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LATE PLEISTOCENE RODENTS FROM CLARK QUARRY, A VERTEBRATE FOSSIL LOCALITY IN SOUTHASTERN GEORGIA

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Recommended Citation

Rhinehart, Parker, "LATE PLEISTOCENE RODENTS FROM CLARK QUARRY, A VERTEBRATE FOSSIL LOCALITY IN SOUTHASTERN GEORGIA" (2021). Biology Theses. 18. [https://kb.gcsu.edu/biology/18](https://kb.gcsu.edu/biology/18?utm_source=kb.gcsu.edu%2Fbiology%2F18&utm_medium=PDF&utm_campaign=PDFCoverPages)

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LATE PLEISTOCENE RODENTS FROM CLARK QUARRY, A VERTEBRATE FOSSIL LOCALITY IN SOUTHEASTERN GEORGIA

by

PARKER DAVID RHINEHART

B.S., Georgia College & State University, 2019

A Thesis Submitted to the Graduate Faculty of Georgia College & State University in

Partial Fulfillment of the Requirements for the Degree

MASTER OF SCIENCE

Milledgeville, GA

2021

Georgia College & State University Department of Biological and Environmental Sciences College of Arts and Sciences

We hereby approve the thesis of

Late Pleistocene Rodents from Clark Quarry, a Vertebrate Fossil Locality in Southeastern Georgia

Parker David Rhinehart

Candidate for the degree of Master of Science

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PREFACE

This thesis has been written in journal format and conforms to the style appropriate to my discipline. This manuscript will be submitted for publication in the Eastern Paleontologist, a peer reviewed interdisciplinary scientific journal, and therefore reflects the required formatting for this publication. This thesis does not contain a list of tables or a list of figures since these are not included in the submission directions for contributors to this journal. Figures and tables follow the text of the manuscript as required by the Eastern Paleontologist and this thesis committee.

LATE PLEISTOCENE RODENTS FROM CLARK QUARRY, A VERTEBRATE FOSSIL LOCALITY IN SOUTHEASTERN GEORGIA

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Abstract

Clark Quarry is a Late Pleistocene fossil locality near Brunswick, GA, United States with a diverse vertebrate fauna. Morphological descriptions of *Mammuthus columbi* (Columbian Mammoth), snakes, amphibians, and birds from Clark Quarry have previously been completed along with a stable isotope analysis of *M. columbi* and *Bison latifrons* (Long-horned Bison) enamel. Herein, the rodent fauna is described using primarily teeth recovered by screen-washing quarry sediment. Nine rodent taxa have been identified, two of which are the extinct species *Synaptomys australis* (Florida Bog Lemming) and *Neochoerus aesopi* (Late Pleistocene Capybara)*.* Of the remaining seven taxa, *Erethizon dorsatum* (North American Porcupine) and *Neofiber alleni* (Round-tailed Mustkrat) are extralimital compared to modern distributions. This is the first reported occurrence of *Reithrodontomys humulis* (Eastern Harvest Mouse) and *Erethizon dorsatum* from the Late Pleistocene of Georgia. The rodent fauna of Clark Quarry suggests a mostly open, grass-dominated environment with vegetated aquatic habitats nearby. This paleoenvironmental assessment agrees with previous paleoecological studies of *M. columbi*, *B. latifrons*, snakes, and birds from Clark Quarry.

Key Words: Rodents, Fossils, Pleistocene, Rancholabrean, Southeast, Georgia

Introduction

The Pleistocene epoch $\left(\frac{2.6 \text{ mya}-10 \text{ ka}}{2.6 \text{ mya}}\right)$ was marked by cyclical glacial and interglacial periods as evidenced from stable isotope data from ice core analyses in Antarctica (Lambert et al. 2008). The Late Pleistocene $\left(\sim 125-10 \text{ ka}\right)$ is noted for the decline of the North American megafauna triggering a cascade of changes in plant and fungal communities (Gill et al. 2009). Large mammals such as *Mammuthus columbi* Falconer (Columbian Mammoth) and *Bison latifrons* Harlan (Long-horned Bison) are some of the well-studied species that became extinct during this time (Bell et al. 2004). Globally, by the end of the Late Pleistocene, 97 of more than 150 of the world's megafauna genera were gone (Barnosky et al. 2004). The Late Pleistocene is of great interest primarily due to its temporal proximity to present day and its implications for early human distribution in North America (Bourgeon et al. 2017). The Late Pleistocene climatic fluctuations are also important for their influences on the distribution patterns of many modern mammal and plant communities (Faith and Surovell 2009, Koch and Barnosky 2006). Although many smaller scale glacial advances and recessions occurred during the Late Pleistocene, there were two main glacial advances, the latter reached the Last Glacial Maximum (LGM) at around 21,000 years ago (Mix et al. 2001). During this time, sea level was 113-133 m lower than modern sea level, exposing large portions of the continental shelf, especially in the southeastern United States (Spratt and Lisiecki 2016).

The majority of Pleistocene vertebrate fossil localities previously described in the southeastern United States are found in Florida and South Carolina (Bentley et al. 1994, Boessenecker et al. 2018, Kurtén and Anderson 1980, McDonald et al. 1996, Ray and Sanders 1984, Roth and Laerm 1980, Sanders 2002). By comparison, Late Pleistocene sites in Georgia are less common with only eight published sites found in the state. The most diverse Late

Pleistocene mammal fauna in Georgia is from Ladds Quarry in Bartow County and it included marsupials, insectivores, chiropterans, xenarthrans, lagomorph, rodents, carnivores, and ungulates (Ray 1967). Four sites in Chatham County along coastal Georgia (Isle of Hope, Mayfair, Jones Girls, and Porters Pit) produced marsupials, xenarthrans, insectivores, carnivores, rodents, lagomorphs, ungulates, and proboscideans (see table 1 of Hulbert and Pratt 1998). Watkins Quarry in Glynn County contained marsupials, xenarthrans, perissodactyls, artiodactyls, and proboscideans (Voorhies 1971). Little Kettle Creek in Wilkes County produced rodents, proboscideans, and ungulates (Voorhies 1974).

The focus of the current study is a survey of the rodents from a more recently described fossil locality named Clark Quarry (hereafter: CQ). The fossil site was discovered on private land in Glynn County (southeast GA) near Brunswick, GA in 2001 (Mead and Spell 2002, Mead et al. 2006; see figure 1 of Patterson et al. 2012). A large collection of amphibian, reptilian, avian, and mammalian fossils have been recovered at the site along with thousands of unreported fish and aquatic invertebrate fossils (Mead et al. 2006). The most thorough description of the locality, including a discussion of the historical significance of the area surrounding the quarry, is found in Patterson et al. (2012). The site is distinguished by its proximity to the Brunswick-Altamaha Canal which, when constructed in 1836-1854, produced a proboscidean molar that was given to Charles Lyell by J. Hamilton Couper (Lyell 1849). This tooth was later identified as the type specimen for *Elephas columbi* (Falconer 1857). The exact location of this fossil's recovery is unknown. However, Patterson et al. (2012) deduced that the type specimen was recovered in close proximity of CQ.

The CQ sediments likely represent a more recent cut-and-fill deposit within the Princess Anne Terrace of the Satilla Formation (Patterson et al. 2012). At the time of deposition, the site

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would have been roughly 100 km inland with sea level approximately 100 m lower due to the relatively flat topography of the southeastern Coastal Plain (Spratt and Lisiecki 2016). Radiocarbon dates derived from *Bison latifrons* and *Mammuthus columbi* teeth indicate an age of 19,840-22,240 radiocarbon years before present (see table 1 of Patterson et al. 2012). The cooccurrence of *Mammuthus columbi* and *Bison latifrons* at CQ indicates the Rancholabrean North American Land Mammal Age (250-12 ka) for the fauna (Bell et al. 2004).

The amphibians and reptiles from CQ have been previously described (Clark 2009a, Parmley et al. 2007, Parmley et al. 2020). The presence of *Amphiuma* Garden (Amphiuma) indicates that a permanent freshwater habitat was readily available during the time of deposition (Parmley et al. 2007). The other four amphibians and 13 reptiles described from CQ were well suited to swamp and marsh habitat as multiple species required non-ephemeral freshwater (Parmley et al. 2020). The avian fauna suggests an edge of woodlands and grasslands near a wetland environment (Clark 2009b). The initial description of the mammalian fauna, which is dominated by *Mammuthus columbi* and *Bison latifrons,* indicated species that would inhabit a riverine system that flows through an open parkland (Bahn 2006). Patterson et al. (2012) described CQ *Mammuthus columbi* morphology and paleoecology and suggested that *Mammuthus* would have converted woodland bush and wooded savannas into more open grasslands, similar to the role of the modern African Elephant. An analysis of carbon and oxygen isotopes from *Mammuthus columbi* and *Bison latifrons* tooth enamel suggested that the large herbivores shifted between browsing and grazing seasonally (Noble et al. 2020). This could be due to migration patterns of the megafauna or by seasonal changes in vegetation growth.

Rodents can be difficult to study due to their small size and difficulty in collecting but are important when interpreting the paleoenvironment of a fossil locality. The vertebrate fauna of a

particular time period is often used as an indicator of the paleoenvironmental conditions at the time of deposition. Rodent fossils are perhaps of greater importance as they are generally deposited in the area in which the organism lived. Rodents are mostly small and inhabit extremely small home ranges, for example adult males of *Sigmodon hispidus* use 0.35 ha (Layne 1974). Fossil specimens are therefore likely to have inhabited exclusively the area of deposition and can offer greater insight into the paleoenvironmental conditions. Larger mammals like *Mammuthus columbi* or *Bison latifrons* may make large migrations which could create a disconnect between the environment they typically lived within and that represented by the deposits in which their bones were buried (Behrensmeyer et al. 2000). Here I provide the first description of the rodent fauna found at Clark Quarry.

Materials and Methods

Microfossils were collected from the CQ sediment following the wet screen washing methods of Hibbard (1949). The concentrate was sorted under a Fiber-Lite Model FL 180 microscope. Unless otherwise specified, all fossils listed here are housed in the Georgia College Vertebrate Paleontology (GCVP) collection. All taxa were identified based on morphological comparison to modern specimens housed in the Georgia College Mammal (GCM) collections, Georgia Museum of Natural History (GMNH) collections, and based on relevant information in published literature. Fossils were identified to the lowest practical taxon identifier.

For the purposes of this text: $I/\mathbf{i} = \text{incisor}$; $C/\mathbf{c} = \text{canine}$; $P/\mathbf{p} = \text{premolar}$; and $M/\mathbf{m} =$ molar. Upper teeth are indicated by capital letters and lower teeth by lower case letters. All measurements are given in millimeters and taken with Chicago Brand digital calipers.

All photographs were taken by the author using a Visionary Digital BK Plus imaging system with a mounted Canon EOS 5DSR. The image stacking was completed using Zerene Stacker Version 1.04 and editing was performed in Adobe Photoshop 13.0 provided by Georgia College & State University.

Systematic Paleontology

Class Mammalia Linnaeus Order Rodentia Bowdich Family Sciuridae Gray Genus *Glaucomys* Thomas *Glaucomys volans* Linnaeus 1758 (Figure 1)

Material- One proximal phalanx (GCVP 19981).

Remarks- GCVP 19981 is identified as a hindfoot proximal phalanx of *Glaucomys volans* Linnaeus (Southern Flying Squirrel) by the size (5.13 mm) and morphology. The proximal and distal articular surfaces are well defined along with ventral elevated tendon attachment sites (entheses) (Figure 1). The elevated tendon attachment sites are prominent in other climbing sciurids such as *Sciurus carolinensis* Gmelin (Eastern Gray Squirrel) and *Tamias striatus* Linnaeus (Eastern Chipmunk), but these species do not correspond in size with the CQ specimen. *Glaucomys volans* is an arboreal gliding species that ranges across the eastern US. It was previously recorded in a Late Pleistocene locality in Georgia (Hulbert and Pratt 1998).

Family Cricetidae Fischer von Waldheim

Subfamily Sigmodontinae Wagner

Genus *Oryzomys* Hibbard

Oryzomys palustris Harlan 1837 (Figure 2 and 3)

Material- Two left I1 (GCVP 17869; 17894); one right I1 (GCVP 17890); one right I1 fragment (GCVP 17872); one left M1 (GCVP 17866); one left M2 (GCVP 17874); two right i1 fragments (GCVP 17873, 19957); three left m1 (GCVP 17864, 17865, 17867); two right m1 (GCVP 17863, 17870); one left m2 (GCVP 17862); one right m2 (GCVP 17868).

Remarks- These incisors are identified as *Oryzomys* based on diameter, curvature, and lack of a groove on the anterior surface (Figure 2A, B; Table 1). The fossil I1s have an average anteriorposterior diameter (APD) of 1.76 mm (1.64-1.96) and a medial-lateral diameter (MLD) of 0.85 mm (0.80-0.89). *Oryzomys* molars display cusps, styles, or tubercules on the occlusal surface arranged in longitudinal series (Hall 1981). *Oryzomys palustris* Harlan (Marsh Rice Rat) has a molar pattern containing clear cusps and valleys (Figure 3). *Oryzomys* maxillary molars have larger lingual cusps, and the mandibular molars have larger buccal cusps (Park 1974). *Oryzomys palustris* molars are similar in form to *Peromyscus* but are 20% larger and have a wider median valley. *Peromyscus* also shows sharper angles on the lingual cusps of the lower molars. Based on these characteristics, the CQ teeth are identified as *O. palustris*. *Oryzomys palustris* is known from the Late Pleistocene to recent (Kurtén and Anderson 1980).

c.f. *Oryzomys palustris*

Material- One left I1 (GCVP 19959); one right i1 (GCVP 19974); one partial femur (GCVP 17956); one left astragalus (GCVP 17980 [Figure 4B]).

Remarks- These specimens match *Oryzomys palustris* in size and morphology but displays no distinctive characteristics to definitively assign them to this species.

> Genus *Sigmodon* Say and Ord *Sigmodon hispidus* Say and Ord 1825 (Figure 5, 6, and 7)

Material- Two left I1 (GCVP 17691; 19936); one right I1 (GCVP 17689); three left M1 (GCVP 17675; 17678; 19983); one left M1 with partial maxilla (GCVP 17695); six left M2 (GCVP 17676-17677; 17680; 17684; 17686; 17688); one left M3 fragment (GCVP 17673); three left i1 (GCVP 17692; 17694; 19984); six right i1 (GCVP 17693; 17696-17697; 17897; 19940; 19951); one left m1 with partial dentary (GCVP 17679); one right m1 and m2 with partial dentary (GCVP 17674); one left m2 (GCVP 17690); three left m3 (GCVP 17672; 17681; 17685); three right m3 (GCVP 17682-17683; 17687).

Remarks- All incisors are identified as *Sigmodon* based on size, curvature, and lack of grooves on the anterior surface of the upper incisors (Figure 5; Table 1). The fossil i1s have an average APD of 1.69 mm (1.58-1.86) and an average MLD of 1.35 mm (1.01-1.47). All cheek teeth are identified as *Sigmodon* based on the distinguishing S-shape occlusal pattern (Figure 6 and 7) of the molars (Nowak 1999). *Sigmodon hispidus* Say and Ord (Hispid Cotton Rat) is commonly reported throughout the United States, including Georgia, in Late Pleistocene fossil sites (Kurtén and Anderson 1980). *Sigmodon hispidus* is the only species from the genus found in the modern CQ area, all others occurring in the Midwest of North America and Mexico (Hall 1981).

c.f. *Sigmodon hispidus* Say and Ord 1825

Material- One partial left I1 (GCVP 19943); one palate fragment (GCVP 19962); one left proximal scapula fragment (GCVP 19931); one scapula fragment (GCVP 17984); two right humeri (GCVP 19963-19964); one partial distal humerus (GCVP 19933); one right humerus fragment (GCVP 17985); two right ulna fragments (GCVP 17990; 19948); three metacarpals (GCVP 17992; 19946; 19968); one forefoot proximal phalanx (GCVP 19966); three right tibia fragments (GCVP 17998-17999; 19949); one distal tibia fragment (GCVP 19961); one forefoot proximal phalanx (GCVP 19932); one left astragalus (GCVP 17981 [Figure 4D]); one right

astragalus (GCVP 17977); one first metatarsal (GCVP 17991); three hindfoot proximal phalanges (GCVP 19944; 19952; 19967); one hindfoot medial phalanx (GCVP 19942). **Remarks-** All cranial and postcranial material is identified as *Sigmodon* based on size and morphology compared to modern specimens. Due to possible intraspecific variation, they cannot be definitively assigned to this species.

Subfamily Arvicolinae Gray

Genus *Neofiber* True

Neofiber alleni True 1884 (Figure 8)

Material- One left I1 (GCVP 17851); four right I1 (GCVP 17849; 17857; 19971; 19979); one right M3 (GCVP 17850); one palate fragment (GCVP 17957); two left i1 (GCVP 17883; 19970); four right i1 (GCVP 17881-17882; 17884-17885); one right m1 fragment (GCVP 17852); one right dentary fragment (GCVP 19979); one right femur (GCVP 19965).

Remarks- *Neofiber* incisors are distinguished by their size compared to other species in the same size range (Figure 8A, B)*.* Rodents in the size range of *Neofiber alleni* True (Round-tailed Muskrat) include *Neotoma floridana* Ord (Eastern Woodrat), *Sciurus carolinensis,* and *Glaucomys volans* (Table 2). Neofiber incisors are much smaller than *Ondatra zibethicus* (Table 4). *Neofiber* has a similar molar occlusal pattern to *Ondatra* but has rootless teeth (Birkenholz 1972). *Neofiber* molars show reentrant angles that cross the midline in the maxillary molars and angles that meet the midline in the mandibular molars (Figure 8C). The femur (GCVP 19965; Figure 8D, E) is identified based on comparison with fossil specimens (see figure 5C, D in Harrington 2015). *Neofiber alleni* is the only extant member of the genus and is no longer native to the CQ region. Its modern range is restricted to Florida and southernmost Georgia. Fossil *N.*

alleni have been found in several sites in Florida (Kurtén and Anderson 1980) and are reported from Ladds Quarry (Ray 1967) and the Isle of Hope Site (Hulbert and Pratt 1998) in Georgia.

c.f. *Neofiber alleni* True 1884

Material- One dentary fragment (GCVP 17951).

Remarks- This specimen matches *Neofiber alleni* in size and morphology but cannot be definitively assigned to this species.

Genus *Synaptomys* Baird

Synaptomys australis Simpson 1928 (Figure 2, 5, and 9)

Material- Six left I1 (GCVP 17650; 17652; 17853; 17856; 17895; 19945); seven right I1 (GCVP 17646; 17649; 17657; 17665; 17854-17855; 19938; 19956); five left M1 (GCVP 17639- 17640; 17645; 17663; 19937); two right M1 (GCVP 17653); two left M2 (GCVP 17638; 17643); one right M2 (GCVP 17654); one right M2 fragment (GCVP 19950); three left M3 (GCVP 17644; 17669; 19939); two right M3 (GCVP 17952; 19958); one right M3 fragment (GCVP 19935); one maxillary fragment (GCVP 19969); one right i1 (GCVP 17648); two left m1 (GCVP 17637; 17670; 19977); four right m1 (GCVP 17641-17642; 17662; 17666); one partial right m1 (GCVP 17656); two left m2 (GCVP 17651; 17668); two right m2 (GCVP 17636; 17955); one right m2 fragment (GCVP 19975); four left m3 (GCVP 17635; 17647; 17658; 17660); three right m3 (GCVP 17661; 17667; 17671); one molar fragment (GCVP 17655); one dentary fragment (GCVP 19976); one complete left dentary (GCVP 17973).

Remarks- *Synaptomys* is distinguished by a prominent groove on the anterior surface of the upper incisors (Figure 2C, D), size (Table 1 and 3) and shape of lower incisors (Figure 5C, D), and upper and lower hypsodont cheek teeth with closed triangles on the labial side and welldeveloped reentrant angles (Figure 9D, E, F) on the lower molars (Linzey 1983). The fossil I1s have an average APD of 1.81 mm (1.54-2.20) and an average MLD of 1.64 mm (1.42-1.94). The referred i1s have an average APD of 1.88 mm (1.79-1.97) and an average MLD of 1.59 mm (1.37-1.81). *Synaptomys australis* Simpson (Florida Bog Lemming) of the Late Pleistocene is a larger fossil species compared to the recent *Synatpomys cooperi* Baird (Southern Bog Lemming) (Hibbard 1955, Hulbert and Pratt 1998, Martin et al. 2003, Olsen 1958, Simpson 1928). Accordingly, the *Synaptomys* specimens collected from CQ are 35% larger on average than the extant *S. cooperi* (Table 1)*.* The CQ material includes one complete dentary (GCVP 17973; Figure 9) that matches sizes of *S. australis* in literature (Hibbard 1955, Olsen 1958, Simpson 1928). Guilday et al. (1978) questioned the validity of *S. australis* and suggested that there may have been an increasing size gradient in *Synaptomys cooperi* from its northernmost reaches in Pennsylvania to its southernmost in Florida during the Late Pleistocene. *Zapus hudsonis* Zimmerman (Meadow Jumping Mouse) and *Napaeozapus insignis* Miller (Woodland Jumping Mouse) are notably smaller than *S. australis* even though both contain a similar anterior groove. In *Zapus* and *Napaeozapus* the groove is similarly located, but deeper and more prominent. *Synaptomys australis* has been reported from Florida (Hulbert and Pratt 1998, Martin et al. 2003, Olsen 1958, Simpson 1928) and Kansas (Hibbard 1955).

c.f. *Synaptomys australis*

Material- Three dentary fragments (GCVP 17664; 17953; 19973); two right astragali (GCVP 17978; 17979 [Figure 4C]); one right calcaneus (GCVP 17975).

Remarks- These specimens match *Synaptomys australis* in size and morphology but contain no distinctive characteristics to match them to this species.

Subfamily Neotominae Merriam

Genus *Peromyscus* Gloger

Peromyscus sp. indet. (Figure 2E, F and 5E, F)

Material- One left I1 (GCVP 17889); five right I1 (GCVP 17860; 17886; 17888; 17891; 19954); three left i1 (GCVP 17887; 17893; 19986); one right i1 (GCVP 17892).

Remarks- *Peromyscus* incisors are identified by diameter, curvature, and lack of grooves on the anterior surface (Figure 2E, F and 5E, F; Table 1). The fossil I1s have an average APD of 1.23 mm (1.11-1.35) and an average MLD of 0.75 mm (0.66-0.84). The CQ i1s have an average APD of 1.22 mm (1.02-1.37) and an average MLD of 0.67 mm (0.57-0.73). *Peromyscus* is relatively small, and only *Reithrodontomys* is smaller in Georgia. *Peromyscus* is a widespread genus of deermice that has bunodont molars and smooth incisors. *Peromyscus* contains 56 extant species, four of which are found in Georgia: *P. leucopus* Rafinesque (White-footed Deermouse)*, P. maniculatus* Wagner (North American Deermouse), *P. gossypinus* Le Conte (Cotton Deermouse)*, P. polionotus* Wagner (Oldfield Deermouse). *Ochrotomys nuttalli* Harlan (Golden Mouse) is a close relative of *Peromyscus*, and after many taxonomic adjustments, it was placed into a separate genus by Packard (1969). *Ochrotomys nuttalli* is morphologically indistinct from *Peromyscus* aside from the position of the posterior palatine foramina. Lacking a skull with a palate intact, we assign these specimens to *Peromyscus* sp. Only *P. gossypinus* and *P. polionotus* are found along the coast of Georgia today and each is identified to species by characteristics requiring the entire body of the individual (Hall 1981). However, some have attempted to classify the different species based on the mesoloph(id) or mesostyle(id) of the upper and lower first and second molars but came to no definite conclusions (Hooper 1957, Pinkham 1971). Ray (1967) subdivided other *Peromyscus* specimens from Ladds Quarry based on molar lengths. The *Peromyscus* material from CQ is all non-molar material. *Peromyscus* is common in Rancholabrean fossil sites across North America (Kurtén and Anderson 1980).

c.f. *Peromyscus* sp. indet.

Material- One partial left I1 (GCVP 17993); three partial right I1 (GCVP 19955; 19960; 19982); one partial proximal right humerus (GCVP 19941); one right distal humerus fragment (GCVP 19972); one left femur (GCVP 19985); one distal tibia fragment (GCVP 17988); two left astragali (GCVP 17982; 17989); one right astragalus (GCVP 17983 [Figure 4A]); four metatarsals (GCVP 17994-17997).

Remarks- *Peromyscus* skeletal material is identified based on comparison to modern specimens from the GCM collections. These specimens match *Peromyscus* in size and morphology but contain no distinctive characteristics to definitively identify them to this species.

Genus *Reithrodontomys* Giglioli

Reithrodontomys humulis Audubon and Bachman 1841 (Figure 2G, H and 5G, H) **Material-** Two left I1 (GCVP 17859; 17898); one right I1 (GCVP 17879); four left i1 (GCVP 17861; 17871; 17875; 17899); one left i1 with attached partial dentary (GCVP 17858); three right i1 (GCVP 17876-17878).

Remarks- *Reithrodontomys* upper incisors have a prominent groove on the midline of the anterior surface (Figure 2G, H). Lower incisors are identified based on diameter and curvature (Figure 5G, H; Table 1). The fossil I1s have an average APD of 1.04 mm (0.94-1.10) and an average MLD of 0.55 mm (0.55-0.56). The fossil i1s have an average APD of 1.09 mm (0.85- 1.29) and an average MLD of 0.52 mm (0.46-0.58). The molars are bunodont and similar to other species in the subfamily Neotominae. *Reithrodontomys* is distinguished as the smallest representative of the subfamily and its teeth are markedly smaller than the next largest member in the southeast, *Peromyscus* sp., which is approximately 23% larger than *R. humulis*. *Reithrodontomys* is a genus of harvest mice found across North America. *Reithrodontomys* is

also notably smaller than *Zapus hudsonis* and *Napaeozapus insignis* even though both contain a similar anterior groove. In *Zapus* and *Napaeozapus* the groove is shallower and located more laterally than *Reithrodontomys*. The only member of the genus found in the modern CQ area is *R. humulis* (Eastern Harvest Mouse). *Reithrodontomys humulis* is known from the Irvingtonian to the present and has been found in fossil localities in Florida during the Rancholabrean. However, this represents the first record of *Reithrodontomys humulis* from the Rancholabrean of Georgia (Kurtén and Anderson 1980). It is unsurprising that *R. humulis* has not been previously reported from the Late Pleistocene of Georgia, as the common practice, and that which was followed here, of screen washing sediment to allow for easier gathering of fossils (Hibbard 1949) often allows isolated *Reithrodontomys* teeth to fall through the screen (Ruez 2000). Ruez (2000) examined a *R. humulis* mandible from the Late Pleistocene of Florida and re-identified it as *R. fulvescens* (Fulvous Harvest Mouse). The distinction was made by comparing the molar row length and occlusal surface morphology of the m3. As there is no molar material from *Reithrodontomys* in this study and with a lack of other evidence, we refer to these specimens as *R. humulis*.

c.f. *Reithrodontomys humulis* Audubon and Bachman 1841

Material- one right humerus fragment (GCVP 17987); one left femur (GCVP 19985); one head of right femur (GCVP 19947); one distal femur epiphysial cap (GCVP 19934); one distal tibia fragment (GCVP 19953).

Remarks- *Reithrodontomys humulis* skeletal material is identified based on comparison to modern specimens from the GCM collections. These specimens match *R. humulis* in size and morphology but contain no distinctive characteristics to definitively identify them to this species.

Family Erethizontidae Bonaparte

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Genus *Erethizon* Cuvier

c.f. *Erethizon dorsatum* Linnaeus 1758 (Figure 10)

Material- One partial right i1 (GCVP 17896).

Remarks- This isolated partial i1 is identified as *Erethizon dorsatum* Linnaeus (North American Porcupine) based on relative size, morphology of the thegosis facet, and position of the lateral and medial enamel-dentine boundaries. Rodents in the size range of *E. dorsatum* include *Marmota monax* Linnaeus (Groundhog or Woodchuck), *Ondatra zibethicus* Linnaeus (Muskrat), and *Castor canadensis* Kuhl (American Beaver) (Table 4). The CQ specimen is closest in medial-lateral diameter to *M*. *monax*. However, the anterior-posterior diameter of the CQ specimen is closer to *O. zibethicus*. The specimen is smaller overall than *E. dorsatum* but lies just outside of the MLD size range, a 0.19 mm difference between the smallest *E. dorsatum* and the CQ fossil. The CQ specimen displays thegosis facet morphology matching *E. dorsatum* (Figure 10B, C)*.* The occlusion of *M. monax* incisors produces a thegosis facet with a distinct shelf near the base of the occlusal surface. The lateral enamel-dentine junction on the CQ specimen is more posteriorly positioned as in *E. dorsatum* rather than the more anterior position in *O*. *zibethicus* and *M. monax* (Figure 10A). The medial enamel-dentine junction also wraps farther on the Clark Quarry fossil than on *M. monax* or *O. zibethicus*. The CQ specimen also displays a slight groove in the anterior surface of the lower incisor which is also seen in *E. dorsatum* and not *O. zibethicus* or *M. monax* (Figure 10C). *Erethizon dorsatum* has been reported across the Late Pleistocene of North America from numerous fossil sites. Florida contains some records of *E. dorsatum* although Georgia has no reported instances of a Late Pleistocene *E. dorsatum* (Martin 1945; White 1970).

Family Caviidae Gray

Subfamily Hydrochoerinae Gill

Genus *Neochoerus* Hay

Neochoerus aesopi Leidy 1853 (Figure 11)

Material- One left P4 fragment (GCVP 17698); one left M1 fragment (GCVP 19859); one left p4 fragment (GCVP 17699); one left m1 fragment (GCVP 19860); one left m2 fragment (GCVP 19978); one cheek tooth fragment (GCVP 11936).

Remarks- Identifying capybara molars to the subfamily level is easily accomplished as even fragments can display the distinct occlusal patterns (Figure 11). The molars are formed by a prism that is divided by re-entrant folds, or flexi(ids) (Vucetich et al. 2013). Late Pleistocene capybaras have been in phylogenetic flux for the past decade. In an attempt to consolidate the phylogeny, Baskin et al. (2020) synonymized *Neochoerus pinckneyi* Hay (Late Pleistocene Capybara) and *Hydrochoerus holmesi* Simpson (Late Pleistocene Capybara) into a single species *Neochoerus aesopi*. Occlusal morphology of extant *Hydrochoerus hydrochaeris* Linnaeus (Capybara) varies greatly with age. Due to this variation, *Hydrochoerus holmesi* and *N. pinckneyi* cannot be distinguished by occlusal morphology alone (Baskin et al. 2020). Additional fossil capybara (previously labelled *N. pinckneyi*) have been identified from the Late Pleistocene of Georgia (Hulbert and Pratt 1998).

Discussion

The Late Pleistocene glaciations were accompanied by fluctuations in faunal and floral ranges, species richness, and the structure of biomes (Williams et al. 2004). The floral communities in the southeast of North America would have been predominately warm mixed forest (Yann et al. 2013). However, during the LGM it appears there was a warm thermal

enclave that stretched across Georgia (Russell et al. 2009). During this period, prairies developed with the aid of large grazing megafauna such as *M. columbi* (Patterson et al. 2012). The presence of grassland habitats at this time is also supported by the occurrence of braided streams in the Altamaha River valley (Leigh 2008). Eolian dunes and braided stream terraces indicate a dryer climate with seasonally large runoff and high overbank flow within the floodplains (Leigh et al. 2004).

In comparison to the number of rodent taxa described at other Late Pleistocene localities in Georgia, CQ fauna is moderately diverse (Table 5). Ladds Quarry (Ray 1967) has the most diverse collection with 15 rodent taxa and contains several taxa not found at CQ, including *Marmota monax, Tamias aristus* Ray (Late Pleistocene Chipmunk)*, T. striatus, Castor canadensis, Neotoma floridana, Peromyscus maniculatus, P. leucopus, Ondatra zibethicus, Synaptomys cooperi, Microtus* (*Pitymys*) *pinetorum* Le Conte (Woodland Vole)*,* and *Zapus hudsonius* Zimmermann (Meadow Jumping Mouse)*.* The CQ rodent fauna shares only three species with Ladds, *Sigmodon hispidus, Peromyscus* sp.*,* and *Neofiber alleni.* Ray (1967) divided the *Peromyscus* into multiple species based on molar size, possibly inflating the number of species compared to CQ.

Of the four sites reported in Hulbert and Pratt (1998), the Isle of Hope Site, the only site extensively screened for microfossils material, has the highest number of rodent species $(n=11)$ and contains a few taxa not found at CQ, *Sciurus carolinensis, Castor canadensis, Peromyscus polionotus,* and *Microtus pennsylvanicus*. Clark Quarry also has a few taxa not seen at the Isle of Hope Site including *Reithrodontomys humulis, Erethizon dorsatum,* and *Neochoerus pinckneyi* (now *Neochoerus aesopi)*. All other taxa are shared at both sites. The presence of the arboreal *Sciurus carolinensis* indicates a more heavily wooded area as this species requires tree cover.

Microtus pennsylvanicus is also found in modern wooded areas, although rarely (Reich 1981). Mayfair Site has one species, *Castor canadensis,* and the Porters Pit site reported only *Neochoerus pinckneyi*. Both species' modern counterparts occur where aquatic habitats are readily available. Both rodent taxa reported from Mayfair Site and Porters Pit are among the largest rodents from the Rancholabrean and would be more easily found without screen washing.

Little Kettle Creek (Voorhies 1974) produced a small total number of species and only two rodent taxa. The *Synaptomys cooperi* from Little Kettle Creek is notably smaller than the *Synpatomys australis* found at CQ and reported elsewhere. The author debated on assigning *S. borealis,* an extralimital species reported as far south as Tennessee (Kurtén and Anderson 1980), but based on size placed the specimens into *S. cooperi.* The second rodent taxa found was *Clethrionomys* sp., now *Myodes* (Red-backed Voles). All extant species of *Myodes* are extralimital to all but the northernmost edge of Georgia.

The previous studies of the CQ fauna indicate an open parkland habitat (Patterson et al. 2012, Parmley et al. 2020) with riverine influences and associated marshy aquatic habitats (Bahn 2006; Clark 2009a, b; Parmley et al. 2020, Noble et al. 2020). This conclusion is supported by the presence of the large grazers *Mammuthus columbi* and *Bison latifrons* along with the aquatic amphibians, reptiles, and birds (Clark 2009a, Clark 2009b, Parmley et al. 2007, Parmley et al. 2020). As previously mentioned, *M. columbi* would have been instrumental in maintaining the open environment (Patterson et al. 2012). Carbon and oxygen isotope data from *M. columbi* and *B. latifrons* suggests elevated C³ vegetation when compared to data from older glaciations. The serial sampling of the *M. columbi* and *B. latifrons* teeth indicate a latitudinal gradient where more C_3 vegetation is available at higher latitudes (Noble et al. 2020). Using the habitat preference of modern rodents, we can determine the most likely paleoenvironment for CQ (Table 6). *Oryzomys palustris, Reithrodontomys humulis, Peromyscus* sp, *Synaptomys, Neofiber alleni, Erethizon dorsatum* and *Neochoerus aesopi* all support the presence of wetland habitat. *Reithrodontomys humulis, Peromyscus* sp., *Sigmodon hispidus, Neofiber alleni,* and *Neochoerus aesopi* all support the existence of open grassland habitat. The only arboreal species, *Glaucomys volans*, suggests an environment not entirely devoid of tree cover. *Erethizon dorsatum* also suggests some tree cover, preferring hard and softwood forests but with a variable habitat preference.

The modern CQ area contains 12 native species of rodents. Five of these are not found in the CQ sediments, *Castor canadensis, Sciurus carolinensis*, *Sciurus niger* Linnaeus (Eastern Fox Squirrel), *Geomys pinetis* Rafinesque (Southeastern Pocket Gopher), and *Neotoma floridana*. Of these species, *C. canadensis, S. carolinensis,* and *N. floridana* have been reported from other Late Pleistocene fossil sites of Georgia (Table 5). Both species of *Sciurus* indicate a more wooded environment, contrary to the suggested paleoenvironment of CQ. *Glaucomys volans, Oryzomys palustris, Reithrodontomys humulis, Peromyscus gossypinus, Peromyscus polionotus, Ochrotomys nutalli,* and *Sigmodon hispidus* all are present in CQ fossil material and in the modern CQ area. However, the *Peromyscus* species and *Ochrotomys nutalli* are all assigned *Peromyscus* sp. in the CQ specimens.

The CQ rodent fauna enhances our understanding of mammal diversity in the Late Pleistocene of Georgia (Table 5). Notably, some arboreal species such as *Sciurus carolinensis* are absent from CQ material, suggesting the overall sparsity of tree cover. *Tamias striatus* and *T. aristus* are also absent. Modern *T. striatus* inhabit deciduous forest environments. Representatives of *Castor canadensis* and *Castoroides ohioensis* Foster (Giant Beaver) are surprisingly absent although they are reported elsewhere from the Late Pleistocene of Georgia.

Neotoma floridana is also missing from the CQ fauna, although it commonly inhabits grasslands. In *Myodes,* the species of vole that is most likely to inhabit Georgia does not stray far from heavily wooded areas and would not match the suggested CQ habitat. However, other voles reported from Georgia include *Microtus pennsylvanicus* and *Microtus pinetorum*, and CQ is at the edge of the modern range of both of these species. The suggested grassy habitat of CQ would be a suitable habitat for both species. *Zapus hudsonius* is currently extralimital to modern CQ but would be inclined to the grassy habitat suggested by this study. The CQ rodent fauna increases our understanding of the rodent diversity in Georgia during the Late Pleistocene. The nine rodent taxa described here suggest mostly open grassland habitat adjacent to permanent freshwater in this part of southeastern North America at approximately 21,000. Additional studies focusing on palynology should help refine this interpretation.

Acknowledgements

Many thanks are due to my major professor, Dr. Alfred Mead, for accepting me into his lab and assisting me in the creation of this thesis and for constantly reminding that he wisely told me I should have started working harder earlier. He has inspired me to reach further and higher in my academic career and to strive to achieve my dreams. Mrs. Heidi Mead also was instrumental in the creation of the final product of this thesis, especially in training me in the use of the imaging system at Georgia College & State University, and in performing the required fossil preparation for this thesis. Both have treated me as family from the day I joined the Mead lab as a wide-eyed undergraduate and for that I will be forever grateful. My committee members, Dr. Samuel Mutiti, Dr. Dominic DeSantis, and Dr. David Patterson were also essential in the completion of this thesis, from providing edits to giving randomly requested life advice

throughout the years, I am grateful. Too many faculty, staff, and students to name individually are responsible for the collection and sorting of the Clark Quarry fossil material, but the collections manager, Ashley Quinn, certainly deserves special thanks for fossil preparation and specimen management. The research at Clark Quarry has also been supported by several faculty research grants.

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Tables

Table 1. Measurements of modern rodent incisors from *Reithrodontomys humuilis* (Eastern Harvest Mouse)*, Peromyscus* sp. (Deermice), *Oryzomys palustris* (Marsh Rice Rat)*, Synaptomys cooperi* (Southern Bog Lemming)*,* and *Sigmodon hispidus* (Hispid Cotton Rat)*.* APD = anterior-posterior diameter; MLD = medial-lateral diameter. All measurements in mm.

¹I1 average of GCM 3593, 3594, 3595, 3596; i1 average of GCM 3594, 3595, 3596.

² Average of GCM 2123, 2498, 2495, 2500.

³ Average of GCM 33, 51, 345, 2465.

4 I1 average of GMNH 328, 496, 3435, 3436; i1 average of GMNH 328, 329, 496, 3435.

5Average of GCM 62, 76, 114, 501.

Table 2. Incisor measurements of fossil incisors from Late Pleistocene Clark Quarry and modern *Neofiber alleni* (Round-tailed Muskrat), *Neotoma floridana* (Eastern Woodrat), *Sciurus carolinensis* (Eastern Gray Squirrel), and *Glaucomys volans* (Southern Flying Squirrel). APD = anterior-posterior diameter, MLD = medial-lateral diameter. All measurements in mm.

¹I1 average of GCVP 17849, 17851, 17857, 19971, 19980; i1 average of GCVP 17881, 17884, 17885, 19970. 2 I1 average of GMNH 2782, 3201, 3203, 3205, 5179; i1 average of GMNH 2783, 3201, 3203, 3205, 5179.

³Average of GCM 77, 82, 2000, 2480.

⁴Average of GCM 1886, 2248, 2452, 2505.

⁵Average of GCM 6, 32, 807, 2526.

Table 3. Cheek teeth measurements of *Synaptomys australis*. APL = anterior-posterior length. All measurements in

mm. AMNH 23440 (Simpson 1928); UMMP 29749 (Hibbard 1955); FGS V-5700 (Olsen 1958).

*Average of GCVP 17637, 17642, 17662, 17666, 17670, 17973, 19977.

Table 4. Incisor measurements for GCVP 17896 from the Late Pleistocene of Clark Quarry, and modern *Marmota monax* (Groundhog)*, Ondatra zibethicus* (Muskrat), *Erethizon dorsatum* (North American Porcupine), and *Castor canadensis* (American Beaver). APD = anterior-posterior diameter, MLD = medial-lateral diameter. All measurements in mm.

¹ Average of GCM 809, 855, 1882, 2117.

² Average of GCM 849, 852, 1950, 1951.

³ Average of GCM 27, 2061, 2065, 2066.

⁴ Average of GCM 789, 792, 793, 908.

Table 5. Late Pleistocene rodents in Georgia. CQ = Clark Quarry; LQ = Ladds Quarry (Ray 1967); LKC = Little Kettle Creek (Voorhies 1974); WQ = Watkins Quarry (Voorhies 1971); IHS = Isle of Hope Site, MS = Mayfair Site, FS = Fossilossa Site, PP = Porters Pit (Hulbert and Pratt 1998).

Taxon	CQ	LQ	LKC	WQ	IHS	MS	FS	${\rm PP}$
Glaucomys volans	$\mathbf X$				$\mathbf X$			
Sciurus carolinensis					$\mathbf X$			
Tamias aristus		$\mathbf X$						
Tamias striatus		$\mathbf X$						
Marmota monax		$\mathbf X$						
Castor canadensis		$\boldsymbol{\mathrm{X}}$			$\mathbf X$	$\mathbf X$		
Oryzomys palustris	$\mathbf X$	$\mathbf X$			$\mathbf X$			
Sigmodon hispidus	$\mathbf X$	$\mathbf X$			$\mathbf X$			
Neotoma floridana		$\mathbf X$			$\mathbf X$			
Peromyscus polionotus					$\mathbf X$			
Peromyscus maniculatus		$\boldsymbol{\mathrm{X}}$						
Peromyscus leucopus		$\mathbf X$						
Peromyscus sp.	$\mathbf X$	$\mathbf X$						
Reithrodontomys humulis	$\mathbf X$							
Neofiber alleni	$\mathbf X$	$\mathbf X$			$\mathbf X$			
Ondatra zibethicus		X						
Synaptomys australis	$\boldsymbol{\mathrm{X}}$				$\mathbf X$			
Synaptomys cooperi		$\boldsymbol{\mathrm{X}}$	$\mathbf X$					
Microtus pennsylvanicus					$\mathbf X$			
Microtus (Pitymys) pinetorum		X			$\mathbf X$			
Clethrionomys (Myodes) sp.			$\mathbf X$					
Zapus hudsonius		$\mathbf X$						
Erethizon dorsatum	X							
Neochoerus pinckneyi			$\boldsymbol{\mathrm{X}}$					$\mathbf X$
Neochoerus aesopi	$\boldsymbol{\mathrm{X}}$							
Total	9	15	\mathfrak{Z}	$\boldsymbol{0}$	11	$\mathbf{1}$	$\boldsymbol{0}$	$\mathbf{1}$

Table 6. Range and habitat descriptions of modern rodent species found in Clark Quarry sediments. All range

information from Hall (1981) and habitat information from Nowak (1999).

Figures

Figure 1. Late Pleistocene Clark Quarry *Glaucomys volans* (GCVP 19981) hindfoot proximal phalanx A) lateral and B) ventral views. Modern *Glaucomys volans* (GCM 2239) hindfoot proximal phalanx C) lateral and D) ventral views. a = ventral elevated tendon attachment sites. Scale bar = 2 mm.

Figure 2. Upper rodent incisors from the Late Pleistocene Clark Quarry. *Oryzomys palustris* left I1 (GCVP 17894) A) lateral and B) anterior views; *Synaptomys australis* right I1 (GCVP 17649) C) lateral and D) anterior views; *Peromyscus* sp. right I1 (GCVP 17891) E) lateral and F) anterior views; *Reithrodontomys humulis* left I1 (GCVP 17859) G) lateral and H) anterior views. $a =$ lateral anterior groove; b, $c =$ medial-lateral anterior groove. Scale bar = 2 mm.

Figure 3. Occlusal view of *Oryzomys palustris* upper and lower cheek teeth from the Late Pleistocene Clark Quarry near Brunswick, GA. A) left M1 (GCVP 17866); B) left M2 (GCVP 17874); C) left m1 (GCVP 17864); D) left m2 (GCVP 17862). Anterior = left, buccal = top of page. Scale bar = 2 mm .

Figure 4. Astragali from Late Pleistocene Clark Quarry rodents. A) right astragalus of *Peromyscus* sp. (GCVP 17983), B) left astragalus of *Oryzomys palustris* (GCVP 17980), C) right astragalus of *Synaptomys australis* (GCVP 17979); D) left astragalus of *Sigmodon hispidus* (GCVP 17981). Scale bar = 2 mm.

Figure 5. Lower incisors from the Late Pleistocene Clark Quarry near Brunswick, GA. *Sigmodon hispidus* left i1 (GCVP 17692) A) occlusal and B) lateral views; *Synaptomys australis* right i1 (GCVP 17648) C) occlusal and D) lateral views; *Peromyscus* sp. left i1 (GCVP 17893) E) occlusal and F) lateral views; *Reithrodontomys humulis* left i1 (GCVP 17875) G) occlusal and H) lateral views. Scale bar = 2 mm.

Figure 6. *Sigmodon hispidus* upper cheek teeth from the Late Pleistocene Clark Quarry near Brunswick, GA. A) left M1 with a partial maxillary fragment (GCVP 17695); B) left M2 (GCVP 17686). Anterior = left, buccal = top of page. Scale bar = 2 mm.

Figure 7. *Sigmodon hispidus* lower cheek teeth from the Late Pleistocene Clark Quarry near Brunswick, GA. A) right dentary fragment with m1 and m2 in place (GCVP 17674), B) right m3 (GCVP 17683). Anterior = left, buccal $=$ top of page. Scale bar $= 2$ mm.

Figure 8. *Neofiber alleni* from the Late Pleistocene Clark Quarry near Brunswick, GA. A) lateral view of a right I1 (GCVP 19971); B) lateral view of a left i1 (GCVP 19970); C) occlusal view of a right M3 (GCVP 17859); D) anterior view of a right femur (GCVP 19965); E) posterior view of a right femur (GCVP 19965). A, B, and C scale $bars = 2 mm$; D and E scale bars = 5 mm.

Figure 9. *Synaptomys australis* cheek teeth from the Late Pleistocene Clark Quarry near Brunswick, GA. A) occlusal, B) lateral, and C) medial views of a left dentary (GCVP 17973) with i1 and m1-m3; D) occlusal view of a left M1 (GCVP 17645); E) occlusal view of a left M2 (GCVP 17638); F) occlusal view of a left M3 (GCVP 17644). Anterior = left in D-F, buccal = top of page in D-F. Scale bars = 2 mm .

Figure 10. Late Pleistocene Clark Quarry *Erethizon dorsatum* (GCVP 17896) upper left incisor A) lateral, B) lingual, and C) occlusal views. $a =$ lateral enamel dentine junction, $b =$ anterior groove. Scale Bar = 2 mm.

Figure 11. Occlusal view of *Neochoerus aesopi* left m1 molar fragment (GCVP 19860) from the Late Pleistocene Clark Quarry near Brunswick, GA. Anterior = left, buccal = bottom of page Scale bar = 2 mm.

Appendix

