The oreodont Merychyus major major (Mammalia: Artiodactyla: Oreodontidae) from the Miocene Popotosa Formation, Bosque del Apache National Wildlife Refuge, Socorro County, New Mexico

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New Mexico Geology, v. 31, n. 4 pp. 91-103, Print ISSN: 0196-948X, Online ISSN: 2837-6420.
https://doi.org/10.58799/NMG-v31n4.91

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The oreodont *Merychyus major major* (Mammalia: Artiodactyla: Oreodontidae) from the Miocene Popotosa Formation, Bosque del Apache National Wildlife Refuge, Socorro County, central New Mexico

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Abstract

A partial fossilized skeleton of an oreodont (Mammalia: Artiodactyla: Oreodontidae) was discovered in 2008 eroding from the wall of an arroyo on the Bosque del Apache National Wildlife Refuge near San Antonio in Socorro County, central New Mexico. The fossil was preserved in a semi-indurated, sandy stream deposit in a distal piedmont facies of the Miocene Popotosa Formation. The specimen includes a nearly intact skull and attached mandible that were associated with a partial articulated postcranial skeleton. The postcranial skeleton consists of a complete set of thoracic, lumbar, and sacral vertebrae, most of the ribs, which are still attached to their respective thoracic vertebrae, both wrists (distal radius and ulna, carpals, proximal metacarpals), left innominate, and an incomplete left hind limb (femur, tibia, fibula, tarsals). A highly unusual feature is the preservation of an ossified larynx and the delicate hyoid bones. The Bosque del Apache oreodont is identified as *Merychyus major major*, a member of the subfamily Ticholeptinae. It is the only record of an oreodont from the Popotosa Formation. The specimen represents one of the largest individuals of the genus currently known and the most derived and tapir-like in the degree of posterior retraction of its external narial opening. *Merychyus major major* is restricted to faunas of early late Miocene (latest Clarendonian) age. Geologic age constraints for the Popotosa Formation in the general vicinity of the oreodont site are provided by two $^{40}Ar/^{39}Ar$ radioisotopic ages. An age of 14.59 ± 0.05 Ma was obtained on pumice clasts in fluvial sandstones near the base of the local section, and an age of 8.57 ± 0.26 Ma was determined for a basalt flow interbedded with conglomerates near the top. The oreodont skeleton was found in strata somewhat below the dated basalt. The radiometric dates for the Popotosa Formation are consistent with those from the Dove Spring Formation of southern California where the stratigraphic range of *M. major major* is bracketed by smaller-bodied subspecies of *M. major* and by vitric tuff units that have been determined to be 11.19 ± 0.10 Ma in age, below, and 9.36 ± 0.20 Ma, above.

Introduction

In February 2008 David Love and Richard Chamberlin of the New Mexico Bureau of Geology and Mineral Resources and Colin Cikoski of the Department of Earth and Environmental Science at New Mexico Tech

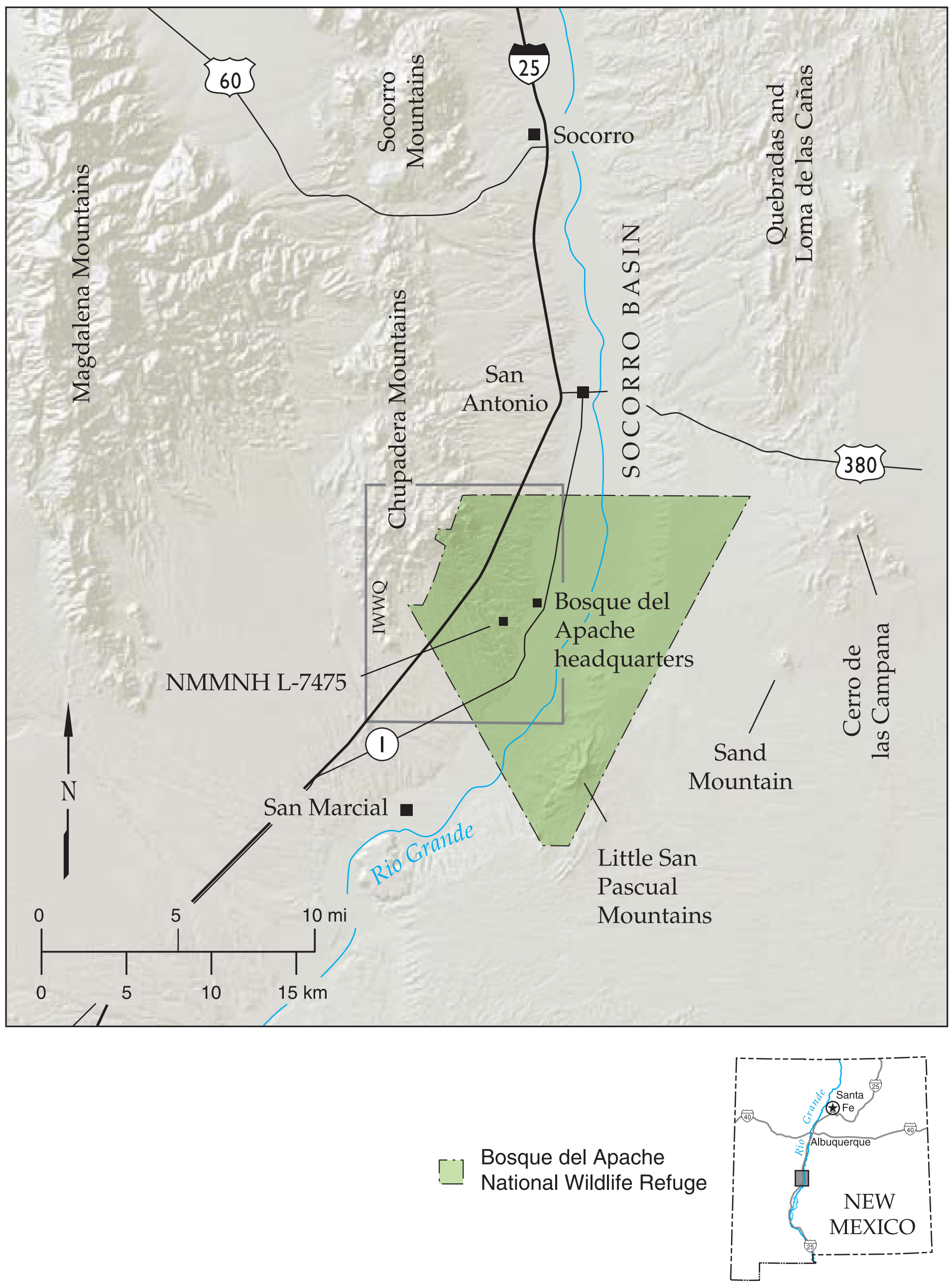

FIGURE 1—Map of a portion of Socorro County in central New Mexico showing Bosque del Apache National Wildlife Refuge, boundary of the Indian Well Wilderness quadrangle (IWWQ), and approximate location of early late Miocene (latest Clarendonian) Bosque del Apache Local Fauna at NMMNH locality L-7475. Small inset map of New Mexico shows general location of Bosque del Apache LF.

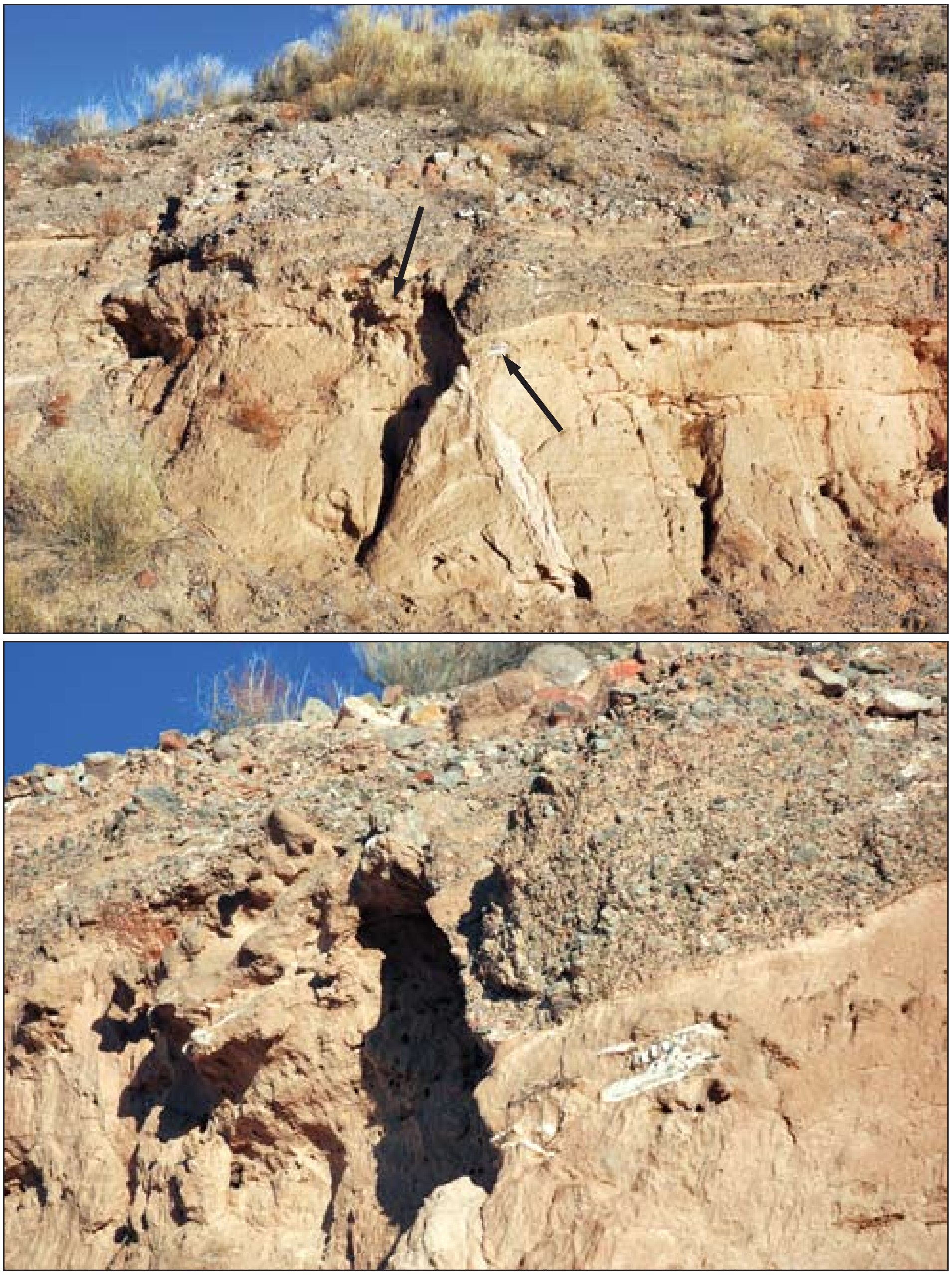

FIGURE 2—Photographs showing stratigraphy and fault cutting through fossil site (NMMNH locality L-7475) offsetting partial skeleton of early late Miocene (latest Clarendonian) oreodont *Merychyus major major* from Popotosa Formation, Bosque del Apache National Wildlife Refuge, Socorro County, central New Mexico. In the top photo the arrow on the right indicates location of oreodont skull and mandible, arrow on the left marks location of the skeleton. Photos courtesy of Colin Lee (USFWS).

discovered a fossilized mammal skeleton while conducting a geological reconnaissance near the Canyon Trail on the Bosque del Apache National Wildlife Refuge in central New Mexico (Fig. 1). The specimen includes a nearly complete skull, mandible, and a partial articulated postcranial skeleton of an extinct species of land mammal known as an oreodont. The fossils were derived from a partially indurated sandstone of the Miocene Popotosa Formation in the Santa Fe Group. After obtaining a permit from the U.S. Fish and Wildlife Service (USFWS), Gary Morgan and Warren Slade from the New Mexico Museum of Natural History (NMMNH) collected the oreodont skeleton in March 2008. They were assisted by David Love, Richard Chamberlin, USFWS personnel from the Bosque del Apache National Wildlife Refuge, and many others who provided logistical support. A small fault offset the skull and mandible from the associated postcranial skeleton by approximately 1 m (3 ft) (Fig. 2). The specimen was collected in two separate plaster jackets. The skull and lower jaws were removed in a smaller jacket on the southern side of the fault, and the postcranial skeleton was collected in a larger jacket on the northern side of the fault, approximately 1 m (3 ft) higher in elevation. The oreodont skeleton was carefully prepared over a period of about 6 months by J. B. Norton in the paleontology preparation laboratory at the NMMNH. The skull and mandible were removed completely from the surrounding sandstone, but are so firmly attached to one another by an indurated sandstone that it was decided not to attempt to separate them for fear of damaging the teeth. The articulated postcranial skeleton was only partially prepared, and still remains embedded in the sandstone matrix to preserve the relative positions and associations of the individual skeletal elements.

Oreodonts are an extinct group of browsing even-toed ungulates (order Artiodactyla) that first appeared in the early middle Eocene (early Uintan North American Land Mammal Age [NALMA]) and went extinct in the latest Miocene (early late Hemphillian NALMA) (Lander 1998). The oreodont from the Bosque del Apache National Wildlife Refuge was briefly mentioned in two previous publications (Morgan et al. 2009a, b). It is a member of the later and more derived oreodont family, Oreodontidae Leidy 1869. Comparisons with other oreodonts indicate that the Bosque del Apache specimen belongs to the very large bodied subspecies *Merychyus major major* Leidy 1859 (subfamily Ticholeptinae Schultz and Falkenbach 1941), which is also known from early late Miocene (latest Clarendonian) sites in California, Nevada, Texas, and Nebraska.

Abbreviations used in this paper are as follows: American Museum of Natural History, New York (AMNH); Frick collection, now housed at the AMNH (F:AM); Vertebrate Paleontology Department, Natural History Museum of Los Angeles County, California (LACM); Local Fauna (LF); North American Land Mammal Age (NALMA); New Mexico Bureau of Geology and Mineral Resources, Socorro, New Mexico (NMBGMR); New Mexico Museum of Natural History and Science, Albuquerque, New Mexico (NMMNH); University of California Museum of Paleontology, Berkeley (UCMP); U.S. Department of the Interior, Fish and Wildlife Service (USFWS); and U.S. National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM). Statistical abbreviations are: mean (M), sample size (N), and observed range (OR). Abbreviations for selected measurements, ratios, and morphologic features of the skull are: narial-orbital length (N-O) and ratio of narial-orbital length to P1-M3 length (N-O/P1-M3). The abbreviations for tooth positions are standard for mammals, with upper case letters for upper teeth and lower case letters for lower teeth: I/i (upper/lower incisor), C/c (upper/lower canine), P/p (upper/lower premolar), and M/m (upper/lower molar). For example, P4 is an upper fourth premolar and m3 is a lower third molar.

Locality

The oreodont skeleton was found in a small unnamed arroyo near the Canyon Trail on the Bosque del Apache National Wildlife Refuge, approximately 14 km (9 mi) south of San Antonio, Socorro County, central New

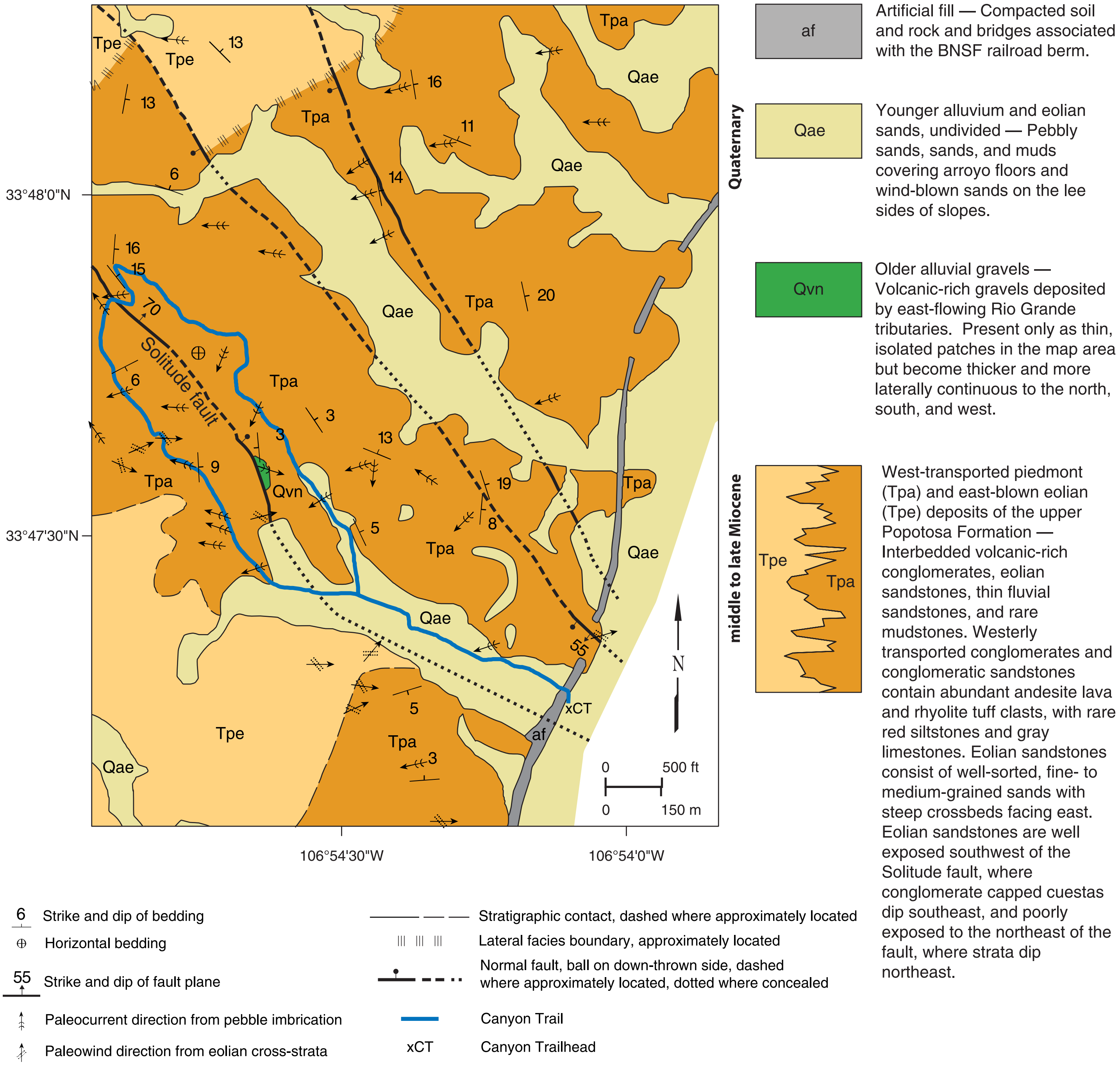

FIGURE 3—Geologic map along Canyon Trail, Bosque del Apache National Wildlife Refuge, Socorro County, central New Mexico. Map compiled by Colin Cikoski, Richard Chamberlin, and David Love.

Mexico (Figs. 1–4). The fossil site (NMMNH locality L-7475) is in the northeastern wall of the arroyo approximately 2–3 m (6.5–10 ft) above the floor of the wash. The fossil land mammal assemblage represented by the specimen is herein named the Bosque del Apache LF. It is located on the Indian Well Wilderness U.S. Geological Survey 7.5-min quadrangle, on land under the jurisdiction of the USFWS. The coordinates of the site are approximately 33°48′ North latitude and 106°54 West longitude, and the elevation is approximately 1,400 m (4,600 ft). NMMNH locality L-7475 consists of a single specimen, a partial skeleton of the oreodont *Merychyus major major* (NMMNH 57623). This is the only fossil so far collected from the Popotosa Formation on the Bosque del Apache National Wildlife Refuge, although a second specimen found by C. Cikoski, a partial limb bone, has yet to be collected.

Geologic setting

The Bosque del Apache National Wildlife Refuge straddles the southern third of the Socorro Basin. This part of the rift basin is a southeast-tilted half-graben bounded on the east by volcanic rocks of Cerro de las Campana and Sand Mountain and by Paleozoic strata at Little San Pascual Mountains, and on the west by the volcanic massif of the Chupadera Mountains. Today, the southwestern flank of the basin is bounded by low volcanic hills that trend in a southerly direction from Chupadera Peak. Gravity data (Cordell et al. 1982) suggest that the Miocene basin terminates southward against a bedrock high, which is masked by a thin veneer of Pleistocene sediments near San Marcial. However, during the Miocene, the sedimentary basin fill might have extended into the San Marcial Basin to the southwest. The rift basin fill is a part of the Santa Fe Group, which is divided locally into the Popotosa Formation, below, and the Sierra Ladrones Formation, above, based on the presence (Sierra Ladrones Formation) or absence (Popotosa Formation) of ancestral Rio Grande deposits.

The strata containing the oreodont site are assigned to the Popotosa Formation. They consist of water-transported conglomerates and sandstones interbedded with eolian sandstones as much as 1,900 m (6,234 ft) thick under the Bosque del Apache Refuge. Based on clast suite and paleocurrent data, the conglomerates and sandstones were derived from

Table 1—Summary of $^{40}Ar/^{39}Ar$ age determinations for the Indian Well Wilderness quadrangle.

Map no.	Field no.	Map unit	Lab no.	Material dated	Method	N	Age (Ma)	± 2σ	MSWD	K/Ca	± 2σ	UTM-E	UTM-N
1	IWW-2004-1	Tbt	55099	groundmass concentrate	RFIH	5	8.57	0.26	1.75	0.26	nc	0322772	3744077
2	CTC-1	Tp2	57746	sanidine	SCLF	12	14.59	0.05	2.76	100.7	36.8	0321323	3744229

NOTES: Method is single crystal laser fusion (SCLF) or resistance furnace incremental heating (RFIH). "N" is number of individual crystals analyzed (SCLF) or number of heating steps used to calculate weighted mean age (RFIH); K/Ca is molar ratio calculated from K-derived ^{39}Ar and Ca-derived ^{37}Ar. Two-sigma variance not calculated (nc) for RFIH samples. Mean sum weighted deviates (MSWD) value with asterisk(*) indicates confidence interval less than 95%.

Methods: Sample preparation: sanidine, –crushing, heavy liquid, Franz, HF; groundmass concentrate–crushing, dilute acid, heavy liquid, hand picking. Samples loaded into machined Al disk and irradiated in D-3 position, Nuclear Science Center, College Station, Texas. The sanidine sample was irradiated for 7 hours while the groundmass concentrate was irradiated for 14 hours. Neutron flux monitor Fish Canyon Tuff sanidine (FC-1); assigned age = 28.02 Ma (Renne et al. 1998). Samples and monitors irradiated in alternating holes in machined Al disks.

Laboratory: New Mexico Geochronology Research Laboratory, Socorro, New Mexico. Instrumentation: Mass Analyzer Products 215-50 mass spectrometer online with automated all-metal extraction system. Heating: sanidine–SCLF, 10W continuous CO_2 laser; RFIH–36 mg aliquot in resistance furnace. Reactive gas cleanup: SAES GP-50 getters operated at 20°C and ~450°C; SCLF – 1 to 2 minutes, RFIH–9 minutes. Error calculation: all errors reported at ±2σ, mean ages calculated using inverse variance weighting of Samson and Alexander (1987); decay constant and isotopic abundances after Steiger and Jaeger (1977).

Analytical parameters: Electron multiplier sensitivity = 4.17×10^{-16} moles/pA for the furnace sample and 5.60×10^{-17} for the laser sample; typical system blanks were 2880, 2.9, 1.3, 0.2, 9.2×10^{-18} moles (furnace) and 230, 5.4 , 1.4 , 1.1, 7.8 (laser) at masses 40, 39, 38, 37, 36 respectively; J-factors determined using SCLF of 4 to 6 crystals from each of 6 or 10 radial positions around irradiation vessel. Correction factors for interfering nuclear reactions, determined using K-glass and CaF_2, $(^{40}Ar/^{39}Ar)_K = 0.0 \pm 0.0004$; $(^{36}Ar/^{37}Ar)_{Ca} = 0.00028 \pm 0.00002$; and $(^{39}Ar/^{37}Ar)_{Ca} = 0.00068 \pm 0.00005$.

Samples: Samples are listed in apparent stratigraphic order. Collected by David Love (IWW-2004) and Colin Cikoski (CTC). Sample locations are in UTM zone 13S and based on 1927 NAD. Map units are shown on Figure 4; Tbt is the basalt of Broken Tank, Tp2 is the ash-bearing member of the lower Popotosa Formation at Bosque del Apache.

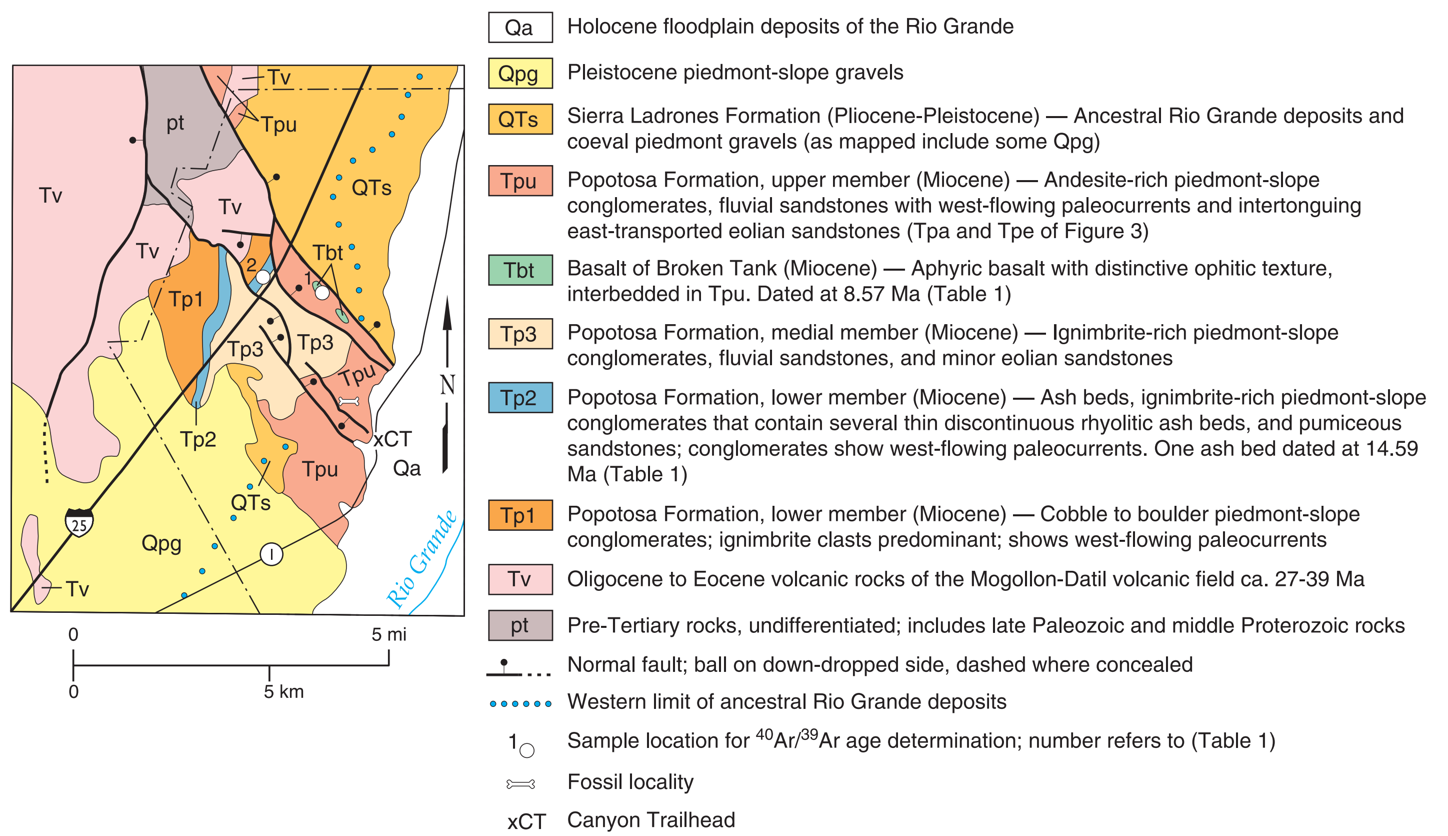

FIGURE 4—Generalized preliminary geologic map of the Indian Well Wilderness quadrangle (Cikoski and Chamberlin, in progress).

a highland to the east, the ancestral "Little" San Pascual Mountains, whereas cross-strata attitudes indicate that the eolian sands were blown eastward across the fossil site and onto the piedmont (Chamberlin et al. 2006). The clast suites of the conglomerate beds grade upsection from rhyolite tuff dominated with rare basalts, to andesite lava dominated with rare red siltstones and limestones. The change in clast type most likely reflects the unroofing of the source area. Rounding and sorting increase upsection, whereas clast size generally decreases and the proportion of sandstone beds increases, suggesting a retreat of the piedmont from the area through time. Geologic age constraints for the Popotosa Formation are provided by $^{40}Ar/^{39}Ar$ radioisotopic ages on pumice clasts in the water-transported pebbly sandstones lying near the base of the local section (14.59 ± 0.05 Ma; Table 1), and on a basalt flow interbedded with sandstones near the top (8.57 ± 0.26 Ma; Fig. 4; Table 1; Chamberlin et al. 2006). The fossil locality is in the upper quarter of the Popotosa Formation and stratigraphically below the down-faulted block that contains the dated basalt.

The skeleton was recovered from a brown, semi-indurated, fine-grained, water-transported sandstone bounded by a crossbedded eolian sandstone below and a conglomerate bed above (Fig. 2). The strata containing the fossil site were probably part of a dynamic boundary between a laterally equivalent erg or dune field and the westward-sloping piedmont (Chamberlin et al. 2006; Figs. 3 and 4). West of the fossil site, eolian sandstones dominate the strata and possibly represent the core of the dune field, whereas to the east, eolian sandstones become less common and give way to more conglomerate beds. Immediately around the skeleton, the two lithotypes interbed, most likely due to the episodic advance and retreat of the dune field onto and off of the eastern piedmont. Figure 3 shows a map of the local geologic units in the vicinity of the Canyon Trail on the Bosque del Apache National Wildlife Refuge.

The Popotosa Formation is deformed by syndepositional fault block rotation and northwest-striking faults. All strata dip to the southeast or northeast as a result of fault block rotation. Syndepositional rotation is suggested by gradually decreasing dip of strata upsection in an area southwest of the oreodont site. The strata are also cut by syndepositional northwesterly trending faults, which show decreasing magnitudes of stratigraphic separation in younger strata. Some faults have remained active until at least the late Pleistocene (Figs. 3 and 4; C. Cikoski, unpublished data). One of these northwest-striking normal faults offsets the oreodont skeleton by approximately 1 m (3 ft) (Fig. 2), and the skeleton makes an almost perfect piercing point. The skull, mandible, atlas vertebra, and parts of the left and right forelimbs were dropped by the fault approximately 1 m (3 ft) below the remainder of the skeleton. The skeletal elements nearest the fault surface, including the cervical vertebrae and the proximal portion of the left front limb (scapula, humerus), were very poorly preserved. Farther from fault surface, the skull, lower jaws, and trunk skeleton (thoracic vertebrae and articulated ribs, lumbar vertebrae, sacrum) were exceptionally well preserved. This is the first New Mexico example of a vertebrate fossil the authors have observed that was severed and subsequently displaced by a fault.

Vertebrate paleontology

Class Mammalia Linnaeus 1758
Order Artiodactyla Owen 1848
Family Oreodontidae Leidy 1869
Subfamily Ticholeptinae Schultz and Falkenbach 1940 (*nomen nudum*), 1941
Genus *Merychyus* Leidy 1859 (imprint 1858)

Merychyus Leidy 1859 (imprint 1858)
Metoreodon Matthew and Cook 1909
Ustatochoerus Schultz and Falkenbach 1941

Genotypic species—*Merychyus elegans* Leidy 1859 (imprint 1858).

Included species (in chronologic order)—*M. calaminthus* Jahns 1940, *M. arenarum* Cope 1884, *M. elegans* (genotype species), *M. relictus* Matthew and Cook 1909, *M. medius* Leidy 1859 (imprint 1858), and *M. major* Leidy 1859 (imprint 1858).

Merychyus major Leidy 1859 (imprint 1858)

Referred subspecies (in chronologic order)—*M. major*? new subspecies of Lander (1998) (older of two unnamed subspecies), *M. major major* Leidy 1859, *M. major*? *profectus* (Matthew and Cook 1909), and *M. major*? new subspecies of Lander (1998) (younger of two unnamed subspecies).

Age and distribution—Early late Clarendonian to early late Hemphillian NALMAs (late Miocene) of California, Kansas, Nebraska, Nevada, New Mexico, Oklahoma, Oregon, and Texas.

Merychyus major major Leidy 1859 (imprint 1858)

Age and distribution—Latest Clarendonian NALMA (early late Miocene) of California, Kansas, Nebraska, Nevada, New Mexico, and Texas.

Emended diagnosis—*Merychyus major major* is the largest form of the genus. It is at least slightly larger than *Merychyus medius*? *santacruzensis*, *M. major*? *profectus*, and two unnamed subspecies assigned questionably to *M. major*. The mean P1-M3 length for a composite sample of *M. major major* from California, Nebraska, and New Mexico (152 mm, OR = 150–157 mm, N = 4) is 7.6% greater than that for the sample of *M. major*? new subspecies from the Kat Channel in Nebraska (141.3 mm, OR = 137–146 mm, N = 8) and 8.2% greater than a composite sample of *M. medius*? *santacruzensis* from the Santa Fe Group in northern New Mexico (140.5 mm, OR = 140–141 mm, N = 2). The external narial opening is somewhat more retracted posteriorly than in *M. major*? new subspecies from the Kat Channel (nasals and dorsal border of maxilla comparatively somewhat shorter; mean N-O/P1-M3 ratio of Bosque del Apache specimen 9.7% less than in sample of *M. major*? new subspecies from Kat Channel). Comparisons based mostly on NMMNH 57623 from the Bosque del Apache LF in New Mexico and on statistical data provided in the tables that follow. Modified from Schultz and Falkenbach (1941, 1968) and Lander (1977, 2005, 2008).

Referred specimen—NMMNH 57623 consists of a nearly complete skull, attached right and left dentaries, and an associated partial articulated postcranial skeleton. The skull contains the right P2-M3 and left I3, C1, and P2-M3, as well as the associated hyoid bones and ossified larynx. The right dentary contains the p3-m3, and the left dentary contains the c, p1-p3, m1-m3. The partial articulated postcranial skeleton includes: the atlas vertebra; a nearly complete series of articulated thoracic vertebrae, most of which still have their respective ribs attached; the articulated series of lumbar vertebrae; the sacrum; the left scapula; the distal half of the left humerus; the proximal end of the left ulna; a partial left innominate; and the left hind limb with the femur, tibia, fibula, patella, calcaneum, and astragalus. The partial articulated right and left forelimbs were found separated slightly from one another and approximately 20 cm (8 in) below the skull and mandible, but were not attached to the remainder of the postcranial skeleton. The forelimbs include the distal ends of the radius and ulna, a complete series of carpals, and the proximal ends of metacarpals 3-5.

Description of Bosque del Apache oreodont specimen (NMMNH 57623)—Photographs of NMMNH 57623 are presented in Figures 5, 7, and 8. Cranial and mandibular measurements are provided in Table 2, dental measurements in Table 3, and comparative statistical data in Table 4. Except for several missing teeth, the skull and dentaries are nearly complete. The right side of the skull and right dentary were partially exposed in the field and have suffered some damage from weathering. All of the incisors except the left I3 are missing, as are the P1s on both sides of the skull, and the left p4. Because the skull and mandible are still attached to one another, it was only possible to study the occlusal morphologies of the dentition anterior to P4 and p4. The hyoid bones and what appears to be an ossified larynx were found associated with the basicranium and posterior portion of the mandible. The anterodorsal portion of the braincase is missing, as is a portion of the right side. Several conical depressions in the dorsal surface of the braincase might

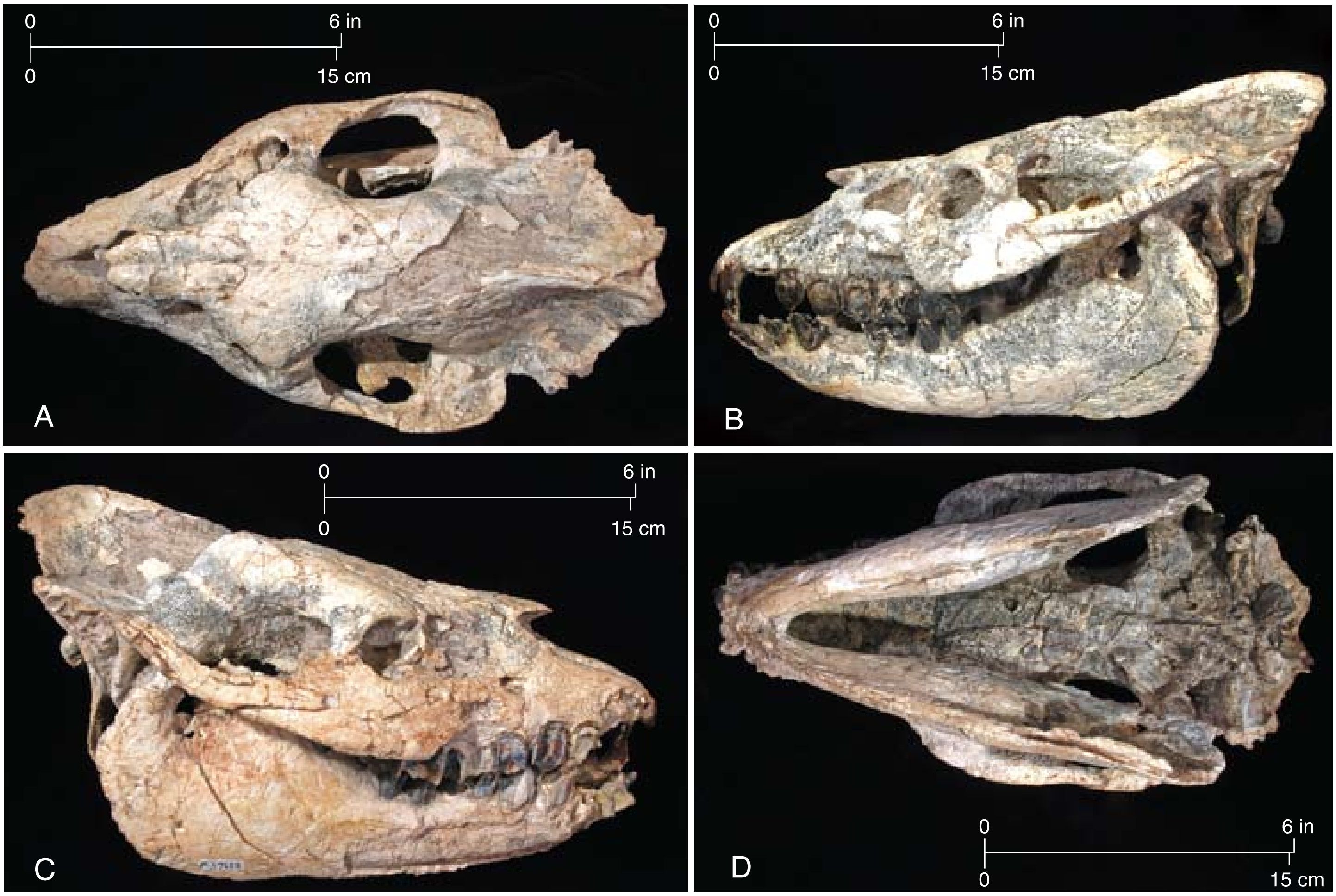

FIGURE 5—Skull and mandible of the early late Miocene (latest Clarendonian) oreodont *Merychyus major major* (NMMNH 57623) from Popotosa Formation, Bosque del Apache National Wildlife Refuge, Socorro County, central New Mexico. **A**. dorsal, **B**. left lateral, **C**. right lateral, and **D**. ventral views.

be tooth impressions or bite marks resulting from predation or scavenging by a carnivore. However, the remainder of the skull and postcranial skeleton does not appear to have suffered any such damage.

The skull is of a very large adult, measuring 325 mm in maximum length from the premaxilla to the posteriormost extension of the occiput. The external narial opening is highly retracted posteriorly, ending at a level dorsal to the middle of the P4. Correspondingly, the rostral-premaxillary suture is comparatively long, and the nasals are relatively short. The anterior tip of the nasals is dorsal to the middle of the P3. The muzzle is low relative to the posterior portion of the skull. The lacrimal fossa is broad, shallow, and flat bottomed. The infraorbital foramen is located dorsal to the anterior half of the P4. The anterior or jugal portion of the zygomatic arch is deep below the orbit. The posterior or squamosal portion of the zygomatic arch is shallow and laterally thin, flat-sided, and recumbent posteriorly. The braincase is inflated. The sagittal crest is prominent, especially posteriorly. The lambdoidal crests are continuous with the paroccipital wings and widely spread to form a broad fan-shaped occiput that overhangs the occipital condyles posteriorly by approximately 25 mm. The paroccipital process is very long, extending approximately 45 mm ventral to the base of the braincase. The postglenoid process is very long and anteroposteriorly thin. The ventral surface of the tympanic bulla is concave and dorsomedially basined relative to the basioccipital. The mandibular symphysis is flattened. The horizontal ramus of the dentary is shallow, especially ventral to the premolars and m1. The dentition is comparatively hypsodont, particularly the molars. The P2 and P3 possess an anterior intermediate crest, which has been modified to form a large distinct cusp at the anteromedial corner of each tooth, as in all other individuals of *Merychyus major*, virtually all examples of *M. medius*, and most specimens of *M. relictus*, but in no other oreodont taxon (Lander 2008). The individual represented by the specimen was not fully mature, based on the essentially unworn dentition and the unerupted m3 hypoconulid.

One of the most unusual features of this specimen is the presence of the ossified thyroid cartilage of the larynx and the associated hyoids that supported the tongue. The ossified larynx and hyoid bones were found in their life positions, with the hyoid apparatus retaining its articulation with the basicranium and the larynx still located posteroventral to the hyoid apparatus and medial to the paroccipital processes and the ascending rami of the dentaries. The larynx is U-shaped or broadly V-shaped in anterior and posterior views, open dorsally, spout-like, and composed of very thin, delicate bone (Fig. 7). In ventral view, this structure is broad in both its anteroposterior and transverse dimensions. Measurements (in mm) of the larynx are: dorsoventral height, 24; anteroposterior length along the midline, 32; transverse width, 45. Scott (1894) described and illustrated the ossified thyroid cartilage of the oreodont *Mesoreodon chelonyx* Scott 1893 from the late Oligocene (earliest Arikareean) Fort Logan Formation of southwestern Montana. Lander (1998) regarded *Mesoreodon* Scott 1893 as a junior synonym of *Eporeodon* Marsh 1875. Scott (1894, p. 131) described the specimen as "…a hollow, compressed semicylinder, or spout-shaped piece of bone, with exceedingly thin walls…" This description and Scott's illustration (1894, plate 3, fig. 29) are similar, although not identical, to the ossified larynx of NMMNH 57623, which represents a considerably larger animal that is also much younger geologically. As noted by Scott (1894), the presence of an ossified larynx is extremely rare among mammals

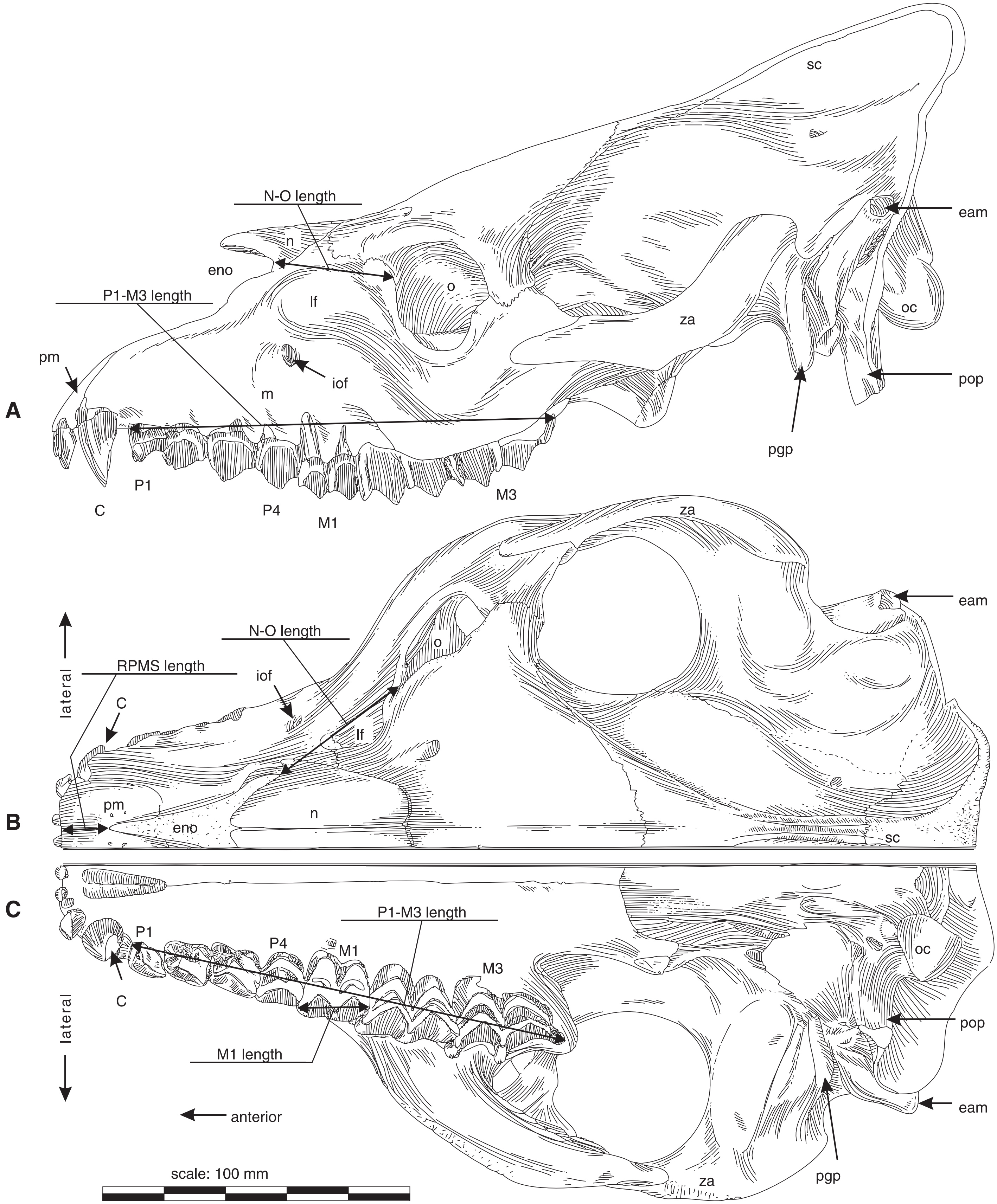

FIGURE 6—Illustration of *Merychyus* skull in **A**. lateral, **B**. dorsal, and **C**. ventral views, showing parameters used in this report and identifying cranial and dental features. Specimen is of *Merychyus major*? new subspecies (F:AM 34220) from Kat Channel, Merritt Dam Member, Ash Hollow Formation, Brown County, north-central Nebraska. After Schultz and Falkenbach (1941, fig. 9; reprinted with permission of T. S. Fischelis). Abbreviations for cranial elements are: **pm** (premaxilla), **m** (maxilla), **n** (nasal), **eno** (external narial opening), **lf** (lacrimal fossa), **iof** (infraorbital foramen), **o** (orbit), **za** (zygomatic arch), **sc** (sagittal crest), **pgp** (postglenoid process), **eam** (external auditory meatus), **oc** (occipital condyle), **pop** (paroccipital process), **C** (upper canine), **P1** (1st upper premolar); **P4** (4th upper premolar); **M1** (1st upper molar); **M3** (3rd upper molar).

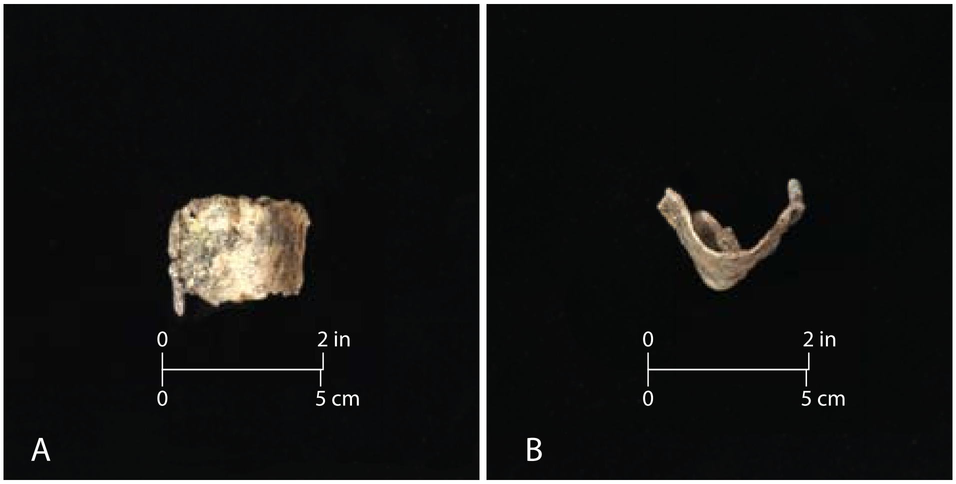

FIGURE 7—Ossified larynx of oreodont *Merychyus major major* (NMMNH 57623) from early late Miocene (latest Clarendonian) Bosque del Apache LF, Popotosa Formation, Bosque del Apache National Wildlife Refuge, Socorro County, central New Mexico. Ossified larynx in **A**. ventral view and **B**. posterior view.

TABLE 2—Measurements (in mm) of skull and mandible of *Merychyus major major* from Bosque del Apache National Wildlife Refuge, Socorro County, New Mexico (NMMNH 57623).

Description of measurement	Measurement (mm)
Length of skull (premaxilla to lambdoidal crest)	325
Condylobasal length of skull (premaxilla to occipital condyles)	296
Maximum width of palate at M3s	114
Maximum width across zygomatic arches	173
Width at external auditory meatus	130
Width of occipital condyles	55
Minimum interorbital width	74
Minimum frontal width	65
Nasal-orbital length	51
Length of nasals	68
Length of rostral-premaxillary suture	31
Depth of jugal below orbit	34
Anteroposterior diameter of orbit	29
Dorsoventral diameter of orbit	34
Length of P1-M3	157[1]
Length of P1-P4	69
Length of M1-M3	103
Total length of dentary	243
Maximum height of dentary at coronoid process	116
Depth of dentary below m1	38
Length of p1-p4	70[2]
Length of p1-m3	175[3]

[1]The P1 is absent from both sides of the skull. Therefore, measurement is from anterior edge of alveolus for P1 to posterior edge of M3 metastyle.
[2]The p4 is absent from the left dentary and the p1 is absent from the right dentary. This measurement was taken on the left side, from the anterior edge of p1 to the posterior edge of the alveolus for p4.
[3]The m3 hypoconulid is not fully erupted but is exposed on the medial surface of the left dentary. This measurement is approximate and minimum value.

TABLE 3—Dental measurements (in mm) of *Merychyus major major* from Bosque del Apache National Wildlife Refuge, Socorro County, New Mexico (NMMNH 57623).

Tooth position	Length	Width
I3	12.8	10.6
C	11.9	13.4
P2	19.6	15.5
P3	17.1	17.6
P4	16.4	—
M1	25.3	—
M2	36.9	—
M3 (at crown, unworn)	38.8	—
M3 (at base of crown)	50.7	—
c1	8.1	12.6
p1	18.8	9.5
p2	18.1	13.3
p3	22.2	14.5
m1	26.2	—
m2	32.4	—

and probably is related to sound production. The living howler monkey *Alouatta* has a bony structure composed of a greatly inflated hyoid (basihyal) that it uses to produce loud vocalizations (Nowak 1999).

The postcranial skeleton of NMMNH 57623 is incomplete (Fig. 8). The epiphyses on the centra of the thoracic vertebrae, the proximal end of the femur, and the distal ends of the radius, tibia, and fibula are unfused, indicating that this individual was not fully mature. However, the eruption of the complete adult dentition, except for the m3 hypoconulid, suggests that this specimen had nearly attained its full adult size.

The atlas vertebra was found attached to the occipital condyles of the skull and is in good condition. The more posterior cervical vertebrae are articulated with the thoracic series, but they are in very poor condition because of the fault that passed through this portion of the skeleton (see discussion above). The remainder of the preserved vertebral column is articulated from the anterior thoracic vertebrae posteriorly to the sacrum, with most of the ribs still attached to their respective thoracic vertebrae. Posterior to the cervical series, the vertebral column includes 14 thoracic, 5 lumbar, and 4 fused sacral vertebrae. The anterior thoracic vertebrae (1-3) have rather elongated neural spines that are more than 100 mm in length. All caudal vertebrae are missing.

The left scapula and partial proximal left forelimb, including the distal half of the humerus and the proximal end of the ulna, are in their near life positions, but they were damaged by the same fault that affected the nearby cervical vertebrae. The skeleton also includes the articulated partial left innominate (pelvis) and left hind limb, which includes the femur, patella, tibia, fibula, astragalus, and calcaneum. The distal right and left forelimbs were separated from the remainder of the postcranial skeleton. The left forelimb includes the distal ends of the radius and ulna, the complete series of articulated carpals (proximal row from medial to lateral consisting of scaphoid, lunar, and cuneiform; distal row from medial to lateral consisting of trapezoid, magnum, and unciform), and the proximal ends of metacarpals 3-5. The right front limb is less complete but better preserved and includes the distal radius and the complete articulated series of six carpals as described for the left front limb. Lengths (in mm) of selected postcranial elements of NMMNH 57623 are as follows (all are from the left side): scapula, 201; femur, 224; tibia, 191. Figure 9 is an artist's reconstruction of the Bosque del Apache oreodont.

Remarks—Schultz and Falkenbach (1941, 1968) assigned *Merychyus major* and its immediate ancestor, *M. medius*, to *Ustatochoerus* Schultz and Falkenbach 1941, considering the genus to have arisen from *Ticholeptus* Cope 1878. In contrast, Lander (1998, 2008) demonstrated that *M. major* actually arose from late Hemingfordian and early Barstovian *M. relictus*. All *Merychyus major* specimens, virtually all examples of *M. medius*, and roughly two-thirds of *M. relictus* individuals are comparatively derived in their mutual development of a prominent isolated cusp from the transversely oriented, anterior intermediate crest at the anteromedial corner of each of the P1-3. In contrast, the crest and its connection to the parametacone are retained in the remaining examples of *M. relictus*, in earlier and more primitive species of *Merychyus*, and in all other ticholeptines, including *Ticholeptus* (Lander 1998, 2008). Moreover, the postglenoid process is anteroposteriorly much thinner in *Merychyus* than in *Ticholeptus* (Lander 1998). Based on these morphologic criteria, Lander (1998, 2008) rejected *Ustatochoerus* and reassigned all of its subordinate taxa except *U. medius mohavensis* Schultz and Falkenbach 1941 to *Merychyus*.

TABLE 4—Mean P1-M3 and nasal-orbital (N-O) lengths (in mm) and mean N-O/P1-M3 ratios for *Merychyus major* and *M. medius* from selected localities in New Mexico, California, and Nebraska. Illustrations of parameters used to develop statistical data are presented in Figure 6 (after Lander 2008). Abbreviations: **M** (mean), **OR** (observed range), **N** (sample size), and **LF** (Local Fauna). "—" indicates specimen not measured.

Taxon, state, stratigraphic unit, and site	Specimen no.	P1-M3 length			N-O length	N-O/PI-M3 ratio		
		M	OR	N		M	OR	N
Merychyus major major								
New Mexico								
Popotosa Formation								
Bosque del Apache LF	NMMNH 57623	157	157	1	51	0.325	0.325	1
California								
Dove Spring Formation								
Member 5	LACM 4153	151	151	1	—	—	—	—
Orinda Formation								
Lafayette Ridge LF	UCMP 55799	150	150	1	—	—	—	—
Nebraska								
Ash Hollow Formation, Merritt Dam Member								
Alligator mefferdi quarry	F:AM 109517	150	150	1	—	—	—	—
Merychyus major? new subspecies								
New Mexico								
Tesuque Formation, Pojoaque Member								
Española Basin	F:AM 34400	147	147	1	56	0.381	0.381	1
Nebraska								
Ash Hollow Formation, Merritt Dam Member								
Kat Channel	F:AM 34129, etc.[a]	141.4	137–146	8	51	0.360	0.350–0.369	2
Merychyus medius santacruzensis								
New Mexico								
Tesuque Formation, Pojoaque Member								
Española Basin	F:AM 32050	140	140	1	—	—	—	—
Zia Formation, Cerro Conejo Member								
Albuquerque Basin	F:AM 104881	141	141	1	64	0.454	0.454	1

[a]F:AM 34220, 34221, 34223, 34225, 34226, 34227, 34232

FIGURE 8—Partial postcranial skeleton of oreodont *Merychyus major major* (NMMNH 57623) from early late Miocene (latest Clarendonian) Bosque del Apache LF, Popotosa Formation, Bosque del Apache National Wildlife Refuge, Socorro County, central New Mexico. Anterior to left, lateral view from left side.

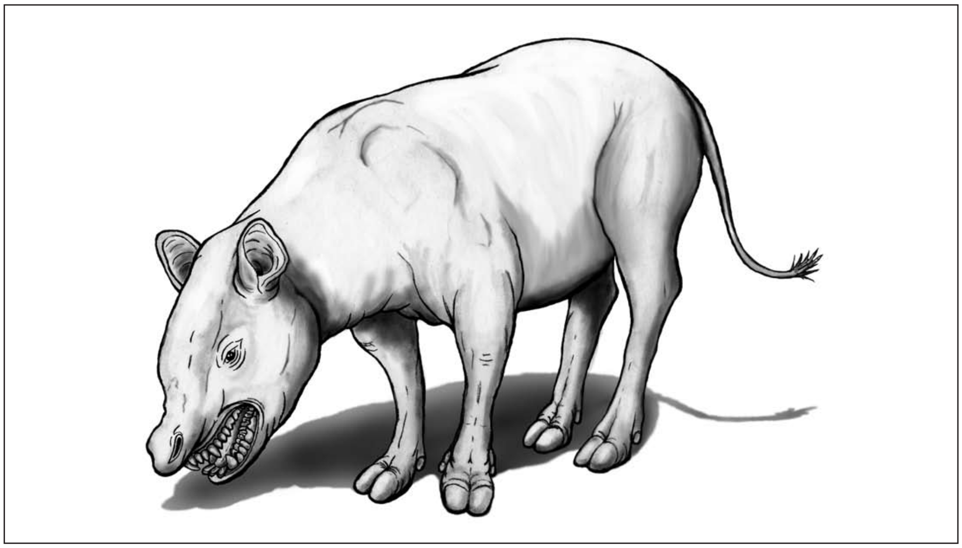

FIGURE 9—Reconstruction of the approximately 1–m (3–ft) tall Bosque del Apache oreodont, *Merychyus major major*, in a browsing pose. Drawing by Leo Gabaldon, cartographer for the New Mexico Bureau of Geology and Mineral Resources.

Lander (2008) documented a progressive size increase in average adult body size through successive generations of *Merychyus* from the early Barstovian to the latest Clarendonian NALMAs (early middle Miocene to early late Miocene), as reflected by an increase in mean P1-M3 length (see Table 4). During this same time interval, *Merychyus* also underwent an increase in the degree of posterior retraction of its external narial opening that was accompanied by the comparative shortening of the nasals and the dorsal border of the maxilla, trends apparently all related to the development of a short, tapir-like proboscis (Lander 1998, 2008). The Bosque del Apache oreodont specimen (NMMNH 57623) is referred to the early late Miocene (latest Clarendonian) subspecies *Merychyus major major*, the largest form of the genus and the largest known ticholeptine. This taxonomic assignment is based on its very large size, especially the P1-M3 length, and on its derived cranial and dental morphologies, including the pronounced posterior retraction of the external narial opening, the correspondingly short nasals, and comparatively long rostral-premaxillary suture, and rather hypsodont molars (Fig. 5, Tables 2–4). With a length of 325 mm, the skull of NMMNH 57623 is somewhat larger than the largest complete skull (317 mm) of an undescribed subspecies of *Merychyus major* from the early late Clarendonian Kat Channel in Nebraska that Schultz and Falkenbach (1941) assigned to *Ustatochoerus major*.

The holotype specimen of *Merychyus major major* (USNM 439) consists of a right maxillary fragment with the P3-M2 from an uncertain locality in Nebraska (Leidy 1859), but it is believed to have been collected in Cherry County in the north-central part of the state (Schultz and Falkenbach 1941). If from Cherry County, then the specimen probably is from the middle part of the Merritt Dam Member of the Ash Hollow Formation (Lander 2008). The P3-M2 length of the holotype specimen (94 mm; Schultz and Falkenbach 1941, p. 51) indicates that it probably represents the largest individual of the genus presently known from Nebraska (Lander 2008), if not the entire central Great Plains. With a P3-M2 length of 96 mm, the Bosque del Apache specimen of *M. major major* (NMMNH 57623) appears to represent an individual that was similar in size to that represented by the holotype specimen. A slightly smaller individual assigned to *M. major major* by Lander (2008) is recorded from the *Alligator mefferdi* quarry (F:AM 109517; P3-M2 length = 85 mm), which he also considered to be in the middle part of the Merritt Dam Member. The *Alligator mefferdi* quarry specimen might be the only other example of the subspecies recorded from the central Great Plains (Lander 2008). The latter and all other records of the subspecies are latest Clarendonian in age according to Lander (2008).

Two other measured individuals of *Merychyus major major* include LACM 4153 from Member 5 of the Dove Spring Formation in Kern County, southern California (P1-M3 length = 151 mm), and UCMP 55799 from the Lafayette Ridge LF in the basal part of the Orinda Formation in the San Francisco Bay area of Contra Costa County, central California (P1-M3 length = 150 mm) (Table 4). With a P1-M3 length of 150 mm, the *Alligator mefferdi* quarry specimen of *M. major major* represents an individual that was very similar in size to those represented by the two California specimens (Table 4). The P1-M3 length of the Bosque del Apache oreodont (157 mm) is greater than that for any other example of the genus, but only 4.7% greater than the P1-M3 length for the two smallest individuals of the subspecies, F:AM 109517 and UCMP 55799 (Table 4; Lander 2008). The holotype specimen of *Ustatochoerus californicus* Merriam 1919 (= *M. major major*; Lander 2008) comprises fragments of a crushed skull with a partial dentition (UCMP 21351) that is too incomplete to allow the measurement of its P1-M3 length. However, its M1-M3 length (ca. 102 mm) is substantially greater than that for F:AM 109517 from the *Alligator mefferdi* quarry (90 mm), but virtually the same as that for NMMNH 57623 (103 mm; Table 2). UCMP 21351 might represent the largest known individual of the genus from California and is similar in size to NMMNH 57623 from New Mexico.

As with its upper dentition, the length of the lower dentition for the Bosque del Apache specimen (NMMNH 57623) also indicates that it represents one of the largest known individuals of *Merychyus*. The p1-m3 length for NMMNH 57623 (ca. 175 mm; Table 2) is a minimum estimate because the hypoconulid or third lobe of the m3 is not fully erupted. With a p1-m3 length of 169 mm, the holotype specimen of *Ustatochoerus californicus raki* Schultz and Falkenbach 1941 (F:AM 42318), a partial mandible with a nearly complete dentition, previously represented the largest known individual of *Merychyus* from New Mexico. Lander (1998) assigned *U. californicus raki* to *M. major*, based on the very large body size indicated by its p1-m3 length. Because it represents an individual similar in size to those referred to *M. major major*, F:AM 42318 is referred to this subspecies, and *U. californicus raki* is rejected. The two New Mexico specimens are the only examples of the subspecies recorded from the southern Basin and Range province.

The *Ustatochoerus californicus raki* type specimen is from First Wash (= Arroyo del Llano on U.S. Geological Survey San Juan Pueblo 7.5-min quadrangle) in the Española Basin of northern New Mexico (Schultz and Falkenbach 1941). Galusha and Blick (1971) mapped the strata in First Wash as the Pojoaque Member of the Tesuque Formation in the Santa Fe Group. Faunas from the Pojoaque Member, including those from First Wash, have been regarded as late Barstovian (early middle and late middle Miocene; about 13.5–14.5 Ma) in age, based on Ar/Ar radioisotopic ages on tephras, paleomagnetic stratigraphy, and mammalian biostratigraphy (Barghoorn 1981; Tedford and Barghoorn 1993; Tedford et al. 2004). However, the presence of the large subspecies *M. major major* (= *Ustatochoerus californicus raki*) in First Wash suggests the presence of younger strata, as the biochron of *M. m. major* is regarded as equivalent to the latest Clarendonian NALMA (Lander 2008). Clarendonian faunas are known from the Chamita Formation, which overlies the Pojoaque Member in the Española Basin (Tedford and Barghoorn 1993; Tedford et al. 2004), but the Chamita Formation was not mapped in First Wash by Galusha and Blick (1971). Unfortunately, the exact provenance of the holotype and only known specimen of *U. californicus raki* is not known. It was collected at an unspecified site in First Wash and lacks stratigraphic data. Despite its inadequate locality and stratigraphic data, this specimen of *M. major major* suggests that fossil-bearing strata of latest Clarendonian age do occur in the immediate vicinity of First Wash.

NMMNH 57623 is the only individual of *Merychyus major major* for which the N-O/P1-M3 ratio can be calculated. The ratio for this specimen (0.325) is below the observed range of the parameter for the early late Clarendonian sample of *M. major*? new subspecies from the Kat Channel in Nebraska (0.350–0.369), and much less than the value of this parameter (0.381) for an example of this same undescribed subspecies (F:AM 34400) from the Santa Fe Group in the Española Basin in northern New Mexico (Table 4). Unfortunately, no specimen of earliest Hemphillian *M. major*? *profectus* is complete enough to allow a determination of the ratio. Therefore, NMMNH 57623 is the most advanced and tapir-like individual of *Merychyus* currently known in terms of the posterior retraction of its external narial opening.

Discussion

Taxonomic implications of fluctuations in average adult body size of *Merychyus*

Based on corresponding changes in its mean P1-M3 length, average adult body size in *Merychyus*, as in most other oreodont lineages, fluctuated dramatically through successive generations (Lander 1998, 2008). Body size increased substantially from *Merychyus medius medius* to *M. major major* during the late Barstovian to latest Clarendonian NALMAs, then decreased from *M. major major* to *M. major*? *profectus* during the latest Clarendonian to earliest Hemphillian NALMAs, and finally increased again from the earliest to late early Hemphillian NALMA (Lander 1998, 2008). Despite such considerable oscillations in their mean P1-M3 lengths (or P2-M3 lengths in agriochoerid oreodonts), simultaneous evolutionary changes, if any, in the cranial and dental morphologies of most oreodont lineages usually were very limited during many of these cycles (Lander 1977, 2008; Lander and Hanson 2006). Consequently, Lander (1977, 1998, 2008) and Lander and Hanson (2006) regarded such short-term changes as phenotypic responses to climatically induced changes in a lineage's food supply. Correspondingly, a sample composed of adults that are smaller bodied than those constituting preceding samples of the same lineage are thought to represent stunted individuals that did not achieve their full growth potentials, which were constrained by the availability of forage (Lander 1977, 1998). Unlike their larger-bodied ancestors, for whom food supply was not a factor limiting adult body size, succeeding generations were composed of smaller-bodied individuals that were unable to obtain as much sustenance as juveniles (Lander 1977, 1998).

Because fluctuations in average adult body size through time do not appear to have been genetically based, successive but morphologically similar samples of *M. medius* and *M. major* were assigned to different subspecies in the same species by Lander (2008) if their P1-M3 lengths differed substantially (i.e., in excess of 10%). Such an approach allows a sample to be distinguished from a morphologically similar one of larger or smaller average adult body size and differing geologic age. This practice follows Lander (1998, 2008) and Lander and Hanson (2006). The recognition of two or more successive subspecies in the same species also permits samples of similar cranial and dental morphologies, adult body size, and geologic age to be included in the same subspecies. In contrast and because similar mean P1-M3 lengths can be recorded at the beginning and end of a cycle characterized by oscillating body size, morphologically similar samples with comparable mean P1-M3 lengths are referred to different subspecies if they are of differing geologic ages and separated by a sample with a demonstrably different mean P1-M3 length. For example, comparatively large-bodied, late early and early late Hemphillian examples of *Merychyus* are assigned to an undescribed subspecies questionably included in *M. major* because they are separated in time from very large-bodied *M. major major* by relatively small-bodied *M. major*? *profectus*. If each body-size group were recognized as a distinct species, then it might be necessary to accept the existence of two successive species of *Merychyus* with essentially identical cranial and dental morphologies and body size. On the other hand, if body-size groups were not distinguished, refined biostratigraphic and biochronologic data critical in accurate long-range correlation and environmental reconstruction would be lost. Lander (1977, 2008) recognized the value of using similarities in mean P1-M3 lengths in conjunction with stage of evolution when correlating oreodont-bearing land mammal assemblages and their respective stratigraphic intervals, even when separated by distances as great as 2,000 km (1,250 mi).

Radioisotopic age of the Bosque del Apache oreodont skeleton compared with other localities

As presented above the geologic age of the Popotosa Formation on the Bosque del Apache National Wildlife Refuge is constrained by two $^{40}Ar/^{39}Ar$ radioisotopic ages (Table 1); pumice clasts dated at 14.59 ± 0.05 Ma near the base of the local section and a basalt flow dated at 8.57 ± 0.26 Ma (Table 1; Chamberlin et al. 2006) near the top of the section, located approximately 1 km (0.6 mi) north of the oreodont site. As shown in Figures 3 and 4 bedding attitudes and slip senses of faults between the oreodont site and the dated basalt indicate that the oreodont site is somewhat lower in the section than the dated basalt flow, and thus is slightly older.

The radioisotopic ages for the Popotosa Formation are consistent with radiometric ages for vitric tuff units in the Dove Spring Formation of southern California that bracket the stratigraphic range of *Merychyus major major*. The first local appearance of *M. major major* in the Dove Spring Formation is from above tuff unit 6 (Lander 2008), which, in turn, lies immediately above the lower basalt unit at the base of Member 4 (Whistler et al. 2009). Tuff unit 6 has been correlated geochemically with Cougar Point Tuff Unit XII, which is estimated to be 11.19 ± 0.10 Ma by interpolation (Perkins et al. 1998; Whistler et al. 2009). The last local occurrence of *M. major major* in the Dove Spring Formation is from just above tuff unit Tra-15 (Lander 2008), which lies at the base of Member 6 (Whistler et al. 2009). Tuff unit Tra-15 is 9.36 ± 0.20 Ma in age by extrapolation (Perkins et al. 1998). The radiometric age determinations from the Dove Spring Formation in California, together with the dated basalt of 8.57 ± 0.26 Ma overlying the Bosque del Apache oreodont site in the Popotosa Formation, suggest that the specimen of *M. major major* from the Bosque del Apache LF is early late Miocene (latest Clarendonian) in age and between about 11 and 9 Ma (Lourens et al. 2004).

Comparison of Bosque del Apache LF and Gabaldon Fauna

The only other fossil vertebrates reported from the Popotosa Formation are from the Gabaldon badlands west of Belen in Valencia County, approximately 100 km (60 mi) north of the Bosque del Apache National Wildlife Refuge (Lozinsky and Tedford 1991). The fossil land mammals in the Gabaldon Fauna are indicative of an early Hemphillian age (ca. 7–9 Ma), based on the presence of the canids (dogs) *Epicyon haydeni* and *Metalopex merriami*, the large felid (cat) *Nimravides* cf. *N. catocopis*, and the castorid (beaver) *Dipoides* cf. *D. vallicula* (Lozinsky and Tedford 1991; Tedford et al. 2004, 2009). Although the Gabaldon Fauna lacks *Merychyus major*? *profectus*, the early Hemphillian age suggested by the mammalian assemblage indicates that it is somewhat younger than the latest Clarendonian Bosque del Apache LF.

Brief review of New Mexico oreodonts

Members of the Oreodontidae were common in faunas of late Eocene to late middle Miocene (early Chadronian to early late Clarendonian) age in the central Great Plains, particularly in adjacent portions of northern Nebraska, southeastern Wyoming, and southern South Dakota, but they were never especially common in correlative strata in New Mexico (Schultz and Falkenbach 1968; Lander 1998). The only stratigraphic units in New Mexico in which oreodonts have been encountered with any frequency are the Skull Ridge, Pojoaque, and Chama–El Rito Members of the Tesuque Formation of the Santa Fe Group in the Española Basin of Santa Fe and Rio

Arriba Counties in northern New Mexico (Frick 1929; Schultz and Falkenbach 1940, 1941, 1947, 1968; Tedford 1981; Tedford and Barghoorn 1997; Lander 1998). Fossil mammal assemblages from these three members of the Tesuque Formation have been regarded as Barstovian (early middle and late middle Miocene) in age (Tedford 1981; Tedford and Barghoorn 1997, Tedford et al. 2004). Oreodonts had not been reported from the Popotosa Formation before the discovery of the *Merychyus major major* specimen described herein from the Bosque del Apache National Wildlife Refuge of Socorro County in central New Mexico.

The earliest members of the Oreodontidae currently known from New Mexico are of Oligocene age from the Seventyfour Draw site in the Black Range of Sierra County, southwestern New Mexico (Morgan and Lucas 2003). Tedford (1981) tentatively referred the specimens from this site to *Promerycochoerus carrikeri* Peterson 1907, a large oreodont typical of assemblages of late Oligocene or earliest Miocene (early late Arikareean) age. However, a reexamination of both the oreodont specimens and the geology of the Seventyfour Draw site suggests a late Oligocene (late early Arikareean) age. Although based on rather fragmentary remains, two taxa of oreodonts were tentatively identified from Seventyfour Draw by Morgan and Lucas (2003), including *Desmatochoerus* cf. *D. megalodon* (Peterson 1907) (= *Eporeodon chelonyx* [Scott 1893]; see Lander 1998) and *Megoreodon* cf. *M. grandis* (= *Merycochoerus superbus* [Leidy 1870]; Lander 1998). Both taxa are typical of late early Arikareean (late Oligocene) faunas from the central Great Plains of Nebraska, Wyoming, and South Dakota that are approximately 28.5–25.5 Ma. The biochrons of the two oreodont taxa are consistent with an $^{40}Ar/^{39}Ar$ radioisotopic age of 27.2 Ma on the South Canyon Tuff, a unit that is correlative with the volcaniclastic strata at the Seventyfour Draw site (McIntosh et al. 1991).

The remaining members of the Oreodontidae presently recorded from New Mexico are from Miocene strata of the Santa Fe Group in the Española and Albuquerque Basins in the northern part of the state. The taxa represented include the following (Lander 1998, 2008): latest Arikareean (earliest Miocene) *Merychyus crabilli crabilli* Schultz and Falkenbach 1947 (regarded as a possible junior synonym of *M. calaminthus* Jahns 1940 by Schultz and Falkenbach 1947, and most subsequent workers; includes *M. crabilli ziaensis* Schultz and Falkenbach 1968) from the Piedra Parada Member of the Zia Formation; late Hemingfordian and early Barstovian (late early and early middle Miocene) *M. relictus* (includes *M.* [*Metoreodon*] species undetermined of Schultz and Falkenbach 1947, 1968) from the Chamisa Mesa Member of the Zia Formation and the Skull Ridge Member of the Tesuque Formation, respectively; latest Hemingfordian (late early or early middle Miocene) *Brachycrus laticeps laticeps* (Douglass 1900) from the uppermost part of the Nambé Member of the Tesuque Formation (E. B. Lander, unpub. data) or the lowermost part of the Skull Ridge Member; early Barstovian (early middle Miocene) *B. laticeps siouense* Sinclair 1915 (includes *B.* species undetermined of Schultz and Falkenbach 1941, *B. rusticus riograndensis* Schultz and Falkenbach 1968, *B. vaughani rioosoensis* Schultz and Falkenbach 1968) from the lower (but not lowermost) part of the Skull Ridge Member and the lower part of the Chama–El Rito Member of the Tesuque Formation; *M. medius novomexicanus* Frick 1929 (includes *Ustatochoerus profectus espanolensis* Schultz and Falkenbach 1941), *M. medius santacruzensis* Schultz and Falkenbach 1941, *M. major*? new subspecies of Lander (2008), and *M. major major* (includes *Ustatochoerus californicus raki* Schultz and Falkenbach 1941), all from the Pojoaque Member of the Tesuque Formation; *M. medius novomexicanus* from the upper part of the Chama–El Rito Member; and *M. medius santacruzensis* from the Cerro Conejo Member of the Zia Formation (E. B. Lander, unpub. data).

There is some disagreement on the age of the Pojoaque and Chama–El Rito Members of the Tesuque Formation and the Cerro Conejo Member of the Zia Formation. Most previous authors (e.g., Tedford and Barghoorn 1993, 1997, 1999; Tedford et al. 2004) regard all mammalian faunas from the Pojoaque, Chama–El Rito, and Cerro Conejo Members to be late Barstovian (early middle Miocene) in age. However, E. B. Lander (unpub. data) believes that the oreodonts from these three units, in particular the Pojoaque Member, are late early Clarendonian (*M. medius novomexicanus*), middle Clarendonian (*M. medius santacruzensis*), early late Clarendonian (*M. major*? new subspecies), and latest Clarendonian in age (*M. major major*).

The skeleton of *Merychyus major major* from the Bosque del Apache LF is latest Clarendonian (early late Miocene) in age and, with the possible exception of the *Ustatochoerus californicus raki* holotype specimen, is younger than any other oreodont record now known from New Mexico. The youngest reported oreodont occurrence is an undescribed subspecies of *Merychyus major*? from the latest Miocene (early late Hemphillian) ZX Bar LF of the Nebraska Panhandle (Lander 2008). Late Hemphillian faunas occur in the upper part of the Chamita Formation in the Española Basin, including the San Juan, Rak Camel, Black Mesa, and Lyden quarries, but none of these sites is known to have produced an oreodont (MacFadden 1977; Morgan et al. 2005). Presumably, the trend toward drier climates and more open habitats during the middle and late Miocene of North America led to the extinction of oreodonts at the end of the epoch (Lander 1998).

Summary

The record of the oreodont *Merychyus major major* from the Bosque del Apache National Wildlife Refuge in central New Mexico is important for a number of reasons. The specimen represents the first identifiable fossil vertebrate occurrence from the Popotosa Formation on the Bosque del Apache National Wildlife Refuge. Moreover, the latest Clarendonian (early late Miocene) age of the oreodont makes it the oldest record of a land mammal from that formation. Additionally, the individual represents one of the youngest examples of an oreodont currently known from New Mexico and one of only two individuals of the subspecies presently recorded from the southern Basin and Range province. Finally, the specimen is especially significant because it includes the most complete skull of the subspecies ever recovered. Because the skull is so complete, it has finally been possible to determine that *M. major major* is the most advanced or tapir-like member of the genus. *Merychyus major major* comprises the largest members of the genus, with the specimen from the Bosque del Apache National Wildlife Refuge likely representing the largest individual.

Acknowledgments

We are especially grateful to Tom Melanson, Colin Lee, and other USFWS staff from the Bosque del Apache National Wildlife Refuge for issuing a permit to collect the oreodont skeleton described herein and for assisting NMMNH staff in organizing and conducting the excavation effort. Colin Lee provided the photographs for Figure 2. Warren Slade helped recover the skeleton, and J. B. Norton prepared the specimen in the NMMNH preparation laboratory with assistance from Larry Rinehart. Tom Williamson assisted with specimen photography, and Phil Miller helped with graphics. We thank Leo Gabaldon for allowing us to reproduce his exquisite drawing of the Bosque del Apache oreodont. Peter Mozley and Richard White provided helpful comments on the manuscript.

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