Journal of Vertebrate Paleontology e2424139 (37 pages)

DOI: 10.1080/02724634.2024.2424139

ARTICLE

A LATEST PALEOCENE MAMMAL FAUNA FROM THE GREAT DIVIDE BASIN IN SOUTHERN WYOMING AND A REVISED BIOZONATION OF THE CLARKFORKIAN LAND MAMMAL AGE

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ABSTRACT—A new latest Paleocene mammal fauna from the Great Divide Basin in southern Wyoming is described and compared with fossil assemblages of similar age elsewhere in Wyoming. The Twelvemile Gulch local fauna is currently documented by 182 mammalian (127 identifiable) specimens from two localities representing 10 orders, 18 families, and 22 species of mammals, including *Phenacolemur cavatus*, new species. Several characteristic taxa indicate a Clarkforkian age, but some taxa that co-occur at Twelvemile Gulch show disjunct stratigraphic ranges in the well-documented stratigraphic sequence exposed in the Clarks Fork Basin of northern Wyoming. Anachronistic occurrences of Clarkforkian taxa in northern and southern Wyoming have now been documented repeatedly. These unexpected faunal associations likely reflect changing climates and associated taxon-specific range shifts across a latitudinal gradient in the Rocky Mountain Interior. The apparently asynchronous first and last appearances of certain taxa across this latitudinal gradient highlight the utility of immigrant clades over endemic taxa in biostratigraphy. A previous biozonation scheme for the Clarkforkian of the Clarks Fork Basin emphasized endemic *Plesiadapis cookei* and *Copecion* as index taxa for Clarkforkian biozones Cf-2 and Cf-3, respectively. However, the applicability of this zonation to Clarkforkian faunas from other parts of Wyoming has been problematic because *Plesiadapis cookei* occurs in all of them, despite substantial evidence for age disparity among these faunas. A revised biozonation for the Clarkforkian leverages first appearances of invasive Coryphodontidae and Miacidae to discriminate later Clarkforkian faunas including Twelvemile Gulch from earlier Clarkforkian faunas such as Big Multi Quarry.

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Citation for this article: Anemone, R. L., Jones, M. F., Van Regenmorter, J., & Beard, K. C. (2024) A latest Paleocene mammal fauna from the Great Divide Basin in southern Wyoming and a revised biozonation of the Clarkforkian land mammal age. *Journal of Vertebrate Paleontology*. https://doi.org/10.1080/02724634.2024.2424139

Submitted: June 25, 2024
Revisions received: October 9, 2024
Accepted: October 17, 2024

INTRODUCTION

The Clarkforkian North American Land Mammal Age (NALMA) has long played a significant role in discussions concerning Paleogene mammalian evolution, biochronology, and biogeography (Archibald et al., 1987; Lofgren et al., 2004; Rose, 1981; Secord, 2008; Secord et al., 2006; Wood, 1967). Originally based on the mammalian fauna described by Granger (1914) from the southwestern end of Polecat Bench in the Clarks Fork Basin of northwestern Wyoming, the Clarkforkian was formally recognized by Wood et al. (1941) as the youngest North American provincial age of the Paleocene. Due to the paucity of mammalian faunas of Clarkforkian age from outside its type area in northern Wyoming, earlier workers expressed skepticism about its usefulness (Wood, 1967). This situation changed following the work of Rose (1981), who responded to these criticisms with a convincing defense of the reality and utility of the Clarkforkian. Rose (1981) demonstrated that a typical Clarkforkian faunal assemblage was present in several Rocky Mountain basins outside its type area and that it was succeeded by the Wasatchian NALMA of earliest Eocene age. Questions concerning the precise position of the Paleocene–Eocene (PE) boundary relative to the Clarkforkian NALMA have since been resolved through paleontological and stratigraphic work across the PE boundary at a number of different

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localities in North America and around the globe (Aubry et al., 2007; Gingerich, 2001; Gingerich & Clyde, 2001; Gingerich & Smith, 2006; Yans et al., 2006). The onset of the Eocene coincides with the base of a high-amplitude negative excursion in δ^{13}C (often designated the carbon isotope excursion or CIE), a worldwide geochemical marker related to a major perturbation in the global carbon cycle (Dupuis et al., 2003; Koch et al., 1992; Luterbacher et al., 2000; Tipple et al., 2011; Turner & Ridgewell, 2016; Yans et al., 2006). Because the onset of the CIE occurs in strata yielding latest Clarkforkian mammals while earliest Wasatchian mammals occur within the body of the CIE (Magioncalda et al., 2004), the Clarkforkian–Wasatchian boundary closely approximates the Paleocene–Eocene boundary (Yans et al., 2006).

Despite a great deal of recent research, especially in the Bighorn Basin, focusing on biotic and environmental changes associated with the Paleocene–Eocene thermal maximum (PETM), Clarkforkian faunas from outside the greater Bighorn Basin are rare, and those that have been identified remain inadequately documented (Holroyd & Rankin, 2014). Clarkforkian faunas have so far been reported only from Montana, Wyoming, and Colorado in North America (Rose, 1981). In addition to the Buckman Hollow fauna from the Green River Basin reviewed by Holroyd and Rankin (2014), Clarkforkian faunas occurring outside the greater Bighorn Basin include those from the Togwotee Pass area in eastern Teton County, Wyoming (McKenna, 1980), the Piceance Creek Basin of northwestern Colorado (Burger, 2012; Burger & Honey, 2008), Big Multi Quarry and nearby sites in the Washakie Basin of southern Wyoming (Beard et al., 2019; Chester & Beard, 2012; Dawson & Beard, 1996; Jones & Beard, 2023; Wilf et al., 1998) and the fauna described here from the Great Divide Basin of south-central Wyoming. Possible Clarkforkian faunas mentioned by Rose (1981) from Big Bend National Park in Texas and Baja California in Mexico are no longer regarded as Clarkforkian in age (Novacek et al., 1991; Schiebout et al., 1987). Clarkforkian equivalent faunas in Asia and Europe probably exist (Beard & Dawson, 1999), but they remain variably problematic because of issues related to intercontinental correlation. Nevertheless, the recently described late Paleocene Petit Pâtis fauna in the Paris Basin is almost certainly a European correlative of the Clarkforkian (Smith et al., 2014).

In this paper we describe the Clarkforkian Twelvemile Gulch local fauna from rocks that are interpreted as belonging to the upper part of the Fort Union Formation in the Great Divide Basin of southern Wyoming. The Twelvemile Gulch local fauna subsumes specimens collected at two closely spaced sites, one of which has been previously cited in the literature as Mark's Locality (Anemone & Dirks, 2009; Holroyd & Rankin, 2014). Nearly all the fossils discussed here are from Mark's Locality. In addition to providing systematic descriptions of the mammal fauna from Twelvemile Gulch, we discuss biostratigraphic implications of the fauna as well as geological aspects of the local and regional setting. Finally, we suggest a revised biozonation of the Clarkforkian NALMA that addresses long-standing issues that have hindered regional correlation of Clarkforkian faunas from southern and western Wyoming with those from the Clarks Fork Basin.

Located primarily in Sweetwater County in southwestern Wyoming, the Great Divide Basin (GDB) is a large (ca. 10,000 km^2) sedimentary basin filled with deposits ranging in age from Paleocene to Quaternary (Fig. 1). It comprises the northeastern

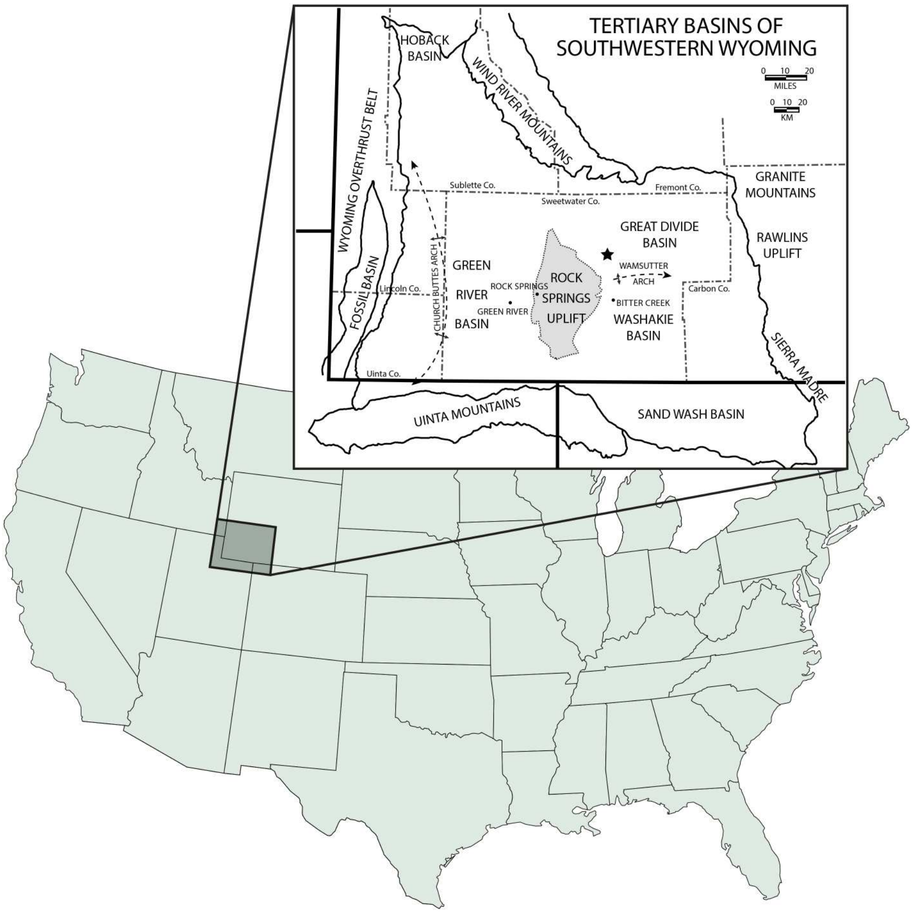

FIGURE 1. Map of southwestern Wyoming, showing important geological features and selected geographic entities. The location of the Twelvemile Gulch local fauna is designated by a black star near the western margin of the Great Divide Basin. Big Multi Quarry is located very close to Bitter Creek.

part of the Greater Green River Basin and is bounded by the Wamsutter Arch to the south, the Wind River Mountains and Granite Mountains Uplift to the north, the Rock Springs Uplift to the west and the Rawlins Uplift to the east (Halverson & Eberle, 2018; Sullivan, 1980). It is an internal drainage basin encircled by the Continental Divide, which splits into two branches near South Pass and rejoins south of Rawlins. With elevations ranging between 2000 and 2500 m, the GDB is today a high desert with less than 250 mm of annual precipitation. Its flora is dominated by sagebrush and various grasses, interspersed with sand dunes and alkali flats, and it lacks any permanent water. Topographic relief is low, especially considering that the GDB straddles the Continental Divide, and typical badland exposures are limited in extent due to the lack of significant rivers or streams crossing the basin. As a result, outcrops of fossiliferous Paleogene strata are limited and exposures are frequently widely separated.

GEOLOGICAL AND PALEONTOLOGICAL BACKGROUND

Geology

First named by Meek and Hayden (1862) for lignite-bearing sandstones and shales of paludal origin in the Williston Basin of northwestern North Dakota, the Fort Union Formation is one of the major units of terrestrial rocks of Paleocene age in the Rocky Mountain Interior of North America (Denson & Gill, 1965; Winterfeld, 1982). In our study area, the Fort Union Formation underlies intertonguing sediments of the Eocene Wasatch and Green River Formations and overlies the Upper Cretaceous Foxhills sandstone and the Hell Creek Formation (Love & Christiansen, 1985). Winterfeld (1982:75) suggested that the base of the Fort Union Formation in the Washakie Basin, just south of our study area "is marked by a distinctive paleosol or thick sandstone," while "placement of the upper boundary is problematic because the formation grades upward into the Wasatch Formation."

Our field investigations confirm the difficulty of identifying a clear boundary between the Fort Union and Wasatch Formations in the Great Divide Basin, where low relief and slow rates of erosion result in large areas of Paleogene outcrops being covered by surficial Quaternary alluvium. The geological map of Wyoming (Love & Christiansen, 1985) indicates that the Fort Union–Wasatch Formation boundary runs along the Bitter Creek Road (Sweetwater County Road 19) in flat-lying strata north of Interstate 80 and the former settlement of Bitter Creek. At the boundary between Townships 20 and 21 North in Range 99 West, the mapped boundary between the Fort Union and Wasatch Formations diverges to the northwest from the Bitter Creek Road. The Twelvemile Gulch assemblage occurs about 9.5 km north of this point, in strata that Love and Christiansen (1985) mapped as Wasatch Formation, although we regard these rocks as being more appropriately assigned to the uppermost Fort Union Formation (Fig. 2). Directly to the west of the Bitter Creek Road at Mark's Locality in Twelvemile Gulch, lithologies suggest paludal deposition with more numerous and substantial coal, lignite, and carbonaceous shale beds that typify the Fort Union Formation. While some thin coal and lignite beds can occur in strata on the east side of the road, the dominant lithologies there tend to be more fluvial in nature and are best considered part of the Wasatch Formation, as suggested by Love and Christensen (1985). Winterfeld (1982:75) suggested that, because this lithological change occurs in conjunction with the disappearance of "limestone- and sandstone-capped cuestas that are characteristic of the

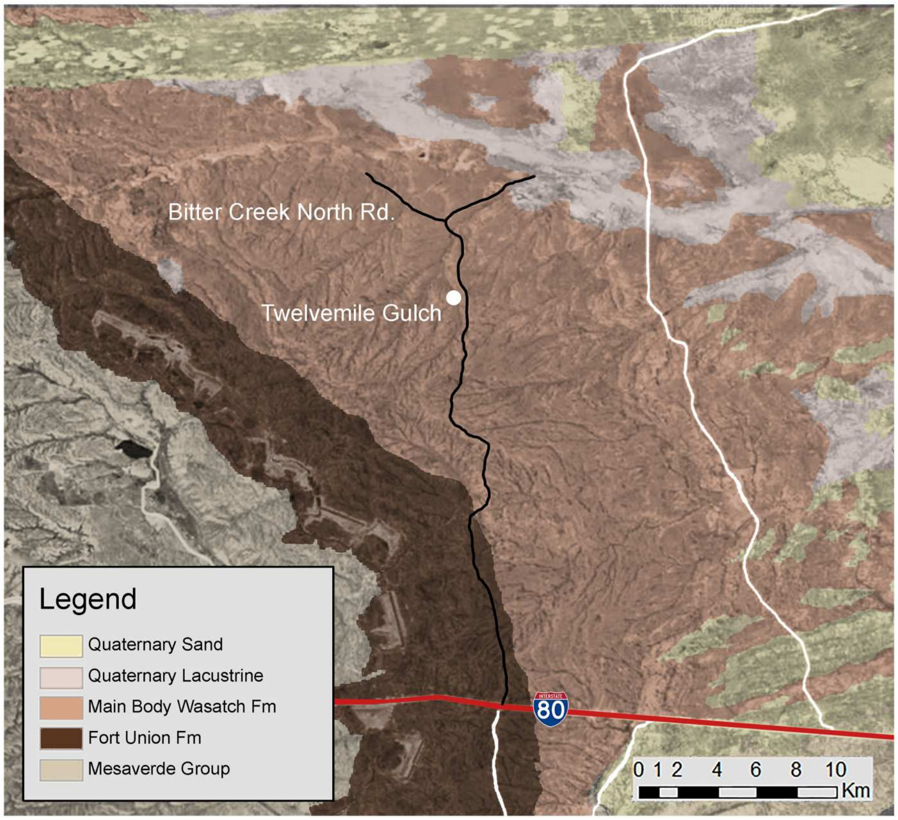

FIGURE 2. Location of the Twelvemile Gulch local fauna superimposed on the geological map of Love and Christiansen (1985) for this part of Wyoming. Note that Twelvemile Gulch is mapped as occurring in the Main Body of the Wasatch Formation, although the boundary between the Fort Union and Wasatch formations is poorly defined locally, partly because of sporadic outcrops.

Fort Union Formation" further to the west, the boundary between the Fort Union and Wasatch Formations in the Washakie Basin should be set at "the upper contact at the last (easternmost) of the cuestas (e.g., NW ¼ of section 17, T 18 N, R 99 W)." This would place the contact 7–8 km north of Bitter Creek, quite close to where it is mapped by Love and Christiansen (1985). We interpret the Fort Union–Wasatch Formation boundary in the vicinity of Twelvemile Gulch to correspond closely to the Bitter Creek Road in the northern part of Township 21, Range 99. Further fieldwork is needed to fully resolve this issue due to the mostly flat-lying and poorly exposed strata in this part of our field area and the lithological similarities between the two formations.

Paleontology

Previous work on Paleocene mammalian faunas from the eastern flank of the Rock Springs Uplift and adjacent parts of the Washakie and Great Divide basins has been sporadic, with intensified activity in recent years. Clarkforkian mammals were first recovered in the Washakie Basin in 1976 at Big Multi Quarry near Bitter Creek by crews from the University of California Museum of Paleontology (UCMP) under the direction of Donald E. Savage (Rose, 1981). In 1992, field parties from the Carnegie Museum of Natural History (and later the University of Kansas) under the direction of K. Christopher Beard reopened the quarry and have continued research at Big Multi Quarry and nearby sites in the succeeding years. Big Multi Quarry is the richest Clarkforkian locality currently known, with 44 mammal species represented and a total of nearly 2000 mammalian specimens collected by small-scale quarrying techniques and screen washing of all fossil-bearing sediment (Beard et al., 2019; Chester & Beard, 2012; Dawson & Beard, 1996; Jones & Beard, 2023; Wilf et al., 1998). A large and diverse flora from Big Multi Quarry and associated strata has yielded significant clues to the paleoecology and climate of southern Wyoming during the latest Paleocene (Wilf et al., 1998).

Winterfeld (1982) conducted a paleontological survey of Fort Union strata in the western part of the Great Divide Basin, the northwestern margin of the Washakie Basin, and the adjacent eastern flank of the Rock Springs Uplift. This work yielded a total of 52 mammalian species from 19 localities spanning the Torrejonian and Tiffanian NALMAs (Winterfeld, 1982). Winterfeld's fieldwork involved surface collecting at most localities, with screen washing and quarrying being carried out at a few localities. Following the initiation of fieldwork in the vicinity of Big Multi Quarry by Beard and colleagues, Beard and Winterfeld collaborated frequently, and their joint efforts yielded additional sites in the Fort Union Formation, notably including the late Tiffanian (Ti-5) Twelvemile Bonanza site located ~8 km south of the Twelvemile Gulch area that is the focus of this report (Mattingly et al., 2018). Detailed taxon-specific studies of Paleocene mammals from this region have also been published (Beard et al., 2019; Chester & Beard, 2012; Dawson & Beard, 1996; Jones & Beard, 2023; Mattingly et al., 2018).

Following up on decades of geological and paleontological work by James Honey and Malcolm McKenna in the eastern part of the Great Divide Basin, Eberle and colleagues named a new arctocyonid (McComas & Eberle, 2016) as well as three new periptychid 'condylarths' (Atteberry & Eberle, 2021) from Puercan (earliest Paleocene) strata of the Fort Union Formation. Halverson and Eberle (2018) published a small early Tiffanian mammal fauna comprising 18 species representing five mammalian orders, mostly collected from anthills in the eastern GDB. Finally, Lofgren and colleagues described Puercan multituberculates from the collections made by Honey and McKenna (Lofgren et al., 2017).

Clarkforkian and the PETM—The Clarkforkian land mammal age is of general interest and importance to paleontologists for several reasons. It marks an important episode of faunal turnover and modernization in North America, characterized most notably by the local first appearance of rodents, a clade that would subsequently become diverse and ecologically ubiquitous (Dawson & Beard, 1996; Rose, 1981). Alongside rodents, the Clarkforkian is defined by the first appearance in North America of tillodonts and the condylarth *Haplomylus* (Archibald et al., 1987; Dawson & Beard, 1996; Lofgren et al., 2004; Rose, 1981, 2006). The pantodont *Coryphodon* has often been cited as occurring near the beginning of the Clarkforkian (Rose, 1981), but *Coryphodon* has not been recorded at several important earlier Clarkforkian sites including Bear Creek, Montana and Big Multi Quarry. Additionally, its first appearance in the Bighorn Basin occurs ~325 m above the Tiffanian–Clarkforkian boundary, after which it becomes relatively common (Secord et al., 2006). Significantly, miacid carnivoramorphans (*Uintacyon*) first appear roughly synchronously with *Coryphodon* in the Clarks Fork Basin sequence (Gingerich, 1983b), marking an important episode of faunal dispersal roughly midway through the Clarkforkian. Most, if not all, of the exotic clades of mammals that first appear in North America at the beginning of the Clarkforkian appear to have originated in Asia, a biogeographic pattern that was replicated in the succeeding (and larger) episode of faunal turnover marking the beginning of the Wasatchian (Beard, 1998; Beard & Dawson, 1999). Accordingly, the Clarkforkian can be viewed as a precursor of the more dramatic biotic and climatic events that transpired across the Paleocene–Eocene boundary.

The Paleocene–Eocene Thermal Maximum was a brief but intense period of global warming (McInerney & Wing, 2011; Wing et al., 2003) associated with an enormous injection of ^{13}C-depleted carbon into the ocean-atmosphere system (Aubry et al., 1998). The resulting negative excursion in atmospheric and oceanic δ^{13}C levels of 3–4‰ was an isochronous and worldwide event that has been located in magnetic polarity chron C24r in both marine and terrestrial strata at 56 Ma (Bains et al., 1999; Bowen et al., 2001; Frieling et al., 2016; Koch et al., 1992; Zachos et al., 2001). The proposed source or sources of the massive amounts of ^{13}C-depleted carbon that would have been required to cause these changes to the global carbon cycle have been debated for decades and include the dissociation of submarine methane hydrates (Dickens et al., 1995, 1997; Katz et al., 1999; Zachos et al., 2008), enhanced volcanism in the North Atlantic (Freiling et al., 2016; Gutjahr et al., 2017; Storey et al., 2007), or the thawing and oxidation of organic matter in terrestrial permafrost (DeConto et al., 2012). One estimate of the mass of the carbon release that propagated the PETM exceeds 10,000 gigatons (Gutjahr et al., 2017).

The environmental effects of the CIE and PETM were enormous, resulting in worldwide environmental disruption including significant acidification and carbonate dissolution in the oceans, and a global temperature increase of between 5–8°C (Bowen et al., 2004; Koch et al., 2003; Tipple et al., 2011). Thus, the PETM, the CIE, the Paleocene–Eocene boundary, and the faunal transition from Clarkforkian to Wasatchian NALMA are all linked events that mark the transition from Paleocene to Eocene time, and record the geochemical evidence and the biological consequences of an intense period of global warming that lasted for approximately 200 Ka (Figueirdo et al., 2012; Frieling et al., 2016; Secord et al., 2012). These warmer temperatures and the associated floral changes may have created a high latitude, forested corridor linking Asia to North America and Europe that allowed the dispersal of Wasatchian mammals between those continents (Beard, 1998, 2008; Beard & Dawson, 1999; Beard et al., 2010; Bowen et al., 2002; Hooker, 1998; Hooker & Dashzeveg, 2003; Smith et al., 2006).

MATERIALS AND METHODS

Institutional Abbreviations—**AMNH FM**, American Museum of Natural History (fossil mammal collection), New York, NY, U.S.A.; **CM**, Carnegie Museum of Natural History, Pittsburgh, PA, U.S.A.; **JSNN**, Joint School of Nanoscience and Nanoengineering, Greensboro, NC, U.S.A.; **SMIF**, Shared Materials Instrumentation Facility, Durham, NC, U.S.A.; **UM**, University of Michigan Museum of Paleontology, Ann Arbor, MI, U.S.A.; **UW**, University of Wyoming, Laramie, WY, U.S.A.

Anatomical Abbreviations—**L**, maximum mesio-distal length; **W**, maximum bucco-lingual width.

Geology and History of Research

Twelvemile Gulch parallels the Bitter Creek Road (Sweetwater CR 19) in Townships 21 and 22 North, Range 99 West, draining in a generally south to north direction just west of the road. Two Clarkforkian localities in this area were first identified in 1994. Mark's Locality (CM locality 3613) and Brett's Booty (CM Locality 3612) are each located just below the rim of Twelvemile Gulch in the northwestern quarter of section 3, Township 21 North, Range 99 West, placing them ~32 km north of Big Multi Quarry. Nearly the entire vertebrate fossil assemblage from Twelvemile Gulch comes from CM locality 3613, while CM 3612 has yielded a partial skeleton of a champsosaur, a single *Phenacodus* lower molar, and multiple fragmentary remains of turtle, crocodile, and gar. Locality CM 3613 has been intensively surface-collected on several occasions since it was first identified in 1994, while CM 3612, located some 800 m south of CM 3613, has been collected less intensively. Although small in number (total number of mammalian specimens, TNS = 182), the vertebrate assemblage from these localities (Table 1) currently

TABLE 1. Faunal list from Twelvemile Gulch local fauna. Total sample includes 127 identified mammals and excludes 55 unidentified mammals and other vertebrates. **Abbreviations**: **TNS**, total number of specimens; **MNI**, minimum number of individuals; **%TNS**, percent of total number of specimens; **%MNI**, percent of minimum number of individuals.

Order	Family	Genus/Species	TNS	MNI	%TNS	%MNI
Multituberculata						
	Neoplagiaulacidae					
		Ectypodus tardus	1	1	0.79	2.33
	Ptilodontidae					
		Prochetodon sp.	2	1	1.57	2.33
Marsupialia						
	Peradectidae					
		Peradectes protinnominatus	2	1	1.57	2.33
Lipotyphla						
	Erinaceomorpha					
		Adunator sp.	3	2	2.36	4.65
	Nyctitheriidae					
		Plagioctenodon goliath	2	1	1.57	2.33
		Plagioctenodon cf. *P. dawsonae*	1	1	0.79	2.33
Cimolesta						
	Pantolestidae					
		Paleosinopa sp.	1	1	0.79	2.33
Apatotheria						
	Apatemyidae					
		Labidolemur kayi	1	1	0.79	2.33
Primatomorpha						
	Carpolestidae					
		Carpolestes nigridens	7	3	5.51	6.98
	Plesiadapidae					
		Plesiadapis cookei	20	6	15.75	13.95
		Plesiadapis dubius	21	4	16.54	9.30
	Paromomyidae					
		Phenacolemur—new species (see below)	6	2	4.72	4.65
	Microsyopidae					
Rodentia		*Arctodontomys simplicidens*	1	1	0.79	2.33
		Arctodontomys sp.	1	1	0.79	2.33
	Paramyidae					
		Acritoparamys atwateri	2	1	1.57	2.33
Mesonychia						
	Mesonychidae					
		Dissacus sp.	1	1	0.79	2.33
Carnivoramorpha						
	Miacidae					
		Uintacyon rudis	1	1	0.79	2.33
	Viverravidae					
		Didymictis proteus	1	1	0.79	2.33
"Condylarthra"						
	Arctocyonidae					
		Thryptacodon sp.	4	1	3.15	2.33
	Phenacodontidae					
		Phenacodus intermedius	2	2	1.57	4.65
		Ectocion osbornianus	8	2	6.30	4.65
	Apheliscidae					
		Apheliscus nitidus	39	9	30.71	20.93
	Totals		127	43		

includes 22 mammal species representing ~18 family-level clades, and at least four sauropsid and fish taxa. The vertebrate assemblage from Twelvemile Gulch is important in part because of the paucity of mammalian fossil-bearing sites in the uppermost part of the Fort Union Formation in our field area. It is particularly interesting, however, because the Twelvemile Gulch assemblage is apparently younger than the Clarkforkian fauna from Big Multi Quarry, enabling a rare opportunity to evaluate the regional validity of biostratigraphic subdivisions of the Clarkforkian proposed in its type area in northern Wyoming.

A detailed stratigraphic section of Twelvemile Gulch (Fig. 3) was measured at Mark's Locality (CM locality 3613) by the third author. The section was measured on a bearing of 090°, up a bluff at 108°36.145′W, 41°49.740′N, at an approximate elevation of 2115 ± 6 m. Total measured thickness was 39.8 meters from the drainage below the locality to the crest of the bluff above the fossil-bearing levels (Fig. 4). Consistent values of strike of 170° were recorded, while dip measurements averaged 5° to the east. Mark's Locality consists of two productive fossil horizons. These two horizons are stratigraphically 3.5 meters apart, but no faunal differences were documented between the two horizons. So, for the purposes of this study, fossils from both horizons were grouped together. Significantly for the arguments presented here, both horizons contain specimens of *Plesiadapis* sp., cf. *P. cookei*.

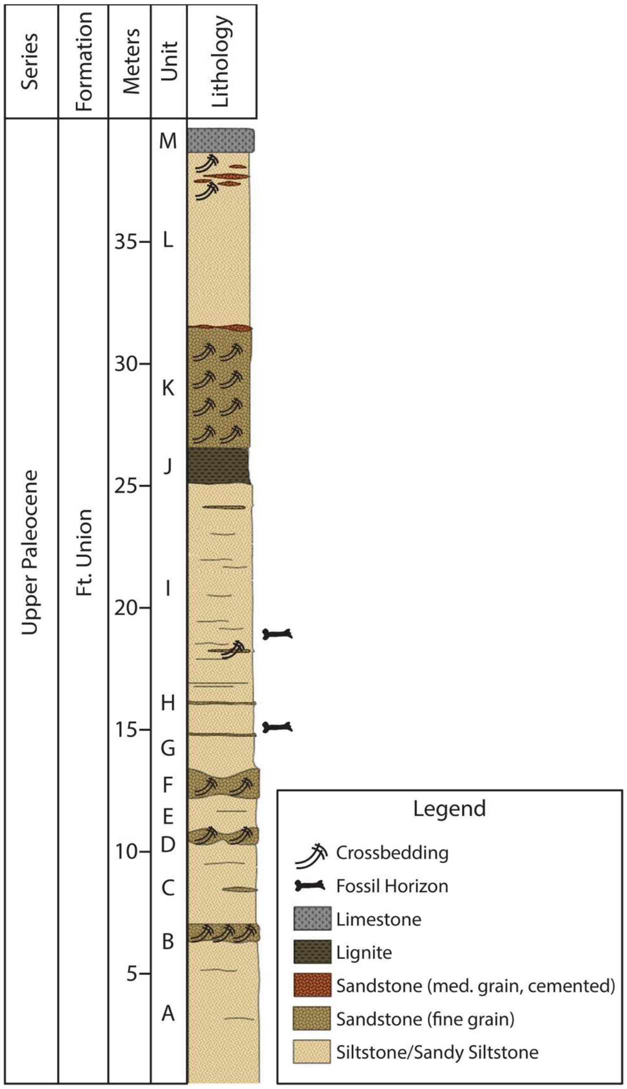

FIGURE 3. Stratigraphic section exposed in the vicinity of the Twelvemile Gulch local fauna, upper Fort Union Formation, Sweetwater County, Wyoming. See Figure 4 for photographs of strata and outcrops.

The measured section (Fig. 3) records essentially a unified stratigraphic succession of fluvial and paludal systems. It contains a relatively thick (1.5 m) lignite (coal) unit and is locally capped by a 1-meter thick laterally persistent limestone unit. Siltstone and sandstone units are uniformly well-sorted, and conglomeratic lithologies are absent from the section. A decrease in silt content accompanies an increase in grain-size and the resulting permeability of the sandstone units. This has resulted in frequent secondary mineralization of these rocks to include bulbous and spindle-shaped carbonate-cemented and ferruginous "nodules" that are a prominent feature of the section transect and the gently sloping land surface east of the bluff. Elsewhere it is clear that secondary cementation of these sandstone beds has resulted in their increased resistance to erosion. This mineralization follows bedding structures in the channel sandstones, with predominant trough cross-bedding resulting in the characteristic shapes of the "nodules" seen eroded out at the surface. The vertebrate fauna described here is associated with fine silty sediment having a characteristic greenish coloration.

Unit A (>6.0 m)—Unit A is exposed in a steep-sided drainage at the foot of the bluff and its base is covered. Exposures consist of a light-colored, weakly consolidated, planar bedded siltstone. Some bedding units were composed of silty sandstone with thin layers containing small sub-angular lithic fragments and infrequent pieces of broken shell, representing local lag deposits. These clasts had a maximum size of ~15 mm.

Unit B (0.7 m)—Unit B represents the first of numerous units of fine- to medium-grained channel sandstone in the measured section. These units are characteristically lenticular and consequently, are variously developed laterally and intermittently exposed along the bluff. The sandstone exhibits trough cross-bedding up to 1 m in height with steep cross-sets. Such units occurring repeatedly throughout the measured section represent channel sands that have experienced secondary carbonate and iron cementation.

Unit C (3.3 m)—Unit C comprises a sequence of light-colored, weakly consolidated siltstones and fine, silty sandstone with a thin lens (max. 0.5 m) of carbonate-cemented medium-grained channel sandstone towards its center.

Unit D (0.6 m)—A distinctly cross-bedded unit of carbonate-cemented, fine-grained channel sandstone that appears more laterally persistent than lower lenticular bodies, although the thickness of the unit is distinctly variable. Sandstone is yellow gray in color and displays oxidation on weathered surfaces.

Unit E (1.3 m)— Unit E is composed of light-colored, weakly consolidated siltstones and fine, silty sandstones. No channel sandstones were present in this part of the measured section.

Unit F (1.2 m)—Variably developed unit of lenticular channel sandstone composed of calcareous-cemented, fine quartz sand. Significant quantities of heavy (ferromagnesian) mineral grains are also apparent in the sandstone, which weathers to a distinct gray carbonate patina. The sandstone exhibits trough cross-bedding, the appearance of which is enhanced by variations in iron-staining on the surface.

Unit G (2.7 m)—Sequence of siltstone and sandy-siltstone containing a thin lens of sandstone. This unit contains the lower of two vertebrate-fossil bearing localities (at 14.6 m) in a weakly laminated greenish siltstone that appears enriched in organic detritus and contains discrete plant material (e.g., fragments of palm frond). The sediment appears oxidized in places, with yellowish brown color and abundant stringers of dark yellowish orange discoloration.

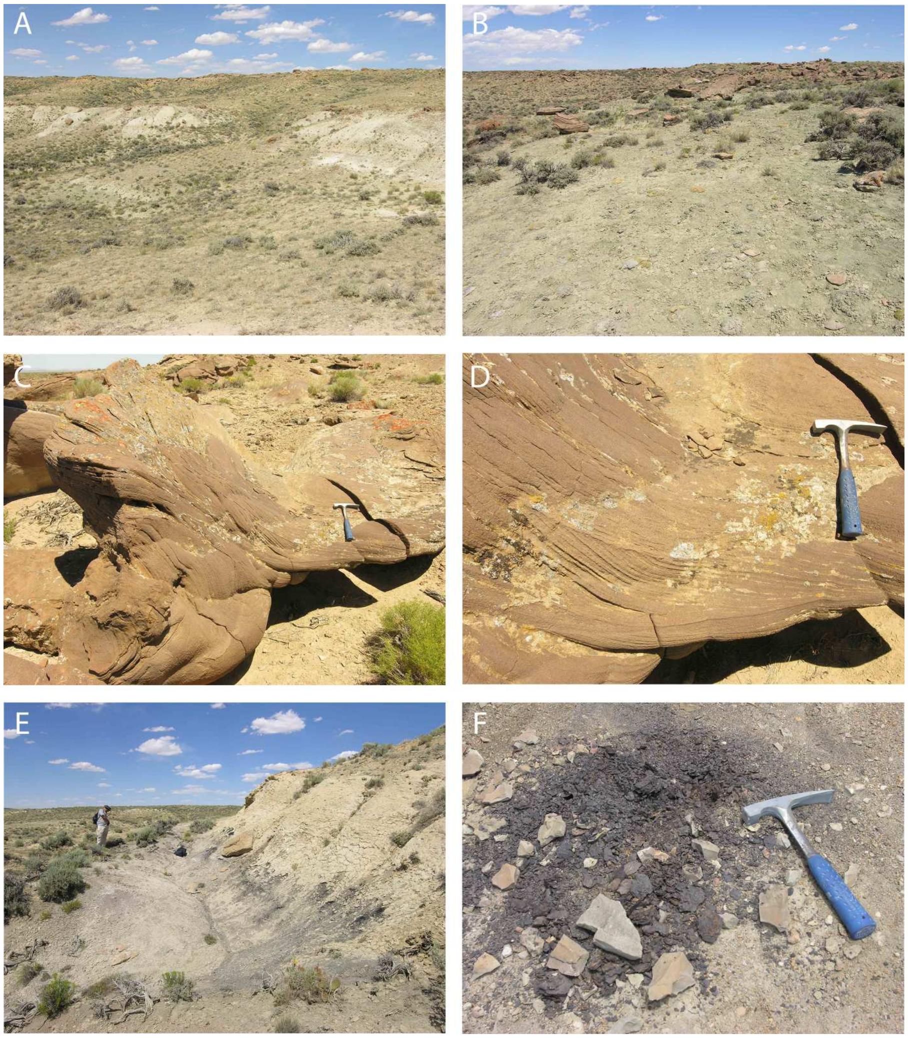

FIGURE 4. Outcrops exposed in the vicinity of the measured section encompassing the Twelvemile Gulch local fauna (see Fig. 3). **A**, general view of upper part of measured section, Units G and above. **B**, distinctive olive-green colored siltstone in upper fossiliferous horizon (Unit I). **C**, trough cross-bedding in calcareous cemented and ferruginous channel sandstones of Unit F. **D**, resilient, cemented channel sandstone of Unit F. **E**, friable, laminated carbonaceous shale ("lignite") comprising Unit J. **F**, close-up view of carbonaceous shale or lignite of Unit J.

Unit H (0.5 m)—Lens of calcareous-cemented fine-grained sandstone.

Unit I (7.2 m)—A series of interbedded siltstones and sandy siltstones of varying coloration and containing thin sandstone lenses. The lower part of the unit is light yellow brown in color, becoming paler upwards beneath the lowermost sandstone lens. The yellow coloration continues immediately above the sandstone but then grades sharply into the distinctly olive colored and fossiliferous siltstone at 18.1 m. The fossil-bearing sediment passes upwards into a sequence of weakly consolidated siltstone and fine sandstone.

Unit J (1.5 m)—A lignite (coal) unit. The lignite unit appears to vary in thickness up to ~1.5 m but is laterally persistent and represents a potentially valuable marker bed. Organic content of the laminated shale appears to be variable with the color of the shale ranging from dusky yellowish brown to grayish black. Sandstone in proximity of the carbonaceous shale is orange in coloration and stringers of similar coloration occur through, and within, the shale.

Unit K (6.6 m)—Fine-grained, silty, trough cross-bedded sandstone, appearing more consolidated and containing less silt in its lower part, and less consolidated and silty in its upper part. Yellowish gray throughout.

Unit L (7.2 m)—Very weakly consolidated siltstones and fine silty sandstone, becoming particularly light-colored towards the top. Contains a small number of thin lenses of channel sandstone. These are a more resistant lithology that appear darker, iron-stained, in color when weathered.

Unit M (1.0 m)—Strongly lithified, resilient limestone forms the crest of the bluff. This is a well-recognized characteristic of the Fort Union Formation. This unit appears more laterally continuous than many others in this section. Although it is of variable thickness, it may also serve as a useful marker bed.

Specimens and Imaging

All specimens were collected by intensive surface collecting under Bureau of Land Management permit 287-WY-PA95, and the permanent repository for these fossils is the Carnegie Museum of Natural History in Pittsburgh, PA. Fossils were measured using several different tools including Helios dial calipers, a Unitron Z series binocular microscope equipped with Mitutoyo digimatic micrometers, and a Leica NZ6 binocular microscope with a measuring reticle. Measurement data are included in Supplementary Data. Fossil material was scanned via computed tomography using Nikon XTH 225-ST micro-CT scanners at Duke University (SMIF) and at the University of North Carolina Greensboro (JSNN). Scans were typically conducted at 120 kV and 70 μA and reconstructed to voxel sizes ranging from 10–20 μm. Scans were visualized and segmented using Materialise Mimics 25.0 software. CT scans are reposited at Morphosource: https://www.morphosource.org/projects/000673731?locale=en

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order MULTITUBERCULATA Cope, 1884
Suborder CIMOLODONTA McKenna, 1975
Superfamily PTILODONTOIDEA Sloan and Van Valen, 1965
Family NEOPLAGIAULACIDAE Ameghino, 1890
ECTYPODUS Matthew and Granger, 1921
ECTYPODUS TARDUS (Jepsen, 1930a)
Fig. 5A, B

Referred Specimen—CM 79212, right p4.

Known Distribution—Upper Eocene (Wasatchian) of Wyoming and Colorado.

Description—CM 79212 (L, 2.78 mm) bears 10 serrations (Fig. 5A, B). Crown height measured at the exodaenodont lobe is 2.36 mm, yielding a ratio of crown height to length of 0.85. The height of the first serration above the dorsal lip of the anterobasal concavity is 1.11 mm, yielding a ratio between the former metric and crown length of 0.40. Minor abrasion along the serrated apex of the crown obscures whether the fourth or fifth serration would have been the highest above the baseline, but there appears to have been little difference in their height. In lateral profile the crown is relatively high, arcuate, and symmetrical. The anterobasal concavity is very shallow, possibly indicating that a peg-like p3 was absent, as is the case for Wasatchian specimens of *E. tardus* (Krause, 1982; Krishtalka, 1984).

The leading edge of the blade is essentially straight from its origin above the anterobasal concavity to the first serration. The profile of the crown is higher anteriorly than posteriorly, being convex between the first and fifth serrations and more nearly straight thereafter. The strength of individual serrations is greatest posteriorly, and the distance between serrations increases posteriorly. Labial and lingual ridges are moderately developed. The exodaenodont lobe is prominent, yielding a

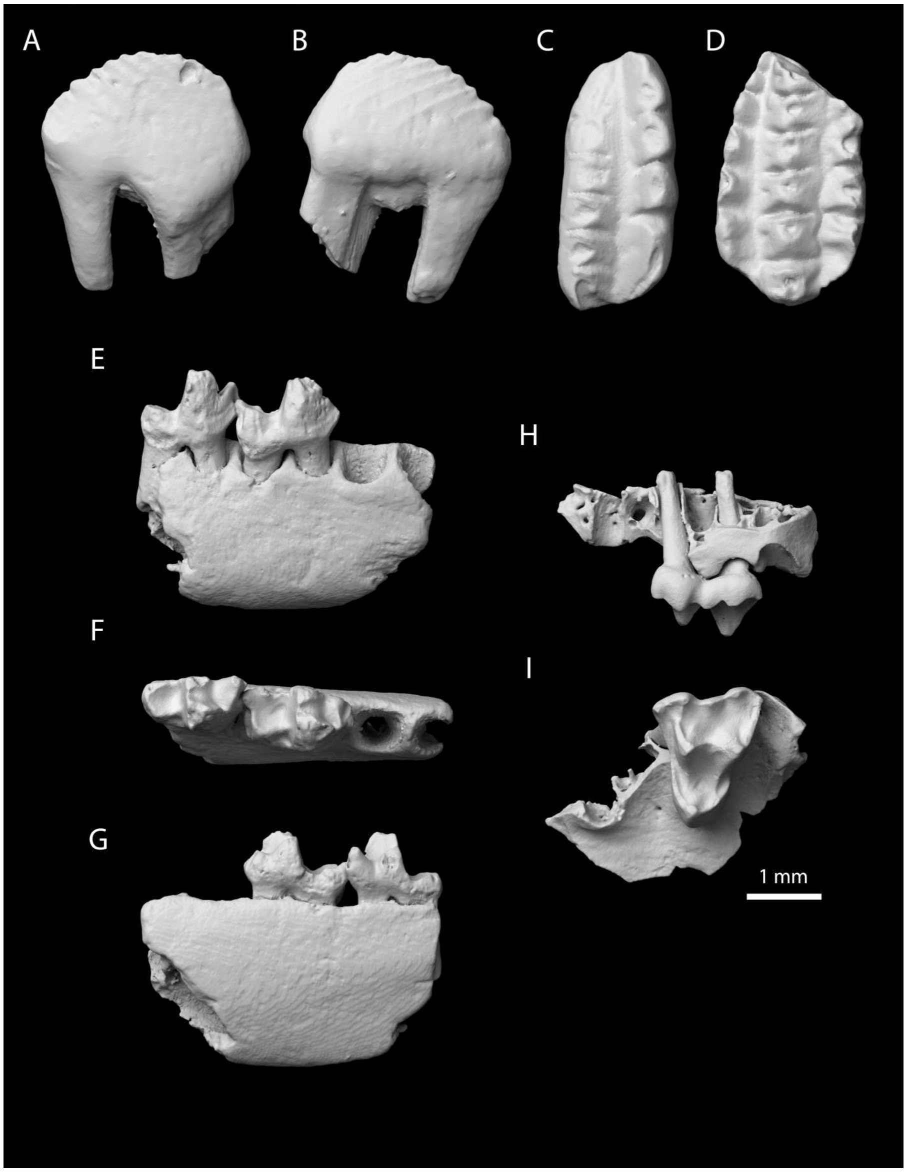

FIGURE 5. Multituberculata and Metatheria from the Twelvemile Gulch local fauna. **A**, **B**, CM 79212, right p4 of *Ectypodus tardus* in **A**, buccal and **B**, lingual views. **C**, CM 79213, left m1 of *Prochetodon* sp. in occlusal view. **D**, CM 79214, partial left M1 of *Prochetodon* sp. in occlusal view. **E**–**G**, CM 79210, right dentary of *Peradectes protinnominatus* preserving m3–4 in **E**, buccal, **F**, occlusal, and **G**, lingual views. **H**, **I**, CM 79211, left maxilla of *Peradectes protinnominatus* preserving M2 in **H**, buccal, and **I**, occlusal views.

narrow and deep incisure between it and the posteroexternal ledge.

Comments—CM 79212 is smaller than the p4 in specimens assigned to *Ectypodus powelli* from Big Multi Quarry and Tiffanian and Clarkforkian sites in the Clarks Fork Basin (Krause, 1980; Secord, 2008). In size and morphology, it fits within the range of variation documented for Wasatchian specimens assigned to *E. tardus* (Krause, 1982; Krishtalka, 1984). This is the first record of *E. tardus* from the Clarkforkian, although Krishtalka et al. (1975) assigned several specimens from Malcolm's Locality, a Tiffanian site in the Wind River Basin, to "*Ectypodus* sp. near *E. tardus*."

Family PTILODONTIDAE Cope 1887
PROCHETODON Jepsen, 1940
PROCHETODON sp.
Fig. 5C, D

Referred Specimens—CM 79213, left m1; CM 79214, partial left M1.

Known Distribution—lower Tiffanian (Ti-1) to upper Clarkforkian (Cf-2) of western North America (Alberta, Saskatchewan, Montana, North Dakota and Wyoming).

Description—CM 79213 (L, 3.45 mm; W, 1.50 mm) is a moderately worn left m1 crown, rendering certain aspects of its occlusal morphology ambiguous (Fig. 5C). The cusp formula (buccal: lingual) is interpreted as 7:5, although wear along the mesiobuccal margin of the crown makes the number of cusps in the buccal row uncertain. Despite the advanced stage of occlusal wear in this specimen, shallow vertical grooves can be observed on the buccal side of the buccal row of cusps. The latter feature is regarded as diagnostic for *Prochetodon* (Krause, 1987).

CM 79214 (W, 1.95 mm) preserves only the distal two-thirds of a left M1 crown (Fig. 5D). As preserved, the cusp formula (buccal:middle:lingual) of this tooth is 4:6:6.5, but there were undoubtedly more cusps occupying at least the buccal and middle rows. The lingual row of cusps is buccolingually compressed, in contrast to the more pyramidal and voluminous cusps of the middle row. The lingual row of cusps extends anteriorly at least as far as the sixth middle cusp.

Comments—The two specimens referred here to *Prochetodon* sp. are smaller than homologous tooth loci in *P. taxus*, which is the only species of *Prochetodon* currently known to occur in the Clarkforkian (Krause, 1987). They are closer in size to *P. cavus* from the late Tiffanian, which is the smallest species of *Prochetodon* documented so far. Given the limited sample of *Prochetodon* currently available from Twelvemile Gulch, we refrain from assigning these specimens to any species.

Krause (1987) and Scott (2004) noted that the range of *Prochetodon* appears to have been limited to more northern faunas in the Western Interior of North America, citing specimens from Malcolm's Locality in the Wind River Basin of central Wyoming as the southernmost record of *Prochetodon* known at that time. The specimens of *Prochetodon* reported here from Sweetwater County in southwestern Wyoming are now the southernmost records of the genus known from the Rocky Mountain region. They are also possibly the youngest specimens of *Prochetodon* currently known.

Supercohort THERIA Parker and Haswell, 1897
Cohort MARSUPIALIA Illiger, 1811
Order DIDELPHIMORPHIA Gill, 1872
Family PERADECTIDAE Crochet, 1979
PERADECTES Matthew and Granger, 1921
PERADECTES PROTINNOMINATUS McKenna, 1960
Fig. 5E–I

Referred Specimens—CM 79210, right dentary preserving m3–4; CM 79211, left maxilla preserving M2.

Known Distribution—upper Paleocene (Clarkforkian) to lower Eocene (Wasatchian) of North America.

Description—CM 79210 is a right dentary fragment preserving m3–4 (m3L, 1.54 mm; m3W, 0.89 mm; m4L, 1.38 mm; m4W, 0.78 mm) and alveoli for m2 (Fig. 5E–G). Both lower molars possess an elongate trigonid with a procumbent paraconid (broken on m3), and strongly notched paracristid. The entoconid on m3 is broken, but the talonid on both teeth is low and buccolingually narrower than the trigonid. The hypoconulid of m3 is low, distally projecting, and distobuccal to the broken entoconid, whereas the talonid of m4 is worn and all talonid cusps are indistinct from the surrounding cristids.

CM 79211 is a maxillary fragment preserving a single molar and alveoli for teeth anterior and posterior to the molar (Fig. 5H, I). The molar is interpreted as M2 due to its relatively short mesiodistal length (L, 1.56 mm; W, 1.96 mm) and nearly symmetrical stylar shelf characterized by a weakly invaginated ectoflexus. In more nearly complete maxillary specimens of *Peradectes protinnominatus* from Big Multi Quarry (e.g., CM 72207, CM 72234) M3 can be distinguished from M2 in having a much deeper ectoflexus. The paracone is somewhat smaller than the metacone, as in M2 and M3 of *Peradectes protinnominatus* but in contrast to M1. Stylar cusps B and D are the largest and most buccally projecting stylar cusps. Stylar cusp C is slightly shorter and less massive than stylar cusps B and D, whereas stylar cusp A is notably smaller and projects only weakly mesially. No paraconule is apparent, but a very faint metaconule is present. Postparaconule and premetaconule cristae are very weak.

Comments—The absence of dilambdodonty and the presence of buccally positioned cristids obliquae differentiate these specimens from Herpetotheriidae. Krishtalka and Stucky (1983) diagnosed the genus *Peradectes* as possessing short talonids on m1–3, low and subequally sized entoconids and hypoconulids, subequal paracones and metacones, weak stylar cusps and conules, and a narrow protocone. *Peradectes protinnominatus* was described by McKenna (1960) as possessing well-developed stylar cusps B and D, and a moderately developed stylar cusp C. Based on the weak conules and relatively pronounced stylar cusps B and D of CM 79211, we assign this specimen to *P. protinnominatus*, known from the upper Paleocene (Cf-1) to lower Eocene (Wa-3) of Colorado and Wyoming (Krishtalka & Stucky, 1983: fig. 8). An earlier report assigning fragmentary Tiffanian specimens from Malcolm's Locality in the Wind River Basin of Wyoming and Police Point in Alberta to *P. protinnominatus* (Krishtalka et al., 1975) is not considered reliable here.

The missing entoconid on m3 of CM 79210 eliminates several key characters used to differentiate Paleogene marsupials. In *P. protinnominatus* the hypoconulid is positioned just distobuccal to the entoconid and is separated from it by only a shallow notch (Gingerich & Smith, 2006; Rose et al., 2012). Hypoconulids of *P. protinnominatus* typically do not project as far distally as in herpetotheriids such as *Peratherium* (Gingerich & Smith, 2006). However, the hypoconulid on m3 in CM 79210 appears to project farther distally than in other published specimens of *P. protinnominatus* and the large sample from Big Multi Quarry. CM 79210 shares with *P. protinnominatus* a shorter m4 talonid than trigonid and relatively weak hypoflexids, and we tentatively refer it to that species on the basis of these similarities. We acknowledge, however, that the Twelvemile Gulch marsupials may ultimately prove to represent two different taxa.

Cohort PLACENTALIA Owen, 1837
Order LIPOTYPHLA Haeckel, 1866
Suborder ERINACEOMORPHA Gregory, 1910
ADUNATOR Russell, 1964

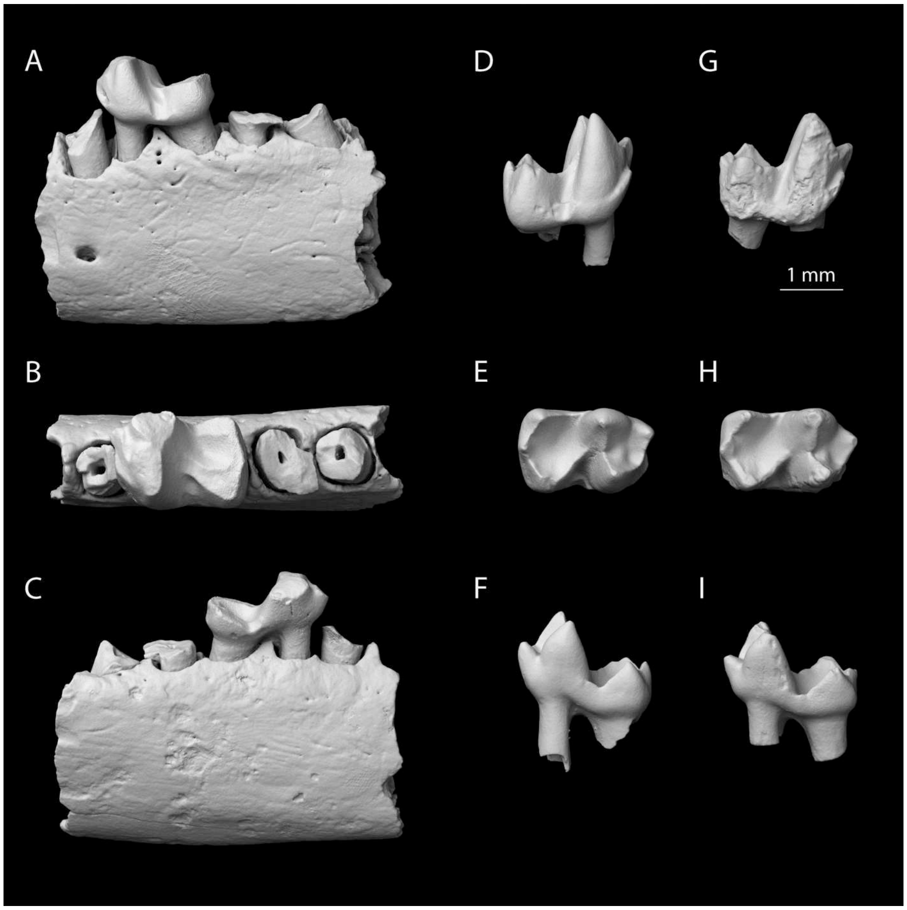

FIGURE 6. *Adunator* sp. from the Twelvemile Gulch local fauna. **A**–**C**, CM 79148, left dentary preserving m1 in **A**, buccal, **B**, occlusal, and **C**, lingual views. **D**–**F**, CM 79149, right m1 in **D**, buccal, **E**, occlusal, and **F**, lingual views. **G**–**I**, CM 79150, right m1 in **G**, buccal, **H**, occlusal, and **I**, lingual views.

ADUNATOR sp.

Fig. 6

Referred Specimens—CM 79148 (Fig. 6A–C), left dentary preserving m1; CM 79149, right m1 (Fig. 6D–F); CM 79150, right m1 (Fig. 6G–I).

Known Distribution—upper Paleocene (Tiffanian) of Wyoming, upper Paleocene of Europe.

Description—Two isolated lower molars and a dentary fragment from Twelvemile Gulch show affinities to members of the lipotyphlan suborder Erinaceomorpha. The lower molar crown preserved in CM 79148 can be readily identified as m1 based on the number and size of alveoli occurring posterior to it, which must have pertained to a double-rooted m2 and the partial alveolus for the mesial root of m3. CM 79148 (L, 1.82 mm; W, 1.28 mm), CM 79149 (L, 2.05 mm, W, 1.23 mm), and CM 79150 (L, 2.19 mm, W, 1.30 mm) are characterized by their relatively simple lower molar morphology with low, cuspidate paraconids and small, centrally placed hypoconulids. The entocristids of these specimens are strongly notched, resulting in talonids that are open lingually. The cristid obliqua is fairly tall, but it does not ascend the back of the postvallid as in many nyctitheriids. One specimen, CM 79150, preserves a small mesoconid on the cristid obliqua.

These specimens are larger than m1 in the holotype of *Mckennatherium ladae* from the Torrejonian of Montana and cf. *Mckennatherium* sp. from Big Multi Quarry (Krishtalka, 1976; Wilf et al., 1998), and they possess more cuspidate paraconids than either of those taxa. They are also larger than m1 in all species of *Adunator* aside from *A. amplus*, and they are likewise larger than m1 in both species of *Diacocherus* (*D. minutus* and *D. meizon*). Unlike the latter genus, they also possess more cuspidate paraconids that do not extend to the lingual margin of the tooth.

Comments—The potential synonymy of *Diacocherus* and *Mckennatherium* with *Adunator*, the latter of which has priority, is debated (Gingerich, 1983a; Krishtalka, 1976; Novacek et al., 1985; Secord, 2008). Unfortunately, our specimens do not preserve the most diagnostic characters that have been proposed to distinguish these genera. According to Gunnell et al. (2007), the m1 and m2 of *Adunator* are nearly equal in size, whereas *Diacocherus* possesses m2 equal to or larger than m1. Additionally, p4 of *Diacocherus* possesses a tall paraconid, whereas that of *Adunator* is lower than the metaconid (Gunnell et al., 2007). Secord (2008) suggested that *Mckennatherium* may be distinct from *Adunator* due to the smaller m2, lower p4 paraconid, and narrower p4 talonid, although other authors have opted to synonymize these genera (e.g., Gunnell et al., 2007; Novacek et al., 1985). Krishtalka (1976) differentiated *Adunator* and "*Diacodon*" *minutus* (*Diacocherus minutus*) from *Mckennatherium* on the basis of their more elongated m1–2 talonids, m2 larger than m1, and compressed m2 paraconid. He also noted that an anteroposterior expansion of the m2 metaconid seems to differentiate *Adunator* and *D. minutus* from *Mckennatherium*.

Regardless of issues of synonymy, we provisionally refer specimens from Twelvemile Gulch to *Adunator* sp. based on their cuspidate paraconids that terminate midway between the protoconid and metaconid—as opposed to those of *Diacocherus*, which terminate near the lingual margin of the tooth—and m1 with an expanded metaconid in lingual view. CM 79148 preserves part of the dentary, and based on alveolar dimensions its m2 was not significantly larger or smaller than m1. Gingerich (1983a) notes that Clarkforkian specimens referred by Rose (1981) to cf. "*Diacodon*" *minutus* are larger than late Tiffanian specimens assigned to *Diacocherus minutus* by Gingerich (1983a). Specimens assigned here to *Adunator* sp. are generally consistent in size with Clarkforkian specimens of cf. "*Diacodon*" *minutus* discussed by Rose (1981), which Gingerich (1983a) regards as likely representing a new species of *Diacocherus*. Whether Twelvemile Gulch specimens assigned here to *Adunator* sp. are conspecific with Rose's (1981) sample assigned to cf. "*Diacodon*" *minutus* requires more nearly complete specimens than are currently available.

Suborder SORICOMORPHA Gregory, 1910
Family NYCTITHERIIDAE Simpson, 1928
PLAGIOCTENODON Bown, 1979
PLAGIOCTENODON GOLIATH Jones and Beard, 2023
Fig. 7D–G

Referred Specimens—CM 79152, right dentary preserving p3–4; CM 79153, right maxilla preserving M2.

Known Distribution—upper Paleocene (Clarkforkian) of Wyoming.

Description—Available specimens include a dentary fragment with p3–4 (Fig. 7D–F) and a maxillary fragment preserving M2 and the base of the zygomatic arch (Fig. 7G). The p4 (L, 1.56 mm; W, 1.02 mm) in CM 79152 conforms with diagnostic characters of *Plagioctenodon* including: a paraconid that is high on the anterior face of the protoconid, somewhat shelf-like, and oriented anterolingually–posterolabially with accompanying anterolabial cingulid (see Bown, 1979). The specimen is somewhat abraded and several features of the talonid cannot be observed clearly; for instance, the hypoconulid is indistinct and the entoconid appears to be broken. Nonetheless, the talonid appears to have been well-developed with a distinct cristid obliqua, entocristid, and talonid basin. Unlike that of *Leptacodon*, p3 in CM 79152 (L, 0.93 mm; W, 0.52 mm) is notably shorter than p4 (Beard & Dawson, 2009), and based on anterior alveoli p2 also appears to have been larger than p3. Premolar dimensions suggest an animal that was larger than all other known species of *Plagioctenodon*, with the exception of Wasatchian *P. savagei*.

The M2 (CM 79153) displays a relatively generalized tribosphenic molar pattern common to Nyctitheriidae, including distinct conules and a small hypocone set on a posterolingual cingulum. This specimen possesses an extensive stylar shelf, with large parastylar and metastylar lobes. These lobes project slightly buccally, converging at a shallow, but distinct, ectoflexus. This tooth is recognized as M2 due to the relatively symmetrical buccal margin resulting from the anterobuccally projecting parastylar region (Manz & Bloch, 2015). The anterior margin of the zygomatic arch in CM 79153 originates buccal to the paracone of M2. This specimen is again larger than all other known species of *Plagioctenodon* (L, 1.64 mm; W, 2.21 mm), compared with means of 1.16, 1.72 in *P. dormaalensis*, 1.52, 2.14 in *P. rosei*, and 1.14, 1.56 in *P. thewisseni* (Manz & Bloch, 2015; Smith, 1996). Unfortunately, *P. savagei* is only known from its lower dentition, and the only published M2 from *P. krausae* is damaged. The length of the latter tooth, however, is listed as 1.95 mm (Bown & Schankler, 1982).

Comments—*Plagioctenodon goliath* is a large species of *Plagioctenodon* (mean p4 dimensions: L, 1.55 mm; W, 0.90 mm. M2 dimensions: L, 1.65 mm, W, 2.27 mm) that was recently described from the nearby early Clarkforkian locality of Big Multi Quarry (Jones & Beard, 2023). Both CM 79152 and CM 79153 share key features with *P. goliath*, including a p4 paraconid that is less procumbent than in other large species of *Plagioctenodon* and relatively small conules on M2. We therefore refer the large *Plagioctenodon* specimens from Twelvemile Gulch to *P. goliath* here.

PLAGIOCTENODON sp., cf. *P. DAWSONAE*
Fig. 7A–C

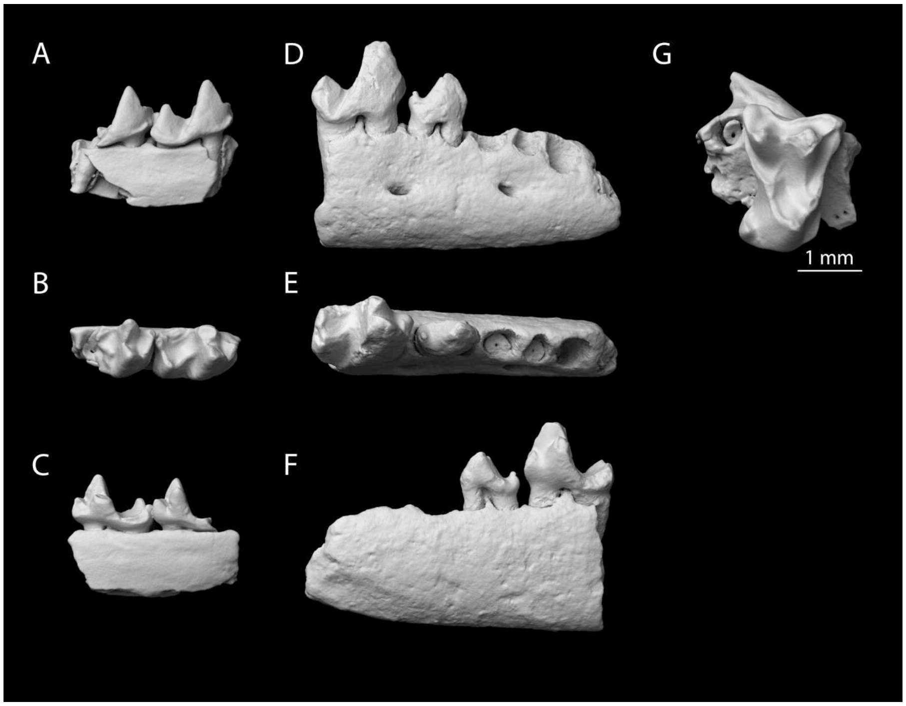

FIGURE 7. *Plagioctenodon* spp. from the Twelvemile Gulch local fauna. **A**–**C**, CM 79151, right dentary of *Plagioctenodon* sp., cf. *P. dawsonae* preserving m1 and fragmentary m2 in **A**, buccal, **B**, occlusal, and **C**, lingual views. **D**–**F**, CM 79152, right dentary of *Plagioctenodon goliath* preserving p3–4 in **D**, buccal, **E**, occlusal, and **F**, lingual views. **G**, CM 79153, right maxilla of *Plagioctenodon goliath* preserving M2 in occlusal view.

Referred Specimen—CM 79151, right dentary preserving m1–2.

Known Distribution—upper Paleocene (Clarkforkian) of Wyoming.

Description—A single dentary fragment preserving m1 and the trigonid of m2 represents a relatively unspecialized small nyctithere (Fig. 7A–C). This specimen is comparable in size to small species of *Plagioctenodon*, including *P. thewisseni* and *P. dawsonae*. The cristid obliqua on m1 is low and contacts the postvallid between the protoconid and metaconid. It does not ascend the postvallid as in *Wyonycteris* and *Limaconyssus* (Gingerich, 1987). The m1 hypoconulid is positioned somewhat lingually on the postcristid, in contrast to the more central location of the hypoconulid in *Leptacodon donkroni* (Rose et al., 2012). The entoconid is broken on m1, eliminating a key character used to distinguish the genera *Plagioctenodon* and *Leptacodon*. In *Leptacodon* lower molar entoconids are subequal in height to the hypoconids, whereas in most *Plagioctenodon* the entoconid is significantly taller than the hypoconid (Manz & Bloch, 2015). Debate exists as to whether *Plagioctenodon* represents a valid genus or should be synonymized with *Leptacodon* (e.g., Beard & Dawson, 2009; Manz & Bloch, 2015; Rose et al., 2012; Smith, 1996). Nonetheless, the lingually positioned hypoconulid and relatively tall paraconids of CM 79151 more closely approximate species that are currently considered to be *Plagioctenodon* than those aligned with *Leptacodon*.

Comments—Most characters differentiating *P. thewisseni* and *P. dawsonae* are found on the premolars, and the absence of preserved premolars in CM 79151 makes a species-level assignment challenging. Unlike the condition in *P. thewisseni,* CM 79151 appears to possess more cuspidate paraconids on m1–2 and less acutely angled trigonids and talonids at their buccal margins. The somewhat less acute molar trigonid and talonid and slightly more lingually positioned hypoconulid suggest closer affinities with *P. dawsonae*, previously described from Big Multi Quarry (Jones & Beard, 2023), although the damage to the entoconid on m1 makes the true position of the hypoconulid difficult to delineate. The metaconid of m2 in CM 79151 is nearly equally as tall and massive as the protoconid, whereas in *P. dawsonae* the metaconid of m2 is more massive than the protoconid. Until additional material from Twelvemile Gulch is available, we conservatively assign this specimen to *Plagioctenodon* sp., cf. *P. dawsonae.*

Order CIMOLESTA McKenna, 1975
Suborder PANTOLESTA McKenna, 1975
Family PANTOLESTIDAE Cope, 1884
PALAEOSINOPA Matthew, 1901
PALAEOSINOPA sp.
Fig. 8C–E

Referred Specimen—CM 79102, left M3.

Known Distribution—upper Paleocene (Tiffanian) to middle Eocene (Bridgerian) of North America, lower Eocene (Ypresian) of Europe.

Description—A single upper molar from Twelvemile Gulch represents a large species of the pantolestid *Palaeosinopa* (Fig. 8C–E). CM 79102 is recognized as an M3 due to its asymmetrical stylar shelf, which is broad in the parastylar region and tapers in the direction of the metacone. The tooth is nearly twice as wide as it is long (L, 3.57 mm; W, 6.20 mm), with the rounded parastylar region projecting much farther buccally and slightly more mesially than the rest of the tooth. The paraconule is slightly larger than the metaconule, and both are present as swellings on the pre- and postprotocrista, respectively. A mesial cingulum is present from roughly the level of the paraconule to the level of the protocone. The enamel in the region of the postcingulum is missing, so the presence or absence of this feature cannot be confirmed. However, there is no cingulum at the lingual base of the protocone.

Comments—CM 79102 displays characters that clearly align it with *Palaeosinopa*, including its markedly transverse dimensions and having an extension of the parastylar region to form a distinct "hook" (Dorr, 1977). Measurements of CM 79102 fall close to published measurements of Clarkforkian *Palaeosinopa* sp. and such large Wasatchian species as *P. didelphoides* and *P. veterrima* (Dunn & Rose, 2015; Rose, 1981). CM 79102 is very similar in buccolingual breadth to earlier Clarkforkian *Palaeosinopa* sp. from Big Multi Quarry (e.g., CM 71725, CM 71913), but is mesiodistally shorter. It also possesses a more distinct parastyle and a more buccally convex, "hook shaped" parastylar region than the Big Multi Quarry taxon. CM 79102 lacks a lingual cingulum, unlike the similarly sized *P. dorri* from the Tiffanian (Dorr, 1977; Gingerich, 1980). Upper molars attributed to *Palaeosinopa* sp. from the lower Eocene of Bitter Creek (Gazin, 1962) are described as being narrower than those of *P. veterrima* with weaker cingula, much as in the M3 from Twelvemile Gulch. Establishing the species-level affinities of the taxon represented by CM 79102 requires more nearly complete material.

Order APATOTHERIA Scott and Jepsen, 1936
Family APATEMYIDAE Matthew, 1909
Genus *LABIDOLEMUR* Matthew and Granger, 1921
LABIDOLEMUR KAYI Simpson, 1929
Fig. 8A, B

Referred Specimen—CM 79101, left edentulous dentary fragment.

Known Distribution—upper Paleocene (Clarkforkian) of Montana and Wyoming and lower Eocene (lower Wasatchian) of Wyoming.

Description—Although it is edentulous, CM 79101 preserves the root of a large, procumbent central incisor mesially and multiple closely spaced alveoli thereafter with no intervening diastemata, leaving no doubt that it represents an apatemyid (Fig. 8A, B). Dorsolateral to the i1 root is a much smaller mesially canted alveolus, interpreted here as pertaining to p2 by analogy with more nearly complete specimens of *L. kayi* described by Gingerich and Rose (1982). The p2 alveolus is displaced laterally with respect to the mesiodistal axis of the remaining alveoli, as is the case for *L. kayi* from Holly's Microsite in the Clarks Fork Basin (Gingerich & Rose, 1982:fig. 2). Distal to the p2 alveolus is a small, somewhat mesially canted alveolus for p3. The p4 was apparently double-rooted in CM 79101, because two relatively circular alveoli occur behind the tiny alveolus for p3, both of which are situated above a shallow fossa on the dorsolateral side of the dentary that may have marked the location of a gland of unknown function (Gingerich & Rose, 1982; West, 1973). The holotype of *L. kayi* apparently bears a single-rooted p4, but other specimens are known to have retained a double-rooted p4 (Silcox et al., 2010:fig. 2A). Distal to the alveoli for p4 is a buccolingually broader alveolus that is interpreted as pertaining to the mesial root of m1. A large mental foramen occurs midway between the alveolar margin and the ventral side of the dentary, below what is interpreted as a partial alveolus for the distal root of m1. The number and location of mental foramina is apparently somewhat variable in *L. kayi* (Silcox et al., 2010).

Comments—In terms of their relative size and angulation, premolar alveoli preserved in CM 79101 generally resemble those in the holotype (AMNH FM 88343) of the much larger and earlier species *Labidolemur major*, known from the lower Tiffanian saddle locality in the Bison Basin of central Wyoming (West,

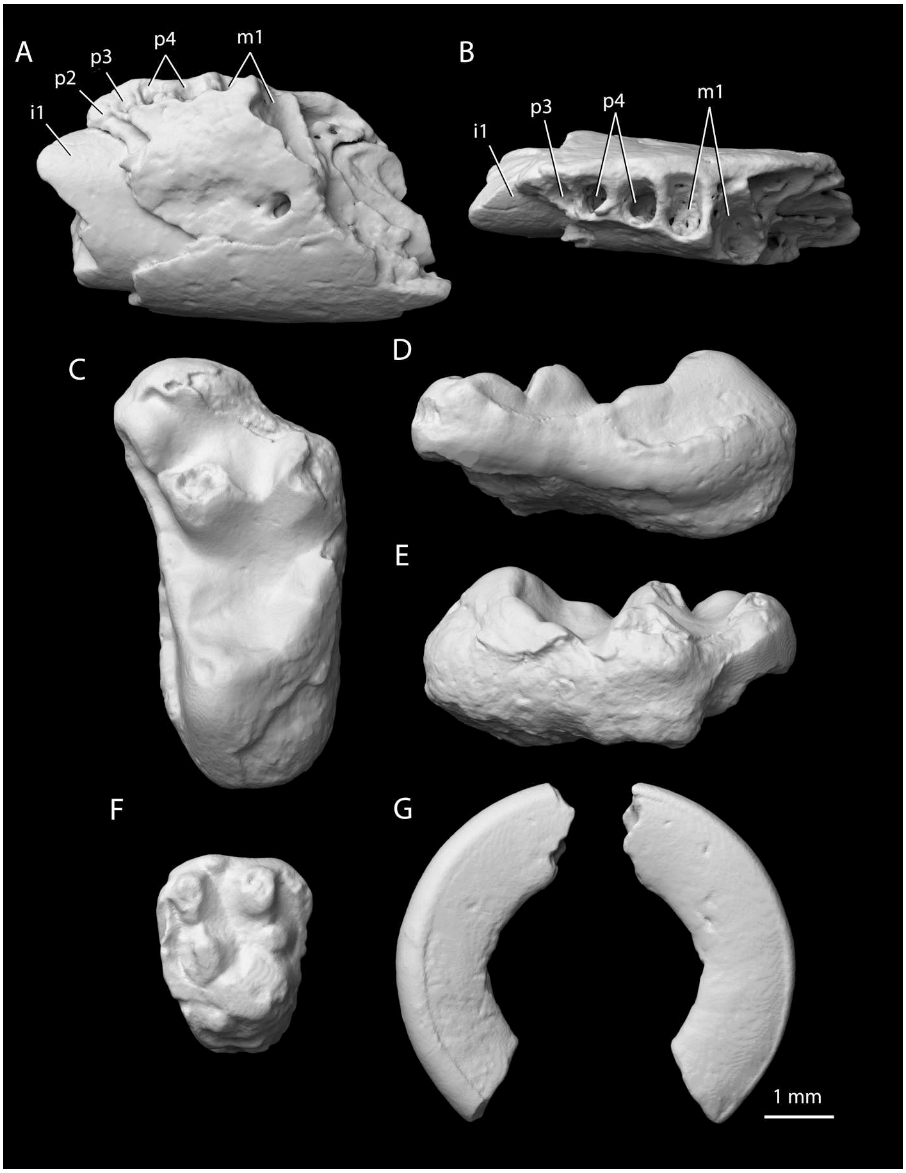

FIGURE 8. Cimolesta, Apatotheria, and Rodentia from the Twelvemile Gulch local fauna. **A**, **B**, CM 79101, left edentulous dentary fragment of *Labidolemur kayi* in **A**, buccal and **B**, occlusal views. **C**–**E**, CM 79102, left M3 of *Palaeosinopa* sp. in **C**, occlusal, **D**, mesial, and **E**, distal views. **F**, CM 79265, right upper molar (probably M1) of *Acritoparamys atwateri* in occlusal view. **G**, CM 79266, upper incisor of *Acritoparamys atwateri* in mesial and distal views.

1972). *L. major* differs from *L. kayi* in having less compaction of the dentary between i1 and p4 caused in part by a short diastema between p3 and p4, retaining relatively larger alveoli for p2 and p3, and lacking the shallow fossa on the lateral side of the dentary beneath p4 that was noted earlier in *L. kayi*. *L. kayi* is the only apatemyid reported so far from the Clarkforkian of North America. Although the fragmentary nature of CM 79101 leaves open the possibility that it may represent some other apatemyid taxon, it is appropriate in size to pertain to *L. kayi*, and we assign it to this species here.

Order RODENTIA Bowdich, 1821
Family PARAMYIDAE Miller and Gidley, 1918
Subfamily REITHROPARAMYINAE Wood, 1962
ACRITOPARAMYS Korth, 1984
ACRITOPARAMYS ATWATERI (Loomis, 1907)
Fig. 8F, G

Referred Specimens—CM 79265, right upper molar (probably M1); CM 79266, two upper incisors.

Known Distribution—upper Paleocene (Clarkforkian) through lower Eocene (Wasatchian) of Wyoming.

Description—CM 79265 (L, 2.34 mm; W, 2.92 mm) is interpreted as a right upper molar (probably M1) rather than P4 on the basis of its inflated protoconule and the broad separation of its paracone and metacone (Fig. 8F). The tooth is notable primarily for the inflated character of its major cusps and conules and the absence of protoloph and metaloph. The protocone, which is situated mesial to the midline of the crown, is the largest and most inflated cusp. From its buccal margin, a linear crease runs distobuccally, separating the paracone and protoconule from the metacone and metaconule. Near the buccal margin of the crease, a weak mesostyle is present. The metaconule is remarkably inflated, such that its volume exceeds that of the metacone. A hypocone is present, but it is much smaller than the protocone and closely appressed to the base of the latter cusp. Anterior and posterior cingula are present, but their lingual extent is unclear because of minor damage to the crown.

Comments—CM 79265 is much larger than upper cheek teeth of *Paramys adamus* from Big Multi Quarry (Dawson & Beard, 1996), and it further differs from the latter taxon in having much more inflated conules and lacking development of protoloph and metaloph. It closely approximates M1 in AMNH FM 15710 in terms of size and morphology (see Korth, 1984:fig. 14A), and it is referred to *A. atwateri* on this basis. Ivy (1990) records *A. atwateri* as ranging from the Clarkforkian into the middle Wasatchian in the Bighorn Basin.

Mirorder CARNIVORAMORPHA Wyss and Flynn, 1993

Family MIACIDAE Cope, 1880

UINTACYON Leidy, 1872

UINTACYON RUDIS Matthew, 1915a

Fig. 9D–F

Referred Specimen—CM 79169, left p4.

Known Distribution—upper Paleocene (Clarkforkian) to lower Eocene (Wasatchian) of Wyoming, lower Eocene (Ypresian) of the U.K.

Description—CM 79169 (L, 5.15 mm; W, 2.51 mm) is the only specimen from Twelvemile Gulch currently assigned to *Uintacyon rudis* (Fig. 9D–F). The crown is simple, being dominated by the large, somewhat distally canted protoconid. A small paraconid and a larger hypoconid are present. The mesial trigonid crest or paracristid is evident but not particularly trenchant. A distal trigonid crest was probably also present, but this part of the p4 crown is obscured by damage in CM 79169. The trigonid as a whole is relatively inflated, and its cingulids are weakly developed if present at all.

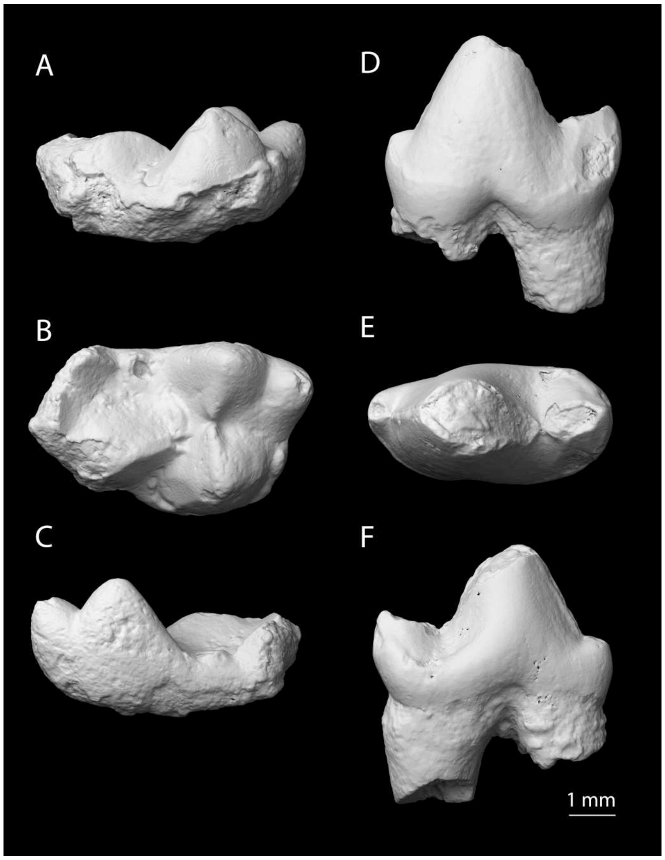

FIGURE 9. Carnivoramorpha from the Twelvemile Gulch local fauna. **A**–**C**, CM 79100, right m2 of *Didymictis proteus* in **A**, buccal, **B**, occlusal, and **C**, lingual views. **D**–**F**, CM 79169, left p4 of *Uintacyon rudis* in **D**, buccal, **E**, occlusal, and **F**, lingual views.

Comments—*Uintacyon rudis* is the only miacid currently documented from the Clarkforkian, and CM 79169 is appropriate in terms of both size and morphology to be referred to this species. The European latest Paleocene miacid *Vassacyon prieuri* has recently been described from the Petit Pâtis fauna in the Paris Basin, which is considered to be closely correlative with the North American Clarkforkian (Smith et al., 2014; Solé et al., 2016). CM 79169 is larger than p4 in *Vassacyon prieuri* and further differs in having a more inflated trigonid and weaker cingulids.

According to Rose (1981) and Gingerich (1983b), *Uintacyon rudis* first appears in middle Clarkforkian (Cf-2) faunas in the Clarks Fork Basin of northwestern Wyoming. Notably, *Uintacyon rudis* has never been documented at Big Multi Quarry, although both larger and smaller viverravid carnivoramorphans are reasonably abundant there (Wilf et al., 1998). This suggests that the first appearance of Miacidae in North America postdates the early Clarkforkian, further supporting the interpretation of Big Multi Quarry as an early Clarkforkian site (Chester & Beard, 2012; Dawson & Beard, 1996; Jones & Beard, 2023; Wilf et al., 1998). Coryphodontid pantodonts show a similar pattern of occurrence, indicating that an important episode of faunal turnover, possibly linked to intercontinental dispersal, occurred within the Clarkforkian, near what has been conventionally regarded as the early–middle Clarkforkian (i.e., Cf-1–Cf-2) boundary.

Family VIVERRAVIDAE Wortman and Matthew, 1899

Subfamily DIDYMICTINAE Flynn and Galiano, 1982

DIDYMICTIS Cope, 1875

DIDYMICTIS PROTEUS Simpson, 1937

Fig. 9A–C

Referred Specimen—CM 79100, right m2.

Known Distribution—upper Paleocene (Tiffanian) through lower Eocene (Wasatchian) of North America.

Description—CM 79100 (W, 4.03 mm) is a fragmentary right m2 that is missing much of the buccal margin of the crown and the distal part of the talonid including most of the hypoconulid (Fig. 9A–C). Crown length therefore cannot be measured. The trigonid is low-crowned, and all three trigonid cusps (especially the protoconid) are basally inflated rather than sectorial. The paraconid and metaconid are in close apposition, in contrast to the condition found in Tiffanian species of *Protictis*, in which these cusps are more widely separated (Gingerich & Winkler, 1985). Remnants of the mesiobuccal and buccal cingulid are present, but minor damage to the mesiobuccal margin of the crown makes it impossible to ascertain whether these structures were once continuous. A tiny cuspule lies near the junction of the cristid obliqua and the postvallid, possibly representing a small mesoconid. A second small, apparently neomorphic, cuspule lies near the lingual base of the postvallid. The hypoconid is taller than the entoconid, and it occurs farther mesially than the latter structure.

Comments—CM 79100 can be assigned to *Didymictis* rather than *Protictis* on the basis of its trigonid morphology. It closely resembles m2 in CM 70099, a more nearly complete dentary of *Didymictis* from Big Multi Quarry near Bitter Creek. Polly (1997) argues that a single species of *Didymictis* occurs in the Clarkforkian of the Bighorn Basin. CM 79100 falls within the range of metric variation for *D. proteus* documented from Cf-2 and Cf-3 levels in the Bighorn Basin (Polly, 1997).

Order MESONYCHIA Van Valen, 1969

Family MESONYCHIDAE Cope, 1875

DISSACUS Cope, 1881

DISSACUS sp.

Fig. 10

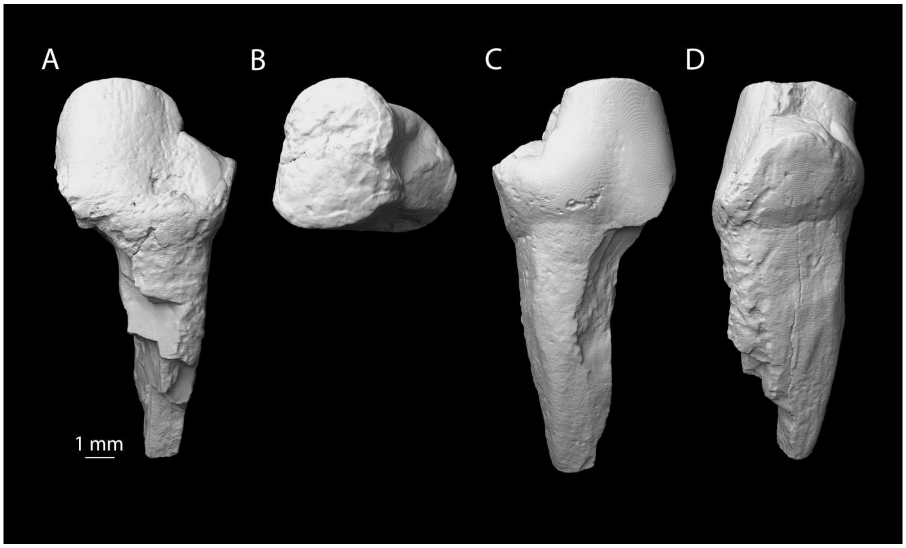

FIGURE 10. Mesonychia from the Twelvemile Gulch local fauna. **A**–**D**, CM 79158, right lower molar trigonid of *Dissacus* sp. in **A**, buccal, **B**, occlusal, **C**, lingual, and **D**, mesial views.

Referred Specimen—CM 79158, right lower molar trigonid.

Known Distribution—upper Paleocene through lower Eocene of Asia (China and Mongolia), North America (Canada, U.S.A., and Mexico) and western Europe (France and Spain).

Description—CM 79158 is a fragment of the trigonid of a right m1 or m2 (Fig. 10). Trigonid width, the only metric that can be assessed in this specimen, is 6.24 mm. Paraconid, protoconid and metaconid all show relatively heavy apical wear, indicating that this individual was fully adult. There is a small interstitial wear facet on the mesial side of the tooth, slightly buccal to its midline (Fig. 10D). The paraconid shows a moderate degree of basal inflation, and it deviates slightly lingually with respect to the protoconid as a result (Fig. 10B). A mesiobuccal cingulid lines the external surface of the paraconid, on which a small neomorphic cuspule occurs (Fig. 10A). The mesial crest from the protoconid is visible near its juncture with the paraconid. A shallow, vertically oriented crease appears to separate this crest from the base of the metaconid, which is fully connate with the protoconid (Fig. 10B). Enamel is slightly wrinkled rather than smooth, which is especially apparent on the buccal side of the trigonid.

Comments—Based on size, this tooth fragment is more compatible with *D. argenteus* than *D. praenuntius*, both of which have been reported from the Clarkforkian of the northern Bighorn Basin (Secord, 2008). *D. willwoodensis* is a third species, roughly equivalent in size to *D. argenteus*, from the lower Wasatchian of the Bighorn Basin. As noted by O'Leary and Rose (1995), individual specimens of *Dissacus* are not always readily diagnostic at the species level because of small sample sizes, the simplified nature of their lower cheek teeth, the possibility of significant sexual dimorphism, and other factors. The fragmentary condition of CM 79158 precludes assigning it to any previously described species of *Dissacus.*

Mirorder PRIMATOMORPHA Beard, 1991
Superfamily PLESIADAPOIDEA Trouessart, 1897
Family CARPOLESTIDAE Simpson, 1935
CARPOLESTES Simpson, 1928
CARPOLESTES NIGRIDENS Simpson, 1928
Fig. 11

Referred Specimens—CM 79215, right maxilla preserving P3–4; CM 79216, right maxilla preserving P3; CM 79217, right p4; CM 79218, left dentary preserving p4–m1; CM 79219, basal fragment of right I1; CM 79220, left p4; CM 79221, right m3.

Known Distribution—upper Paleocene (uppermost Tiffanian and lower Clarkforkian) of Montana and Wyoming.

Description—The third upper premolar is represented by two specimens from Twelvemile Gulch. CM 79215 is a right maxillary fragment preserving P3–4 (Fig. 11A, B), and CM 79216 is a right maxillary fragment preserving right P3 (Fig. 11C, D). P3 in both specimens bears three parallel rows of cusps running mesiodistally, with five (CM 79215) or six (CM 79216) prominent cusps in the buccal row, the two most anterior of which are slightly separated from the posterior three or four, much as described by Rose (1975) in his emended diagnosis of *Carpolestes nigridens.* The occlusal outline of P3 is highly asymmetrical as a result of its elongated anteroexternal spur, which bears the additional (neomorphic) cusps comprising the buccal row. A narrow and shallow trough runs along the lingual side of the buccal row of cusps, separating it from structures occupying the central part of the crown. Included in the latter are a central cuspule, located lingual to the gap between the anterior and posterior cusps comprising the buccal row, and an intermediate ridge or crest that bears one or more variably developed cuspules. A deeper and broader trough separates the central cuspule and intermediate ridge from a lingual row of cusps. The lingual row of cusps includes a prominent anterior cusp that is often described as a protocone, which is connected by a mesiodistally oriented crest to a distolingual cuspule that is often described as a hypocone. Note that Beard et al. (2016) argue that both of these lingual cusps are neomorphic structures that are not strictly homologous with the protocone and hypocone of more basally branching plesiadapoid taxa.

The P4 in CM 79215 also has three parallel rows of cusps, with five prominent cusps along its buccal side occurring in direct continuity with the buccal row of cusps on P3 (Fig. 11A, B). While its length is somewhat greater buccally than lingually, P4 lacks the anteroexternal spur that characterizes P3, and is more nearly symmetrical in occlusal outline as a result. As in P3, a narrow trough separates the buccal row of cusps from an intermediate ridge or crest that bears multiple small cuspules. The intermediate ridge runs mesiodistally along the entire length of the crown, being confluent mesially with the intermediate ridge or crest of P3. The lingual row consists of three distinct cusps, including a relatively large and centrally located protocone that is flanked mesially and distally by a smaller pericone and hypocone,

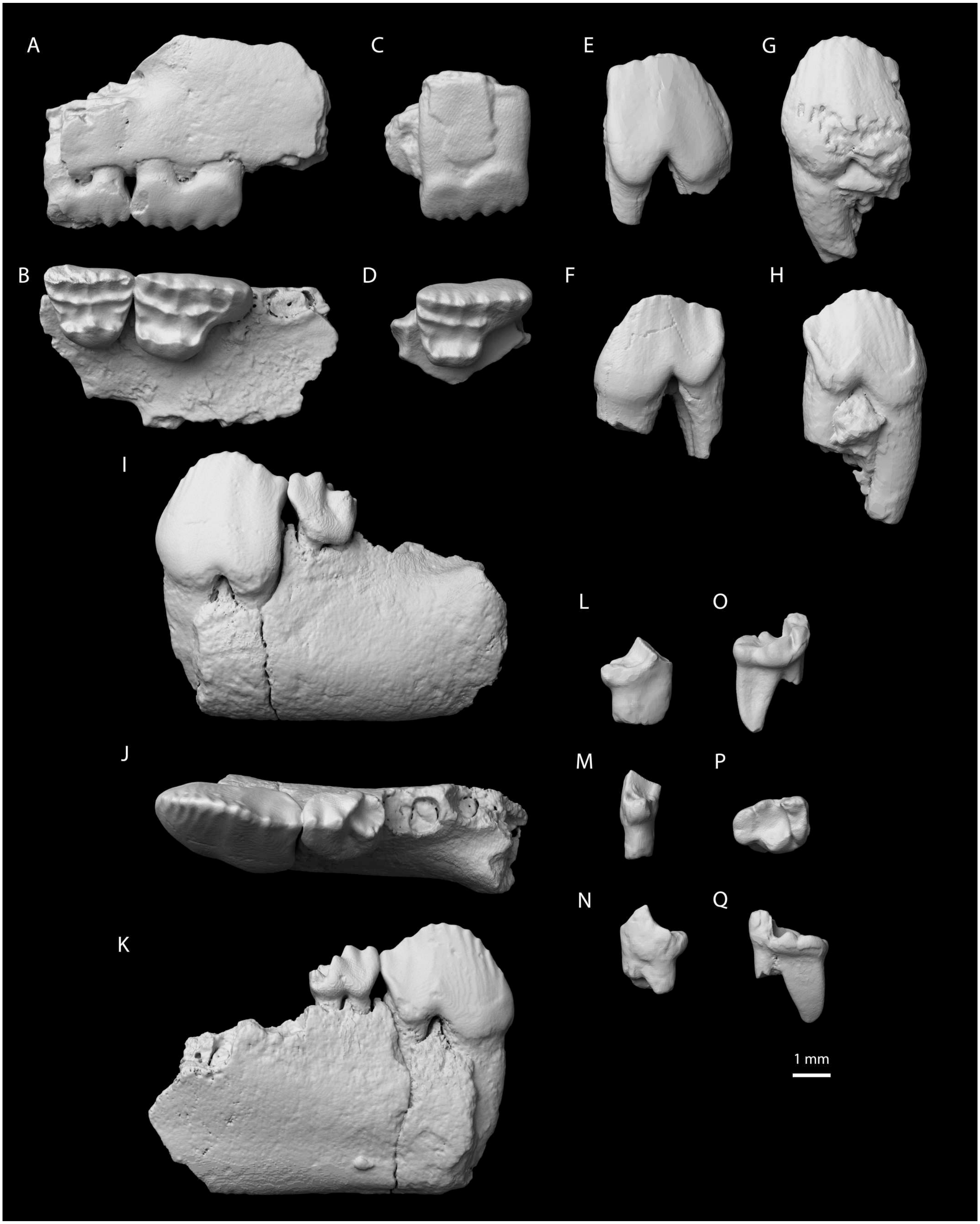

FIGURE 11. *Carpolestes nigridens* from the Twelvemile Gulch local fauna. **A**, **B**, CM 79215, right maxilla preserving P3–4 in **A**, buccal, and **B**, occlusal views. **C**, **D**, CM 79216, right maxilla preserving P3 in **C**, buccal, and **D**, occlusal views. **E**, **F**, CM 79217, right p4 in **E**, buccal, and **F**, lingual views. **G**, **H**, CM 79220, left p4 in **G**, buccal, and **H**, lingual views. **I**–**K**, CM 79218, left dentary preserving p4–m1 in **I**, buccal, **J**, occlusal, and **K**, lingual views. **L**–**N**, CM 79219, basal fragment of right I1 in **L**, mesial, **M**, lingual, and **N**, distal views. **O**–**Q**, CM 79221, right m3 in **O**, buccal, **P**, occlusal, and **Q**, lingual views.

respectively. The latter cusps are linked with the protocone by variably developed crests.

CM 79218 is a left dentary fragment with p4-m1 (Fig. 11I–K). As is typical for *Carpolestes*, p4 forms a large, plagiaulacoid blade with nine apical cusps that are mesiodistally aligned with the paraconid and protoconid of m1. The dentary is broken posterior to p4 and repaired, so that the positions of p4 and m1 are not aligned as precisely as they would be if the dentary were intact, although their current positions appear to closely approximate their natural condition. The paraconid of m1 is directly mesial to the protoconid, and these two cusps essentially merge with the apical cusps of p4 to form a continuous cutting blade. A distinct metaconid is positioned distolingually with respect to the protoconid, resulting in a trigonid that is widely open lingually. The cristid obliqua runs mesiolingually from the hypoconid to the postvallid. The entoconid occurs directly distal to the metaconid, from which it is separated by a deep notch. Another deep notch separates the hypoconid from the entoconid, and there is no hypoconulid. Two isolated p4 specimens, CM 79217 (Fig. 11E, F) and CM 79220 (Fig. 11J, K), have been collected, both of which have nine apical cusps and closely resemble the morphology described for CM 79218.

CM 79221 is an isolated right m3 (Fig. 11O–Q). The trigonid bears three cusps, although the paraconid and metaconid are very closely appressed and barely distinguishable. The metaconid is the most prominent cusp, forming the bulk of the lingual side of the trigonid, and the protoconid is worn. The cristid obliqua runs mesiolingually from the prominent hypoconid to the postvallid directly below the protoconid. A deep notch separates the metaconid from the entoconid, and the hypoconulid lobe is pronounced with a twinned hypoconulid. CM 79219 is a fragmentary right I1 that preserves part of the root and crown, although its apex including the anterocone and laterocone is broken away (Fig. 11L–N).

Comments—The plagiaulacoid p4 and the P3–4 with which it occludes are the most specialized teeth in carpolestids, and these tooth loci have traditionally provided reliable data for assessing systematic and phylogenetic relationships within this clade (Beard, 2000; Beard et al., 2016; Beard & Wang, 1995; Bloch & Gingerich, 1998; Bloch et al., 2001; Mattingly et al., 2018; Rose, 1975; Silcox et al., 2001). In Clarkforkian species of *Carpolestes*, these teeth are highly autapomorphic (Bloch & Gingerich, 1998). Specifically, P3 in both *Carpolestes nigridens* and *Carpolestes simpsoni* bears five or six buccal cusps and an elongated anteroexternal spur that projects significantly farther mesially than the remainder of the crown. P3 in older and more primitive species of *Carpolestes*, including *Carpolestes dubius* from the late Tiffanian Princeton Quarry in the Bighorn Basin and *Carpolestes twelvemilensis* from the upper Tiffanian Twelvemile Bonanza locality ~8 km south of the Twelvemile Gulch sites being discussed here, has only four buccal cusps and lacks an exaggerated anteroexternal spur, rendering the entire crown more nearly symmetrical in occlusal outline (Mattingly et al., 2018; Rose, 1975). Later Clarkforkian *C. simpsoni* differs from earlier Clarkforkian *C. nigridens* chiefly in being smaller and having lost the vestigial p3 (Bloch & Gingerich, 1998). Dental measurements (Table 2) for the Twelvemile Gulch sample of *Carpolestes* suggest that they can be referred to the larger species, *C. nigridens*. For example, metric data for CM 79218 (Fig. 11I–K) are consistent with *C. nigridens*, with both p4 and m1 being longer and wider than the range reported by Bloch and Gingerich (1998) for *C. simpsoni*. Both CM 79220 (left p4) and CM 79217 (right p4) are also longer and wider than p4 of *C. simpsoni*. Essentially the same situation exists with respect to lengths and widths of the upper premolars and the m3 (Table 2).

Bloch and Gingerich (1998) reported the stratigraphic range of *C. simpsoni* in the Clarks Fork Basin as being middle and late Clarkforkian (Cf-2 and Cf-3), whereas *C. nigridens* was thought to be restricted to the early Clarkforkian (Cf-1). Subsequently, Secord (2008) interpreted a sample of *Carpolestes* from the Paint Creek locality in the Clarks Fork Basin (lower part of Cf-2) as pertaining to *C. nigridens*, while noting that the earliest occurrence of *C. nigridens* antedates the local first appearance of Rodentia, thereby extending the range of *C. nigridens* into the latest Tiffanian. There appears to be a significant gap in the record of *Carpolestes* during the early part of Cf-2 in the Clarks Fork Basin (see Bloch & Gingerich, 1998), making it unclear precisely when earlier Clarkforkian *C. nigridens* was replaced by younger *C. simpsoni*.

Family PLESIADAPIDAE Trouessart, 1897
PLESIADAPIS Gervais, 1877
PLESIADAPIS DUBIUS Matthew, 1915b
Fig. 12

Referred Specimens—CM 79247, right M3; CM 79248, right dentary preserving m1–2; CM 79249, right dentary preserving m2–3; CM 79250, left m3; CM 79251, left m2; CM 79252, left maxilla preserving M2; CM 79253, left m1; CM 79254, right

TABLE 2. Dental measurements (mm) of Twelvemile Gulch *Carpolestes nigridens* compared to *C. nigridens* (Bloch, pers. comm.) and *C. simpsoni* (Table 1, Bloch & Gingerich, 1998), both from the Bighorn Basin. **Abbreviations**: **mm**, millimeters; **n**, sample size; **sd**, standard deviation.

	C. nidridens Twelvemile Gulch			*C. nigridens* Bighorn Basin			*C. simpsoni* Bighorn Basin		
	mean	sd	n	mean	sd	n	mean	sd	n
P3 length	3.09	0.12	2	3.18	0.16	7	2.63	0.15	13
P3 width	2.32	0.18	2	2.44	0.09	7	2.05	0.15	13
P4 length	2.26		1	2.29		1	2.02	0.08	8
P4 width	2.07		1	2.11		1	1.78	0.12	8
p4 length	3.31	0.10	3	3.21	0.16	19	2.96	0.15	27
p4 width	1.88	0.11	3	1.99	0.18	19	1.60	0.12	26
m1 length	1.95		1	1.77	0.28	14	1.32	0.08	17
m1 width	1.62		1	1.53	0.10	14	1.32	0.08	17
m3 length	2.26		1	2.30		1	2.12	0.09	10
m3 width	1.49		1	1.40		1	1.30	0.05	9

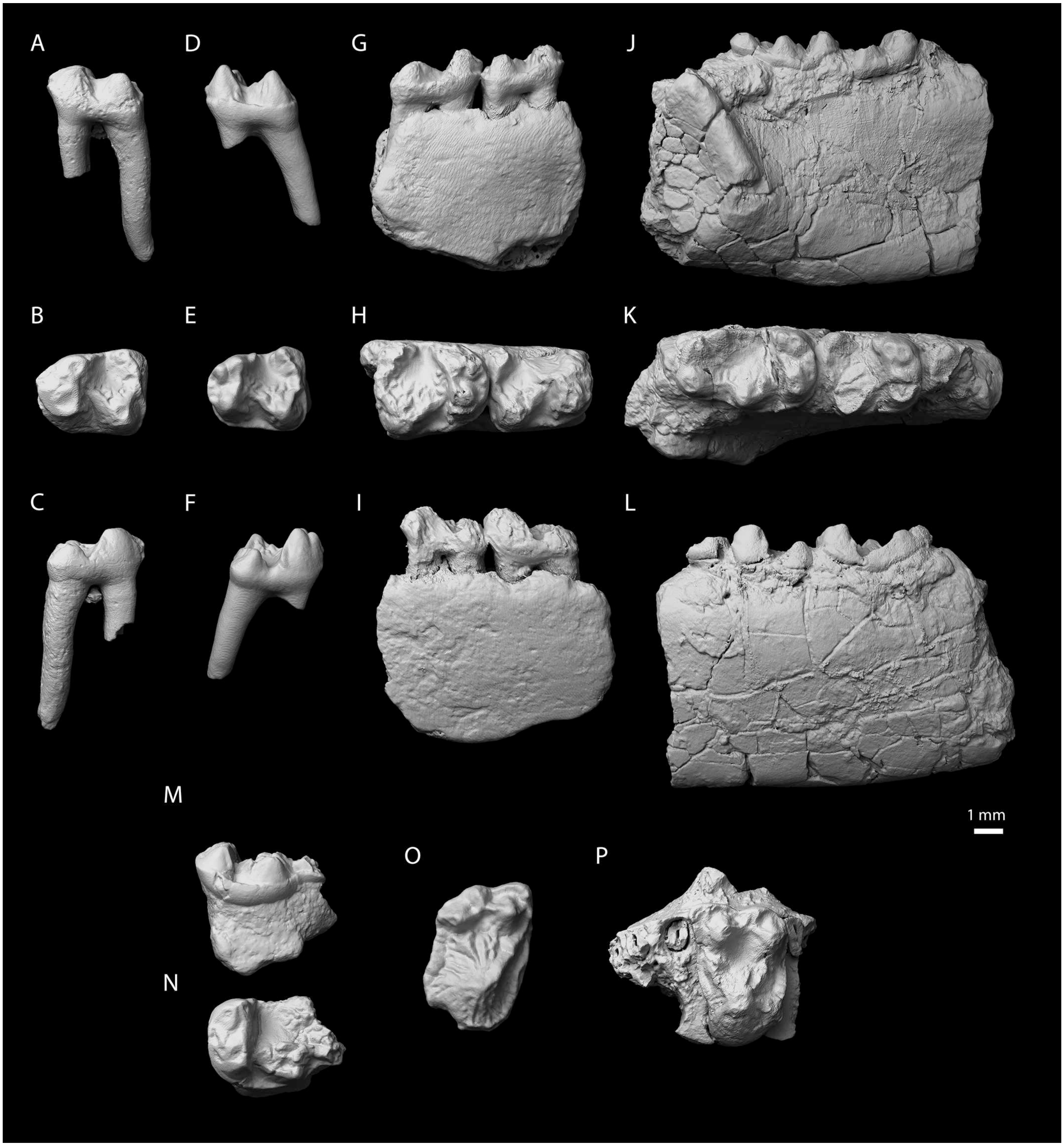

FIGURE 12. *Plesiadapis dubius* from the Twelvemile Gulch local fauna. **A**–**C**, CM 79258, left m1 in **A**, buccal, **B**, occlusal, and **C**, lingual views. **D**–**F**, CM 79251, left m2 in **D**, buccal, **E**, occlusal, and **F**, lingual views. **G**–**I**, CM 79248, right dentary preserving m1–2 in **G**, buccal, **H**, occlusal, and **I**, lingual views. **J**–**L**, CM 79249, right dentary preserving m2–3 in **J**, buccal, **K**, occlusal, and **L**, lingual views. **M**, **N**, CM 79250, left m3 in **M**, buccal, and **N**, occlusal views. **O**, CM 79247, right M3 in occlusal view. **P**, CM 79252, left maxilla preserving M2 in occlusal view.

m3; CM 79255, left M1; 79256, left m3; CM 79257, right m3; CM 79258, left m1; CM 79259, right partial M3; CM 79260, left M1; CM 79261, partial right lower molar; CM 79262, right M3; CM 79263, right m1; CM 79264, left m2; CM 95829, right m2; CM 95832, left M2; CM 95833, right M2.

Distribution—upper Paleocene (upper Tiffanian Ti-5b) to lower Eocene (lower Wasatchian) of Wyoming, upper Paleocene (Clarkforkian) of Colorado.

Description—The Twelvemile Gulch sample of *P. dubius* is morphologically consistent with the holotype dentary of

P. dubius (AMNH FM 16073) and referred specimens from the Paint Creek locality in the Bighorn Basin, Buckman Hollow in the Green River Basin, and the upper part of the Fort Union Formation in the Piceance Creek Basin (Burger & Honey, 2008; Gingerich, 1976; Holroyd & Rankin, 2014; Rose, 1981). Upper molars from Twelvemile Gulch are characterized by tall, weakly inflated paracone, metacone, and protocone; strong pre- and postprotocristae; a tendency toward dilambdodonty with well-developed parastyle and mesostyle; a small pseudohypocone; and crenulated enamel. Lower molars bear relatively acute cusps and angular crests. Variably developed neomorphic crests run inferiorly down either side of the lower molar postvallids, including a stronger lingual crest originating at the apex of the metaconid that can include a weak metastylid and a weaker buccal crest originating near the apex of the protoconid. The cristid obliqua of m1 runs toward (or merges with) the metaconid, while this structure on m2–3 typically joins the postvallid farther buccally. A strong lingual notch separates the lower molar entoconid from the postvallid. A short distobuccal cingulid typically occurs behind the hypoconid on lower molars, but this structure is not always continuous with a buccal crest from the entoconid, as is the case in the holotype of *P. dubius*. The m3 talonid bears a prominent, squared, and crenulated third lobe bearing a twinned hypoconulid that is separated from the hypoconid by a wide valley and from the entoconid by a narrow groove. Linear measurements indicate that the Twelvemile Gulch sample is consistent with the metric range of variation of *P. dubius* from the Bighorn Basin (Table 3).

Comments—*P. dubius* differs only subtly from the earlier and closely related *P. fodinatus*, primarily in being slightly smaller, having relatively narrower lower molars, and consistently lacking p2 (Gingerich, 1976; Rose, 1981; Secord, 2008). Upper and lower incisors of *P. dubius* are also said to differ from their counterparts in *P. fodinatus* in having smaller margoconids on i1 and reduced mediocone and lack of centroconule on I1 (Secord, 2008). Unfortunately, only upper and lower molars of *P. dubius* are currently recognized from Twelvemile Gulch. The sample of *P. dubius* from Twelvemile Gulch conforms with Clarkforkian samples of this species known from the Clarks Fork Basin, Big Multi Quarry, and related sites in the vicinity of Bitter Creek, the Buckman Hollow local fauna from the Green River Basin, and sites in the Piceance Creek Basin of northwestern Colorado (Burger & Honey, 2008; Gingerich, 1976; Holroyd & Rankin, 2014; Rose, 1981).

A single specimen of *P. dubius* has been reported from lower Wasatchian strata in the Bighorn Basin (Rose & Bown, 1982). North American plesiadapids have not otherwise been

TABLE 3. Dental measurements (mm) of Twelvemile Gulch *Plesiadapis dubius* compared to conspecific sample from the Paint Creek locality (UM Locality SC-143) in the Bighorn Basin (Table A-12, Gingerich, 1976). **Abbreviations**: **mm**, millimeters; **n**, sample size; **sd**, standard deviation.

	Twelvemile Gulch			Bighorn Basin		
	mean	sd	n	mean	sd	n
M1 length	2.85	0.09	2	3.06	0.17	5
M1 width	3.56	0	2	4.20	0.20	5
M2 length	3.17	0.12	3	3.22	0.16	5
M2 width	4.28	0.06	3	4.64	0.29	5
M3 length	3.24	0	2	3.10	0.14	4
M3 width	4.76	0.13	2	4.45	0.19	4
m1 length	3.07	0.05	4	2.90	0.20	3
m1 width	2.61	0.23	4	2.60	0.10	3
m2 length	3.23	0.11	5	3.07	0.10	4
m2 width	2.80	0.13	5	2.85	0.06	4
m3 length	4.65	0.31	3	4.90	0.28	2
m3 width	2.90	0.38	5	3.10	0.25	1

TABLE 4. Dental measurements (mm) of Twelvemile Gulch *Plesiadapis cookei* compared to conspecific samples from the Little Sand Coulee area in the Clarks Fork Basin (Table 14, Rose, 1981). **Abbreviations**: **mm**, millimeters; **n**, sample size; **sd**, standard deviation.

	Twelvemile Gulch			Clarks Fork Basin		
	mean	sd	n	mean	sd	n
P3 length	4.68		1			
P3 width	5.98		1			
P4 length	4.68	0.23	3	4.18	0.20	3
P4 width	6.76	0.60	3	6.48	0.57	3
M1 length	5.39	0.13	3	5.54	0.24	9
M1 width	7.09	0.18	3	7.13	0.28	9
M2 length	6.18	0.09	2	5.66	0.27	6
M2 width	7.76	1.07	2	7.98	0.50	6
M3 length	5.68	0.28	4	5.15	0.21	7
M3 width	8.06	0.39	4	7.78	0.70	6
m2 length	6.04	0.13	2	5.63	0.23	16
m2 width	5.35	0.19	2	5.41	0.28	17
m3 length	7.29		1	9.05	0.44	11
m3 width	3.83		1	.25	0.25	11

documented from the Eocene, although the clade did persist into the Eocene of western Europe (Jehle et al., 2019; Russell et al., 1967).

PLESIADAPIS sp., cf. *P. COOKEI* Jepsen, 1930
Figs. 13–15

Referred Specimens—CM 79228, left M3; CM 79229, right M1; CM 79230, right m2; CM 79231, left m2; CM 79232, left maxilla preserving P4–M2; CM 79233, left maxilla preserving M2–3; CM 79234, left P4; CM 79235, left dentary preserving damaged m3; CM 79236, left maxilla preserving M3; CM 79237, left P3; CM 79238, right M1; CM 79239, right m3; CM 79240, cuboid; CM 79241, left M3; CM 79242, left M3; CM 79243, right M3; CM 79244, left P4; CM 79245, left m3; CM 79246, distal fragment of right p3.

Known Distribution—upper Paleocene (Clarkforkian) of Wyoming.

Description—*Plesiadapis* sp., cf. *P. cookei* is the most abundant primatomorphan in the Twelvemile Gulch fauna, and many cheek tooth loci are represented in the available sample (Table 1). Relatively unworn cheek teeth tend to have heavily crenulated enamel. A maxillary fragment, CM 79233, preserves the roots of P3 and crowns of P4–M2, although the tooth crowns are variably abraded or otherwise damaged in this specimen (Fig. 14E). P3 is poorly represented in *P. cookei*, but this tooth locus is documented at Twelvemile Gulch by CM 79237 (Fig. 14A). Previously described specimens of *Plesiadapis cookei* that preserve P3 are limited to AMNH FM 16077 and UM 87990 from the Clarks Fork Basin. Unlike P3 in the latter specimens, CM 79237 possesses a distinct metacone and is larger. P4 is documented by three specimens from Twelvemile Gulch (Fig. 14B, C, E). Each bears a large protocone with a smaller paracone and even smaller metacone that is very closely appressed to the paracone. There is no distinct paraconule on P4, although a weakly inflated cuspule lingual to the paracone may represent a remnant of this structure. One of the P4 specimens known from Twelvemile Gulch, CM 79234 (L, 4.91 mm; W, 7.36 mm), is substantially larger than specimens of *P. cookei* from the Clarks Fork Basin (Table 4) measured by Rose. Mesial and distal cingula are well-developed and can be shelf-like, as is the case for the mesiobuccal cingulum on CM 79234 and CM 79244 (Fig. 14B, C). The buccal cingulum is variably developed, being particularly weak or absent near the base of the paracone. A short postmetacrista runs distally from the metacone to merge with the buccal margin of the distal cingulum. A relatively trenchant postprotocingulum runs distally

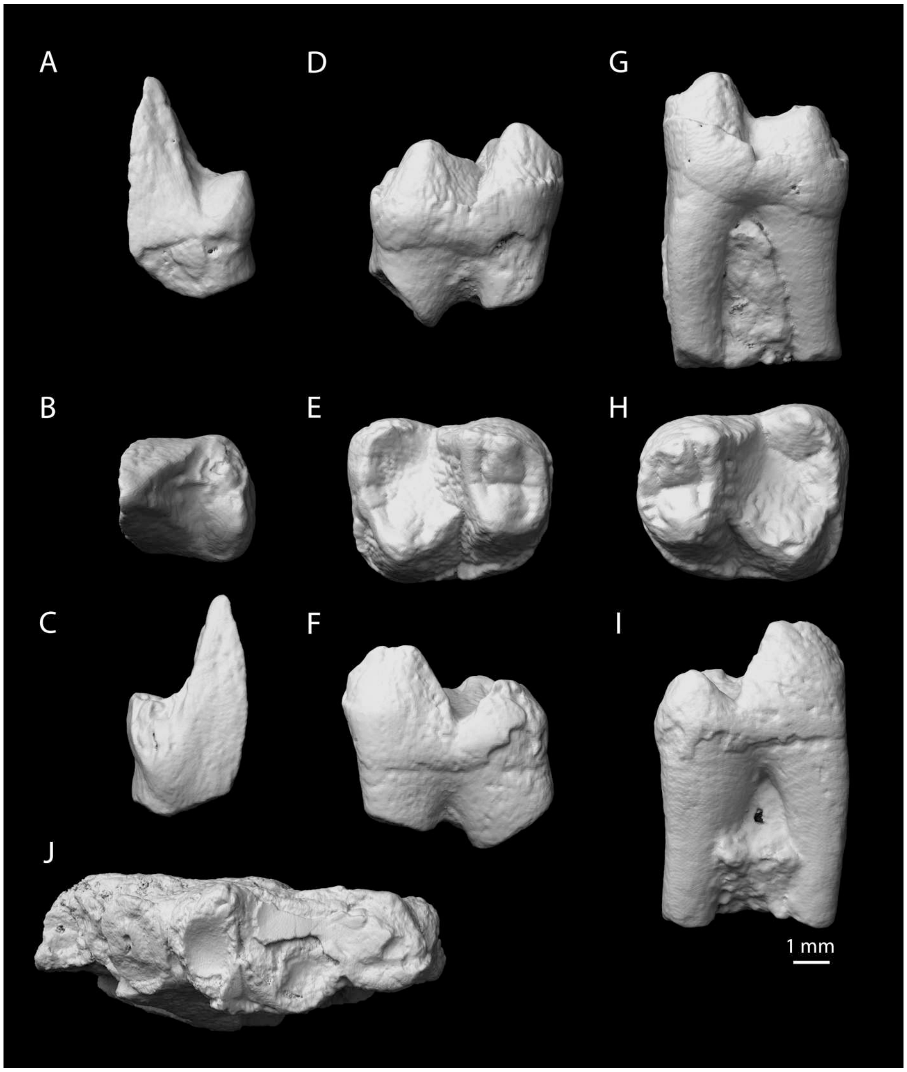

FIGURE 13. Lower teeth of *Plesiadapis* sp., cf. *P. cookei* from the Twelvemile Gulch local fauna. **A**–**C**, CM 79246, distal fragment of left p3 in **A**, buccal, **B**, occlusal, and **C**, lingual views. **D**–**F**, CM 79230, right m2 in **D**, buccal, **E**, occlusal, and **F**, lingual views. **G**–**I**, CM 79231, left m2 in **G**, buccal, **H**, occlusal, and **I**, lingual views. **J**, CM 79235, left dentary preserving damaged m3 in occlusal view.

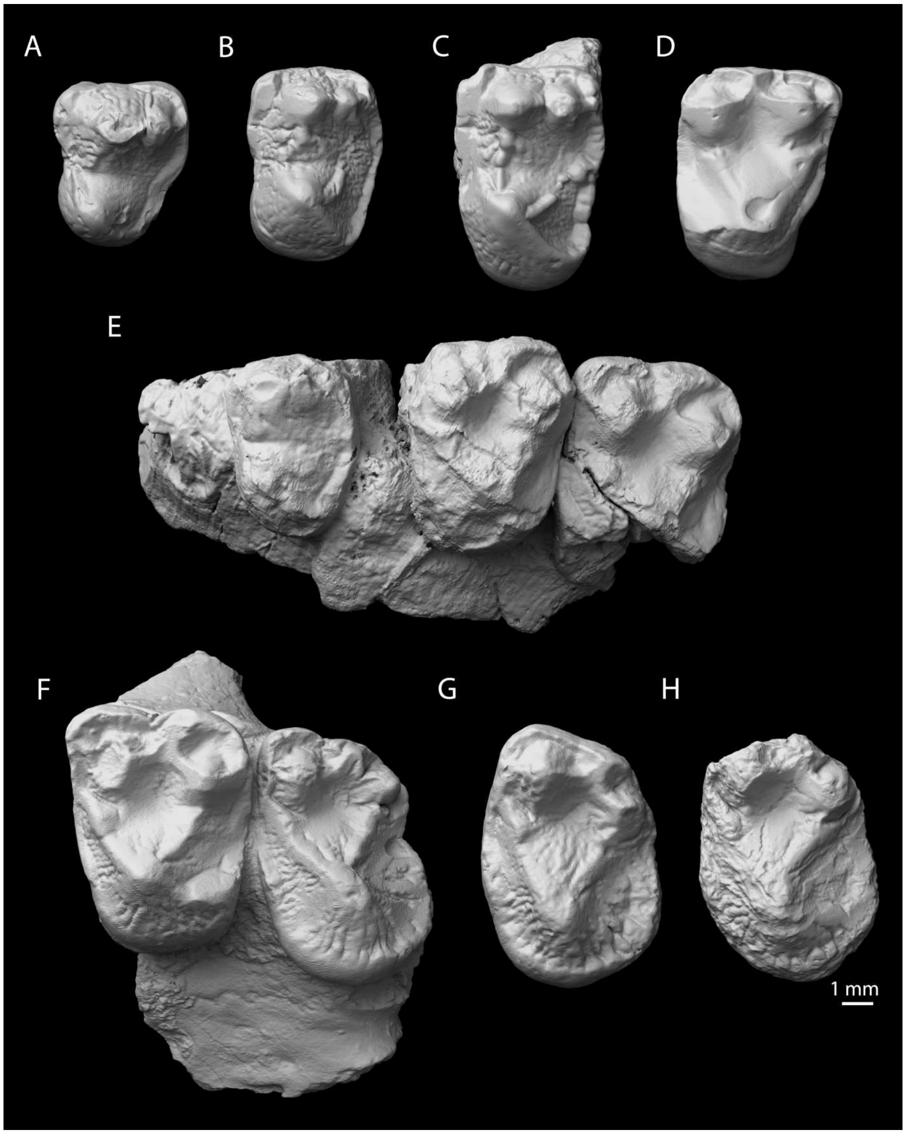

FIGURE 14. Upper teeth of *Plesiadapis* sp., cf. *P. cookei* from the Twelvemile Gulch local fauna, all in occlusal view. **A**, CM 79237, left P3. **B**, CM 79244, left P4. **C**, CM 79234, left P4. **D**, CM 79238, right M1. **E**, CM 79232, left maxilla preserving P4–M2 (upper molars damaged). **F**, CM 79233, left maxilla preserving M2–3. **G**, CM 79228, left M3. **H**, CM 79241, left M3.

from the protocone to merge with the lingual margin of the distal cingulum, while weaker preprotocrista and postprotocrista run mesiobuccally and distobuccally, respectively, from the tip of the protocone.

Upper molars are characterized by strong mesostyles that link postparacrista and premetacrista with relatively complete buccal cingula that tend to be raised and semi-crestiform (Fig. 14D–H). Paracone, metacone, and protocone are conical and weakly inflated. The preprotocrista and postprotocrista are trenchant, particularly on unworn molars, and the paraconule is generally more inflated than the metaconule (Fig. 14F–H). Hypocones (technically, pseudohypocones) are generally weak to absent on upper molars, although a small hypocone occurs on M2 in CM 79233 (Fig. 14F). Unworn examples of M3 are typically asymmetrical in occlusal outline, as a result of the distally expanded talon with heavily crenulated enamel (Fig. 14F–H).

Lower cheek tooth loci, especially lower premolars, are poorly represented at Twelvemile Gulch. CM 79246 is a distal fragment of a right p3 preserving the talonid, the postvallid, and the distal half of the protoconid (Fig. 13A–C). It can be identified as to locus based on its narrow postvallid and its lack of a discrete cristid obliqua. Lower molar loci include two examples of m2, which can be identified as to locus based on the close apposition of their paraconid and metaconid (Fig. 13D–I). The loop-like paracristid runs mesially from the protoconid before curving back to connect to the paraconid, while the protocristid is more nearly linear, connecting the protoconid with the metaconid. The wide talonid basin is open lingually because of a deep notch between the cuspidate entoconid and postvallid. The hypoconid is tall and voluminous, giving rise to a raised postcristid that connects the hypoconid to the entoconid while bearing several small cuspules along its length. Several specimens document m3, none of which is complete or unabraded (Fig. 13J).

A complete and well-preserved left cuboid, CM 79240, is assigned to *Plesiadapis* sp., cf. *P. cookei* (Fig. 15). It preserves several typical plesiadapiform characters as described and discussed in publications by Szalay and colleagues (e.g., Decker & Szalay, 1974; Szalay, 1994; Szalay & Decker, 1974; Szalay & Delson, 1979; Szalay et al., 1975). It closely resembles the cuboid of European *Plesiadapis tricuspidens* figured by Szalay and Delson (1979), and it is also an excellent match in both size and morphology to that of North American *Plesiadapis*

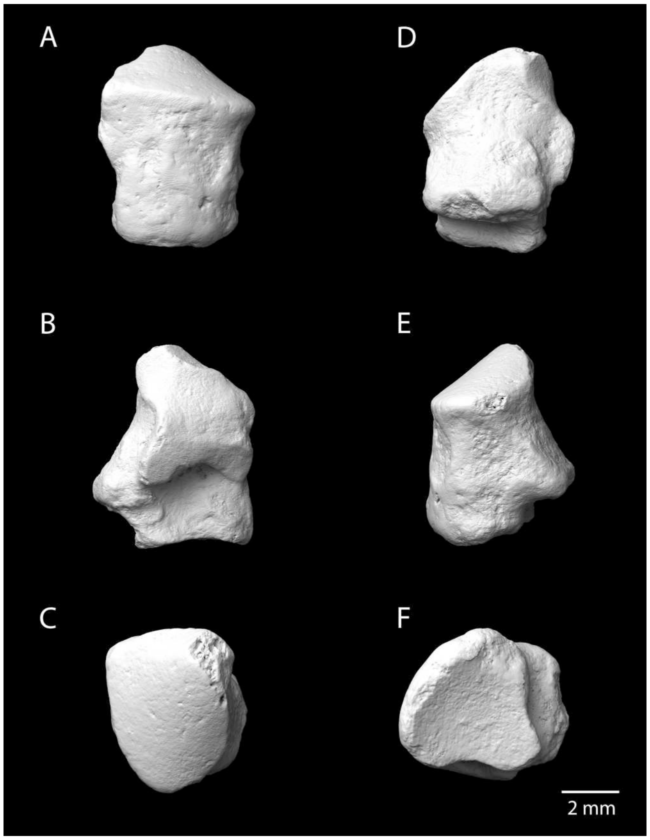

FIGURE 15. Left cuboid of *Plesiadapis* sp., cf. *P. cookei* (CM 79240) from the Twelvemile Gulch local fauna in **A**, dorsal, **B**, medial, **C**, proximal, **D**, plantar, **E**, lateral, and **F**, distal views.

cookei, based on comparison with this element from an associated skeleton from the Clarks Fork Basin (UM 87990, Boyer & Gingerich, 2019). CM 79240 measures 8.00 mm in length and 6.30 mm in width, and it bears a mostly flat calcaneal facet on its proximal surface with a small pivot on the inferior-medial surface that articulates with a congruent concavity on the distal end of the calcaneus. This joint is best described as an incipient calcaneocuboid pivot, being a reasonable structural intermediate between those of early Eutheria and the more fully developed pivot joint of Euprimates. While the calcaneocuboid pivot joint of Euprimates is a structural innovation clearly associated with rotation along the long axis of the pes (Dagosto, 1988), this specimen suggests that *Plesiadapis* may have already been engaging in some degree of pedal rotation at the calcaneocuboid joint (contra Dagosto, 1988). Distally the cuboid bears a triangular, flat facet for articulation with metatarsals 4 and 5. On its medial proximal surface, the cuboid bears a flat, rectangular facet for articulation with the ectocuneiform. Distal to the facet for the ectocuneiform on the medial surface of the cuboid is a large and deep pit for a ligamentous attachment. No articular surfaces are found on the dorsal or lateral sides of the bone, while the plantar surface bears a large tuberosity with a well-marked groove for the peroneus longus muscle running medio-laterally across the bone near its distal end.

Comments—The specimens referred here to *Plesiadapis* sp., cf. *P. cookei* are distinctive enough with respect to the holotype and referred specimens of *P. cookei* (including the remarkably well-preserved UM 87990) that they could conceivably represent a new species. Specifically, upper premolars from Twelvemile Gulch differ from those of *P. cookei* specimens from the Clarks Fork Basin in having more heavily crenulated enamel, a distinct metacone on P3, trenchant pre- and postprotocrista and postprotocingulum on P4, and greater disparity between the paracone and metacone on P4 (with the paracone being dominant). While there is broad metric overlap between the sample from Twelvemile Gulch and that from the Clarks Fork Basin for most tooth loci, specimens from Twelvemile Gulch tend to be larger, and certain specimens (including the P4, CM 79234) fall well outside the documented range for homologous tooth loci of *P. cookei* from the Clarks Fork Basin (Rose, 1981:table 14).

Superfamily PAROMOMYOIDEA Simpson, 1940
Family PAROMOMYIDAE Simpson, 1940
PHENACOLEMUR Matthew, 1915b
PHENACOLEMUR CAVATUS, sp. nov.
Fig. 16A–K

Holotype—CM 79226, right dentary preserving p4 (Fig. 16D–F).

Etymology—Latin *cavatus* (hollowed out), in allusion to the concave nature of the distobuccal side of the p4 trigonid and the proximity of the type locality to Dugout Draw.

Referred Specimens—CM 79222, left dentary preserving m2–3; CM 79223, right m3 talonid; CM 79224, apical part of right I1; CM 79225, apical part of right I1; CM 90249, apical part of left I1.

Diagnosis—Differs from all other species of *Phenacolemur* in having p4 oriented more obliquely in the dentary (with long axis running mesiobuccal to distolingual), p4 with neomorphic crest on mesiobuccal side of protoconid, slightly concave buccal margin of crown in vicinity of hypoflexid, and extremely narrow talonid with faintly discernible hypoconid and entoconid. Further differs from *P. simonsi*, *P. willwoodensis*, and *P. jepseni* in having p4 with greater mesiobasal expansion of the crown. Lower molars smaller than those of *P. praecox* and *P. fortior*, larger than those of *P. simonsi.* Further differs from *P. pagei*, *P. archus*, and *P. simonsi* in having I1 without mediocone and associated mediocrista.

Locality, Horizon, and Age—Twelvemile Gulch local fauna, CM Locality 3613, upper part of Fort Union Formation, Clarkforkian of Great Divide Basin, Sweetwater County, Wyoming.

Description—The holotype p4 (Fig. 16D–F; L, 2.88 mm; W, 2.04 mm) is unique in being oriented more obliquely in the dentary than is the case in other species of *Phenacolemur*. Although only a small part of the dentary is preserved in the holotype, the obliquity of p4 is validated by reference to the interstitial wear facet for m1 on the distal margin of p4, which is invariably oriented transversely with respect to the mesiodistal axis of the lower toothrow. Relative to the transverse plane occupied by this interstitial facet, the trigonid of p4 (and especially its mesiobasal expansion) diverges strongly mesiobuccally. The p4 in *P. cavatus* is also distinct in having four surprisingly well-marked crests emanating from the apex of the protoconid. In addition to the paracristid, which is located mesiolingually on the trigonid and which occurs in more or less muted form in many species of *Phenacolemur*, a neomorphic crest adorns the mesiobuccal side of the trigonid. The latter structure marks a boundary between the convex leading edge of the p4 trigonid and its modestly excavated or semi-planar distobuccal margin, which is continuous distally with the buccal side of the talonid. In addition to the two mesial crests, two distal crests define the margins of a triangular area on the postvallid of p4. These distolingual and distobuccal p4 crests typify many species of *Phenacolemur* (Silcox et al., 2008), but they are closer together than in other species of *Phenacolemur* because of the excavation of the distobuccal side of p4 noted previously. As a result, the triangular area on the

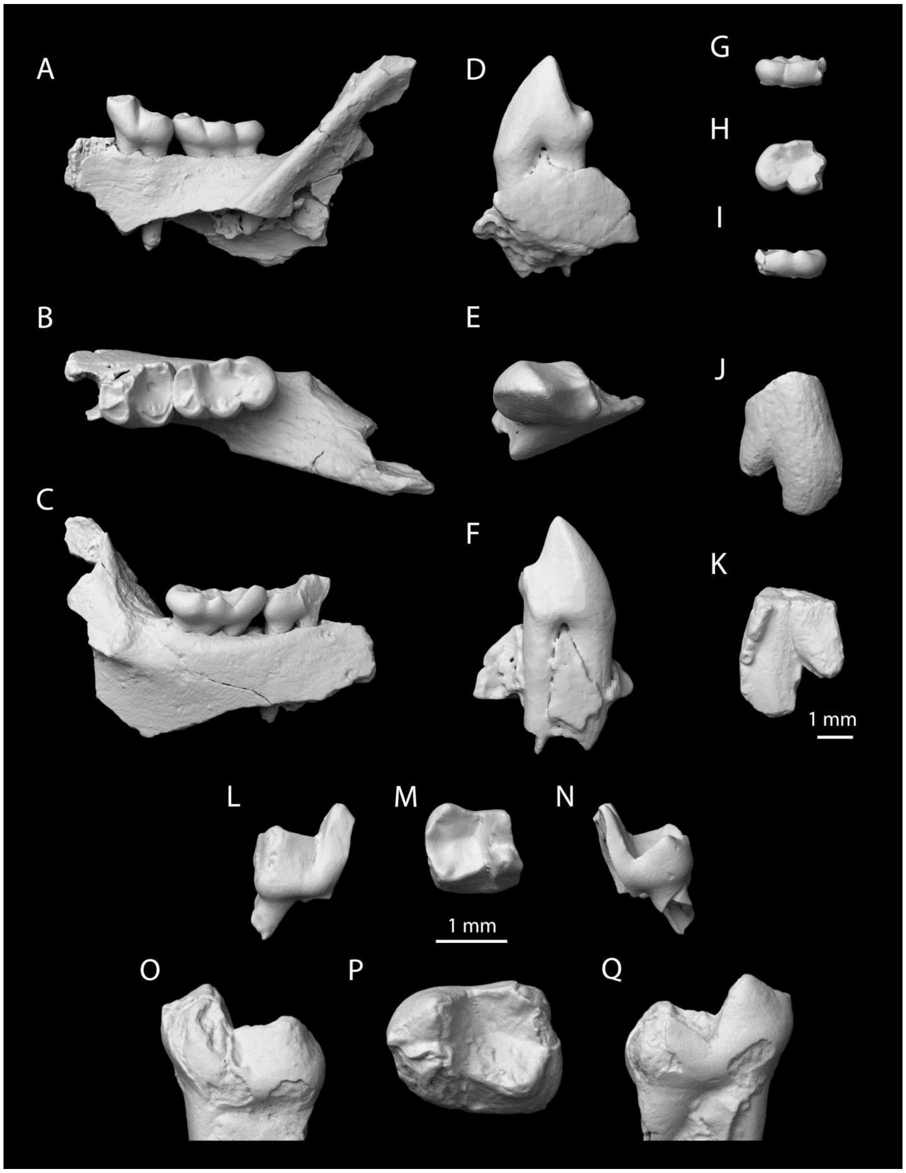

FIGURE 16. Paromomyidae and Microsyopidae from the Twelvemile Gulch local fauna. **A**–**C**, CM 79222, left dentary preserving m2–3 of *Phenacolemur cavatus* in **A**, buccal, **B**, occlusal, and **C**, lingual views. **D**–**F**, CM 79226, holotype right dentary preserving p4 of *Phenacolemur cavatus* in **D**, lingual, **E**, occlusal, and **F**, buccal views. **G**–**I**, CM 79223, right m3 talonid of *Phenacolemur cavatus* in **G**, buccal, **H**, occlusal, and **I**, lingual views. **J**, **K**, CM 79225, apical part of right I1 of *Phenacolemur cavatus* in **J**, labial, and **K**, lingual views. **L**–**N**, CM 92158, right lower molar fragment of *Arctodontomys* sp. in **L**, buccal, **M**, occlusal, and **N**, lingual views. **O**–**Q**, CM 95836, left m2 of *Arctodontomys simplicidens* in **O**, buccal, **P**, occlusal, and **Q**, lingual views.

postvallid of p4 is buccolingually narrower than in other species of *Phenacolemur*. The surprisingly trenchant distobuccal crest on p4 is continuous with the cristid obliqua, whereas the distolingual crest terminates in front of a lingual talonid notch. The talonid of p4 is remarkably abbreviated, particularly buccolingually, and it is not deeply excavated. Neither the hypoconid nor the entoconid is pronounced. In buccal view the crown of p4 lacks the strong mesiobasal expansion that typically occurs in *P. pagei* (Rose 1981:fig. 29B), *P. praecox* and *P. fortior*, but this may partly reflect the obliquity of p4 in *P. cavatus*. The p4 of *P. cavatus* shows greater mesiobasal expansion than occurs in *P. jepseni*, *P. simonsi*, and *P. willwoodensis*.

CM 79222 is a dentary with m2–3 (Fig. 16A–C; m2L, 2.10 mm; m2W, 1.93 mm; m3L, 3.12 mm; m3W, 1.80 mm) that shows the morphology characteristic of *Phenacolemur*, combining low and mesially canted trigonids with broad and deeply basined talonids. The trigonid of m2 is damaged lingually, precluding determination of whether a distinct paraconid would have been present. The trigonid of m3 is moderately worn, but there is no clear evidence of a paraconid. Silcox et al. (2008) report that the presence of distinct paraconids on m2–3 is variable in many Wasatchian species of *Phenacolemur*.

Three fragmentary I1 crowns, all of which preserve the apical part of the crown, are known (Fig. 16J, K). All these specimens differ from I1 crowns attributed to *P. simonsi*, *P. archus*, *P. pagei*, and *Ignacius frugivorus* in lacking the mediocone and its associated crest, the mediocrista (Rose et al., 1993; Secord, 2008; Silcox et al., 2008). Rather, I1 in *P. cavatus* bears two well-developed apical cusps, the anterocone and laterocone. A slightly raised crest or cingulum that bears several tiny cuspules lines the mesial side of the crown, running from near the base of the anterocone toward the posterocone. This structure may be partly homologous with the mediocrista found on I1 in other species of *Phenacolemur*, but it differs in being relatively straight and extending farther toward the base of the crown.

Comments—*P. cavatus* remains poorly known, but p4 and I1 morphology clearly distinguish this species from *P. pagei*, which is reasonably well-documented from late Tiffanian and

Clarkforkian sites in the Bighorn Basin and at Big Multi Quarry. The p4 morphology in *P. cavatus* is clearly autapomorphic, but the loss of the mediocone on I1 could be a synapomorphy linking this species with Wasatchian forms such as *P. fortior*.

Superfamily MICROSYPOIDEA Osborn and Wortman, 1892
Family MICROSYOPIDAE Osborn and Wortman, 1892
ARCTODONTOMYS Gunnell, 1985
ARCTODONTOMYS sp.
Fig. 16L–N

Referred Specimen—CM 92158, right lower molar fragment.

Known Distribution—upper Paleocene (upper Tiffanian) through lower Eocene (Wasatchian) of North America.

Description—CM 92158 (W, 1.28 mm) is a right lower molar fragment missing the mesial part of the trigonid including the paraconid (Fig. 16L–N). The trigonid is elevated well above the level of the talonid, and the postvallid is relatively vertical. The trigonid is relatively narrow, and the metaconid and protoconid are closely spaced as a result. The base of the metaconid is swollen, so that a bulge of enamel extends buccally from the metaconid toward the base of the protoconid. On the distal face of the metaconid a weak crest loops down the surface of the postvallid before connecting with a similar crest from the protoconid. The latter structure may be homologous with the protocristid that typically connects the protoconid and metaconid somewhat more mesially. A weak paracristid runs mesially from the protoconid, but its full extent is obscured by the breakage noted earlier. The talonid is deeply excavated but asymmetrical. Its buccal margin is formed by the elevated cristid obiqua, which terminates on the postvallid below the protoconid. Its lingual margin is much lower because the entocristid is weak or even absent. As a result, the talonid is open lingually near the base of the postvallid. The hypoconid is the tallest talonid cusp, situated near the junction of the cristid obliqua and the weakly developed postcristid. The latter structure connects the hypoconid with the weakly cuspidate hypoconulid, which occurs lingual to the midline of the talonid, closely approximating the entoconid. There is no development of a buccal cingulid, and the hypoflexid is shallow.

Comments—CM 92158 probably represents a fragmentary m2 based on comparisons with similarly small microsyopid specimens from Big Multi Quarry preserving serially associated teeth (e.g., CM 69336). Wilf et al. (1998) cited the Big Multi sample as *Arctodontomys* sp. nov. because the species is extremely small, approximating the size of *Navajovius kohlhaasae*. Secord (2008) described a single dentary fragment from the late Tiffanian of the Bighorn Basin as possibly pertaining to the same taxon represented at Big Multi Quarry. CM 92158 may or may not prove to be conspecific with the sample from Big Multi Quarry, but additional specimens are required.

ARCTODONTOMYS SIMPLICIDENS (Rose, 1981)
Fig. 16O–Q

Referred Specimen—CM 95836, left m2.

Known Distribution—upper Paleocene (Clarkforkian) of Wyoming.

Description—CM 95836 (L, 3.00 mm; W, 2.07 mm) is a left m2 that suffers from abrasion on the mesiobuccal margin of the trigonid, impacting the buccal side of the protoconid, and around the distolingual perimeter of the talonid, affecting the entoconid and hypoconulid (Fig. 16O–Q). The specimen is identified as m2 rather than m1 based on the close approximation of the paraconid and metaconid. As is typical for m2 in *A. simplicidens*, the paraconid is much smaller than the metaconid and situated mesiobuccal to the latter cusp. As a result, the paraconid is not fully lingual in position. The hypoconulid is located lingual to the midline on the distal margin of the talonid, being virtually twinned with the entoconid.

Comments—CM 95836 conforms in terms of both size and morphology with *A. simplicidens*, and it is assigned to this species here. CM 95836 is much larger than the lower molar fragment (CM 92158) described previously from Twelvemile Gulch, which was referred to *Arctodontomys* sp. Accordingly, two species of *Arctodontomys* are represented in the Twelvemile Gulch local fauna, as is also the case at Big Multi Quarry (Wilf et al., 1998).

Order "CONDYLARTHRA" Cope, 1881
Family ARCTOCYONIDAE Giebel, 1855
Subfamily ARCTOCYONINAE Giebel, 1855
THRYPTACODON Matthew, 1915a
THRYPTACODON sp.
Fig. 17

Referred Specimens—CM 79103, right p4; CM 79104, right m2; CM 79168, left P4.

Known Distribution—Middle Paleocene (Torrejonian) to lower Eocene (Wasatchian) of North America.

Description—The only upper tooth in the current sample is P4 (CM 79168, Fig. 17G–I; L, 4.94 mm; W, 4.09 mm). Its crown is relatively simple and vaguely T-shaped in occlusal outline, comprising a mesiodistally elongated buccal margin dominated by a tall, relatively pyramidal paracone and a much shorter, smoothly rounded lingual lobe. The mesiobuccal side of the tooth is broken, so it remains unclear whether a minor parastyle would have been present. The mesial side of the paracone is relatively rounded, but the distal side is marked by a

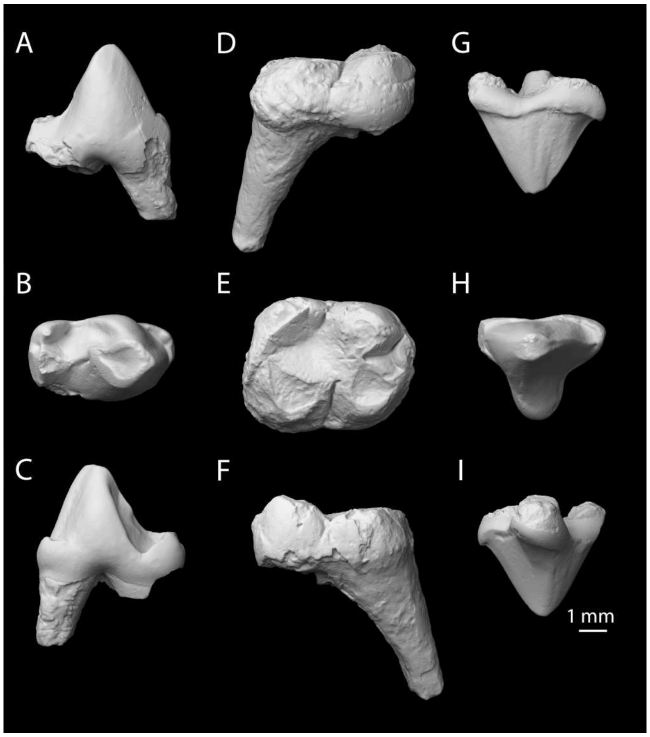

FIGURE 17. *Thryptacodon* sp. from the Twelvemile Gulch local fauna. **A–C**, CM 79103, right p4 in **A**, buccal, **B**, occlusal, and **C**, lingual views. **D–F**, CM 79104, right m2 in **D**, buccal, **E**, occlusal, and **F**, lingual views. **G–I**, CM 79168, left P4 in **G**, buccal, **H**, occlusal, and **I**, lingual views.

moderately developed postparacrista. A buccal cingulum is present and continuous, but this structure is sinuous in buccal view and best developed mesially and distally. There is no cuspate protocone, although the lingual lobe of the tooth is reasonably well developed.

CM 79103 is a right p4 (Fig. 17A–C; L, 4.98 mm; W, 2.95 mm), with approximately 2.2 mm of the mesial root preserved. Its trigonid is dominated by the protoconid, from the apex of which a modestly developed paracristid and postvallid crest emanate. The buccal side of the trigonid is gently convex, but the lingual side is marked by a prominent metaconid ridge that is not cuspidate but stronger than that in the holotype of *T. australis.* A thick mesiolingual cingulid occupies the space at the base of the crown between the paracristid and the metaconid ridge. The talonid is simple and limited to the lingual half of the distal part of the crown. It bears a small but distinct entoconid and a hypoconid, the latter of which connects to the postvallid crest via a short cristid obliqua.

CM 79104 is a right m2 (Fig. 17D–F; L, 5.96 mm; W, 5.17 mm). Its crown is remarkably bunodont, and its talonid is inflated buccally. The trigonid bears a small paraconid that is not fully lingual in position. The paraconid is connected by weak crests to both the metaconid and protoconid, the latter of which was the largest trigonid cusp in terms of volume and basal circumference. The talonid is marked by the inflated hypoconid, which crowds the space that would otherwise accommodate the hypoflexid, which is mesiodistally very short. A weak buccal cingulid appears to have been complete; the latter structure was likely confluent with a stronger distobuccal cingulid. The lingual side of the talonid bears an entoconid and entoconulid.

Comments—The specific identity of the sample of *Thryptacodon* known from the Twelvemile Gulch local fauna remains unclear. According to Secord (2008), P4 dimensions discriminate between *T. antiquus* and *Thryptacodon* sp., cf. *T. antiquus* (both of which have relatively short and wide P4 with a distinct protocone) and *T. australis* and *T. pseudarctos* (which have relatively long and narrow P4 without a distinct protocone). The dimensions and morphology of P4 in CM 79168 therefore distinguish the species occurring at Twelvemile Gulch from *T. antiquus* and *Thryptacodon* sp., cf. *T. antiquus.* However, the lower molar (CM 79103) from this locality is probably too small to pertain to *T. pseudarctos.* Likewise, p4 morphology distinguishes this taxon from *T. australis.* Additional material will be required to assign the sample of *Thryptacodon* from Twelvemile Gulch at the species level.

Family APHELISCIDAE Matthew, 1918
APHELISCUS Cope, 1875
APHELISCUS NITIDUS Simpson, 1937
Figs. 18 and 19

Referred Specimens—CM 79105, right dentary preserving p4–m2; CM 79106, left m3 talonid; CM 79107, right dentary preserving m2–3; CM 79108, right maxilla preserving M2–3; CM 79109, right dentary preserving m3; CM 79110, left M1; CM 79111, right M2; CM 79112, left dentary preserving m2–3; CM 79113, left dentary m2; CM 79114, right dentary preserving m2; CM 79115, right m3; CM 79116, left P4; CM 79117, left M3; CM 79118, partial right lower molar; CM 79119, left M3; CM 79120, left M2; CM 79121, left M1; CM 79122, left M2; CM 79123, right M3; CM 79124, left M2; CM 79125, right M1; CM 79126, left dP4; CM 79127, right dentary preserving m1; CM 79128, left lower molar; CM 79129, right dentary preserving m2-3; CM 79130, right M3; CM 79131, left m2; CM 79132, left M1; CM 79133, right M2; CM 79134, right M3; CM 79135, left p4; CM 79136, left M2; CM 79137, right m3; CM 79138, right dp4; CM 79139, left M3; CM 79178, left molar trigonid; CM 79189, right astragalus; CM 79199, right calcaneus; CM 95835, left m2.

Known Distribution—upper Paleocene (Clarkforkian) of North America.

Description—*Apheliscus nitidis* from Twelvemile Gulch are metrically similar to Rose's (1981) published sample from the Clarks Fork Basin (Table 5). P4 bears a large wear facet on its distal face, while its protocone is smaller (Fig. 18H). Upper molars of *Apheliscus* are low-crowned and essentially tritubercular, although small hypocones are present on M1–2 (Fig. 18I–M). Pre- and postprotocristae connect the protocone to the paracone and metacone, respectively, and these crests bear small conules positioned near the paracone and metacone. Upper molars have bunodont cusps and prominent mesial, distal, and buccal cingula. The preparacrista and postmetacrista are weak or absent on upper molars, while the postparacrista and premetacrista are typically better developed, even though they fail to unite to form a continuous centrocrista. M1–2 have a small parastyle. The metacone is reduced or absent on M3 (Fig. 18M). M1 differs from M2 in being smaller, having a weaker hypocone, and having a more nearly triangular occlusal outline caused by decreased mesiodistal expansion in the vicinity of the protocone. The distinctive M3 is triangular in outline and always lacks a hypocone. The paracone is the largest cusp on M3 and it is encircled buccally and mesially by a prominent cingulum.

The p4 is a distinctive, elongate tooth that is dominated by a large protoconid and a mesiodistally expansive talonid marked by raised distal margin that bears one or more small cusps along its postcristid (Fig. 18A–C). The cristid obliqua runs nearly directly mesially from the hypoconid to the postvallid, which forms a nearly vertically oriented shearing facet. Lower molars are elongate, constricted between trigonid and talonid, and the cusps are notably bunodont (Fig. 18A–F). A small paraconid occurs on m1 but is missing on m2–3. In the latter teeth a small paracristid runs mesially and lingually from the protoconid. The metaconid is larger than the protoconid in all lower molars, and the three talonid cusps are all well developed, with a large hypoconid, smaller entoconid, and small but distinct hypoconulid that is lingually displaced and separated from the hypoconid by a groove. The talonid basin is open lingually just distal to the base of the postvallid. While m3 has a distinct hypoconulid, it is not particularly elongated into a distinct talonid heel.

A right astragalus (Fig. 19A–C) and calcaneus (Fig. 19D–F) from Twelvemile Gulch bear many of the morphological features identified by Zack et al. (2005) as indicating cursorial or saltatorial terrestrial locomotion in Wasatchian *Apheliscus chydaeus* from the Bighorn Basin. Highlighted features on the astragalus include a moderately grooved trochlea, an elongate neck, and the absence of an astragalar foramen. However, the astragalus of *A. nitidus* from Twelvemile Gulch differs from that of *A. chydaeus* from the Bighorn Basin in lacking a distinctly concave cotylar fossa for the tibial malleolus. The calcaneus of *A. nitidus* is elongate and likely bears a small and distally located peroneal tubercle (this region is damaged on the Twelvemile Gulch specimen), generally resembling that of *A. chydaeus* (Zack et al., 2005). However, it remains unclear whether a distinct fibular facet was present adjacent to the ectal facet on the calcaneus in *A. nitidus.*

Comments—Represented by 39 specimens, *Apheliscus nitidus* is the most common mammal in the Twelvemile Gulch fauna and one of only two taxa with identified postcranial elements. Simpson (1937) described *Apheliscus nitidus* based on a left maxilla with P4–M1 (AMNH FM 15849) from upper Clarkforkian beds near the head of Big Sand Coulee in the Clarks Fork Basin. Species of *Apheliscus* are relatively common in

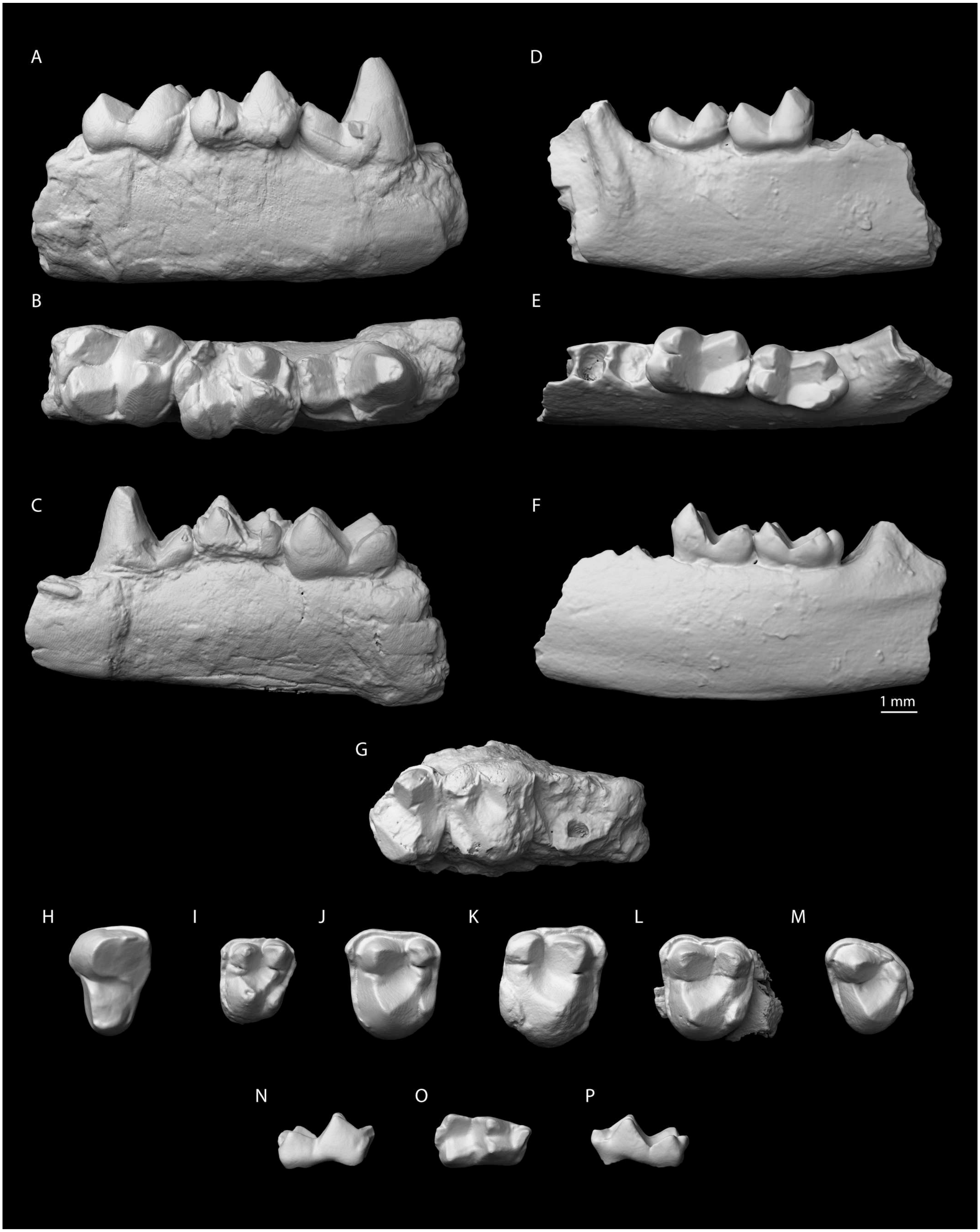

FIGURE 18. *Apheliscus nitidus* from the Twelvemile Gulch local fauna. **A**–**C**, CM 79105, right dentary preserving p4–m2 in **A**, buccal, **B**, occlusal, and **C**, lingual views. **D**–**F**, CM 79107, right dentary preserving m2–3 in **D**, buccal, **E**, occlusal, and **F**, lingual views. **G**, CM 79108, right maxilla preserving M2–3 in occlusal view. **H**, CM 79116, left P4 in occlusal view. **I**, CM 79121, left M1 in occlusal view. **J**, CM 79132, left M2 in occlusal view. **K**, CM 79111, right M2 in occlusal view. **L**, CM 79122, left M2 in occlusal view. **M**, CM 79123, left M3 in occlusal view. **N**–**P**, CM 79138, right dp4 in **N**, buccal, **O**, occlusal, and **P**, lingual views.

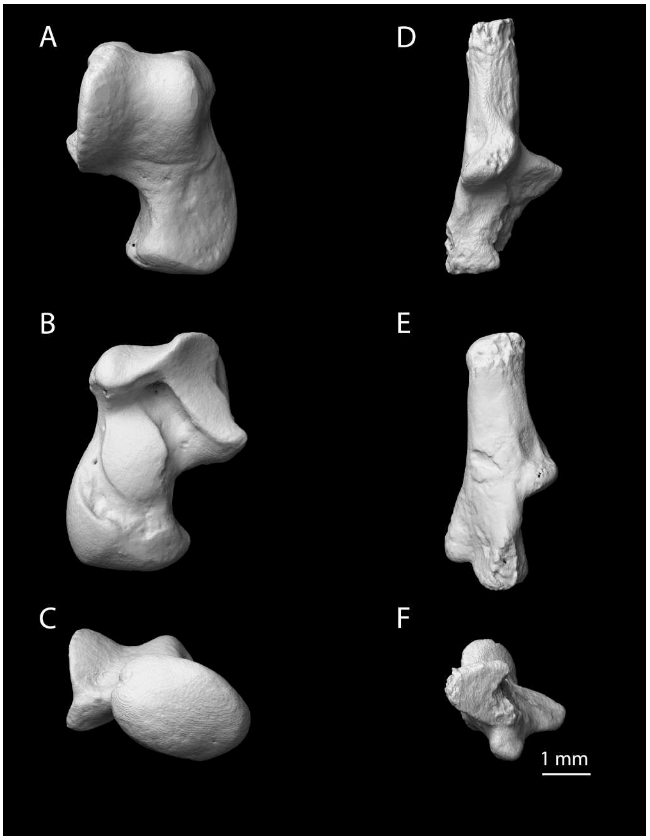

FIGURE 19. Tarsals of *Apheliscus nitidus* from the Twelvemile Gulch local fauna. **A**–**C**, CM 79189, right astragalus in **A**, dorsal, **B**, plantar, and **C**, distal views. **D**–**F**, CM 79199, right calcaneus in **D**, dorsal, **E**, lateral, and **F**, distal views.

Clarkforkian and Wasatchian strata of the Rocky Mountain West, being documented in Wyoming from the Powder River Basin (Delson, 1971) and Bighorn Basin (Bown, 1979; Gazin, 1959; Gingerich, 1994; Rose, 1981), in Colorado from the Sand Wash Basin (McKenna, 1960) and Piceance Creek Basin (Kihm, 1984), and in New Mexico from the San Juan Basin (Cope, 1874). Rose (1981) and Gingerich (1994) restrict *A. nitidus* to the Clarkforkian. Gingerich (1994) recognizes two smaller early Wasatchian species of *Apheliscus*, *A. chydaeus*, and *A. wapitiensis.*

Apheliscus has frequently been allied with hyopsodontid condylarths, sometimes as a subfamily (Apheliscinae) within Hyopsodontidae (Gingerich, 1994; McKenna, 1960; Rose, 1981), or as a separate family (Apheliscidae) within "Condylarthra" (Rose et al., 2012; Zack et al., 2005). A recently described partial skeleton of *Apheliscus chydaeus* from Wasatchian strata in the Bighorn Basin has been cited in support of a possible phylogenetic link between apheliscines and extant macroscelidean afrotherians (Zack et al., 2005). While the astragalus and calcaneus attributed here to *A. nitidus* (Fig. 19) agree closely with those described by Zack et al. (2005:fig. 2a, b) for *A. chydaeus*, the tarsal morphology of *A. nitidus* appears to be more primitive than that of *A. chydaeus* in lacking a deep cotylar fossa on the astragalus and a fibular facet on the calcaneus. In these respects, *A. nitidus* differs more profoundly from extant macroscelideans than does *A. chydaeus*, raising the possibility that tarsal features shared by macroscelideans and Eocene apheliscines are the result of homoplasy.

Family PHENACODONTIDAE Cope, 1881
PHENACODUS Cope, 1873
PHENACODUS INTERMEDIUS Granger, 1915
Fig. 20I–N

Referred Specimens—CM 79147, left m1 or m2 talonid; CM 95885, left m1 or m2.

Known Distribution—upper Paleocene (Clarkforkian) to middle Eocene (Bridgerian) of Wyoming, Colorado, New Mexico, Utah, and Texas.

Description—Two specimens from the Twelvemile Gulch local fauna can be referred to *Phenacodus intermedius.* CM 95885 (Fig. 20I–K) is a relatively complete left m1 or m2 (L, 12.55 mm; W, 10.90 mm) while CM 79147 (Fig. 20L–N) is the talonid of a left m1 or m2 (W, 10.20 mm). The former is more heavily worn than the latter, with oval dentine exposures marking each of the five main cusps (there is no paraconid). The hypoconid and hypoconulid on CM 79147 have small dentine exposures while

TABLE 5. Dental measurements (mm) of Twelvemile Gulch *Apheliscus nitidus* compared to conspecific sample from Clarks Fork Basin (Rose, 1981, Table 25). Note that Rose (1981) did not report standard deviations for samples with n = 2 (i.e., M1 and M3 length and width. The Standard Deviation numbers presented here for these tooth loci were calculated by the authors. **Abbreviations**: **mm**, millimeters; **n**, sample size; **sd**, standard deviation.

	Twelvemile Gulch			Clarks Fork Basin		
	mean	sd	n	mean	sd	n
P4 length	2.35		1	2.57	0.425	3
P4 width	3.09		1	3.10	0.377	3
M1 length	2.48	0.141	4	2.78	0.247	2
M1 width	2.74	0.137	4	2.98	0.318	2
M2 length	2.73	0.178	7			
M2 width	3.13	0.171	6			
M3 length	2.25	0.122	7	2.68	0.106	2
M3 width	2.91	0.128	7	2.88	0.106	2
p4 length	3.00	0.115	2	3.13	0.058	3
p4 width	1.87	0.344	2	1.77	0.115	3
m1 length	3.05	0.057	2	2.49	0.152	5
m1 width	2.35	0.115	2	1.90	0.070	4
m2 length	3.05	0.123	6	2.92	0.115	13
m2 width	2.22	0.210	6	2.25	0.131	13
m3 length	3.09	0.103	6	2.76	0.309	4
m3 wiidth	2.07	0.234	6	2.04	0.210	4

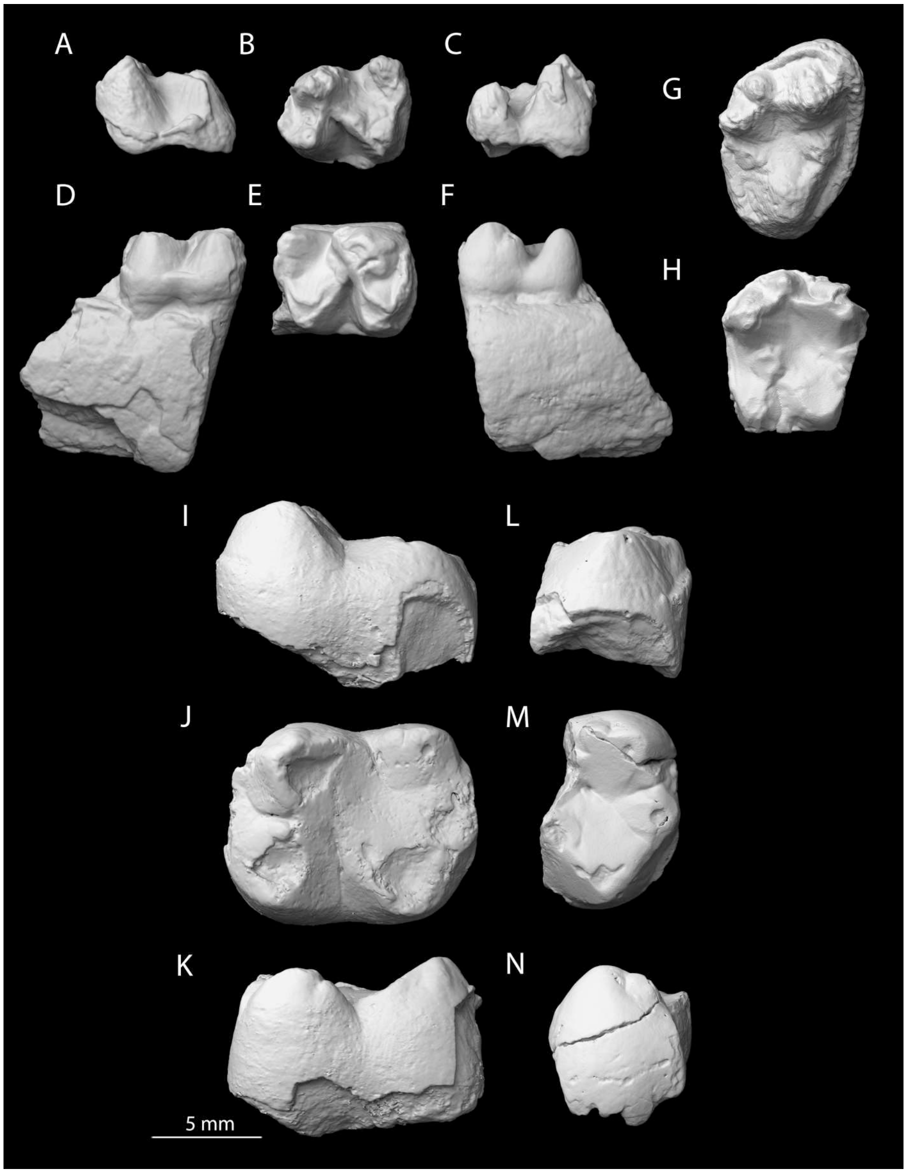

FIGURE 20. Phenacodontidae from the Twelvemile Gulch local fauna. **A**–**C**, CM 79141, left m1 of *Ectocion osbornianus* in **A**, buccal, **B**, occlusal, and **C**, lingual views. **D**–**F**, CM 79144, right m1 or m2 of *Ectocion osbornianus* in **D**, buccal, **E**, occlusal, and **F**, lingual views. **G**, CM 79146, right M3 of *Ectocion osbornianus* in occlusal view. **H**, CM 79143, fragmentary right M1 or M2 of *Ectocion osbornianus* in occlusal view. **I**–**K**, CM 95885, left m1 or m2 of *Phenacodus intermedius* in **I**, buccal, **J**, occlusal, and **K**, lingual views. **L**–**N**, CM 79147, talonid of left m1 or m2 of *Phenacodus intermedius* in **L**, buccal, **M**, occlusal, and **N**, lingual views.

the entoconid is barely worn. Both teeth are low crowned and rectangular, and both bear a small but distinct cristid obliqua running mesiolingually from a prominent hypoconid. The hypoconulid is located centrally at the distal margin of the tooth, separated from both the hypoconid and entoconid by small grooves. An accessory cuspule lies just mesial to the entoconid, marking the mesiolingual extent of the talonid basin on CM 79147. Both molars are low (brachyodont) with rounded (bunodont) cusps, as is typical for the genus.

Comments—In his revision of the Phenacodontidae, Thewissen (1990) regarded Clarkforkian records of *Phenacodus* as pertaining to one of two species, the smaller and long-ranging *P. vortmani* and the larger *P. intermedius*, which first appears in the Clarkforkian and persists into the early Bridgerian. Both specimens from Twelvemile Gulch are similar in size to lower second molars of *P. intermedius*, and they are assigned to this species here.

ECTOCION Cope, 1882
ECTOCION OSBORNIANUS Cope, 1882
Fig. 20A–H

Referred Specimens—CM 79140, left dentary preserving p4-m1, m3; CM 79141, left m1; CM 79142, right lower molar; CM 79143, fragmentary right M1 or M2; CM 79144, right m1 or m2; CM 79145, right M2; CM 79146, right M3; CM 95830, left M3.

Known Distribution—upper Paleocene (Clarkforkian) through lower Eocene (Wasatchian) of North America.

Description—The small sample of *Ectocion* from Twelvemile Gulch agrees in size and morphology with Clarkforkian specimens of *E. osbornianus* from Big Multi Quarry and the Clarks Fork Basin. First and second upper molars of *Ectocion* are quadritubercular, with well-developed hypocones and strong conules. M3 lacks a hypocone but retains conules. The stylar area on all upper molars is well developed and distinctive, with a large parastyle and mesostyle connected to the paracone and metacone by a W-shaped ectoloph. Cingula encircle most, if not all, of the perimeter of upper molar crowns, although the lingual cingulum can be very weak. Lower molars lack a paraconid but have a paracristid that runs mesially from the protoconid before curving lingually to enclose a small trigonid basin. The metaconid is situated

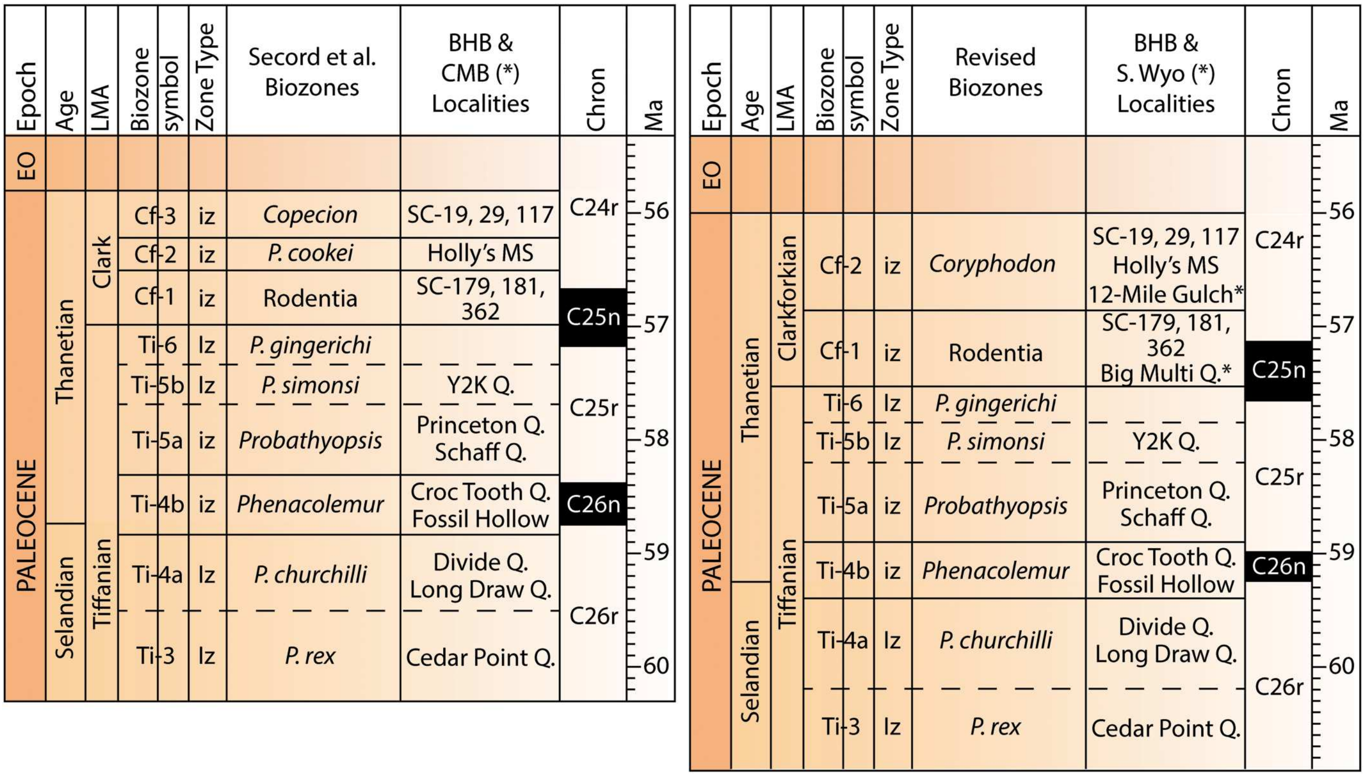

FIGURE 21. Comparison of late Paleocene biozonation scheme adopted by Secord et al. (2006), which was calibrated to Gradstein et al. (2004), with the revised biozonation being proposed here, which is calibrated to Speijer et al. (2020). Biozones are named after the taxon that defines its base; succeeding taxon defines the top of each biozone. Correlation of biozones to the geomagnetic polarity time scale is based on measured stratigraphic section across the southeast side of Polecat Bench and associated mean accumulation rates for individual magnetochrons (Secord et al., 2006:table 1), recently revised age estimates for magnetochron boundaries (Speijer et al., 2020:table 28.1), and the earliest occurrence of *Coryphodon* in the Clarks Fork Basin at locality SC-108, located 325 m above the base of Cf-1. **Abbreviations**: **BHB**, Bighorn Basin; **Cf,** Clarkforkian; **CMB**, Crazy Mountains Basin; **iz**, interval zone; **lz**, lineage zone; **P.**, Plesiadapis; **Q.**, Quarry; **S. Wyo.**, Southern Wyoming; **Ti.**, Tiffanian.

distolingually with respect to the protoconid and is only slightly lower and smaller than the protoconid. The cristid obliqua forms a linear crest running from the hypoconid to join the postvallid near the base of the metaconid. The hypoconulid on m1–2 is positioned lingually, close to the entoconid. On m3 the hypoconulid lobe is extended distally and centrally located. A deep entoconid notch is preserved in even heavily worn lower molars.

Comments—*Ectocion osbornianus* is the only species of *Ectocion* documented from the Clarkforkian of Wyoming, and we refer Twelvemile Gulch specimens to this species here. Farther to the south, in the Piceance Creek Basin of western Colorado, Burger (2012) has reported the co-occurrence of *E. osbornianus* and the smaller species *E. parvus* in Clarkforkian strata of the Atwell Gulch Member of the Fort Union Formation. Specimens of *Ectocion* from the Twelvemile Gulch local fauna are too large to pertain to *E. parvus.*

DISCUSSION

As recently emphasized by Holroyd and Rankin (2014), Clarkforkian faunas outside the Clarks Fork Basin in northern Wyoming are limited in number, and they have generally been inadequately documented, often being represented in the literature by published faunal lists rather than formal descriptions of the included taxa and associated voucher specimens. The Twelvemile Gulch local fauna from the Great Divide Basin (Anemone & Dirks, 2009) and the Big Multi Quarry fauna from the nearby Washakie Basin (Beard et al., 2019; Chester & Beard, 2012; Dawson & Beard, 1996; Jones & Beard, 2023; Wilf et al., 1998) provide insights into the nature of Clarkforkian faunas in southwestern Wyoming, nearly 500 km south of the Clarks Fork Basin. These more southerly faunas differ compositionally from Clarkforkian faunas from northern Wyoming in ways that highlight some of the limitations in our current understanding of upper Paleocene mammalian biostratigraphy in the Rocky Mountain West, and they invite questions about correlation and the interpretation of faunal similarities and differences across substantial latitudinal gradients.

In his monographic review of the Clarkforkian, Rose (1981) created three faunal zones corresponding roughly to early, middle, and late Clarkforkian. Rose's *Plesiadapis gingerichi* zone extends from the late Tiffanian through the early Clarkforkian, the *Plesiadapis cookei* zone equates to the middle Clarkforkian, and the *Phenacodus–Ectocion* zone corresponds to the late Clarkforkian. The *Plesiadapis gingerichi* zone can be considered an interval zone (or possibly a lineage zone) in the sense of Woodburne (2004), because it spans the interval from the lowest occurrence of *P. gingerichi* to the lowest occurrence of *P. cookei.* When *P. gingerichi* was first described, Rose (1981) interpreted it as the phylogenetically intermediate segment of a single lineage linking the earlier *P. simonsi* with the younger *P. cookei*. If such an anagenetic relationship among these late Paleocene species of *Plesiadapis* were to be validated, it would be appropriate to regard the corresponding biozone as a lineage zone. However, these relationships have been disputed by more recent phylogenetic analyses (Boyer & Gingerich, 2019; Boyer et al., 2012). Regardless of the precise phylogenetic affinities of *P. gingerichi*, the Clarkforkian part of the *Plesiadapis gingerichi* zone, defined as the interval between the lowest occurrence of Rodentia and the lowest occurrence of *P. cookei*, is an interval zone that equates with the Cf-1 biochron of Gingerich (2001) and Secord et al. (2006). Under Rose's (1981) original formulation, the *Plesiadapis cookei* zone is best considered as a lineage zone, because it equates with the duration of the *P. cookei* lineage. Gingerich (2001) equated the *Plesiadapis cookei* lineage zone with the Cf-2 biochron. Secord et al. (2006) transformed the *Plesiadapis cookei* lineage zone of Rose (1981) into an interval zone by redefining its upper boundary as the lowest occurrence of the phenacodontid condylarth *Copecion*. As noted by Boyer and Gingerich (2019), this alteration effectively shortened the duration of Cf-2, because the earliest record of *Copecion* occurs below the highest record of *P. cookei* in the Clarks Fork Basin. Some potential problems with the *Plesiadapis cookei* interval zone of Secord et al. (2006) are discussed below as they relate to Clarkforkian faunas from outside the Bighorn Basin. Rose's (1981) *Phenacodus–Ectocion* zone corresponds to an assemblage zone (Woodburne 2004), or more precisely an abundance zone in the sense of Salvador (1994), defined by the unusual commonality of these two phenacodontid taxa. Rose (1981) recognized the base of the *Phenacodus–Ectocion* zone as corresponding to the highest occurrence of *Plesiadapis cookei*. Cognizant of the potential taphonomic biases associated with abundance zones and recognizing that the base of a biozone is optimally defined by the lowest, rather than the highest, occurrence of a taxon, Secord et al. (2006) proposed the *Copecion* interval zone as the interval between the lowest occurrence of *Copecion* and the lowest occurrence of Wasatchian immigrant mammal taxa (Perissodactyla, Artiodactyla, and euprimates). The *Copecion* interval zone of Secord et al. (2006) closely approximates the Cf-3 biochron of Gingerich (2001), although Gingerich (2001) continued to follow Rose (1981) in recognizing the base of Cf-3 by the highest occurrence of *Plesiadapis cookei*, which, as noted earlier, does not correspond precisely with the lowest occurrence of *Copecion*. Gingerich (2001) defined the top of the Cf-3 biochron as the lowest occurrence of *Meniscotherium priscum*, which would later define the base of the succeeding Wa-M biochron (Gingerich & Smith, 2006).

Extending the biostratigraphic zonation scheme established for the Clarkforkian of the Bighorn Basin to other Clarkforkian faunas in Wyoming has proven to be problematic. As noted by Holroyd and Rankin (2014), all the Clarkforkian faunas currently known from outside the Clarks Fork Basin in Wyoming include *Plesiadapis cookei*, possibly indicating that all such faunas are close in age, being correlative with the *Plesiadapis cookei* interval zone (Cf-2) in the Clarks Fork Basin. These faunas include those from various Purdy Basin sites near Togwotee Pass in eastern Teton County, Wyoming (McKenna, 1980; Rose, 1981), the Buckman Hollow fauna from the Green River Basin in Lincoln County, Wyoming (Holroyd & Rankin, 2014), Big Multi Quarry and closely related sites in the Washakie Basin in Sweetwater County, Wyoming (Beard et al., 2019; Chester & Beard, 2012; Dawson & Beard, 1996; Jones & Beard, 2023; Wilf et al., 1998), and the Twelvemile Gulch fauna from the western Great Divide Basin that is the subject of this report. Despite the shared occurrence of *Plesiadapis cookei* or *Plesiadapis* sp., cf. *P. cookei* in all these faunas, there is compelling evidence for some degree of age disparity among them. For example, Big Multi Quarry and Twelvemile Gulch are geographically proximate and derived from apparently similar paleoenvironments, yet the Twelvemile Gulch fauna includes multiple taxa that have never been recorded from the more extensively sampled Big Multi Quarry assemblage. Examples include the neoplagiaulacid multituberculate *Ectypodus tardus*, the paramyid rodent *Acritoparamys atwateri*, the miacid carnivoramorphan *Uintacyon rudis* and the paromomyid primatomorphan *Phenacolemur cavatus*. Most, if not all, of these taxa suggest that the Twelvemile Gulch fauna is younger than Big Multi Quarry. For example, *Ectypodus tardus* is otherwise documented from early Wasatchian faunas, whereas *Ectypodus powelli* occurs at Big Multi Quarry and is also known from the upper Tiffanian and lower Clarkforkian of the Bighorn Basin (Secord, 2008; Wilf et al., 1998). *Acritoparamys atwateri* is substantially larger than *Paramys adamus* from Big Multi Quarry (Dawson & Beard, 1996), and its upper molar morphology is seemingly more derived in having enlarged and inflated conules. *Uintacyon rudis* pertains to a carnivoramorphan clade (Miacidae) that has never been documented at Big Multi Quarry, although both larger (*Didymictis*) and smaller (*Viverravus*) carnivoramorphans occur there (Wilf et al., 1998). *Phenacolemur cavatus* is distinguished by its seemingly autapomorphic p4 morphology, which contrasts with the more conservative morphology found in *Phenacolemur pagei* from Big Multi Quarry, a species also known from late Tiffanian and earlier Clarkforkian sites in the Bighorn Basin (Secord, 2008). Likewise, several biostratigraphically significant taxa occur at Big Multi Quarry that remain undocumented from Twelvemile Gulch. Notable examples include the microcosmodontid multituberculate *Microcosmodon conus*, which is documented in the Bighorn Basin only from the late Tiffanian (Secord, 2008), and the plagiomenid *Planetetherium*, which in the Bighorn Basin is restricted to Eagle Coal Mine, a site that is widely regarded as early (if not earliest) Clarkforkian (Secord, 2008).

Plesiadapis cookei is a distinctive member of the North American plesiadapid radiation, but its precise phylogenetic relationships with respect to other plesiadapids is debated. Gingerich (1976) and Rose (1981) interpreted *P. cookei* as the youngest member of a large-bodied lineage of North American *Plesiadapis* that also includes *P. simonsi* and *P. gingerichi*. In contrast, Boyer et al. (2012) and Boyer and Gingerich (2019) reconstructed *P. cookei* as being specially related to European *Platychoerops*. This phylogenetic discrepancy has implications for interpreting *P. cookei* in a biostratigraphic context. That is, if *P. cookei* does not pertain to the same lineage as *P. simonsi* and *P. gingerichi*, then its stratigraphic range in the Bighorn Basin cannot be interpreted as a lineage zone. Lineage zones are accorded special status by Woodburne (2004) because evolutionary changes are temporally unique. As such, lineage zones theoretically function as chronozones that lack gaps and do not overlap adjacent lineage zones. Paradoxically, at the Paint Creek locality in the Bighorn Basin, *P. cookei* is reported to co-occur with its purported ancestor *P. gingerichi* (Bloch & Gingerich, 1998), suggesting that, while these species may be closely related, they are not members of a single anagenetic lineage. As noted earlier, *Plesiadapis* sp., cf. *P. cookei* from Twelvemile Gulch tends to be larger than *P. cookei* from the Clarks Fork Basin and elsewhere, and it is further distinguished in having a metacone on P3, which is plausibly interpreted as an autapomorphic character. Whether these distinctions eventually warrant taxonomic recognition must await the recovery of additional specimens, but they emphasize the tenuous nature of the morphological boundaries of *P. cookei*, a situation that is equally applicable to other species of *Plesiadapis* (e.g., Jehle et al., 2019; Secord, 2008).

A further complication related to *P. cookei* is ambiguity regarding its lowest occurrence in the Clarks Fork Basin. As noted by Secord (2008), while the base of the Rodentia interval zone (i.e., the base of Cf-1) is reasonably well exposed along the western flank of Polecat Bench, most of the stratigraphic section between the lowest occurrence of rodents and the lowest occurrence of *P. cookei* is covered. Gingerich (2001:fig. 2) depicts an interval of ~285 m between the last occurrence of *P. gingerichi* (low in the Rodentia interval zone) and the first occurrence of *P. cookei* in the upper part of the Fort Union Formation in the Clarks Fork Basin. Accordingly, the actual duration of the Rodentia interval zone in the Clarks Fork Basin, the end of which has previously been defined by the lowest occurrence of *P. cookei*, remains poorly constrained because of the intervening covered section. If the actual first occurrence of *P. cookei* occurs relatively low in the covered stratigraphic interval spanning much of Cf-1, then the Rodentia interval zone would become remarkably brief, potentially explaining why Clarkforkian faunas from elsewhere in Wyoming all appear to correlate with Cf-2.

An alternative to relying so heavily on *P. cookei* for biozonation of the Clarkforkian would focus instead on immigrant mammalian taxa. As noted by Woodburne (1977, 2004) and others, immigrant clades offer certain advantages over endemic taxa for biostratigraphic correlation, because they are readily identifiable and frequently common, and because they often disperse widely and rapidly once colonization has occurred. Two clades of mammals appear to have immigrated into North America during the Clarkforkian, almost certainly from Asia (Beard, 1998). Coryphodontid pantodonts were originally cited by Rose (1981) as appearing at or near the beginning of the Clarkforkian, but a more recent review of *Coryphodon* in the Clarks Fork Basin indicates that it first appears within the *Plesiadapis cookei* interval zone, roughly midway through the local Polecat Bench–Sand Coulee Clarkforkian stratigraphic section (Uhen & Gingerich, 1995). Secord et al. (2006) note that *Coryphodon* is not clearly documented in the Clarks Fork Basin until ~325 m above the Tiffanian–Clarkforkian boundary. Being one of the largest mammals known from the Clarkforkian, *Coryphodon* is not easily overlooked by collectors, and following its lowest occurrence in the Clarks Fork Basin, it is typically abundant. A second immigrant mammal clade, the miacid carnivoramorphan *Uintacyon*, appears at roughly the same time in the Clarks Fork Basin (Gingerich, 1983b; Rose, 1981), suggesting that this episode of faunal turnover in the middle of the Clarkforkian is more important than has been widely recognized.

To achieve more accurate correlation between Clarkforkian faunas from southern and western Wyoming and those from the Clarks Fork Basin, we propose to revise the tripartite biozonation scheme for the Clarkforkian of Secord et al. (2006) by relying explicitly on immigrant mammal taxa. The beginning of the Clarkforkian, and the early Clarkforkian Cf-1 interval zone, remains defined by the first appearance of the invasive clade Rodentia. We recognize a new late Clarkforkian interval zone (Cf-2), the base of which is defined by the first appearance of *Coryphodon* and the top of which is defined by the first appearance of Perissodactyla (Fig. 21). The *Coryphodon* interval zone, which can also be recognized by the first appearance of Miacidae (*Uintacyon*) in western North America, equates roughly with the second half of the Clarkforkian, because it begins later than the *Plesiadapis cookei* interval zone of Secord et al. (2006) and includes the *Copecion* interval zone of those authors. We justify recognition of a bipartite, rather than tripartite, subdivision of the Clarkforkian for several reasons, including our philosophical preference for relying on invasive clades over endemic taxa in defining biozones. Likewise, *Copecion* is a rare taxon (Secord et al., 2006), making it less than ideal as an index fossil. Finally, a bipartite division of the Clarkforkian prioritizes accuracy over precision in correlation. Recognition of the *Coryphodon* interval zone requires modification of the Rodentia interval zone of Secord et al. (2006), by extending it beyond the lowest occurrence of *Plesiadapis cookei* to the lowest occurrence of *Coryphodon* (and/or Miacidae). Following prior nomenclatural practice, we designate our revised version of the Rodentia interval zone as Cf-1 (or early Clarkforkian) and the *Coryphodon* interval zone as Cf-2 (or late Clarkforkian). This biozonation scheme addresses the significant gap in the stratigraphic record of large-bodied plesiadapids in the Clarks Fork Basin and the related possibility of asynchronous local first appearances of *P. cookei* across a latitudinal gradient in the Rocky Mountain Interior. Such a pattern has previously been suggested with respect to *P. cookei* (Anemone & Dirks, 2009; Chester & Beard, 2012) and documented with respect to *Ectocion parvus* (Burger, 2012). Based on current understanding of their faunas, Big Multi Quarry and Buckman Hollow appear to correlate to Cf-1, while Twelvemile Gulch and at least some of the Purdy Basin Clarkforkian sites documented by McKenna (1980) pertain to Cf-2 (Fig. 21). This revised biozonation scheme for the Clarkforkian accommodates the evidence cited above for Twelvemile Gulch being younger than Big Multi Quarry, while potentially reconciling previously conflicting interpretations regarding correlation of Big Multi Quarry with the Clarkforkian sequence of faunas in the Clarks Fork Basin. That is, the occurrence of *Plesiadapis cookei* at Big Multi Quarry could indicate correlation with the narrow stratigraphic interval in the Clarks Fork Basin between the local first appearance of *Plesiadapis cookei* and the local first appearance of *Coryphodon* (i.e., early in the Cf-2 biochron of Secord et al. [2006] or late in the Cf-1 biochron of our biozonation scheme). Alternatively, *Plesiadapis cookei* at Big Multi Quarry may antedate its first occurrence in the Clarks Fork Basin, either because of the stratigraphic gap in the record of large-bodied plesiadapids in the Clarks Fork Basin or because *P. cookei* appears asynchronously across a latitudinal gradient because of a Clarkforkian warming trend that coincides with northward range expansions of multiple plant and animal taxa (Burger, 2012; Wilf, 2000; Wilf et al., 1998).

Another example of the potential utility of a Clarkforkian biozonation scheme focused on immigrant clades (Rodentia, Coryphodontidae, and Miacidae) rather than endemic North American plesiadapids and phenacodontids is its application to intercontinental correlation. In western Europe, the late Paleocene Petit Pâtis fauna from the northern Paris Basin has previously been correlated with the North American Clarkforkian based on the presence of rodents and the miacid carnivoramorphan *Vassacyon* (Smith et al., 2014; Solé et al., 2016). Although different miacid genera are represented in the North American Western Interior and western Europe, the presence of *Vassacyon* at Petit Pâtis suggests correlation with Cf-2 (late Clarkforkian). If so, western European faunas that potentially correlate with Cf-1 remain undocumented, because the classical Cernay fauna almost certainly correlates with later Tiffanian faunas from North America (Beard & Dawson, 1999; Beard et al., 2019; Jehle et al., 2019).

The Twelvemile Gulch local fauna contributes to our knowledge of regional diversity in late Paleocene mammalian faunas from the Clarkforkian NALMA and raises a series of questions concerning so-called anachronistic faunas (Black, 1967; Gunnell & Bartels, 2001a, b; Robinson et al., 1964), latitudinal gradients and their effects on faunal composition (Anemone & Dirks, 2009), and mammalian dispersal (Holroyd & Rankin, 2014). In describing basin margin faunas from upland localities near South Pass, Wyoming, Gunnell and Bartels (2001a, b) developed and applied the concept of "anachronistic faunas." They suggested that basin margin faunas tended to differ from the faunal assemblages typically found closer to the center of sedimentary basins by virtue of possessing (1) distinctive or unique taxa, (2) taxa with distinctive morphology, and (3) faunal co-occurrences of typically ancestor-descendant (i.e., "anachronistic") taxa. While the Twelvemile Gulch fauna includes several anachronistic faunal associations (e.g., *Ectypodus tardus*, *Plesiadapis* sp., cf. *P. cookei*, and *Carpolestes nigridens*) as well as some distinctive taxa (*Phenacolemur cavatus* sp. nov., and *Arctodontomys* sp.), it is not located particularly close to the basin margin (i.e., the Rock Springs Uplift), and it does not include ancestor-descendant taxa. We therefore are not convinced that the basin margin hypothesis applies here (Anemone & Dirks, 2009).

We suggest a better explanation may be found in latitudinal variation and concomitant environmental and climatic gradients between sedimentary basins in southern (i.e., Washakie and Great Divide basins) and northern Wyoming (i.e., the Clarks Fork Basin). The late Paleocene was a time of significant global warming (Aubry et al., 1998) that was accompanied by major evolutionary transitions among mammalian lineages (e.g., origins, extinctions, and dispersals), with much evidence supporting a causal role of climate change in these evolutionary events (Erwin, 2009; Gingerich, 2003, 2006). However, the notion that fossil assemblages from particular geographic regions (e.g., the Clarks Fork Basin of northern Wyoming) appear and disappear synchronously over regional or continental scales is not likely to be strictly true, especially for large and mobile animals like mammals. We suggest that seemingly anachronistic mammal assemblages in southern Wyoming, characterized by the co-occurrence of taxa that never co-occur in contemporary faunal assemblages from northern Wyoming, may reflect a combination of taxon-specific shifts in geographic ranges across a latitudinal and climatic gradient and gaps in the local record of the Clarks Fork Basin. As regional climate warmed during the late Paleocene, the first and last appearances of individual taxa would be expected to be somewhat asynchronous across a latitudinal gradient, leading to the anachronistic associations of taxa that are found at Twelvemile Gulch and Big Multi Quarry. Relying on immigrant taxa such as Rodentia, Coryphodontidae, and Miacidae as index fossils for Clarkforkian biostratigraphy is justified because of their highly diagnostic morphology and their presumed ability to disperse widely and rapidly once colonization has occurred. In contrast, endemic North American clades such as Plesiadapidae and Phenacodontidae, which already boasted long evolutionary histories in North America by the Clarkforkian, may be more prone to asynchronous range shifts in response to changes in regional climate or local environments through time.

ACKNOWLEDGMENTS

The authors thank K. Tietjen for her artistry and skill at producing fossil images based on CT scans. All CT scan data were collected using the Nikon XTH-225 ST micro-CT scanner at the Joint School of Nanoscience and Nanoengineering (JSNN) in Greensboro, NC. JSNN is a member of the National Nanotechnology Coordinated Infrastructure (NNCI), which is supported by the National Science Foundation (Grant ECCS-2025462).

We thank J.I. Bloch, H.H. Covert, P.D. Gingerich, K.D. Rose and the late G.F. Gunnell for helpful discussions, and D. Hansen and B. Breithaupt of the Wyoming BLM for their support and permission to collect fossils on federal lands in Sweetwater County. We thank all of the students, colleagues, and friends who have collected with us over the years in the Great Divide Basin, especially J. Emerson, N. Laudicina, E. Johnson, B. Nachman, J. Carrico, J. Crowe, J. Crowell, T. Yokley, M. Furtner, and C. Kufeldt. We owe a special debt of gratitude to the good people of Point of Rocks, WY for their help, support, and friendship over the nearly 30 years that we have been working in Sweetwater County. We might have been able to do this work without the logistical help and companionship of the Varley family of Point of Rocks (Ed, Roger, Mark, Megan, and Amanda) and especially G. Johnson, but it wouldn't have been nearly as much fun. A heartfelt thanks to M. Brotherton, who collected the first fossils from Mark's Locality and who has provided much help, support, and friendship in and out of the field for 30 years.

We thank the reviewers and Editors for their constructive comments and suggestions for improving this paper.

All fossils discussed here were collected under Bureau of Land Management paleontology collecting permit 287-WY-PA95 to RLA.

We dedicate this paper to our deceased colleague Wendy Dirks, who collected and contributed to the description of many of the fossils from Twelvemile Gulch.

AUTHOR CONTRIBUTIONS

RLA initiated the project and collected the fossils described here and took the photographs of Mark's Locality in Figure 4. RLA, KCB, and MFJ wrote the systematic descriptions. JVR measured the section and described the geology of Mark's Locality. RLA and KCB wrote the remainder of the paper.

DATA AVAILABILITY STATEMENT

All data generated in the course of this study are provided in the text or supplementary information. CT scans are reposited at Morphosource: https://www.morphosource.org/projects/000673731?locale=en

DISCLOSURE STATEMENT

No potential conflict of interest was reported by the author(s).

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SUPPLEMENTARY FILE(S)

Supplementary File 1.xlsx: data set of raw measurements.

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Handling Editor: Matthew Borths.