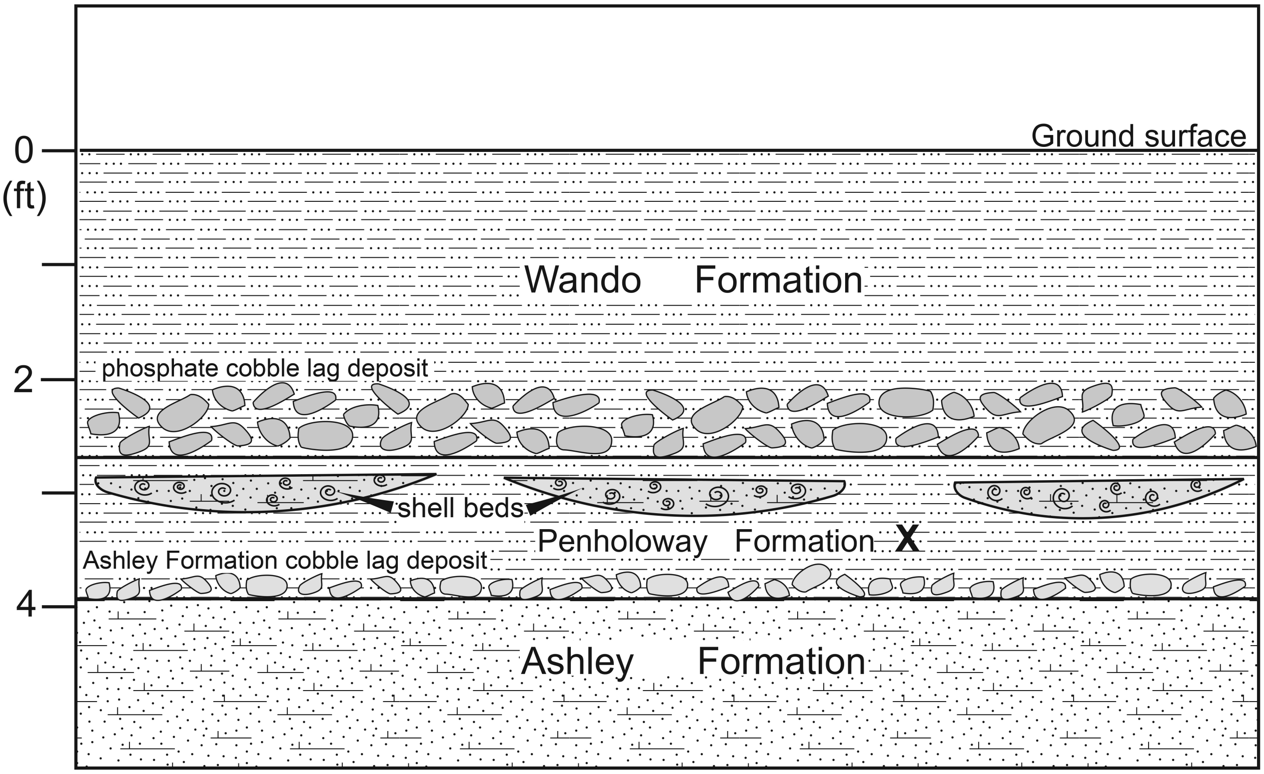


Figure 12. Stratigraphic context of ChM PV4748, *Eremotherium laurillardi* (marked by "**X**"), recovered from the Penholoway Formation near Trailwood Trailer Park, North Charleston, Charleston County (see Fields et al., 2012:6 for further details).

(2002) noted the following terrestrial vertebrates from this unit: *Megalonyx jeffersonii* (late Irvingtonian to Rancholabrean), *Eremotherium laurillardi*, *Arctodus pristinus* (late Blancan to late Irvingtonian), *Equus* sp., and *Tapirus veroensis* (late Irvingtonian to Rancholabrean). In addition, however, is the spectacular assemblage of beautifully preserved fossil mammals that comprise the Camelot Local Fauna (Kohn et al., 2005; Beaty et al., 2007; Fields, 2010; Barbiarz, et al., 2018). Considered most similar to the latest Irvingtonian (0.3–0.4 Ma) Coleman 2A Local Fauna of Florida (Martin, 1974; Morgan, 2005), Kohn et al. (2005:649) noted that "the site is one of the most productive and diverse middle Pleistocene sites in eastern North America outside of Florida, and it contains some of the best preserved examples of specific taxa such as saber-toothed cats (*Smilodon fatalis*) outside of the La Brea tar pits, California." The Camelot assemblage was recovered from fluvial sediments resting unconformably above the Tupelo Bay Formation at the Giant Cement quarry in Dorchester County that are considered equivalent to the Ladson Formation. The fauna includes *Megalonyx jeffersonii* (or a form transitional between *M. wheatleyi* and M. *jeffersonii* per Fields, 2010), *Holmesina septentrionalis*, *Dasypus bellus*, *Didelphis virginiana*, *Scalopus* sp., *Lepus* sp., *Sylvilagus palustris*, *Sciurus carolinensis*, *Thomomys* sp., *Sigmodon bakeri*, *Neofiber ?alleni*, *Neochoerus* sp., *Procyon lotor*, *Urocyon cinereoargenteus*, *Smilodon fatalis*, *Miracinonyx inexpectatus*, *Canis armbrusteri*, *Mylohyus* sp., *Platygonus* sp., *Paleolama mirifica*, *Hemiauchenia macrocephala*, *Odocoileus virginianus*, *Tapirus veroensis*, and *Equus* sp.

Ten Mile Hill Formation (Upper Middle Pleistocene). Another complex of fluvial, estuarine, and barrier island deposits, the "Ten Mile Hill beds" of Weems and Lemon (1984a, b), and named for Sloan's (1908) "sands on Ten Mile Hill," were originally included within the Ladson Formation of Malde (1959). But Weems and Lemon (1984a, b) separated these beds out as a different unit "because they record a different and younger transgression and regression of the sea than that recorded by the beds of the Ladson type section." This was confirmed by Szabo's (1985) uranium series dating of corals from these beds, indicating deposition from around 202 to 230 kyr ago. Deposition over this interval results in a correlation, as noted by Szabo (1985), to MIS 7 (Fig. 3C). The Ten Mile Hill beds are also equivalent to unit Q3 of McCartan et al. (1990), who considered this unit correlative (in part) with the Socastee Formation of the Myrtle Beach area (see below).

Sanders et al. (2009) elevated these beds to formational status and noted their particular importance insomuch as they yielded the oldest well dated remains of *Bison* in the conterminous USA. The appearance of *Bison* in North America south of the 55th parallel defines the beginning of the Rancholabrean NALMA, and prior to the recovery of the specimen from the Ten Mile Hill Formation there was little temporally well-constrained material that might provide an accurate date for the Irvingtonian/Rancholabrean boundary (see Bell et al., 2004). Thus, we consider the fauna derived from this formation as the oldest in North America (south of the 55th parallel) representative of the Rancholabrean.

In addition to *Bison*, Sanders et al. (2009) listed the following taxa from the Ten Mile Hill Formation: *Dasypus bellus, Holmesina septentrionalis, Eremotherium laurillardi*, *Odobenus* sp., *Hydrochoerus holmesi*, *Tapirus haysii*, *Equus* sp., and *Cuvieronius* sp. In this report we add *Sylvilagus palustris* and *Castor canadensis*. Last occurring in Florida in the middle Irvingtonian, the record of *T. haysii* from the Ten Mile Hill Formation provides an extension of this taxon into the earliest Rancholabrean and a relatively short temporal interval of overlap with *T. veroensis*, which first appears in Florida in the late Irvingtonian (Hulbert, 1995).

Socastee Formation (Upper Pleistocene). The Socastee Formation of DuBar (1971) and DuBar et al. (1974) is represented by back-barrier or estuarine deposits that, according to McCartan et al. (1982:351), comprise "the major surficial unit along the [Intracoastal] Waterway" in the Myrtle Beach area. As noted by Szabo (1985), however, McCartan et al's. (1982) interpretation of this unit was much broader than that of DuBar et al. (1980). The latter considered only the narrow, uppermost deposit of sand overlying the Canepatch Formation (= Ladson Formation) along the waterway near the Route 501 bridge as Socastee, designating all the underlying sediment at that location to the Canepatch Formation. In an attempt to resolve this, Szabo (1985) analyzed samples from the Route 501 bridge locality for uranium-series dating, but the equivocal results were disregarded as unreliable. Weems and Lemon (1993) consider this unit correlative with the lower member of the Wando Formation.

Sanders (2002) noted the recovery of the distal end of a humerus of the phocid seal *Erignathus barbatus* from a coarse sand deposit that evidently is exposed intermittently along the south bank of the Intracoastal Waterway toward the northeastern limits of Myrtle Beach. He also reported a partial dentary of *Monachus tropicalis* from "along the Intracoastal Waterway at the Possum Trot Golf Course near the town of Crescent Beach, Horry County, South Carolina ..." (Sanders, 2002:76). Although both specimens were reported as being recovered from the Socastee Formation, whether they came from correlative sediments cannot be determined; nor is it unequivocal that they were recovered from the Socastee Formation given the varying interpretation of this unit noted above. However, supporting assignment of these vertebrate-bearing beds to the Socastee Formation, rather than to the older Canepatch (= Ladson) Formation, is the fact that both species are currently extant; i.e., taxa that range from the Rancholabrean to Recent are somewhat more likely to occur in Socastee deposits than in Canepatch (late Irvingtonian) deposits. Sanders (2002) also noted the questionable recovery of *Holmesina septentrionalis* and *Tremarctos floridanus* from the Socastee, but these specimens, having been found on Myrtle Beach, may also have originated from an undetermined late Pleistocene unit, or units, that lie offshore.

Wando Formation (Upper Pleistocene). As noted by Edwards et al. (2000), this unit was originally named by McCartan et al. (1980) for outcrops near the Wando River representative of "a coastal complex of fluvial, estuarine, lagoonal, barrier-island, and shallow-marine shelf deposits." It also includes the beds of shelly sand, clayey sand, and clay mapped as unit Q2 by McCartan et al. (1984; also see McCartan, 1990, and McCartan et al., 1990) that underlie the Pamlico and Prince Anne terraces of Colquhoun (1974). Szabo (1985) recognized two depositional episodes within the Wando which he referred to as "early Wando deposits" and "late Wando deposits." He reported an average age for the lower Wando of 129,000 ± 10 kyr and 87,000 ± 4 kyr for the upper, with a consequent correlation to oxygen isotope stage 5. Sanders (2002), following Weems and Lemon (1993), further divided the Wando into upper, middle, and lower members, and it is the middle member that he determined to be the unit of origin for most of the Charleston area's fossil vertebrates collected from the famous "Ashley River phosphate beds."

The principle collection of fossils from the Ashley River phosphate beds curated at The Charleston Museum includes nearly 200 specimens that were provided by Charles C. Pinckney, Jr. From 1869 until 1910, Pinckney owned the Magnolia Phosphate Mine in the vicinity of Runnymede Plantation about 11 miles northwest of Charleston along the Ashley River (Sanders 2002). In addition to Domning's (1989b) discussion of the Charleston phosphate beds, Sanders (2002) provided a thorough discussion of the Pinckney collection with details of its provenance and acquisition. Sanders (2002) listed the following taxa from the Wando Formation: *Megalonyx jeffersonii*, *Neochoerus pinckneyi*, *Hydrochoerus holmesi*, *Castor canadensis*, *Neofiber alleni*, *Canis dirus*, *Arctodus pristinus* (but see discussion below), *Ursus americanus*, *Odobenus rosmarus*, *Hemiachenia* sp. cf. *H. macrocephala*, *Rangifer* sp. cf. *R. tarandus*, *Cervalces scotti*, *Cuvieronius* sp., and *Mammut americanum*. To this can be added *Equus* sp., *Tapirus veroensis*, *Bootherium bombifrons*, and *Mammuthus columbi*.

It has long been recognized that several species known from the Ashley River phosphate beds are much older than the Rancholabrean age implied by Szabo's (1985) dates on the Wando Formation, evidently having been reworked into this unit from subjacent strata. This was noted as early as Leidy (1877:210) in which he stated: "Besides the phosphate nodules, the Ashley beds present a remarkable intermixture of the remains of marine and terrestrial animals, consisting of bones, teeth, coprolites, shells, etc., derived from the contiguous formations of various ages from the early tertiary [sic] to those of a comparatively recent period." Domning (1989b) also noted the temporally (and ecologically) mixed nature of the fossils from the phosphate beds and their likely stratigraphic provenance. In fact, the Wando Formation rests unconformably on a variety of older units including the Oligocene Ashley, Chandler Bridge, and Edisto formations, the lower Pliocene Goose Creek Limestone, and the Pleistocene Penholoway Formation.

Some of the most dramatic examples of this reworking are specimens of late to latest Oligocene age including the horse *Anchippus texanus*, the entelodont *Daeodon mento*, the dugongids *Dioplotherium manigaulti* and *Crenatosiren olseni*, and the early odontocete cetaceans *Agorophius pygmaeus* and *Xenorophus sloanii*. *Daeodon*, and possibly *Anchippus*, may be reworked from the Edisto Formation, whereas the dugongids and cetaceans are known from the Ashley and Chandler Bridge formations. Another cetacean from the phosphate beds, the beaked whale *Choneziphius trachops* Leidy, 1876a, is also known from the lower Miocene (Burdigalian) Pungo River Formation at the Lee Creek Mine, NC (Whitmore and Kaltenbach, 2008). Its presence in the Wando, therefore, suggests reworking from what may have been the Marks Head Formation based on the correlation of Ward (2008:fig. 3). The same may hold true for several additional, highly worn, fossil beaked whale specimens (noted previously) reported from the phosphate beds by Leidy (1877) and Allen (1926), as well as the holotype of another ziphiid, *Anoplanassa forcipata* Cope, 1869 (also see True, 1907), recovered during dredging operations for phosphate rock in the Coosaw River of Beaufort County. On the other hand, these specimens may have also been reworked from the Goose Creek Limestone or perhaps from another, now missing Pliocene unit, such as the Wabasso beds or a bed correlative with the Sunken Meadow Member of the Yorktown Formation. This supposition is based on the abundant fossil material of beaked whales from the Pliocene of Italy (Bianucci, 1997) that very closely resembles specimens from SC, as well as on the recovery of another species, *Tusciziphius crispus* Bianucci, 1997, originaly described from the Pliocene of Italy, but which is now known from what is thought to be the Goose Creek Limestone from the bottom of the Morgan River in Beaufort County (Post et al., 2008).

Another example may be Leidy's (1854) holotype of the bear *Arctodus pristinus*. That now lost specimen consisted of a single isolated molar that was recovered from the Ashley phosphate beds (= Wando Formation) at Bee's Ferry on the west bank of the Ashley River northwest of Charleston (Sanders, 2002). Discussed in detail in the "Systematic Paleontology" section on this taxon below, it is now thought to have been reworked into the Wando Formation from a more age-appropriate subjacent unit, as *A. pristinus* is no longer considered to have existed during the Rancholabrean (Emslie, 1995; Schubert, 2008; Schubert et al., 2010).

More recent collections from the Wando Formation include the highly diverse assemblage of vertebrates that comprise the Crowfield Local Fauna (Chandler and Knight, 2009; Fields et al., 2012). Recovered as a result of the excavation of a lake in the Crowfield subdivision between Goose Creek and Summerville "along the Dorchester-Berkeley county line," the fauna includes 55 identified mammalian taxa, 11 species of birds, and "a substantial herpetofauna" (Chandler and Knight, 2009:143). Although not yet studied in detail, the mammals of the Crowfield Local Fauna are listed in Table 4.

"Silver Bluff beds." Thin deposits of sand, mud, and clay are present beneath a coastal terrace about 2 m above modern sea level known as the Silver Bluff terrace (Puri and Vernon, 1964). Rec-

Table 4. Mammals of the Rancholabrean-aged Crowfield Local Fauna.

Didelphis virginiana
Megalonyx jeffersonii
Holmesina septentrionalis
Dasypus bellus
Sorex longirostris
Sorex sp. cf. *S. arcticus*
Sorex sp. cf. *S. palustris*
Microsorex hoyi
Blarina brevicauda
Blarina sp.
Cryptotis parva
Scalopus aquaticus
Condylura cristata
Sylvilagus floridanus
Sylvilagus palustris
Sciurus carolinensis
Ictidomys tridecemlineatus
Glaucomys volans
Castoroides dilophidus
Castor canadensis
Oryzomys sp.
Peromyscus sp.
Sigmodon hispidus
Neotoma floridana
Microtus pennsylvanicus
Microtus pinetorum
Microtus ochrogaster
Synaptomys cooperi
Synaptomys australis
Neofiber alleni
Ondatra zibethicus
Erethizon dorsatum
Lynx rufus
Urocyon cinereoargenteus
Canis sp.
Tremarctos floridanus
Ursus americanus
Lontra canadensis
Spilogale putorius
Mephitis mephitis
Neovison vison
Procyon lotor
Odobenus rosmarus
Equus sp.
Tapirus veroensis
Mylohyus sp.
Hemiauchenia macrocephala
Palaeolama mirifica
Rangifer tarandus
Cervus elephus
Odocoileus virginianus
Bison sp.
Mammut americanum
Trichechus manatus

ognized and mapped in Florida, Georgia, and South Carolina as far north as the vicinity of the Santee River, deposits immediately beneath this terrace are typically between 1.5 and 3 m thick, but locally can be up to 10.5 m thick in filled buried channels (Weems and Lemon, 1993). These deposits previously have been assigned either to the uppermost Sangamon stage (MIS 5A) or the middle Wisconsian stage (MIS 3) (Colquhoun, 1974), although the bulk of this unit is probably middle Wisconsian in age based on a ^{14}C date of 33,070 ± 1830 years (Beta Analytic Laboratory Report B-20188, 1979). This date was obtained from surf-polished wood chips found near the base of the unit in a sand pit in the Fort Moultrie quadrangle near the Atlantic coast (between localities FM 24 and FM 17 in Weems and Lemon, 1993). However, other samples of woody material recovered by augering 1.5 m below the terrace surface in the Fort Moultrie quadrangle (at locality FM 23) yielded ^{14}C ages of only 7,860 ± 80 years (USGS Radiocarbon Laboratory Report W-5038, 1982) and of 6,960 ± 200 years (USGS Radiocarbon Laboratory Report W-5322, 1984). This suggests that in some areas there are local deposits of early Holocene age also present within this terrace complex. The "Silver Bluff beds" have not yet yielded any vertebrate remains that can be unequivocally assigned to them, but it is possible that Wisconsian-age vertebrates found along Edisto and Myrtle beaches derive from offshore deposits of this unit which were scoured from the coastal sea floor and transported to the shoreline.

Additional deposits younger than the Wando Formation. From upper Pleistocene sediments that filled previously noted solution cavities eroded into the top of the upper Eocene Tupelo Bay Formation and into the overlying Harleyville Formation at the Giant Cement quarry, Bentley et al. (1994) recovered the Ardis Local Fauna. ^{14}C dates place the fauna between 18,530 and 18,940 years old, which coincides with the last glacial maximum, and the 43 mammalian species support this. According to Bentley et al. (1994:1) they reflect "a more equitable climate, cooler summers and warmer winters, than that presently occurring in the region." Occasionally, additional specimens turn up in these upper Pleistocene sands, including a virtually complete skull of *Canis dirus* (USNM 437648) that was collected and donated to the USNM by R. Ogilvie (Sanders, 2002), as well as a mammoth molar col-

Table 5. Mammals of the late Rancholabrean Ardis Local Fauna.

Didelphis virginiana
Megalonyx jeffersonii
Holmesina septentrionalis
Dasypus bellus
Sorex sp. cf. *S. longirostris*
Blarina brevicauda
Scalopus aquaticus
Condylura cristata
Sylvilagus palustris
Sylvilagus floridanus
Sciurus carolinensis
Ictidomys tridecemlineatus
Glaucomys volans
Castor canadensis
Oryzomys palustris
Peromyscus sp.
Neotoma floridana
Microtus pennsylvanicus
Microtus pinetorum
Synaptomys cooperi
Synaptomys australis
Neofiber alleni
Ondatra zibethicus
Hydrocheoridae
Smilodon fatalis
Lynx rufus
Urocyon cinereoargenteus
Canis dirus
Tremarctos floridanus
Lontra canadensis
Spilogale putorius
Mephitis mephitis
Conepatus robustus
Neovison vison
Procyon lotor
Equus sp. cf. *E. complicatus*
Tapirus veroensis
Mylohyus nasutus
Palaeolama mirifica
Odocoileus virginianus
Bison antiquus
Mammut americanum
Mammuthus columbi

Table 6. Terrestrial mammals represented from fossils collected on Edisto and Myrtle beaches.

Megalonyx leptostomus
Megalonyx jeffersonii
Eremotherium laurillardi
Paramylodon harlani
Holmesina septentrionalis
Glyptotherium floridanum
Dasypus bellus
Sylvilagus sp.
Castoroides sp.
Castor canadensis
Erethizon dorsatum
Neochoerus pinckneyi
Miracinonyx inexpectatus
Miracinonyx trumani
Smilodon fatalis
Panthera atrox
Felis onca augusta
Puma concolor
Lynx rufus
Urocyon cinereoargenteus
Canis dirus
Canis latrans
Tremarctos floridanus
Ursus americanus
Procyon lotor
Halichoerus grypus
Monachus tropicalis
Odobenus rosmarus
Equus sp.
Tapirus veroensis
Mylohyus fossilis
Palaeolama mirifica
Cervus elephus
Odocoileus virginianus
Bison antiquus
Bootherium bombifrons
Mammuthus columbi
Mammut americanum
Trichechus manatus

lected by JLK after a bulldozer destroyed a partial skeleton. A faunal list of mammals from the Ardis Local Fauna is provided in Table 5.

In addition to the unit that yielded the Ardis Local Fauna are the "undetermined offshore units" from which the late Rancholabrean remains found on Edisto and Myrtle beaches originate (Table 6). As Sanders (2002:7) noted, these units were obviously exposed "during the periods of extremely low sea level that accompanied Wisconsinan glaciation" (~18 to 60 kyrs), but to date there has been no underwater investigation seaward of these beaches that might provide more detailed information about these units. Roth and Laerm (1980) provided an account of the fossil mammals and turtles from Edisto Beach, with additions by Sanders (2002), but there has been no formal treatment of those from Myrtle Beach. Similarly aged vertebrate remains also wash ashore onto Fernandina, Jacksonville, and Ponte Vedra beaches in northern Florida, but as in SC, the unit of origin has not been determined, and there has been no formal treatment of the northern Florida Rancholabrean fauna.

To date there are 36 known taxa in the Edisto Rancholabrean fauna including a new record of *Miracinonyx trumani* (discussed below). Five additional taxa from Myrtle Beach include *Holmesina septentrionalis*, the first report of *Canis latrans* from SC, *Tremarctos floridanus*, *Mylohyus fossilis*, and *Bootherium bombifrons*. Most assuredly, remains of additional Rancholabrean taxa have been recovered from Myrtle Beach (and nearby beaches in Horry County), but these have not been reported or, as far as we know, curated into accessible collections. A similar situation exists regarding fossils from Edisto Beach, including a number of unstudied specimens held in private collections.

Fossils representing several taxa of marine mammals are also recorded from Edisto Beach, and these include *Tursiops truncatus* (Bottlenose Dolphin), *Pseudorca crassidens* (False Killer Whale), *Physeter catodon* (Sperm Whale), *Monachus tropicalis* (Monk Seal), and *Halichoerus grypus* (Gray Seal) (Ray et al., 1968). However, these taxa seem more likely to have been eroded from Holocene sediments found at the top of an augered section drilled by AES and REW at Edisto Beach, rather than from offshore Rancholabrean deposits. The uppermost stratum consisted of 13 feet of shelly sand deposited during the Holocene, probably at the time of the last transgression to its present stand no more than 7600 years ago (Cronin et al., 2007). All are from extant taxa known to have occurred in western Atlantic waters by the Holocene.

In addition to a marine component to the fauna from Edisto Beach and an apparent Holocene component, there are also remains of terrestrial taxa older than those Rancholabrean taxa that comprise the bulk of the fauna (e.g., *Megalonyx leptostomus*; see discussion below). Thus, the "Edisto Beach fauna" actually consists of a temporally mixed assemblage.

ADDITIONS TO THE CENOZOIC MAMMALIAN FAUNA OF SOUTH CAROLINA

Locality information more detailed than that provided below can be found on file in the institutions where the specimens are curated. The use of the question mark ("?") in association with a taxonomic name follows Kornicker (1979).

SYSTEMATIC PALEONTOLOGY
MAMMALIA Linnaeus, 1758
MARSUPIALIA (Illiger, 1811)
DIDELPHIDAE Gray, 1821
DIDELPHIS Linnaeus, 1758
DIDELPHIS VIRGINIANA Kerr, 1792
Figure 13A

Referred Specimens.—SC75.31.70, left dentary with p3–m4; SC2003.75.293, right maxillary fragment with P3–M1; SC2003.75.294, left dentary fragment with p2–3, m2–3, partial m4; SC2003.75.295, left dentary fragment with m4; SC2003.75.296, left dentary fragment with p2-3, m1–4; SC2003.75.297, right dentary fragment with p1, p3; SC2003.75.298, left dentary fragment with p3, m4; SC2004.1.239, right dentary with c, p2–3, m1–4; SC2004.1.240, right dentary with p3, partial m1 and m3, m4; SC2003.75.693, left humerus; SC2003.75.694, partial left humerus; ChM PV7692, atlas vertebra.

Locality, Stratigraphic Horizon, and Age.—SC75.31.70 from Cooper River, ?Wando Formation, late Pleistocene, Rancholabrean; all other SCSM specimens from Camelot locality, Dorchester County, Ladson Formation, middle Pleistocene, late Irvingtonian; ChM PV7692 from "near Bee's Ferry Rd.," Charleston County, Wando Formation, late Pleistocene, Rancholabrean.

Discussion.—Bentley et al. (1994) first reported fossil remains of the Virginia opossum in SC from the very late Rancholabrean Ardis Local Fauna (18–19 kyrs), and Morgan (2002) noted that the earliest records of *D. virginiana* in North America are from two late Irvingtonian faunas in Florida. Although not identified to species, older specimens of the genus were recorded from the middle Irvingtonian Fyllan Cave LF, Texas, by Winkler and Gose (2003). These late Irvingtonian records from Florida are now matched in South Carolina by the presence of *D. virginiana* in the similarly aged Camelot Local Fauna. ChM PV7692 was collected by G. Pettus in 2006 and is considered to have originated from the Wando Formation on the basis of the proximity of Bee's Ferry Road to the old Charleston phosphate mining district.

PLACENTALIA Owen, 1837
XENARTHRA Cope, 1889
PILOSA Flower, 1883
MEGALONYCHIDAE Gervais, 1855
MEGALONYX Harlan, 1825
MEGALONYX LEPTOSTOMUS Cope, 1893
Figure 13B

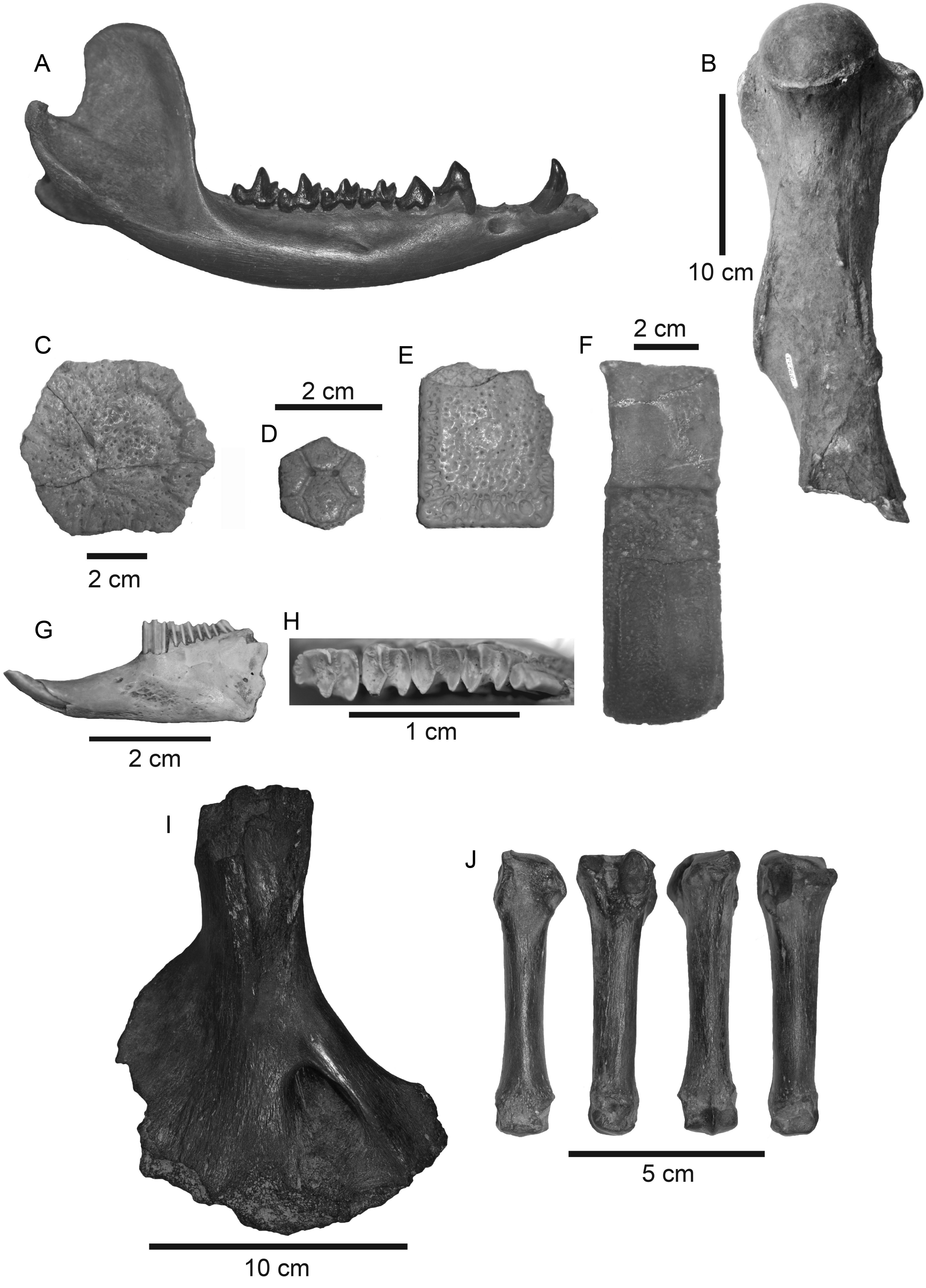
Referred Specimens.—See Fields et al. (2012).

Locality, Stratigraphic Horizon, and Age.—See Fields et al. (2012).

Discussion.—In a recent paper on all the ground sloth material known from South Carolina, Fields et al. (2012) noted the occurrence of *Megalonyx leptostomus* from two localities, including several elements from the late Blancan Walrus Ditch LF of Dorchester County. A fragment of humerus from the bottom of the Cooper River in Berkeley County is thought to have originated from the ~3.8 myr old Goose Creek Limestone based on the nature of the matrix adhering to the specimen.

The oldest occurrence of *Megalonyx* in the USA is in the early late Hemphillian (Hh3, 6–7 Ma) ZX Bar Local Fauna, Nebraska (Hirschfeld and Webb, 1968; Morgan, 2005). In the southeastern USA, *Megalonyx* is first recorded in the latest Hemphillian (Hh4, 4.7–5 Ma) Palmetto Fauna of Florida as *M. curvidens* (Morgan, 2005; Webb et al., 2008).

The oldest and youngest records of *M. lep-*


A
B
10 cm
C
2 cm
D
2 cm
E
F
2 cm
G
2 cm
H
1 cm
I
10 cm
J
5 cm

tostomus occur, respectively, in the Hagerman Local Fauna, Idaho, at a level considered approximately 3.98 Ma by D. Ruez (pers. comm. to LBA, 2008), and in the Inglis 1A site, Florida (1.8 Ma), apparently confining this taxon to the Blancan NALMA (Bell et al., 2004; Morgan, 2005). Thus, as Fields et al. (2012) noted, the partial humerus (ChM PV7681) purportedly from the Goose Creek Limestone represents the oldest record of a ground sloth in the state, and for the first time confirms the presence of this species in the Southeastern USA during the early Blancan.

A fragment of cheek tooth (SC2008.8.16) from Edisto Beach is similar in size and morphology to those of *M. leptostomus*, and JLK has observed additional teeth from Edisto Beach the size of *M. leptostomus* in a private collection. However, given that the "Edisto Beach fauna" *per se* is of Rancholabrean age, the possibility exists that these teeth belonged to a juvenile or subadult species of *M. jeffersonii*. The Edisto Beach "fauna" comprises a temporally mixed assemblage based on the recovery of both terrestrial and marine fossils, and on taxa of apparent Holocene age, as well.

CINGULATA Illinger, 1811
GLYPTODONTIDAE Gray, 1869
GLYPTOTHERIUM Osborn, 1903
GLYPTOTHERIUM TEXANUM Osborn, 1903
Figure 13C

Referred Specimen.—SC 90.121.1, carapacial osteoderm.

Locality, Stratigraphic Horizon, and Age.—Collected by R. Ogilvie in a spoil pile that consisted of a "bed of white sand" near the town of Florence, Florence County, about 0.34 km north of the intersection of US Route 52/301 and County Road 107 (= Alligator Road). Formation and age unknown, but possibly from the Duplin Formation.

Description and Discussion.—Following the revised taxonomy of Gillette et al. (2016), *Glyptotherium texanum* is the valid species name for Blancan and Irvingtonian glyptodonts in the southeastern USA, superseding the usage of *Glyptotherium arizonae* advocated by Gillette and Ray (1981). SC 90.121.1 is a large carapacial osteoderm, measuring about 61 mm in diameter by 20.6 mm thick. It matches osteoderms referred to *G. arizonae* by Gillette and Ray (1981:13) in its large size, flat to weakly convex external surface, and in the central figure occupying greater than half the scute diameter (about 32 mm; distinctively broader than the relatively narrow peripherals). In *G. floridanum* the central figure of carapacial osteoderms is "approximately equal in size to peripherals, usually slightly raised and weakly concave" (Gillette and Ray, 1981:15).

SC 90.121.1 was found on a spoil pile of sediments described as a white sand by the collector. These sediments were originally thought to match those representative of the Duplin Formation from a site near Darlington, SC, (~16 km WNW of the Florence site) where a specimen of *Phugatherium dichroplax* (discussed below) was found. This would have resulted in the oldest record of *Glyptotherium* in the USA. Further inquiry regarding the provenance of this specimen, however, revealed that the sediment from the two sites was

Figure 13. **A**, *Didelphis virginiana*, SC2004.1.239, right dentary with c, p2–3, m1–4, from Camelot locality, Ladson Formation; **B,** *Megalonyx leptostomus*, ChM PV7681, partial left humerus from Cooper River, Goose Creek Limestone; **C**, *Glyptotherium texanum*, SC90.121.1, carapacial osteoderm, from ?Duplin Formation; **D**, *Pachyarmatherium leiseyi*, SC2006.1.123, carapacial osteoderm, from Walrus Ditch locality, Waccamaw Formation; **E**, *Holmesina floridanus*, SC2006.1.19, partial carapacial osteoderm, from Walrus Ditch locality, Waccamaw Formation; **F**, *Holmesina septentrionalis*, SC2003.75.129, movable osteoderm from Camelot locality, Ladson Formation; **G**, *Sylvilagus palustris*, ChM PV7675, labial view of left dentary with incisor plus p3–m3, from Ten Mile Hill Formation; **H**, same specimen, occlusal view; **I**, *Castoroides dilophidus*, SC2017.10.25, distal right humerus from Broad River, Beaufort County; **J**, *Castoroides dilophidus*, SC2015.53.5, right metatarsal III from Broad River, Beaufort County, in (left to right) anterior, lateral, posterior, and medial view.

not similar, leaving the geologic unit from which the *Glyptotherium* scute originated unresolved. Interestingly, the *Glyptotherium* locality is also the site from which Late Cretaceous (Maastrichtian) reptile material was recovered (Schwimmer et al., 2015), the "white sands" evidently being the unit capping the upper Cretaceous Peedee Formation.

The oldest USA records of *Glyptotherium* are those from early late Blancan sites in the Southwest, such as Cita Canyon, Texas, and 111 Ranch, Arizona, which occur magnetostratigraphically just below the Gauss-Matuyama boundary at about 2.6–2.7 Ma (Bell et al., 2004; Morgan and White, 2005; Morgan, 2005, 2008). Even older records are known from the Guanajuato region of central Mexico (Carranza-Castenada and Miller, 1988) where Flynn et al. (2005:304) dated the strata yielding these specimens to about 3.6 Ma. Younger records from the Southeast include specimens from late Blancan sites in Florida such as the De Soto Shell Pit and the Santa Fe River 1 faunas, where Morgan (2005:292) noted that *G. arizonae* co-occurs with *Nannippus*, and also from the early Irvingtonian Leisey site.

GLYPTOTHERIUM FLORIDANUM
(Simpson, 1929)

Referred Specimens.—ChM PV2415, postglenoid cranial fragment; ChM PV2417, 2418, 2090, isolated carapace osteoderms (Gillette and Ray, 1981); ChM PV4879, osteoderm; ChM PV4880, osteoderm; SC94.57.8b, osteoderm.

Locality, Stratigraphic Horizon, and Age.—ChM PV2415, 2417, 2418, 2090, 4879, and SC94.57.8b from Edisto Beach, Colleton County, undetermined offshore unit; ChM PV4880 from Garden City Beach, Horry County, undetermined offshore unit, late Pleistocene, Rancholabrean.

Discussion.—These elements are referred to *G. floridanum* on the basis of their much smaller size relative to those of *G. texanum*, and on the diameter of the central figure (about 17 mm), which is less than half the total scute diameter (about 43 mm). They are noted here to complement those specimens previously reported by Ray (1965) and Roth and Laerm (1980). Taxonomy of *Glyptotherium* species here follows Gillette et al. (2016); some favor synonymy of *G. floridanum* with a species named from Mexico (Ramírez-Cruz and Montellano-Ballesteros, 2014; Zurita et al., 2018).

PACHYARMATHERIIDAE Fernincola et al., 2018
PACHYARMATHERIUM Downing and White, 1995
PACHYARMATHERIUM LEISEYI Downing and White, 1995
Figure 13D

Referred Specimens.—SC2006.1.123, osteoderm (plus several others with SC2006.1 prefix).

Locality, Stratigraphic Horizon, and Age.—Walrus Ditch locality, Dorchester County, lower Waccamaw Formation, early Pleistocene, late Blancan.

Discussion—The specimens noted here from the Walrus Ditch locality were mentioned, but not discussed in detail, in Downing's and White's (1995) original description of *Pachyarmatherium leiseyi* from the early Irvingtonian Leisey Shell Pit Local Fauna of Florida. Although specimens are also known from Costa Rica (Laurito et al., 2005), the Walrus Ditch material provides the first USA record of this taxon outside of Florida. A more detailed account of the SC material will be presented upon completion of the study on the Walrus Ditch LF.

PAMPATHERIIDAE Paula Couto, 1954
HOLMESINA Simpson, 1930
HOLMESINA FLORIDANUS (Robertson, 1976)
Figure 13E

Kraglievichia floridanus Robertson, 1976.
Holmesina floridanus (Robertson). Edmond, 1987; Hulbert and Morgan, 1993; Downing and White, 1995.

Referred Specimens.—ChM PV7596, tooth 4; SC2006.1.19, partial imbricating osteoderm.

Locality, Stratigraphic Horizon, and Age.—ChM PV7596 from Clapp Creek locality, Kingstree, Williamsburg County, ?lower Waccamaw Formation; SC2006.1.19 from Walrus Ditch locality, Dorchester County, lower Waccamaw Formation, early Pleistocene, late Blancan.

Discussion.—These specimens represent the first records of *H. floridanus* from SC, a taxon known previously from late Blancan to early Irvingtonian sites in Florida (Hulbert and Morgan, 1993; Morgan, 2005). The small size of the osteoderm (21.2 mm wide by 6.6 mm thick; length indeterminable due to breakage), together with other elements of the Walrus Ditch Local Fauna indicative of a late Blancan age, supports referral to *H. floridanus* rather than the much larger and later occurring *H. septentrionalis* (Fig. 13F). The latter is known from the late Irvingtonian Camelot Local Fauna, in addition to several unnamed sites in the Summerville area. The tooth from the Clapp Creek locality is 12 mm long by about 5 mm wide, which is slightly smaller than material described from the early Irvingtonian Leisey Shell Pit Local Fauna, Florida (Downing and White, 1995; Hulbert and Morgan, 1993; Morgan and Hulbert, 1995). As noted in Downing and White (1995), Edmund (1987) quantified a trend in *Holmesina* from smallest size in Blancan species to increasingly larger size through the Irvingtonian and Rancholabrean. The slightly smaller size of ChM PV7596 relative to the Leisey specimens, together with the recovery of *Ondatra idahoensis* and *Nannippus peninsulatus* (discussed below), supports our late Blancan assignment for many of the mammalian fossils from the Clapp Creek site.

LAGOMORPHA Brandt, 1855
LEPORIDAE Gray, 1821
SYLVILAGUS Gray, 1867
SYLVILAGUS PALUSTRIS Chapman and Willner, 1981
Figure 13G–H

Referred Specimens.—ChM PV7675, left dentary with incisor plus p3–m3; ChM PV7733, right dentary with incisor plus p3–m2.

Locality, Stratigraphic Horizon, and Age.—ChM PV7675 from Tall Pines subdivision, Berkeley County, Ten Mile Hill Formation, late middle Pleistocene, early Rancholabrean; ChM PV7733 from Trailwood Trailer Park, Charleston County, Penholoway Formation, late early Pleistocene, middle Irvingtonian.

Description.—Descriptive terminology of leporid dentition follows White (1991). In leporids the p3 is the most diagnostic tooth with which to determine species. In PV7675, the p3 measures 3.9 mm AP by 3.02 mm TR. The anterior surface of the tooth has multiple anterior reentrants, the anteroexternal reentrant (AER) is shallow and heavily cemented, and the posteroexternal reentrant (PER) extends across the entire occlusal surface. The thick enamel of the anterior wall of the PER has no crenulations, whereas the thin enamel of the posterior wall is highly crenulated, as in p4–m2. Measuring along the occlusal surfaces, the length of p3–m3 = 14.8 mm. PV7733 is smaller than PV7675, but of similar morphology with the exception that the anterior surface of p3 is not as highly crenulated. The AP length of p3 measures 3.3 mm and the length of p3–m2 = 11.5 mm.

Discussion.—The extant marsh rabbit *Sylvilagus palustris* differs from the extinct species *S. hibbardi*, known from Blancan and Irvingtonian sites in western North America, in its larger size, greater number of anterior reentrants, and extension of the PER to the lingual border. It closely resembles the extinct *S. webbi*, from the Blancan and very early Irvingtonian of Florida, but differs in having a PER that extends across the tooth to the lingual border (White, 1991). White (1991) suggested that *S. palustris* may have evolved from *S. webbi*. Bentley et al. (1994) also noted this species from the late Rancholabrean Ardis Local Fauna.

RODENTIA Bowdich, 1821
CASTORIDAE Hemprich, 1820
CASTOROIDES Foster, 1838
CASTOROIDES DILOPHIDUS (Martin, 1969)
Figure 13I–J

Castoroides ohioensis dilophidus Martin, 1969; Martin, 1975.

Castoroides leiseyorum Morgan and White, 1995; Parmalee and Graham, 2002.

Castoroides dilophidus (Martin, 1969). Hulbert, Kerner, and Morgan, 2014.

Referred Specimens.—SC75.33.1, nearly complete cranium; SC2016.1.24, fragment of upper incisor; SC2015.17.6, right p4; USNM PAL 530187, two cheek teeth; SC2017.10.25, distal end of right humerus; SC2015.53.5, right metatarsal III.

Locality, Stratigraphic Horizon, and Age.—SC2016.1.24, and SC2017.10.25 from Broad River, seaward of Edward B. Rogers Bridge (SC Highway 170) and SC2015.53.5 from Whale Branch region of Broad River inland from Edward B. Rogers

Bridge, Beaufort County, likely derived from a unit equivalent to the Wando Formation, late Pleistocene, Rancholabrean; SC75.33.1 and SC2015.17.6 from Cooper River, Berkeley County, thought to be derived from the Wando Formation, late Pleistocene, Rancholabrean; USNM PAL 530187 from Myrtle Beach, Horry County, from undetermined offshore upper Pleistocene unit, Rancholabrean.

Discussion.—Parmalee and Graham (2002) provided a full description, plus illustrations, of the skull, SC75.33.1, referring it to *Castoroides leiseyorum*. Recently, Hulbert et al. (2014) determined that *C. leiseyorum* is the junior synonym of *C. dilophidus* (Martin, 1969). This, in turn, resulted in their referral of the other known specimens of *Castoroides* from Florida, Georgia, and SC (the Southeastern Coastal Plain) to *C. dilophidus*, noting several characters that distinguish it from *C. ohioensis*, now putatively restricted to the northeastern and mid-continental USA and Canada. Although SC2015.17.6, the right p4 from the Cooper River, does not have the "dilophid" pattern in which the second anterior lophid of the p4 is divided as do many of the specimens from Florida, Hulbert et al. (2014) do not consider this morphology as necessarily diagnostic or characteristic of *C. dilophidus* because of individual variation of this feature.

It is interesting to note that SC75.33.1 exhibits nearly identical preservation to that of three other specimens recovered from the same general area of the Cooper River: the cranial material of *Neochoerus pinckneyi* (ChM PV2796) noted in Sanders (2002) and discussed further below, the well preserved skull of *Tapirus veroensis* (ChM PV4257) described by Ray and Sanders (1984), and the dentary of *Canis dirus* (SC83.118.1) also noted below. All four specimens are brown in color, not strongly permineralized, and essentially pristine in preservation. Although their exact stratigraphic origin is unknown, Sanders (2002) provided information based on USGS mapping in the region to support a Wando Formation provenance. However, also noteworthy is the discussion by Sanders (2002:13) regarding the preservation of vertebrate material in the late Pleistocene deposits of the Charleston area:

> There are four Pleistocene units within a ten mile radius of Runnymede Plantation, *viz*, the early Pleistocene Penholoway Formation, the Ladson Formation and the Ten Mile Hill Beds, both of middle Pleistocene age, and the late Pleistocene Wando Formation. Fossil bones found in place in the Penholoway Formation are medium to dark brown in color, while those from the Ladson and Ten Mile Hill Beds are usually of light brown or buff color, sometimes with light orange or black iron stains. As noted in the *Megalonyx* account in the present paper, the only specimens yet found in place in the Wando Formation are well mineralized and almost uniformly black, particularly those from the lag deposit at the base.

Although difficult to confirm, the above statement suggests a unit of origin for these four specimens other than the Wando Formation. The color of the specimens suggests a Penholoway origin, and the early Irvingtonian to late Rancholabrean range of *Castoroides dilophidus* does not preclude this suggestion. Nor do the ranges of *Tapirus veroensis* and *Canis dirus* (late Irvingtonian to Rancholabrean) or *Neochoerus pinckneyi* (Blancan to Rancholabrean). Their excellent preservation indicates (1) that they had not been long on the floor of the river since eroding from their entrapping matrix, (2) that they certainly had not been transported very far from their point of origin, and (3) that they did not originate from a basal lag deposit. Plans are currently underway to resume scuba diving efforts at the localities where these specimens were recovered in hopes of shedding new light on the accuracy of our hypotheses regarding their geological provenance.

CASTOR Linnaeus, 1758
CASTOR CANADENIS Kuhl, 1820

Referred Specimen.—ChM PV5027, incisor; ChM PV9635, distal end of right humerus.

Locality, Stratigraphic Horizon, and Age.—ChM PV5027, collected by V. McCollum from a ditch adjacent to County Road 199, Dorchester County, Ten Mile Hill Formation, late middle Pleistocene, early Rancholabrean; ChM PV9635, Myrtle Beach, Horry County, from undetermined offshore upper Pleistocene unit, Rancholabrean.

Discussion.—Whereas *Castor canadensis* is relatively common in the fossil record of South Carolina, we note these specimens simply as additions to the known material from the state. ChM PV5027 represents the first occurrence of *Castor* from the Ten Mile Hill Formation. A label with ChM PV9635 identified that specimen as belonging to *Castoroides*, but the specimen is not nearly the size of the giant beaver; it is similar in size to that of *Castor*, and, as in the latter taxon, the element lacks the entepicondylar foramen.

ARVICOLIDAE Gray, 1821
ONDATRINAE Repenning, 1982
ONDATRA Link, 1795
ONDATRA IDAHOENSIS Wilson, 1933

Figures 14A–I

Ondatra idahoensis Wilson, 1933.
Ondatra idahoensis Wilson. Hibbard, 1959; Martin, 1972; Eshelman, 1975; Repenning et al., 1995; Albright, 1999a.
Ondatra annectens (Brown). Repenning and Grady, 1988.
Neofiber cf. *N. diluvianus* (Cope). Sanders, 2002.

Referred Specimens.—ChM PV7579, left m1; SC87.158 (accession number only), unassociated right and left m3.

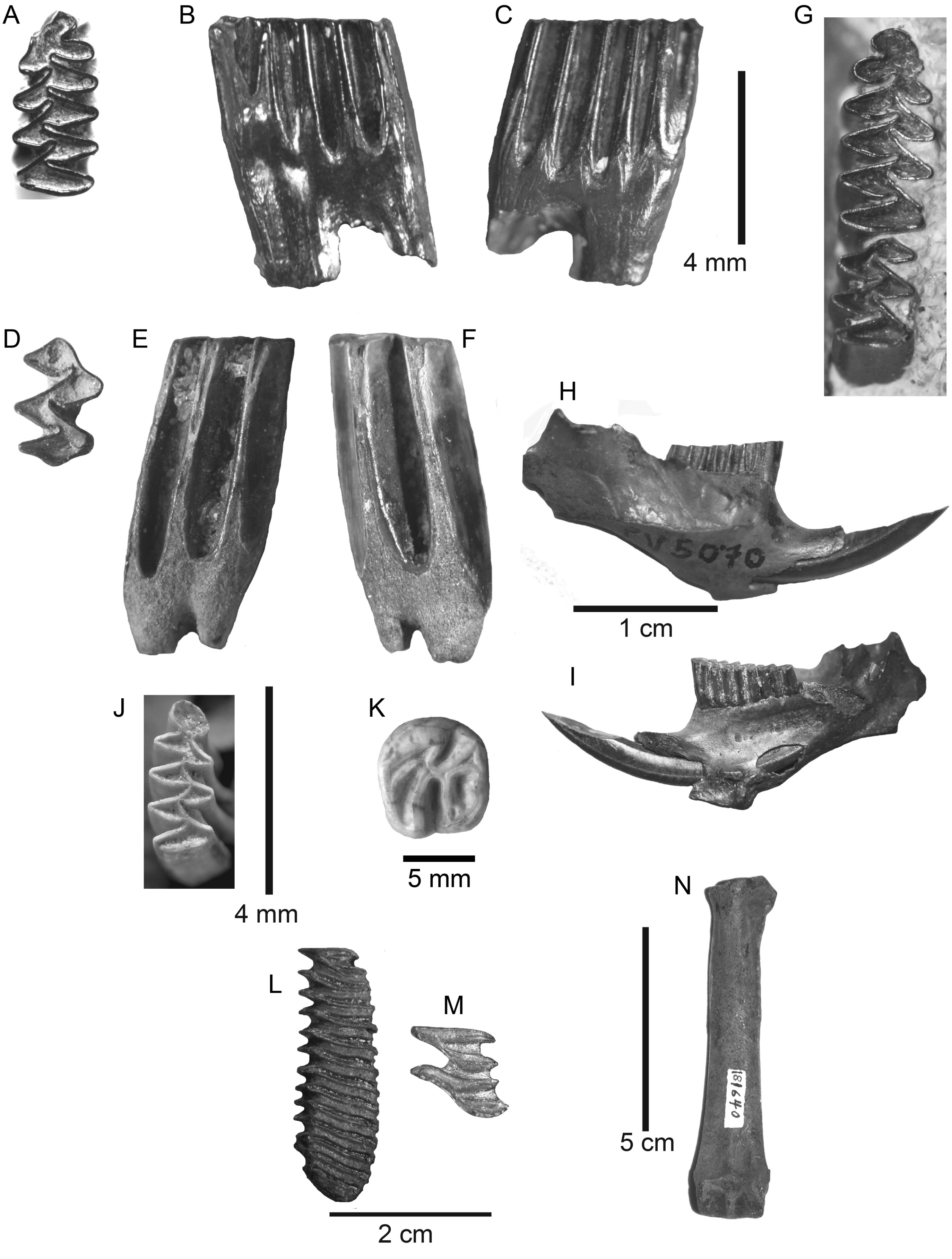
Locality, Stratigraphic Horizon, and Age.—ChM PV7579 and SC87.158 from Clapp Creek site in Kingstree, Williamsburg County, ?lower Waccamaw Formation, early Pleistocene, late Blancan.

Description.—The m1 from Clapp Creek is nearly identical to those from the latest Blancan Inglis 1A Local Fauna, Florida, and with an AP measurement of 4.3 mm, it falls within the 4.2–4.8 mm size range of the Inglis sample (Morgan and White, 1995:439). The tooth has a posterior loop followed by five alternating triangles and an anteroconid (or anterior cap). The anteroconid has a well-developed lingual reentrant (the fifth lingual reentrant) that isolates a seventh triangle, but it is not nearly as deep as the four lingual reentrants posterior to it. The opposing sixth triangle, on the labial side of the anteroconid, is not as distinct as the second and fourth triangles posterior to it due to the absence of an anterolabial (fourth labial) reentrant. Thus there are three (prominent) labial reentrants and five lingual reentrants, the fifth somewhat less developed than the others. All dentinal commissures are very narrow and nearly equal in width. The tooth has well developed roots, enamel of equal width everywhere except on the anterolabial surface, and little if any cement in the reentrants. Both labial and lingual dentine tracts are well developed, although the former are more so than the latter. As in many arvicolids, including several of the Inglis 1A specimens, the only dentine that extends up the crown to the occlusal surface in these teeth is that at the labial termination of the posterior loop.

The m2 (based on specimens from North Carolina; see discussion below) has a posterior loop followed by three alternating triangles, with a smaller fourth anterior triangle. Thus there are two lingual and labial reentrants. As in the m1, the reentrants are very narrow and the dental commissures between triangles are nearly closed except for a very narrow commissure between the third and fourth triangles. The enamel is of equal width everywhere, and there is minimal cement in the reentrants.

The m3 has a posterior loop followed by three alternating triangles, the third being the anterior triangle; there is only a single labial reentrant. The labial dentine tracts extend up to the occlusal surface. The lingual dentine tract of triangle two extends approximately half way up the crown; that of triangle three extends about one-third the way up the crown. There is another dentine tract on the anterior face of the third triangle that extends about two-thirds the way up the crown. The left m3 associated with SC87.158 measures about 2.9 mm AP with a crown height of about 5.3 mm.

Discussion.—ChM PV7579 and SC87.158 represent the first records of *Ondatra idahoensis* from South Carolina. Germane to this discussion, however, are two specimens from North Carolina: ChM PV5070, a partial right dentary with i1, m1, m2, and root of m3 and ChM PV5398, a partial right dentary with the base of i1, m1, and m2. These specimens were collected from the approximately 1.6 Ma upper Waccamaw Formation (middle early Pleistocene, latest Blancan) at Marsh Harbor Marina on the Intracoastal Waterway near Calabash, Brunswick County, North Carolina (see Sanders, 2002:85). Although Sanders (2002) origi-


A
B
C
G
4 mm
D
E
F
H
V5070
1 cm
I
J
K
4 mm
5 mm
N
L
M
5 cm
181640
2 cm

nally referred these specimens to *Neofiber* cf. *N. diluvianus*, more recent analysis has determined that they differ considerably from the poorly known middle to late Irvingtonian *N. diluvianus*, the middle to late Irvingtonian (1.0–0.6 Ma) *N. leonardi*, and the latest Irvingtonian (~0.4 Ma) to Recent *N. alleni*. All the aforementioned round-tailed muskrats have ever-growing teeth, ample cement in the reentrants, and well-developed dentine tracts. The Waccamaw and Clapp Creek specimens show none of these derived features; close inspection of the NC specimens has determined that they have rooted teeth (*contra* Sanders, 2002) and only very limited cement in the reentrants, if any. For this reason we herein revise the identification of ChM PV5070 and PV5398 from *Neofiber* cf. *N. diluvianus* to *Ondatra idahoensis*, an assignment much more temporally and taxonomically consistent with their morphology and their recovery from the Waccamaw Formation. Antero-posterior measurements of the m1s of ChM PV5070 and 5398 are 4.8 mm and 4.7 mm, respectively; thus, they too fall within the 4.2–4.8 mm size range of the Inglis 1A sample (Morgan and White, 1995:439).

It is interesting that Sanders (2002:90) commented on the inconsistency of finding an arvicoline rodent, his *Neofiber* cf. *N. diluvianus*, with what he thought were rootless teeth in sediments of such early age "inasmuch as the latter specimens appear to be as old or slightly older than the proposed ancestor of *Neofiber*" (i.e., *Proneofiber* from the 1.4–1.6 Ma Gilliland Local Fauna of Texas [Hibbard and Dalquest, 1973]). Our new findings explain this temporal/morphological inconsistency insomuch as the Waccamaw specimens are not members of either *Neofiber* or *Proneofiber*.

Like so many of the terrestrial Miocene and Pliocene vertebrate fossils from SC found in lag deposits, the exact formation from which the Clapp Creek specimens originated cannot be determined. The oldest occurrence of *O. idahoensis* is in the Tusker (111 Ranch) LF, Arizona, and the Cita Canyon LF, Texas, where it occurs in normally magnetized strata just below the Gauss-Matuyama boundary at about 2.6 Ma, which is also the base of Blancan V within which *O. idahoensis* is a characterizing taxon (Bell et al., 2004). Its latest occurrence is in the 1.3–1.4 Ma El Casco Local Fauna, California (Albright, 1999a). However, additional taxa from the Clapp Creek locality, such as the dwarf horse *Nannippus*, confirm the late Blancan age of some material from this site, in turn suggesting derivation from the Waccamaw Formation.

ONDATRA ZIBETHICUS (Linnaeus, 1766)

Referred Specimen.—ChM 55.103.117, right dentary with partial i1 plus m1–m3, and humerus.

Locality, Stratigraphic Horizon, and Age.—The only information accompanying this specimen is the following: "W. B. Cormark. Loc. Santee & Cooper rivers. June, 1941. Identified by Gilmore, U.S.N. Museum." ?Wando Formation; late Pleistocene, Rancholabrean.

Description and Discussion.—The m1 of ChM 55.103.117 has a posterior loop followed by seven alternating triangles and an anteroconid. The anteroconid has a weakly-developed lingual reentrant and no anterolabial reentrant. There are five lingual reentrants (excluding the weak one of the anteroconid) and four labial reentrants. All triangles are closed (i.e., there are no dentinal commissures between them) and enamel thickness on their

Figure 14. **A**–**F**, *Ondatra idahoensis* from Clapp Creek site, Kingstree, SC. **A**, **B**, **C**, ChM PV7579, left m1, in (left to right) occlusal, labial, and lingual views, respectively; **D**, SC87.158, right m3, in occlusal view; **E**, **F**, SC87.158, left m3, in (left to right) lingual and labial views, respectively. **G, H, I**, *Ondatra idahoensis* from Waccamaw Formation, Brunswick County, NC. ChM PV5070, right dentary, in occlusal (top), labial (middle), and lingual (lower) views, respectively; **J**, *Allophaiomys pliocaenicus*, SC2001.51.4, right m1, from Walrus Ditch site, Waccamaw Formation; **K**, *Erethizon ?bathygnathum*, SC2006.1.105, right M1, from Walrus Ditch site; **L**, *Phugatherium dichroplax*, USNM 181573, left M3, occlusal view, from Duplin Formation; **M**, *Neochoerus pinckneyi*, left M2, from Cooper River; **N**, *Phugatherium dichroplax*, USNM 181640, right metacarpal III, from Duplin Formation.

posterior and anterior surfaces is equal. This tooth, as well as the m2 and m3, has no cement in the reentrants, no dentine tracts that reach the occlusal surface, and were ever-growing. The length of the m1 is 7.6 mm. The m2 has a posterior loop followed by four alternating triangles, with two lingual and two labial reentrants; it measures 4.0 mm in length. The m3 is similar to the m2 except smaller, measuring 3.5 mm. A right humerus catalogued together with this specimen under the same number, although similar in color, appears to be that of a recent individual.

The extant muskrat, *Ondatra zibethicus*, was noted by Bentley et al. (1994) to be the most common mammal of the latest Rancholabrean Ardis Local Fauna (in which they also noted the first record from SC of the round-tailed muskrat *Neofiber alleni*). The vague information accompanying ChM 55.103.117 precludes an accurate determination of the unit of origin, and therefore age, of this specimen, but its size is indicative of very late Pleistocene populations (Martin et al., 2009); hence, the tentative referral of this specimen from the Wando Formation.

ARVICOLINAE Bonaparte, 1837
ARVICOLINI Kretzoi, 1954
ALLOPHAIOMYS Kormos, 1932
ALLOPHAIOMYS PLIOCAENICUS Kormos, 1932
Figure 14J

Referred Specimen.—SC2001.51.4, right m1.

Locality, Stratigraphic Horizon, and Age.—Walrus Ditch locality, Dorchester County, lower Waccamaw Formation, early Pleistocene, late Blancan.

Description.—In his revised diagnosis of the Tribe Arvicolini, Repenning (1992:24) noted "a first lower molar with posterior loop preceded successively by three substantially closed and alternating triangles and terminated by an Anteroconid Complex with confluent, lingual and buccal Primary Wings and an uncomplicated, more or less globular Cap." He further noted that *Allophaiomys* was one of only three rootless genera in the Tribe Arvicolini, and that enamel-thickness differentiation was typically intermediate (i.e., equal thickness on the anterior and posterior edges of the triangles) vs. "*Mimomys*" or "*Microtus*" like. This diagnosis exactly describes the morphology of SC2001.51.4. The tooth measures 3.1 mm AP by 1.4 mm TR. Although cement is present in the reentrants, the tooth would not be considered heavily cemented. (Note: Storer [2003] subscribes to a different interpretation of *Allophaiomys* in which included specimens retain rooted cheek teeth).

Discussion.—According to Repenning and Grady (1988), *Allophaiomys* "is known from perhaps 2.5 million years ago in Asia." But in North America the oldest occurrence is based on a specimen (not necessarily diagnostic of the genus; see Bell et al., 2004:279) recovered from a core drilled at the foot of Hansen Bluff, Colorado, in the eastern part of the Rocky Mountains that Repenning (1992:32) placed "either during the oldest part of the Olduvai event or just before it," indicating a date for that specimen of approximately 1.95 to 2.0 Ma. More diagnostic specimens of *Allophaiomys* occur in the Nash Fauna of Kansas, which may be slightly older (see Bell et al., 2004), although Martin et al. (2008:202) considered the appearance of "*Microtus* cf *pliocaenicus*" in the Short Haul and Aries A local faunas, also in Kansas, at "about 2.0 Ma" as the oldest records. At the time of Repenning's (1992) publication, *Allophaiomys* was only known from east of the Rocky Mountains. It has since been noted from the Irvingtonian of Nevada (Bell et al., 2004:280).

Martin et al. (2008) recommended "the *Microtus* immigration event," constrained in the Meade Basin of southwestern Kansas to between 1.95 and 2.06 Ma, as a replacement for the first appearance of *Mammuthus* to define the Blancan/Irvingtonian NALMA boundary. The record of *Allophaiomys* in the late Blancan Walrus Ditch Local Fauna, dated to between 2.3 and 2.4 Ma, presents an interesting record, as it represents an even older appearance (the oldest in North America) and a geographic extension resulting in its eastern-most and southern-most occurrence.

ERETHIZONTIDAE Thomas, 1897
ERETHIZON Cuvier, 1822
ERETHIZON ?BATHYGNATHUM Wilson, 1935
Figure 14K

Erethizon bathygnathum Wilson, 1935.
?Coendou brachignathum [sic] (Wilson). White, 1968.
Coendou stirtoni White, 1968.
Coendou brachygnathum [sic] (Wilson). White, 1970.
Erethizon bathygnathum Wilson. Shotwell, 1970; Albright, 1999a; Sussman et al., 2016.
Coendou stirtoni White, 1968. Harrison, 1978.

Referred Specimens.—SC2006.1.105, right M1; SC2001.51.5, left m1.

Locality, Stratigraphic Horizon, and Age.—Walrus Ditch locality, Dorchester County, lower Waccamaw Formation, early Pleistocene, late Blancan.

Discussion.—Erethizontids are members of the first major suite of Neotropical mammals that dispersed through Central America into North America during the Great American Biotic Interchange upon development of the Panamanian Isthmus (GABI 1 of Woodburne, 2010), although the earliest immigrants were megalonychid and mylodontid sloths, which arrived during the early Hemphillian (Lindsay et al., 1984). The oldest occurrence of erethizontids in the USA is based on a specimen of "*Coendou stirtoni*" from the Wolf Ranch Local Fauna of Arizona (Harrison, 1978; later synonymized with *E. bathygnathum* by Frazier, 1981) dated magnetostratigraphically to about 2.6 Ma (just below the Gauss/Matuyama boundary; early late Blancan). Additional records of this species are found elsewhere across the American West in late middle to late Blancan sites (Frazier, 1981; Albright, 1999a).

Prior to the recovery of the Walrus Ditch specimens, the oldest known records of porcupine in the southeastern USA were *E. poyeri* Hulbert, 1997, from the middle late Blancan Haile 7C locality (1.9–2.2 Ma) of Florida, and the much smaller *E. kleini* Frazier, 1981, from the slightly younger latest Blancan Inglis 1A locality (1.6–1.9 Ma) (Hulbert, 1997, 2010; Morgan, 2005, 2008). The extant North American porcupine *E. dorsatum* (Linnaeus, 1758) is first recorded from Florida's earliest Irvingtonian Haile 16A Local Fauna after the demise of *E. poyeri* and *E. kleini* (Morgan and White, 1995; Hulbert, 1997; Morgan, 2005, 2008). This species is also recorded from the primarily Rancholabrean Edisto Beach fauna (SC83.17.1; Sanders, 2002).

Prompted by the study of new erethizontid material from the El Golfo region of northern-most Mexico (~1.0 Ma), Sussman et al. (2016) reviewed the taxonomy of the North American species. They concluded that all Florida taxa older than Rancholabrean age (i.e., those noted above) represent *Coendou*, rather than *Erethizon*; thus, *C. poyeri*, *C. kleini*, and for the pre-Rancholabrean material previously referred to *E. dorsatum*, *Coendou* spp. They referred the El Golfo material to *C.* cf. *C. kleini*. The evidence for their conclusions focused on morphological changes that took place in the erethizontid lineage as the tropical taxon, *Coendou*, adapted to colder climatic conditions as it dispersed into (northern and western) North America, resulting in *Erethizon*. Their hypothesis (supported with morphological data) postulated that these pre-Rancholabrean Florida taxa constituted a southeastern population of *Coendou* that, living in the subtropical part of North America, were not subjected to the selection pressures of inclement climatic conditions that led to the evolution of *Erethizon*.

The relatively large size of the Walrus Ditch M1 (7.64 mm AP by 7.98 mm TR) compared with those of *E. kleini*, *E. poyeri*, and *E. dorsatum* from Florida suggests referral to *E. bathygnathum*, although this species has never before been recorded beyond western North America (hence, the questionable specific assignment). The early late Blancan age (2.2–2.6 Ma; Hulbert, 2010) of the Walrus Ditch specimens (~2.3 Ma), however, which predates all other southeastern records of *Erethizon*, is consistent with that of *E. bathygnathum* at its western localities. The size of the unerupted m1 crown, at 6.39 mm AP by 6.96 mm TR, is similar in size to those of *E. poyeri* and also falls within the range of *E. dorsatum* (Hulbert, 1997:table 1; Sussman et al., 2016, also provided extensive tables of dental measurements for both extant and extinct North American species of porcupines). This m1 differs from those of *E. poyeri* and *E. dorsatum* in being slightly wider transversely than it is long anteroposteriorly, but this may be a variable trait. As noted above, however, *E. dorsatum* is not known from the Southeast (i.e., Florida) until the early Irvingtonian (Morgan and White, 1995; Hulbert, 1997).

If the Walrus Ditch specimens are correctly identified, and if our estimation of the age of the Walrus Ditch LF is accurate (~2.3 Ma), then this occurrence not only provides the oldest record of an erethizontid in the southeastern USA, it also provides the first record of *Erethizon* (i.e., *E. bathygnathum*) beyond the western USA. This record, in turn, directly contradicts the findings of Sussman et al. (2016) that *Erethizon* was confined to western and northern regions of North America until the Rancholabrean. As an explanation for the late Blancan appearance of a porcupine (*E. poyeri*) in Florida, Hulbert (1997; also see Morgan and Emslie, 2010) noted the influx of xeric adapted western mammals during this time. *Erethizon bathygnathum* could well have been among that group, appearing earlier in South Carolina than in Florida due to high earlier Blancan sea levels which inundated peninsula Florida. Given this scenario, however, *E. bathygnathum* might then be expected to appear in Florida by the late Blancan, in turn hinting that the Walrus Ditch material might better be referred to a large individual of *E. poyeri*. Only more diagnostic material from the Walrus Ditch site will resolve these hypotheses, including whether *all* erethizontid material from the pre-Rancholabrean Southeast should be assigned to *Coendou* per Sussman et al. (2016).

CAVIIDAE Fischer von Waldheim, 1817
HYDROCHOERINAE Gill, 1872

The relatively recent consensus reached by nearly all those who study fossil and extant capybaras is that the taxonomy of, particularly, North American species is in a state of confusion and in much need of revision (e.g., Mones, 1984; Mones and Ojasti, 1986; Morgan and White, 1995; Morgan, 2008; Pérez et al., 2017; Vucetich et al., 2015). An attempt to resolve these issues is currently underway and being led primarily by the Argentine paleontologists C. M. Deschamps, M. E. Pérez, and M. G. Vucetich (e.g., Deschamps et al., 2007, 2013; Vucetich et al., 2015; Pérez et al., 2017, and references therein). The main reason for such confusion is that capybaras have ever-growing cheek teeth that change *in size and morphology* throughout life. The result, therefore, has been an interpretation of higher taxonomic diversity in the fossil record than actually exists. Fossils of different size and morphology at a single locality are now known to represent different ontogenetic stages of a single taxon, not multiple taxa (e.g., Deschamps et al., 2007; Vucetich et al., 2015). Adding to this problem is the referral of North American Pliocene species to genera that do not appear in the fossil record of South America until the Pleistocene. Specifically, species referred to *Neochoerus* Hay, 1926, and *Hydrochoerus* Brisson, 1762, appear in North America (Arizona, Texas, Florida, South Carolina) before their ancestors are known from South America (see Vucetich et al., 2015). Also problematic is the questionable provenance of many specimens. For example, several of the specimens from South Carolina (referred to two different species) were recovered as a result of phosphate dredging and mining operations within and near the Ashley River in the earliest 1900s (Sanders, 2002).

In an attempt to stem this tide of confusion, we herein adopt the more parsimonious hypothesis of North American capybara taxonomy as advocated by Vucetich et al. (2015). They referred all North American species recovered from Blancan aged sites previously assigned to *Neochoerus dichroplax* (from Arizona and Florida) and *Neochoerus cordobai* (from the Guanajuato region of central Mexico [Carranza-Castenada and Miller, 1988]) to the South American genus *Phugatherium* Ameghino, 1887; hence *Phugatherium dichroplax*. In addition to the lineage represented by *Phugatherium*, Vucetich et al. (2015:331) recognized a second "*Neochoerus-Hydrochoerus*" lineage that they noted "was undoubtedly represented in the Pleistocene with *N. aesopi*, *N. pinckneyi*, and *H. holmesi*." (Note: Sanders (2002) regarded *N. aesopi* a junior synonym of *N. pinckneyi*). They added, however, that "the Pliocene records of the two latter [species] must be revised both taxonomically and stratigraphically." Although we make an attempt below to align our evaluation of SC capybaras with these recent findings, a revision such as that suggested by Vucetich et al. (2015) is beyond the scope of this report.

As noted by Morgan and White (1995) and Morgan (2008), Mones (1984) and Mones and Ojasti (1986) argued that *Hydrochoerus*, the genus to which extant capybaras belong, does not occur in North America; i.e., that specimens referred to this taxon (e.g., *Hydrochoerus holmesi* Simpson, 1928) have been done so in error and that they are instead representative of *Neochoerus pinckneyi* (Hay, 1923), considered by Ahearn and Lance (1980) to be the only species of *Neochoerus* in North America (also see discussion in Sanders, 2002:96). Until further research provides new information on the relationships between *Phugatherium*, *Neochoerus*, and *Hydrochoerus*, we provisionally follow the conclusions of Mones (1984) and Mones and Ojasti (1986) that specimens from the USA previously assigned to *Hydrochoerus* are more likely representatives of either of the other two taxa. This results in the reassignment of the nine specimens that Sanders (2002) referred to *Hydrochoerus holmesi* to *Neochoerus pinckneyi* and in the referral of all the capybara material found in the Ashley River phosphate mining region to one species rather than two. Moreover, we maintain that all the capybara material currently known from SC, with the exception of limited material discussed below but including the numerous specimens currently curated at the SCSM, is referable only to *N. pinckneyi*.

PHUGATHERIUM Ameghino, 1887
PHUGATHERIUM DICHROPLAX (Ahearn and Lance, 1980)
Figure 14L–N

Referred Specimens.—USNM 181573, left M3; USNM 181640, right metacarpal III.

Locality, Stratigraphic Horizon, and Age.—“Middle Swamp, approximately 100 yards southeast of SC Rte. 340 on Myrtle Branch, 8.5 mi. SW Darlington,” (approximate location 34º 11’ 36” N, 79º 55’ 57”), Darlington County; collected in 1971 by A. Langley of Darlington, SC, from correspondence archived at the USNM; see discussion below); Duplin Formation, early late Pliocene, middle Blancan.

Description.—The small size of USNM 181573 (~ 32 mm AP by ~ 8 mm TR) implies that it represents a juvenile (or subadult) individual; it is not indicative of which species is represented. The tooth has an anterior prism (the first lamina, following terminology of Ahearn and Lance, 1980) followed by 13 posterior lamina prisms. None of the laminae show the distinct, prominently bifurcated morphology on the labial edge that characterizes *Phugatherium dichroplax*, although this may be a variable character (see below). The metacarpal, USNM 181640, was found at the same locality as the M3, but represents an adult, as the epiphyses are fused. It has a total length of 83.9 mm; the width of the proximal end = 16.9 mm; the width of the distal end = 18.9 mm.

Discussion.—Although USNM 181573 and 181640 are labeled “*Neochoerus* cf. *dichroplax*” in the collections at the USNM, the former was referred to *Hydrochoerus holmesi* by Ahearn (1981:59), and this identification was seconded by Sanders (2002:98). But as noted above, Mones (1984) and Mones and Ojasti (1986) do not consider *Hydrochoerus* a North American taxon. Nor are North American specimens referred to *Hydrochoerus* recorded from the Blancan (*contra* Morgan, 2008, who assigned the late Blancan Haile 1A material to that genus). Following these criteria, therefore, it may be more appropriate (and accurate) to assign USNM 181573 and USNM 181640 to either *Phugatherium dichroplax* or to *Neochoerus pinckneyi*. Although the morphology of USNM 181573 does not fit the description of *P. dichroplax* in that it lacks the prominent bifurcations on the anterior few laminae that Vucetich et al. (2015) considered a synapomorphy of the genus, Morgan (2008) noted that the specimens of *N. cordobai* from central Mexico, which Vucetich et al. (2015) synonymized with *Phugatherium dichroplax*, also lack this character. If that is indeed the case, then it will be difficult to distinguish *P. phugatherium* from *N. pinckneyi* if only teeth are available. Differentiation of these two taxa is based primarily on characters of the skull (Vucetich et al., 2015). We provisionally refer this material to *Phugatherium dichroplax* to maintain consistency with the currently associated USNM label, fully realizing, however, that this is certainly subject to change upon future study of the *Neochoerus-Hydrochoerus* lineage.

The oldest records of capybara in the USA *from well-calibrated sites* are those of "*Neochoerus*" *dichroplax* (i.e., *Phugatherium dichroplax*) from the early late Blancan 111 Ranch fauna, Arizona. These date to about 2.6–2.7 Ma, or just below the Gauss-Matuyama magnetochron boundary (Ahearn and Lance, 1980; Galusha et al., 1984; Bell et al., 2004; White and Morgan, 2005; Morgan and White, 2005; Morgan, 2005, 2008). The same species is also known from late Blancan faunas of Florida, such as Sommer's Pit, Mule Pen Quarry, Macasphalt Shell Pit, Kissimmee River, and Inglis 1A (Morgan and White, 1995; Morgan, 2008; R. Hulbert, pers. comm. to LBA, May, 2019). The specimens noted above from Mexico which were originally assigned to *Neochoerus cordobai* by Carranza-Castenada and Miller (1988), but more recently synonymized with *Phugatherium dichroplax* by Vucetich et al. (2015), were recovered from even older, early Blancan sites from the Rancho Viejo area of Guanajuato. Flynn et al. (2005:304) dated the strata yielding these specimens (including *Glyptotherium*) as "at least as old as 3.1–3.5 Ma ... or older ... correlative with levels slightly above a 3.9 Ma FT [fission track] date in La Pantera II ...." In summary, *Phugatherium dichroplax* is recorded in North America from the early middle Blancan (approx. 3.6 Ma) in Mexico, then again in the early late Blancan of Arizona (approx. 2.7 Ma), and finally in the early late to latest Blancan of Florida (approx. 1.8 Ma).

Bearing on the age of USNM 181573 and 181640 is a series of correspondence archived at the USNM and dated from March, 1971, to August, 1972, between the collector of the material, a Mr. A. A. Langley of Darlington, SC, and Drs. T. R. Waller, who at the time was the Associate Curator of Invertebrate Paleontology, and C. E. Ray, who was the Curator of Vertebrate Paleontology. Included in this correspondence is a list of molluscs collected by Mr. Langley together with the capybara material. The list includes *Oliva carolinensis*, *Siphocypraecea carolinensis*, *Glycymeris subovata*, "*Ostrea*" *sculpturata*, "*Ostrea*" *disparilis*, *Mercenaria* sp., *Argopecten eboreus*, and *Nassarius vibex*. Upon seeing this list, L. D. Campbell (pers. comm. to LBA, May, 2019) noted that several of these were long-ranged taxa, but that one in particular, *Siphocypraecea carolinensis*, was quite age diagnostic. Occurring only in the Duplin Formation's Natural Well, NC, stratotype[5] and in South Carolina sites considered equivalent (and also in the slightly older Stokes quarry located 9.65 km directly NE from the capybara site and closer to the town of Darlington; see discussion of Duplin Formation in section above on the fossil bearing beds of SC), *S. carolinensis* is confined to about 3.0–3.6 Ma, i.e., middle Blancan. Matrix extracted from between the enamel laminae of USNM 181573 was examined under a microscope by AES and found to be identical to that collected at the nearby Stokes quarry site in grain size, color, condition, and in the presence of tiny shell fragments. L. D. Campbell considers the Stokes quarry to be 3.4 to 3.6 myr old. This range of dates, 3.0–3.6 Ma, places a capybara (regardless of its identification) in the southeastern USA at about the same time, perhaps slightly more recently, than "*Neochoerus*" *cordobai* (= *Phugatherium dichroplax*) is recorded in Mexico. The SC specimens would therefore represent some of the oldest records of capybara in the USA.

Even older, however, may be several specimens from the Ashley River phosphate beds that Sanders (2002) referred to *Neochoerus pinckneyi*. This older age was based on his conclusion that these specimens, including the holotype (ChM PV2506), apparently originated from the Goose Creek Limestone as determined from the presence of its distinctive matrix adhering to the teeth. The Goose Creek Limestone underlies the Duplin Formation (Figs. 2C, 3C) and was considered no younger than calcareous nannofossil zone NN15 by Weems et al. (1982). GTS2012 places NN15 in the late Zanclean (middle Pliocene) at about 3.8 Ma, and Campbell and Campbell (1995) suggested an age for the Goose Creek Limestone of between about 3.55 and 3.75 Ma on the basis of their mollusc studies. Both of these estimates fall within

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[5] L. D. Campbell notes that there are about 360 species of molluscs from the Duplin Formation's Natural Well, NC, stratotype curated in the Florida Museum of Natural History's Locklin Collection (L. D. Campbell, pers. comm. to AES, October 2007).

magnetochron C2Ar, and recent paleomagnetic analysis by LBA suggesting reversed polarity for the Goose Creek Limestone lends additional support. These teeth therefore, appear to represent the oldest records of this Neotropical rodent in what is now the USA. If correctly identified, *Neochoerus* must have entered what is now the southern USA at a time correlative with, or even earlier, than the *P. dichroplax* occurrence in central Mexico.

It appears, therefore, that capybaras not only reached North America much earlier than what has typically been considered the primary pulse of the GABI beginning about 2.7 myr ago, but that two lineages, *Phugatherium* and the *Neochoerus-Hydrochoerus* lineage, apparently reached the southeastern USA at about the same time as their arrival in the Guanajuato region of Mexico. As noted above in the discussion of *Glyptotherium texanum*, the apparent absence of capybara in the early to middle Blancan of Florida, in contrast to their early and middle Blancan records in SC, is likely attributable to the absence in Florida of terrestrial faunas of this age due to high sea levels during that time.

NEOCHOERUS Hay, 1926
NEOCHOERUS PINCKNEYI (Hay, 1923)
Figure 14M

Referred Specimens.—Additions to ChM PV2796: right I1, left M2; SC2017.10.24, left lower incisor; SC2015.17.7, sacrum; SC2015.17.8, distal right tibia; SC2015.17.9, metacarpal III.

Locality, Stratigraphic Horizon, and Age.—ChM PV2796, SC2017.10.24, SC2015.17.7, and SC2015.17.8 from west branch of Cooper River, Berkeley County, thought to be derived from Wando Formation (see Sanders, 2002:102–104); SC2017.10.24 from Broad River, seaward of Edward B. Rogers Bridge (SC Highway 170), Beaufort County, likely derived from a unit equivalent to Wando Formation; late Pleistocene, Rancholabrean.

Discussion.—Sanders (2002:102) noted cranial elements and teeth collected by LBA in 1977 from the west branch of the Cooper River catalogued as ChM PV2796. In the Spring of 2015, Ms. Susan Wallace, who was LBA's scuba diving partner throughout the 1970s (and the collector of the beautiful *Tapirus* skull described in Ray and Sanders, 1984), came across a box of fossil specimens while preparing for a move from her Isle of Palms, SC, residence. Contacting LBA to look over the long-packed specimens, two capybara teeth were noted that identically matched those of ChM PV2796 in color, degree of wear, and in the matrix remaining in the reentrants of the teeth. In conversation it became apparent that the teeth "re-discovered" by Ms. Wallace were almost assuredly collected on the same dive, at the same location, as those specimens collected by LBA, resulting in the consequent conclusion that they likely belonged to the same individual. Upon comparison by LBA, this hunch was confirmed, and Ms. Wallace agreed to donate the newly found specimens to The Charleston Museum where they are now included with the material earlier assigned to ChM PV2796. Confirmation was supported by the perfect fit of the "re-discovered" right incisor into the empty right alveolus seen in figure 42B of Sanders (2002).

The sacrum, distal tibia, and metacarpal III were also among the specimens in the box of Ms. Wallace's fossils. Although they too were collected in the Cooper River, they were not recovered from the identical location as ChM PV2796, nor does their preservation match that of the same individual.

EULIPOTYPHLA Haeckel, 1866
TALPIDAE Fischer von Waldheim, 1817
CONDYLURA Illinger, 1811
CONDYLURA CRISTATA (Linnaeus, 1758)

Referred Specimen.—ChM PV9636, right humerus.

Locality, Stratigraphic Horizon, and Age.—Bank of Eagle Creek near junction with Ashley River, Dorchester County (Fig. 10), in proximity to outcrops of Chandler Bridge Formation, but likely derived from overlying Wando Formation; late Pleistocene, Rancholabrean.

Discussion.—This specimen is an addition to the known fossil talpid material from South Carolina. It was originally thought to have originated from the upper Oligocene Chandler Bridge Formation due to the occurrence of the latter unit in the vicinity of the site where the specimen was collected, but identification of the element as belonging to the extant star-nosed mole, *Condylura cristata*, resulted in the realization that the specimen had to have originated in much younger sediments overlying the Chandler Bridge. In South Carolina *Condylura cristata* is also recorded from the Rancholabrean aged Crowfield and Ardis local faunas (Bentley et al., 1994; Chandler and Knight, 2009).

North American fossil talpids that span the interval of time represented by the Chandler Bridge Formation (late Arikareean) include *Mystipterus* Hall, 1930, *Proscalops* Matthew, 1901, *Mesoscalops* Reed, 1960, *Quadrodens* Macdonald, 1970, and *Scalopoides* Wilson, 1960 (Gunnell et al., 2008). The humeri of *Mystipterus*, *Proscalops*, *Mesoscalops*, and *Quadrodens* are entirely unlike that of ChM PV9636. *Mystipterus* has a narrow, non-expanded humerus with a rounded head, indicative of an ambulatory adaptive mode (Hutchison, 1976), whereas *Proscalops* and *Mesoscalops* have the derived, greatly broadened humeri characteristic of a fully fossorial adaptive niche (Hutchison, 1972; Barnosky, 1981, 1982). *Quadrodens* is a poorly known form from the early Arikareean aged Sharps Formation of South Dakota, the humerus of which Gunnell et al. (2008:102) described as having a "long, medially directed distal pectoral process."

Although ChM PV9636 resembles the humerus of *Scalopoides* more so than that of any other Oligocene talpid, comparison with humeri of *Condylura cristata* leaves little doubt regarding its taxonomic assignment. In contrast to *Scalopoides*, ChM PV9636 has the humeral head angled laterally to the long axis vs. parallel in *Scalopoides*, a clavicular articular facet that is nearly parallel to the long axis, vs. strongly angled in *Scalopoides*, and a teres tubercle that is angled medially relative to the long axis, vs. parallel in *Scalopoides*.

CARNIVORA Bowdich, 1821
VIVERRAVIDAE Wortman and Matthew, 1899
DIDYMICTIS Cope, 1875
DIDYMICTIS PROTEUS Simpson, 1937
Figure 15

Referred Specimen.—ChM PV7687, trigonid of right m1.

Locality, Stratigraphic Horizon, and Age.—Collected by B. Palmer from a spoil pile of sediment obtained from stratigraphically below the Santee Limestone at the Martin Marietta Aggregates Jamestown Quarry, Berkeley County, "Jamestown beds" (Chicora Member of the Williamsburg Formation); late Paleocene, calcareous nannoplankton zone NP9a, late Thanetian, Clarkforkian.

Description and Discussion.—Polly (1997) concluded that there were seven species of viverravid carnivorans from the Bighorn and Clarks Fork basins of Wyoming, represented by two genera, *Viverravus* and *Didymictis*. ChM PV7687, which consists only of the trigonid, is referred to *Didymictis* on the basis of its much more closely appressed paraconid and metaconid relative to *Viverravus*, in which the more anterior position of the paraconid gives the trigonid a more "open" morphology (Polly, 1997). Of the three recognized species of *Didymictis*, ChM PV7687 most closely resembles that of *Didymictis proteus*, a late Tiffanian (Ti5) through earliest Wasatchian (Wa0) species, although the SC tooth is slightly smaller than specimens from Wyoming. *Didymictis leptomylus* Cope, 1880, and *D. protenus* (Cope, 1874) are larger and occur later in the Wasatchian (Polly, 1997). Measurements of this trigonid are 3.6 mm AP by 4.3 mm TR.

Prior to the discovery of latest Paleocene/earliest Eocene fossil-bearing sediments at the Jamestown quarry (calcareous nannoplankton zone NP9a; Cicimurri et al., 2016), only three sites along the Eastern Coastal Plain had yielded terrestrial fossils of this age: (1) land mammals from the Chicora Member of the Williamsburg Formation exposed in the St. Stephen pit, Berkeley County, referred to as the Black Mingo Fauna, are considered to be late Tiffanian (Ti5) in age (Schoch, 1985, 1998; Lofgren et al., 2004); (2) from the Fisher/Sullivan site near Fredericksburg, Virginia, Rose (1999, 2010) identified eight mammalian taxa of Wasatchian age from the Potapaco Member of the Nanjemoy Formation (Weems and Grimsley, 1999); and (3) from the Aquia Formation in Maryland, Rose (2000) described three Clarkforkian aged mammals. None of these faunas include taxa representative of the Viverravidae, thus making ChM PV7687 the first

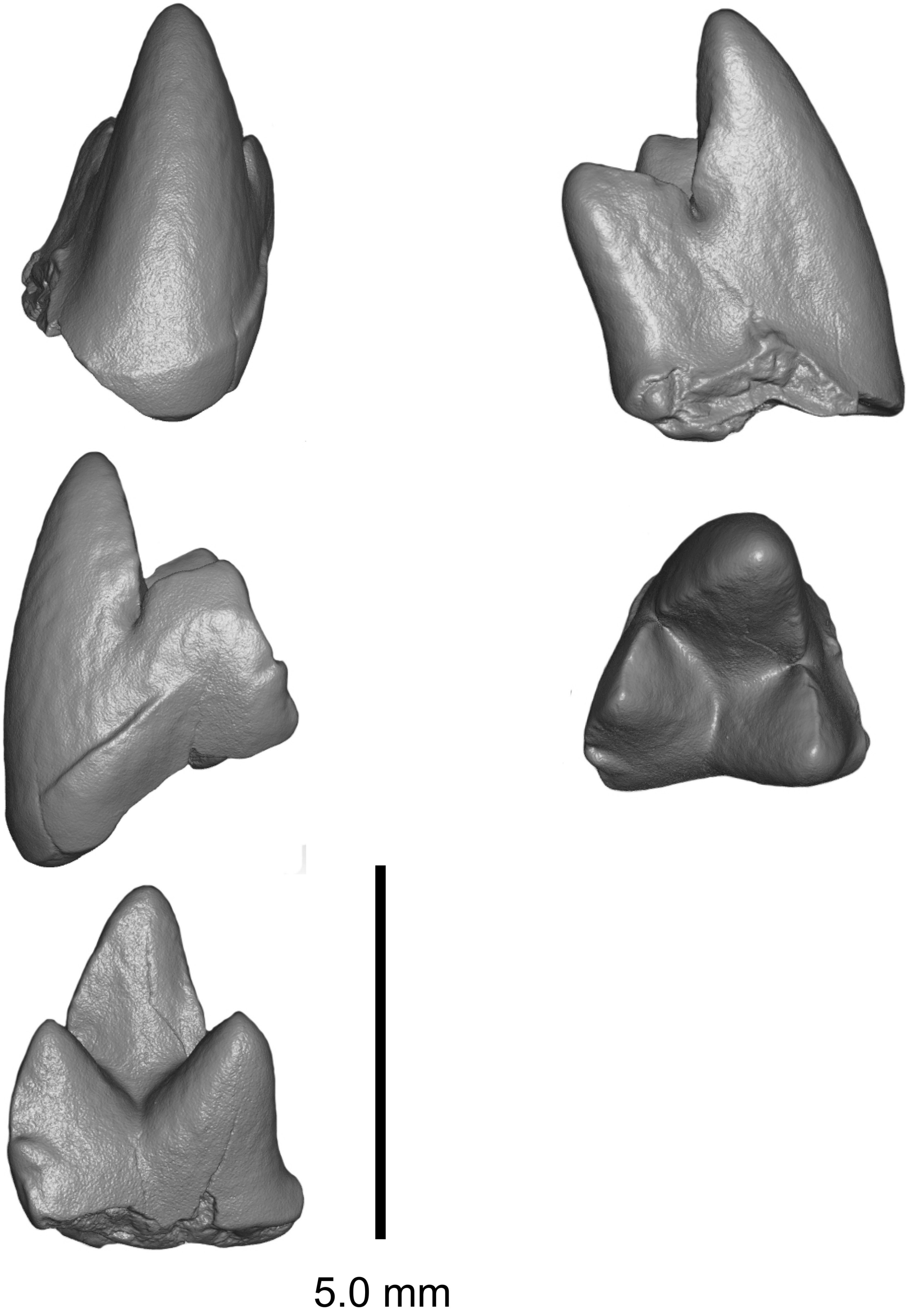


Figure 15. CT scanned images of *Didymictis proteus*, ChM PV7687, partial right m1 (trigonid only), from “Jamestown beds.” Left column: labial, anterior, and lingual views (top to bottom). Right column: posterior and occlusal views.

known occurrence of a viverravid from the Eastern Coastal Plain of the USA. The nearest known occurrence of viverravids to SC are those described by Beard and Dawson (2009) from the early Wasatchian Red Hot Local Fauna from the uppermost Tuscahoma Formation of Mississippi along the Gulf Coastal Plain.

FELIDAE Gray, 1821
LEOPARDUS Gray, 1842
LEOPARDUS AMNICOLA (Gillette, 1976)
Figure 16A–B

Felis amnicola Gillette, 1976.
Leopardus wiedii amnicola Werdelin, 1985.
Felis amnicola Gillette. Spearing, 2006.
Leopardus amnicola (Gillette). Hulbert and Pratt, 1998.

Referred Specimen.—ChM PV2636, partial left dentary with p3–4.

Locality, Stratigraphic Horizon, and Age.—"Ashley River Phosphate beds," Magnolia Phosphate Mine, Runnymede Plantation, Charleston County, Wando Formation, late Pleistocene, Rancholabrean.

Discussion.—ChM PV2636 represents the first record of *Leopardus amnicola* from SC. In size and morphology it appears closest to specimens found primarily in the Aucilla River of the Florida panhandle originally described by Gillette (1976) as *Felis amnicola*. Considered a subspecies of the margay, *L. wiedii* (*L. wiedii amnicola*), by Werdelin (1985), this taxon was maintained as a separate species, *F. amnicola*, by Spearing (2006). The Charleston specimen plots out at what would be the largest specimen of the species (p3: 7.27 mm AP x 3.47 max TR; p4: 9.05 AP x 4.01 max TR; depth of dentary below p3: 14.5 mm), but not so large as to warrant referral to a new species. According to Werdelin (1985:195), *L. amnicola* differs from *L. yagouaroundi* in having "the principal cusps of the cheek teeth aligned nearly in parallel" and a p4 that is transversely narrower for its length. In *L. yagouaroundi*, *Leopardus* sp. from coastal Georgia (Hulbert and Pratt, 1998), and even more so in the larger *Lynx rufus*, the p4 is relatively shorter and broader.

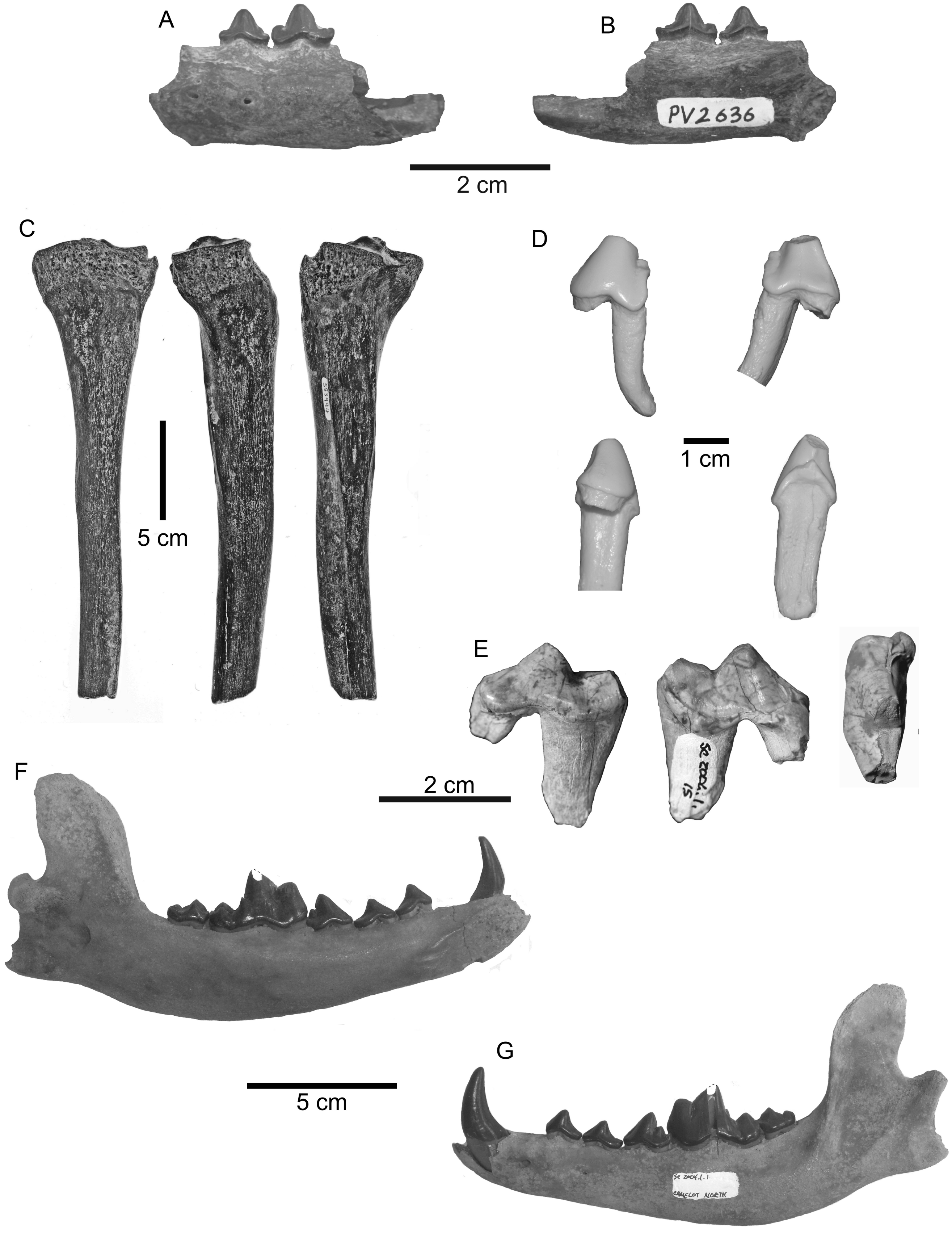
MIRACINONYX Adams, 1979
MIRACINONYX ?TRUMANI (Orr, 1969)
Figure 16C

Referred Specimen.—USNM 533994, partial right tibia collected by E. A. Crawford.

Locality, Stratigraphic Horizon, and Age.—Edisto Beach, Colleton County, from undetermined offshore upper Pleistocene unit; late Pleistocene, Rancholabrean.

Discussion.—Identification of this partial tibia as belonging to the North American cheetah-like cat *Miracinonyx* was based on comparisons with material referred to *M. inexpectatus* (Cope, 1895) from Hamilton Cave, West Virginia, by F. Grady (USNM). That species is known from late Blancan and Irvingtonian localities, including sites in SC (Sanders, 2002), with a last known occurrence of about 0.6 Ma (Van Valkenburgh et al., 1990). More recently, material referred to this taxon has been recovered from the approximately 0.41 Ma Camelot Local Fauna, thus extending its range into the latter part of the Irvingtonian. Though not yet studied in detail, the material from Camelot includes a radius, the distal part of a humerus, the proximal part of a femur, and two phalanges (SC2003.75.148–151, 153). A partial mandible with m1 (SC2003.75.147) is provisionally assigned to *M. inexpectatus*, but detailed comparisons with other cats have not yet confirmed this

Figure 16. *Leopardus amnicola*, ChM PV2636, partial left dentary with p3–4, in **A**, labial and **B**, lingual views, from "Ashley River phosphate beds"; **C**, *Miracinonyx ?trumani*, ChM PV553994, partial right tibia, in (left to right) anterior, lateral, and medial views, from Edisto Beach; **D**, *Borophagus hilli*, cast of AMNH 144657, left p4, in (left to right, top) labial and lingual view, and (left to right, bottom) anterior and posterior views, from Martin Marietta Orangeburg Quarry, Raysor Formation; **E**, *Canis lepophagus,* SC2006.1.15, right P4, in (left to right) labial, lingual, and occlusal views, from Walrus Ditch site, Waccamaw Formation; **F**, lingual and **G**, labial views of *Canis armbrusteri*, SC2004.1.2, right dentary with c, p2–m2, from Camelot locality, Ladson Formation.


A
B
PV2636
2 cm
C
5 cm
D
1 cm
E
2 cm
F
G
5 cm
CAMELOT NORTH

identification.

A second species, *M. trumani*, is apparently confined to the Rancholabrean, with an earliest known occurrence in Crypt Cave, Nevada, which has been dated to 19,750 ± 650 years BP (Van Valkenburgh et al., 1990). *Miracinonyx trumani* was originally recorded from Natural Trap Cave in the Bighorn Mountains of Wyoming, the oldest stratum in which was radiocarbon dated to 12,770 ± 900 years (Martin et al., 1977). From a biochronologic perspective, therefore, USNM 533994 seems referable to *M. trumani* rather than *M. inexpectatus*, as the fauna from Edisto Beach is primarily Rancholabrean. On the other hand, F. Grady (pers. comm. to LBA, May, 2019) noted that the size of the Edisto tibia was similar to *M. inexpectatus*. Further study of this specimen is warranted before a definitive identification to species can be made.

CANIDAE Fischer von Waldheim, 1817
BOROPHAGINAE Simpson, 1945
BOROPHAGUS Cope, 1892
BOROPHAGUS HILLI (Johnston, 1939)
Figure 16D

See Wang et al. (1999:296) for synonymy.

Referred Specimen.—AMNH 144657, left p4.

Locality, Stratigraphic Horizon, and Age.—Martin Marietta Aggregates Cross Quarry, Orangeburg County, Raysor Formation, early Pliocene, early Blancan.

Description.—Because detailed description of this tooth was recently provided by Tseng and Geisler (2016), only a brief summary is provided here. Referral of AMNH 144657 to *Borophagus hilli*, rather than to the other Blancan borophagine, *B. diversidens* Cope, 1892, is based on the presence of a posterior accessory cusplet (absent in *B. diversidens*) and on the absence of the strongly posteriorly-sloped crown noted for the latter (Wang et al., 1999; Tseng and Geisler, 2016). *Borophagus dudleyi* (White, 1941), from the latest Hemphillian Palmetto Fauna of Florida (Bone Valley Formation), is known only from an edentulous skull, therefore precluding comparison with the SC tooth, although the latter matches very closely those p4s from the same fauna but referred to *B. hilli* (see discussion in Wang et al., 1999:301). *Borophagus dudleyi* was also reported from the late Hemphillian Lee Creek Local Fauna of North Carolina (Eshelman and Whitmore, 2008), but the absence of a p4 again precludes comparison with the SC specimen. Measurements provided by Tseng and Geisler (2016) place the tooth at 15.4 mm long by 13.1 mm wide, slightly shorter but comparable in width to the smallest specimen of *B. hilli* noted in Appendix III of Wang et al. (1999).

Discussion.—In May 2006, Ms. D. Young, searching for fossils with Mr. B. Palmer, found an isolated carnivoran p4 in spoil material on the floor of the Martin Marietta Aggregates Orangeburg quarry west of Cross, SC. In the part of the quarry from which the tooth was found, when it was found, excavation had yet to cut into the Eocene units which are the source of the limestone being mined. Unconformably overlying the Eocene units is the Pliocene age Raysor Formation, and it is from this unit the tooth is considered to have originated, although Tseng and Geisler (2016) suggested the Goose Creek Limestone as a possible source. Examination by LBA of the area of the quarry from which the tooth was recovered revealed exposures of the Raysor Formation, but not of the Goose Creek Limestone. AMNH 144657 represents the only known occurrence of a borophagine canid from SC.

CANINAE Fischer de Waldheim, 1817
CANIS Linnaeus, 1758
CANIS LEPOPHAGUS Johnston, 1938
Figure 16E

Canis lepophagus Johnston, 1938.
Canis latrans lepophagus Giles, 1960.
Canis lepophagus Johnston. Tedford et al., 2009.

Referred Specimen.—SC 2006.1.15, right P4.

Locality, Stratigraphic Horizon, and Age.—Walrus Ditch locality, Dorchester County, lower Waccamaw Formation, early Pleistocene, late Blancan.

Description and Discussion.—This tooth represents the first reported occurrence of *C. lepophagus* in SC. It measures 22.6 mm AP by 11.7 mm TR at the paracone by 10.5 mm TR at the protocone. In Florida, *C. lepophagus* is known from the late Blancan Santa Fe River and Withlacoochee River 1A faunas.

CANIS ARMBRUSTERI Gidley, 1913
Figure 16F–G

See Tedford et al. (2009) for synonymy.

Referred Specimens.—SC 2004.1.1, right dentary with broken canine, p2, p4–m2; SC 2004.1.2, right dentary with canine, p2–m2; SC2003.75.152, left Mt II; SC2003.75.692, left Mt V.

Locality, Stratigraphic Horizon, and Age.—Camelot locality, near Harleyville, Dorchester County, from fluvial channel sediments likely correlative with the Ladson Formation; middle Pleistocene, late Irvingtonian.

Discussion.—Known from the early Irvingtonian of Arizona and Florida to the early Rancholabrean of Florida, *Canis armbrusteri* is broadly distributed across the USA (Tedford et al., 2009). Taxonomically the Camelot Local Fauna appears similar to the late Irvingtonian Coleman 2A Local Fauna of Florida (Martin, 1974), and this is supported by the 400–450 kyr dates on the Ladson Formation from which the Camelot LF is thought to be derived. The two above noted rami were utilized by Kohn et al. (2005) for isotopic analysis of enamel in an attempt to infer trophic levels, habitat, etc. Additional undescribed material of this taxon is currently catalogued and under study by DJC, JLK, and associates at the SCSM.

CANIS DIRUS Leidy, 1858
Figure 17A–D

See Tedford et al. (2009) for synonymy.

Referred Specimens.—ChM PV2637, partial right mandibular dentary with p4; SC 83.118.1, left dentary with p2, partial p3, p4–m2; ChM PV7697, right medial phalanx, pes digit 3.

Locality, Stratigraphic Horizon, and Age.—ChM PV2637 from "Ashley River phosphate beds" (Wando Formation) near Runnymede Plantation, about 15 km northwest of Charleston; SC 83.118.1 from Cooper River, Berkeley County, likely derived from Wando Formation; ChM PV7697 from "near Summerville," exact locality unknown, likely derived from Wando Formation; late Pleistocene, Rancholabrean.

Discussion.—The partial right dentary, ChM PV2637, was originally mentioned and figured by Hay (1923:365-366) who noted its similarity to "*C. occidentalis*," but he did not assign it to a specific taxon. Comparisons with material at the SCSM and the FLMNH, and with measurements in Nowak (1979, 2002) and Kurtén (1984), result in a confident referral of the specimen to the dire wolf. The p4 measures about 18.5 mm AP by 9.5 mm TR (max). Measurements for SC 83.118.1 are as follows: p2, 14.6 mm; p3, 16.9 mm; p4, 19.9 mm; m1, 34.6 mm; m2, 14.2 mm; p2-m2, 102.9 mm. See the above discussion on *Castoroides* regarding the unit of origin for this specimen. ChM PV7697, the medial phalanx, measures about 2.8 cm long.

CANIS LATRANS Say, 1823
Figure 17E–F

Referred Specimens.—SC2016.20.1, right dentary with p1–4, m1–2; SC2016.21.1, edentulous dentary showing alveoli for p3–m3; USNM 533995, right m1.

Locality, Stratigraphic Horizon, and Age.—SC2016.20.1 collected by J. Thompson from Edisto River, south of Highway 17, Colleton County, ?Wando Formation, Rancholabrean; SC2016.21.1 collected by B. Orr from the Cooper River, Berkeley County, ?Wando Formation, Rancholabrean; USNM 533995 from Myrtle Beach, Horry County, undetermined offshore upper Pleistocene unit, Rancholabrean.

Discussion.—These specimens represent the first reported fossil occurrences of *C. latrans* in SC. Measurements of the teeth are provided in Table 7, and they fall within the range of variation for this species as presented in figure 4 of Nowak (2002:106). SC2016.21.1, the edentulous dentary, shows no diastemata whatsoever between any of the alveoli. SC2016.20.1, on the other hand, shows prominent diastemata between all the teeth. Examination of several coyote jaws in the collections of the SCSM shows this feature to be variable. The m1s have a robust hypoconulid, diminutive entoconid, and weak posterior cingulum.

As Nowak (2002:118) noted, fossil material of eastern coyotes is rare, although late Rancho-

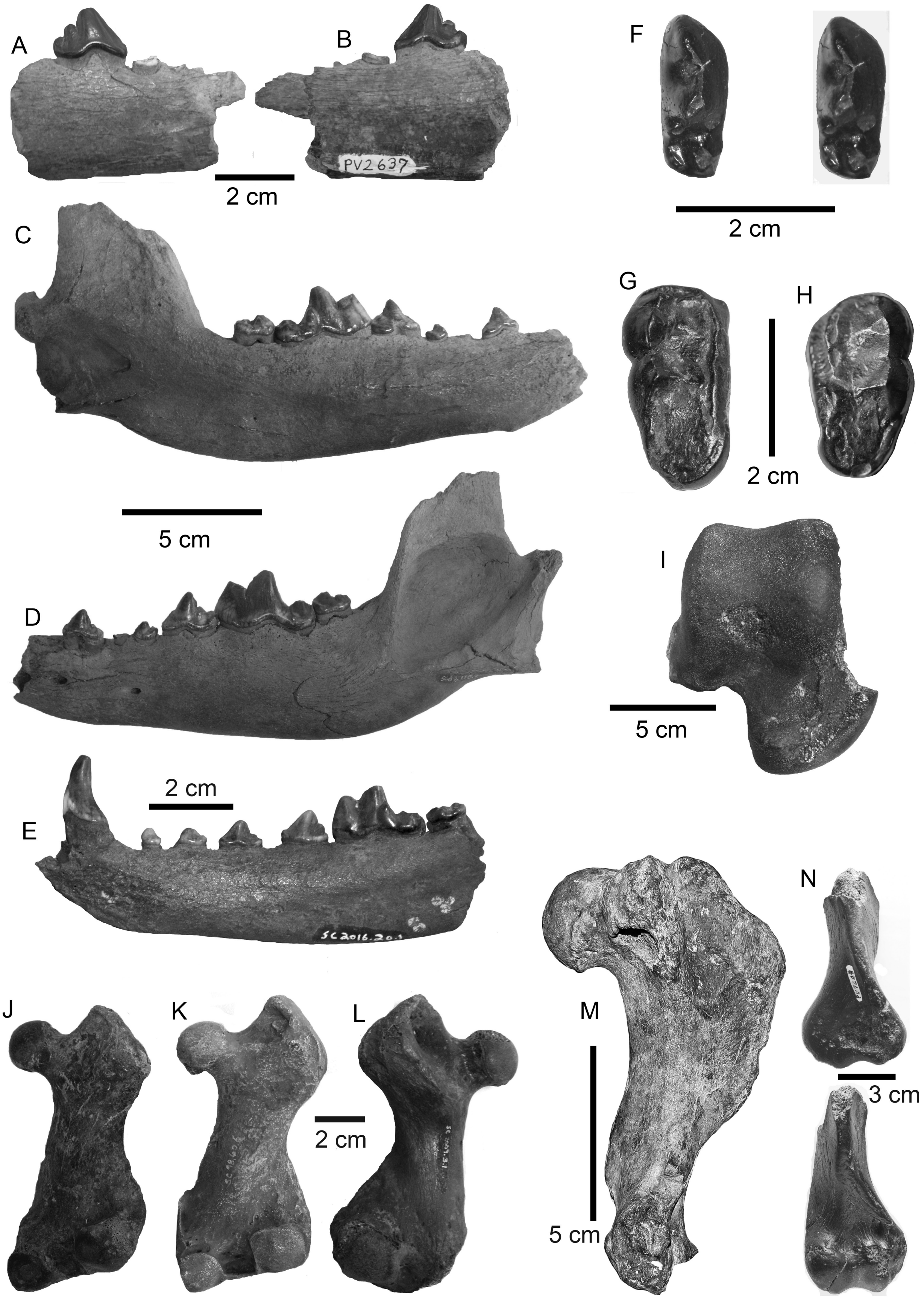

A
B
PV2637
2 cm
F
2 cm
C
G
H
2 cm
5 cm
I
D
5 cm
2 cm
E
SC2016.20.1
N
J
K
L
M
2 cm
5 cm
3 cm

Table 7. Measurements (mm) of lower teeth in selected specimens of *Canis latrans*.

Specimen/Tooth	AP	TR
SC2016.20.1		
canine	7.0	6.4
p1	4.7	3.2
p2	8.0	4.4
p3	10.3	5.0
p4	11.2	6.2
m1	22.2	9.0
m2	9.3	7.0
USNM 533995		
m1	19.5	8.5

labrean records have been reported from Indiana, Pennsylvania, West Virginia, Mississippi, Alabama, and Florida. This rarity of coyotes in the east during the late Rancholabrean, Nowak concluded, is most likely due to the influx of the small wolf, *C. rufus*, at that time.

URSIDAE Gray, 1825
ARCTODUS Leidy, 1854
ARCTODUS PRISTINUS Leidy, 1854

Referred Specimen.—USNM PAL 530189, left m2.

Locality, Stratigraphic Horizon, and Age.—Myrtle Beach, Horry County, from undetermined offshore Pleistocene unit.

Discussion.—In his discussion of *A. pristinus*, Sanders (2002:40) noted the provenance of two specimens, ChM PV5472 and ChM PV2536, as the Wando Formation, and also concluded that Leidy's lost holotype was derived from that unit, as well. He also cited Kurten's and Anderson's (1980) range for this taxon as "only from a few Irvingtonian and Rancholabrean localities in the eastern United States." More recent studies of *A. pristinus*, however, from a variety of localities across the eastern USA, especially Florida and Pennsylvania where several much more complete specimens have been recovered, have determined that there are no confirmed Rancholabrean occurrences, and that this taxon is diagnostic of the late Blancan to late Irvingtonian (Emslie, 1995; Schubert, 2008; Schubert et al., 2010). The Rancholabrean species, *A. simus*, is much larger than *A. pristinus* and apparently extremely rare in southeastern North America, currently known only from two localities in Florida (Schubert et al., 2010). These findings, therefore, prompt a reevaluation of the age and provenance of specimens discussed by Sanders (2002) as having been recovered from the Wando Formation.

First is Leidy's (1854) holotype. That now lost specimen consisted of a single isolated m2 that was recovered from the Ashley phosphate beds at Bee's Ferry on the west bank of the Ashley River about 17 km northwest of Charleston, and Sanders (2002) convincingly argued that it was *collected*

Figure 17. *Canis dirus*, ChM PV2637, partial right mandibular dentary with p4, in **A**, labial, and **B**, lingual view, from the "Ashley River phosphate beds"; *Canis dirus*, SC 83.118.1, left dentary with p2, partial p3, p4–m2, in **C**, lingual, and **D**, labial view, from the Cooper River; **E**, *Canis latrans*, SC2016.20.1, lingual view of right dentary with c–m2 from Edisto River, ?Wando Formation; **F**, USNM 533995, stereo view of right m1, from Myrtle Beach; **G**, *Tremarctos floridanus*, ChM PV3463, right M2, from Edisto Beach; **H**, *Ursus americanus*, SC83.99.3, left M2, from Horry County; **I,** *Ontocetus emmonsi*, ChM PV6949, right astragalus, from Cross quarry, Goose Creek Limestone or Raysor Formation; **J**, *Phocanella pumila*, SC2015.18.4, right femur, from Ashepoo River, Colleton County; **K**, *Phocanella pumila*, SC98.60.6 (cast of USNM 181649), right femur, from Yorktown Formation, Lee Creek Mine, NC; **L**, *Phocanella pumila*, SC2009.3.1, left femur, from Morgan River, Beaufort County, ?Wabasso beds or ?Goose Creek Limestone; **M**, *Callophoca obscura*, SC2012.16.1, left humerus, from Broad River, Beaufort County, ?Wabasso beds or ?Goose Creek Limestone; **N**, *Monatherium* sp., ChM PV7688, distal part of humerus, in dorsal (top) and ventral (bottom) view, from Summerville area, ?Ebenezer Formation.

from the Wando Formation. To the extent, however, that the Wando Formation is correlative with the Rancholabrean NALMA within which *A. pristinus* apparently does not occur, the Leidy specimen more likely *originated* from the Penholoway or Ladson formations from which middle and late Irvingtonian taxa, respectively, are known, followed by reworking into the Wando at a later time. Determining that the tooth was found in the Wando Formation, Sanders (2002:42) suggested that it perhaps had been "transported [to the Wando Formation in the vicinity of Bee's Ferry] by water from an inland source." That is likely correct, the "inland source," however, being the older, more age-appropriate formations noted above. Further supporting this is a statement by Sanders (2002:61) regarding the provenance of another specimen collected from the Ashely phosphate beds in the same region. Referring to MCZ 16512, an edentulous dentary of *Miracinonyx inexpectatus*, Sanders stated, "since most of the land mining operations in the Charleston area were located along the Ashley River this specimen probably came from one of the mines on the north side of the river, where the early Pleistocene (Middle Irvingtonian) Penholoway Formation underlies the Wando Formation …." The same might be said about Leidy's holotype.

ChM PV2536, a lower left canine, was found in the same area as Leidy's holotype (the Ashley phosphate beds on the west bank of the Ashley River), and like the latter tooth was also likely reworked into the Wando. Supporting these conclusions is the presence of *A. pristinus* in the late Blancan Walrus Ditch LF (lower Waccamaw Formation) and another m2 from the middle Pleistocene aged Ladson Formation (ChM PV5146: Sanders, 2002), units whose age is consistent with that of this species.

Another specimen noted from the Wando Formation is ChM PV5472, a partial dentary with m1-m2. This specimen was actually found on the bottom of Tail Race Canal (see Sanders, 2002:40 and fig. 16), which refers to the upper-most west branch of the Cooper River, not in situ. Pleistocene fossils from the Cooper River are always found as isolated specimens in lag deposits that have accumulated on the bottom of the channel – never in situ (LBA, pers. observ.). Thus, based on the biochronological findings of Schubert et al. (2010) noted above, it is more likely that this specimen originated from the Waccamaw, Penholoway, or Ladson formations from which late Blancan to late Irvingtonian taxa, respectively, are known, rather than from the Wando Formation as reported.

USNM PAL 530189, from deposits off of Myrtle Beach, is noted here simply as an addition to the known *Arctodus* material from SC. This specimen, too, was likely reworked into the offshore upper Pleistocene deposits from a subjacent, older unit.

TREMARCTOS Gervais, 1855
TREMARCTOS FLORIDANUS (Gidley, 1928)
Figure 17G

Arctodus floridanus Gidley, 1928.
Tremarctos mexicanus Stock, 1950.
Tremarctos floridanus (Gidley). Stock, 1950; Kurtén, 1966.

Referred Specimen.—SC81.140.1, right M2.

Locality, Stratigraphic Horizon, and Age.—Edisto Beach, Colleton County, undetermined offshore upper Pleistocene unit; late Pleistocene, Rancholabrean.

Discussion.—The photograph of the M2 of *Tremarctos floridanus* in Figure 16G is of ChM PV3463 (also from Edisto Beach) rather than SC81.140.1. The two specimens are nearly identical, however, and we note the latter as an addition to material previously referred to this taxon from SC, such as specimens from the Ardis LF (Bentley et al., 1994; Sanders, 2002). SC81.140.1 measures 29.9 mm AP x 15.0 mm TR; ChM PV3463 measures 29.83 mm AP x 15.7 mm TR.

URSUS Linnaeus, 1758
URSUS AMERICANUS Pallas, 1780
Figure 17H

Referred Specimen.—SC83.99.3, left M2.

Locality, Stratigraphic Horizon, and Age.—SC83.99.3 from Horry County, undetermined offshore upper Pleistocene unit; late Pleistocene, Rancholabrean.

Discussion.—Measuring 27.02 mm AP by 16.16 mm TR, SC83.99.3 is considerably smaller than the late Blancan to late Irvingtonian lesser short-faced bear, *Arctodus pristinus*, and the even larger late Rancholabrean greater short-faced bear, *A. simus*. SC83.99.3 also lacks the dramatic reduction of the posterior portion of the tooth that is characteristic of *Arctodus*. Although the late Pleistocene *Ursus americanus* did not overlap temporally with *A. pristinus*, it did co-occur with *Tremarctos floridanus* (Schubert et al., 2010). According to B. Schubert (pers. comm. to LBA, November, 2016), the M2 of *U. americanus* has a cingulum and the lingual side of the occlusal surface is concave, whereas *Tremarctos* tends to lack a cingulum ridge and the lingual side of the tooth forms a straight line. We note this specimen simply as an addition to the known *Ursus* material from SC.

PROCYONIDAE Gray, 1825
PROCYON Storr, 1780
PROCYON LOTOR (Linnaeus, 1758)

Referred Specimen.—ChM PV7696, axis vertebra.

Locality, Stratigraphic Horizon, and Age.—Near Summerville (exact locality unknown), Berkeley County, ?Wando Formation; late Pleistocene, late Rancholabrean.

Discussion.—Identification of this well preserved specimen is based on the nearly identical morphology it shares with the axis vertebra of the extant raccoon. Fossil remains of raccoon are also known from Edisto Beach (Roth and Laerm, 1980), the Ardis Local Fauna (Bentley et al., 1994), the Crowfield Local Fauna, plus the older, late Irvingtonian aged Camelot Local Fauna.

ODOBENIDAE Allen, 1880
ONTOCETUS Leidy, 1859
ONTOCETUS EMMONSI Leidy, 1859
Figure 17I

See Kohno and Ray, 2008, for synonymy.

Referred Specimens (in part from Kohno and Ray, 2008:77; also see Boessenecker et al., 2018).—USNM 437544, 437545, 475484, upper canines, from Little River, Horry County; USNM 475463, upper canine, from Martin Marietta Cross quarry, Berkeley County; USNM 521227, upper canine, Walrus Ditch locality, Dorchester County; SC2017.14.2 (original number SC98.51.1), right tusk, Austin Sand Pit, Ridgeville, Dorchester County; CCNHM 1144, left tusk, Austin Sand Pit, Ridgeville, Dorchester County; SC76.15.9, 77.14.1, 77.14.2, 77.14.3, 79.38.199, and 84.37.1, upper canines, from Cooper River, Berkeley County; AMNH 104788, 104790, upper canines, from "Ashley River phosphate beds" (Sanders, 2002:66); ChM PV1028, 1029, upper canines, from "Charleston"; ChM PV13296, upper canine, from Coosaw River, Beaufort County; SC2017.10.6, proximal left tusk, from Broad River, Beaufort County; SC2016.1.23, distal right tusk, from Broad River, Beaufort County; ChM PV13497, upper canine, from "?Charleston"; USNM 481879, upper canine, from Beaufort County; USNM 475482 left dentary with i3, c, p1–3 (cast ChM PV7213), from Martin Marietta Cross quarry, Berkeley County; ChM PV6949, right astragalus, from Martin Marietta Cross quarry, Berkeley County.

Stratigraphic Horizon and Age.—Specimens from Cross quarry from Raysor Formation or Goose Creek Limestone, late early Pliocene, late Zanclean, early Blancan; specimens from Cooper River probably from Goose Creek Limestone, late early Pliocene, late Zanclean, early Blancan; specimens from Ashley River phosphate beds probably from Goose Creek Limestone, late early Pliocene, late Zanclean, early Blancan; specimen from Walrus Ditch locality from lower Waccamaw Formation, early Pleistocene, late Blancan; specimen from Ridgeville LF (= Austin pit locality) from ?upper Waccamaw Formation, early Pleistocene, latest Blancan-earliest Irvingtonian.

Discussion.—Kohno and Ray (2008) reviewed all Pliocene walruses from North America, Europe, and northern Africa, which constituted several named genera and species, and concluded that they all belonged to a single taxon, *Ontocetus emmonsi* (also see Deméré, 1994, and Deméré et al., 2003). Found in Pliocene coastal deposits of the eastern and western North Atlantic (and the early Pliocene of the North Pacific), *O. emmonsi* is best represented in North America from the Yorktown Formation at the Lee Creek Mine, NC.

Several specimens have also been recovered from equivalent strata in South Carolina, primarily the Goose Creek Limestone and/or Raysor Formation (listed above from Kohno and Ray, 2008:77). Although Kohno and Ray (2008) noted the questionable occurrence of USNM specimens 437544, 437545, 475484 (upper canines) from the Canepatch (= Ladson) Formation of Horry County, it is highly unlikely that they are from that unit given its middle Pleistocene age; *O. emmonsi* is not known to have survived along the Eastern Coastal Plain of North America later than the early late Pliocene (Kohno and Ray, 2008:63; but note the following). Similarly, they noted the questionable occurrence of the Walrus Ditch specimen (USNM 521227) from the Goose Creek Limestone. This, too, is untenable, as the Walrus Ditch LF is not derived from the Goose Creek Limestone; it includes a rich late Blancan terrestrial mammal fauna from what is considered to be the lower Waccamaw Formation (approx. 2.4 Ma). The Walrus Ditch specimen, in addition to the specimen noted in Boessenecker et al. (2018) from the Ridgeville LF, therefore, extends the range of *O. emmonsi* into what is now considered the early Pleistocene based on the recent extension of the Pleistocene downward to the base of the Gelasian Stage (Gibbard et al., 2010; Pillans and Gibbard, 2012).

Kohno and Ray (2008:77) also referred two upper canines from the Ashley River phosphate beds near Charleston to *O. emmonsi* (AMNH 104788 and 104790), whereas Sanders (2002) assigned these specimens to *Odobenus rosmarus*. The morphology of the specimens indicates referral to the former, i.e., laterally compressed with fluting along the length of the tusk. Based on *O. emmonsi*'s termination by (what is now considered) the early Pleistocene, and on the non-overlapping ranges of *O. emmonsi* and *Odobenus rosmarus*, these specimens evidently were reworked into the Ashley phosphate beds (within the Wando Formation) from an older unit, presumably the Goose Creek Limestone upon which the Wando unconformably rests in many places.

PHOCIDAE Gray, 1825
PHOCINAE Gill, 1866
PHOCANELLA Van Beneden, 1877
PHOCANELLA PUMILA Van Beneden, 1877

Figure 17J–L

See Koretsky and Ray (2008) for synonymy.

Referred Specimens.—SC2016.1.16, partial left innominate; SC2016.1.17, partial right innominate; SC2015.18.4, right femur; SC2009.3.1, left femur; SC2017.14.1, proximal left femur. (Note: SC2016.1.16, SC2016.1.17, and SC2015.18.4 may be associated).

Locality, Stratigraphic Horizon, and Age.—SC2016.1.16, SC2016.1.17, and SC2015.18.4 collected by M. Swilp from the Ashepoo River, Colleton County (exact locality unknown); SC2017.14.1 collected by M. Swilp from Whale Branch region of Broad River, Beaufort County; SC2009.3.1 collected by scuba divers from the Morgan River, Beaufort County; questionably from Wabasso beds, although matrix in pores suggests possible derivation from Goose Creek Limestone; early Pliocene, late Zanclean, early Blancan (see further discussion below).

Discussion.—Originally described by Van Beneden (1877) from the Zanclean of Belgium, *Phocanella pumila* is known from the USA Atlantic Coastal Plain from the Yorktown Formation, NC (Ray, 1976a; Koretsky and Barnes, 2008; Koretsky and Ray, 2008), and from the latest Hemphillian Palmetto Local Fauna of the upper Bone Valley Formation, central Florida (Morgan, 1994). To our knowledge, this is the first report of this taxon from SC. Referral of the SC femora to *P. pumila* is based on the nearly identical morphology they share with the Lee Creek specimen (USNM 181649) described by Koretsky and Ray (2008) as determined from direct comparisons with a cast of the same (SC98.60.6; Fig. 17K). The larger size of SC2009.3.1 may be a function of ontogenetic stage or sexual dimorphism (Table 8).

USNM 181649 was stated to be from the "lower beds of the Yorktown Formation" in the Lee Creek Mine (Koretsky and Ray, 2008:121), which indicates its likely derivation from the Sunken Meadow Member. Terrestrial mammals from this unit, the Lee Creek Local Fauna (Eshelman and Whitmore, 2008), are indicative of a latest Hemphillian age – the same age as the Palmetto Local Fauna. In addition to the mutual occurrence of

Table 8. Measurements (mm) of femora of *Phocanella pumila*; (brkn = broken, sl worn = slightly worn).

Specimen	Maximum length	Max. Width (proximal end)	Max. Width (distal end)
SC 98.60.6 (cast of USNM 181649)	124.3	60.2	58.8
SC 2009.3.1	125.2 (sl worn)	70.4	59.2 (brkn)
SC 2015.18.4	120.3 (worn)	61.8 (worn)	59.6

Phocanella pumila in these two faunas, the pinnipeds *Callophoca obscura* and *Ontocetus emmonsi* are also shared, as well as the cetacean *Ninoziphius platyrostris* (Morgan, 1994). This suggests that the specimens from the Broad and Morgan rivers near Beaufort, SC, may have originated from a Sunken Meadow Member equivalent, perhaps the Wabasso beds, which, as noted previously, apparently occur in the shallow subsurface near Beaufort (Huddlestun, 1988:98). This is further supported by the quality and, at one time, common and abundant presence of *Megaselachus megalodon* teeth from the Morgan River, given that this taxon last occurs during Sunken Meadow (= Wabasso) time (Ward, 2008). On the other hand, there is a cream-colored matrix within pore spaces of SC2009.3.1 that resembles Goose Creek Limestone. To the extent that *Phocanella* has not been found in strata more recent in age than Zanclean, the latest Zanclean age of the Goose Creek Limestone does not preclude that unit as the specimen's source.

MONACHINAE Gray, 1869
CALLOPHOCA Van Beneden, 1877
CALLOPHOCA OBSCURA Van Beneden, 1877
Figure 17M

See Koretsky and Ray (2008) for synonymy.

Referred Specimen.—SC2012.16.1, partial left humerus, collected by M. Swilp from Whale Branch region of Broad River, Beaufort County.

Locality, Stratigraphic Horizon, and Age.—Questionably from Wabasso beds (or possibly Goose Creek Limestone); early Pliocene, late Zanclean, early Blancan.

Discussion.—Referral of SC2012.16.1 is based primarily on its similarity in size and morphology to those specimens assigned to this taxon from the Lee Creek Mine by Koretsky and Ray (2008). This humerus differs significantly from that of *Phocanella pumila* in being relatively shorter with a more stocky appearance and in the much larger size of the capitulum relative to the total length, which is 131 mm. This length, together with its somewhat gracile morphology, suggests that the element belonged to a female (see measurements in Koretsky and Ray, 2008).

SC2012.16.1 represents the first record of *Callophoca obscura* in SC. Like *Phocanella pumila* discussed above, *C. obscura* was also originally described from the Zanclean of Belgium (Van Beneden, 1877), but it too occurs in the Lee Creek and Palmetto faunas (Ray, 1976a; Morgan, 1994; Koretsky and Barnes, 2008; Koretsky and Ray, 2008). Its presence in South Carolina, therefore, from deposits that also yielded *Phocanella* is not particularly unexpected.

MONATHERIUM Van Beneden, 1877
MONATHERIUM sp.
Figure 17N

Referred Specimen.—ChM PV7688, distal part of humerus.

Locality, Stratigraphic Horizon, and Age.—Near Summerville, Berkeley County (exact locality unknown), ?Ebenezer Formation; late Miocene, late Tortonian, late Barstovian.

Discussion.—Identification of this specimen as *Monatherium* was provided by I. Koretsky (pers. comm. to AES, 2010). First described from Europe, this taxon ranges in age from the middle to late Miocene (Langhian to Messinian) and is known in North America from the Calvert, St. Mary's, and Eastover formations of Virginia and Maryland

(Ray, 1976a, b; Deméré et al., 2003); it is not known from the Yorktown or other Pliocene formations of the Atlantic Coastal Plain. In South Carolina the only middle to upper Miocene units are the Coosawhatchie and Ebenezer formations, respectively. According to Weems and Lewis (2002:29), the Ebenezer Formation is only known in the Charleston/Summerville area from "two small patches of shelly shelf sand, informally named the Rudd Branch beds …" They further noted that these beds represent "the only occurrences of any strata representing the late Miocene" in that region. The middle Miocene (lower Serravallian) Coosawhatchie Formation does not occur in the Charleston/Summerville area (Weems and Lewis, 2002). As with many of South Carolina's vertebrate fossil occurrences, however, and given the extremely limited distribution of these two "small patches," it is likely that this specimen was reworked from the Ebenezer Formation into a younger formation of greater extent in the Summerville area, such as the Goose Creek Limestone (see Weems and Lewis, 2002:fig. 5), if Koretsky's identification of this fragmentary specimen is correct.

PERISSODACTYLA Owen, 1848
EQUIDAE Gray, 1821
ANCHIPPUS Leidy, 1868b
ANCHIPPUS TEXANUS Leidy, 1868b
Figure 18A

Anchippus texanus Leidy, 1868b.
Anchippus texanus Leidy. Leidy, 1869; Albright, 1999b.
Parahippus texanus (Leidy). Gidley, 1907; Osborn, 1918; Stirton, 1940.
Parahippus cf. *P. texanus* (Leidy). Forsten, 1975, in part.

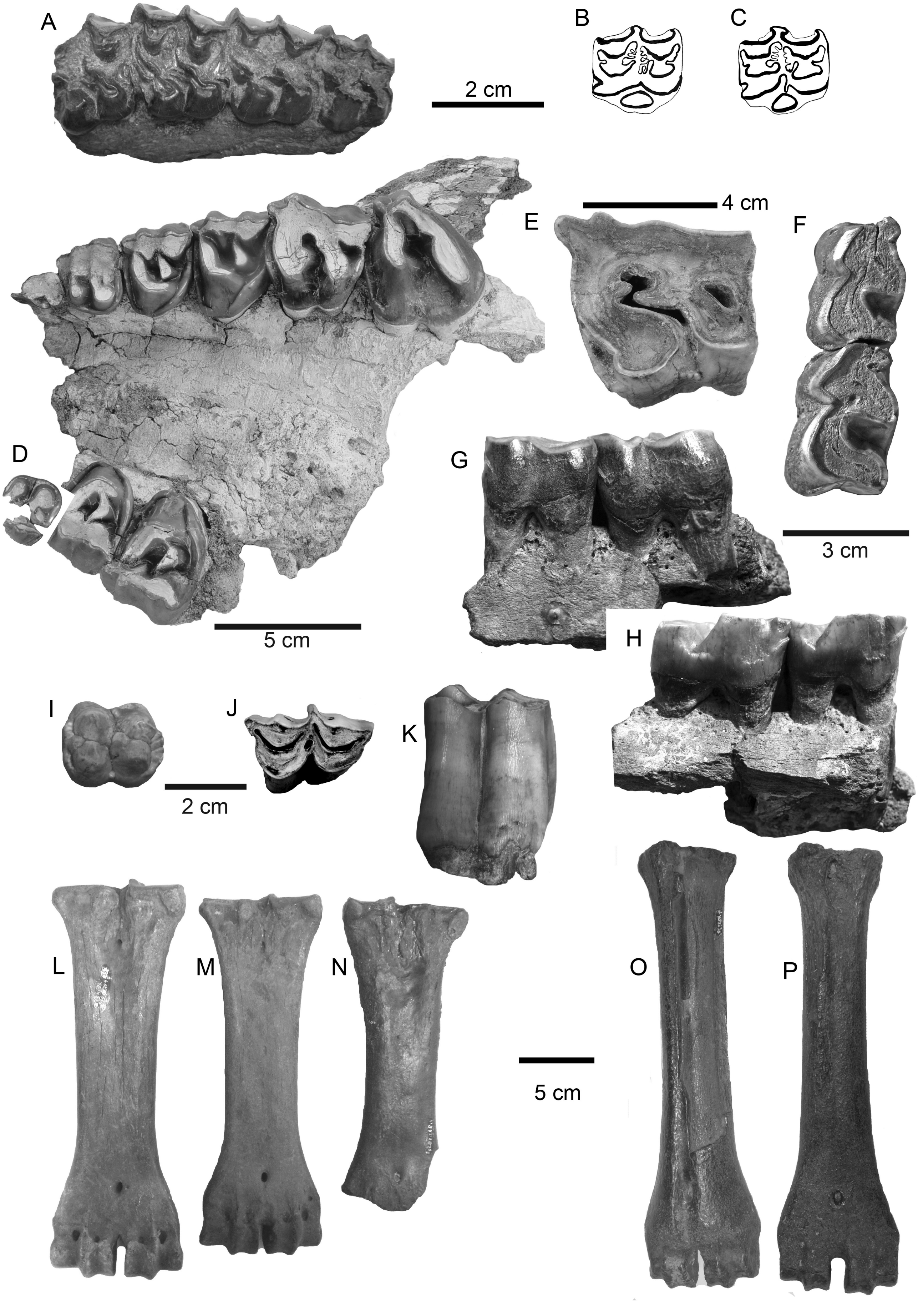
Referred Specimen.—ChM PV13526, partial left maxillary with P4–M3.

Locality, Stratigraphic Horizon, and Age.—"Ashley River phosphate beds" near Runnymede Plantation, about 15 km northwest of Charleston. Likely reworked into the upper Pleistocene Wando Formation from either the Chandler Bridge or Edisto formations; late Oligocene, late Chattian, Arikareean 3.

Discussion.—ChM PV13526 is here referred to *Anchippus texanus* on the basis of the nearly identical morphology that the teeth share with the type specimen and with those referred to this taxon from the late Arikareean Toledo Bend Local Fauna of easternmost Texas (Albright, 1991, 1999b). Just as in *A. texanus* from Toledo Bend, the Charleston teeth, although slightly smaller (M1 = 17.5 AP x 20.0 TR, M2 = 16.8 AP x 19.3 TR, M3 = 15.3 AP x 18.3 TR; M1–M3 = 48.4 mm; P4 broken anteriorly), are low-crowned, they lack cement, they have slightly crenulated enamel, the protocone and protoconule, as well as the metacone and metaconule, are distinctly separated and remain so at least through medium wear, and there is a single crochet extending anteriorly from the metaloph toward the division between the protocone and protoconule.

The teeth also closely resemble those of the late Arikareean *Parahippus nebrascensis* and *P. wyomingensis* from the Great Plains. This simi-

Figure 18. A, *Anchippus texanus*, ChM PV13526, partial left maxillary with P4–M3, from "Ashley River phosphate beds"; **B**, *Nannippus* sp., SC2006.1.24, and **C**, SC2006.1.23, upper left cheek teeth, from the Walrus Ditch locality, Waccamaw Formation; **D**, *Subhyracodon mitis*, right P2 (SCTC400; the palate shown, from which the P2 is derived, with right P2–4 and left P1–4, M1 or M2, and M3 is held in a private collection [see text for discussion]), from the Argos Cement quarry, Harleyville Formation; **E**, *Aphelops* ?*malacorhinus*, photograph of original left M2 from Wright River, Jasper County, from which cast SC2010.12.1 was made; **F**, ?*Teleoceras gymonense*, left p3–4, occlusal view, from Morgan River, Beaufort County; **G**, **H**, same specimen in lateral and lingual views, respectively; **I**, *Perchoerus* sp., ChM PV5025, right m2, from Chandler Bridge Formation; **J**–**P**, *Bootherium bombifrons*: **J**, USNM 533996, left M3, occlusal view, Surfside Beach, Horry County; **K**, labial view of same; **L**, SC75.31.204, right metacarpal III–IV, Edisto Beach; **M**, ChM PV40.183.17, right metacarpal III–IV, Edisto Beach; **N**, SC83.168.1, left metacarpal III–IV missing distal end, Edisto Beach; **O**, SC77.14.4, right metatarsal III–IV, dorsal view, Edisto Beach; **P**, ventral view of same.


A
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larity is further emphasized through an unpublished manuscript prepared by O. P. Hay sometime between 1915 and 1923, and currently archived in The Charleston Museum, in which he described the Charleston specimen as the new species "*Parahippus carolinus*." Hay also noted in this manuscript with "great interest ... that at least one species of the genus extended to the Atlantic coast" (O. P. Hay, unpublished ms, p. 4).

ChM PV13526 is thought to have been collected, like so many other fossils from the Charleston area, from the "Ashley River phosphate beds," which, as noted previously, occur in the middle member of the upper Pleistocene Wando Formation according to Sanders (2002). However, this specimen is particularly intriguing because there is no doubt that it belongs to a taxon of late Arikareean (latest Oligocene to early Miocene) age based on its early parahippine grade. Thus, this specimen could not have originated from the Wando Formation, but must have been reworked into that unit from subjacent strata. Dinoflagellates found in matrix taken from the specimen do not include particularly restrictive species, although one is indicative of the Oligocene to middle Miocene (L. Edwards, pers. comm. to LBA, 2007). This limits the units from which the specimen could have originated to the upper Chattian Chandler Bridge Formation, the uppermost Chattian Tiger Leap or Edisto formations, or the upper Aquitanian Parachucla Formation, all of which occur in the subsurface of the Charleston area (see Weems and Lewis, 2002:fig.5). The morphological grade of PV13526 appears too primitive to be considered as having originated from the middle Burdigalian Marks Head Formation, which falls within the interval of time represented by the Hemingfordian NALMA. Although a recently reported ^{87}Sr/^{86}Sr date of 23.4 Ma for the Edisto Formation (a date that falls within late Arikareean 3 of Albright et al., 2008) supports origination of the specimen from this unit (Weems et al., 2006), the matrix found within the specimen, and from which samples were collected for microfossil analysis, most closely resembles the lithology of Bed 2 of the Chandler Bridge Formation. Another Arikareean taxon recovered from the Ashley phosphate beds is the giant entelodont, *Daeodon mento*. But, as is discussed in more detail below, this specimen (MCZ 17015) has matrix adhering to it that is entirely unlike that associated with PV13526, and more indicative of an Edisto Formation origin.

As Voorhies (1990) observed, many of the species currently referred to *Parahippus* are done so in error. *Anchippus*, therefore, may well be considered a valid genus, and the one to which many horses of this grade previously assigned to *Parahippus* should be referred, particularly *P. nebrascensis* and *P. wyomingensis*. MacFadden's (1998:546) approach was to place the low-crowned "primitive parahippines," including *Anchippus*, in the genus *Desmatippus* Scott, 1893. But, *Anchippus* has priority, having been erected by Leidy in 1868(b). In addition, there is now an abundance of material of *A. texanus*, rather than the single, damaged type specimen, based on the correlation of the Hutchen's Well type specimen locality in Washington County, Texas, to the Cedar Run Local Fauna locality, also in Washington County, and to the Toledo Bend Local Fauna in Newton County. Due to (1) the uncertain state of the genus *Parahippus* at this time, (2) the fact that the Charleston species lacks the derived features that typify *Parahippus* sensu stricto, and (3) because the Charleston specimen so closely resembles the type specimen and those specimens from Toledo Bend referred to *A. texanus*, ChM PV13526 is here referred to that taxon.

NANNIPPUS Matthew, 1926

NANNIPPUS PENINSULATUS (Cope, 1885)

See MacFadden (1984) and Hulbert (1993) for synonymy.

Referred Specimens.—ChM PV7563, left M1 or M2; ChM PV7576, right M3; ChM PV7564, left M3; ChM PV7575, left M3; ChM PV7568, right p3 or p4; ChM PV7577, right ?m2; ChM PV7569, partial left m3.

Locality, Stratigraphic Horizon, and Age.—Clapp Creek locality, Kingstree, Williamsburg County, ?lower Waccamaw Formation, early Pleistocene, late Blancan.

Description.—ChM PV7563 is a worn M1 or M2, with only about 22 mm of tooth crown remaining. The tooth measures about 15 mm long (AP) by 16 mm wide (TR) and the oval protocone is about

5.7 mm long. There is no pli caballin or hypoconal groove, and fossette borders are relatively simple (weakly plicated).

Although not collected in SC, another tooth here referred to *N. peninsulatus* is ChM PV7567 (55.103.41), a right M2. According to Charleston Museum archives, this tooth was collected by Ivan Tomkins in 1938 from spoil piles near Brunswick, Georgia (exact locality unknown). It thus represents the first record (although unpublished) of *Nannippus* from that state. This tooth differs from ChM PV7563 in the presence of a hypoconal groove and a more transversely compressed protocone. It has a crown height of about 33 mm and measures about 15 mm AP by 14 mm TR. Additional teeth of *Nannippus* from a Hemphillian site in Georgia were noted by Voorhies (1974).

ChM PV7564, an M3, is relatively well worn with a crown height of about 30 mm. It measures about 16 mm AP by 13 mm TR, and has an elongate, transversely compressed protocone, a weak pli caballin, weakly plicated fossette borders, and a hypoconal groove. ChM PV7575 has a similar morphology to PV7564, although it lacks a pli caballin; it has a crown height of about 50 mm and it measures about 15.5 mm AP by 10 mm TR. The broken base of the crown of another M3, ChM PV7576, precludes an estimate of its crown height, but its occlusal morphology resembles that of PV7575 in the absence of a pli caballin; it measures 16 mm AP by 12 mm TR.

ChM PV7568, the p3 or p4, has a crown height of about 42 mm and it measures about 19 mm AP by 11 mm TR; the right ?m2, ChM PV7577, has a crown height of about 48 mm and it measures about 16 mm AP by 10 mm TR. Both teeth are similar in having a moderately deep ectoflexid, no protostylid, and no pli caballinid.

Discussion.—MacFadden (1984) recognized four valid species of *Nannippus*: *N. minor*, *N. ingenuus*, *N. peninsulatus* (to which he synonymized *N. phlegon*), and *N. beckensis*. Hulbert (1990) assigned populations previously referred to *N. minor* to *N. aztecus*, and then later (1993) established a fifth species, *N. westoni*, for late Clarendonian and earliest Hemphillian specimens previously referred to the latter. Hulbert (1993) also referred *N. ingenuus* of MacFadden (1984) to *N. lenticularis*, and he described a sixth species, *N. morgani*, from the late early Hemphillian of Florida.

The teeth from the Clapp Creek locality are larger than those of *N. morgani*, thus far known only from late early Hemphillian sites in Florida; and they also differ in the absence of features that characterize the latter, such as well-developed pli caballins and pli caballinids, a shallow ectoflexid, and moderately complex fossette borders. The late early to late Hemphillian *Nannippus aztecus* (= *N. minor*) is also smaller than the Clapp Creek species. The largest species of *Nannippus*, the early to late Hemphillian *N. lenticularis* (= *N. ingenuus* of MacFadden, 1984), is larger than the Clapp Creek species, although its morphology is similar in having simple to moderate fossette plications, weak to absent pli caballins and pli caballinids, and moderately deep ectoflexids. *Nannippus westoni*, a latest Clarendonian through early Hemphillian species, is of similar size to that from Clapp Creek, but it differs in having a weak metastyle and prominent pli caballins and pli caballinids.

The two species most similar to that from Clapp Creek are *N. beckensis* and *N. peninsulatus*. The former is known only from the early Blancan of Texas, whereas the latter is widely distributed and known best from late Blancan faunas. It is to the latter species that we refer the Clapp Creek material. The Clapp Creek species shares with *N. peninsulatus* a prominent mesostyle with a restricted neck, a reduced hypocone that is labially retracted relative to the protocone (also seen in *N. beckensis*), a protocone that is divided nearly in half if a line is drawn transversely across the occlusal surface from the mesostyle (Hulbert, 1993:358), relatively simple fossette borders, a moderately deep ectoflexid, and no protostylid. Apparently limited to the Blancan (Bell et al., 2004), *N. peninsulatus* was originally described from the "Loop Fork" shales of Tehuichila, Mexico (see MacFadden, 1984:138), but is well represented from Mt. Blanco, Texas, and is also known from several late Blancan sites in Florida (MacFadden and Waldrop, 1980; MacFadden, 1984; Hulbert, 1993; Morgan and Hulbert, 1995; Morgan, 2005). As noted in Bell et al. (2004), one of the youngest occurrences is in the Macasphalt Shell Pit fauna at about 2.2 Ma (Morgan, 2005), although R. Hulbert (pers. comm. to LBA May, 2019) noted what may be the youngest occurrence in North America at Florida's Withlacoochee River 1A site dated biochronologically to approximately 2.0 Ma. The disappearance of *Nannippus* in the southwest (New Mexico) nearly coincides with the first arrival of South American immigrants near the Gauss-Matuyama boundary at approximately 2.6 Ma (Tedford, 1981). Additionally supporting our referral of the Clapp Creek material to *N. peninsulatus* is the co-occurrence there with *Ondatra idahoensis* (see above), a late Blancan rodent. The mutual presence of these late Blancan taxa implies a likely origin from either the Cypresshead or the lower Waccamaw formations.

Efforts to locate the tooth described by Leidy (1859) as *Hipparion venustum* from the "Ashley River phosphate beds," also mentioned by Voorhies (1974) and MacFadden (1984:126), and illustrated by Osborn (1918:200), were unsuccessful.

NANNIPPUS sp.
Figure 18B–C

Referred Specimens.—SC2006.1.23, right P4 or M1; SC2006.1.24, right upper cheek tooth; SC2006.1.26, fragment of upper cheek tooth; SC2006.1.22, partial upper cheek tooth; SC2006.1.27, partial left upper cheek tooth; SC2006.1.25, labial half of upper cheek tooth; SC89.245.11, fragment of lower cheek tooth; SC89.245.12, fragment of lower cheek tooth; SC2006.1.21, left m3.

Locality, Stratigraphic Horizon, and Age.—Walrus Ditch locality, Dorchester County, lower Waccamaw Formation; early Pleistocene, late Blancan.

Description.—SC2006.1.23, a P4 or M1, measures 16.4 mm AP by 15.3 mm TR. It has a "necked" metastyle, a hypoconal groove, a single pli caballin, an oval protocone that is somewhat flattened medially, and the posterior pre-fossette and anterior post-fossette borders are well crenulated. SC2006.1.24, another upper cheek tooth, also has a "necked" metastyle, a hypoconal groove, well crenulated opposing fossette borders but no pli caballin, and an oval protocone although more elongate than in SC2006.1.23. SC2006.1.24 measures 16.3 mm AP by 16.0 mm TR.

Discussion.—In the collections at the SCSM are several teeth from the Walrus Ditch locality that represent a different species than that from Clapp Creek. They are larger than the Clapp Creek specimens, and the upper cheek teeth have highly plicated opposing pre- and post fossette borders. The occlusal pattern of the upper teeth most closely resembles that of *N. aztecus* from the latest Hemphillian Palmetto Fauna of Florida (Webb et al., 2008:fig. 8A) and *Nannippus* sp. A from gravel pits along the Nueces River, Texas (Baskin, 1991), but the Walrus Ditch teeth are distinctly larger. Although listed as *Nannippus peninsulatus* by Fields et al. (2012:15) in their discussion of the Walrus Ditch assemblage, we consider these teeth referable to a different, yet-to-be determined, species.

RHINOCEROTIDAE Owen, 1845
SUBHYRACODON Brandt, 1878
SUBHYRACODON MITIS (Cope, 1875)
Figure 18D

See Prothero (2005:46) for synonymy.

Referred Specimen.—Right P2; SCTC400.

Locality, Stratigraphic Horizon, and Age.—Argos Cement quarry, near Harleyville, Dorchester County, Harleyville Formation; lower calcareous nannoplankton zone NP21, late Eocene, latest Priabonian, late Chadronian.

Discussion.—As noted in the discussion of the Harleyville Formation earlier in this report, a rhinoceros specimen was collected from the Argos Cement quarry near Harleyville, SC, by Mr. J. Metts, an avocational fossil collector who allowed the first author to examine it. The specimen consists of a palate with teeth of the primarily Chadronian to Whitneyan taxon, *Subhyracodon*. It includes the right P3–4 and the left P1–4, M1 or M2, and M3. The identification of the M1 or M2 is equivocal because the palate is evidently pathologic – only a single molar is emplaced between the P4 and M3 – but the tooth is most likely M2 based on size and morphology. Unfortunately, the palate is currently retained in Mr. Metts' private collection, and therefore not immediately available for further study. Fortunately, however, a fragmentary P2 belonging to the same individual as the palate is curated in the

SCSM collection, thus providing the basis for this most important record.

According to Prothero (2005:47), *Subhyracodon mitis* is "the common late Chadronian rhino." Although *S. occidentalis* is also known from the late Chadronian, referral of the SC specimen to *S. mitis* is based on the primitive, non-molariform morphology of the P3 and P4 and on its smaller size. As Prothero (2005) further noted, P3 and P4 of *S. mitis* have strongly posteriorly projecting protolophs and unconnected metalophs, exactly the condition of the SC specimen, whereas in *S. occidentalis* the protoloph shows only a trace of posterior projection with a strong and merged metaloph.

The specimen was collected from one of the many shallow solution pits filled with Harleyville Formation that commonly occur across the upper surface of the Pregnall Member of the Tupelo Bay Formation. Dinocysts (e.g., *Batiacasphaera baculata*, *B. compta*, *Cordosphaeridium funiculatum*, *Homotryblium plectilum*, *Samlandia chlamydophora*, and *Trigonopyxidia fiscellata*) and calcareous nannoplankton (e.g., *Ismolithus recurvus*, *Ericsonia formosa*, and *Reticulofenestra umbilicus*) analyzed from matrix associated with the palate indicate assignment to lower nannoplankton zone NP21 (USGS Paleobotanical sample number R6747, L. Edwards and J. Self-Trail, pers. comm. to LBA, 2012). Although NP21 spans the Priabonian-Rupelian boundary (Eocene-Oligocene boundary), which closely approximates the Chadronian-Orellan boundary, we consider this specimen to be latest Chadronian (Ch3) in age. The Chadronian rather than Orellan age assignment is based on the additional discovery of a brontothere upper molar from the same horizon at the nearby Giant Cement quarry (also retained by the same owner as the *Subhyracodon* palate); brontotheres are not known to have extended into the Oligocene in North America (Mihlbachler, 2008).

Although the bulk of this specimen is currently held in a private collection, the curated P2 from the same individual provides the first and only record of *Subhyracodon* east of Mississippi (Manning, 1997; Albright et al., 2016), as all other records are from California, the northern and central Great Plains, and Oregon (Prothero, 1998, 2005).

APHELOPS Owen, 1845

APHELOPS ?MALACORHINUS Cope, 1878

Figure 18E

Referred Specimens.—SC2010.12.1, cast of left M2 (labeled "*Teleoceras*"); SC2015.18.3, ectoloph of right M2.

Locality, Stratigraphic Horizon, and Age.—SC2010.12.1, Wright River, Jasper County; SC2015.18.3, Chechessee River, Beaufort County; stratigraphic unit undetermined, but possibly Coosawhatchie or Ebenezer formations; middle to late Miocene, late Barstovian or early Hemphillian, respectively.

Discussion.—Like the brontothere tooth and *Subhyracodon* palate noted above, the original specimen from which SC2010.12.1 was cast resides in a private collection. Fortunately, the first author was allowed to observe, measure, and photograph the original specimen. It is in medium wear stage with a crown height of about 38 mm, a maximum AP length of about 60 mm, and a TR width of about 53 mm.

Aphelops and *Teleoceras* are represented by several species that collectively range from the late Hemingfordian to the latest Hemphillian, and species of both genera have been recorded from Florida (Hulbert, 2001; Prothero, 2005). Although the stage of wear of SC2010.12.1 makes it difficult to discern which taxon may be represented, it does not appear to be *Teleoceras*. Upper molars of *Teleoceras* typically have a prominent antecrochet that extends posteriorly from the protoloph, lingual to the crochet - a feature lacking in both *Aphelops* and in the SC tooth. The tooth does have what might be considered a small antecrochet, but this is not the same structure as in *Teleoceras*; the structure in SC2010.12.1 is *labial* to the crochet (i.e., it does not originate from the protoloph). Regardless of which taxon is represented, these specimens provide an exceptionally rare record of a Miocene land mammal from SC.

TELEOCERAS Hatcher, 1894

TELEOCERAS ?GUYMONENSE Prothero, 2005

Figure 18F–H

Referred Specimens.—SC2017.14.4a and b,

cast of associated left p3–4 in fragment of mandible (fragment with p3 = SC2017.14.4a; fragment with p4 = SC2017.14.4b).

Locality, Stratigraphic Horizon, and Age.—Morgan River, Beaufort County; stratigraphic unit undetermined, but possibly Ebenezer Formation or Wabasso beds; late Miocene to earliest Pliocene, early to latest Hemphillian.

Description and Discussion.—This specimen, too, currently resides in a private collection, but the collector, M. Swilp, graciously allowed the first author to observe, measure, and photograph it, and to have it cast by the SCSM. A digital file of this specimen was also created by scanning the specimen with a CT scanner at the Johnson and Johnson Laboratory within the Department of Engineering at the University of North Florida.

Measurements of the teeth are as follows: p3, 28 mm AP x 19.7 mm TR; p4, 32 mm AP x 22.2 mm. Both the p3 and p4 have a small, but distinct cingulum that wraps around the anterior surface of the tooth from the antero-labial corner to the antero-lingual corner. There is also evidence of a posterior cingulum, but it is worn down due to abutment of the teeth. Approximately 1 cm above the base of the crown on the labial surface is a weak, nearly indistinguishable rugosely textured cingulum (which does not appear to be due to water wear), and there is a weak cingular segment protecting the posterior lingual reentrant of the p4, as well. The anterior lingual reentrant of both teeth is very shallow. The teeth are in medium wear stage and they show no cement. There is a wear facet on the anterior surface of p3 indicating the presence of a p2.

Rhinoceroses in North America are known to have gone extinct in the latest Hemphillian, the last known taxa including *Teleoceras hicksi* Cook, 1927, from Florida's Palmetto Fauna; the dwarf species *T. guymonense* Prothero, 2005, known only from Oklahoma, Texas, Kansas, and New Mexico; and *T. aepysoma* Short et al., 2019, from the Gray Fossil Site of eastern Tennessee. The species from SC is much smaller than *T. hicksi*, *T. aepysoma*, and the above noted *Aphelops malacorhinus*, but is similar in size to *T. guymonense*. It differs from the latter in having a wear facet on the anterior surface of p3, thus indicating the presence of p2. Although the p2 is typically lost in later species of the genus, Prothero and Manning (1987) noted that the p2 is occasionally retained, and this was recently exemplified by specimens of *T. aepysoma* described by Short et al. (2019) that ranged from having no p2s, to having vestigial p2s, to specimens that retained the p2s. *Aphelops malacorhinus* also retains p2, but this species is considerably larger than the Morgan River taxon. Measurements of the small Barstovian rhino *Peraceras hessei* Prothero and Manning, 1987, indicate a size similar to the SC species, and *P. hessei* retains the p2, but the lower teeth of the latter differ from those from SC in the presence of prominent labial cingula. Another small, but primarily Barstovian species is *T. meridianum* (Leidy, 1865), known from the Texas Coastal Plain. It too shows variation in the presence/absence of the p2 and, like the Morgan River species, it lacks prominent cingula (Prothero and Manning, 1987).

In size and morphology, therefore, the Morgan River species most closely resembles *T. meridianum* and *T. guymonense*. Our referral of these small rhino teeth from SC to the latter species rather than the former is based more on their purported age than on any particulars of morphology – the mainly Barstovian age of *T. meridianum* vs. the late Hemphillian age of *T. guymonense*. Although the SC specimen was found out of stratigraphic context on the bottom of a river, support for its latest Hemphillian age is provided by the recovery of specimens of *Phocanella pumila* and gomphothere teeth likely representative of *Rhynchotherium* from the same locality – two taxa also known from Florida's latest Hemphillian Palmetto Fauna (and from which *T. hicksi* is also known). The recovery of upper molars from the Morgan River locality would help refine our identification because, according to Prothero (2005:124), those of *T. guymonense* show a unique character in the form of a "short but distinct rib on the lingual face of the crochet, which produces a short lingual spur on the wear surface."

Rhinocerotidae, Genus and species indeterminate

Referred Specimen.—MCZ 17134, "a large flake from the outer side of a molar," from the Robert Wilson collection (Allen, 1926:454).

Locality, Stratigraphic Horizon, and Age.—from the "phosphate beds of Ashley River, South Carolina" near Charleston (Allen, 1926:447); age not determinable.

Discussion.—In his paper on fossil mammals from South Carolina, Allen (1926:454) noted a fragment "from the outer side" of an upper molar of a rhinoceros that he referred to ?*Teleoceras proterus* (Leidy)." In the same discussion, he also mentioned the note of rhinoceros remains from the Ashley River beds by Packard (1871). Because the Ashley phosphate beds include a temporally mixed assemblage, rhinoceros remains from this unit could be referable to a number of species including *Diceratherium*, *Menoceras*, *Teleoceras*, or *Aphelops*. The MCZ fragment is non-diagnostic.

ARTIODACTYLA Owen, 1848
ENTELODONTIDAE Lydecker, 1883
DAEODON Cope, 1878
DAEODON MENTO (Allen, 1926)

Dinohyus (?) *mento* Allen, 1926.

Referred Specimen.—MCZ 17015, symphyseal region of mandible, from the Robert Wilson Collection (Allen, 1926).

Locality, Stratigraphic Horizon, and Age.—"Ashley River phosphate deposits," considered to have been reworked into the Wando Formation from the uppermost Chattian Edisto Formation; late Arikareean (Ar3).

Discussion.—This specimen still represents the only record of an entelodont from SC (although rumors suggest that additional material may exist in private collections), and is noted again here because of its record as a second Arikareean land mammal taxon from the "Ashley River phosphate beds" together with the above noted *Anchippus texanus*. MCZ 17015 was evidently reworked into the Wando Formation from the Edisto Formation, which has been determined to be of latest Chattian age (Weems and Harris, 2008; Weems et al., 2006; Weems et al., 2016). Other possible units of origin include the upper Rupelian Ashley Formation, the upper Chattian Chandler Bridge Formation, the lower Miocene (Aquitanian) Parachucla Formation, and the lower Miocene (Burdigalian) Marks Head Formation, as all span, respectively, the early Arikareean to early Hemingfordian – the interval of time over which the giant entelodonts are known in North America. These formations, however, are excluded as the units of origin on the basis of information provided below.

Although Effinger (1998) listed "?*D. mento*" from the Hawthorn Formation, it should be noted that this formation is no longer recognized in SC. The Hawthorn Formation was once represented in SC by the Marks Head Member, but this unit has more recently been elevated to formational status (Huddlestun, 1988). The Marks Head Formation, described in the Dorchester County area by Edwards et al. (2000) as a "clayey phosphatic quartz sand," is excluded as the unit of origin for MCZ 17015 on the basis of its dissimilar lithology relative to the matrix still adhering to the specimen. Another option is that the entelodont specimen originated from the upper Rupelian (earliest Arikareean) Ashley Formation, often referred to as the "Ashley marl." As Allen (1926) noted for MCZ 17015, "the fact that the posterior tooth-sockets are filled with indurated marl may indicate that the fragment was deposited in the earlier Tertiary marl beds while they were forming."

However, it is our opinion that this specimen originated from the Edisto Formation, rather than the Ashley Formation. First, Edwards et al. (2000) described the Edisto Formation as a "quartz and phosphate sandy, calcarenite." This description closely matches the lithology of the matrix adhering to MCZ 17015, particularly considering that the matrix also effervesces when hydrochloric acid is applied (R. Weems, pers. observ., 2009). Further precluding origination from the Ashley Formation, and additionally supporting derivation from the Edisto Formation, are two lines of circumstantial evidence: (1) the Edisto Formation is a more inshore and shallow water unit, and therefore more amenable to harboring fossils of terrestrial mammals, than the mid-shelf depositional environment of the Ashley Formation, and (2) the reported ^{87}Sr/^{86}Sr date of 23.4 Ma for the Edisto Formation is a more likely age for *Daeodon*, based on its temporal span, than is the 28-29 myr age of the Ashley Formation.

TAYASSUIDAE Palmer, 1897
PERCHOERUS Leidy, 1869
PERCHOERUS sp.
Figure 18I

Referred Specimen.—ChM PV5025, right m2.

Locality, Stratigraphic Horizon, and Age.—Bank of drainage ditch approximately 0.52 km south of County Road 996, Goose Creek, Charleston County, Chandler Bridge Formation; late Oligocene, Chattian, Arikareean 3.

Discussion.—The serendipitous discovery of this isolated peccary tooth (16.4 mm AP, 14.9 mm TR, crown height 10 mm) during excavation of fossil whale material from the Chandler Bridge Formation represents the only terrestrial mammal material found in situ from the Oligocene of South Carolina. Material of other latest Oligocene/earliest Miocene land mammals (*Anchippus* and *Daeodon*) were found as specimens reworked into the "Ashley River phosphate beds."

According to Wright (1998:fig. 26.5) and Prothero (2009), there are only two valid North American genera of Oligocene tayassuids, *Thinohyus* and *Perchoerus*. The Chandler Bridge tooth is similar in size to those of both taxa. Although its morphology more closely resembles that of *Thinohyus*, peccary teeth are highly variable and notoriously unsuitable for alpha level taxonomy. With only a single tooth available, we tentatively assign this specimen to *Perchoerus* based on the broader geographic distribution this taxon had than that of *Thinohyus*, which is known only from the John Day Formation, Oregon (Prothero, 2009).

MYLOHYUS Cope, 1889
MYLOHYUS FOSSILIS (Leidy, 1860)

Referred Specimens.—ChM PV2499, right m1; ChM PV4986, right m2; USNM 530190, left m3 (additional specimens from SC noted in Roth and Laerm [1980] and Bentley et al. [1994]).

Locality, Stratigraphic Horizon, and Age.—ChM PV2499 and ChM PV4986 from Edisto Beach, Colleton County, undetermined offshore unit; late Pleistocene, late Rancholabrean. USNM 530190 from Myrtle Beach, Horry County, undetermined offshore unit; late Pleistocene, late Rancholabrean.

Discussion.—The m1 is represented by what appears to be an unerupted crown, and it measures 15.5 mm AP by 12.5 mm TR; the m2 is somewhat worn and measures 16 mm AP by 13 mm TR; and the m3 measures 18.5 mm AP by 14 mm TR. Referral to *M. fossilis* rather than *M. nasutus* (Leidy, 1869) follows Lundelius (1960:34), who concluded that the former was the east coast species, whereas the latter was "more western in its distribution," and Wright (1995, 1998) rather than Kurtén and Anderson (1980). Wright (1998) also noted that *M. fossilis* spans the late Blancan through Rancholabrean. In the collections of the SCSM are additional specimens currently under study from the late Irvingtonian Camelot Local Fauna.

CERVIDAE Gray, 1821
CERVUS Linnaeus, 1758
CERVUS ELAPHUS Linnaeus, 1758

Referred Specimens.—ChM PV7595, partial right m3; McK67.41.169, unerupted M2.

Locality, Stratigraphic Horizon, and Age.—ChM PV7595 from Clapp Creek locality, Kingstree, Williamsburg County, unit of origin unknown; McK67.41.169 from Eddingsville Beach, Colleton County, undetermined offshore unit, late Pleistocene, Rancholabrean.

Discussion.—Sanders (2002) reported the first remains of fossil *Cervus* in SC from Edisto Beach and from a site northwest of Charleston in the Penholoway Formation, providing a middle Irvingtonian through Rancholabrean age range. Although the majority of mammal fossils recovered from the Clapp Creek locality are of middle-to-late Blancan age, the nature of the deposit there (a lag deposit resting upon the Maastrichtian Steel Creek Formation; see above) results in a mixed fauna that includes taxa from the late Blancan, late Rancholabrean, and even the late Cretaceous and early Paleocene. (Note: Ludt et al. [2004] considered the species of *Cervus* that dispersed from NE Asia into North America to be *Cervus canadensis* rather than *C. elaphus*.)

RANGIFER Hamilton-Smith, 1827
RANGIFER TARANDUS (Linnaeus, 1758)

Referred Specimen.—SC2010.13.151, right

dP3.

Locality, Stratigraphic Horizon, and Age.—Crowfield locality, Dorchester County, Wando Formation; late Pleistocene, late Rancholabrean.

Discussion.—Although records of caribou in SC were noted previously by McDonald et al. (1996, 2000) and Sanders (2002), the importance of such boreal taxa occurring at what is likely the southern extreme of their Pleistocene range in the eastern USA warrants mention of this isolated specimen, as well. The tooth measures about 15 mm AP by 11 mm TR, and is from the Rancholabrean-aged Crowfield locality currently under study by JLK, DJC, and F. Grady (USNM). The southern-most extent of Pleistocene *Rangifer* appears to be based on a specimen from Bartow County, Georgia (Martin and Sneed, 1989).

BOVIDAE Gray, 1821
BOOTHERIUM Leidy, 1852
BOOTHERIUM BOMBIFRONS (Harlan, 1825)
Figure 18J–P

Referred Specimens.—USNM 533996, left M3, collected "near pier at Surfside Beach," Horry County; USNM PAL 530183, partial cheek tooth, Myrtle Beach, Horry County; SC92.121.1, cast of partial m3, from St. Helena Sound, Beaufort County; SC77.8.17, radius-ulna, from Edisto Beach, Colleton County; ChM PV40.183.17, right Mc III–IV from Edisto Beach; SC75.31.204, right Mc III–IV, from Edisto Beach; SC83.168.1, left Mc III–IV missing distal end, from Edisto Beach; SC2015.17.1, left Mc III–IV, from west branch of Cooper River; SC77.14.4, right Mt III–IV, from Edisto Beach; ChM PV7199, left calcaneum, from the Holcim (formerly Holnam) Cement Company quarry, Harleyville, Dorchester County.

Stratigraphic Horizon and Age.—Specimens from Myrtle, Surfside, and Edisto beaches, undetermined offshore unit, late Pleistocene, late Rancholabrean; SC2015.17.1 from the Cooper River, ?Wando Formation, late Pleistocene, Rancholabrean; ChM PV7199, unnamed Pleistocene deposits overlying Harleyville Formation; late Rancholabrean.

Description.—USNM 553996, the well preserved M3, measures about 4.1 cm long by 2.9 cm wide and it has a crown height of about 4.5 cm. Additional elements of *Bootherium* from SC include a partial radius-ulna and fused metacarpals and metatarsals, measurements of which are provided in Table 9. Referral to *Bootherium* rather than to *Bison* is based primarily on the significantly more robust morphology of matching elements for the latter. The calcaneum was determined to represent that of *Bootherium* on the basis of its similarity to that of *Ovibos moschatus*, the extant Musk Ox. It is of similar size to calcanea of *Hemiauchenia* and *Palaeolama* (from Leisey), but differs in the following features: (1) it has relatively parallel dorsal and ventral surfaces when viewed from a lateral perspective vs. distally diverging dorsal and ventral surfaces in the camels (resulting in significantly more bone ventral to the sustentacular facet); (2) the dorsal surface of the calcaneal heel is pinched and forms a ridge vs. the broad dorsal surface in camels; (3) the dorsal surface of the calcaneal heel has a concavity immediately before the calcaneal tuberosity.

Discussion.—One previous record of the woodland musk ox, *Bootherium bombifrons*, from SC was reported by McDonald et al. (2000) in which they noted an m3 from Saint Helena Sound, Beaufort County – the southern-most occurrence of musk ox along the Atlantic Coastal Plain. That record, together with those noted herein, indicates that *Bootherium* was broadly distributed along the coastal plain of SC during the Wisconsian, if not before (Fig. 19). The presence of both *Bootherium* and *Rangifer* in SC supports the existence of what McDonald et al. (2000:132) referred to as a "cohort of large-bodied boreal ungulates ... in the southeastern extremes of their ranges." To date, *Bootherium* is not known from Georgia or Florida.

The calcaneum, ChM PV7199, was collected by B. Palmer in October, 2001, from Pleistocene sediments overlying the Harleyville Formation in the Holcim Cement plant quarry near Harleyville, Dorchester County. Based on his familiarity with the stratigraphy and paleontology of the Harleyville area, Palmer concluded that the sediments from which the specimen originated were very likely equivalent to those from which the nearby Ardis

Table 9. Measurements (mm) of selected postcranial elements of *Bootherium bombifrons* from SC.

Specimen	Maximum Length	Width (prox. end)	Width (distal end)
Metacarpals III–IV			
ChM PV40.183.17	230		
SC75.31.204	253	81.5	82.1
SC83.168.1	--	81.3	missing
Metatarsal III–IV			
SC77.14.4	284	62.5	74.2
Radius/ulna			
SC77.8.17	410	87.8	92.6
Calcaneum			
ChM PV7199	121	33.8	--

Local Fauna was recovered. In light of the fact that Palmer did not know to which taxon the specimen belonged, his conclusion was an astute one, as the Ardis LF was recovered from beds ^{14}C dated to between 18,530 and 18,940 years old (Bentley et al., 1994). This is exactly the interval of time over which *Bootherium* would be expected to be as far south as South Carolina, i.e., during the last glacial maximum.

SIRENIA Illiger, 1811
PROTOSIRENIDAE Sickenberg, 1934
PROTOSIREN Abel, 1907
PROTOSIREN sp. indet.
Figure 20A

Referred Specimens.—GSM 1333, partial left inominate; SC2015.65.1, parietal-supraoccipital skull cap.

Locality, Stratigraphic Horizon, and Age.—GSM 1333, Martin Marietta Orangeburg Quarry, Orangeburg County, lower part of Cross Member of Tupelo Bay Formation "within 30 cm of the Santee Limestone/Tupelo Bay Formation contact" (Beatty and Geisler, 2010:2); NP17, late Eocene, Bartonian, late Uintan. SC2015.65.1, Giant Cement quarry, Dorchester County, Tupelo Bay Formation; NP17 or 18, late Eocene, Bartonian or Priabonian,

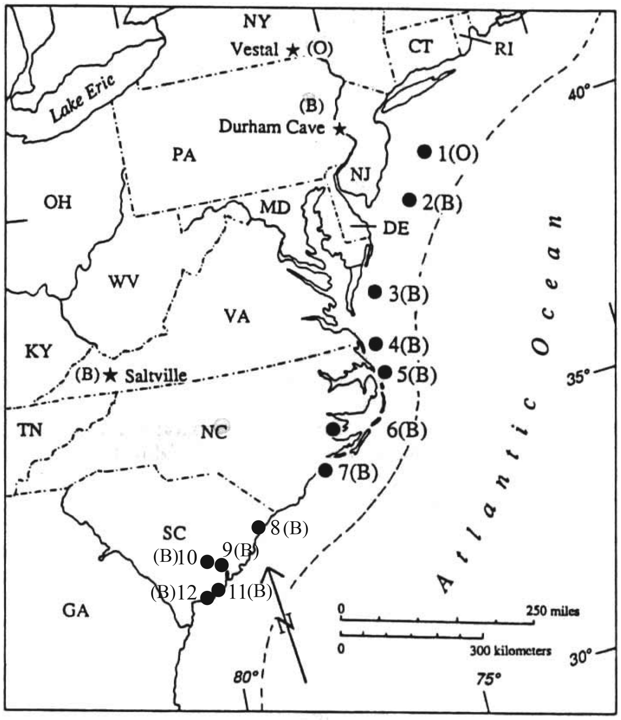

Figure 19. Atlantic Coastal Plain of USA showing localities where specimens of fossil musk ox (O = *Ovibus*; B = *Bootherium*) have been recovered. Base map, localities **1**–**7**, and cave localities after McDonald and Ray (1993:fig. 1); SC localities **8**–**12**: **8**, Surfside and Myrtle beaches, Horry County; **9**, Cooper River, Berkeley County; **10**, Harleyville, Dorchester County; **11**, Edisto Beach, Colleton County; **12**, St. Helena Sound, Beaufort County.

Duchesnean to early Chadronian.

Discussion.—GSM 1333 was collected by B. Palmer from the same stratigraphic horizon as the holotype of *Carolinacetus gingerichi* Geisler et al., 2005. Noting the "striking similarity" of this specimen to that of *Protosiren sattaensis* from the Bartonian of Pakistan, Beatty and Geisler (2010:2) conservatively referred it to *Protosiren* sp. Another specimen provisionally referred to *Protosiren*, SC2015.65.1, was collected by V. McCollum from a spoil pile at the bottom of the Giant Cement plant quarry.

DUGONGIDAE Gray, 1821
EOTHEROIDES Palmer, 1899
EOTHEROIDES sp.

Referred Specimens.—SC2006.30.1–15, partial skull with limb material (15 elements numbered individually); SC2013.32.1, partial skull with M1–2; USNM 537206, partial skull and partial skeleton; ChM PV7639, fragment of skull cap.

Locality, Stratigraphic Horizon, and Age.—SC2006.30.1–15 and USNM 537206 from Giant Cement quarry, Dorchester County, Tupelo Bay Formation, Pregnall Member, late Eocene, NP18, early Priabonian, early Chadronian; SC2013.32.1 from Argos Cement quarry, Dorchester County, Tupelo Bay Formation, Pregnall Member, late Eocene, NP18, early Priabonian, early Chadronian; ChM PV7639 from Giant Cement quarry, Harleyville Formation-filled pits eroded into upper surface of Pregnall Member of Tupelo Bay Formation, late Eocene, NP21, late Priabonian, Chadronian (possibly reworked into Harleyville Formation from underlying Pregnall Member).

Discussion.—Because these specimens are currently being described as potential new species of *Eotheroides* by D. Domning and I. Zalmout, we mention them only as records of this genus from SC. The two SCSM specimens were collected by V. McCollum and the USNM skeleton was collected by B. Palmer.

METAXYTHERIUM de Christol, 1840
?*METAXYTHERIUM ALBIFONTANUM* Vélez-Juarbe and Domning, 2014b
Figure 20B–C

Referred Specimen.—ChM PV9480, partial left m3.

Locality, Stratigraphic Horizon, and Age.—Drainage ditch south to southwest, and between 0.6 and 1.7 km, of the Charleston Airport Terminal, Charleston County, Ashley Formation; early Oligocene, late Rupelian, Arikareean 1.

Description and Discussion.—ChM PV9480 is missing the anterior portions of the protoconid and metaconid, as well as the lingual surface of the metaconid, entoconid, and the lingual hypoconulid lophule (terminology follows Vélez-Juarbe and Domning, 2014b:fig.8, p. 453). A prominent cristid obliqua blocks the transverse valley, and the hypoconulid lophule consists of two cusps, the lingual of which is crescentic in shape. In its broken state it measures about 18 mm AP by 14 mm TR. Both measurements would be slightly greater if the tooth was complete. The morphology of the tooth closely resembles that of the middle to late Miocene *Metaxytherium floridanum* Hay, 1922, but ChM PV9480 is smaller. Furthermore, the tooth is thought to have originated from the middle Oligocene (upper Rupelian) Ashley Formation based on the nature of the matrix adhering to it; thus it is much older than *M. floridanum*.

According to Vélez-Juarbe et al. (2012) and Vélez-Juarbe and Domning (2014a), three species of late Oligocene dugongids were sympatric across at least part of their ranges in the western Atlantic region, and remains of each of these, *Metaxytherium albifontanum*, *Crenatosiren olseni* (Reinhart, 1976), and *Dioplotherium manigaulti*, are known from the Chandler Bridge Formation. Recently, Vélez-Juarbe and Domning (2015) described a fourth late Oligocene species from this region (Puerto Rico), *Callistosiren boriquensis*.

Early Oligocene taxa in this region include *Priscosiren atlantica* Vélez-Juarbe and Domning (2014a) from the San Sebastian Formation of Puerto Rico, of similar age to the Ashley Formation, as well as the above noted *Crenatosiren olseni*, which has also been recorded from the Ashley (Domning, 1997). The m3s of both of these taxa are significantly smaller and different in morphology than ChM PV9480 (LBA, pers. observ.).

Although the larger Chandler Bridge taxa, *Metaxytherium albifontanum* and *Dioplotherium*

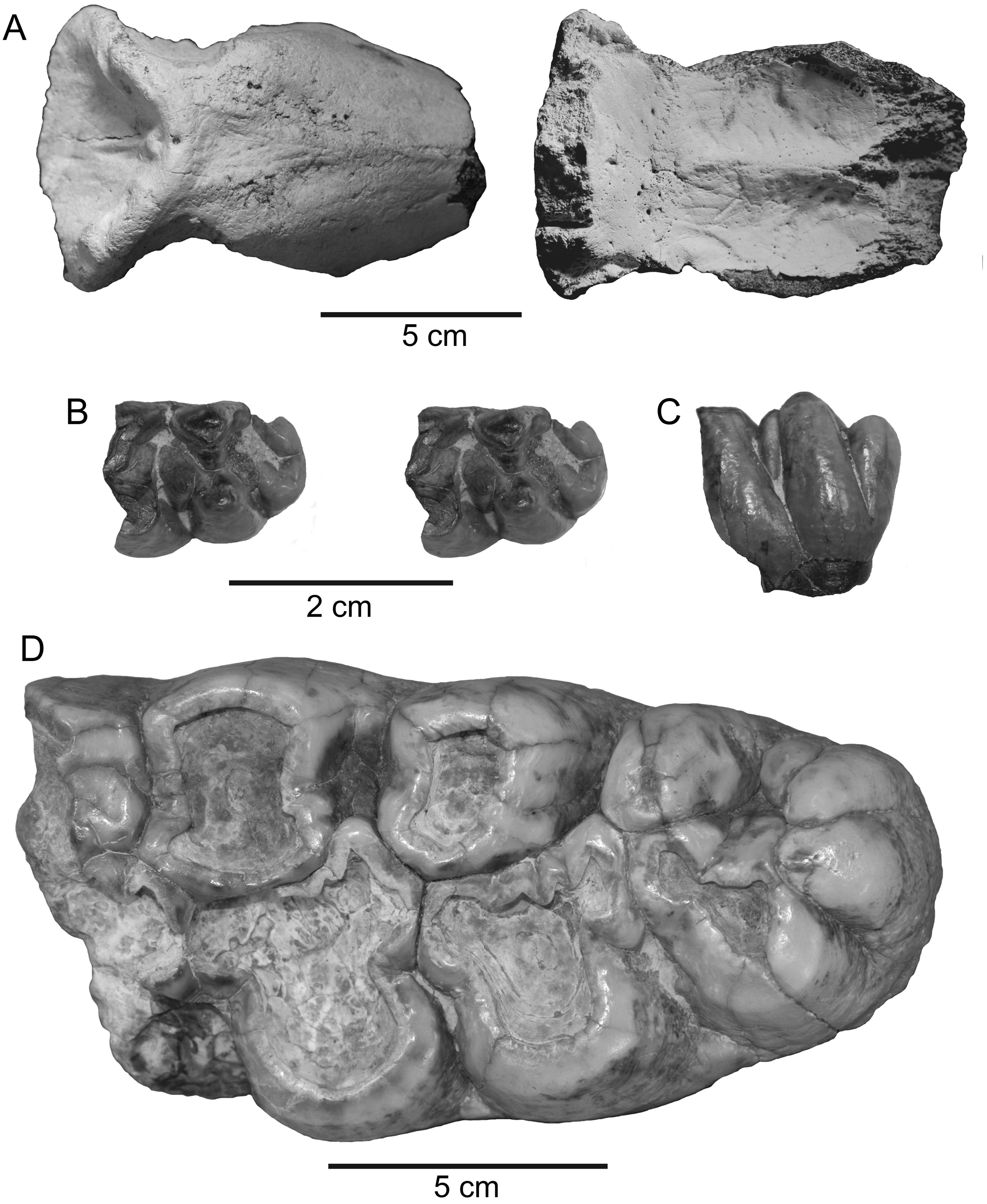

Figure 20. A, *Protosiren* sp., SC2015.65.1, parietal-supraoccipital skull cap, from the Giant Cement quarry, Dorchester County, in dorsal (left) and ventral (right) views; **B**, ?*Metaxytherium albifontanum*, ChM PV9480, partial left m3, stereo occlusal view and **C**, labial view, Ashley Formation, Charleston County; **D**, *Rhynchotherium falconeri*, SC2017.6.1, left m3.

manigaulti, are not yet known from the Ashley Formation, their teeth (no m3s are known for the latter) are similar in size to ChM PV9480. So too are the M3s of *Callistosiren boriquensis,* but this taxon is not yet recorded from the Oligocene of South Carolina (nor are m3s known yet). This suggests that ChM PV9480 may belong to one of the former two species if either of them are ever determined to have ranged down into the Ashley Formation. *Metaxytherium albifontanum* specimens SC89.255.1 and SC89.255.2 include only upper teeth, but another specimen, SC89.115, includes an m3, which measures 22.2 mm AP x 13.66 mm TR. The partial ChM PV9480 would be similar in size if it was complete. If our identification to *M. albifontanum* is correct, then its range, too, is herein adjusted down into the upper Rupelian from the Chattian.

PROBOSCIDEA Illiger, 1811

GOMPHOTHERIIDAE Hay, 1922

RHYNCHOTHERIUM Falconer, 1868

RHYNCHOTHERIUM FALCONERI Osborn, 1923

Figure 20D

Referred Specimens.—SC2017.6.1, left m3; SC2017.6.2, partial right M3; SC2006.1 (accession number only), partial molar.

Locality, Stratigraphic Horizon and Age.—SC2017.6.1 and SC2017.6.2 from a site in Dorchester County with a Walrus Ditch-equivalent assemblage (detailed locality information on file at SCSM); SC2006.1 from Walrus Ditch locality, Dorchester County, Waccamaw Formation, late Pliocene, late Blancan.

Discussion.—Based on evidence from Florida, there are three different proboscidean families that occurred in the southeast: the Mammutidae, the Gomphotheriidae, and the Elephantidae (Hulbert, 2001). The various species recorded from Florida include the mammutids *Zygolophodon tapiroides*, *Mammut sellardsi*, and *Mammut americanum*; the gomphotheriids *Gomphotherium calvertense*, *G. simplicidens*, *Amebelodon floridanus*, *A. britti*, *Platybelodon* sp., *Rhynchotherium falconeri* (see below), and *Cuvieronius hyodon*; and the elephantid *Mammuthus columbi* (Hulbert, 2001; Lister and Sher, 2015; Morgan and Harris, 2015; Morgan et al., 2016). These are the taxa, therefore, that might be expected to be found in the fossil proboscidean record of South Carolina. Excluding the abundance of material, both dental and skeletal, confidently referred to the American Mastodon, *Mammut americanum*, and to the Columbian Mammoth, *Mammuthus columbi*, the remainder of fossil proboscidean material from the state is almost exclusively comprised of teeth, fragments of teeth, and fragments of jaws. Unfortunately, the highly variable condition of the gomphothere dentition makes it nearly impossible to determine which taxon is represented when teeth are the only record available (see Lucas and Morgan, 2008:74). As Hulbert (2001:315) noted, “Relatively complete skulls and jaws with the mandibular symphysis and lower tusks are needed for secure identifications.”

The temporal range of these taxa can be used with some utility as an aid to identification, but only cautiously, as several taxa overlap in age. For example, *Zygolophodon*, *Gomphotherium*, *Amebelodon*, and *Platybelodon* are all present in the late Miocene (although the former two also occur in the middle Miocene), which due to the paucity of fossil-bearing exposures in SC of that age would not be expected to be found in the state, at least not commonly. On the other hand, the few, rare, fossil rhinoceros specimens reported herein provide tantalizing glimpses into this interval of time and portend the possibility that late Miocene proboscidians may eventually be found, if they haven’t been already.

That leaves *Rhynchotherium* and *Cuvieronius*. In a detailed and much needed study on the taxonomy of *Rhynchotherium*, Lucas and Morgan (2008) concluded that only one of several named species was valid, *Rhynchotherium tlascalae* Osborn, 1918, although they considered the holotype lower jaw of this species as representative of the genus *Gomphotherium*, not *Rhynchotherium*. Therefore, they established as a neotype for *R. tlascalae* the type specimen lower jaw of *R. browni* Osborn, 1936, AMNH 15550. Synonymizing *R. browni*, *R. edense*, *R. falconeri*, and *R. simpsoni* with *R. tlascalae*, they also concluded that *Rhynchotherium sensu stricto* was solely a North American taxon. Subsequently, however, Lucas (2010) applied for and obtained a ruling from the ICZN to recognize *R. falconeri* as the type species based on Osborne's (1923) holotype lower jaw (AMNH 8532) from the late Blancan Mt. Blanco LF of Texas, which "shows the key diagnostic features of *Rhynchotherium sensu stricto*" (Lucas and Morgan, 2008:78).

Typically considered a late Hemphillian through late Blancan taxon with a broad North American distribution, *R. falconeri* is known from the Palmetto (latest Hemphillian) and Macasphalt Shell Pit (late Blancan) faunas of Florida. The late Hemphillian *Rhynchotherium* from Florida was originally named *R. simpsoni* by Olsen (1957), then referred to *R. edense* by Webb et al. (2008), but synonymized with *R. falconeri* by Lucas and Morgan (2008; also see Morgan and Harris, 2015). *Cuvieronius*, however, is considered to have an early Irvingtonian through Rancholabrean range, and extensive research on these two taxa by G. Morgan, S. Lucas, and others has resulted in the conclusion that they do not temporally overlap; that *Rhynchotherium* went extinct around 2 my ago and that *Cuvieronius* first appeared about 1.5 my ago (Morgan et al., 2016). This, therefore, provides for our assignment of the specimens from the Walrus Ditch LF to *R. falconeri*. It should be noted, however, that there are several gomphothere teeth in the collections of the SCSM, the Charleston Museum, and the Mace Brown Museum of Natural History, as well as in known private collections, for which detailed identification is not available due to their highly variable morphology and lack of detailed provenance data.

SUMMARY AND CONCLUSIONS

Approximately 107 species of terrestrial fossil mammalian taxa and approximately 56 marine mammalian taxa (not including several undescribed species) are known from at least 18 of 41 named formations (and at least two unnamed units) underlying the SC Coastal Plain. Paleocene and Eocene terrestrial vertebrates are exceptionally rare, as they are only recovered from quarries or construction sites where deep excavation reached strata of that age. One of these, the viverravid *Didymictis proteus* from the approximately 57 my old (late Clarkforkian/earliest Wasatchian) Williamsburg Formation, provides a new first occurrence for the Atlantic Coastal Plain. Two others, a brontothere molar and rhinoceros palate with teeth (*Subhyracodon mitis*) from the approximately 34 my old Harleyville Formation (latest Chadronian) also deserve mention because they too represent new Eocene records for SC, but sadly they are currently in a private collection and inaccessible to study. Fortunately, a partial tooth from the rhinoceros specimen is housed at the SCSM and is formally recognized in this report. A third specimen that deserves mention is a metatarsal of the hyena *Chasmaporthetes*. Although the first author was allowed to examine, measure, and photograph the specimen (a left Mt III), it is not included in the "Systematic Paleontology" section of this work because it too resides in the same private collection. Collected from the Ashepoo River by a scuba diver, the exact location and unit of origin are unknown. This specimen represents the first eastern occurrence of this taxon outside of Florida. Additional first occurrences for SC reported herein include *Ondatra idahoensis*, *Canis lepophagus*, *Phocanella pumila*, *Callophoca obscura*, *Anchippus texanus*, and possibly *Teleoceras guymonense*. Other notable occurrences include what may be the oldest records of capybara and *Allophaiomys* in the USA and the oldest record of *Erethizon* in the southeastern USA. The latter two specimens were recovered from the approximately 2.3 my old, late Blancan, Walrus Ditch LF.

Particularly impressive is the stunning diversity of fossil cetaceans from the state, which helps to document their evolution from rear-legged protocetids with the nasal opening still far forward on the snout, through their cladogenesis into primitive odontocetes and bizarre toothed mysticetes, to the earliest baleen-bearing mysticetes and echolocating odontocetes. Indeed, SC's fossil cetacean record rivals the very best on the planet, including those of western Pakistan and the Fayum of Egypt.

With its wealth of paleontological resources, in particular those from the famous "Ashley River phosphate beds," the SC Coastal Plain played a seminal role in the development of vertebrate paleontology as a scientific discipline in the United

States. Were it not for phosphate and limestone mining operations, however, this potential may not have been realized as early as it was, considering that natural exposures of fossil-bearing strata are exceptionally rare in the Carolina "Low Country." But now, many decades later, explosive escalation in development and construction, particularly in the Charleston-Berkeley-Dorchester tri-county area, has resulted in at least ephemeral exposure of fossil-bearing beds that lie in some cases just below the surface. The consequent dramatic increase in avocational fossil collecting has often led to important specimens remaining in private hands, but fortunately many are now housed within museum collections where they can be accessed in perpetuity for study.

The discovery in the late 1960s and early 1970s that the bottoms of many South Carolina coastal rivers were littered with fossils eventually led to the inclusion of fossils in the SC Underwater Antiquities Act (1991). This Act identifies fossils occurring in coastal waterways as State property, but also allows for avocational collectors to recover and in most cases keep the material they find. Such specimens that have been donated to and placed within museum collections, many of which are included in this report, have provided an even greater understanding of the state's record of prehistoric life.

With progressively increasing study of these new finds over the last few decades came the realization that the weak link in a thorough understanding of the state's vertebrate paleontology was the lack of a refined, modern, temporal framework. Our attempt in this report has been to provide, in a single body of literature, (1) a statewide review of all the vertebrate fossil-bearing geologic units, (2) an update and refinement of their temporal placement with the consequent development of a refined chronostratigraphic context for the state's vertebrate fossil record, (3) a comprehensive review of that record, including several additions previously unknown from the state (or in some cases from the Southeastern Atlantic Coastal Plain), plus (4) revised taxonomic assessment of some previously reported species.

We have provided this interpretation in the hope that our initial attempt will aid other researchers interested in the vertebrate paleontology of South Carolina, and inspire at least occasional updates as the GPTS and understanding of the state's stratigraphy further refines our knowledge of the age of the state's vertebrate fossil-bearing units. As less than half of the recognized units within the South Carolina Coastal Plain are known to contain vertebrate fossils, we fully recognize that our effort may be altered dramatically as additional field and laboratory work results in the discovery of new fossil-bearing localities and analysis of new specimens, respectively. Publication of data on non-mammalian fossils will also add to the robustness of the findings presented here.

ACKNOWLEDGEMENTS

First, we extend our gratitude to the following avocational fossil collectors: Aura Baker† (and volunteers from the Myrtle Beach Fossil Club who helped her), Mace Brown (Director, Mace Brown Museum of Natural History, College of Charleston), Michael Bruggeman, Alan Devier, Doris Holt†, Derwin Hudson, Jeremy Jacobs, Daniel Lesesne, James Malcolm, Vance McCollum, John Metts†, Frank Morning, Ray Ogilvie, Bruce Orr, Bill Palmer†, Richard Patterson, Sammy Peek, Alan Schoemaker, Matthew Swilp, Jason Thompson, and Susan Wallace (extensive discussions with V. McCollum and M. Swilp were particularly helpful); plus Jason Osborne and Aaron Alford, founders and principals of Paleo Quest, a non-profit (503c) organization established to enhance paleontological collections, research, and education through "citizen science." It is only through the enthusiastic and professional efforts of all the above, and their understanding of the importance of having fossils curated in public repositories, that scientific study of many of South Carolina's fossil vertebrates has been possible. († = Deceased)

Additional gratitude is extended to the following colleagues who took time from their busy schedules to identify molluscs and/or microfossils from samples of stratigraphic units for which we sought refined age determinations, and for helpful discussions on SC stratigraphy: Lyle Campbell (University of South Carolina, Spartanburg), David Campbell (University of North Carolina, Chapel Hill), Matthew Campbell (Erskine College, Due West, SC), William Doar (SC Department of Natural Resources), W. B. Harris (University of North Carolina, Wilmington), Tom Cronin (USGS), and especially Jean Self-Trail and Lucy Edwards (USGS) who we bombarded with sediment samples for which we needed microfossil analyses. Matthew Campbell is also thanked for allowing us to include his unpublished lists of molluscs from the Ashley and Chandler Bridge formations that have resulted from his extensive studies of these units.

Special gratitude is extended to Matthew Gibson for assisting LBA and AES with study of specimens under his care at The Charleston Museum, and to Richard Hulbert for similar assistance during visits by LBA and JLK to the Florida Museum of Natural History. Jonathan Bloch, Paul Morse, and David Steadman were also integral to our studies of specimens at the latter institution. We also thank David Bohaska, Fred Grady, Robert Purdy, and Steve Gotte at the Smithsonian Institution, Washington, DC, and Stephanie Pierce and Jessica Cundiff at the Museum of Comparative Zoology, Harvard. Gary Morgan at the New Mexico Museum of Natural History and Science is thanked for helpful discussions on fossils and Neogene sites of Florida and also for help with identification of some specimens. Matthew Mihlbachler provided helpful discussions on North American brontotheres and Jonathan Geisler was always generous in sharing his knowledge of SC's fossil cetacean record. Charles Ciampaglio (Wright State University, Celina, Ohio) introduced LBA to the Clapp Creek locality in Kingstree. Adam Rountrey (University of Michigan Museum of Paleontology) provided photographs of the genoholotype of *Proneofiber guildayi*, as did Ted Daeschler (ANSP) for *Phoca modesta* and *P. debilis*, and Stephen Godfrey (Calvert Marine Museum) for *Agorophius pygmaeus*. Finally, Nicholas Emord, Joshua Nevin, and Joshua Oglesby of Johnson and Johnson's 3-D Printing Laboratory at UNF are thanked for the time they took from their busy schedules to CT scan some of the specimens. Michael Woodburne is thanked for reviewing an early version of the manuscript, as are formal reviewers Jonathan Geisler, Richard Hulbert, and Gary Morgan, whose attention to details plus comments and suggestions resulted in a much improved final product. Funding for this project was provided in part by a grant to LBA from the Charleston Scientific and Cultural Education Fund. Finally, LBA would like to extend a personal debt of gratitude to his friend of over 55 years, Howard G. Costa. It was their childhood fossil forays around the Charleston area and the deep interest in natural history they shared during their formative years that in large part galvanized the first author's early decision to become a scientist, with particular interests in paleontology. Both of us were in very large part inspired by our early association with Albert E. Sanders.

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APPENDIX 1

All known non-marine mammalian taxa from South Carolina including age and unit from which the remains were recovered (or thought to have originated). *Denotes South Carolina as type locality; † Denotes specimens examined by LBA but retained in a private collection; **Boldface** denotes taxon previously unreported from South Carolina; **"APBs"**, "Ashley Phosphate Beds"; **ARD**, Ardis Local Fauna; **"BPBs"**, "Beaufort Phosphate Beds"; **BMF**, Black Mingo Fauna; **CAM**, Camelot Local Fauna; **CB**, Chandler Bridge Formation; **CLP**, Clapp Creek locality; **COOS**, Coosawhatchie Formation; **CR**, Cooper River; **CRO**, Crowfield Local Fauna; **DUP**, Duplin Formation; **EB**, Edisto Beach; **EBEN**, Ebenezer Formation; **EF**, Edisto Formation; **GCL**, Goose Creek Limestone; **HAR**, Harleyville Formation; **IRV**, Irvingtonian NALMA; **JMS**, "Jamestown beds"; **LAD**, Ladson Formation; **MB**, Myrtle Beach; **PEN**, Penholoway Formation; **RAY**, Raysor Formation; **RLF**, Ridgeville Local Fauna; **RLB**, Rancholabrean NALMA; **TMH**, Ten Mile Hill Formation; **WAC**, Waccamaw Formation; **Wa0**, Wasatchian 0 (earliest Wasatchian) NALMA; **WAN**, Wando Formation; **WD**, Walrus Ditch Local Fauna. Compiled from Leidy (1860, 1877); Hay (1923); Allen (1926); Ray (1965, 1967); Ray et al. (1968); Ray and Sanders (1984); Roth and Laerm (1980); Bentley et al. (1994); McDonald et al. (1996); Downing and White (1995); Schoch (1985, 1998); Sanders (2002); Kohn et al. (2005); Fields et al. (2012); and this paper.

Taxon	Fauna, Stratigraphic Unit, or Locality	North American Land Mammal Age
Marsupialia		
Didelphis virginiana	ARD, CAM, CRO, EB	Late Irvingtonian–Late Rancholabrean
Eutheria incertae sedis		
**Mingotherium holtae*	BMF	Late Tiffanian (Ti5)
Xenarthra		
Megalonyx leptostomus	CR, WD	Early(?)–Late Blancan
Megalonyx jeffersonii	ARD, CAM, CRO, EB, LAD, WAN	Late Irvingtonian–Late Rancholabrean
Eremotherium laurillardi	EB, LAD, PEN, TMH	Irvingtonian-Late Rancholabrean
Eremotherium eomigrans	WD, RLF	Late Blancan
Paramylodon harlani	CR, EB, ?WAN	Late Irvingtonian(?)–Late Rancholabrean
Glyptotherium texanum	?	?Middle Blancan
Glyptotherium floridanum	EB	Late Rancholabrean
Pachyarmatherium leiseyi	WD	Late Blancan
Holmesina septentrionalis	ARD, CAM, CRO, EB, TMH	Late Irvingtonian–Late Rancholabrean
Holmesina floridanus	CLP, WD, RLF	Late Blancan
Dasypus bellus	ARD, CAM, CRO, EB, TMH, WD	Late Blancan–Late Rancholabrean
Taeniodonta		
Ectoganus gliriformis lobdelli	BMF	Late Tiffanian (Ti5)
Lagomorpha		
Sylvilagus floridanus	ARD, CRO, EB	Rancholabrean
Sylvilagus palustris	ARD, CAM, CRO, TMH	Late Irvingtonian–Late Rancholabrean
Sylvilagus webbi	WD	Late Blancan
Lepus sp.	CAM	Late Irvingtonian
Rodentia		
Sciurus carolinensis	ARD, CAM, CRO	Late Irvingtonian–Late Rancholabrean
Sciurus sp.	CRO	Rancholabrean
Ictidomys tridecemlineatus	ARD, CRO	Rancholabrean

APPENDIX 1 (Continued)

Taxon	Fauna, Stratigraphic Unit, or Locality	North American Land Mammal Age
Glaucomys volans	ARD, CRO	Rancholabrean
Castoroides dilophidus	CRO, EB, WAN	Rancholabrean
Castor canadensis	ARD, EB, CRO, TMH, WAN	Rancholabrean
Thomomys sp.	CAM	Late Irvingtonian
Oryzomys palustris	ARD	Rancholabrean
Oryzomys sp.	CRO	Rancholabrean
Peromyscus sp.	ARD, CRO	Rancholabrean
Sigmodon hispidus	CRO	Rancholabrean
Sigmodon bakeri	CAM	Late Irvingtonian
Neotoma floridana	ARD, CRO	Rancholabrean
Allophaiomys pliocaenicus	WD	Late Blancan
Microtus pennsylvanicus	ARD, CRO	Rancholabrean
Microtus pinetorum	ARD, CRO	Rancholabrean
Microtus ochrogaster	CRO	Rancholabrean
Synaptomys cooperi	ARD, CRO	Rancholabrean
Synaptomys australis	ARD, CRO	Rancholabrean
Neofiber alleni	ARD, CRO, TMH, WAN	Rancholabrean
Neofiber ?alleni	CAM	Late Irvingtonian
Ondatra idahoensis	CLP	Late Blancan
Ondatra zibethicus	ARD, CRO	Rancholabrean
Erethizon ?bathygnathum	WD	Rancholabrean
Erethizon dorsatum	CRO, EB	Rancholabrean
Phugatherium dichroplax	DUP	Middle Blancan
**Neochoerus pinckneyi*	GCL, DUP, WAC, WD, RLF, CAM, TMH, WAN, ARD, EB	Early Blancan–Rancholabrean
Insectivora		
Sorex sp. cf. *S. longirostris*	ARD, CRO	Rancholabrean
Sorex sp. cf. *S. arcticus*	CRO	Rancholabrean
Sorex sp. cf. *S. palustris*	CRO	Rancholabrean
Microsorex hoyi	CRO	Rancholabrean
Blarina brevicauda	ARD, CRO	Rancholabrean
Blarina sp.	CRO	Rancholabrean
Cryptotis parva	CRO	Rancholabrean
Scalopus aquaticus	ARD, CRO	Rancholabrean
Scalopus sp.	CAM	Late Irvingtonian
Condylura cristata	ARD, CRO	Rancholabrean
Carnivora		
Didymictis proteus	JMS	Clarkforkian–earliest Wasatchian
Leopardus amnicola	WAN	Rancholabrean

APPENDIX 1 (Continued)

Taxon	Fauna, Stratigraphic Unit, or Locality	North American Land Mammal Age
Miracinonyx ?trumani	EB	Late Rancholabrean
Miracinonyx inexpectatus	CAM, PEN, WAC	Irvingtonian
Smilodon fatalis	ARD, CAM, EB	Late Irvingtonian–Late Rancholabrean
Smilodon gracilis	WD	Late Blancan
Panthera atrox	EB	Late Rancholabrean
Panthera onca augusta	EB	Late Rancholabrean
Puma concolor	EB	Late Rancholabrean
Lynx rufus	ARD, CRO, EB	Rancholabrean
†***Chasmaporthetes ossifragus***	?	Late Blancan–Early Irvingtonian
Borophagus hilli	RAY	Early Blancan
Canis lepophagus	WD	Late Blancan
Canis armbrusteri	CAM	Late Rancholabrean
Canis dirus	ARD, EB, WAN	Rancholabrean
Canis latrans	MB	Late Irvingtonian
Urocyon cinereoargenteus	ARD, CAM, EB, CRO	Late Irvingtonian–Late Rancholabrean
Arctodus pristinus	LAD, WD	Late Blancan–Late Irvingtonian
Tremarctos floridanus	ARD, CRO, EB, MB	Rancholabrean
Ursus americanus	CRO, WAN	Rancholabrean
Lontra canadensis	ARD, CRO	Rancholabrean
Spilogale putorius	ARD, CRO	Rancholabrean
Mephitis mephitis	ARD, CRO	Late Rancholabrean
Conepatus robustus	ARD	Late Rancholabrean
Neovison vison	ARD, CRO	Rancholabrean
Procyon lotor	ARD, CAM, EB, CRO	Late Irvingtonian–Late Rancholabrean
Procyon sp.	WD	Late Blancan
Cetungulata		
**Phenacodus grangeri mccollumi*	BMF	Late Tiffanian (Ti5)
Perissodactyla		
†***?Megacerops*** sp.	HAR	Late Chadronian
Anchippus texanus	EF?	Late Arikareean
Nannippus peninsulatus	CLP	Late Blancan
Nannippus sp.	WD	Late Blancan
Cormohipparion sp.	CLP	Late Blancan
Equus “*complicatus*”	ARD	Late Rancholabrean
Equus “*fraternus*”	“APBs”	Rancholabrean
Equus “*leidyi*”	“APBs”	Rancholabrean
Equus sp.	CAM, CLP, CRO, EB, LAD, TMH, WAN, WD, RLF	Blancan–Late Rancholabrean

APPENDIX 1 (Continued)

Taxon	Fauna, Stratigraphic Unit, or Locality	North American Land Mammal Age
Equus “*littoralis*”	“APBs”	Rancholabrean
Tapirus sp.	RLF	Late Blancan
Tapirus haysii	TMH, WAC, WD	Late Blancan–Early Rancholabrean
Tapirus veroensis	ARD, CAM, CLP, CRO, EB, LAD, WAN	Late Irvingtonian–Rancholabrean
Subhyracodon mitis	HAR	Late Chadronian
Aphelops ?malacorhinus	?COOS or ?EBEN	?Barstovian–Hemphillian
Teleoceras ?guymonense	?COOS or ?EBEN	?Barstovian–Late Hemphillian
Artiodactyla		
**Daeodon mento*	EF	Late Arikareean
Mylohyus fossilis	ARD, MB, EB	Late Rancholabrean
Mylohyus sp.	CAM, CRO, WD	Late Irvingtonian–Rancholabrean
Platygonus compressus	CAM	Late Irvingtonian
Perchoerus sp.	CB	Late Arikareean
Hemiauchenia macrocephala	CAM, CRO, WD	Late Blancan–Rancholabrean
Palaeolama mirifica	ARD, CAM, CRO, EB	Late Irvingtonian–Late Rancholabrean
Rangifer tarandus	CRO, WAN	Rancholabrean
Cervalces scotti	WAN	Rancholabrean
Cervus elaphus	CLP, CRO, EB	Rancholabrean
Odocoileus virginianus	ARD, CAM, CRO, EB, WD	Late Blancan–Recent
Bison antiquus	ARD, EB	Late Rancholabrean
Bison sp.	CRO	Rancholabrean
Bootherium bombifrons	ARD, MB, WAN	Rancholabrean
Proboscidea		
Gomphothere	“APBs”, “BPBs”	Rancholabrean
Rhynchotherium falconeri	WD, RLF	Late Blancan
Cuvieronius hyodon	TMH, WAN	Rancholabrean
Mammut americanum	ARD, CRO, EB, WAN	Rancholabrean
Mammuthus columbi	ARD, EB, WAN	Rancholabrean

APPENDIX 2

Marine mammalian taxa from South Carolina, including age and unit from which the remains were recovered (or thought to have been recovered). " " denotes doubtful generic assignment; *Denotes South Carolina as type locality; **GCL** = Goose Creek Limestone; **TBF** = Tupelo Bay Formation; **UOPD** = Unnamed Offshore Pleistocene Deposits. **NOTE**: Not included in this list are dozens of yet-to-be-described cetacean taxa including new representatives of the Protocetidae, Basilosauridae, Xenorophidae, Agorophiidae, "Waipatiidae," "Squalodontidae," and Eomysticetidae, in addition to several new sirenian taxa of Protosirenidae and early members of the Dugongidae.

Taxon	Formation	Stage/Age
Cetacea		
Protocetidae		
Georgiacetus sp. cf. *G. vogtlensis*	Santee Limestone	Upper Lutetian/Lower Bartonian
**Carolinacetus gingerichi*	Cross Mbr., TBF	Upper Bartonian
**Tupelocetus palmeri*	Cross Mbr., TBF	Upper Bartonian
Basilosauridae		
Basilosaurus cetoides	Pregnall Mbr., TBF	Lower Priabonian
Basilosaurus sp.	Pregnall Mbr., TBF	Lower Priabonian
Zygorhiza kochii	Pregnall Mbr., TBF	Lower Priabonian
**Chrysocetus healyorum*	Pregnall Mbr., TBF	Lower Priabonian
**Dorudon serratus*	?Pregnall Mbr., TBF	Lower Priabonian
Basilosauridae indet.	Parkers Ferry Fm.	Upper Priabonian
Basilosaurus sp.	?Harleyville Fm.	Upper Priabonian/Lower Rupelian
Odontoceti		
Xenorophidae		
**Xenorophus sloanii*	Ashley Fm.	Upper Rupelian
Albertocetus meffordorum	Ashley Fm.	Upper Rupelian
**Inermorostrum xenops*	Ashley Fm.	Upper Rupelian
**Cotylocara macei*	Chandler Bridge Fm.	Upper Chattian
**Echovenator sandersi*	Chandler Bridge Fm.	Upper Chattian
Ashleycetidae		
**Ashleycetus planicapitis*	Ashley Fm.	Upper Rupelian
Agorophiidae		
**Agorophius pygmaeus*	Ashley and Chandler Bridge Fms.	Upper Rupelian/Upper Chattian
Family indet.		
**Ediscetus osbornei*	Ashley Fm.	Upper Rupelian
"Squalodon" tiedemani ("Genus Y"?)	Ashley and Chandler Bridge Fms.	Upper Rupelian/Upper Chattian
"Squalodon" atlanticus	Chandler Bridge Fm.	Upper Chattian
Eurhinodelphinidae		
"*Rhabdosteus latiradix*"	?Marks Head Fm.	Burdigalian

APPENDIX 2 (Continued)

Taxon	Formation	Stage/Age
Ziphiidae		
Anoplanassa forcipata	?Marks Head Fm.	Burdigalian
**Dioplodon proprops*	?Marks Head Fm.	Burdigalian
**Choneziphius chonops*	?Marks Head Fm.	Burdigalian
**Choneziphius liops*	?Marks Head Fm.	Burdigalian
**Choneziphius tracops*	?Marks Head Fm.	Burdigalian
**Choneziphius macrops*	?Marks Head Fm.	Burdigalian
**Eboroziphius coelops*	?Marks Head Fm.	Burdigalian
**Ceterhinops longifrons*	?Goose Creek Limestone	Zanclean
Tusciziphius crispus	?Goose Creek Limestone	Zanclean
Physeteridae		
**Dinoziphius carolinensis* (= *Physeter carolinensis*)	?Marks Head Fm.	Burdigalian
Physeterula sp.	?Waccamaw Fm.	Lower Pleistocene
Scaldicetus sp.	?Waccamaw Fm.	Lower Pleistocene
Physeter macrocephalus	UOPD (Edisto Beach)	Upper Pleistocene–Holocene
Delphinidae		
Tursiops truncatus	UOPD (Edisto Beach)	Upper Pleistocene–Holocene
Stenella sp.	UOPD (Edisto Beach)	Upper Pleistocene–Holocene
Pseudorca crassidens	UOPD (Edisto Beach)	Upper Pleistocene–Holocene
Mysticeti		
**Coronodon havensteini*	Ashley and Chandler Bridge Fms.	Upper Rupelian/Upper Chattian
**Micromysticetus rothauseni*	Ashley Fm.	Upper Rupelian
**Eomysticetus whitmorei*	Chandler Bridge Fm.	Upper Chattian
**Eomysticetus carolinensis*	Chandler Bridge Fm.	Upper Chattian
Balaenopteridae		
Eschrichtius sp.	?Waccamaw Fm.	Lower Pleistocene
Gen. et sp. indeterminate	Goose Creek Limestone	Upper Zanclean
Pinnipedia		
Odobenidae		
Ontocetus emmonsi	GCL, Raysor, Waccamaw Fms.	Upper Zanclean–Lower Pleistocene
Odobenus rosmarus	?Wando Fm.	Upper Pleistocene
Odobenus sp.	Ten Mile Hill Fm.	Upper Middle Pleistocene
Phocidae		
Monatherium sp.	?Ebenezer Fm.	?Tortonian
Phocanella pumila	?Wabasso beds, ?GCL	Zanclean
Callophoca obscura	?Wabasso beds, ?GCL	Zanclean
Erignathus barbatus	Socastee Fm.	Upper Pleistocene

APPENDIX 2 (Continued)

Taxon	Formation	Stage/Age
Monachus tropicalis	Socastee Fm., UOPD	Upper Pleistocene
Halichoerus grypus	UOPD (Edisto Beach)	Upper Pleistocene–Lower Holocene
Sirenia		
Protosirenidae		
Protosiren sp.	Cross Mbr., TBF	Upper Bartonian
Protosiren sp.	Pregnall Mbr., TBF	Lower Priabonian
Dugongidae		
Eotheroides sp.	Pregnall Mbr, TBF	Lower Priabonian
Priscosiren atlantica	Ashley Fm.	Upper Rupelian
**Stegosiren macei*	Ashley and ?Chandler Bridge Fms.	Upper Rupelian/?Upper Chattian
Crenatosiren olseni	Ashley and Chandler Bridge Fms.	Upper Rupelian/Upper Chattian
Metaxytherium albifontanum	?Ashley Fm., Chandler Bridge Fm.	?Upper Rupelian/Upper Chattian
Metaxytherium sp.	Ashley Fm.	Upper Rupelian
**Dioplotherium manigaulti*	Chandler Bridge Fm.	Upper Chattian
**"Halitherium" alleni*	Uncertain	Uncertain
Corystosiren sp.	Uncertain	Uncertain
Trichechidae		
Trichechus manatus[1]	UOPD (Edisto Beach)	Upper Pleistocene–Holocene

[1] Includes **Manatus antiquus* Leidy, 1856 and **Manatus inornatus* Leidy, 1873 (see Domning, 1989b).

APPENDIX 3

Recognized Faunas, Local Faunas, faunal assemblages, and/or stratigraphic units from which known non-marine mammalian taxa from SC originate, plus associated age and NALMA, with faunas from Florida mentioned throughout text included for temporal comparison. * denotes the primarily Rancholabrean aspect of the mammals from Edisto Beach, but see text for discussion regarding additional taxa of non-Rancholabrean age.

South Carolina	Florida	Epoch	NALMA
Ashley River Phosphate Beds		Mixed faunas	See text
Beaufort Phosphate Beds		Mixed faunas	See text
Cooper River		Mixed faunas	See text
Clapp Creek locality		Mixed faunas	See text
Ardis Local Fauna		Latest Pleistocene	Late Rancholabrean
Edisto Beach Fauna		Mixed faunas	Rancholabrean*
Myrtle Beach Fauna		Mixed faunas	Rancholabrean*
Crowfield Local Fauna		Late Pleistocene	Rancholabrean
Wando Formation		Late Pleistocene	Rancholabrean
Socastee Formation		Late Pleistocene	Rancholabrean
Ten Mile Hill Formation		Late Mid. Pleistocene	Earliest Rancholabrean
	Coleman 2A LF	Mid. Pleistocene	Late Irvingtonian
Camelot Local Fauna		Mid. Pleistocene	Late Irvingtonian
Ladson Formation		Mid. Pleistocene	Late Irvingtonian
Penholoway Formation		Late Earl. Pleistocene	Middle Irvingtonian
	Leisey Shell Pit LF	Early Pleistocene	Late Early Irvingtonian
	Haile 16A LF	Early Pleistocene	Earliest Irvingtonian
Ridgeville Local Fauna		Early Pleistocene	Latest Blancan-E. Irv.
Upper Waccamaw Formation		Early Pleistocene	Late Blancan
	Inglis 1A LF	Early Pleistocene	Latest Blancan
	De Soto Shell Pit	Early Pleistocene	Latest Blancan
	Haile 7C LF	Early Pleistocene	Middle late Blancan
	Withlacoochee River 1A		
	Haile 15A LF	Early Pleistocene	Early Late Blancan
	Santa Fe River 1 LF	Early Pleistocene	Early Late Blancan
	Macasphalt Shell Pit LF	Early Pleistocene	Early Late Blancan
Lower Waccamaw Formation		Early Pleistocene	Early Late Blancan
Walrus Ditch Local Fauna		Early Pleistocene	Early Late Blancan
Duplin Formation		Late Pliocene	Middle Blancan
Raysor Formation		Middle Pliocene	Early Blancan
Goose Creek Limestone		Middle Pliocene	Early Blancan
Wabasso beds	Palmetto Fauna	Early Pliocene	Latest Hemphillian
Edisto Formation		Latest Oligocene	Late Arikareean (Ar3)

APPENDIX 3 (Continued)

South Carolina	Florida	Epoch	NALMA
Chandler Bridge Formation	White Springs LF	Late Oligocene	Late Arikareean (Ar3)
Ashley Formation		Early Oligocene	Early Arikareean (Ar2)
Harleyville Formation		Latest Eocene	Late Chadronian
Parkers Ferry Formation		Late Eocene	Late Chadronian
Tupelo Bay Formation		Late Eocene	Late Duchesnean-Early Chadronian
Santee Limestone		Middle Eocene	Late Uintan
“Jamestown beds” (= Chicora Mbr., Williamsburg Formation)		Latest Paleocene-Earliest Eocene	Clarkforkian-Earliest Wasatchian
Black Mingo Fauna		Late Paleocene	Late Tiffanian (Ti5)

APPENDIX 4

Molluscan Fauna of the Ashley Formation

The Ashley Formation contains abundant well-preserved valves of a small, thin-shelled, finely ribbed pectenid-like bivalve that often occurs in densely packed layers. Tuomey (1848) reported this locally abundant mollusc as *Pecten calvatus*, an Eocene form, and one of three molluscan taxa upon which he based his referral of the Charleston marl beds to the Eocene. Dall (1894:301), however, noted that "The pecten referred to [by Tuomey] is not *Pecten calvatus*" and he expressed doubt that the sediments in which it occurred were of Eocene age, as indeed they are not. Dall (1894, 1896, 1903) considered the Ashely Formation to be Miocene in age, and therefore used Miocene names for the species. Dall (1894:300) reported "about twenty species" of molluscs from the Ashley Formation from an 1877 shipwreck in Maine that carried phosphate from "the east bank of the Ashely River about 10 miles from Charleston, SC." That bivalve has recently been identified by M. Campbell as *Eburneopecten subminutus* (Aldrich, 1903).

During his survey of the geology of South Carolina in the first decade of the 20th Century, State Geologist Earle Sloan collected molluscs from the Ashley Formation at several localities near Charleston. On some occasions he was accompanied by T. W. Vaughn (USGS), who may well have provided many of the identifications of the specimens. In 1907 Sloan and Vaughn collected specimens from the Ashley Formation in the Lambs and Ingleside marl pits and from an unspecified location near the Ingleside railroad station; but because of the nature of the publication, Sloan did not include detailed faunal lists in his *Mineral Localities of South Carolina* (Sloan, 1908), and for many years thereafter the molluscan fauna of this unit remained virtually unknown. Sloan's extensive collection of geological and paleontological material from South Carolina, Virginia, and the Gulf Coast is housed in The Charleston Museum.

C. W. Johnson (1931) described five new wentletraps from the vicinity of Charleston. The type specimens of four of them, *Epitonium chamberlaini*, *E. charlestonensis*, *E. cooperensis*, and *E. subexpansum* (now *Sthenorytis subexpansum* (Johnson, 1931)) were collected by E. Bernham Chamberlain of The Charleston Museum on a small island of dredgings of Ashley Formation sediments from the Cooper River opposite its west bank approximately 1.5 miles above the Etiwan Fertilizer works, north of Charleston (Johnson, 1931). The label with the holotype of the fifth taxon, *E. raveneli* Johnson, 1931 (ChM PI26233 [Ravenel No. 11 30]), discovered by Johnson in the Edmund Ravenel collection, states that the specimen is from the "Eocene" of "St. Johns Parish," Berkeley County, indicating that it was collected from the Ashley Formation, then thought to be of Eocene age. The holotype of *Sthenorhytis mazyckii* (Dall, 1896), originally described by Dall as *Scala* (*Sthenorhytis*) *mazyckii* and considered Miocene age, was collected by W. G. Mazyck at Cainhoy, Berkeley County; but a specimen of the same taxon collected from the Ashley Formation at The Charleston Museum's Chandler Bridge excavation site (Sanders, 1980; see below) demonstrates this taxon to be a late Rupelian (early Oligocene) form. In concluding his report of these taxa, Johnson (1931:10) noted that 35 species of foraminifera from matrix removed from the specimens were identified as Eocene forms by J. A. Cushman, "thus definitely determining the age of this formation." But as detailed above, overwhelming evidence now proves the Ashley Formation to be of Oligocene age.

More recently, extensive studies of unpublished collections of specimens from the Ashley Formation at The Charleston Museum and the SCSM have been conducted by Dr. Matthew Campbell. In his assessment he noted that calcitic taxa were preserved as the original shell, but aragonitic taxa are preserved as internal or external molds resulting in identification only to the genus level. He also noted that earlier literature that published notifications of molluscs from the Ashley Formation often assigned Eocene through Miocene ages to this unit. In turn, these papers used species names that are now known to be restricted to different ages, including the Cretaceous to Eocene through Pliocene. The species with affinities listed below are taken from the published literature.

APPENDIX 4 (Continued)

As Campbell further noted (pers. com. to LBA, August 2019), “examination of the original specimens is needed to determine whether or not sufficient morphological details are preserved to assign more appropriate names …” The following table provides his updated assessment of the molluscs from this unit. This represents the second extensive list of upper Rupelian molluscs from the Atlantic coast, subsequent to the fauna from the Lower River Bend Formation of North Carolina (Rossbach and Carter, 1991).

Bivalves

Yoldia sp.
Nuculana sp. aff. *N. flexuosa*
Nuculana sp.
Brachidontes mississippiensis
Crenella sp.
Modiolus sp.
Glycymeris sp.
Pteria sp. cf. *P. argentea*
Aequipecten cocoana
Amusium sp.
Chlamys sp.
Eburneopecten subminutus
Aequipecten sp. cf. *A. acanikos*
Pecten sp. aff. *P. humphreysii*
Pecten sp.
Pseudamussium sp.
Pseudamussium sp. aff. *P. claibornense*
Plicatula? sp.
Spondylus sp.
Anomia sp. aff. *A. simplex*
Anomia jugosa
Anomia sp.
Pododesmus sp. aff. *P. philippi*
Ostrea sp. aff. *O. carolinensis*
Ostrea sp. aff. *O. podagrina*
Ostrea sp. aff. *O. queteleti*
Ostrea sp. aff. *O. thomasii*
Ostrea sp.
“Ostrea” n. sp.
Pycnodonte paroxis
Gryphaeostrea sp. aff. *G. plicatella*
Phacoides? sp.
Phacoides sp. aff. *P. contractus*
Cyclocardia sp. aff. *C. granulata*
Cyclocardia sp. aff. *C. castrana*
Cardita sp.
Astarte sp.
Astarte sp. aff. *A. vacina*
Astarte sp. aff. *A. thomasii*
Lucina sp.
Cardiidae sp.
Cardium sp.
Dinocardium sp. aff. *D. taphrium*
Nemocardium? sp.
Solen sp.
Tellina sp.
Antigona (Artena) undulata
Antigona (A.) n. sp. aff. *A. lamellacea*
Antigona (A.) sp.
Callista sp.
Veneridae sp.
Anomalocardia? sp.
Corbula sp.
Gastrochaena sp.
Panopea sp. aff. *P. elongata*
Panopea sp.
Thracia? sp.

Gastropods

Modulus? sp.
Turitella sp. cf. *T. tampae*
Turitella sp. aff. *T. bowenae*
Calyptraea (Trochita) sp. cf. *C. (T.) aperta*
Xenophora sp. cf. *X. conchyliophora*
Xenophora sp.
Apiocypraea sp.
Naticid sp.
Galeodea petersoni
Galeodea sp.
Malea sp. aff. *M. camura*
Ficus sp.
Cirsotrema sp.
Sthenorytis mazyckii
Sthenorytis subexpansum
Epitonium chamberlaini
Epitonium charlestonensis
Epitonium raveneli
Epitonium cooperensis
Chicoreus sp. aff. *C. mississippiensis*
Ecphora sp.
Levifusus? sp.
Lyria sp.
Athleta sp. aff. *A. petrosa*
Athelta sp.
Olivella sp.
Prunum sp.
Mitra sp.
Pyropsis sp.
Conus sp.

APPENDIX 4 (Continued)

Scaphopods

Dentalium sp.	*Dentalium* sp. aff. *D. attenuatum*

Cephalopods

Aturia alabamensis