

## New Skeletal Remains of *Mammuthus columbi* from Glynn County, Georgia with Notes on their Historical and Paleocological Significance

David B. Patterson<sup>1,\*</sup>, Alfred J. Mead<sup>2</sup>, and Robert A. Bahn<sup>3</sup>

**Abstract** - Although *Mammuthus columbi* (Columbian Mammoth) remains have been collected and extensively studied throughout the United States, limited in situ material has been discovered in Georgia. Here we describe new Columbian Mammoth material from Clark Quarry, a recently excavated late-Pleistocene locality near Brunswick, GA, and discuss their historical and paleocological significance. The site has yielded 12 genera of birds, 18 genera of amphibians and reptiles, and 12 species of mammals. Radiocarbon analyses bracket the locality between 19,840 and 22,240 radiocarbon years before present. In 1857, Falconer designated a partial third upper molar unearthed during the excavation of the Brunswick Altamaha Canal as the type specimen for *Mammuthus (Elephas) columbi*. Clark Quarry borders the abandoned Brunswick Altamaha Canal, and presents the possibility that this new material could be from the type locality of *Mammuthus columbi*. Material identified thus far indicates a minimum of two individuals and includes a juvenile palate and lower jaw with cheek teeth, adult tooth fragments, complete and partial adult long-bones, carpals, tarsals, ribs, sternal elements, and cervical, thoracic, and caudal vertebrae.

### Introduction

Although fossils of *Mammuthus columbi* (Falconer) (Columbian Mammoth) have been collected extensively throughout the United States (Agenbroad 1984, Dutrow 1977) relatively little in situ (anthropogenically undisturbed) material is known from the Southeast (Kurtén and Anderson 1980). Of the five states bordering Georgia, the greatest quantities of mammoth material have been reported from Florida and South Carolina (Hay 1923, Kurtén and Anderson 1980). Some of this material includes cranial and postcranial elements, but most consist primarily of cheekteeth. While not as abundant as in Florida, mammoth material from Georgia is taxonomically significant (Hay 1923, Hulbert and Pratt 1988, Hurst 1957, Voorhies 1974). One geographic area within Georgia of paleontological significance is the Brunswick Altamaha Canal in Glynn County, where the type specimen for *Mammuthus (Elephas) columbi*, an isolated 10-plate partial molar, was unearthed during the canal's excavation in 1838 (Couper 1842).

The systematics of the Columbian Mammoth have been somewhat controversial since its initial description. The holotype described by Falconer (1857)

<sup>1</sup>Department of Anthropology, George Washington University, Washington, DC 20052.

<sup>2</sup>Department of Biological and Environmental Sciences, Georgia College and State University, Milledgeville, GA 31061. <sup>3</sup>Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA 30602.

\*Corresponding author - dbpatter@gwmail.gwu.edu.

consisted of a single molar with no additional cranial or post-cranial material. Osborn (1942) questioned the validity of Falconer's (1857) type specimen and subsequently recognized 16 North American mammoth species based primarily upon variations in molar plate numbers. Maglio (1973) reconfirmed the legitimacy of Falconer's (1857) type specimen and suggested that the differences noted by Osborn (1942) were most likely the result of intraspecific variation. More recent discussions of Columbian Mammoths adopt Maglio's (1973) systematics (Agenbroad 2005, Haynes 1991).

Here we report new fossil material, and discuss the historical and paleoecological significance of the Columbian Mammoth from Clark Quarry, a recently excavated late-Pleistocene locality near Brunswick, GA (Mead et al. 2006).

### Materials and Methods

For the present study, molar terminology and eruption sequences are based on Laws (1966) and Shoshani and Tassy (1996). All *Mammuthus columbi* material from Clark Quarry is housed in the Georgia College and State University Vertebrate Paleontology Collection (GCVP). Mammoth material was identified using published descriptions and comparative material in the following research collections: Georgia College and State University Mammal Collection (GCM), The Florida Museum of Natural History (UF), The National Museum of Natural History (USNM), and The Academy of Natural Sciences of Philadelphia (ANSP). Historical maps were obtained from the Coastal Georgia Historical Society. Georgia Department of Transportation maps (1995) were used to determine the location of the modern canal. Radiocarbon analyses were performed at the University of Georgia Center for Applied Isotope Studies.

### Historical Significance

Besides the abundance of the in situ vertebrate fossils recovered from Clark Quarry (Fig.1), the significance of the mammoth material stems from the locality's proximity to the area described as yielding the type specimen of *Mammuthus columbi* (Couper 1842). Work on the Brunswick Altamaha Barge Canal (herein referred to as the Brunswick Canal) began in 1838 in an attempt to unite the Altamaha and Turtle rivers (Hodgson 1846, Lyell 1849). The canal was constructed along a 12-mile distance separating the two rivers and traversed an area that was referred to as the "six-mile swamp" (Hurst 1957), however it was never functional (Cate 1930). During the excavation, J. Hamilton Couper, a local naturalist from Hopeton, GA (near Darien) collected a diversity of mammalian fossils including mastodon, mammoth, giant sloth, horse, bison, hog and what he thought to be hippopotamus (Couper 1842). Couper, a former student of Benjamin Silliman at Yale, was a well-educated progressive agriculturist with a passion for geology and paleontology (Wilson 1998).

Over the next decade, this fossil material collected by Couper was dispersed to a number of museums within the United States. Harlan (1842) provided the first

record of this material in July of 1842, in which he acknowledged the donation of mammoth, mastodon, giant ground sloth, horse and whale to the collections of the Academy of Natural Sciences in Philadelphia. Additional material from the Brunswick Canal was sent to the National Museum of Natural History in Washington (Lyell 1846) and the Natural History Society of Boston (Leidy 1853). Lipps et al. (1988) noted that some of the fossils may have been sent to the Lyceum of Natural History in New York and were probably destroyed by fire in 1846 (Fairchild 1887).

Couper (1846:45) described the proboscidean material from the Brunswick Canal as “two lower maxillary bones with teeth, two rotula, several detached teeth, two tusks and several vertebrae” of *Elephas* (now = *Mammuthus*) *primigenius* (Blumenbach) (Woolly Mammoth). Of the aforementioned collections, only ANSP contains a significant portion of the proboscidean material from the Brunswick Canal. The collection at the Academy currently consists of 4 partial molars and an unlabeled box of podials that may have come from the canal. The other mammoth material collected by Couper appears to have been lost to science.

In January of 1846, during his second visit to the United States, Sir Charles Lyell visited Couper, with whom he had previously corresponded concerning “geological matters” (Lyell 1849:244). Under the guidance of Couper, Lyell toured the area around the coastal confluence of the Altamaha River, a few barrier islands, and the Brunswick Canal. Couper presented Lyell with a proboscidean molar collected during the excavation of the Brunswick Canal (Lyell 1849). Upon his return to England, Lyell presented the tooth to Dr. Hugh Falconer, who found sufficient variation in comparison with the Woolly Mammoth to constitute a new species, *Elephas columbi* (Falconer 1857). The type molar is now housed in the British Museum of Natural History [BM(NH)40769] (Lipps et al. 1988).

The precise geographical location where the Columbian Mammoth type specimen was unearthed is unknown, but an approximate location can be deduced based upon descriptions by Couper (1842, 1846). The best description of the area given by Couper (1842:216–217) states that “... the bones of terrestrial mammalia were found in the bed of the canal, at the southern end of this swamp, at six different points, extending up from its junction with the salt marsh to a distance of three miles (4.8 kilometers).”

### Site Description

Clark Quarry was initially discovered in 2001 and is located on private property adjacent to the Brunswick Canal (Fig. 1). The site is located approximately 1.5 km southwest along the Brunswick Canal from the Pleistocene-aged Watkin’s Quarry described by Voorhies (1971). Due to the prevailing flat topography, dense vegetation, and relatively uniform sedimentology of the region, there remains a lack of general consensus among researchers as to the specific characteristics of

Georgia's Pleistocene units (Hails and Hoyt 1969, Huddlestun 1988, Markewich et al. 1992). However, all agree that the late Pleistocene sedimentary environments were similar to the fluvial and marsh environments that exist along the Georgia coast today (Hulbert and Pratt 1998).

Based on maps of the region generated by Huddlestun (1988:134), Clark Quarry lies within the Princess Anne Terrace of the Satilla Formation, a unit characterized by "coastal marine ('coastal terrace') deposits and the presumed equivalent river terrace deposits of Pleistocene age." However, radiocarbon analyses of material from Clark Quarry bracket the age of the locality between 19,840 and 22,240 radiocarbon years before present (rcybp; Table 1). This age for the fauna indicates that the Clark Quarry fluvial deposit likely represents a younger Pleistocene cut and fill deposit within the Satilla Formation sediments and places it during the height of the Last Glacial Maximum (LGM). At roughly 20,000 rcybp, sea level should have been approximately 80 m lower than at present time, placing Clark Quarry approximately 100 km

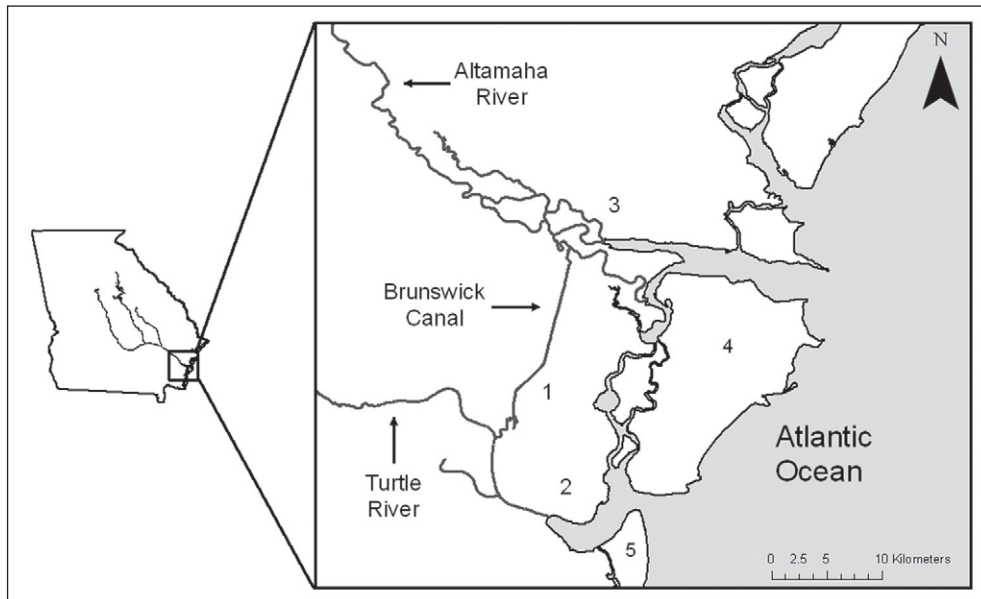


Figure 1. Map of Georgia with a close-up of the section of the coastal area showing the geographical relationship of Clark Quarry (1) to the Altamaha and Turtle rivers, Brunswick (2), Darien (3), St. Simon's Island (4), and Jekyll Island (5).

Table 1. Radiocarbon analyses of Clark Quarry *Mammuthus columbi* and *Bison latifrons* material. Abbreviations: GCVP = Georgia College & State University Vertebrate Paleontology, EA = enamel apatite, BA = bone apatite, YBP = years before present.

Sample	Taxon	$^{14}\text{C}$ Age (YBP)	$\delta^{13}\text{C}$
GCVP 10515	<i>M. columbi</i> (EA)	19,840 $\pm$ 50	-7.0
GCVP 13119	<i>M. columbi</i> (BA)	22,240 $\pm$ 60	-6.8
GCVP 11352	<i>M. columbi</i> (EA)	21,900 $\pm$ 50	-6.8
GCVP 10504	<i>B. latifrons</i> (EA)	20,390 $\pm$ 50	-4.1

inland (Ervin Garrison, University of Georgia, Athens, GA, March 2011 pers. comm.). To date, excavations at Clark Quarry have yielded 12 genera of birds, 18 genera of amphibians and reptiles, and 12 species of mammals. The site is dominated by fossils of *Mammuthus columbi* and *Bison latifrons* Harlan (Giant Bison).

### Systematic Paleontology

Order: Proboscidea Illiger, 1811

Family: Elephantidae Gray, 1821

Genus: *Mammuthus* Burnett, 1830

*Mammuthus columbi* (Falconer, 1857)

### Referred material

*Cranial*—partial juvenile right mandible with complete Rm1 (GCVP 8300); partial juvenile palate with complete LM1 and RM1 (GCVP 11350); unerupted juvenile molar (GCVP 11928); distal end of adult tusk (GCVP 8318); adult molar fragment with 4 plates (GCVP 11353); partial juvenile horizontal ramus with complete mandibular condyle (GCVP 10597); partial juvenile horizontal ramus with fragmentary cheek teeth (GCVP 10534); complete adult mandibular condyle with partial ascending ramus and partial horizontal ramus (GCVP 11351)

*Axial*—adult atlas (GCVP 10559); adult cervicals 3–5 (GCVP 10514, 8352, 10533); partial adult cervicals 6–7 (GCVP 11335, 10596); adult thoracic 1–4 (GCVP 8351, 10530, 10531, 10532); 3 adult posterior thoracic vertebra (GCVP 10016, 11332, 11337); adult right rib (GCVP 8349); adult left rib (GCVP 8312); 3 fragmentary ribs (GCVP 11358, 11359, 11360); partial lumbar (GCVP 10023)

*Appendicular*—partial caudal angle of right scapula (GCVP 11354); partial adult left humerus with complete olecranon fossa (GCVP 11349); partial adult ulna with fragmentary olecranon and trochlear notch (GCVP 11356); adult right trapezium (GCVP 10528); partial juvenile right cuneiform (GCVP 10040); adult right cuneiform (GCVP 10524); adult right scaphoid (GCVP 10525); adult right pisiform (GCVP 10527); juvenile right pisiform (GCVP 10020); adult right unciform (GCVP 10017); adult left metacarpal 1 (GCVP 10526); sesmoids (GCVP 10031, 10008, 10000, 10005); adult distal phalanx (GCVP 10522); fragmentary sternal material (GCVP 11336, 10539, 11355); fragmentary adult pelvis with acetabular fossa, ischium and pubis (GCVP 11357); partial adult right femur (GCVP 11352); complete adult right tibia (GCVP 10502); adult right astragalus (GCVP 10516); adult left astragalus (GCVP 8308); juvenile right metatarsal 1 (GCVP 10007); adult left navicular (GCVP 8316); 5 adult metapodials (GCVP 8350, 10022, 10515, 10529, 11333)

### Descriptions

Adult *M. columbi* skeletal elements recovered from Clark Quarry are depicted in Figure 2. Cervicals 3–7 and thoracics 1–4 articulate with a high degree of

certainty, which, along with the lack of duplicate material from the locality, suggests they are from the same individual.

The teeth within the juvenile dentary and palate appear identical in size and wear stage, and are most likely from the same individual. Based upon molar eruption and wear (Laws 1966), the individual appears to have been approximately 8 AEY (African Elephant [*Loxodonta Africana* (Blumenbach)] years) at the time of death. The size of the juvenile lower jaw material compares favorably to that of *Elephas maximus* L. (Asian Elephant) material (GCM 2187) of approximately the same age.

### Discussion

Thus far, Clark Quarry has yielded the most extensive collection of in situ mammoth material known from Georgia. Besides earlier material from the Brunswick Canal, much of the Columbian Mammoth material from coastal Georgia consists of teeth collected as a by-product of river dredging operations. Similarly, most collections from surrounding states are dominated by dental elements and contain little associated postcranial material suitable for morphometric analysis (Hay 1923, Hulbert and Pratt 1998).

The Columbian Mammoth was undoubtedly a keystone species within the late Pleistocene paleoecosystem of North America, and its removal from the ecological landscape had a profound impact on the vegetation (Haynes 2002). Much like contemporary elephants in Africa and Asia, the Columbian Mammoth would have converted wooded savannas into open grasslands and

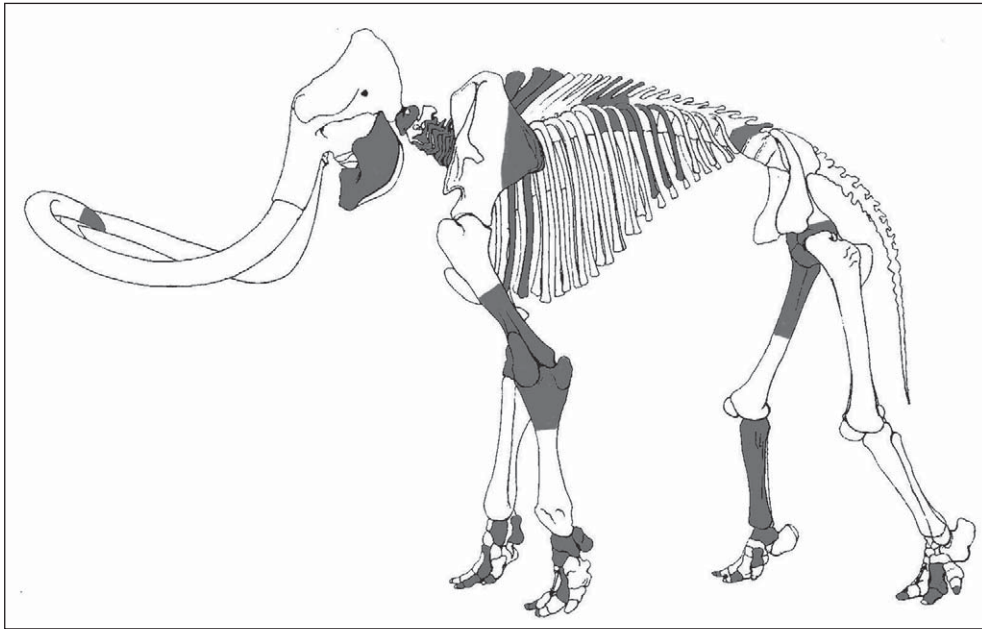


Figure 2. Adult *Mammuthus columbi* material collected at Clark Quarry, Glynn County, GA. Recovered elements are depicted in grey. Figure modified from Osborn (1942).

expanded the available territory for grazing species. In the absence of African Elephants, the grasslands of Africa give way to dense woodland brush (Western 1989) less suitable to the maintenance of healthy populations of smaller grazing organisms.

Most studies of the late Pleistocene vegetation and climate of Georgia's Coastal Plain are in general agreement. Watts' (1983) analysis of southeastern late Pleistocene vegetation indicated a dominance of herbs characteristic of prairies and sandhills. Using fossil pollen data, Williams et al. (2004) described the region as mixed parkland to the south giving way to warm mixed forest to the north. Based on the geomorphology of Coastal Plain rivers, Leigh (2008) noted the presence of braided rivers with broad floodplains containing eolian dunes in an open savanna landscape. Summarizing all available information, Russell et al. (2009) proposed the occurrence of a late Pleistocene "warm thermal enclave" across the southeast with mixed forest and prairie habitats. The presence of mammoths in this late Pleistocene deposit is congruent with these proposed environments.

The mixed vegetative community indicated by Russell et al. (2009) is supported by isotopic analyses of Clark Quarry mammoth and bison material. After adjusting  $\delta^{13}\text{C}$  values for herbivore diet-apatite fractionation (+13.5%; Bocherens et al. 1996, Koch et al. 1991), Clark Quarry mammoth and bison paleodietary reconstructions indicate a mixture of  $\text{C}_3$  and  $\text{C}_4$  plant material. Mammoth material from Clark Quarry has slightly depleted  $\delta^{13}\text{C}$  values compared to those of northern Florida (Koch et al. 1998), which is most likely indicative of increased  $\text{C}_3$  plant abundance at higher latitudes. The isotopic signature of Clark Quarry mammoth material lends support to Haynes' (1991) supposition that elephant and mammoth teeth may be more dietarily flexible than indicated by morphology alone.

The historical significance of the *Mammuthus columbi* material from Clark Quarry is derived from its geographical proximity to the species type locality and the involvement by some of the pioneers of North American paleontology who played a role in the collection and description of the fossil material obtained from the Brunswick Canal in the early to mid-1800s. When both historical and modern maps are analyzed, it is evident that Clark Quarry lies well within the described area from which the type specimen was unearthed. Since the species was named based upon the description of a single molar, the mammoth material from Clark Quarry provides the opportunity to better understand this historically significant species.

#### Acknowledgments

We thank Les and Deborah Clark for granting access to the locality and Josh and Kelly Clark for their assistance at Clark Quarry. We are indebted to Richard Hulbert (Florida Museum of Natural History) for advice throughout the duration of this project. Thank you to Heidi Mead for fossil preparation. For access to collections and historical information we thank Ted Daeschler (Academy of Natural Sciences, Philadelphia), Michael

Brett-Surman (National Museum of Natural History), Jessica Cundiff (Harvard Museum of Comparative Zoology), Kathlyn Smith (Georgia Southern University) and Jennifer Herring (Coastal Georgia Historical Society). We would also like to thank Alexander Cherkinsky (University of Georgia) for radiocarbon analyses. Thank you to Heidi Mead, Dennis Parmley, Ervin Garrison, and René Bobe for useful comments on earlier drafts of this paper.

### Literature Cited

- Agenbroad, L.D. 1984. New World mammoth distributions. Pp. 90–108, *In* P.S. Martin and R.G. Klein (Eds.). *Quaternary Extinctions: A Prehistoric Revolution*. University of Arizona Press, Tucson, AZ. 892 pp.
- Agenbroad, L.D. 2005. North American proboscideans: Mammoths—the state of knowledge 2003. *Quaternary International* 126–128:73–92.
- Bocherens, H., P.L. Koch, A. Mariotti, D. Geraads, and J.J. Jaeger. 1996. Isotopic biogeochemistry ( $^{13}\text{C}$ ,  $^{18}\text{O}$ ) of mammalian enamel from African Pleistocene hominid sites. *PALAIOS* 11:306–318.
- Cate, M.D. 1930. *Our Todays and Yesterdays: A Story of Brunswick and the Coastal Islands*. Revised Edition. Glover Brothers, Brunswick, GA. 302 pp.
- Couper, H. 1842. On fossil bones and shells from the Brunswick Canal, GA. *Proceedings of the Academy of Natural Sciences of Philadelphia* 1:216–217.
- Couper, H. 1846. On the geology of a part of the sea coast of the state of Georgia; with a description of the fossil remains of the megatherium, mastodon, and other contemporaneous Mammalia and fossil marine shells, found in the Brunswick Canal and at Skidaway Island. Pp. 25–50, *In* W.B. Hodgson (Ed.). *Memoir on the Megatherium and other Extinct Gigantic Quadrupeds of the Coast of Georgia and its Geologic Features*. Bartlett and Welford, New York, NY. 47 pp.
- Dutrow, B.L. 1977. Preliminary postcranial metric analysis of mammoths from Hot Springs Mammoth site, South Dakota. *Transactions of the Nebraska Academy of Sciences and Affiliated Societies* 4:223–227.
- Fairchild, H.L. 1887. *A history of the New York Academy of Sciences, formerly the Lyceum of Natural History*. Privately published. New York, NY. 190 pp.
- Falconer, H. 1857. On the species of mastodon and elephant occurring in the fossil state of Great Britain. *Quarterly Journal of the Geological Society of London* 13:307–360.
- Hails, J.R., and J.H. Hoyt. 1969. An appraisal of the evolution of the lower Atlantic Coastal Plain of Georgia, USA. *Transactions of the Institute of British Geographers* 46:53–68.
- Harlan, R. 1842. Meeting for business, July 12, 1842. *Proceedings of the Academy of Natural Sciences of Philadelphia* 1:189.
- Hay, O.P. 1923. *The Pleistocene of North America and its vertebrated animals from the states east of the Mississippi river and the Canadian provinces east of longitude 95°*. Carnegie Institution of Washington Publication 322:1–499.
- Haynes, G. 1991. *Mammoths, Mastodonts, and Elephants: Biology, Behavior, and the Fossil Record*. Cambridge University Press, New York, NY. 413 pp.
- Haynes, G. 2002. The catastrophic extinction of North American mammoths and mastodonts. *World Archaeology* 33:391–416.
- Hodgson, W.B. 1846. *Memoir on the Megatherium and Other Extinct Gigantic Quadrupeds of the Coast of Georgia with Observation on its Geologic Features*. Bartlett and Welford, New York, NY. 47 pp.



- Huddlestun, P.F. 1988. A revision of the lithostratigraphic units of the Coastal Plain of Georgia, the Miocene through the Holocene. *Bulletin of the Georgia Geological Survey* 104:1–162.
- Hulbert, R.C., and A.E. Pratt. 1998. New Pleistocene (Rancholabrean) vertebrate faunas from Coastal Georgia. *Journal of Vertebrate Paleontology* 18:412–429.
- Hurst, V.J. 1957. Prehistoric vertebrates of the Georgia coast. *Georgia Mineral Newsletter* 10:77–93.
- Koch, P.L., A.K. Behrensmeyer, and M.L. Fogel. 1991. The isotopic ecology of plants and animals in Amboseli National Park, Kenya. *Annual Report of the Director Geological Laboratory, Washington, DC*. Pp. 163–171.
- Koch, P.L., K.A. Hoppe, and S.D. Webb. 1998. The isotopic ecology of late Pleistocene mammals in North America Part 1. Florida. *Chemical Geology* 152:119–138.
- Kurtén, B., and E. Anderson. 1980. *Pleistocene Mammals of North America*. Columbia University Press, New York, NY. 442 pp.
- Laws, R.M. 1966. Age criteria for the African Elephant. *East African Wildlife Journal* 4:1–37.
- Leidy, J. 1853. Memoir on the extinct species of American ox. *Smithsonian Contributions to Knowledge* 5:1–20.
- Leigh, D.S. 2008. Late Quaternary climates and river channels of the Atlantic Coastal Plain, Southeastern USA. *Geomorphology* 101:90–108.
- Lipps, E.L., R.W. Purdy, and R.A. Martin. 1988. An annotated bibliography of the Pleistocene vertebrates of Georgia. *Georgia Journal of Science* 25:113–119.
- Lyell, C. 1846. On the newer deposits of the southern states of North America. *Quarterly Journal of the Geological Society* 2:405–410
- Lyell, C. 1849. *A Second Visit to the United States of North America*. Vol. 1. Harper and Brothers, New York, NY. 273 pp.
- Maglio, V.J. 1973. Origin and evolution of the Elephantidae. *Transactions of the American Philosophical Society* 63:1–149.
- Markewich, H.W., C. M. Hacke, and P.F. Huddlestun. 1992. Emergent Pliocene and Pleistocene sediments of southeastern Georgia: An anomalous, fossil-poor, clastic section. Pp. 173–189, *In* C.H. Fletcher and J.F. Wehmiller (Eds.). *Quaternary Coasts of the United States: Marine and Lacustrine Systems*. Society for Sedimentary Geology, Tulsa, OK. 450 pp.
- Mead, A.J., R.B. Bahn, R.M. Chandler and D. Parmley. 2006. Preliminary comments on the Pleistocene vertebrate fauna from Clark Quarry, Brunswick, GA. *Current Research in the Pleistocene* 23:174–176.
- Osborn, H.F. 1942. *Proboscidea: A Monograph on the Discovery, Evolution, Migration, and Extinction of the Mastodonts and Elephants of the World*. Vol II. Stegodontia, Elephantoidae. American Museum Press, New York, NY. 870 pp.
- Russell, D.A., F.J. Rich, V. Schneider, and J. Lynch-Stieglitz. 2009. A warm thermal enclave in the Late Pleistocene of the southeastern United States. *Biological Reviews* 84:173–202.
- Shoshani, J., and P. Tassy. 1996. *The Proboscidea: Evolution and Paleoecology of the Elephants and Their Relatives*. Oxford University Press, New York, NY. 472 pp.
- Voorhies, M.R. 1971. The Watkins Quarry: A new Late Pleistocene mammal locality in Glynn County, Georgia. *Bulletin of the Georgia Academy of Sciences* 29:128.

- Voorhies, M.R. 1974. Pleistocene vertebrates with boreal affinities in the Georgia Piedmont. *Quaternary Research* 4:85–93.
- Watts, W.A. 1983. Vegetational history of the eastern United States 25,000 to 10,000 years ago. Pp. 294–310, *In* H.E. Wright and S.C. Porter (Eds.). *Late-Quaternary Environments of the United States, Volume 1, The Late Pleistocene*. University of Minnesota Press, Minneapolis, MN. 424 pp.
- Western, D. 1989. The ecological role of elephants in Africa. *Pachyderm* 12:43–46.
- Williams, J.W., B.N. Shuman, T. Webb, P.J. Bartlein, and P.L. Leduc. 2004. Late-Quaternary vegetation dynamics in North America: Scaling from taxa to biomes. *Ecological Monographs* 74:309–334.
- Wilson, L.G. 1998. *Lyell in America, Transatlantic Geology, 1841–1853*. Johns Hopkins University Press, Baltimore, MD. 429 pp.