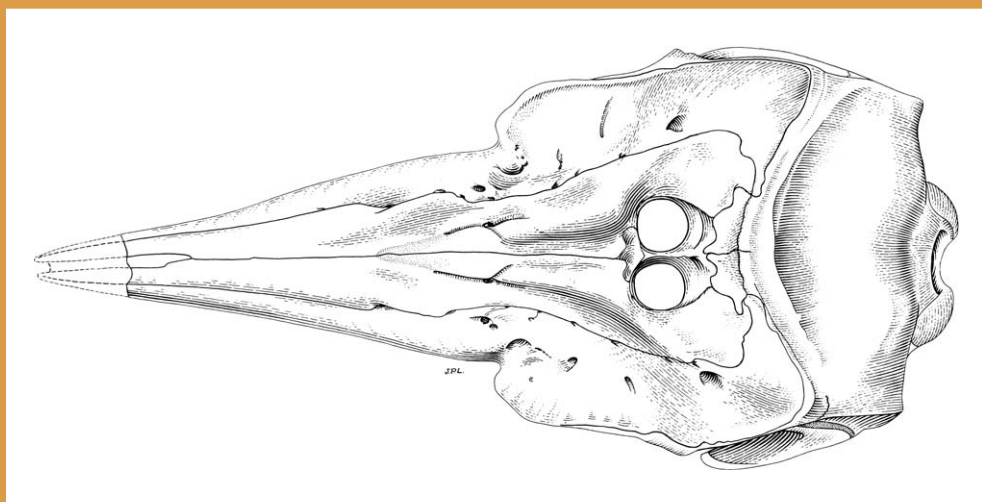


# Geology and Vertebrate Paleontology of Western and Southern North America

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Edited By Xiaoming Wang and Lawrence G. Barnes



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# Paleocene primates from the Goler Formation of the Mojave Desert in California

Donald L. Lofgren,<sup>1</sup> James G. Honey,<sup>2</sup> Malcolm C. McKenna,<sup>2,†</sup>  
Robert L. Zondervan,<sup>3</sup> and Erin E. Smith<sup>3</sup>

**ABSTRACT.** Recent collecting efforts in the Goler Formation in California's Mojave Desert have yielded new records of turtles, rays, lizards, crocodilians, and mammals, including the primates *Paromomys depressidens* Gidley, 1923; *Ignacius frugivorus* Matthew and Granger, 1921; *Plesiadapis* cf. *P. anceps*; and *Plesiadapis* cf. *P. churchilli*. The species of *Plesiadapis* Gervais, 1877, indicate that Member 4b of the Goler Formation is Tiffanian. In correlation with Tiffanian (Ti) lineage zones, *Plesiadapis* cf. *P. anceps* indicates that the Laudate Discovery Site and Edentulous Jaw Site are Ti2–Ti3 and *Plesiadapis* cf. *P. churchilli* indicates that Primate Gulch is Ti4. The presence of *Paromomys* Gidley, 1923, at the Laudate Discovery Site suggests that the Goler Formation occurrence is the youngest known for the genus. Fossils from Member 3 and the lower part of Member 4 indicate a possible marine influence as Goler Formation sediments accumulated. On the basis of these specimens and a previously documented occurrence of marine invertebrates in Member 4d, the Goler Basin probably was in close proximity to the ocean throughout much of its existence. Member 4 of the Goler Formation was deposited primarily by rivers that contained a diverse assemblage of turtles and mammals, with lizards, crocodilians, and particularly fish being rarer. An abundance of fossil wood in Member 4 suggests that Goler primates lived within stands of trees adjacent to the rivers. The Goler Formation provides the only diverse sample of Paleocene continental vertebrates from the west coast of North America. Goler mammalian assemblages are generally similar to Tiffanian faunas from the Rocky Mountain states; therefore, generally favorable conditions for dispersal between the coast and western interior must have existed. However, significant endemism is also evident in that Goler specimens of *Plesiadapis* cannot confidently be referred to existing species, and some new species of turtles and mammals are present in Goler vertebrate assemblages.

## INTRODUCTION

The Goler Formation crops out in the El Paso Mountains in the southwestern Great Basin in the Mojave Desert of California (Fig. 1). It is immensely thick, more than 3 km, and is subdivided into four members (Fig. 2) comprising mainly fluvial deposits (Dibblee, 1952; Cox, 1982, 1987), although the uppermost member contains a thin interval of marine sediments (Cox and Edwards, 1984; Cox, 1987). Originally, Goler sediments were thought to be late Eocene to Miocene in age on the basis of fossil plants (Axelrod, 1949) and other evidence (Dibblee, 1952).

The first vertebrate data potentially useful in determining the age of the Goler Formation came in 1950 when a turtle carapace and mammal tooth were found by Richard H. Tedford and R. Shultz in Member 3. They took the fossils to Chester Stock at the California Institute of Technology, but unfortunately, before the specimens could be studied, Stock died, and the fossils were lost. However, soon thereafter, M. McKenna collected a peripitychid mammal jaw fragment at the Laudate Discovery Site (base of Member 4b), which is higher in the section than the Tedford-Schultz site. This discovery indicated a Paleocene age for this part of the formation (McKenna, 1955). Over the next 35 years only about a dozen identifiable vertebrate specimens were found (all but one from Member 4a and 4b), but they corroborated the Paleocene age (McKenna, 1960; West, 1970; McKenna et al., 1987). More specifically, the mammalian fauna from Member 4b suggested that this part of the Goler Formation was Torrejonian or early

<sup>1</sup> Raymond M. Alf Museum of Paleontology, The Webb Schools, 1175 West Baseline Road, Claremont, California 91711. Email: dlofgren@webb.org

<sup>2</sup> University of Colorado Museum, 1035 Broadway Street, Boulder, Colorado 80309

<sup>3</sup> The Webb Schools, 1175 West Baseline Road, Claremont, California 91711

† Deceased

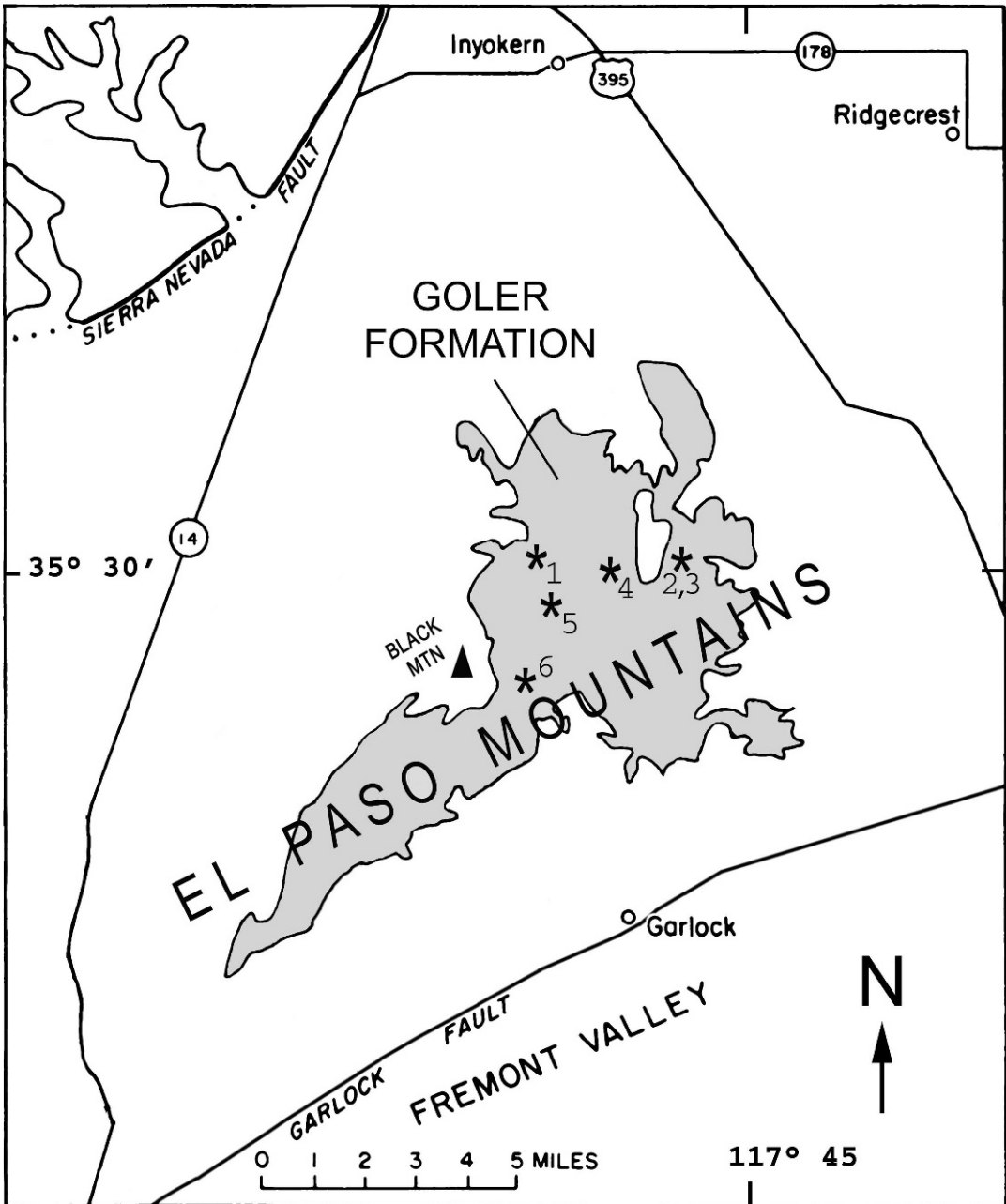
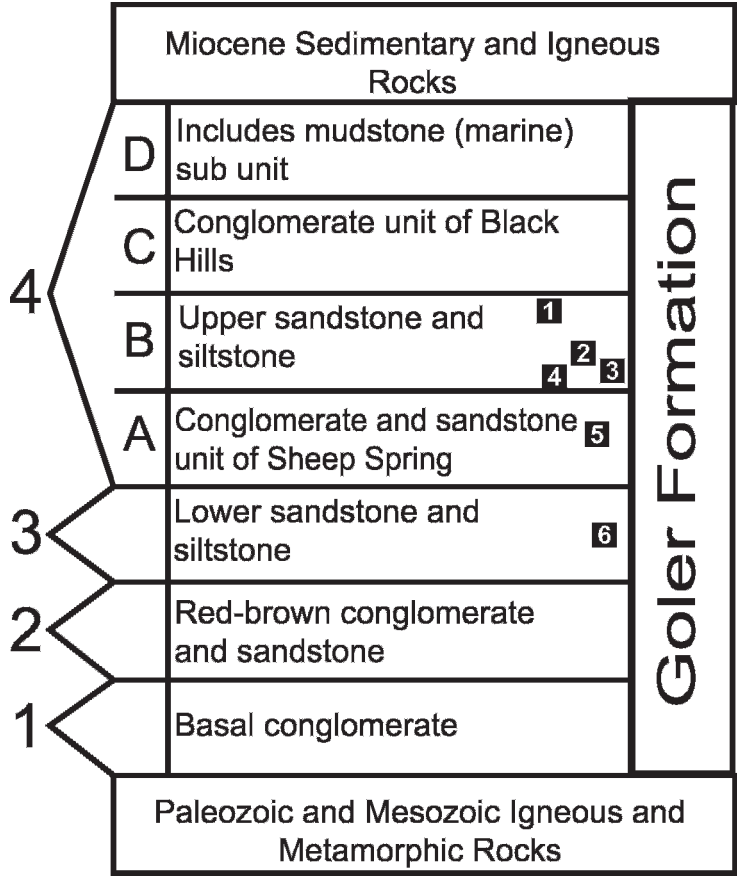


Figure 1 Outcrop map of the Goler Formation (shaded), with major vertebrate sites numbered; see Figure 2 for site names and Figure 3 for location of the El Paso Mountains within California; map adapted from Cox (1987).

Tiffanian in age (McKenna, 1960; McKenna et al., 1987).

By 1990, the Goler Formation was widely recognized as being critically important in elucidating California's early Cenozoic history. It was the only known Paleocene rock unit on the west coast of North America that could potentially yield a diverse assemblage of fossil vertebrates.

Accordingly, field crews from the Raymond M. Alf Museum of Paleontology and other institutions initiated a long-term effort in 1993 to recover a large sample of Goler vertebrates, primarily through the use of screen-washing techniques. Important new mammal localities were discovered, both lower and higher in Member 4 than the original Laudate Discovery

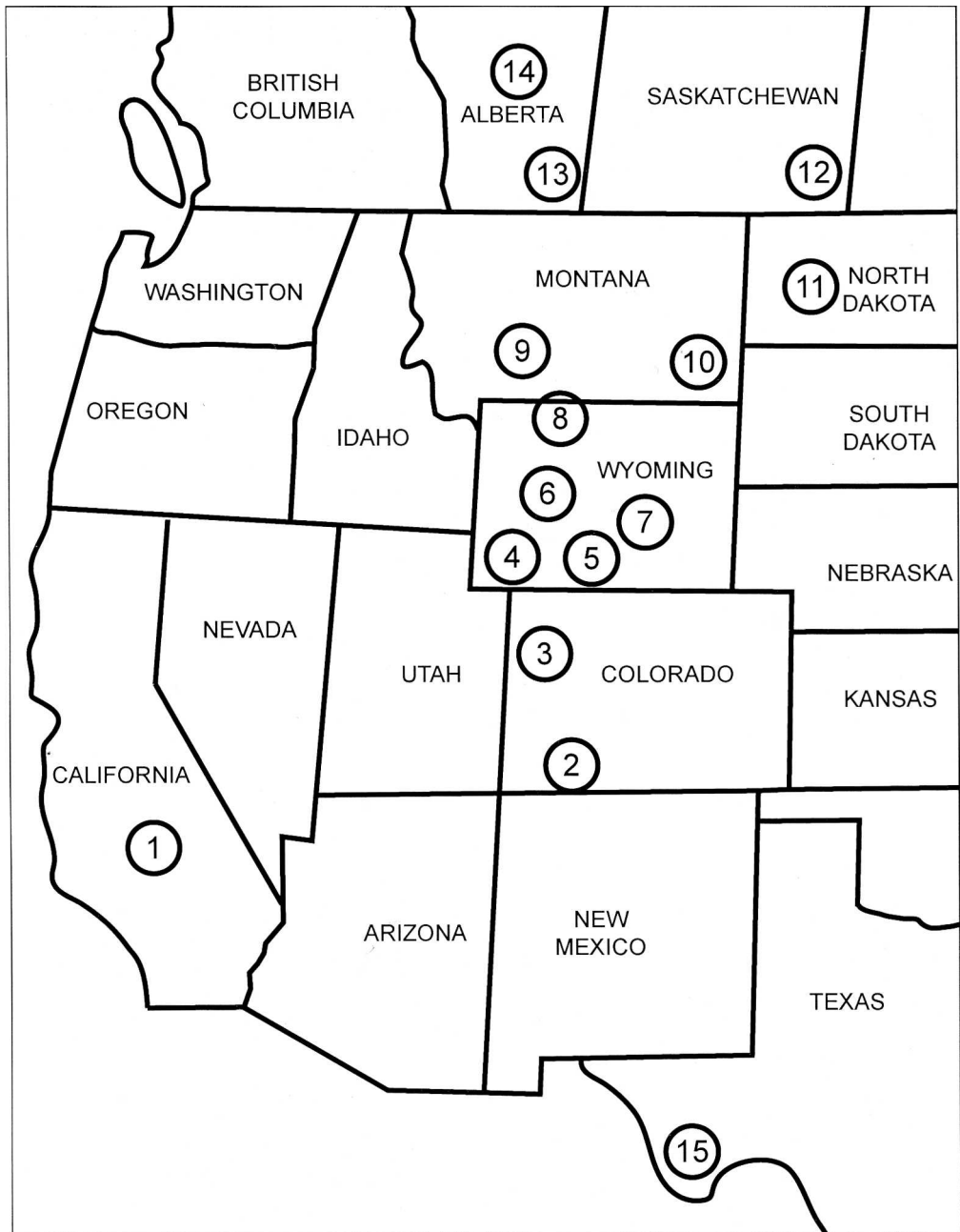


**Figure 2** Stratigraphic subdivision of the Goler Formation showing the four members and subdivisions of Member 4 (after Cox, 1987), with approximate stratigraphic location of major vertebrate-yielding sites numbered as 1, Honey Pot, locality V200120; 2, Primate Gulch, locality V200202; 3, Edentulous Jaw Site, locality V98012; 4, Laudate Discovery Site, locality V94014; 5, Land of Oz, locality V20001; and 6, the Tedford-Shultz Site. See text for discussion of stratigraphic relations between sites 2 through 4.

Site (Fig. 2). More than 15 tons of sediment were screen-washed, and a few hundred additional specimens were recovered. Many species represent new records for the Goler Formation, including several kinds of turtles (baenids, “macrobaenids,” and trionychids), rays (cf. *Hypolophodon* Capetta, 1980), lizards (cf. *Proxestops* Gauthier, 1982; cf. *Paleoxantusia* Hecht, 1956), crocodilians (cf. *Allognathosuchus* Mook, 1921), and mammals (multituberculates, marsupials, plesiadapid and paromomyid primates, carnivores, and mesonychids, as well as arctocyonid, hyopsodontid, phenacodontid, and peripitychid ungulates) (Lofgren et al., 1999, 2002, 2004c; McKenna and Lofgren, 2003). The newly expanded assemblage of mammals is diverse and represents the oldest known record of Mammalia from California other than the metacarpal recently described from late Cretaceous marine rocks in Butte County (Wilson et al., 2003). The Goler Formation specimens are

also the oldest mammalian dental remains from the west coast of North America other than the few specimens described by Lillegraven (1972, 1976) from Upper Cretaceous rocks of Baja California.

Of particular interest is the recovery of the primates *Plesiadapis*, *Ignacius* Matthew and Granger, 1921, and *Paromomys*. Their occurrence in California during the Paleocene raises interesting paleoecological and paleobiogeographic issues. The nearest sites that have yielded *Plesiadapis* are in Colorado and Wyoming (Fig. 3). Also, the presence of *Plesiadapis* indicates that the mammal-bearing part of Member 4 is younger than was previously thought. Here we describe California’s first record of Paleocene primates, their utility in determining the age of the mammal-yielding part of the formation, and implications of their presence to Paleocene paleobiogeography and paleoecology of this part of western North America.



**Figure 3** Map of western North America with areas (basins, formations, or localities) that have yielded Paleocene plesiadapids: 1, Goler Formation; 2, Animas Formation; 3, Piceance Creek Basin; 4, Green River and Fossil basins; 5, Washakie and Bison basins; 6, Wind River and Hoback basins; 7, Hanna and Carbon basins; 8, Bighorn and Clarks Fork basins; 9, Crazy Mountains Basin; 10, Western Williston and Powder River basins; 11, Eastern Williston Basin; 12, Roche Percée; 13, Police Point; 14, Paskapoo and Porcupine Hills formations; and 15, Blacks Peak Member of Tornillo Formation. Adapted from Gingerich (1976).

# METHODS AND MATERIALS

Primates described here were recovered from three sites: (A) V200202, Primate Gulch, RAM

7193; (B) V98012, Edentulous Jaw Site, RAM 6431, 6433, 6446, 6700, 6929, 6931, 6934, 6935, 6946, 6957, 6960, 6961, 6962, 6963; and (C) V94014, Laudate Discovery Site, RAM 6426,

6925. RAM 6925 and 7193 were found by surface collecting. All of the others were recovered through the screen-washing process. The classification scheme used here follows that of McKenna and Bell (1997). An ocular micrometer (RAM 7193) and digital calipers (all other specimens) were used to measure teeth. Measurements are in millimeters. Cusp terminology for teeth is that of Van Valen (1966:fig. 1) and Gingerich (1976:figs. 4 and 5). Measurements of teeth were taken following Lillegraven (1969:fig. 5). For plesiadapid upper incisors, maximum width was measured at the widest part of the laterocone, perpendicular to the long axis of the tooth.

The Raymond M. Alf Museum of Paleontology (RAM) records each vertebrate locality with a V followed by numbers (e.g., V98012). Specimens are given a numerical code preceded by RAM (e.g., RAM 6925).

## ABBREVIATIONS

AMNH	American Museum of Natural History, New York, New York USA
GH Wa	Geiseltalmuseum, Halle, Germany
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts USA
PU	Princeton University (now at Peabody Museum, Yale University), New Haven, Connecticut USA
RAM	Raymond M. Alf Museum of Paleontology, The Webb Schools, Claremont, California USA
SMM	Science Museum of Minnesota, St. Paul, Minnesota USA
UA	University of Alberta, Calgary, Alberta Canada
UCMP	Museum of Paleontology, University of California, Berkeley, California USA
USNM	Department of Paleobiology United States National Museum, Smithsonian Institution, Washington, D.C. USA

## SYSTEMATICS

### Order Primates

### Suborder Dermoptera

### Family Paromomyidae Simpson, 1940

### Subfamily Paromomyinae Simpson, 1940

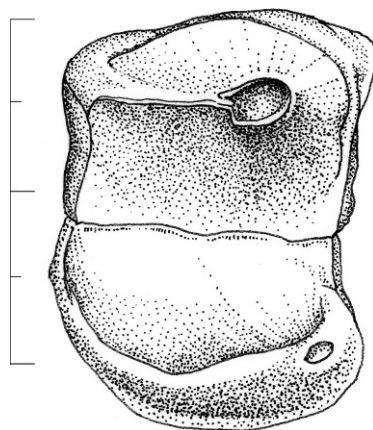
### *Paromomys* Gidley, 1923

### *Paromomys depressidens* Gidley, 1923

Figure 4

**HOLOTYPE.** USNM 9546, part of upper jaw with P4–M3, Gidley Quarry, Fort Union Formation, Montana (middle Torrejonian).

**REFERRED SPECIMEN.** One P4 (RAM 6426) from locality V94014.



**Figure 4** *Paromomys depressidens* Gidley, 1923, right P4, RAM 6426 from locality V94014, occlusal view. Scale bar = 2 mm.

**DESCRIPTION.** The only specimen from the Goler Formation that can be assigned to *Paromomys* is a slightly damaged P4 (RAM 6426). Damage is primarily limited to the tooth's edge as the thin veneer of enamel that should coat the tooth is absent from its posterolabial, anterolabial, and labial margins. The absence of enamel in these regions does not appear to alter significantly the tooth's general morphology, except that the small metastyle and parastyle were probably more pronounced. The paracone is large and connected to a small metastyle by a very well developed postparacrista. A metacone is not present. The protocone is less elevated and significantly smaller than the paracone, and it is positioned anterior to the paracone on the anterolingual edge of the tooth. A prominent cingulum runs posterior from the protocone, becoming progressively less developed as it curves around to the tooth's posterior edge. Between this cingulum, the protocone, and the paracone-postparacrista is a large posterolingual basin. Between the parastyle and metastyle, a buccal cingulum was almost certainly present because a distinct lineation is evident that appears to approximate the former position of the cingulum. A cingulum does not appear to have been present between the parastyle and protocone. However, owing to the lack of enamel in this region of the tooth, a cingulum could have been present, but if so, it was very diminutive. The length of RAM 6426 is 1.85 mm, width is 2.36 mm.

**DISCUSSION.** Gidley (1923) erected the genus *Paromomys* and named two species, *Paromomys maturus* Gidley, 1923, and *Paromomys depressidens*, both from the Gidley Quarry, Lebo Formation, Crazy Mountains, Montana. They were differentiated by size and morphology (Gidley, 1923). The type of *P. depressidens* (USNM 9546) is a right maxillary fragment with P4–M3. The P4 of the type was described as having a well-



developed posterior cingulum with a “postproto-crista” that forms with the protocone a posterolingual basin on the tooth, with an incipient metacone placed on the postparacrista near the external cingulum (Gidley, 1923). No measurements of the P4 of the type were given. However, Simpson (1937) later noted that the P4 of USNM 9546 was  $1.9 \times 2.0$  mm (length  $\times$  width) and also that the metacone of *P. depressidens* was very small or indistinct on P4 (Simpson, 1955).

RAM 6426 is referred to *Paromomys depressidens* because it is much smaller than the P4 of *P. maturus*, it lacks a distinct metacone and, although slightly larger, it is very similar in size and morphology to specimens referred to the species, especially those from the Swain Quarry, Fort Union Formation, Wyoming, described by Rigby (1980). Lack of a metacone on RAM 6426 clearly distinguishes it from *Phenacolemur* Matthew, 1915, *Ignacius*, and *Palaechthon* Gidley, 1923, all of which have distinct P4 metacones (Simpson, 1955). Compared with P4s referred to *P. depressidens* from other sites, RAM 6426 is large ( $1.85 \times 2.36$  mm), more transverse than the holotype ( $1.9 \times 2.0$  mm) from Gidley Quarry, and larger than single P4s referred to *Paromomys* cf. *P. depressidens* from Cochrane 2, Porcupine Hills Formation, Alberta (UA 11744,  $1.5 \times 1.8$  mm) (Krause, 1978) and *Paromomys* near *P. depressidens* from the Shotgun Fauna, Fort Union Formation, Wyoming (MCZ 18764,  $1.6 \times 1.9$  mm; Gazin, 1971). Unlike RAM 6426, the latter two specimens have a small metacone (Gazin, 1971; Krause, 1978). RAM 6426 is most similar to the Swain Quarry sample of *P. depressidens* where measurements of four P4s are presented (observed range  $1.77\text{--}1.85$  mm  $\times$   $2.1\text{--}2.25$  mm; Rigby, 1980:table 32). Also, the Swain Quarry sample is described as being inseparable from the Gidley Quarry sample from which the holotype was collected (Rigby, 1980). Specimens from the Gidley Quarry were not studied, but those from the Swain Quarry sample were compared directly with the Goler specimen. RAM 6426 is virtually identical to both AMNH 80976a and AMNH 80976b, although RAM 6426 is slightly more transverse than either AMNH specimen.

#### Subfamily Phenacolemurinae Simpson, 1955

##### *Ignacius* Matthew and Granger, 1921

##### *Ignacius frugivorus* Matthew and Granger, 1921

Figure 5

**HOLOTYPE.** AMNH 17368, left maxilla with P2, P4–M2. Mason Pocket, Animas Formation, late Tiffanian, Colorado.

**REFERRED SPECIMEN.** One m3 (RAM 6433) from locality V98012.

**DESCRIPTION.** The slightly damaged lower molar (RAM 6433) assigned to *Ignacius* is small;

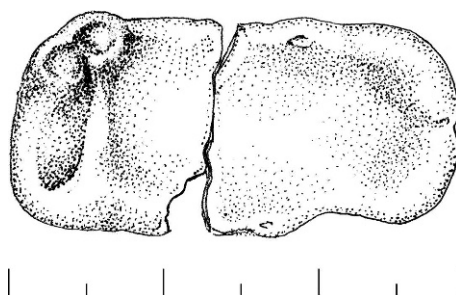


Figure 5 *Ignacius frugivorus* Matthew and Granger, 1921, left m3, RAM 6433 from locality V98012, occlusal view. Scale bar = 3 mm.

length 2.94 mm, width 1.47 mm. It was found in two pieces during sorting of screen-washed concentrate (the small fragments missing from the lingual and labial margins of the talonid were not recovered). RAM 6433 is slightly worn, with significant wear evident only on the paraconid and metaconid. The paraconid and metaconid are small, subequal in size, and separated by a narrow, but distinct, valley. Only after moderate to heavy wear would the paraconid and metaconid merge into a single cusp. The paraconid is deflected labially relative to the metaconid. The protoconid is the largest of the trigonid cusps, and it is connected to the metaconid by a well-developed protocristid. The paracristid is lower and less developed than the protocristid and curves at its labial edge to connect with the protoconid. The protoconid and metaconid are approximately parallel in relation to the lingual–labial axis of the trigonid. RAM 6433 has a rounded and well-developed hypoconulid lobe that is broad and elevated. The hypoconulid lobe is separated into two distinct bulbous cusps by a shallow valley. A small, slightly elevated hypoconid is present. Immediately posterior to the hypoconid, the talonid’s margin deflects lingually, forming a distinct notch that separates the hypoconulid lobe from the hypoconid. A distinct entoconid is present on a well-developed and sharply elevated crest that borders the lingual margin of the talonid. The entoconid is larger and much higher than the hypoconid and is positioned more posteriorly on the talonid. A notch is not present on the lingual margin of the talonid, anterior to the hypoconulid lobe.

**DISCUSSION.** Distinguishing between species of *Ignacius* and *Phenacolemur* based on isolated teeth is difficult (Rose, 1981). Matthew’s (1915) genus *Phenacolemur* was based on a lower jaw of *Phenacolemur praecox* Matthew, 1915. Soon thereafter, Matthew and Granger (1921) described a new genus and species, *I. frugivorus*, based on a maxillary fragment. Simpson (1935) synonymized the genera, noting that the type and other specimens referred to *Ignacius frugivorus* were exactly like those of *Phenacolemur*, only smaller. Bown and Rose (1976) resurrected the

genus *Ignacius*, noting differences in tooth morphology and that *Ignacius* has a deeper and narrower mandible in relation to the cheek teeth. Rose and Gingerich (1976) and Rose (1981) further supported the separation of *Ignacius* and *Phenacolemur* on the basis of tooth and cranial morphology. The isolated m3 (RAM 6433) from the Goler Formation is most similar to m3s referred to *Ignacius*.

The Goler m3 is very similar to specimens referred to *Ignacius frugivorus* by Krause (1978) from the Roche Percée Local Fauna, Ravenscrag Formation, Saskatchewan, Canada. The Roche Percée specimens and RAM 6433 have small paraconids and metaconids and a notch posterior to their hypoconids (Krause, 1978:fig. 5, UA 8839) and are almost identical in size (length 2.5–2.8 mm, width 1.4–1.5 mm; Krause, 1978:table 7; RAM 6433 length 2.94 mm, width 1.47 mm). RAM 6433 is also very similar in size to AMNH 17405 (length 2.9 mm, width 1.6 mm) from Mason Pocket, Animas Formation, Colorado, which was referred to *Ignacius* (“*Phenacolemur*”) *frugivorus* by Simpson (1935). Compared with other Paleocene–Early Eocene species of *Ignacius*, RAM 6433 is larger than m3s of *Ignacius fremontensis* Gazin, 1971, from the Shotgun Fauna, Fort Union Formation, Wyoming (Gazin, 1971), and much smaller than *Ignacius graybullianus* Bown and Rose, 1976, from the Willwood Formation, Wyoming (Bown and Rose, 1976:table II).

Two m3s referred to *Ignacius frugivorus* (length  $\times$  width,  $2.80 \times 1.20$  mm and  $2.60 \times 1.50$  mm) from the Tongue River Formation of North Dakota by Holtzman (1978) are smaller than RAM 6433 ( $2.94 \times 1.47$  mm), but morphologically they are nearly identical to the Goler specimen. Especially significant is their trigonid morphology, as both RAM 6433 and SMM P77.7.131 have a small, but distinct, paraconid and metaconid, a labially deflected paraconid, and a metaconid and protoconid that are positioned subparallel to one another (Holtzman, 1978:fig. 8).

Compared with m3s of species of *Phenacolemur*, RAM 6433 is much larger than that of *Phenacolemur simonsi* Bown and Rose, 1976 (Bown and Rose, 1976:table III; Robinson and Ivy, 1994:table 4), and much smaller than those of *Phenacolemur praecox* and *Phenacolemur jepseni* Simpson, 1955 (Simpson, 1955:tables 4 and 6). *Phenacolemur pagei* Jepsen, 1930, is most similar to RAM 6433 in morphology and size, although *P. pagei* is slightly larger (Simpson, 1955:table 2). However, in his description of the dentition of *Phenacolemur*, Simpson (1955) drew heavily on the specimens of *P. pagei* from the Silver Coulee Quarry, Polecat Bench Formation, Wyoming, and noted that “the paraconid is so small and so nearly fused with the metaconid that it cannot be distinguished at all except when practically unworn” (Simpson, 1955:431). In

contrast, the paraconid and metaconid on the Goler m3 would merge only after moderate to heavy wear. Finally, the talonid notch is poorly defined or absent in *Ignacius* and typically well marked in *Phenacolemur* (Rose, 1981). RAM 6433 lacks a well defined talonid notch.

## Family Plesiadapidae Trouessart, 1897

### *Plesiadapis* Gervais, 1877

### *Plesiadapis anceps* Simpson, 1936

### *Plesiadapis* cf. *P. anceps*

Figure 6A–E; Table 1

**HOLOTYPE.** AMNH 33822, left lower jaw with incisor and m1–3, right p4 and m1, right P3–M1, left M1–2, and other fragments, all from one individual. Scarritt Quarry, Fort Union Formation, early Tiffanian, Montana.

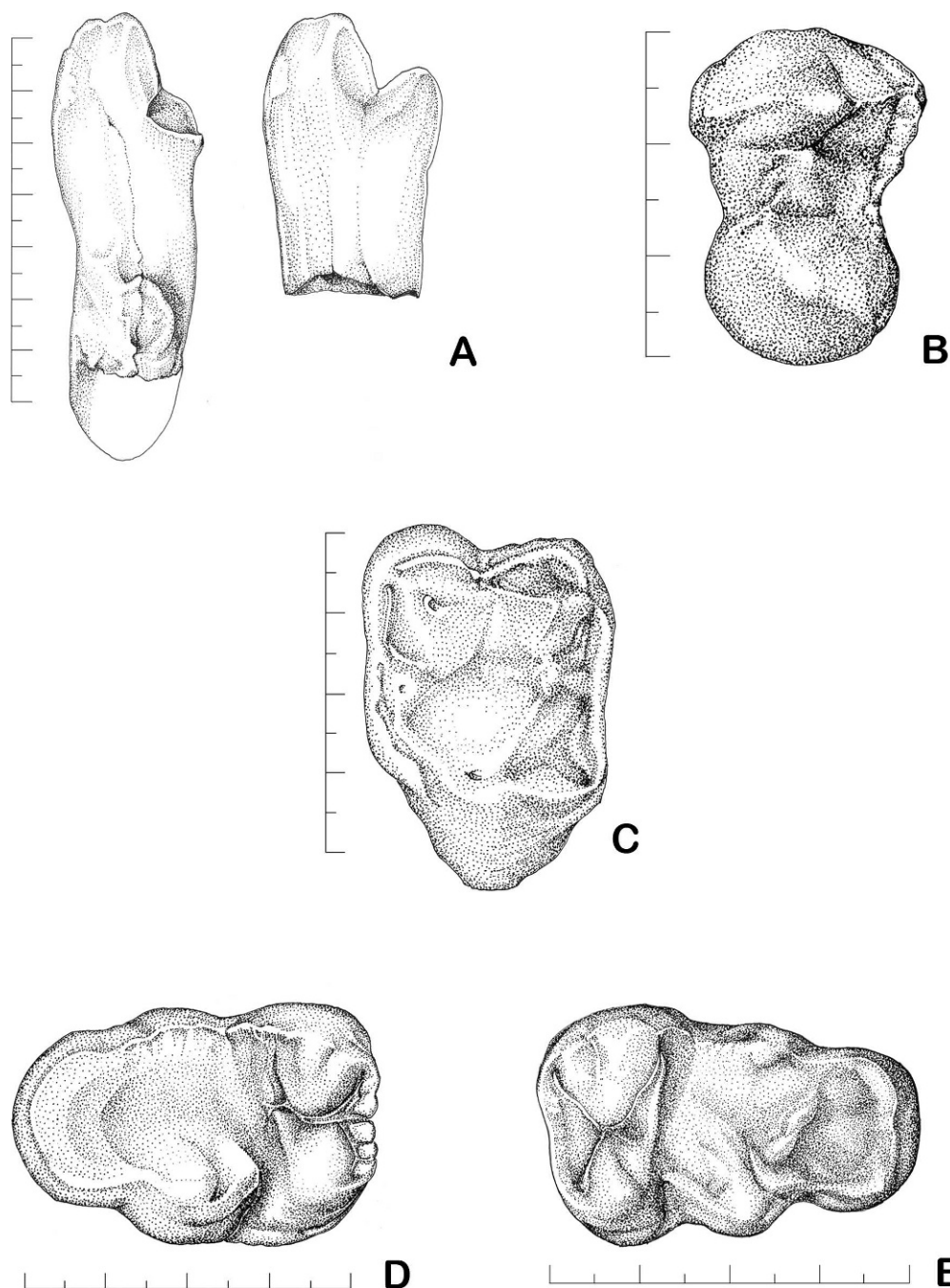
**REFERRED SPECIMENS.** Five m3s (RAM 6960, RAM 6963, RAM 6700, RAM 6961, RAM 6934), 1 m2 (RAM 6446), 1 mx fragment (RAM 6935), 1 mx trigonid (RAM 6946), 1 M3 (RAM 6957), 1 M2 (RAM 6962), 1 P4 (RAM 6931), and 2 I1s (RAM 6431, RAM 6929) from locality V98012. One m3 (RAM 6925) from locality V94014.

**DESCRIPTION.** Compared with *Paromomys* and *Ignacius*, the sample referred to *Plesiadapis* cf. *P. anceps* from the Goler Formation is relatively large, consisting of 14 complete or partial teeth whose measurements are given in Table 1 (except RAM 6946).

**Incisors.** Two damaged upper left incisors were recovered (Fig. 6A). Only the crown is present on RAM 6929 because the tooth is broken just above the position of the posterocone. RAM 6929 has a prominent anterocone and laterocone and a minute mediocone. The tip of the tiny mediocone is missing because of breakage. A centroconule is not present. RAM 6431 has a prominent anterocone. Both the laterocone and posterocone are broken off at their base, but both cusps were large, as shown by the size of the breaks. There is no trace of a mediocone or centroconule.

**Premolars.** Only a single premolar was recovered, an unworn and well-preserved P4 (RAM 6931; Fig. 6B). RAM 6931 has a very large paracone and a smaller but prominent protocone. There is no trace of a metacone. A small paraconule is closely appressed to, and positioned high on the lingual slope of, the paracone. The paraconule and protocone are subequal in height. A weakly developed paracrista extends from the paracone to the anterolabial margin of the tooth where a very small parastyle is present. A well-developed crest runs posteriorly from the paracone and terminates at a small metastyle. A cingulum is developed only on the posterior margin of RAM 6931 between the posterior slope of the protocone and the metastyle.





**Figure 6** *Plesiadapis* cf. *P. anceps* Simpson, 1936, occlusal views of isolated teeth from locality V98012: A, RAM 6431 (left) and RAM 6929 (right), left I1's, scale bar = 7 mm; B, RAM 6931, left P4, scale bar = 3 mm; C, RAM 6962, left M2, scale bar = 4 mm; D, RAM 6700, right m3, scale bar = 4 mm; E, RAM 6963, left m3, scale bar = 4 mm.

**Upper Molars.** Two upper molars were recovered, a damaged M3 (RAM 6957), and a well-preserved M2 (RAM 6962; Fig. 6C). RAM 6957 is slightly worn and is missing its anterolabial corner (paracone is entirely absent). A small metacone is present, as are a very small para-

conule and metaconule. A strongly developed preprotocrista connects the paraconule with the protocone. The protocone is large and broad, with 2 to 3 enamel crenulations developed both on its anterolingual and posterolabial slopes, with those on the latter being much better developed.

**Table 1** Measurements (mm) of isolated *Plesiadapis* teeth from the Goler Formation.

Specimen no.	Tooth position	Length	Width
RAM 6963	m3	4.32	2.95
RAM 6960	m3	4.52	3.16
RAM 6700	m3	4.59	3.15
RAM 6961	m3	4.84	3.20
RAM 6934	m3	—	2.82*
RAM 6925	m3	4.79	3.38
RAM 6446	m2	3.55*	3.15*
RAM 6935	mx	—	2.75*
RAM 6931	P4	2.30	3.11
RAM 6962	M2	3.35	4.62
RAM 6957	M3	2.94*	3.61*
RAM 6929	I1	—	3.22
RAM 6431	I1	—	2.96*

RAM 6925 from V94014; all others from V98012.

\* Tooth incomplete, so measurement is a minimum.

Both a precingulum and a postcingulum are present, and they terminate labially at the paraconule and metaconule, respectively. A weakly developed ridge stretches posteriorly from the protocone to the postcingulum, but a distinct hypocone is not evident.

RAM 6962 is slightly worn and its paracone and metacone are large, with the paracone being slightly broader. A strong ectoflexus is present, as are a centrocrista, paracrista, and metacrista. RAM 6962 has no trace of a metastyle, parastyle, or mesostyle. Both a small paraconule and metaconule are present, and well-developed pre-protocrista and postprotocrista connect these cusps to a large and broad protocone. A small hypocone is located on a crest that runs posteriorly from the protocone and merges with the postcingulum. A well-developed cingulum rings the tooth's margin except along the lingual slope of the protocone and hypocone and at the terminus of the metacrista.

**Lower Molars.** These nine teeth provide the most comprehensive data for this species and six of them are complete or partial m3s that give some perspective on variation at a particular tooth site. A general description of these m3s is given on the basis of RAM 6700, a slightly worn specimen (Fig. 6D). Variations in morphology or important features are noted in the brief descriptions of the other m3s.

RAM 6700 has a small metaconid and paraconid, with the former being slightly higher and much larger. The protoconid is subequal in size to, but lower than, the metaconid. The paracristid is well developed, the protocristid much less so. The talonid is dominated by a very large, rounded hypoconulid lobe that is not fissured and has no evidence of crenulations. The hypoconid is large, and it is separated by a lingually sloping, shallow valley from a smaller

and less elevated mesoconid, which is very close to the trigonid. An entocristid is well developed, but a distinct entoconid is not present. The entocristid rises in elevation from the talonid notch to merge with the hypoconulid lobe. The deep talonid basin is deepest adjacent to the talonid notch. RAM 6700 is widest at the hypoconid region of the talonid. Directly posterior to the hypoconid, the tooth's margin deflects lingually, which demarks the beginning of the hypoconulid lobe. A distinct labial cingulum is present.

RAM 6934 is very slightly worn, and only the talonid is preserved. The hypoconulid lobe is rounded, and a few shallow crenulations are developed on the posterior part of the talonid basin that impinge slightly onto the hypoconulid lobe.

RAM 6961 is moderately worn. Its hypoconulid lobe is squared and most of the enamel on the talonid is missing because of wear and breakage. If fissures were present, they have been obscured.

RAM 6960 is heavily worn and the enamel on the talonid has been breached by wear in many places. The hypoconulid lobe is rounded. An area of enamel is preserved near the rear of the talonid basin, which has a few shallow crenulations.

RAM 6925 is moderately worn and slightly damaged. A section of enamel is missing from the lingual trigonid wall. The hypoconulid lobe of RAM 6925 is rounded and has 2 small fissures that are deepest on the anterior part of the lobe. These fissures terminate before reaching the posterior margin of the lobe. The talonid of RAM 6925 is more strongly crenulated than any of the other m3s, with 4 or 5 deep crenulations developed in the posterior part of the talonid basin. These crenulations also extend onto the lingual slope of the hypoconid. Unlike other m3s, the entocristid remains elevated as it merges with the trigonid, and thus a talonid notch is not present.

RAM 6963 is unworn and well preserved (Fig. 6E). The talonid is different from the other m3s in a number of ways. The talonid basin is relatively shallow, being deepest just anterior to the hypoconulid lobe. In this same area, a few shallow crenulations are developed that extend onto the anterior part of the hypoconulid lobe. The hypoconid of RAM 6963 is similar to that of other m3s, but its mesoconid is ridgelike, lacking a distinct apex. Also, there is a distinct cusp on the entocristid, subparallel to the hypoconid. Posterior to this entocristid cusp, the tooth's margin deflects slightly labially, more so than in the other Goler m3s. Also, unlike the other m3s, there is a small cusp developed just posterior to the hypoconid. Posterior to this cusp, the tooth's margin is deflected strongly lingually. Thus, with both its labial and lingual anterior margins deflected toward the axis of the talonid basin,

the hypoconulid lobe of RAM 6963 is markedly squared in appearance.

Three other teeth are identified as lower molars; a nearly complete m2 (RAM 6446) and two broken teeth (RAM 6935 and 6946). Both RAM 6935 and RAM 6946 are too damaged to determine which tooth site they represent. RAM 6946 is a fragment of a trigonid that is missing its lingual wall, including all of the metacone. On the basis of color and wear, RAM 6946 might be the missing trigonid of RAM 6934 (m3). RAM 6935 is more complete, having preserved the entire trigonid and the anterior portion of the talonid.

RAM 6446 is a nearly complete m2 that is chipped along its entire exterior edge. Thus, much of the base of the tooth is missing, including a large part of the lingual wall of the trigonid. The paraconid and metaconid of RAM 6446 are subequal in size, with both a paracristid and protocristid present, the former being better developed. The hypoconid is much larger than the entoconid, and the entoconid corner is curved. A small labial cingulum is present.

**DISCUSSION.** On the basis of size and general morphology, we conclude that these 14 isolated teeth are from a single species. All but RAM 6925 are from a single locality, which lends support to the single species hypothesis. The six m3s provide information about variability at a single tooth site, and their morphology does exhibit significant variation, indicating that perhaps more than one species is present. However, without more complete material, this cannot be determined. Bearing in mind this caveat, we discuss the various genera and species of plesiadapids in relation to the Goler Formation specimens.

Five genera of plesiadapids are known from Torrejonian through Clarkforkian rocks in North America: *Pronothodectes* Gidley, 1923; *Saxonella* Russell, 1964; *Nannodectes* Gingerich, 1975; *Chiromyoides* Stehlin, 1916; and *Plesiadapis*. Specimens referred to *Saxonella* and *Pronothodectes* are much smaller than those of the Goler Formation sample listed in Table 1 (for *Pronothodectes* see Gingerich, 1976; for *Saxonella* see Fox, 1991). Also, upper central incisors of *Chiromyoides* are extraordinarily robust (Gingerich, 1976), which contrasts with the conservative morphology of the two Goler incisors.

Of the four species of *Nannodectes*, the two largest species, *Nannodectes simpsoni* Gazin, 1971, and *Nannodectes gidleyi* Matthew, 1917, are nearly equal in size to Goler specimens (Gingerich, 1976:tables A-5 and A-6). However, unlike the Goler sample, *N. gidleyi* has highly crenulated m3 talonid enamel and M2s with mesostyles (Gingerich, 1976). The m3s of *N. simpsoni* (USNM 20756, 20751) have uncrenulated talonid enamel, but they are smaller and have narrower hypoconulid lobes than the Goler Formation specimens.

With regard to European species of *Plesiadapis*, the only one that approaches the general morphology seen in the Goler sample is *Plesiadapis walbeckensis* Russell, 1964. The m3 of Walbeck specimen GH Wa 392 is similar to Goler m3s in most respects, but GH Wa 392 has a fissured heel and its number of talonid enamel crenulations exceeds anything seen in Goler m3s. Also, *P. walbeckensis* has a large mediocone on the central upper incisor (Gingerich, 1976), unlike either of the two Goler incisors.

There are many North American species of *Plesiadapis*, but most can be quickly eliminated. On the basis of size, compared with the Goler specimens, *Plesiadapis praecursor* Gingerich, 1975, is too small and *Plesiadapis simonsi* Gingerich, 1975; *Plesiadapis cookei* Jepsen, 1930; and *Plesiadapis gingerichi* Rose, 1981, are far too large. *Plesiadapis dubius* Matthew, 1915; *Plesiadapis fodinatus* Jepsen, 1930; and *Plesiadapis churchilli* are closer in size to the Goler Formation sample, but the smallest specimens of these species at each particular tooth site (Gingerich, 1976:tables A-9–A-12) exceed or equal the size of the largest tooth from the comparable tooth site in the Goler Formation sample (Table 1). Furthermore, unlike the Goler sample, *P. fodinatus*, *P. dubius*, and *P. churchilli* have strong mesostyles on upper molars and fissured heels on m3s; *P. fodinatus* and *P. dubius* have highly crenulated talonid enamel on m3s, and *P. churchilli* and *P. fodinatus* have small or well-developed centroconules on upper central incisors (Gingerich, 1976).

The Goler Formation specimens are most similar to *Plesiadapis rex* Gidley, 1923, and *Plesiadapis anceps* in size and general morphology. With regard to size, there is considerable overlap between the samples referred to *P. anceps* from the Bison Basin Saddle locality (Gingerich, 1976:table A-7) and the holotype of *P. anceps* (AMNH 33822) from Scarritt Quarry (Simpson, 1936) with that of the sample referred to *P. rex* from the Cedar Point Quarry (Gingerich, 1976:table A-8). The Goler Formation sample generally falls into this zone of overlap or it is more similar to *P. rex* (Table 1).

In his monograph on plesiadapids, Gingerich (1976) described various morphological features used to distinguish *Plesiadapis anceps* from *P. rex*, some of which are evident in the small Goler sample of isolated teeth. Key features of the Goler Formation specimens are: upper incisors lack centroconules, mediocone absent on RAM 6431 and minute on RAM 6929, the only complete upper molar (RAM 6962) lacks a mesostyle, and m3s have squared to rounded hypoconulid lobes with smooth to slightly crenulated talonid enamel. Also, hypoconulid lobe fissures are absent except on RAM 6925, whose weakly developed fissures do not divide the lobe into medial and lateral parts.

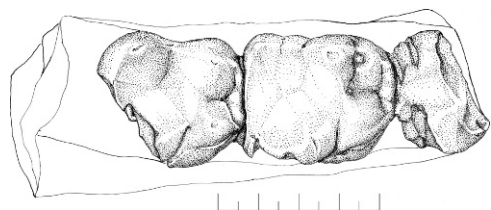


Figure 7 *Plesiadapis* cf. *P. churchilli* Gingerich, 1975, right mandible fragment with damaged p4, m1, and m2, RAM 7193 from locality V200202, occlusal view. Scale bar = 4 mm.

*Plesiadapis anceps* lacks an M2 mesostyle, has a small mediocone but no centroconule on the central upper incisor, and has a hypoconulid lobe that varies from squared to rounded, with smooth enamel and small fissures on half of known specimens (Gingerich, 1976). In contrast, *P. rex* usually has a mesostyle on M2, a centroconule and small mediocone on the central upper incisor, and an m3 hypoconulid lobe that tends to be broad, squared, usually with moderately crenulated enamel, and a single, small fissure that divides the lobe into medial and lateral parts (Gingerich, 1976).

In general, the Goler sample is more similar to *P. anceps* than to *P. rex*. Key features that contrast Goler specimens with *P. rex* are: lack of a mesostyle on RAM 6962 (M2), lack of a centroconule on both Goler upper incisors, and lack of a fissure on the hypoconulid lobe of m3 that divides it into two parts, and the lobe of Goler m3s tend to range between rounded and squared. Key features that contrast Goler specimens with *P. anceps* are: presence of crenulations on some hypoconulid lobes of Goler m3s, lack of a mediocone on RAM 6931, and slightly larger size of some Goler specimens. Thus, in most features, the Goler sample resembles *P. anceps*. Also, certain Goler specimens, such as RAM 6700 (m3), are almost identical to specimens of *P. anceps* from the Bison Basin Saddle locality (USNM 20587).

The Goler sample of isolated teeth is more similar to *Plesiadapis rex* in size, but it is more similar to *P. anceps* in morphology. Therefore, these teeth are designated *Plesiadapis* cf. *P. anceps*, denoting their close morphological similarity to *Plesiadapis anceps*.

#### *Plesiadapis churchilli* Gingerich, 1975

##### *Plesiadapis* cf. *P. churchilli* Figure 7

**HOLOTYPE.** PU 21234, left mandible with i1, p3–4, and m1–3. Long Draw Quarry, Polecat Bench Formation, late Tiffanian, Wyoming.

**REFERRED SPECIMEN.** Partial right mandible with talonid fragment of p4, m1, and broken m2 (RAM 7193) from locality V200202.

**DESCRIPTION.** RAM 7193 is a fragmentary right ramus containing a damaged p4, m1, and m2. The p4 is broken anterior to the heel. The damaged heel has a shallow talonid basin with a hypoconid and broken entoconid. Both m1 and m2 are broken at the hypoconid corner. The two molars appear to be water worn, with consequent reduction of morphological detail; for example, no enamel crenulation is observable, if it were ever present. A prominent basal cingulum is present on the protoconid and continues posteriorly to the break on the hypoconid. A worn cusplule is present in the m1 talonid notch. A slight swelling is present in nearly the same position on the anterolingual margin of the entoconid of m2. The m1 entoconid corner is squared, whereas the m2 entoconid corner is curved, resulting in the anterior displacement of the entoconid. Because of breakage of the hypoconid on m1 and m2, widths of these teeth are only approximate. Measurements (in mm): p4 width, 2.68 (estimated); m1 length  $\times$  width, 3.80  $\times$  3.15 (estimated); m2 length  $\times$  width, 3.80  $\times$  3.40 (both estimated).

**DISCUSSION.** Compared with various species of *Plesiadapis*, RAM 7193 differs from *Plesiadapis praecursor* and *P. anceps* in its larger size (Table 2). In addition, the buccal cingula on m1 and m2 of RAM 7193 are more robust. Compared with *P. rex*, the m1–2 of RAM 7193 are longer, but of similar estimated width (Table 2), and the p4 estimated talonid width is at the upper end of the size range for *P. rex* given by Gingerich (1976). On the p4 of RAM 7193, the short talonid is transversely broader and more basined than on *P. rex* (cast of PU 20058 from Cedar Point Quarry). Although the p4 entoconid of the Goler specimen is partly broken, it appears to have been a larger, more distinct cusp than in *P. rex*. The m1 entoconid corner on RAM 7193 is squared as in *P. rex*, but the m2 entoconid corner is more curved. The m1–2 labial cingula are more robust than on *P. rex*.

The Goler Formation specimen is similar in size to specimens of *Plesiadapis churchilli*. Compared with the sample from Long Draw Quarry (Gingerich, 1976), RAM 7193 differs in having a longer m1 (Table 2). Compared with Winterfeld's (1982) sample of *Plesiadapis* sp., probably *P. churchilli* from the Rock Springs Uplift, RAM 7193 also has a slightly longer m1 and a wider p4 talonid. However, all measurements for the Goler specimen fall within the ranges given by Krause (1978) for the *P. churchilli* sample from the Roche Percée Local Fauna. The p4 talonid on RAM 7193 is weakly basined and transversely broader than that of *P. churchilli* (PU 21235 type), in which the talonid is domed, and the entoconid of RAM 7193 is more distinct than on *P. churchilli*. The m1 entoconid corner is squared in both RAM 7193 and *P. churchilli*, and the m2 entoconid corner is rounded on RAM 7193 and



**Table 2** Measurements (mm) of *Plesiadapis* m1s from North America compared with RAM 7193 from the Goler Formation in Primate Gulch (locality V200202).

<i>Plesiadapis</i> species	Locality and age	Length	Width	Number
<i>praecursor</i>	Douglas Quarry/Keefer Hill: Ti1	2.6–2.7	2.5–2.7	5
<i>anceps</i>	Bison Basin Saddle: Ti2	2.6–3.0	2.7–3.0	11
<i>rex</i>	Cedar Point Quarry: Ti3	2.7–3.4	2.6–3.4	126
<i>Churchill</i>	Long Draw Quarry: Ti4	3.4–3.6	3.2–3.5	4
cf. <i>churchilli</i>	Primate Gulch: Ti4?	3.80	3.15*	1
<i>fodinatus</i>	Princeton Quarry: Ti5	2.8–3.5	2.7–3.2	34
<i>simonsi</i>	Midlevel Sand Draw: Ti5	3.9–4.0*	3.9*	2
<i>gingerichi</i>	Clark's Fork Basin: Ti6-Cf1	4.5–4.75	3.9–4.4	3
<i>cookie</i>	Little Sand Coulee area: Cf1	5.1–5.7	4.8–5.4	7
<i>dubius</i>	Paint Creek: Cf2	2.7–3.1	2.5–2.7	3

Measurements of *P. gingerichi* from Rose (1981); all others, except RAM 7193, from Gingerich (1976).

\* Estimated.

some specimens of *P. churchilli*, including the holotype. A prominent buccal cingulum is present on the molars of some specimens in Winterfeld's (1982) sample. RAM 7193 resembles *P. churchilli* from Roche Percée in having the small cuspule at the base of the talonid notch on m1. This cuspule fills the talonid notch, whereas it appears to be a little smaller in the Roche Percée specimens illustrated by Krause (1978). A tiny cuspule appears also to be present in the m2 talonid notch of *P. churchilli* from Roche Percée. On the m2 of RAM 7193, the talonid notch is reduced to a narrow crease, and only the aforementioned slight swelling is present.

RAM 7193 is also similar in size to *Plesiadapis fodinatus*, differing by having a greater m1 length (Table 2). The p4 of RAM 7193 resembles that of *P. fodinatus* (cast of PU 13930) in having a short, weakly basined talonid (in contrast to *P. churchilli*), with a distinct entoconid cusp present; this cusp, absent in *P. churchilli*, is said to be present on most specimens of *P. fodinatus* (Gingerich, 1976). *Plesiadapis fodinatus* differs from the Goler specimen in having noticeably curved entoconid corners on both m1 and m2, whereas the m1 entoconid corner of RAM 7193 is squared and the m2 corner is less curved (comparison made with PU 13930). Because the m1 posterolingual corner in *P. fodinatus* is curved, with the entoconid anteriorly displaced, the talonid notch is distinctly narrower than on RAM 7193. The m2 notch is also slightly narrower on *P. fodinatus* because of the greater anterior displacement of the entoconid. The curved, rather than squared, entoconid corners of m1–2 are features associated with later species of *Plesiadapis* (Gingerich, 1976). *Plesiadapis fodinatus* also is characterized by having more crenellated enamel than *P. churchilli*; no distinct crenellation is observable on the Goler specimen, but some morphological detail has probably been lost because of wear.

RAM 7193 differs from *Plesiadapis simonsi* in having a squared entoconid corner on m1, whereas

in *P. simonsi*, the m1 posterolingual corner is strongly curved, with the entoconid displaced anteriorly. The m1–2 lengths of RAM 7193 and PU 17814 (holotype of *P. simonsi*) are similar (Table 2), but the trigonid widths are greater in *P. simonsi* (because of breakage, the talonid widths on RAM 7193 cannot be obtained).

*Plesiadapis dubius* differs from RAM 7193 in being much smaller (Table 2) and having curved entoconid corners on both m1 and m2. *Plesiadapis gingerichi*, *P. cookei*, and the European *Plesiadapis tricuspidens* Gervais, 1877, are much larger than RAM 7193 (Table 2), with the latter two species having curved, crested entoconids on the m1 (in addition to m2). The European species *Plesiadapis insignis* Piton, 1940, and *Plesiadapis walbeckensis* are much smaller than RAM 7193; in addition, the heel on the p4 of *P. walbeckensis* is unbasined and without a distinct entoconid. The European *Plesiadapis remensis* Lemoine, 1887, is similar in size to RAM 7193, but it has been reported to have curved entoconid crests on both m1 and m2 and an unbasined p4 heel (Gingerich, 1976). Also, RAM 7193 is much larger than the largest species of *Nannodectes*, *N. gidleyi*.

The size and morphological similarities that RAM 7193 shows with teeth of *Plesiadapis churchilli* and *P. fodinatus* make it unlikely that this specimen belongs to a genus other than *Plesiadapis*. Based on the comparisons made above, RAM 7193 is most similar to *P. churchilli*, with fewer similarities to *P. fodinatus*. The Goler Formation specimen is closest in size to *P. churchilli*, and it resembles that species in retaining a squared entoconid corner on the m1. The molar entoconid corners of *P. fodinatus* are noticeably more curved than on RAM 7193. Also, absence of enamel crenulation on the molars suggests that, although the molars are water worn, intense enamel crenulation as found in *P. fodinatus* might never have been present. Thus, the overall molar morphology of RAM 7193 more closely resembles that of *P. churchilli*



than that of *P. fodinatus*. However, the p4 of RAM 7193 is advanced and resembles that of *P. fodinatus* in having a short, weakly basined talonid with a distinct entoconid, features absent in *P. churchilli*. These two species are closely related, and Gingerich (1976) suggested that *P. fodinatus* evolved from *P. churchilli*. Thus, it is not unexpected to find a specimen showing features of both named species.

### MAMMALIAN BIOSTRATIGRAPHY AND BIOCHRONOLOGY

Until the 1990s, the age of the Goler Formation was a matter of considerable uncertainty, as few fossils were available. Based on admittedly sparse data, McKenna (1960) and McKenna et al. (1987) argued that the only major mammal-yielding locality, the Laudate Discovery Site, was probably late Torrejonian or early Tiffanian in age. The late Paleocene or early Eocene invertebrates in Member 4d (Cox and Edwards, 1984; Cox and Diggles, 1986; McDougall, 1987; Squires et al., 1988; Reid and Cox, 1989) helped constrain the age of strata near the top of the formation, but they were of little utility in constraining the age of the subdivisions below.

Recent efforts have yielded new mammal sites both higher and lower in the formation than the Laudate Discovery Site (Fig. 2), and more fossils are now available primarily because of the success of screen-wash sampling. On the basis of structural orientation of the formation, where beds dip generally north, the highest locality, Honey Pot, is approximately 590 m above the Member 4a–4b contact, and the lowest, Land of Oz, is approximately 300 m below the same contact. These two sites have not, as yet, yielded primates. However, *Plesiadapis* has been recovered from the Laudate Discovery Site (lowermost part of Member 4b), as well as Primate Gulch and the Edentulous Jaw Site (both in the lower part of Member 4b). *Plesiadapis* is not known from rocks older than Tiffanian (Archibald et al., 1987; Lofgren et al., 2004a), indicating that the lower part of Member 4b is Tiffanian in age or younger.

Gingerich (1976) proposed a lineage zone subdivision of the Tiffanian on the basis of nonoverlapping species of *Plesiadapis* (Fig. 8). As discussed earlier, the species from the Laudate Discovery Site and the Edentulous Jaw Site, referred to *Plesiadapis* cf. *P. anceps*, is more similar to *P. rex* in size but more similar to *P. anceps* in morphology. On the basis of Gingerich's (1976) zonation, the presence of *P. anceps* denotes Tiffanian (Ti) lineage zone Ti2, and the presence of *P. rex* denotes Tiffanian lineage zone Ti3. If this zonation can be extended to California, the two sites, and thus the lower part of Member 4b, is roughly correlative to lineage zone

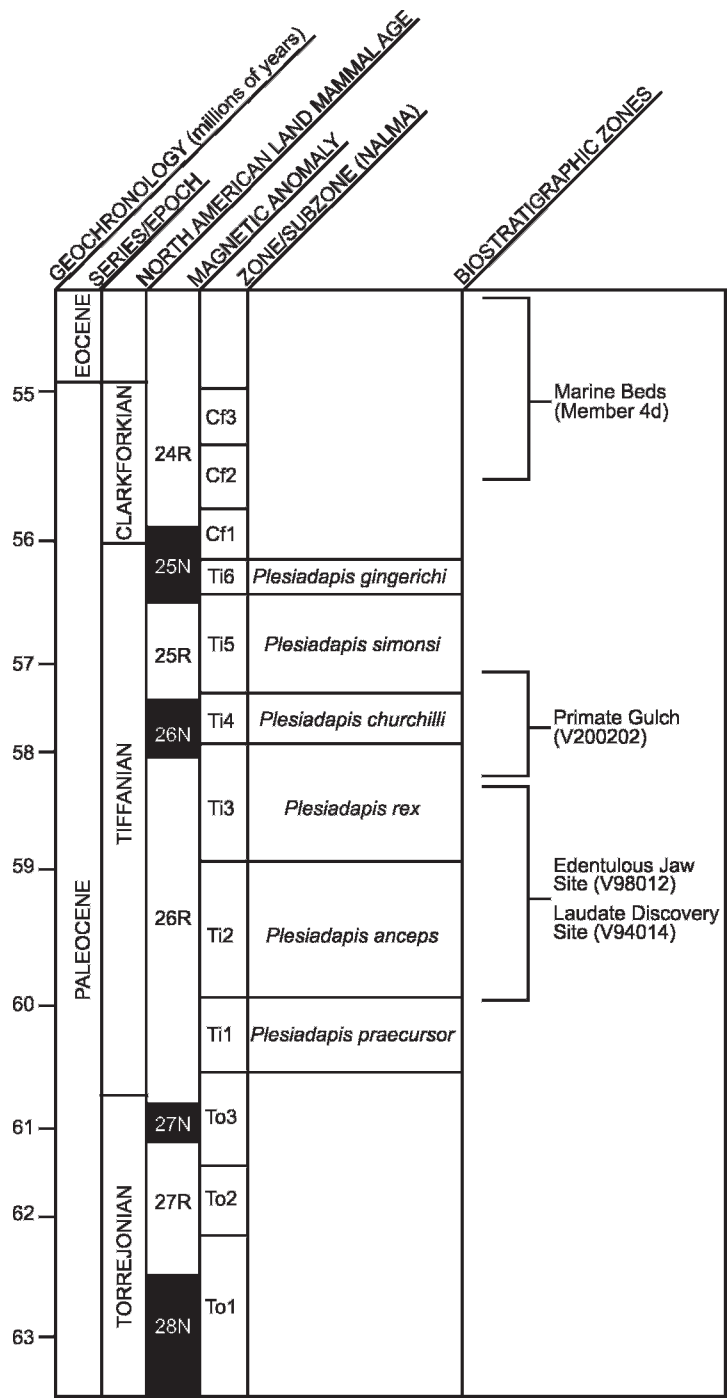
Ti2, or perhaps Ti3 (Fig. 8). Similarly, Primate Gulch yielded a single jaw fragment referred to *Plesiadapis* cf. *P. churchilli*, and on the basis of Gingerich's (1976) zonation, Primate Gulch would correlate approximately to Tiffanian lineage zone Ti4 (Fig. 8).

It is important to note that stratigraphic relationships between the three sites yielding *Plesiadapis* are very uncertain. The Goler Formation can be well exposed locally, but most of the formation is covered. Because the Laudate Discovery Site and Edentulous Jaw Site are separated by over 2 km of mostly covered exposures, physical correlation of the sites is not possible. Primate Gulch is only 0.3 km north of the Edentulous Jaw Site, and it appears to be stratigraphically higher on the basis of the general structural trend of the formation where beds usually dip north. But physical correlation of Primate Gulch and the Edentulous Jaw Site is not possible, because intervening outcrops are covered, local outcrops show evidence of folds, and Cox (1982) mapped a geological fault between the sites. Consequently, interpretations of the relative ages of the Laudate Discovery Site, Edentulous Jaw Site, and Primate Gulch are based almost solely on fossils.

The presence of *Paromomys depressidens* at the Laudate Discovery Site and *Ignacius frugivorus* at the Edentulous Jaw Site provide both supporting and conflicting data compared with correlations based on species of *Plesiadapis*. *Paromomys* is relatively common in Torrejonian assemblages, but rare in Tiffanian ones. The youngest records of the genus are specimens referred to *Paromomys* cf. *P. depressidens* from the Cochrane 2 site (Porcupine Hills Formation) in Alberta, Canada (Krause, 1978), and the Shotgun Fauna (Keefer Hill) (Fort Union Formation) in Wyoming (Gazin, 1971). Both sites are interpreted to be earliest Tiffanian (Ti1) (Archibald et al., 1987; Lofgren et al., 2004a). If the Laudate Discovery Site is indeed Ti2–Ti3, then the Goler Formation occurrence would be the youngest known for *Paromomys*. Conversely, but less likely, the Laudate Discovery Site could be Ti1.

In contrast, *Ignacius frugivorus* is known from sites that are similar in age (on the basis of *Plesiadapis* zonation) to the Edentulous Jaw Site (Ti2–Ti3). For example, Cedar Point Quarry (Rose, 1981), Scarritt Quarry (Rose, 1981), and Brisbane (Holtzman, 1978) are either Ti2 or Ti3 (Archibald et al., 1987; Lofgren et al., 2004a). Therefore, the Goler Formation occurrence, interpreted to be Ti2–Ti3, is consistent with the age of other sites yielding *I. frugivorus*.

The Goler Formation primates are generally similar to those from early-middle Tiffanian rocks in the Rocky Mountain States, with the exception of *Paromomys depressidens*, whose Goler occurrence appears to be a temporal vestige.



**Figure 8** Correlation of the three primate-yielding sites from the Goler Formation to the Tiffanian North American Land Mammal Age. Tiffanian subdivisions are lineage zones of Gingerich (1976) based on nonoverlapping species of *Plesiadapis*. Correlation of Member 4d marine beds is also shown on the basis of invertebrate fossils (Cox and Edwards, 1984; Cox and Diggles, 1986; McDougall, 1987; and Reid and Cox, 1989). Adapted from Lofgren et al. (2004a).

## PALEOECOLOGY AND PALEOBIOGEOGRAPHY

Before the 1980s, the Goler Formation was thought to be entirely nonmarine. More recently, marine sediments were identified that indicated that the Goler Basin was inundated by a marine transgression in the late Paleocene or early Eocene (Cox and Edwards, 1984; Cox and Diggles, 1986; McDougall, 1987; Squires et al., 1988; Reid and Cox, 1989). The marine sediments near the top of the formation in Member 4d (Fig. 2) yielded invertebrate fossils, including foraminifera. Paleocological interpretations based on Goler foraminiferal assemblages indicate a maximum water depth of up to, or exceeding, 150 m (McDougall, 1987). Recently, shark teeth (*Striatolamia* Gluckman, 1964) were recovered from Member 4d (Lofgren et al., 2004b). The marine invertebrates from Member 4d and other fossils noted below from Members 3 and 4 indicate that, before the marine transgression, the Goler Basin was probably in close proximity to the Pacific Ocean throughout much of its history.

A single ray tooth (RAM 7180)—suborder Batoidea, family Dasyatidae, cf. *Hypolophodon* (Lofgren et al., 2002)—was recovered from the Edentulous Jaw Site (Member 4b). Batoids are characteristically nearshore marine fishes that are quite tolerant of brackish water and are often found in rivers (Bryant, 1989). Also, the species represented by a large section of turtle shell found at UCMP locality V81035 (Member 4a) is thought to be related to sea turtles (McKenna et al., 1987). Finally, a concretion from UCMP locality V5250 (Member 3) contains a bass-shaped osteichthyan fish whose fin morphology resembles beryciform fish (McKenna et al., 1987). Extant beryciforms are marine (Zehren, 1979). Cumulatively, these fossils suggest a marine influence as Goler sediments accumulated.

The depositional setting of the Goler Formation indicates that the Goler Basin was a suitable environment for aquatic vertebrates. The formation consists of 1) a lower sequence of mostly alluvial fan and braided stream deposits (Members 1–3) whose detritus was derived from nearby sources, primarily to the north, and 2) an upper sequence of braided and meandering stream deposits (Member 4, except for marine beds) containing sediment derived from more distant sources to the east (Cox, 1982). The westward-flowing river system represented by Member 4 probably emptied into the Pacific Ocean not far west of the Goler Basin. In contrast to the rarity of most other types of vertebrates in the Goler Formation, Member 4 has a relatively diverse assemblage of turtles (McKenna et al., 1987; Lofgren et al., 2002). Also, crocodilian teeth and scutes have been recovered from the Edentulous

Jaw Site and Laudate Discovery Site, the two screen-wash samples from the Goler Formation. This is to be expected because turtles and crocodilians are common in Paleocene nonmarine rocks from the Rocky Mountain states. However, what is unusual is the paucity of teeth and scales of fish in Goler screen-wash samples. For example, gar scales are often very common in Paleocene fluvial deposits from elsewhere in North America, but they have not been recovered from the Goler Formation. Whether the paucity of fish remains has some ecological significance is a question that can be addressed through further sampling.

Fully terrestrial vertebrates in the Goler Formation are represented thus far only by mammals and lizards. At least three genera of lizards are present (Lofgren et al., 2002), and lizard scutes are the most common fossils in screen-wash samples (about 200 specimens). The Goler mammalian fauna is relatively diverse and contains arctocyonid, hyopsodontid, phenacodontid, and peripitychid ungulates; multituberculates; marsupials; carnivores; mesonychids; and plesiadapid and paromomyid primates (Lofgren et al., 2002).

The Goler Formation primates, represented by the paromomyids, *Paromomys* and *Ignacius*, and the plesiadapid, *Plesiadapis*, were probably both terrestrial and arboreal in habit. On the basis of limb proportions, forelimb resemblances to the extant rodent *Marmota* Blumenbach, 1779, and other evidence, *Plesiadapis* is interpreted to have been primarily terrestrial (see discussion in Gingerich, 1976). In contrast, the osteology of the manus and pes of paromomyids indicates that they might have been gliders (Beard 1990, 1993). The Goler Basin would have provided ample habitat for gliders, as the presence of numerous trees is indicated by an abundance of fossil wood in Member 4. Large logs, up to a few meters in length, are commonly present in outcrops of thick, cross-bedded conglomeratic sandstone. Fossil wood is less abundant in Member 3, but pieces more than 20 cm in length are not uncommon (in contrast, sites that yield well-preserved fossil leaves or pollen are rare). Thus, coursed by meandering and braided streams that were probably lined with thick stands of vegetation, the Goler Basin provided a suitable habitat for a diverse assemblage of vertebrates, including arboreal primates.

Given that the Goler Formation now lies hundreds of miles west of other similarly aged Paleocene sites that yield plesiadapid primates (Fig. 3), Goler Formation vertebrate assemblages provide important information concerning western North American paleobiogeography. Goler vertebrate assemblages are generally similar to those from early-middle Tiffanian rocks in the Rocky Mountain states (Lofgren et al., 2002).

Therefore, considerable interchange of taxa occurred between these areas and probably no major dispersal barriers were in place. This is especially evident with regard to the arboreal Goler Formation primates, as *Paromomys depressidens* is also known from Wyoming to Alberta, and *Ignacius frugivorus* from Texas to Saskatchewan.

Conversely, even at this early stage of analysis of Goler Formation vertebrate assemblages, there is a significant indication of endemism as well. Goler Formation taxa, such as the plesiadapids referred to *Plesiadapis* cf. *P. anceps* and *P. cf. P. churchilli*, two new mammal taxa (arctocyonid *Mimotricentes tedfordi*, McKenna and Lofgren, 2003; peripitychid *Goleroconus alfi* gen. and sp. nov., McKenna et al., 2008), and new species of turtles represented by two recently collected skulls (Lofgren et al., 2002), indicate that there was a notable degree of geographic and/or latitudinal difference between coastal California and other early-middle Tiffanian sites from western North America.

## CONCLUSIONS

1. Before 1990, the Goler Formation had yielded only a few vertebrate fossils. Recent collecting efforts, using screen-washing techniques, provide a much larger sample of vertebrates, including new records of turtles, rays, lizards, crocodilians, and mammals.

With its emerging diverse assemblage of continental vertebrates, the Goler Formation provides a unique opportunity for study of the Paleocene vertebrate fauna from the west coast of North America.

2. New records of Goler Formation mammals include three genera of primates (*Paromomys*, *Ignacius*, and *Plesiadapis*), the oldest known from California. These specimens are referred to *Paromomys depressidens*, *Ignacius frugivorus*, *Plesiadapis* cf. *P. anceps*, and *Plesiadapis* cf. *P. churchilli*.
3. The presence of *Plesiadapis* indicates that the lower part of Member 4b of the Goler Formation is Tiffanian. More specifically, the occurrence of *Plesiadapis* cf. *P. anceps* at the Laudate Discovery Site and Edentulous Jaw Site and *Plesiadapis* cf. *P. churchilli* at Primate Gulch indicates an approximate age of Ti2–Ti3 for the Laudate Discovery Site and Edentulous Jaw Site and Ti4 for Primate Gulch.
4. The occurrence of *Ignacius frugivorus* at the Edentulous Jaw Site is consistent with Ti2–Ti3, but the presence of *Paromomys depressidens* at the Laudate Discovery Site suggests either an older age or that the Goler occurrence is the youngest known for the genus.
5. Exposures of the Goler Formation are entirely nonmarine except for Member 4d, which

contains late Paleocene or early Eocene marine invertebrates. A few fossils from Members 3 and 4a–b indicate a possible marine influence on the Goler Basin. These data suggest that the Goler Basin was in close proximity to the Pacific Ocean throughout much of its existence.

6. The part of the Goler Formation that has yielded vertebrate fossils (Members 3–4) was deposited primarily by braided and meandering streams. Member 4 contains a relatively diverse assemblage of vertebrates, with the remains of turtles, mammals, and lizards being somewhat common, but those of crocodilians and, particularly fish, much less so. The absence of gars is puzzling as their fossils are usually common in Paleocene nonmarine basins elsewhere in North America.
7. Goler Formation paromomyids (*Paromomys* and *Ignacius*) and plesiadapids probably lived within stands of trees that lined large streams, an interpretation supported by the abundance of fossil wood in Member 4.
8. Goler Formation vertebrate assemblages provide important information concerning North American paleobiogeography. Goler Formation vertebrates, especially the mammals, are generally similar to those from early-middle Tiffanian rocks in the Rocky Mountain states, and some taxa must have been able to move freely between the areas. However, there is also evidence of significant endemism on the basis of Goler *Plesiadapis* specimens that cannot be confidently referred to existing species, as well as new species of turtles and mammals.

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