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Using Geometric Morphometrics to Differentiate Lower First Molars of Microtus Species: A Review of the Clark's Cave Bone Deposit, VA

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Using Geometric Morphometrics to Differentiate Lower First Molars of *Microtus* Species: with A Review of the Clark's Cave Bone Deposit, VA

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by

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ABSTRACT

Using Geometric Morphometrics to Differentiate Lower First Molars of *Microtus* Species: A Review of the Clark's Cave Bone Deposit, VA

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Clark's Cave contains a large collection of late Pleistocene mammal material. In particular, it contains a sizable amount of *Microtus* spp. which can be valuable paleoclimate indicators. Identification techniques traditionally used to classify these species have been shown to be unreliable. Recent studies have shown that using geometric morphometric techniques on lower first molars can be more successful. By placing landmarks and running a discriminate analysis on new and previously collected material from the cave, significant differences in *Microtus* species proportions were found. Specifically, showing the deposit has a larger proportion of *M. xanthognathus* than previously reported; resulting in a subsequent drop in the number of *M. pennsylvanicus* and *M. chrotorrhinus* present. Moreover, previously unreported *M. ochrogaster* was determined to be an important component of the fauna. The results presented here show the importance of applying new techniques to previous studies.

DEDICATION

To Jon Silver, Mr. Hains, Max Christie, and Dr. Russ Graham. At the end of the day it's you guys that got me here.

ACKNOWLEDMENTS

There are so many people that I would like and need to thank for making this project possible:

Huge thanks must go to my committee. To Dr. Steven Wallace, chair, for being there throughout the whole process, including enduring the days where you would get nothing done as I would bombard you with questions. Your knowledge of caves, microtines, morphometrics, Corel, and computers as a whole was most useful. To Dr. Blaine Schubert for suggesting Clark's Cave in the very beginning and for acquiring the extended loan of specimens used. To Dr. Jim Mead for keeping on top of us to make sure progress was being made and for all the lil' nuggets and reassurance along the way. To Sandy Swift who really is an honorary committee member. Thank you for showing me how to use the microscope camera, use PhotoShop, and for always seemingly giving me a lighter work load when I most needed it.

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A special thanks must be extended to the Breeden family for permission to visit and remove sediment from the cave. To Larry Smith and the Virginia Department of Conservation and Recreation for granting us a permit to collect. To Rick Lambert, for basically being our guide of the cave, you made the whole process much easier and more fun. To Wally, Blaine, Molly Witter, Joshua Doby, Kevin Chovanec, Diana Velasco, Hannah Darcy, and Will Harris for helping explore the cave and assessing potential excavation spots.

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CHAPTER 1

INTRODUCTION

Overview

To insure the proper interpretation of Quaternary paleoenvironments, it is vital that correct identifications are made on mammalian fossils from that time. Improper identifications can lead to inappropriate inferences on species' ranges and misrepresent climatic and environmental conditions in a particular region. Small mammals (micromammals), especially insectivores and rodents, are very useful for climate studies, due to their restrictive ecologic tolerances and inability to migrate large distances over short periods of time (e.g. Graham 1986). Many studies (e.g. Guilday & Parmalee 1972; Grady & Garton 1981; Bell & Bever 2006; Wallace 2009; McGuire 2010; Renvoise et al. 2012) have focused around arvicoline (microtine) rodents.

One micromammal genus that is often used as a proxy for climate studies is *Microtus*, consisting of both New and Old World voles (Rodentia; Arvicolidae). Fossil records of *Microtus* often consist of only isolated molars (i.e. Martin 1968; Hallberg et al. 1974; Zakrzewski 1985; Bell & Repenning 1999; Wallace 2006) and are therefore problematic. Such scrappy material can create a challenge to identify members of this genus down to species level, due to variability of characters within a species, along with a lack of diagnostic characters (Zakrzewski 1985; Bell & Repenning 1999; Bell & Bever 2006). Consequently, improved methods for classification of isolated fossil teeth have been the focus of many recent studies (e.g. Wallace 2006; McGuire 2010, 2011; McGuire & Davis 2013).

Solely relying on traditional *Microtus* identification methods is often not enough to confidently place fossil material to species level. These traditional techniques should be the first step in an ongoing process. The advent of the digital age provides us with statistical and spatial software that allow a more thorough examination. Additionally, recent DNA studies on many lemming taxa have showed different species composition than previously thought (Burns 1980; Ehrich et al. 2000; Fedorov et al. 2003; Fulton et al. 2013). Moreover, similar studies show that dispersion and re-colonization was different than expected before and after the Pleistocene (Fedorov et al. 2003; Wallace 2009; Semken et al. 2010; Shafer et al. 2010; Hope et al. 2011; Fulton et al. 2013).

The project presented here focuses on four interrelated topics, so the organization is written in a manner that follows the compounding nature of the study. In other words, results of a chapter directly affect the outcome of subsequent chapters (i.e. results from Ch. 3 generate the questions in Ch. 4). Consequently, the primary goals here are:

1. Comparing superimpositions using generalized rotational fitting (GRF) (Adams, Rohlf & Slice 2004), as preformed in Wallace (2006) to create Bookstein Shape Coordinates (see Bookstein 1991), versus using a Generalized Procrustes fit (GPA) (Rohlf & Slice 1990), used in McGuire (2010; 2011), McGuire & Davis (2013), to generate the shape variables used in the analysis of landmark data on the lower m_1s of *Microtus*. Both methods have produced viable data and conclusions, but there has not been a direct comparison of the two methods using the same dataset. By comparing both methods on the same species (*M. pennsylvanicus* (Meadow vole) and *M. xanthognathus* (Taiga vole)), a preferred method can be ascertained for identifying *Microtus* spp.

2. Differentiating *M. xanthognathus*, *M. richardsoni* (Water vole), and *M. pennsylvanicus* lower first molars (m_1). *Microtus xanthognathus* and *M. richardsoni* have the two largest (on average) sized sets of molars of the extant *Microtus* spp. (Ludwig 1984; Conroy & Cook 1999). Historically these two species have been separated from the rest of the extant *Microtus* species by having lower first molars greater than 3.2 mm in length (Hallberg et al. 1974; Semken & Wallace 2002). However, Wallace (2006) shows that molar size alone is not a reliable method to distinguish *Microtus* species. For this reason *M. pennsylvanicus* is also included here due to its wide geographic range and high molar variability (Martin 1968; Guilday 1982b; Davis 1987; Barnosky 1990). *Microtus richardsoni* is often distinguished from other *Microtus* spp. by a bulbous anterior complex on the lower m_1 (Burns 1982; Semken & Wallace 2002). Here, the above stated superimposition and landmark techniques will be tested to see if such methods can successfully differentiate these three vole species. Due to the varying nature of *M. xanthognathus* molars in the fossil record (Guilday & Bender 1960; Guilday 1982b), this could be a useful alternative method of identification.

Currently the range of *M. xanthognathus* includes the boreal forests of central Alaska and northwestern Canada, across to the Hudson Bay, down into south central Alberta (**Fig. 1**) (Conroy & Cook 1999). However, fossil specimens of *M. xanthognathus* have been found as far south as Arkansas (Hallberg et al 1974). *M. richardsoni*'s geographic range today forms two distinct bands (**Fig. 1**). One that extends from southern Oregon into British Colombia along the Cascades; and a larger eastern band that follows the Rocky Mountains from Northern Utah up to Alberta; with fossil remains found in a similar region (Ludwig 1984). *M. pennsylvanicus* has a wide distribution spanning most northern North American grasslands; from Alaska, through Canada, into the southeastern US and into the west (**Fig. 1**), with a fossil record that is equally as

broad (Reich 1981). Given their overlapping ranges in the past and present, it is possible to have all three species recovered from the same paleontological/archeological site. It should be noted that *M. pennsylvanicus*'s fossil range may be overestimated. Other species such as *M. chrotorrhinus, M. mexicanus, M. montanus, M. longicaudus,* and *M. californicus* show similar occlusal m_1 patterns.

3. Revisiting Guilday's (1977) report on Clark's Cave, VA., by applying the methods lined out above to review the ratio of 5-closed triangle morph *Microtus* (specifically *M. pennsylvanicus* vs. *M. xanthognathus*); then the 3-closed triangle morph *Microtus* (*M. pinetorum* (Pine vole) vs. *M. ochrogaster*(Prairie vole)) collected from Clark's Cave. All of the 3-closed triangle morph *Microtus* were classified as *M. pinetorum* by Guilday et al (1997), based upon geographic probability. Therefore, the presences of *M. ochrogaster* is tested using geometric morphometric techniques.

Microtus pinetorum's range covers most of the eastern United States (**Fig. 2**); stretching from southern Maine to northern Florida across to eastern Texas up into Wisconsin (Smolen 1981). Clark's Cave would be an extra-limital occurrence for *M. ochrogaster*. Its current most eastern range is western West Virginia (**Fig. 2**). It ranges into the northeastern corner of New Mexico up to Alberta (Stalling 1990). Most extra-limital records found are from Oklahoma, Texas and more southern New Mexico (Smartt 1977; Stalling 1990).

4. Collecting and screening new samples from the cave to look for species that were previously not found or recognized in Guilday et al. (1977). The volume of new sediment collected compared to that which was reported from Guilday et al. (1977) is much less; however, the new site is in a slightly different location within the cave. Updated identification techniques can also lead to new or different identifications.

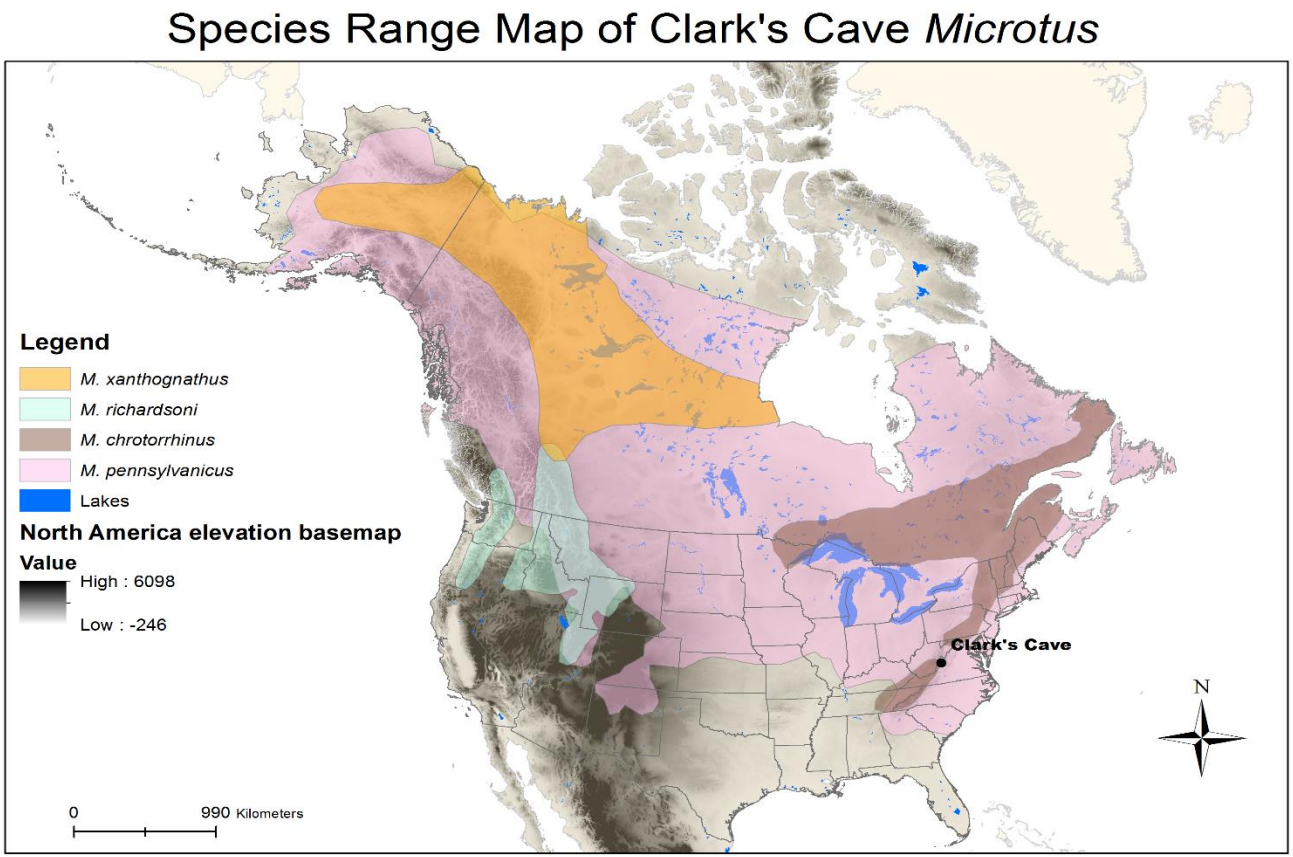

Fig. 1 - Modern geographic distribution of *Microtus pennsylvanicus*, *M. xanthognathus*, *M. richardsoni*, *M. chrotorrhinus* including the location of Clark's Cave, Virginia. Modified from Hall (1981).

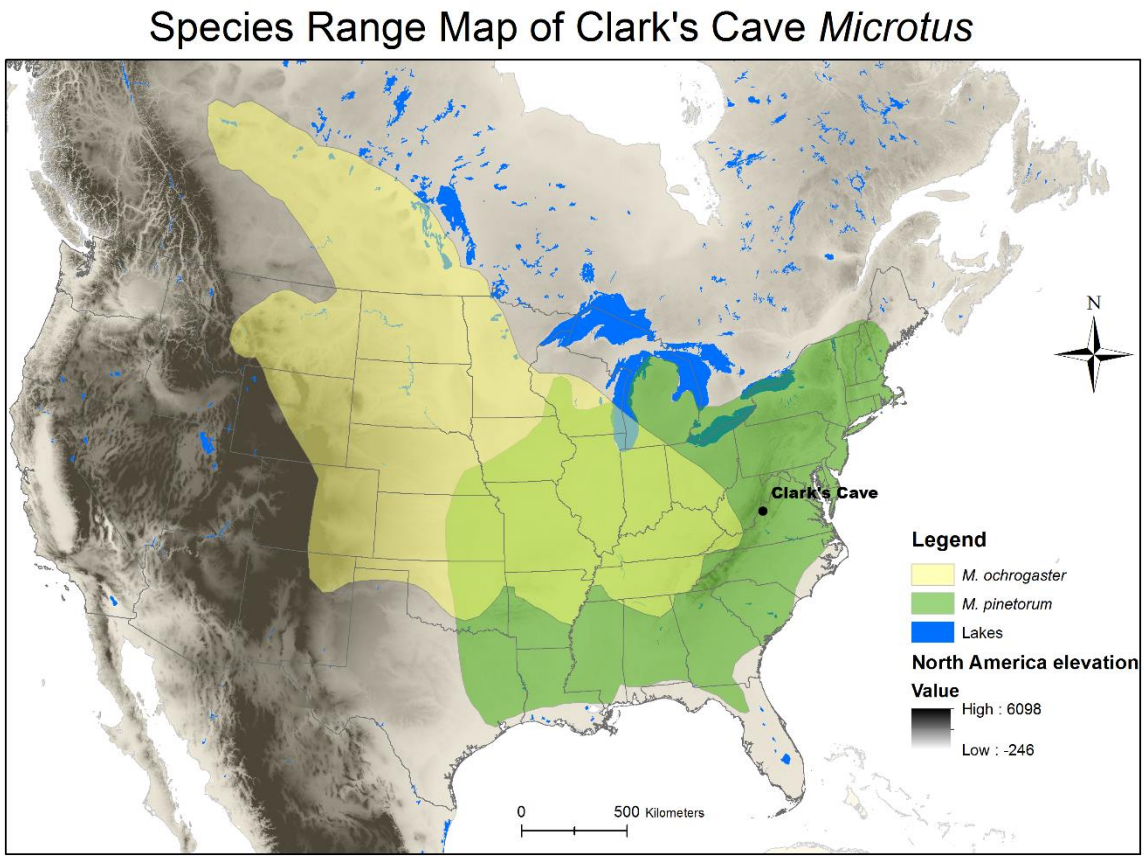

Fig. 2 - Modern geographic distribution of *Microtus pinetorum* and *M. ochrogaster* including the of location Clark's Cave, Virginia. Modified from Hall (1981).

Background

Schubert (1997) states:

> "Studies of well documented Quaternary environmental changes are necessary for 1) Understanding the intricacies of past climatic fluctuations, 2) Providing a foundation for interpreting modern biological communities, and 3) Testing and refining models used to predict future climatic change."

When using mammal fossil material (especially micromammal) to interpret the paleoclimate or environment there is an inherent advantage to working in the Quaternary. Most late Pleistocene and Holocene species are extant today (i.e. Guilday 1982b; Graham, 1986; Graham & Mead 1987; Graham & Grimm 1990), which provides a modern analog for comparison. However, such comparisons are made under the assumption that the diet, behavior, and environmental preferences of modern species still apply to their Quaternary counterparts (Bell & Bever 2006; Stewart 2009; George 2012). Predicting how extreme environmental pressures (such as those caused by the last ice age) would alter the behaviors of species can be difficult. It can also be challenging to interpret how modern species reacted and interacted with extinct species (Stewart 2009; George 2012). Pressures such as these can lead to non-analog faunas (i.e. Graham & Mead 1987; Semken et al. 2010) and different groupings of taxa than would otherwise be expected (Graham & Grimm 1990). These communities and groupings can persist even after the pressure has subsided (Graham & Mead 1987; Graham & Grimm 1990). Many such variables along with a limited amount of identifiable characters in small mammal material, can lead to inaccurate species richness models. As a result, it is highly likely that the number of identified Quaternary species from the fossil record is either inflated from the use of

geographic assumption to identify species, or underrepresented; due to an inability to differentiate species based solely on crainodental characters (George 2012).

Mid-Appalachian regions provide examples of non-analog faunas from the end and post last glacial maximum (LGM). Guilday (1982a) bounds this region between 34 and 36 degrees north latitude. This region of the Appalachian Plateau and Ridge and Valley includes: most of Pennsylvania, West Virginia, the eastern halves of Kentucky, Ohio, and Tennessee, and the western parts of Virginia and Maryland (Guilday 1982a). Palynological studies by Watts (1979) and Wright (1981) indicate that during the late glacial (18-12kya) the region would have been predominantly covered with coniferous forests, intermixed with grasslands. By the Holocene the region switched to predominately deciduous forest (Guilday 1982a).

Guilday (1982a) divides the late Pleistocene fauna into four categories: (1) species that are extinct, (2) present day boreal species, (3) present day Midwestern prairie species, and (4) species that still remain in the area today. Much of the megafauna of the area did not survive into the Holocene (e.g. Graham & Lundelius 1984; Barnosky et al. 2004; etc.). Microfauna of Mid-Appalachia at the time were dominated by boreal taxa, highlighted by arctic adapted voles and lemmings restricted to northern Canada and Alaska today. *Dicrostonyx* sp. (the collared lemming) is one of the best examples of this; today restricted to the Arctic tundra (Hall 1981), but has been collected from various Pleistocene aged deposits (Grady & Garton 1981; Mead & Mead 1989). Prairie species such as ground squirrels indicate that there were grasslands during the late Pleistocene. Temperate species found in the region today would have been found at lower volumes than presently. A slightly dryer climate that had less severe temperature swings in the summer and winters is one proposed model that may have permitted the cohabitation of these taxa (Graham & Grimm 1990).

Cave Paleontology

Cave deposits are a vital part of the Quaternary fossil record. As of 1994 based on records from FAUNMAP Working Group (1994) nearly 52% of the late Pleistocene taxonomic record comes from cave deposits (Jass & George 2010). Bones accumulate in caves as a result of animals living in, falling into, becoming trapped in, washing in post mortem, or being deposited by predators (Andrews 1990). When looking at Quaternary cave faunas, the geographic location of the cave will not have changed drastically, but the climate, and subsequently the taxa that inhabited the cave will have changed through time.

During the 1960's-70's there was an explosion of central Appalachian cave exploration. During this time many reports on the flora and fauna found from these karst system deposits were being published. John Guilday and his teams were at the forefront (Guilday & Bender 1958; Guilday 1962; Guilday et al. 1964; Guilday & Parmalee 1965; Guilday et al. 1966; Guilday 1967; Guilday 1971; Guilday et al. 1977; Guilday & Hamilton 1978; Guilday et al. 1978) of this and are responsible for much of our knowledge of the area's prehistoric fauna. Sites like this provide large numbers of microfauna that were often not found, or overlooked at archeological sites and other non-karst paleontological sites.

Clark's Cave

Focus here is on one particular site, Clark's Cave, Virginia. From the original report (Guilday et al. 1977) 3.9 m^3 of sediment was extracted for entrance 2 of the cave. Five hundred and forty kg of matrix was dry screened through 6mm mesh screens. The remaining 180 kg of sediment was screened and washed through 1 mm mesh at the New Paris field laboratory. Bone and teeth material was further sorted and is stored at the Carnegie Museum, PA.

The aim of the Guilday et al. (1977) study was threefold: (1) Identification to species if possible, (2) Establishing minimum number of individuals (MNI) for each taxon, (3) Looking at possible size differences between recent and fossil populations. For the mammals in this study, identifications were focused primarily on dental and cranial material. Very little mammalian postcranial material was cataloged or identified (but is still stored at the Carnegie Museum). However, identifications of avian, amphibian, reptilian, and fish material was primarily on postcranial material.

Preservation of bone and teeth was chemically good, but rather fragmented, with very little articulation. All of the bird and micromammal material recovered were from extant species (Guilday et al. 1977). Other material recovered was from reptiles, amphibians, fish, crayfish, insects, gastropods, bivalves, along with plant material. Two groups that represented the highest number of individuals were Arvicolinae (voles) and Vespertilionidae (common bats) (Guilday et al. 1977). The number of species identified from the deposit by group are: Flora (8), Insetca (11), Crustacea (2), Gastropoda (20), Bivalvia (2), Osteichthyes (bony fish) (7), Amphibia (9), Reptilia (5), Aves (68), Mammalia (53). Some of these species identifications are best guesses (cf.) or have names that are no longer proper nomenclature.

Clark's Cave (CC) is located is 12 km southwest of Williamsville in Bath County, Virginia (Guilday et al. 1977). It is located in north-central Virginia (**Fig. 2**), in the George Washington National Forrest, along the south bank of the Cowpasture River (a relatively slow and meandering river). CC is a large maze style cave, with complex passageways 10,355 meters in length (**Fig. 3**), formed in lower Devonian limestone cliffs (Helderberg group, New Scottland member) (Bick 1962), capped by the mainly sandstone Oriskany formation (Palmer 2009). There are 6 major entrances in the limestone cliff side; located about 30m above the river

(Guilday et al. 1977). Entrances open up to talus slopes and old collapse features. The rest of the hillside is vegetated and slopes down to the bank of the river at a steep to moderately steep gradient; depending on location. CC is mostly dry especially in the more explored regions near the entrances.

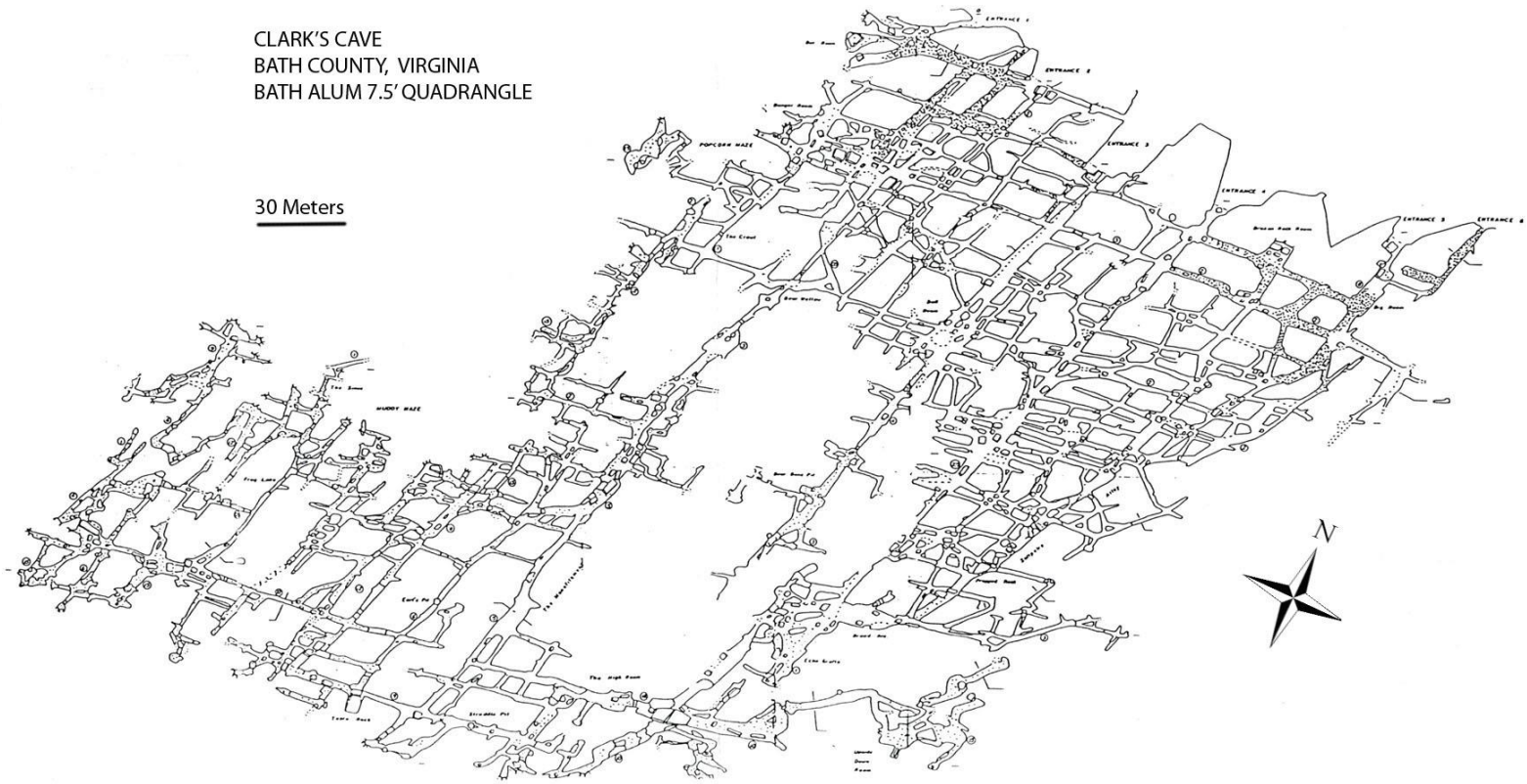

Fig. 3 - Passageways of Clark's Cave (Modified from Rod Morris map, 1965) courtesy of Rick Lambert.

Specimens used in this study, and from Guilday et al. (1977), come from entrance 2, as seen in (**Fig 4**). Entrance 2's amphitheater traditionally serves as the main entrance to the cave, as entrance 1 is not accessible by foot (one would need to rappel in from above). While standing in the amphitheater there are 3 separate passages one can take. The right and center passages (while facing the cliff) lead into the cave, while the left passage is a small off shoot that leads back to the bluff face.

Material used in both studies was collected out of the right passageway. Field Site No. 3 (the Clark's Cave faunal deposit (Guilday et al. 1977) was collected near the top of a loose unconsolidated talus slope that fed into the amphitheater talus slope. Ninety percent of the material collected in that study was cliff wastage, the remaining 10% was organic material and dark brown dry soil (Guilday et al. 1977). A datum (labeled: 7/19/14 – 002) now marks the site of their excavation.

Material excavated on July 19-20, 2015 by the East Tennessee State University (ETSU) team came from sediment just down-slope from Field Site No. 3 (of Guilday et al. 1977). Sediment was collected from a small ledge, raised about 40 cm from the floor (**Fig. 4**). Material appears to have been winnowed out from deeper inside the cave. Since this material had been slightly raised off the floor it was less disturbed and more packed down than the loose talus on the cave floor. There was a thin layer of moss or lichen on top of the sediment in a few regions. The matrix was made up of mostly organic material and dark soil/clay with the remaining material being wastage from the cave.

Fig. 4 - Right passageway of Entrance 2 in Clark's Cave, VA. Material was collected from the ledge in the bottom left corner of the right image, marked by black oval.

No radiocarbon dates were collected or published from Guilday et al. (1977); it was hypothesized that the deposit was created between 11-20kya. This age range was chosen based on the taxa collected, hypothesized rate of accumulation based on modern raptor roosts, and similarities in a previously dated site at New Paris No. 4, PA. (Guilday et al. 1964). Subsequent dates have been obtained from material from Clark's Cave that back up the suggested age. These dates point to a late glacial age (10-15kya) deposit: [Radiocarbon years before present ± 1 standard deviation (RC yr. BP ± 1 SD)] [*M. xanthognathus* (14,440 ± 70), *T. striatus* (13,570 ± 70), *P. breweri* (12,930 ± 70), *N. floridana* (12,530 ± 60; 12,340 ± 60; 12,270 ± 60; 11,170 ± 60)] (Semken et al. 2010).

Microtus Morphometrics

Microtus spp. are commonly used to reconstruct paleoclimate and environment (e.g. Guilday & Hamilton 1978; Martin 1991; Bell & Barnosky 2000; McGuire 2011; Renvoise et al. 2011). *Microtus* molars have diagnostic occlusal patterns (**Fig. 5)**. The lower first molar has historically been used to differentiate species. Due to their variant molar morphology (most common method of identification) multiple studies have been published cautioning the classification to species, especially with very small sample sizes (Guilday 1982b; Bell & Repenning 1999; Bell and Barnosky 2000; Bell & Bever 2006; Jass & Bell 2011).

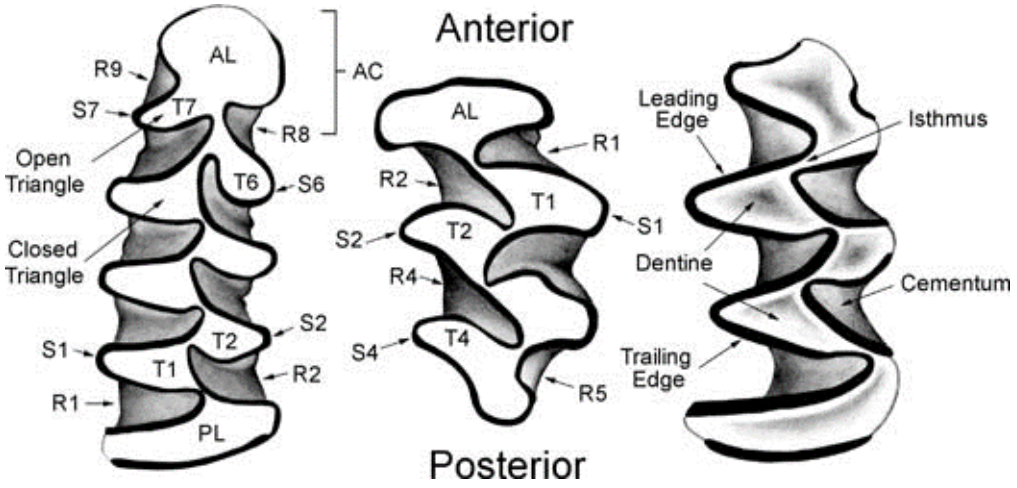

Fig. 5 - Basic arvicoline molar nomenclature. Left to right: lower right 1st molar (m_1) and upper right 1st molar (M^1) of *Microtus richardsoni*, and m1 of *Synaptomys cooperi*. Enamel is the black band surrounding each element of the tooth; whereas dentine is the white or lightly shaded regions. Dentine wears more easily than enamel creating depressions on the surface of the tooth. Cementum is the darker shaded region on the external surface of the tooth, primarily within the re-entrant angles. Lower molars: the intervening triangles (T1, T2, etc.), re-entrant angles (R1, R2, etc.), and salient angles (S1, S2, etc.) are numbered in increasing order starting anterior to the posterior loop; ending at the anterior loop. Reverse is applied to upper molars. Anterior complex (AC), posterior loop (PL), and anterior loop (AL) are labeled accordingly. Specimens are not to scale. Modified from van der Meulen (1978) & Wallace (2006).

Wallace (2006) was the first published study to use landmarks along with morphometric techniques to differentiate species of *Microtus*. He was able to show that using a 3.2mm length

of the lower first molar to separate *M. xanthognathus* from *M. pennsylvanicus* was an inadequate method of differentiation. The landmark scheme developed in that study is applicable to fossil and extant *Microtus* worldwide. Using the same landmark scheme but slightly different statistical procedure McGuire (2010; 2011]) and McGuire & Davis (2013) looked at inter / intra-species difference between western North American *Microtus* spp. to infer geographic and climatic changes. Similar questions were examined in a study by Renvoise et al. (2012) using different landmark techniques, on European *Microtus* spp.

Abbreviations

ADW = Animal Diversity Website; CC = Clark's Cave, Virginia; cf. = confer; DA = Discriminant analysis; ETMNH = East Tennessee State University & General Shale Natural History Museum; ETSU = East Tennessee State University; ETVP = East Tennessee Vertebrate Paleontology; GPA = Generalized Procrustes analysis; GRF = Generalized rotational fit; kya = Thousand years ago; LGM = Last Glacial Maximum; M = Upper molar; m = Lower molar; MDA = Multidiscriminant analysis; MNI = Minimum number of individuals; MPM = *Microtus pennsylvanicus* morph; MXM = *Microtus xanthognathus* morph; NISP = Number of identified specimens; PCA = Principle component analysis; R = re-entrant angle; S = salient angle; sp. = Species; spp. = Species (plural); T = triangle.

CHAPTER 2

MATERIALS AND METHODS

Excavation

On July 19th and 20th, 2014 sediment was collected from Clark's Cave, by a group affiliated with the Geoscience Department at East Tennessee State University (ETSU) and the East Tennessee State University & General Shale Natural History Museum (ETMNH). Excavation was permitted by the Virginia Department of Conservation and Recreation (see **Appendix B**). Multiple locations within the cave and around Entrance 2 were sampled, however specimens used here come from sample: Clark's Cave 7/19/14 – 003; 6 sediment bags collected as a bulk sample. Specimens and sediment from this and the other locations that were collected are stored at the ETMNH.

Specimens

Specimens Used in Chapter 3

Material used in chapter 3 is composed of extant specimens borrowed from the Smithsonian included: *Microtus xanthognathus* from Alaska and Canada (n=32) and *M. richardsoni* from Wyoming, Washington and Canada (n=30). All specimens were collected as skin and skull. *M. pennsylvanicus* data was from Wallace (2006), see **Appendix A**. Only m_1s were used because they are the most common tooth used to distinguishing different species of *Microtus*. To limit sources of error, only right m_1s were used. If the right molar was too damaged, the left molar was used, and specimens were converted by multiplying the x variable by (-1) (after the specimen was photographed and digitized) to produce a mirror image. Being able to use both rights and lefts is also critical for fossil specimens; where a large sample size (of

the same side) would most likely be unavailable. Moreover, because identification is the primary goal when looking at fossil specimens, not to establish each taxon's morphospace, utilization of every specimen is critical.

Specimens Used in Chapter 4

Material from Wallace (2006) and the Smithsonian were also used in chapter 4, along with the specimens collected from the 2014 Clark's Cave excavation and specimens from Guilday's 1977 excavation. Specimens collected by Guilday et al. (1977) were borrowed from the Carnegie Museum of Natural History, Vertebrate Paleontology Collection. All specimens borrowed from the Smithsonian (for this study) were cataloged as *M. pinetorum* (see **Appendix A**), per identifications made by Guilday et al. (1977). Identifications and comparison to previously collected specimens was the main focus, therefore, both left and right molars were used in the chapter 4 study; facilitating a larger sample size.

Unlike in the study in chapter 3, there were no specimens that possessed a complete dentary with both sets of molars on either side of the mandibular symphysis. Therefore, if a molar was too damaged it was excluded from the data set. To stay consistent with, and incorporate the data from chapter 3, all left molars were converted to "rights" by multiplying the x variable by (-1) as before. This was done for all 5-closed triangle morph *Microtus*; however, because a majority of left molars were present for the 3-closed triangle clade *Microtus*, the opposite conversion was performed for those specimens. Three- and 5-closed triangle morph molars were never included together in the same data set, thus posing no potential source of error in this study.

Identification

All *Microtus* lower first molars collected from Clark's Cave by Guilday et al. (1977) and ETSU were treated as unknowns. Initial identification was only taken to either 3- or 5-closed triangle morph *Microtus*. This can easily be performed via observation via a microscope. The next step was to place tentative identifications (or morphotypes) to the species level, using traditional methods of identification. Specimens identified as 5-closed triangle morph were assigned to one of two morphotypes: *M. pennsylvanicus* morph (encompassing *M. pennsylvanicus* or *M. chrotorrhinus*) or *M. xanthognathus* morph (encompassing *M. xanthognathus* or *M. richardsoni*). If the length of the m1 was greater than or equal to 3.2 mm (Hallberg et al. 1974) it was assigned to *M. xanthognathus* morph (MXM). Less than 3.2 mm (Hallberg et al. 1974) was assigned to *M. pennsylvanicus* morph (MPM). Unknowns were then combined with the specimens from chapter 3 (which are taken to be knowns) to test what percentage of the assigned morphotypes were correct.

Three-closed triangle morph specimens were assigned to one of two morphotypes: *M. pinetorum* or *M. ochrogaster*. Molars with enamel that has roughly the same thickness on the leading and trailing edges (van der Meulen 1978; Martin 1991; Semken & Wallace 2002), and an anteriorly directed, deep 6th re-entrant angle (Martin 1987; Semken & Wallace 2002) were assigned as *M. pinetorum*. If the molar had a sixth re-entrant angle that was shallower (Martin 1987; Semken & Wallace 2002), and enamel that was the same thickness on the leading end and trailing end (van der Meulen 1978; Martin 1991; Semken & Wallace 2002) it was assigned to *M. ochrogaster*.

Assumptions of *Microtus* spp.

Assumptions 1-4 are modified from Wallace (2006) and are listed below.

1. Occlusal patterns of *Microtus* m_1s have not experienced significant change, which would impact these analyses, since the Pleistocene. Individual species have likely experienced morphological change both spatially and temporally, but as long as such interspecific changes are less significant than current intraspecific differences, the changes should prove irrelevant to the analyses.

2. Fossil molars of a particular taxon are more similar to extant specimens, of said taxon, than they are to any other taxon's molars. This is similar to assumption one and must apply regardless of the specimen's geologic age.

3. All recognized Quaternary species of North American *Microtus* are extant. None of the widely distributed continental micromammals have been included in the end-Pleistocene extinction in North America (Martin 1967; Graham & Lundelius 1984; FAUNMAP 1994; Jass & Bell 2011).

4. Morphotypes are equivalent to biological species. Complete correlation between morphotypes and biological species in the fossil record may be unreachable. Regardless, most specimens can be placed within a morphotype with a high degree of confidence.

Landmarks

The 21 landmarks developed by Wallace (2006) are used in this study (**Table 1)**. These landmarks (**Fig**. **6**) were selected for ease of repeatability by another user, their likely preservation in the fossil record, and the shared ability to be used across *Microtus* spp.

Table 1 - Description of Landmarks Used in Analysis (adapted from Wallace 2006).

Landmark No.	Description of landmark
1	Terminal end of the enamel band on lingual side of posterior loop.
2	Most medial point of re-entrant angle 1 at the boundary between enamel and cement.
3	Intersection of leading and trailing edges of enamel on triangle 1. At the boarder of enamel and dentine.
4	Most medial point of re-entrant angle 3 at the boundary between enamel and cement.
5	Intersection of leading and trailing edges of enamel on triangle 3. At the boarder of enamel and dentine.
6	Most medial point of re-entrant angle 5 at the boundary between enamel and cement.
7	Intersection of leading and trailing edges of enamel on triangle 5. At the boarder of enamel and dentine.
8	Most medial point of re-entrant angle 7 at the boundary between enamel and cement.
9	Intersection of leading and trailing edges of enamel on triangle 7. At the boarder of enamel and dentine.
10	Intersection of leading and trailing edges of enamel on triangle 6. At the boarder of enamel and dentine.
11	Most medial point of re-entrant angle 6 at the boundary between enamel and cement.
12	Outside edge of enamel band at point of maximum curvature along the leading edge of triangle 4.
13	Intersection of leading and trailing edges of enamel on triangle 4. At the boarder of enamel and dentine.
14	Most posterior position along the boundary of dentine and enamel of the trailing edge of triangle 4.
15	Most medial point of re-entrant angle 4 at the boundary between enamel and cement.
16	Outside edge of enamel band at point of maximum curvature along the leading edge of triangle 2.
17	Intersection of leading and trailing edges of enamel on triangle 2. At the boarder of enamel and dentine.
18	Most posterior position along the boundary of dentine and enamel of the trailing edge of triangle 2.
19	Most medial point of re-entrant angle 2 at the boundary between enamel and cement.
20	Outside edge of enamel band at point of maximum curvature along the leading edge of the posterior loop.
21	Terminal end of the enamel band on labial side of posterior loop.

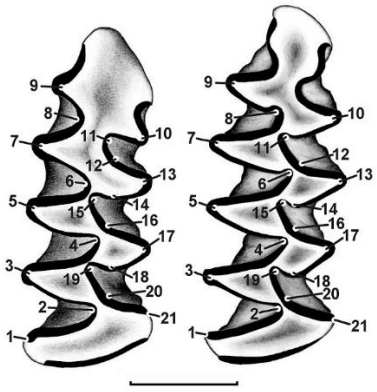

Fig 6 - Landmarks used in this study (Modified from Wallace 2006). Occlusal view of "*Microtus ochrogaster*"- morph (left) and "*M. pennsylvanicus*"- morph (right) m1s. Landmark location homologous for both morphs. Scale bar equals 1 mm.

Shape Variables

Photographs of the specimens were taken with a Leica EZ4 HD stereo microscope, using the computer program Leica Application Suite V4, in the East Tennessee State University

(ETSU) Department of Geosciences microscope/camera lab. Damaged specimens (if a landmark could not be placed due to damage or extreme weathering) were not used in the analysis. Two-dimensional coordinates were digitized on images using tpsDig2 ver. 2.17 (Rohlf 2013a), using the 21 landmarks from Wallace (2006). All data was then combined into one tps file (including the original *M. pennsylvanicus* data from Wallace (2006)) using tpsUtil ver. 1.58 (Rohlf 2013c). A Generalized Procrustes analysis (GPA) was then preformed on the data, using tpsSuper ver. 2.00 (Rohlf 2013b), that superimposes the specimens by translating the centroid of each specimen (having an x and y coordinate) with that of the mean specimen. Consequently, overall size is normalized across all specimens. Specimens were then oriented in a manner that creates the smallest summed squared distances between each of the landmarks (this is part of the superimposition). These new coordinates were then used to compare shape differences between samples (Adams et al. 2004). Results of the GPA produce 42 shape variables, with each landmark contributing an x and y coordinate. The steps in the above paragraph were repeated for each individual analysis.

Analysis

Shape variables were then uploaded into the program SPSS for windows (version 21.0; SPSS Inc., Chicago, Illinois). A principle component analysis (PCA) was run for both groupings, to look for initial separation. Discriminant analysis / Multidiscriminant analysis (DA/MDA) were run to look for separation among species. Stepwise discriminant analyses, with a P=.05 (significance), were used to isolate the most significant variables (that separate out the species).

CHAPTER 3

USING GEROMETRIC MORPHOMETRICS TO DIFFERENTIATE *MICROTUS RICHARDSONI*, *MICROTUS XANTHOGNATHUS*, AND *MICROTUS PENNSYLVANICUS* LOWER FIRST MOLARS

Results

Principle Component Analysis (PCA)

M. xanthognathus vs. *M. richardsoni*.

Results of the PCA show a noticeable separation between the two species (**Fig. 7a**). Separation between the two species occurs around the first axis; with almost all of the *M. xanthognathus* plotting in the negative range of the first axis and the vast majority of the *M. richardsoni* plotting in the positive range. Results of the PCA warranted preforming a DA to look for further separation between the two species, and to isolate the landmarks that best separate the two taxa.

M. xanthognathus vs. *M. richardsoni* vs. *M. pennsylvanicus*.

Results of the PCA show a good separation between the three species (**Fig. 7b**). As was seen in (**Fig. 7a**), *M. xanthognathus* and *M. richardsoni* separate by the first axis. *Microtus pennsylvanicus* separates from the other two species around the second axis. Results of this PCA also warranted preforming a DA.

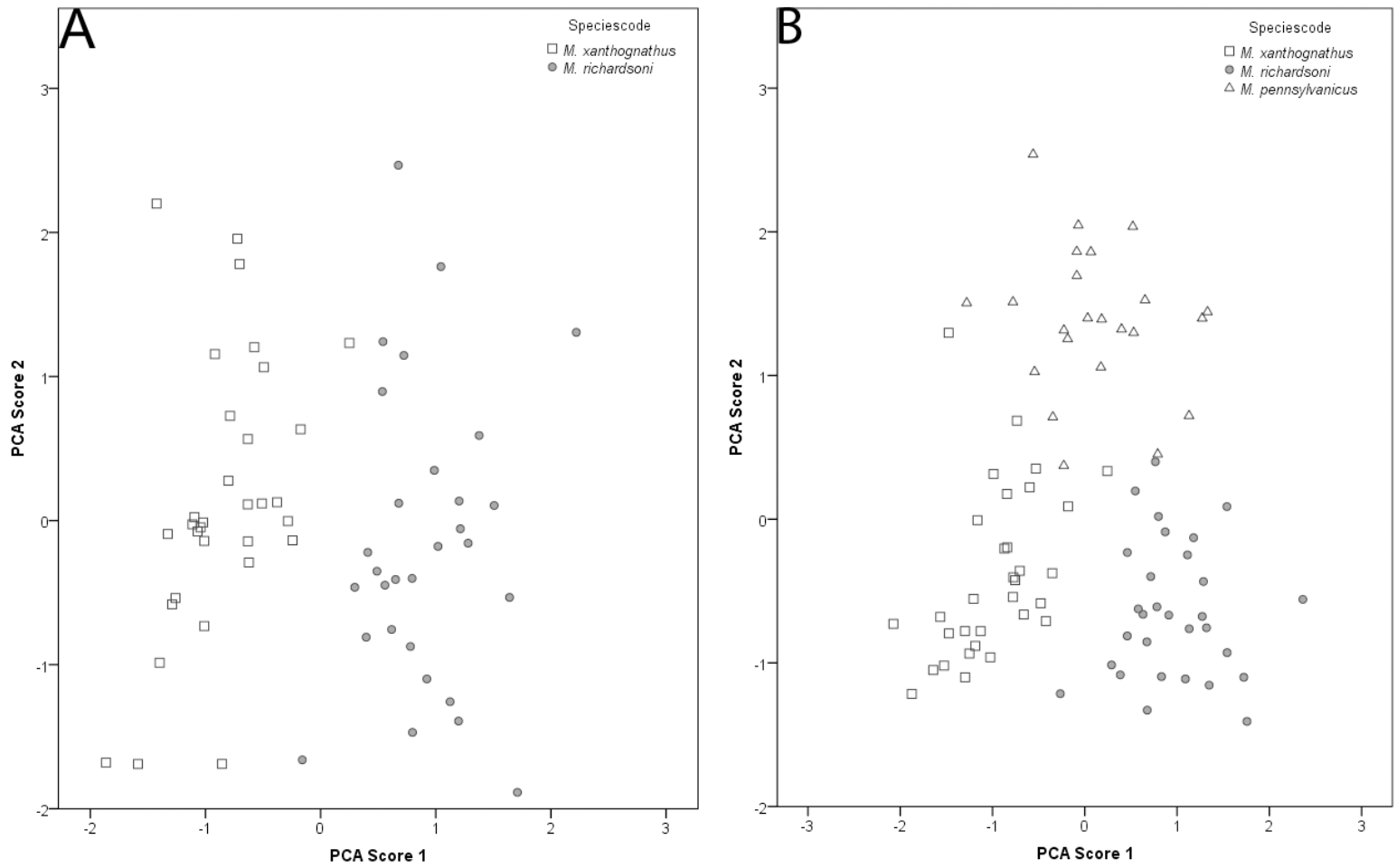

Fig. 7. - Results of Principle Component Analysis with first two scores plotted, against each other a) *M. xanthognathus* and *M. richardsoni*. PCA score 1 accounts for 28.2% of the variance while PCA score 2 accounts for 9.9% and with b) *Microtus xanthognathus*, *M. richardsoni*, and *M. pennsylvanicus*. PCA score 1 accounts for 22.9% of the variance while PCA score 2 accounts for 17.6%.

Discriminant Analysis (DA)

M. xanthognathus vs. *M. richardsoni*.

All specimens were correctly classified to species by the analysis including all variables and when a stepwise was performed. This held true for the original and cross-validated results. The stepwise discriminant function isolated 10 significant variables (X9, Y9, X11, Y8, X10, X18, Y12, Y7, Y17, X5) with a probability F= .05 (**Table 2**). *Microtus xanthognathus* specimens plot as positive values of the discriminant function, whereas *M. richardsoni* specimens plot as negative values (**Fig. 8a**). These values change drastically when a stepwise is performed (**Fig. 9a**). The five most correlated scores from both the DA and Stepwise DA are listed in **Table 3**.

Table 2 - Variables Selected by the Stepwise Discriminant Analysis.

Variables	Wilks' Lambda
X9	0.068
Y9	0.094
X11	0.075
Y8	0.082
X10	0.077
X18	0.058
Y12	0.061
Y7	0.059
Y17	0.061
X5	0.058

Table 3 - Top Five Most Correlated Scores from Structure Matrix.

DA Variables	Correlation score	Stepwise DA Variables	Correlation score
Y13	0.249	X9	-0.347
X9	0.225	Y17	-0.261
Y10	0.217	X10	0.233
X19	-0.173	X11	0.184
Y17	0.169	X18	0.183

Multidiscriminant Analysis (MDA)

M. xanthognathus vs. *M. richardsoni* vs. *M. pennsylvanicus.*

100% of the original "known" cases classified correctly to species in the standard MDA. However, only 96.5% of the cross-validated grouped cases correctly classified to species (**Table 4**): with one *M. richardsoni* classified as *M. pennsylvanicus* and two *M. pennsylvanicus* classified as *M. richardsoni*. When a stepwise MDA was performed both the original and cross-validated identified 100% of the species correctly. The stepwise multidiscriminant function isolated 12 significant variables (X9, Y19, Y2, Y9, X21, Y10, X11, Y17, X10, Y4, Y16, Y8) with a probability F= .05 (**Table 5**). *Microtus richardsoni* and *M. pennsylvanicus* plot as positive values of the first discriminant function, with *M. xanthognathus* plotting as negative values. *Microtus richardsoni* plots with negative values of the second discriminant function, with *M. pennsylvanicus* plotting as positive values. *M. xanthognathus* has positive and negative values of the second discriminant function (**Fig. 8b**).

Table 4 - Classification and Cross-Validated Table from Multidiscriminant Analysis. Species Code 1) *Microtus xanthognathus*, 2) *M. richardsoni*, 3) *M. pennsylvanicus*.

			Predicted Group Membership			
		Species Code	1	2	3	Total
Original	Count	1	32	0	0	32
		2	0	30	0	30
		3	0	0	23	23
	%	1	100	0	0	100
		2	0	100	0	100
		3	0	0	100	100
Cross-validated	Count	1	32	0	0	32
		2	0	28	2	30
		3	2	1	22	23
	%	1	100.0	0	0	100
		2	0	93.3	6.7	100
		3	0	4.3	95.7	100

Table 5 - Variables Selected by Stepwise Multidiscriminant Analysis.

Variables	Wilks' Lambda
X9	.021
Y19	.021
Y2	.021
Y9	.020
X21	.024
Y10	.019
X11	.023
Y17	.021
X10	.019
Y4	.019
Y16	.019
Y8	.018

Stepwise MDA is not as clean as the standard MDA. First discriminant function plots *M. xanthognathus* as positive values and *M. richardsoni* as negative values with most *M. pennsylvanicus* plotting as negative values. Second discriminant function plots *M. richardsoni* and most *M. xanthognathus* as positive points, whereas the *M. pennsylvanicus* plot as negative

points (**Fig. 9b**). The five most correlated scores for the first two functions used in the MDA are listed in **Table 6**.

Table 6 - Top Five Most Correlated Scores Used in MDA from Structure Matrix.

Variables	Correlation score function 1	Variables	Correlation score function 2
X9	-0.325	Y13	0.285
Y13	-0.241	Y8	-0.273
X7	-0.232	Y2	-0.264
X10	0.202	Y10	0.254
Y10	-0.197	Y15	-0.241

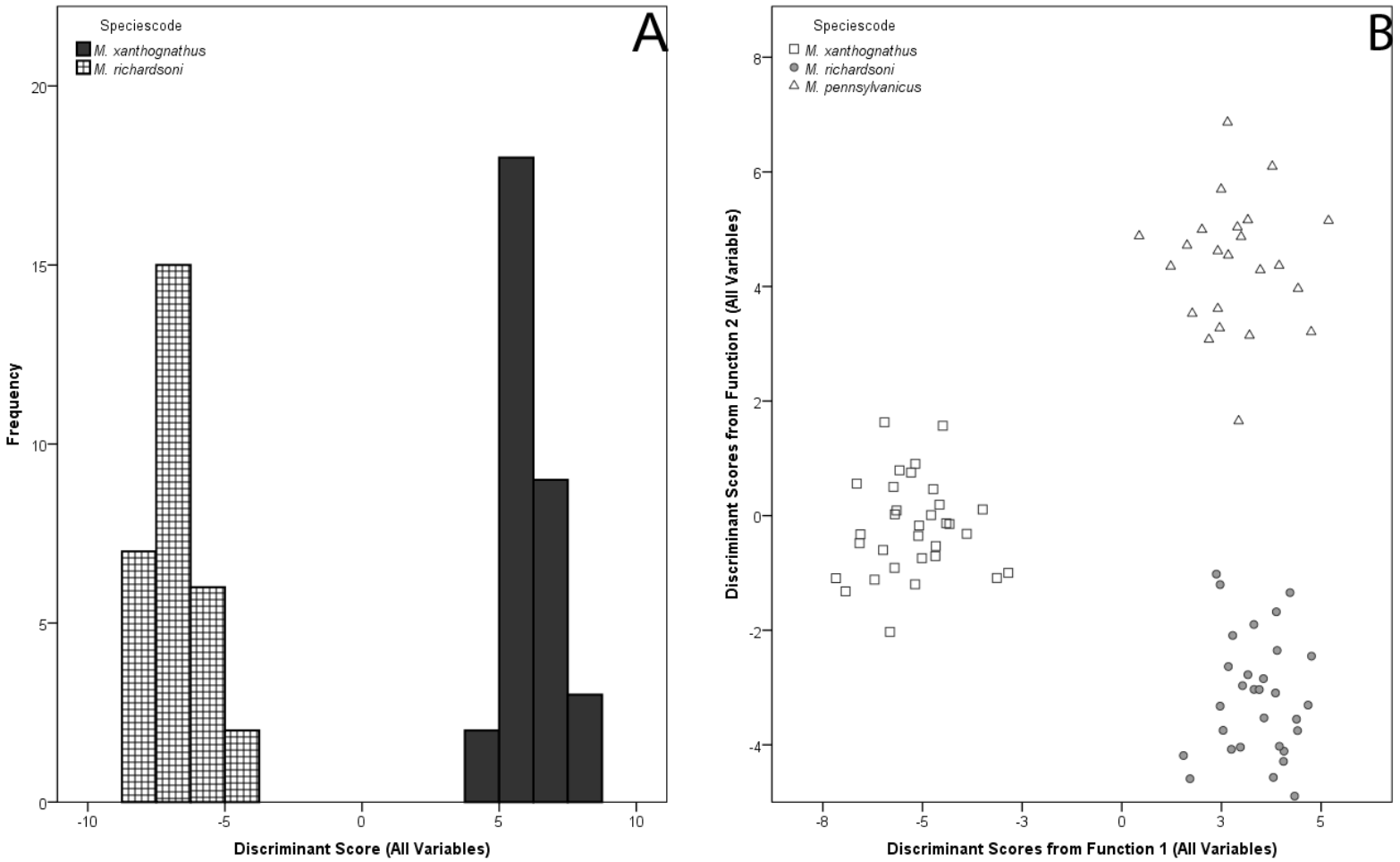

Fig. 8 - A) Results of Discriminant Analysis for *Microtus xanthognathus* and *M. richardsoni* with all variables included and B) Results of Multidiscriminant Analysis with first two scores plotted, against each other for *M. xanthognathus*, *M. richardsoni*, and *M. pennsylvanicus* with all variables included. Function 1 accounts for 65.4% of the variance with Function 2 accounting for the remaining 34.6%.

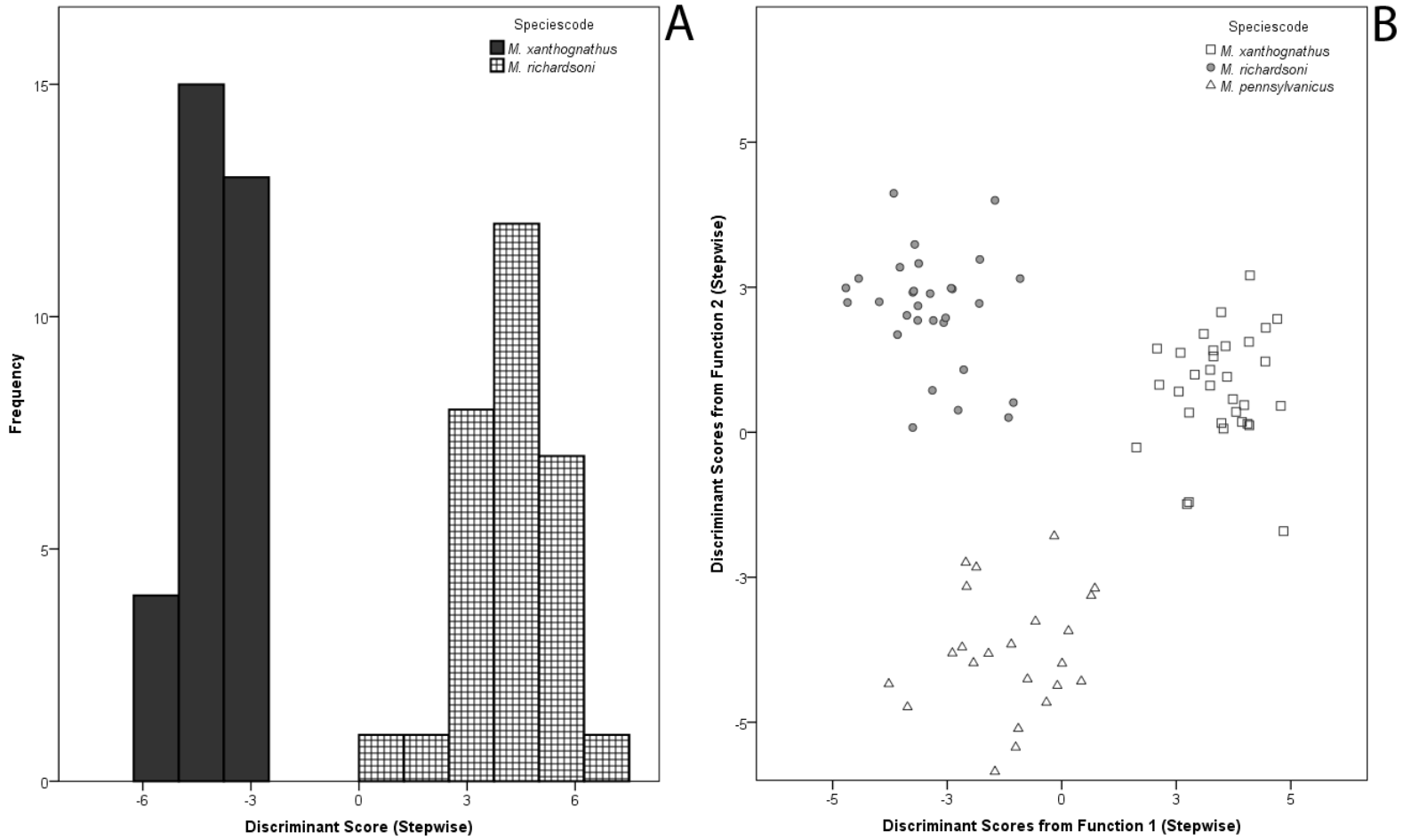

Fig. 9 - A) Results of Discriminant Analysis for *Microtus xanthognathus* and *M. richardsoni* with only those variables selected by the stepwise analysis and B) Results of Multidiscriminant Analysis with first two scores plotted, against each other for *M. xanthognathus*, *M. richardsoni*, and *M. pennsylvanicus* with only those variables selected by the stepwise analysis. Function 1 accounts for 57.7% of the variance with Function 2 accounting for the remaining 42.3%.

Discussion

Previous studies have primarily separated *Microtus richardsoni* from *M. xanthognathus* by the presence of a bulbous anterior complex of the lower m_1 of *M. richardsoni* (Burns 1982; Semken & Wallace 2002) (**Fig. 10**). The current study provides an alternative method of differentiating the two species even if the anterior complex is slightly damaged or missing. In comparison with other 5-closed triangle *Microtus*, *M. xanthognathus* m_1s have a more pronounced lingual curvature (**Fig. 10**). *M. pennsylvanicus* tend to have much sharper salient angles in comparison to the other two species. **Figure 11** shows a linear scatter plot of all 21 landmarks from all specimens used here.

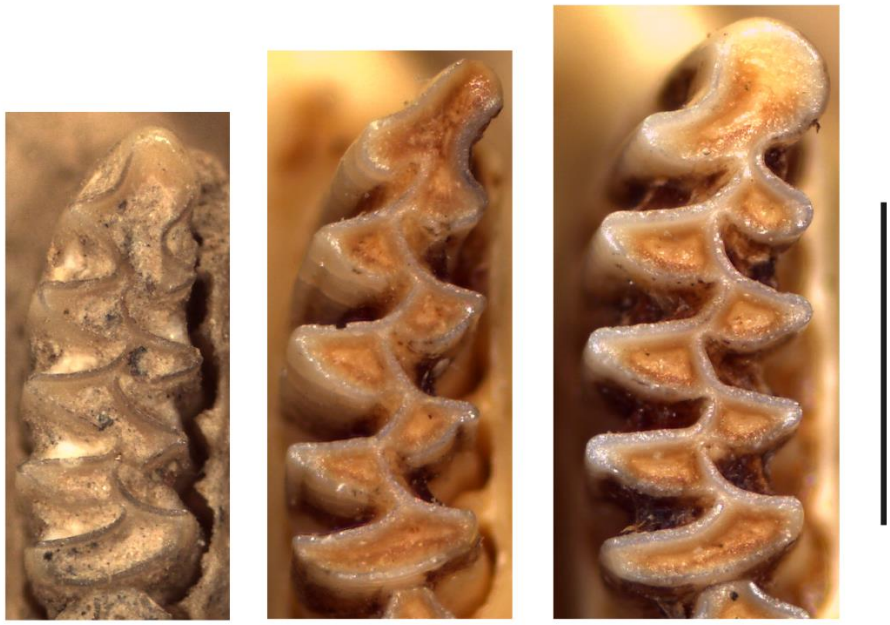

Fig. 10 - Occlusal views of lower first molars from: Left) *Microtus pennsylvanicus* (left molar, rotated for the purpose of this figure), collected from Clark's Cave tentative ID CCD-201L; Center) *M. xanthognathus* (right molar), USNM-109459; *M. richardsoni* (right molar), USNM-170391. Scale bar = 2mm.

The five most significant variables that make up the discriminant function separating *M. xanthognathus* and *M. richardsoni* are listed in **Table 3**. The more robust nature of the *M.*

richardsoni triangles seems to be driving the function. Four of the five variables (Y13, X9, Y10, Y17) are from landmarks on the salient edge of the triangles. **Figure 11** shows that for landmarks 10, 13, and 17 *M. xanthognathus* consistently occupies a more anterior location (higher "morphospace") on the tooth than *M. richardsoni*. *M. xanthognathus* m1s show a more pronounced curvature compared to most other *Microtus* species as seen from the plotting of landmark 9 (**Fig. 11**). The variable with the fourth strongest correlation with the function is X19. This may be a character that would have been easily overlooked, but upon looking, R2 on *M. richardsoni* tend to have a more anterior curve to them. This results in landmark 19 plotting in a higher morphospace for *M. richardsoni*.

When comparing the variables selected for differentiating *M. xanthognathus* and *M. richardsoni* vs. all three species (inclusion of *M. pennsylvanicus*) there are many similarities, but also important differences. The five most correlated variables that make up multidiscriminant function 1 separating *M. xanthognathus*, *M. richardsoni*, and *M. pennsylvanicus* are listed in **Table 6**. The top five most correlative variables with function 1 are all from salient triangle angles (X9, Y13, X7, X10, Y10). As can be seen from **Figure 9a** function 1 separates *M. xanthognathus* from the other two species. It is not surprising that variables X9 and X7 are among the top five most correlated as they show the characteristic lingual curvature on the labial side of the M_1, which is diagnostic of *M. xanthognathus* (Semken & Wallace 2002; **Fig. 11**). Variables X10 and X13 correspond to T6 and T4 respectively. Both these variables show a more lingual occupation of "morphospace". **Figure 11** shows that variable Y10 for *M. xanthognathus* and *M. pennsylvanicus* plot in a higher morphospace than *M. richardsoni*.

As seen in **Fig. 8b**, MDA function 2 separates *M. richardsoni* from *M. pennsylvanicus*. The five most correlated variables with function 2 can be seen in **Table 6**. **Figure 11** shows that

landmarks 10 and 13 in *M. pennsylvanicus* plot more anteriorly than *M. richardsoni*. This is logical as S4 and S6 are angled anteriorly in *M. pennsylvanicus* and posteriorly to medially in *M. richardsoni*. Variables Y8, Y2, and Y15 also show strong correlation with function 2 and **Figure 11** indicates that *M. richardsoni* have deeper more anteriorly curved R1, R4, and R7.

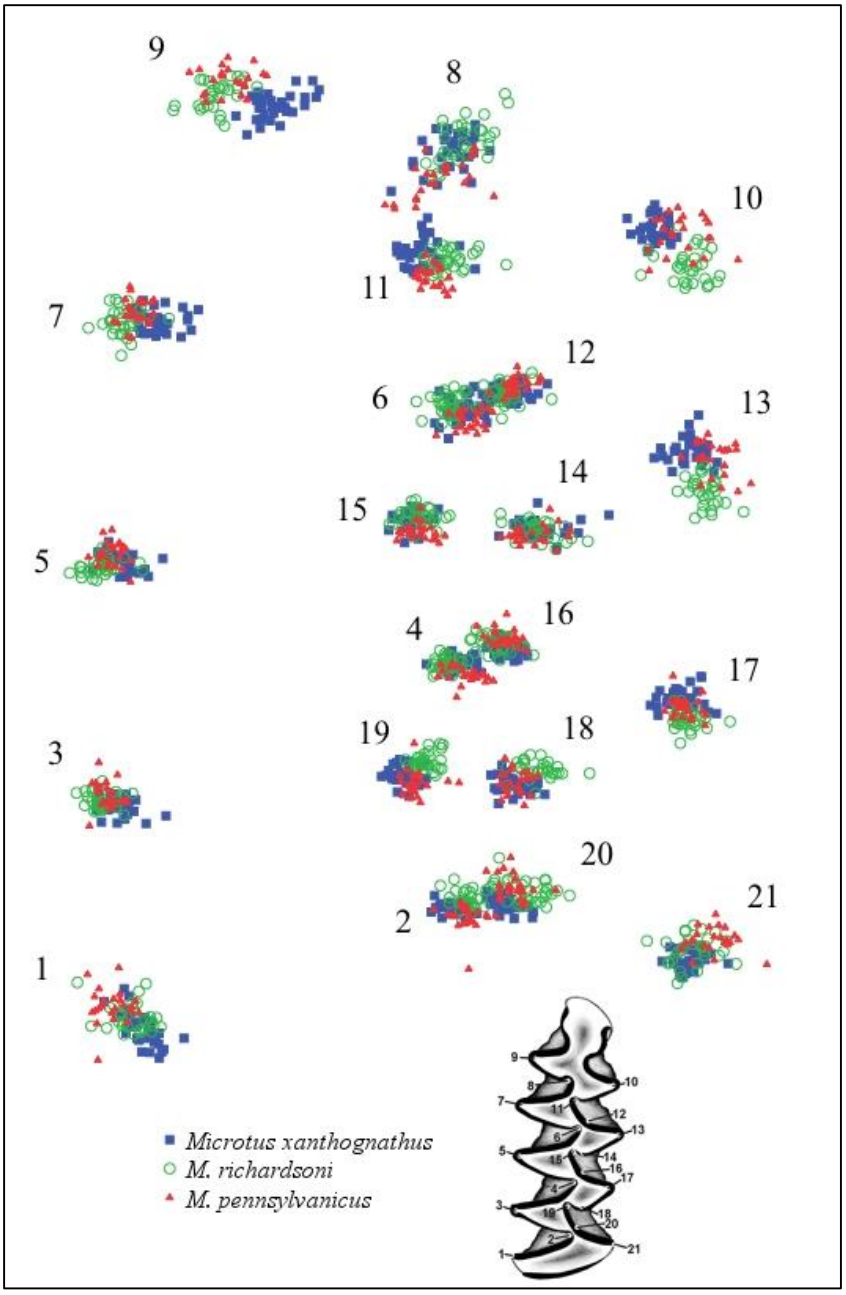

Fig. 11 - Generalized scatter plot of the 21 landmarks (see figure 3) for all 3 species. Note that the greatest spread of the landmarks (and most telling morphology) is at the anterior end of the tooth; whereas the posterior-medial portion exhibits the least variation (more conservative). Also note the distinct spread of landmarks for each of the three taxa: *Microtus xanthognathus* exhibiting a relatively "thin" tooth (more medially placed landmarks), *M. richardsoni* exhibiting a very "wide" tooth, and *M. pennsylvanicus* exhibiting an intermediate spread. Numbers next to clusters indicate the landmark.

Errors in proper identification of the species in the MDA may have stemmed from an unequal sample size of *M. pennsylvanicus* in comparison to the other two species. As in Wallace

(2006), a standard discriminant function produces better separation, in all of the analyses, than with a stepwise discriminant. Such disparity may indicate that *Microtus* m_1s share enough morphological similarity that all variables should be included. Careful evaluation of each variable should be considered before elimination from any future analyses.

Conclusions

Wallace (2006) used a Bookstein (1991) shape coordinates method to analysis landmark data, resulting in variables produced from landmarks 2 and 9 (**Fig. 6**) being excluded from said analysis, in order to align the remaining landmarks. The study presented here points to the importance of those two landmarks in identifying the three *Microtus* species in this and future studies. In the stepwise DA of *M. xanthognathus* and *M. richardsoni* variables X9 and Y9 were significant to classifying the taxa (**Table 2**). In the stepwise MDA of *M. xanthognathus*, *M. richardsoni* and *M. pennsylvanicus*, X9, Y9, and Y2 are the three most important variables in classifying the specimens, based on Wilks' Lambda values (**Table 5**). The importance of these variables in the stepwise DA's points to the favorable use of a GPA over GRF for this and similar *Microtus* studies.

"Bulbous" or "broad" are vague terms, and leave room for question when trying to differentiate between the m_1 of a *M. richardsoni* and *M. xanthognathus*. This study provides a more concrete method of differentiating the two. This study also builds on the work produced by Wallace (2006) and provides an improved method for differentiating *Microtus* lower first molars. Proper identification of *Microtus* and other microtine species will aide in the proper reconstruction of paleoenvironments in the Quaternary; especially important for species that share, or have shared, similar geographic ranges. Studies such as these can help shed light on errors on identifications in the past and open new doors for future research.

CHAPTER 4

RE-EXAMING THE CLARK'S CAVE *MICROTUS* USING MORPHOMETIRCS

Three distinct tests will be performed in this chapter, looking for: 1) the presence of *Microtus richardsoni*; 2) the ratio of *M. pennsylvanicus* morph vs *M. xanthognathus* morph, and 3) the ratio / presence of *M. pinetorum* and *M. ochrogaster*, in the CC deposit. The first two tests use 106 5-closed triangle morph *Microtus* m_1s collected from Clark's Cave (ETSU group) to test traditional vs morphometric techniques of identification. Of those specimens, 87 had a lower first molar length of less than 3.2 mm (classified as *M. pennsylvanicus* morph using the traditional measurement division), and 19 possessed an m_1 length of greater than or equal to 3.2mm (assigned to *M. xanthognathus*).

Clark's Cave *Microtus richardsoni* test

Results

PCA.

Following the methods outlined in chapter 2, results of PCA show noticeable separation between the known *M. richardsoni* specimens and the *M. pennsylvanicus* and *M. xanthognathus* fossils (**Fig. 12)**. *Microtus richardsoni* specimens plot in the bottom right quadrant of (**Fig. 12)**, while the majority of the unknowns plot within the *M. pennsylvanicus* cluster or *M. xanthognathus* cluster. The first two eigenvalues (10.214 and 5.236) make up 24.320% and 12.467% of the variance respectively. Sufficient separation is shown by the PCA, warranting a MDA be performed.

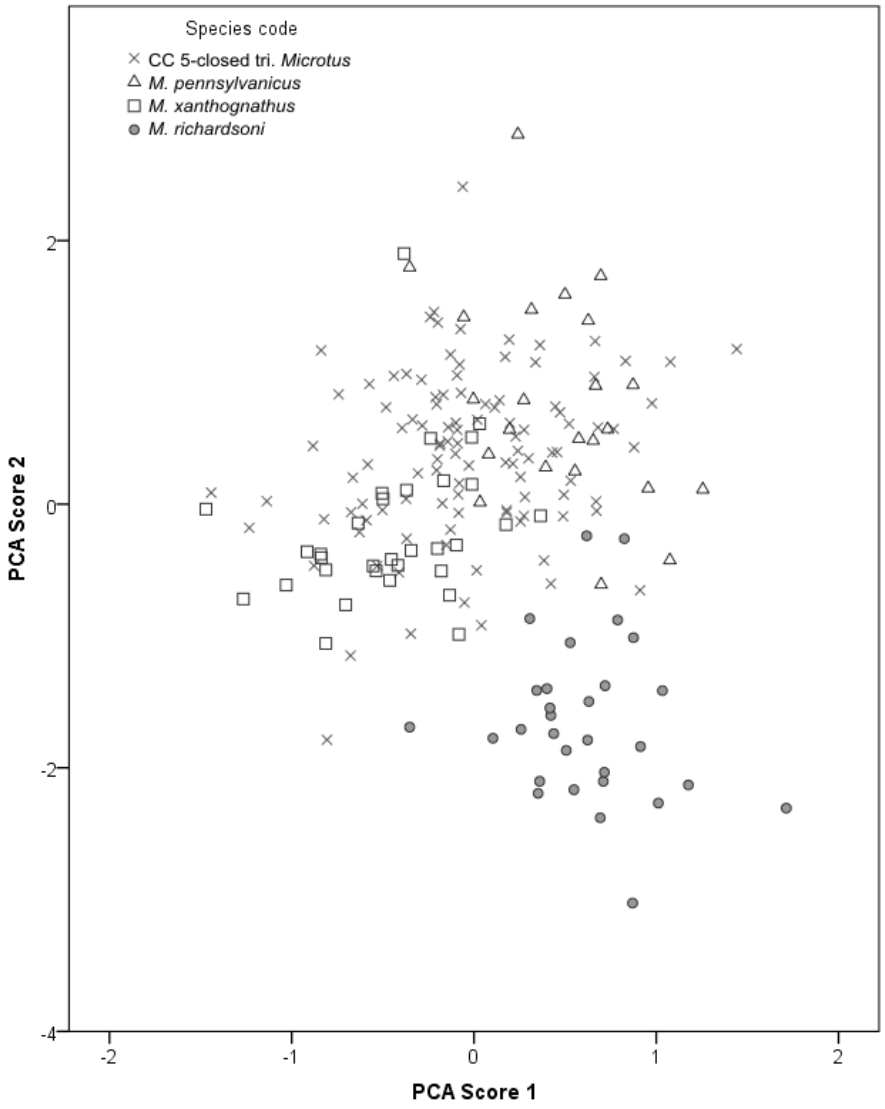

Fig. 12. - Results of Principle Component Analysis with first two scores plotted, against each other for *Microtus pennsylvanicus*, *M. xanthognathus, M. richardsoni,* and 5-closed triangle morph *Microtus* from Clark's Cave (CC). PCA score 1 is responsible for 24.32% of the variance with PCA score 2 responsible for 12.47% of the variance. Known specimens were wild caught and collected skin and skull.

MDA.

Unlike in the PCA there is not a uniform break between the *M. richardsoni* specimens and the unknowns, especially amongst the unknowns assigned as MPM (**Fig. 13a**). Of the 106 unknowns: 31 (29.2%) were classified as *M. pennsylvanicus*, 45 (41.5%) were classified as *M.*

xanthognathus, and 31 (29.2%) were classified as *M. richardsoni* (**Table 6**). The majority of the unknowns classified as *M. xanthognathus* grouped with the known specimens of that species. The same is not true of the unknowns classified as *M. pennsylvanicus*; with the bulk of these specimens grouping within the middle range between the three knowns, spilling into all three clusters. Function 1 has an eigenvalue of 17.109 and accounts for 65.4% of the variance. Function 2 has an eigenvalue of 9.069 accounting for the remaining 34.6% of the variance.

Table 7 - Classification and Cross-Validated Table from Multidiscriminant Analysis. Species Code 1) *M. pennsylvanicus*, 2) *M. xanthognathus*, 3) *M. richardsoni*, Ungrouped Cases are the Unknown 5 Closed Triangle Morph *Microtus*.

			Predicted Group Membership			
		Species Code	1	2	3	Total
Original	Count	1	23	0	0	23
		2	0	32	0	32
		3	0	0	30	30
		Ungrouped cases	31	44	31	106
	%	1	100	0	0	100
		2	0	100	0	100
		3	0	0	100	100
		Ungrouped cases	29.2	41.5	29.2	100
Cross-validated	Count	1	22	0	1	23
		2	0	32	0	32
		3	2	0	28	30
	%	1	95.7	0	4.3	100
		2	0	100	0	100
		3	6.7	0	93.3	100

When a stepwise MDA is preformed there is a change in the ratio of unknowns assigned to either *M. xanthognathus* or *M. pennsylvanicus* (**Fig. 13b**). Number of unknowns classified as *M. richardsoni* remained the same at 31 (making up 29.2% of the unknowns); however unknowns classified as *M. pennsylvanicus* increased to 42 (39.6%), while the number of *M. xanthognathus* classified fell to 33 (31.1%) (**Table 8**). Function 1 has an eigenvalue of 7.989 responsible for 59.9% of the variance. Function 2 has an eigenvalue of 5.358 responsible for

40.1 % of the variance. The stepwise multidiscriminant function isolated 11 significant variables (X9, Y19, Y2, Y9, X21, Y10, X11, Y17, X10, Y4, Y16) with a probability F = .05.

Table 8 - Classification and Cross-Validated Table from Stepwise Multidiscriminant Analysis. Species Code 1) *M. pennsylvanicus*, 2) *M. xanthognathus*, 3) *M. richardsoni*, Ungrouped Cases are the Unknown 5-closed Triangle Morph *Microtus*.

			Predicted Group Membership			
		Species Code	1	2	3	Total
Original	Count	1	23	0	0	23
		2	0	32	0	32
		3	0	0	30	30
		Ungrouped cases	42	33	31	106
	%	1	100	0	0	100
		2	0	100	0	100
		3	0	0	100	100
		Ungrouped cases	39.62264	31.13208	29.24528	100
Cross-validated	Count	1	23	0	0	23
		2	0	32	0	32
		3	0	0	30	30
	%	1	100	0	0	100
		2	0	100	0	100
		3	0	0	100	100

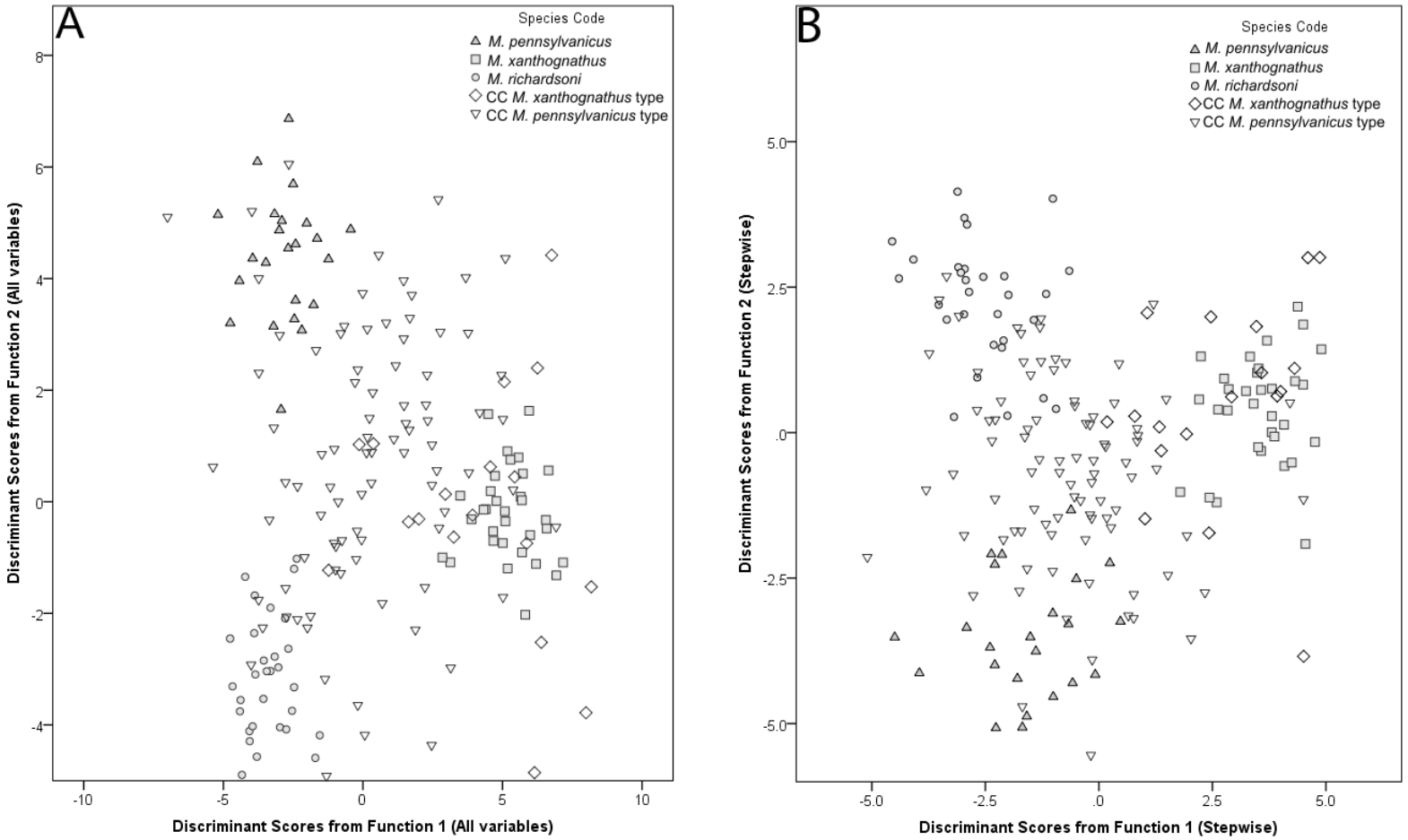

Fig. 13 - Results of Multidiscriminant Analysis with first two scores plotted, against each other for *Microtus pennsylvanicus*, *M. xanthognathus*, *M. richardsoni*, and 5-closed triangle morph *Microtus* from Clark's Cave (CC) with A) all variables included. Function 1 accounts for 65.4% of the variance with Function 2 accounting for the remaining 34.6%, and B) with only those variables selected by the stepwise analysis. Function 1 accounts for 59.9% of the variance with Function 2 accounting for the remaining 40.1%. Known specimens were wild caught and collected skin and skull.

Discussion

Results of the PCA seems to support the notion that there were no *M. richardsoni* collected from the site; a not surprising result as fossil records only come out of the western US and Canada, similar to its current range today (Ludwig 1984) (**Fig. 1**). That is not to suggest that it would be impossible to find *M. richardsoni* in an eastern deposit as there are taxa such as *M. xanthognathus* which has much wider extra-limital fossil ranges. Circular reasoning is commonly used in identifying *Microtus* spp. and should be avoided to assure more accurate and unbiased identifications. If no one is expecting to find *M. richardsoni* in eastern deposits they could be misidentified as *M. xanthognathus*. Guilday and Bender (1960) discuss the variation seen in yellow-cheeked vole molars and how some specimens show a bulb like anterior complex. A lack of *M. richardsoni* in eastern NA could be an indication that: 1) their range did not drastically shift as a result of glaciation, 2) the species is not that old, or 3) that there is a sampling error.

After running an MDA I expected a more clear separation between the *M. richardsoni* and the rest of the specimens, because of the separation seen from the PCA. Results from chapter 3 showed, if good separation is seen from the results of a PCA, the results from a MDA will show greater separation. However, the opposite proved true as the MDA classified 29% of the unknown specimens as *M. richardsoni*. As I see it, the PCA depicts a more accurate representation of the *Microtus* collected from the site and I do not feel comfortable classifying any of the specimens as water voles. Data presented in **Figure 13a** and **Table 7** show that all of the unknowns classified as *M. richardsoni* were assigned as *M. pennsylvanicus* morph. These unknowns in both the standard and stepwise MDA do not fully penetrate the *M. richardsoni* cluster, unlike the unknowns that grouped with the other two known clusters. Unknowns

classified as *M. richardsoni* group around the central region of the chart. For *M. pennsylvanicus* and *M. xanthognathus* clusters, unknowns show up at the extreme end of their respected clusters.

The results suggest that all of the unknowns classified as *M. richardsoni* were assigned to the MPM group. Unknowns assigned as MXM grouped in the *M. xanthognathus* third of the graph. More than the 19 specimens in the MXM group were classified as *M. xanthognathus*, meaning that some of the MPM group were classified as *M. xanthognathus*, as was expected. When visually comparing tooth morphology, *M. richardsoni* and *M. xanthognathus* m_1s look more similar to each other than they do to *M. pennsylvanicus* (Semken & Wallace 2002). At first glance this is true for size and sharpness of the salient angles of the triangles (**Fig. 10**). *M. richardsoni* on average have the largest m_1 of the NA *Microtus*, and all of the MPM group molars are less than 3.2mm in length. Their size coupled with the fact that during the initial classification stage there were very few teeth that even resembled a *M. richardsoni* morphology, support Guilday et al. (1977)'s assessment that there are no *M. richardsoni* in the Clark's Cave deposit.

A number of potential factors may have led to the MDA classifying unknowns as *M. richardsoni*. 1) The variant nature of *M. pennsylvanicus* occlusal tooth morphology. It would not be surprising that a population of meadow voles developed a morphology resembling the triangle orientation of water voles. 2) Assumption 1 from chapter 2 is false and *M. pennsylvanicus* has changed morphologically since the Pleistocene. 3) At the end Pleistocene, the climate and landscape of Virginia would be different than present and *M. pennsylvanicus* may have adapted a set of characters more similar to another *Microtus* species as a response to environmental pressures. 4) Weathering process may have altered some of the MPM group leading to misclassification. 5) A fifth and more likely scenario is that other than T6 on *M.*

richardsoni, the water vole and meadow vole share more anteriorly pointing salient angles, in comparison to the taiga vole. After performing a superimposition and normalizing size, the orientation of the salient angles would group *M. richardsoni* and *M. pennsylvanicus* specimens closer together in comparison to *M. xanthognathus* specimens.

As a result, I feel comfortable in stating that there were no *M. richardsoni* collected in the (ETSU) sample and most likely the sample from Guilday et al. (1977). Consequently, *M. richardsoni* will no longer be considered a species option in the MXM specimens. This should increase the accuracy on the rest of the analyses. Removing one of the species allows the analysis to focus on just the characters that separate out *M. pennsylvanicus* and *M. xanthognathus* (in this case). With each subsequent group added to a DA, a weaker result is produced. Ideally MDA's should be used as a means of parsing out groups (species, options, etc.), performed in this study.

Clark's Cave *Microtus pennsylvanicus* morph / *M. xanthognathus* morph ratio test

Results

PCA.

Results of the PCA do not show any unsurprising trends. A rough line of separation seems to be running diagonally from the bottom left to the top right (**Fig. 14**). MXM unknowns plot well with their known counterparts; while MPM unknowns show more mixing. The first two eigenvalues (7.988 and 8.261) make up 19.019% and 8.261% of the variance respectively. Sufficient separation is shown in the PCA that an MDA was worth performing.

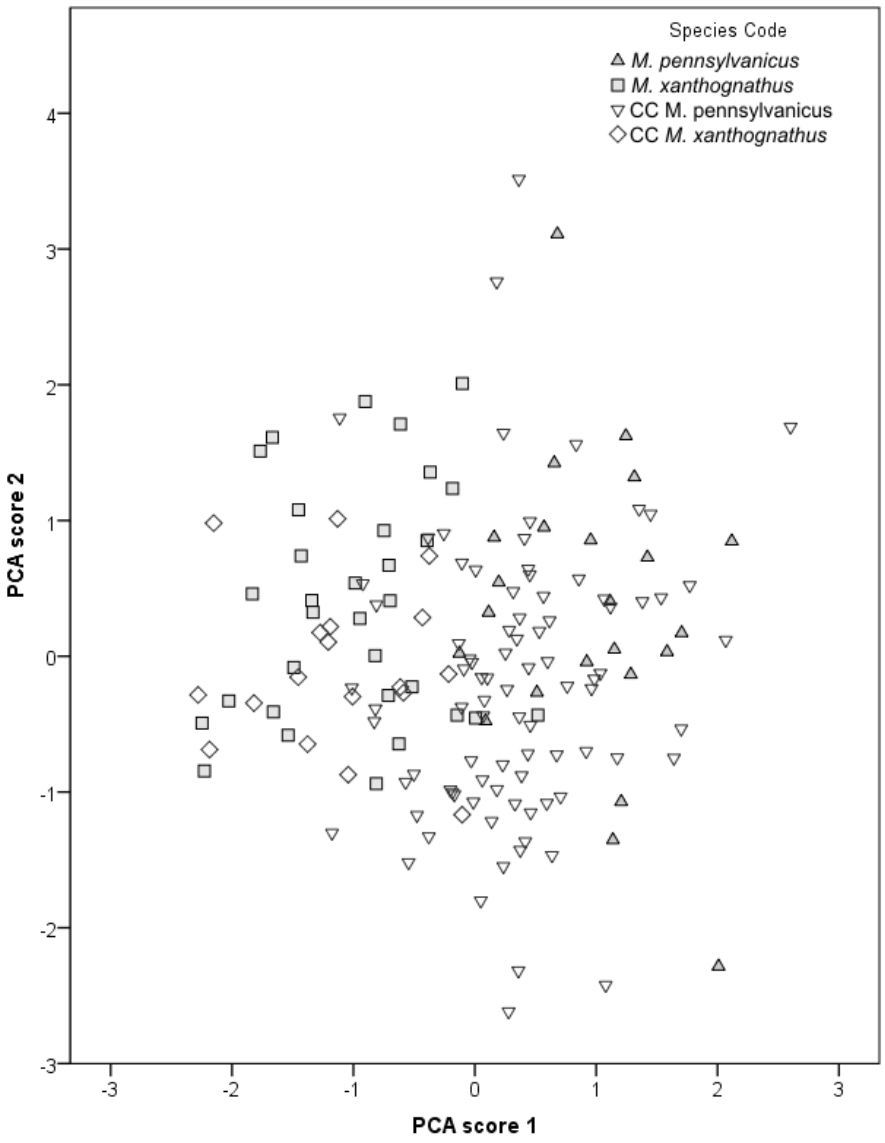

Fig. 14 - Results of Principle Component Analysis with first two scores plotted against each other for *Microtus pennsylvanicus*, *M. xanthognathus*, and 5-closed triangle morph *Microtus* from Clark's Cave (CC). PCA score 1 accounts for 19% of the variance and PCA score 2 accounts for 8.3% of the variance. Known specimens were wild caught and collected skin and skull.

DA.

Results of the DA give a similar result to the PCA. Specimens fall out on one side or the other, but there are also a lot of unknowns that fall near the boundary of both species (**Fig. 15a)**. Of the 106 unknown specimens: 38 (35.8%) were classified as *M. pennsylvanicus* and the

remaining 68 (64.2%) were classified as *M. xanthognathus* (**Table 9**); a noticeable amount of variation from the assigned morphotypes. Results of the stepwise DA shows a more even separation than the standard DA and PCA. A cluster of *M. pennsylvanicus* morphs still remain in the middle, but they are much more concentrated (**Fig. 15b**). Of the 106 unknown specimens: 47 (44.3%) were classified as *M. pennsylvanicus* and the remaining 59 (55.7%) were classified as *M. xanthognathus* (**Table 10**). Nine variables were used in the stepwise analysis: (X9, Y9, Y12, Y2, X14, Y17, X3, Y19, Y16).

Table 9 - Classification and Cross-Validated Table from Discriminant Analysis. Species Code 1) *Microtus pennsylvanicus*, 2) *M. xanthognathus*, the Ungrouped Cases are the Unknown 5-closed Triangle Morph *Microtus*.

			Predicted Group Membership		
		Species Code	1	2	Total
Original	Count	1	23	0	23
		2	0	32	32
		Ungrouped cases	38	68	106
	%	1	100	0	100
		2	0	100	100
		Ungrouped cases	35.8490566	64.1509434	100
Cross-validated	Count	1	21	2	23
		2	3	29	32
	%	1	91.30434783	8.695652174	100
		2	9.375	90.625	100

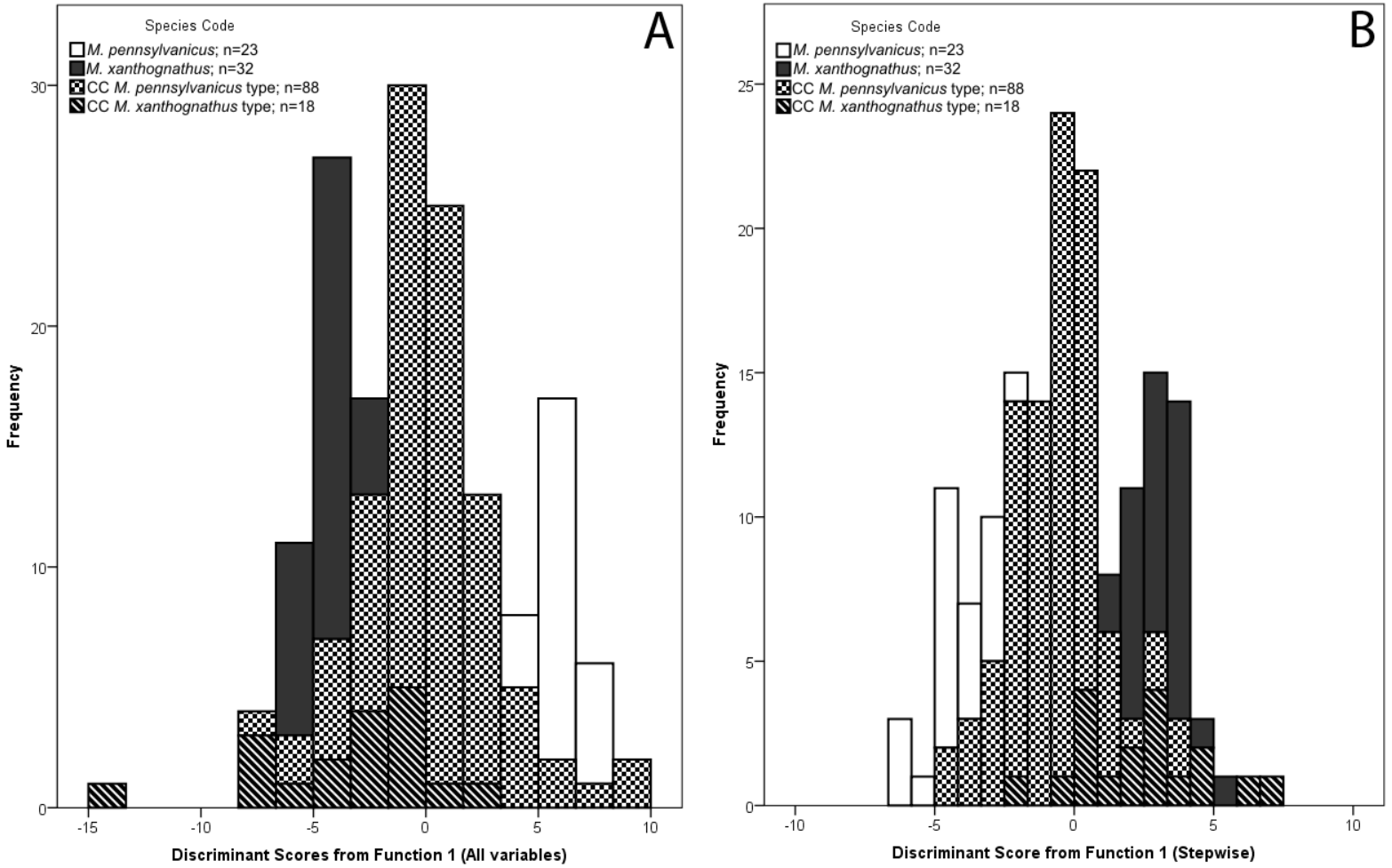

Fig. 15 - Results of Discriminant Analysis for *Microtus pennsylvanicus*, *M. xanthognathus*, and Clark's Cave (CC) unknowns with A) all variables included and B) only those variable selected by the stepwise analysis. Known specimens were wild caught and collected skin and skull.

Table 10 - Classification and Cross-Validated Table from Stepwise Discriminant Analysis. Species Code 1) *Microtus pennsylvanicus*, 2) *M. xanthognathus*, Ungrouped Cases are the Unknown 5-closed Triangle Morph *Microtus*.

			Predicted Group Membership		
		Species Code	1	2	Total
Original	Count	1	23	0	23
		2	0	32	32
		Ungrouped cases	47	59	106
	%	1	100	0	100
		2	0	100	100
		Ungrouped cases	44.33962264	55.66037736	100
Cross-validated	Count	1	23	0	23
		2	0	32	32
	%	1	100	0	100
		2	0	100	100

Discussion

Both the DA and the stepwise DA indicate that there is a much higher proportion of *M. xanthognathus* in the deposit than would previously have been assumed, helping confirm the conclusion that size alone is an inadequate method of differentiating MPM from *M. xanthognathus*. Morphological analyses should be the primary focus of future and past identification. Ideally whole dentitions should be used for corrected identifications. However, when working in the fossil record, complete *Microtus* skulls are few and far between.

It should not be surprising that the average length of MPM and *M. xanthognathus* molars from the past are different than that of modern specimens. *M. pennsylvanicus* occlusal molar patterns have already been shown to have high levels of variation, it is not that hard to believe that size will vary as well. A host of ecological pressures could select for different size and morphology. With time averaging you could have very different populations providing different

morphologies. Even within the same depositional time range, a multitude of predators at the sight may have significantly different hunting ranges pulling from different populations.

Clark's Cave is so far from the current range that it should not be a surprise that there is a significant size difference in some *M. xanthognathus* specimens. Bergmann's rule could be a simple answer to this question. Virginia is much further south than the arctic. The taiga vole has a limited range today; were it to have a much larger southern range today, I see no reason why we wouldn't see significant variation is size. Though I know of no study, it's worth testing variation in occlusal molar pattern in sympatric vole species, in comparison to populations of those same species that are isolated from each other. To see if competition over the same resources causes a change in morphology. If this were to occur, size and morphology differences could be the result of competition in non-analog faunas.

The useable minimum number of individuals (MNI) of MPM collected from the ETSU sample was 48 specimens (right m_1). The useable MNI of *M. xanthognathus* (ETSU sample) was 11 (right m_1). Total this puts the useable MNI for five closed triangle morph *Microtus* at 59. A DA was run using these numbers to allow for comparison to the MNI's reported in Guilday et al. (1977). Of the 59 specimens: 21 (35.6%) were classified as MPM, the remaining 38 (64.4%) specimens were classified as *M. xanthognathus* (**Table 11**).

Table 11 - Classification and Cross-Validated Table from Discriminant Analysis. Species Code 1) *Microtus pennsylvanicus*, 2) *M. xanthognathus*, the Ungrouped Cases are the Unknown 5-closed Triangle Morph *Microtus*.

			Predicted Group Membership		
		Species Code	1	2	Total
Original	Count	1	23	0	23
		2	0	30	30
		Ungrouped cases	21	38	59
	%	1	100	0	100
		2	0	100	100
		Ungrouped cases	35.59322034	64.40677966	100
Cross-validated	Count	1	21	2	23
		2	2	28	30
	%	1	91.30434783	8.695652174	100
		2	6.666666667	93.33333333	100

Using a DA the MNI of *M. xanthognathus* from the ETSU sample is 38, accounting for 64.4% of the total MNI for 5-closed triangle morph *Microtus* collected from the site. Though this is a much smaller sample size than that collected in Guilday et al. (1977) I feel the same ratio can be applied to that sample collected. There the MNI of MPM collected was 950 (m_1s). The MNI on the subsequent *M. xanthognathus* was 511 (m_1s). Resulting in a total MNI of 5 closed triangle morph *Microtus* as 1461 (m_1s). Applying the ratio stated above on this sample would result in an MNI of roughly 941 *M. xanthognathus* and 520 MPM, resulting in a nearly 180 degree flip in classification.

Without whole skulls it is difficult to determine the ratio of *M. pennsylvanicus* to *M. chrotorrhinus*. I do not feel comfortable using the ratio of upper M^2s or M^3s and extrapolating to the number of MPM m_1s. Guilday et al. (1977) obtained adjusted MNI's for *M. pennsylvanicus* and *M. chrotorrhinus* in this way. All three of these teeth are different sizes and will therefore, likely preserved in different quantities. Examination of the collected M^3s (using techniques in Guilday (1982b) and Semken & Wallace (2002)) show all three species of the 5-closed triangle

morph *Microtus* are present. Therefore the best this study can say is that both MPM species are present at the sight. This is the safest assumption.

Clark's Cave *Microtus pinetorum* / *M. ochrogaster* ratio test

For this study 194 specimens *M. pinetorum* from the Carnegie collection were used in the analysis along with eight 3-closed triangle morph *Microtus* from the ETVP collection. Using traditional methods (van der Meulen 1978; Martin 1987; Martin 1991; Semken & Wallace 2002) 43 of the total 202 specimens were classified as *M. pinetorum* and the remaining 155 were classified as *M. ochrogaster*. A stark difference from only *M. pinetorum* being present in the deposit.

Results

PCA.

Results of the PCA shows a distinct gap between the two clusters created. With the *M. ochrogaster* group clustered at the bottom right of **Figure 16a** and the *M. pinetorum* group clustered in the upper left section of the graph. Some intermixing of the two species occurs within their respected clusters, suggesting misidentifications were made. The first two eigenvalues (12.893 and 5.540) make up 30.697% and 13.190% of the variance respectively. Results of the PCA showed sufficient separation that a MDA was worth preforming.

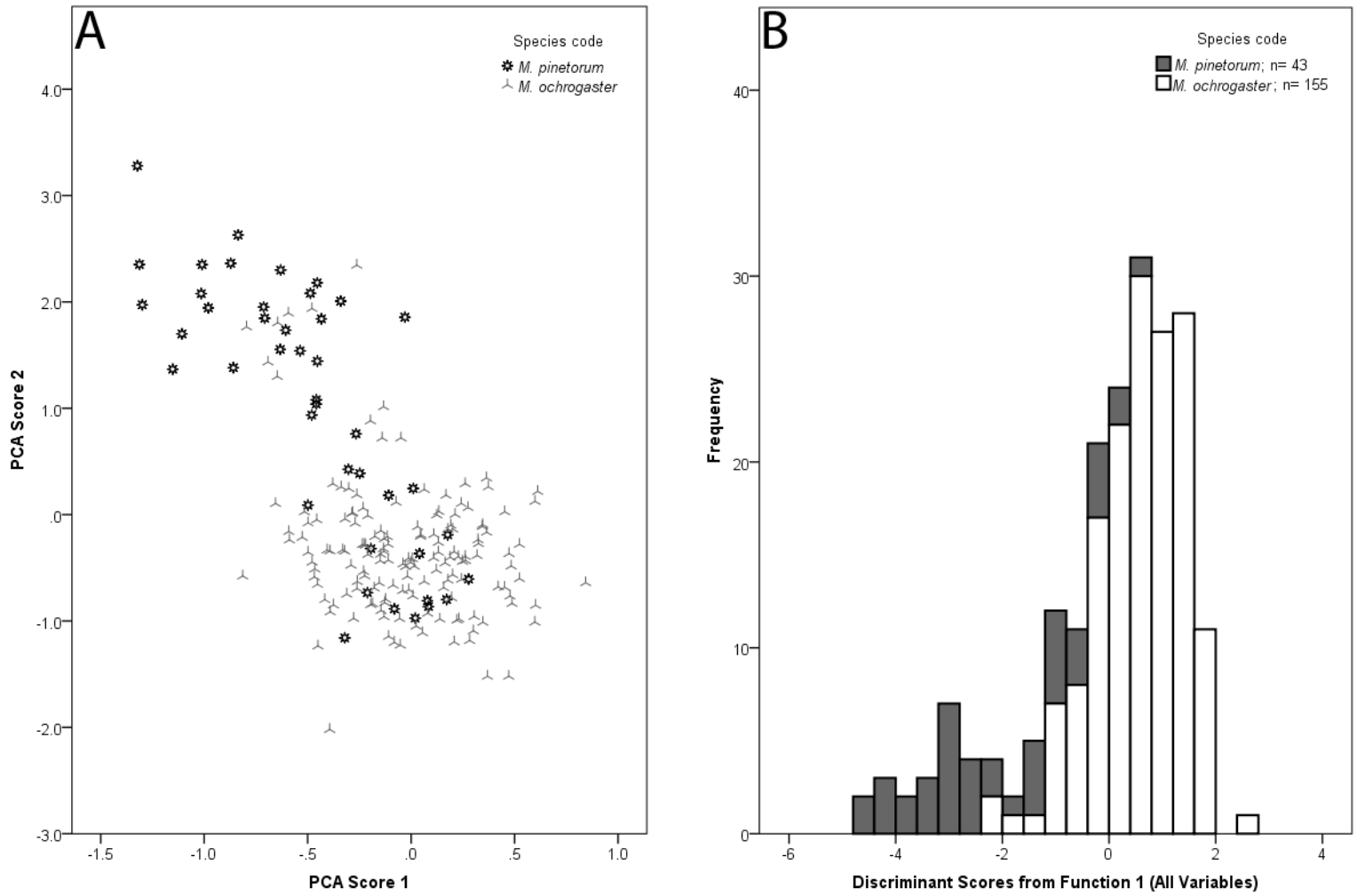

Fig. 16 - A) Results of Principle Component Analysis with first two scores plotted, against each other for *Microtus pinetorum* and *M. ochrogaster*. PCA score 1 accounts for 30.7% of the variance with PCA score 2 accounting for 13.2% of the variance and B) Results of Discriminant Analysis for *M. pinetorum* and *M. ochrogaster* with all variables included.

DA.

No modern analogs (knowns) were included in this study. A sizeable modern comparative sample was not obtained. Therefore, no specimen was assigned as an unknown in this analysis. Results of the discriminate may have shown some variance if modern specimens were included. **Figure 16b** shows separation amongst the two species. Overlap occurs towards the middle of the graph. Of the 43 specimens assigned as *M. pinetorum*: the discriminate classified 33 (76.7%) of these as woodland voles and the other 10 (23.3%) as prairie voles (**Table 12**). Of the 155 specimens assigned as *M. ochrogaster*: the discriminate classified 11 (7.1%) of these as woodland voles and the other 144 (92.9%) specimens as prairie voles.

Table 12 - Classification and Cross-Validated Table from Discriminant Analysis. Species Code 1) *Microtus pinetorum,* 2) *M. ochrogaster*.

			Predicted Group Membership		
		Species Code	1	2	Total
Original	Count	1	33	10	43
		2	11	144	155
	%	1	76.74418605	23.25581395	100
		2	7.096774194	92.90322581	100
Cross-validated	Count	1	24	19	43
		2	20	135	155
	%	1	55.81395349	44.18604651	100
		2	12.90322581	87.09677419	100

Upon observation of the PCA results, 7 *M. ochrogaster* are plotted in the *M. pinetorum* bubble and 17 *M. pinetorum* are plotted in the *M. ochrogaster* range. Interpreted to be specimens that fall into the in-between category (where it was hard to confidently assign which species the molar belonged to). These 24 teeth were then assigned to the opposite species from which they were originally identified and a DA was run again. Resulting in a 99% grouping of

specimens as they were newly assigned (**Table 13**). With all of the *M. pinetorum* grouping correctly and only 2 *M. ochrogaster* grouping as woodland voles.

Table 13 - Classification and Cross-Validated Table from Discriminant Analysis, with Adjusted Classifications. Species Code 1) *Microtus pinetorum*, 2) *M. ochrogaster*.

			Predicted Group Membership		
		Species Code	1	2	Total
Original	Count	1	33	0	33
		2	2	163	165
	%	1	100	0	100
		2	1.2121	98.7878	100
Cross-validated	Count	1	32	1	33
		2	4	161	165
	%	1	96.9696	3.03	100
		2	2.4242	97.5757	100

Discussion

I feel confident saying that *M. ochrogaster* was collected from the Clark's Cave deposit, based on my identification and the results of the PCA and DAs. Both methods support this conclusion, suggesting that using geographic probability to classify 3-closed triangle *Microtus* in this case was a poor assumption. The ratio of *M. pinetorum* to *M. ochrogaster* was not as expected. Initial expectations were that a few prairie voles would show up in the deposit. The current study suggests that the deposit is much richer in prairie voles than woodland voles.

The initial discriminate classifies about 21% (**Table 12**) of the 3-closed triangle morph *Microtus* molars to be *M. pinetorum*. While, the DA with modified identifications classifies only about 17% (**Table 13**) of the 3-closed triangle morph *Microtus* molars to be *M. pinetorum*. Results from the initial discriminate were less conclusive because a DA will try to group like specimens together. This resulted in the analysis trying to group some *M. ochrogaster* as *M.*

pinetorum and vice versa. After identifications were adjusted / corrected base off the PCA results, classifications made by the second DA were much cleaner.

Results of the discriminate analysis were most helpful in identifying the "in-between" 3-closed triangle morph *Microtus* specimens. While examining the specimens under a scope it became very obvious that there were three types of m_1s. Those that were clearly *M. pinetorum* (**Fig. 17**), those that were clearly *M. ochrogaster* (**Fig. 17**), and those that showed characteristics of both species. Results the PCA and DAs show that I misidentified some of these in-between specimens, as was expected. Using morphometric analysis helps in eliminating some of the guess work.

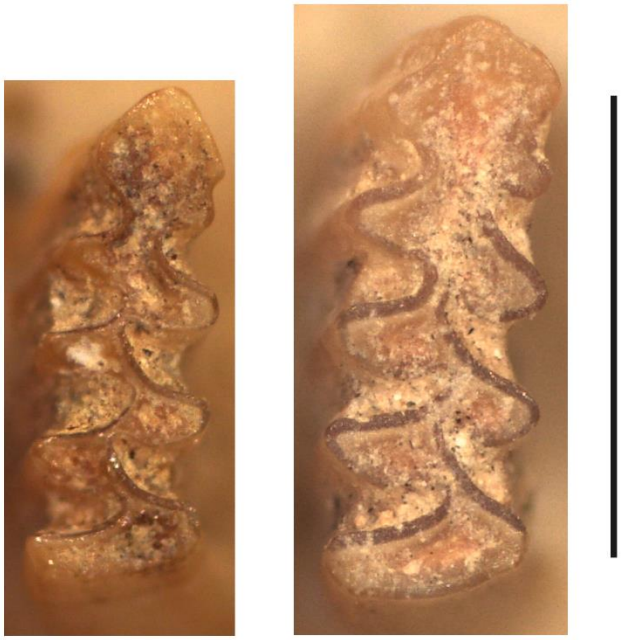

Fig. 17 - Occlusal view of right lower first molars for: Left) *Microtus ochrogaster*, tentative ID TCT-35R; *M. pinetorum*, tentative ID TCT-252R. Both specimens part of CM-24576. Scale bar = 2mm.

One of the limitations in using landmark data to perform a discriminate analysis is that some of your collection is not included in the analysis. Fragmented or damaged material was excluded from the analysis as it either deviates to far from the normal range or prohibited the placement of landmarks. Because of this I would expect a slightly higher proportion of *M. pinetorum* specimens. During the examination process it was evident that in general *M. pinetorum* like specimens showed more signs of weathering. In particular doming of the occlusal surface of the tooth (**Fig. 18**). In count and proportions *M. pinetorum* molars tended to show much higher signs of exaggerated doming, a strong indicator of digestion (Andrews 1990). Potential evidence that there was more than one predator source for the material in the deposit.

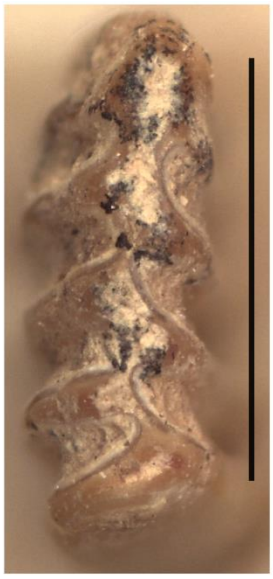

Fig. 18 - Severe doming of occlusal surface of *Microtus pinetorum* (CM-24576, tentative ID: TCT 100). Indicative of digestion. Scale bar = 2mm.

Both of these species occupy very different niches. Having both in the same deposits suggests one of two things. 1) That both a forested and more open grassland biome were within the hunting range of the raptor(s) roosting at the cave site at the time. 2) The two different species were deposited at different times, representing a changing landscape during glacial and interstadial periods. Dates on the deposit (Semken et al. 2010) would suggest that particular taxa

show periods of presence and absence in accordance with Heinrich events (Alley & MacAyeal 1994) and other climatic fluctuations. It should be noted that the lack of presence does not necessarily mean absence and should be considered in climate studies.

Conclusions

In using the Clark's Cave fossil deposit as a case study we see that when modern techniques of species identification can result in significant changes in species accounts. This was true of both 5 and 3 closed triangle morph *Microtus*, even resulting in the recording of a previously unreported taxa from the site (*M. ochrogaster*). These results stress the importance that these and similar techniques continue to be used and developed.

This study also brings to light the importance of going back and revisiting fossil collections in museums. Studies like Guilday et al. (1977) are important as they are the foundation upon which we build knowledge. Everything in our power should be done to strengthen our foundation as this can only lead to clearer more accurate studies in the future. Work presented here may not be classified as "sexy" and most journals these days are looking for new original research, but that should not dampen the importance of these studies. Someone could spend many lifetimes of research revisiting past studies.

Another important issue raised here is the danger of over classifying. Species level identifications are frequently sought, but the reality is that sometimes this is not feasible. Saying you can only take a particular taxon to Genus sp. still tells you something. It can also be dangerous to try and stretch and assume a classification. If incorrect this can then paint an improper interpretation of environment. Leaving something as Genus sp. can lead to someone developing a new technique in the future that can better solve this problem.

CHAPTER 5

CLARK'S CAVE BONE DEPOSIT

Taxonomic Remarks

Below is a tentative faunal list of species collected from CC 7/19/14 – 003 (**Table 14**). Material recorded in this section is limited to mammalian material that was identifiable.

Table 14 - Faunal List, Entrance 2, Site 7/19/14 -003, Clark's Cave.

MAMMALIA (Identified by M.H.S)	Scientific name	Common name	NISP	MNI
1	*Sorex arcticus*	Arctic shrew	2	1
2	*Sorex longirostris*	Southeastern Shrew	1	1
3	*Blarina* sp.	Short-tailed Shrew	36	3
4	*Parascalops breweri*	Hairy-tailed Mole	3	1
5	*Condylura cristata*	Star-nosed Mole	2	1
6	*Myotis* sp.	Little Brown Bats	17	11
7	cf. *Perimyotis* sp.	Pipistrelles	3	3
8	*Eptesicus fuscus*	Big Brown Bat	10	5
9	cf. *Lasiurus* sp.	Hairy-tailed Bats	8	6
10	cf. *Corynorhinus* sp.	Big-eared Bats	1	1
11	*Tamias* cf. *T striatus*	Eastern Chipmunk	1	1
12	*Tamias minimus*	Least Chipmunk	1	1
13	cf. *Sciurus* sp.	Tree Squirrels	1	1
14	*Glaucomys* cf. *G. volans*	Southern Flying Squirrel	1	1
15	*Peromyscus* cf. *P. leucopus*	White-footed Mouse	33	10
16	*Peromyscus* cf. *P. maniculatus*	Deer Mouse	57	15
17	*Neotoma* sp.	Woodrat	27	6
18	*Myodes gapperi*	Southern Red-backed Vole	27	9
19	*Phenacomys* sp.	Heather Vole	3	2
20	*Microtus pennsylvanicus*	Meadow Vole	38	21
21	*Microtus chrotorrhinus*	Rock Vole	22	13
22	*Microtus xanthognathus*	Yellow-cheeked Vole	68	38
23	*Microtus pinetorum* or *M. ochrogaster*	Woodland Vole or Prairie Vole	15	7
24	*Ondatra zibethicus*	Muskrat	3	1
25	*Synaptomys borealis*	Northern Bog Lemming	5	2
26	*Synaptomys cooperi*	Southern Bog Lemming	4	2
27	*Napaeozapus* cf. *N. insignis*	Woodland Jumping Mouse	3	1
28	*Zapus* cf. *Z. hudsonicus*	Meadow Jumping Mouse	6	1
29	*Mustela nivalis*	Least Weasel	4	2

Recorded material is limited to mainly dental and some cranial material. In rare cases such as with moles a post-cranial element was used in an identification. Fragmented and post-cranial material is not listed but is a large portion of the deposit.

Mammalia – Mammals

Order: Eulipotyphla – Insectivores

Family: Soricidae – Shrews

REFERRED MATERIAL: 10 partial dentaries; 5 lower 1st incisors.

REMARKS: This material could be easily classified as shrew but was either too broken or too weathered to identify below.

Sorex arcticus – Arctic shrew

REFERRED MATERIAL: 1 right, 1 left dentary.

REMARKS: Arctic shrews are a medium sized shrew with a distinctive tri-color pelage. Found in the boreal forests of Canada and small portions of northcentral United States (Kirkland & Schmidt 1996). Though they are confined to boreal forest regions, they prefer open wet areas such as marshes and meadows. Fossil remains are common from Pleistocene deposits in the central and southern Appalachian region, along with from the Great Plains. Much of this region is south of its current distribution. Almost all Pleistocene records are south of the furthest extent of the Laurentide ice sheet during the LGM (Kirkland & Schmidt 1996). Identifications were made using Carraway (1995).

Sorex longirostris – Southeastern Shrew

REFERRED MATERIAL: 1 right dentary.

REMARKS: Southeastern shrews are a small member of the genus *Sorex* and possess short tails. As the name suggest they are found throughout the southeastern United States. With their northern range spanning from Maryland over to Missouri, and their southern extent into Louisiana across to Florida (French 1980). Favors wet areas, but have also been found in dry sandy soils. They are synonymous with thick ground cover. Due to the sparseness of its capture in snare traps it has been deemed a rare shrew. Similar in appearance to *S. cinereus*; there has been one tentative fossil identification (Parmalee 1967) from a fissure fill deposit in Monroe County, Illinois. Identification made using Carraway (1995). Characters that separated from similar members of the genus were length of dentary (≤ 6.5mm), pigment arrangement on the i1 (1st lower incisor), and width of the m1 (≥ 1.1 mm).

Sorex sp. – Unidentified *Sorex*

REFERRED MATERIAL: 1 right, 1 left dentary.

REMARKS: Based off size and coloration could say it wasn't *Blarina*, but could not identify to species within *Sorex*.

Blarina sp. - Short-tailed Shrew

REFERRED MATERIAL: 4 partial skulls; 3 right dentary; 4 right, 2 left partial dentaries; 7 maxillary fragments with molars; 5 lower, 4 upper 1st incisors; 4 lower, 3 upper molars.

REMARKS: Short-tailed shrews are large and robust shrew having a shorter and more robust snout. There range includes much of the northeastern and northcentral United States and adjacent southern regions of Canada (George et al. 1986). The southern extent of the range is northern Georgia. Most commonly found in deep leaf liter of hardwood forests, but can be found in grasslands and pine forests. Increase in size with latitude. Fossil remains are found

throughout their range. Measurements collected from Guilday et al. (1977) would indicate a more northern locality. Suggesting a colder climate. Identification made using Carraway (1995).

Family: Talpidae – Moles

Parascalops breweri – Hairy-tailed Mole

REFERRED MATERIAL: 1 right dentary with no molars; 1 right ulna, 1 humerus.

REMARKS: Hairy-tailed moles are a medium sized mole with a short tail and a long narrow snout. Ranging is from the northeaster US and southeastern Canada down the Appalachian plateau to the very northeastern tip of South Carolina (Hallett 1978). Found in both coniferous and deciduous woodlands. Most commonly found in sandy loam soils that have good surface coverage and sufficient moister. Tend to avoid saturated clay rich soils (Hallett 1978). Fossil specimens are not abundant but have been found from Pleistocene cave faunas. Identifications were made with modern specimens from East Tennessee State Vertebrate Paleontology (ETVP) Comparative Collection.

Condylura cristata – Star-nosed Mole

REFERRED MATERIAL: 1 right, 1 left partial dentary.

REMARKS: Star nose moles are named for the star shaped ring at the end of its nose made up of 22 fleshy tentacle-like appendages. They are reported as excellent swimmers and much less fossorial than other moles. Found in wet areas in meadows, woods, and swamps; usually found in mucky soil (Petersen & Yates 1980). Current range is in eastern Canada and the US, spanning from Minnesota into Georgia. Pleistocene records of the mole are found from deposits in the

central Appalachians and Missouri. Identifications were made with modern specimens from the (ETVP) Comparative Collection.

Order: Chiroptera – Bats

REFERRED MATERIAL: 144 dentary fragments; 32 maxillary fragments; 255 lower molars; 110 upper M^1s and M^2s; 12 upper M^3s; 116 premolars; 234 incisors and canines.

Family: Vespertilionidae – Common bats

REFERRED MATERIAL: 15 dentary fragments with 2 premolar alveoli present; 58 dentary fragments with 3 premolar alveoli present; 9 maxillary fragments with 3 premolars alveoli present.

Myotis spp. – Little Brown Bats (Mouse Eared Bats)

REFERRED MATERIAL: 11 right, 6 left dentaries.

REMARKS: *Myotis* is a large and diverse genus with over 100 species; 38 in the New World (Simons 2005). When dealing with fragmentary or fossil specimens it can be very challenging to classify down to species level (Toomey 1993; Jansky 2013). Guilday et al. (1977) classifies 5 species: (*M. lucifugus, M. sodalis, M. keeni, M. leibii, and M. grisescens*), some that are common to the eastern US today. I did not feel there was enough material to classify to species. However, it is likely that there are multiple members of the genus in the deposit. Gannon & Raez (2006) and Jansky (2013) showed evidence for identification to the species level using geometric morphometrics. Identifications were made via modern comparisons from ETVP collections, Hillson (2005), and the Animal Diversity Website (ADW) (produced by the University of Michigan, Museum of Zoology).

cf. *Perimyotis* sp. – Pipistrelles

REFERRED MATERIAL: 3 right partial dentaries.

REMARKS: Pipistrelles or tri colored bats are a small bat that has two species in the US today: *P. Hesperus* (Western Pipistrelle) and *P. subflavus* (Eastern Pipistrelle) (Hall 1981). Guilday et al. (1977) reported the eastern pipistrelle making up 53% of the bats recorded from a three hours mist net trapping at entrance no. 3 (Guilday et al. 1977). Making it highly probable that this is in fact the species in the deposit. However, with the fragmented dentary material in the deposit I did not feel comfortable taking it to species. Identifications were made via modern comparisons from ETVP collections, Hillson (2005), and the ADW.

Eptesicus fuscus – Big Brown Bat

REFERRED MATERIAL: 4 right, 5 left partial dentaries; 1 upper premolar.

REMARKS: Big brown bats are distinguishable from most Vespertilionids in their range by their large broad head, husky body, short rounded ears, and short, broad wings. This species is found in and around forests; deciduous much more than coniferous (Kurta & Baker 1990). Ranging throughout much of North America: from southern Canada, throughout the US into Mexico and the highlands of Central America to Columbia. It is the most abundant Pleistocene bat found in North America (Kurta & Baker 1990). Identifications were made via modern comparisons from ETVP collections, Hillson (2005), and the ADW. This is a common species found at the cave today. Composed of 15% of the mist-netted sample (Guilday et al. 1977).

cf. *Lasiurus* sp. – Hairy-tailed Bats

REFERRED MATERIAL: 2 right, 6 left dentaries.

REMARKS: Hairy-tailed bats have long, robust wings for fast and strong flight. These bats will roost on tree branches as opposed to in caves. Many of the northern taxa migrate south in the winter (Simmons 2005). Found throughout North America (Hall 1981). They are generally found living in forests. As they are not a cave dwelling bat it is not surprising that none were noted from the mist-netting sample (Guilday et al. 1977). Identifications were made via modern comparisons from ETVP collections, Hillson (2005), and the ADW.

cf. *Corynorhinus* sp. – Big-eared Bats

REFERRED MATERIAL: 1 left partial dentary.

REMARKS: As their name suggest these bats have very large ears. Guilday et al. (1977) reports a few specimens of *Plecotus* cf. *townsendii*. Townsend Big-eared bats are now classified under the genus *Corynorhinus*. This bat is found in woodlands in the eastern US (Burford & Lacki 1995) however, there range is mainly western in nature however. Ranging from Mexico to southwestern Canada, stretching east to Texas. There are isolated populations in West Virginia, Kentucky, Tennessee / North Carolina border, and the four corners of Oklahoma, Missouri, Kansas, and Arkansas (Hall 1981). *Corynorhinus rafinesquii* (Rafinesque's big-eared bat) has a more eastern range but also is not found at the cave locality today (Hall 1981). There was not enough material to classify to species. Identifications were made via modern comparisons from ETVP collections, Hillson (2005), and the ADW.

Order: Lagomorpha – Rabbits, Hares, Pikas

Family: Leporidae – Rabbits, Hares

REFERRED MATERIAL: 1 maxillary fragment with alveoli; 5 lower, 4 upper molars.

REMARKS: Guilday et al. (1977) reports both snowshoe hare (*Lepus americanus*) and New England cottontail (cf. *Sylvilagus transitionalis*). In this deposit there were only lone molars and incisors that were not conducive to classification to species. Eastern cottontail (*Sylvilagus floridanus*) are present in the area today (Hall 1981).

Order: Rodentia – Rodents

Family: Sciuridae – Squirrels

Tamias cf. *T. striatus* – Eastern Chipmunk

REFERRED MATERIAL: 1 right partial dentary.

REMARKS: Eastern chipmunk are small, moderately heavy set squirrel with prominent longitudinal stripes along its body. Common in and along the edges of deciduous forests (Synder 1982). Their range extends from southeastern Canada to Oklahoma and Louisiana up to southcentral Canada. Pleistocene records are common and extend much further west than the modern range (Synder 1982). Identifications were made via modern comparisons from ETVP collections and Hillson (2005).

Tamias minimus – Least Chipmunk

REFERRED MATERIAL: 1 left dentary.

REMARKS: Least chipmunks are a small sciurid with a long tail. Ranging from the Canadian Yukon to central Canada and adjacent northcentral US, down the Great Plains and western US (Verts & Carraway 2001). Inhabiting a wide range of environments from montane coniferous forests, sagebrush deserts, to meadows and alpine tundra. Previous to Guilday et al. (1977) the least chipmunk had not been reported from the Appalachians. Pleistocene remains are

commonly found in the western US (Verts & Carraway 2001). Identifications were made via modern comparisons from ETVP collections and Hillson (2005).

cf. *Sciurus* spp. – Tree Squirrels

REFERRED MATERIAL: 1 left partial maxilla with M^2 and M^3.

REMARKS: There are multiple types of tree squirrels that are native to the region today (Hall 1981). Guilday et al. (1977) reported *Sciurus* cf. *carolinensis* (gray squirrel) and *Tamiasciurus hudsonicus* (red squirrel). It is likely that both of the above species are in the ETSU deposit. There is very little material from this deposit and barely enough to place to genus. Identifications were made via modern comparisons from ETVP collections and Hillson (2005).

Glaucomys cf. *G. volans* – Southern Flying Squirrel

REFERRED MATERIAL: 1 right partial dentary.

REMARKS: Southern flying squirrel are small sciurids that have adapted to gliding. They have a broad, hairy, dorsoventraly compressed tail and skin membranes along the side of their bodies, which allow them to glide (Dolan & Carter 1977). Found predominantly in deciduous forests. Their range encompasses most of the eastern US, and a small segment of southeastern Canada; ending at the Great Plains. Pleistocene records come mainly from Appalachian cave deposits (Dolan & Carter 1977). Identifications were made via modern comparisons from ETVP collections and Hillson (2005).

Peromyscus cf. *P. leucopus* type – White-footed Mouse

REFERRED MATERIAL: 1 partial dentary; 2 lower, 4 upper m1s; 7 lower, 6 upper m2s; 10 lower, 3 upper m3s.

REMARKS: The white footed mouse is a fairly small member of the genus, with a narrow slightly haired tail. Abundant and occupying many habitats from deciduous and mixed forests, brushlands, and semidesert regions. Stretching from very southern SE Canada to Mexico (excluding Florida) (Lackey & Huckaby 1985). Pleistocene records have been found through the US. Identifications were made via modern comparisons from ETVP collections and Hillson (2005).

Peromyscus cf. *P. maniculatus* type – Deer Mouse

REFERRED MATERIAL: 1 right dentary; 2 left partial dentaries; 8 lower, 8 upper m1s; 15 lower, 10 upper m2s; 12 lower, 1 upper m3s.

REMARKS: The North American deer mouse looks very similar to the white-footed mouse. Difference between the species come from slight differences in pelage and tail appearance. Can be found through much of the northern region of the continent. It ranges from southern Mexico up to the Yukon, across to the northeastern Canada; excluding the SE US (Banfield 1974; Hall 1981). Fossil records are found throughout the range. Identifications were made via modern comparisons from ETVP collections and Hillson (2005).

Neotoma spp. – Woodrat (Packrat)

REFERRED MATERIAL: 1 left partial dentary with m_1 and m_2; 1 right partial maxilla with M^2 and M^3; 6 right, 3 left lower m_1s; 1 left lower m_2; 2 lower m_3s; 3 right, 3 left upper M^1s; 2 right, 1 left upper M^2s; 4 right upper M^3s.

REMARKS: Woodrats are medium sized rodents with fairly large ears. There are many different species of woodrat that range from Florida to Mexico and western Canada (Hall 1981). *Neotoma* teeth do no vary much by species and can be hard to differentiate especially with lone teeth.

Woodrats are present and active today at Clark's Cave. Evidence of middens and active collecting can be seen at CC. Guilday et al. (1977) classified all *Neotoma* remain as the eastern woodrat (*Neotoma floridana*). The northern populations (from Tennessee to New York) are now classified as *Neotoma magister* (Allegheny woodrat) (Whitaker & Hamilton 1998). I would expect both of the above species, and potentially others to be part of this deposit cycling in and out with glacial stages. Samples collected are mainly isolated teeth and was not conducive to classification to species.

Family: Cricetidae – Hamster, Voles, Lemmings, New and Old World Mice

"Arvicolinae" – Unidentified microtine rodent

REFERRED MATERIAL: 235 upper M^1s; 149 lower, 58 upper m2s; 173 m's.

Myodes "*Clethrionomys" gapperi* – Southern Red-backed Vole

REFERRED MATERIAL: 1 right dentary; 6 right, 6 left partial dentaries; 9 right, 5 left lower m_1s.

REMARKS: Red-backed voles have commonly been placed under the genus *Clethrionomys*. It has been recently determined that the proper name associated to this genus was *Myodes* (Carleton et al. 2014). It is a small slender vole. Ranging throughout most of southern Canada and adjacent northern regions of the US. Also extending south along the Rockies and Appalachians (Hall 1981). Found predominantly in damp coniferous forests along with mountain meadows and bogs (Guilday et al. 1977). Fossil remains are common amongst Appalachian cave fauns. Identifications were made via modern comparisons from ETVP collections and Semken and Wallace (2002).

Phenacomys sp. – Heather Vole

REFERRED MATERIAL: 2 left partial dentaries; 1 left lower m_1.

REMARKS: Heather voles are small short tailed voles that greatly resemble montane voles (*Microtus montanus*). They are generally located at altitude and typically found in heather meadows, alpine areas, and open coniferous forests (McAllister & Hoffman 1988). There are two species in North America: the western heather vole (*Phenacomys intermedius*) and eastern heather vole (*Phenacomys ungava*). Neither species' current range is close to Clark's cave; with the eastern species ranging across most of Canada and the western species being along the Rockies and western region of US and Canada (Banfield 1974). Guilday et al. (1977) reported *Phenacomys intermedius*. However, it has been shown to be difficult to differentiate between species of the genus with fossil material (Guilday & Parmalee 1972). For this reason specimens were not taken to species. Identifications were made via modern comparisons from ETVP collections and Semken and Wallace (2002).

Microtus pennsylvanicus – Meadow Vole

REFERRED MATERIAL: 48 up M^2s; 52 upper M^3s.

REMARKS: The meadow vole is an average sized vole with a relatively long tail. As the name suggest they prefer damp meadows or other areas with thick grasses. It has the largest range of any NA member of the genus *Microtus* (**Fig. 1**). Their range includes most of Alaska, Canada, the northern and central eastern US, into the northern and central Great Plains (Reich 1981). Possessing a large late Pleistocene record of the species throughout their range. Identifications were made via modern comparisons from ETVP collections, Guilday (1982b), and Semken and Wallace (2002). Traditionally the occlusal pattern of the lower first molar has been reported as

the diagnostic character of this species. This character has shown to have large degrees of variability (Guilday 1982b) and to be confident in identification one should have the corresponding upper second molar (M2) of the specimen (Semken and Wallace 2002).

Microtus chrotorrhinus – Rock Vole

REFERRED MATERIAL: 13 right, 9 left upper M^3s.

REMARKS: Rock voles are very similar in their appearance to the meadow vole. Slight differences in pelage color separate the two species. Found primarily in SE Canada, into New England and northeastern Minnesota (**Fig. 1**). They also range down the Appalachians into eastern Tennessee and western North Carolina (Kirkland & Jannett 1982). One has never been trapped in Virginia (Guilday et al. 1977). Generally live in rocky areas in cool moist mixed and hardwood forests; often near a source of water. Fossil records are from late Pleistocene Appalachian cave deposits (Kirkland & Jannett 1982). Identifications were made via modern comparisons from ETVP collections, Guilday (1982b), and Semken and Wallace (2002). Most teeth are indistinguishable from those of the meadow vole. The two species are separated based on differences in occlusal pattern on the upper 3rd molars (M^3) (Guilday 1982b).

Microtus pennsylvanicus morph – *M. pennsylvanicus* or *M. chrotorrhinus*

REFERRED MATERIAL: 21 right, 17 left lower m_1s.

REMARKS: No reliable method to differentiate *M. pennsylvanicus* or *M. chrotorrhinus* m_1s from each other. This would be an excellent area for further study.

Microtus xanthognathus – Yellow-cheeked Vole

REFERRED MATERIAL: 38 right, 30 left lower m_1s.

REMARKS: The yellow-cheeked vole (taiga vole) is generally one of the largest of the North American *Microtus*. Along with *M. richardsoni*, *M. xanthognathus* have on average the largest lower first molars amongst New World *Microtus* (Semken & Wallace 2002). This is a boreal adapted taxa that inhabits wet forests, thriving in recently burned upland regions. Ranging from the west coast of the Hudson Bay into central Alaska (Conroy & Cook 1999) (**Fig. 1**). Fossil ranges includes many regions of northern North America south of the Laurentide ice sheet (Hallberg et al. 1974). Morphotype placement was made via modern comparisons from ETVP collections and Semken and Wallace (2002).

Microtus pinetorum or *M. ochrogaster*

REFERRED MATERIAL: 4 right, 7 left lower m_1s; 4 upper M^3s.

REMARKS: Prairie voles often have long coarse fur and are found primarily in prairies and grasslands, preferring dry soil. They range throughout the central US into Canada (Stalling 1990) (**Fig. 2**). Many Pleistocene and Holocene records of the prairie vole exist inside their range. Like *Microtus pinetorum* they share a 3 closed triangle pattern on the occlusal surface of their lower first molar (Semken & Wallace 2002). Morphotype placement was made via modern comparisons from ETVP collections and Semken and Wallace (2002).

Woodland voles has a slender cylindrical body plan modified for a semifossorial life. These voles prefer sandy soils found in deciduous forests with thick leaf litter or grassy fields with lots of brush (Smolen 1981). Their range spreads throughout much of the eastern and Midwestern US, entering small adjacent regions of Canada (**Fig. 2**). There are many late Pleistocene records throughout the range including some extra-limital accounts (Smolen 1981).

Identifications were made via modern comparisons from ETVP collections and Semken and Wallace (2002).

Ondatra zibethicus - Muskrat

REFERRED MATERIAL: 1 left partial dentary with m_1; 1 upper M^1; 1 lower m_2.

REMARKS: The muskrat is the largest NA microtine and has a large blunt head and is chunky in appearance. Found in shallow marshes and less commonly along lakes and streams. Their range covers most of Alaska and Canada, along with the majority of the US except Florida and the arid Southwest (Willner et al. 1980). Good fossil records have come from Kansas and the Appalachians. Identifications were made via modern comparisons from ETVP collections and Semken and Wallace (2002). Teeth are very large for microtines. Also the cement that fills in the re-entrant angles of the m_1s is divided into horizontal bars (Semken & Wallace 2002).

Synaptomys borealis – Northern Bog Lemming

REFERRED MATERIAL: 1 right dentary; 1 right partial dentary with m_1; 1 right, 2 left lower m_1s.

REMARKS: The northern bog lemming is small with a cylindrically shaped body. They are found mainly in bogs, wet meadows, or alpine tundra (Banfield 1974). Their range covers most of Alaska and western Canada, along with northeastern Canada and northern New England (Hall 1981). Fossil remains have been found from Pleistocene deposits in the northern and central Appalachians. Identifications were made via modern comparisons from ETVP collections and Semken and Wallace (2002).

Synaptomys cooperi – Southern Bog Lemming

REFERRED MATERIAL: 2 right, 2 left lower m_1s.

REMARKS: Southern bog lemmings are similar in appearance to the northern bog lemming. However, occupying a wider variety of habitat then their northern counter parts. Are usually found in green grass or sedge; around bogs, dense woodland, and grass fields (Banfield 1974). Their range is eastern and Midwestern US and adjacent southeastern Canada (Hall 1981). Pleistocene records have been found as far south as Alabama. Identifications were made via modern comparisons from ETVP collections and Semken and Wallace (2002).

Family: Zapodidae – Jumping Mice

Napaeozapus cf. *N. insignis* – Woodland Jumping Mouse

REFERRED MATERIAL: 3 molars.

REMARKS: The woodland jumping mouse has very long and narrow hind feet along with a long narrow tail. Found in wet cool woods, often in areas of dense vegetation along streams. Typically associated with mixed forest type biomes (Whitaker & Wrigley 1972). Their current range is in southeastern Canada and northeastern US, down the Appalachians into Georgia. Fossil remains are found from deposits throughout the central Appalachians (Whitaker & Wrigley 1972). Identifications were made via modern comparisons from ETVP collections, Krutzsch (1954), and Hillson (2005), and the ADW.

Zapus cf. *Z. hudsonicus* – Meadow Jumping Mouse

REFERRED MATERIAL: 1 right dentary; 1 left partial maxilla with M^2 and M^3; 4 molars.

REMARKS: The meadow jumping mouse has very long and narrow back feet, with hind limbs that are longer than the forelimbs. They also have long narrow tails. Most commonly found in wet or dry grassy fields, but can also be found along streams and bogs (Whitaker 1972). Stretching

from southern Alaska, throughout much of southern and eastern Canada, and along much of the eastern and Midwestern US. Late Pleistocene records have been found throughout the range (Whitaker 1972). Identifications were made via modern comparisons from ETVP collections, Krutzsch (1954), and Hillson (2005). The meadow jumping mouse is similar in appearance and tooth morphology to the woodland jumping mouse (*Napaeozapus insignis*) (Whitaker 1972).

Order: Carnivora – Carnivorans

Family: Mustelidae – Weasels

Mustela nivalis – Least Weasel

REFERRED MATERIAL: 2 right, 2 left partial dentaries.

REMARKS: Least weasel are the smallest members of the order Carnivora. Like most members of the genus *Mustela, M. nivalis* it has a long slender body with short limbs. *M. nivalis* prefer open areas: meadows, brush, and marshlands, but can be found in coniferous forests (Sheffield & King 1994). Their range covers much of northern North America, Europe, northern Asia, and parts of North Africa. Pleistocene records have been throughout the range on both sides of the old land bridge (Hall 1981). Identifications were made via modern comparisons from ETVP collections.

Discussion and Conclusions

There are two species reported here that were not reported in Guilday et al. (1977), the southeastern shrew (*Sorex longirostirs*) and the prairie vole (*Microtus ochrogaster*). Presence of the southeastern shrew would be a logical because Clark's Cave is within its current distribution (French 1980). It is regarded as one of the more rare shrews in its distribution; not commonly caught in traps. At the time there may have been little to no comparative samples of this shrew,

inhibiting it from being identified. It is quite possible that southeastern shrew material was collected and has been classified as *Sorex* sp. in Guilday et al. (1977).

Lack of *M. ochrogaster* from the original publication was based on a faulty assumption by Guilday et al. (1977). "Identification to species is based upon geographic probability. It is conceivable that *M. ochrogaster* may be represented as well" (Guilday et al. 1977). The clarification given when discussing the *M. pinetorum* specimens. An assumption made most likely due to the current wooded nature of the surrounding area along with the fact that the woodland vole is found at the site today, whereas the prairie vole is not. Unfortunately circular reasoning like this can lead to misidentifications or in this case the exclusion of a taxa. Woodland voles and the prairie voles suggest two distinctly different environments. Without the prairie vole report we see a more limited view of paleoenvironment.

I was much more hesitant to take specimens to the species level than was Guilday et al. (1977). With the specimens collected by ETSU I did not feel there was enough diagnostic material at times that would warrant a species or even genus classification. This is especially true for things like bats, which do not show much variation in their dentition across the species level (Toomey 1993; Jansky 2013). When bats were taken to species they were often classified using "cf.", as identification confidence was low. Much of the bat material in the ETSU sample was isolated teeth.

Much more material was collected from Guilday et al. (1977) and as a result they had a much larger sample size. More than likely providing them the opportunity to obtain more complete specimens then, what was extracted by ETSU. However, if the bulk of Guilday et al. (1977)'s classifications to the species level were done using geography, I feel this is an unsafe

assumption, especially without many of these taxa having dates associated with them. I took a similar approach to identifications when it came to lone squirrel or rabbit teeth.

Unlike in Guilday et al. (1977) there is a noticeable lack of medium to large animals in size in my sample. Most likely due to the difference in size of the material collected. Even with the Carnegie sample being much bigger, larger animals still have very low MNI's in comparison to the rest of the deposit. This is to be expected when dealing with a raptor deposit (Guilday et al. 1977; Andrews 1990). During the ETSU trip to the cave, black bear (*Ursus americanus*) and white-tailed deer (*Odocoileus virginianus*) remains were found within the cave. They were not included within the species account as this material was not collected at site 7/19/14 – 003. This material was found lying on the surface, deeper within the cave, and not within any sediment, likely suggesting a younger age.

CHAPTER 6

SUMMARY

For years efforts to solve the "*Microtus* problem" had been mostly fruitless; especially when looking at the fossil record, which rarely provides complete specimens with a large sample sizes. The use of geometric morphometrics on m_1s is helping to un-muddy the waters. Results of the study presented here help build on previously published works, by stating:

- Until the presentation of a more accurate method, the use of a GPA should be the preferred method to perform a superimposition on *Microtus* molars.
- Using geometric morphometrics is a reliable method to differentiate m_1s of *Microtus richardsoni* from other *Microtus* spp., especially *M. pennsylvanicus* and *M. xanthognathus*.
- Results of a PCA would suggest that *M. richardsoni* is not present at Clark's Cave in agreement with the reporting's of Guilday et al. (1977).
- Results of DAs indicate that *Microtus xanthognathus* is the most abundant vole in the Clark's Cave deposit.
- Further examination of previously collected specimens and the results of a PCA on said specimens, indicate that *Microtus ochrogaster* is present in the CC deposit. Worthy of note is that not only is it present but makes up the majority of the 3 closed triangle morph *Microtus* from the deposit.
- A tentative list of faunal identifications is listed in this report.

Clark's Cave is a vast cave system with the potential for much further study. Guilday et al. (1977) and this study have focused on one small locality at one particular entrance. It is likely

that this cave hold deposits of multiple ages. Other regions of the cave were sampled by the ETSU team, but not included in this report. Acquisition of more radiocarbon (14C) dates from the entrance 2 deposit and other sites throughout the cave would help piece together a more complete picture. The information that we have now from this cave is still very isolated. It should be emphasized that just because a particular site has been reported on does not mean that everything is known about that site.

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APPENDICES

APPENDIX A

LIST OF SPECIMENS ANALYSED

Abbreviations: SUI = University of Iowa, Department of Geoscience Repository (CC= Comparative); YPM= Yale Peabody Museum; UMMZ= University of Michigan Museum of Zoology; USNM= United States National Museum; CM= Carnegie Museum.

Specimens from Wallace (2006):

Microtus pennsylvanicus (n=23): SUI-365, Wisconsin; SUI-828, 831, Iowa; SUI-CC-922, Kansas; YPM-1172, Virginia; YPM-1175, Maine; YPM-1176, Quebec; YPM-1184, Connecticut; YPM-1196, Nova Scotia; YPM-1199, British Columbia; YPM-1902, Manitoba; YPM-2034, New Mexico; YPM-2268, West Virginia; YPM-2271, New York; YPM-3655-3656, Minnesota; YPM-3758 Rhode Island; YPM-4045, Minnesota; UMMZ-117715-117719, Michigan.

Specimens from the (USNM) collection:

Specimens with an asterisk indicate a left molar was photographed.

Microtus xanthognathus (n=32): USNM-109355-109356, 109358, 109364, 109366, 109368*, 109370, 109373, Saskatchewan; USNM-109459-109460, Alberta; USNM-110601, Northwest Territory; USNM-128301, 128328*, 128330, Alaska; USNM-134073-134077, Alberta; USNM-157281-157282, 178112, 178114, Alaska; USNM-235921-235923, Alberta; USNM-271710, 286851-286853, 286855, Alaska; USNM-7702, Northwest Territory.

Microtus richardsoni (n=30): USNM-55288, 55290, 55708, 55751, Wyoming; USNM-90091-90092, 142023, Washington; USNM-170391, 170396, 170398*, 170421, 170485, 170492, 170525, 176759, 177243-177244, 177246, 177252, 177256, 223107, Wyoming; USNM-227130-227131, 227137, 229936, 230456, 233191, Washington; USNM-248602, 298292, 298608, Wyoming.

Specimens from the (CM) collection:

Microtus pinetorum: CM-24524, (3 left, 4 right mandibles with m1; 7 left, 5 right m1); CM-24576, (24 left, 18 right mandibles with m1; 136 left, 114 right m1; 31 left, 33 right M3).

APPENDIX B

COLLETCION PERMIT

Molly Joseph Ward
Secretary of Natural Resources

Joe Elton
Interim Director

COMMONWEALTH of VIRGINIA
DEPARTMENT OF CONSERVATION AND RECREATION

600 East Main Street, 24th Floor
Richmond, Virginia 23219
(804) 786-6124

June 26, 2014

Dr. Steven C. Wallace
Professor, Department of Geosciences
P.O. Box 70357
East Tennessee State University
Johnson City, TN 37614

Dear Dr. Wallace:

The Virginia Department of Conservation and Recreation (DCR) and the Virginia Department of Historic Resources (DHR) have reviewed your request for a Cave Collection Permit for your work involving excavation of sediment and small fossils from Clark's Cave, Bath County Virginia.

In accordance with terms of the Virginia Cave Protection Act (section 10.1-1003 of the Code of Virginia), a cave collection permit for your work is granted with the following conditions:

1. This permit is for the work outlined in your proposal dated June 13, 2014 and sent to me via email on June 18, 2014.
2. No archaeological, prehistoric or historic features shall be intentionally disturbed or removed pursuant to Section 10.1-1004 of the *Code of Virginia*. If any historic or prehistoric artifacts or human remains are encountered during your work you must immediately stop work and inform the Department of Historic Resources Office of Review and Compliance (804-367-2323). If cultural remains are identified, the find should be recorded with DHR as an archaeological site and summary report of the findings should be submitted to DHR. .
3. You will restrict the numbers of persons conducting research within Clark's Cave to the minimum required to accomplish the study.
4. You must provide summaries of data and results of ongoing research, study or collections by the first day of the year following the year of this letter and you must submit a final report within 3 months of the expiration date. Reporting shall include:

A) Identification of specimens to the most detailed taxonomic level known at the time of collection.

B) If specimens are identified at a later date, notification of the chain of custody and subsequent species identification is requested.

5. You must carry this permit while exercising the privileges granted.
6. Written permission from owners of the caves to be visited must be obtained prior to visiting the caves. Failure to obtain such permission will violate the Virginia Cave Protection Act (10.1-1000 through 1008, *Code of Virginia*) and will serve to invalidate this permit.

This permit shall be valid for 24 months following the date of this letter. This permit is not transferable and will confer the above-stated conditions to you and those assistants accompanying you.

If you have any questions about this permit, please call Larry Smith at 804-371-6205.

Thank you for your contributions to gaining a greater understanding of the cave resources of Virginia.

Sincerely,

Larry Smith

cc: Roger Kirchen, Department of Historic Resources
Wil Orndorff, DCR Karst Program

APPENDIX C

MEASUREMENTS OF OCCLUSAL SURFACES OF COLLETCED 5 CLOSED TRIANGLE MORPH *MICROTUS*

Table including the measurements of the occlusal lengths of lower first molars for the 5 closed triangle morph *Microtus* from Clarks Cave 7/19/14 – 003. All specimens have a tentative CCD tag. All measurements are in mm.

Specimen #	Element	Length
16	m1	2.8
17	m1	3.1
18	m1	3.2
19	m1	2.9
20	m1	3.5
21	m1	2.7
22	m1	2.8
23	m1	2.3
24	m1	2.6
25	m1	2.7
26	jaw w/ m1	2.8
27	jaw w/ m1 & m2	3.7
28	jaw w/ m1 & m2	2.7
29	jaw w/ m1	3.5
30	m1	2.6
31	m1	3.3
32	m1	2.7
33	m1	3
34	m1	3.5
35	m1	2.8
36	m1	3.4
37	m1	2.7
38	m1	2.5
39	m1	2.5
40	m1	2.5
41	m1	2.5
42	m1	2.8
43	m1	2.8
44	m1	2.7
45	m1	2.8
46	m1	2.6
47	m1	2.5
48	m1	2.8
49	m1	2.6
50	m1	2.7
51	m1	3.5
52	m1	2.3
53	m1	2.7
54	m1	2.6
55	m1	2.5
56	m1	2.6
57	m1	2.7
58	m1	2.5
59	m1	2.6
60	m1	2.1
61	m1	2.9
62	m1	2.5
63	m1	2.7
96	m1	2.9
97	m1	3.1
98	m1	3.3
99	m1	3.8
100	m1	2.6
101	m1	2.8
102	m1	2.2
103	m1	2.2
104	m1	3.3
105	m1	2.6
106	m1	2.8
107	m1	2.7
108	m1	2.8
109	m1	2.6
110	m1	3.1
111	m1	3.5
112	m1	2.8
113	m1	2.8
114	m1	2.8
115	m1	3.4

116	m1	2.5	151	m1	2.9	200	dentary	3.5
117	m1	2.8	152	jaw w/ m1 & m2	3.6	201	dentary	2.8
118	m1	2.6	153	m1	3.6	202	dentary	2.8
119	m1	2.7	154	m1	3.4	203	dentary	3
120	m1	2.7	155	m1	3.1	204	dentary	2.9
121	m1	3.5	156	m1	3.6	205	dentary	2.8
122	m1	2.9	157	m1	3.6	206	dentary	3.3
123	m1	2.7	158	m1	2.7	207	dentary	3.4
124	m1	2.4	159	m1	2.6	208	dentary	3.4
125	m1	2.6	160	m1	2.7	209	dentary	3
126	m1	2.6	161	jaw w/ m1 & m2	3.1	210	dentary	3
127	m1	2.8	162	jaw w/ m1 & m2	3.4	211	dentary	3.4
128	m1	2.5	163	jaw w/ m1 & m2	3.3	212	dentary	3
129	m1	2.8	164	jaw w/ m1	2.9	213	dentary	3.7
130	m1	2.9	165	jaw w/ m1 & m2	3.4	214	dentary	2.8
131	m1	2.8	184	m1	2.8	215	dentary	3
132	m1	2.7	185	m1	2.8	216	dentary	2.8
133	m1	2.6	186	m1	2.7	217	dentary	2.7
134	m1	2.7	187	m1	2.6	218	dentary	2.6
135	m1	2.6	188	jaw w/ m1	2.6	219	dentary	2.6
136	m1	2.7	189	m1	2.8	220	dentary	2.6
137	m1	3.2	190	dentary	2.7	221	dentary	2.7
138	jaw w/ m1	2.7	191	dentary	3	222	dentary	2.7
139	jaw w/ m1	2.7	192	dentary	2.7	223	dentary	3.1
140	jaw w/ m1	2.5	193	dentary	3.5	224	dentary	2.9
141	jaw w/ m1 & m2	2.7	194	dentary	3	225	dentary	2.6
142	jaw w/ m1	2.7	195	dentary	3.2	226	dentary	2.7
143	complete jaw	2.6	196	dentary	3.4	227	dentary	2.8
144	jaw w/ m1 & m2	3.4	197	dentary	2.8	228	dentary	2.7
149	m1	2.7	198	dentary	3.3	229	dentary	2.4
150	m1	2.5	199	dentary	2.6	230	dentary	2.5

231	dentary	2.5
232	dentary	2.5
233	dentary	2.9
234	dentary	2.6
235	dentary	2.7
236	dentary	2.8
237	dentary	2.7
238	dentary	3.5
239	dentary	3.6
240	dentary	3.3
241	dentary	3
242	dentary	3.3
243	dentary	3.5
244	dentary	3.5
245	dentary	3.5
246	dentary	3.4
247	dentary	3.4
248	dentary	3.4
249	dentary	3.5

APPENDIX D

ADDITIONAL FIGURES

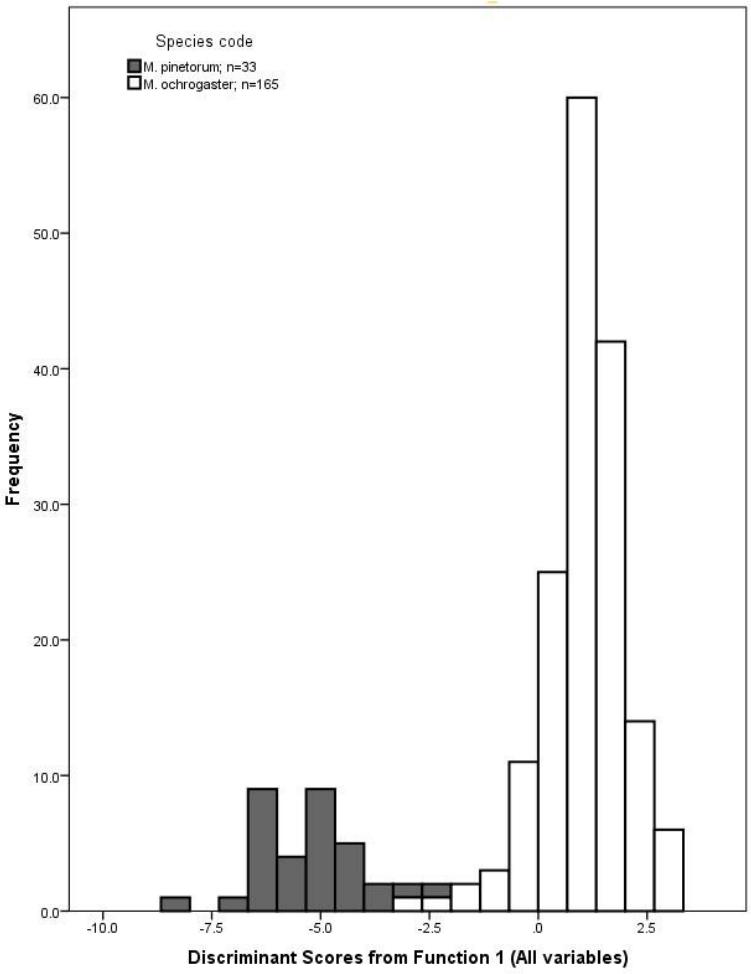

Fig. 19 - Results of DA after classifications of 3-closed triangle morph *Microtus* were corrected based off results of PCA, with all variables included.

VITA

MARK SHELLEMAN

Personal Information:	Date of Birth: November 26, 1991
	Place of Birth: Poughkeepsie, New York
Education:	Public Schools, Arlington, New York
	B.S. Geosciences, Pennsylvania State University, University Park, Pennsylvania, 2013
	M.S. Geosciences, East Tennessee State University, Johnson City, Tennessee, 2015
Professional Societies:	Geological Society of America
Professional Experience:	ETSU Department of Geosciences Research/Teaching Assistant, August 2013 – May 2015