Anchitheriomys buceei (Rodentia, Castoridae) from the Miocene of Texas and a review of the Miocene beavers from the Texas Coastal Plain, USA

Steven R. May and Matthew A. Brown

ABSTRACT

The record of fossil beavers from Miocene age strata in the Texas Coastal Plain is sparse. The first occurrence of fossil beavers is in Arikareean age faunas. One fossil beaver specimen was reported from a Hemingfordian fauna near Navasota, TX. Both *Monosaulax* and *Anchitheriomys* are described here from multiple early Barstovian faunas including a new taxon, *Anchitheriomys buceei*. The taxon, *A. buceei,* was a relatively large beaver, similar to *A. fluminis* in size, and shares characters with both *A. fluminis* and *A. nanus*. The holotype of *Anchitheriomys buceei* is a partial skull and endocast that preserves key features of the orbital foramina and palatine. Referred specimens include a partial dentary, isolated cheek teeth, and two post-cranial elements. The co-occurrence of this taxon and a small beaver identified as *Monosaulax* sp. in early Barstovian faunas is coeval with the first occurrence of proboscideans along the Texas Coastal Plain. Beavers are unknown in late Barstovian and Clarendonian faunas, although rodent fossils are uncommon from these faunas in general. Most of the fossil beaver specimens were obtained in the early twentieth century by collectors affiliated with Dr. Mark Francis at Texas A&M University, or with the State-Wide Paleontologic-Mineralogic Survey in Texas and are curated at the Texas Vertebrate Paleontology Collections. Archival materials housed at that facility have been instrumental in unraveling the history of collection, the distribution of localities and the evolving understanding of Miocene vertebrate biostratigraphy on the Texas Coastal Plain.

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INTRODUCTION

The specimens described below are curated at the Texas Vertebrate Paleontology Collections at The University of Texas at Austin. Some of the material was initially housed in a museum at Texas A&M University. Most of the Texas A&M collection was assembled under the direction of Dr. Mark Francis, a veterinarian at the university and an early champion of Texas vertebrate paleontology. Dr. Francis and his colleagues collected fossil vertebrates from the Texas Coastal Plain from the late 1800s through the 1930s. Some of this material was being studied by C.J. Hesse, who was hired by Texas A&M in 1938, in part to act as curator of the Francis collections. Hesse's (1942) paper describing the Miocene vertebrate localities from Southeast Texas remains a valuable reference, however, due to his death in 1945, much of the work Hesse started was left unfinished. The museum at Texas A&M was demolished in 1972 and many of the specimens were sent to Austin. In 1983, the collection was formally transferred by the President of Texas A&M to The University of Texas at Austin. Additional specimens described below were collected by the State-Wide Paleontologic-Mineralogic Survey conducted by the Works Progress Administration (WPA) under the direction of the University of Texas Bureau of Economic Geology (BEG) from 1939-1942. A few castorid specimens were later added in the 1950s by John A. Wilson and his students.

A number of papers have been published on Miocene vertebrates from the Texas Coastal Plain including Quinn (1952, 1955), Wilson (1956, 1960), Patton (1969), Forsten (1975), Webb and Hulbert (1986), Hulbert (1987a, 1987b, 1988a, 1988b), Prothero and Manning (1987), and May (2019). With a few exceptions, fossil rodents are poorly represented in the Miocene faunas. Wood and Wood (1937) described two castorid teeth from the Arikareean Cedar Run Local Fauna and Albright (1998) described a series of isolated teeth from the Toledo Bend Local Fauna of similar age in far east Texas. A review of all material in the TMM collection has resulted in the recognition of multiple specimens described here representing two different castorid taxa from a number of early Barstovian faunas. A large beaver is identified as a new species of *Anchitheriomys*, and a small beaver is identified as *Monosaulax* sp. Many of these specimens had been recognized as castorids on specimen cards, but not described in publication. Following these early Barstovian (Ba1) occurrences, there is a gap in the record of fossil beavers from the Texas Coastal Plain from the late Barstovian through the Pliocene. Relatively rare specimens of *Castor* and *Castoroidies* are known from the Quaternary although most specimens are from cave faunas of the Edwards Plateau region. *Castor canadensis* is a common element of modern faunas in the Texas Coastal Plain.

Materials and Methods

Abbreviations. AMNH, American Museum of Natural History; F:AM, Frick Collection, American Museum of Natural History; TAMU, Texas A&M University; TMM, Texas Vertebrate Paleontology Collections, The University of Texas at Austin; UCMP, Museum of Paleontology University of California, Berkeley; USNM, United States National Museum (Smithsonian Institution); NALMA, North American Land Mammal Age; AP, anteroposterior; HI, hypsodonty index; I incisor; M, upper molar; m, lower molar; P, upper premolar; p, lower premolar; TRL, tooth row length; L, left; R, right; mm, millimeters. Specimens and archival material at The University of Texas at Austin are curated in the Texas Vertebrate Paleontology Collections. Locality numbers are formatted TMM ##### and specimen numbers include the locality number, followed by a dash and the catalog number, i.e., TMM #####-####. Records of Mark Francis, Curtis Hesse, John Wilson and the Statewide Paleontologic-Mineralogic Survey are housed in the Texas Vertebrate Paleontology Archives.

Anatomical Terminology. Dental terminology used here is based on Stirton (1935) and the cranial terminology used for *Anchitheriomys* is based on Korth and Emry (1997).

Faunal Terminology. The terms local fauna and fauna are used following the definitions in Woodburne (2004). Locality, local fauna, and fauna names have been complicated historically by varied use in publications, archival records and specimen cards. We have largely followed the use of local fauna names as described in Tedford et al. (2004) for the Texas Coastal Plain.

Preparation. Fossils were originally prepared prior to this study by preparators at both The University of Texas and Texas A&M University using undocu-

mented methods and materials. However, techniques likely followed the Handbook of Recommended Procedures (McAnulty, 1939) as outlined by Brown (2013). During this study, additional preparation was performed on TMM 40197-2665 by Deborah Wagner and Matthew Brown, and on TMM 31244-6 by Brown. Matrix was removed from the left and right orbital walls and palate to expose foramina, around the posterior margins of the palate, and other diagnostic areas of TMM 40197-2665. A rotated and displaced M3 was also removed from the matrix. Care was taken to preserve the endocast while uncovering additional bone surfaces. All preparation was done with a carbide needle and pin vise or an HW-1 airscribe under 10-50x magnification using a Wild M8 binocular microscope. Paraloid B-72 (Rohm & Haas) was used to consolidate friable bone. An unknown yellowed resin (possibly Duco Cement) was removed from TMM 31244-6, as well as a paper label attached with string and adhesive. A small amount of preparation using a pin vise was performed by Brown on TMM 1465-1.1 (*Anchitheriomys nanus*) to better expose foramina in the palatine region.

Photography. Specimens were photographed using an iPhone 11 or a Canon Power Shot D20 and processed using Adobe Photoshop.

Computed Tomography (CT). All CT imaging was performed at The University of Texas High-Resolution X-ray CT Facility at The University of Texas at Austin using a North Star Imaging micro-computed tomography scanner with a Fein Focus High Power source and a Perkin Elmer detector. TMM 40197-2665 was scanned at kV = 150; μA = 130 with a voxel size of 0.0799 mm x 0.0799 mm x 0.0799 mm. TMM 31244-6 was scanned at kV = 120; μA = 100 with a voxel size of 0.0914 mm x 0.0914 mm x .0914 mm. TMM 1465-1.1 was scanned at kV = 185; μA = 185 with a voxel size of 0.0417 mm x 0.0417 mm x 0.0417 mm. Scans are archived at https://www.morphosource.org. ImageVis3D, ImageJ, and Avizo software were used to visualize and analyze the CT data.

MIOCENE STRATIGRAPHY OF THE TEXAS COASTAL PLAIN

Wilson (1956) reviewed the history of stratigraphic terminology and vertebrate biostratigraphy from Miocene strata of the Texas Coastal Plain. In that paper, he used the name Oakville Formation containing the Garvin Gully fauna and the Fleming Formation containing the younger Burkeville and Cold Spring faunas. However, Plummer (1932) and

Renick (1936) had previously elevated the Fleming to group status composed of the underlying Oakville Formation and the overlying Lagarto Formation. Recent authors (Galloway et al., 1986; Young et al., 2010) consider the Oakville and Lagarto Formations to be part of the Fleming Group, and that is the stratigraphic nomenclature used here (Figure 1).

The Fleming Group includes a number of large fluvial systems in up-dip areas that transition to deltaic and marginal marine systems down-dip and to fully marine offshore (Galloway et al., 1986; Morton et al., 1988). Measured thicknesses from outcrop include 215-430 meters in the Lagarto Formation and 90-215 meters in the underlying Oakville Formation (Galloway et al., 1986). Recognition of the up-dip, non-marine subdivisions of the Fleming Group is difficult. While the Oakville Formation is mapped in some areas, the Fleming Group is recognized as undifferentiated in others. Furthermore, the boundary between the Catahoula Formation and the Fleming Group is not well defined (Albright, 1998). In the offshore Gulf of Mexico, the formations of the Fleming Group thicken significantly. The Oakville Formation is a sandy progradational sequence above a maximum transgression associated with the Anahuac Shale. The Lagarto Formation is muddy with an aggradational to retrogradational architecture, including a peak transgression near the top of the formation associated with the *Amphistega* B Shale (Galloway et al., 1986). Projection of the maximum flooding surface up-dip into the outcrop is uncertain, but a possible candidate is the marginal marine facies described within the Fleming Group near Burkeville, Texas (Stenzel et al., 1944). Marine fossils from this area, as identified in Stenzel et al. (1944), include ray teeth, an oyster, and a foraminifer. As will be discussed later, the age of the Burkeville Local Fauna is early Barstovian (Ba1) consistent with the Langhian age for the *Amphistega* B transgression (Figure 1).

Because formations of the Fleming Group are difficult to differentiate in up-dip outcrop areas of the Texas Coastal Plain, detailed stratigraphic correlation between localities is not possible. The relative stratigraphic positions of local faunas from the Fleming Group are based on general location with respect to the lower and upper lithostratigraphic boundaries. While the upper boundary with the Goliad Formation is reasonably well constrained, the lower boundary with the Catahoula Formation is often problematic.
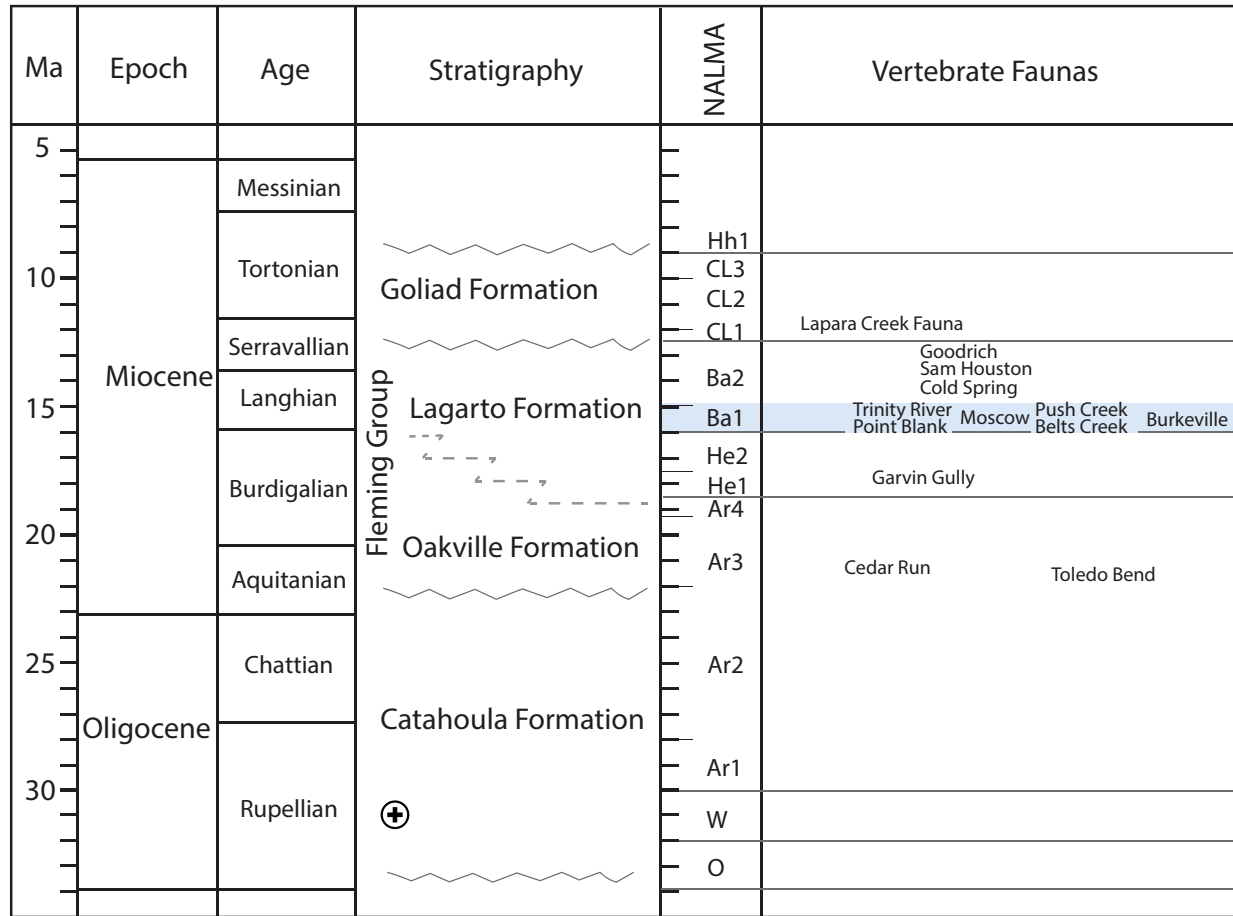
Ma	Epoch	Age	Stratigraphy	NALMA	Vertebrate Faunas
5					
	Miocene	Messinian		Hh1	
10		Tortonian	Goliad Formation	CL3, CL2	
		Serravallian		CL1	Lapara Creek Fauna
		Langhian	Lagarto Formation (Fleming Group)	Ba2	Goodrich, Sam Houston, Cold Spring
15				Ba1	Trinity River, Point Blank, Moscow, Push Creek, Belts Creek, Burkeville
		Burdigalian		He2	Garvin Gully
				He1	
20			Oakville Formation	Ar4	
		Aquitanian		Ar3	Cedar Run, Toledo Bend
25	Oligocene	Chattian		Ar2	
			Catahoula Formation		
30		Rupellian	⊕	Ar1	
				W	
				O	

FIGURE 1. Miocene stratigraphy and temporal distribution of vertebrate faunas. Stratigraphy primarily based on Galloway et al. (1986) and reflects marine biostratigraphic control in down-dip locations. Symbol in the Catahoula Formation identifies approximate age of multiple Ar/Ar radiometric dates (Jordan et al., 2019). Blue bar highlights the Ba1 North American Land Mammal Age (NALMA). Time scale from Hilgren et al. (2012); Raffi, Wade and Pälike (2020). O = Orellan, W = Whitneyan, Ar = Arikareean, He = Hemingfordian, Ba = Barstovian, CL = Clarendonian, H = Hemphillian. Names shown for the vertebrate assemblages are local fauna names except for Lapara Creek Fauna (composed of multiple local faunas), and Belts Creek (single locality with three known taxa).

Based on correlation of outcrop and subsurface, both planktonic and benthonic foraminifera constrain the age of the Oakville Formation to be Aquitanian through middle Burdigalian with the Lagarto Formation being middle Burdigalian through Langhian (Galloway et al., 1986). According to the time scale of Hilgren et al. (2012); Raffi, Wade and Pälike (2020), this correlation suggests that the Oakville Formation would be largely Arikareean (Ar3-Ar4) through early Hemingfordian (He1) in age and the Lagarto Formation would be late Hemingfordian and Barstovian (Figure 1). Although generally consistent with ages interpreted from the fossil vertebrates, late Barstovian (Ba2) faunas from the Lagarto Formation suggest that the upper part of the Fleming Group extends into the early Serrivalian.

Considering the vertebrate faunas, the age of the lower part of the Fleming Group may become younger from the Hemingfordian Garvin Gully locality on the west to the early Barstovian Moscow and Belts Creek localities to the east. However, as discussed previously, the Catahoula Formation – Fleming Group boundary is not well defined and this apparent diachroneity may be an artifact of geologic mapping (Albright, 1998).

MIOCENE VERTEBRATE BIOSTRATIGRAPHY

Two Arikareean local faunas (Cedar Run, Toledo Bend) include the three equids *Archaeohip-*
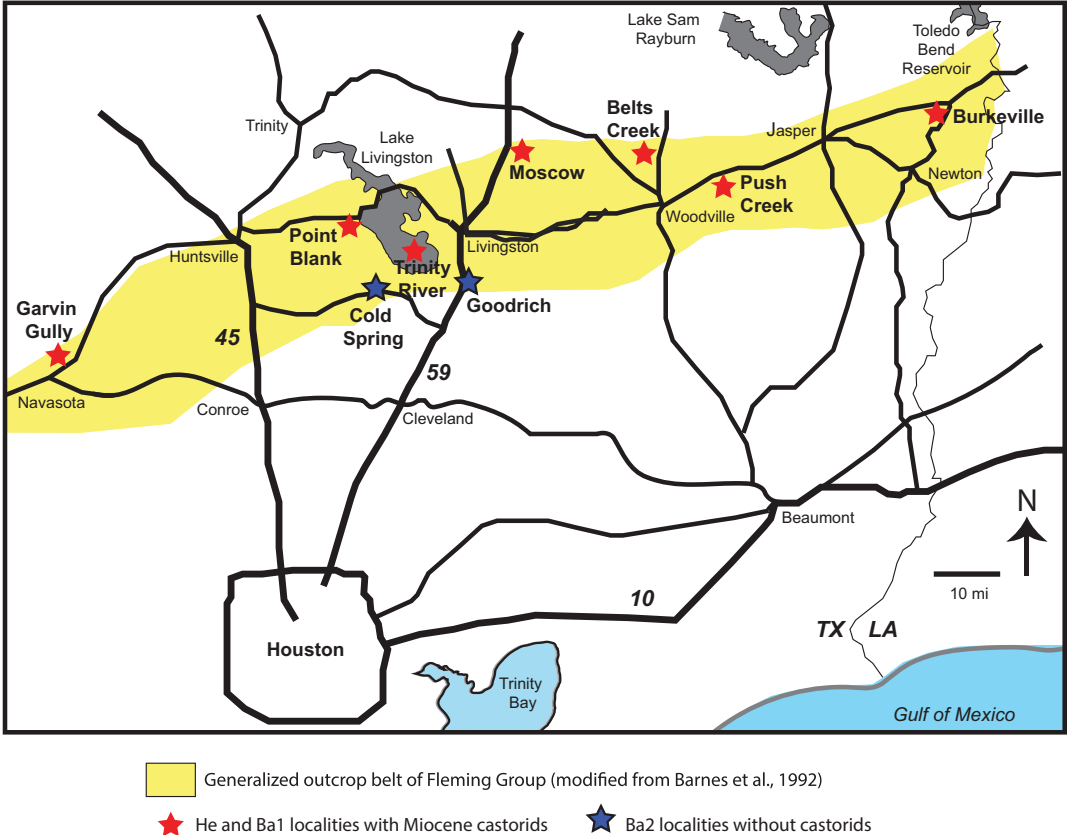
FIGURE 2. Distribution of selected vertebrate localities in the Fleming Group. See Table 1 for locality names, numbers, and associated faunal names.

pus, *Anchippus,* and *Miohippus* along with *Diceratherium, Prosynthetoceras, Floridatragulus, Daphoenodon,* and *Dinohyus* (Albright, 1998). The Hemingfordian fauna associated with the Garvin Gully localities includes the horses *Archaeohippus, Anchitherium,* and *Parahippus*, a diverse suite of camelids and *Prosynthetoceras* as well as the rhino *Menoceras barbouri* (Prothero and Manning, 1987) and the carnivore *Amphicyon*.

Vertebrate faunas from the early Barstovian (Ba1) localities (Point Blank, Belts Creek, Trinity River, Moscow, Push Creek, Burkeville, Figure 2; see Table 1 for locality names, numbers, and associated faunal names) are characterized by the continued presence of *Prosynthetoceras* and *Floridatragulus*, but also by the appearance of horses with hypsodont cheek teeth commonly assigned to *Merychippus, Protohippus,* and *Cormohipparion* (MacFadden, 1984). Instead of the single genus *Menoceras*, rhinos included *Aphelops, Peraceras,* and *Teleoceras,* all of which continued through the Ba2 Cold Spring Fauna (Prothero and Manning, 1987). The carnivores *Paratomarctus* (Wang et al., 1999) and possibly

TABLE 1. Local fauna names, locality descriptors, and counties for fossil castorid occurrences discussed in this paper. A number of these local faunas include additional localities that lack castorids. Archival records for TMM 71 (Point Blank) are somewhat uncertain. Our use of this locality descriptor is based on Hesse (1942) and locality maps at The University of Texas Vertebrate Paleontology Collections.

Local Fauna	Locality	County
	TMM 40622 (Belts Creek)	Tyler
Burkeville	TMM 40197 (TAMU 42)	Newton
Cedar Run	TMM 40068 Cedar Creek, Derrick Farm	Washington
Garvin Gully	V-3507 (Floyd Quarry)	Washington
Moscow	TMM 31057 (Barringer Farm)	Polk
Point Blank	TMM 71 (TAMU 71) TMM 31244 (Wanza Farm)	San Jacinto
Push Creek	TMM 40623	Tyler
Toledo Bend	TMM 43231	Newton
Trinity River	Pit 1 (AMNH)	San Jacinto

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Tomarctus (T. brivirostris from Noble Farm according to Wang et al., 1999) and the procyonid *Edaphocyon* (Wilson, 1960) appeared in the Ba1 faunas as well. Based on studies of various vertebrate groups, Tedford et al. (2004) considered the Point Blank, Trinity River, Moscow, and Burkeville Local Faunas to be Ba1 in age. Proboscideans are known from the Ba1 faunas at Noble Farm, Belts Creek, and possibly Burkeville. Stenzel et al. (1944) provided a vertebrate faunal list for the Burkeville area that included ?*Desmostylus*. Reinhart (1976) reviewed these specimens and concluded they were fragments of a proboscidean tooth or perhaps were better considered indeterminate. Further examination leads us to the same conclusion. These are the fragments listed as proboscidean from the Burkeville Local Fauna by Tedford et al. (1987) and Tedford et al. (2004).

The Ba2 local faunas from the upper part of the Lagarto Formation (Cold Spring, Sam Houston, Goodrich) are clearly differentiated by the appearance of additional horse taxa including *Calippus, Hipparion, Protohippus,* and *Neohipparion*. The carnivore *Aelurodon ferox* appears in the Goodrich and Cold Spring Local Faunas (Wang et al., 1999). The Ba2 faunas also include *Aepycamelus, Longirostromeryx,* and *Cranioceras* (Tedford et al., 2004). These local faunas were referred to as the Cold Spring fauna by Quinn (1955), Wilson (1956, 1960), and Patton (1969).

DISTRIBUTION OF MIOCENE FOSSIL BEAVERS

The oldest fossil beavers from the Texas Coastal Plain are known from two Arikareean local faunas: Cedar Run (also referred to as Cedar Creek, Derrick Farm) and Toledo Bend. Wood and Wood (1937) described a small fauna of mostly isolated bones and teeth from "stream-channel" sandstones in what they interpreted as the basal part of the Oakville Formation. Geologic mapping compiled by Barnes et al. (1992) would place the Cedar Run locality well within the bounds of the Catahoula Formation. However, as discussed by Albright (1998), the boundary between the Catahoula Formation and Fleming Group has long been problematic and was never clearly defined. Jordan et al. (2019) report an Ar40/Ar39 radiometric date of 30.65 +/- 0.06 Ma for a volcanic ash from the Catahoula Formation near Sam Rayburn reservoir in east Texas. This is consistent with other dates from the Catahoula ranging from 29.98-32.72 Ma all of which suggest a Whitneyan age (early Oligocene) for at least part of the Catahoula (Jordan et

al., 2019). Albright (1998) and Tedford et al. (2004) concluded that both the Cedar Run and Toledo Bend Local Faunas are most likely Ar3 in age or approximately 22-23 Ma. The age of the Cedar Run Local Fauna is consistent with the stratigraphic interpretation of Wood and Wood (1937) (Oakville Formation).

Wood and Wood (1937) included photos of two beaver teeth from the Cedar Run Local Fauna. AMNH No. 30088 was identified as a left p4 of *Palaeocastor* cf. *simplicidens* and AMNH No. 30090 was identified as a right M1? of *Palaeocastor* cf. *barbouri*. Albright (1998) included *Palaeocastor* cf. *P. simplicidens* and *P.* cf. *P. barbouri* in a faunal list for Cedar Run, but considered the possibility that only a single castorid taxon was present. Martin (1987) had reassigned *P. barbouri* (Stirton, 1935) to a new genus *Pseudopalaeocastor*, and Tedford et al. (2004) list both *Palaeocastor* and *Pseudopalaeocastor* in their faunal list from Cedar Run. Figure 3 illustrates a previously unreported castorid tooth from TMM 40068, which is the Cedar Run (Cedar Creek) locality of Wood and Wood (1937) that was collected by J. A. Wilson in 1950 (Wilson, 1960). TMM 40068-24 is a slightly worn left m1 with a simple hypoflexid and three simple fossettids (para, meso, and meta). It is small (3.38 mm x 4.06 mm AP x W) and has a hypsodonty index of approximately 2. The base of the enamel is preserved, but the roots are not. The hypoflexid would be lost after only modest wear leaving four
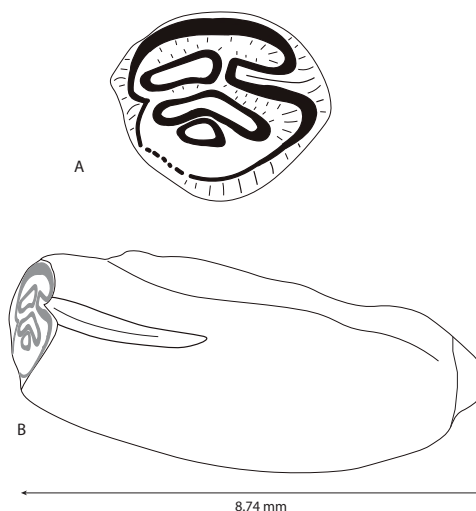

FIGURE 3. TMM 40068-24, left m1, cf. *Palaeocastor.* A – line drawing occlusal view, B – labial view.

simple fossettids. Short striae are characteristic of the palaeocastoines according to Korth (2001b). The size, occlusal pattern, and degree of hypsodonty are all similar to *Palaeocastor fossor* (Peterson, 1905). Martin (1987) described *P. fossor* as having "high-crowned cheek teeth", a character that is also illustrated in Peterson (1905). It is often difficult to identify Miocene castorids on the basis of isolated cheek teeth. Although TMM 40068-24 is closely comparable to *P. fossor*, it is here identified as cf. *Palaeocastor*.

The Toledo Bend Local Fauna from near the Louisiana-Texas border was collected from strata mapped as Catahoula Formation on the Texas side of the Red River but as Fleming Group on the Louisiana side (Albright, 1998). Albright (1998) described the stratigraphic relationships and provided a complete review of the fauna with comparisons to the Great Plains and Florida. He concluded that the Toledo Bend Local Fauna was Ar3 in age and correlative with Cedar Run. Albright (1996) identified a castorid based on isolated teeth as *"Monosaulax" hesperus* but noted a number of issues with this generic assignment. Korth (1996) proposed the species *hesperus*, (previously assigned to *Steneofiber* or *Monosaulax*) as the type species for the new genus *Neatocastor*. He described the cheek teeth as having complex occlusal patterns, sub-hypsodont and rooted. Albright (1998) listed the beaver from the Toledo Bend Local Fauna as cf. *Neatocastor hesperus*.

The record of Arikareean castorids from the Texas Coastal Plain is sparse although it appears that both Palaeocastorines and Angotocastorines may be represented. The record of Hemingfordian castorids is even more limited. The only known Hemingfordian beaver from the Texas Coastal Plain is a single tooth (UCMP 32614) from the Garvin Gully Local Fauna collected by R.A. Stirton in 1935 and is curated at the University of California Museum of Paleontology (UCMP). Unfortunately, the status of this specimen is uncertain after it was borrowed in 1990 and never returned. The Garvin Gully Local Fauna is known from a few localities northeast of Navasota, TX (Figure 2). Stirton's field notes from 1935 (UCMP archives) indicate that the UCMP material was collected at the Floyd Quarry (V-3507) and referred to as the Navasota fauna including a field identification of *"Palaeocastor"*. A sketch map with his notes suggests that the Floyd Quarry was located very close to the main Texas A&M locality, TAMU 20. Stirton's field notes refer to discussions with "Dr. Francis" about collecting sites in the area. Mark Francis and

his staff collected fossils in the Garvin Gully area from 1919-1922 (TAMU 20) resulting in a collection of numerous specimens now in The University of Texas Vertebrate Paleontology Collections. Based on correspondence in the TMM archives, Frick collectors also visited this site and there is a small collection at AMNH. Additional material was collected from Garvin Gully by The University of Texas in 1950 (TMM 31084). Wilson (1956) recognized that a number localities from the Oakville Formation (lower Fleming of others) were approximately correlative, and he referred to all of these occurrences as the Garvin Gully fauna. None of these localities other than the Floyd Quarry (V-3507) from the Garvin Gully area contain fossil castorids. Tedford et al. (1987) suggested comparison of the Garvin Gully taxa with those from the Runningwater Formation in Nebraska and Tedford et al. (2004) interpreted the Garvin Gully Local Fauna as Hemingfordian in age.

The castorids *Monosaulax* and *Anchitheriomys* are described in this paper from Ba1 faunas of the Texas Coastal Plain and make their appearance along with proboscideans, hypsodont equids *(Merychippus, Cormohipparion)* the rhinos *Aphelops, Peraceras,* and *Teleoceras*, and the carnivores *Paratomarctus*, *Tomarctus*, and *Edaphocyon*. The Moscow (= Barrington Farm) Local Fauna and Belts Creek locality are from near the lower part of the Fleming Group as mapped by Barnes et al. (1992), while the Point Blank, Trinity River, Push Creek, and Burkeville Local Faunas are from localities stratigraphically higher near the middle part of the Fleming Group. All of these faunas are interpreted as Ba1 in age based on faunal composition and stratigraphic position.

No fossil castorids are currently known from Ba2 faunas located in the upper part of the Fleming Group, nor from the Cl1-Cl2 Lapara Creek Fauna in the Goliad Formation (May, 2019) (Figure 4). Fossil castorids are not recognized again until the Quaternary of the Texas Coastal Plain where both *Castor* and one specimen assigned to *Castoroides* are present in the TMM collection.

SYSTEMATIC PALEONTOLOGY

Order Rodentia Bowdich, 1821
Family Castoridae Hemprich, 1820
Subfamily Anchitheriomyinae Korth, 2001a
Anchitheriomys Roger, 1898
Anchitheriomys buceei, new species
Amblycastor Matthew, 1918

Type Species. *Anchitheriomys suevicus* (Schlosser, 1884)

Ma	Epoch	NALMA		Washington	Grimes	San Jacinto	Polk	Tyler	Newton
12				No beavers in the early Clarendonian Lapara Creek Fauna, first occurrence of mylagaulids					
13		Ba2				Goodrich L.F.	No beavers in the Texas coastal plain Ba2 faunas		
14						Sam Houston L.F.			
15	Miocene / Barstovian					Cold Spring L.F.		Push Creek *Anchitheriomys*	Burkeville L.F. *Anchitheriomys*
16		Ba1				Trinity River L.F. *Anchitheriomys* Point Blank L.F. *Monosaulax* *Anchitheriomys*	Moscow L.F. *Anchitheriomys* *Monosaulax*	Belts Creek *Anchitheriomys*	
17	Miocene / Hemingfordian	He2							
18		He1			Garvin Gully L.F. *Palaeocastor?*				
19		Ar4							
20									
21									
22	Miocene / Arikareean	Ar3		Cedar Run L.F. *Palaeocastor*					Toledo Bend L.F. cf. *Neatocastor hesperus*
23		Ar2							

FIGURE 4. Distribution of local faunas and castorids in the Miocene strata of the Texas Coastal Plain. Texas counties displayed roughly west to east, left to right. Time scale from Hilgren et al. (2012); Raffi, Wade and Pälike (2020).

Referred Species. *Anchitheriomys fluminis* (Matthew, 1918), *Anchitheriomys tungurensis* (Stirton, 1934), *Anchitheriomys stouti* (Korth, 2001a), *Anchitheriomys nanus* (Korth, 2004), and *Anchitheriomys buceei* new species.

Range. Early to middle Miocene (Hemingfordian to Barstovian) of North America and Eurasia.

Anchitheriomys buceei new species
(Figures 5-15, Table 2)

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Type Specimen. TMM 40197-2665, partial skull with M3 and roots for P4-M3.

Referred Specimens. TMM 31057-7 LM2; TMM 31057-59 Rm2; TMM 31057-141 RM3; TMM 31057-163 Lm1; TMM 31057-185 Lm1; TMM 40622-13 LP4; TMM 40623-12 left dentary; TMM 71-2666 distal humerus, proximal ulna, TMM 71-2667 Rp4; TMM 71-2668 – molar; TMM 71-2669 – RM2. F:AM 64023A - partial left maxilla with P4; F:AM 64023B - P4; F:AM64024A edentulous partial left ramus; F:AM 64024B left lower cheek tooth. (Note: TMM 71-2770, an isolated tooth was borrowed in the 1940s and never returned. The specimen number at that time would have been TAMU 2770.)

Horizon and Locality. Lagarto Formation, Fleming Group, Burkeville, Newton Co. (TMM 40197); Push Creek, Belts Creek, Tyler Co. (TMM 40623, TMM 40622); Moscow (Barrington Farm), Polk Co. (TMM 31057); Trinity River (Pit 1 AMNH speci-

mens), Point Blank, San Jacinto Co. (TMM 71); Texas.

Age. Early Barstovian, Ba1, (middle Miocene).

Etymology. Species named in recognition of Bucee's roadside attraction travel centers that have re-popularized beavers in Texas.

Diagnosis. *Anchitheriomys buceei* is larger than both *A. stouti* from the early Hemingfordian of Nebraska (Korth, 2001a) and *A. nanus* from the early Hemingfordian of Nebraska (Korth and Martin, 2007). The cheek teeth have much simpler enamel patterns than *A. tungurensis* (Stirton, 1934). The dentary has a well-developed symphyseal flange differing from both *A. suevicus* and *A fluminis*. A relatively large mental foramen is located on the labial side of the dentary anterior to p4 and well above the midline of the horizontal ramus with much smaller foramen just anterior to the primary foramen. The ridges on i1 are much more prominent than in *A. nanus* and possess secondary corrugations along their length. *Anchitheriomys buceei* is similar to *A. fluminis* in size and elongated rostrum, but differs in having grooves on the palatine, the more posterior position of the posterior palatine foramina, a single nasolacrimal foramen, the ethmoidal foramen is located more dorsal relative to the optic foramen, and the posterior divergence of the upper cheek teeth is less pronounced. The posterior terminus of the palatine in *A. buceei* forms a broadly curving arc as in *A. fluminis* and unlike the tight u-shaped terminus in *A. nanus.* The cheek teeth are large with a very large P4/p4 relative to the molars.

Description. TMM 40197-2665 is a partial skull of a relatively large castorid that preserves portions of the cranium and dentition, with much of the cranial anatomy preserved as an endocast (Figures 5, 6). The length of the preserved skull is 152.6 mm, but with both anterior and posterior elements missing. The greatest width of the preserved rostrum is 47.3 mm, again representing a minimum value. Although the anterior portion of the rostrum is missing, the I1-P4 diastema is at least 55 mm. The depth of the skull from palate to the frontals is approximately 51 mm. This compares well with the value of 50.8 mm for the skull of *Anchitheriomys*
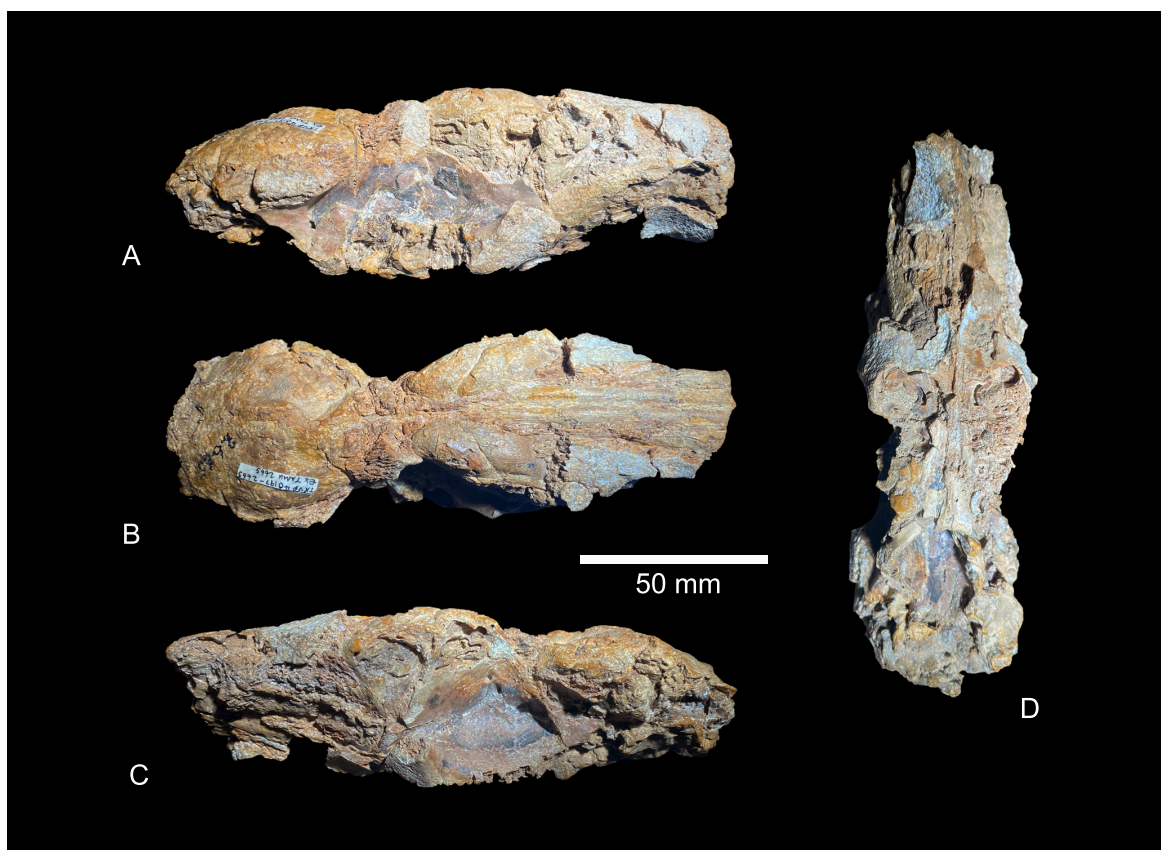

FIGURE 5. TMM 40197-2665. *Anchitheriomys buceei* (holotype), A – right side (anterior to right), B – dorsal view, C – left side (anterior to left), D – ventral view. Photographs in normal light.
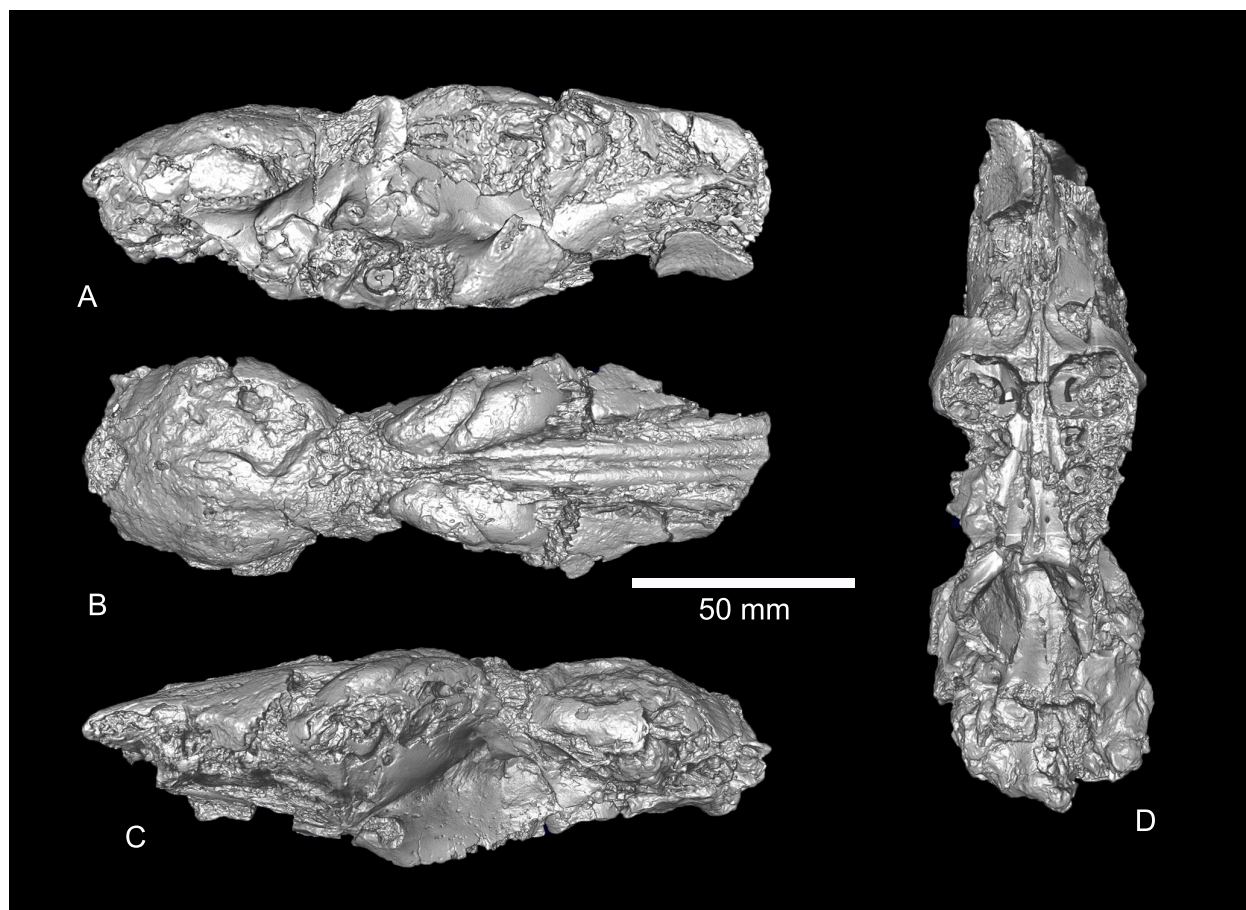
FIGURE 6. TMM 40197-2665. *Anchitheriomys buceei* (holotype), A – right side (anterior to right), B – dorsal view (anterior to right), C – left side (anterior to left), D – ventral view (anterior to top). Images rendered from CT data volume.

fluminis (USNM 299914, Korth and Emry, 1997). The size of the skull of *A. buceei* is significantly larger than the Hemingfordian taxa *A. nanus* and *A. stouti* and similar to the mid Barstovian *A. fluminis* (USNM 299914, Korth and Emry, 1997).

The upper tooth rows of *Anchitheriomys buceei* diverge posteriorly as in the skull of *A. fluminis* (USNM 299914) described by Korth and Emry (1997), but the degree of divergence is less (Figure 7). The width of the palatine on TMM 40197-2665 varies from 10.2 mm at P4 to 13.3 mm at M3. The ratio of palatal width measurements at P4 and M3 is 0.76 for *A. buceei*, but 0.56 for *A fluminis*. The two skulls of *A. nanus* described by Korth and Martin (2007) illustrate variability in this character with the larger skull at 0.67 and the smaller skull at 0.56. The anterior portion of the palatine is grooved, as in *A. nanus*, while the posterior portion is slightly concave with no distinct grooves. There is a prominent ridge along the midline of the palatine. The palatine grooves terminate anterior to the palatine foramina, similar to *A. nanus* (Korth and Martin, 2007) and unlike *A. fluminis* (Korth and Emry, 1997) (Figure 7). Recent preparation of *A. nanus* skull (TMM 1465-1.1) revealed that the palatine grooves terminate posteriorly in foramina. This appears to be the same in *A. buceei*, although the palatine bone is poorly preserved at that location. The palatine foramina are located entirely within the palatine bone as in other species of *Anchitheriomys*. Whereas *A. nanus* has a single palatine foramen on each side of the palatine bone, *A. buceei* has two, as does *A. fluminis* (Korth and Emry, 1997). The left side of the palatine includes a larger posterior foramen aligned with the middle of M3 and a smaller anterior foramen. The locations of the posterior palatine foramina in *A. buceei* are more posterior than in *A. fluminis*. The palatine/maxilla suture is not preserved, but the palatine bone extends at least to the posterior edge of M1. The posterior margin of the palatine structure in *A. buceei* forms a broadly
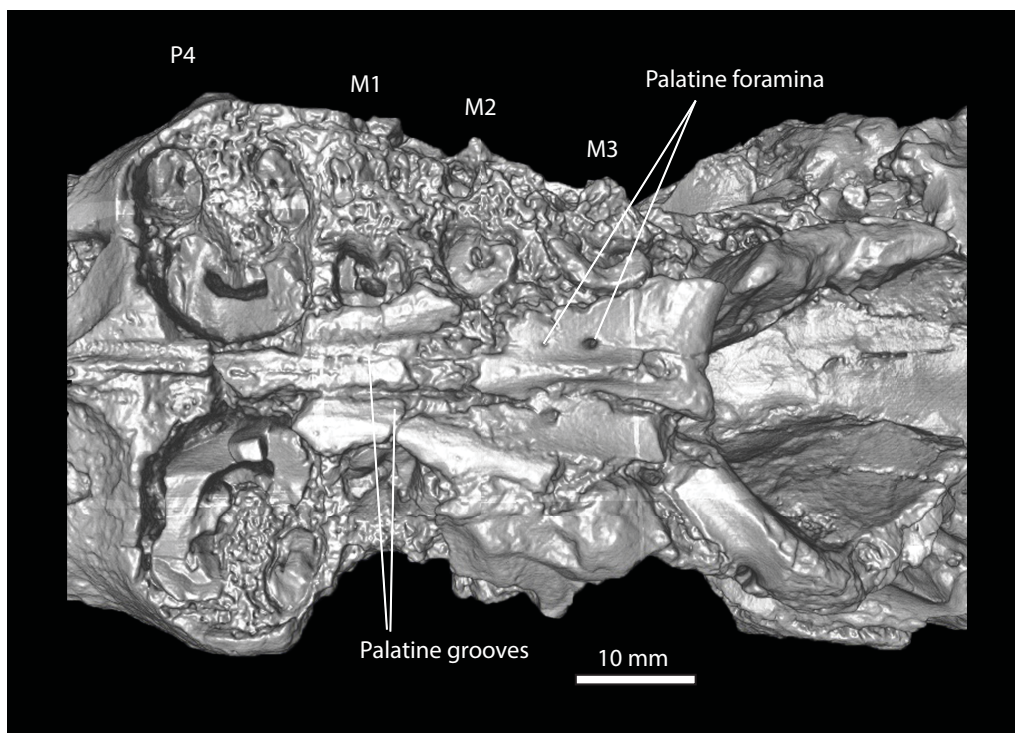
FIGURE 7. TMM 40197-2665. *Anchitheriomys buceei* (holotype), ventral view of skull, isosurface rendered from CT volume, anterior to left, illustrating roots of the upper cheek teeth, palatine grooves and foramina, posterior geometry of palatine.
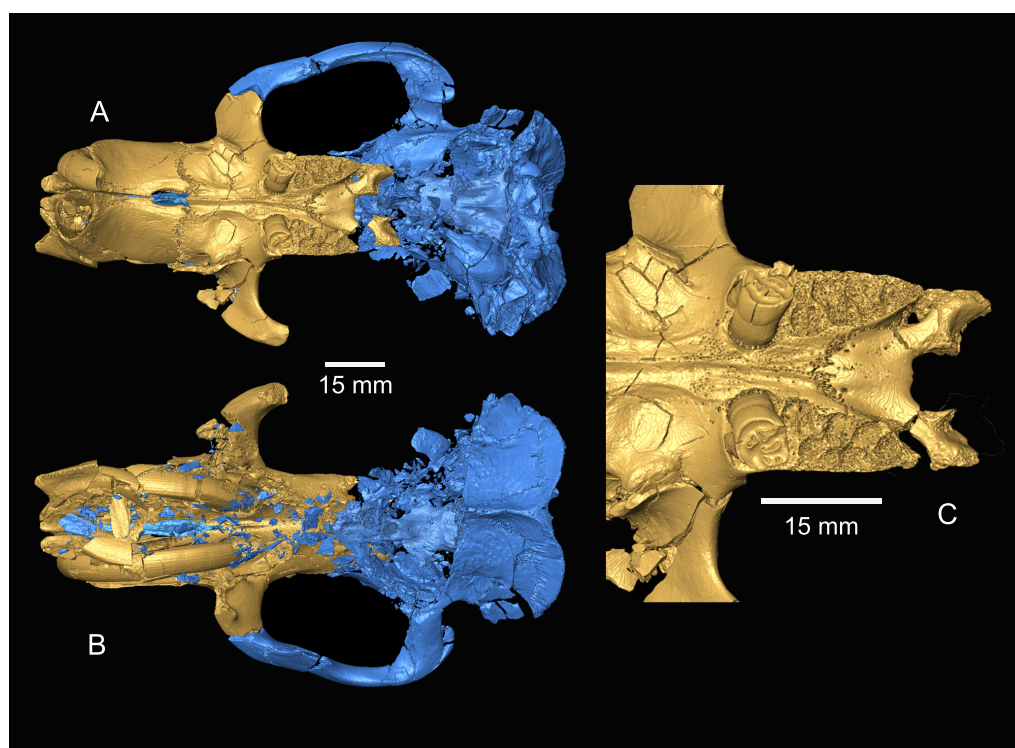

FIGURE 8. A - TMM 1465-1.1. *Anchitheriomys nanus*, isosurface rendering of CT data showing the ventral view of the skull. Bones of the palate and associated facial features are rendered in gold, anterior to the left. B – dorsal view of the skull. C – details of the palatine morphology, anterior to the left. The right pterygoid process has been restored to near its original position in the image. Grooves in the palatine are clear as is the foramen at the posterior terminus of the groove. The two teeth are right and left P4.

curving arc as in *A. fluminis* (Figure 7). In contrast, the posterior edge of the palatine in *A. nanus*, forms a narrow, u-shaped margin along with the pterygoid processes (Figure 8C).

Although the nasal bones are mostly missing on TMM 40197-2665, the endocast of the nasal cavities is long and narrow with a preserved length of 78.0 mm and a combined width of approximately 10.6 mm (Figures 9, 10). Fragments of both premaxilla are preserved. These fragments terminate at approximately the same position posteriorly probably reflecting the original suture with the frontal bones. A small bone fragment, presumably part of the right nasal, also terminates at approximately this position and the nasal cavity endocast exhibits a slight change in orientation at this position as well. The nasals and the premaxilla bones joined the frontals near the anterior terminus of the zygomatic arch. This geometry is similar to the skull of *Anchitheriomys fluminis* shown in Korth and Emry (1997).

The frontal sinus is large and bilobed with dimensions of 44.1 mm x 14.6 mm (L x maximum width) (Figures 9, 10). The infraorbital canal on the right side of the skull is relatively large with four small foramina present in two paired groups (Figure 9). A post-glenoid foramen is preserved on the right side of the skull and appears to be more rounded as in *Anchitheriomys fluminis* compared to the elongated geometry of *A. nanus* (Korth and Martin, 2007).

Approximate dimensions of the alveolus endocast for the right I1 are 12.5 mm x 11.5 mm and similar to *Anchitheriomys fluminis* (10.6 mm x 9.4 mm, 10.9 mm x 9.5 mm, I1 L x W in Korth and Emry, 1997). P4 is the largest of the cheek teeth and all cheek teeth have three roots. The lingual root is large and bladelike while the two labial roots are more peg-like (Figure 7). There is no evidence of cheek teeth anterior to P4.

Except for the right M3, only the roots of the cheek teeth are present in TMM 40197-2665. The left side tooth row is more complete with an alveolar length of ~41.6 mm. This is similar to the tooth row length of *Anchitheriomys fluminis* (41.4 mm, 39.2 mm in Korth and Emry, 1997). Measured at the roots, the left P4 is 13.1 mm x 15.3 mm. The right P4 at the roots is 12.0 mm x 14.1 mm.

The single isolated right M3 associated with TMM 40197-2665 is moderately worn. It had been rotated out of position and was prepared from the matrix of the original specimen. It is 7.8 mm x 8.3 mm (L x W) at the occlusal surface and 9.7 mm x 8.7 mm at the base of the enamel. The preserved crown height is 9.3 mm. The alveolar dimensions of the left M3 are 6.8 mm x 8.1 mm (L x W). The roots of the right M2 are also rotated so that they point laterally rather than ventrally.

The orbital foramina are well preserved on TMM 40197-2665 and imaged in the CT data (Figure 11). The size and locations of these foramina are different in detail than either *Anchitheriomys fluminis* or *A. nanus*, but are more similar to *A. nanus*. According to Korth and Martin (2007), *A. nanus* differs from *A. fluminis* in the more posterior position of the optic and ethmoidal foramina which Korth and Martin (2007) interpreted as a primitive condition. The relative locations of the ethmoidal and optic foramina in *A. buceei* are similar to *A. nanus*, but the sphenopalatine foramen is elongate and dorso-ventrally oriented, and the optic foramen is sub-circular as in *A. fluminis*. Both the optic and interorbital foramina are larger than in *A. fluminis*. The ethmoidal foramen is located more dorsal relative to the optic foramen as in *A. nanus*. The large interorbital foramen in *A. buceei* is located just dorsal to a small dorsal palatine foramen. This positioning is similar to *A. nanus* and unlike *A. fluminis*. A pair of nasolacrimal foramina are present in *A. buceei*, as in *A. fluminis*, and unlike the single foramen described in *A. nanus* (Korth and Emry, 1997; Korth and Martin, 2007) (Figure 11).

TMM 40623-12 is a partial left dentary assigned to *Anchitheriomys buceei* from the Push Creek Local Fauna (Figure 12). The dentary is robust. The medio-lateral width at the symphysis is 15.5 mm, at the diastema is 16.02 mm, at p4 is 21.7 mm, at m1 is 23.7 mm, and at m2 is 23.1 mm. The minimum dorso-ventral depth at the diastema is 22.9 mm while the depth below m1 is 30.6 mm (minimum measurement as the ventral portion of the dentary is missing). The diastema of *A. buceei* is relatively shallow compared to *A. fluminis* (FAM 64020 in Korth 2017b). The symphyseal flange (digastric process) is much better developed than in *A. suevicus* (Stefen and Mörs, 2008) and *A. fluminis* (Korth, 2017b). *Anchitheriomys stouti* (Korth, 2001a) also has a prominent symphyseal flange as does the large castorid (UF 223914) from Suwannee River, Florida (Mörs and Hulbert, 2010). Mörs and Hulbert (2010) assigned UF 223914 to *Amblycastor fluminis,* but Korth (2017b) argued that the Florida specimen is of uncertain taxonomic identity. The symphysis is oval in shape and narrows ventrally. It is 38.7 mm in dorso-ventral height with a maximum width of 23.7 mm.

A relatively large mental foramen is located on the labial side of the dentary anterior to p4 and well
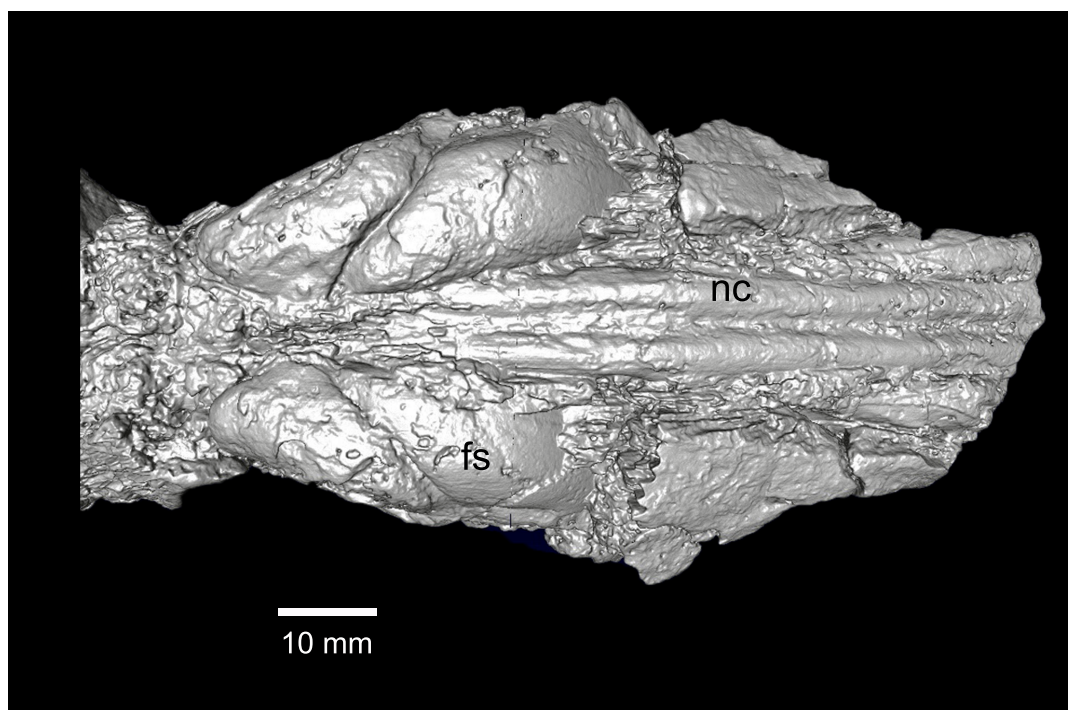
FIGURE 9. TMM 40197-2665. *Anchitheriomys buceei* (holotype), dorsal view of skull, isosurface from CT volume, anterior to the right, nc – nasal cavity, fs – frontal sinus.
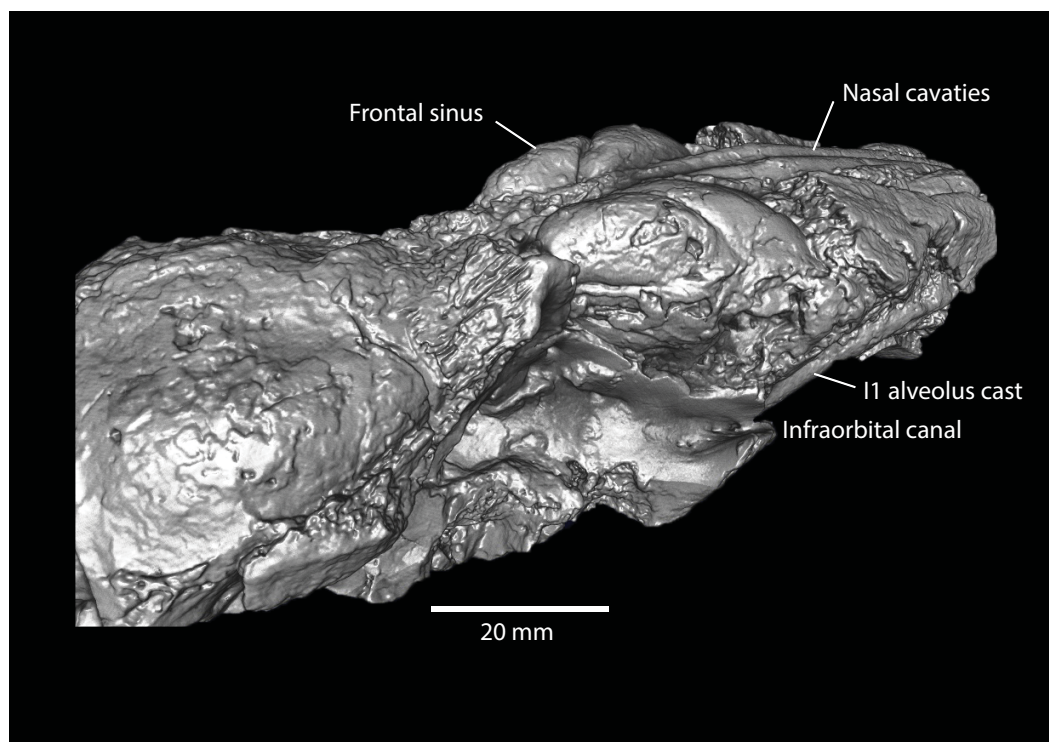

FIGURE 10. TMM 40197-2665. *Anchitheriomys buceei* (holotype), right oblique view of skull illustrating endocast of brain, frontal sinus, nasal cavity, infraorbital canal, and endocast of I1 alveolus, isosurface rendered from CT volume, anterior to right.
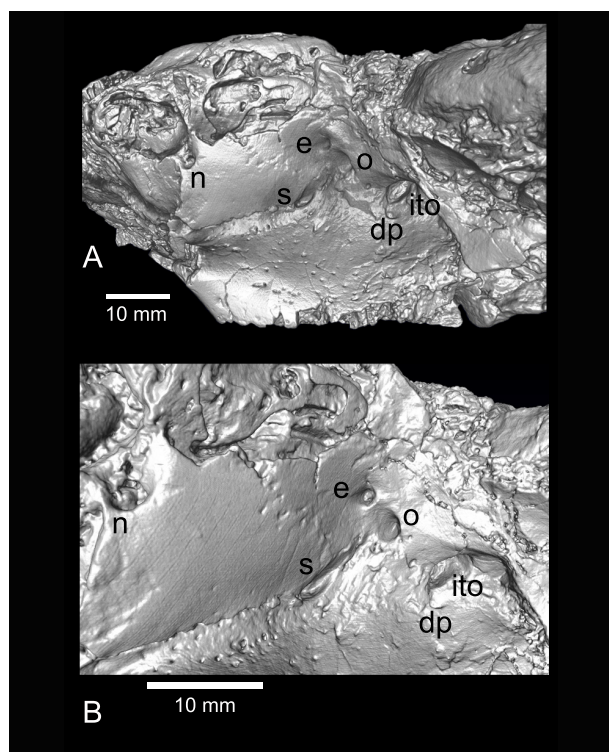
FIGURE 11 (left). TMM 40197-2665. *Anchitheriomys buceei* (holotype), lateral view of left orbital illustrating orbital foramina from CT volume. n – nasolacrimal, s – sphenopalatine, e – ethmoidal, o – optic, dp – dorsal palatine, ito – interorbital, anterior to the left. Isosurface rendered from CT volume. B – closer view of the same from a more anterior angle.

above the midline of the horizontal ramus. A much smaller foramen is located just anterior to the primary foramen. *Anchitheriomys suevicus* exhibits a single mental foramen located near the middle of the horizontal ramus (Stefen and Mörs, 2008), while *A. stouti* has a double mental foramen that is located below the center of the diastema at about the dorso-ventral midline of the horizontal ramus (Korth, 2001a). TMM 40623-12 clearly differs from both of these morphologies. *Anchitheriomys fluminis* (FAM 64020) shown in Korth (2017b) appears to have a single small foramen located near the midline of the horizontal ramus and more posterior than in *A. buceei*. However, the holotype of *A. fluminis* figured in Matthew (1918) shows a large sub-
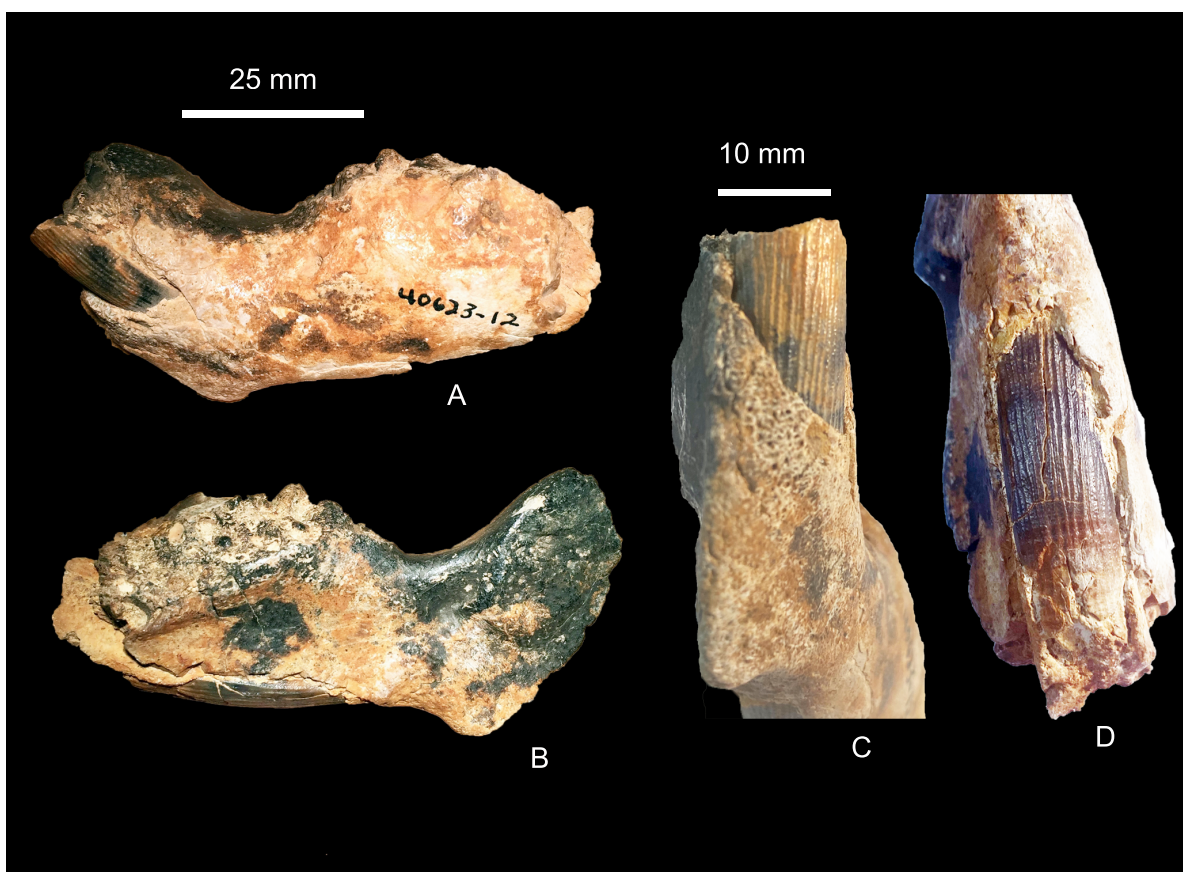

FIGURE 12. TMM 40623-12. *Anchitheriomys buceei,* partial left dentary, A – labial view anterior to the left, B – lingual view anterior to the right, C – oblique anterior view showing well developed ridges on i1 and symphyseal flange, D – ventral view showing posterior continuation of i1.
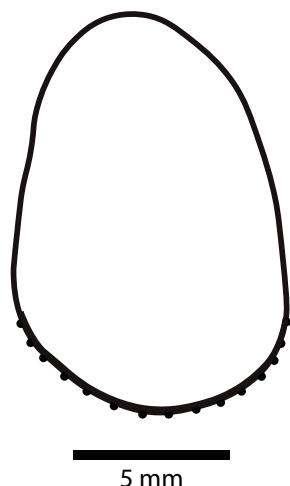
5 mm

FIGURE 13. TMM 40623-12, *Anchitheriomys buceei*, line drawing showing cross section of i1 at natural break near alveolus with general location of well-defined ridges along the anterior face.

5 mm

FIGURE 14. TMM 40623-12, *Anchitheriomys buceei*, oblique view of i1 showing corrugations on ridges of incisor.

circular mental foramen slightly posterior to the midline of the dentary.

The lower incisor of *Anchitheriomys buceei* is ovoid in cross-section with very prominent longitudinal ridges on the anterior face (Figure 13). Approximately 15-16 ridges are generally sub-parallel, but occasionally anastomose. The ridges are individually corrugated with small culminations along their length as shown in Figure 14. Because the ventral portion of the dentary is broken, the ridges can be seen to run the entire length of the incisor (Figure 12). Measured at the natural break, i1 is 12.8 mm x 11.3 mm in cross section with a preserved length of 73.5 mm. The ridges on i1 are much more prominent than in *A. nanus*.

The dimensions of p4 on TMM 40623-12 measured at the roots (alveolar) are 14.0 mm x 13.6 mm (L x W). This is much larger than *A. stouti* (Korth 2001a), *A. nanus* (Korth 2004) and near the largest reported dimensions for *A. fluminis* and *A. suevicus* (Stefen and Mörs, 2008), but smaller than the large castorid described by Mörs and Hulbert (2010). The alveolar tooth row length is difficult to measure, but is at least 39 mm.

Isolated Cheek Teeth: Six isolated upper cheek teeth are illustrated in Figure 15 including two P4s, two M2s and two M3s at various stages of wear. These teeth are from the Burkeville, Moscow, Belts Creek, and Point Blank Local Faunas. Dimensions are summarized in Table 2. TMM 40197-2665 (Figure 15) is a moderately worn R M3 that was associated with the skull of the same specimen number.

This tooth was embedded in the matrix surrounding the skull, but was rotated out of the alveolus. It has a well-developed mesoflexus that curves posteriorly and an antero-lingually oriented hypoflexus. There are four anterior fossettes and three posterior fossettes. The fossette pattern is somewhat simpler than *A. fluminis* (Korth and Emry, 1997), but more complex than *A. nanus* (Korth and Martin, 2007). The size is slightly smaller than *A. fluminis*, but significantly larger than *A. nanus*.

TMM 40622-13 (Figure 15) is a moderately worn left P4 with a well-developed mesoflexus that curves posteriorly and an antero-lingually oriented hypoflexus. The parafossette is broad and the metafossette is relatively narrow with accessory fossettes on either end. The lack of accessory anterior fossettes seems to differ from *A. fluminis* (Emry and Korth, 1997). This specimen is 9.6 mm x 10.7 mm at the occlusal surface (L x W) and broadens to 10.2 mm x 11.6 mm at the base of the enamel.
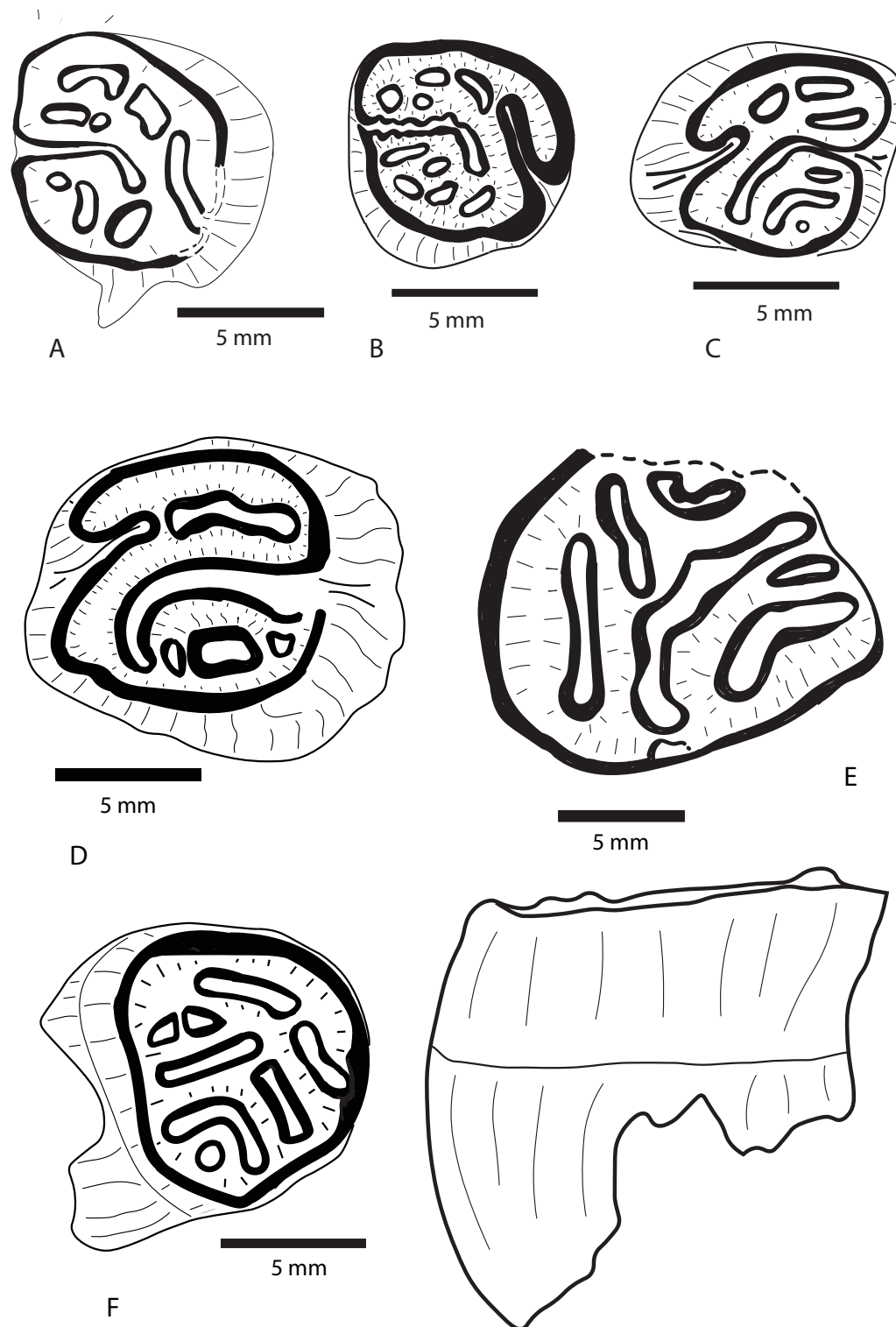
FIGURE 15. *Anchitheriomys buceei*, isolated upper cheek teeth (all measurements are L x W, anterior up). A - TMM 40197-2665 R M3, molar associated with holotype skull 7.9 mm x 8.2 mm; B - TMM 31057-141 R M3, 7.1 mm x 7.5 mm; C - TMM 31057-7 L M2, 7.33 mm x 7.38 mm; D - TMM 40622-13 L P4, 9.4 mm x 10.3 mm; E – 2666 L P4 very worn, 14.5 mm x 12.8 mm, occlusal view above, posterior view below with large blade-like root on the lingual side of the tooth; F – TMM 71-2669 R M2, 8.9 mm x 9.6 mm.

TABLE 2. *Anchitheriomys buceei*, cheek teeth dimensions.

Anchitheriomys buceei		Length (mm)	Width (mm)
TMM 40197-2665	P4 alveolar	13.1	15.3
TMM 71-2666	P4 very worn	14.5	12.8
TMM 40623-13	P4 moderately worn	9.4	10.3
TMM 31057-7	M2 occlusal	7.3	7.4
TMM 71-2669	M2 occlusal	8.9	9.6
TMM 40197-2665	M3 occlusal	7.9	8.2
TMM 31057-141	M3 occlusal	7.1	7.5
TMM 40197-2665	Tooth row alveolar (left)	41.6	
TMM 40623-12	p4 alveolar	14.0	13.6
TMM 71-2667	p4 occlusal	12.3	10.8
TMM 31057-185	m1	8.8	9.2
TMM 31057-163	m1	7.4	9.6
TMM 31057-59	m2	8.0	7.5

Four isolated lower cheek teeth are illustrated in Figure 16 including one p4, two m1's, and one m2. Three of the four specimens are from the Moscow Local Fauna (TMM 31057), and one is from the Point Blank Local fauna (TMM 71). TMM 71-2667 is the only p4 in the collection (Figure 16). It is very worn and broken, but illustrates some of the occlusal pattern. It is a large tooth measuring 12.3 mm x 10.8 mm near the occlusal surface, but broadens to 13.3 mm x 12.5 mm at the base of the enamel. This is consistent with the alveolar measurements of p4 on TMM 40623-12 of 14.0 mm x 13.6 mm (L x W). The dimensions of p4 for *A. buceei* are similar to those reported for *A. suevicus* and for *A. fluminis* and much larger than *A. nanus* and *A. stouti* (Stefen and Mörs, 2008). The occlusal pattern is similar to *A. suevicus* with crescentic and branching fossettids.

TMM 31057-185 and TMM 31057-163 are both very worn left m1s. The posteriorly directed hypoflexid is distinct. The anterior parafossetid complex includes four separate fossettids on TMM 31057-185 and only two on TMM 31057-163, while the mesofossettid is a single loop at this stage of wear. The metafossettid is a single loop on TMM 31057-185 but includes a pair of fossettids on TMM 31057-163 in addition to a small accessory fossettid. This variability is at least partly due to slight variation in the amount of wear on these two teeth.

TMM 31057-59 is a moderately well-worn right m2 with a distinct posteriorly directed hypoflexid, and a short mesoflexid. The parafossettid is crescent shaped as seen in specimens of *A. suevicus* (Stefen and Mörs, 2008). The metafossettid appears to be two separate fossettids.

Post Cranial: Two post-cranial elements were recovered from the Point Blank Local Fauna (TMM 71) (Figure 17). A distal right humerus (TMM 71-2666) and a proximal right ulna (TMM 71-2666) were associated with the box of isolated teeth labeled "topotype material" discussed above. Both specimens are broken and appear to have been tumbled. The epicondylar width of the humerus is 32.0 mm. The trochlear surface is shallow as is the olecranon fossa. There is no trochlear foramen. The lateral supracondylar ridge is not strongly developed as it is in modern *Castor canadensis*. The olecranon process of the partial right ulna is relatively short. The trochlear notch is relatively shallow and the coronoid process is not strongly developed. Based on multiple measurements of the ulna from *A. buceei* and multiple specimens of *C. canadensis* in the TMM comparative collection, this element of *A. buceei* was approximately 25-30% larger than adult specimens of the modern American beaver.

Discussion. Stenzel et al. (1944) discussed the stratigraphy and paleontology of Miocene sedimentary rocks exposed near Burkeville, TX. The area includes rocks of both brackish marine and non-marine facies including both marine invertebrate and non-marine vertebrate fossils. The significance of this stratigraphic relationship had been recognized for years and discussed in publications by Veatch (1902, 1906), Dall (1913), Ellisor (1936), Stenzel and Turner (1944), and others. In his 1942 paper, Hesse lists *Amblycastor* n. sp. (skull) from
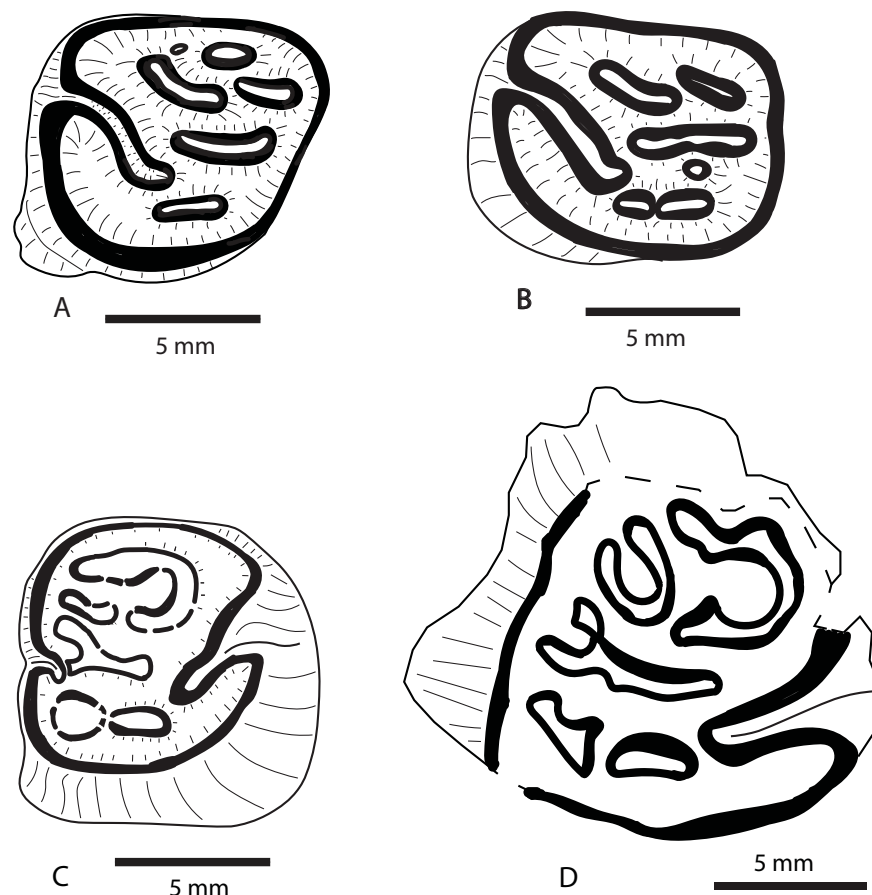
FIGURE 16. *Anchitheriomys buceei*, isolated lower cheek teeth (all measurements are L x W, anterior up). A – TMM 31057-185 L m1, 8.8 mm x 9.2 mm; B - TMM 31057-163 L m1, 7.4 mm x 9.6 mm, very worn; C - TMM 31057-59 R m2, 8.0 mm x 7.5 mm, D – TMM 71-2667 R p4, 10.6 mm x 10.8 (broken along dashed line).

the A. & M. Museum Locality No. 42 (TAMU 42) (p. 175). This is undoubtedly a reference to TMM 40197-2665. Stenzel et al. (1944) list *Amblycastor* n. sp. Hesse, without a date, but cite a paper by C.J. Hesse listed as "Fossil Vertebrates of the Burkeville Area, Newton County, Texas", American Journal of Science, in press (1944). Stenzel and Turner (1944) improperly list the name *Amblycastor stirtoni* citing the same Hesse paper as "in preparation". Hesse never described this material nor officially proposed the name in a publication, as he died in 1945. An untitled, unpublished manuscript housed in the archives at the Texas Vertebrate Paleontology Archives (Mark Francis Papers, Series I: Correspondence/Manuscripts), includes a note from Hesse: "For a description of this material see *Amblycastor stirtoni*, in the discussion of the Burkeville fauna." There is no record of that part of the manuscript, and discussion of the Burkeville fauna only includes the name *Amblycastor* n. sp.

Although it seems clear that Hesse intended to name a new species of castorid, in fact, the specimens were never described in the literature and no holotype was ever specified. Furthermore, much of the cranial anatomy has only become observable since 2019 through preparation of TMM 40197-2665. The use of *Amblycastor stirtoni*, therefore, does not conform to the International Code of Zoological Nomenclature Article 13.1, and the name used in Stenzel and Turner (1944) is a *nomen nudum*.

Four specimens of a relatively large castorid were recovered from the Trinity River Pit 1 locality by Frick collectors in 1964 and are now curated at the AMNH (F:AM 64023A, B, F:AM 64024A, B). 64023A is a partial left maxilla with P4 and 64023B is an isolated P4. F:AM64024A is an edentulous partial left ramus, while 64024B is an isolated left lower cheek tooth. Due to inaccessibility during the Covid pandemic, these specimens have only been
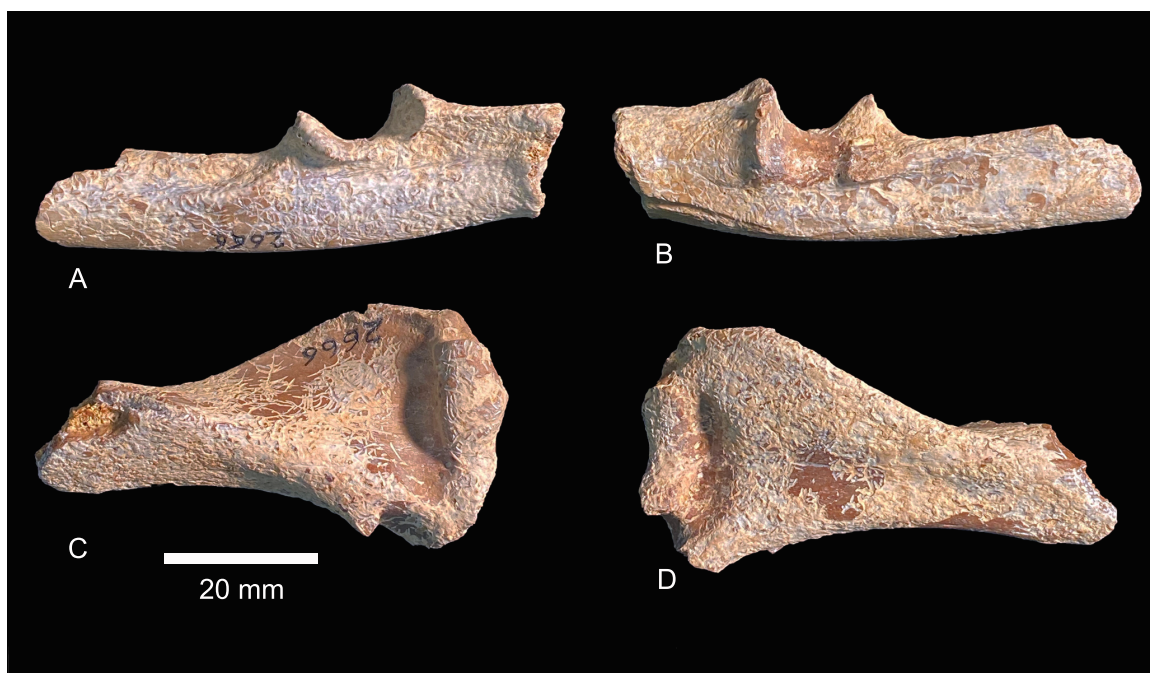
FIGURE 17. *Anchitheriomys buceei*, A, B - TMM 71-2666, proximal right ulna. C, D – TMM 71-2666 distal right humerus.

studied in photographs, but are consistent in size and morphology with *A. buceei*.

Matthew (1918) described the type material (AMNH 17213) for *Amblycastor fluminis* from the Snake Creek fauna of Nebraska. The holotype is a waterworn partial mandible with p4 and a partial i1. Additional specimens of *A. fluminis* from the Ba1 Olcott Formation have been described by Stirton (1935) and Korth (2017b). These Ba1 occurrences of *A. fluminis* include dentaries, fragments of dentaries, and isolated teeth. The skull of *A. fluminis* is only known from the Ba2 Valentine Formation (Korth and Emry, 1997). No skulls of *A. suevicus* are known from Europe. *Anchitheriomys tungurensis* is known from dentaries, partial dentaries, and isolated teeth. Stefen and Mörs (2008) reviewed the age constraints for *A. tungurensis* and concluded that it is from latest Barstovian to earliest Clarendonian equivalent faunas and therefore younger than both *A. fluminis* (Ba) and *A. suevicus* (MN5-MN6). The only other species of *Anchitheriomys* known from skull material is *A. nanus* from the early Hemingfordian Runningwater Formation in Nebraska (Korth and Martin, 2007).

The skull, dentary, and isolated teeth of *A. buceei* from the Ba1 Lagarto Formation of the Texas Coastal Plain are similar in size to *A. fluminis*, but exhibit a number of characters that differ from that taxon. Some characters are similar to *A.*

nanus such as the grooved palatine. *A. buceei* represents a permissible member of the *A. nanus – A. fluminis* lineage.

Family Castoridae Hemprich, 1820
Subfamily Castoroidinae Allen, 1877
Tribe Castoroidini Allen, 1877
Genus *Monosaulax* Stirton, 1935
Steneofiber Cope, 1874

Type Species. *Steneofiber pansus* Cope, 1874; Barstovian (Miocene), New Mexico, USA.
Referred Species. *Monosaulax curtus* Matthew and Cook (1909); *Monosaulax typicus* Shotwell (1968); *Monosaulax skinneri* (in Evander, 1999); *Monosaulax tedi* Korth (1999).
Range. Barstovian (middle Miocene).

Monosaulax sp.
(Figures 18-20)

Description. A small castorid from two Ba1 local faunas of the Texas Coastal Plain is identified as *Monosaulax* sp. based primarily on dental and mandibular morphology and size. TMM 31057-300 (Moscow Local Fauna, Barringer Farm) is a partial maxilla with P4-M3 (Figure 18). TMM 31244-6 was collected by the Statewide Paleontologic-Mineralogic Survey at the Wanza Farm locality in San Jacinto County (Point Blank Local Fauna). The specimen includes a partial mandible with fragmentary right and left i1, p4-m3. P4-M2 of presum-
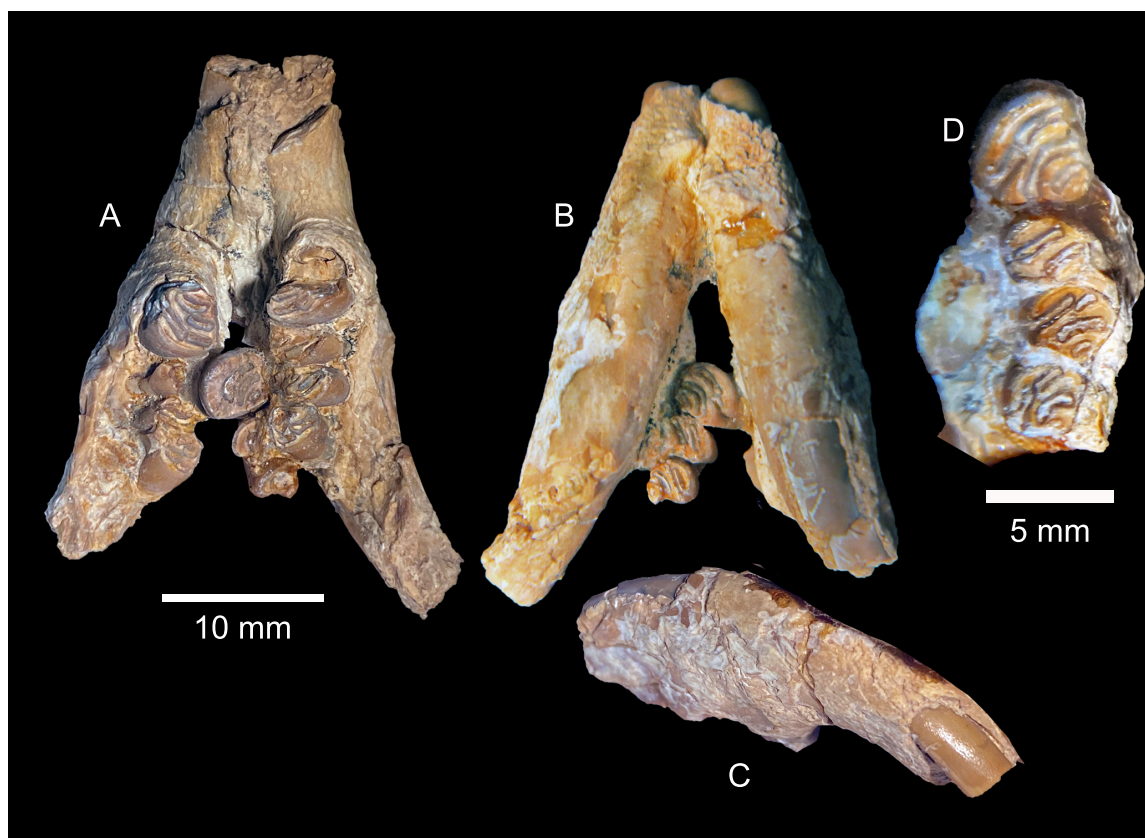
FIGURE 18. *Monosaulax* sp. A, TMM 31244-6 mandible dorsal view. B, TMM 31244-6 mandible ventral view showing occlusal surface of P4-M2 between left and right dentaries. C, TMM 31244-6 mandible ventro-lateral view showing smooth nature of anterior face of lower incisors. D, TMM 31057-300, maxillary fragment with P4-M3, occlusal view, anterior towards top.

ably the same individual is wedged between the right and left dentaries (Figure 18). This artifact of taphonomy results in a clear association of upper and lower cheek teeth. The cheek teeth are well worn in both specimens but appear to be mesodont. It is not possible to determine if the cheek teeth have two or three roots. The fourth premolar is the largest of the cheek teeth.

The incisors of TMM 31244-6 are subtriangular in cross section, rounded anteriorly, and have a slight rugosity, but lack ridges (Figure 19). The width of the left incisor where it is broken at the alveolus is 3.8 mm. The left p4 of TMM 31244-6 is 4.4 mm x 4.1 mm (L x W) at the occlusal surface but the length increases to 5.0 mm near the base of the enamel. The parafossetid is curved rather than straight, one of the characters separating *Monosaulax* from *Eucastor* (Korth, 1999). Accessory fossettes (fossettids) are absent in these two specimens and generally rare in the genus *Monosaulax* as compared to the similarly sized *Temperocastor* (Korth, 2008). At the moderate level of wear in both of the specimens, the hypoflexus (id)

is the only striae (id) still open. All others have closed as fossettes (ids) indicating that the striae (ids) are short, a primitive character for the genus and similar to *M. tedi* (Korth, 1999) and *M. typicus* (Shotwell, 1968). Because the striae (ids) are short, the molars lack the S-pattern. At a similar degree of wear, the lingual striid is still open in *M. pansus* (RAM 7618) from the Barstow Formation (Lofgren et al., 2019). Korth (1999) stated that *M. pansus* has deeper lingual striids than *M. tedi*.

Monosaulax typicus (Shotwell, 1968) from the early Barstovian of southeastern Oregon is slightly smaller than *Monosaulax* sp. from the Texas Coastal Plain, but appears to be similar in terms of crown height and length of striae (ids). The occlusal patterns of *M. typicus* figured in Shotwell (1968) are similar to *Monosaulax* sp. from Texas except that the parafossettid on p4 is straighter. Shotwell (1968) stated that the cheek teeth of *M. typicus* were shorter crowned and possessed shorter striae (ids) than *M. pansus*. *Monosaulax baylei* from the early Hemingfordian Runningwater Formation of Nebraska (Korth, 2004) is slightly larger,
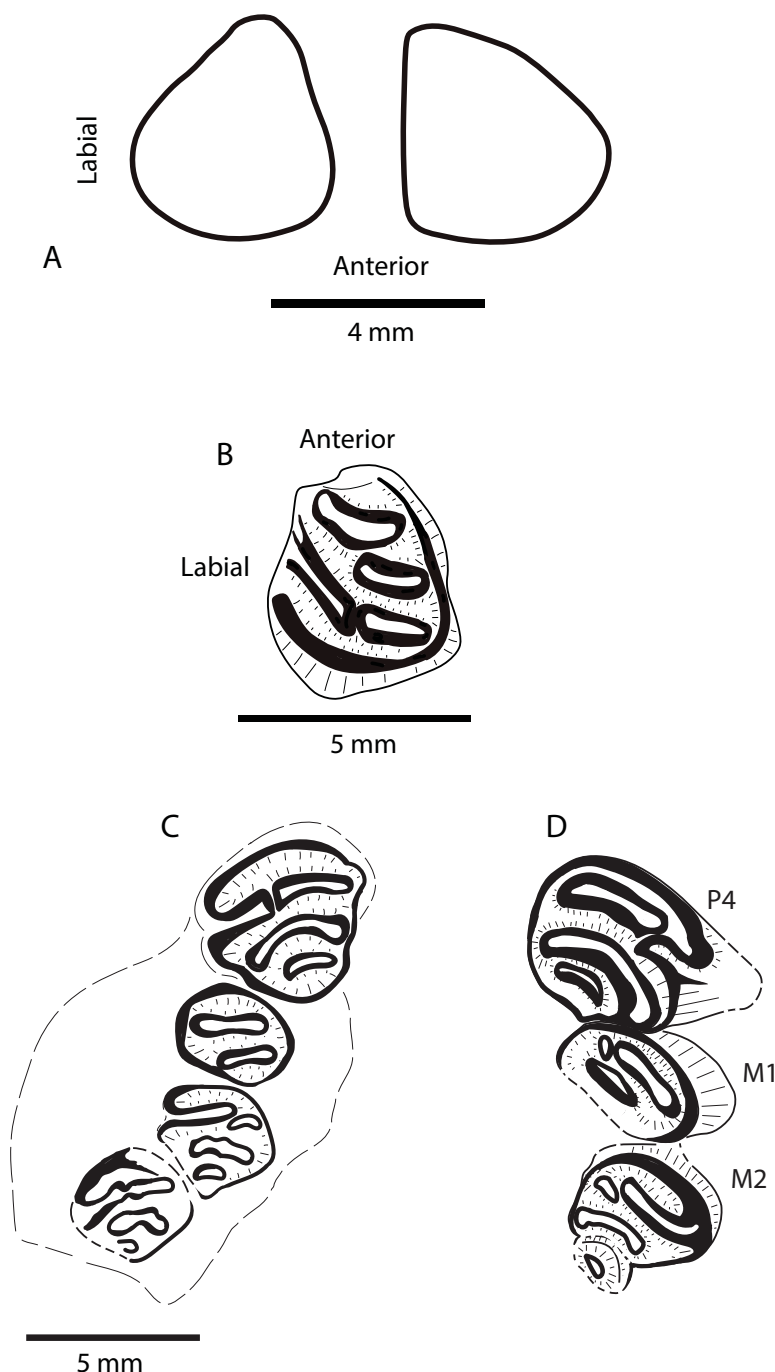
FIGURE 19. *Monosaulax* sp. A - TMM 31244-6, left and right i1, cross-section drawn at natural break. B – TMM 31244-6, L p4 occlusal view. C – TMM 31057-300, maxillary fragment with P4-M3 occlusal view, anterior towards top. D – TMM 31244-6, P4-M2 associated with mandible.

but the p4 has a v-shaped parafossettid unlike the gently curved parafossettid in *Monosaulax* sp.

The p4 of TMM 31244-6 is significantly smaller than *Monosaulax skinneri* (Korth, 2008) (Figure 19). The p4-m3 tooth row length (13.1-13.4 mm) is shorter than *M. skinneri* (Korth, 2008), *M. pansus* (Korth, 2002) and *M. baylei* (Korth, 2004), and similar to *M. tedi* and *M. curtus* (Korth, 1999), but the latter has a straight parafossetid while that of TMM 31244-6 is curved. The tooth row length is
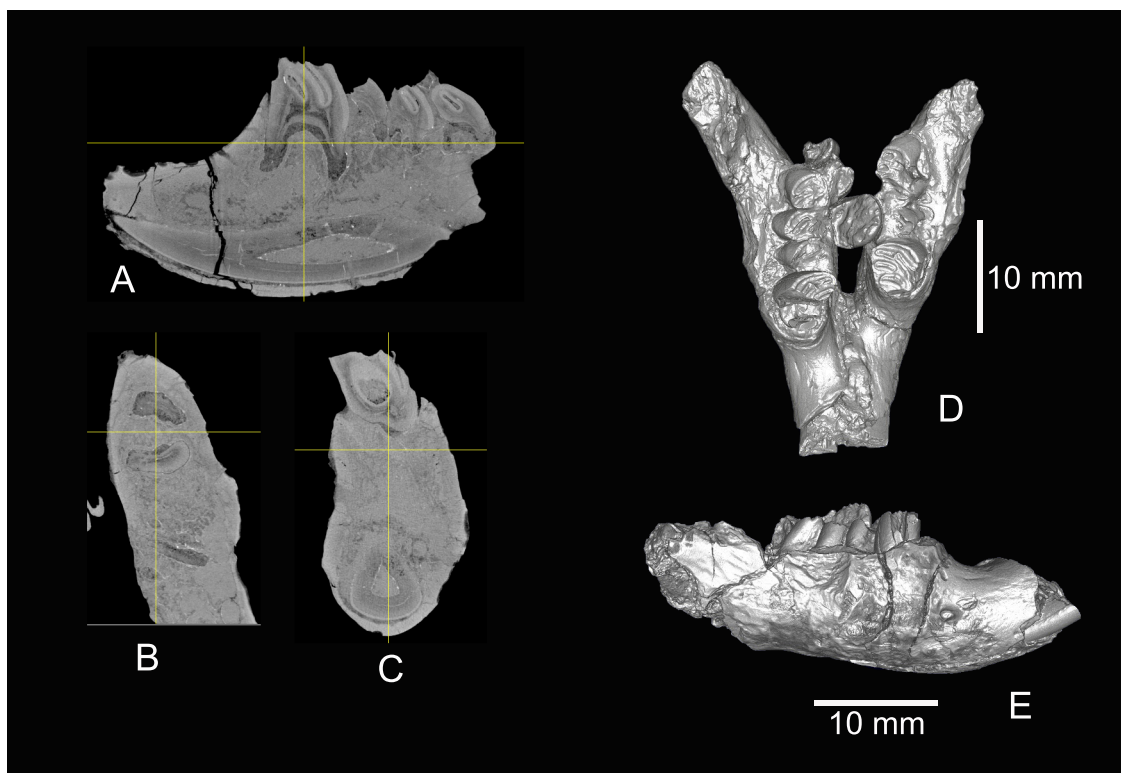
FIGURE 20. *Monosaulax* sp. TMM 31244-6 CT data. A – vertical longitudinal slice through anterior part of left dentary showing two roots on left p4 and oblique view of incisor, anterior to the left. B – horizontal slice through anterior part of left dentary showing two roots on left p4, anterior to the top. C – vertical transverse slice of left dentary between roots of p4 and showing cross-sectional view of incisor. D – dorsal view of mandible as isosurface rendering. E– labial view of right dentary as isosurface rendering, anterior to the right.

just slightly longer than the measurements reported for *M. typicus* (Shotwell, 1968). The P4–M2 length of TMM 31244-6 is approximately 10.4 mm.

The preserved length of the right dentary is 35.5 mm, and the minimum depth below the diastema is 9.5 mm. The diastema is relatively shallow. A single mental foramen is located anterior to p4 near the midline of the horizontal ramus and is 1.8 mm in its long dimension (Figure 20). There is no symphyseal flange. These characters are similar to the dentaries of *M. typicus* figured in Shotwell (1968). A virtual slice through the CT volume of TMM 31244-6 shows two roots on p4 (Figure 20). Korth (1999) described this as the common character state in all species of *Monosaulax* except for *M. skinneri.*

The P4-M3 tooth row length of TMM 31057-300 is 12.9 mm. Individual tooth measurements are P4: 4.6 mm x 4.3 mm (L x W), M1: 2.8* mm x 3.6 mm (*broken), M2: 2.8 mm x 3.2 mm, M3: 2.7 mm x 2.7 mm. The occlusal patterns of the upper cheek teeth are simple with 2-3 fossettes and a

hypoflexus. Even the hypoflexus on M1 has been lost with wear so the tooth only contains two fossettes (Figure 19).

Discussion. A small castorid from the early Barstovian (Ba1) Moscow and Point Blank Local Faunas is identified as *Monosaulax* sp. The small size, low crown height, lack of accessory fossettes(ids), short striae (ids), and lack of S-shaped molars are all interpreted to be primitive characters for the genus. The two specimens of *Monosaulax* from the Moscow and Point Blank Local Faunas are most similar to *M. typicus*, but minor differences in occlusal patterns (e.g., less curved parafossettid on *M. typicus*) and the limited number of specimens from Texas causes us to be cautious about that assignment.

Monosaulax is known from a number of Barstovian localities in North America. The older and more primitive species (*M. typicus, M. tedi*) are most similar to *Monosaulax* sp. from the Texas Coastal Plain. The suite of primitive characters and similarity with *M. typicus* are consistent with a Ba1 age assignment for the Moscow and Point Blank

local faunas. Korth (1999) suggested that *Monosaulax* was close to the basal castoroidine. *Prisaulax* was described as a new genus by Korth and Bailey (2006) from the late Arikareean and early Hemingfordian of Nebraska, and they proposed a basal castoroidine phylogenetic position for that taxon. *Monosaulax* and *Prisaulax* appear to be closely related, and Korth (2017a) removed the species *serundi* from the genus *Monosaulax* and placed it in the genus *Prisaulax*.

DISCUSSION

Fossil castorids are rare in the Miocene vertebrate faunas from the Texas Coastal Plain. The first record appears to be that of Dumble (1915), who listed *Hystricops* sp. based on a report from W.D. Matthew concerning an "upper jaw with M1 and a lower molar" from "one and one-fourth miles north of Cold Springs", TX. Stirton (1935) referred this material to *Amblycastor*, but did not examine it. The descriptions of *Anchitheriomys buceei* and *Monosaulax* sp. presented in this paper are based on specimens that were collected in the first half of the twentieth century. The holotype of the new species *Anchitheriomys buceei* was collected from outcrops near Burkeville, Texas, by H. Turner, F. Stenzel, and C. Hesse in 1941. A number of the referred specimens were collected between 1932 and 1940 from near Point Blank, TX (TMM 71) by C. Riley, a collector for Dr. Mark Francis. Dr. Francis and his collectors made important contributions to the knowledge of fossil vertebrates in Texas from the late 1800s through the 1920s. His contributions have been recognized by a number of taxa with patronyms reflecting his influence (e.g., *Aleurodon francisi, Equus francisi, Rhynchotherium francisi)*. Many of the fossils collected by Francis were described by W.D. Matthew of the American Museum and by O.P. Hay of the Smithsonian Institution and, after his death, became part of the first museum at Texas A & M University, then known as the Museum of the Agricultural and Mechanical College of Texas. C.J. Hesse was hired in 1938 and promoted to curator at the museum in 1943. He recognized the significance of the castorid material from Miocene localities on the Texas Coastal Plain. Although it is clear from publications by Stenzel et al. (1944), Stenzel and Turner (1944), as well as archival material at the University of Texas that Hesse intended to name a new species, in fact, the specimens were never described in the literature, were never illustrated, and no holotype was ever specified. Hesse died in 1945 at the age of 40 before he could complete his study.

In addition to the TAMU material, specimens of Miocene castorids were collected by the Statewide Paleontologic-Mineralogic Survey including material from the Barringer Farm near Moscow (TMM 31057) collected by J.T. Gregory in 1940, and material from the Wanza Farm locality in San Jacinto Co. (TMM 31244) collected by G.H. Schafer in 1941. The material from Push Creek (TMM 40623) and Belts Creek (TMM 40622) was collected by J.A. Wilson in 1963.

Previous work on Miocene castorids from the Texas Coastal Plain included the recognition of rare occurrences from Arikareean and Hemingfordian faunas. *Palaeocastor* and perhaps *Pseudopalaeocastor* are reported from the Cedar Run Local Fauna and cf. *Neatocastor* from the Toledo Bend Local Fauna (Wood and Wood, 1937; Tedford et al., 2004; Albright, 1998). There is also an unpublished report of *Palaeocastor* from Garvin Gully (R.A. Stirton field notes, 1935). These occurrences are limited to isolated teeth and identifications remain uncertain. The palaeocastorines are best known from fossil burrows in the Great Plains and were interpreted by Rybczynski (2007) to be part of a North American clade of castorids associated with an open-habitat fossorial environments.

A number of Miocene castorid fossils in The University of Texas Vertebrate Paleontology Collection represent a large form now recognized as a new species of *Anchitheriomys*. *Anchitheriomys buceei* is distinct from other species of this genus based on a suite of cranial and dental characters. We interpret the skull, mandible, isolated cheek teeth, and limited post-cranial elements as all representing this new taxon. Reconstruction of the skull and measurements of the post-cranial material suggests that this castorid was about 20-30% larger than adult individuals of the modern *Castor canadensis*. Rybczynski (2007) proposed that *Anchitheriomys* was part of a "swimming clade" of Holarctic castorids. According to her analysis, semi-aquatic/woodcutting behaviors interpreted for this clade also appear to be associated with immigration between Europe and North America. The oldest occurrence of *Anchitheriomys* is from the early Hemingfordian Runningwater Formation of Nebraska (Korth, 2001a; Korth and Martin, 2007). *Anchitheriomys suevicus* and *A. tungurensis* appear in European and Asian faunas correlative with the Barstovian (Stefen and Mörs, 2008). Interpretation of migration between North America and Eurasia is based in part on the synonymy of *Amblycastor* with *Anchitheriomys* as discussed in Mörs and Hulbert (2010) and Korth (2017a).

A small castorid is identified as *Monosaulax sp.* The specimens from the Texas Coastal Plain represent a primitive form of the genus most similar to the early Barstovian *M. typicus* and *M. tedi*. *Monosaulax* is known from Barstovian faunas in North America and is thought to be a primitive member of the *Eucastor-Dipoides-Castoroides* lineage. Although not addressed in the analysis of Rybczynski (2007), the phylogenetic association of *Monosaulax* with castoridines such as *Eucastor, Dipoides,* and *Castoroides* suggests that *Monosaulax* was also a semi-aquatic form.

Both *Anchitheriomys buceei* and *Monosaulax. sp.* are currently known from Ba1 local faunas in the Texas Coastal Plain. These faunas include *Prosynthetoceras, Floridatragulus, Merychippus, Protohippus, Cormohipparion, Aphelops, Peraceras, Teleoceras, Paratomarctus, Tomarctus*? and *Edaphocyon*. The later Barstovian faunas from the upper part of the Lagarto Formation contain no known castorids, but are differentiated by the appearance of *Calippus, Hipparion, Protohippus, Neohipparion, Aelurodon ferox, Aepycamelus, Longirostomeryx* and *Cranioceras*. At least two of the Ba1 local faunas also contain the earliest records of fossil proboscideans in the Texas Coastal Plain.

ACKNOWLEDGMENTS

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