FOSSIL RODENTS FROM BONE CAVE AT THE KOANAKA HILLS LOCALITY, BOTSWANA

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by

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DEDICATION

This work is dedicated to my mom and dad, Drs. Maria and Robert Pierce. None of this is possible without the hard work and perseverance exhibited throughout their lives, and I am eternally grateful for this sacrifice. This work is also dedicated to my wife Lillian Pierce who provided constant love and support during this process which gave me the perseverance and motivation to finish.

ABSTRACT

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In this study I analyze a Middle Pleistocene rodent fauna from Bone Cave locality, Koanaka Hills, northwestern Botswana and attempt to reconstruct the paleoenvironment of the surrounding area. Only a few Pliocene and Pleistocene fossil localities exist between eastern and southern Africa, and the fossil rodents collected from within the Koanaka Hills partially fills this significant geographic and temporal gap in the paleontological record of Africa. Rodent remains from owl accumulations are frequently found in the fossil record and used to reconstruct the paleoenvironment Similarly, prey remains from owl accumulations are used to reconstruct modern community composition. Rodents are seen as particularly useful for reconstructing paleoenvironments over larger mammals as most genera commonly found at Pliocene and Pleistocene fossil localities in Africa are extant, which allows scientist to project modern environmental and habitat preferences to the past as a way to reconstruct past environments. However, there is no defined set of osteological apomorphies with which to identify some rodent taxa to an environmentally informative taxonomic level. This issue makes it difficult to accurately and systematically identify rodents from southern African fossil localities and reconstruct the paleoenvironment. To address this issue, a character matrix is created in this project of cranio-dental characters reported in resources and augmented with new characters derived from comparative images of museum specimens for representative rodent genera from southern Africa ≤ 5 kg. Results from the analysis of fossil specimens is the compared to trapping data of rodents in the area surrounding Koanaka Hills and two

modern barn owl pellet assemblages from within the cave at Koanaka Hills allowing a unique opportunity to compare the fossil assemblage with the modern community in a known environment. One-hundred ninety-six fossil maxillary rodent specimens were identified to the genus and subfamily taxonomic level. Some rodent and nonmammalian fossil specimens identified suggest the environment around Bone Cave was similar to todays, but at some point during the Middle Pleistocene, there was a nearby source of water and wooded vegetation due to the presence of taxon such as *Pelomys*. While the presence of *Pelomys*, buttonquail, and amphibians in the fossil record of Bone Cave allows for the possibility of a more mesic past, they are not convincing by themselves. *Pelomys* and buttonquail are each represented by a single specimen, and amphibians occur at the Koanaka Hills today. The overwhelming majority of fossils found in the Bone Cave deposit represent taxa still found there today. Given these data, the most parsimonious interpretation is one of no change.

KEY WORDS: Rodents, Bone Cave, Koanaka Hills, Botswana, Middle Pleistocene, Micromammals.

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CHAPTER I

INTRODUCTION

Significance and Aims

Several independent lines of evidence ranging from faunal analyses of productive fossil localities (e.g., Vrba, 1975, 1988; Alemseged et al., 2006; Behrensmeyer et al., 1997; Bobe and Eck, 2001; Bobe and Behrensmeyer, 2004; Reed, 2011; Reed and Geraads, 2012) to eolian dust records from deep sea ocean cores (e.g., DeMenocal, 1995; Shackelton, 1995) and stable isotope analysis (e.g., Lehmann et al., 2016), suggest a dramatic shift in climate took place in Sub-Saharan Africa accompanied by significant changes in the plant and animal communities during the Pliocene and Pleistocene epochs. There are numerous fossil localities with a chronology ranging from the Plio-Pleistocene in South Africa, such as Sterkfontein, Swartkrans, Drimolen, Gladysvale, Plover's Lake, Makapansgat, Taung, Malapa, and Rising Star (Dart, 1925; Broom and Robinson, 1950; Berger et al., 1993 2010, 2015, 2017; Thackeray, 1994; Keyser et al., 2000; Clarke, 2013). In eastern Africa some of these localities include Omo Valley (Alemseged, 2003), Olduvai Gorge (Leakey et al., 1964, 1971, 2001), and Turkana Basin (Wesselman, 1984; Behrensmeyer et al., 1997; Bobe and Behrensmeyer, 2004; Frost, 2007). However, only a few productive Plio-Pleistocene fossil localities are known between these east and south African sites, such as Humpata in southern Angola and the Otavi Mountains in Namibia (Pickford et al., 1994). Hypotheses linking rapid faunal change with environmental changes can only be refined as both the fossil record and our understanding of past environments increase. The rodent fossils from the Koanaka Hills, a Plio-Pleistocene

locality in Botswana, partially fills this significant geographic and temporal gap in the paleontological record of Africa.

The Koanaka Hills, also known as !Ncumtsa Hills, are located in western Ngamiland, Botswana, roughly 30 km east of the Botswana-Namibia border, and 150 km west of the Okavango Inland Delta (Pickford and Mein, 1988). The local San term !Ncumsta translates to "two hills" referring to Koanaka North and South. The Koanaka Hills today refers three hills, consisting of Koanaka North (34 S 521875 7772653), Koanaka South (34 S 520382, 7771021), and Koanaka West (34 S 508380 7771379) (Figure 1). The local term for Koanaka West is !Ncumxee (Williams et al., 2012). Bone Cave is located on the northern end of Koanaka South (Ritter and Mann, 1995).

Micromammal (mammals weighing <5 kg) accumulations found at fossil localities such as Bone Cave are typically attributed to owls. Studies have identified biases inherent in micromammals assemblages generated by owls which suggest caution should be used when using these assemblages to reconstruct paleoenvironments (Avery, 1982a, 1997, 2002, 2007; Andrews, 1990; Denys et al., 1996; Yom-Tov and Wool, 1997; Leichliter, 2011). The term micromammal, defined here as mammal weighing less than 500 g, incorporates most adult rodent species in southern Africa except springhares (*Pedetes capensis*), cane-rats (*Thryonomys* spp.), Gambian giant pouched rats (*Cricetomys gambianus*), and cape porcupines (*Hystrix africaeaustralis*) (Stuart and Stuart, 2015; Wilson and Reeder, 2005). Rodents are seen as particularly useful for reconstructing paleoenvironments because of their speciose nature, relatively small home ranges, precise environmental tolerances for some taxa, and rich array of dietary adaptations (DeGraff, 1981; Wesselman, 1984, 1995; Andrews, 1990; Reed, 2003, 2005,

2007; Skinner and Chimimba, 2005; Reed and Geraads, 2012). Most genera commonly found at Pliocene and Pleistocene fossil-bearing localities in Africa are extant, which allows scientist to project modern environmental and habitat preferences to the past as a way to reconstruct past environments (Andrews 1990). However, possible misidentification of fossil rodent specimens due to the fragmentary nature of most fossils, as well as a lack of defined apomorphies, have led to difficulties inferring paleoenvironments (Skinner and Chimimba, 2005; Barr, 2008; Monadjem et al., 2015). Additionally, overstating environmental preferences of some rodents, such as gerbils and vlei rats, can lead to inaccurate paleoenvironmental reconstructions (Robbins et al., 1996; Reed, 2007; Barr, 2008; Campbell et al., 2011)

The goal of this thesis is to reconstruct the paleoenvironment of Koanaka South through an analysis of rodent fossils collected from Middle Pleistocene deposits within Bone Cave (Williams et al., 2012). This goal is facilitated by comparisons of fossil specimens with modern rodents trapped in the area surrounding Koanaka South, as well as with two modern barn owl pellet assemblages from the site. Due to the availability of these multiple lines of data, Koanaka South provides a unique opportunity to compare paleontological and neontological data from the same site in order to interpret how the environment has changed. However, there is currently no guide to identify fragmentary rodent fossils using craniodental remains. To address this issue, a suite of characters identified from literature resources (e.g., Hanney, 1962; Misonne, 1969; Smithers, 1971; Perrin and Curtis, 1980; Wesselman, 1984; Denys et al., 1992; Chimimba, 1998; Skinner and Chimimba, 2005; Wilson and Reeder, 2005; Monadjem et al., 2015; Stuart and Stuart, 2015) and photographs of museum specimens of all rodent genera from southern

Africa with body masses ≤ 5 kg will be used. The suite of characters identified will potentially provide guidance for future researchers to identify fossil rodents from southern Africa with body masses ≤ 5 kg using maxillary characteristics, and will thereby lead to more accurate paleoenvironmental reconstructions. The Middle Pleistocene paleoenvironment at Koanaka South will be reconstructed by comparing the fossil rodent community with the modern rodent community at Koanaka South and other modern and fossil rodent communities in southern Africa.

Environment of Africa During the Pliocene and Pleistocene Epochs

Many studies exist which investigate the environment during the Pliocene and Pleistocene Epochs in Africa through analyses of eolian dust records from deep-sea ocean cores (DeMenocal, 1995, 2004; Shackelton, 1995), and isotopic analysis of fossil mammal teeth (Lehmann et al., 2016). Various faunal analyses are also used at fossil sites mostly focused on bovids (Vrba, 1975, 1980, 1993; Thackeray, 1994; Bobe and Eck, 2001; Bobe et al., 2002; Kappleman et al., 1997; Alemseged, 2003) and other mammalian taxa such as suids, equids, cercopithecids (Bobe et al., 2002; Alemseged, 2003), and rodents (Avery, 1982b, 1986, 1992a; Denys, 1985; Thackeray, 1987; Fernandez-Jalvo et al., 1998; Bobe and Behrensmeyer, 2004; Reed, 2011). These studies suggest the environment in Africa began to get colder and drier around the transition from the Pliocene to the Pleistocene. The colder and drier conditions are a result of large-scale climate changes due to variations in the position of the earth relative to the sun, as changes in the earth's eccentricity, axial tilt, and precession significantly impact the amount of solar radiation reaching it (Bennet, 1990). Collectively known as Milankovitch cycles variations in eccentricity of earth's orbit occurs periodically every 100,000 years,

variation in oscillations of Earth's axial tilt occurs periodically every 41,000 years, and variation in precessions of Earth's orbit occurs periodically every 23,000 years (Bennet, 1990). Studies involving mammal taxa from fossil localities in eastern and South Africa suggests the abundance of wetland-adapted mammals significantly decreased and the abundance of arid-adapted mammals significantly increased during a relatively short period of time, coined the turnover-pulse hypothesis (Vrba, 1980, 1988, 1995). The change in climate and environments is seen as being the catalyst for the radiation of hominins during different periods in the Pliocene and Pleistocene (Vrba, 1988; Bobe et al., 2002; Alemseged, 2003).

Evidence from eastern Africa. At the Turkana Basin fossil site in Ethiopia, a large turnover in woodland-adapted and forest-adapted bovids and rodents was followed by a pulse in grassland-adapted bovids and rodents at 2.5 Ma suggesting the environment oscillated between humid and dry during the transition from the Pliocene to the Pleistocene (Wesselman, 1984; Vrba, 1995). Paleosol and paleobotanical evidence dating from 1.39-3.59 Ma at the Omo Valley in Ethiopia also suggest the environment became cooler and drier during the Pleistocene (Bobe and Eck, 2001). This evidence for an oscillating environment during the Pliocene and Pleistocene transition is corroborated by eolian dust variability from deep sea ocean cores off the coast of West Africa (DeMenocal, 1995, 2004). There are a few disagreements in the turnover-pulse hypothesis regarding the severity, intensity, and timing of climate change and its impact on African biota. For example, first appearance datum (FAD) and last appearance datum (LAD) of cercopithecids from the Dawaitoli in formation Afar Depression dating to the

Middle Pleistocene suggests the habitat had more wooded vegetation than expected (Frost, 2007).

Evidence from South Africa. In South Africa, the Pliocene and Pleistocene environment has been inferred in a study analyzing carbon and oxygen isotope data from the teeth from large mammals at Langebaanweg (~ 5 Ma), Elandsfontein (1.0–0.6 Ma), and Hoedjiespunt (0.35–0.20 Ma) (Lehmann et al., 2016). The results indicate the main diet of the mammals from these sites and their associated time period consisted of C_3 plants associated cool and wet climates (Lehmann et al., 2016). A different result was indicated at three additional sites in South Africa at Makapansgat (3.0-2.5 Ma), Sterkfontein (3.0-2.0 Ma), and Swartkrans (1.8-1.0 Ma) evidenced by stable carbon isotopes from fossil tooth enamel (Lee-Thorp et al., 2007). At all three sites, the results confirm a general trend towards more open environments since 3 Ma and a marked change to open grassy habitats in the latest Pliocene/early Pleistocene enamel (Lee-Thorp et al., 2007). Micromammal remains from Sterkfontein and Swartkrans also suggest more open environments in the Pleistocene (Avery, 2001). The fossil rodents identified from these two sites indicate a succession from riverine grassland, sometimes with *Acacia* trees, to plains with an open savanna woodland (Avery, 2001). While there are a few disagreements in the turnover-pulse hypothesis, these studies from eastern Africa and South Africa agree that the Pleistocene was cooler and drier than the Pliocene, and as a result the abundance of woodland-adapted taxa began to decrease while the abundance of taxa adapted to more open habitats began to increase (Vrba, 1975; Thackery, 1987; Avery, 1982b; 2001; Lee-Thorp et al., 2007). These environmental changes had significant impacts on the biota of the region.

Previous Paleontological Research in Northwestern Botswana

Koanaka Hills and Gcwihaba Hills. Wayland (1944) first published on the caves of Northwestern Botswana starting with Drotsky's Cave in the Gcwihaba Hills located approximately 20 km from Koanaka South. His work included a brief description of the cave's position, sediments, layout, and major cave features (e.g., chambers and speleothems). In 1969, the first excavations at Drotsky's Cave were performed and yielded 61 *in situ* stone artifacts, 848 faunal elements, and several ostrich eggshell fragments which all indicated human occupation (Yellen et al., 1987). Radiocarbon dating of charcoal found within the cave established that humans occupied the cave during the terminal Pleistocene around 12,200 +/- 150 BP (Yellen et al., 1987).

In 1988 further work identified three additional fossiliferous deposits Gcwihaba Hills, Gcw A North, Gcw C South, and Gcw C North, as well as two fossil localities at Koanaka South (Pickford and Mein, 1988; Pickford, 1990). The fossil deposits at Gcwihaba consisted of three localities, Gew A North, Gew C South, and Gew C North, that were rich in small mammals and contained fewer large mammal fossils including a partially complete bovid and a fragmented proboscidean skeleton (Pickford, 1990). Taphonomic analysis of the two partially complete mammal skeletons suggest they fell from an opening in the roof of the cave and became trapped (Pickford, 1990). Other large mammal material was attributed to predation from leopards or from porcupines as the latter have frequently been recorded collecting dry bone in caves in order to gnaw on them and thus reduce their constantly growing incisors (Brain et al., 1980; Pickford and Mein, 1988; Pickford, 1990). Gcw A North is located on the northerly opening of Drotsky's Cave, while the other two localities, Gcw C South and Gcw C North, are

located 0.7 km northwest of Drotsky's Cave and are likely ancient caves destroyed by roof collapse (Pickford, 1990). All three localities lie roughly at the same altitude and are ~15 m above the floor of Drotsky's cave (Pickford, 1990).

The Koanaka Hills are comprised of three hills, Koanaka North, Koanaka South, and Koanaka West (Pickford, 1990). Two fossil localities, termed Koa W and Koa N, were discovered in Koanaka South (Pickford, 1990). During this initial expedition leopards, porcupines, barn owls, and bats were reported to inhabit both Koanaka and Gcwihaba, although there were only a few signs indicating regular use of the caves by leopards (Pickford and Mein, 1988). At Koa W and Koa N, several fossil-rich patches of micromammals and a few large mammal fossils including a set of baboon teeth were collected (Pickford and Mein, 1988) (Table 1). The presence of fossilized remains of arid-adapted rodents from the Dendromurinae and Gerbillinae subfamilies suggests the fossiliferous sediments of the Koanaka Hills were deposited under semi-arid conditions (Pickford and Mein, 1988; Pickford, 1990). According to Pickford (1990) and Pickford and Mein (1988), the presence of several fossilized rodents including *Paleotomys gracilis, Protomys campbelli,* and *Graphiurus* spp. suggest a nearby swampy area bordered by trees. However, this interpretation should be viewed with caution as *Paleotomys gracilis* and *Protomys campbelli* have no extant representatives that may be used to infer the environment (Wilson and Reeder, 2005). Additionally, members of the genus *Graphiurus* are not exclusive to swampy areas as there are populations distributed in semiarid biotic zones in southern Africa, such as the spectacled dormouse, *Graphiurus ocularis* (Monadjem et al., 2015; Stuart and Stuart, 2015). Overstating the environmental

tolerances of fossil specimens identified as *Graphiurus* could lead to inaccurate paleoenvironment reconstructions.

In 1991, a third team excavated at Drotsky's Cave utilizing a sieve to increase artifact recovery (Robbins et al., 1996). Nine rodent genera were identified, all of which were presumably deposited by the barn or grass owl, with exception to the spring hare due to its weight (~3kg) being well above that of prey taken by either raptor (Robbins et al., 1996) (Table 2). Of the rodent material, 27.8% occurred in a band of sediment with charcoal 0-80 cm below the surface and radio-carbon dating indicated a terminal Pleistocene/ Holocene date between 5,470 +/- 90 BP and 12,450 +/- 80 BP (Robbins et al., 1996). The remaining 72.2% of the rodent material was recovered 100-130 cm below the surface, indicating owls occupied the cave for a period of time before 12,450 +/- 80 BP (Robbins et al., 1996). Diatom and grain size analysis of cave clastic sediments suggest the environment was wetter and cooler during the terminal Pleistocene than during the Holocene (Robbins et al., 1996). The presence of the aquatic frog, *Xenopus sp*., and the side-neck turtle, *Pelusios sp,* also suggests wetter conditions as these two taxa need a constant source of water (Robbins et al., 1996). More mesic conditions were also inferred due to the presence of members of the genus *Otomys* and the climbing mouse *Dendromus* sp., as many extant members of this species are currently found in areas near a major water source with heavy vegetation (Robbins et al., 1996). This inference, however, is an oversimplification of the potential habitats occupied by these taxa. For example, while it is true that extant species of *Otomys* typically occur in mesic and/or montane ecosystems in Africa, populations of Angoni vlei rats, *O. angoniensis,* are distributed in drier areas such as open savanna's and grassy hillsides and are not always

associated with a major water source with heavy vegetation (De Graaff, 1981; Monadjem et al., 2015). The same is true for *Dendromus* as most species in this genus are found in habitats with tall grasses and rank vegetation; however, large populations of *Dendromus melanotis* exist in arid (semi-desert) biotic zones in southern Africa where annual rainfall rarely exceeds 500mm (Stuart and Stuart, 2015). Over-stating the environmental signal of fossil specimens identified as *Otomys* and *Dendromus* at other fossil localities can lead to inaccurate environmental reconstruction.

The Koanaka Hills and Gcwihaba Hills were investigated for a fourth time in 1994 by members of the Gcwihaba Cave Project and the National Museum of Botswana. This team initially went to search for the two localities (Koa N and Koa W) to provide a detailed description of the known caves features and search for more caves (Ritter and Mann, 1995). This team also identified another cave at Koanaka West and named it Blue Cave (Ritter and Mann, 1995). Although no fossils were found within Blue Cave, a dead juvenile barn owl was present on the cave floor (Ritter and Mann, 1995). Their project has some different terms for the Koanaka Hills than Pickford (1990). For example, Ritter and Mann (1995) referred to Koanaka North as K1, Koanaka South as K2, and Koanaka West as K3. This thesis will follow the terminology of Pickford (1990) than Ritter and Mann (1995). This thesis also has different terms for the chambers within Bone Cave (Ritter and Mann, 1995). An index is provided to clarify the terminology between this project and the work of Ritter and Mann (1995) (Appendix A).

A subsequent joint field project from 1994 to 1996 consisting of field crews representing Duke University, Stony Brook University, and the National Museum, Monuments and Art Gallery of Botswana resulted in the recovery of the cranium of a

new fossil baboon subspecies, *Papio hamadryas botswanae* at Bone Cave in Koanaka South (Williams et al., 2012). Additionally, this team also obtained the first absolute dates for the Bone Cave through thermoluminescence of two breccia samples, one taken just above the cranium from the chamber wall and the other taken from the main chamber of the cave known as the Atrium (Williams et al., 2012). The sample located above the cranium yielded a minimum age of 317 +/- 114 ka, while that from the Atrium yielded a minimum age of >383 ka (Williams et al., 2012). Both samples indicate at least a Middle Pleistocene age for the deposits, but the deposits could possibly be much older as both samples either approached or exceeded thermoluminescences saturation levels (Williams et al., 2012). When saturation occurs, there is no way to accurately measure increases in thermoluminescence levels (Williams et al., 2012). Therefore, while the dates indicate at least a Middle Pleistocene age for the deposits, they could be much older (Williams et al., 2012).

Tsodilo Hills. The Tsodilo Hills, a UNESCO World Heritage Site in northwestern Botswana known for its rock art paintings, are located 125 km north of Gcwihaba. (Rudner, 1965). There are three main hills named Male, Female, and Child, which are predominantly comprised of quartzite, schist, and marble (Rudner, 1965; Robbins et al., 1996; Thomas et al., 2003). Fossil remains and lithics have been recovered from three deposits within Female Hill and Male Hill: Rhino Cave (RC) and Depression Rock Shelter Site (DRS) within Female Hill, and White Paintings Rock Shelter (WPS) at Male Hill (Robbins and Campbell, 1989; Robbins et al., 1996, 2000; Feathers, 1997). Dating of these deposits utilized optically stimulated luminescence (OSL) and radio-carbon dating, yielding a reliable chronology ranging from around 95 to 5 ka (Robbins and Campbell,

1989; Robbins et al., 1994, 2000). At WPS, 68,296 bone fragments were recovered, 77% of which belonged to mammals and 21% belonged to fish (Robbins et al., 2000). The fish remains were found among lithics, and several barbed bone tips in deposits dating from 65 to 4 ka (Robbins et al., 1994, 2000; Feathers, 1997). Rodent fossils were recovered in sediments dating from 48 to 5 ka and interpreted to be barn owl accumulations, with exception to *Pedetes capensis* and *Hystrix africaeaustralis* as these taxa are not recorded as prey items for barn owls (Robbins et al., 2000). A list of the rodent taxa collected from WPS is provided in Table 3. Freshwater mollusks and diatoms identified within lacustrine carbonates in an ephemeral pan near Female and Male Hill suggest the presence of a semi-permanent lake that varied in size seasonally at 40- 32 ka, 27- 22 ka, and 19-12 ka with the possibility of a drying period at 22-19 ka (Robbins et al., 1994, 2000; Thomas et al., 2003). The twelve species of freshwater mollusks identified in the lacustrine carbonates all occur in the Okavango River system today (Robbins et al., 1994, 2000; Thomas et al., 2003). The abundant fish fossils, mollusks, and diatoms suggest wetter conditions and a nearby permanent source of water in the area around the Tsodilo Hills during the terminal Pleistocene. Currently, the closest permanently flowing water source is several walking days away (Robbins et al., 1994, 2000; Thomas et al., 2003).

Gi. About 60 km northwest of Koanaka South is the site of Gi, which is an ephemeral pan similar to those that surround the immediate area around the Koanaka and Tsodilo Hills (Helgren and Brooks, 1983). The site was first discovered in 1969 and excavated from 1969-70 (Yellen, 1971). A list of the taxa identified from this expedition is provided in Table 4. The site was excavated again from 1975-77 yielding thousands of teeth and tooth fragments and hundreds of bone fragments associated with the Middle

Stone Age (MSA) lithic assemblage (Helgren and Brooks, 1983). The assemblage included three extinct species, the giant zebra (*Equus capensis*), giant buffalo (*Pelorovis antiquus*), and a giant alcelaphine bovid attributed to *Megalotragus priscus* (Helgren and Brooks 1983). No micromammals have been reported from Gi excavations (Yellen, 1971; Helgren and Brooks, 1983). An analysis of the geology, lithostratigraphy, and geomorphology of Gi showed the existence of a palaeolake up to nine meters deep around ~30 ka, and again at ~23 ka (Helgren and Brooks, 1983).

Sua, Nwetwe, and Nxai Pans. Two much larger palaeolakes, Lake Palaeo-Makgadikgadi and Palaeolake Deception, were identified in northwestern Botswana and the Sua, Nwetwe, and Nxai pans are the dried up remains of these once large lakes (Grey and Cooke, 1977; McFarlane and Eckardt, 2006). These pans are over 200 km from the outer reaches of the Okavango Delta. The larger of the two palaeolakes, Palaeolake Deception, occurred at an elevation of ~990 m at its greatest extent based on the height of independent ridge components that are relict shorelines (McFarlane and Eckardt, 2006). Stone tools found in the fossil lake-bed suggest a minimum age of ~200-500 ka (McFarlane and Segadika, 2003; McFarlane and Eckardt, 2006). The area of Palaeolake Deception cannot be estimated due the extreme modification of some of the relict ridges, hence the name (McFarlane and Eckardt, 2006). Nonetheless, evidence from the ridges present suggests its area was at least twice the size of Lake Palaeo-Makgadikgadi, which at its largest covered an area of 37,000 kM2 (McFarlane and Eckardt, 2006). Carbon dating from relict shorelines of Lake Palaeo-Makgadikgadi suggest it had an elevation of 945 m between ~40-35 ka. Around 26-10 ka lake level elevation dropped to 920 m. The presence of these massive palaeolakes in northwestern Botswana suggests a wetter

climate during the mid- Pleistocene and Holocene than today (Helgren and Brooks, 1983).

Rodents as Proxies to the Past

Rodents compared to larger mammals. Rodents are particularly useful for paleoenvironmental reconstructions relative to larger mammals for reasons including: rodents are more speciose, they have smaller home ranges, precise environmental tolerances for some taxa, a rich array of dietary adaptations, typically larger sample sizes, and the fact that most rodent genera commonly found at Pliocene and Pleistocene fossil localities in Africa are extant (DeGraff, 1981; Wesselman, 1984, 1995; Denys, 1985; Andrews, 1990; Reed, 2003, 2005, 2007; Skinner and Chimimba, 2005; Reed and Geraads, 2012). These characteristics allow scientists to project modern environmental and habitat preferences to the past as a way to reconstruct past environments It is further suggested that, when compared to larger mammals, rodents are more useful for paleoecological reconstruction because they provide paleoenvironmental signals at a finer scale as they are closely tied to specific microhabitats (Avery, 1982b; Wesselman, 1984, 1995; Reed, 2007).

Barn owls as accumulating agents of rodents. The barn owl (*Tyto alba*) is the presumed accumulating agent of the rodent fossil assemblage at Bone Cave because they prefer to roost in closed shelters like caves whereas other owl species from southern Africa, like the spotted eagle owl (*Bubo africanus*) prefer to roost in open areas such as tree crowns, the ground, and on rocky outcrops (Fry et al., 1982; Steyn, 1983; Campbell et al., 2018). Additionally, barn owls have been identified as the accumulating agent at several cave fossil localities in southern Africa (e.g., Avery 1982b). Barn owls prey on

invertebrates and several vertebrate classes including Reptilia, Aves, Amphibia, Mammalia, and Pisces and regurgitate the indigestible material such as fur, bone, chitin, and feathers in the form of a compact pellet (Reed and Reed, 1928; Grimm and Whitehouse, 1963; Glue, 1967, 1974; Perrin, 1982; Andrews, 1990; Taylor, 1994). Barn owls typically occupy the same roost sites and nest sites. These sites can vary seasonally for their entire life of the owl, and the owls tend to regurgitate an average of 1.4 pellets per day at these sites (Andrews, 1990). Over time, these pellets can accumulate and, under the right conditions, the large bone accumulations within the pellets can fossilize and provide a large sample of the small mammals in the surrounding area (Andrews, 1990; Yom-Tov and Wool, 1997). As such, large accumulations of fossils found at closed sites (i.e., caves or rock shelters) are typically attributed to owls (Brain, 1981; Andrews, 1990; Avery, 1997, 2002, 2007). Raptors such as kestrels and hawks regurgitate pellets like owls, but can sometimes be eliminated as possible sources of large bone accumulations as the pellets of raptors and kestrels contain fewer skeletal elements (Duke et al., 1975; Dodson and Wexlar, 1979; Andrews, 1990). This difference is skeletal preservation is due to the lower degree of bone breakage from mechanical processes that occur to bone during consumption and digestion, and acid etching on the bone from chemical processes due slightly higher pH levels of digestive juices within the stomachs of owls (Clark, 1972; Dodson and Wexlar, 1979; Brain, 1981; Andrews, 1990). As a result, barn owls in general tend to regurgitate around 72% intact bones, compared to only 6.5% for hawks (Duke et al., 1975; Dodson and Wexlar, 1979; Andrews, 1990).

Studies comparing pellets from modern owl assemblages indicate some owl species return more bones in their pellets due to differences in mechanical and chemical

digestion making them more useful for paleoenvironmental reconstruction (Dodson and Wexlar, 1979). For example, an analysis of owl pellet taphonomy Dodson and Wexler (1979) found that 82.4% of skulls were recovered from barn owl pellets while only 2.9-12.5% of skulls were recovered from the pellets of great horned owls (*Bubo virginianus)* and screech owls (*Otus asio*). Additionally, the barn owl returned 81.7% (72% of which were complete) of all large skeletal elements, which includes the skull, mandible, scapula, humerus, radius, ulna, pelvis, femur, and tibia. The relatively small amount of damage barn owls produce on bones minimizes the taphonomic imprint on the prey remains found in their pellets, making them particularly useful in reconstructing paleoenvironments relative to other owl species.

While barn owls are capable of providing a large sample of the rodent community, there are biases inherent in these assemblages that could ultimately alter the paleoenvironmental signal inferred from it. Acknowledging the potential biases barn owls introduce to micromammal assemblages will allow for a more accurate interpretation of the paleoenvironment of Koanaka South.

Prey preference: The barn owl ranges in weight from 280 to 450 g, and the daily food intake in terms of live prey weight of barn owls in South Africa is 42-82 g (Steyn, 1983). Generally, 90% of prey taken by barn owls consists of members of the superfamily Muroidea (i.e. hamsters, mice, rats, gerbils, voles), and shrews from the family Soricidae (Andrews, 1990). The other 10% typically consists other small mammals, birds, amphibians, reptiles, and fish (Andrews, 1990). A sample of 52 barn owl dietary studies found approximately 74-100% of remains recovered from the barn owl pellets were micromammals (Taylor, 1994). Additionally, barn owl pellets analyzed

from 28 localities in South Africa and Namibia revealed rodents consisted of 46-100% of their diet (Vernon, 1972).

Although the barn owl is sometimes described as an opportunistic (non-selective) predator, this label is an over-simplification as several studies have shown barn owl prey assemblages do not fully correspond with relative abundances, presence/absence, and weight distribution (within the barn owls' potential prey size) of the surrounding small animal community (Andrews, 1990). Prey preference has been analyzed in studies comparing barn owl prey assemblages with the small mammal community and most suggest they are at least partially selective of their prey (Hanney, 1962; Glue, 1974; Bunn et al., 1982; Steyn, 1983; Fernandez-Jalvo, 1998; Avenant, 2005). For example, a comparison between a modern barn owl assemblage from the Great Fish River Valley of the Eastern Cape Province and the surrounding small mammal community found that barn owls prefer prey with a mass below 100-110 g (Perrin, 1982). Due to this preference, southern African rodent taxa with species that have a mass at or above this level, such as *Otomys, Gerbilliscus,* and *Pelomys,* may be underrepresented in barn owl pellet assemblages. Selectivity is further suggested by an analysis of 439 barn owl pellets from three sites at the Serengeti National Park in Tanzania found that the spiny mouse, *Acomys,* was not identified in a single pellet despite comprising of over 40% of the trapped rodents within the area (Laurie, 1971). The absence of this genus once again suggests barn owls are at least partially selective hunters and not strictly opportunistic (Laurie, 1971). The posterior dorsal hairs in *Acomys* are composed of rigid spines could discourage the barn owl from preying upon this genus and could be the reason as to why this genus was avoided by the barn owl.

Hunting behavior and habitat: Barn owls are exceptional hunters of small terrestrial fauna in open habitats exhibited through several anatomical specializations (Payne, 1971; Andrews, 1990; Reed, 2003). These include a relatively long legs, a facial disc that tunnels noises from below into their ears located near the center of their facial disc, specialized feathers which create a silent flight, and a low wing-loading creating a slow and buoyant flight pattern (Payne, 1971; Reed, 2003). Radio telemetry and long-term observations have confirmed their preference for open habitats; however, they also spend time in margin habitats between closed and open vegetation (Glue, 1967, 1974; Bunn et al., 1982). As a result, open habitat prey are expected to be represented more frequently in pellets than closed habitat prey, but this bias may be mitigated by time spent hunting in habitat margins (Reed, 2007).

Barn owls are mainly nocturnal, but are also occasionally crepuscular (Bunn, 1972), resulting in prey items being predominately, but not exclusively, nocturnal (Andrews, 1990). This bias was noted in the Great Fish River Valley pellet analysis where the diurnal/crepuscular rodent *Rhabdomys pumilio* only comprised of 15% of the small mammal remains from the barn owl pellets despite representing at least 50% of the small mammal community from trapping data (Perrin, 1982). A such, diurnal and/or crepuscular prey may be underrepresented in the rodent fossil assemblage from Bone Cave; however, this potential bias is limited in barn owls due to their crepuscular behavior (Andrews, 1990). Similarly, rodents from southern Africa that are arboreal (e.g., *Thallomys*) or fossorial (e.g., *Georychus capensis*) are likely to be underrepresented or absent in owl pellet assemblages; however, on occasion they are preyed upon and recovered in barn owl assemblages (Perrin 1982).

Although the home range of a barn owl may not result in a taxonomically biased assemblage, it does limit how far around a prey assemblage a paleoenvironmental can be inferred. The barn owl's home range is typically several square kilometers and is occupied throughout the year (Bunn et al., 1982; Andrews, 1990; Taylor, 1994). It should be noted that most of the time spent by the barn owls in their home range was between 0.4 km and 1.6 km from their nest, which would suggest the paleoenvironmental signal is going to be strongest within the 1.6 km radius surrounding the nest (Colvin, 1984).

Actualism. Paleoenvironmental reconstructions of fossil localities using owl-accumulated rodent assemblages are often based on actualistic principles. Actualism is the inference that present-day events and their effects occurred in the past (Simpson, 1970; Gifford, 1981; Gifford-Gonzalez, 1991). In studies that rely on actualistic principles for paleoenvironmental reconstruction, environmental tolerances and behaviors of extant taxa are interpreted to be similar to fossil specimens which they cannot be distinguished from morphologically. For example, all species of extant acacia rats in the genus *Thallomys* are arboreal and are found in biotic zones in southern Africa with *Acacia* savannas (Roberts, 1951; Smithers, 1968, 1971; DeGraaff 1981; Rautenbach, 1982; Monadjem et al., 2015). Under the principles of actualism, one can infer fossil specimens identified as *Thallomys* also occurred in similar biotic zones with *Acacia* savannas. Unfortunately, a downside to this assumption is that it is not possible to account for all interactions that existed in the past that could alter the fundamental niche of potential barn owl prey. Factors such as competition, predation, and other biotic interactions may limit a taxon's biogeographical distribution or behaviors to a smaller

subset of its fundamental niche, called a realized niche (Lomolino et al., 2006; Campbell et al., 2011).

Methodologies for reconstructing paleoenvironments using rodents. Environments inferred from rodents often use descriptions of the environment, habitat, diet, distribution, and ecology of modern faunas and apply these to fossil-bearing localities that contain the same taxa (Avery, 1981; Evans et al., 1981; Fernandez-Jalvo et al., 1998; Reed, 2007). For example, if the rodent fossil taxa identified from Bone Cave are all currently found in deserts and sandy substrates, one could infer the paleoenvironment was also a desert. Indicator species are particularly useful as they are specialized for a specific environment and provide general interpretations of the paleoenvironment (Avery 1981; Evans et al., 1981; Fernandez-Jalvo et al., 1998; Reed, 2007). A significant issue with this method is that few taxa exhibit habitat specificity to such a degree that they can unequivocally be used to indicate a specific environment (Evans et al., 1981).

A common index used to interpret the paleoenvironment of a fossil locality using rodent assemblages is the Gerbillinae:Murinae (G:M) ratio (Dauphin et al., 1994; Fernandez-Jalvo et al., 1998; Manthi, 2007; Reed, 2007; Stoetzel et al., 2011; Geraads et al., 2013). Measured as the proportional representation of the minimum number of individuals (MNI) from the rodent subfamilies Gerbillinae and Murinae, the G:M ratio has been proposed to be an indicator of open and arid habitats as the abundance of Gerbillinae taxa increases from northern Africa to south of the Sahara, while Murinae taxa shows the opposite trend (Dauphin et al., 1994; Fernandez-Jalvo et al., 1998). Reed (2007) tested the accuracy of the (G:M) ratio by comparing nine separate modern barn

and spotted eagle owl pellet assemblages collected from the Serengeti National Park in northern Tanzania with the amount of open vegetation 5 km around each assemblage. The results showed a significant trend toward decreasing proportions of gerbils with roost environments that had more wooded vegetation which would indicate of open environments; however, one roost had a higher than expected G:M ratio, with Murinae taxa being slightly more abundant than Gerbillinae taxa despite being in a grassland area (Reed, 2007). The author attributed this discrepancy to the fact that the area around the roost used to be more wooded in the past. However, he also recognized the important role the arid-adapted genus *Gerbillus* played in this ratio, and acknowledges this genus is found in wooded habitats which makes it less reliable as an indicator of open habitats. Similarly, a gerbil currently endemic to southern Africa, *Gerbillurus paeba*, is also distributed in savanna woodland biotic zones suggesting it is not always a useful indicator of open habitats (Stuart and Stuart, 2015). The same is true for the gerbil species, *Desmodillus auricularis*. Populations of this species are prevalent throughout the desert and semi-desert biotic zones in southern Africa; however, populations also exist in the Cape Fynbos biotic zone which is abundant in shrubs (Stuart and Stuart, 2015). The large roles *Desmodillus*, *Gerbillus*, and *Gerbillurus* play in G:M ratios all suggests this value may not be appropriate to use at southern and central African fossil sites. For these reasons, the G:M ratio will not be calculated at Bone Cave.

Another method utilizing rodents to infer the paleoenvironment at a fossil locality, is the taxonomic habitat index (THI). This method combines niche models from each taxon identified from a fossil locality which creates an overall picture of the habitat preferred by the fossil assemblage (Evans et al., 1981; Andrews, 1990; Fernandez-Jalvo

et al., 1998; Matthews et al. 2007; Reed, 2007). Niche models are values indicating the probability of a taxon being found in a particular habitat and are constructed from autecological summaries of current habitat use (Evans et al., 1981; Reed, 2007). For example, if a taxon is found with equal frequency in grasslands, forests, deserts, and savannas, each unique category would be scored 0.25. The pooled value given to each habitat class is the THI (Evans et al., 1981; Reed, 2007). If the fossils are only identified to the genus level, scores are added up for each individual species and divided by the total number of species in the genus (Evans et al., 1981; Reed 2007). This also applies to fossils identified to the family level by summing all species scores within a family and dividing by the total number of species (Evans et al., 1981; Reed 2007). As the number of species used to generate values at the genus and family level increases, the resolving power of the THI is diminished (Evans et al., 1981; Reed 2007). THI will not be utilized as the taxa identified in this project can only be identified to the genus level.

Trapping and Modern Owl Pellets from Koanaka South

A collection of two modern barn owl pellet assemblages and small mammals trapped from the area around the Koanaka South provides an opportunity to determine the taxonomic biases from barn owl assemblages, which can be applied to the fossil assemblage (Ferguson et al., 2010; Tutalo, 2012; Thies and Lewis, 2015). Additionally, the two sampling methods provides a unique opportunity to infer the paleoenvironment surrounding Koanaka South by comparing the modern rodent community composition with the fossil rodent community composition (Tutalo, 2012; Thies and Lewis, 2015).

The small mammal fauna was trapped at Koanaka South for roughly two weeks in July of 2008 and again in 2009 (Ferguson et al., 2010; Thies and Lewis, 2015). Trapping

was performed using baited Sherman traps and snare traps during both field seasons. Traps were set during the day and left out overnight to ensure the best possible chance of sampling both the diurnal and nocturnal rodents in the area, and were placed in six different areas which best represented the diverse microhabitats of Koanaka South locality (Thies and Lewis, 2015; Ferguson et al., 2010). Between the two field seasons, 25 different small mammal species were trapped (Table 5) (Thies and Lewis, 2015). It should be noted that some trapped individuals were released and the recording methods utilized did not allow for the numbers of individuals released and potentially recaptured to be estimated. The released taxa consisted of *Aethomys chrysophilus*, *Mastomys natalensis*, and *Micaelamys namaquensis* (Thies and Lewis, 2015).

The two modern barn owl assemblages collected from Koanaka South consisted of 91 pellets (Tutalo, 2012). A minimum of 233 individuals were recovered including rodents, shrews, and unidentified individuals belonging to the classes Reptilia and Aves (Figure 2). *Steatomys* was the most abundant taxon in the pellets, with 75 individuals recovered, accounting for 32.19% of the identifiable rodent specimens. *Mus* was the second most abundant rodent prey with 26 individuals accounting for 11.16% of the owl pellets rodent remains (Tutalo, 2012). Also noteworthy was the presence of 19 individuals of both *Aethomys* and *Saccostomus*, each making up 8.15% of the rodents in the barn owl pellets, and twelve *Gerbilliscus* individuals, making up 5.15% of the rodents in the barn owl pellets (Tutalo, 2012). Eleven specimens, representing 4.72% of the rodent prey from the barn owl pellets, could not be distinguished between *Zelotomys* or *Mastomys*. All other taxa range from 3% to less than 1% including *Lemniscomys, Mastomys, Micaelamys, Mus, Zelotomys, Murinae gen., Saccostomus, Dendromus,*

Steatomys Desmodillus/Geribillurus, Gerbillurus, Gerbilliscus, Gerbilliscus/Gerbilliurus, Gerbillinae gen., and *Fukomys* (*Cryptomys*).

A comparison of the taxa from the traps and pellets indicates all of the rodents identified in the pellets were also identified in the traps (Tutalo, 2012). However, some genera present in both the owl pellets and traps were rare in one while abundant in the other (Tutalo, 2012). One of the most significant disagreements between pellets and trapping at Koanaka South involves the fat mouse, *Steatomys*. This genus made up the highest percentage of the pellet remains but the lowest percentage of the trapping records. The lone specimen was trapped near a rocky, woodland microhabitat where this genus is known to occur (Stuart and Stuart, 2015). The abundance of *Steatomys* in the owl pellets relative to the other genera is possibly explained by the tendency of barn owls to sample taxa adapted to habitats with open vegetation over taxa adapted to habitats with closed vegetation (Torre et al., 2004). A discrepancy between the two sampling methods also occurred for *Mastomys* as it accounted for a large percentage of the trapped individuals, but only one individual was identified from the barn owl pellets (Tutalo, 2012). Similarly, *Micaelamys* accounted for eight percent of the trapping, but only one individual was recovered from the pellets (Tutalo, 2012). It should be noted that numerous elephant shrews (*Elephantulus intufi*) were trapped at Koanaka South, but none were identified in the owl pellets despite elephant shrews being in the size range of barn owl prey (Tutalo, 2012). Elephant shrew fossils also occur in the Bone Cave deposit.

The significant differences that exist in the relative abundance of some taxa between the two sampling methods indicate relative abundances of taxa from barn owl assemblages are not representative of the surrounding community. These results suggest

relative abundance of taxa should not be a factor in determining the paleoenvironment of a fossil locality. The results from this study also suggest barn owls are capable of providing a large sample of the rodent community composition but the relative abundance of the rodent taxa are not always in proportion to the trapping data collected from the rodent community. These results could be due to biases inherent in both owl pellets and trapping. For example, some rodent taxa are described as difficult to catch through trapping alone suggesting and some may have been missed or underrepresented (Smithers, 1971; Monadjem et al., 2015). For example, Stuart and Stuart (2015) state that *Dendromus* rarely enter traps, which could be why only two individuals were trapped in 2008-2009. Low numbers from the traps may be attributed to a number of variables such a type of trap, type of bait, or even time of year trapped (dry season). Since this was one of the first times small mammal trapping was conducted in this area, more research needs to be conducted in order to accurately address these issues.

Description of Koanaka South and Bone Cave

Modern environmental conditions at Koanaka South.

Presently, annual temperature at Koanaka South ranges from -6.1°C to 39.6°C (Botswana Department of Meteorological Services, 2017). Mean annual precipitation (MAP) is 250–650 mm and mostly occurs during the summer months between November and March (Wright, 1978). Adjacent to Koanaka South locality are two pans, which are small closed basins containing ephemeral lakes that are characteristics of semi-arid regions with little topographic relief (Thomas and Shaw, 1991). One is located ~1.5 km west of Koanaka South and the second is ~2 km west of Koanaka North. The pan's substrate consists of calcareous clays that overly calcrete (Cooke, 1975; Kennedy et al., 2012). These pans are only filled with water for short periods of time after the summer

rainy season; however, the exact duration or frequency of when they are filled is not known (Bauer et al., 2009; Kennedy et al., 2012). A large system of linear dunes surrounds Koanaka South today. These dunes are aeolian (wind-derived) depositional landforms composed of coarse sand (Cooke, 1975; Thomas and Shaw, 1991).

Currently, there are six major biotic zones defined in southern Africa (*sensu* Skinner and Chimimba, 2005) including Angola, Zambia and Malawi: desert, semi-desert, savanna woodland, savanna grassland, cape fynbos, and indigenous forest (Stuart and Stuart, 2015). The southern African subregion proper is comprised of the area south of the Zambezi and Kunene Rivers, and the northern border of Namibia (Skinner and Chimimba, 2005). The Koanaka Hills fall within the semi-desert or arid biotic zone. These areas are described as xeric, though they receive higher rainfall than deserts (Stuart and Stuart, 2015). MAP in semi-deserts rarely exceeds 500mm/year (Stuart and Stuart, 2015). In southern Africa this biome is represented in most of Namibia outside the desert zone, the Kalahari in Botswana, and extends south into South Africa in the Karoo and Namibia (Stuart and Stuart, 2015). The sparse vegetation in this area is mostly comprised of woody shrubs and trees, and meandering rivers are also common in semi-desert zones (Stuart and Stuart, 2015).

Description of Bone Cave. The entrance into Bone Cave is known as the Entrance Room (Pickford and Mein 1988; Pickford 1990; Williams et al., 2012) (Figure 3). At the southern end of the Entrance Room (about 30 m into Koanaka South) is a narrow shaft called the Squeeze, which is ~1 m in diameter. Leopard's Dining Room (LDR) is the first chamber beyond the Squeeze (Figure 4), consisting of a room with a < 3 m high ceiling and about 10-12 m wide (Ritter and Mann, 1995). Leopards (*Panthera*

pardus) inhabited Bone Cave in 1994 as Ritter and Mann (1995) reported encountering one while crawling through the squeeze, and they also found many bird and antelope bones on the floor of the LDR. Many bones, some with dried meat still on them, were also reported in the 2007-2009 expedition suggesting the cave was still being used actively by leopards (Tutalo, 2012). The cave continues on to another room with a 2-3 m pit near the center known as Drop Room (DR) (Figure 4). Stalactites, stalagmites, breccia, and flowstones cover the walls of DR, and in some places, breccia surrounds older stalactites (Ritter and Mann, 1995). The baboon skull and the breccia sample taken just above the skull dating to ≥317+/-114 ka were collected in the DR (Williams et al., 2012). Beyond DR is the main cavern known as the Atrium (Figure 5), which is about 75 m in diameter and ranges from 1-7 m in height (Ritter and Mann, 1995). Moving east-west around the Atrium is the Micro-Mammal room, which contains three 2-3 m deep pits (Ritter and Mann, 1995). In the southern portion of the cave is the Sand Slide, which has a sandy mound that slopes 3-4 m down into the Atrium (Figure 5). North of the Sand Slide is Elephant Room, which contains several speleothems including one that resembles an elephant (Figure 5). The fossil rodent material analyzed in this study were found in several parts of the cave, including DR, Atrium, LDR, Micro-Mammal Room, and Sand Slide.

Goals of This Study

The goal of this project is to infer the paleoenvironment of Koanaka South around 317 +/- 114 k using fossil rodents recovered from Bone Cave. To achieve this goal, I will use maxillary characters for identifying southern Africa rodents ≤ 5 kg to the lowest taxonomic level. The fossil rodent community composition will then be compared against

the modern community as assessed from trapping and pellet data to determine if they are identical in taxonomic composition. If both the modern and fossil rodent community compositions are the same, this would suggest the environment of Koanaka South around 317 +/- 114 ka was similar to today. Additionally, other regions of Africa where the modern rodent community composition is identical or similar to the fossil rodents will be identified and described to interpret the paleoenvironment of Koanaka South. Descriptions of the environment, habitat, distribution, and ecology of modern faunas will also be applied to the fossil rodent taxa identified from Koanaka South.

1. H_O: Fossil rodent taxa identified from Bone Cave are all distributed at Koanaka South today.

   H_A: Fossil rodent taxa identified from Bone Cave are not all distributed at Koanaka South today.

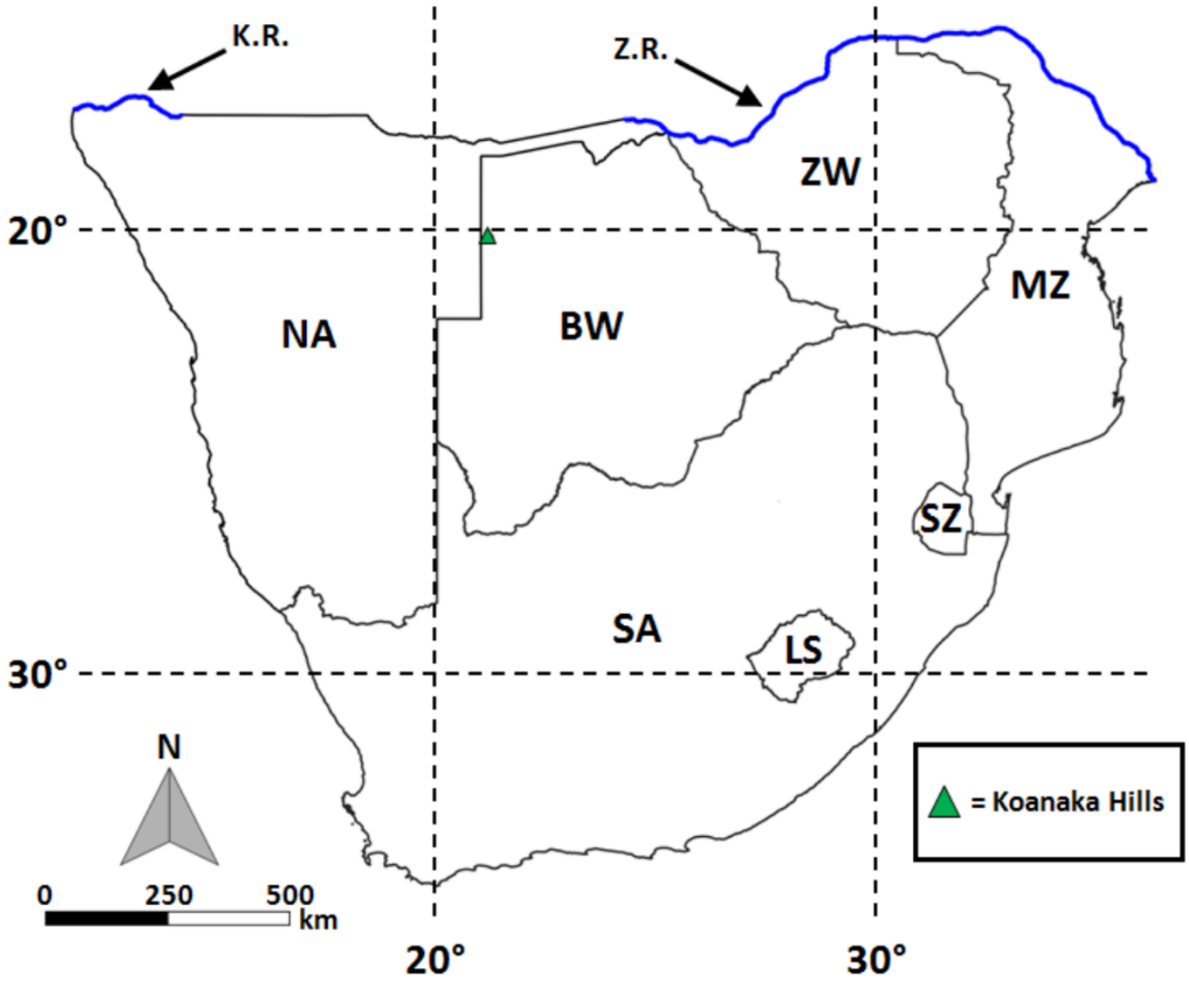


FIGURE 1. Geographic location of the Koanaka Hills within southern Africa. Abbreviations in the figure: K.R. Kunene River, Z.R. Zambezi River, SA South Africa, LS Lesotho, SZ Swaziland, MZ Mozambique, ZW Zimbabwe, BW Botswana, and NA Namibia.

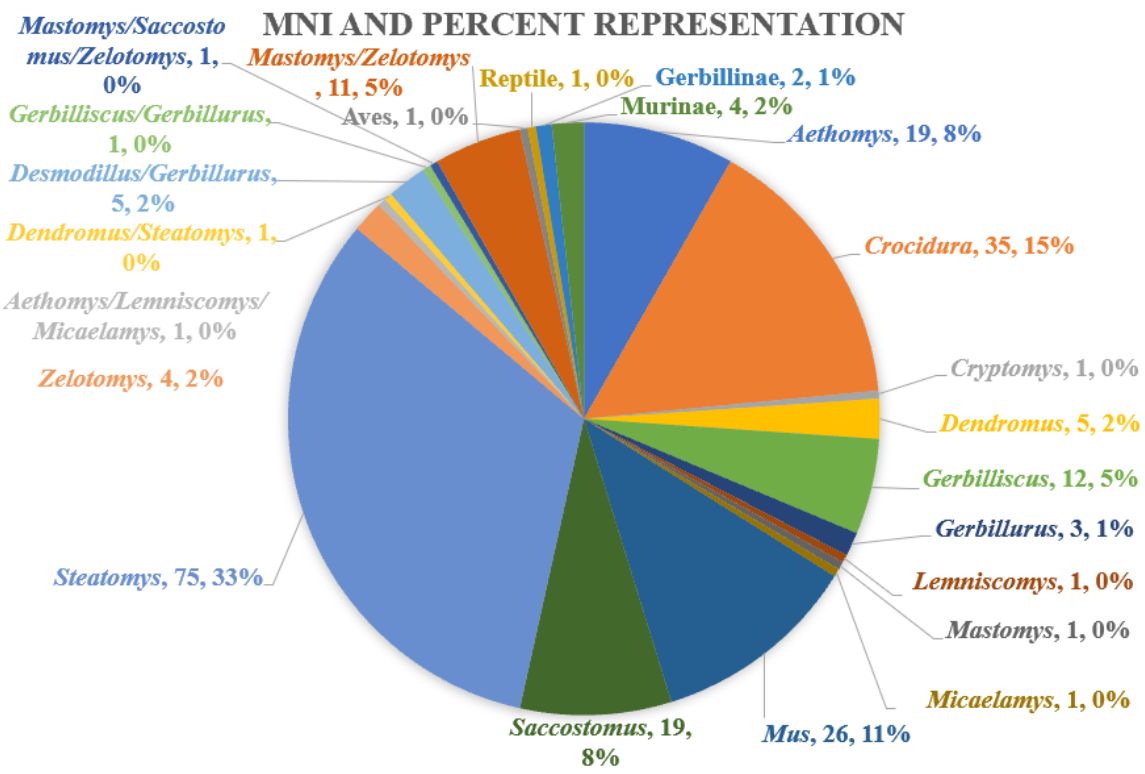


FIGURE 2. MNI and percent representation of prey remains identified from barn owl pellets collected from Koanaka South in 2008-2009 (Tutalo, 2012).

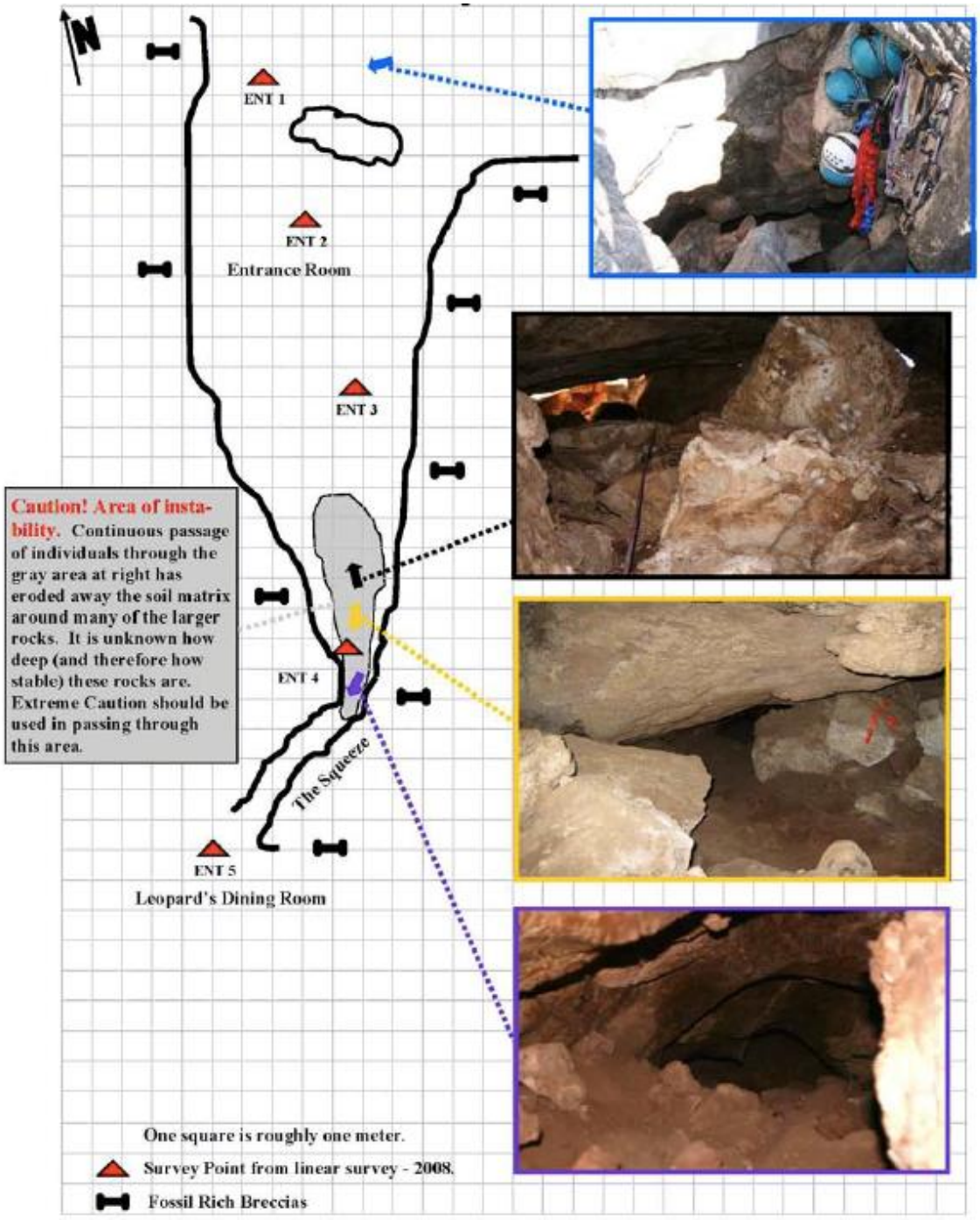


FIGURE 3. The Entrance and Squeeze in Bone Cave, Koanaka South (map courtesy of Steve Thompson and Mohutsiwa Gabadirwe).

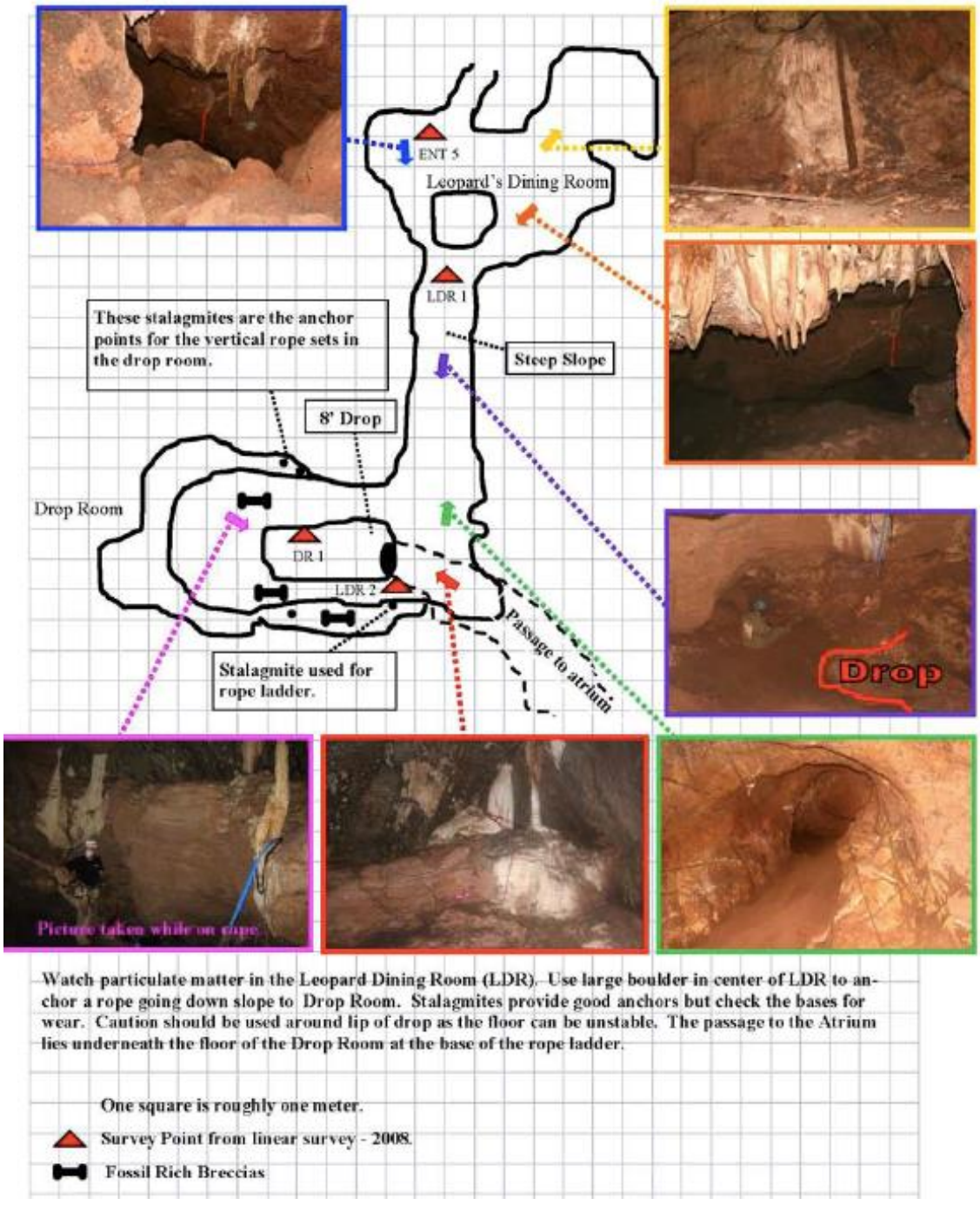


FIGURE 4. The Leopard's Dining Room and the Drop Room in Bone Cave, Koanaka South (map courtesy of Steve Thompson and Mohutsiwa Gabadirwe).

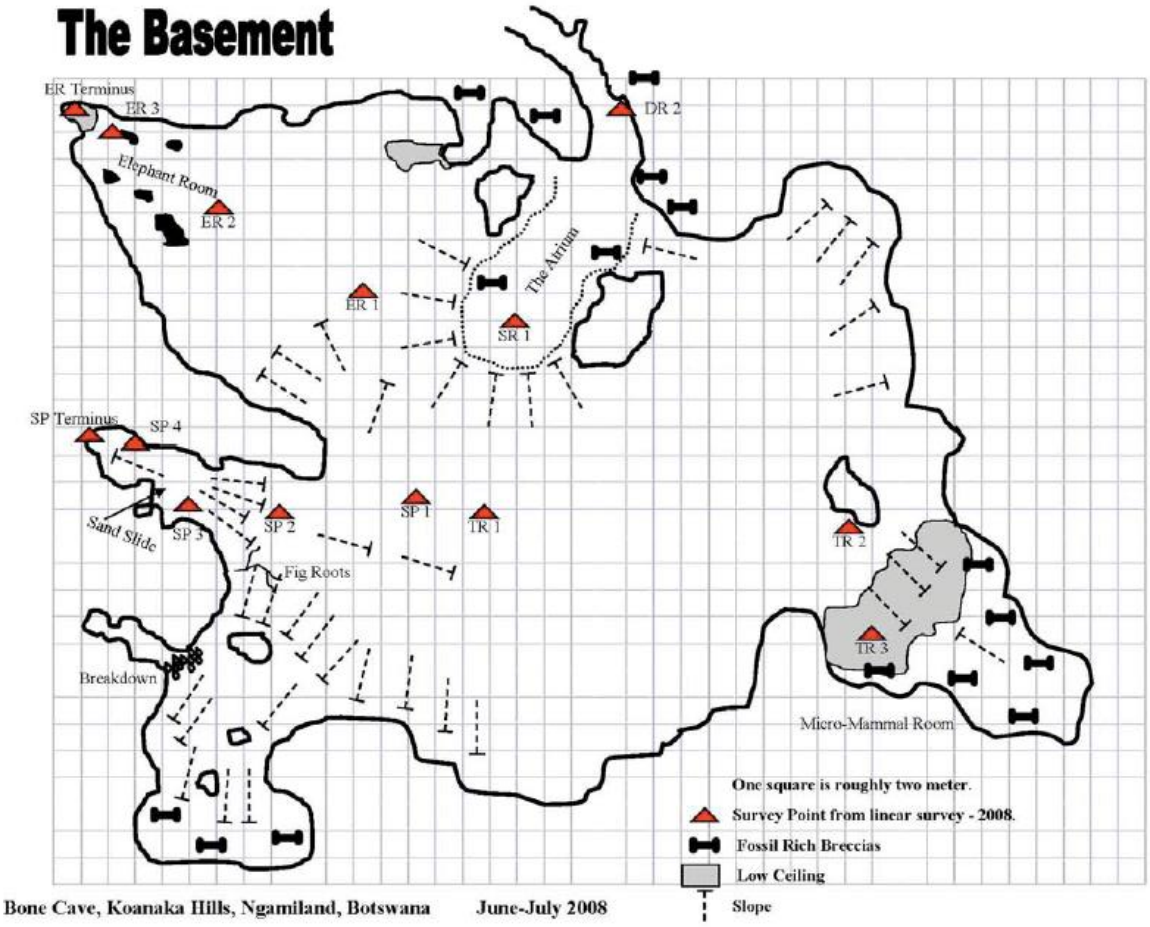


FIGURE 5. The Basement, with the Elephant Room, Micro-Mammal room, Breakdown and Atrium in Bone Cave, Koanaka South (map courtesy of Steve Thompson and Mohutsiwa Gabadirwe).

TABLE 1. Mammals from Gcwihaba and Koanaka combined from 1988 expedition (Pickford 1990).

Scientific name	Common name
Rinolophus sp. 1	Horseshoe Bat
Rinolophus sp. 2	Horseshoe Bat
Vespertilionidae	Vesper Bat
Myosorex sp.	Forest Shrew
Suncus sp.	Dwarf Shrew
Elephantulus sp.	Elephant Shrew
Lepus sp.	Hare
Zelotomys aff. *woosnami*	Woosnam's broad-headed mouse
Millardia aff. *kathleenae*	Miss Ryley's soft-furred rat
Mus sp.	Mouse
Steatomys sp.	Fat mouse
Malacothrix sp.	Large-eared mouse
Dendromus sp.	Climbing mouse
Gerbilliscus (*Tatera*) cf *brantsi*	Highveld Gerbil
Taterillus sp. 1	Gerbil
Taterillus sp. 2	Gerbil
Gerbillus sp.	Gerbil
Otomys gracilis	Vlei rat
Otomys campbelli	Vlei rat
Graphiurus sp.	Dormouse
Georychus sp.	Molerat
Hystrix sp.	Porcupine
Pedetes sp.	Springhare
Procavia sp.	Hyrax
Parapapio sp.	Baboon
Phacochoerus sp.	Warthog
cf. *Raphicerus* or *Cephalophus*	Grysbok or Duiker

TABLE 2. Rodent taxa identified at Drotsky's Cave during the 1991 expedition (Robbins et al., 1996).

Taxon	Common Name	Minimum Number of Individuals (MNI)
Pedetes capensis	Springhare	8
Mystromys albicaudatus	White-tailed rat	3
Gerbillurus paeba	Hairy-footed gerbil	4
Gerbilliscus (*Tatera*) cf. *G. leucogaster*	Bushveld gerbil	1
Gerbilliscus (*Tatera*) cf. *G. brantsii*	Highveld gerbil	34
Gerbilliscus (*Tatera*) sp.	Gerbil	9
Dendromus sp.	Climbing Mouse	1
Steatomys or *Malacothrix* sp.	Fat mouse or Large eared mouse	2
Otomys cf. *angoniensis*	Angoni vlei rat	11
Muridae	Murids	1
Unidentified muroidea	Muroids	7

TABLE 3. Rodents from Tsodilo Hills (Robbins et al., 1996).

Scientific Name	Common Name	Late Prehistoric/Historic MNI	Late Latter Stone Age MNI	Upper Fish Deposits MNI	Lower Fish Deposits MNI
Pedetes capensis	Springhare	3	8	19	5
Fukomys (*Cryptomys*) *damarensis*	Damaraland mole rat	1	1	3	0
Saccostomus campestris	Pouched mouse	0	1	1	0
Gerbillurus paeba	Hairy-footed Gerbil	1	0	1	0
Gerbiliscus (*Tatera*) cf. *leucogaster*	Probable bushveld gerbil	1	2	8	0
Otomys cf. *angoniensis*	Probable Angoni vlei rat	1	1	1	0
Hystrix africaeaustralis	Cape Porcupine	1	1	1	1

TABLE 4. List of taxa identified from 1969-1970 expedition at Gi Pan fossil locality in northwestern Botswana (Brooks and Yellen, 1977).

Scientific name	Common name
*Equus capensis**	Giant zebra
*Phacochoerus ethiopicus**	Cape warthog
*Homoioceras bainii**	Giant buffalo
Alcelaphus cf. *helmei*	Giant hartebeest
Ceratotherium simum	White rhinoceros
Connochaetes taurinus	Brindled gnu
Antelopini sp.	Antelopine
Girrafa cf. *camelopardalis*	Giraffe

** indicates extinct species*

TABLE 5. Small mammals trapped from 2007-2009 Koanaka South expedition (Ferguson et al., 2010; Tutalo, 2012).

Order	Species	N
Eulipotyphyla	*Crocidura hirta*	10
Chiroptera	*Chaerephon nigeriae*	1
	Hipposideros commersoni	9
	Neoromicia capensis	10
	Nycteris thebaica	31
	Rhinolophus denti	20
Carnivora	*Cynictis penicillata*	8
	Galerella sanguinea	2
	Genetta genetta	1
	Mellivora capensis	2
Macroscelidea	*Elephantulus intufi*	1
Rodentia	*Aethomys chrysophilus*	131
	Cryptomys damarensis	2
	Dendromus melanotis	2
	Gerbilliscus brantsi	61
	Gerbilliscus leucogaster	66
	Gerbillurus paeba	31
	Lemniscomys rosalia	6
	Mastomys natalensis	129
	Micaelamys namaquensis	42
	Mus indutus	6
	Mus minutoides	5
	Saccostomus campestris	8
	Steatomys parvus	1
	Xerus inauris	2
	Zelotomys woosnami	2

CHAPTER II

MATERIALS AND METHODS

Field Methods Used at Koanaka South

From 2007-2009 three field seasons were conducted at Koanaka South for approximately two weeks each year. Collecting at Koanaka South was focused on an internal deposit in the Atrium with an estimated minimum age of >383 ka (Williams et al., 2012). Additional samples were also collected from the Drop Room and Micro-Mammal Room, LDR, and Sand Slide. The fossiliferous deposits from the Koanaka South cave site is expansive and covers many large rooms of the cave to several meters. Fossiliferous deposits are also exposed on the surface of the cave, and this exposure was conservatively estimated to encompass at least 300 m^2. Much of the internal deposits are loosely consolidated, allowing for easy excavation of materials, but other parts, including the external deposits, consist of calcified breccia. In 2007, the cave interior was initially surveyed for areas of high fossil concentration and specimens were collected opportunistically if they were readily identifiable and gathered without risk of damage (Lewis et al., 2011). This survey identified several areas with high a density of fossils including Drop Room, Atrium, Leopard's Dining Room (LDR), Micro-mammal room, and Sand Slide. The rodents collected from theses rooms could have been altered post-depositionally through trampling, water transport, weathering, and erosion (Andrews, 1990). These processes could result in a fossil assemblage that is temporally mixed. For example, the rodent collected from the Leopard Dining Room could have been deposited and from a different time period than those in the Atrium and if the cave was flooded these samples could become mixed.

In 2008-2009 these areas were again sampled and small test pits were dug that resulted in several bags of fossil bearing sediments which were removed from the cave. These sediments were allowed to dry by spreading them out on plastic tarps. Once dry, sediments were then passed through 1 mm gauge screens to isolate the fossils (Lewis et al., 2011). Sensitive areas within the cave, such as where cave formations are located or active, were avoided. All test pits were refilled so that the cave retained its original appearance. Half of the fossils were then returned to the Paleobiology Lab at Sam Houston State University (SHSU) where they were cleaned, cataloged, identified, and curated for long term storage, and the other half were set to the Botswana National Museum (BNM) for permanent curation (Lewis et al., 2011). The fossils sent to the BNM and the Paleobiology Lab at SHSU were chosen randomly (Lewis et al., 2011).

Qualitative Analysis

Fossil rodent identification. Since fossil remains are often fragmentary, identification of fossil rodent specimens is typically achieved through the examination of cranio-dental features such as the number of cusps on a molar and position of the anterior palatal foramina (e.g., Roberts, 1951; Hanney, 1962; Davis, 1965; Misonne, 1969). Alternately, extant rodents are often identified to the species level through characteristics such as: genetic variation, pelage variation, number of mammae, skull size, and other parts of soft and hard tissue anatomy (Wilson and Reeder, 2005; Monadjem et al., 2015). This presents an issue for paleontologists attempting to identify fossil rodents as most of these features are not preserved during the fossilization process.

Further complicating fossil identifications is the lack of a systematic guide to identify all African rodent genera using only those characters present on the typically

fragmentary remains recovered. Despite this, most fossil rodent identifications reported are at the genus or even the species-level and are frequently made without explicit reference to the characters or sources used (Avery, 1981, 2001; Pickford, 1990; Pickford et al., 1994; Robbins et al., 1996; Reed, 2003; Leichlitter, 2011). A character matrix was created to accurately identify fossilized rodent specimens collected from Bone Cave in a manner that is replicable and can be applied to other rodents. The character matrix was created drawing on maxillary characters found in literature and modified using a comparative image library of all rodent genera with geographic distribution in southern Africa with body mass ≤ 5 kg (excluding the suborder Sciuromorpha) (Tables 6 and 7) (Misonne, 1969; DeGraaff, 1981; Carleton and Musser, 1984; Denys et al., 1994; Kingdon, 1997; Reed, 2003; Wesselman, 1984; Skinner and Chimimba, 2005; Wilson and Reeder, 2005 Avery, 2007). Sciuromorphs were not included because we did not take photos of the museum specimens for the species found in southern Africa. However, sciuromorphs are relatively easy to identify as they have four molars whereas the majority of southern African rodents have three molars (Kingdon, 1997; Monadjem et al., 2015). The rodent maxilla, as opposed to the mandible, contains more characteristics that are unique to different genera of the rodent subfamily Murinae in Africa (Barr, 2008). For this reason, only fossil maxillae with at least one tooth were included in the analysis. A character matrix for mandibles could help diagnose rodent taxa from fossil localities in southern Africa as there are apomorphic characteristics in the mandible, but time limited the ability for this to be done in this project. In order to assist in replicating rodent identifications for future researchers, a photograph of a rodent maxilla was labelled with the characters used in the character matrix (Figure 6). A photographic example of each

character state is also provided in the appendices as well as a list of all the modern museum specimens used in this project (Appendices B-S). Dental nomenclature for this project follows that used in previous studies (Table 8). Identifications for each specimen first began by scoring them for each of the seventeen characters. If a genus-level identification was not possible with the character matrix scores alone, dental metrics were taken for each tooth available on the fossil specimen and compared against dental metrics of the museum specimens for all possible remaining genera.

Comparative images were taken by T.L. Campbell and included specimens from Ditsong National Museum of Natural History (formerly Transvaal Museum [TM]), National Museum, Bloemfontein (NMB), Field Museum of Natural History (FMNH), American Museum of Natural History (AMNH), Natural Science Research Laboratory (NSRL), and National Museum of Natural History (USNM). To aid in identification of genera not readily identifiable using the character matrix alone, molar dimensions were also taken on digital photos for both the museum and fossil specimens. Scaled specimen photos were taken with the occlusal surface of the teeth parallel to the camera lens. Molar measurements were acquired using tpsDIGw32 version 2.31 (Rohlf, 2017) and consisted of maximum lengths and widths for each available tooth (Figure 7).

Paleoenvironmental reconstruction. Once the fossil rodent specimens from Bone Cave are identified, a description of the environment, habitat, diet, distribution, and ecology of their modern counterparts will be outlined to infer the paleoenvironment of Koanaka South. For example, if the rodent taxa identified from Bone Cave are all currently found along streams and rivers with *Acacia* trees, we could infer the paleoenvironment was similar. The fossil rodent community will also be compared

against the modern rodent community at Koanaka South and other modern rodent communities in Africa. If the fossil community composition is taxonomically identical to the modern community composition inhabiting Koanaka South, this would suggest the environment around 317 +/- 114 ka was similar to the modern environment. If the community composition differs significantly from Koanaka South biota, other regions (if any) in Africa with indistinguishable or similar rodent community compositions will be identified and described as an analog to the paleoenvironment around Koanaka South during fossil deposition. A downside to methods utilizing actualistic principles is that it is impossible to accurately interpret all biotic interactions that existed in the past, and one must recognize that these interactions could significantly alter potential barn owl prey. However, in spite of the inability to qualify and quantify these interactions, this principle is freely applied by all paleontologists using fauna to reconstruct the paleoenvironment of fossil localities.

Quantitative Analysis

MNI and NISP. The MNI (minimum number of individuals) is a way to tabulate the fewest possible number of individuals identified from a fossil locality using defined criteria with physical remains (White, 1953). MNI for the fossil rodents at Bone Cave was calculated for all specimens with at least one mostly complete molar attached to a maxilla. Molars and maxillae with small cracks and chips were included if they were able to be identified to the genus taxonomic level. To calculate MNI, each specimen was tallied according to its anatomical side and taxonomic identification. The most abundant side for each taxon or taxonomic group used. The NISP (number of identified specimens)

is a count of the number of identified specimens for each identified taxonomic group and was determined for Bone Cave specimens by combining sided elements per taxon.

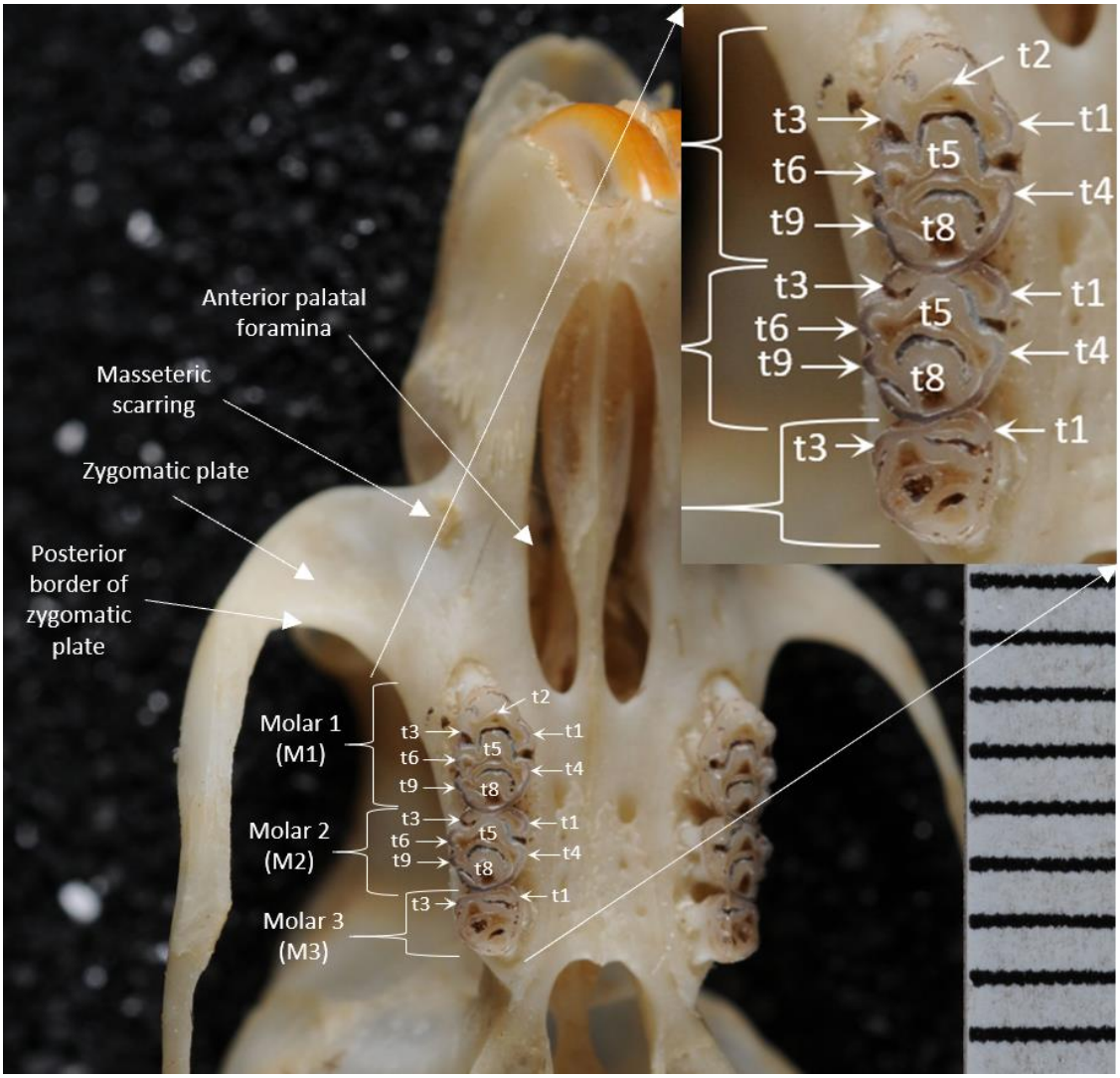


FIGURE 6. Cranio-dental nomenclature used in the character matrix. Reference specimen: *Grammomys cometes* (FM 214896).

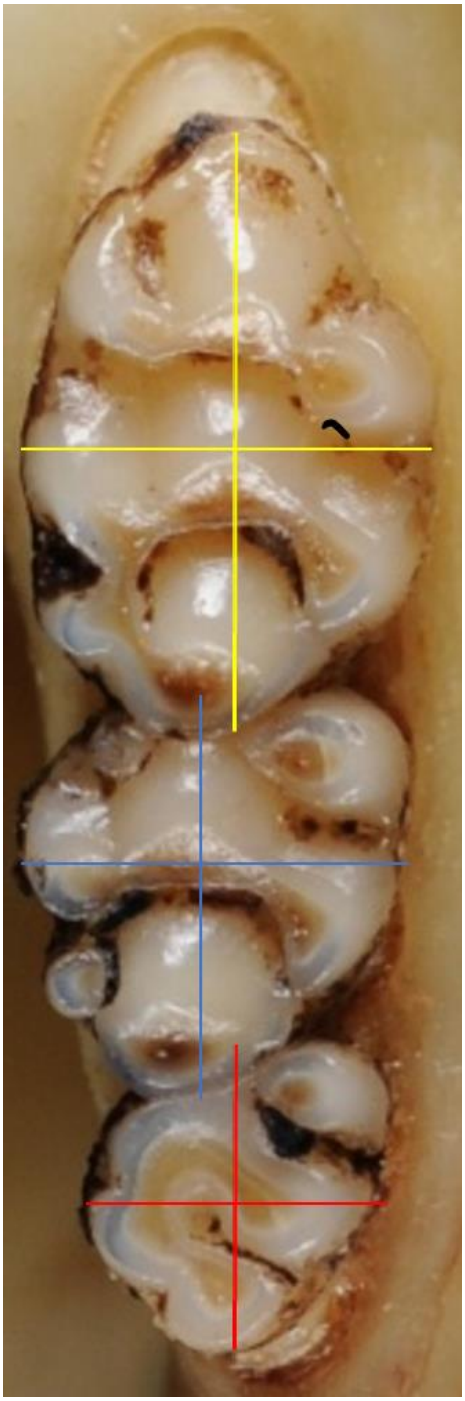


FIGURE 7. Representation of measurements for M1 (yellow lines), M2 (blue lines), and M3 (red lines) dimensions. Reference specimen: *Aethomys chrysophilus* (TM. 45247*).*

TABLE 6. List of all southern African rodents ≤ 5 kg excluding Sciuromorphs.

Family	Subfamily	Genus
Muridae	Murinae	*Aethomys* spp.
		Dasymys sp.
		Grammomys spp.
		Lemniscomys sp.
		Mastomys sp.
		Micaelamys spp.
		Mus spp.
		Pelomys spp.
		Otomys spp.
		Myotomys spp.
		Rhabdomys spp.
		Thallomys spp.
		Zelotomys spp.
	Dendromurinae	*Desmodillus* sp.
		Gerbilliscus spp.
		Gerbillurus spp.
	Deomyinae	*Acomys* spp.
Nesomyidae	Mystromyinae	*Mystromys* sp.
	Dendromurinae	*Steatomys* spp.
		Dendromus spp.
		Malacothrix sp.
	Cricetomyinae	*Saccostomus* sp.
		Cricetomys sp.
	Petromyscinae	*Petromyscus* spp.
Petromuridae	Petromurinae	*Petromus* sp.
Pedetidae	Pedetinae	*Pedetes* sp.
Bathyergidae	Bathyerginae	*Fukomys* spp.
		Cryptomys sp.

TABLE 7. Characters and character states for southern African rodents (excluding Sciuromorphs) used to identify fossil specimens. A not available (n/a) character state means the character state is not present in the specimen.

Anterior Palatal Foramen Posterior Length Character 1	
State	Description
0	Does not reach first alveoli on M1
1	Reaches anterior border of first alveoli on M1
2	Reaches first lamina of M1 (i.e. T2/T3) (For Mystromys, Petromyscus, Petromus, and Gerbils – at anterocone)
3	Reaches second lamina of M1 (i.e. T5/T6) (For Mystromys, Petromyscus, Petromus, and Gerbils – at protocone)

Anterior Alveoli Position to Posterior Curve of Zygomatic Plate Character 2	
State	Description
0	Alveoli border posterior to zygomatic plate
1	Alveoli border at zygomatic plate
2	Alveoli border anterior to zygomatic plate

t1 on M1 Character 3	
State	Description
0	N/A
1	Absent
2	Incipient
3	Present

Position of t1 on M1 Character 4	
State	Description
0	Approximately parallel with t2/t3 on M1
1	Slightly posteriorly displaced
2	Highly posteriorly displaced
3	Absent
4	N/A

Position of t4 on M1 Character 5	
State	Description
0	Approximately parallel with t5/t6 on M1
1	Slightly posteriorly displaced
2	Highly posteriorly displaced
3	Absent
4	N/A

TABLE 7. (CONTINUED).

t9 on M1 Character 6	
State	Description
0	N/A
1	Absent
2	Present

t9 on M2 Character 7	
State	Description
0	N/A
1	Absent
2	Present

t3 on M2 Character 8	
State	Description
0	N/A
1	Absent
2	Present

M3 Development Character 9	
State	Description
0	Incipient
1	Developed (containing at least two rows with cusps)

Cingular Conule or t2 Extention on M1 Character 10	
State	Description
0	Absent/ Slight depression or cingulum
1	Developed cusp or extention of anterior border of T2
2	N/A

Masseteric Knob Character 11	
State	Description
0	Absent (absent or small scarring on zygomatic plate)
1	Present (knob on zygomatic plate)
2	Well-developed (knob on narrow and vertically-oriented zygomatic plate though these features not as extreme as in *Malacothrix*)
3	Pronounced (large knob on narrow, vertically-oriented zygomatic plate)

TABLE 7. (CONTINUED).

Molar type Character 12	
State	Description
0	Loxodont
1	Lophodont/Semi-lophodont/Advanced-lophodont

t7 on M1 Character 13	
State	Description
0	N/A
1	Absent
2	Present

t7 on M2 Character 14	
State	Description
0	N/A
1	Absent
2	Present

Number of Molars Character 15	
State	Description
0	3 molars
1	4 molars

Molars with re-entrent folds Character 16	
State	Description
0	Absent
1	Present

Number of Lamina on M3 Character 17	
State	Description
0	Six or more lamina
1	Five lamina
2	Four-three lamina
3	Two or less lamina

TABLE 8. Sources for the dental terminology used in this study.

Family	Subfamily	Publication
Nesomyidae	Cricetomyinae	Miller 1912
	Dendromurinae	Miller 1912
	Petromyscinae	Lindsay 1988
	Mystromyinae	Lindsay 1988
Muridae	Gerbillinae	Flynn *et al.*, 2003
	Deomyinae	Miller 1912
	Murinae	Miller 1912

CHAPTER III

RESULTS

Overview of Specimens Identified from Bone Cave

Using the character matrix and molar measurements, 196 maxillary rodent specimens with a minimum of 126 individuals were identified from Bone Cave. All of the specimens identified belong to the superfamily Muroidea, a species rich and diverse clade found on every continent except Antarctica (Musser and Carlton, 2005). The Muroids identified from Bone Cave include members from two families, Muridae and Nesomyidae, six subfamilies Deomyinae, Gerbillinae, Murinae, Cricetomyinae, Mystromyinae, and Dendromurinae, and twenty potential genera including *Acomys Gerbilliscus, Gerbillurus, Desmodillus, Lemniscomys Mastomys, Micaelamys Rhabdomys, Thallomys, Mus, Otomys, Pelomys, Grammomys, Saccostomus, Dendromus, Malacothrix, Steatomys,* and *Mystromys* (Table 9).

The character matrix and molar dimensions taken from museum specimens used in this analysis indicate it is possible to identify most but not all southern African rodent fossils to the genus level especially if they retain all molars and portions of both the anterior palatal foramina and zygomatic arch are retained. For the murines, *Aethomys*, *Mastomys, Rhabdomys, Zelotomys*, and *Grammomys* specimens were all not identifiable to the genus level to the exclusion of all other rodents from southern Africa using the character matrix and molar measurements. For the deomyines, if all three molars are present, molar dimensions as well as character matrix scores can be used to identify *Acomys* to the generic level. Among the Gerbillinae only *Gerbilliscus* can be identified to the genus level with the character matrix scores and molar dimensions to the exclusion of

the other two gerbil genera with populations in southern Africa, *Gerbillurus* and *Desmodillus*. These two gerbil genera cannot be distinguished from each other using molar dimensions and the character matrix. All three southern African genera from the Dendromurinae subfamily, *Dendromus, Steatomys*, and *Malacothrix*, can be identified to the genus level using character matrix scores if the masseteric knob is present. The two genera in the Cricetomyinae subfamily, *Cricetomys* and *Saccostomus* can be identified to the genus level using scores from the character matrix alone. The one southern African genus from the Mystromyinae subfamily, *Mystromys*, can be identified to the genus level using character matrix scores alone, even if only the M1 or M2 are present.

Specimens with two or three potential genus-level identifications are grouped together, whereas specimens with more than three potential genus-level identifications are labelled at the subfamily level. Character matrix scores for each fossil rodent specimen identified from Bone Cave are listed in appendix T, while character matrix scores for the museum specimens are listed in appendix U. The molars present for each specimen are listed in appendix V.

Murinae gen sp. indet/Deomyinae gen sp. indet. Identification of genera within the subfamily Murinae is complex relative to the other represented subfamilies. Moreover, murine genera including *Grammomys, Mastomys, Thallomys, Zelotomys,* and *Mus* (if the M1 is absent), are indistinguishable from the deomyine genus *Acomys* using the maxillary characters and molar dimensions examined here. Although the presence of t3 on M3 has been considered a useful characteristic for identifying *Acomys* (Denys et al., 1994), this study found that some murine genera also exhibit this character such as *Mastomys* (TM 44488) and *Pelomys* (AMNH 213089 and 213087) (Figure 8). Thus, this

character cannot be considered diagnostic for *Acomys*. While the presence of t3 on M3 can be used to eliminate several murine taxa. However, the size of the M3 in addition to the maxillary characters can be used to distinguish *Acomys* from all murines. In total 12 specimens, representing 9 individuals lacked the necessary elements to achieve a genus-level identification (Table 9; Figure 9). These twelve specimens are missing both the M3 needed to distinguish most murines from *Acomys,* and have an M1 or M2 within the size range of *Acomys* and several murine genera.

***Grammomys, Thallomys,* or *Acomys*.** Two specimens could not be distinguished among *Grammomys*, *Thallomys,* or *Acomys* (Figure 9). These specimens lack an M3, although M1 and M2 dimensions along with character matrix scores eliminate all other possible genera (Figures 10 and 11).

***Acomys*.** Two specimens retaining all three molars present represent two individuals (Table 9; Figure 9). As mentioned above, it is not possible to distinguish *Acomys* from murines using maxillary features alone thus the presence of t3 as well as the small dimensions of the M3 distinguishes these two specimens (Figure 12). Also known as spiny mice, *Acomys* are typically found in savanna and desert areas with rocky outcrops; however, *A. subspinosus* is found within the mountains and hill country in the fynbos biotic zone suggesting that not all members of the genus are restricted to dry and semi-desert areas (Monadjem et al., 2015; Stuart and Stuart, 2015). There are fifteen species currently recognized in Sub-Saharan Africa, although only one species, *A. selousi,* has a recorded distribution in Botswana, (Monadjem et al., 2015).

Murinae gen sp. indet. Two specimens are identified at the subfamily level and represent one individual (Table 9; Figure 9). These specimens have an M3 without a t3

which exclude *Acomys* as a possible identification; however, molar dimensions fell within the range of several murine genera.

***Mastomys, Thallomys,* or *Rhabdomys*.** One specimen, with only an M2, cannot be distinguished from *Mastomys, Thallomys,* or *Rhabdomys* based on the character matrix or molar dimensions (Table 9). *Acomys* and all other murine genera can be excluded due to the size of the M2 (Figure 13).

***Micaelamys, Thallomys,* or *Rhabdomys*.** One specimen, composed of an M1 and M2, cannot be distinguished from *Micaelamys*, *Thallomys,* or *Rhabdomys* based on character matrix scores and molar dimensions. *Acomys* and all other murine genera aside from these three can be excluded due to the size of the M1 and M2 (Figures 14 and 15).

***Mastomys, Micaelamys,* or *Rhabdomys*.** One specimen, possessing only a second molar, cannot be distinguished from *Mastomys*, *Micaelamys,* or *Rhabdomys* based on character matrix scores and molar dimensions. *Acomys* and all other murine genera can be excluded based on the size of the M2 (Figure 16).

***Micaelamys*.** Two specimens representing a MNI of one can be identified as *Micaelamys* to the exclusion of all other rodents taxa (Table 9; Figure 9). Both specimens retain only the first molar. Character matrix scores suggested several possible genera; however, with the addition of the M1 dimensions, genus-level identification was possible (Figure 17). Only one species, *Micaelamys namaquensis*, has modern populations distributed within Botswana (Meester and Setzer, 1971; DeGraff 1981; Rautenbach 1982; Monadjem et al., 2015).

***Lemniscomys*.** Three specimens with complete molar tooth rows can be identified as *Lemniscomys* to the exclusion of all other taxa resulting in an MNI of 2 (Table 9;

Figure 9). Use of the character matrix resulted in five possible genera identifications; however, molar dimensions allowed for genus-level identifications (Figures 18-20). Also known as grass mice, *Lemniscomys* typically occur in savannas, forest clearings, alpine habitats, and/or disturbed rainforests (Monadjem et al., 2015). In Sub-Saharan Africa they are currently distributed from Senegal to Ethiopia to South Africa (Monadjem et al., 2015). Members of this genus are terrestrial, diurnal and crepuscular, and considered herbivorous, granivorous, insectivorous, and frugivorous (Monadjem, 1997; Monadjem et al., 2015; Stuart and Stuart, 2015). Ten species are currently recognized in Sub-Sharan Africa, one of which has a current distribution in Botswana, *Lemniscomys rosalia*.

Thallomys. One specimen retaining both an M1 and M2 can be identified as *Thallomys*. Using the character matrix three genera were identified; however, M1 dimensions excluded all other possibilities aside from *Thallomys* (Figure 21). Also known as acacia tree rats, *Thallomys* occur typically in arid to mesic *Acacia* savannas Smithers, 1968, 1971; DeGraff, 1981; Rautenbach, 1982; Meyer et al., 2008; Monadjem et al., 2015). Members of this genus are nocturnal, arboreal, and folivorous, foraging and building nests in *Acacia* shrubs (Smithers, 1968, 1971; DeGraff, 1981; Rautenbach, 1982; Meyer et al., 2008; Monadjem et al., 2015). There are four species currently recognized in *Thallomys* in Sub-Saharan Africa with populations in northern South Africa, Botswana, Namibia, Angola, Tanzania, Kenya, and Ethiopia (Monadjem et al., 2015). Two of the four species are found in Botswana, *Thallomys nigricauda* and *Thallomys paedulcus*.

Pelomys. One specimen retaining an M1, M2, and M3 can be identified as *Pelomys* (Table 9; Figure 9). Using the character matrix several possible genera were

identified; however, in conjunction with molar dimensions one genus was identified (Figures 22-24). Also known as creek rats, *Pelomys* occur along streams, rivers, grasslands, and marshes (Roberts, 1951; Smithers, 1968, 1971; DeGraff, 1981; Monadjem et al., 2015). There are five species of *Pelomys* currently recognized in Sub-Saharan Africa and the genus is widespread in moist habitats within the southern savannas in East and Central Africa (Smithers, 1971; Monadjem et al., 2015). *Pelomys* are described as being strictly nocturnal, partly aquatic, and feeding mainly on aquatic vegetation such as reed shoots (Smithers, 1971; Monadjem et al., 2015; Stuart and Stuart, 2015). Only one species has a modern distribution in Botswana, *Pelomys fallax* (Monadjem et al., 2015).

***Otomys*.** Eight specimens can be identified as *Otomys* (Table 9; Figure 9). Character matrix scores alone were enough to eliminate all other possible genera, including the closely related genera *Myotomys* and *Parotomys*. For this reason, molar dimensions were not taken. The number of laminae on the M3 is diagnostic for this genus as they have at least six laminae on the M3 (including the terminal heel) whereas *Myotomys* has a maximum of five laminae (including the terminal heel) and *Parotomys* has a maximum of four laminae (including the terminal heel). Also known as groove-toothed rats or swamp rats, members of this genus typically occur in mesic and/or montane ecosystems in Africa; however, two species, *Otomys angoniensis* and *Otomys irroratus* are distributed in drier areas such as open savannas and grassy hillsides (De Graaff, 1981; Monadjem et al., 2015). In sub-Saharan Africa, *Otomys* has a wide distribution throughout the continent ranging from Cameroon in the west to Ethiopia in the east and all the way to the southern coast of South Africa (Monadjem et al., 2015).

The 29 currently recognized species in Sub-Saharan Africa are diurnal, herbivorous, and often found within the vicinity of marshes and are considered competent swimmers (De Graaff, 1981; Monadjem et al., 2015). Only one species, *Otomys angoniensis,* has a current distribution in Botswana and is found around the northern rivers of the Okavango delta. The presence of this genus at Bone Cave suggest there was a permanent or ephemeral source of water like a river or a marsh nearby when the fossils were deposited.

Mus. Twenty specimens can be identified as *Mus* (Table 9; Figure 9). *Mus* can be identified through the character matrix alone as it is the only murine with a singular conule on the anterior portion of t2 on M1 and/or an extension of t2 on M1 (character 10 – Table 9; Figure 9). Members of *Mus* have a wide habitat tolerance. They can be found in arid shrub savannas, where mean annual rainfall is 200 mm, as well as in rich riverine forests where mean annual rainfall is over 700 mm (Smithers, 1971). They have a wide distribution throughout the entire continent of Africa including two species currently distributed in Botswana, *Mus musculus* and *Mus minutoides*. All nineteen species in the genus in Sub-Saharan Africa are nocturnal, terrestrial, and have a granivorous, herbivorous, and omnivorous diet (Monadjem, 1997; Monadjem et al., 2015).

***Gerbillurus/Desmodillus*.** Thirty-eight specimens cannot be differentiated as *Gerbillurus* or *Desmodillus* from the character matrix and molar dimensions (Table 9; Figure 9). In particular, first and second molar dimensions overlap between these genera but distinguish them from *Gerbilliscus* (Figures 25 and 26).

Gerbilliscus. Thirty-nine specimens representing 19 individuals can be identified as *Gerbilliscus* using the character matrix and molar dimensions (Table 9; Figure 9). Although the character matrix scores alone cannot differentiate the three possible

southern African gerbil genera, M1 and M2 dimensions readily distinguish *Gerbilliscus* from *Gerbillurus* and *Desmodillus* (Figures 25 and 26). Also known as hairy-footed gerbils, in Sub-Saharan Africa *Gerbilliscus* occurs in a wide variety of habitats with sandy soils including wooded and open grasslands (Monadjem et al., 2015). Members of this genus are nocturnal, terrestrial, and their diet is described as granivorous, herbivorous, and omnivorous (Monadjem et al., 2015). In Sub-Saharan Africa there are fourteen species currently recognized, two of which are found in Botswana, *Gerbilliscus brantsii* and *G. leucogaster* (Monadjem et al., 2015). The presence of this genus at the Bone Cave suggest the habitat surrounding the area was semi-arid or arid when the fossils were deposited.

***Dendromus*.** Nine specimens are identified as *Dendromus* (Table 9; Figure 9). *Dendromus* was identified from all other taxa using the character matrix scores alone, although the small M2 dimensions can also help to distinguish it from *Malacothrix* (Figure 27). Also known as African climbing mice, *Dendromus* is widespread throughout Sub-Saharan Africa with exception to desert regions (Monadjem et al., 2015). Populations can be found in high-elevation grasslands, montane forests, or gallery forests, and are associated with wetlands and aquatic vegetation (Monadjem et al., 2015). Members of this genus are nocturnal, arboreal, and their diet is granivorous, omnivorous, and insectivorous (Monadjem et al., 2015). Fourteen species are currently recognized in Sub-Saharan Africa, two of which have current distributions around the northern rivers of the Okavango delta in Botswana, *D. melanotis* and *D. mesomelas.* (Monadjem et al., 2015). The presence of this genus suggests there was a permanent or ephemeral source of water nearby when the fossils were deposited at Bone Cave.

***Malacothrix*.** Fifteen specimens can be identified as *Malacothrix* (Table 9; Figure 9). *Malacothrix* can be identified from all other taxa using the character matrix scores alone, in particular, the large size and orientation of the masseteric knob (character 11) can distinguish this genus from all others in southern Africa. Additionally, while M2 dimensions do not help to distinguish *Malacothrix* from *Steatomys*, it can be used to distinguish it from *Dendromus* due to a larger tooth size (Figure 26). Also known as long-eared mice, *Malacothrix* is only found in semi-arid savannahs and deserts in four countries in Africa: South Africa, Botswana, Namibia, and Angola (Monadjem et al., 2015). This genus is monotypic, with *Malacothrix typica* the only recognized extant species (Monadjem et al., 2015). Members of this genus are terrestrial, and their diet is described as omnivorous, graminivorous, and insectivorous (Monadjem et al., 2015). The presence of this genus at Bone Cave suggest the habitat surrounding the area was semi-arid or arid when the fossils were deposited.

Malacothrix/Dendromus. One specimen cannot be identified as either *Malacothrix* or *Dendromus* (Table 9; Figure 9). While this specimen possesses an M1, it is missing the posterior portion inhibiting resolution using the character matrix. Additionally, the diagnostic masseteric knob is partially broken.

Steatomys. Thirty-four specimens can be identified as *Steatomys* representing an MNI of 26 (Table 9; Figure 9). *Steatomys* is identified from all other taxa using the character matrix scores alone, specifically, the size and orientation of the masseteric knob (character 11). Also known as fat mice, *Steatomys* typically occurs in savanna habitats and is widespread throughout Sub-Saharan Africa (Monadjem et al., 2015). Members of this genus are terrestrial and prefer areas with soft grounds to build burrows for their

nesting chambers (Hanney, 1962; Monadjem et al., 2015). Their diet is described as omnivorous, graminivorous, insectivorous, and herbivorous (Monadjem et al., 2015). There are eight species currently recognized in Sub-Saharan Africa, two of which are distributed in Botswana, *S. parvus* and *S. pratensis.* The wide habitat tolerance of this genus is not useful in reconstructing the paleoenvironment of Koanaka South.

Saccostomus. Two specimens are identified as *Saccostomus* (Table 9; Figure 9). Character matrix scores are enough to identify this genus to the exclusion of all other southern African rodents. Character 5 distinguishes *Saccostomus* from *Cricetomys* as the latter has a t4 that is parallel with t5 and t6 on the M1, whereas t5 and t6 on the M1 of *Saccostomus* is slightly posteriorly displaced. Also known as pouched mice, in Sub-Saharan Africa *Saccostomus* is adapted to woodlands and grasslands of southern and eastern Africa, and occurs in a wide variety of habitats such as acacia woodlands and dry river-beds (DeGraaff, 1981; Monadjem et al., 2015; Stuart and Stuart, 2015). Members of this genus are nocturnal, dwell in the ground, and their diet is mostly granivorous though also includes insects and other vegetable matter (DeGraaff, 1981; Monadjem et al., 2015; Stuart and Stuart, 2015). Two species are currently recognized in Sub-Saharan Africa, with *S. campestris* distributed in Botswana (Monadjem et al., 2015).

Mystromyinae. Mystromyinae has one genus with modern distributions in southern Africa, *Mystromys*.

Mystromys. Two specimens are identified as *Mystromys* (Table 9; Figure 9). Character matrix scores are enough to identify this genus to the exclusion of all others, with character 16 being featuring prominently. For this reason, molar dimensions were not taken. Also known as African white-tailed rats, this genus is monotypic and the one

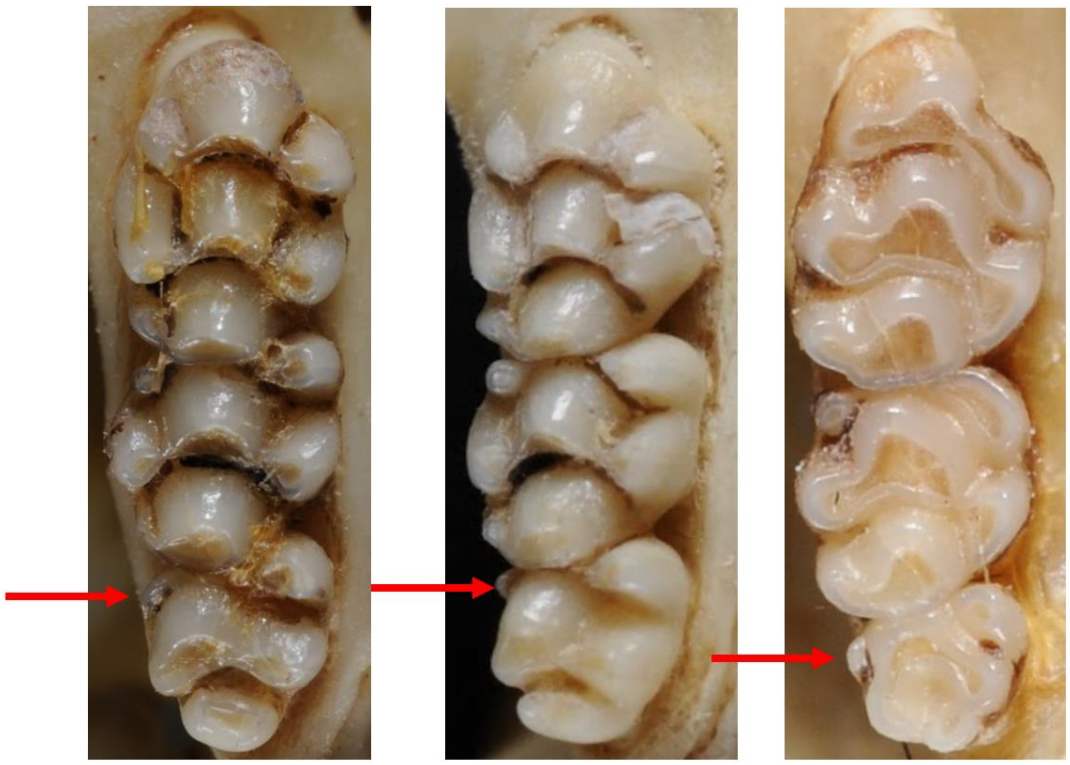
species, *Mystromys albicaudatus*, currently endemic to the grasslands of South Africa and Lesotho. This is the first time any modern or prehistoric *Mystromys* specimen has been identified in Botswana, extending the prehistoric range of this genus over 800km. Members of this genus are terrestrial, nocturnal, and their diet is predominately herbivorous (Monadjem et al., 2015).

Fossil Owl Prey Assemblage from Bone Cave Compared with Modern and Fossil Assemblages Throughout Southern Africa

Seven rodent genera identified from the fossil assemblage are also represented in both the modern pellets and trap records including *Gerbilliscus, Lemniscomys, Micaelamys, Mus, Saccostomus, Dendromus,* and *Steatomys* (Table 10). Alternately, *Gerbillurus* and/or *Desmodillus* were represented in the pellet data and fossil assemblage, but not trap data. An additional six genera are represented in the fossil assemblage but not the pellet or trap data including *Otomys, Pelomys Thallomys, Malacothrix, Acomys,* and *Mystromys. Finally,* four genera are represented in the pellets and traps, but not the fossil assemblage including *Aethomys, Cryptomys, Mastomys,* and *Zelotomys*.

Mystromys, *Malacothrix*, and *Pelomys* are all represented in the Bone Cave assemblage; however, there are no areas where these three genera are today sympatric (Stuart and Stuart, 2005) suggesting the rodent paleocommunity represented at Bone Cave has no modern analog. As such, the null hypothesis stating fossil rodent taxa identified from Bone Cave are all distributed at Koanaka South today is rejected. The alternative hypothesis stating the fossil rodent taxa identified from Bone Cave are not all distributed at Koanaka South today is accepted (Table 11). To my knowledge, there are modern rodent communities in southern Africa containing the majority of the rodent taxa

identified from Bone Cave, such as within Pilanesberg National Park and Lower Zambezi National Park, but to my knowledge none are identical in taxonomic composition (Table 11). To my knowledge, there are also no fossil rodent communities from southern Africa that are identical to the composition of the fossil rodents from Bone Cave (e.g. Avery, 1981, 1982b, 1997, 2001; Thackery, 1987; Pickford, 1990; Pickford et al., 1994; Robbins et al., 1996; Matthews et al., 2007; Fernandez-Jalvo and Avery, 2015). Once again, *Mystromys*, *Malacothrix*, and *Pelomys* are the specific taxa that have never been identified in the same excavation units at fossil sites. These three genera have been identified at Border Cave site located in Swaziland, but they were never found in the same unit (Avery, 1982b). Border Cave contains eleven sedimentary units ranging in dates from 90 ± 105 bp to > 40,000 bp (Avery, 1982b). *Malacothrix* is only identified in the younger units dating to the Holocene whereas *Mystromys* was identified in almost every unit including those older than >40, 000 bp (Avery, 1982b). *Pelomys* is strictly identified in units older than 40,00 bp and is extirpated from the site around 35,000 bp. This is the only instance *Pelomys* and *Mystromys* are found in the same units, but this only occurs for a short period of time before *Pelomys* are extirpated from the area. Regardless of this one brief instance where these taxa are sympatric, *Mystromys*, *Malacothrix*, and *Pelomys* have never been identified at a locality in the same unit.



Pelomys (AMNH 213087) *Pelomys* (AMNH 213089) *Mastomys* (TM 44488)

FIGURE 8. Arrow indicates t3 on M3 for *Mastomys* and *Pelomys* museum specimens suggesting this trait is not diagnostic for *Acomys.*

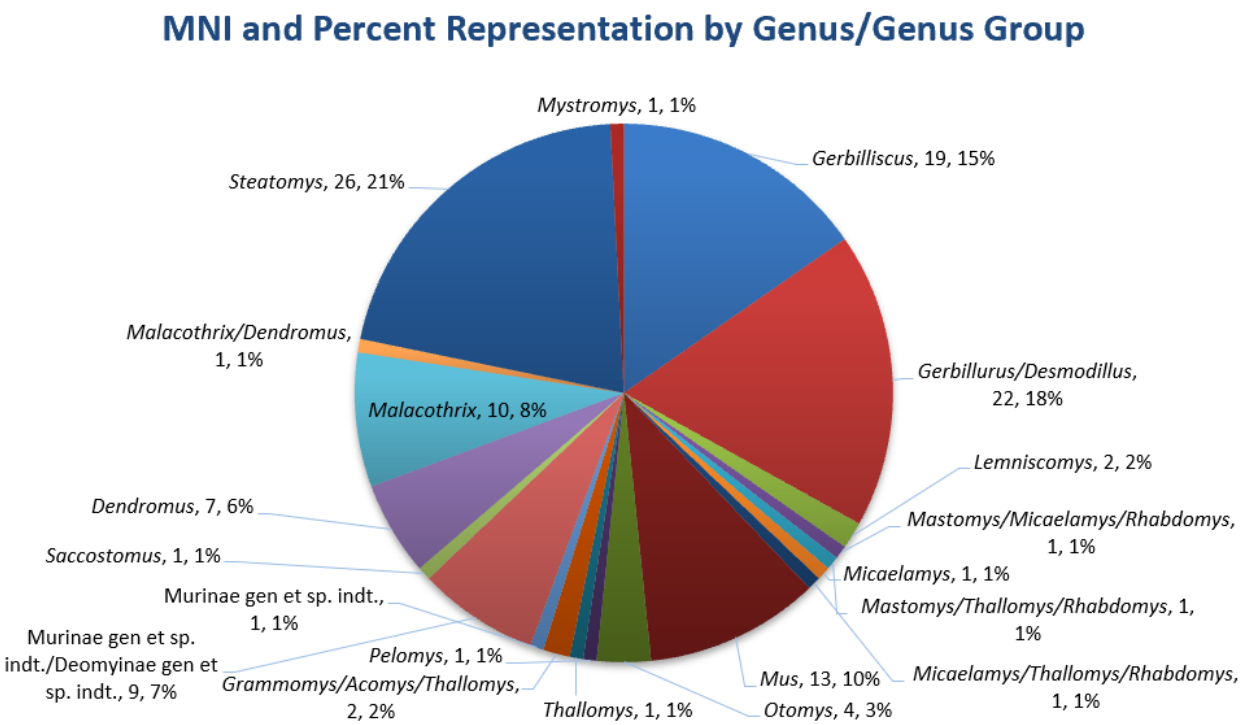


FIGURE 9. MNI and percent representation of rodent fossils from Bone Cave.

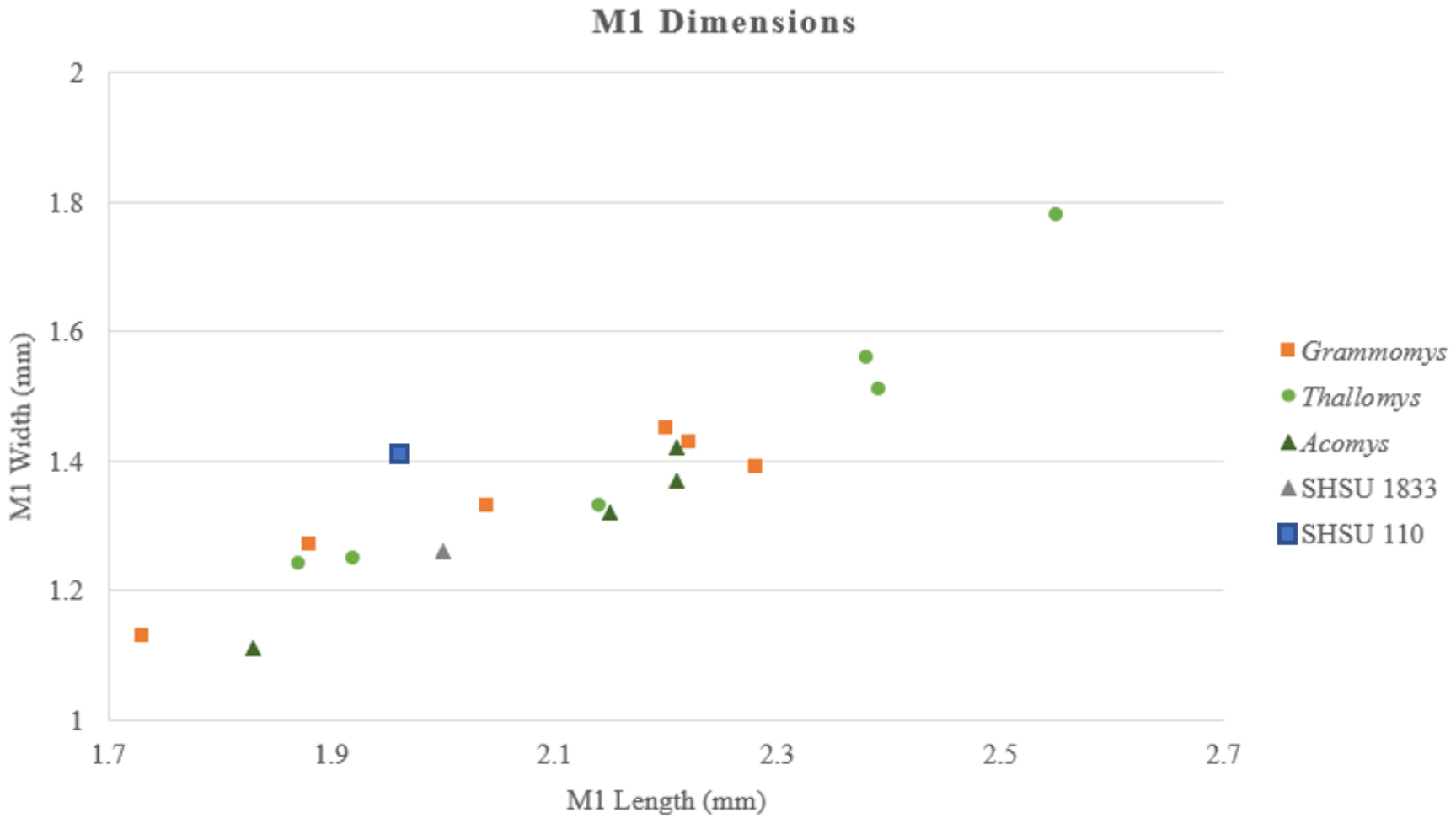


FIGURE 10. M1 dimensions of select Murine and *Acomys* museum specimens and fossil rodents from Bone Cave SHSU 1833 and SHSU 110) identified as *Grammomys*, *Thallomys*, or *Acomys*.

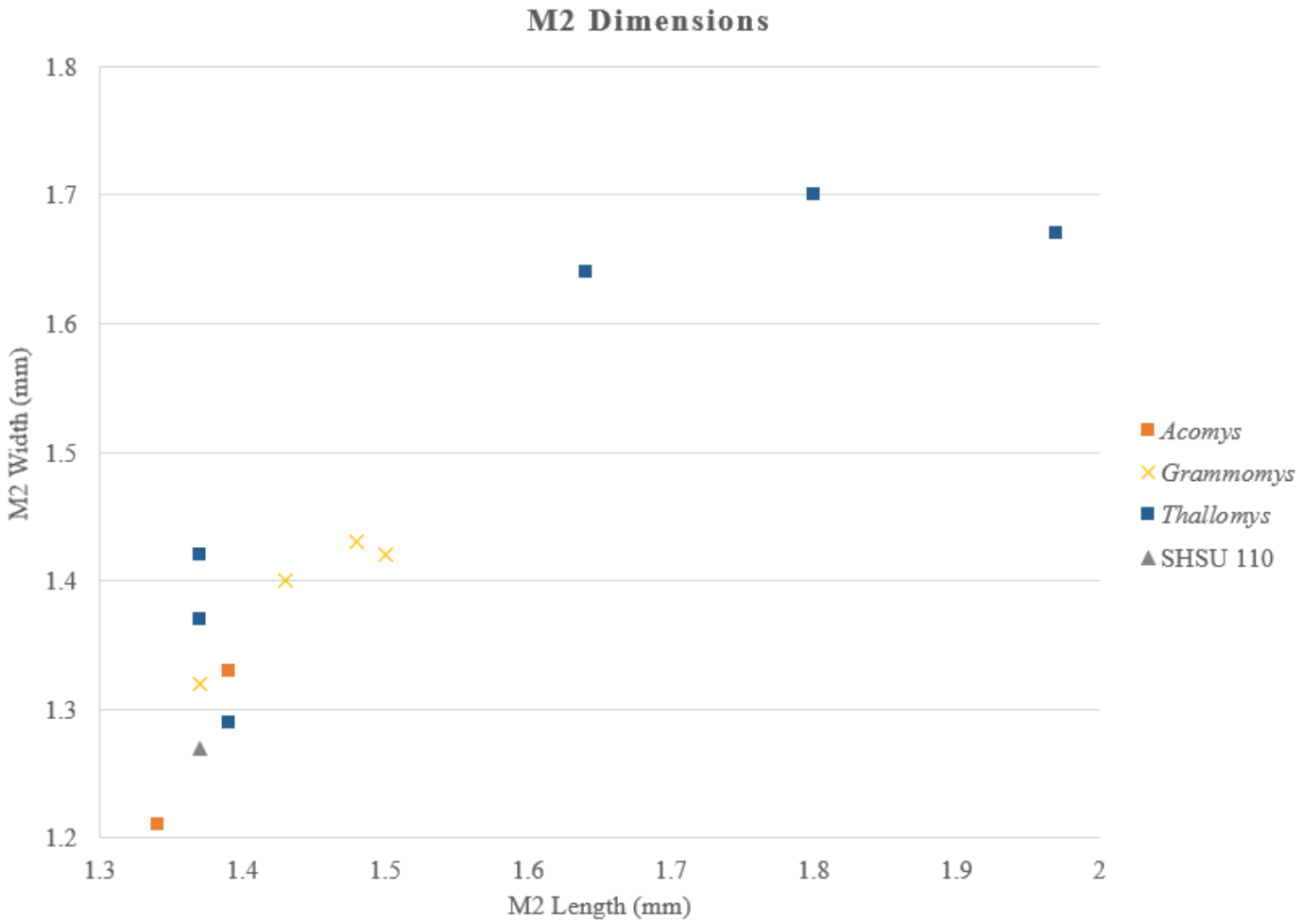


FIGURE 11. M2 dimensions of select Murine and *Acomys* museum specimens and SHSU 110 from Bone Cave identified as *Grammomys*, *Thallomys*, or *Acomys*.

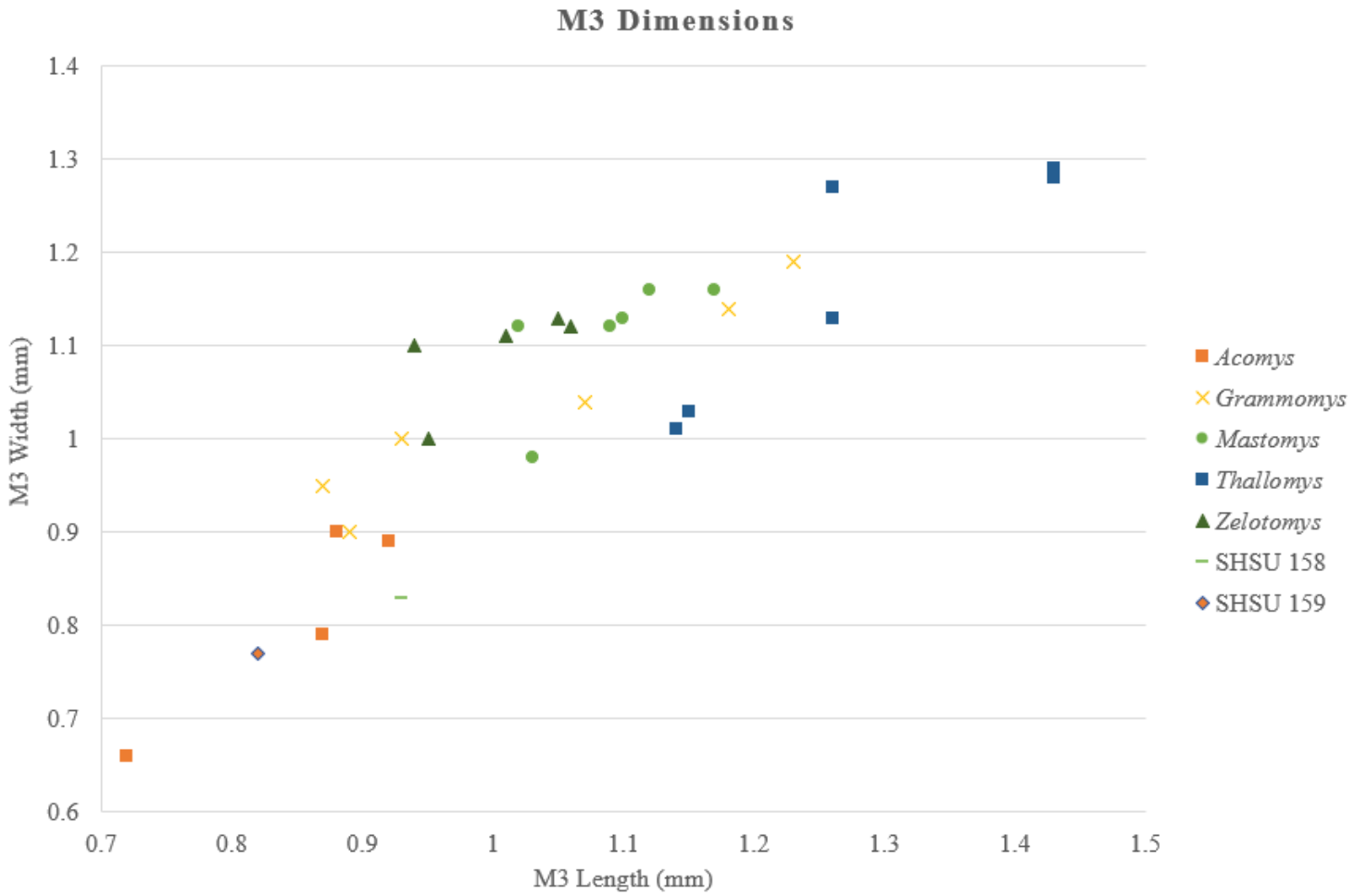


FIGURE 12. M3 dimensions of select Murine and *Acomys* museum specimens and fossil rodents from Bone Cave identified as the genus *Acomys* (SHSU 158, SHSU 159).

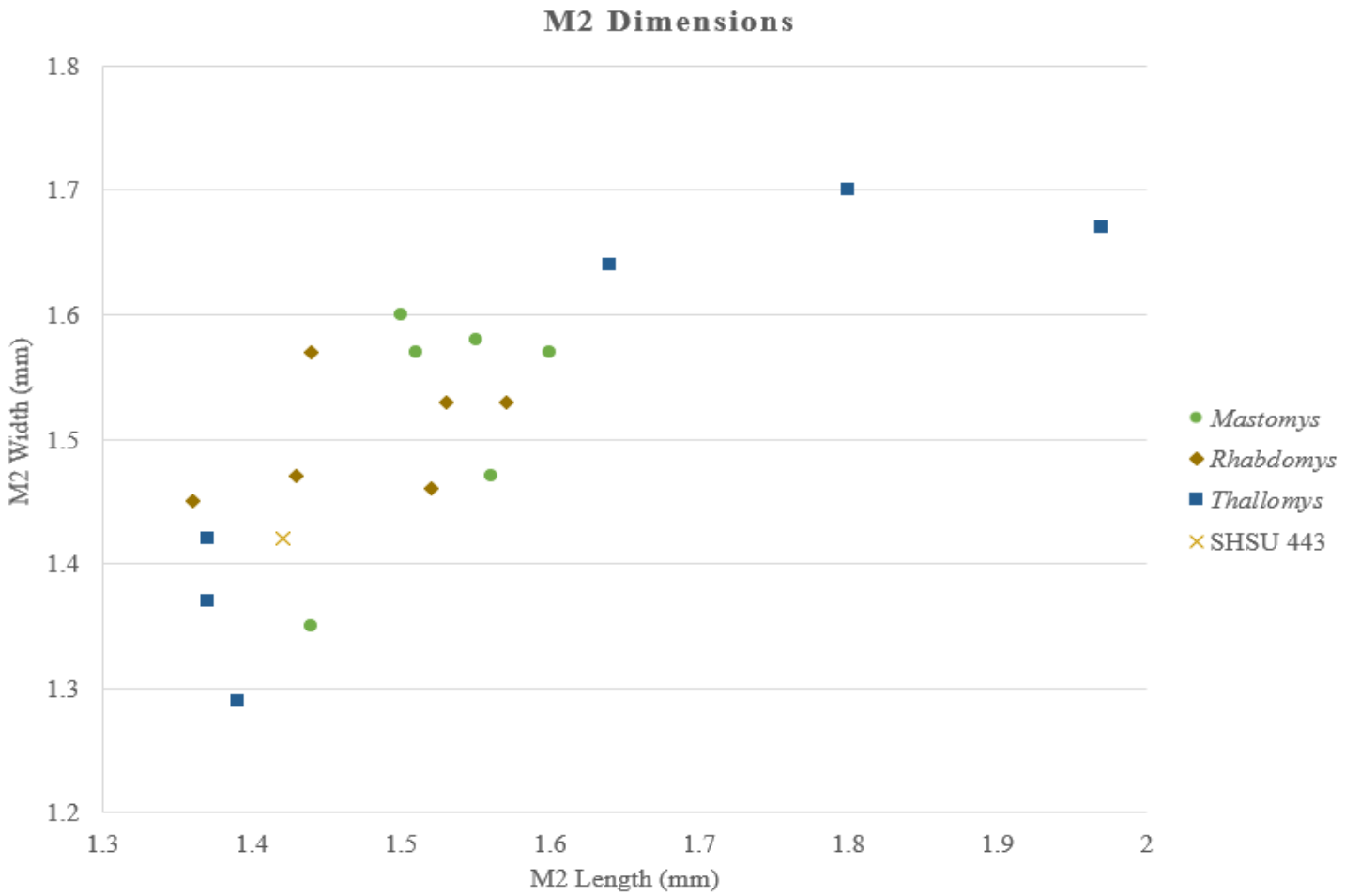


FIGURE 13. M2 dimensions of select Murine museum specimens and SHSU 443 from Bone Cave identified as *Mastomys, Thallomys,* or *Rhabdomys*.

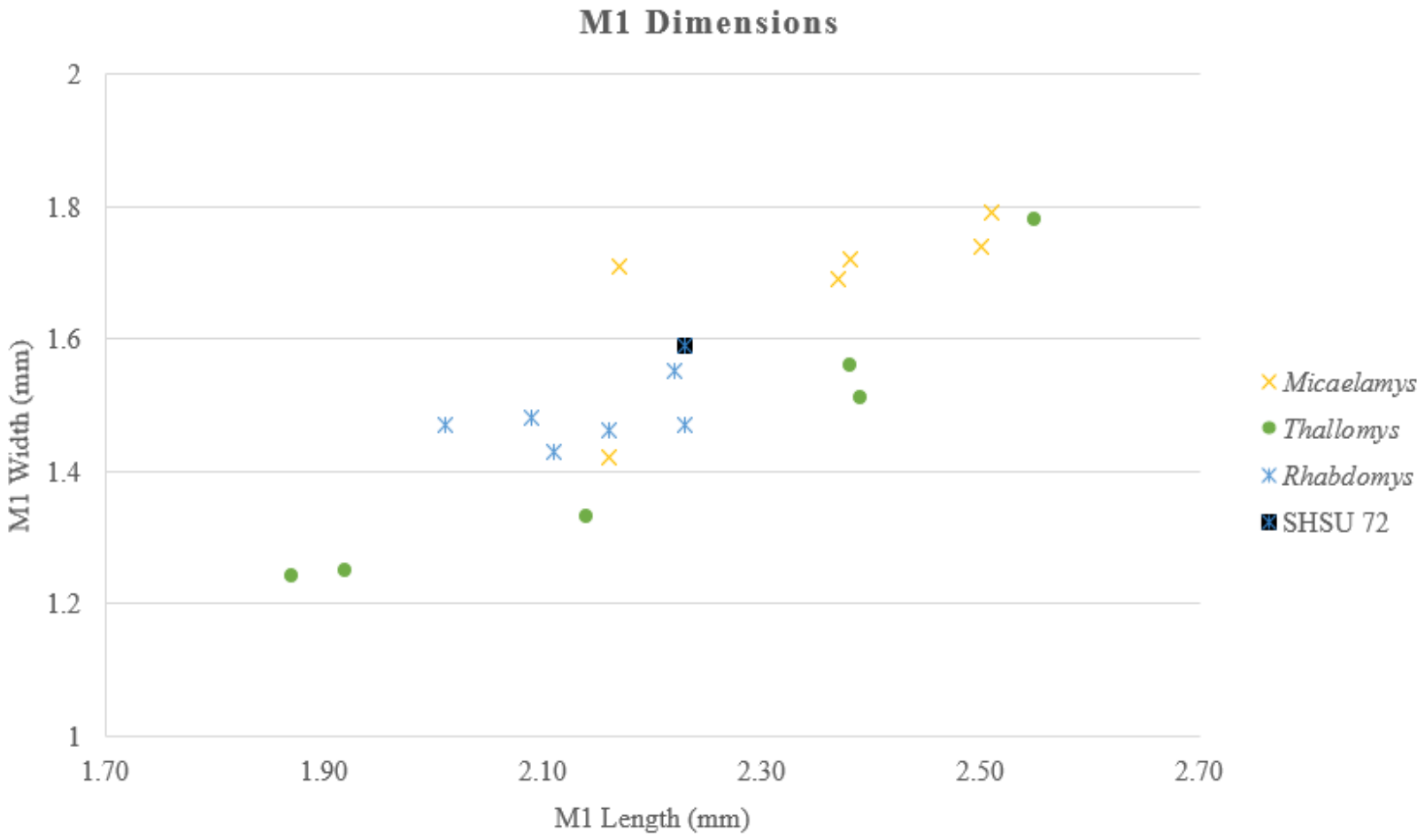


FIGURE 14. M1 dimensions of select Murine museum specimens and SHSU 72 from Bone Cave identified as *Micaelamys*, *Thallomys*, or *Rhabdomys*.

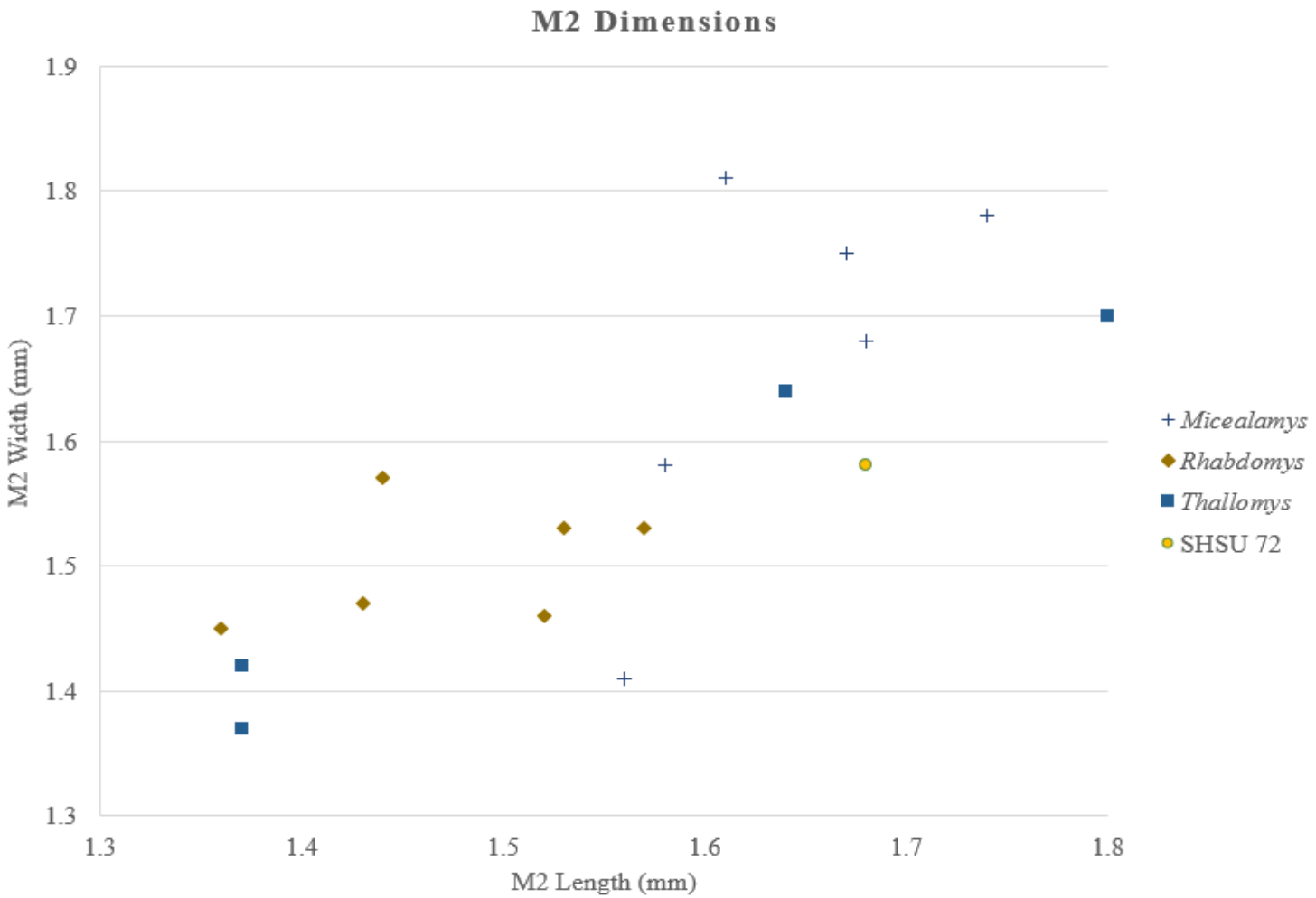


FIGURE 15. M2 dimensions of select Murine museum specimens and SHSU 72 from Bone Cave identified as *Micaelamys*, *Thallomys*, or *Rhabdomys*.

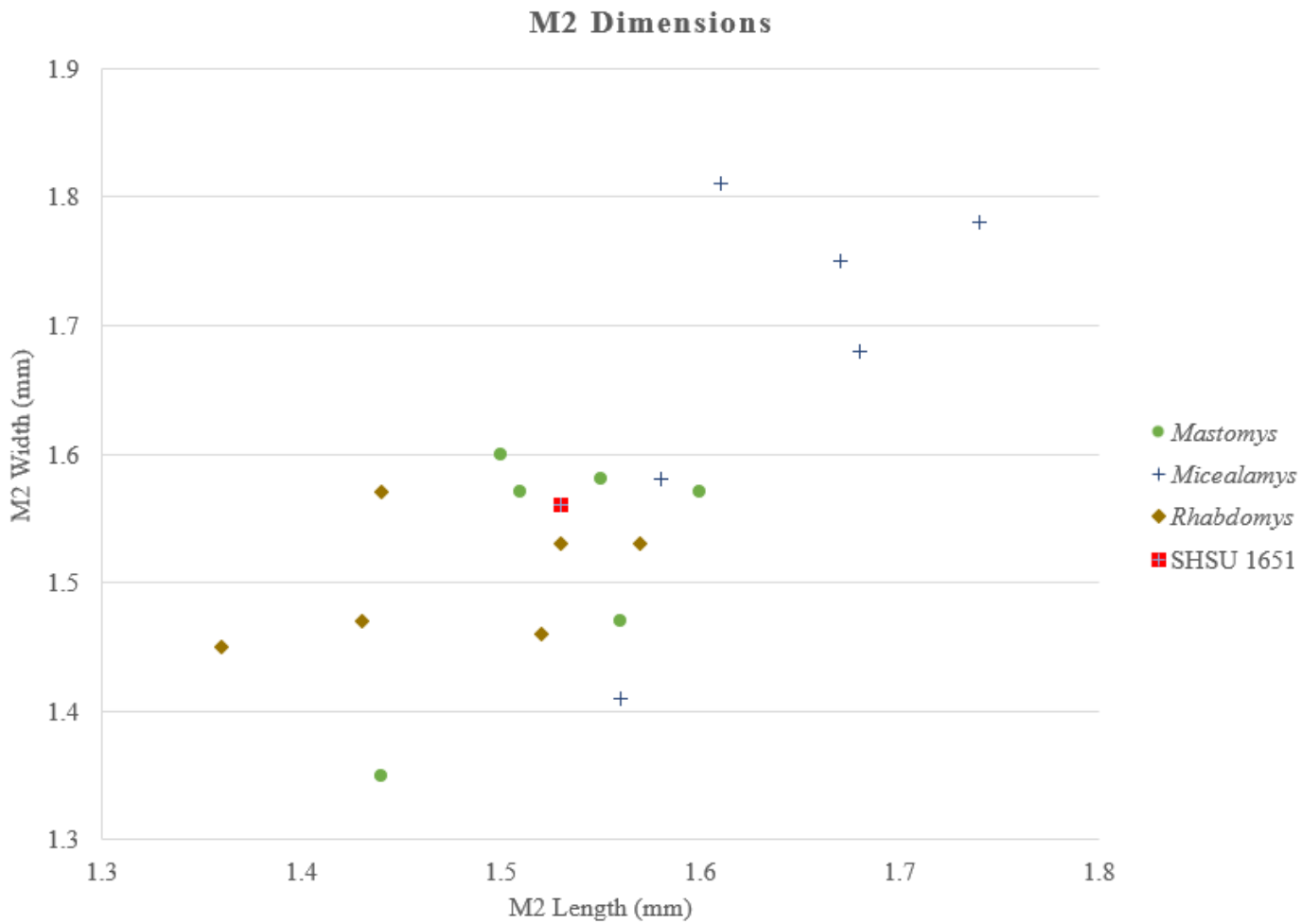


FIGURE 16. M2 dimensions of select Murine museum specimens and SHSU 1651 from Bone Cave identified as *Mastomys*, *Micaelamys,* or *Rhabdomys*.

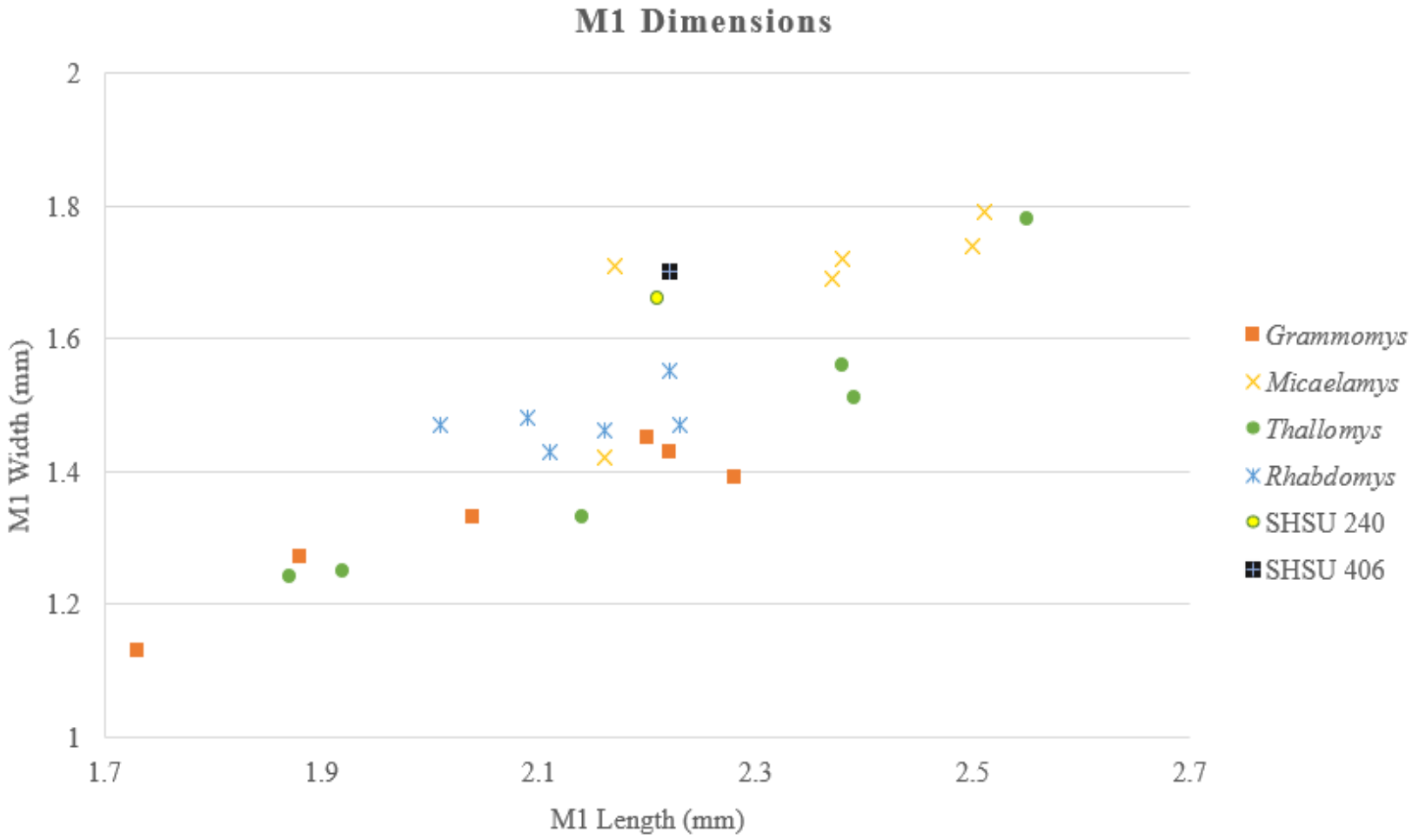


FIGURE 17. M1 dimensions of select Murine museum specimens and SHSU 406 and SHSU 240 from Bone Cave identified as *Micaelamys*.

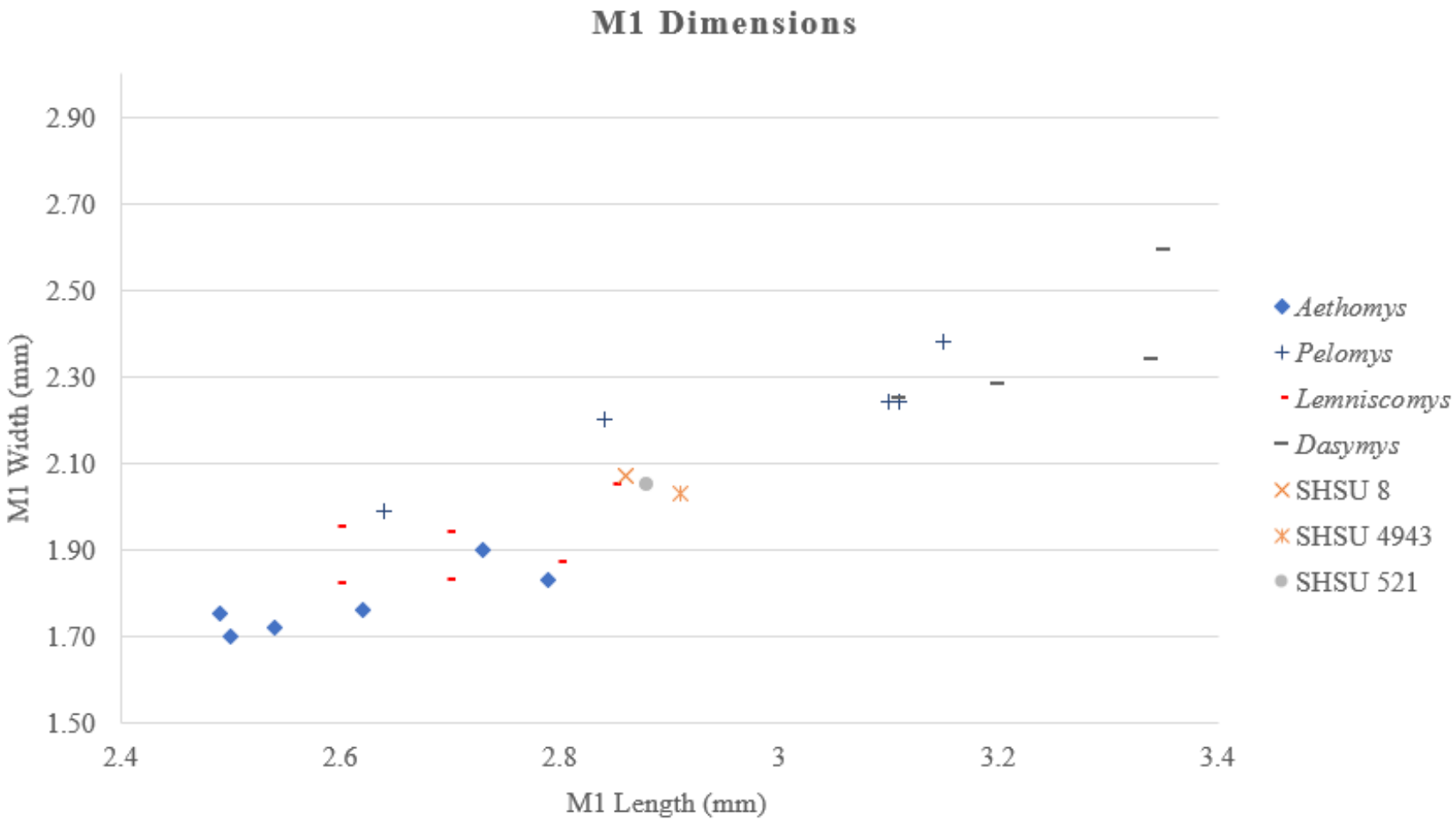


FIGURE 18. M1 dimensions of select Murine museum specimens and SHSU 8, SHSU 521, and SHSU 4943 from Bone Cave identified as *Lemniscomys*.

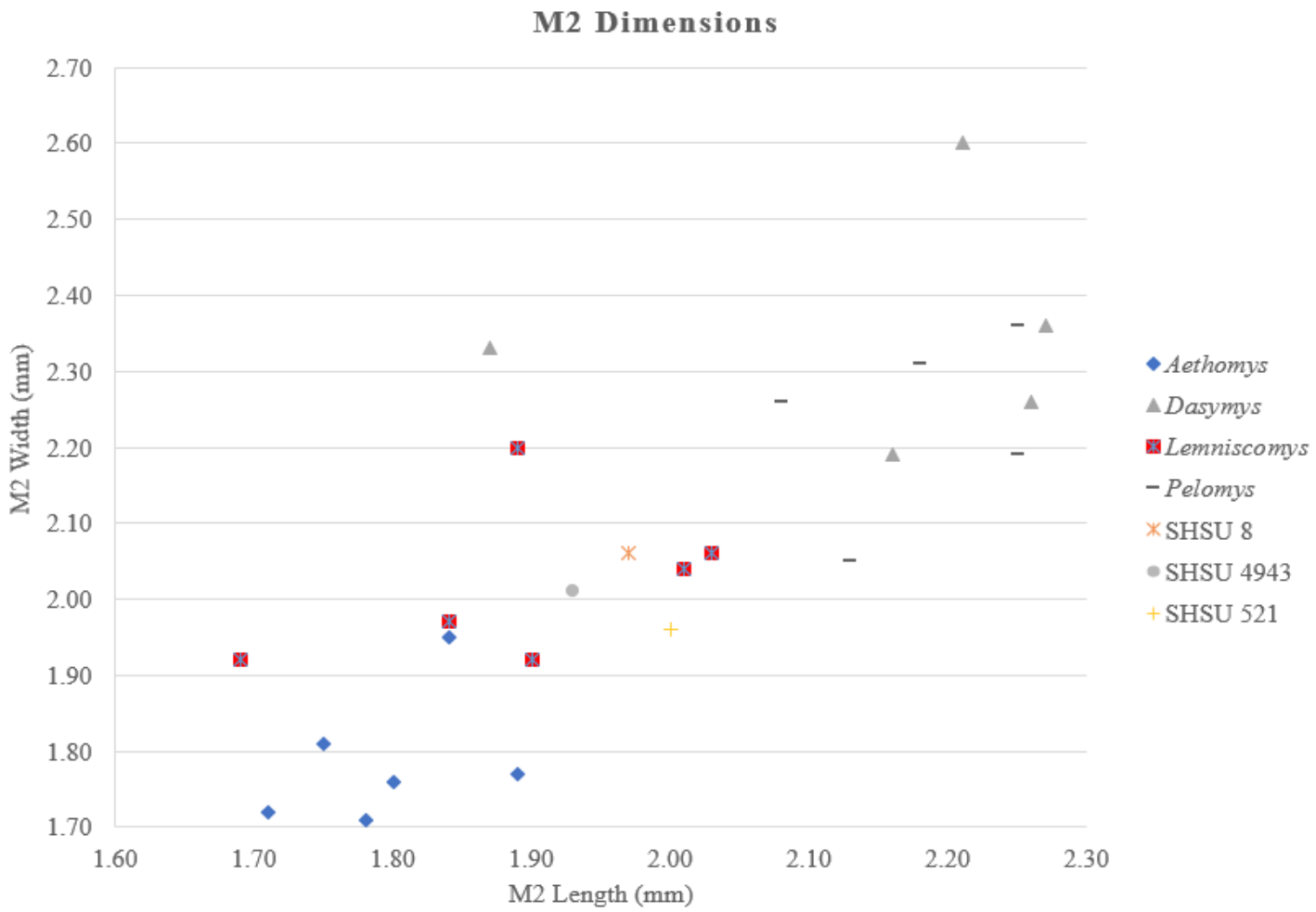


FIGURE 19. M2 dimensions of select Murine museum specimens and SHSU 8, SHSU 521, and SHSU 4943 from Bone Cave identified as *Lemniscomys*.

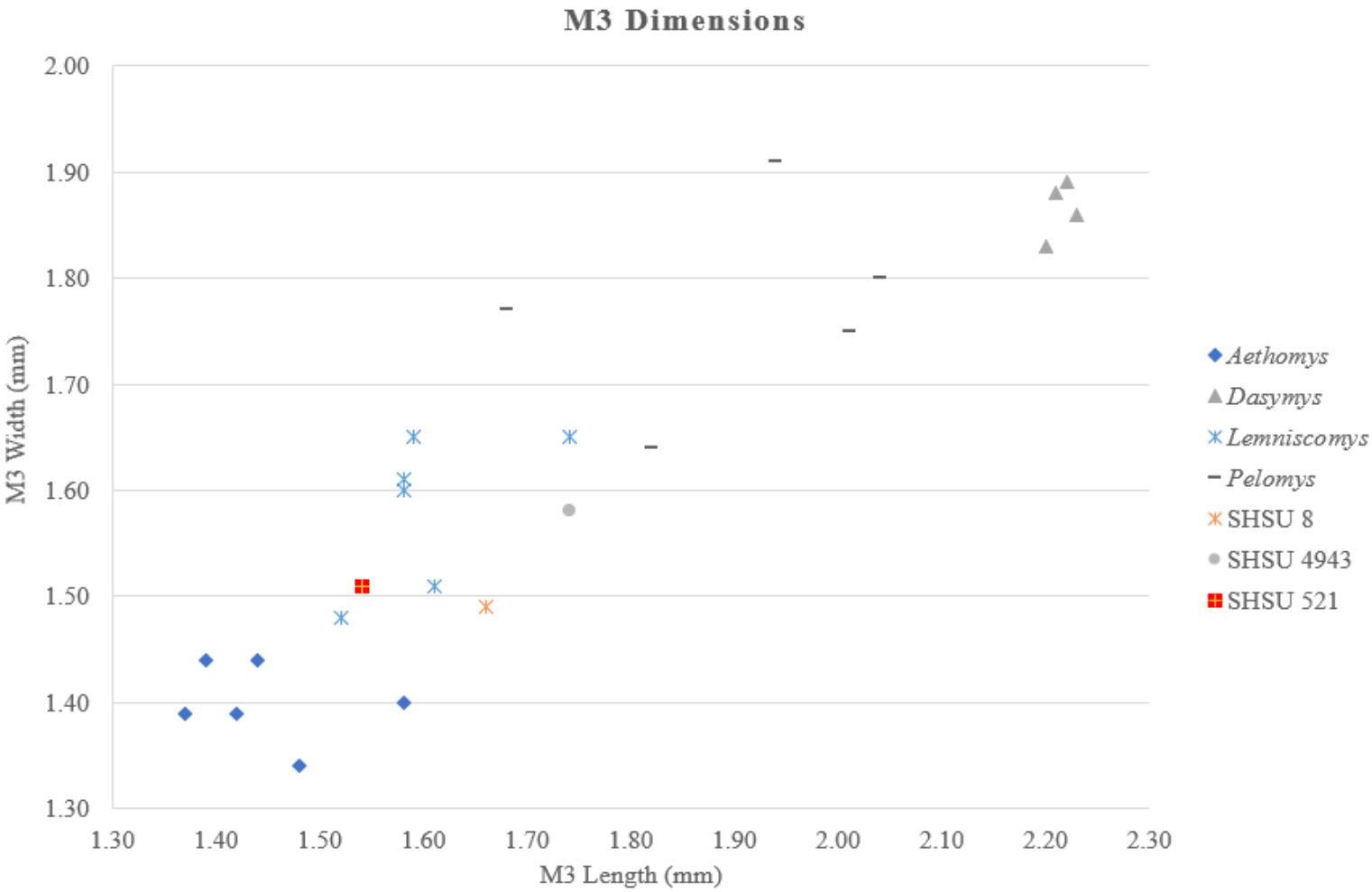


FIGURE 20. M3 dimensions of select Murine museum specimens and SHSU 8, SHSU 521, and SHSU 4943 from Bone Cave identified as *Lemniscomys*.

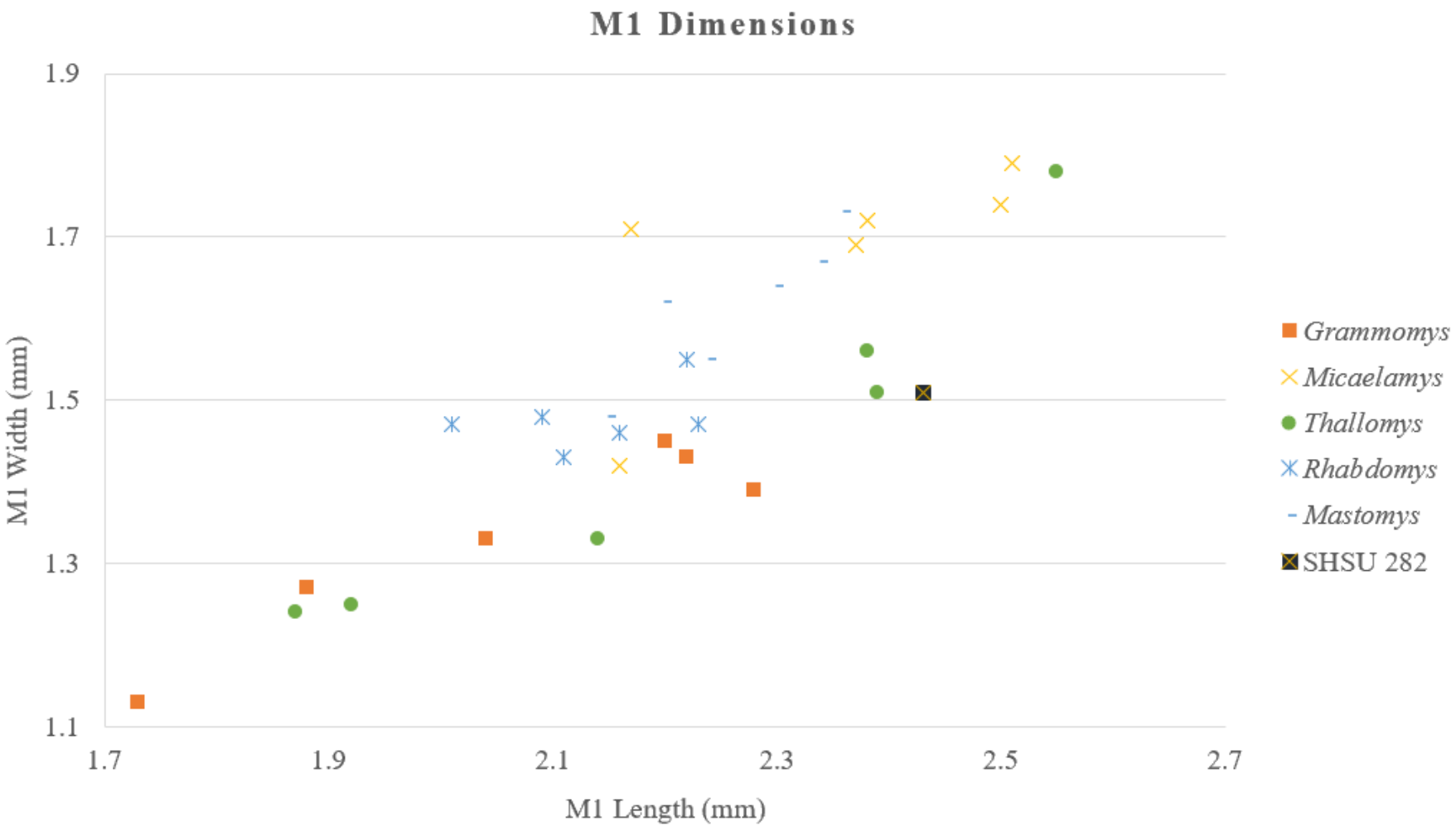


FIGURE 21. M1 dimensions of select Murine museum specimens and SHSU 282 from Bone Cave identified as *Thallomys*.

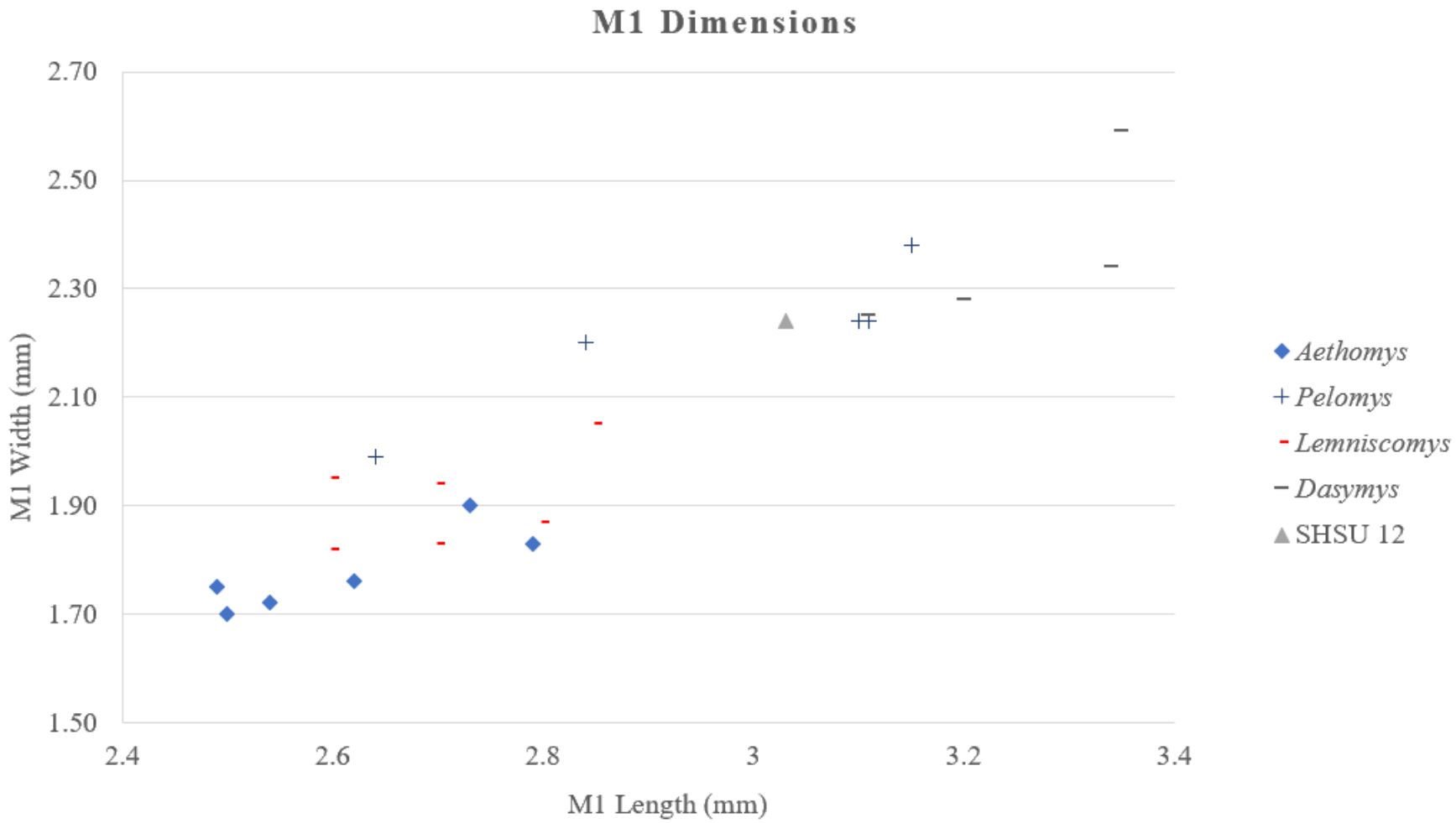


FIGURE 22. M1 dimensions of select Murine museum specimens and SHSU 12 from Bone Cave identified as *Pelomys*.

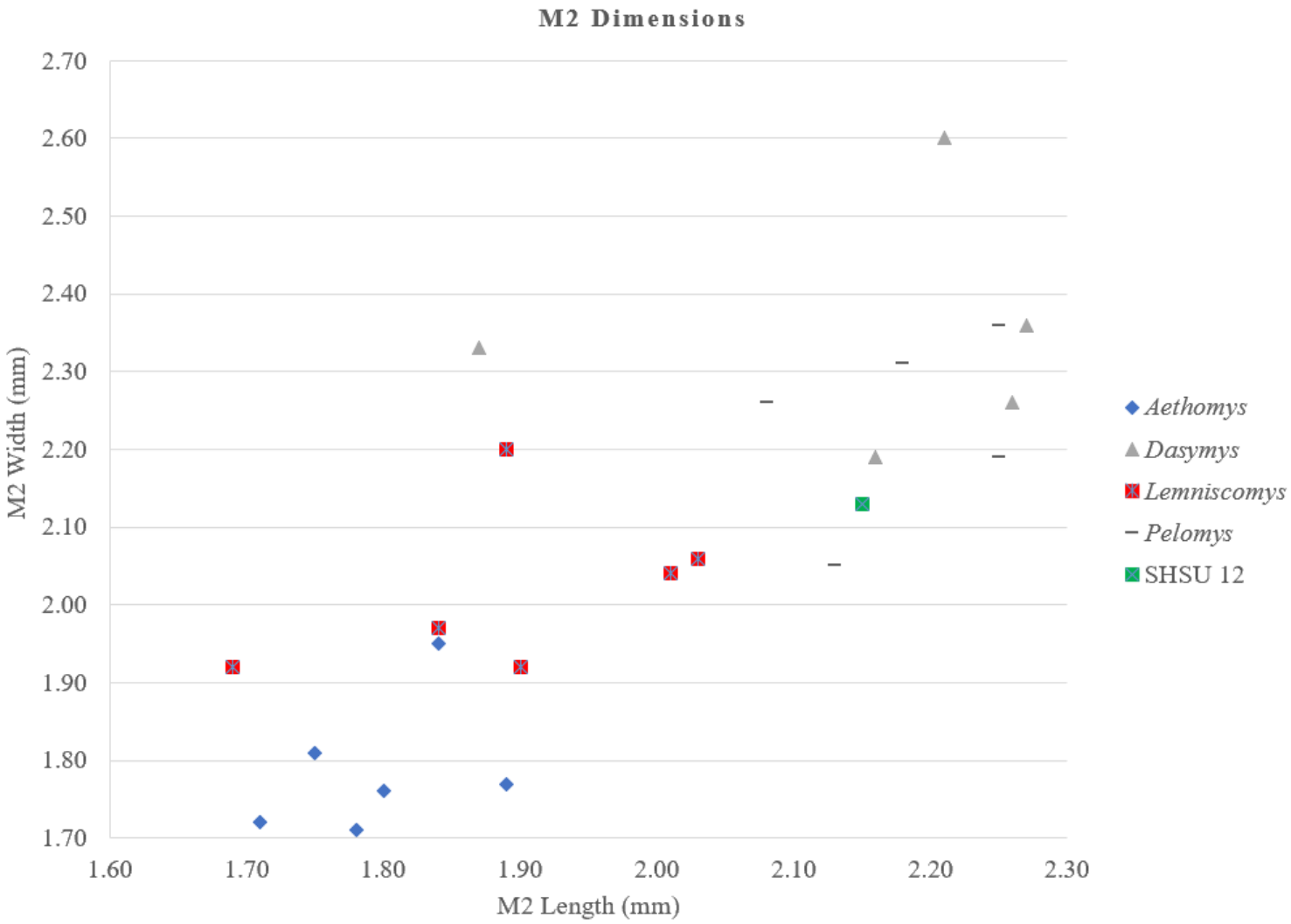


FIGURE 23. M2 dimensions of select Murine museum specimens and SHSU 12 from Bone Cave identified as *Pelomys*.

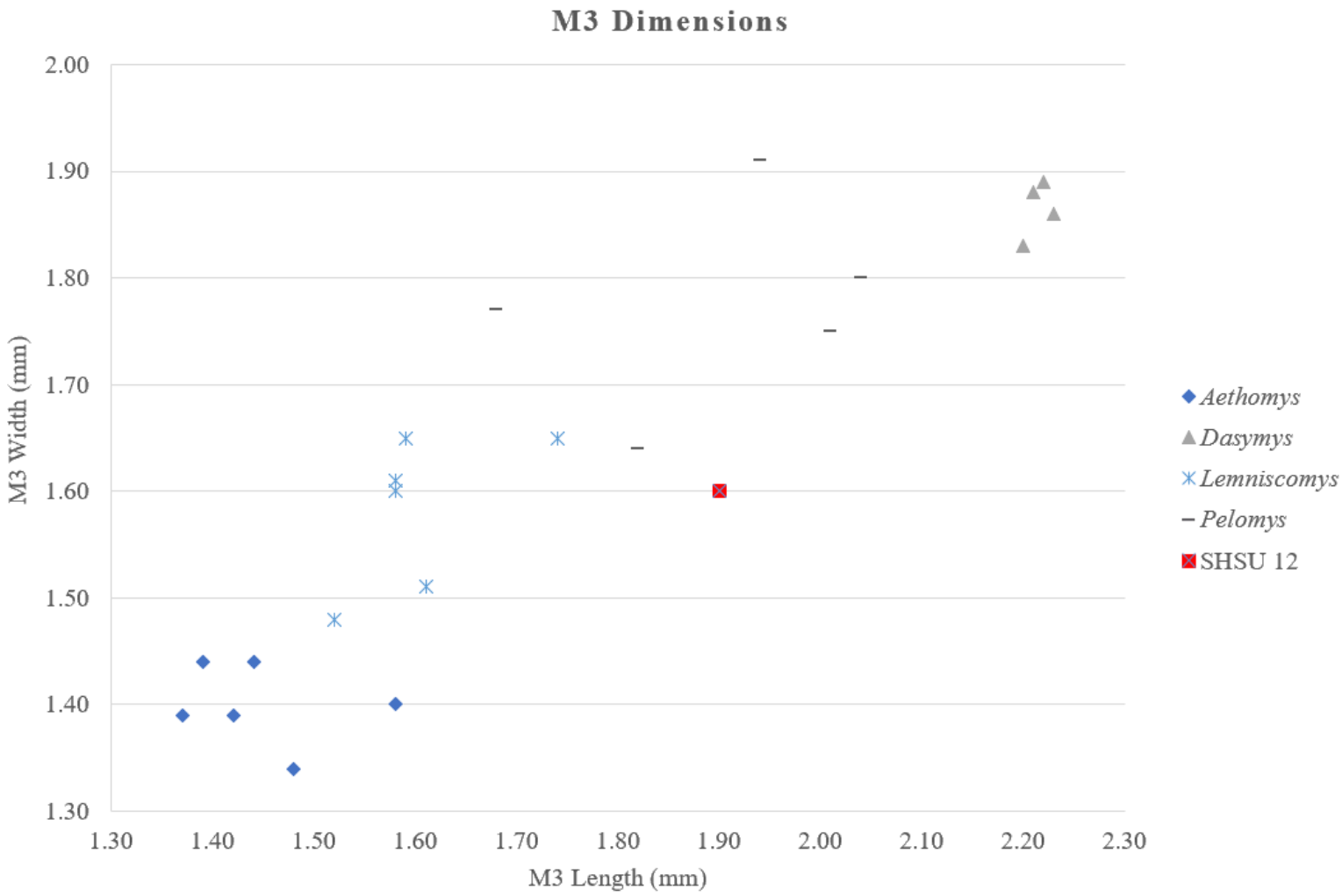


FIGURE 24. M3 dimensions of select Murine museum specimens and SHSU 12 from Bone Cave identified as *Pelomys*.

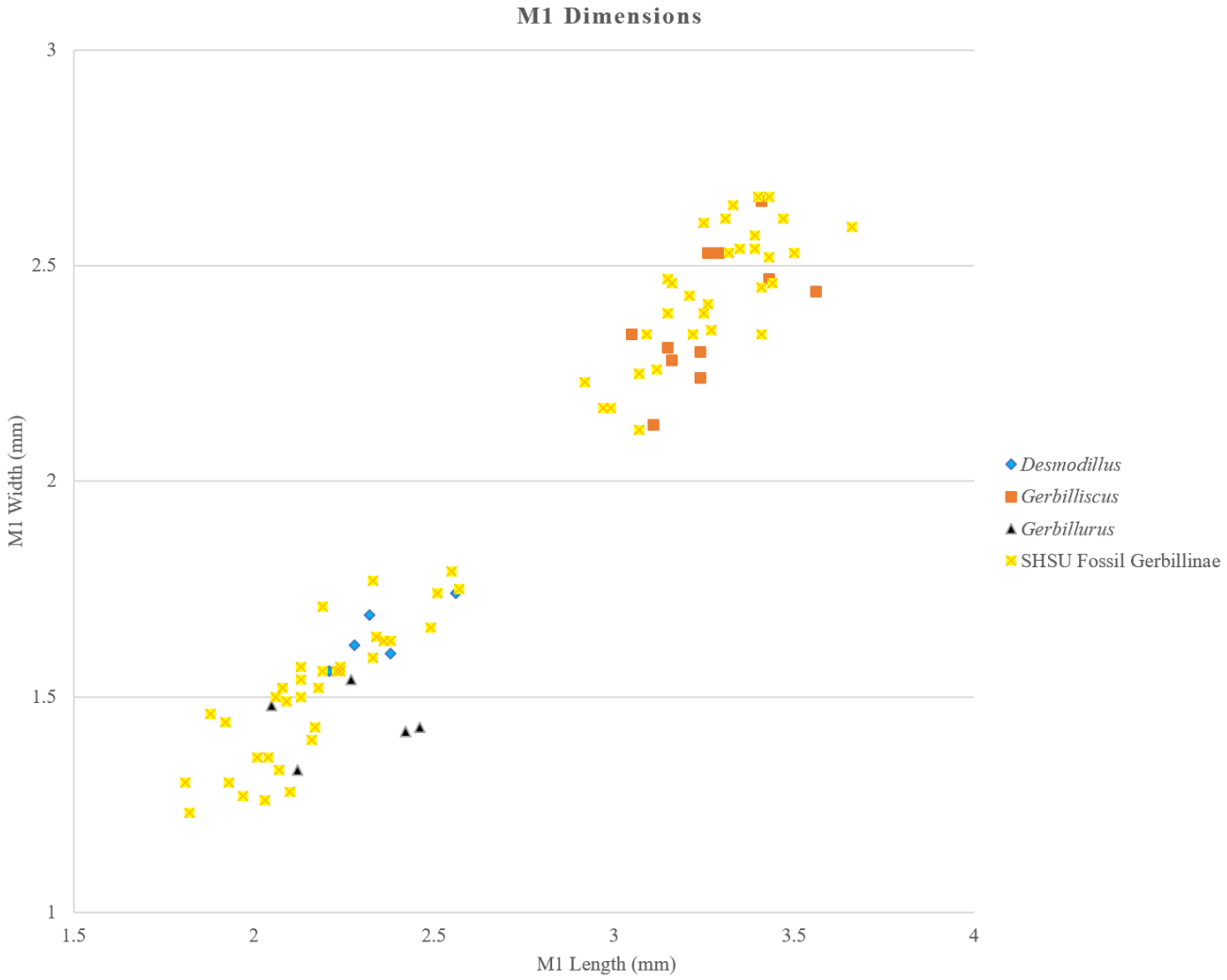


FIGURE 25. M1 dimensions of museum gerbil specimens and fossil gerbil specimens from Bone Cave.

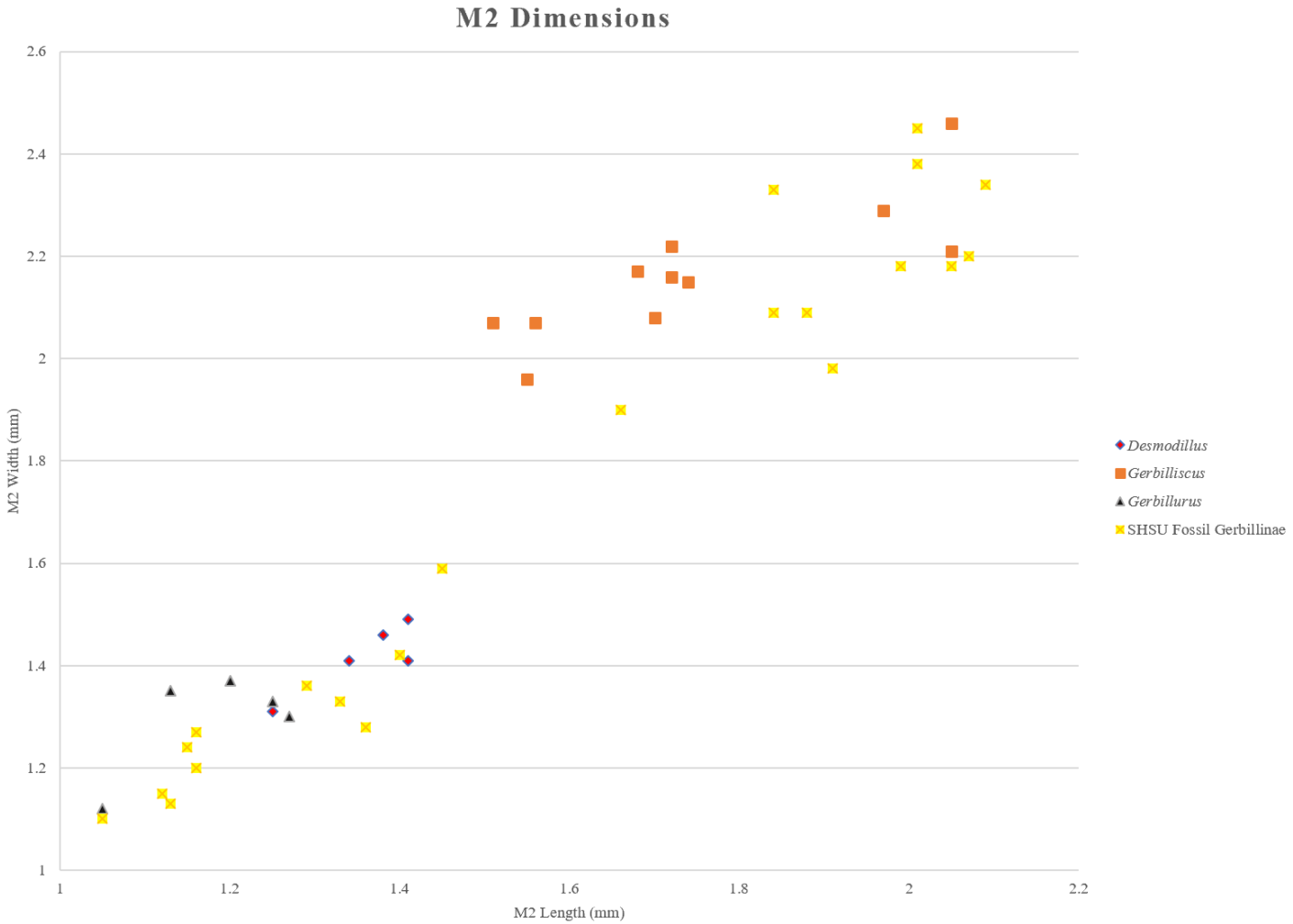


FIGURE 26. M2 dimensions of museum gerbil specimens and fossil gerbil specimens from Bone Cave.

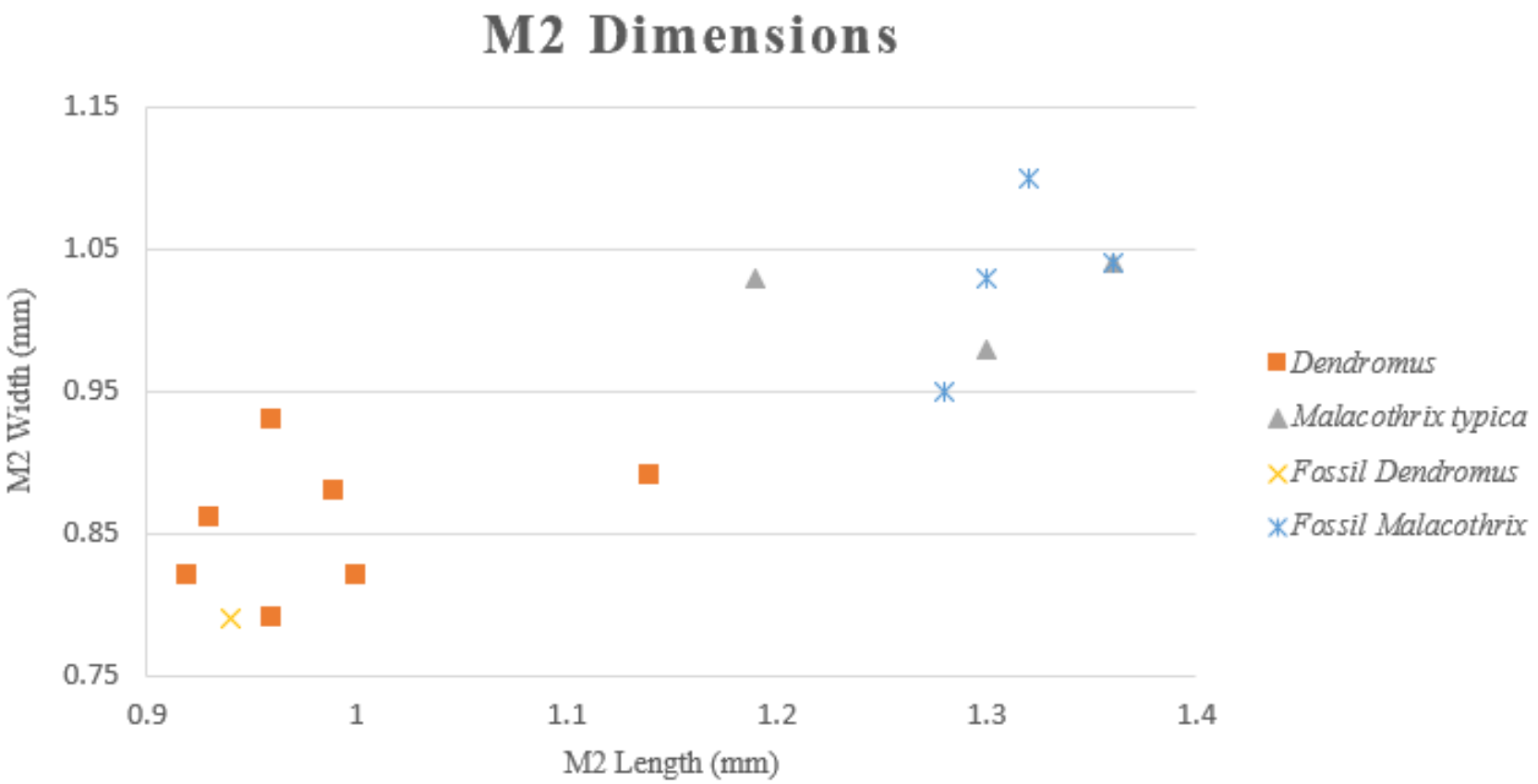


FIGURE 27. M2 dimensions of *Dendromus* and *Malacothrix* museum specimens and *Dendromus* and *Malacothrix* fossil specimens from Bone Cave.

TABLE 9. MNI and NISP of fossil rodents from Bone Cave. Total count is based on the sum of each genus or genus groups.

Family	Subfamily	Genus/Genus group	MNI	NISP
Muridae			80	133
	Deomyinae		2	2
		Acomys	2	2
	Gerbillinae		41	77
		Gerbilliscus	19	37
		Gerbillurus/Desmodillus	22	40
	Murinae		26	40
		Mus	13	20
		Otomys	4	8
		Pelomys	1	1
		Thallomys	1	1
		Micaelamys	1	2
		Lemniscomys	2	3
		Mastomys/Micaelamys/Rhabdomys	1	1
		Mastomys/Thallomys/Rhabdomys	1	1
		Micaelamys/Thallomys/Rhabdomys	1	1
		Murinae gen. *et sp. indet.*	1	2
	Murinae/Deomyinae		11	14
		Murinae gen. *sp. indet*/Deomyinae gen, *sp. indet.*	9	12
		Grammomys/Acomys/Thallomys	2	2
Nesomyidae			46	63
	Cricetomyinae		1	2
		Saccostomus	1	2
	Dendromurinae		44	59
		Dendromus	7	9
		Malacothrix	10	15
		Malacothrix/Dendromus	1	1
		Steatomys	26	34
	Mystromyinae		1	2
		Mystromys	1	2
Total			126	196

TABLE 10. Comparison of rodents identified from the fossil assemblage, traps, and pellet assemblage.

Family	Subfamily	Genus/Genera	Fossil	Pellet	Trap
Muridae	Deomyinae	*Acomys*	X		
	Gerbillinae	*Gerbilliscus*	X	X	X
		Gerbillurus/Desmodillus	X	X	
	Murinae	*Aethomys*		X	X
		Lemniscomys	X	X	X
		Mastomys/Micaelamys/Rhabdomys	X		
		Mastomys/Thallomys/Rhabdomys	X		
		Micaelamys	X	X	X
		Micaelamys/Thallomys/Rhabdomys	X		
		Mus	X	X	X
		Otomys	X		
		Pelomys	X		
		Thallomys	X		
		Mastomys		X	X
		Zelotomys		X	X
	Murinae/Deomyinae	*Grammomys/Acomys/Thallomys*	X		
Nesomyidae	Cricetomyinae	*Saccostomus*	X	X	X
	Dendromurinae	*Dendromus*	X	X	X

TABLE 10. (Continued)

Family	Subfamily	Genus/Genera	Fossil	Pellet	Trap
		Malacothrix	X		
		Malacothrix/Dendromus	X		
		Steatomys	X	X	X
	Mystromyinae	*Mystromys*	X		
Bathyergidae	Bathyerginae	*Fukomys* (*Cryptomys*)		X	X

TABLE 11. Comparison of fossil rodent community identified from Koanaka South with rodent communities from modern ecosystems in southern Africa.

Koanaka South Fossils	Pilanesburg National Park	Koanaka South	Okavango Delta	Tankwa Karoo National Park	Lower Zambezi National Park	Uitkomst and Jack Scott Nature Reserve
Acomys	Yes	No	No	Yes	Yes	Yes
Dendromus	Yes	Yes	Yes	Yes	Yes	Yes
Gerbilliscus	Yes	Yes	Yes	Yes	Yes	Yes
Lemniscomys	Yes	Yes	Yes	No	Yes	Yes
Micaelamys	Yes	Yes	Yes	Yes	Yes	No
Malacothrix	No	No	No	Yes	No	Yes
Mus	Yes	Yes	Yes	Yes	Yes	Yes
Mystromys	Yes	No	No	Yes	No	Yes
Otomys	Yes	No	Yes	Yes	No	Yes
Pelomys	No	No	Yes	No	Yes	No
Saccostomus	Yes	Yes	Yes	No	Yes	No
Steatomys	Yes	Yes	Yes	Yes	Yes	Yes
Thallomys	Yes	No	Yes	No	Yes	Yes

CHAPTER IV

DISCUSSION

Characters used to identify rodents from southern Africa ≤ 5 kg (excluding Sciuromorphs

The maxillary character matrix and dental metrics presented in this project allows for genus-level identification for several taxa ≤ 5 kg including: *Gerbilliscus*, *Dasymys, Micaelamys, Otomys, Parotomys*, *Myotomys*, *Pelomys, Thallomys*, *Lemniscomys, Thallomys, Mus, Mystromys*, *Saccostomus, Cricetomys*, *Steatomys, Dendromus, Malacothrix, Petromus*, *Petromyscus,* and *Acomys*. Genera that were unidentifiable using the character matrix and dental metrics include: *Aethomys*, *Mastomys*, *Zelotomys*, *Rhabdomys, Grammomys, Gerbillurus,* and *Desmodillus*. For murines, the maxilla has more diagnostic characters as opposed to the mandible (Barr, 2008); despite this, five murine taxa are not identifiable to the genus taxonomic level using maxillary characters.

Several maxillary characters identified from this project are particularly useful for genus-level identifications of fossil rodent specimens from southern Africa. Specifically, the size and shape of the masseteric knob (character 11) is particularly useful for separating the three dendromurines genera, *Dendromus, Steatomys,* and *Malacothrix*. An incipient t1 on the M1 (character 3) also helps separate *Steatomys* from the other dendromurines genera; however, this character is not always present in *Steatomys*. The number of laminae on the M3 (character 17) is useful for separating the three Otomyine genera, *Myotomys, Parotomys,* and *Otomys*. The presence of a t9 on the M1 and M2 (characters 6 and 7) is useful for separating *Dasymys* from other murinae genera. The presence of the t7 on the M1 and M2 (characters 13 and 14) is useful for separating

cricetomyines from all other rodent subfamilies and the position of the t4 on the M1 (character 5) is useful for separating the two cricetomyines genera distributed in southern Africa, *Cricetomys* and *Saccostomus*.

Using the character matrix, maxillary dental metrics can distinguish *Gerbilliscus* from *Gerbillurus* and *Desmodillus.* Similarly, molar dimensions can help distinguish the murine genera, *Pelomys, Lemniscomys, Micaelamys,* and *Thallomys*. The museum specimens used here also indicate that the presence of t3 on the M3 can no longer be considered diagnostic for *Acomys,* as the t3 was also present on the M3 of *Mastomys* and *Pelomys*. Species-level identification for fossil rodent specimens from southern Africa is often not possible with maxillary characteristics alone. This is not surprising given how difficult it is to identify some modern rodent species from southern Africa such as *Mus indutus* and *Mus minutoides* to the species-level due to their highly conserved morphology (McDonough et al., 2013). This suggests species-level identifications for some genera such as *Mus* may not be possible at any fossil site where only maxillary teeth are used for identifications.

Paleoenvironment of Koanaka South

As *Mystromys*, *Malacothrix*, and *Pelomys* are currently distributed in different environmental conditions, biotic zones, and are not known to occur together (Kingdon, 2013; Monadjem et al., 2015, Stuart and Stuart, 2015), their presence in the Bone Cave fauna may be explained in two ways: 1) the fauna is a non-analog fauna with no modern correlates; or 2) the fossil assemblage is mixed and sampling different environments from different periods. Non-analog communities are known in late Pleistocene paleoecological records for plants (Blinnikov et al., 2002; Jackson and Overpeck, 2000), coleopterans

(Morgan and Morgan, 1980), mammals (Semken et al., 2010; Stafford et al., 1999; Graham, 2005), mollusks (Kitamura, 2004), and foraminifera (Mix et al. 1999). If the assemblage is a non-analog community and sampling one habitat from one period of time, the co-occurrence of *Mystromys*, *Malacothrix*, and *Pelomys* suggests the environment was transitioning during the Middle-Pleistocene and had habitats suitable for these three genera.

The second explanation, that the fossil assemblage is mixed and sampling different environments from different periods, appears more likely as the fossils were collected from different chambers in the cave and processes such as aeolian or water transport may have mixed the fossil assemblage. The Sand Slide in the Atrium indicates aeolian processes could have transported the fossils. The breccia samples from Bone Cave dating to the Middle Pleistocene using thermoluminescence reached saturation levels meaning the deposits could be much older. As such, the fossil rodents from Bone Cave, from which the paleoenvironmental conditions are inferred, were deposited at some point during the Middle Pleistocene, but could have occurred earlier in the Pleistocene or even the Pliocene.

While there are no modern or fossil localities with a rodent community identical to that at Bone Cave, many of the rodent taxa identified from Bone Cave suggest that the paleoenvironment during the Middle Pleistocene was similar to the modern environment at Koanaka South today. This is evidenced by the presence of several genera that are all located at Koanaka South today (e.g., *Gerbilliscus, Lemniscomys, Micaelamys, Mus, Saccostomus, Dendromus*, and *Steatomys*). Additionally, *Aethomys*, *Gerbillurus*, *Mastomys*, and *Zelotomys* were both trapped and identified in the pellets, but fossil

specimens of these taxa are not identifiable to the genus level because no apomorphies were found to distinguish any one genus from the others. This inability to resolve these taxa at the genus level means we cannot say with confidence if any, some, or all of them were present in the past. As such, their presence does not help resolve the paleoenvironment of Koanaka South during the Middle Pleistocene.

Populations of *Pelomys* are only found within habitats such as swamps, streams, lakes and marshes making them reliable indicators of mesic conditions (Stuart and Stuart, 2015). *Pelomys* at Bone Cave, therefore, may suggest there was a permanent source of water within a few kilometers of the cave during the Middle Pleistocene that is not there today. The closest source of water to Koanaka South is sub-surface or seasonally available from rainfall that fills the ephemeral pans alongside Koanaka South. The nearest location this genus is found today is ~180 km away along the northern rivers of the Okavango Delta (Stuart and Stuart, 2015). The southern rivers of the Okavango Delta are ~120 km from Koanaka South. Several other genera identified at Bone Cave also have species that are currently distributed along the northern rivers of the Okavango Delta including: *Gerbilliscus, Dendromus, Steatomys, Mus, Micaelamys, Thallomys, Lemniscomys,* and *Saccostomus*. However, these genera are common in a wide range of environments and were also trapped at Koanaka South suggesting that they are not reliable indicators of mesic conditions (Monadjem et al., 2015; Stuart and Stuart, 2015). Although *Pelomys* was not identified from the modern pellet and trapping data, there are biases in both methodologies that could explain why this taxon was not present. The prey size bias exhibited by barn owls could explain why *Pelomys* was absent in the pellets. Similarly, since traps were only set during the summer season, seasonal variations in

Pelomys populations could explain why they were absent in the traps. Only a single specimen of *Pelomys* was recovered in the fossil assemblage. For these reasons, the mesic conditions inferred from the fossil rodents at Bone Cave cannot confidently be supported.

Otomys was also identified at Bone Cave, and although otomyines have been described as being associated with moist habitats (Pickford, 1990), some species such as *Otomys sloggetti* and *Otomys unisculatus* are located in more arid regions of southern Africa. This suggests that they, too, are not reliable indicators of mesic conditions (Kingdon, 2013; Monadjem et al., 2015, Stuart and Stuart, 2015).

Among the nonmammalian taxa recovered were several birds, including buttonquail, rails, and passerines, as well as reptiles and amphibians (Lewis et al., 2007). The presence of *Turnix* sp. (buttonquail) supports the possibility of a water source within a few kilometers of Koanaka South during the Middle Pleistocene. Forty-four fossil amphibian and reptile elements were identified from Bone Cave (Kennedy and Bhullar, 2007). Five specimens were attributed to the amphibian order Anura. Squamate clades represented include Caenophidia, Gekkonidae, Lacertidae, Scincoidea, and Agamidae, with Gekkonids (n=22) representing the most common taxon in the assemblage (Kennedy and Bhullar, 2007). The presence of Anura suggests the past presence of a seasonal source of water. Anurans are also found in the modern biota at Koanaka South today (Bauer et al., 2009). It is unknown if buttonquail, absent in the dry season during which collections were made, are present in the wet season when the pans at Koanaka South are presumably full (based on the presence of hibernating frogs in the dry season).

Regionally, mesic conditions during the Middle Pleistocene are supported by the presence of, *Xenopus* sp. and *Pelusios* sp. from fossil deposits at Drotsky's Cave. These conditions are also supported by the diatom and mollusk taxa identified from the Tsodilo Hills and Drotsky's Cave, and analysis of relict shore lines from the Sua, Nwetwe, and Nxai pans.

CHAPTER V

CONCLUSION

Results from this study show that species-level identification for fossil rodent specimens from southern Africa are often not possible with maxillary characteristics. The maxillary character matrix and dental metrics presented in this project allows for genus-level identification for several taxa ≤ 5 kg. Genera that were unidentifiable using the character matrix and dental metrics include: *Aethomys, Mastomys, Zelotomys, Rhabdomys, Grammomys, Gerbillurus,* and *Desmodillu*s. It might be possible to identify these genera to a lower taxonomic level by incorporating additional characters from the maxilla, such as the incisors, or from other skeletal remains also commonly found in owl assemblages, such as mandibles or postcranial elements like the femur and humerus (Andrews, 1990). Future research can build on this work by incorporating these additional elements from the mandible or postcrania along with the characters used in this project. Adding these elements may allow for the identification of more taxa and thereby improve the accuracy of paleoenvironmental reconstructions. Studies of pollen, sediments from the cave, and invertebrate fossils would also be useful in determining the paleoenvironment at Bone Cave.

The characters used in building character matrix from this project are only accurate if the assumption holds true that the museum specimens used to create the matrix were identified correctly and are representative of current taxonomy. Since taxonomy for rodents frequently changes (even at the genus level), it is likely at least one museum specimen was not identified properly. Also, recent work on modern rodents supports the presence of cryptic species (e.g., McDonough et al. 2013) that trapping projects may have

misidentified and mislabeled. It would be beneficial for future researchers to confirm the taxonomic identification of museum specimens using DNA analyses whenever possible. This clarification of taxonomic identity would increase the confidence of morphology-based studies, such as that presented here.

Two methods frequently used to reconstruct paleoenvironments using rodents, the G:M ratio and THI, may not be as reliable or useful in certain circumstances. Given that species-level identifications of rodent fossil remains from southern Africa are often not possible, the resolving power and usefulness of THI's from rodents is limited and may be unreliable. Similarly, although G:M ratios may be reliable indicators for the amount of vegetation in the surrounding habitats in northern and eastern Africa, the large role *Desmodillus*, *Gerbillus*, and *Gerbillurus* play in G:M ratios suggests this value may not be appropriate to use in southern and central African fossil sites as these taxa are not reliable indicators of open habitats.

Mystromys, *Malacothrix*, and *Pelomys* are all represented in the Bone Cave assemblage. The fact that these taxa are not found together today (Stuart and Stuart, 2015) suggests that the rodent paleocommunity represented at Bone Cave has no modern analog. As such, the null hypothesis stating fossil rodent taxa identified from Bone Cave are all distributed at Koanaka South today is rejected. The alternative hypothesis stating the fossil rodent taxa identified from Bone Cave are not all distributed at Koanaka South today is accepted.

While the presence of *Pelomys*, buttonquail, and amphibians in the fossil record of Bone Cave allows for the possibility of a more mesic past, they are not convincing by themselves. *Pelomys* and buttonquail are each represented by a single specimen, and

amphibians occur at Koanaka South today. The overwhelming majority of fossils found in the Bone Cave deposit represent taxa still found there today. Given these data, the most parsimonious interpretation is one of no change. Hypotheses linking faunal change with environmental change at Koanaka South, like those at every locality, can only be refined as both the fossil record and our understanding of past environments increases. The rodent fauna from Koanaka South partially fills this significant geographic and temporal gap in the paleontological record of Africa.

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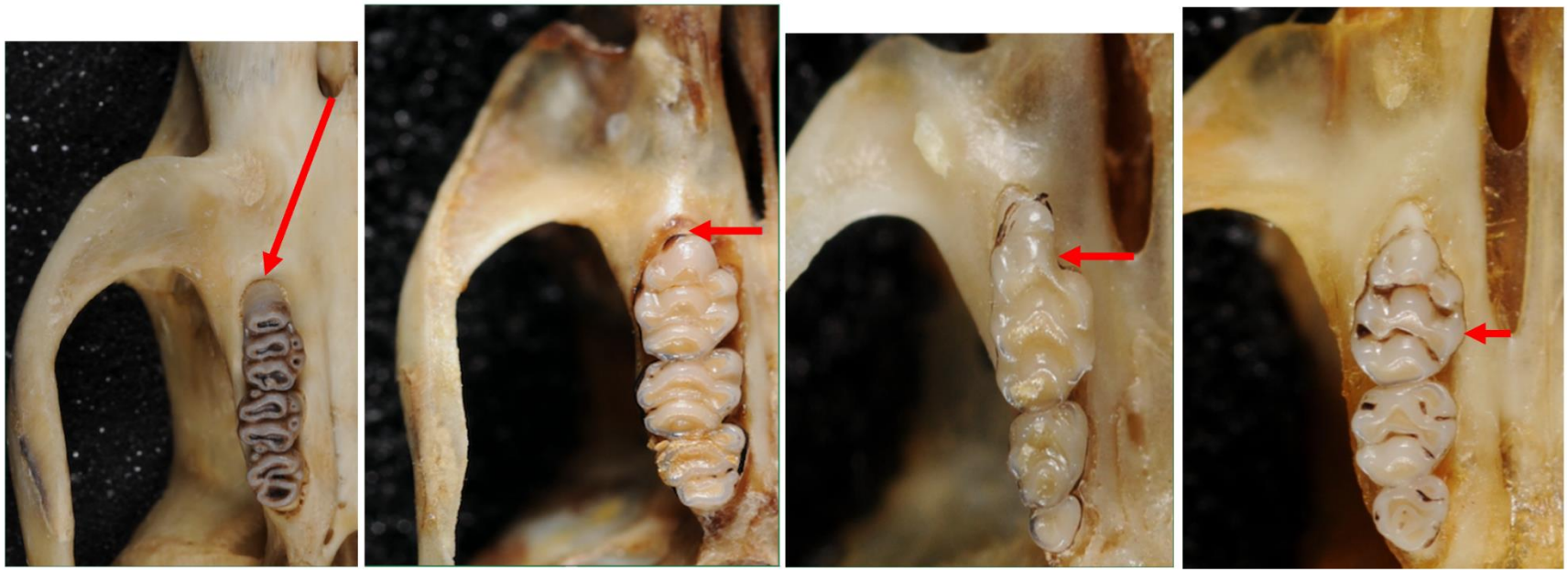
APPENDIX A

Index comparing names of various chambers within Koanaka Hills and Bone Cave from this project and Ritter and Mann, 1995.

This Project	Ritter and Mann 1995
Koanaka North	K1
Koanaka South	K2
Koanaka West	K3
Bone Cave	Bone Cave
Atrium	Central Chamber
Micromammal Room	Pit's Room
Sand Slide	Sloping Chambers
Elephant Room	Elephant Room
Leopard's Dining Room	Leopard's Dining Room
Drop Room	Drop Room

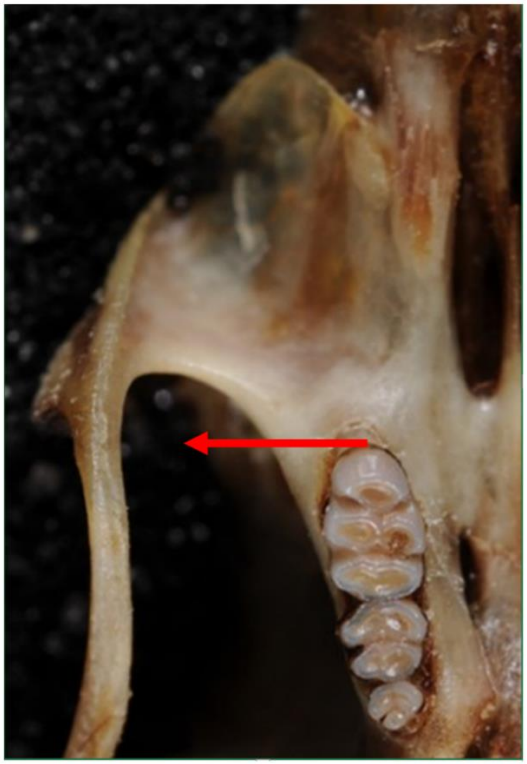
APPENDIX B



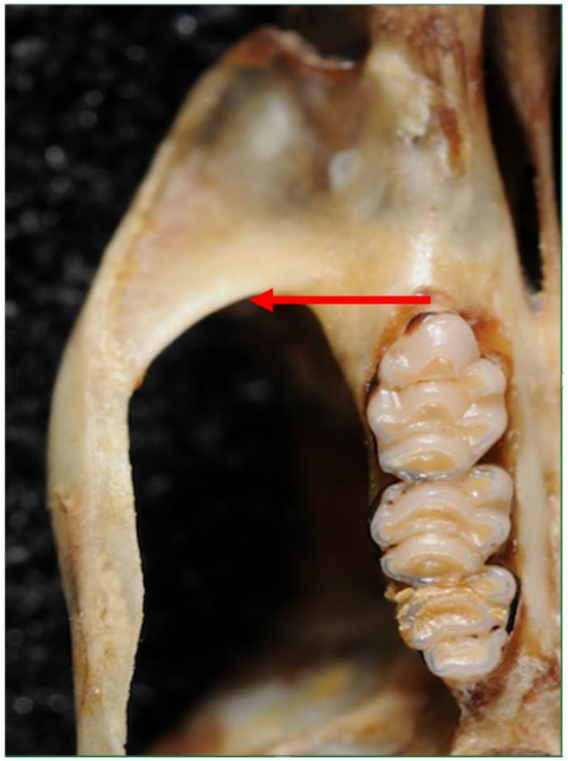
Character state examples for character 1. Arrow indicates position of anterior palatal foramina relative to M1.

State	Description
0	Does not reach first alveoli on M1
1	Reaches anterior border of first alveoli on M1
2	Reaches first lamina of M1 (i.e. T2/T3) (For *Mystromys, Petromyscus, Petromus*, and Gerbils – at anterocone)
3	Reaches second lamina of M1 (i.e. T5/T6) (For *Mystromys, Petromyscus, Petromus*, and Gerbils – at protocone)

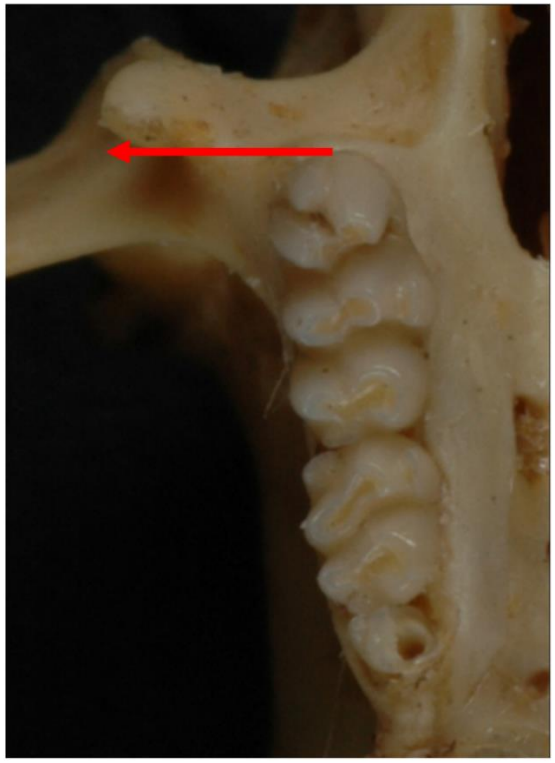
APPENDIX C



Character 2 State 0



Character 2 State 1

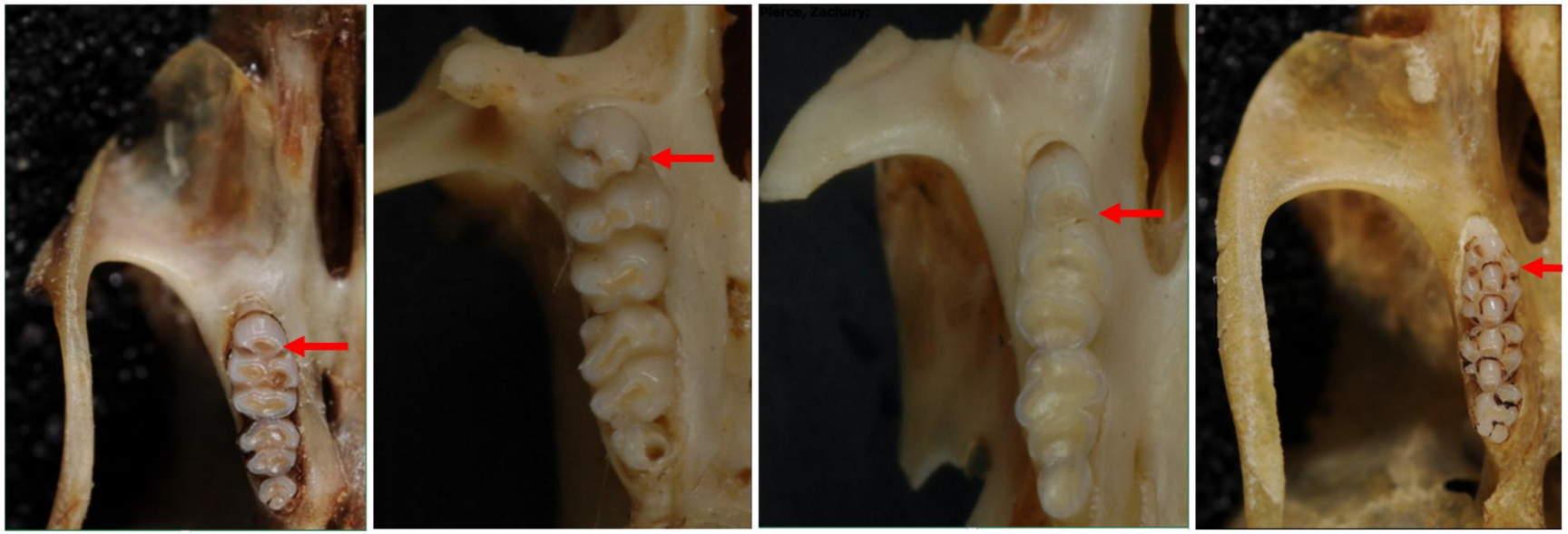


Character 2 State 2

Character state examples for character 2. Arrow indicates position of anterior alveoli relative to zygomatic plate.

State	Description
0	Alveoli border posterior to zygomatic plate
1	Alveoli border at zygomatic plate
2	Alveoli border anterior to zygomatic plate.

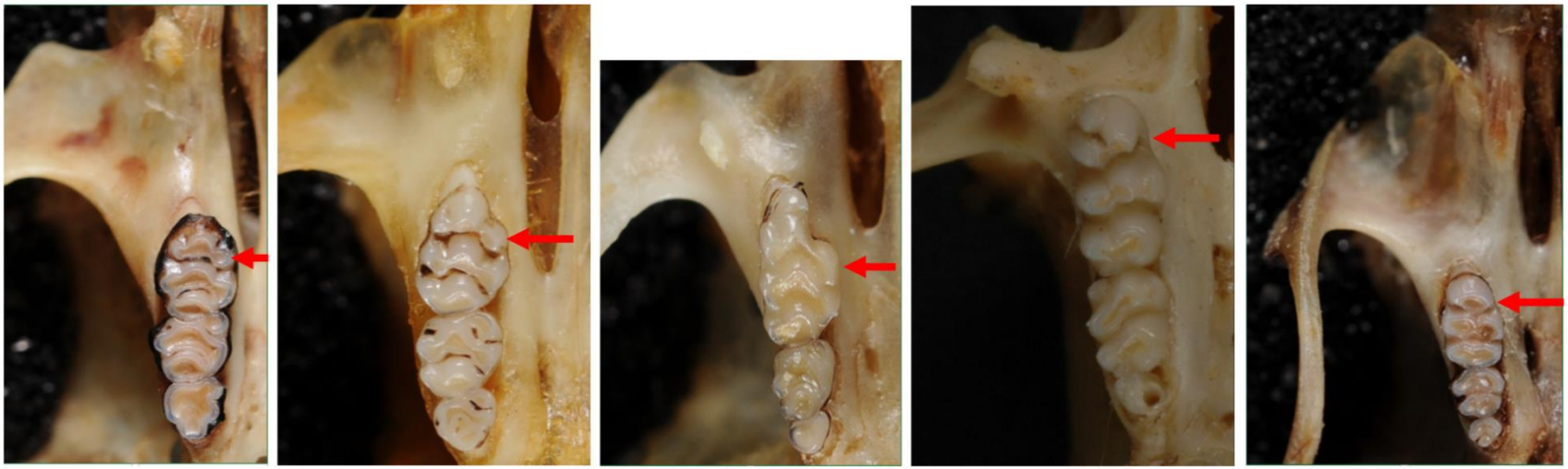
APPENDIX D



Character state examples for character 3. Arrow indicates the presence and absence of a t1 on M1.

State	Description
0	N/A
1	Absent
2	Incipient
3	Present.

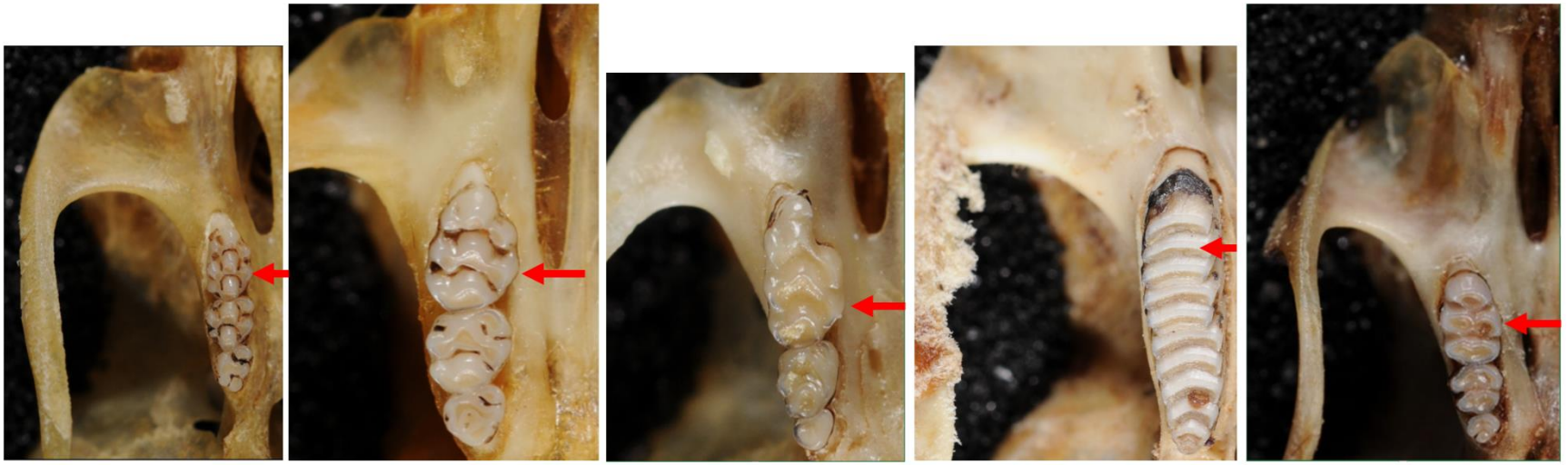
APPENDIX E



Character state examples for character 4. Arrow indicates the position of a t1 on M1.

State	Description
0	Approximately parallel with t2/t3 on M1
1	Slightly posteriorly displaced
2	Highly posteriorly displaced
3	Absent
4	N/A

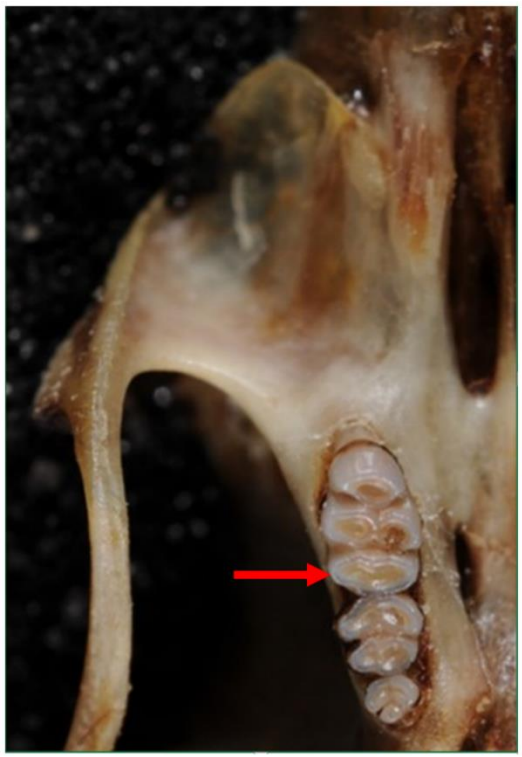
APPENDIX F



Character state examples for character 5. Arrow indicates the presence, absence, and position of a t4 on M1.

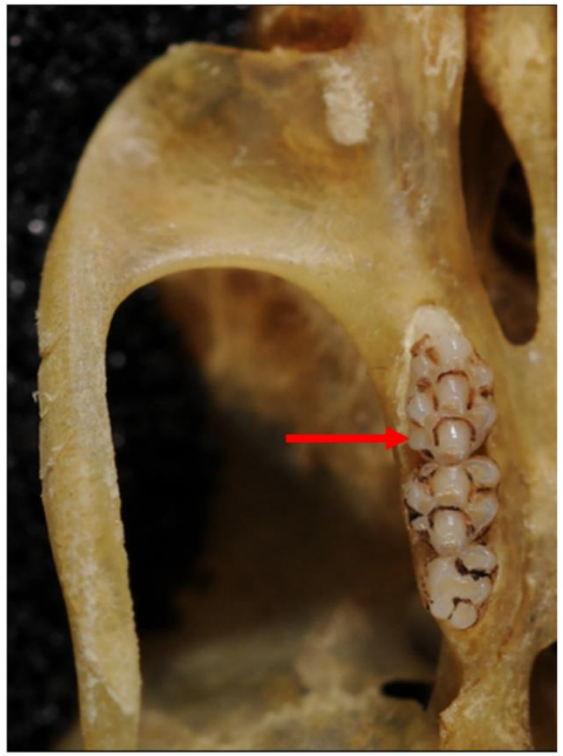
State	Description
0	Approximately parallel with t5/t6 on M1
1	Slightly posteriorly displaced
2	Highly posteriorly displaced
3	Absent
4	N/A

APPENDIX G



Character 6 State 0

Character 6 State 1



Character 6 State 2

Character state examples for character 6. Arrow indicates the presence or absence of a t9 on M1.

State	Description
0	N/A
1	Absent
2	Present

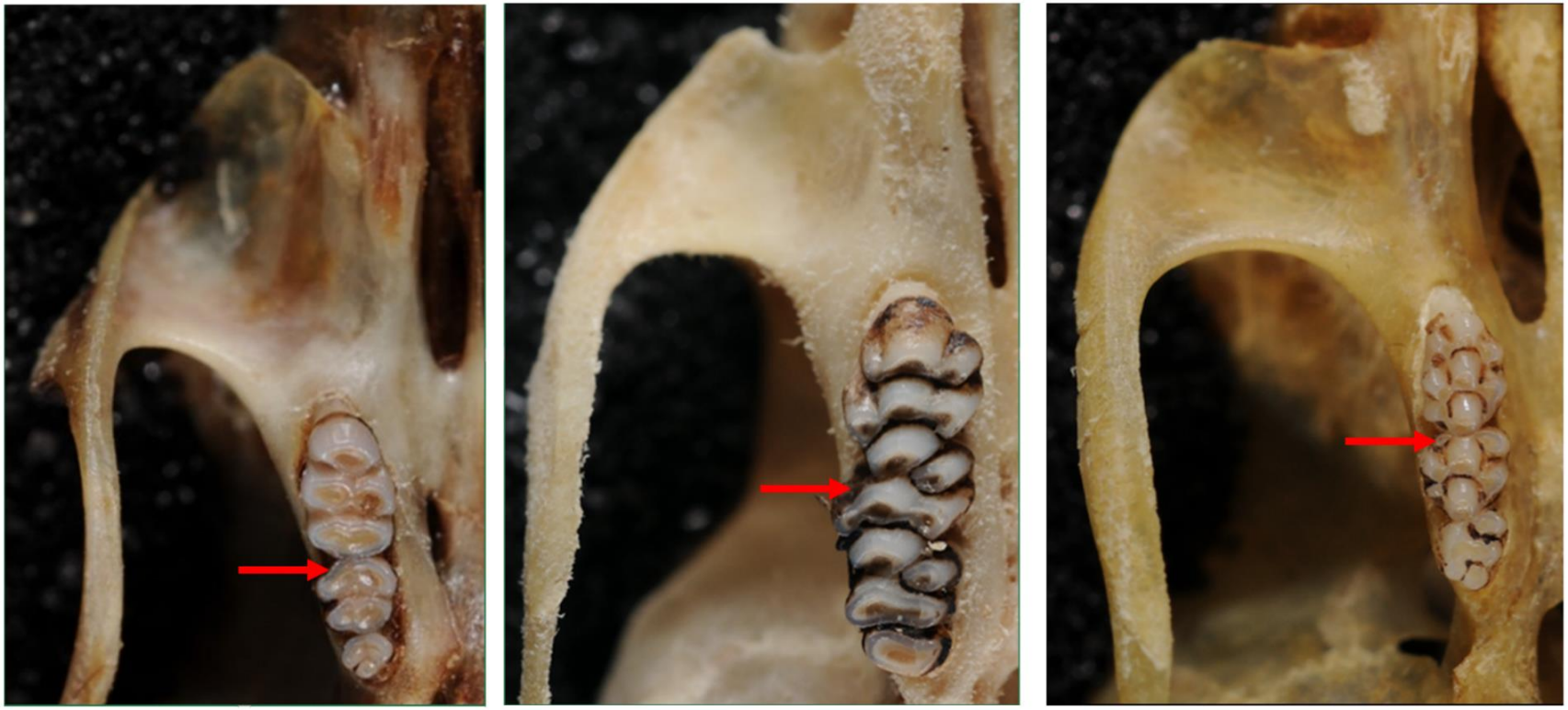
APPENDIX H

Character 7 State 0 | Character 7 State 1 | Character 7 State 2

Character state examples for character 7. Arrow indicates the presence or absence of a t9 on M2.

State	Description
0	N/A
1	Absent
2	Present

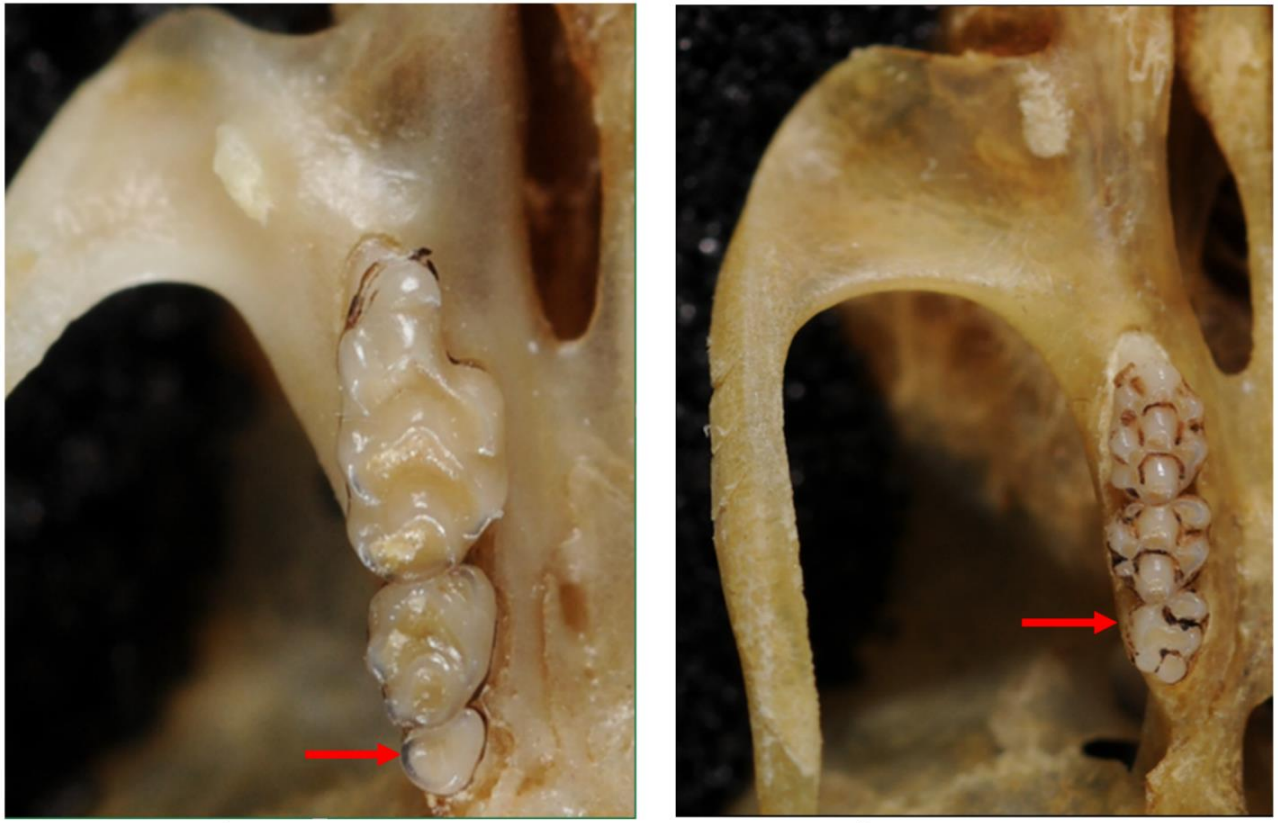
APPENDIX I



Character state examples for character 8. Arrow indicates the presence or absence of a t3 on M2.

State	Description
0	N/A
1	Absent
2	Present

APPENDIX J

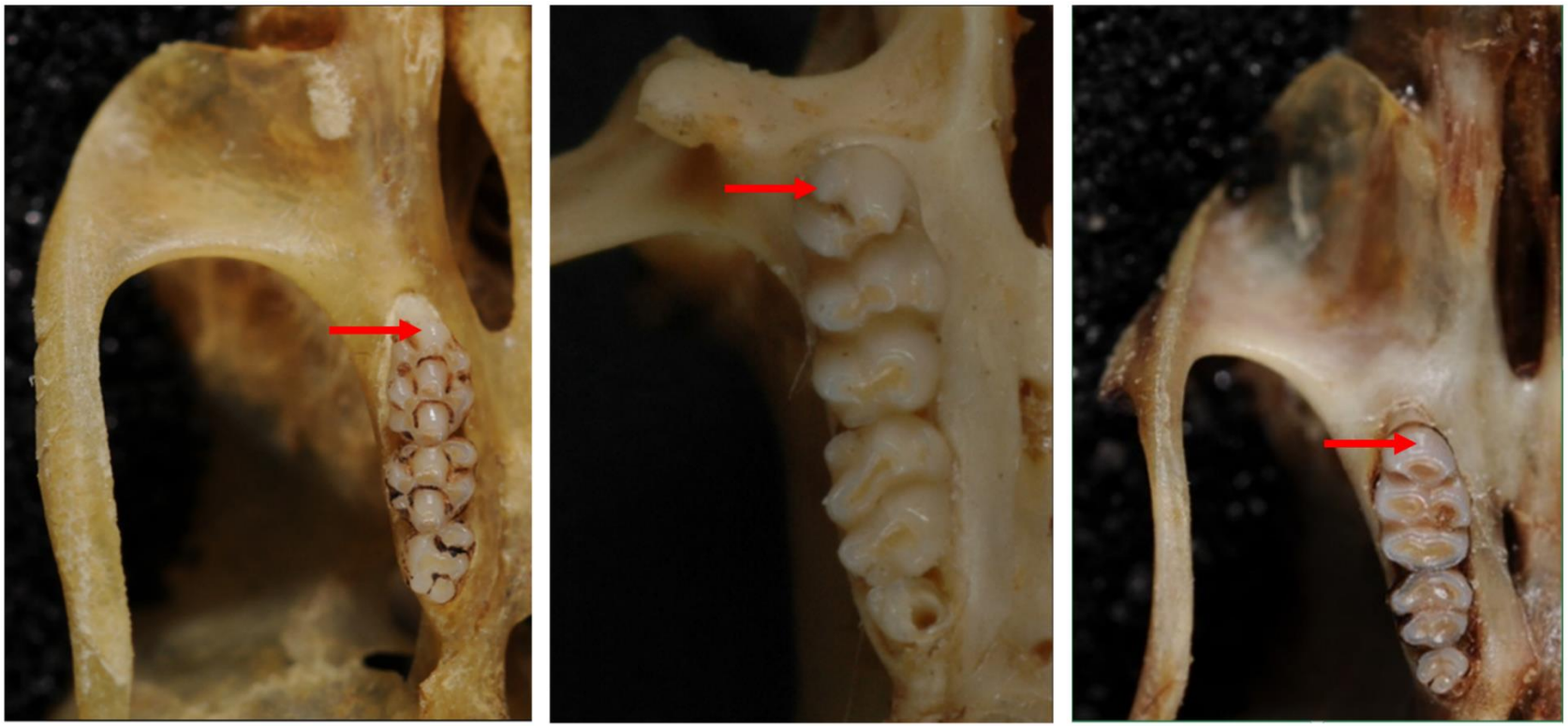


Character 9 State 0 Character 9 State 1

Character state examples for character 9. Arrow indicates M3 development

State	Description
0	Incipient
1	Developed (containing at least two rows with cusps)

APPENDIX K

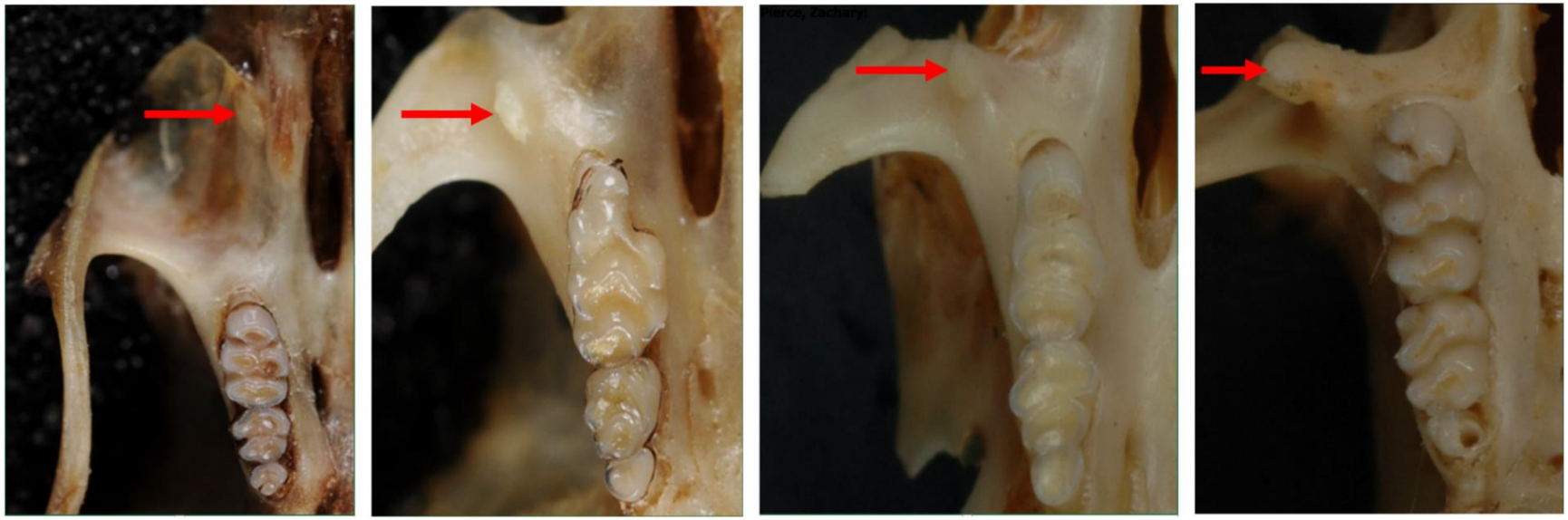


Character 10 State 0 | Character 10 State 1 | Character 10 State 2

Character state examples for character 10. Arrow indicates a cingular conule, extension of a t2 on M1.

State	Description
0	Absent/ Slight depression or cingulum
1	Developed cusp or extention of anterior border of T2
2	N/A

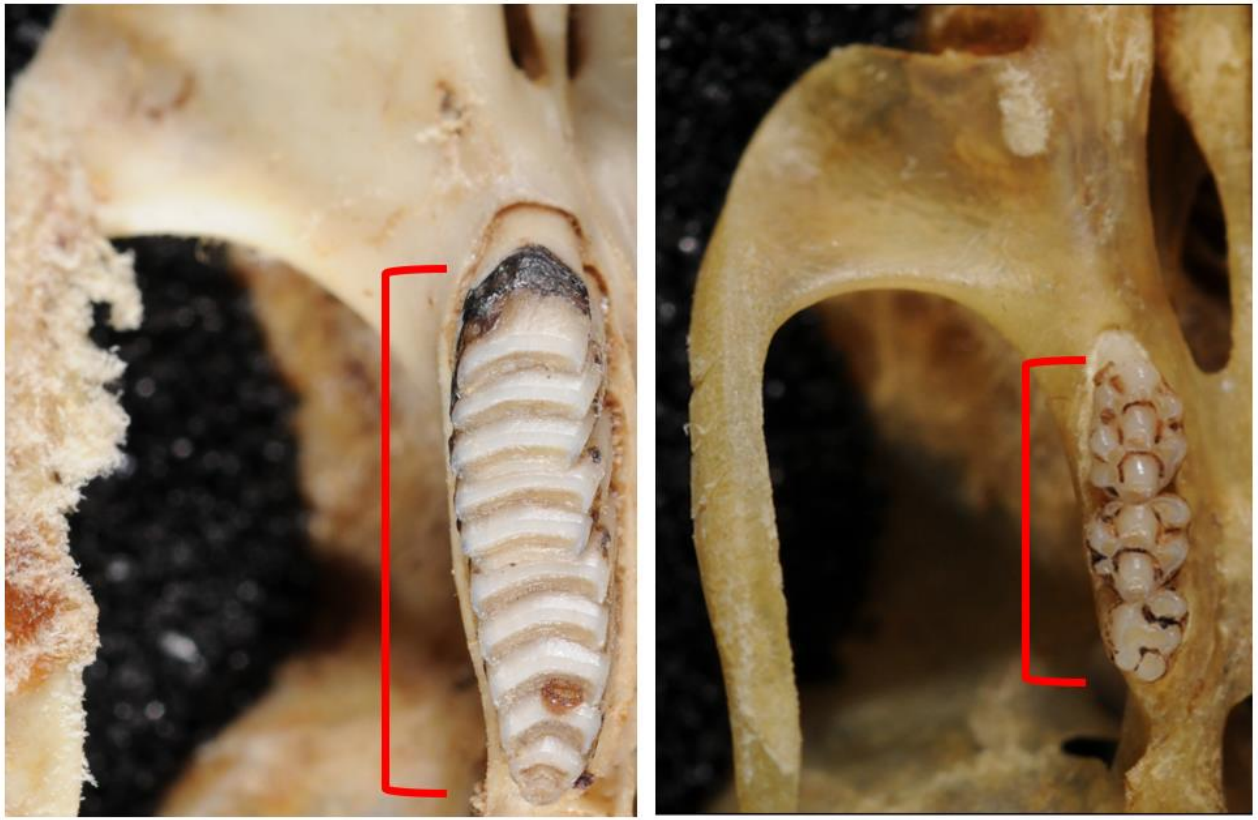
APPENDIX L



Character state examples for character 11. Arrow indicates masseteric knob or masseteric scarring.

State	Description
0	Absent (absent or small scarring on zygomatic plate)
1	Present (knob on zygomatic plate)
2	Well-developed (knob on narrow and vertically-oriented zygomatic plate though these features not as extreme as in Malacothrix)
3	Pronounced (large knob on narrow, vertically-oriented zygomatic plate)

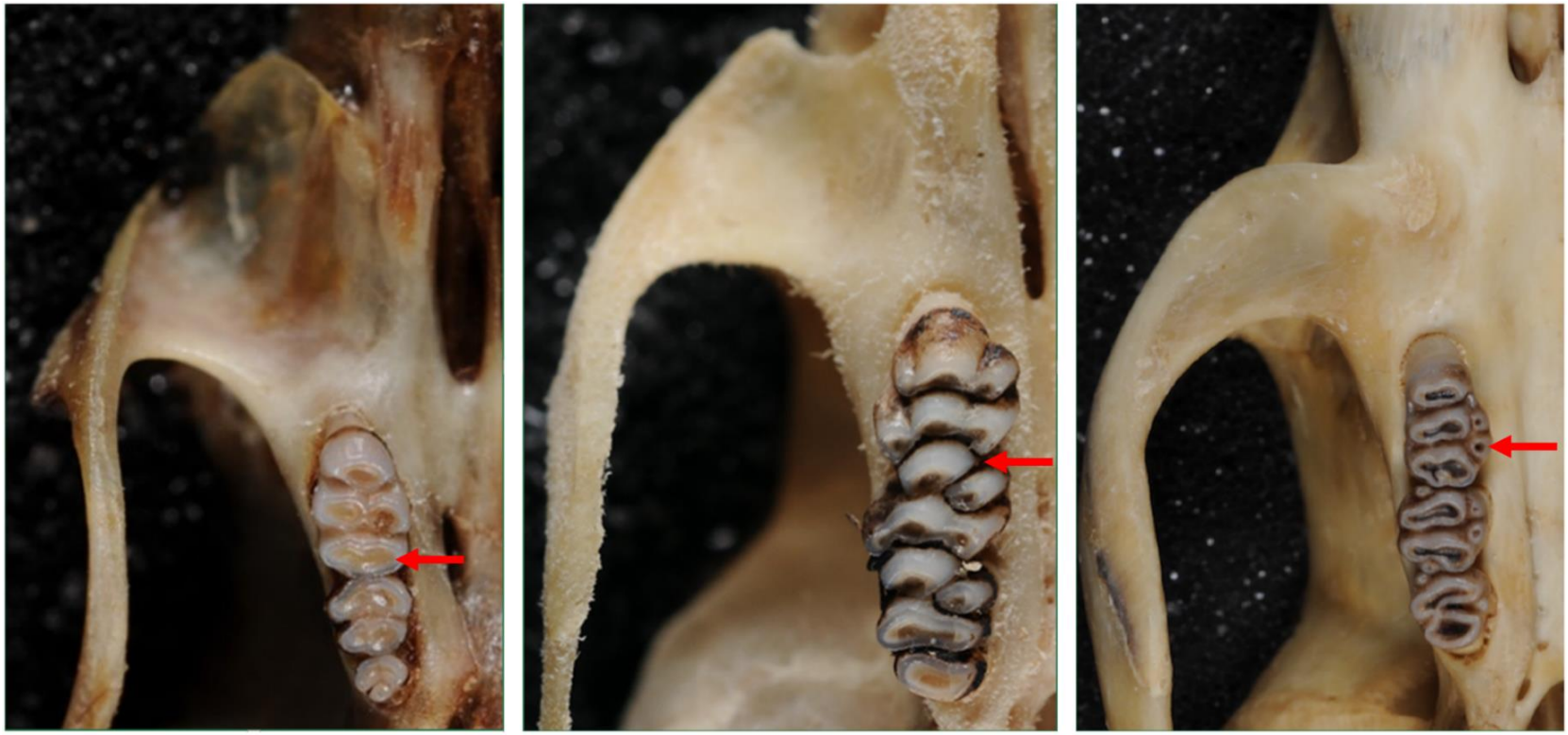
APPENDIX M



Character state examples for character 12. Bracket indicates the presence of loxodont or lophodont molars.

State	Description
0	Loxodont
1	Lophodont/Semi-lophodont/Advanced-lophodont

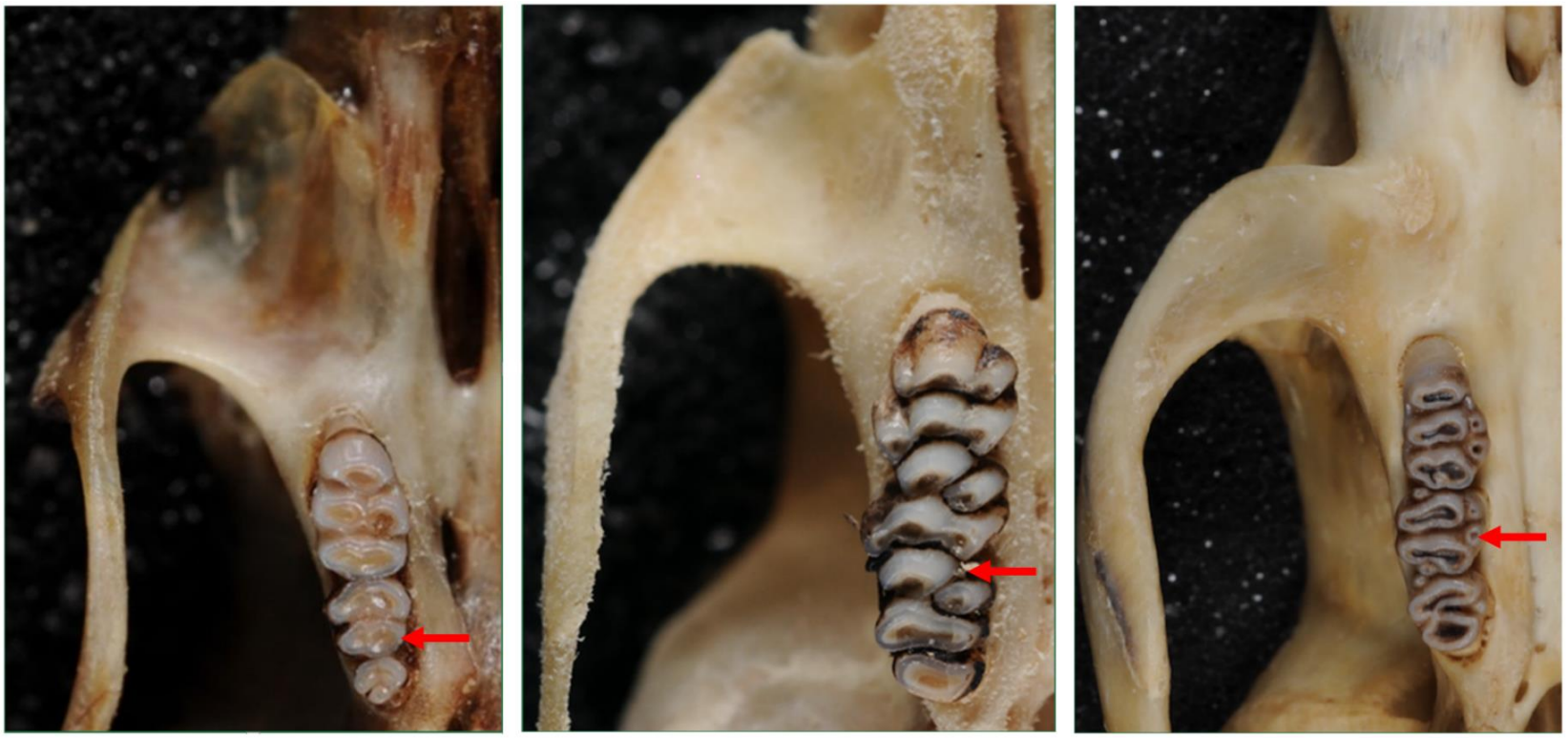
APPENDIX N



Character state examples for character 13. Arrow indicates the presence or absence of a t7 on M1.

State	Description
0	N/A
1	Absent
2	Present

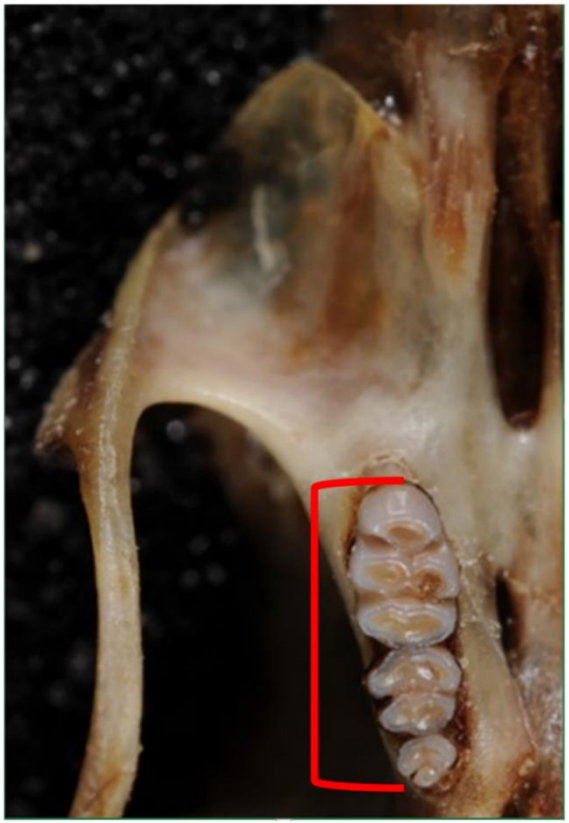
APPENDIX O



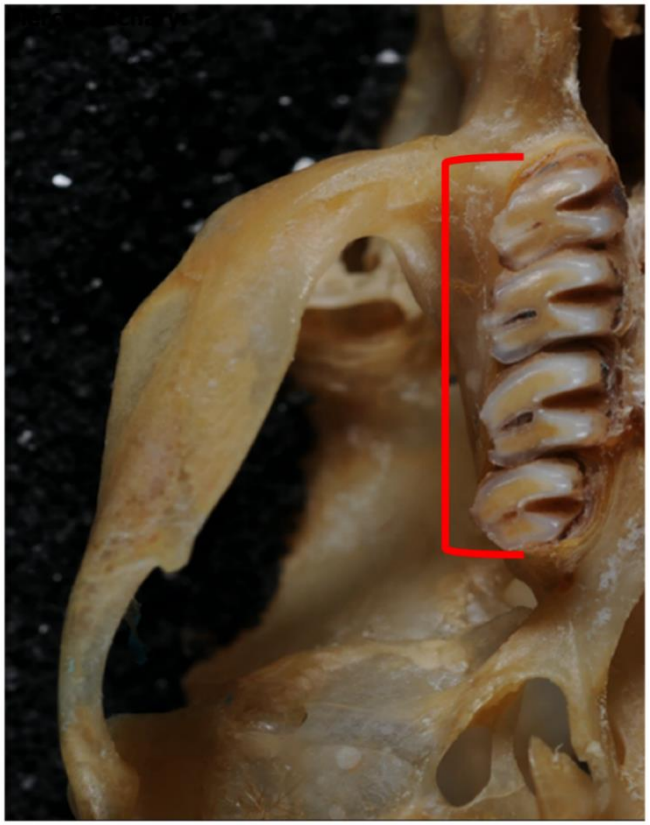
Character state examples for character 14. Arrow indicates the presence or absence of a t7 on M2.

State	Description
0	N/A
1	Absent
2	Present

APPENDIX P



Character 15 State 0

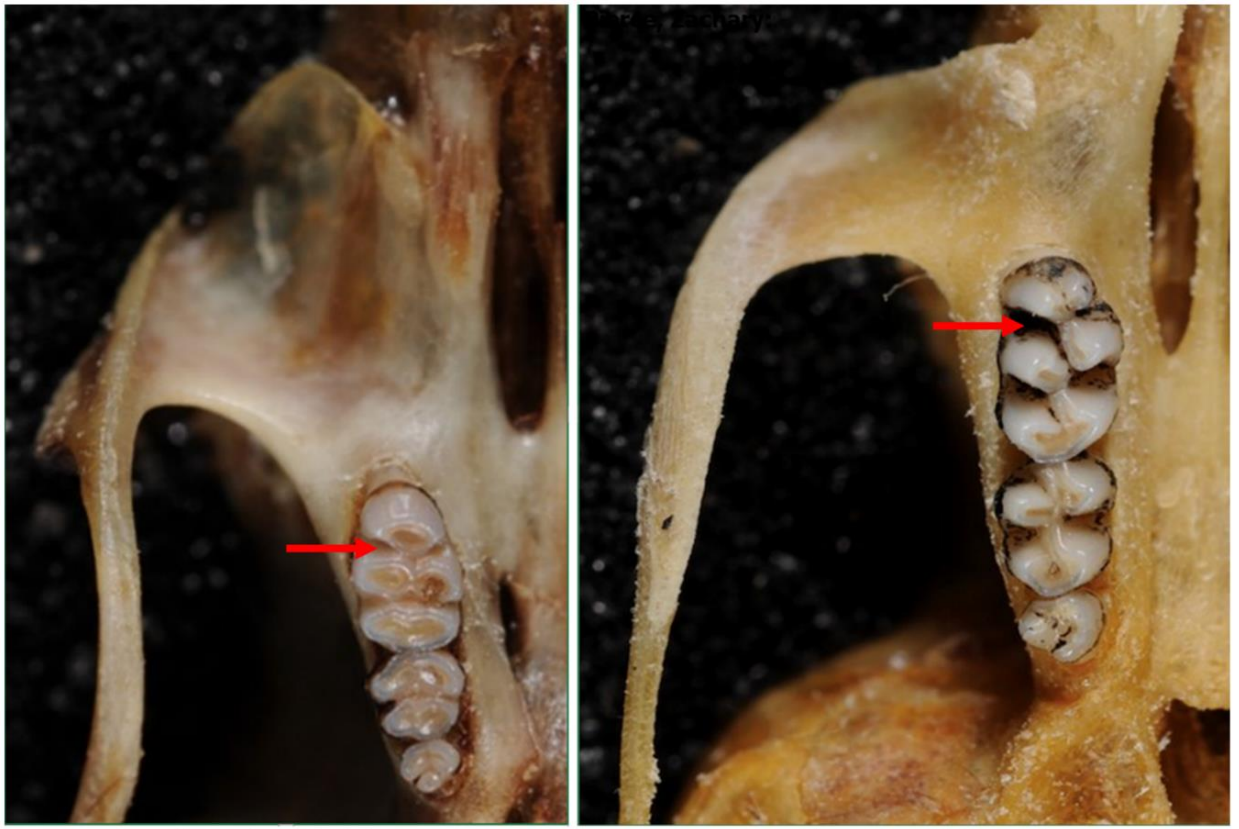


Character 15 State 1

Character state examples for character 15. Bracket indicates the number of molars.

State	Description
0	3 molars
1	4 molars

APPENDIX Q

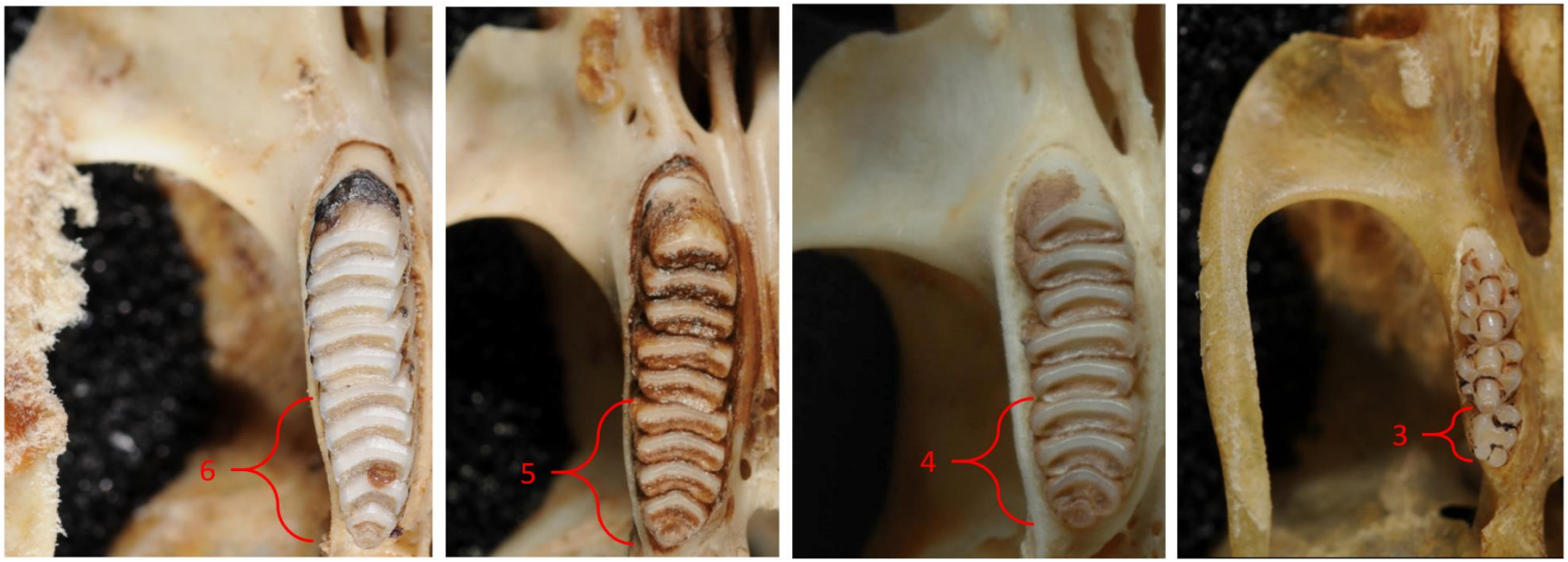


Character 16 State 0 Character 16 State 1

Character state examples for character 16. Arrow indicates the presence or absence of re-entrant folds.

State	Description
0	Absent
1	Present

APPENDIX R



Character state examples for character 17. Bracket and associated number indicate the number of laminae on M3.

State	Description
0	Six or more laminae
1	Five laminae
2	Four-three laminae
3	Two or less laminae

APPENDIX S

List of museum specimens used in character matrix scores and molar measurements as reference for fossil specimens.

Genus	Species	Museum	Specimen ID #
Aethomys	*chrysophilus*	TM	19806
Aethomys	*chrysophilus*	TM	45247
Aethomys	*chrysophilus*	TM	19807
Aethomys	*chrysophilus*	TM	19817
Aethomys	*ineptus*	TM	46971
Aethomys	*ineptus*	TM	46509
Acomys	*spinosis*	TM	40754
Acomys	*spinosis*	TM	44810
Acomys	*spinosis*	TM	45107
Acomys	*spinosis*	USNM	367353
Dasymys	*incomtus*	FM	183756
Dasymys	*incomtus*	FM	183758
Dasymys	*incomtus*	FM	183760
Dasymys	*incomtus*	FM	183761
Dasymys	*incomtus*	TM	45265
Grammomys	*cometes*	FM	165600
Grammomys	*cometes*	FM	214896
Grammomys	*cometes*	FM	214895
Grammomys	*dolichurus*	FM	214898
Grammomys	*dolichurus*	FM	214904
Grammomys	*dolichurus*	FM	214907
Lemniscomys	*rosalia*	TM	45841
Lemniscomys	*rosalia*	TM	42053
Lemniscomys	*rosalia*	TM	45967
Lemniscomys	*rosalia*	TM	45843
Lemniscomys	*rosalia*	TM	45320
Lemniscomys	*rosalia*	TM	44410
Mastomys	*coucha*	TM	44488
Mastomys	*coucha*	TM	42448
Mastomys	*natalensis*	TM	45664
Mastomys	*natalensis*	TM	45665
Mastomys	*natalensis*	TM	45775
Mastomys	*natalensis*	AMNH	168662
Micaelamys	*namaquensis*	TM	16274
Micaelamys	*namaquensis*	TM	25882
Micaelamys	*namaquensis*	TM	43625
Micaelamys	*namaquensis*	TM	45909
Micaelamys	*namaquensis*	TM	45694
Micaelamys	*namaquensis*	TM	42171
Mus	*indutus*	TM	45484
Mus	*indutus*	TM	45888
Mus	*indutus*	TM	45489
Mus	*indutus*	TM	45736
Mus	*minutoides*	TM	13549
Mus	*minutoides*	USNM	45547
Mus	*minutoides*	USNM	351810
Pelomys	*fallax*	AMNH	169404
Pelomys	*fallax*	AMNH	213087
Pelomys	*fallax*	FM	183807
Pelomys	*fallax*	FM	183806
Pelomys	*fallax*	AMNH	213089
Otomys	*angoniensis*	TM	46524
Otomys	*irroratus*	TM	42185
Otomys	*laminatus*	TM	29647
Otomys	*saundersiae*	TM	22639
Myotomys	*unisulcatus*	TM	42141
Myotomys	*unisulcatus*	TM	42169
Myotomys	*sloggetti*	TM	22683
Myotomys	*sloggetti*	TM	22668
Parotomys	*brantsii*	TM	3453
Parotomys	*littledalei*	TM	5083
Parotomys	*littledalei*	TM	11072
Parotomys	*littledalei*	TM	10982
Rhabdomys	*pumilio*	TM	23946
Rhabdomys	*pumilio*	TM	24132
Rhabdomys	*pumilio*	TM	45303
Rhabdomys	*pumilio*	TM	46507
Rhabdomys	*pumilio*	TM	23974
Rhabdomys	*pumilio*	TM	46510
Thallomys	*nigricauda*	USNM	295700
Thallomys	*paedulcus*	TM	41115
Thallomys	*paedulcus*	TM	41161
Thallomys	*paedulcus*	TM	45485
Thallomys	*paedulcus*	TM	46972
Thallomys	*paedulcus*	TM	44735
Zelotomys	*woosnami*	TK	164762
Zelotomys	*woosnami*	TK	154622
Zelotomys	*woosnami*	USNM	295830
Zelotomys	*woosnami*	TM	28450
Zelotomys	*woosnami*	TM	25421
Mystromys	*albicaudatus*	TM	41851
Mystromys	*albicaudatus*	TM	44173
Mystromys	*albicaudatus*	TM	39331
Desmodillus	*auricularis*	TM	41041
Desmodillus	*auricularis*	TM	12121
Desmodillus	*auricularis*	TM	45478
Desmodillus	*auricularis*	TK	55158
Desmodillus	*auricularis*	TM	43634
Gerbilliscus	*leucogaster*	USNM	295381
Gerbilliscus	*leucogaster*	USNM	295447
Gerbilliscus	*inclusus*	FM	214890
Gerbilliscus	*inclusus*	TM	45949
Gerbilliscus	*brantsii*	TM	42394
Gerbilliscus	*brantsii*	TM	45496
Gerbilliscus	*afra*	TM	21604
Gerbilliscus	*afra*	TM	2213
Gerbilliscus	*afra*	TM	41554
Gerbilliscus	*afra*	TM	4801
Gerbilliscus	*afra*	TM	9039
Gerbillurus	*paeba*	USNM	344068
Gerbillurus	*paeba*	TM	42148
Gerbillurus	*paeba*	TM	45735
Gerbillurus	*vallinus*	TM	41037
Gerbillurus	*vallinus*	TM	41038
Steatomys	*pratensis*	TM	45114
Steatomys	*pratensis*	TM	45910
Steatomys	*pratensis*	TM	45948
Steatomys	*parvus*	TK	164993
Steatomys	*parvus*	TM	7604
Steatomys	*krebsi*	USNM	296024
Steatomys	*krebsi*	USNM	296011
Steatomys	*krebsi*	TM	3779
Dendromus	*melanotis*	TM	41304
Dendromus	*melanotis*	USNM	295975
Dendromus	*mysticalis*	TM	45830
Dendromus	*mysticalis*	TM	46416
Dendromus	*mesomelas*	TM	45729
Dendromus	*mesomelas*	TM	3220
Dendromus	*nyikae*	TM	40108
Malacothrix	*typica*	TM	2661
Malacothrix	*typica*	NMB	11601
Malacothrix	*typica*	TM	2652
Saccostomus	*campestris*	USNM	295948
Saccostomus	*campestris*	TM	44214
Saccostomus	*campestris*	TM	46471
Saccostomus	*campestris*	TM	44591
Saccostomus	*campestris*	TM	46423
Saccostomus	*campestris*	TM	46467
Cricetomys	*gambianus*	TM	43334
Cricetomys	*gambianus*	TM	43349
Cricetomys	*ansorgei*	FM	183756
Petromyscus	*collinus*	TK	55216
Petromyscus	*collinus*	TK	55217
Petromyscus	sp.	TM	43628
Petromyscus	*collinus*	USNM	344080
Petromus	*typicus*	AMNH	168337
Petromus	*typicus*	AMNH	34393

APPENDIX T

Bone Cave rodent fossil scores.

SHSU #	Palatal Foramen (1)	Alveoli - Zygomatic (2)	T1 on M1 (3)	Position T1 - M1 (4)	Position T4 -M1 (5)	T9 on M1 (6)	T9 on M2 (7)	T3 on M2 (8)	M3 Development (9)	M1 CC or E (10)	Masseteric Knob (11)	Molar type (12)	t7 on M1 (13)	t7 on M2 (14)	# of Molars (15)	re-entrent folds (16)	# of lamina on m3 (17)
3	n/p	2	1	n/p	n/p	n/p	1	1	1	n/p	n/p	0	n/p	1	0	0	0
8	2	n/p	3	1	1	2	2	2	1	0	n/p	1	1	1	0	0	3
12	n/p	n/p	3	0	0	2	2	2	1	0	n/p	1	1	1	0	0	3
15	2	n/p	0	4	4	0	n/p	n/p	n/p	2	n/p	1	0	n/p	0	0	3
17	3	2	1	3	0	2	n/p	n/p	n/p	0	2	1	1	n/p	0	0	3
18	3	1	2	3	0	2	2	2	0	0	2	1	1	1	0	0	3
24	n/p	2	1	n/p	n/p	n/p	n/p	n/p	1	n/p	n/p	0	n/p	n/p	0	0	0
25	1	n/p	0	n/p	4	0	n/p	n/p	n/p	n/p	n/p	1	0	n/p	0	0	3
40	2	1	0	4	4	0	n/p	n/p	n/p	2	n/p	1	0	n/p	0	0	3
72	1	1	3	1	1	2	2	2	n/p	0	0	1	1	1	0	0	3
73	n/p	n/p	0	4	4	0	0	0	n/p	2	0	1	0	0	0	1	3
96	n/p	1	3	2	2	1	1	1	n/p	1	1	1	1	1	0	0	3
110	2	0	3	1	1	2	2	2	n/p	0	0	1	1	1	0	0	3
112	3	2	2	3	0	2	n/p	n/p	n/p	0	2	1	1	n/p	0	0	3
113	2	n/p	3	2	2	2	2	1	n/p	1	n/p	1	1	1	0	0	3
117	2	n/p	0	4	4	0	n/p	n/p	n/p	2	n/p	1	0	n/p	0	0	3
118	2	n/p	0	4	4	0	n/p	n/p	n/p	2	n/p	1	0	n/p	0	0	3
128	1	0	0	4	4	0	n/p	n/p	n/p	2	n/p	1	0	n/p	0	0	3
134	n/p	2	1	3	3	1	1	1	1	0	n/p	0	1	1	0	0	0
136	n/p	1	3	n/p	n/p	n/p	2	2	1	n/p	0	1	n/p	1	0	0	3
137	3	2	2	3	0	2	n/p	n/p	n/p	0	2	1	1	n/p	0	0	3
138	n/p	0	2	3	0	2	2	2	0	0	2	1	1	1	0	0	3
139	n/p	1	1	3	0	2	n/p	n/p	n/p	0	2	1	1	n/p	0	0	3
140	3	2	2	3	0	2	n/p	n/p	n/p	0	2	1	1	n/p	0	0	3
144	3	1	1	3	0	2	n/p	n/p	n/p	1	2	1	1	n/p	0	0	3
145	3	2	2	3	0	2	n/p	n/p	n/p	0	2	1	1	n/p	0	0	3
154	3	1	2	3	0	2	2	2	n/p	0	2	1	1	1	0	0	3
155	2	1	1	3	0	2	n/p	n/p	n/p	0	2	1	1	n/p	0	0	3
156	2	1	3	2	2	2	n/p	n/p	n/p	1	1	1	1	n/p	0	0	3
157	3	2	1	3	0	2	n/p	n/p	n/p	0	2	1	1	n/p	0	0	3
158	2	1	3	1	1	2	2	2	1	0	0	1	1	1	0	0	3
159	2	1	3	1	1	2	2	2	1	0	0	1	1	1	0	0	3
160	3	1	2	3	0	2	2	2	n/p	0	2	1	1	1	0	0	3
236	2	1	0	4	4	0	n/p	n/p	n/p	2	n/p	1	0	n/p	0	0	3
237	1	1	0	4	4	0	n/p	n/p	n/p	2	n/p	1	0	n/p	0	0	3
238	2	0	0	4	4	0	n/p	n/p	n/p	2	n/p	1	0	n/p	0	0	3
239	2	n/p	3	1	1	n/p	n/p	n/p	n/p	0	n/p	1	n/p	n/p	0	0	3
240	2	n/p	3	1	1	2	n/p	n/p	n/p	0	n/p	1	1	n/p	0	0	3
241	2	n/p	0	4	4	0	n/p	n/p	n/p	2	n/p	1	0	n/p	0	0	3
242	n/p	0	0	n/p	n/p	n/p	0	0	n/p	n/p	n/p	1	n/p	0	0	0	3
243	1	0	0	4	4	0	n/p	n/p	n/p	2	0	1	0	n/p	0	0	3
244	2	1	0	4	4	0	n/p	n/p	n/p	2	n/p	1	0	n/p	0	0	3
272	2	n/p	0	4	4	0	n/p	n/p	n/p	2	n/p	1	0	n/p	0	0	3
273	3	1	3	n/p	n/p	n/p	2	2	n/p	n/p	0	1	n/p	1	0	0	3
280	n/p	1	2	3	0	2	n/p	n/p	n/p	0	2	1	1	n/p	0	0	3
282	2	1	3	1	1	2	2	2	n/p	0	0	1	1	1	0	0	3
397	2	1	3	1	n/p	n/p	n/p	n/p	n/p	0	n/p	1	n/p	n/p	0	0	3
398	3	1	1	3	0	2	n/p	n/p	n/p	0	2	1	1	n/p	0	0	3
404	2	0	3	1	1	2	n/p	n/p	n/p	0	0	1	1	n/p	0	0	3
405	3	2	1	3	0	2	n/p	n/p	n/p	0	2	1	1	n/p	0	0	3
406	1	n/p	3	1	1	2	n/p	n/p	n/p	0	n/p	1	1	n/p	0	0	3
443	3	0	3	n/p	n/p	n/p	2	2	n/p	n/p	0	1	n/p	1	0	0	3
456	n/p	1	1	3	0	2	2	2	n/p	0	2	1	1	1	0	0	3
458	3	2	1	3	0	2	n/p	n/p	n/p	0	2	1	1	n/p	0	0	3
467	1	0	0	4	4	0	n/p	n/p	n/p	2	n/p	1	0	n/p	0	0	3
475	1	0	0	4	4	0	n/p	n/p	n/p	2	0	1	0	n/p	0	0	3
479	3	1	2	3	0	2	2	2	n/p	0	2	1	1	1	0	0	3
510	2	0	0	4	4	0	n/p	n/p	n/p	2	n/p	1	0	n/p	0	0	3
511	2	1	3	2	2	2	2	2	0	1	1	1	1	1	0	0	3
512	2	1	1	3	0	2	n/p	n/p	n/p	0	2	1	1	n/p	0	0	3
513	3	1	1	3	0	2	n/p	n/p	n/p	0	2	1	1	n/p	0	0	3
519	2	n/p	0	4	4	0	n/p	n/p	n/p	2	n/p	1	0	n/p	0	0	3
521	2/3	1	3	1	1	2	2	2	1	0	n/p	1	1	1	0	0	3
522	2	0	0	4	4	0	n/p	n/p	n/p	2	n/p	1	0	n/p	0	0	3
523	3	2	1	3	0	2	n/p	n/p	n/p	0	2	1	1	n/p	0	0	3
524	2	0	0	4	4	0	n/p	n/p	n/p	2	?	1	0	n/p	0	0	3
527	3	1	2	3	0	2	n/p	n/p	n/p	0	2	1	1	n/p	0	0	3
542	3	1	1	3	0	2	2	2	n/p	1	2	1	1	1	0	0	3
543	n/p	n/p	1	n/p	n/p	n/p	1	1	1	n/p	n/p	0	n/p	1	0	0	0
549	n/p	n/p	1	n/p	n/p	n/p	1	1	1	n/p	n/p	0	n/p	1	0	0	0
580	1	0	0	4	4	0	n/p	n/p	n/p	2	n/p	1	0	n/p	0	0	3
612	1	n/p	0	4	4	0	n/p	n/p	n/p	2	n/p	1	0	n/p	0	0	3
613	3	2	1	3	0	2	2	2	n/p	1	3	1	1	1	0	0	3
614	3	n/p	0	4	4	0	0	0	0	2	n/p	1	0	0	0	1	3
648	1	n/p	0	n/p	n/p	n/p	0	0	n/p	n/p	n/p	1	n/p	0	0	0	3
649	2	1	1	3	0	n/p	2	n/p	n/p	0	0	1	n/p	2	0	0	3

Bone Cave rodent fossil scores (continued).

SHSU #	Palatal Foramen (1)	Alveoli - Zygomatic (2)	T1 on M1 (3)	Position T1 - M1 (4)	Position T4 -M1 (5)	T9 on M1 (6)	T9 on M2 (7)	T3 on M2 (8)	M3 Development (9)	M1 CC or E (10)	Masseteric Knob (11)	Molar type (12)	t7 on M1 (13)	t7 on M2 (14)	# of Molars (15)	re-entrent folds (16)	# of lamina on m3 (17)
651	1	0	0	4	4	0	0	0	n/p	2	n/p	1	0	0	0	0	3
680	2	1	3	2	1	n/p	n/p	n/p	n/p	0	n/p	1	n/p	n/p	0	0	3
681	1	n/p	0	4	4	0	n/p	n/p	n/p	2	0	1	0	n/p	0	0	3
682	2	n/p	0	4	4	0	n/p	n/p	n/p	2	n/p	1	0	n/p	0	0	3
688	0	0	0	4	4	0	0	0	n/p	2	n/p	1	0	0	0	0	3
689	0	0	0	4	4	0	0	0	1	2	n/p	1	0	0	0	0	3
762	1	0	0	4	4	0	0	0	n/p	2	n/p	1	0	0	0	0	3
804	n/p	0	1	3	0	2	n/p	n/p	n/p	0	0	1	2	n/p	0	0	3
836	3	2	1	3	0	2	2	2	n/p	1	3	1	1	1	0	0	3
1502	1	0	0	4	4	0	0	0	n/p	2	n/p	1	0	0	0	0	3
1535	2	2	n/p	n/p	0	2	n/p	n/p	n/p	n/p	3	1	1	n/p	0	0	3
1539	2	n/p	3	1	0	2	n/p	n/p	n/p	0	n/p	1	1	n/p	0	0	3
1651	n/p	n/p	3	n/p	n/p	n/p	2	2	n/p	n/p	0	1	n/p	1	0	0	3
1750	n/p	n/p	3	n/p	n/p	n/p	n/p	n/p	1	n/p	n/p	1	n/p	1	0	0	3
1751	2	1	3	2	2	2	2	1	n/p	1	1	1	1	1	0	0	3
1791	1	n/p	0	4	4	0	n/p	n/p	n/p	2	n/p	1	0	n/p	0	0	3
1798	2	1	3	2	2	2	2	2	n/p	1	1	1	1	1	0	0	3
1833	2	1	3	1	0	2	n/p	n/p	n/p	0	0	1	1	n/p	0	0	3
1897	2	n/p	3	1	1	2	2	2	n/p	0	n/p	1	1	1	0	0	3
1918	2	n/p	3	1	1	2	2	2	n/p	0	n/p	1	1	1	0	0	3
1948	0	0	0	4	4	0	0	0	0	2	0	1	0	0	0	0	3
1961	1	0	0	4	4	0	0	0	n/p	2	n/p	1	0	0	0	0	3
1962	1	0	0	4	4	0	n/p	n/p	n/p	2	n/p	1	0	n/p	0	0	3
1979	2	n/p	3	1	1	2	2	2	1	0	n/p	1	1	1	0	0	3
2027	2	0	3	1	1	n/p	n/p	n/p	n/p	0	0	1	n/p	n/p	0	0	3
2028	0	0	0	4	4	0	0	0	1	2	n/p	1	0	0	0	0	3
2080	2	0	0	4	4	0	0	0	n/p	2	n/p	1	0	0	0	0	3
2163	2	1	3	2	2	n/p	2	1	n/p	1	1	1	1	1	0	0	3
2177	1	1	0	4	4	0	0	0	n/p	2	n/p	1	0	0	0	0	3
2191	2	n/p	0	n/p	n/p	n/p	0	0	n/p	n/p	n/p	1	n/p	0	0	0	3
2210	2	0	0	n/p	n/p	n/p	0	0	n/p	n/p	0	1	n/p	0	0	0	3
2214	1	0	0	4	4	0	0	0	n/p	2	n/p	1	0	0	0	0	3
2236	2	1	3	2	2	n/p	n/p	n/p	n/p	1	1	1	n/p	n/p	0	0	3
2237	3	1	3	1	1	2	2	2	n/p	0	n/p	1	1	1	0	0	3
2241	3	n/p	1	3	0	n/p	n/p	n/p	n/p	1	2	1	1	n/p	0	0	3
2243	3	1	1	3	0	2	n/p	n/p	n/p	1	2	1	1	n/p	0	0	3
2244	1	0	0	4	4	0	n/p	n/p	n/p	2	0	1	0	n/p	0	0	3
2442	1	0	0	4	4	0	n/p	n/p	n/p	2	n/p	1	0	n/p	0	0	3
2443	1	0	0	4	4	0	n/p	n/p	n/p	2	n/p	1	0	n/p	0	0	3
2475	1	0	0	4	4	0	n/p	n/p	n/p	2	n/p	1	0	n/p	0	0	3
2495	1	n/p	0	4	4	n/p	n/p	n/p	n/p	2	n/p	1	0	n/p	0	0	3
2510	n/p	2	1	3	0	2	n/p	n/p	n/p	1	3	1	1	n/p	0	0	3
2527	3	1	3	2	2	n/p	2	2	n/p	n/p	0	1	1	1	0	0	3
2694	n/p	n/p	0	4	4	0	n/p	n/p	n/p	2	n/p	1	0	n/p	0	0	3
2724	2	1	3	2	2	2	n/p	1	n/p	1	1	1	1	n/p	0	0	3
2773	2	0	0	4	4	0	0	0	1	2	n/p	1	0	0	0	0	3
2774	1	0	0	4	4	0	n/p	n/p	n/p	2	n/p	1	0	n/p	0	0	3
2775	1	n/p	0	4	4	0	n/p	n/p	n/p	2	n/p	1	0	n/p	0	0	3
2776	3	2	2	3	0	2	n/p	n/p	n/p	0	2	1	1	n/p	0	0	3
2813	1	0	0	4	4	0	n/p	n/p	n/p	2	n/p	1	0	n/p	0	0	3
2840	2	1	3	2	2	2	2	2	0	1	1	1	1	1	0	0	3
2873	3	2	1	3	0	2	n/p	n/p	n/p	1	3	1	1	n/p	0	0	3
2941	2	1	0	4	4	0	0	0	n/p	2	n/p	1	0	0	0	0	3
2944	3	2	1	3	0	2	n/p	n/p	n/p	1	3	1	1	n/p	0	0	3
2945	2	1	3	2	2	2	2	1	0	1	1	1	1	1	0	0	3
3047	1	n/p	0	4	4	0	n/p	n/p	n/p	2	n/p	1	0	n/p	0	0	3
3052	1	0	0	4	4	0	n/p	n/p	n/p	2	n/p	1	0	n/p	0	0	3
3222	2	n/p	0	4	4	0	n/p	n/p	n/p	2	n/p	1	0	n/p	0	0	3
3223	1	0	0	4	4	0	0	0	0	2	0	1	0	0	0	0	3
3254	2	n/p	0	n/p	n/p	n/p	0	0	n/p	n/p	n/p	1	n/p	0	0	0	3
3264	n/p	2	3	2	2	n/p	n/p	n/p	n/p	1	1	1	n/p	n/p	0	0	3
3279	1	0	0	4	4	0	0	0	n/p	2	n/p	1	0	0	0	0	3
3280	3	2	1	3	0	2	2	2	n/p	1	3	1	1	1	0	0	3
3298	3	2	1	3	0	2	2	2	n/p	1	2/3	1	1	1	0	0	3
3332	n/p	2	1	3	0	2	n/p	n/p	n/p	1	3	1	1	n/p	0	0	3
3333	n/p	1	2	3	0	2	n/p	n/p	n/p	0	2	1	1	n/p	0	0	3
3351	1	0	0	4	4	0	0	0	n/p	2	n/p	1	0	0	0	0	3
3515	3	2	1	3	0	2	n/p	n/p	n/p	1	2/3	1	1	n/p	0	0	3
3519	3	2	2	3	0	2	n/p	n/p	n/p	0	2	1	1	n/p	0	0	3
3555	2	n/p	0	4	4	0	n/p	n/p	n/p	2	n/p	1	0	n/p	0	0	3
3571	1	0	0	3	n/p	n/p	3	3	n/p	2	n/p	1	0	0	0	0	3
3629	2	n/p	0	4	4	0	n/p	n/p	n/p	2	n/p	1	0	n/p	0	0	3
3631	n/p	n/p	0	n/p	n/p	n/p	0	0	n/p	n/p	n/p	1	n/p	0	0	0	3
3636	3	2	1	3	0	2	n/p	n/p	n/p	1	2	1	1	n/p	0	0	3
3704	3	1	2	3	0	2	n/p	n/p	n/p	0	2	1	1	n/p	0	0	3
3708	3	1	2	3	0	2	2	2	n/p	0	2	1	1	1	0	0	3

Bone Cave rodent fossil scores (continued).

SHSU #	Palatal Foramen (1)	Alveoli - Zygomatic (2)	T1 on M1 (3)	Position T1 - M1 (4)	Position T4 -M1 (5)	T9 on M1 (6)	T9 on M2 (7)	T3 on M2 (8)	M3 Development (9)	M1 CC or E (10)	Masseteric Knob (11)	Molar type (12)	t7 on M1 (13)	t7 on M2 (14)	# of Molars (15)	re-entrent folds (16)	# of lamina on m3 (17)
3715	2	1	3	2	2	2	2	2	0	1	1	1	1	1	0	0	3
3718	3	2	1	3	0	2	2	2	n/p	1	3	1	1	1	0	0	3
3720	2	1	3	2	2	2	1	2	n/p	1	1	1	1	1	0	0	3
3721	n/p	n/p	0	n/p	n/p	n/p	0	0	n/p	2	n/p	1	n/p	0	0	0	3
3722	3	2	1	3	0	2	n/p	n/p	n/p	1	3	1	1	n/p	0	0	3
3727	1	0	0	4	4	0	n/p	n/p	n/p	2	n/p	1	0	n/p	0	0	3
3733	3	1	1	3	0	2	2	2	n/p	0	2	1	1	1	0	0	3
3757	2	0	0	n/p	n/p	n/p	0	0	n/p	n/p	n/p	1	n/p	0	0	0	3
3781	1	1	0	4	4	0	n/p	n/p	n/p	2	n/p	1	0	n/p	0	0	3
3782	3	1	3	2	2	2	2	2	n/p	1	1	1	1	1	0	0	3
3814	3	2	1	3	0	2	n/p	n/p	n/p	1	2	1	1	n/p	0	0	3
3859	1	0	0	4	4	0	n/p	n/p	n/p	2	n/p	1	0	n/p	0	0	3
3911	3	2	2	3	0	2	n/p	n/p	n/p	0	2	1	1	n/p	0	0	3
3973	1	0	0	4	4	0	n/p	n/p	n/p	2	n/p	1	0	n/p	0	0	3
4043	3	1	1	3	0	2	n/p	n/p	n/p	1	2	1	1	n/p	0	0	3
4127	1	0	0	4	4	0	n/p	n/p	n/p	2	n/p	1	0	n/p	0	0	3
4196	1	n/p	0	4	4	0	n/p	n/p	n/p	2	n/p	1	0	n/p	0	0	3
4212	n/p	n/p	1	3	0	n/p	n/p	n/p	n/p	1	2	1	1	n/p	0	0	3
4250	3	n/p	1	3	0	2	n/p	n/p	n/p	1	2	1	1	n/p	0	0	3
4279	1	0	0	4	4	0	0	0	n/p	2	n/p	1	0	0	0	0	3
4293	3	1	1	3	0	2	n/p	n/p	n/p	1	2	1	1	n/p	0	0	3
4297	3	1	2	3	0	2	n/p	n/p	n/p	0	2	1	1	n/p	0	0	3
4407	2	0	0	4	4	0	n/p	n/p	n/p	2	n/p	1	0	n/p	0	0	3
4457	3	2	3	2	2	2	2	2	n/p	1	1	1	1	1	0	0	3
4506	2	1	3	2	2	2	2	2	n/p	1	1	1	1	1	0	0	3
4545	2	n/p	0	4	4	0	0	0	n/p	2	0	1	0	0	0	0	3
4591	3	n/p	1	3	0	2	n/p	n/p	n/p	1	3	1	1	n/p	0	0	3
4628	3	2	1	3	0	2	n/p	n/p	n/p	1	3	1	1	n/p	0	0	3
4630	2	1	3	2	2	2	2	2	n/p	1	1	1	1	1	0	0	3
4884	3	2	1	3	0	2	n/p	n/p	n/p	1	2	1	1	n/p	0	0	3
4942	n/p	n/p	1	n/p	n/p	n/p	n/p	n/p	1	n/p	n/p	0	n/p	n/p	0	0	0
4943	3	n/p	3	1	1	2	2	2	1	0	n/p	1	1	1	0	0	3
4945	2	1	1	3	0	2	n/p	n/p	n/p	0	2	1	1	n/p	0	0	3
4947	1	0	0	4	4	0	0	0	n/p	2	n/p	1	0	0	0	0	3
4951	2	n/p	0	n/p	n/p	n/p	0	0	n/p	n/p	n/p	1	n/p	0	0	0	3
4952	2	1	2	3	0	2	n/p	n/p	n/p	0	2	1	1	n/p	0	0	3
4953	3	1	2	3	0	2	n/p	n/p	n/p	0	2	1	1	n/p	0	0	3
4959	n/p	n/p	0	4	4	0	n/p	n/p	n/p	2	n/p	1	0	n/p	0	0	3
4961	3	1	1	3	0	n/p	n/p	n/p	n/p	0	2	1	1	n/p	0	0	3
4963	n/p	1	3	2	2	n/p	n/p	n/p	n/p	1	1	1	n/p	n/p	0	0	3
5008	1	n/p	0	4	4	0	n/p	n/p	n/p	2	n/p	1	0	n/p	0	0	3
5015	n/p	n/p	1	n/p	n/p	n/p	n/p	n/p	1	n/p	n/p	0	n/p	n/p	0	0	0
5251	n/p	n/p	1	n/p	n/p	n/p	n/p	n/p	1	n/p	n/p	0	n/p	n/p	0	0	0
5261	1	n/p	3	1	1	2	n/p	n/p	n/p	0	n/p	1	1	1	0	0	3

APPENDIX U

Character scores for museum specimens of southern African rodents ≤ 5 kg (except Scuriomorpha). Scores based on character matrix created from this thesis.

Sub Family	Genus	Palatal Foramen (1)	Alveoli - Zygomatic (2)	t1 on M1 (3)	Position t1 - M1 (4)	Position t4 -M1 (5)	t9 on M1 (6)	t9 on M2 (7)	t3 on M2 (8)	M3 Development (9)	M1 CC or E (10)	Masseteric Knob (11)	Molar type (12)	t7 on m1 (13)	t7 on m2 (14)	# of Molars (15)	Re-entrent folds (16)	# of lamina on m3 (17)
Cricetomyinae	Cricetomys	0	0/1	1	3	0	2	2	2	1	0	0	1	2	2	0	0	3
Cricetomyinae	Saccostomys	0/1/2	0/1	1	3	1	2	2	2	1	0	0	1	2	2	0	0	3
Dendromurinae	Dendromus	2/3	0/1/2	1	3	0	2	2	2	0	1	2	1	1	1	0	0	3
Dendromurinae	Malacothrix	2/3	2	1	3	0	2	2	2	0	1	3	1	1	1	0	0	3
Dendromurinae	Steatomys	2/3	1/2	1/2	3	0	2	2	1/2	0	0	2	1	1	1	0	0	3
Deomyinae	Acomys	2	0/1	3	1	1	2	2	2	0/1	0	0	1	1	1	0	0	3
Gerbillinae	Desmodillus	0/1/2	0	0	4	4	0	0	0	0	2	0	1	0	0	0	0	3
Gerbillinae	Gerbilliscus	0/1/2	0/1	0	4	4	0	0	0	1	2	0	1	0	0	0	0	3
Gerbillinae	Gerbillurus	0/1/2	0	0	4	4	0	0	0	0/1	2	0	1	0	0	0	0	3
Murinae	Aethomys	2/3	0/1	3	1	1	2	2	2	1	0	0	1	1	1	0	0	3
Murinae	Dasymys	1	0/1	3	0/1	0/1	1	1	1	1	0	0	1	1	1	0	0	3
Murinae	Grammomys	1/2	0	3	1	1	2	2	2	1	0	0/1	1	1	1	0	0	3
Murinae	Lemniscomys	1/2	1	3	1	0/1	2	2	2	1	0	0/1	1	1	1	0	0	3
Murinae	Mastomys	2/3	1/2	3	1/2	1/2	2	2	2	0/1	0	0/1	1	1	1	0	0	3
Murinae	Micaelamys	2/3	0/1	3	0/1	0/1	2	2	2	1	0	0/1	1	1	1	0	0	3
Murinae	Mus	2/3	1/2	3	2	1/2	2	1/2	1/2	0	1	0/1	1	1	1	0	0	3
Murinae	Pelomys	1/2	0/1	3	0/1	0/1	1/2	1/2	2	1	0	0	1	1	1	0	0	3
Murinae	Rhabdomys	1/2	0/1	3	1/2	1/2	1/2	1/2	2	1	0	0	1	1	1	0	0	3
Murinae	Thallomys	2	0/1	3	0/1	0/1	2	2	2	1	0	0/1	1	1	1	0	0	3
Murinae	Zelotomys	2/3	1	3	1/2	1	2	2	2	0	0	0	1	1	1	0	0	3
Mystromyinae	Mystromys	3	1/2	0	4	4	0	0	0	0	2	0	1	0	0	0	1	3
Otomyinae	Myotomys	0/1	2	1	3	3	1	1	1	1	0	0	0	1	1	0	0	1
Otomyinae	Otomys	0/1	2	1	3	3	1	1	1	1	0	0	0	1	1	0	0	0
Otomyinae	Parotomys	0/1	2	1	3	3	1	1	1	1	0	0	0	1	1	0	0	2/3
Petromurinae	Petromus	3	2	0	4	4	0	0	0	1	2	0	1	0	0	1	0	3
Petromyscinae	Petromyscus	0/1	0/1	0	4	4	0	0	0	0	2	0	1	0	0	0	1	3

APPENDIX V

Molar presence/absence for fossil rodent specimen from Bone Cave. X indicates a tooth was present in the specimen.

SHSU ID	Genus/Genus group	M1	M2	M3
804	*Saccostomus*	X		
649		X	X	
4043	*Dendromus*	X		
4250		X		
144		X		
542		X	X	
2243		X		
4293		X		
4884		X		
2944		X		
4212		X		
613	*Malacothrix*	X	X	
3298		X	X	
3332		X		
4591		X		
4628		X		
3515		X		
3636		X		
2510		X		
2873		X		
3280		X	X	
3718		X	X	
3722		X		
3814		X		
836		X	X	
1535		X		
2241	*Malacothrix/Dendromus*	X		
3333	*Steatomys*	X		
4945		X		
398		X		
4297		X		
154		X	X	
155		X		
513		X		
4953		X		

SHSU ID	Genus/Genus group	M1	M2	M3
527	*Steatomys*	X		
3519		X		
3704		X		
3708		X	X	
3911		X		
4961		X		
18		X	X	X
112		X		
137		X		
138		X	X	X
139		X		
140		X		
145		X		
157		X		
160		X	X	
280		X		
456		X	X	
458		X		
479		X	X	
512		X		
523		X		
4952		X		
17		X		
405		X		
2776		X		
3733		X	X	
158	*Acomys*	X	X	X
159		X	X	X
15	*Gerbilliscus*	X		
40		X		
117		X		
236		X		
238		X		
241		X		
244		X		
1791		X		
2495		X		
2694		X		
2813		X		
3047		X		
3555		X		

SHSU ID	Genus/Genus group	M1	M2	M3
4545		X	X	
519	*Gerbilliscus*	X		
3222		X		
3571			X	
4951			X	
118		X		
237		X		
243		X		
272		X		
467		X		
475		X		
510		X		
522		X		
580		X		
612		X		
2773		X	X	X
2941		X	X	
3351		X	X	
3629		X		
5008		X		
242			X	
648		X		
2177		X	X	
2210			X	
3781		X		
3254			X	X
1961	*Gerbillurus/Desmodillus*	X	X	
2028		X	X	
2214		X		
2244		X		
2775		X		
4407		X	X	
651		X		X
681		X	X	
1948		X		
3052		X		
3973		X		
4127		X		
25		X		
3859		X	X	
2191			X	

SHSU ID	Genus/Genus group	M1	M2	M3
3631			X	
3721			X	
762	*Gerbillurus/Desmodillus*	X		
1962		X		
3727		X		
2443		X		
2475		X		
2774		X	X	X
3223		X	X	
3279		X		
128		X		
524		X		
682		X	X	
688		X	X	
1502		X		
2442		X		
4196		X	X	
4279		X	X	
4947		X		
4959		X	X	
3757			X	
689		X	X	X
2080		X	X	
8	*Lemniscomys*	X	X	X
521		X	X	X
4943		X	X	X
1651	*Mastomys, Micaelamys,* or *Rhabdomys*		X	
443			X	
240	*Micaelamys*	X		
406		X		
72	*Micaelamys, Thallomys,* or *Rhabdomys*	X	X	
1979	Murinae gen sp. indt.	X	X	X
136		X		
2027	Murinae gen sp. indt./Deomyinae gen sp. indt	X		
5261		X		
404		X		
1539		X		
1897		X	X	
1918		X	X	
239		X		
680		X		

SHSU ID	Genus/Genus group	M1	M2	M3
2527		X	X	
2237		X	X	
397		X		
1750	Murinae gen sp. indt./Deomyinae gen sp. indt		X	X
96	*Mus*	X		
113		X	X	
156		X		
511		X	X	X
2840		X	X	
3782		X	X	
4630		X	X	
1751		X	X	
1798		X	X	
2163		X	X	
2724		X	X	
2945		X	X	X
3264		X		
3715		X	X	X
3720		X		
4457		X	X	
4506		X	X	
273			X	
2236		X		
4963		X		
24	*Otomys*			X
134		X	X	X
4942				X
5015				X
3			X	X
543			X	X
549			X	X
5251				X
12	*Pelomys*	X	X	X
282	*Thallomys*	X	X	
110	*Grammomys, Thallomys,* or *Acomys*	X	X	
1833		X		
73	*Mystromys*	X	X	
614		X	X	X

VITA

Zachary W. Pierce
Sam Houston State University
Department of Biological Sciences
Huntsville, Texas 77341-2116

EDUCATION

Sam Houston State University
Master of Science in Biology (Department of Biological Sciences), January 2016- May 2019. Thesis Title: "Fossil rodents from Bone Cave locality, Botswana."
Committee Chair: Dr. Patrick J. Lewis
Committee Members: Dr. Jeffrey R. Wozniak and Dr. Monte L. Thies

University of Texas at San Antonio
Bachelor of Arts in Anthropology, May 2014 (College of Liberal and Fine Arts)

RESEARCH INTERESTS

Micromammals
Ecology
Taphonomy
Paleoanthropology

PROFESSIONAL EXPERIENCE

Sam Houston State University Department of Biological Sciences
Teaching Assistant
January 2016 – January 2018

Southwest National Primate Research Institute
Volunteer in the Primate Enrichment department
August 2013 – August 2014

COURSES TAUGHT

BIOL 1413 – Zoology, Spring 2016, Fall 2016, Fall 2017

BIOL 1401– Environmental Science, Spring 2017, Summer 2017

PUBLICATIONS

Bauer, A.M., Beach-Mehrotra, M., Bermudez, Y., Clark, G.E., Daza, J.D., Glynne, E., Hagyari, D., Harnden, J.M., Holovacs, N., Kanasiro, A., Lofthus, A.J., **Pierce, Z.W.,** Aaliyah, R., Syed, S., Vallejo-Pareja, M.C., Walker B.A. and Willett, J. 2018. The Tiny Skull of the Peruvian Gecko *Pseudogonatodes barbouri* (Gekkota: Sphaerodactylidae) Obtained via a Divide-And-Conquer Approach to Morphological Data Acquisition**.** South American Journal of Herpetology, 13(1), pp.102-116.

Campbell, T.L., **Pierce, Z.W.,** Dollman, K.N., Bamford, M.K., Musiba, C.M. and Magori, C. 2017. Syntopy and co-utilization of a "roosting area" by the barn owl (*Tyto alba*) and spotted eagle owl (*Bubo africanus*) in Tanzania. African Journal of Ecology.

PRESENTATIONS

Zachary W. Pierce. Fossil rodents from Bone Cave at the Koanaka Hills Locality, Botswana. Thesis defense, Sam Houston State University, Huntsville, Texas. 25 March 2020.

Zachary W. Pierce. Owl Vomit. Three-Minute Thesis Competition Final Round, Sam Houston State University, Huntsville, Texas. 4 April 2017

Zachary W. Pierce. Owl Vomit. Three-Minute Thesis Competition Preliminary Round, Sam Houston State University, Huntsville, Texas. 28 February 2017.

Zachary W. Pierce. A Primer on Salamander Territoriality. Sam Houston State University Herpetology Symposium, Sam Houston State University, Huntsville, Texas. 29 April 2016.

Zachary W. Pierce. Phylogenetic relationship of the Acacia Rat (Genus *Thallomys*). Sam Houston State University Principles of Systematics Symposium, Sam Houston State University, Huntsville, December 8, 2016.

Zachary W. Pierce, Timothy L. Campbell, Patrick J. Lewis. Using Microfauna to Reconstruct a Pleistocene Cave Site in Botswana. Texas Association of Biological Anthropologist, Austin, Texas. November 18-19, 2016.

Timothy L. Campbell, **Zachary W. Pierce**, Frank Senegas, Patrick J. Lewis. Analysis of skeletal part proportions of mammalian microvertebrates taken by barn owls (*Tyto abla*) in southern Africa. Texas Association of Biological Anthropologist, Austin, Texas. November 18-19, 2016.

Zachary W. Pierce, Justin Levy, Maria C. Vallejo-Pareja, and Patrick J. Lewis. 2016. A Reanalysis of Muskrat Taxonomy Using Morphological Characteristics of the First Molar. The Society of Vertebrate Paleontology, Salt Lake City, Utah. October 26-29, 2016.

MEETINGS ATTENDED

American Association of Physical Anthropologists – April 19-22, 2017. New Orleans, Louisiana

Texas Association of Biological Anthropologists – November 18-19, 2016. Austin, Texas

Society of Vertebrate Paleontology – October 26-29, 2016. Salt Lake City, Utah.

Texas Academy of Science – March 4-6, 2016. Junction, Texas

Texas Association of Biological Anthropologists – October 23-24, 2015. Lubbock, Texas

FIELD WORK

Push Creek, Texas
Director: Dr. Patrick J. Lewis
Survey and collect new fossils
June 2018

Driefontein, South Africa
Director: Dr. Patrick J. Lewis
Survey and collect new fossils
June- July 2017

Laetoli, Tanzania
Director: Dr. Charles Musiba
Collected owl pellets and disaggregated remains for analysis
June- July 2016

Olduvai Gorge, Tanzania
Director: Dr. Charles Egeland
Field school at sites PTK, BKE, and DK
June- July 2014

SOCIETIES

Paleoanthropology Society 2015-present
American Association of Physical Anthropology 2014-present
Biological Sciences Graduate Student Organization 2016-present
Society for Vertebrate Paleontology 2016-present
Texas Academy of Science, 2016- present
Travis County Archaeological Society, 2014-2015
Society for Conservation Biology, 2010

OUTREACH

Sam Houston State University 2016 Undergraduate Research Symposium, Moderator, Huntsville, TX. (23 April 2016)

Sam Houston Elementary School, presentation on dinosaurs to elementary school children. Huntsville, TX. (2 March 2016)

Sam Houston State University 2017 Undergraduate Research Symposium, Moderator, Huntsville, TX. (29 April 2017)

AWARDS AND ACHIEVEMENTS

Dean's List, University of Texas at San Antonio, Fall 2011, Summer 2013, Spring 2014.

Honor Roll, University of Texas at San Antonio, Fall 2012, Spring 2013, Fall 2014.

Sam Houston State University 3-minute thesis finalist