Introduction

The transition between the Bridgerian and Uintan North American Land Mammal ages (NALMAs) remains one of the most problematic biostratigraphic intervals in the Eocene. Although several well-documented faunal assemblages are known from the late Bridgerian and early Uintan, few continuous fossiliferous sequences span the Bridgerian–Uintan transition [1,2]. Furthermore, patterns of regional endemism complicate attempts to make precise biostratigraphic correlations between localities [3,4]. The Devil’s Graveyard Formation (DGF) of Trans-Pecos Texas (Figure 1) is particularly relevant for understanding the tempo and mode of mammalian evolution during the early Uintan because it preserves abundant middle Eocene faunal assemblages stratified within volcaniclastic sediments dateable by both radiometric and paleomagnetic techniques.

Fossil materials assigned to the Whistler Squat local fauna of the DGF were collected by University of Texas field parties under the direction of J.A. Wilson from 1970–1974 and are curated at the Jackson School of Geosciences Vertebrate Paleontology Laboratory at the University of Texas at Austin. As defined by Walton [5,6], the Whistler Squat local fauna consists of material from four localities recovered from an equivalent stratigraphic sequence in the DGF: (1) TMM 41372 (“Whistler Squat Quarry”); (2) TMM 41466, described as “located about 300 yards east of” TMM 41372 ([7]; p. 354) although specimen notes document that these fossils were collected over a large area adjacent to the quarry as opposed to a discrete locality (E.C.K., pers. obs.); (3) TMM 41576 (“Wax Camp”), located ~1.5 km west of TMM 41372; and (4) TMM 41747 (“Boneanza”), located ~750 m northeast of TMM 41372. This study focuses only on specimens from the Whistler Squat Quarry ($n=815$) and TMM 41466 ($n=16$), which are derived from the same stratum (M.S. Stevens, pers. comm., May, 2013) and together comprise 84% of the specimens in the Whistler Squat local fauna. Fossils from Wax Camp and Boneanza are not considered here because the exact stratigraphic provenance of these two localities is not as well documented, Wilson [7] originally grouped fossils from the “basal Tertiary conglomerate” of the lowermost DGF with those of the stratigraphically higher Whistler Squat Quarry level as comprising the Whistler Squat local fauna. However, he also noted that further collecting might favor the

Abstract

The Whistler Squat Quarry (TMM 41372) of the lower Devil’s Graveyard Formation in Trans-Pecos Texas is a middle Eocene fossil locality attributed to Uintan biochronological zone Ui1b. Specimens from the Whistler Squat Quarry were collected immediately above a volcanic tuff with prior K/Ar ages ranging from ~47–50 Ma and below a tuff previously dated to ~44 Ma. New $^{40}\text{Ar}/^{39}\text{Ar}$ analyses of both of the original tuff samples provide statistically indistinguishable ages of 44.88±0.04 Ma for the lower tuff and 45.04±0.10 Ma for the upper tuff. These dates are compatible with magnetically reversed sediments at the site attributable to C20r (43.505–45.942 Ma) and a stratigraphic position above a basalt dated to 46.80 Ma. Our reanalysis of mammalian specimens from the Whistler Squat Quarry and a stratigraphically equivalent locality significantly revises their faunal lists, confirms the early Uintan designation for the sites, and highlights several biogeographic and biochronological differences when compared to stratotypes in the Bridger and Uinta Formations. Previous suggestions of regional endemism in the early Uintan are supported by the recognition of six endemic taxa (26% of mammalian taxa) from the Whistler Squat Quarry alone, including three new taxa. The revised faunal list for the Whistler Squat Quarry also extends the biostratigraphic ranges of nine non-endemic mammalian taxa to Ui1b.

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* Email: campisano@asu.edu
allocation of localities in these two stratigraphic intervals to
different local faunas [7]. Walton [5,6] subsequently recognized a
Basal Tertiary local fauna for the older DGF localities (Figure 2)
based on key differences between these two stratigraphic intervals,
such as the first appearance of Amynodon in the Whistler Squat
Quarry. Reviews by Robinson et al. [1] and Gunnell et al. [2] also
recognize a biostratigraphic difference between these two intervals
within the lower member of the DGF, but do not use the term
Basal Tertiary local fauna for the older material.

Robinson et al. [1] erected the Uintan biochron Ui1 to
accommodate those assemblages that represent a transitional
interval between Bridgerian biochron Br3 and the early Uintan
faunal assemblages typified by Uinta B localities in Utah and
assigned to Uintan biochron Ui2. Furthermore, Robinson et al. [1]
assigned the Whistler Squat local fauna of the DGF to either Ui1
or Ui2. Gunnell et al. [2] subsequently subdivided Ui1 into
biochrons Ui1a and Ui1b based on differences in the number of
Bridgerian holdover taxa, the diversity of selenodont artiodactyls,
and the first appearance of Amynodon. The Turtle Bluff Member
(=Bridger E) of the Bridger Formation was selected as the
statotype for the Ui1 biochron, but due to the lack of high
resolution lithostratigraphic data associated with Ui1b faunal
assemblages, no stratotype was assigned to biochron Ui1b. Instead,
the biochron is associated with a half-dozen well-documented
faunal assemblages including the Whistler Squat local fauna of the
DGF.

In this study, we revise the radiometric age and reassess the
mammalian specimens from two localities of the Whistler Squat
local fauna for the first time in nearly three decades. Our
geochronological results provide a tightly constrained age for the
Whistler Squat localities, and our reanalysis of fossil specimens
significantly revises the Whistler Squat faunal list. These results
have important implications for early Uintan biochronology and
for documenting regional patterns of endemism in the middle
Eocene of North America.

Abbreviations: TMM, Jackson School of Geosciences Verte-
brate Paleontology Laboratory at the University of Texas at
Austin, formerly “Texas Memorial Museum”, Austin, Texas,
USA; USNM, Smithsonian Institution National Museum of
Natural History, Washington, D.C., USA; YPM, Yale University
Peabody Museum of Natural History, New Haven, Connecticut,
USA; p, mandibular premolar; P, maxillary premolar; m, mandibular molar; M, maxillary molar; Ma, mega-annum.

Geological Context

The Devil’s Graveyard Formation (DGF), part of the Buck Hill
Group, is composed of more than 472 meters of middle Eocene to
early Oligocene continental volcaniclastic sediments located in the
south-central part of the Trans-Pecos volcanic field of West Texas
[8]. The DGF is exposed principally at the western edge of
Brewster County in the Agua Fria region between Big Bend
National Park and Big Bend Ranch State Park (Figure 1).
Additional exposures attributed to the DGF have been mapped to
the southeast of Agua Fria in the vicinity of Hen Egg Mountain
and Dogie Mountain [9,10] (Figure 1). In its type area, the DGF

Figure 1. Satellite image of the Devil’s Graveyard Formation study area and surrounding region. WSQ = Whistler Squat Quarry; JCT = Junction locality; AF = Agua Fria Mountain; HE = Hen Egg Mountain; DB = Devil’s Graveyard basalt; DM = Dogie Mountain.
unconformably overlies late Cretaceous marine sediments, and is capped by the Mitchell Mesa Rhyolite [8,11]. Stevens et al. [8] divided the DGF into three units based principally on local disconformities, the informal lower and middle members and the formal Bandera Mesa Member (Figure 2). Fossil localities in the basal portion of the lower member comprise the early Uintan Basal Tertiary local fauna, those in the upper portion of the lower member comprise the early Uintan Whistler Squat local fauna, those from the middle member comprise the late Uintan Serendipity local fauna, and those from the Bandera Mesa Member comprise the Duchesnean Skyline local fauna [5,6,7,12] (Figure 2).

Wilson [7] described the main fossiliferous unit of the Whistler Squat Quarry as a weakly calcareously cemented bentonitic clay-pebble conglomerate with sanidine and biotite grains. This unit ranges up to 35 cm thick and is likely a fluvial channel remnant because it grades upward into cross-bedded sands and preserves variable degrees of water-worn bone [J.A. Wilson, 1970 field notes, TMM]. At the Whistler Squat Quarry a 15–50 cm thick calcareous tuff, referred to as the “Quarry Tuff” by Walton [5], directly underlies the fossiliferous unit [7,8] (Figure 3). The Quarry Tuff was described as a welded tuff discontinuously exposed from the southwest to northeast corners of the type area with a distinctive fractured, yellow-stained surface in outcrop [5,8]. At the Whistler Squat Quarry, the resistant tuff forms a low bluff that the fossiliferous unit rests upon, with several areas excavated across the exposed platform (Figure 3). The tuff and clay-pebble conglomerate grade laterally into a tuffaceous limestone, reported to represent a depositional environment close to the edge of a small lake [7]. In some locations, an additional 10–90 cm of mottled yellow and purple bentonite that is sparsely fossiliferous separates the tuff from the channel deposit (J.A. Wilson, 1971 field notes, TMM). Samples JW-1 and 72-WS33-2 were collected for dating from the Quarry Tuff at the Whistler Squat Quarry. The Lunch Locality sandstone, 5–6 m above the Quarry Tuff at the Whistler Squat Quarry, is a ledge forming sandstone on the west side of the excavated areas (Figure 3) that along with several other localized channel sands at the same approximate stratigraphic level have been referred to as the “Lunch Complex” [5,8]. Approximately 1.5 km south of the Whistler Squat Quarry, sample JW-2 was collected from a biotite-rich ash in the lowest part of the Lunch Complex associated with the “orange clinoptilolite” (a product of altered volcanic glass) [5], J.A. Wilson, 1971 field notes, TMM). Thus, the two samples from the Quarry Tuff and JW-2 bracket the Whistler Squat Quarry, and a biotite tuff with associated orange clinoptilolite identified in the Quarry Tuff at the Whistler Squat Quarry is a ledge forming sandstone on the west side of the excavated areas (Figure 3) that along with several other localized channel sands at the same approximate stratigraphic level have been referred to as the “Lunch Complex” [5,8]. Approximately 1.5 km south of the Whistler Squat Quarry, sample JW-2 was collected from a biotite-rich ash in the lowest part of the Lunch Complex associated with the “orange clinoptilolite” (a product of altered volcanic glass) [5], J.A. Wilson, 1971 field notes, TMM). Thus, the two samples from the Quarry Tuff and JW-2 bracket the Whistler Squat Quarry and TMM 41466, although the Quarry Tuff is more directly associated with the fossil fauna in both geographic and stratigraphic context.

Samples JW-1, 72-WS33-2, and JW-2 were first dated in the 1970s by F. McDowell at the University of Texas at Austin. Age results have been reported in several publications (e.g., [8,13,14]), but the complete analytical details and data reduction have never been published. Sanidine separates from JW-1 and plagioclase separates from 72-WS33-2 yielded K/Ar ages of 46.9±1.0 Ma and 49.7±1.2 Ma, respectively. Biotite separates from JW-2

| EPOCH | NALMA | LITHOLOGIC UNIT | LOCALITY | LOCAL FAUNA | BIOCHRON ZONE | AGE (MA) | DATED HORIZON |
|-------|-------|----------------|---------|-------------|--------------|----------|---------------|
| Oligocene | | | | | | 33.25 | Mitchell Mesa Rhyolite |
| | | | | | | 42.77 | biotite tuff (B-5367) |
| | | | | | | 45.04 | orange clinoptilolite biotite (JW-2) |
| | | | | | | 44.88 | Quarry Tuff (JW-2) |
| | | | | | | 46.8 | basalt (H86-92) |

Figure 2. Lithostratigraphy, biochronology and radiometric ages of the Devil’s Graveyard Formation in the Agua Fria and Hen Egg Mountain region. Sample numbers for dated horizons are in parentheses. The 1980s K/Ar age for sample B-5367 of 42.7±1.6 Ma [8,14] has been assumed to be erroneously old by others (e.g., [96]) and is being redated. Locality numbers: Hen Egg Mountain (TMM 42028, TMM 42287); 0.6 miles east of Junction (TMM 41444); Junction (TMM 41443); Boneanza (TMM 41747); Wax Camp (TMM 41576); Whistler Squat Quarry (TMM 41372); 300 yd east of Whistler Squat Quarry (TMM 41466); Titanothere Hill (TMM 41723); Serendipity (41745); Purple Bench (TMM 41672); Tepee Canyon (TMM 41578); Above Skyline (TMM 41580); Dalquest’s Canyon (TMM 41715).

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yielded a K/Ar age of 43.9±0.7 Ma. This study takes advantage of the significant technological advances over the last several decades to provide single-crystal ^{40}Ar/^{39}Ar analyses of samples JW-1 and JW-2 and the Whistler Squat Quarry assemblage.

Figure 3. Photos of the Whistler Squat Quarry locality. From the archives of the Vertebrate Paleontology Laboratory and courtesy of Sarah Wilson. A, 1970 aerial view of the locality prior to any significant quarrying with key features marked; B, excavation at the quarry, July 1971; C, close-up of the ~20 cm fossiliferous horizon immediately overlying the Quarry Tuff, August 1971.

doi:10.1371/journal.pone.0101516.g003

Materials and Methods

Geochronology

Tephra samples JW-1 and JW-2 were collected by J. Wilson in 1970 and 1971, respectively. Both samples are distal tuffs. JW-1 is well indurated, whereas JW-2 is soft and friable. In thin section, both samples are matrix supported by a groundmass of fine clay that is likely the alteration product of volcanic glass shards. The phenocryst population includes quartz and potassium feldspar of
approximately equal amounts, with subordinate plagioclase and biotite and sparse lithic fragments (J.W. McDowell, pers. comm., March, 2013). Sample JW-1 appears to be an undisturbed ash-fall deposit, confirming the original description of the Quarry Tuff as a primary tephra deposit. The JW-2 thin section indicates some degree of winnowing of ash compared to JW-1, but we still interpret it as an unworked fallout tuff as opposed to a "tuffaceous sediment" as noted in Henry et al. [14].

Sample preparation was principally conducted at the University of Texas at Austin by J.W. McDowell in the 1970s. Both samples were processed through a jaw crushe and disk mill, the latter at a close adjustment to liberate crystals from ground mass. Samples were screened to retain the 60–80 mesh (180–250 micron) size fraction. They were then washed and passed through a magnetic separator, in the case of JW-1 to eliminate all magnetic particles and for JW-2 to roughly define the range of magnetic susceptibility for the biotite. Sample JW-2 was processed through bromoform with a specific gravity of 2.86 and further refined by ultrasonic cleaning and sieving, followed by more careful magnetic separation. The finished separate was checked by x-ray diffraction for crystallinity and chlorite content. For JW-1, following a leach in 10% hydroflouric acid and sonification to remove fines, the feldspar of JW-1 was separated with bromoform adjusted with acetone to a specific gravity of approximately 2.60 or lighter to eliminate quartz and then at 2.56 to eliminate groundmass. Finally, X-ray diffraction was used to assess residual quartz content. The original feldspar separates from JW-1 and biotite separates from JW-2 were subsequently re-screened for the 40–60 mesh (250–425 micron) size fraction, with the most euhedral and unaltered crystals hand-picked under a stereomicroscope at Arizona State University.

The crystal concentrates were irradiated in a single batch for 50 hours in the Cd-lined, in-core CLICIT facility of the Oregon State University TRIGA reactor. Sanidine from the Fish Canyon Tuff of Colorado was used as the neutron fluence monitor, with an astronomically calibrated reference age of 28,201 ± 0.046 Ma [15]. Standards and unknowns were placed in 2 mm deep wells in circular configurations on 18 mm diameter aluminum disks, with standards placed strategically so that the lateral neutron flux gradients across the disk could be evaluated. Planar regressions were fit to the standard data, and the 40Ar/39Ar neutron fluence parameter, J, interpolated for the unknowns. J's are measured independently for each machine and approach, and in this case differ by ~1% between the systems. Uncertainties in J are estimated at ~0.05% for the single-crystal total-fusion (SCFT) data set on the MAP machine, and ~0.2% for the single-crystal incremental-heating (SCH) work on the Noblesse, based on Monte Carlo error analysis of the planar regressions [16].

All 40Ar/39Ar analytical work was performed at the Berkeley Geochronology Center (BGC). Argon extractions from the irradiated material were performed on two separate systems. The SCFT work utilized a partially defocused CO2 laser beam delivering ~5–8 Watts of power to rapidly fuse individual feldspars over an interval of ~6 seconds. Released gasses were exposed for several minutes to an approximately 143 K cryo-surface to trap H2O, and to SAES getters to remove reactive compounds (CO, CO2, N2, O2, and H2). After approximately three minutes of cleanup, the gas was admitted to an MAP 215–50 mass spectrometer. Five argon isotopes were measured by peak hopping on a single analog multiplier over a period of approximately 30 minutes. Measured isotope abundances were corrected for extraction-line blanks. A value of 293.5 was used for the atmospheric 40Ar/36Ar ratio [17] for the purposes of routine measurement of mass spectrometer discrimination using air aliquots, and correction for atmospheric argon in the 40Ar/39Ar age calculation. Additional details of the total-fusion feldspar dating methodology as applied at BGC are provided elsewhere [16,18,19,20].

The SCH work was performed on a completely separate extraction line and mass spectrometer combination. Laser heating was achieved using a CO2 laser fitted with a beam-shaping lens that generates a flat energy profile of variable diameter. Individual grains of biotite were heated for ~30 seconds at progressively increasing power levels until fusion was achieved (5–8 steps). After a cleanup interval of several minutes analogous to that described above, the argon isotopes were measured by ion counting on a 5-collector Noblesse mass spectrometer over a period of about eight minutes. Isotopes 40Ar, 39Ar, 37Ar, and 38Ar were detected simultaneously on separate ion counters, interspersed with a brief peak hop to bring 36Ar onto an ion counter for measurement. Count rates were kept below 200 kcps to minimize dead-time corrections. Detector intercalibrations were performed with periodic measurement of air argon (40Ar/36Ar by comparison of simultaneous measurement to the expected air ratio of 295.5, and 40Ar/39Ar, 40Ar/38Ar, and 40Ar/36Ar by repeated measurement of 40Ar on relevant detectors). Measurement of the neutron flux standard (FG Sanidine) was also performed by SCH on the same machine using the same protocols as the unknown.

Paleontology

This study examined mammalian specimens from localities TMM 41372 (Whistler Squat Quarry) and TMM 41466 (representing the same stratigraphic interval as the Whistler Squat Quarry) housed at the Jackson School of Geosciences Vertebrate Paleontology Laboratory at the University of Texas at Austin, a publicly accessible paleontological repository. No permits were required for the described study, which compiled with all relevant regulations. All fossil specimens were collected in the 1970s on private land (Agua Fria Ranch) with permission of the landowners (M. Richmond and J.H. Burton) and lessees (B.P. and S. McKinney). All examined specimens are listed in the Systematic Paleontology section below. Some of these specimens were previously used to generate a faunal list for the "Whistler Squat quarry and equivalent localities" by Wilson [17; p. 371]. No other systematic re-assessment of the mammalian fossil sample from these two localities has been undertaken in the intervening 27 years. Although some specimens from TMM 41372 and TMM 41466 have been included in earlier descriptions of the DGF mammalian fauna (see below), formal examination and comparison of other specimens used in this analysis have not been completed previously.

Results

Geochronology

Single-crystal total-fusion 40Ar/39Ar dating of 27 sanidine phenocrysts from JW-1 yielded a simple unimodal distribution of ages (Figure 4) and a weighted mean age of 44.88 ± 0.04 Ma (1σ error including error in J, MSWD = 0.73) (Table 1, Table S1). This high-precision result (± ~0.08%) serves as an excellent chronostratigraphic tie-point for the section.

Fourteen SCH 40Ar/39Ar dating experiments on single biotite grains from JW-2 are illustrated as incremental release spectra in Figure 5, with analytical data provided in Table 2 and Table S1. Note that these data sets exclude steps yielding less than 2% of the total 40Ar released. Every experiment yielded a plateau (defined by consecutive steps in which there is greater than a 95% chance that the Mean Square of Weighted Deviates [MSWD] of ages is
accounted by measurement error alone) encompassing >90% of the total 39Ar released. Further, each experiment revealed high radiogenic content vs. atmospheric contamination, registering >90% radiogenic argon (40Ar*) in all but a few of the earliest steps. Thus, the internal systematics of the individual biotite spectra suggest that they are fresh, undisturbed grains that potentially yield accurate geological information. The population distribution of the plateau ages for JW-2 yielded a simple unimodal distribution (Figure 6), with a weighted mean of 45.04 ± 0.10 Ma (1σ error including error in \( J \), MSWD = 1.03, n = 14) (Table 2).

The biotite mean plateau age for sample JW-2 is statistically indistinguishable at the 95% confidence level from the sanidine age of the stratigraphically lower sample JW-1. Of these two sample ages, the result that best defines the age of the fossiliferous horizon is clearly the sanidine determination from JW-1 of 44.88 ± 0.04 Ma. This result is not only more analytically precise, but sanidine is potentially more geologically accurate due to the greater susceptibility to alteration of biotite. The chronostratigraphic tie point provided by the sanidine date is also convenient because the dated tuff lies immediately below the fossil horizon.

### Table 1. Summary single-crystal total-fusion 40Ar/39Ar analytical results for JW-1 sanidine phenocrysts.

| Lab ID# | 39Ar Mol x10^-14 | %40Ar* | Ca/K | Age ±1σ (Ma) | 1σ error in \( J \) |
|---------|-----------------|--------|------|--------------|------------------|
| 25958-01 | 5.25            | 99.0   | 0.0249 | 44.90 ± 0.20 |                  |
| 25958-03 | 9.22            | 98.9   | 0.0169 | 44.95 ± 0.15 |                  |
| 25958-05 | 7.09            | 99.1   | 0.0240 | 44.88 ± 0.17 |                  |
| 25958-09 | 10.96           | 99.1   | 0.0258 | 44.84 ± 0.13 |                  |
| 25958-10 | 10.16           | 99.6   | 0.0219 | 45.07 ± 0.14 |                  |
| 25958-11 | 6.92            | 99.3   | 0.0248 | 44.91 ± 0.18 |                  |
| 25958-12 | 7.84            | 99.6   | 0.0229 | 45.02 ± 0.16 |                  |
| 25958-13 | 10.50           | 98.8   | 0.0333 | 44.72 ± 0.12 |                  |
| 25958-14 | 7.08            | 99.3   | 0.0295 | 45.00 ± 0.17 |                  |
| 25958-15 | 8.04            | 95.9   | 0.0270 | 44.84 ± 0.15 |                  |
| 25958-16 | 9.12            | 98.7   | 0.0252 | 44.76 ± 0.14 |                  |
| 25958-17 | 6.04            | 99.0   | 0.0338 | 45.00 ± 0.18 |                  |
| 25958-18 | 7.36            | 98.8   | 0.0178 | 44.85 ± 0.16 |                  |
| 25958-19 | 6.53            | 98.6   | 0.0844 | 45.01 ± 0.17 |                  |
| 25958-20 | 6.52            | 98.1   | 0.0440 | 44.94 ± 0.18 |                  |
| 25958-21 | 9.00            | 99.1   | 0.0290 | 44.99 ± 0.14 |                  |
| 25958-22 | 7.34            | 99.6   | 0.0338 | 44.96 ± 0.15 |                  |
| 25958-23 | 8.29            | 98.7   | 0.0284 | 44.65 ± 0.15 |                  |
| 25958-24 | 8.15            | 99.2   | 0.0327 | 44.94 ± 0.15 |                  |
| 25958-25 | 7.79            | 99.1   | 0.0227 | 44.75 ± 0.15 |                  |
| 25958-26 | 5.16            | 98.8   | 0.0303 | 45.13 ± 0.22 |                  |
| 25958-27 | 6.97            | 99.0   | 0.0178 | 45.06 ± 0.18 |                  |
| 25958-28 | 7.05            | 99.0   | 0.0218 | 45.02 ± 0.18 |                  |
| 25958-29 | 6.74            | 98.8   | 0.0291 | 44.71 ± 0.17 |                  |
| 25958-30 | 5.19            | 98.9   | 0.0266 | 45.01 ± 0.20 |                  |
| 25958-31 | 8.43            | 98.8   | 0.0295 | 44.66 ± 0.14 |                  |
| 25958-32 | 7.19            | 98.7   | 0.0260 | 44.79 ± 0.16 |                  |
| Weighted Mean |                  |        |        | 44.88 ± 0.04 |                  |

1σ error in \( J \), the neutron fluence parameter. 
MSWD = Mean Square Weighted Deviation.
Complete analytical data provided in Table S1. 
doi:10.1371/journal.pone.0101516.t001

### Systematic Paleontology

Order DIDELPHIMORPHIA Gill, 1872 [21].
Family HERPETOTHERIIDAE Trouessart, 1879 [22].
Genus HERPETOTHERIUM Cope, 1873 [23].
HERPETOTHERIUM sp.
Specimens: TMM 41372-239, -403.

These two isolated lower molars from the Whistler Squat Quarry were included by West [24] in an assemblage of isolated teeth that he attributed to *Herpetotherium marsupium* (Figure 7A-B).

**Herpetotherium** is known from many North American Eocene localities and ranges from the Wasatchian through the Duchesnean [25]. Species level designations for *Herpetotherium* are primarily based on characters of the upper molars, which are not represented in the Whistler Squat Quarry sample. Lower molars of the known species of *Herpetotherium* may differ in size, but are very similar in occlusal morphology [26,27]. Accordingly, West’s [24] attribution of the Whistler Squat Quarry specimens to *H. marsupium* was based on the morphology of upper molars recovered from U1a localities that are stratigraphically lower in the Devil’s Graveyard Formation (i.e., TMM 41443 “Junction”...
and TMM 41444 “0.6 miles east of Junction”; Figure 2). TMM 41372-403 very closely resembles the m2 of the holotype mandible of *H. marsupium* (YPM 13518; [28]) in both size and morphology. The Whistler Squat Quarry *Herpetotherium* lower molars also compare favorably in size with lower molars attributed to *H. marsupium* from the Uintan Swift Creek local fauna [29] and with *Herpetotherium* cf. *H. marsupium* from the Duchesnean Lac Pelletier local fauna [26,27]. Nevertheless, TMM 41372-403 is also similar in size to lower molars attributed to the Bridgerian-Duchesnean species *H. knighti* and TMM 41372-239 is similar in size to lower molars attributed to the Wasatchian-Duchesnean species *H. innominatum* [2,24,26,30,31]. Given this size overlap with multiple Uintan species of *Herpetotherium* and the lack of associated upper molars from the Whistler Squat Quarry that might be used for species identification, we refer TMM 41372-239 and TMM 41372-403 to *Herpetotherium* sp.

Both of the Whistler Squat Quarry specimens are either first or second lower molars. The first through third mandibular molars of

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**Figure 4.** $^{40}$Ar/$^{39}$Ar age distribution of JW-1 phenocrysts. Age-probability density function and weighted-mean age of the $^{40}$Ar/$^{39}$Ar single-crystal total-fusion (SCTF) analyses of individual sanidine phenocrysts from sample JW-1. Complete analytical data provided in Table S1. doi:10.1371/journal.pone.0101516.g004
Herpetotherium are nearly identical in cusp morphology and differ primarily in their size and the relative proportions of the trigonid and talonid [26]. Until more specimens can be recovered we defer identifying tooth position for these specimens.

Order LIPOTYPHA Haeckel, 1866 [32].
Suborder ERINACEOMORPHA Gregory, 1910 [33].
Family AMPHILEMURIDAE Hill, 1953 [34].
Genus SCENOPAGUS McKenna and Simpson, 1959 [35].

SCENOPAGUS cf. S. EDENENSIS McGrew, 1959 [31].

Two isolated and worn lower molars are here referred to the genus Scenopagus (Figure 7C). Gunnell et al. [2] report that three species of Scenopagus are known from Br3 (S. curtidens, S. edenensis, and S. priscus), but only S. priscus is currently known to persist into the Uintan (Ui1a and Ui1b). Both of the Whistler Squat Quarry Scenopagus specimens are substantially larger than S. priscus and S. curtidens, but closely match dental dimensions reported for S. edenensis [36]. However, the talonid breadth of 41372-118 (an M3) slightly exceeds that of S. edenensis and the advanced state of wear of both specimens prohibits detailed comparisons of occlusal morphology. Nonetheless, we attribute both specimens to Scenopagus cf. S. edenensis based on their large size.

Subfamily SESPEDECTINAE Novacek, 1985 [37].
Genus PROTERIXOIDES Stock, 1935 [38].
PROTERIXOIDES sp. nov.
Specimens: TMM 41372-118, -281.

TMM 41372-118 and -281, both referred by West [24] to Proterixoides. The Whistler Squat Quarry specimens are also similar to Proterixoides in being buccolingually narrower, in possessing a mesiobuccal cingulum, in possessing a metastylid, in having a more oblique distal talonid margin, and in having a more projecting hypoconulid that is in closer proximity to the entoconid. Although the recovery of additional fossil material may favor attribution of these specimens to a new genus, we provisionally attribute both specimens to Proterixoides sp. nov. A full description of this new taxon will be published separately.

Order PRIMATES Linnaeus, 1758 [39].
Suborder PLESIADAPIFORMES Simons and Tattersall, 1972 [40].
Family MICROSYOPIDAE Osborn and Wortman, 1892 [41].
Genus MICROSYOPS Leidy, 1872 [42].
MICROSYOPS ANNECTENS Marsh, 1872 [43].
Specimen: TMM 41466-7.

This partial maxilla (Figure 7D) was referred by West [24] to Microsyops annectens. The morphology and smaller size of the cheek teeth of this specimen are inconsistent with attribution to either Crasops or Megadelphys. Dental dimensions of TMM 41466-7 are larger than those reported for the Bridgerian species Microsyops elegans but are similar to those reported for M. annectens [44]. M. annectens is known from localities spanning Br2 through Ui1b, and the only other Uintan species of Microsyops (M. kratos) is slightly larger than M. annectens [44]. TMM 41466-7 differs from some specimens of M. annectens in having well-developed lingual cingulae on M2-M3 and an M2 that lacks a distinct cuspatc hypocone, but these features appear to be variable in M. annectens [45]. TMM 41466-7 also lacks the rugose enamel that is variably present in M. annectens [44]. Nonetheless, the size and anatomy of this specimen favor continued attribution to M. annectens.

Order PRIMATES Linnaeus, 1758 [39].
Family OMMOMYIDAE Gazin, 1958 [46].
Genus OURAILA Gazin, 1958 [47].

Table 2. Summary single-crystal incremental-heating $^{40}$Ar/$^{39}$Ar analytical results for JW-2 biotite phenocrysts.

| Run ID    | Age ± 1e (Ma)$^1$ | MSWD | $n/n_{tot}$ | $\%^{39}$Ar | Age ± 1e (Ma)$^2$ |
|-----------|-------------------|------|-------------|-------------|-------------------|
| 25960-01  | 45.3±0.3          | 1.2  | 3/3         | 100.0       | 45.4±0.4          |
| 25960-02  | 45.00±0.18        | 1.2  | 4/5         | 93.2        | 45.3±0.2          |
| 25960-03  | 44.9±0.2          | 1.1  | 5/5         | 100.0       | 44.8±0.3          |
| 25960-04  | 44.8±0.2          | 0.2  | 5/5         | 100.0       | 44.7±0.3          |
| 25960-05  | 45.1±0.3          | 0.1  | 5/5         | 100.0       | 45.1±0.3          |
| 25960-06  | 45.3±0.2          | 0.6  | 5/5         | 100.0       | 45.3±0.3          |
| 25960-07  | 44.9±0.2          | 0.2  | 4/4         | 100.0       | 44.9±0.3          |
| 25960-08  | 45.09±0.16        | 1.2  | 5/5         | 100.0       | 45.2±0.2          |
| 25960-09  | 45.2±0.2          | 1.3  | 5/5         | 100.0       | 45.1±0.3          |
| 25960-10  | 44.5±0.2          | 0.4  | 6/6         | 100.0       | 44.5±0.3          |
| 25960-11  | 45.3±0.3          | 0.1  | 4/4         | 100.0       | 45.4±0.4          |
| 25960-12  | 45.13±0.12        | 0.7  | 5/5         | 100.0       | 45.14±0.17        |
| 25960-13  | 44.8±0.19         | 1.9  | 5/6         | 90.7        | 45.1±0.2          |
| 25960-14  | 45.13±0.15        | 0.5  | 5/5         | 100.0       | 45.13±0.18        |
| Mean      | 45.04±0.10 $^2$   |      |             | 45.1±0.11   |                   |

$^1$Excludes error in $J$, the neutron fluence parameter, except as noted.
$^2$Includes error in $J$.
$n/n_{tot} =$ steps used to calculate age/steps yielding >2% of the total 39Ar released.
MSWD = Mean Square Weighted Deviation.

Complete analytical data provided in Table S1.

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doi:10.1371/journal.pone.0101516.t002

Revisions of the Eocene Whistler Squat Quarry...
**OURAYIA UINTENSIS** Osborn, 1895 [47].

This specimen is an isolated m2 trigonid from an omomyid primate (Figure 7E). Its large size and substantial buccolingual breadth, low postvallid height, rounded mesial occlusal profile, high degree of bunodonty, well-developed mesiobuccal cingulid, and crenulated enamel are consistent with attribution to *Ourayia uintensis*. This species is also known from the Ui1a locality TMM 41443 ("Junction" [12]), which is stratigraphically below the Whistler Squat Quarry in the Devil’s Graveyard Formation (Figure 2) [2,7]. In the Uinta Basin, *O. uintensis* has historically been associated with Ui2 localities [43] but is now known to also occur at the Ui3 locality WU-26 (K.E.T., pers. obs.). If these alpha taxonomic and biostratigraphic attributions are correct, then *Ourayia uintensis* persists over a longer time interval (Ui1a–Ui3) than has been previously recognized [2,12].

**ORDER** RODENTIA Bowdich, 1821 [48].

**FAMILY** ISCHYROMYIDAE Alston, 1876 [49].

**GENUS** THISBEMYS Wood, 1959 [50].

**THISBEMYS PLICATUS** Wood, 1962 [51].

Specimens: TMM 41372-25, -56, -117, -122, -129, -130, -131, -133, -135, -237, -270, -274, -296, -402.

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**Figure 5.** 40Ar/39Ar incremental heating spectra of JW-2 phenocrysts. Spectra derived from 40Ar/39Ar single-crystal incremental-heating (SCIH) analyses of individual biotite phenocrysts from sample JW-2. Excludes steps yielding less than 2% of the total 39Ar released. Complete analytical data provided in Table S1.

doi:10.1371/journal.pone.0101516.g005
Wood [52] identified *Thisbemys plicatus* as occurring at the Whistler Squat Quarry and two other localities that are stratigraphically lower in the Devil's Graveyard Formation (TMM 41443 “Junction” and TMM 41444 “0.6 miles east of Junction”, Figure 2). The genus *Thisbemys* is distinctive in having cheek teeth with highly crenulated enamel [50,51]. In fact, Korth [53] indicates that enamel crenulation is the only feature that distinguishes *Thisbemys* from *Paramys nini* and *Paramys woodi*. Wood [52] assigned the Devil’s Graveyard Formation assemblage to *Thisbemys plicatus* because the dimensions of most specimens are less than two standard deviations from the mean of the original *T. plicatus* assemblage found in the Bridger Formation of the Green River Basin, Wyoming. Whistler Squat Quarry *T. plicatus* (Figure 8A–H) have cheek tooth enamel crenulations without dentinal cores that may be obliterated by wear (typical of other *Thisbemys*) and narrow lower incisors with a faint anterior sulcus. Here we follow Wood’s [52] specific attribution because the Whistler Squat Quarry specimens resemble *T. plicatus* and differ from *T. corrugatus* in having less pronounced enamel crenulation and mandibular molars that lack a massive hypocone connected to the metaloph.

**ISCHYROMYIDAE gen. et sp. nov.**

Specimens: TMM 41372-259, -278, -297, -305.

Four isolated rodent teeth from the Whistler Squat Quarry represent a new genus and species of ischyromyid. Two P4s in this assemblage (41372-278 and 41372-297) were described as *Prolapsus sibilatoris* by Wood [52], but were attributed by Wilson and Runkel to “a new undescribed genus and species” ([54]: p. 2). According to J.W. Westgate (pers. comm., July, 2013), these specimens were included in an unpublished multi-authored manuscript in the early 1990s describing new Eocene rodents from Texas. In preparation for publication, these fossil rodents were cataloged using the

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**Figure 6.** $^{40}$Ar/$^{39}$Ar age distribution of JW-2 phenocrysts. Age-probability density function and weighted-mean age of the plateau ages from the single-grain biotite $^{40}$Ar/$^{39}$Ar SCIH analyses. Complete analytical data provided in Table S1.

doi:10.1371/journal.pone.0101516.g006
generic name proposed in the manuscript - “Faustimys”. Williams and Kirk [12] subsequently listed the unpublished genus “Faustimys” as occurring in the Devil’s Graveyard Formation, an error that we correct here. A description of this new taxon will be published separately, and thus the Whistler Squat Quarry specimens are included here as “Ischyromyidae gen. et sp. nov.”.

Subfamily MICROPARAMYINAE Wood, 1962 [51].
Genus MICROPARAMYS Wood, 1959 [50].
MICROPARAMYS MINUTUS Wilson, 1937 [55].
Specimens: TMM 41372-260, -298.
An isolated lower molar (41372-260) and p4 (41372-298) from the Whistler Squat Quarry (Figure 8I–J) were identified by Wood [52] as Microparamys minutus. M. minutus was initially described as a species of Paramys by Wilson [55]. Wood [50] subsequently erected the new genus Microparamys to include Wilson’s assemblage and others that were discovered at various Wasatchian through Bridgerian localities across Wyoming. The teeth of Microparamys are very small, with most mandibular and maxillary teeth ranging in size from less than 1 mm to 2 mm in length [51]. The assemblage from the Whistler Squat Quarry is no different in this respect, with all specimens less than 2.0 mm in mesiodistal length. Furthermore, these specimens exhibit occlusal morphology typical of M. minutus. In particular, 41372-260 resembles other lower molars of M. minutus in exhibiting a wide talonid basin that is defined mesially by an anterolophid, prominent protoconid, and metaconid and distally by a conspicuous entoconid, a distinct posterolophid, and prominent hypoconid.

MICROPARAMYINAE gen. et sp. indet.
Specimen: TMM 41372-286.

Figure 7. Select dental specimens from the Whistler Squat local fauna. A–B, Herpetotherium sp., left m1/2 (TMM 41372-403), lingual view (A) and occlusal view (B); C, Scenopagus cf. S. edenensis, right mandibular molar (TMM 41372-118), occlusal view; D, Microsyops annectens, partial right maxilla with P4-M3 (TMM 41466-7), occlusal view; E, Ourayia uintensis, right m2 trigonid (TMM 41372-301), occlusal view. doi:10.1371/journal.pone.0101516.g007
This single specimen of a left lower third molar (Figure 8K) was referred to “Lophiparamys sp. indet.” by Wood [52]. Lophiparamys has occlusal anatomy that is similar to Microparamys but is diagnosed as a separate genus primarily on the basis of strong enamel crenulation [51]. Wood [52] argued that the high metaconid and enamel crenulation of the Whistler Squat Quarry specimen favor attribution to Lophiparamys. However, a high metaconid is not unusual for the genus Microparamys, and crenulations are sometimes found in the talonid basins of Microparamys specimens (K.E.T., pers. obs.). TMM 41372-286 is too worn to permit further comparisons of occlusal morphology with Lophiparamys and Microparamys, and we therefore refer this specimen to the Microparmyinae gen. et sp. indet.

Family CYLINDRODONTIDAE Miller and Gidley, 1918 [56].

Genus MYSOPS Leidy, 1871 [57].

MYSOPS BOSKEYI Wood, 1973 [52].

Specimens: TMM 41372-47, -137, -138, -139, -140, -141, -142, -144, -145, -146, -147, -148, -149, -150, -249, -250, -251, -253, -257, -258, -261, -264, -267, -268, -271, -272, -273, -275, -276, -277, -280, -292, -293, -296, -303, -307, -376, -379, -408, -470, -473, -773, -777, -779, -783, -786, -787, -789, -789.

Mysops boskeyi is currently only known from the lower member of the Devil’s Graveyard Formation [7] (Figure 2). This large assemblage of M. boskeyi from the Whistler Squat Quarry includes the holotype and many additional specimens that Wood [52] used to diagnose the species (Figure 8L–S). All specimens are isolated teeth. According to Korth [58], Mysops is the earliest occurring cylindrodontid genus. Wood [52] describes M. boskeyi as a high-crowned species of Mysops, with a clear difference in height between the trigonid and talonid that is not characteristic of later cylindrodontids. By contrast, Korth [58] suggested that M. boskeyi should be referred to Pareumys, which would make “Pareumys boskeyi” the most primitive member of this genus. Although we acknowledge Korth’s [58] opinion here, in the absence of a stronger formal argument for transferring the species to Pareumys we have chosen to retain M. boskeyi from the Whistler Squat Quarry in the genus Mysops.

Family SCIURAVIDAE Miller and Gidley, 1918 [56].

Genus PROLAPSUS Wood, 1973 [52].

PROLAPSUS SIBILATORIS Wood, 1973 [52].

Specimens: TMM 41372-179, -252, -256, -262, -263, -265, -266, -269, -284, -285, -291, -295, -299, -300, -304, -381, -778, -782.
Wood [52] originally named *Prolapsus sibilatoris* based on specimens recovered exclusively from the Whistler Squat Quarry (Figure 9F–Y). However, Wilson and Runkel [54] described additional specimens of *P. sibilatoris* from localities in the Devil’s Graveyard and Canoe Formations that span the entire Uintan (Ui1–Ui3). The only other described member of the genus (*P. junctum*) has a similar geographic and temporal distribution [54], and thus known occurrences of *Prolapsus* are currently restricted to the Big Bend region of Texas. Wood [52] considered *Prolapsus* to be an early ancestor of extant caviomorphs, but later studies have shown that *Prolapsus* is a sciuravid and a probable sister taxon to *Knightonyx*, a widely distributed genus known from the Wasatchian and Bridgerian [54,58]. While Wood [52] did not identify a family for this taxon, the sciuravid affinities of *P. sibilatoris* are clearly indicated by (1) its quadriradiculare upper molars and (2) its quadrangular lower molars with three transverse crests derived from cingulids and transversely expanded cusps.

**Genus PAUROMYS** Troxell, 1923 [59].

**Genus Pauromys texensis** Walton, 1993 [60].

Specimen: TMM 41372-279.

This isolated M2 (Figure 8Z) was initially designated *Prolapsus* sp. indet. by Wood [52], although he noted that it is “much smaller” than other species of *Prolapsus*. However, TMM 41372-279 exhibits the highly lophate cusps that are typical of the genus *Pauromys*. This specimen was included by Walton [60] in the hypodigm of *P. texensis*, and we see no reason to revise this attribution. All other known specimens of *P. texensis* occur at a single locality that is located higher in the Devil’s Graveyard Formation stratigraphic section (TMM 41745; “Serenity”, Figure 2) and considered to be Ui3 in age by Robinson et al. [1].

Order **CONYLAURIA** Cope, 1881 [61].

**Family HOMACODONTIDAE** Trouessart, 1879 [22].

Genus **HYOPSODUS** Leidy, 1870 [62].

**HYOPSODUS** sp.

Specimen: TMM 41372-227.

This isolated and worn M2 (Figure 9A) was originally attributed by West [24] to *Hyopsodus uintensis*. However, *H. uintensis* is currently only known from Ui2 and Ui3 localities [2]. The length and width of TMM 41372-227 are also below the range of all upper molar dimensions provided by Krishtalka [63] for *H. uintensis*. Given the small size of this isolated tooth and the lack of preserved anatomical detail, we have chosen to attribute this specimen to *Hyopsodus* sp.

Order **ARTIODACTyla** Owen, 1848 [64].

Family **HOMACODONTIDAE** Marsh, 1894 [65].

**HOMACODONTIDAE** sp. nov.

Specimens: TMM 41372-28, -233, -234, -245, -471.

These specimens represent a new species of bunodont homacodontid artiodactyl that is most similar to the Ui3 Devil’s Graveyard Formation endemic species *T Texodon menidanaus* [24]. An m1 or m2 of this taxon (TMM 41372-245) was described as “*Microsus cf. cuspidatus*” by West [24]. This specimen resembles both *Microsus* and *Homacodon* in lacking a paraconid. However, TMM 41372-245 differs from *M. cuspidatus* and resembles “*Microsus* sp.” of Stucky [66] in possessing a complete hypolophid connecting the hypoconid and entoconid and a strongly developed crestid connecting the hypoconulid and hypoconid. In these respects, TMM 41372-245 differs from *Texodon* and the Bridgerian genus *Homacodon* but is more similar to the Bridgerian-early Uintan genus *Antiacodon* and the Ui3 genus *Auxontodon*. TMM 41372-245 also lacks the small stylid twinned with the hypoconulid seen in m2–3 of the genotype of *Microsus* (USNM 1178). An M1 or M2 of the new taxon from the Whistler Squat Quarry (TMM 41372-233) occludes well with TMM 41372-245 and is distinctive

![Image](image-url)

**Figure 9. Select dental specimens from the Whistler Squat local fauna.** A, *Hyopsodus* sp., right M2 (TMM 41372-227), occlusal view; B–C, *Helohyus* sp., left m1/2 (TMM 41446-12), buccal view (B) and occlusal view (C). [doi:10.1371/journal.pone.0101516.g009](http://doi.org/10.1371/journal.pone.0101516.g009)

in possessing a complete postprotocone crista between the protocone and metaconule. In this respect, TMM 41372-233 resembles *Texodon* but differs from *Microsus, Homacodon, Auxontodon*, and *Antiacodon*. These two molars from the Whistler Squat Quarry are closely matched in size and morphology by a well-preserved m3 (TMM 41372-471) and two worn M3s (TMM 41372-28 and TMM 41372-234). A complete diagnosis and description of the new Whistler Squat taxon will be published separately, and we have therefore grouped the specimens here as Homacodontidae sp. nov.

Family **HELOHYIDAE** Marsh, 1877 [67].

**Genus HELOHYUS** Marsh, 1872 [43].

**HELOHYUS** sp.

Specimen: TMM 41446-12.

This m1 or m2 of a bunodont artiodactyl (Figure 9B–C) was attributed by West [24] to *Lophiohyus* based on perceived similarities to the type specimen of *Lophiohyus aliceps* [68]. According to Stucky [66], however, *L. aliceps* is a junior synonym of *Helohyus milleri*. The occlusal anatomy and precise taxonomic affinities of TMM 41446-12 are difficult to assess due to damage, particularly to the lingual portion of the trigonid and the distal portion of the talonid. Contrary to West [24], it is not possible to discern the presence and/or size of a paraconid and hypoconulid on this specimen. Nonetheless, the size and morphology of this specimen is most consistent with attribution to *Helohyus*. TMM 41446-12 is considerably larger than any known leptochoerine, antiacodontine, or homacodontine but has a length (approx. 12.3 mm) within the range of m2 lengths reported for *Helohyus* (8.4–14.3 mm) by Stucky [66]. *Helohyus* is also known from other localities spanning the early Bridgerian through early Uintan, including Ui1a and Ui1b [2,66]. Accordingly, we attribute this specimen to *Helohyus* sp.
Family PROTOCERATIDAE Marsh, 1891 [69].
Genus LEPTOREODON Wortman, 1898 [70].
LEPTOREODON MARSHI Wortman, 1898 [70].
Specimens: TMM 41372-2, -5, -7, -10, -13, -23, -43, -44, -468, -62, -124, -125, -170, -175, -176, -177, -178, -210, -212, -214, -220, -230, -238, -242, -247, -312, -316, -361, -368, -371, -391, -395, -400, -412, -417, -434, -474, -476, -477, -486, -487, -488, -489, -490, -491, -494, -510, -519, -532, -569, -573, -581, -589, -609, -615, -616, -631, -633, -636, -638, -639, -663, -665, -666, -669, -670, -672, -676, -678, -682.

The presence of p4 metaconids in this large sample of *Leptoreodon marshi* from the Whistler Squat Quarry (Figure 10) help to distinguish this taxon from *Leptotragulus*, a common and slightly smaller Uintan protoceratid [71]. Wilson [72] attributed the entire Whistler Squat Quarry assemblage of *Leptoreodon* to *L. marshi* based on metric comparisons with the smaller California species *L. edwardsi* [71,73]. We find no reason to question Wilson's [72] assessment and we therefore retain his species attribution for these specimens.

LEPTOREODON MAJOR Golz, 1976 [73].
Specimen: TMM 41466-2.
TMM 41466-2 is a partial right maxilla with M1–M3 (Figure 11A). The M1 crown is largely missing, the M2 paracone is damaged, and the M3 crown is intact. Golz [73] identified several characters distinguishing *L. major* from other species of *Leptoreodon* that are evident in this specimen, including its larger overall size and upper molars with strong cingulars, broad styles, and square occlusal profiles. We therefore attribute TMM 41466-2 to *Leptoreodon major*. This specimen is particularly important for biochronological correlation because *L. major* is an index taxon of biochron Oib [2].

Order PERISSODACTYLA Owen, 1848 [64].
Family BRONTOTHERIIDAE Marsh, 1873 [74].
Genus PROTITANOTHERIUM Hatcher, 1895 [75].
PROTITANOTHERIUM EMARGINATUM Hatcher, 1895 [75].
Specimens: TMM 41372-3, -431, -536, TMM 41466-6, -10.

**Figure 10.** Select *Leptoreodon marshi* specimens from the Whistler Squat local fauna. A, left maxilla with C–P3, M1–3 (TMM 41372-175), occlusal view; B, left mandible with dp2–dp4, m1–m2 (TMM 41372-176), oblique occlusal view and C, buccal view; D, right mandible with p2–m3 (TMM 41372-178), oblique occlusal view and E, lingual view.
doi:10.1371/journal.pone.0101516.g010
This isolated astragalus is clearly equid in morphology, displaying a medially projecting astragalar head, a smooth navicular facet, and a trochleated proximal articular surface that is oriented oblique to the long axis of the bone (Figure 11D). There are two genera of equids that occur during the Uintan: the early Uintan *Protitanotherium*, a holdover taxon from the Bridgerian, and *Epihippus*, which ranges through the Uintan [2]. In comparison with an astragalus of *Epihippus* associated with dental material from the Uinta Formation of Utah, the Whistler Squat Quarry specimen has a more elongated astragalar head (K.E.T., pers. obs.). Because no dental remains are associated with the Whistler Squat Quarry astragalus, there is some possibility that this specimen could be attributed to *Protitanotherium*, particularly since this taxon’s highest range datum is known from U1b in Wyoming [2]. Given this uncertainty whether the Whistler Squat Quarry astragalus represents *Protitanotherium* or *Epihippus*, we refer the specimen to Equidae gen. et sp. indet.

Family AMYNOBLASTIDAE Scott and Osborn, 1883 [80].

Genus AMYNOBLASTUS Marsh, 1877 [81].

*AMYNOBLASTUS ADVENTUS* Marsh, 1875 [82].

Specimens: TMM 41372-2, -3, -5, -6, -8, -11, -12, -13, -14, -18, -20, -24, -45, -46, -48, -49, -50, -51, -52,-60, -61, -64, -65, -66, -68, -69, -71, -72, -73, -74, -75, -76, -77, -78, -79, -80, -81, -82, -83, -84, -85, -86, -87, -88, -89, -90, -91, -92, -94, -95, -96, -99, -100, -101, -102, -115, -127, -159, -164, -166, -171, -186, -194, -203, -206, -207, -240, -310, -325, -328, -329, -330, -331, -333, -334, -335, -336, -337, -338, -340, -342, -344, -345, -346, -347, -348, -349, -350, -351, -352, -353, -354, -355, -357, -358, -359, -360, -372, -393, -394, -399, -410, -413, -414, -415, -416, -478, -421, -422, -426, -429, -430, -432, -433, -434, -435, -437, -438, -439, -440, -441, -442, -443, -444, -446, -451, -452, -453, -454, -455, -456, -457, -458, -459, -460, -461, -462, -493, -497, -498, -500, -501, -504, -505, -507, -508, -509, -511, -512, -514, -521, -524, -526, -530, -533, -535, -537, -538, -539, -540, -542, -544, -545, -546, -547, -548, -549, -550, -551, -552, -553, -554, -555, -556, -557, -558, -561, -566, -567, -570, -571, -572, -577, -578, -579, -582, -583, -585, -586, -589, -591, -594, -596, -598, -599, -600, -601, -602, -603, -604, -605, -606, -610, -611, -612, -613, -617, -618, -619, -621, -622, -623, -624, -626, -627, -628, -629, -630, -637, -639, -644, -645, -646, -649, -650, -651, -652, -677, -684, -685, -686, -687, -689, -690, -691, -692, -693, -694, -695, -696, -697, -698, -699, -700, -701, -702, -703, -704, -705, -706, -707, -708, -709, -710, -711, -712, -713, -714, -716, -717, -718, -719, -720, -721, -722, -723, -724, -725, -726, -740, -742, -744, -745, -746, -747, -748, -750, -753, -755, -756, -757, -758, -759, -760, -761, -762, -763, -764, -765, -766, -771, -772, -790, -791, -793, -795, -796, -797, -798, -799, -800, -802, -803, -804, -806, -809, -810, -814.

This large assemblage from the Whistler Squat Quarry includes multiple skull fragments (Figure 12) from at least 11 individuals, multiple isolated teeth from all dental loci, and a large sample of postcrania. Many of these specimens were identified as *Amynodon advenus* by Wilson and Schiebout [63] in their description of the amynodontids of Trans-Pecos Texas. *A. advenus* is an index species of biochron U1b and is known from numerous U1b–U3 localities throughout North America [2]. The Whistler Squat Quarry cranial material shows features typical of the genus *Amynodon*, including a large preorbital fossa, a long preorbital region of the skull, and a nasal incision terminating at the level of the diastema [84]. Two species of *Amynodon* are currently recognized from the Uintan [83,84]: *A. advenus* and *A. reedi*. The main feature that distinguishes these two species is size, with *A. reedi* approximately 23% smaller than *A. advenus* [83]. Because the Whistler Squat Quarry *Amynodon* assemblage falls within the size

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Figure 11. Select specimens from the Whistler Squat local fauna. A, Leptotyphon major, partial right maxilla with M1 crown base and M2-M3 (TMM 41466-2), occlusal view; B-C, Protitanotherium emarginatum, (B) right p2 (TMM 41372-536), occlusal view, (C) left M2 (TMM 41466-6), occlusal view; D, Equidae gen. et sp. indet., right astragalus (TMM 41372-204), superior view. doi:10.1371/journal.pone.0101516.g011

This assemblage includes a large M2 (TMM 41466-6) that Wilson [76] listed in the hypodigm of *Sthenodectes australis* and three isolated lower premolars (Figure 11B–C). Milhnic [77] noted that although *Sthenodectes* was described by Osborn [78] as having a horn, the genotype in fact lacks horns. The holotype of *S. australis* (TMM 41723-3) [76] exhibits small elliptical frontonasal horns and is therefore more appropriately assigned to *Protitanotherium emarginatum* [77]. The anatomy and dimensions of the four isolated teeth from Whistler Squat are also consistent with attribution of these specimens to *P. emarginatum*.

Family EQUIDAE Gray, 1821 [79].

Equidae gen. et sp. indet.

Specimen: TMM 41372-204.
range of *A. advenus*, we see no reason to revise the specific attribution of Wilson and Schiebout [83].

Order CREODONTA Cope, 1875 [85].
Family HYAENODONTIDAE Leidy, 1869 [86].
Genus *SINOPA* Leidy, 1871 [57].
*SINOPA MAJOR* Leidy, 1871 [57].
Specimen: TMM 41466-9.
This partial mandibular ramus with a broken m1 and worn m2 (Figure 13A–B) was referred to “?Proviverra major” by Gustafson [87]. The same specimen was attributed to *Sinopa major* by Gunnell [88]. Gustafson [87] published dental metrics showing that TMM 41466-9 is similar in size to Bridgerian specimens of *Sinopa major* (including the holotype YPM 11878). Our review of more detailed descriptions of this species [89] indicate that TMM 41466-9 is comparable in morphology to specimens originally referred to *Sinopa major* [88,90]. Recent taxonomic revisions have indicated that *Proviverra* is a genus restricted to Europe, and we therefore retain Gunnell’s [88] attribution of this specimen to *Sinopa major* [88,90].

Order CARNIVORAMORPHA Wyss and Flynn, 1993 [91].
Family MIACIDAE Cope, 1880 [92].
*MIACIDAE gen. et sp. indet.*
Specimen: TMM 41372-367.
This isolated p4 (Figure 13F–H) was tentatively referred to *Uintacyon scotti* by Gustafson [87]. However, as explained by Friscia and Rasmussen [95], the correct generic attribution for this miacid species is *Miocyon*. In the Uinta Formation of Utah, *Miocyon* is probably represented by two species that co-occur at some fossil localities: *M. vallisrubrae* and the larger species *M. scotti* [95]. Other than size, the main characters that potentially distinguish *M. vallisrubrae and M. scotti* are found on the m2, which is unknown from the Whistler Squat Quarry and equivalent localities. However, Friscia and Rasmussen [95] could not exclude the possibility that specimens of *M. vallisrubrae and M. scotti* represent a single sexually dimorphic species. Wear of the Whistler Squat

This specimen is the distobuccal portion of a carnivoramorph P4, including the paracone and metastylar blade (Figure 13C–E). Although the mesial portion of the crown is missing, the slightly conical morphology of the paracone and the rounded, more open carnassial notch, not typical of taxa known in Viverravidae, favors attribution of this tooth to the Miacidae [93]. We have therefore referred this specimen to Miacidae gen. et sp. indet.

Genus *MIOCYON* Matthew, 1909 [94].
*MIOCYON sp.*
Specimen: TMM 41372-367.
This isolated p4 (Figure 13F–H) was tentatively referred to *Uintacyon scotti* by Gustafson [87]. However, as explained by Friscia and Rasmussen [95], the correct generic attribution for this miacid species is *Miocyon*. In the Uinta Formation of Utah, *Miocyon* is probably represented by two species that co-occur at some fossil localities: *M. vallisrubrae* and the larger species *M. scotti* [95]. Other than size, the main characters that potentially distinguish *M. vallisrubrae and M. scotti* are found on the m2, which is unknown from the Whistler Squat Quarry and equivalent localities. However, Friscia and Rasmussen [95] could not exclude the possibility that specimens of *M. vallisrubrae and M. scotti* represent a single sexually dimorphic species. Wear of the Whistler Squat

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Figure 12. Select *Amynodon advenus* specimens from the Whistler Squat local fauna. A, partial left maxilla with C–M3 (TMM 41372-45), occlusal view; B, partial left maxilla with P4–M3 (TMM 41372-72), occlusal view; C, partial left mandible with p3–m3 (TMM 41372-99), buccal view and D, occlusal view.

doi:10.1371/journal.pone.0101516.g012
Quarry specimen also hinders comparisons with known species of *Miocyon*, and we therefore refer this specimen to *Miocyon* sp.

**Discussion**

In his synthesis of Eocene vertebrate faunas from Trans-Pecos Texas, Wilson [7] variously referred to the localities comprising the Whistler Squat local fauna as both “early Uintan” and as belonging to the “Uinta B” land mammal age. However, as noted by Prothero [96], Walsh [97], and Townsend et al. [98], “Uinta B” refers specifically to a local lithostratigraphic unit in the Uinta Basin that has yielded characteristically U2 faunas. Further confusion is introduced by Figure 3 in Wilson [7], which identifies the stratigraphically lowest localities in the Whistler Squat local fauna (e.g., “Junction”, “0.6 miles east of Junction”, and “Hen Egg Mountain”) as potentially late Bridgerian. Robinson et al. [1] also called attention to faunal differences between the “Junction localities” (labeled as “Ui1” and “Ui1–Ui2”) respectively, Gunnell et al. [2] subsequently subdivided Ui1 into biochrons Ui1a and Ui1b, recognizing Ui1b by the first appearance of the selenodont artiodactyls *Protoreodon*, *Leptoreodon*, and *Protylopus*, the rhinocerotid *Amynodon*, and the uintathere *Eobasileus*. Gunnell et al. ([2]: p. 313) designated the “basal Tertiary conglomerate” localities of the Devil’s Graveyard Formation as a Ui1a reference section. However, Gunnell et al. ([2]: p. 314) also designated the “Whistler Squat Local Fauna…” (Wilson, 1986) as a Ui1b reference section despite the fact that the “basal Tertiary conglomerate” localities comprise part of Wilson’s [7] Whistler Squat local fauna. Because the “basal Tertiary conglomerate” localities lack the genera identified by Gunnell et al. [2] as definitive of Ui1b (cf. [7]: table 1), Gunnell et al. [2] intended to include only the Whistler Squat Quarry and equivalent localities (cf. [7]: table 2) as a Ui1b reference section (P.C. Murphey, pers. comm., March, 2014) in accord with Walton’s alternative use of the “Whistler Squat local fauna” [3,6].

Our revised faunal list for TMM 41372 and TMM 4166 (Figure 14) reinforces the conclusion that the fauna from Whistler Squat Quarry and equivalent localities in the Devil’s Graveyard Formation are attributable to biochron Ui1b. Most significantly, our revised faunal list includes two index species of biochron Ui1b: *Leptoreodon major* and *Amynodon advenus* [2]. As noted previously, the first appearances of the genera *Leptoreodon* and *Amynodon* help to define Ui1b as distinct from Ui1a. Our revised faunal list also includes one genus (*Microsyops*) and one species (*Microparamys minutus*) that are last known to occur in Ui1b [2].

As discussed by Gunnell et al. [2], other Ui1b localities in southern California and the northern Rocky Mountains demonstrate striking patterns of regional endemism. The mammalian fauna from the Whistler Squat Quarry is similar in this respect, with two new undescribed taxa (a homacodontid artiodactyl related to *Texodon meridianus* and a sespedectine erinaceomorph related to *Proterixoides davisi*) currently known only from the Whistler Squat Quarry (TMM 41372). Similarly, the sciuravid rodent species *Pauromys texensis* and the cylindrodontid rodent species *Mysops boskeyi* are currently only known from the Whistler Squat Quarry and other middle Eocene localities in Texas. Research in progress describing the anatomy and phylogenetic relationships of the various new regionally

![Figure 13. Select dental specimens from the Whistler Squat local fauna. A-B, Sinopa major, partial left mandible with m1–m2 (TMM 41466-9), buccal view (A) and occlusal view (B); C-E, Miacidae gen. et sp. indet., partial left P4 (TMM 41372-389), lingual view (C), buccal view (D), and occlusal view (E); F-H, Miocyon sp., left p4 (TMM 41372-367), buccal view (F), lingual view (G), and occlusal view (H). doi:10.1371/journal.pone.0101516.g013](https://www.plosone.org/doi/10.1371/journal.pone.0101516.g013)
endemic taxa from the Whistler Squat Quarry will help to further clarify the pattern of faunal endemism characteristic of the early Uintan in Texas.

This reanalysis of Whistler Squat Quarry specimens has also led to the extension of biochronological zone ranges to Ui1b for several taxa compared to recent compilations by Robinson et al. [1] and Gunnel et al. [2], and this study. Gray bars indicate range extension of non-endemic taxa compared to Robinson et al. [1] and Gunnell et al. [2]. *Herpetotherium* species candidates range throughout the Bridgerian and Uintan. **Range listed is for *S. edenensis***. *Endemic species, but extends LRD of genus from Ui3. 4Endemic species, but extends HRD of genus from Ui1a. 5Range is genus/species specific. 6Extends LRD of genus from Ui2.*  

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**Figure 14. Whistler Squat faunal list and associated Bridgerian and Uintan biochronological zone ranges.** Mammalian taxa identified from Whistler Squat local fauna localities TMM-41372 and TMM-41466 and their Bridgerian (Br) and Uintan (Ui) biochronological zone ranges based on Wilson [7], Wilson and Runkel [51], Walton [60], Williams and Kirk [12], Robinson [1], Gunnell et al. [2], and this study. Gray bars indicate range extension of non-endemic taxa compared to Robinson et al. [1] and Gunnell et al. [2]. *Herpetotherium* species candidates range throughout the Bridgerian and Uintan. **Range listed is for *S. edenensis***. *Endemic species, but extends LRD of genus from Ui3. 4Endemic species, but extends HRD of genus from Ui1a. 5Range is genus/species specific. 6Extends LRD of genus from Ui2.*

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### Table

| Taxon | Index taxon | Endemic | Br1 | Br2 | Br3 | Ui1a | Ui1b | Ui2 | Ui3 |
|-------|-------------|---------|-----|-----|-----|------|------|-----|-----|
| Didelphimorpha | *Herpetotherium* sp. ⁴ | | | | | | | | |
| Lipotyphla | *Scenopagus* cf. *S. edenensis* ² | | | | | | | | |
| | *Proterixoides* sp. nov. ³ | | | | | | | | |
| Plesiadapiformes | *Microsops* annectens | | | | | | | | |
| | *Ourayia uintensis* | | | | | | | | |
| Primates | | | | | | | | | |
| Rodentia | *Thisbemys* plicatus | | | | | | | | |
| | *Ischyromyidae* gen. et sp. nov. | | | | | | | | |
| | *Microparamys* minutus | | | | | | | | |
| | *Mysops* boskeyi ⁴ | | | | | | | | |
| | *Prolapsus* sibilatoris | | | | | | | | |
| | *Pauromys* texensis | | | | | | | | |
| Condylarthra | *Hyopsodus* sp. ⁵ | | | | | | | | |
| Artiodactyla | *Homoconodontidae* sp. nov. | | | | | | | | |
| | *Helohys* sp. | | | | | | | | |
| | *Leptoreodon* marshi | | | | | | | | |
| | *Leptoreodon* major | | | | | | | | |
| Perissodactyla | *Protitanotherium* emarginatum | | | | | | | | |
| | *Equidae* gen. et sp. indet. ⁵ | | | | | | | | |
| | *Amynodon* advenus | | | | | | | | |
| Cretodonta | *Sinopa* major | | | | | | | | |
| Carnivoramorpha | *Miacidae* gen. et sp. indet. ⁵ | | | | | | | | |
| | *Miocyon* sp. indet. ⁶ | | | | | | | | |

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**Legend**

- **White Bar**: Non-endemic taxa.
- **Gray Bar**: Endemic taxa extending the LRD of genus from Ui3.
- **Black Bar**: Endemic taxa extending the HRD of genus from Ui1a.
- **X**: Taxa extending range at the Whistler Squat Quarry.

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**Endemic taxa from the Whistler Squat Quarry**

endemic taxa from the Whistler Squat Quarry will help to further clarify the pattern of faunal endemism characteristic of the early Uintan in Texas.
documented *Ourayia uintensis* from the Ui1a “Junction” locality, extending the LRD for both species from Ui2 [2]. The reallocation of *Sthenodectes australis* specimens [7] to *Prothodontherium emarginatum* [77] extends the LRD for the genus from Ui3 and the presence of *Protoioides* and *Miocyon* at the Whistler Squat Quarry extends the LRD for these genera to Ui1b from Ui3 and Ui2, respectively [1,2].

Well-characterized faunal assemblages in a highly resolved chronostratigraphic framework are key to understanding the Bridgerian to Uintan faunal transition. Our study provides an essential first step in this process by presenting a well-constrained chronostratigraphy for an early Uintan locality. New geochronological analysis of tephra bracketing the Whistler Squat Quarry assemblage has provided a high-precision age estimate of 44.88 ± 0.04 Ma, a significant improvement compared to the previous age range that spanned almost 5 million years (43.2–47.9 Ma with ±1σ uncertainty). These new dates are compatible with magnetically reversed sediments at the site [5,6] attributable to C20r (43.505–45.942 Ma [99]). The revised date for the Whistler Squat Quarry is also consistent with a date of 46.80 ± 0.08 Ma for a stratigraphically lower basalt outcropping on the southeast side of Hen Egg Mountain [100] (recalibrated to Fish Canyon standard of 28.201 ± 0.046 Ma) that is likely to contain the Alamo Creek Basalt of the Chisos Formation and Basalt A of the Canoe Formation [9,10,100,101]. Significantly, this basalt overlies the Hen Egg Mountain fossil localities (TMM 42026 and TMM 42287) that constitute part of the basal Tertiary local fauna [5,7]. If Wilson [7] and Runkel [9] are correct that the Hen Egg Mountain fossil localities are roughly contemporaneous with TMM 41443 (“Junction”) and TMM 41444 (“0.6 miles east of Junction”), then the Ui1b localities of the Whistler Squat local fauna are ~2 Ma younger than the localities of the Basal Tertiary local fauna. Renewed fieldwork in late Uintan (Ui3) deposits of the DGF has yielded abundant fossil remains, including several new primate species [12,102]. New 40Ar/39Ar and paleomagnetic analyses of these Ui3 sediments are currently in progress. The work presented here provides the first 40Ar/39Ar date directly associated with a fossil assemblage attributed to the Ui1b biochron and the most precise radiometric date directly associated with an early Uintan assemblage. This study also highlights the need for thorough reexaminations of collections with decades-old taxonomic identifications in order to properly document patterns of endemism and biogeochronological ranges in the Eocene. As noted by Prothero [96], the DGF and correlative deposits in the Trans-Pecos region hold the potential to significantly increase our knowledge of Uintan biochronology and biogeography. With the inclusion of the localities of the basal Tertiary local fauna, the Devil’s Graveyard Formation is an ideal setting to document the Bridgerian–Uintan transition (biochrons Br3–Ui1b) within a well-dated continuous sequence. This objective is the focus of ongoing and future work. Combined with a refined understanding of the Bridger Formation of Wyoming (e.g., [4,103]), continued paleontological and geochronological research in the DGF may also significantly improve our understanding of the details of the Bridgerian–Uintan transition across North America, including any geographical variation in the timing of this transition.

**Supporting Information**

**Table S1 Complete 40Ar/39Ar analytical data for samples JW-1 and JW-2.**

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**Author Contributions**

Conceived and designed the experiments: CJC ECK KET ALD. Performed the experiments: CJC ECK KET ALD. Analyzed the data: CJC. Contributed reagents/materials/analysis tools: CJC. Performed the experiments: CJC ECK KET ALD. Analyzed the data: CJC. Conceived and designed the experiments: CJC ECK KET ALD. For this manuscript: CJC. Preparation: CJC. We thank the geological context of the DGF sites. We thank Tim Rowe, Chris Sagebiel, Matthew Brown, Ernest Lundelius, and the staff of the Jackson School of Geosciences Vertebrate Paleontology Laboratory for assistance and access to the fossil collections. We thank Tony Friscia for discussions on carnivoromorph morphology. Thanks are also due to Sarah Wilson, Anne Walton, Rich Kay, and Blythe Williams for providing photos of fieldwork conducted in the DGF and to Brent Adrian for specimen photo preparation. This manuscript benefited from constructive reviews by Gregg Gunnell, Paul Murphey, Andrew Farke, and an anonymous reviewer. Thanks are also due to the Richmond and Burton families for providing Wilson and colleagues with permission to collect the fossils described in this paper. Finally, this research was only possible due to the considerable efforts of Jack “Doc” Wilson (dec.), Bob Rainey (dec.), Margaret Stevens, Jim Stevens, and many others who helped to collect the fossil sample analyzed in this paper.

**Author Contributions**

Conceived and designed the experiments: CJC ECK KET ALD. Performed the experiments: CJC ECK KET ALD. Analyzed the data: CJC ECK KET ALD. Contributed reagents/materials/analysis tools: CJC ECK KET ALD. Wrote the paper: CJC ECK KET ALD.

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**Table S1 Complete 40Ar/39Ar analytical data for samples JW-1 and JW-2.**

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