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A Systematic Review of the Soricimorph Eulipotyphla (Soricidae: Mammalia) from the Gray Fossil Site (Hemphillian), Tennessee

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A Systematic Review of the Soricimorph Eulipotyphla (Soricidae: Mammalia) from the Gray Fossil Site (Hemphillian), Tennessee

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presented to
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by
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ABSTRACT

A Systematic Review of the Soricimorph Eulipotyphla (Soricidae: Mammalia) from the Gray Fossil Site (Hemphillian), Tennessee

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Joshua R. Doby

Due in part to the incompleteness of the Cenozoic fossil record in the eastern U.S., the evolution and immigration of shrews (Soricidae) is not well understood. A rich soricid fauna from the Gray Fossil Site (GFS), Washington County, TN, has enabled many new inferences to be made. There are 7 new species in 6 genera: *Paenelimnoecus*, *"Blarinella", Petenyia, Tregosorex, Crusafontina,* and Gen et sp. nov. GFS species of the genera *Paenelimnoecus*, *"Blarinella",* and *Petenyia* are the first occurrence of each genus in the New World. *Tregosorex, Crusafontina,* and the N.A. taxon *Limnoecus* all have their latest documented occurrence at the GFS, extending their temporal range by at least 1 million years. "*Blarinella*" sp. nov. has a complete lateral groove in the inferior incisor, providing the earliest evidence for venom in soricids by at least 4 million years. GFS taxa also provide insight into the evolution of both Soricini and Blarinini.

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I would like to think the chair of my committee Dr. Steven (Wally) Wallace and my other committee members Dr. James Mead and Dr. Blaine Schubert for their support and guidance throughout this project. I would also like to thank: Shawn Haugrud for his work preparing the specimens used in this thesis and for discussions about the specimens, Sandy Swift for her work picking through the sediment and her initial identifications of the specimens as shrews, Brett Woodward for allowing me access to the specimens and providing them with new numbers when necessary, Dr. Joyner for his help with making a map, Dr. Rountre for access to specimens at the University of Michigan, and Dr. Reumer for his helpful comments about the systematics within the thesis. I would like to thank my fellow graduate students and Gray fossil Museum staff for all of their support during my time at ETSU. Finally, I would like to thank Connor Behrmann for his limitless patience and support over the last year of this project.

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Pictured is *Lunanosorex* with a view of the articular condyle. 90

LIST OF ABBREVIATIONS

ETMNH-East Tennessee State University Museum of Natural History Collection

UMMP-University of Michigan Museum of Paleontology

INSM-Indiana State Museum

UNSM-University of Nebraska State Museum

UW-University of Washington

UO-University of Oregon

IVPP-Institute of Vertebrate Paleontology and Paleoanthropology

WINE-Working group on Insectivores from the Neogene of Eurasia

M1-Upper first molar

m1-Lower first molar

M2-Upper second molar

m2-Lower second molar

M3-Upper third molar

m3-Lower third molar

P4-Upper fourth premolar

AA-Upper antemolar

I-Upper incisor

I sup-Superior incisor (Upper)

i-Lower incisor

I inf- Inferior incisor (Lower)

CHAPTER 1

INTRODUCTION

Background

Many early mammals have been considered 'Insectivora' at some point in their classification. The former, poorly defined group has been eliminated and most of the basal groups have been more appropriately placed. In particular, nyctitherids (large Antillean eulipotyphlan), erinaceids (hedgehogs), soricids (shrews) and talpids (moles) have been placed into the Order Eulipotyphla (MacPhee et al. 1993; Symonds 1999; Douady and Douzery 2003; Symonds 2004). Eulipotyphla diversified during the extinction event at the end of the Middle Eocene (Engesser, 1979; Rzebik-Kowalski 1998; Rossner and Heissig 1999; Douady et al. 2002). This extinction saw the end of many insectivorous groups: multituberculates, pleisiadapiforms and leptictids; allowing Eulipotyphla to thrive (Agusti and Anton 2002). Nyctitherids were the first group of Eulipotyphla; they originated in North America during the Paleocene, and by the Middle Eocene soricomorphs had evolved as well (Harris 1998; Rzebik-Kowalska 1998; Reumer 1998; Rzebik-Kowalska 2003).

It was during the Eocene a critical divergence in Soricomorpha occurred and two groups, the basal and now extinct Heterosoricidae and the more derived and extant Soricidae, originated (Reumer 1998). The level of classification of the two groups is still debated. Storch et al. (1998) actively refutes the familial level of Heterosoricidae and Soricidae and insists that the subfamilial placement from Repenning (1967) be kept. This thesis agrees with and uses the familial identifications, Heterosoricidae and Soricidae, proposed by Reumer (1998) because having the two taxa as sister subfamilies make the entire group (in this case "Soricidae") polyphyletic (Reumer 1998; Rzebik-Kowalska 1998). Other than the use of the heterosoricid *Domnina* as the outgroup in the phylogenetic analysis and the discussion that comes with it, heterosoricids and their relationships to soricids will not be discussed here because it is outside the scope of this project.

Soricid Fossil Record

European

Significantly more is known about eulipotyphlan evolution in Europe due to the well-studied fossil record. There is a group of paleontologists whose goal is solely to study the soricid fossil record. The group is called Working group on Insectivores from the Neogene of Eurasia (WINE) and every few years they put out a total overview of all of the fossil soricids in a region (Hoek Ostende et al. 2005a). These publications include a volume in 2001 and more recently in 2005 (Hoek Ostende 2001; Hoek Ostende et al. 2005b; Fejfar and Sabol 2005).

Asian

Qui and Storch saw the necessity of studying Asian microfossils and wrote a number of publications describing numerous new species of small extinct mammals (Storch and Qui 1991; Storch and Qui 1995; Qui and Storch 2000; Qui and Storch 2005). Beginning in 1983 with the faunas of Ertemte and Harr Obo in Mongolia, Qui and Storch began collecting, identifying, and compiling insectivoran remains (Storch and Qui 1983). By 2005 the two had written a combined 16 papers on Chinese and Mongolian insectivoran faunas (see Qui and Storch 2005 and citations therein). Prior to Qui and Storch (1983) only a handful of papers had been published on fossil insectivorans, and even less on soricids. Microfossils have been overlooked at most localities for over 30 years (Kowalski and Li 1963; Storch and Qui 2005). Storch et al. (1998) and Storch and Qui (2005) summarize the known Asian soricid fossil record.

North American

There has been no large scale assessment of fossil North American soricids since Repenning (1967). From 1967 to present a number of new soricid faunas have been disparately published. Hibbard and Bjork (1971) described the Hagerman (Upper Pliocene of Idaho) soricids, and that same year Hibbard and Jammot (1971) published on the soricids of the WaKeeney fauna (Lower Pliocene of Kansas). The following year Dalquest (1972) described a new genus and species (*Beckiasorex hibbardi*) from the Upper Pliocene of Texas. Bown (1980) describes the most diverse Hemphillian soricid fauna from the Great Plains (latest Miocene/ earliest Pliocene, Lemoyne Quarry, Keith Co. Nebraska). Voorhies (1990) created a faunal list of all Upper Cenozoic sites within Nebraska. The only known, frugivorous shrew was described, *Arctisorex polaris,* in Hutchison and Harington (2002), which is also the most northern found shrew taxon, extant or fossil. Most recently Czaplewski (2012) published on two specimens of *Sorex* found in Indiana at the Pipe Creek Sinkhole (Latest Hemphillian). There are two reviews of American Eulipotyphla, Gunnell et al. (2007), a chapter in *Evolution of Tertiary Mammals of North America Volume 2* and Harris (1998). Harris (1998) is older, but takes into consideration Eurasian taxa when analyzing systematic placement.

The Gray Fossil Site (GFS), TN, is the first site older than Pleistocene in eastern North America to yield more than one taxon of soricid. This extremely well- preserved fauna is crucial in understanding global soricid evolution. Here, the taxa from GFS are identified and their evolutionary affinities are discussed along with their influences on the understanding of Eurasian faunas. Meticulous screening and picking of fossils from the GFS sediment, following Hibbard (1949), has yielded over 30 soricid fossils; including a large number of morphotypes. Considering the rarity of identifiable soricid fossils and their significance in everything from biochronology to evolution, biogeography, metabolism and paleoecology, a systematic review of an eastern North American soricid fauna will prove invaluable across fields (Reumer 1989; Peltonen and Hanski 1991; Harris 1998; Woodburne 2004; Hoek Ostende et al. 2005; Peigne et al. 2009).

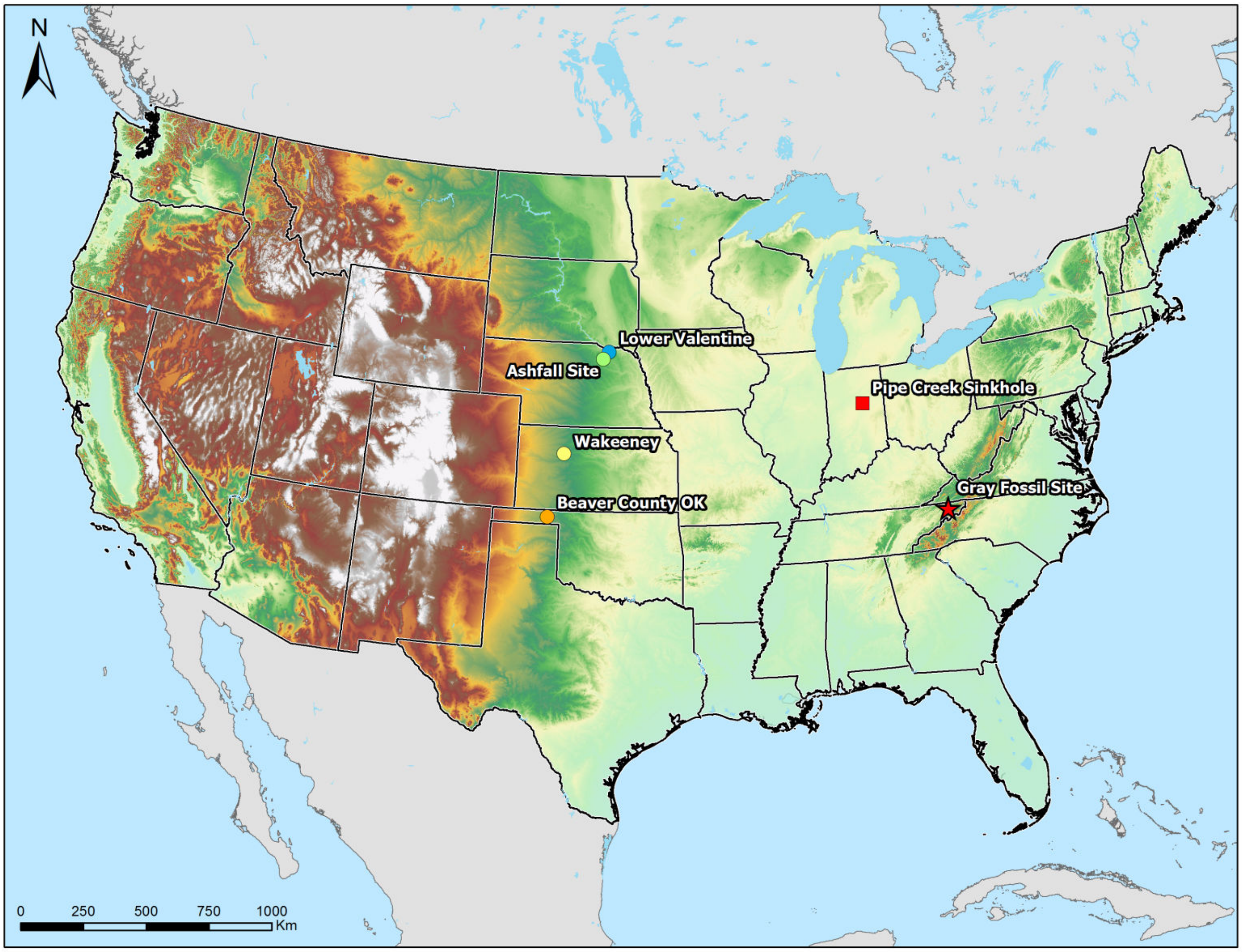

Figure 1. United States with location of the Gray Fossil Site, TN, and the Pipe Creek Sinkhole, IN; the two Neogene localities in the eastern (as defined by the Mississippi River) United States with soricid fossils. Lower Valentine, Ashfall Fossil Beds State Historical Park, WaKeeney, and Beaver County are Midwestern fossil sites contemporary with the Gray Fossil Site.

CHAPTER 2

MATERIALS AND METHODS

Methods of Differential Diagnosis

There are over 250 named shrew species in about 75 genera (Wolsan and Wojcik 1998). The large number of genera makes understanding evolutionary relationships difficult because of the seemingly arbitrary splits between taxa. Early paleontologists created numerous new genera due to the vast gaps in the fossil record and the limited number of individuals from each species. More recent paleontologists divide genera based on locality, making the assumption that if it is on a different continent it is a different genus. This paper follows the method of discernment described in Bell et al. (2010) which strongly recommends the use of apomorphies. Apomorphies are divided into two categories by Badyaev and Foresman (2000), integrated and non-integrated traits. Integrated traits are codependent on other morphological traits in order to carry out their function; while non-integrated traits are independent. According to Badyaev and Foresman (2000) and Young (2008) the quantitative genetics theory states that integrated morphological features will evolve in concert with the other features to carry out a particular function; while non-integrated features evolve independently. This difference in the rate of evolution should allow for the differentiation of an apomorphy for the designation of a species and a synapomorphy for the designation of a genus or higher level of organization.

An experiment by Badyaev and Foresman (2004) looked at which characters were integrated, and which were not, by measuring changes in jaw morphology after shrews were put under high stress (Figure 2). A population of shrews had their ground cover stripped and then members of the population were captured and their mandibles measured (Badyaev and Foresman 2004). Figure 2 shows the integrated structures highlighted in gray; these are the features that should stay conservative within a genus along with the teeth. If there is an adaptation in one of the features it should be reflected across multiple features to maintain the functionality. Landmarks 2, 3, 10, 11, 12, 13, 16, and 17 are highly plastic and can vary slightly in individuals within a single species (Badyaev and Foresman 2004; Badyaev and Young 2006). Because there is variation in the amount of individual variation from species to species (Badyaev and Foresman 2004), it is best to avoid using morphological differences in the areas of landmarks 2, 3,10, 11, 12, 13, 16, and 17 as apomorphies unless there are significant differences in multiple areas. Size and changes due to robustness should not be considered significant differences. Changes in the teeth, or in one of the integrated areas, represent a more definitive apomorphy. Changes in multiple integrated areas, or in multiple changes in the teeth, should be viewed as a synapomorphy due to the substantial selective pressure needed to force these changes.

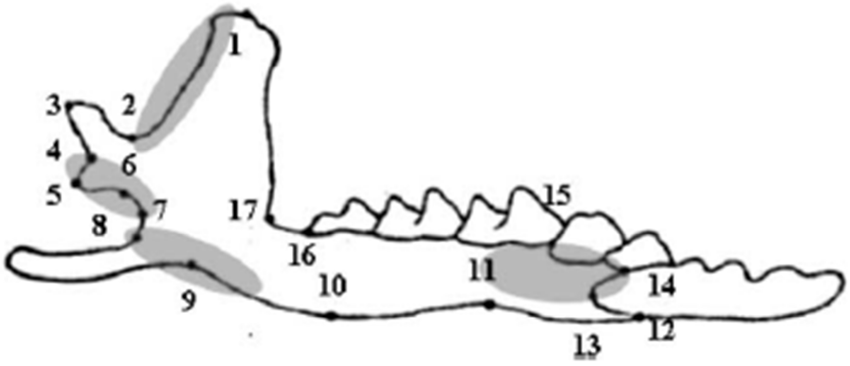

Figure 2. *Sorex* mandible with functionally integrated regions shaded. Numbers 1-17 are the landmarks used by Badyaev and Foresman (2004) to test which parts of the mandible were integrated and non-integrated. Modified from Badyaev and Foresman (2004).

Morphology

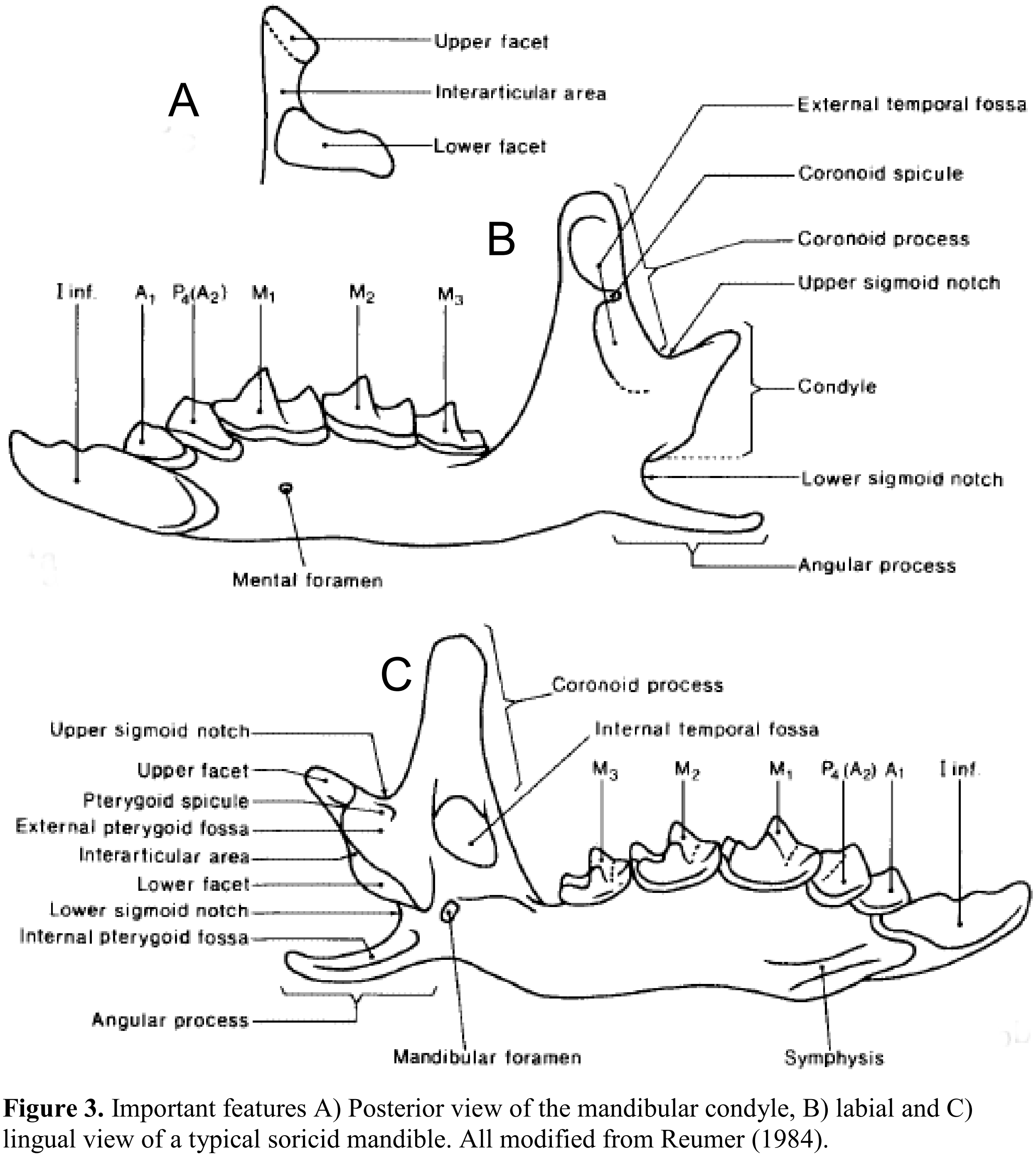

Figure 3. Important features A) Posterior view of the mandibular condyle, B) labial and C) lingual view of a typical soricid mandible. All modified from Reumer (1984).

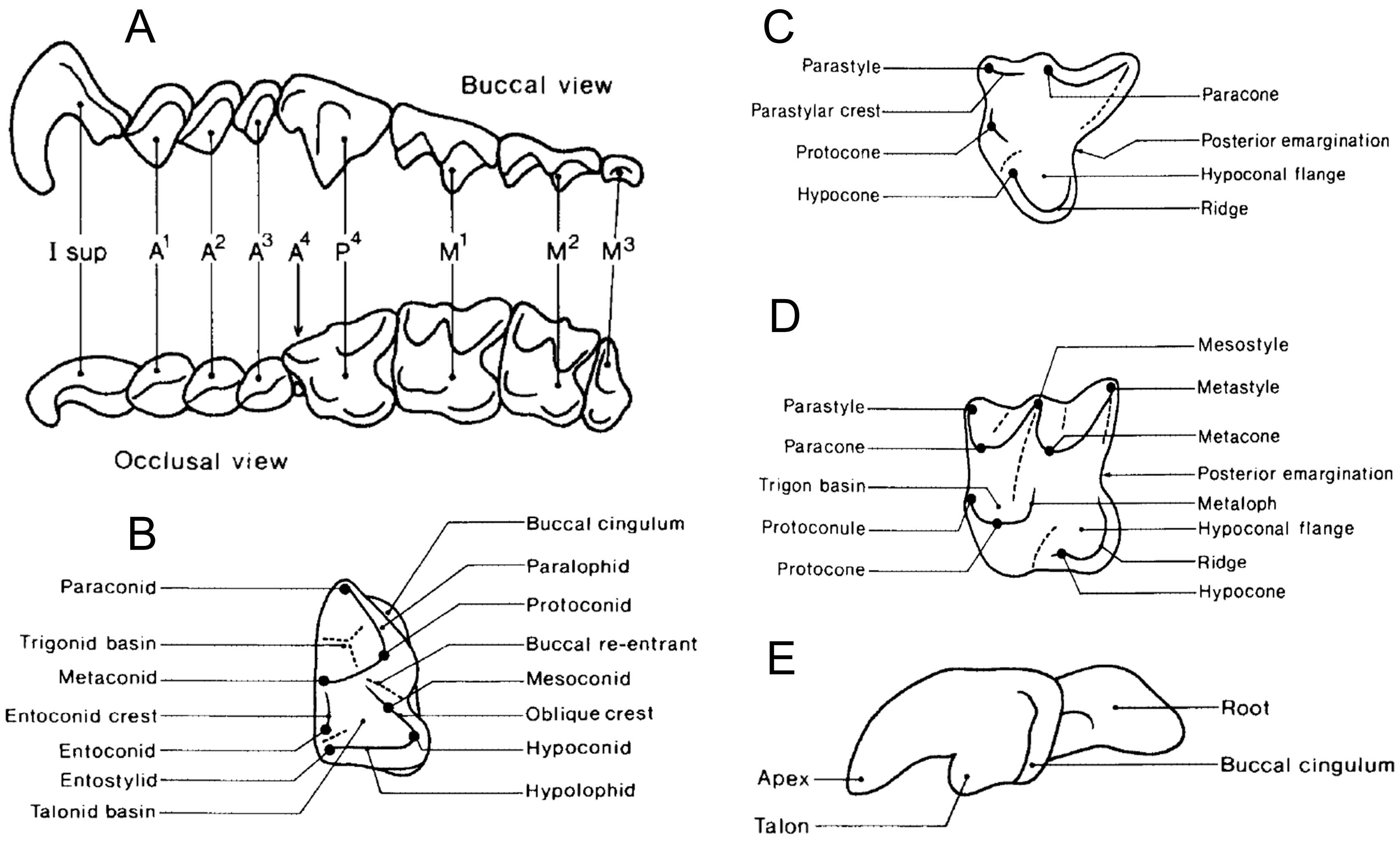

Figure 4. Important features of the A) upper dentition of a soricid in a lingual and occlusal view. B) Occlusal view of lower m1/m2. C) Occlusal view of upper 4rth premolar. D) Occlusal view of the upper M1/M2. E) Features of the superior incisor. All modified from Reumer (1984).

Locality (Gray Fossil Site)

North American soricid evolution is poorly understood due to the lack of described fossil evidence and unrevised mid-20th century publications. Eurasian soricids have been well studied (Reumer 1998; Rzebik-Kowalski 2003; Qui and Storch 2005), but without data from the Western Hemisphere a complete understanding of soricid evolution is impossible. An exquisitely preserved soricid fauna from the Gray Fossil Site (GFS), TN, provides a critical perspective that aids in the elucidation of their complex evolutionary history. The GFS is unique among North American sites of similar age in that it is the only Neogene site in the Appalachians and is one of only two Neogene sites in eastern North America that are not coastal, the other being Pipe Creek (Wallace and Wang 2004; Czaplewski 2013).

Both the macrofossil and pollen records are well preserved at GFS. A number of plant taxa have been identified. *Quercus* (oak), *Pinus* (pine), *Carya* (hickory), Asteraceae (composites), *Betula* (birch), *Tsuga* (hemlock), *Juglans* (walnut), Apiaceae (parsley), *Ambrosia* (ragweed), *Abies* (fir), *Taxus* (yew), Onagraceae (primrose), *Ulmus* (elm), *Viburnum*, *Ilex vomitaria* (southeastern holly), *Fraxinus* (lilac), *Euphorbia* (spurge), *Xanthium* (cocklebur), *Tilia* (lime trees), Malvaceae (mallows), and *Rhus* (sumac); all contain native North American species (Gong et al. 2010; Ochoa et al. 2012; Baumgartner 2014), many of which still live in the southeastern United States. Some like Malvaceae, which contain cotton, cacao, and hibiscus, are much more prevalent in tropical Central and South America. Ochoa et al. (2012) show findings of a woodland with 90% oak, hickory, and pine and they compare the assemblage to many others and found the analog to be the warmer and drier regions in North America. Baumgartner (2014) found the Hemphillian climate of the GFS to be similar to present day coastal South Carolina using the Coexistence Approach from Mosbrugger and Utescher (1997). Using coastal South

Carolina as a modern analogue is further supported by the presence of *Alligator*, which needs a minimum average temperature no colder than 22˚C (Markwick 1998).

Many plants and animals, which are found exclusively in Asia today are present at the GFS. *Pterocarya* (wingnut), found at the GFS (Ochoa et al. 2012), is a genus closely related to North American *Juglans*, but are now restricted to a few species in Asia (Ochoa et al. 2012). This trend is seen again in the genus *Vitis* (grape), which has extant species in both North America and Asia, but none currently living in Europe (Gong et al. 2010). *Vitis* has a substantial fossil record stretching back to the Paleocene and has a range containing the entire North Hemisphere until the late Cenozoic (Gong et al. 2010), probably into the Pliocene. Three new species of *Vitis* have been described from the GFS, *V. grayensis, V. lanatoides,* and *V. latisulcata*, of which only *V. latisulcata* is closely related to North American taxa (Gong et al. 2010). *Vitis grayensis* and *V. lanatoides* are more closely related to modern Asian and extinct Eurasian taxa (Gong et al. 2010). The first substantiated North American occurrence of the large woody vine *Simomenium* is another example of an exclusively Eurasian taxon present at the GFS (Liu and Jacques 2010). The numerous species of Eurasian plant taxa found at the GFS provides overwhelming evidence for the American-Asian disjunct distribution hypothesis that has been discussed since Gray (1878). The GFS is unique in that it is the latest known North American site of many shared Eurasian taxa.

By the Hemphillian the fauna at the Pipe Creek sinkhole had already begun exhibiting the effects of aridification (Farlow et al. 2001). Based on the fauna, the environment was dry and prairie-like with nearby trees (Farlow et al. 2001), similar to that of the Clarendonian of Kansas, Nebraska, and Texas (Wilson 1968). At the same time sites such as Palmetto Florida, on the Gulf Coast, were experiencing far wetter climates (Shunk et al. 2006), similar to the tropics.

While the GFS was experiencing a climate more similar to the one in Csakar, Hungry was experiencing as described in Meszaros (2000) with lush forests.

CHAPTER 3

SYSTEMATIC PALEONTOLOGY

Order Eulipotyphla

Family Soricidae, Gray, 1821

Soricidae is characterized by the absence of a zygomatic arch, the internal temporal fossa is deeply pocketed and the mandibular condyle is separated dorsoventrally (Reumer 1998). Soricid crania with zygomatic regions are not available from the Gray Fossil Site, but all specimens found with a preserved mandible have a deeply pocketed internal temporal fossa and a mandibular condyle that is separated dorsoventrally. Based on these two characters all of the following taxa being described belong to the family Soricidae (Repenning 1967).

Subfamily Allosoricinae Fejfar, 1966

Allosoricinae is characterized by having a short interarticular area of the mandibular condyle and a triangular upper facet. It also has a vestigial, or absent, entoconid and/or entoconid crest, so that the hypolophid is ended in the entostylid (synapomorphy). The metaconid is low and close to the protoconid, while the paralophid is long and nearly parallel to the longitudinal axis of the dentary, resembling a carnassial blade especially in the m1 (Reumer 1984).

The GFS specimen ETMNH 11029 exhibits the vestigial entoconid and entoconid crest (Figure 5) and the hypolophid ends in the entostylid. Presence of this synapomorphy places ETMNH 11029 into the subfamily Allosoricinae (Reumer 1992).

Paenelimnoecus Baudelot, 1972

ETMNH 11029 lacks the long paralophid that resembles a carnassial blade; absence of this character places the specimen in the genus *Paenelimnoecus* rather than *Allosorex* the only other genus in the subfamily (Baudelot 1972; Engesser 1979).

There are 5 species of *Paenelimnoecus* in Europe spanning the early Miocene to the late Pliocene, they include: *Paenelimnoecus micromorphus* from the early Miocene, *P. truyolsi* from the middle Miocene (Hoek Ostende et al. 2009), *P. crouzeli* from the middle Miocene*, P. repenningi* from the late Miocene, and *P. pannonicus* from the early Pliocene (Reumer 1992; Rzebik-Kowalska 1998) and 2 from China, *P. obtusus* from the Miocene (Storch 1995) and *P. chinensis* from the early Pliocene (Jin and Kawamura 1997). For this paper, *Paenelimnoecus* will remain in Allosoricinae, however a few possibilities of alternative taxonomic allocations will be discussed.

Paenelimnoecus sp. nov.

Holotype: ETMNH 11029, ascending ramus with m2 and m3 (Figure 5).

Differential Diagnosis: Based on the presence of a remnant entoconid, ETMNH 11029 can be differentiated from *Paenelimnoecus pannonicus* which has no sign of a remnant entoconid. *Paenelimnoecus crouzeli* has a similar ridge running the length of the ascending ramus (Figure 5), but has a distinctively reduced articular condyle not present in the GFS form. *Paenelimnoecus obtusus* differs from *P.* sp. nov. in that is has a very distinctive coronoid process that leans dramatically forward. *Paenelimnoecus truyolsi* has a mesoconid that abuts the trigonid causing the oblique crest to end abruptly, whereas, *P.* sp. nov. the oblique crest that instead forms a U-shaped talonid basin (Figure 5).

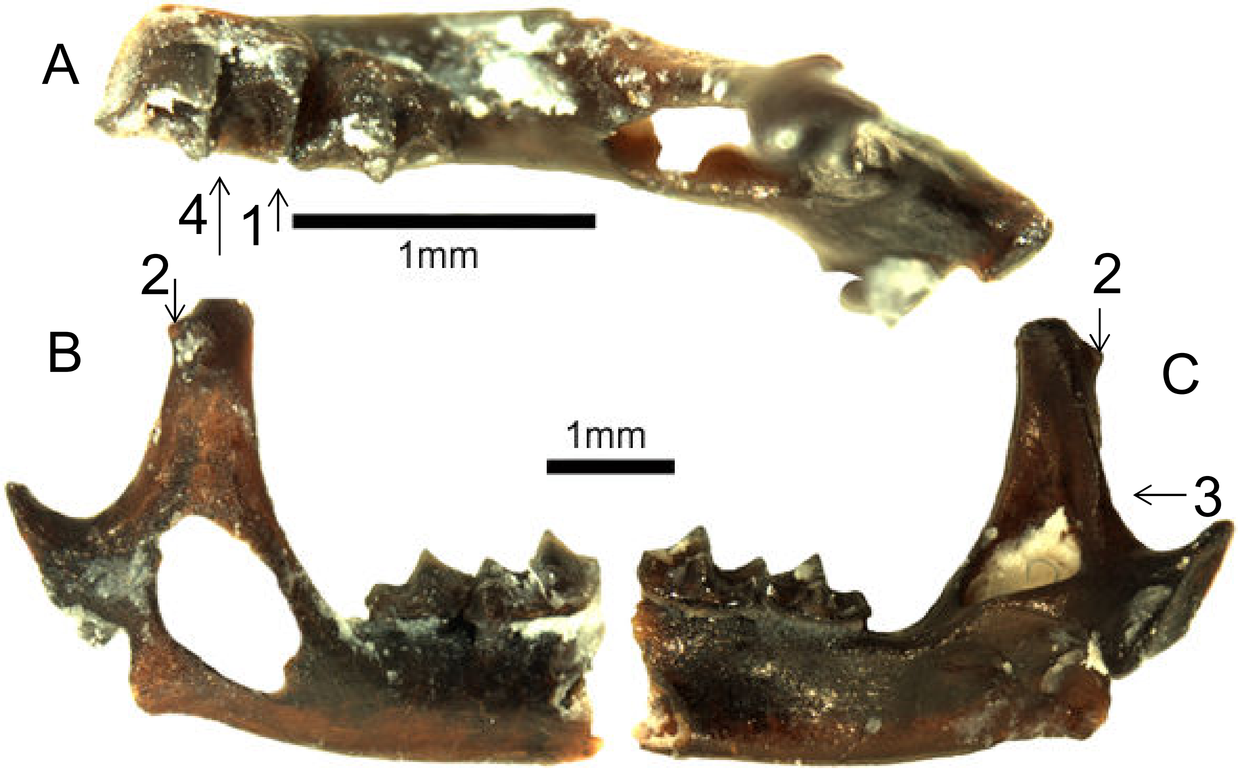

Figure 5. Characters of holotype of *Paenelimnoecus* sp. nov. ETMNH 11029, A) occlusal, B) labial, C) lingual. 1) lack of an entoconid and the hypolophid extending lingually to a point, 2) projection present distally on the coronoid process, 3) raised ridge extending the length of the ascending ramus causing a depression in the dorsal portion of the internal temporal fossa. *Paenelimnoecus truyolsi* has a mesoconid that abuts the trigonid causing the oblique crest to end abruptly, whereas, *P.* sp. nov. the oblique crest that instead forms a 4) U-shaped talonid basin.

Subfamily Limnoecinae Repenning, 1967

Limnoecinae is characterized by a lingually displaced lower facet of the articular condyle (Figure 6), p4 with little or no lingual segment or posteriolingual ridge of basal triangular cusp, labial shearing blade is not developed, posteriolingual basin little or not developed and the talonid basis in lost through emphasis of metalophid by the late Miocene (Repenning 1967).

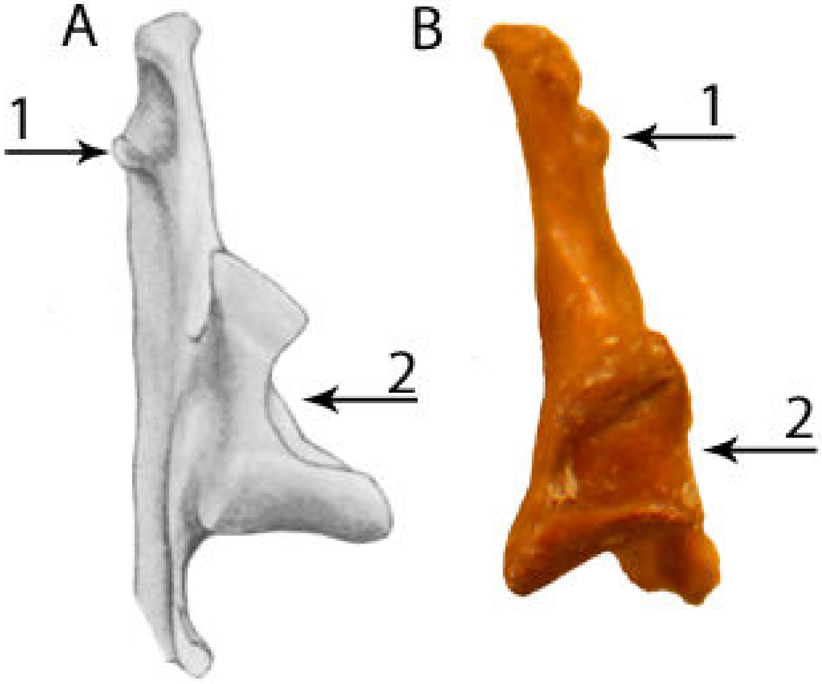

Figure 6. Two taxa showing the difference in labial and lingual dispacements of the lower facet. A) *Crusafontina minimus* has the typical labially displaced lower facet, evident by the 1) coronoid spicule being on the opposite side of the 2) opening of the articular condyle (Modified from Bown 1980). B) ETMNH 9724 has a lingually displaced lower facet indicative of the Limnoecinae, which is seen by the 1) coronoid spicule being on the same side of the 2) opening of the articular condyle.

Limnoecus Stirton, 1930

Limnoecus sp. indet**.**

Limnoecus is characterized by p4 with posteriolingual crest of basal triangular p4 forming medial crest which hooks lingually where it merges with posterior cingulum, posterior crest nearly or entirely lost; reentrant valley between hypoconid and protoconid of m1 emerges on labial face well above the cingulum; talonid of m3 reduced to trenchant heel formed by posteriorly directed metalophid and hypoconid and talonid basin is virtually lost except for a trace of the entoconid crest (Repenning 1967).

Referred specimen: ETMNH 9724 Ascending ramus with fragment of m2. (Figure 6 and 7)

Differential Diagnosis: There are 3 species of Limnoecinae, all in North America, in 2 genera: *Angustidens vireti* from the late Arikareean, *Limnoecus niobrarensis* from the Barstovian and *Limnoecus tricuspus* from the Barstovian to the Hemphillian (Stirton 1930; Repenning 1967; Harris 1998; Rzebik-Kowalska 2003). Unfortunately the specimen from the GFS only has half of a tooth so dental features are limited. The ascending ramus is very different than that of *Limnoecus niobrarensis*, with ETMNH 9724 exhibiting a much more robust ascending ramus that leans back and as a result is closer to the articular condyle. The condyle of ETMNH 9724 is larger and the interarticular area is wider. There is a distinctive projection on the back of the coronoid process that appears to be for extra muscular attachment on ETMNH 9724. A large coronoid spicule is present on ETMNH 9724 which is extremely reduced on *Limnoecus niobrarensis*. Unfortunately there is no complete coronoid process or articular condyle from *Limnoecus tricuspus* so it not possible at this point to tell if the GFS specimen is *Limnoecus niobrarensis*, *L. tricuspus*, or a new species.

Figure 7. Referred specimen *Limnoecus* sp. ETMNH 9724 in lingual view. 1) Diagnostic lingually displaced lower facet. 2) A large projection on the coronoid and 3) the enlargement of the coronoid could later be used as apomorphies if a complete coronoid is found for *Limnoecus tricuspus*. The features are very different than those seen on *L. niobrarensis* which has the typical rounded coronoid.

Subfamily Soricinae Fischer von Waldheim, 1817

All of the soricid specimens from the GFS, with the exception of two, belong to the subfamily Soricinae: this is supported by several features: by the condyle, which has two articular facets; by the interarticular area, which is lingualy emarginated; and by the presence of an entoconid (Repenning 1967, Reumer 1984, Reumer 1998).

Tribe Blarinellini Reumer, 1998

Tregosorex Hibbard and Jammot, 1971

Tregosorex sp. nov.

Holotype: ETMNH 8411, right mandible with m1, m2 and m3. (Figure 8)

Referred specimen: ETMNH 9726, left P4. (Figure 9)

Differential Diagnosis: Due to the reduced coronoid process and the extremely enlarged and deepened inter-temporal fossa, *Tregosorex* is an extremely diagnostic genus and is not easily confused with anything else. The squat acuspulate incisor, reduction of the coronoid, deep rugose internal temporal fossa, robustness of the horizontal ramus, and the twisted articular condyle are all distinctly characteristic of the genus. *Tregosorex* sp. nov. differs from *T. holmani* in the enlarged articular condyle, more greatly reduced coronoid process, the deeper internal temporal fossa and higher entoconid crest.

Discussion: There are at least 3 million years between the only currently named species in *Tregosorex* and the GFS species, and yet the cheek teeth and even the less conservative inferior incisors are nearly unchanged, while the coronoid and internal temporal fossa are distinctly different. Both differences can be explained by a single shift in musculature, a reduction in the temporalis. The temporalis is the main muscle used in crushing prey (Young 2008), so the reduction likely started after a new feeding method was adapted earlier in the genus's history.

No upper dentition has yet been associated with the genus *Tregosorex*. ETMNH 9726 has been associated with ETMNH 8411because of its derived loss of the hypocone and protocone. An analogous P4 is seen in *Suncus murinus*. *Suncus murinus* is clearly adapted for predation; the P4 is extremely carnassial-form and the first antemolars and sup. incisors are extremely caniniform. *Tregosorex* sp. nov. and *Suncus murinus* both exhibit the acuspulate incisor.

Tribal Affiliation

Reumer (1998) attempts to classify *Tregosorex,* but struggles due to figures in Hibbard and Jammot (1971) that contradict the description. Hibbard and Jammot (1971) allude to an entoconid crest by stating that the entoconid and metaconid are joined, but Reumer (1998) tentatively placed *Tregosorex* into Blarinini based on the lack of an entoconid crest in the figure. Reumer stated that if it turned out to have an entoconid crest *Tregosorex* may belong to Blarinellini, but an analysis of the holotype has shown that it does have an entoconid crest (Figure 10). The GFS contains well preserved specimens of multiple members of Blarinellini and a well preserved specimen of *Tregosorex.* From comparisons made, it is evident that the m1 and m2 of *Tregosorex* are nearly identical to "*Blarinella"* except for a shorter entoconid crest, a slightly longer talonid basin, a slightly higher paraconid, and the entoconid and metaconid are closer together in *Tregosorex*. *Tregosorex* differs from *Petenyia* in that the molars in *Petenyia* have the more elongated W pattern. Based on the presence of the entoconid crest it is clear that *Tregosorex* belongs to the tribe Blarinellini and is a close sister taxon to "*Blarinella*" (Figure 8).

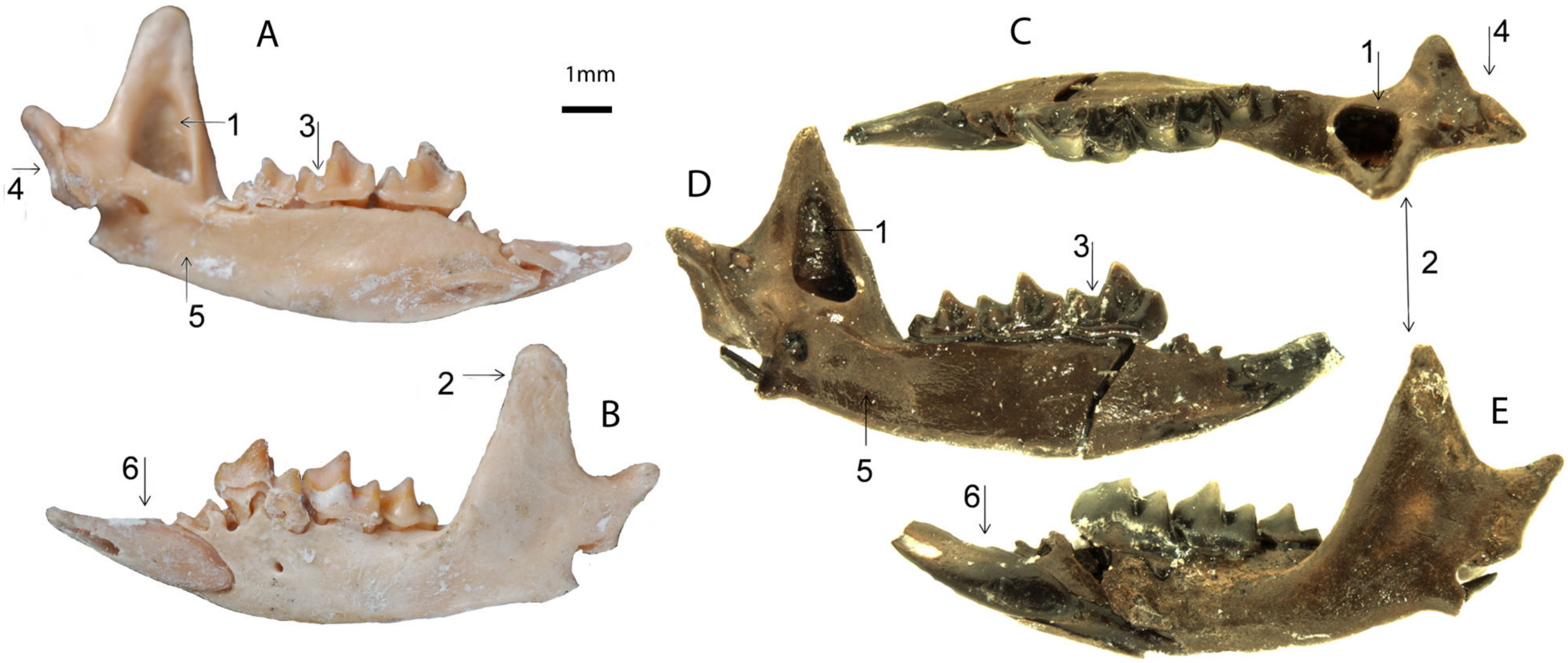

Figure 8. *Tregosorex holmani* UMMP 0604445 from the Clarendonian of Kansas compared with the holotype of *Tregosorex* sp. nov. ETMNH 8411, A) occlusal view of *T. holmani* , B) lingual view of *T. holmani*, C) Occlusal view of *Tregosorex* sp. nov. D) lingual view of *T.* sp. nov. E) labial view of *T.* sp. nov.. 1) Deep and dorsally elongated internal temporal fossa, deeper in *T.* sp. nov. 2) coronoid process is reduced and comes to a point, 3) entoconid crest of *T.* sp. nov. slightly higher than that of *T. holmani*, 4) slight lingual twisting in the articular condyle on *T.* sp. nov., but not *T holmani*, 5) fossa at the junction of the horizontal and ascending ramus, 6) acuspulate incisor.

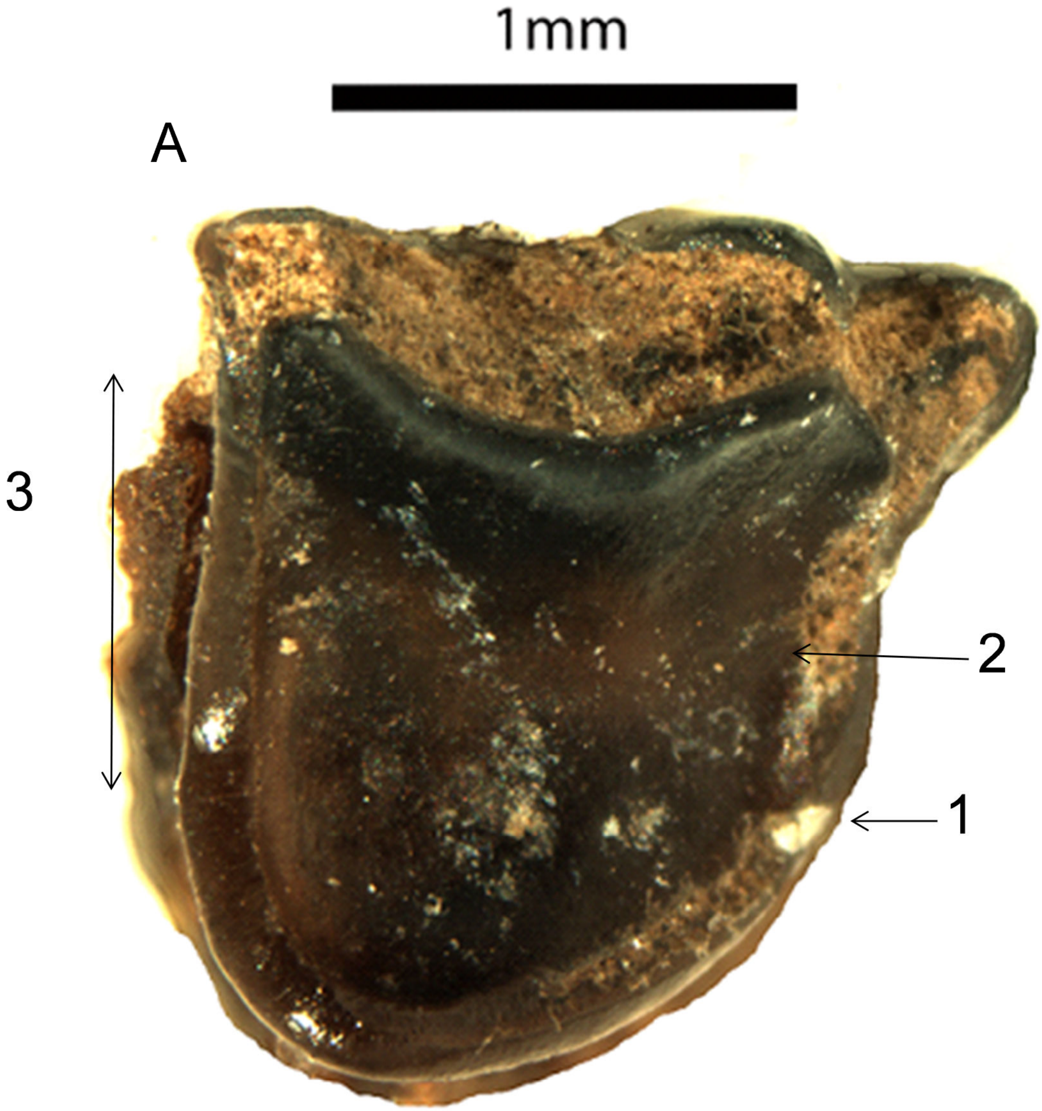

Figure 9. Referred specimen *Tregosorex* sp. nov. ETMNH 9726, A) occlusal view of upper fourth premolar. The reduction of the 1) hypocone and 2) protocone is similar to that seen in more carnivorous soricids. 3) The very slight lingual emargination is characteristic of the tribe Blarinellini which agrees with the diagnosis from the lower dentition.

Petenyia Kormos, 1934

Petenyia sp. nov.

Holotype: ETMNH 17661 left mandible with m1- m3.

Referred specimens: ETMNH 9566 right mandible with m2 and m3; ETMNH 9720 left mandible with m1, m2, and m3; and right mandible with m1, m2, and m3, ETMNH 12295, M1 and M2. The upper dentition is absent so the important differentiation based on the number of antemolars is impossible to make, but the series of other characters suffice for an accurate identification.

Differential Diagnosis: ETMNH 17661shares many basal traits with members of Anourosoricini, but the non-reduced m3 and the broad interarticular area of the condyle are a clear indication that it belongs instead to Blarinellini.

Table 1 Differences Between *“Blarinella”* and *Petenyia.* From Reumer (1984)

Petenyia	*“Blarinella”*
Pigmentation moderate to strong	Pigmentation extremely strong
Superior incisor and Inferior incisor with pointed apex	Superior incisor and Inferior incisor with spatulate apex
Inferior incisor with nearly straight ventral border of the apex	I Inferior incisor with S-curved ventral border in unworn
4 upper antemolars	5 upper antemolars
Coronoid spicule in center of external temporal fossa	Coronoid spicule above center of external temporal fossa
Internal temporal fossa without horizontal bar	Internal temporal fossa with a horizontal bar
Lower molars less quadrate	Lower molars more quadrate
Lower molars with elongated W-pattern (less sharp angles between lophids)	Lower molars with compressed W-pattern (sharp angles between lophids)
Entoconid crests moderately high	Entoconid crests extremely high

Zelceina and *Petenyia* are very similar, both have a reduced talonid on the m3, slight posterior emargination of the upper molars, a bicuspulate inf. incisor and 4 upper antemolars (Reumer 1984). Due to the limited material and how basal the lower dentition is within members of the *Petenyia-Zelceina* complex both genera are pictured with similarities and differences highlighted (Figure 10). Direct observation has shown the differences between the two genera are also clear in the lower teeth and mandible. The entoconid and metaconid are closer together in *Zelceina* than in *Petenyia*. The internal temporal fossa is lower, wider and more round in *Petenyia* and there is an elongation of the “heel” below the intersection of the ascending and horizontal rami in *Zelceina*.

Reumer (1984) sunk all but one species of *Petenyia, P. hungarica* and in Qui and Storch (2000) a Chinese species, *P. katrinae* was erected. *Petenyia* sp. nov. differs from *P. hungarica* by having a reduced coronoid, reduced coronoid spicule, a shelf on the lingual side below the m3, much more space between the ascending ramus and the m3 and a lower internal temporal fossa. *Petenyia* sp. nov. differs from *P. katrinae* in having a more gracile coronoid process and coronoid spicule and a more narrow and elongated interarticular area of the condyle and an upper facet that is not round.

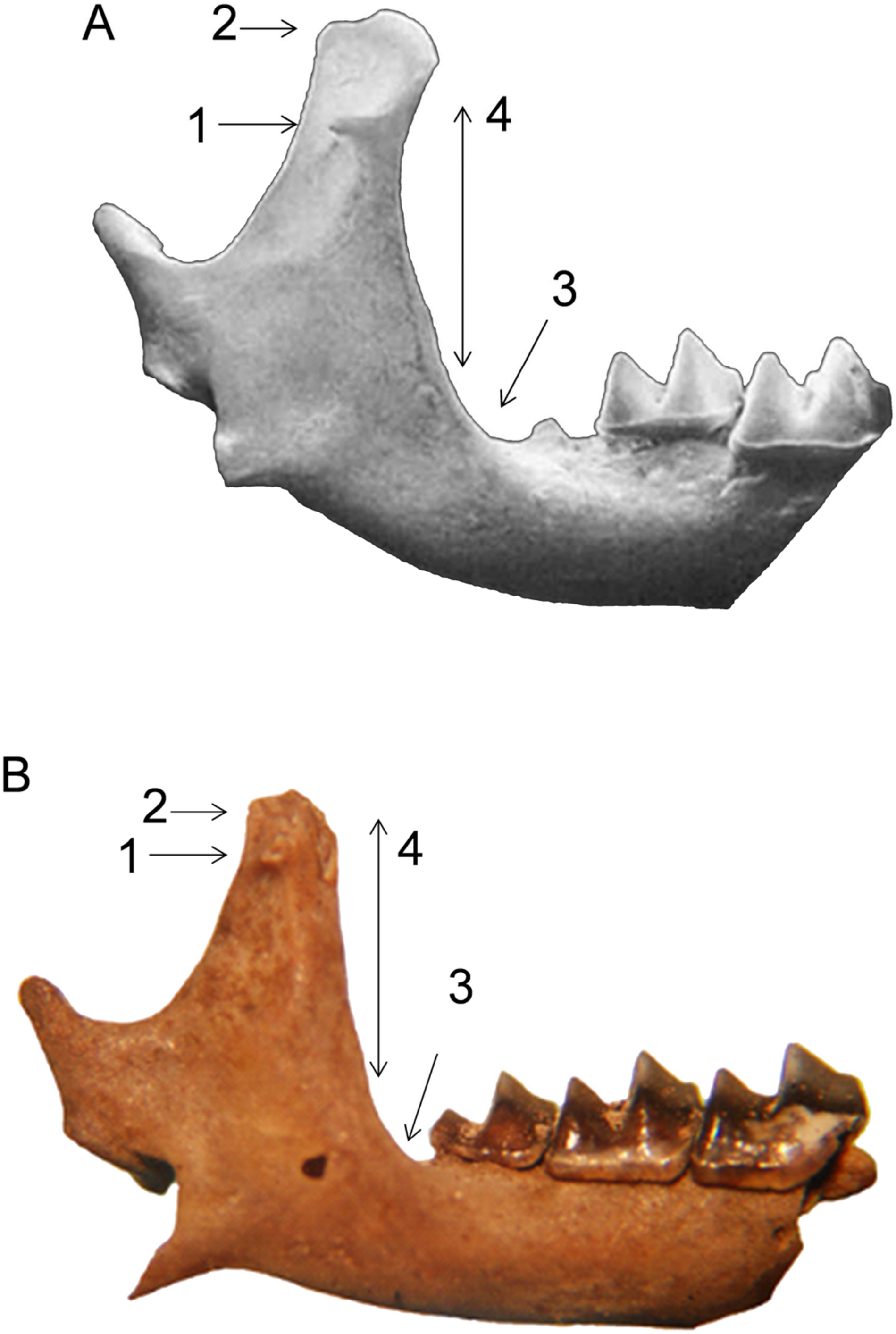

Figure 10. Comparison of A) *Zelceina kormosi* IVPP V 12121.13. (Modified from Storch 1995). and B) *Petenyia* sp. nov. ETMNH 17661, observed differences include 1) placement of coronoid spicule, 2) projection on the back of the coronoid process, 3) curvature of horizontal ramus's transition to ascending ramus, 4) angle of coronoid process. There is damage on the coronoid of B) ETMNH *Petenyia* sp. nov.17661.

“*Blarinella”* (Reumer, 1984)

“*Blarinella”* gen. et sp. nov.

Sorex dubia, Blarinella dubia and *Petenyia dubia* are considered junior synonyms.

Holotype: ETMNH 18218, complete dentary with inf. I, a1, p4, m1, m2, and m3. (Figure 11)

Paratypes: ETMNH 12299, partial skull with 1 sup. I, 1 A1, 2 A2, 2 P4, 2 M1, 2 M2, and 2 M3. (Figure 11)

Referred specimens: ETMNH 11028; ETMNH 12300 P4, M1, M2, and M3; ETMNH 14144 P4 and, M1.

Differential Diagnosis: ETMNH 18218 and ETMNH 12299 match Reumer’s (1984, p. 66-68) description of *“Blarinella”* including: I sup. and I inf. with spatulate apex, I sup. with S-curved ventral border in unworn specimens 5 upper antemolars, coronoid spicule above center of external temporal fossa, internal temporal fossa with a horizontal bar, lower molars more quadrate, lower molars with compressed W-pattern (sharp angles between lophids), and an extremely high entoconid crest. Here are additional observations: ETMNH 12299 is closer to “*B”. dubia* than *“B” europaea* based on the presence of a well-developed protocone on the P4. ETMNH 12299 differs from “*B”. dubia* in that the hypoconal flange on the M1 and M2 is reduced, the parastyle of the P4 is more pronounced, the internal temporal fossa is much larger above the bar, and ETMNH 18218 lacks the projection on the coronoid process. The inf. incisor of ETMNH 18218 has a more upturned apex like in *“B” europaea.*

Reumer (1984) reassigned a specimen to this genus using in a way that Storch and Qui (1995) considered circular reasoning. Storch and Qui (1995) placed it back into *Petenyia*. I agree with Reumer (1984) in taking it out of *Petenyia,* but agree with Storch and Qui (1995) in its placement in *Blarinella*.

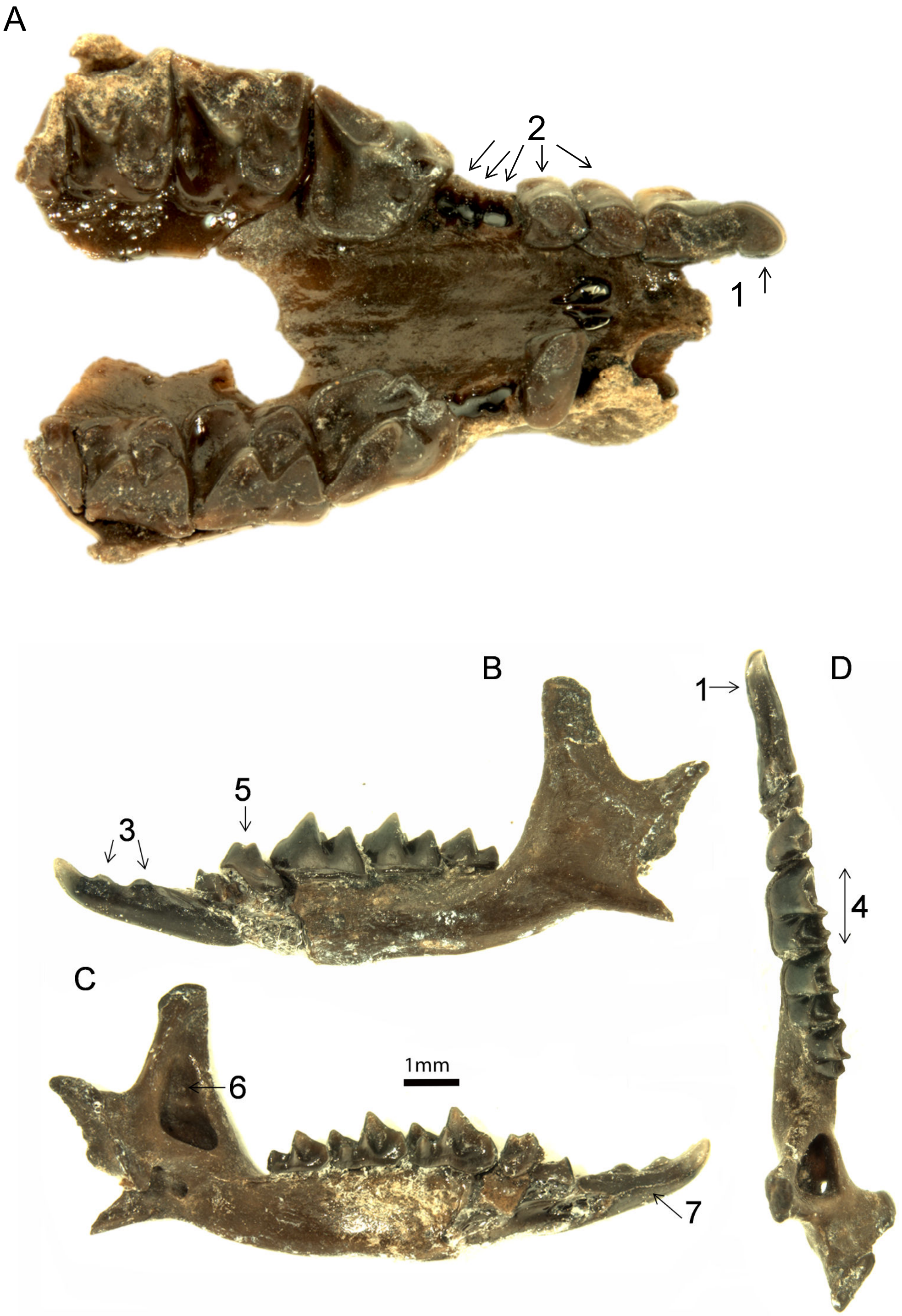

Figure 11. "*Blarinella*" gen et sp. nov. ETMNH 12299 A) Upper dentition, ETMNH 18218, Lower B) labial, C) lingual, D) occlusal with highlights of apomorphies, B, C, and D to scale. Note, 1) spatulate incisor 2) 5 upper antemolars 3) bicuspulate incisor 4) proximo-distally compressed molars 5) distinct cusps of the p4 are the same height 6) horizontal bar present in the internal temporal fossa, 7) medial groove on inferior incisor.

gen et sp. nov.

Gen et sp. nov. is defined by moderately wide inter-articular area and the wide horizontal ramus like those seen in members of the Blarinellini in combination with molars similar to *Sorex*. (Figure 12)

Holotype: ETMNH 9718, left mandible with m1. (Figure 13)

Differential Diagnosis: m1: Both ETMNH 9718 and *Crusafontina minimus* exhibit the following: exodaenodont teeth, the entoconid is well defined, but is the shortest cusp (Bown (1980) calls the metaconid and entoconid subequal, but Figure 11 clearly shows the metaconid being taller), the entoconid and metaconid are close and separated by a very low entoconid crest, the protoconid is the tallest and largest cusp. A hypoconlulid is present close to the entoconid, but separated by a deep notch. The metaconid and protoconid are connected by a notched paracristid. A broad buccal cingulum is present and a weak lingual cingulum.

The differences in ETMNH 9718 and *Crusafontina minimus* are: the trigonid in ETMNH 9718 is much more proximal-distally compressed, likely from the presence of a pronounced paraconid that is missing in *C. minimus*. The width of the interarticular area is also less in *C. minimus* (Figure 13).

Mandible: ETMNH 9718 and *Crusafontina minimus* both exhibit the following: a distinctively long and narrow coronoid (although a bit more exaggerated in ETMNH 9718), presence of a slight projection on the back of the coronoid process, the position of the mandibular foramen is distinctive and close in both taxa, a shelf behind the m3 at the junction between the ascending and horizontal ramus is present.

Differences in the mandible of ETMNH 9718 and *Crusafontina minimus* are: the width of the interarticular area is less in *Crusafontina minimus.* The coronoid spicule is defined in both taxa, but is much longer in ETMNH 9718 spanning the entire width of the coronoid, whereas it only extends half way across in *Crusafontina minimus.* The mental foramen is much smaller on ETMNH and is under the talonid basin of the m1 rather than under the center of the m1. The interarticular area is far too broad to be considered a Soricini, much less a member of *Sorex* (Figure 12). Ontogeny as a possible cause for these traits has ruled out by comparing an older individual of gen. et sp. nov. to younger individuals of *Sorex*. Age was inferred by the amount of wear on the teeth. (Figure 12)

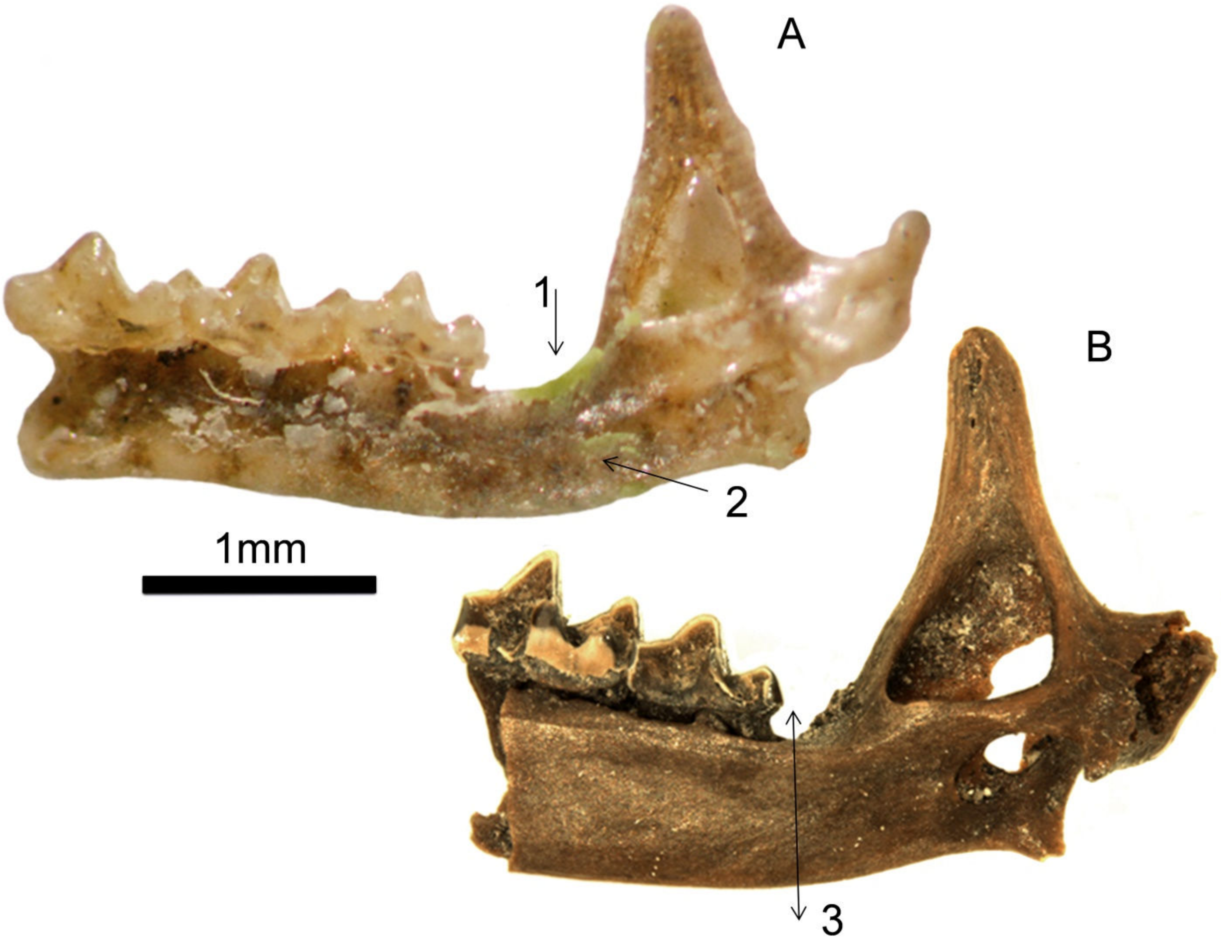

Figure 12. Comparison of A) *Sorex meltoni* to B) gen et sp. nov. ETMNH 97212. *S. meltoni*'s convergence with gen et sp. nov. 2 makes it an excellent comparison for showing synapomorphies of the genus. 1) The difference in space between the m3 and beginning of the ascending ramus, 2) the "heel" with is a synapomorphy for *Sorex* and 3) the width of the horizontal ramus which is much less in *Sorex.* Ontogeny is accounted for by using a specimen of *Sorex* that is an older individual than the specimen ETMNH 97212, age is evident from the amount of tooth wear.

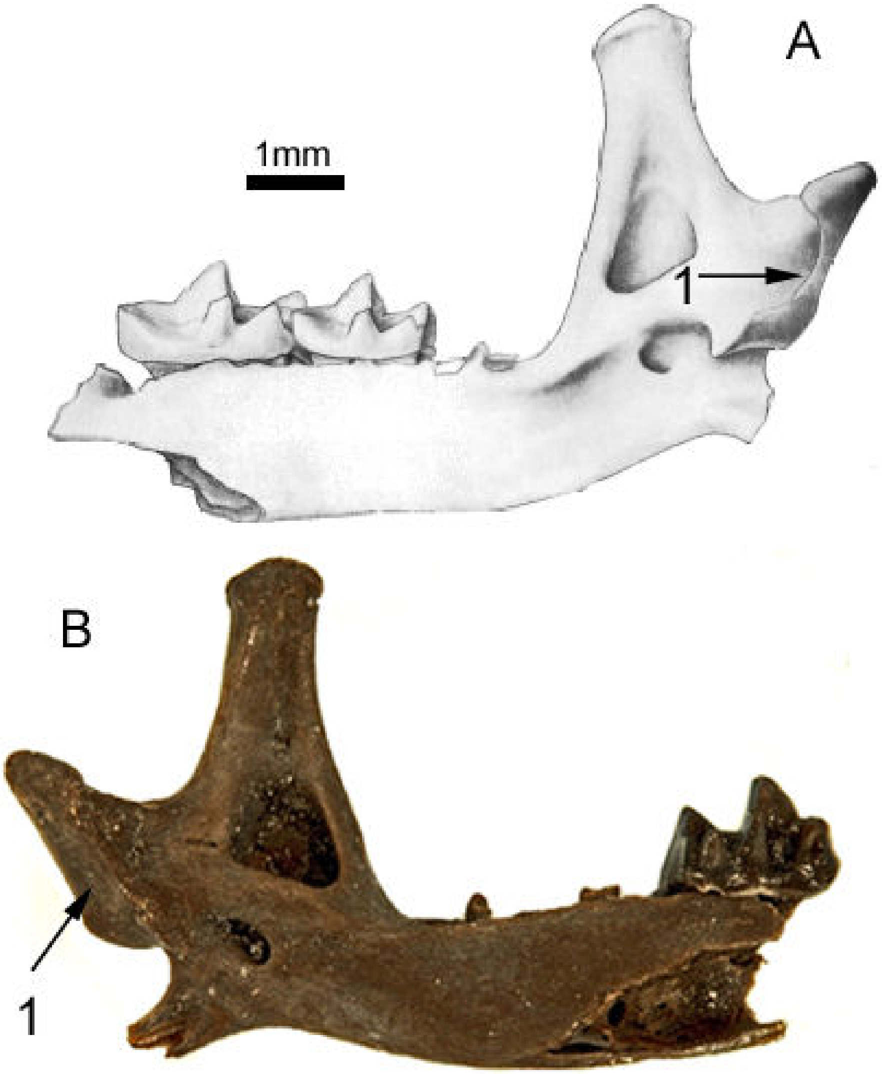

Figure 13. Comparison of A) UO 24711 *Crusafontina minimus* to B) gen et sp. nov. ETMNH 9718. Although superficially similar, the upper and lower facets of the articular condyle of *C. minimus* have a much more 1) narrow interarticular area. Modified from Bown (1980)

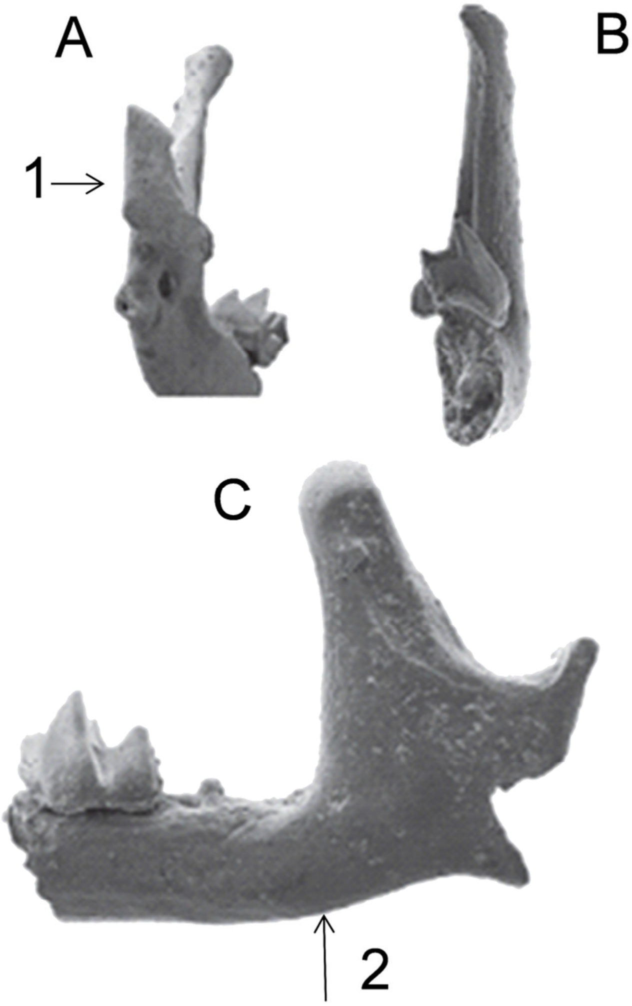

Figure 14. Pipe Creek *Sorex* INSM 71.3.144.3011, in A) posterior, B) anterior, and C) labial views, highlighting defining features of the new genus 1) shows the expanded interarticular area more similar to the Blarinellini and 2) shows the very beginning of the *Sorex* "heel." Modified from Czaplewski (2013).

gen et sp. nov. 2

Etymology: Named for the genus being ancestral to *Sorex*

Holotype: ETMNH 9721, dentary with m2 and m3. (Figure 15)

Paratypes: ETMNH 9567, dentary with m2; ETMNH 9568, dentary with m2; ETMNH 9716, m2 and m3 in jaw fragment; ETMNH 9725, m2 in jaw fragment; ETMNH 18126, front half of horizontal ramus with proximal half of m2, distal half of m1 and half of the inf. incisor.

Differential Diagnosis: m1 and m2: Unlike *Adeloblarina berklandi* the protoconid and entoconid are far away from each other and have a low entoconid crest. The endostylid is extremely pronounced resulting in a cusp the same height as the entoconid. The m1 and m2 are remarkably similar in morphology to *Crusafontina*, issues related to this will be discussed in more depth. *Crusafontina* and ETMNH 9567 and others of the morphotype have in common: a well-defined entoconid, the entoconid and metaconid are close and separated by a very low entoconid crest, the protoconid is the tallest and largest cusp. A hypoconlulid is present close to the entoconid, but separated by a deep notch. The metaconid and protoconid are connected by a notched paracristid. A broad buccal cingulum is present and a weak lingual cingulum.

m3: The m3 not being reduced is an indicator that this morphotype does not belong to *Crusafontina.* As seen in many members of Blarinellini and a couple species of *Crusafontina*, the talonid basin has been reduced and only a single large cone remains.

Mandible: The coronoid is extremely reduced and comes to a point. Despite the heavy reduction there are still coronoid spicules present. All of the individuals have the modified coronoid, but the height varies between individuals. The condyle looks much more similar to those in Blarinellini despite superficial similarities in the rest of the jaw morphology with *Sorex meltoni*. The condyle is the best indicator in this case of tribal placement. Despite the condyle being slightly reduced, the interarticular area is broad as is seen in Blarinini and Blarinellini, and due to the presence of an entoconid crest gen et sp. nov. can only belong to Blarinellini.

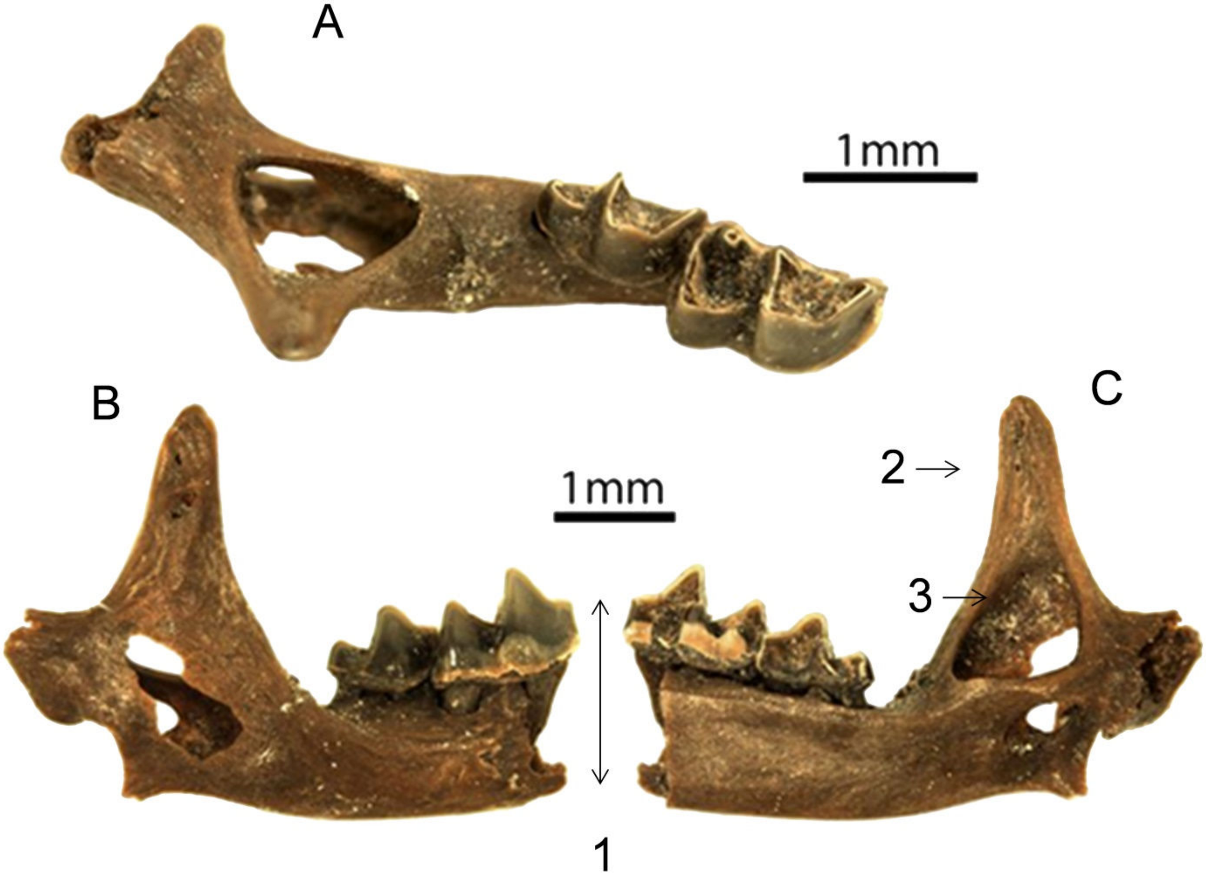

Figure 15. Gen. et sp. nov. 2 ETMNH 9721, A) occlusal, B) labial, C) lingual views, with highlights of apomorphies. 1) The stout horizontal ramus is a synapomorphy of the new genus, 2) the reduced coronoid, while the 3) large internal temporal fossa and forward leaning distal end of the coronoid process are apomorphies.

Anourosoricini Anderson, 1879

Crusafontina Gilbert, 1975

Crusafontina sp. nov.

Holotype: ETMNH 14850, right mandible with m1 and p4 and left mandible with p4. (Figure 16)

Referred Specimens: ETMNH 15660, m1/2 and ascending ramus; ETMNH 16020, i1, m2 and horizontal ramus fragment; ETMNH 9723, m1 in horizontal ramus fragment; ETMNH 16022, ascending ramus.

Differential Diagnosis: There are 6 species of *Crusafontina* in Europe spanning the early Miocene to the late Pliocene, they include: *C. endemic, C. fastigia, C. kormosi, C. magna, C. minima,* and *C. vandeweerdi.* Size is not an accurate character on its own, but it is of mention that *Crusafontina* sp. nov. dwarfs most species of soricid including many within *Crusafontina.* The two other genera within the clade, *Amblycoptus* and *Kordosia,* are acknowledged as being generally larger and more robust than *Crusafontina* (van Dam 2004). Despite the size similarities and bulbousness of the teeth, *Crusafontina* still retains its m3 and M3 and has not gained the characteristic larger and more quadrate P4. van Dam (2004) acknowledges a trend that the younger the *Crusafontina* species is the larger it is, he proposes the Hemphillian *Crusafontina magna* could have arisen from the smaller Clarendonian *Crusafontina minima* and *C. minima* from cf. *Crusafontina*, an even smaller species from the Middle Miocene of Europe. If this trend continued it suggests that the GFS specimen is the youngest, making the GFS Pliocene. Size is not an accurate character by itself, but it is worth mentioning that the largest *Crusafontina* species previously found, *C. kormosi,* has a mean m1 length of 2.29mm. The GFS species has an average m1 size of 3mm. *C. endemic*a differs from *C.* sp. nov. in that it still has a remnant cusp on the inf. incisor, the incisor is also much shorter in relation to the rest of the mandible compared to *C.* sp. nov., there is also a lingual cingulum on the inf. incisor that has been lost in *C.* sp. nov. *Crusafontina.* sp. nov. is more similar in morphology to *Kordosia* than to other *Crusafontina,* but the presence of the m3 implies a closer affiliation to *Crusafontina* despite convergent morphology. *Crusafontina.* sp. nov. stands out as a new species in the structure of the ascending ramus, the internal temporal fossa is very small and deep, the area between the coronoid and the upper facet of the articular condyle is greatly reduced and the lower facet almost to the dorsal portion of the horizontal ramus. These features make the ascending ramus extremely broad. There is also a reservoir present in the inf. incisor that is not seen in any other taxa.

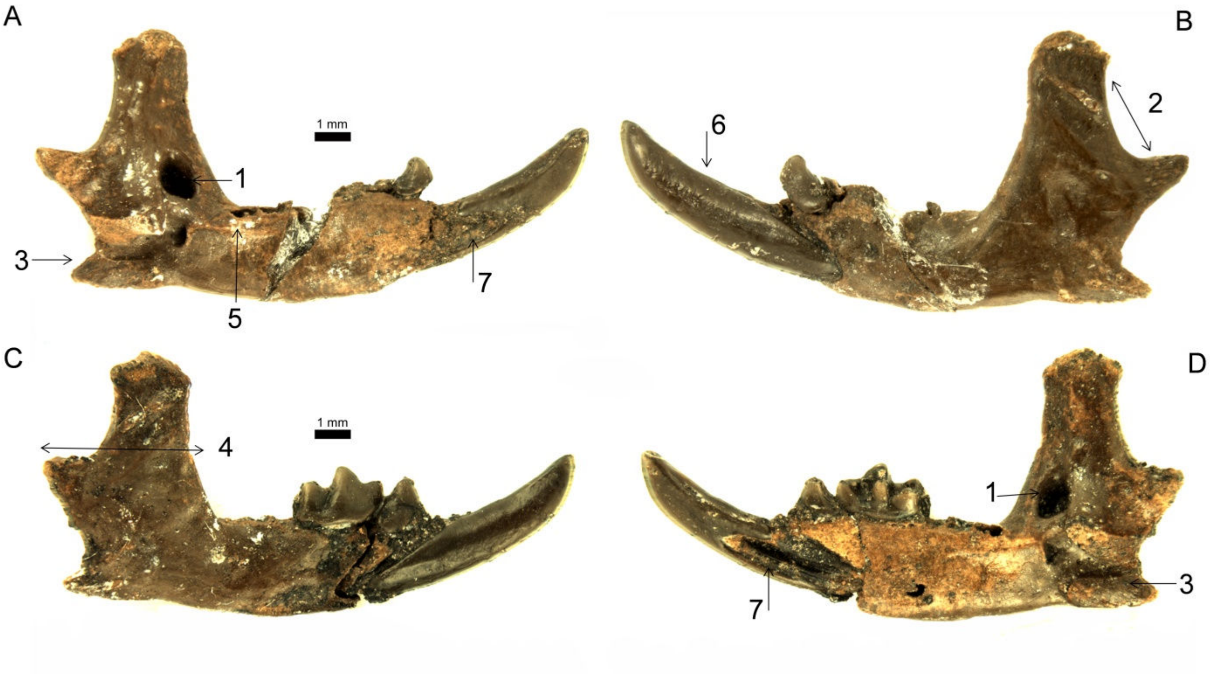

Figure 16. *Crusafontina* sp. nov. ETMNH 14850, A) left lingual, B) left labial, C) right labial, D) right lingual. *Crusafontina* sp. nov. stands out as a new species in the structure of the ascending ramus, 1) the internal temporal fossa is very small and deep, 2) the area between the coronoid and the upper facet of the articular condyle is greatly reduced and 3) the lower facet almost to the dorsal portion of the horizontal ramus. These features make the 4) ascending ramus extremely broad. 5) The m3 is extremely reduced, but still present. 6) The inferior incisor is acuspulate and there is also a 7) reservoir present in the inf. incisor that is not seen in any other taxa.

CHAPTER 4

PHYLOGENETICS

Domnina was chosen as the first outgroup because it is well-studied and one of the earliest members of Soricimorpha. Belonging to Heterosoricidae, *Domnina* is an earlier sister taxa to the Soricidae making the characters extremely basal. The characters that make *Domnina* derived within Heterosoricidae were left out of the analysis here; however they include: position of the mental foramen and the transversely broadened or double-rooted premolars (Repenning 1967). The non-pocketed internal temporal fossa and the presence of the masseteric fossa have been left in the analysis as plesiomorphies of the Heterosoricidae (Repenning 1967, Reumer 1998)

Unfortunately, due to the black and white nature of character states true relationships cannot be parsed out through cladistics. There is no accurate way to score the difference in a hypocone that is reduced to a small bump on the cingulum to a poorly developed hypocone. Because all fossils are transitional forms and all taxa change at different rates, to lump all forms into camps with those individuals closest to them is to overlook the subtle differences that make the forms distinct. If the fossil record were perfect an accurate cladogram may be possible. However, due to the number of missing or possibly incorrectly associated upper material are present, and the staggering conservatism of the lower dentition, true relationships cannot accurately be inferred. Two cladistic analysis were attempted, one with 45 characters and one with the most differential 17 characters. Both analyses proved inconclusive. There were thousands of most parsimonious trees and of those viewed none were able to sort out useful evolutionary relationships, all results were unresolved.

Past Attempts

An enormous cladistic analysis using dental and mandibular characters was undertaken by Rofes and Cuenca-Bescos (2009b) using 900 specimens included in 30 genera. Problematically the results contradict most other publications on shrew systematics and genetic analysis. The results of the analysis showed the tribes Blarinellini, Neomyini, Nectogalini, and Soricini being polyphyletic and showed Anourosoricini and Beremendini being paraphyletic (Rofes and Cuenca-Bescos 2009b). Only Blarinini was shown to be monophyletic (Rofes and Cuenca-Bescos 2009b) and this is likely because the more specious North American genera *Blarina* and *Cryptotis* were not included. Rofes and Cuenca-Bescos (2009b) admit to the questionable validity of their analysis and forfeited the option to propose new taxonomic names. The issues were in part due to the choice to use *Sorex* to polarize the characters, a decision made based on the assumption that the genus *Sorex* dates back at least 16 million years and is a crown clade of the Soricinae (Rofes and Cuenca-Bescos 2009b).

A number of small mistakes were also made in their analysis including the number of upper antemolars present in *Blarinella*. The study had four upper antemolars whereas one of the synapomorphies of the genus is the presence of a fifth antemolar (Abramov et al. 2007). The importance of this feature is described in a section of Abramov et al. (2007) on upper antemolars as an evolutionary marker. This mistake could in part explain why *Blarinella quadraticauda* placed out within the very different Anourosoricini. Despite all of the issues with the analysis insights can still be drawn. *Alloblarinella, Paenepetenyia, Cokia, Petenyia,* and *"Blarinella,"* all members of Blarinellini, group together. What is interesting is *Zelceina* and *Deinsdorfia* also fall out into this group, both genera's placement in Soricini is called into question in the section on Soricini. Many members of *Sorex* are also called into question as to their correct taxonomic placement. This paper’s earlier discussions of problems within Blarinini and Soricini as well as the inability to run cladistic analysis on Soricidae point out the ineffectuality of the tribe system within Soricidae. Reumer’s (1984) efforts to give plesiomorphies to the tribes was a practical and helpful step in the understanding of soricid evolution, but it appears that a next step needs to be taken and the tribes need to be broken down into smaller monophyletic groups. A more effective method of classification may be to lump similar taxa into the same genus, then subdivide those into subgenera. This would allow for morphological relationships within the tribe to be more easily associated, while still differentiating differences seen in species with more recent diversification. Unfortunately this is outside the scope of this thesis. Arbitrary differentiations based on geography or chronology should also be avoided, they are detrimental in the understanding of a taxon’s evolutionary history and biogeography. This is why nearly all of the GFS specimens were assigned to known genera despite perceived geographic barriers.

Figure 17. Adapted from Rofes and Cuenca-Bescos (2009b) cladogram showing many of the Eurasian taxa with 2 American taxa added, "*Blarinella"* sp. nov. and *Blarina brevicauda*.

Evolutionary Implications

Relationship Between Blarinellini and Blarinini

The first member of the tribe Blarinellini, *Hemisorex robustus,* is also the first member of the subfamily Soricinae (Ziegler 1989; Rzebik-Kowalska 1998). The type specimen is from the middle Miocene of France, but a tentative identification has been made of a specimen from the early Miocene of Germany (Ziegler 1989; Rzebik-Kowalska 1998). The Barstovian of Oregon yields the next oldest soricine remains, *Alluvisorex arcadentes*, a member of *Blarinella* and *Adeloblarina berklandi,* a member of Blarinini (Hutchison 1966; Repenning 1967). Divergence of the tribe Blarinini from Blarinellini likely occurred quickly, this is evident from the remarkably similar morphology between the two. Loss of the entoconid crest is the sole pleisiomorphy of the Blarinini, but because of the near impossibility of reacquiring a trait completely lost the missing entoconid crest is still observed in extant members of Blarinini. After the disappearance of *Adeloblarina berklandi* no other member of Blarinini is seen again until the Blancan. Blarinellini diversifies in the Clarendonian giving rise to three other genera (all monotypic): *Anchiblarinella, Parydrosorex,* and *Tregosorex*, as well as another species of *Alluvisorex* (Wilson 1968; Hibbard and Jammot 1971; Reumer 1998; Harris 1998). *Alluvisorex* survives into the Hemphillian and appears to go extinct at the beginning of the Blancan. It is also evident from the GFS fauna that Blarinellini continued to diversify throughout the Hemphillian. *Tregosorex* is highly derived; reduction of the coronoid process and subsequent deepening of the internal temporal fossa as well as the thickening of the horizontal ramus make it very different from any other contemporaneous species. Despite these differences the teeth are remarkably similar to other Blarinellini, except for the reduction in the entoconid crest. The entoconid crest height is similar in both the Clarendonian *Tregosorex wakeeneyensis* and the Hemphillian

Tregosorex sp. nov.; this feature and the many other similarities between the species suggest that there was gene flow between these populations for millions of years. By the late Hemphillian at least 11 million years had passed since the last known occurrence of a member of Blarinini. This large gap despite having soricine faunas from each intervening land mammal age combined with the evidence of members of Blarinellini reducing their entoconid crest in the late Miocene, it seems more parsimonious that *Adeloblarina berklandi* belongs to a branch of the soricine tree that split off around 20 million years ago and went extinct shortly thereafter and a more recent member of Blarinellini also reduced its entoconid crest, but this time gave rise to the successful Blarinini.

<u>*Paenelimnoecus*</u>

Specimens of modern *Blarinella* have also been found with a reduced entoconid (Storch 1995); due to the common place of misidentifications of soricids in collections, it is possible that they are not *Blarinella*. Another possibility is that the loss of an entoconid is not evolutionarily that difficult and if that is the case it could have occurred more than once in the same or different groups in order to fill a niche. Considering that there is still no consensus on the placement of *Paenelimnoecus*, Reumer (1992) allocates the genus to the subfamily Allosoricinae. Storch and Qui (1995) refutes this claim and leaves it as *Incertae sedis*. Observations from the GFS specimens provide evidence that it may fit within Blarinellini, Blarinini or a sister to *Adeloblarina berklandi. Paenelimnoecus* being found in North America begs more questions than it answers, but it may also shed light on a possible taxonomic position. The first is that *Paenelimnoecus* is sister to *Adeloblarina berklandi*. Both appear in the early Miocene, *Adeloblarina berklandi* loses just the entoconid crest and then goes extinct, while *Paenelimnoecus* loses both the entoconid crest and the entoconid. The evidence to support this hypothesis is the vestigial entoconid crest seen in the mid Miocene *Paenelimnoecus truyolsi* and the remnants of the entoconid seen in the late Miocene *Paenelimnoecus repenningi* (Furio and Santos-Cubedo 2009) and now the GFS taxon, *Paenelimnoecus* sp. nov.

Relationship of *"Blarinella"* to *Anchiblarinella wakeeneyensis*

The age of the WaKeeney site is unclear in Hibbard and Jammot (1971). It is cited as both Clarendonian, which is now considered to be from 12.5-9 Ma, and Lower Pliocene now dated to 4.8-3 Ma. To get a more accurate age, the ranges of the WaKeeney mammalian fauna were overlaid (*Plesiogulo, Martes, Eucastor, Copemys* (*Tregomys*), *Gnomomys, Astrohippus* and, *Neohipparion*); based on the fauna, the WaKeeney site is 13.6-5.3 Ma (Clarendonian/Hemphillian) (Hibbard and Jammot 1971, Paleodatabase). The paleoecology of the site is described by Wilson (1968) as similar to the lower Valentine of Nebraska (as described by MacGinitie (1962); warm-temperate to subtropical and savanna with forests along the streams). The presence of savanna rather than grasslands is indicative of Clarendonian rather than Hemphillian, making WaKeeney between 2 and 8 million years older than the GFS (Webb 1977, Wallace and Wang 2004). *"Blarinella"* sp. nov. and *Anchiblarinella wakeeneyensis* are very similar in ways that support that *Anchiblarinella* is ancestral to *Paenepetenyia*. *Anchiblarinella* is also similar to the modern *Blarinella*, even more so than to *Paenepetenyia*, implying a more direct lineage from *Anchiblarinella* to *Blarinella* with *Paenepetenyia* being a derived Hemphillian off shoot. The earliest documented occurrences of *Blarinella* are latest Miocene from the Ramapithecus fossil locality in Lufeng in the Yunnan Province of China (Guoqin 1985) and the Maritsa locality in Rhodes, Greece (Bruijn et al. 1970). More than 10 years after Storch and Qui (1995) dismisses a number of *Blarinella* species including "*B". europaea* and "*B". kormosi, "B". dubia* stating *Blarinella* is known only from the Pleistocene and recent of China. Citing circular reasoning as the reason for misidentification, Storch and Qui (1995), shows that Reumer (1984) used a Mio-Pliocene taxa he was describing when identifying the characters of the genus rather than using the extant namesake of the genus. Storch and Qui (1995) amended his original diagnosis from Fahlbusch et al. (1983); taking both "*B. zhudingi*" and "*B. kormosi*" out of *Blarinella* and placing them into *Paenepetenyia,* and *Alloblarinella* respectively. Storch et al. (1998) and Storch and Qui (2005) both make mention of a *Blarinella* sp. from the late Miocene, Lufeng site in China (Storch and Qui 1991). The diagnosis was made on: 5 upper incisors, 1 fragmentary lower incisor, 1 M1 or M2 talonid, 1 M1, one M2 and 1 M1 or M2 fragment (Storch 1991). Solitary upper incisors are indistinguishable from *Petenyia* and fragments are hardly substantial for such a drastic range extension. The M1 and M2 look very similar to Storch's (1995) *"Blarinella*" which he redefined as *Paenepetenyia*. It appears that *Paenepetenyia, Anchiblarinella,* and *"Blarinella"* are very closely related with *Anchiblarinella* being ancestral and the other 2 taxa as contemporaries.

Upper Antemolars as an Evolutionary Marker

A lot can be inferred about evolutionary heritage based on the number of upper antemolars. Similar work has been done looking at the vestigial lower antemolar found across disparate taxa (Hugueney and Maridet 2011; Klietmann et al. 2013); but despite being acknowledged as a character on the generic level, no lineages have been drawn based on the number of upper antemolars. Five antemolars appears to be the basal state and many taxa across tribes still have all five antemolars. There is a trend seen that an occasional genus will become more derived and lose an upper antemolar; the first to do this was *Petenyia* 12 million years ago. This is useful because *Petenyia* is one of only five genera of Soricidae, excluding the extremely basal Crocidosoricinae, present in the Middle Miocene. Of those five genera: *Adeloblarina* is missing an entoconid crest (Repenning 1967), and *Paenelimnoecus* is missing an entoconid (Reumer 1992) and *Petenyia* only has four antemolars (Reumer 1984). Based on these definitive characters the common ancestors of different groups that diversified in the Late Miocene/ Early Pliocene can be inferred. It is clear that *Paenelimnoecus* did not give rise to anything outside of its subfamily, Allosoricinae, or there would be more species lacking the entoconid because the likelihood of reacquiring a cusp is slim. *Adeloblarina* may be an evolutionary dead end or may give rise to the Blarinini (Harris 1998). *Petenyia*'s ancestors will all have four antemolars or less due to the unlikelihood of regaining a lost tooth. There are only a handful of taxa that are known to have four or less upper antemolars, *Zelceina* (Reumer 1984)*, Cryptotis parva* (Repenning 1967)*, Paracryptotis rex* (Hibbard 1953)*, Notiosorex* (which only has 3) (Hibbard 1953), and *Beremendia* (Rofes and Cuenca-Bescos 2009a). It is likely that the loss of the 5th antemolar in *Cryptotis parva* and *Paracryptotis rex* was convergence since the Plio/Pleistocene sister genera, *Blarina, Blarinoides, Mafia,* and *Sulimskia* all have 5 upper antemolars. *Zelceina* and *Beremendia* both appear during the middle of *Petenyia*'s time range and geographic range (Rzebik-Kowalski 1998), making *Petenyia* a possible candidate for ancestry. The problem with *Petenyia* being ancestral to *Zelceina* is that the tribe Soricini then becomes polyphyletic.

Soricini

The correct placement of many members of the Soricini is unclear. Storch and Qui (1995) has *Zelceina* in the *Petenyia-Zelceina* complex within Soricini, but *Petenyia* has been placed into Blarinellini in all later works including Storch and Qui (1998) while *Zelceina* has remained in Soricini. This can be resolved in one of two ways, place *Zelceina* into Blarinellini or say that the *Petenyia-Zelceina* split marks the beginning of the Soricini line. *Zelceina* is found alongside other Soricini in Asia, Europe, and N.A. Sorex in all and *Deinsdorfia* in Europe (Furio and Mein 2008). The *Sorex* found contemporaneously lack the typical *Sorex* "heel" and the *Deinsdorfia* is more than superficially similar to the Blarinellini. In the publications where *Zelceina* and *Deinsdorfia* are discussed they are never compared to each other despite both being compared to *Petenyia* because of similar morphology (Reumer 1984; Storch and Qui 1995). *Sorex*, the tribe's namesake, is by far the most muddled soricid genus.

Discussion of the Problems with *Sorex.*

Many overviews of American Eulipotyphla, like Gunnell et al. (2007), show the genus *Sorex* being in North America as early as 12 million years ago. As it stands, there is no fossil evidence placing *Sorex* in North America earlier than 9 million years ago. Two Clarendonian *Sorex* were identified tentatively and erroneously as "*Sorex*" sp. by Whistler and Burbank (1992) and ?*Sorex* sp. by Dalquest et al. (1996). There are two species, *S. edwardsi* and *S. yatkolai*, from the poorly constrained Lemoyne Quarry site in the Ash Hollow Formation of Nebraska, which spreads the entire breadth of the Hemphillian. North American *Sorex,* as far as is known from the fossil record, only lasted at most 3 million years, and all but three species in Europe follow that trend (Figure 18). The arbitrary assignment of many different morphotypes to *Sorex* has done more to obscure the understanding of soricid evolution than anything else. The original diagnosis of *Soricini* by Repenning (1967) is often not followed when naming new species (Figure 19).

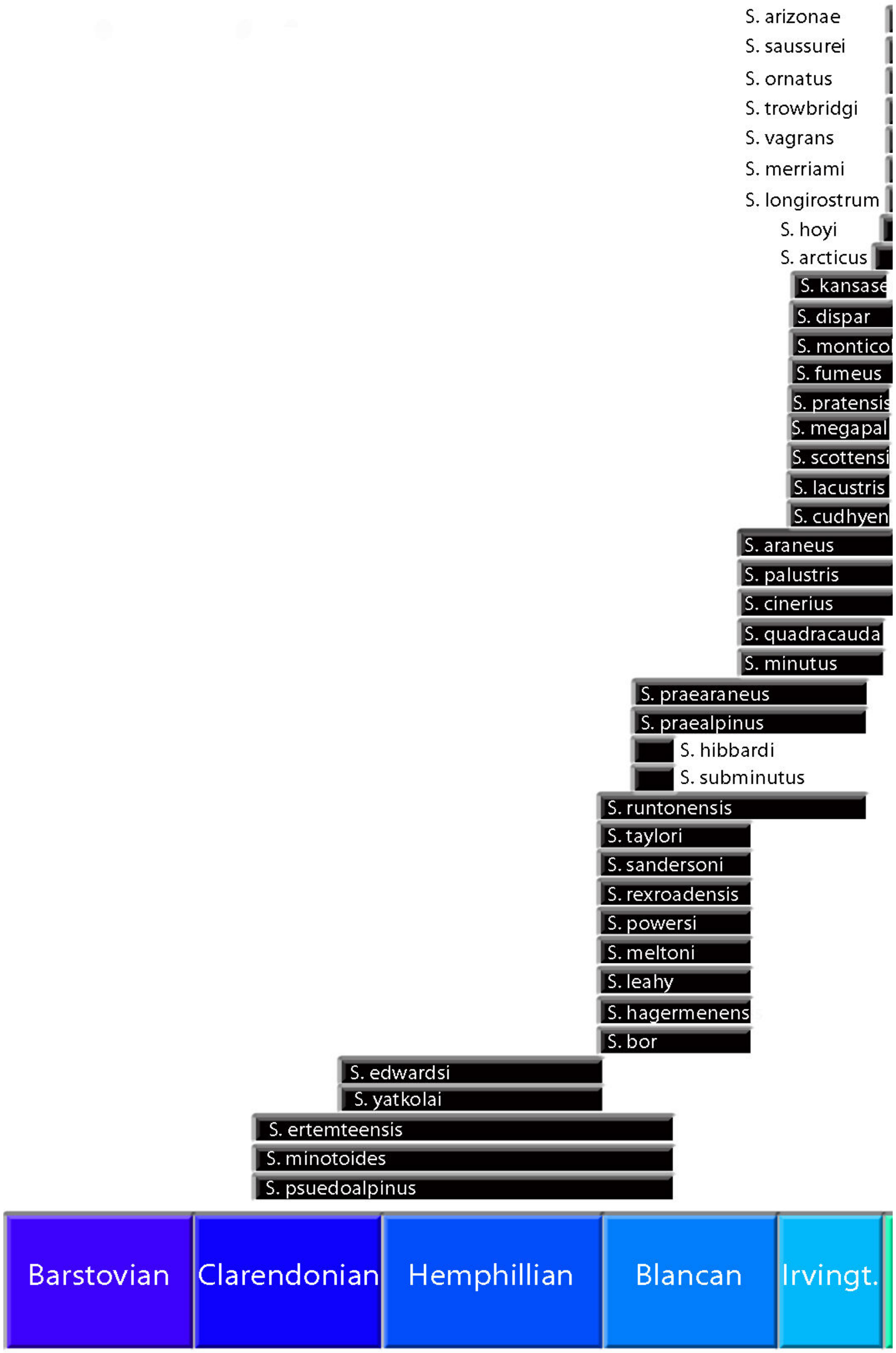

Figure 18. Fossil *Sorex* across time to illustrate trends in the longevity of species. Note that only five species predate the Blancan. Of those five species three (*Sorex ertemteensis, S. minotoides,* and *S. pseudoalpinus*) are from a poorly constrained site and the other two (*S. edwardsi* and *S. yatkolai*) may be a different genus. The figure also shows distinct faunal turnovers at the end of each land mammal age, but this could be an artifact of poorly constrained fossil localities.

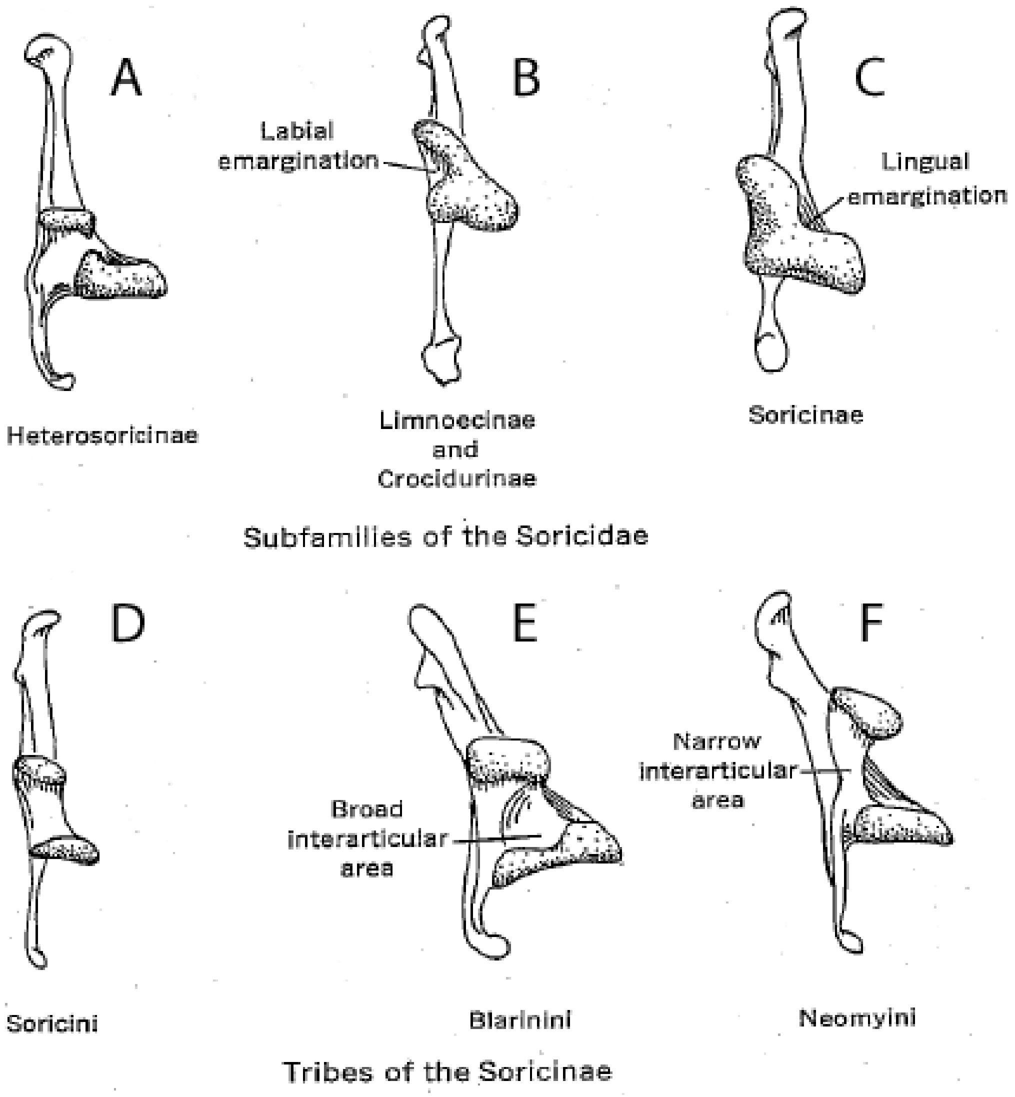

Figure 19. A-C represent the 4 Subfamilies in Repenning (1967), but Heterosoricinae is considered a Family here. A-C show the different types of emargination in the articular condyle. The upper and lower facets do not connect in A so there is no emargination. Limnoecinae and Crocodurinae have the same emargination which can be viewed as a shared trait on a phylogenetic node, seen in B. Soricini (D), Blarinini (E), and Neomyini (F) are Tribes within Soricinae (C). The width of the interarticular area is supposed to be a definitive way to classify to Tribe, but many "Soricini" have been named with a broad interarticular area. Modified from Repenning (1967).

All three of the soricids represented in Figure (20) were identified as *Sorex* in Bown (1980). They are the only specimens of *"Sorex"*, other than a couple of Chinese specimens that are not constrained, that date beyond the Blancan. It is evident from the broad interarticular area that these specimens are not members of Soricini, but of some intermediate group. In Reumer (1984) a group with an interarticular area like this was described, Blarinellini. This leads to many issues within both Soricini and Blarinellini because countless species have this intermediate interarticular area.

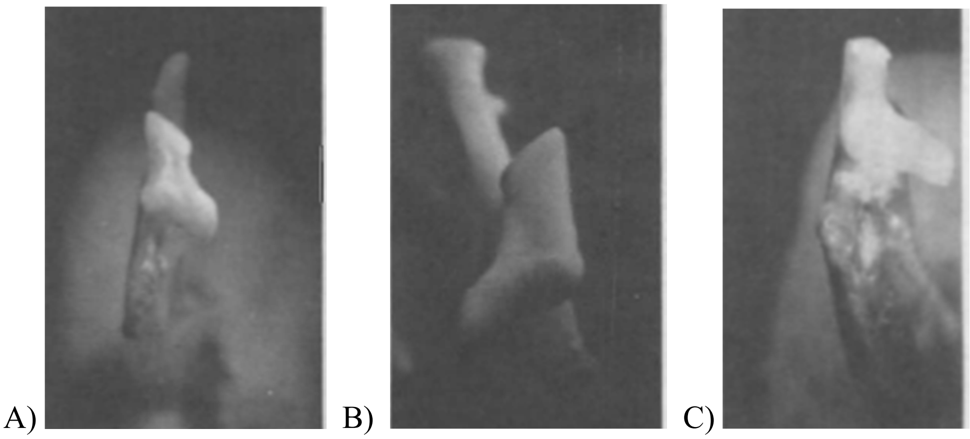

Figure 20. Three Hemphillian species identified as *Sorex*, but have a relatively broad inter-articular area. A) *S. yatkolai* UNSM 27624 B) *S.*sp. UW 6733 C) *S. edwardsi* UW 6737. Modified from Bown (1980).

Circular Reasoning in Phylogenies

Many phylogenies that take into account the fossil record use the hypothetical split of *Neomys* and *Sorex* to calibrate their analysis. That point is between 17.5 and 26.8 Mya (Fumagalli et al. 1999), problematically if future analyses are constrained to particular dates only certain answers are going to be obtained. Many of these assumptions are made on poorly constrained sites or misidentified taxa. Dubey et al. (2007) uses the oldest known *Cryptotis* to calibrate their points. The oldest known *Cryptotis* date was obtained through a secondhand source, Harris (1998), an overview of North American taxa. That date was 9 Mya, upon further research it becomes evident that the site is actually Blancan in age (Hibbard 1953). Dubey et al. (2007) also uses the assumption that *Adeloblarina* gave rise to all members of Blarinini at 12.9 Mya. When this assumption is made Blarinellini and Blarinini will always split at 12.9 Mya. Ohdachi et al. (2005) ran a molecular phylogeny without using the fossil record as a constraint and in one of the cladograms *Blarinella* fell out within *Blarina*, making the node paraphyletic. A result like that may mean Blarinellini and Blarinini are not as far displaced as originally thought.

CHAPTER 5

DISCUSSION

Paleobiology

Venom

The *Crusafontina* and "*Blarinella"* from the GFS add to the understanding of the evolution of venom within soricids. "*Blarinella"* sp. nov. has the earliest described incisoral venom groove by four million years (Figure 23). The earliest prior to this is *Dolinosorex* around the Middle Pleistocene (Cuenca-Bescos and Rofes 2007). Venom is common among multiple modern soricid species including *Blarina* (Martin 1981), but *Blarina* does not retain the groove. There is still debate as to what modern shrews are venomous, and whether or not any of the modern still administers venom through a groove (Furio et al. 2010). Considering the groove's completeness, it stands to reason that an even earlier soricid ancestor had venom, and based on the numerous occurrences of envenomation related morphology at distant nodes, a minimum time of acquisition can be inferred. *Crusafontina* sp. nov. has an incomplete groove, more incomplete than modern *Sorex* and an enlarged reservoir on the lingual side of the incisor (Figure 22). The length of the groove differs between individuals showing that the selective pressure is not that great and that acquisition or reduction of the groove, at least in the case of *Crusafontina*, is gradual. It is unclear whether *C.* sp. nov. is losing the groove or gaining it. If it is being gained, the robust morphology of the mandible and the long acuspulate incisor would imply that the pocket at the base of the incisor, possibly a reservoir, could be for venom and that the administration method is capillary action rather than injection. If the groove is being lost while the smaller "*Blarinella"* retains it, then it nullifies the hypothesis that venom is acquired as a species gets larger in order to obtain larger food as is presented in Cuenca-Bescos and Rofes

(2007). It is, however, a logical assumption that since the tendency is when soricids reach a certain size they acquire Carnivora-like traits for acquiring larger prey (Peigne et al. 2009); for example in *Crusafontina* a long, blade-like incisor, reduced number of upper antemolars, reduced m3, and a carnasiform p4. With those adaptations, venom may be unneeded to be a sufficient predator, as seen in felids and canids.

Figure 21. 1) Medial groove in the inferior incisor of ETMNH 18218 *"Blarinella"*sp. nov. Presence of a medial groove indicates the use of venom, the earliest known medial groove in a soricid.

Figure 22. 1) Vestigial groove and the 2) large reservoir in the inferior incisor of ETMNH 14850 *Crusafontina* sp. nov. Presence of a minute groove is not uncommon, but is significant in understanding the evolution of venom in soricids.

Paleoecology

"Blarinella" and *Paenelimnoecus* have, until now, only been known from Eurasia, but their occurrence in North America is no surprise. *Crusafontina,* also found at the GFS as well as western North America, are found across Europe and Asia during the Miocene and Pliocene (van Dam 2004; Prieto and van Dam 2012). *Crusafontina* and *Paenelimnoecus* are well documented paleoecological indicators of a forested environment with a body of water (Meszaros 2000). "*Blarinella"* also has a tendency of being found in similar environments, but this is often attributed to a generalist lifestyle (Meszaros 2000). Popov (2003) disagrees with the generalist description and states that they are more specialized, but gives no information on what niche they

might be specialized for. Although extant *Blarinella* have a highly specialized lifestyle due to shrinking ranges, most evidence shows that some fossil species were generalists. WaKeeney, the other North American site where *Anchiblarinella* is present, was described by Wilson (1968) as similar to the lower Valentine of Nebraska as described by MacGinitie (1962); warm-temperate to subtropical and savanna with forests along the streams. Chaney and Elias (1936) are also cited describing the contemporaneous Beaver Co. Oklahoma as being more humid during the Mio-Pliocene than western Nebraska (Figure 1).

Sorex underwent a massive diversification during the cooling and drying trend that occurs at the end of the Miocene. According to Reumer (1989), this diversification was spurred by the extirpation and extinction of many woodland taxa. The presence of other fauna, isotope analysis of their teeth, and plant fossils (macro and micro) at the GFS provide support for the hypothesis that the GFS is a refugium (Wallace and Wang 2004; DeSantis and Wallace 2008; Gong et al. 2010; Ochoa et al. 2012). Pipe Creek is also the only other site in eastern North America to yield soricid remains older than Pleistocene, and as of now the only described taxon is *Sorex* (Czaplewski 2013). The GFS is close in age to Pipe Creek, both are considered to be Hemphillian (Latest Miocene) (Czaplewski 2013; Wallace and Wang 2004), but GFS has not yielded any *Sorex*. Thus, the absence of *Sorex* at GFS may provide additional support for the refugium hypothesis. If this hypothesis is correct, then many of the plants and animals found will be holdovers from earlier parts of the Miocene before the spread of grasslands. Evidence from DeSantis and Wallace (2008) includes a *Teleoceros* species that has been identified as a browser, despite other contemporaneous forms of rhinoceroses from other sites being grazers. Only the proboscidian, a group known for traveling great distances, is a grazer (DeSantis and Wallace 2008). The grazing proboscidian and the limited, but present grass pollen are indications that, despite the apparent lack of grass in the GFS ecosystem, there could be grasslands or savannas in an adjacent area (Ochoa et al. 2010). The absence of the soricid genera *Cryptotis*, *Notiosorex*, and *Paracryptotis* is also a good indicator that the GFS was an ecosystem without grasslands.

Interpretations of GFS Soricid Associations

Eight soricid taxa are found at the GFS; remarkably high diversity. Extant systems usually yield 4 to 7 species, the high end if humid and the low if arid (Fox and Kirkland 1992; Dickman 1988). Soricid diversity has a tendency to correlate with arthropod abundance (Fox and Kirkland 1992; Dickman 1988), implying the GFS could have had high arthropod abundance. Fossil localities when *in situ* usually contain even less diversity due to incompleteness of the fossil record. Some cave deposits tend to yield high soricid diversity because of the abundance of raptor roosts (Mayhew 1977; Mellet 1974) and the sampling of an overall environment.

Arguments for Multiple Similar Species at a Single Site

Sexual dimorphism does not account for the high diversity. Modern *Cryptotis* species show very little sexual dimorphism. Woodman and Timm (1993) show that the only statistically significant cranial difference between males and females is a longer unicuspid tooth row in females. The same limited differences are seen between the sexes of *Sorex* (Badyaev and Foreman 2000). All of the morphotypes from the GFS differ by distinct apomorphies that cannot be attributed to sexual dimorphism or individual variation.

Niche Partitioning

Churchfield et al. (1999) analyzed stomach contents of 6 sympatric forest shrews in Russia. This study showed that smaller shrews had less diverse diets. The smallest species fed exclusively on arthropods, whereas the larger species also fed on oligochaetes and gastropods (Churchfield et al. 1999). Diptera larvae were also absent from the diet of the smallest shrews.

With the exception of *Crocidura lasiura*, smaller shrews fed predominately on the surface and in the litter; while the larger species fed in the soil (Churchfield et al. 1999). The reason for *Crocidura lasiura* having similar prey and feeding habits to the smaller shrews could be a similarity of tooth morphology or specialization from past ecological restraints within the genus (Churchfield et al. 1999).

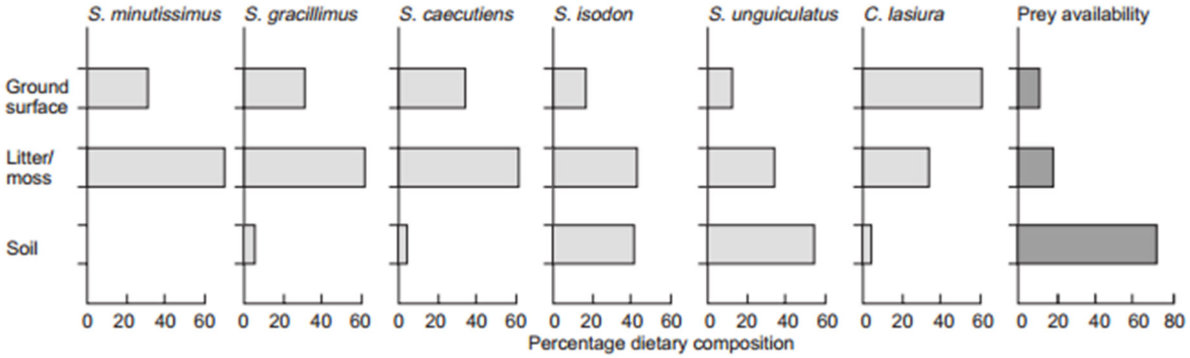

Figure 23. Percentage dietary composition of invertebrates taken from different vertical strata by coexisting shrews of the Russian Far East, together with their percentage occurrence quantitative field samples. Modified from Churchfield et al. (1999).

Shrews from the GFS can be divided into 4 size classes using jaw length: <7mm, 7-10mm, 10-15mm and 15<mm. Contrary to the predictions made by Fox and Kirkland (1992) and Dickman (1988), large shrews were not the most prevalent. Those studies showed that size did not directly affect prey choice, but gave evidence that larger shrews were better adapted for fossoriality and movement through dense microenvironments; they showed that larger shrews were just outcompeting the smaller ones (Dickman 1988; Fox and Kirkland 1992). The GFS community is significantly different with 6 of the 9 species present representing the smaller size classes. Of those smaller shrews only 1 species does not have another taxon overlapping in size. What is seen in the fossil community that was not discussed in modern ecology papers is a

difference in tooth morphology. In one of the species, "*Blarinella*" basal dilambdodont teeth are present; whereas another three have more derived, broad, cuspy teeth; some possibly durophagus. Two species, *Crusafontina* sp. nov. and *Tregosorex* sp. nov., have taken on a carivoran role possibly in response to competition. The presence of *Crusafontina* sp. nov. could account for the absence of a least weasel size carivoran; it is even possible that the extinction of most of the Anourosoricini could have opened up a small carivoran niche that was quickly filled during the diversification of mustelids in the Pliocene. Another species, *Paenelimnoecus* sp. nov., has lost its entoconids possibly filling a niche that has no modern analogue. Fox and Kirkland (1992) and Dickman (1988) also suggest that the amount of invertebrates available heavily influences the amount of competition, so it may be a possible that there were significantly more invertebrates during the late Miocene in the area (than are currently present) allowing for more small species to coexist. Another possibility is that large shrews were drifting towards a carnivoran diet, allowing the proliferation of smaller species that were restricted to arthropods; like what was seen when large shrews were removed in the Dickman (1988) study.

Preservational Bias

Evidence of digestion on some GFS shrew dentaries implies (Figure 15) some of the species could have been brought to the site of deposition by owls, hawks or mammalian predators. This could mean that some species present may be from unrelated ecosystems. If this is the case, the number of sympatric species could be significantly lower and perhaps more similar to the modern diversity of species.

Another Dickman (1991) paper showed that owls most often took small female mice due to the small mice's habit of traveling in more open vegetation. Males and other larger mice tended to travel in more densely vegetated areas. It can then be inferred that since smaller shrews are less able to travel through dense vegetation or through the topsoil (Churchfield et al. 1999, Figure 23) that they are more often eaten by owls than large shrews, perhaps supporting a preservation bias of small shrew species at the GFS. One of the smallest species gen. et sp. nov. has multiple individuals found in the same unit (on roughly the same day): ETMNH 9715, ETMNH 9716, ETMNH 9117, ETMNH 9721, and ETMNH 12298. At least two of the individuals are acid etched providing evidence that this may have been below a bird of prey roost (Metter 1974; Mayhew 1977) (Figure 15). The genus found appears to be closer to Soricini, suggesting there are grasslands within flying distance of a bird of prey or within the hunting range of a carivoran.

CHAPTER 6

CONCLUSIONS

Eulipotyphla at the GFS play a critical role in understanding the evolution and migration patterns of a large group of mammals that continue to thrive worldwide by filling in gaps in the scanty North American fossil record.

Based on the fossil soricids found at the Gray Fossil Site, it can now be inferred that:

- *Paenelimnoecus, "Blarinella",* and *Petenyia* have a distribution across the entire north-temperate zone.
- Origination of venom in soricids dates back at least 4 million years.
- A trend of *Crusafontina* species getting larger as time moves towards the present is supported by the GFS *Crusafontina* being the largest and youngest member of the genus.
- *Crusafontina, Tregosorex,* and *Limnoecus* survive until the latest Miocene.
- *Sorex* may not be present in the region until, at earliest, the early Pliocene.
- *Sorex* has an ancestor similar to members of Blarinellini.
- Blarinellini gave rise to Blarinini, instead of being a sister group.
- Eastern North American soricids are more morphologically similar to European taxa than Asian.

- There were larger and more diverse soricid communities during the Late Miocene than before or after the expansion of grasslands.

Publication of the GFS shrew fauna will enable a massive leap forward in the understanding of soricid evolution. Based on *Crusafontina* and *Limnoecus*, the Gray Fossil Site can possibly be constrained to closer to the 7Ma age estimation, but, because the species are considered to be new it is impossible to know if their extinction at 7.75 million years ago elsewhere holds true for those at the Gray Fossil Site as well. This latest occurrence would provide more evidence of the GFS being a refugium and constrain the age closer to the younger 4.5 Ma date.

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APPENDICES

Appendix A

List of 40 soricid taxa used in the data matrix of the phylogenetic analysis including 45 character states. Primitive state based on comparisons with genus

Sorex ertmentensis
S. minutoides
S. bor
S. minutus
S. fumeus
Drepanosore kordosi
D. janossyi
Zelceina. kormorsi
Z. soriculoides
Petenyia hungarica
Neomys fodiens
N. newtoni

Alloblarinella. europeoa
Blarinella.quadraticauda
"Blarinella"dubia
Adeloblarina. sincia
A. berklandi
Blarina. brevicauda
Cryptotis parva
"Cryptotis" meadensis
Paracryptotis rex
Tregosorex. holmani
T. sp. nov.

Al. chasseae
Al. arcadensis
Anchiblarinella
Petenyia" concisus
Antesorex
Bekiasorex
Notiosorex
Gen et sp. nov.
Paenepenenyia

Domnina
Mafia csarnotensis
Blarinoides aliciae
Bl. mariae
ETMNH13343
Berimendia fissidens
Lananosorex
GFS mystery

List of 45 soricid characters used in the data matrix of the phylogenetic analysis including 17 character states. Primitive state based on comparisons with genus *Domnina*.

1. Teeth: **(0)** pigmented; **(1)** without pigment.
2. I1 apex: **(0)** bifid; **(1)** non-bifid.
3. AA number: **(0)** five; **(1)** four; **(2)** three **(3)** two. Excluding P4 which is not considered an antemolar.
4. AA postero-lingual cusps: **(0)** absent; **(1)** present.
5. P4 posterior emargination **(0)** absent; **(1)** weak; **(2)** strong.
6. P4 protocone **(0)** absent; **(1)** present.
7. P4 paracone **(0)** prominent; **(1)** reduced.
8. P4 hypocone development: **(0)** poor; **(1)** good.
9. P4 parastyle **(0)** minute; **(1)** defined.
10. P4 parastylar crest: **(0)** low; **(1)** high **(2)** absent.
11. M1 posterior emargination/hypoconal flange (present w/ emargination) **(0)** absent; **(1)** present.
12. M1 hypocone: **(0)** present; **(1)** absent.
13. M1 hypocone development: **(0)** poor; **(1)** good.

14. M1 mesostyle: **(0)** present; **(1)** absent.

15. M2 shape: **(0)** rectangular; **(1)** trapezoidal.

16. M3: **(0)** present; **(1)** absent.

17. i1 serrations: **(0)** present; **(1)** absent.

18. i1 **(0)** tricuspulate/tetracuspulate; **(1)** bicuspulate; **(2)** monocuspulate; **(3)** acuspulate.

19. i1 buccal cingulum: **(0)** present; **(1)** absent.

20. i1 apex upturning: **(0)** slight; **(1)** strong.

21. i1 medial groove continues to end of incisor: **(0)** absent; **(1)** present.

22. aa number: **(0)** four; **(1)** three; **(2)** two; **(3)**; one. Excluding P4 which is not an AA.

23. a1 cingulum: **(0)** present; **(1)** absent.

24. a1 buccal cingulum: **(0)** pronounced; **(1)** weak.

25. a1 lingual cingulum: **(0)** pronounced; **(1)** weak.

26. p4 postero-lingual basin: **(0)** deep; **(1)** shallow; **(2)** absent.

27. p4 cingulum: **(0)** present; **(1)** absent.

28. p4 buccal cingulum: **(0)** pronounced; **(1)** weak.

29. p4 lingual cingulum: **(0)** pronounced; **(1)** weak.

30. m1 entoconid: **(0)** present **(1)** reduced; (2) absent.

31. m1 entoconid crest: **(0)** present high; **(1)** present low; **(2)** absent.

32. m3: **(0)** present; **(1)** absent.

33. m3 number of cusps in talonid: **(0)** two; **(1)** one.

34. mm buccal cingula: **(0)** pronounced; **(1)** weak.

35. mm lingual cingula: **(0)** weak; **(1)** strong; **(2)** absent.

36. Ascending ramus to vertical ramus **(0)** perpendicular; **(1)** not perpendicular.

37. Coronoid process leaning forward: **(0)** no; **(1)** yes.

38. Coronoid spicule: **(0)** small; **(1)** large; **(2)** absent.

39. Coronoid spicule: **(0)** weak; **(1)** pronounced.

40. External temporal fossa: **(0)** shallow; **(1)** deep.

41. Masseteric fossa: **(0)** present; **(1)** absent.

42. Internal temporal fossa: **(0)** not pocketed; **(1)** pocketed.

43. Internal temporal fossa horizontal bar: **(0)** absent; **(1)** present.

44. Symphyseal fossa: **(0)** absent; **(1)** shallow; **(2)** deep.

45. M1 metalophid: (0) present; (1) absent.

Appendix B

Issues with Particular Characters

Character 1: All fossils go through individual taphonomic processes. These processes alter the chemical state of the fossils; this includes color. Color is a problematic indicator due to the fact it changes through time, deposition, and erosion. This is extremely problematic when the two modern subfamilies, Crocidurinae and Soricinae, are differentiated based on whether the teeth are pigmented; this problem is further amplified when the amount of pigmentation is used as a character when differentiating between different genera and species.

Character 2: Bifurcation (Figure 24), number of upper antemolars and the presence/absence of the upper 4rth premolar posterial-lingual cusps all seem to be solid characters. The only problem is there is no good measure of the stage of development of each of these adaptations.

Figure 24. Illustration of bifurcation with arrow highlighting the secondary cusp which makes the tooth bifid. Modified from Rzebik-Kowalski (2013).

Characters 5 and 11: Posterior emargination is a distinctive yet highly varied character. The strong posterior emargination in *Sorex* is immediately apparent when compared to a member of Blarinellini who have almost no posterior emargination. Posterior emargination is very much a gradation from taxa to taxa and is heavily influenced by the inflation and reduction of the hypocone and protocone. The reliance on other features however does make posterior emargination an integrated trait, which makes it useful in discerning differences between taxa on the generic and subfamily level. (Figure 25)

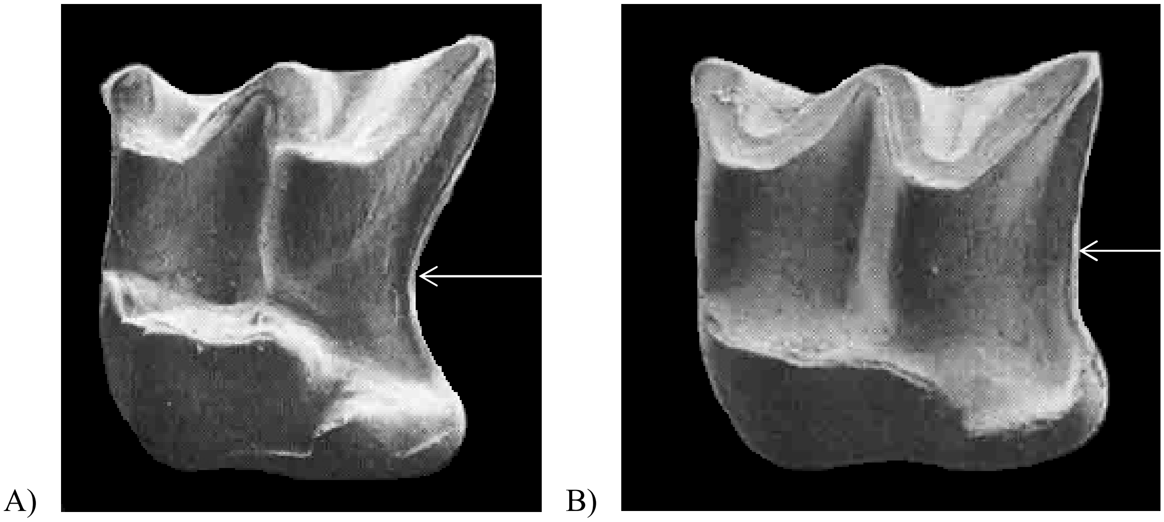

Figure 25. A) *Sorex pseudoalpinus* with extreme posterior emargination compared to B) *Alloblarinella sincia* with minor posterior emargination. Modified from Storch (1995).

Characters 6-10, 12-14, 30, and 32: The presence and prominence of cones, especially on the highly variable upper 4rth premolar (Figure 26), proves useful in all levels of identification. The upper dentition appears to be more variable than the conservative lower dentition, making it valuable in not only the differentiation of species, but the tracing of heritage through time. This can be seen very evidently in the appearance and growth of the metaconule in the red panda. Problematically, there is no defined way to mark the exact size and placement of a cone in a cladistic analysis, resulting in a significant loss of data. Another problem marking cones in a cladistic analysis is the lack of individual conicular description in soricid publication until the 1980s; aspects such as the height of the parastylar crest were not described and cannot be made out from line drawings or old photographs.

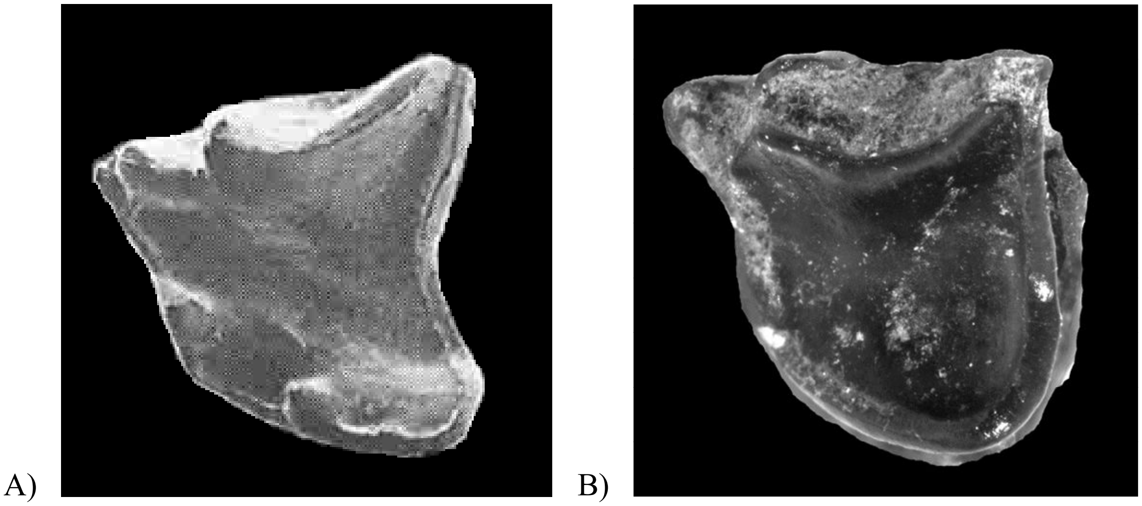

Figure 26. Comparison of upper P4 of two different genera. A) *Sorex pseudoalpinus* and B) *Tregosorex* sp. nov. showing the extreme emargination and well defined cusps in A and the lack of these traits in B. Modified from Storch (1995).

Character 15: Shape of the upper 2nd molar is slightly subjective, but seems to be a viable character if the same definition is used throughout the analysis.

Characters 17 and 18: The number of cusps in the inferior incisor is extremely useful (Reumer 1984). Even the problem of the same species sometimes developing an extra cusp or losing a diminished cusp is valuable in helping to understand the evolutionary history. A single species capable of having multiple numbers of cusps did prove problematic in the analysis. Those with three and four cusps had to be lumped because of the tendency of individuals to gain or lose a small cusp. A judgment call also had to be made when deciding what constituted as a cusp; in this paper any identifiable raise on the incisor, as is seen in *Notiosorex* constituted monocuspulate as opposed to the acuspulate *Crusafontina* (Figure 27).

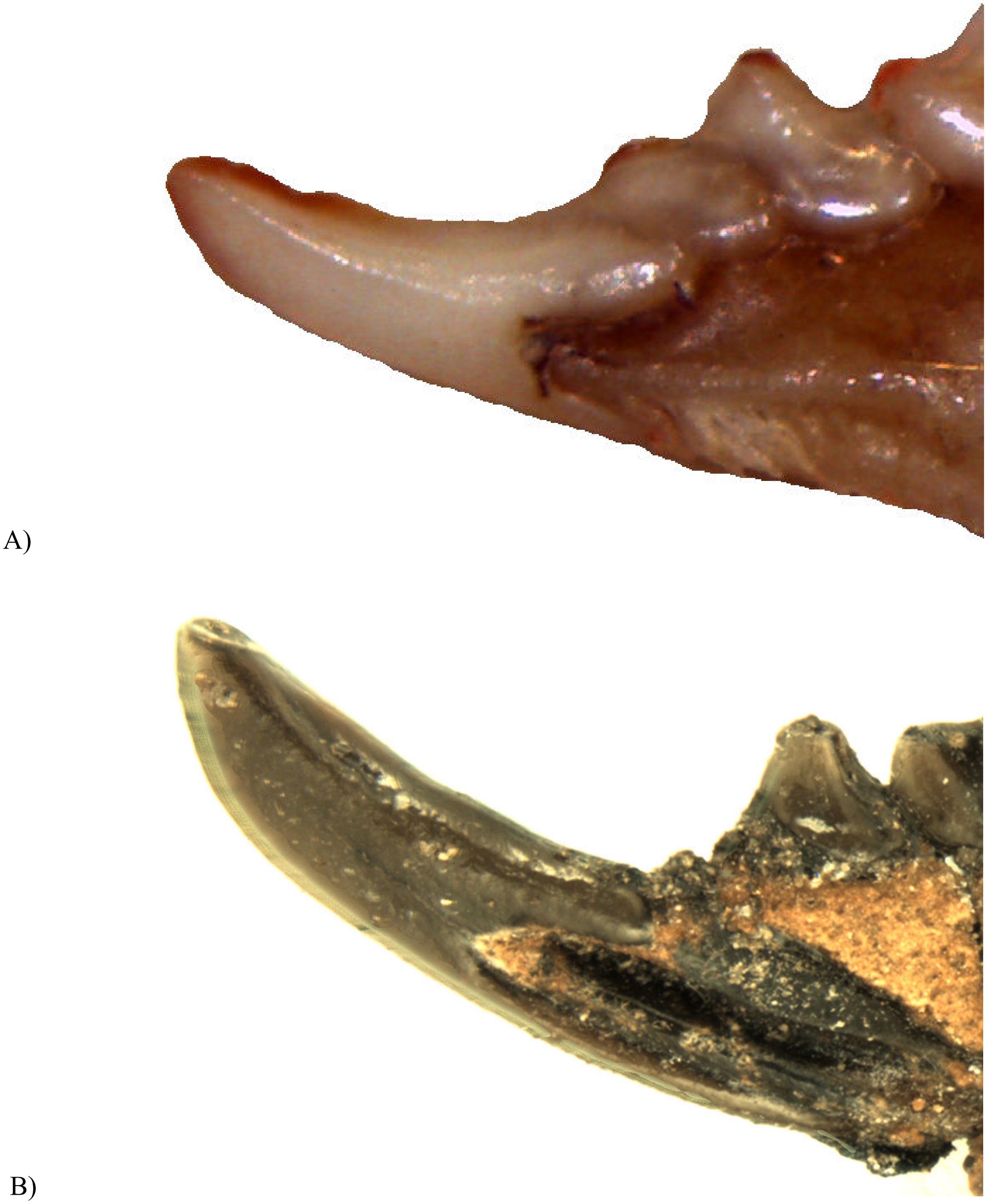

Figure 27. The difference between monocuspulate A) *Notiosorex* and acuspulate B) *Crusafontina* inferior incisors.

Character 19: Presence or absence of the buccal cingulum of the inferior incisor is a good character, but in order for better differentiation note should be made as to the size.

Character 20: Upturning of the incisor’s apex seems to be informative, but when reproducing these character states it is left to the judgment of the author what constitutes as slight or strong.

Character 21: Another important trait that has been overlooked in the literature in the presence or absence of a medial groove (Figure 21), that extends to the end of the incisor (Cuenca-Bescos and Rofes 2007). It would appear that this groove indicates the presence of venom, there needs to be a study done that examines at all of the known inferior incisors and plots the presence of the medial groove (Cuenca-Bescos and Rofes 2007).

Character 22: The lower antemolar number is extremely helpful in determining evolutionary relationships (Klietmann et al. 2013).

Characters 23-29: Cingula are extremely variable, easily worn and subjectively documented.

Character 30: The presence of an entoconid is important in separating members of the Allosoricinae (Reumer 1992; van de Hoek Ostende et al. 2009), but because members of Allosoricinae are not included in this analysis so the character proved non useful.

Character 31: Entoconid crests, particularly on the m1, are heavily relied on to differentiate taxa on the tribe level. The reliance may be in part unjustified due to the variability observed in the feature within a species when large numbers of individuals are studied (Storch 1995).

Character 32: Presence or absence on the lower third molar is extremely descriptive, it is only lost in a few highly derived taxa (Meszaros 1997; van Dam 2004).

Character 33: The number of cusps in the talonid of the lower third molar is also a very helpful character because of the tendency of certain taxa to reduce their talonid basin (Figure 28).

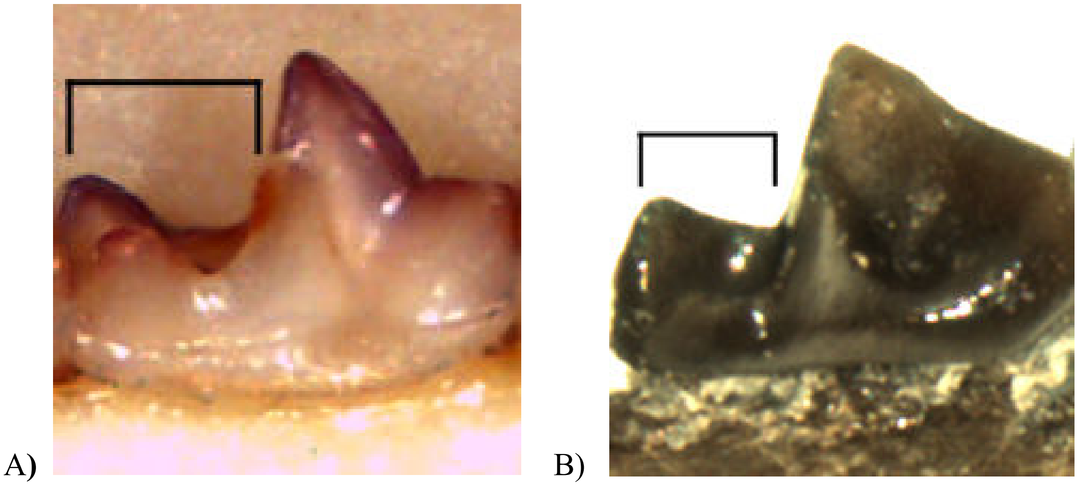

Figure 28. The number of cusps in the talonid of the lower third molar is also a very helpful character because of the tendency of certain taxa to reduce their talonid basin. Example of a A) basal talonid and a B) reduced talonid.

Character 36: A non-perpendicular ramus is only found in the tribe Beremendini (Rofes and Cuenca-Bescos 2009a; Rofes and Cuenca-Bescos 2009b) (Figure 29), if a member of the tribe is not present in the analysis then the character is not useful.

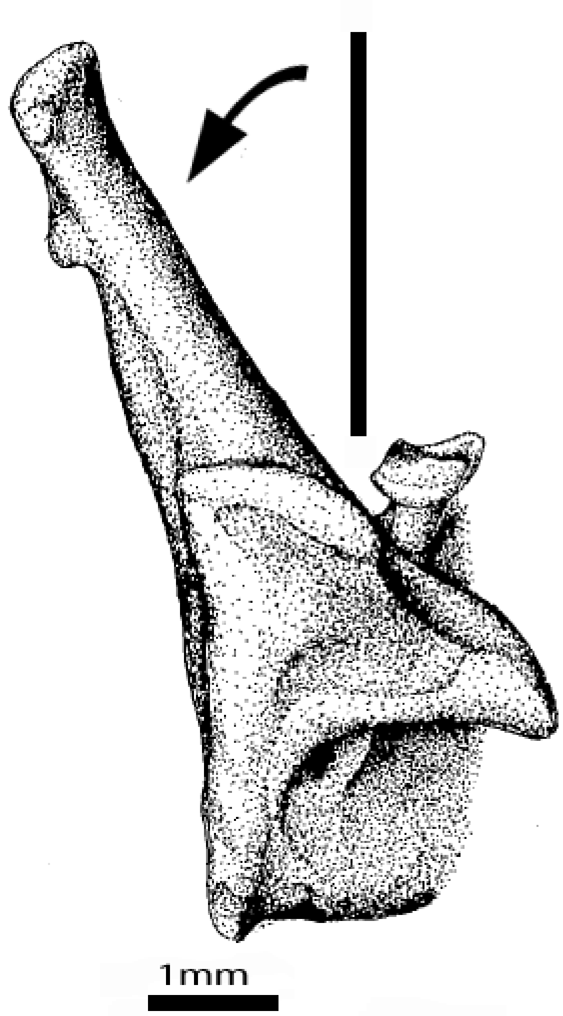

Figure 29. A non-perpendicular ramus is only found in the tribe Beremendini. Pictured is *Lunanosorex* with a view of the articular condyle. Modified from Jin and Kawamura (1996).

Character 37: The lean of the coronoid process is very plastic (Rychlik et al.2006; Young and Badyaev 2006) and may be helpful when parsing out some groups, but it should not be heavily relied on (Figure 4).

Characters 38-40: The size and pronunciation of the coronoid spicule and the depth of the external temporal fossa are integrated traits. Change in one or two should indicate differentiation at the species level, while a change of all three should allocate the differentiation of genera (Figure 4).

Character 43: Presence of an internal temporal fossa bar implies a difference in musculature that is only present in select groups making it a helpful character (Figure 12).

Character 44: Depth or absence of the symphyseal fossa appears to be a good trait for showing relationships. The problem with the character is that the mandible is often broken on or before the symphyseal fossa (Figure 3).

Appendix C

List of 17 soricid characters used in the data matrix of the phylogenetic analysis including 17 character states. Primitive state based on comparisons with genus *Domnina*.

1. I1 apex: **(0)** bifid; **(1)** non-bifid.
2. AA number: **(0)** five; **(1)** four; **(2)** three **(3)** two. Excluding P4 which is not an AA.
3. AA postero-lingual cusps: **(0)** absent; **(1)** present.
4. P4 posterior emargination: **(0)** absent; **(1)** weak; **(2)** strong.
5. P4 protocone: **(0)** absent; **(1)** present.
6. P4 hypocone development: **(0)** poor; **(1)** good.
7. M1 posterior emargination/ hypoconal flange (present with emargination): **(0)** absent; **(1)** present.
8. M1 hypocone: **(0)** present; **(1)** absent.
9. M1 hypocone development: **(0)** poor; **(1)** good.
10. i1 **(0)** tricuspulate/tetracuspulate; **(1)** bicuspulate; **(2)** monocuspulate; **(3)** acuspulate.
11. p4 postero-lingual basin: **(0)** deep; **(1)** shallow; **(2)** absent.
12. m1 entoconid crest: **(0)** present high; **(1)** present low **(2)** absent.
13. m3 number of cusps in talonid: **(0)** two; **(1)** one.
14. Ascending ramus to vertical ramus: **(0)** perpendicular; **(1)** not perpendicular.
15. Coronoid spicule: **(0)** small; **(1)** large **(2)** absent.
16. Coronoid spicule: **(0)** weak; **(1)** pronounced.
17. Internal temporal fossa horizontal bar: **(0)** absent; **(1)** present.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
S. ertmentensis	0	?	?	1	1	1	1	0	0	0	0	0	0	0	0	1	1
S. minutoides	0	?	?	1	1	1	1	0	1	0	0	0	0	0	2	0	1
S. bor	1	0	?	1	1	1	1	1	0	0	0	0	0	0	0	0	0
S. minutus	0	0	0	?	1	0	1	0	0	0	0	1	0	0	2	0	0
S. fumeus	0	0	0	2	1	1	1	0	1	1	0	1	0	0	0	0	0
D. kordosi	1	?	?	?	1	0	0	1	0	1	?	0	0	0	1	1	0
D. janossyi	1	0	1	1	1	0	0	1	0	0	0	1	1	0	1	1	1
Z. kormorsi	1	?	?	1	1	0	1	0	0	0	1	1	0	0	0	1	1
Z. soriculoides	?	1	?	1	1	0	1	0	1	1	0	1	1	0	0	0	0
P. hungarica	1	1	0	0	1	0	1	0	0	1	0	0	1	0	1	1	0
N. fodiens	1	0	0	2	1	1	1	0	1	2	0	1	0	0	0	0	0
N. newtoni	0	?	?	?	?	1	?	0	1	?	0	1	0	0	0	0	0
Al. europeoa	1	0	0	1	0	0	?	1	0	1	1	0	1	0	?	?	1
Bl. quadraticauda	?	?	?	?	?	?	1	0	1	1	1	1	?	0	0	1	0
"Blarinella" dubia	?	?	0	1	1	0	1	1	0	1	1	0	1	0	0	1	1
A. sincia	1	?	?	0	0	0	?	0	0	0	?	0	1	0	1	1	0
Ad. berklandi	?	?	?	?	?	?	?	?	?	?	?	2	?	0	1	1	1
B. brevicauda	1	0	1	1	1	1	1	0	1	1	1	2	0	0	1	1	0
C. parva	1	1	1	2	1	1	1	0	1	2	1	2	1	0	1	1	0
"C". meadensis	?	?	?	?	?	?	?	?	?	?	2	?	1	0	0	0	?
P. rex	1	1	0	?	1	1	0	0	1	3	?	2	1	0	1	1	0
T. holmani	?	?	?	?	?	?	?	?	?	3	?	1	1	0	0	0	0
T. sp. nov.	?	?	?	?	?	?	?	?	?	3	?	1	1	0	2	1	1
Al. chaseae	?	?	?	?	?	?	?	?	?	0	0	0	?	0	?	?	?
Al. arcadensis	?	?	?	?	?	?	?	?	?	0	0	0	?	?	?	?	0
Anchiblarinella	?	?	?	?	?	?	?	?	?	?	0	0	1	0	1	1	0
P. concisus	?	?	?	?	?	?	?	?	?	?	?	?	1	0	0	1	0
Antesorex	?	?	?	2	1	0	1	0	0	?	1	0	0	0	1	1	0
Bekiasorex	?	?	?	?	?	?	?	?	?	?	?	2	?	0	2	0	0
Notiosorex	1	2	0	2	1	0	1	0	1	2	0	1	0	0	0	0	0
gen. et sp. nov.	1	0	0	0	1	1	0	0	0	1	1	0	0	0	0	0	1
Paenepenenyia	1	0	?	2	0	0	1	0	?	1	0	0	1	0	1	1	1
Domnina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
M. csarnotensis	1	?	?	0	1	0	1	1	0	?	0	2	?	0	0	0	0
Blarinoides aliciae	1	?	?	1	1	1	0	0	1	0	?	2	0	0	?	?	?
Bl. mariae	1	0	?	1	1	1	0	0	1	1	0	2	1	0	1	1	1
ETMNH13343	?	?	?	1	1	0	1	0	0	?	?	1	0	?	?	?	?
Berimendia fissidens	0	1	0	2	1	1	1	0	0	3	1	1	0	1	1	1	0
Lananosorex	?	?	?	?	?	?	?	?	?	3	1	1	0	1	1	1	0
GFS mystery	?	?	?	?	?	?	?	?	?	?	?	1	1	0	1	1	0

Appendix D

Translation of the description of Hemisorex from German, Ziegler (1989)

The lower jaw fragment from Stubersheim 3 cannot be assigned to the admitted taxa based on the strong morphometric deviation. It is distinguished by strongly reduced rust colored central part, with only 2 antemolar alveoli whose back part is bigger (?). The edge of the rust colored center is easily worn off, but the damage did not result in the loss of an alveolus. Therefore the mental foramen lies under the trigonid of the m1 and or under the aboral antemolar alveoli. The incisor has only one root. Of both molars, especially of the m1they are comparatively amblyodont and easily exoedaenodont. It has a free ending hypolophid and a short but strong entocristid a continuous thin but strong cingulum that pulls that on the paraconule over the labial side to entostylid (hypoconulid) The lingual cingulum is wider, but very weak. The hypoflexid is high especially on the m1, through which the hibitus compact (passage) is accented.

VITA

JOSHUA DOBY

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Published Abstracts:

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