

New records of eutherian mammals from the Goler Formation (Tiffanian, Paleocene) of California and their biostratigraphic and paleobiogeographic implications

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ABSTRACT

The Goler Formation is the only rock unit on the West Coast of North America that has yielded a diverse assemblage of Paleocene vertebrates. Intense prospecting of strata representing member 4 of the formation over the past two decades has resulted in recovery of over 70 specimens of eutherian mammals, representing 18 species. All specimens were recovered from member 4a and the lower part of member 4b, except an isolated tooth referred to *Phenacodus* cf. *P. vortmani* from member 4d in the uppermost part of the formation. Three taxa are new, the plesiadapid, *Nannodectes lynasi*, and two hyopsodontid condylarths, *Promioclaenus walshi* and *Protoselene ashtoni*. Also present are four species of *Phenacodus*, two species of *Protictis*, and single species representing *Goleroconus*, *Mimotricentes*, *Lambertocyon*, *Ignacius*, *Paromomys*, *Bessoecetor*, *Thryptacodon*, *Dissacus*, and a taeniodont. The mammalian fauna from member 4a and the lower part of member 4b is collectively referred to as the Goler Assemblage because taxa recovered from sites throughout this 500 m stratigraphic interval are too similar to subdivide into discrete biostratigraphic units. Based on comparison to faunas from well-known Tif-

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fanian sites in the Western Interior, the Goler Assemblage is probably middle Tiffanian (Ti3–Ti4a), although a Ti5a age is also possible. The Goler Assemblage exhibits significant endemism as 40% of its taxa are not reported elsewhere and only four of 18 Goler Assemblage eutherians can be confidently referred to known species. Comparison to seven Ti3–Ti4a aged sites from the Western Interior indicates that the Goler Assemblage has a closer affinity to more southern faunas (southern Wyoming, Colorado, and Texas), than northern faunas (northern Wyoming, North Dakota, and western Canada), and is most similar to the mammalian assemblage from the Ledge Locality in the Bison Basin of southern Wyoming. Presence of late Paleocene–early Eocene marine strata in the uppermost member of the Goler Formation indicates that the Goler Basin was probably adjacent to the Pacific Ocean during most of its existence. Also, significant distances and one or more paleodrainage divides separated the Goler Basin from Western Interior basins, factors that limited the dispersal of mammals between the West Coast and the continental interior and contributed to the formation of a discrete faunal province on the West Coast of North America during the late Paleocene.

INTRODUCTION

The Goler Formation is composed of more than 3000 m of mostly nonmarine sedimentary strata that crop out in the El Paso Mountains in the northern Mojave Desert (fig. 1). The formation was named by Dibblee (1952), and later divided into four members (numbered 1–4), with member 4 consisting of four informal units, listed in ascending stratigraphic order, 4a, 4b, 4c, and 4d (fig. 1) (Cox, 1982, 1987). The Goler Formation is sparsely fossiliferous, as extensive prospecting efforts between 1954 and 1987 yielded fewer than 12 identifiable mammalian fossils (McKenna, 1955, 1960; McKenna et al., 1987). Although these initial results were sparse, they did demonstrate that the Goler Formation was the only known rock unit on the West Coast of North America with the potential to yield a diverse assemblage of Paleocene terrestrial vertebrates.

Beginning in 1993, two of us (M. M. and D. L.) began a long-term effort to exploit this potential, focusing primarily on recovery of mammals from members 3 and 4. Although a few partial turtle shells were found, mammalian fossils were not recovered from member 3. In contrast, screenwashing and intense prospecting of member 4 yielded a diverse assemblage of Tiffanian mammals, as well as, turtles, crocodylians, lizards, sharks, and rays (Lofgren et al., 2002; Lofgren et al., 2004a; Lofgren et al., 2008; McKenna et al., 2008; Lofgren et al., 2009; Albright et al., 2009; Lofgren et al., 2010). All mammalian fossils were recovered from member 4a and member 4b, except for an isolated tooth of *Phenacodus* from member 4d, an interval of marine sediments in the uppermost part of the Goler Formation that also yields invertebrate fossils (Cox and Edwards, 1984; Cox and Diggles, 1986; McDougall, 1987; Squires et al., 1988; Lofgren et al., 2010).

Here we describe the eutherian mammalian fauna from the Goler Formation, based on more than 70 identifiable specimens, representing 18 taxa, including three new species. Goler eutherians are compared to Tiffanian eutherian assemblages from the Western Interior to pro-

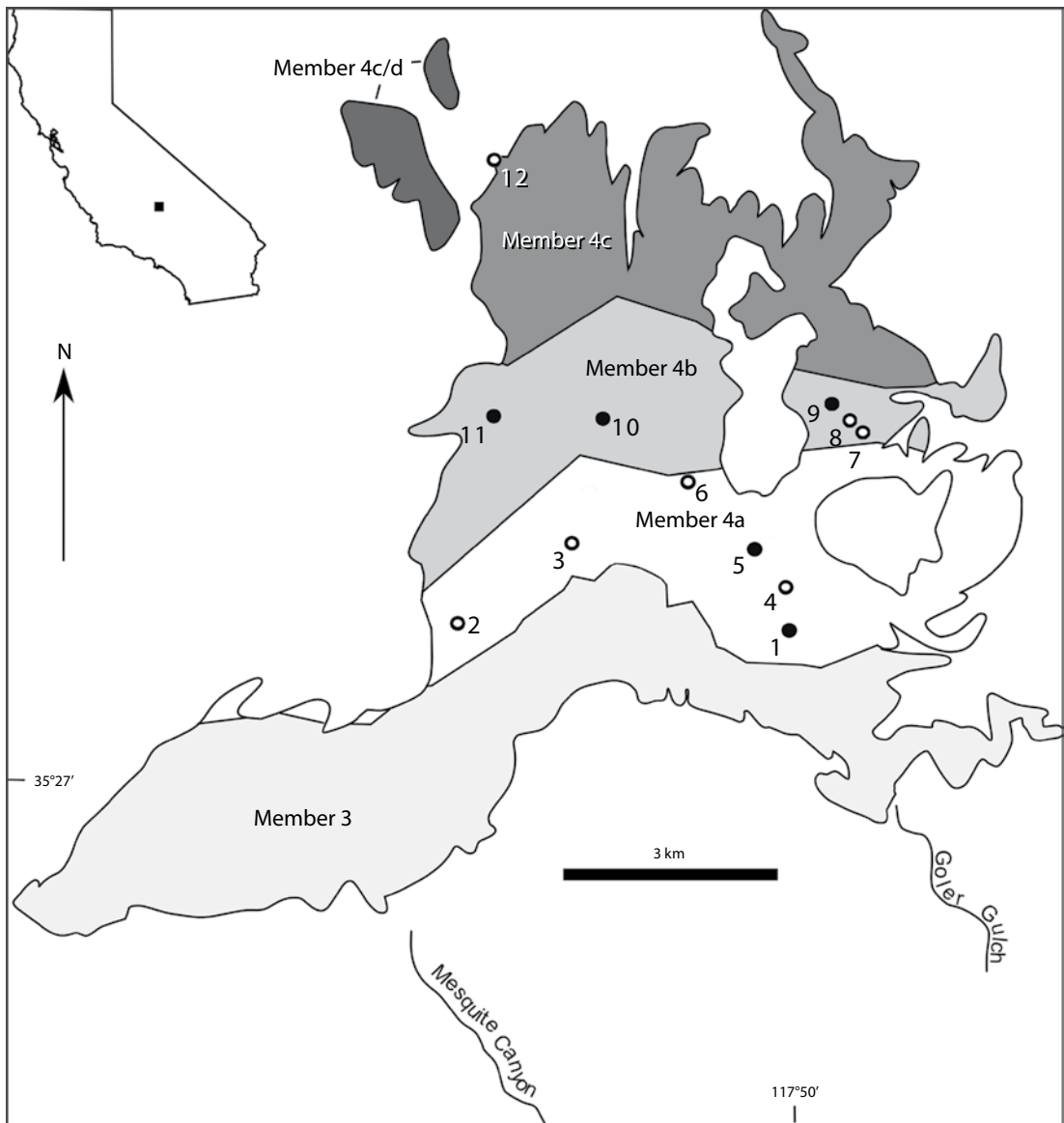


FIGURE 1. Map of California (inset) with location of study area shaded and outcrop map of member 3 and member 4 of the Goler Formation within the El Paso Mountains (adapted from Cox, 1982; Cox and Diggles, 1986) showing location of sites discussed in text; members 1–2 not shown. Numbers refer to a specific site or group of sites within a limited geographic area, with the numerical order reflecting the approximate stratigraphic sequence of localities referred to in the text. Open circles are areas where strata at a specific site underwent paleomagnetic analysis; results presented in Albright et al. (2009). **1**, Red Flat area (V201014, V201122); **2**, Grand Canyon area (V200508, V200510, V200706, V200802, V200804); **3**, Land of Oz (V200001); **4**, *Phenacodus* Pocket area (V200603, V200612); **5**, R-Z Zone area (V200303, V200304, V200702); **6**, Laudate Discovery Site area (V94014, V94133); **7**, Edentulous Jaw Site (V98012); **8**, Primate Gulch (V200202); **9**, Lone Tooth (V200704); **10**, Butte Tooth (V200613); **11**, Honey Pot (V200120); **12**, Shark Site (V200307).

vide a refined age for member 4 of the formation and to determine the degree of endemism exhibited by the Goler eutherian assemblage and its implication for Tiffanian paleobiogeography of western North America.

MATERIALS AND METHODS

The Goler Formation has rightly earned its reputation as a difficult rock unit in which to locate fossils, but vertebrate fossils can be found in member 4a and member 4b with some regularity by systematically scanning the surface of all isolated outcrops while crawling on hands and knees. This methodology is laborious, but proved effective, as between 1993 and 2012, RAM field crews (usually 3–5 members) found one or two mammalian specimens for every three days in the field, which over many years, resulted in recovery of the fossils described in this report.

The hundreds of weathered and often broken concretions that litter the surface of some localities are the source of the most complete specimens. For example, in May 2000, a nearly complete dentary with its teeth sheared off at root level, was found by R. Leggewie. After repeated visits to the same site, M. McKenna found a concretion with the protruding roots of multiple teeth that exactly matched the Leggewie dentary. This specimen (RAM 6927, *Protictis paralus*), and others like it from indurated concretions, was painstaking prepared by M. Stokes. The Laudate Discovery Site (RAM locality V94014) and Edentulous Jaw Site (RAM locality V98012) were screenwashed, which yielded about 200 isolated mammal teeth, but the great majority were broken and could not be identified. Mammalian specimens from the Goler Formation collected prior to 1990 are housed at the University of California Museum of Paleontology (UCMP). Those from 1993 to the present are housed at the Raymond M. Alf Museum of Paleontology (RAM). Part of the Goler Formation eutherian fauna collected after 1993 was described (McKenna and Lofgren, 2003; Lofgren et al., 2008; McKenna et al., 2008) and those specimens are listed here, but not redescribed.

The classification scheme employed here is that of McKenna and Bell (1997), except for *Pro-mioclaenus* and *Protoselene*, which are placed in Hyposodontidae following Zack et al. (2005). Cusp terminology follows Van Valen (1966: fig. 1), with exceptions being Gingerich (1976: figs. 4–5) for plesiadapids, and Meehan and Wilson (2002: fig. 7) for viverravid p4s. A Mitutoyo digital caliper was used to measure teeth and measurements are in millimeters, taken following Lille-graven (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 by using a V followed by numbers (e.g., V98012) and specimens are given a unique number following RAM (e.g., RAM 9044).

ABBREVIATIONS

AMNH, American Museum of Natural History, New York; **Cf**, Clarkforkian North American Land Mammal Age; **FMNH**, Field Museum of Natural History, Chicago, Illinois; **NALMA**, North American Land Mammal Age; **PU**, Princeton University Collection at Yale University, New Haven, Connecticut; **RAM**, Raymond Alf Museum of Paleontology, The Webb Schools,

Claremont, California; **SMM**, Science Museum of Minnesota, St Paul, Minnesota; **Ti**, Tiffanian North American Land Mammal Age; **TMM**, Texas Memorial Museum, Austin, Texas; **To**, Torrejonian North American Land Mammal Age; **UALVP**, University of Alberta Laboratory of Vertebrate Paleontology, Calgary, Alberta, Canada; **UCMP**, University of California Museum of Paleontology, Berkeley, California; **UM**, University of Michigan Museum of Paleontology, Ann Arbor, Michigan; **USNM**, Department of Paleobiology, United States National Museum of Natural History, Smithsonian Institution, Washington D.C.; **UW**, University of Wyoming, Laramie, Wyoming (now housed at the University of Colorado Museum, Boulder, Colorado); **Wa**, Geiseltal Museum, Halle, Germany.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758

Order CIMOLESTA McKenna, 1975

Family PANTOLESTIDAE Cope, 1884

Bessoecetor Simpson, 1936

Bessoecetor septentrionalis Scott et al., 2002

HOLOTYPE: AMNH 33810, left dentary with p2–m3 from Scarritt Quarry, Fort Union Formation, Montana.

REFERRED SPECIMEN: RAM 9099, right dentary fragment with m2–m3 from RAM locality V200510, member 4a (fig. 2A–B).

DESCRIPTION AND DISCUSSION: “*Propalaeosinopa*” was the generic name employed for a common North American Torrejonian–Tiffanian pantolestid, but Scott et al. (2002) demonstrated that the type of “*Propalaeosinopa*,” *P. albertensis*, is a nomen dubium. Van Valen (1967) originally proposed the synonymy of *Bessoecetor thomsoni*, *B. diliculi*, and “*Propalaeosinopa*” *albertensis*. Scott et al. (2002) argued that *B. diliculi* is identical to the type of “*Diacodon*” *septentrionalis* described by Russell (1929), and thus has priority. Scott et al. (2002) then resurrected *Bessoecetor* and transferred the four species of “*Propalaeosinopa*” (*P. thomsoni*, *P. diliculi*, *P. albertensis*, *P. septentrionalis*) to the new combination, *Bessoecetor septentrionalis*. This synonymy was provisionally followed by Secord (2008), but he noted that the type specimen of the genus should be the holotype of *B. thomsoni* (AMNH 33810) from Scarritt Quarry, not the type of “*Diacodon*” *septentrionalis* (UALVP 126).

The m2–m3 of RAM 9099 have tall trigonids with large protoconids and metaconids and small paraconids that are shifted labially and low talonids with large hypoconids and slightly smaller entoconids, with small and medially placed hypoconulids (fig. 2A–B); features present in both known species of *Bessoecetor*, *B. septentrionalis* and *B. pilodontus*. However, *B. septentrionalis* can be differentiated from *B. pilodontus* by size, although teeth of *B. pilodontus* and *B. septentrionalis* may overlap slightly in length (Secord, 2008). Tooth dimensions of RAM 9099 are very similar to the holotype of *B. septentrionalis* and are significantly smaller than the holotype of *B. pilodontus* (table 1). Therefore, RAM 9099 is referred to *B. septentrionalis*.

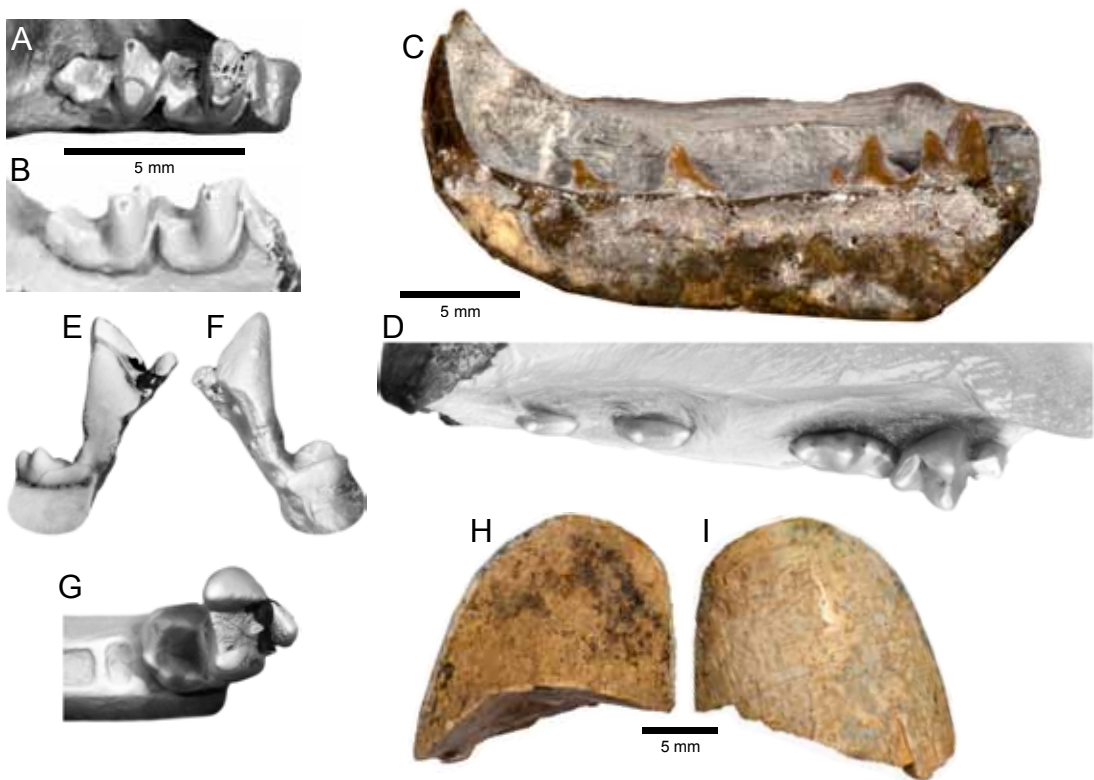


FIGURE 2. Mandibles and teeth of *Protictis*, *Bessoecetor*, and *Taeniodonta*. **A.** Occlusal view of RAM 9099, right dentary fragment with m2–3 of *Bessoecetor septentrionalis* from RAM locality V200510; **B.** labial view of RAM 9099. **C.** Lingual view of RAM 6927, a right dentary fragment with c, p1–p2, p4, and partial m1 of *Protictis paralus* from RAM locality V200001 (with partial imprint of dentary); **D.** occlusal view of p1–2, p4–m1 of RAM 6927. **E.** Lingual view of partial m1 of RAM 7246, left dentary fragment with partial m1 of *Protictis* cf. *P. agastor* from RAM locality V200001; **F.** labial view of partial m1 of RAM 7246; **G.** occlusal view of RAM 7246. **H.** Posterior view of RAM 15328, partial lower canine of a taeniodont from RAM locality V200612; **I.** anterior view of RAM 15328. Scale bar for C–D also applies to E–G.

Order CARNIVORA Bowdich, 1821

Family VIVERRAVIDAE Wortman and Matthew, 1899

Protictis Matthew, 1937

Protictis paralus Holtzman, 1978

HOLOTYPE: SMM P77.6.64, right dentary with canine and p4–m2 from the Judson Locality, Tongue River Formation, North Dakota.

REFERRED SPECIMEN: RAM 6927, right dentary fragment with c, p1–2, p4, and partial m1 from RAM locality V200001, member 4a (fig. 2C–D).

DESCRIPTION: The canine of RAM 6927 is large. Its apex extends anteriorly and its root curves posteriorly underneath p1. A wide diastema separates the canine and p1, which has a tall and narrow anterior cusp, and a small and low posterior accessory cusp (fig. 2C–D). The

TABLE 1. Measurements of *Bessoecetor septentrionalis* from the Goler Formation (RAM 9099) and the holotypes of *B. septentrionalis* (AMNH 33810) and *B. pilodontus* (UM 91332). Measurements of AMNH 33810 from Simpson (1936) and UM 91332 from Secord (2008: table 17).

Tooth site	RAM 9099	AMNH 33810	UM 91332
m2 length	2.31	2.3	2.70
WTri	1.92	1.8	2.65
WTal	1.88	—	2.40
m3 length	2.67	2.6	3.25
WTri	1.66	1.8	2.55
WTal	1.22	—	1.75

diastema separating p1 and p2 is short, and p1 and p2 are similar in morphology, with p2 a larger version of p1, but with a relatively tall anterior cusp. Two alveoli filled with sediment mark the position of the missing p3, which indicates the p2–p3 diastema was short and the p3–p4 diastema was absent. A mental foramen is positioned below the anterior root of p3.

A well-developed anterior cuspule and large main cusp and two small posterior cuspules are present on p4. The apex of the anterior cuspule is conical and separated from the main cusp by a broad carnassiform notch. The first posterior cuspule is positioned on the posterior slope of the main cusp, with a small carnassiform notch separating them. A third carnassiform notch separates the first posterior cuspule from the slightly lower second posterior cuspule. A small talonid basin is developed between the posterior cuspules that opens lingually and cusps and cuspules of p4 are aligned in a slight arc that opens lingually in occlusal view.

The m1 of RAM 6927 has a tall and well-preserved trigonid and a low and damaged talonid. The protoconid is the tallest cusp, with a distinctly smaller metaconid that is taller and slightly larger than the paraconid. Part of the talonid is missing and only a small hypoconid is present whose position is significantly lingual to the protoconid, suggesting that the talonid was small. Depth of the mandible below p2 is 1.09 mm, and 2.01 mm below m1.

DISCUSSION: The presence of a sectorial main cusp, a smaller but well-developed anterior cuspule, small posterior cuspules developed on the posterior flank of the main cusp, and a small talonid basin, are features of the p4 of RAM 6927 that indicate it represents *Protictis*. Torrejonian and Tiffanian species of *Protictis* from the Bighorn and Clark's Fork basins, including *P. schaffi*, *P. agastor*, *P. dellensis*, *P. haydenianus*, *P. laytoni*, and *P. paralus*, were noted by Gingerich and Winkler (1985) as usually differentiated by size. Later, Polly (1997) removed *P. schaffi*, *P. dellensis*, *P. laytoni* from *Protictis* by synonymizing *P. schaffi* with *Viverravus politus*, *Protictis dellensis* with *Didymictus proteus*, and *Protictis laytoni* with *Viverravus bowni*. More recently, two Torrejonian species of *Protictis*, *P. simpsoni* and *P. minor* from the San Juan Basin of New Mexico, were described by Meehan and Wilson (2002). *Protictis agastor*, *P. minor*, *P. simpsoni*, and *P. haydenianus* are larger than *P. paralus* (Gingerich and Winkler, 1985: tables 4–5, 8; Meehan and Wilson, 2002: table 2; Holtzman, 1978: table 31). Direct comparison of the holotype of *P. paralus* (SMM P77.6.64) and RAM 6927 indicates that the p4 of RAM 6927 is nearly identical in all respects to the p4 of the holotype, except the anterior accessory cusp of

TABLE 2. Measurements of the lower dentition of *Protictis paralus* from the Goler Formation and the Judson locality from the Fort Union Formation of North Dakota. Measurements of SMM P77.6.64 (holotype) and SMM P77.8.190 from Holtzman (1978: table 31).

Tooth site	RAM 6927	SMM P77.6.64	SMM P77.8.190
p1 L	2.00	—	—
W	0.90	—	—
p2 L	2.75	—	—
W	1.10	—	—
p4 L	3.95	4.0	—
W	1.60	1.8	—
m1 L	—	4.5	4.5
WTri	3.00	3.0	3.0
WTal	—	2.3	2.2

RAM 6927 is slightly larger. The p4 of both the holotype and RAM 6927 have a small talonid basin and are similar in size (table 2).

The m1 of RAM 6927 has a metaconid that is slightly taller and larger than the paraconid. In the m1 of the holotype, the paraconid is slightly larger than the metaconid, but a second m1 (SMM P77.8.190) of *P. paralus* from the type locality has a paraconid and metaconid equal in size and height, indicating that some variation can be expected in m1 trigonid cusp morphology in *P. paralus*. These three m1s (RAM 6927, SMM P77.6.64, SMM P77.8.190) have identical trigonid widths (table 2). Based on nearly identical p4s, little difference in m1 trigonid cusp development, and close similarity in size between RAM 6927 and the holotype of *P. paralus*, RAM 6927 is confidently referred to this rarely reported small species of *Protictis*.

Protictis cf. *P. agastor* Gingerich and Winkler, 1985

HOLOTYPE: PU 21311, left dentary with m1–2 from Cedar Point Quarry, Polecat Bench Formation, Wyoming.

REFERRED SPECIMEN: RAM 7246, left dentary fragment with partial m1 and alveoli of m2 from RAM locality V200001, member 4a (fig. 2E–G).

DESCRIPTION: RAM 7246 is a dentary fragment found in a broken concretion whose m1 is missing the anterior face of the trigonid below the apex of the paraconid (fig. 2E–F). The trigonid is much taller than the talonid. RAM 7246 has a large protoconid and smaller paraconid and metaconid that are equal in height. The talonid basin is deepest adjacent to the trigonid, and a large hypoconid, smaller hypoconulid and entoconid, and low and very small entocristid are present (fig. 2G). The hypoconulid is medial, with the entoconid positioned directly adjacent, so they appear twinned. The alveoli of m2 are sediment filled, with the anterior alveolus wider than long, and the posterior alveolus longer than wide. RAM 7246 has a length of 5.0 mm (minimum, because of breakage) with a trigonid width of 4.39 mm and talonid width of 3.37 mm. Mandible depth beneath the talonid of m1 is 8.75 mm.

DISCUSSION: RAM 7246 represents a second species of *Protictis* from RAM locality V200001, which is larger than *P. paralus* (RAM 6927). Species of *Protictis* can usually be separated by size (Gingerich and Winkler, 1985; Meehan and Wilson, 2002) and RAM 7246 is most similar to *P. haydenianus* and *P. agastor* in this respect. *P. haydenianus* differs from *P. agastor* in having a more sectorial m2, with a shorter and less massive trigonid (Gingerich and Winkler, 1985), but m2 is not present in RAM 7246. However, two lines of evidence suggest RAM 7246 is probably *P. agastor*. *Protictis haydenianus* is well known from Torrejonian strata and questionably known from Tiffanian strata (Gingerich and Winkler, 1985), and *Protictis agastor* and RAM 7246 are both known from mid-Tiffanian strata (this report). Also, *P. paralus* (RAM 6927) is found at the same locality as RAM 7246, which is important because *P. agastor* and *P. paralus* are rarely found in Tiffanian strata but occur together at the Chappo Type locality and Cedar Point Quarry in Wyoming (Gingerich and Winkler, 1985; Gunnell, 1994), both mid-Tiffanian sites (Archibald et al., 1987; Lofgren et al., 2004b). Based on size and its Tiffanian occurrence, RAM 7246 is tentatively referred to *Protictis* cf. *P. agastor*.

Order TAENIODONTA Cope, 1876

Family STYLINODONTIDAE Marsh, 1875

Genus indeterminate

REFERRED SPECIMEN: RAM 15328, lower canine fragment from RAM locality V200612, member 4a (fig. 2H–I).

DESCRIPTION AND DISCUSSION: RAM 15328 is the distal end of a tooth about 2 cm in length and width, with enamel coating half of the tooth's longitudinal axis, a strong indicator that it represents a taeniodont (fig. 2H–I). RAM 15328 was compared directly to canines and incisors of *Psittacotherium* and *Ectoganus* housed at the AMNH and it was most similar in size and shape to AMNH 3392 and AMNH 3390, lower canines identified as *Psittacotherium* (Schoch, 1986). Although RAM 15328 too is fragmentary to be assigned to *Psittacotherium* with confidence, it does represent the only reported record of a taeniodont from the West Coast of North America.

Order PRIMATES Linnaeus, 1758

Family PAROMOMYIDAE Simpson, 1940

Paromomys Gidley, 1923

Paromomys depressidens Gidley, 1923

HOLOTYPE: USNM 9546, part of maxilla with P4–M3 from Gidley Quarry, Fort Union Formation, Montana.

REFERRED SPECIMEN: RAM 6426, right P4 from RAM locality V94014, member 4a.

DISCUSSION: This isolated tooth was described and figured by Lofgren et al. (2008: fig. 4). RAM 6426 closely resembles P4s of *Paromomys* from Swain Quarry that are inseparable from those of *P. depressidens* from Gidley Quarry (Rigby, 1980), the type locality.

Ignacius Matthew and Granger, 1921

Ignacius frugivorus Matthew and Granger, 1921

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

REFERRED SPECIMEN: RAM 6433, left m3 from RAM locality V98012, member 4b.

DISCUSSION: RAM 6433 was described and figured by Lofgren et al. (2008: fig. 5). The morphology of this isolated m3 is nearly identical to m3s referred to *Ignacius frugivorus* from the Roche Percee Local Fauna in Saskatchewan, Canada, the Brisbane and Judson localities in North Dakota, and Mason Pocket, the type locality in Colorado (Lofgren et al., 2008).

FAMILY PLESIADAPIDAE Trouessart, 1897

Nannodectes Gingerich, 1975

Nannodectes lynasi, new species

Plesiadapis cf. *P. anceps* Lofgren et al., 2008

Plesiadapis cf. *P. churchilli* Lofgren et al., 2008

HOLOTYPE: RAM 9044, right dentary fragment with damaged i1, p2 alveolus, and p3–m3 from RAM locality V200510, member 4a, Goler Formation, California (fig. 3A).

REFERRED SPECIMENS: RAM 9668, left maxilla fragment with C, alveoli of P2 and P3, P4–M1 (fig. 5C), and RAM 9669, crushed skull fragment with broken left I1, right P4, M1–2 and associated right p3 (fig. 5E–F) from RAM locality V200510, member 4a; RAM 9429, right dentary fragment with i1 root and p3–m3 from RAM locality V200706, member 4a (fig. 3B); RAM 10029, right dentary fragment with damaged p4–m3 from RAM locality V200804, member 4a (fig. 3C); five m3s RAM 6961 (fig. 4A), RAM 6963 (fig. 4B), RAM 6960 (fig. 4C), RAM 6700 (fig. 4D), RAM 6934, m2 RAM 6446, mx fragment RAM 6935, mx trigonid RAM 6946, M3 RAM 6957 (fig. 5H), M2 RAM 6962 (fig. 5G), P3 RAM 6931 (fig. 5D), and 2 I1s RAM 6431 (fig. 5A), RAM 6929 (fig. 5B) from RAM locality V98012, member 4b; RAM 7193, partial right dentary with talonid fragment of p4, m1 and broken m2 from RAM locality V200202, member 4b; RAM 6925, partial left m3 from RAM locality V94014, member 4a.

ETYMOLOGY: Named in honor of Richard “Dick” Lynas, for his dedicated efforts in support of collection and study of Goler Formation vertebrate fossils.

DIAGNOSIS: Midsized plesiadapid with a narrow p4 and m2 that align it with *Nannodectes* and a unique combination of other features that separates it from all known plesiadapid species, which include, I1 with mediocone small or absent and centroconule absent, upper molars with no significant development of crenulated enamel and lacking mesostyles, p3–4 with inflated protoconids and distinct talonid basins, m1–2 with squared entoconids, and m3 with slight to moderate talonid enamel crenulations and broad and unfissured hypoconulid that is usually rounded.

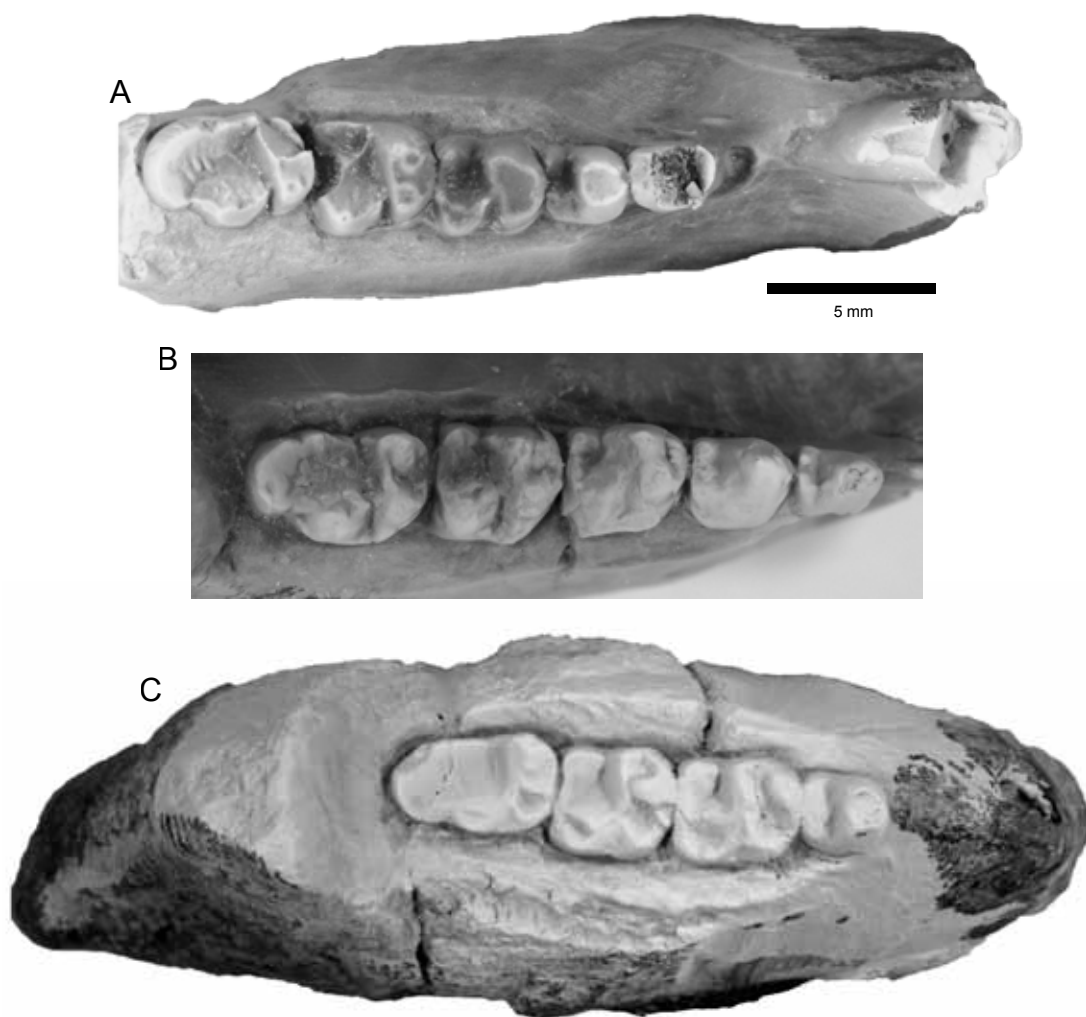


FIGURE 3. Occlusal views of mandibles of *Nannodectes lynasi*, new species. **A.** RAM 9044, holotype of *Nannodectes lynasi*, right dentary fragment with damaged i1, alveolus of p2, p3–m3 from RAM locality V200510. **B.** RAM 9429, right dentary fragment with i1 root and p3–m3 from RAM locality V200706. **C.** RAM 10029, right dentary fragment with damaged p4–m3 from RAM locality V200804.

DESCRIPTION: The holotype of *Nannodectes lynasi* (RAM 9044) has a damaged i1, p3, m2, and m3 (fig. 3A). Only the triangular-shaped posterior part of i1 is preserved. A single round depression, posterior to i1 and directly anterior to p3, represents the p2 alveolus. The trigonid of p3 is missing due to breakage. The talonid of p3 has two small medial cusps on its posterior margin (labially positioned cusp largest), and a very small, but distinct basin is present. The trigonid of p4 is dominated by a massive and worn protoconid (if a paraconid and metaconid were present, all trace has been removed by wear), and a distinct cristid obliqua connects the trigonid to a large hypoconid. The posterior margin of the talonid is defined by a postcristid developed between the hypoconid and smaller entoconid. The talonid basin of p4 is large, but

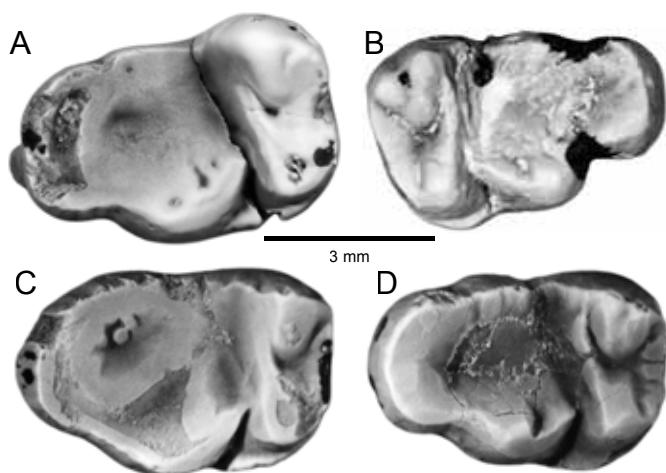


FIGURE 4. Occlusal views of m3s of *Nannodectes lynasi* from RAM locality V98012. **A.** RAM 6961, right m3. **B.** RAM 6963, left m3. **C.** RAM 6960, right m3. **D.** RAM 6700, right m3.

relatively small compared to m1–m2. Molar trigonids are simple, with large metaconids and protoconids, and smaller labially shifted paraconids (breakage removed metaconid and paraconid of m3). Talonids of m1–2 have large hypoconids and the entoconid of m1 is squared (entoconid of m2 broken). Crenulated enamel is not developed on m1–2. Notable features of the m3 talonid are faint to moderately developed crenulations, a labially projecting hypoconid lobe, and a broad, rounded, and unfissured hypoconulid.

RAM 9429 represents another mostly complete dentary of *N. lynasi* (fig. 3B), but one with significant enamel corrosion. RAM 9429 has a small, laterally crushed depression directly anterior to p3 that may represent the p2 alveolus, and a large, anteroposteriorly elongate protoconid dominate the trigonid of p3. The entoconid, hypoconid, cristid obliqua, and talonid basin are more developed in the p3 of RAM 9429 than the p3 of the holotype (RAM 9044). The trigonid of p4 has a very large protoconid, but unlike the holotype, a small metaconid and labially shifted paraconid are also present. Similar to p3, the hypoconid and entoconid are larger, and cristid obliqua and talonid basin more developed in the p4 of RAM 9429 than the holotype. The m1 of RAM 9429 has a large protoconid and metaconid and a smaller, linguallly positioned paraconid (less linguallly positioned than in p4). In m2, the paraconid is more linguallly positioned and more closely appressed to the metaconid. Entoconids of m1 and m2 are squared in RAM 9429. The talonid of m3 has a broad, rounded, and unfissured hypoconulid like the holotype, but differs in having a narrower hypoconulid lobe and a small entoconid that forms a distinct lingual bulge.

RAM 10029 is a partial dentary with heavily damaged p4–m3 as the crowns are partially dissolved (fig. 3C). Only the most robust crown features of RAM 10029 are visible, but in general shape and size, RAM 10029 closely resembles the holotype (RAM 9044) and RAM 9429. Also, the p4 talonid basin of RAM 10029 was large, like the p4 of RAM 9429. RAM 10029 also has a broad and rounded m3 hypoconulid and lacks an entoconid lobe, features more like the holotype than RAM 9429.

The partial dentary (RAM 7193) and isolated m3s previously referred to *Plesiadapis* cf. *P. churchilli* or *P. cf. P. anceps* (Lofgren et al., 2008), compare favorably to the holotype of *Nannodectes lynasi* and RAM 9429, except for RAM 6963. Isolated m3s of *N. lynasi* from the Goler Formation are uniform in morphology (fig. 4A, C–D), but RAM 6963 is smaller than all other m3s (table 3) and its hypoconulid is distinctly squared (fig. 4B). Because RAM 6963 comes

TABLE 3. Measurements of the lower dentition of *Nannodectes lynasi* from the Goler Formation. All specimens from V98012, except RAM 9669 and RAM 9044 (holotype) from V200510, RAM 9429 from V200706, RAM 10029 from V200804, and RAM 6925 from V94014.

Specimen	Tooth Site	Length	Width
9669	p3	2.50	2.08
9044	p3	2.41	1.89
	p4	2.75	2.29
	m1	3.25	2.97
	m2	3.93	3.40
	m3	5.10	2.97
9429	p3	2.45	1.91
	p4	3.05	2.71
	m1	3.74	3.32
	m2	3.90	3.60
	m3	5.43	3.44
10029	p4	2.52	2.39
	m1	3.68	3.39
	m2	3.59	3.41
	m3	4.92	3.02
6963	m3	4.32	2.95
6960	m3	4.52	3.16
6700	m3	4.59	3.15
6961	m3	4.84	3.20
6934	m3	—	2.82*
6925	m3	4.79	3.38
6446	m2	3.55*	3.15*
6935	mx	—	2.75*

* Minimum because tooth incomplete.

from the same site as four other m3s of *N. lynasi* (fig. 4A, C–D), it most likely represents an extreme morphological variant of the species.

Upper incisors of *N. lynasi* are broken, but RAM 6929 and RAM 6431 preserve a significant part of the crown (fig. 5A–B), and RAM 9669 just the alveolar rim. RAM 6929 and RAM 6431 were described by Lofgren et al. (2008), and their important features are the minute mediocone and lack of a centroconule in RAM 6929 and the absence of both a mediocone and centroconule in RAM 6431 (fig. 5A–B). The alveolar rim of RAM 9669 is 2.54 mm in width and 4.34 mm in length.

The upper canine and premolars of *N. lynasi* are represented by RAM 9668 (C and P4, with alveoli of P2–3), RAM 6931 (P3), and RAM 9669 (P4). In RAM 9668 (fig. 5C), a single-rooted tooth is positioned adjacent to the anterior alveolus of P2, indicating the lack of a diastema between the teeth. This rarely preserved tooth has been identified as the canine in plesiadapids (Gingerich, 1976; Boyer, 2009), although at first glance it would appear to be P1 based on its

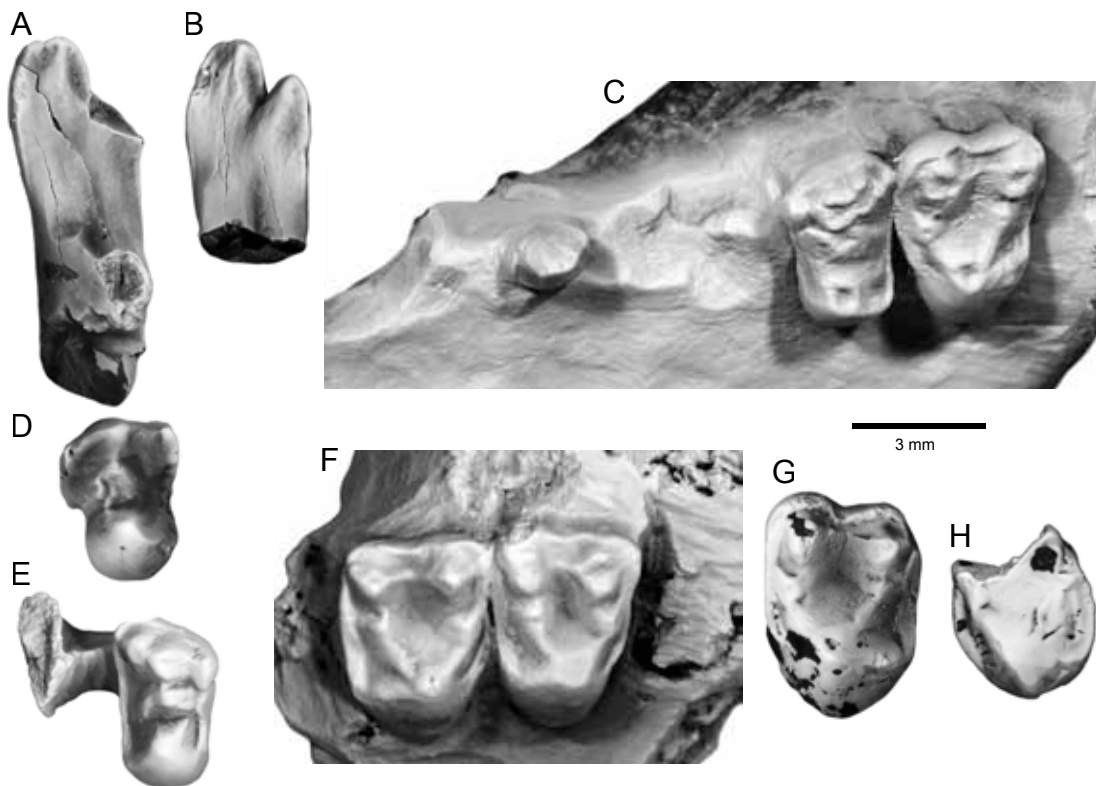


FIGURE 5. Upper dentition of *Nannodectes lynasi*. **A.** Occlusal view of RAM 6431, left I1 from RAM locality V98012. **B.** Occlusal view of RAM 6929, left I1 from RAM locality V98012. **C.** Occlusal view of RAM 9668, left maxilla fragment with C, alveoli of P2–3, and P4–M1 from RAM locality V200510. **D.** Occlusal view of RAM 6931, left P3 from RAM locality V98012. **E.** Occlusal view of right P4 of RAM 9669, skull fragment with broken I1, right P4, M1–2 and associated right p3 from RAM locality V200510; **F.** occlusal view of right M1–2 of RAM 9669. **G.** Occlusal view of RAM 6962, left M2 from RAM locality V98012. **H.** Occlusal view of RAM 6957, partial left M3 from RAM locality V98012.

position adjacent to P2. The canine of RAM 9668 is a single upright cusp elongated anteroposteriorly, with a small shelf positioned low on the anterior face of the tooth. The close placement of the canine and P2 in RAM 9668 is reminiscent of the condition seen in Wa 282, a partial maxilla of *Plesiadaptis walbeckensis*. In contrast, a canine to P2 diastema is present in PU13393, a partial maxilla of *P. fodinatus*. Alveoli present anterior to the P4 in RAM 9668 indicate that P2 had two circular roots orientated anteroposteriorly, with the anterior one approximately half the diameter of the posterior root and P3 had two roots of equal size, oriented transversely. Diastemas apparently were not developed between premolars in RAM 9668.

The only known P3 of *Nannodectes lynasi* (RAM 6931), described by Lofgren et al. (2008) as a P4, lacks a metacone and metaconule, but has a prominent protocone, and a paracone with a paraconule developed on its lingual face (fig. 5D). Both P4s (RAM 9669 and RAM 9668) of *N. lynasi* have a closely appressed paracone and metacone, small parastyle, prominent paraconule with a small enamel bulge positioned posteriorly (that could represent an incipient metaconule), large protocone, well-developed anterior and posterior cingulum, and weakly developed stylar

TABLE 4. Measurements of the upper dentition of *Nannodectes lynasi* from the Goler Formation. All specimens from V98012, except RAM 9668 and RAM 9669 from V200510.

Specimen	Tooth Site	Length	Width
9668	C	1.85	1.44
	P4	2.63	4.30
	M1	3.48	5.17
9669	P4	2.52	4.03
	M1	3.25	4.94
	M2	3.18	4.83
6931	P3	2.30	3.11
6962	M2	3.35	4.62
6957	M3	2.94*	3.61*
6929	I1	—	3.22
6431	I1	—	2.96*

* Minimum because tooth incomplete.

shelf and labial cingulum (fig. 5C, E). Also, the lingual cingulum is not continuous in P4 and the mesostyle and metastyle are absent. In contrast to P3, whose paracone is positioned on the lingual face of the paracone, the paracone and paracone of P4 are separated by a distinct valley.

Features of the M1 and M2 in *N. lynasi* are similar and include: widely spaced paracone and metacone subequal in size and connected by centrocrista, metacone positioned posteriorly, parastyle small and connected to paracone by weak paracrista, ectoflexus weak, labial cingulum present, protocone larger than metacone and paracone and connected to paracone and metacone by preprotocrista and postprotocrista, small hypocone present on crest extending posteriorly from protocone that merges with postcingulum, well-developed precingulum, lingual cingulum not continuous across protocone, and mesostyle and metastyle absent (fig. 5C, F, G). The only differences between M1 and M2 are a more developed centrocrista and parastyle on M2, and a stronger M2 ectoflexus in RAM 6962 (fig. 5G), compared to both the M1 of RAM 9668 and the M1–2 of RAM 9669 (fig. 5C, F). RAM 6957, the only known M3 of *N. lynasi* (fig. 5H) is damaged and has slightly crenulated enamel and lacks a distinct hypocone (Lofgren et al., 2008). Measurements of the dentition of *N. lynasi* are provided in tables 3–4.

DISCUSSION AND COMPARISONS: The initial sample of this Goler plesiadapid consisted of 14 isolated teeth and a dentary fragment found before 2003 that were referred to *Plesiadapis* cf. *P. churchilli* (dentary fragment) and *P. cf. P. anceps* (isolated teeth) because the specimens could not be confidently assigned to a known species (Lofgren et al., 2008). Between 2007 and 2009, three partial dentaries and two partial maxillae were recovered from a 300 m thick sequence of member 4a strata in a large canyon informally termed Grand Canyon (no. 2 in fig. 1). RAM locality V200510 in Grand Canyon yielded a dentary with p3–m3 (RAM 9044) and two partial upper dentitions (RAM 9668, RAM 9669), specimens reasonably certain to represent the upper and lower dentition of a single species.

During the early and middle Tiffanian in North America, lineages of similar plesiadapid genera, *Nannodectes* and *Plesiadapis*, evolved in parallel, with *Nannodectes* distinctly smaller

than *Plesiadapis* when both genera are found at the same site (Gingerich, 1976). Also, *Nannodectes* was distinguished from contemporaneous species of *Plesiadapis* by its narrower cheek teeth (especially in the lower premolars), more triangular P3 (usually lacking a paraconule), and lack of a centroconule on I1 (Gingerich, 1976).

In the Goler Formation, a single plesiadapid species is present, so size comparison between morphotypes is not possible. Also, the lack of a centroconule on I1 and a more triangular P3 are characters that do not reliably distinguish the two genera as they are found in *Nannodectes* and some species of *Plesiadapis*. However, narrower cheek teeth appear to distinguish *Nannodectes* and *Plesiadapis* as a cladogram based on dental characters of plesiadapid species indicates that *Nannodectes* is monophyletic, based on proportional differences between length and width of p4, M1–3, and m1–3 (Boyer, 2009: fig. 5.1, table 5.1, characters 18, 23, and 31). Thus, the lower cheek teeth of *Nannodectes* should be narrower than those of *Plesiadapis* and upper molars of *Nannodectes* more squared compared to more rectangular upper molars of *Plesiadapis*. To test this, ratios of length versus width of cheek teeth of *Nannodectes* and North American species of *Plesiadapis* were calculated using length and width means provided by Gingerich (1976: table 2, tables A3–A13) for each species. These ratios were compared to similarly derived ratios for the cheek teeth of *Nannodectes lynasi* from the Goler Formation (table 5). For the lower dentition, a number above 1.00 for a tooth site indicates that the teeth are longer than wide (narrower). For the upper dentition, all teeth are wider than long, but a number close to 1.00 for a tooth site indicates that these teeth are more squared (less rectangular).

Length versus width ratios of cheek teeth provide limited support for distinguishing *Nannodectes* from *Plesiadapis*. Ratios of the p4 of *N. intermedius*, *N. gazini*, *N. simpsoni*, and *N. gidleyi* are all above 1.00, indicating that the p4 of *Nannodectes* is consistently narrow. Early and middle Tiffanian species of *Plesiadapis* (*P. praecursor*, *P. anceps*, *P. rex*, *P. churchilli*) have a p4 that is wider than long (ratio less than 1.00), but later Tiffanian species (*P. fodinatus*, *P. dubius*, *P. cookei*) have narrow p4s like *Nannodectes* (table 5). The m2 of *Nannodectes* is slightly narrower than the m2 of *Plesiadapis praecursor*, *P. anceps*, and *P. rex*, but not narrower than the m2 of *P. churchilli*, *P. fodinatus*, *P. dubius*, and *P. cookei* (table 5). For the p3, m1 or m3, there is no significant difference in length versus width ratios between genera. For the upper dentition, the P3 of *Nannodectes gazini*, *N. simpsoni*, and *N. gidleyi* is more squared than in any North American species of *Plesiadapis*, while the P4 of *Nannodectes gazini*, *N. simpsoni*, and *N. gidleyi* is significantly more squared than only *Plesiadapis praecursor*, *P. rex*, and *P. churchilli* (table 5). There are no significant differences in ratios of length and width in the upper molars of *Nannodectes* and North American species of *Plesiadapis* (table 5). Length versus width ratios indicates that only a narrow p4 and more squared P3 and P4 are measurable characters that separate *Nannodectes* from early and middle Tiffanian species of *Plesiadapis*.

Goler dentaries (RAM 9044, RAM 9429, and RAM 10029) have narrow p4s and m2s with ratios above 1.00 (table 5), which supports their referral to *Nannodectes*, but Goler P4s and the single P3 have ratios not clearly aligned with either *Nannodectes* or *Plesiadapis* (table 5). Thus, proportional differences in certain cheek teeth of *Nannodectes* and *Plesiadapis* that distinguish the two genera are valid only for the lower dentition of the Goler sample. However, comparison of the dentition of this Goler plesiadapid to all species of *Nannodectes*, *Plesiadapis*, and *Chiromyoides*

TABLE 5. Length versus width ratios of cheek teeth of species of *Nannodectes* and North American species of *Plesiadapis*. Ratios based on means provided by Gingerich (1976). Ratios of *Nannodectes lynasi* based on measurements in tables 3 and 4.

TAXON	P ₃	P ₄	M ₁	M ₂	M ₃	p ³	p ⁴	M ¹	M ²	M ³
<i>N. intermedius</i>	1.17	1.06	1.08	1.00	1.56	—	—	—	—	—
<i>N. gazini</i>	1.27	1.13	1.12	1.04	1.67	0.85	0.69	0.69	0.68	0.78
<i>N. simpsoni</i>	1.42	1.16	1.04	1.03	1.57	0.85	0.73	0.68	0.62	0.82
<i>N. gidleyi</i>	1.23	1.06	1.07	1.03	1.61	0.85	0.69	0.70	0.66	0.73
<i>N. lynasi</i>	1.25	1.14	1.10	1.10	1.53	0.74	0.62	0.67	0.70	—
<i>P. praecursor</i>	1.22	0.91	1.02	0.99	1.52	0.73	0.59	0.61	—	—
<i>P. anceps</i>	1.13	0.95	1.01	0.95	1.51	—	—	—	—	—
<i>P. rex</i>	1.10	0.96	1.04	0.99	1.58	0.72	0.59	0.67	0.63	0.75
<i>P. churchilli</i>	1.13	0.97	1.06	1.07	1.58	0.66	0.60	0.72	0.66	0.68
<i>P. fodinatus</i>	1.27	1.11	1.10	1.06	1.60	0.74	0.64	0.71	0.68	0.70
<i>P. dubius</i>	—	1.22	1.12	1.08	1.58	0.71	0.65	0.73	0.69	0.70
<i>P. cookei</i>	1.29	1.04	1.06	1.06	1.60	—	0.71	0.75	0.68	0.76

indicates a closer morphological affinity to *Nannodectes gidleyi* and *N. aff. gidleyi*, which also supports referral of the Goler sample to *Nannodectes* and the diagnosis of the new species, *N. lynasi*.

When compared to middle and late Tiffanian species of *Plesiadapis*, *Nannodectes lynasi* is much smaller than *Plesiadapis simonsi*, *P. gingerichi*, *P. cookei*, *P. tricuspiciens*, and *P. remensis*, and lacks the more derived dental features seen in some combination in *P. fodinatus*, *P. dubius*, and *P. churchilli*. These features include highly crenulated upper molar enamel, m3 hypoconulid squared and fissured, m3 with highly crenulated talonid enamel, rounded m1–2 entoconids, centroconule on I1, and upper molars with mesostyles (Gingerich, 1976).

Compared to the early and middle Tiffanian species of *Plesiadapis*, *Nannodectes lynasi* is much larger than *Plesiadapis praecursor*, *P. insignis*, and *P. anceps*. Previously, isolated plesiadapid teeth from the Goler Formation were referred to *Plesiadapis* cf. *P. anceps* (Lofgren et al., 2008), but molars and premolars of the three recently collected dentaries (RAM 9429, RAM 9044, and RAM 10029) indicate the size of the lower dentition of *Nannodectes lynasi* significantly exceeds *Plesiadapis anceps* (table 6). Also, the lower premolars from these dentaries show the size of the p3 and p4 protoconid and talonid basin of p4 in *Nannodectes lynasi* far surpass development of these features in *Plesiadapis anceps*.

The European species, *P. walbeckensis*, is similar to *Nannodectes lynasi* in size and some other features, but it has poorly developed p3–4 talonids and a fissured m3 hypoconulid with more talonid crenulations than the m3 of *N. lynasi*. *Plesiadapis rex*, is also generally similar to *Nannodectes lynasi* in size, but differs in having an m3 hypoconulid that is usually fissured and squared, a centroconule on I1, mesostyles on M2–3, and a mesostyle sometimes on M1 (Gingerich, 1976). Also, *Plesiadapis rex* has weakly developed p3–4 talonids, compared to the relatively well-developed p3–4 talonids of *Nannodectes lynasi*.

Chiromyoides (particularly *C. minor*) shares some features with *Nannodectes lynasi* as it has a rounded, broad, and unfissured m3 hypoconulid with uncrenulated talonid enamel, but its

TABLE 6. Measurements of the lower dentition of *Nannodectes lynasi*, *Nannodectes gidleyi*, *Nannodectes* aff. *N. gidleyi*, and *Plesiadapis anceps*. Measurements of *Nannodectes gidleyi* and *Plesiadapis anceps* from Gingerich (1976: tables A-6, A-7), and *Nannodectes* aff. *N. gidleyi* from Schiebout (1974: table 9).

TAXON		P ₃	P ₄	M ₁	M ₂	M ₃
<i>Nannodectes lynasi</i>	Length	2.41–2.50	2.52–3.05	3.25–3.74	3.59–3.93	4.32–5.43
	Width	1.89–2.08	2.29–2.71	2.97–3.39	3.40–3.60	2.95–3.44
<i>Nannodectes gidleyi</i>	Length	2.1–2.3	2.2–2.4	2.7–3.1	3.0–3.3	4.4–5.0
	Width	1.7–2.0	1.9–2.5	2.5–3.1	2.9–3.3	2.7–3.2
<i>Nannodectes</i> aff. <i>gidleyi</i>	Length	—	2.7–3.1	2.6–2.9	3.1–3.3	4.5–4.7
	Width	—	2.3–2.4	2.6–2.8	3.0–3.2	3.1–3.2
<i>Plesiadapis anceps</i>	Length	2.1–2.2	2.2–2.5	2.6–3.0	2.8–3.1	4.2–4.5
	Width	1.8–2.0	2.2–2.6	2.7–3.0	3.0–3.3	2.8–3.0

p4 lacks a talonid basin. Also, the central upper incisors of *Chiromyoides* are extraordinarily robust (Gingerich, 1976), unlike Goler I1s.

In comparison to species of *Nannodectes*, *N. lynasi* is much larger than *N. intermedius*, *N. gazini*, and *N. simpsoni*. The lengths of the m3s and p4s in these species do not exceed 4.3 mm and 2.4 mm respectively (Gingerich, 1976: tables A3–A5), while in *N. lynasi* the lengths of m3s range from 4.32–5.43 mm and p4s from 2.52–3.05 mm (table 6).

Nannodectes gidleyi has many similarities to *N. lynasi* as it has a rounded, unfissured m3 hypoconulid, lacks a centroconule on I1, and has a small talonid basin on p3–4, usually with a small but distinct cristid obliqua (Gingerich, 1976). Also, a hypoconid and entoconid are developed on the labial and lingual edges of the posterior talonid margin of the p4 in AMNH 17389 of *N. gidleyi*, a feature shared with the holotype of *N. lynasi* (RAM 9044). Finally, some m3s of *N. gidleyi* (such as AMNH 17365 and AMNH 17174) have talonid enamel crenulations that are slightly or moderately developed, indicating some overlap in this feature with *N. lynasi*. However, development of crenulated talonid enamel in most m3s of *N. gidleyi* (for example, AMNH 17171 and AMNH 17389) exceeds anything seen in *N. lynasi*. Also, *N. gidleyi* usually has mesostyles on M1 and mesostyles always on M2–3 (Gingerich, 1976) and relatively small protoconids on p3–4. *Nannodectes lynasi* lacks upper molar mesostyles and has large p3–4 protoconids. Also, lower premolars and molars of *N. lynasi* are distinctly larger than those of *N. gidleyi*, although this distinction is less evident when comparing m3s (table 6).

Nannodectes aff. *N. gidleyi* from Big Bend, Texas, has a p4 that is closer in size to *N. lynasi*, but its lower molars are smaller, about the same size as *N. gidleyi* (table 6). *Nannodectes* aff. *N. gidleyi* apparently lacks a centroconule on I1 (see TMM 41365–274 in Schiebout, 1974: fig. 16b) and has an unfissured and often rounded m3 hypoconulid lobe (Gingerich, 1976), features shared with *N. lynasi*. However, *Nannodectes* aff. *N. gidleyi* has distinct upper molar mesostyles, squared hypoconulid lobes on some m3s, and highly crenulated m3 talonid enamel (Gingerich, 1976), although the two m3s illustrated by Schiebout (1974: TMM 41365–541: fig. 16k and TMM 41366–77: fig. 17) show slightly crenulated m3 talonid enamel. In any case, *N. aff. N. gidleyi* and *N. gidleyi* are closer in morphology to *N. lynasi* than any other plesiadapid species.

Order PROCREODI Matthew, 1915

Family OXYCLAENIDAE Scott, 1892

Thryptacodon Matthew, 1915*Thryptacodon* sp.

REFERRED SPECIMEN: RAM 9041, right m1 from RAM locality V200510, member 4a (fig. 6A).

DESCRIPTION: RAM 9041 is missing the metaconid due to breakage, but the protoconid, hypoconid, hypoconulid, and entoconid are all well preserved (fig. 6A). A small paraconid is connected to the protoconid by a long and arcuate paracristid. Broadly and deeply basined, the talonid is significantly longer and slightly wider than the trigonid. The hypoconid is large and the entoconid and hypoconulid are much smaller, with the hypoconulid slightly smaller than the entoconid. The hypoconulid is markedly shifted lingually, positioned immediately adjacent to the entoconid, so that the two cusps appear twinned, and a small entoconulid is present. The talonid basin is deepest against the back wall of the trigonid and a talonid notch is not present. A prominent shelf-like labial cingulid extends continuously from the anterior face of the trigonid below the paraconid, across the protoconid, to the most labial margin of the hypoconid. On the posterior face of the talonid a shelflike postcingulid descends labially to the posterolabial corner of the hypoconid, where only a short gap separates it from the posterior terminus of the labial cingulid.

DISCUSSION: RAM 9041 is most closely aligned with oxyclaenids and is most similar to *Thryptacodon*, based upon crown height, and occurrence and relative position of primary and secondary cusps. Based on size, RAM 9041 is much smaller than *Thryptacodon antiquus*, *T. australis*, and *T. pseudarctos* and is most similar to specimens included by Gazin (1956) in *T. demari* and *T. belli*, which were synonymized by Van Valen (1978) as *T. demari*. Similarities of RAM 9041 with *T. demari* include paraconid lingual and positioned anteriorly, talonid basin much wider than trigonid, distinct entoconulid, talonid notch closed, and hypoconulid lingually displaced and close to the entoconid. Only its smaller size and presence of a strong labial cingulid keep RAM 9041 from being identified as the Bison Basin species, now synonymized with *T. orthogonius* (Scott et al., 2002). RAM 9041 measures 4.95 mm in length, with a trigonid width of 2.64 mm and talonid width of 3.05 mm, compared to the m1 of the holotype of *T. "belli"* (UW 1045), whose length and width are 5.6 mm and 3.8 mm respectively (Gazin, 1956). Thus, RAM 9041 is assigned to *Thryptacodon* species indeterminate until more specimens are recovered of this oxyclaenid.

Family ARCTOCYONIDAE Murray, 1866

Mimotricentes Simpson, 1937*Mimotricentes tedfordi* McKenna and Lofgren, 2003

HOLOTYPE: RAM 6908, right maxilla with P4–M3 from RAM locality V94133, member 4a, Goler Formation, California.

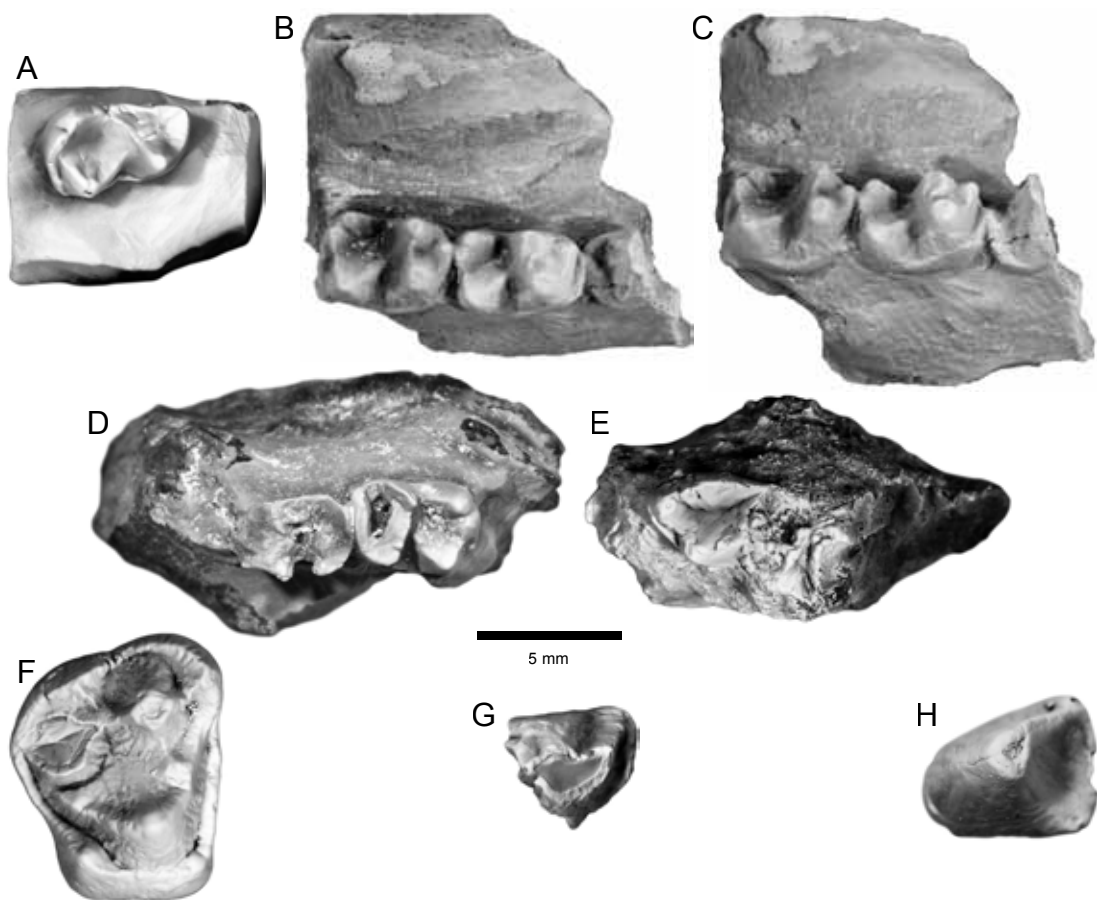


FIGURE 6. Dentition of oxyclaenids and arctocyonids. **A.** Occlusal view of RAM 9041, right m1 of *Thryptacodon* sp. from RAM locality V200510. **B.** Occlusal view of RAM 15622, right dentary fragment with talonid of p4, and m1–2 of *Mimotricentes tedfordi* from RAM locality V201014; **C.** oblique labial view of RAM 15622. **D.** Occlusal view of RAM 9670, left dentary fragment of *Mimotricentes tedfordi* with damaged m1 and base of p4 from RAM locality V200510. **E.** Occlusal view of RAM 6928, right dentary fragment of *Mimotricentes tedfordi* with m3 talonid and base of trigonid from RAM locality V200001. **F.** Occlusal view of RAM 9040, right M1 of *Lambertocyon* cf. *L. gingerichi* from RAM locality V200001. **G.** Occlusal view of RAM 9043, left p3 fragment of *Lambertocyon* cf. *L. gingerichi* from RAM locality V200001. **H.** Occlusal view of RAM 9660, premolar of undetermined arctocyonid from RAM locality V200613.

REFERRED SPECIMENS: RAM 15622, right dentary fragment with talonid of p4, and m1–2 from RAM locality V201014, member 4a (fig. 6B–C); RAM 9670, left dentary fragment with the base of p4 and damaged m1 from RAM locality V200510, member 4a (fig. 6D); RAM 6928, right dentary fragment with m3 talonid and base of trigonid (fig. 6E), and RAM 15333, left M2 from RAM locality V200001, member 4a.

DISCUSSION: The holotype of *M. tedfordi*, a maxillary fragment with P4–M3 (RAM 6908), from V94133, high in member 4a, was described by McKenna and Lofgren (2003), who noted that *M. tedfordi* was significantly smaller than *M. subtrigonus* and all other described species of *Mimotricentes* and *Lambertocyon*. The holotype was the only known specimen of *Mimotricentes tedfordi*, so the lower dentition was not described.

In 2010, a dentary fragment (RAM 15622) was recovered from V201014, a site low in member 4a, about 3 km south of the type locality of *M. tedfordi*. RAM 15622 represents the lower dentition of a small arctocyonid that almost certainly is *M. tedfordi*. Two other fragmentary arctocyonid dentaries (RAM 6928 and RAM 9670), collected prior to 2008, probably also represent *M. tedfordi*. Also, an isolated M2 (RAM 15333), found in 2012, is nearly identical to the M2 of the holotype. These four specimens are described below.

DESCRIPTION: The M2 of the holotype of *M. tedfordi* (RAM 6908) and RAM 15333 are similar in all features, their unusually large crestlike parastyles being especially noteworthy. Also, the length of RAM 15333 is 4.54 mm and the width 5.19 mm, dimensions similar to that of the M2 of the holotype (length 4.62 mm and width 5.50 mm).

RAM 15622 is a dentary fragment with a broken p4, and m1–2, with only the talonid and posterior wall of the trigonid of the p4 preserved (fig. 6B–C). The p4 has a low, 1.2 mm long, posterior shelf, which has a weakly developed posteromedial cusp connected to the trigonid wall by a small crest, features often seen in arctocyonids. The metaconid and protoconid of m1 are subequal in size and height, both larger than the low, labially shifted paraconid, and a protocristid and paracrista are present. The precingulid and a partial labial cingulid are present (labial cingulid terminates posteriorly at ectoflexid). The cristid obliqua is well developed and terminates at a large hypoconid, and a small but deep talonid basin, with steep posterior and labial slopes is present. A small posterolingually positioned entoconid and hypoconulid are closely appressed, with the hypoconulid slightly posterior to the transversely aligned hypoconid and entoconid. The m2 is similar to m1 in most respects, but m2 is more quadrate in outline and has a more labially shifted paraconid. Depth of the mandible below m1 is 6.15 mm.

The p4 of RAM 9670 is sheared off just above the gum line and the anterior part of the tooth is missing (fig. 6D), but its length was at least 3.5 mm, and width about 2.5 mm. The talonid of m1 is well preserved but the trigonid crown is missing due to breakage. The dimensions of the m1 of RAM 9670 are similar to those of the m1 of RAM 15622, but the talonid of RAM 9670 has crenulated enamel, a broader and shallower basin, and greater spacing of the entoconid and hypoconulid, differences suggesting they could represent different taxa. However, significant variation in lower molar morphology is well documented in *Mimotricentes subtrigonus*, a larger species than *M. tedfordi* (table 7), from Swain Quarry in Wyoming, where sample sizes of isolated teeth can exceed 60 specimens (Rigby, 1980: table 38). Teeth of *M. subtrigonus* exhibit considerable variation in talonid development, as the proximity of the hypoconulid and entoconid can vary from nearly fused to well separated with the hypoconulid medially located (Rigby, 1980). Also, some m1s from Swain Quarry in the AMNH collections lack crenulated talonid enamel, while in others it is well developed. If this amount of variation is also present in *M. tedfordi*, RAM 9670 likely represents the same species as RAM 15622.

RAM 6928 is a dentary fragment with a damaged m3 that may also represent *M. tedfordi*. RAM 6928 has an intact m3 talonid, but its trigonid is broken at the gum line (fig. 6E). The talonid has a low hypoconulid, an entoconid crest with three cusps, and a large hypoconid. The talonid basin of m3 is broad and shallow and opens lingually through a small talonid notch. The morphology of the m3 talonid in *Mimotricentes subtrigonus* from Swain Quarry, varies even more than the m1 talonid, so much so that the m3 is “posteriorly too variable for

TABLE 7. Measurements of the lower dentition of *Mimotricentes tedfordi* from the Goler Formation and *Mimotricentes subtrigonus* from Swain Quarry, Fort Union Formation, Wyoming. Measurements of *M. subtrigonus* from Rigby (1980: table 38). Measurements of *M. tedfordi* from RAM 9670 (p4–m1), RAM 6928 (m3), and RAM 15622 (p4–m2).

Tooth Site		<i>M. tedfordi</i>	<i>M. subtrigonus</i>
P ₄	L	3.5*	5.10–5.40
	W	2.50*–2.79*	3.15–3.30
M ₁	L	4.38–4.49	5.10–6.45
	WTri	2.78–2.94*	3.30–4.35
	WTal	2.93–3.14	3.75–4.95
M ₂	L	4.41	5.55–6.90
	WTri	3.15	4.20–5.10
	WTal	3.22	4.05–5.25
M ₃	L	5.27*	5.70–7.20
	W	3.18*	3.30–4.80

* Estimate.

taxonomic use” (Rigby, 1980: 104). Specimens of *M. subtrigonus* observed at the AMNH from Swain Quarry have m3 talonids of similar construction as RAM 6928, but are much larger (table 7). Thus, RAM 6928 probably also represents *M. tedfordi*.

Lambertocyon Gingerich, 1979

Lambertocyon cf. *L. gingerichi* Gunnell, 1994

HOLOTYPE: UM 81147, left M1 from Chappo Type Locality, Wasatch Formation, Wyoming.

REFERRED SPECIMENS: RAM 9040, right M1 (fig. 6F), and RAM 9043, left p3 fragment (fig. 6G) from RAM locality V200001, member 4a.

DESCRIPTION: RAM 9040 is an unworn M1 that is in pristine condition except for the metacone, which is missing due to breakage (fig. 6F). Based on the size of its base, the metacone was about as tall and broad as the large paracone. The protocone is massive, taller and larger than the paracone. A small and low hypocone is positioned slightly lingual to the protocone on the posterolingual corner of the postcingulum. The paraconule is larger than the metaconule, and a postparaconule wing connects the paraconule with the lingual base of the paracone (a premetaconule wing is not developed). The parastyle is large and crescent shaped, but a metastyle is not present. The lingual cingulum is complete, but weakly developed across the base of the protocone. The labial cingulum is also complete, but is weakest labial to the base of the paracone. The mesostyle is large and elongate, with its apex forming a large part of the labial cingulum. Also, a series of cuspules are present on the anteroposterior axis of the mesostyle and a small ridge projects linguallly from its apex to the base of the cusp.

RAM 9043 is broken and only the anterolabial third of the tooth is present (fig. 6G), but what remains is nearly identical in morphology to p3s of *L. gingerichi* from the Chappo Type Locality. Distinct enamel crenulations on the anterolabial face of p3, its size, and the wear facet on its broken crown all mirror features observed in *Lambertocyon*.

DISCUSSION: Three species of *Lambertocyon* have been described, *L. ischyryus* (Gingerich, 1978, 1979), *L. eximius* (Gingerich, 1979), and *L. gingerichi* (Gunnell, 1994), with the following reported occurrences: (1) *L. ischyryus*, Debeque Formation, Colorado (Gingerich, 1978, 1979; Kihm, 1984); (2) *L. eximius*, Blacks Peak Formation, Texas, (Schiebout, 1974; listed as *Arctocyonidae*, undescribed genus and species), Fort Union Formation, Wyoming (Winterfeld, 1982), and Polecat Bench Formation, Wyoming (Gingerich, 1979; Secord, 2008); and (3) *L. gingerichi*, Polecat Bench and Wasatch formations, Wyoming (Gunnell, 1994; Secord, 2008). The Goler specimens of *Lambertocyon* are both from the Land of Oz site (V200001), so they almost certainly represent the same species.

Species of *Lambertocyon* are differentiated by mesostyle development and size, with *L. eximius* significantly larger than *L. ischyryus* (Gingerich, 1979), and *L. gingerichi* 8%–10% larger than *L. eximius* (on average) and also having a well-developed mesostyle (Gunnell, 1994). Based on size, RAM 9040 is more like the holotype of *L. eximius* than the holotype of *L. gingerichi*, but measurements of the two species overlap (table 8), demonstrating that distinguishing species of *Lambertocyon* by size is problematic. For example, the sample of *Lambertocyon* from Divide Quarry was referred to *L. gingerichi* (Secord, 2008), but one of the two M1s from Divide Quarry (UM 87040), has a length of 7.7 mm and a width of 8.1 mm (table 8), dimensions closer to the holotype of *L. eximius*, than that of *L. gingerichi* (table 8). The only reported M1 of *L. ischyryus* (FMNH P15545) is 6.86 mm in length and 7.87 mm in width, which is significantly smaller than M1s of *L. eximius* and *L. gingerichi* (table 8).

The very large mesostyle of RAM 9040 is unique for *Lambertocyon*. Secord (2008) noted that M1 mesostyle development varies from strong to weak in *L. gingerichi* from Divide Quarry and larger samples are needed to conclusively demonstrate *L. eximius* and *L. gingerichi* are distinct species. RAM 9040 was compared directly to M1s of *L. gingerichi* (UM 81147 holotype and UM 85163 from Chappo Type locality; UM 87040 and UM 110259 from Divide Quarry), and these specimens have small mesostyles, in comparison to the distinctly larger mesostyle of RAM 9040. Also, the complete lingual cingulum of RAM 9040 is not reported for any M1 of *Lambertocyon* or observed in M1s of *L. gingerichi* from Chappo Type Locality or Divide Quarry.

The large mesostyle and complete lingual cingulum of RAM 9040 demonstrate that morphological variation within *Lambertocyon* is greater than previously documented and the Goler Formation occurrence may represent a new species. RAM 9043, the fragmentary p3, adds little to this discussion. An unusually large mesostyle and a weak but complete lingual cingulum on a single tooth is an inadequate basis from which to diagnose a new species, especially considering *L. eximius* and *L. gingerichi* require larger samples to confirm they represent distinct species. Thus, RAM 9040 and RAM 9043 are referred to *Lambertocyon* cf. *L. gingerichi* until more specimens of *Lambertocyon* are recovered from the Goler Formation, as the mesostyle development of RAM 9040 is more aligned with that species than *L. eximius*.

TABLE 8. Measurements of *Lambertocyon* cf. *L. gingerichi* (RAM 9040) from the Goler Formation compared to other M1s of *Lambertocyon*.¹

Specimen no.	Length	Width
FMNH P15545	6.9	7.9
PU19576 (holotype)	7.4	8.3
UW 13325	7.1	7.5
UW 13221	6.8*	7.3*
TMM 41365-764	6.9	6.9
UM 81147 (holotype)	7.5	8.8
UM 87040	7.7	8.1
UM 110259	7.7	8.9
RAM 9040	7.3	8.5

*Estimated.
¹ *L. ischyrius*: cast of FMNH P15545. *L. eximius*: TMM 41365-764 (Schiebout, 1974: table 14); UM 13325, UM 13221 (Winterfeld, 1982: table 18); PU 19576, holotype (Gingerich, 1979: table 1). *L. gingerichi*: UM 81147, holotype (Gunnell, 1994: table 3); UM 87040, UM 110259 (Secord, 2008: table 53).

ARCTOCYONIDAE?

REFERRED SPECIMEN: RAM 9660, a p2, p3, P2, or P3 from RAM locality V200613, member 4b (fig. 6H).

DESCRIPTION: RAM 9660 is a large premolar with slightly crenulated enamel that is 5.75 mm in length and 4.30 mm in width if the long axis of the tooth is its anterior-posterior orientation. RAM 9660 has a large and swollen anterior cusp that is connected by a pair of posteriorly directed cristae that terminate at small cusps on the tooth margin (fig. 6H). These low cusps are connected by a weakly developed cingulum or cingulid that forms the posterior (?) edge of the tooth.

DISCUSSION: RAM 9660 probably indicates the presence of an additional eutherian from the Goler Formation. RAM 9660 may be an arctocyonid, but this is uncertain, as is which tooth site RAM 9660 represents. Another possibility is that RAM 9660 represents an upper premolar of *Goleroconus*.

Order CONDYLARTHA Cope, 1881a

Family HYOPSONDONTIDAE Trouessart, 1897

Protoselene Matthew, 1897

Protoselene ashtoni, new species

HOLOTYPE: RAM 9047, left dentary fragment with a partially erupted p4 and m1 from RAM locality V200702, member 4a, Goler Formation, California (fig. 7A–C).

ETYMOLOGY: Named in honor of R. Larry Ashton, Jr., for his support of the research programs of the Raymond M. Alf Museum of Paleontology.

DIAGNOSIS: Protoconid of p4 highly inflated, significantly more than other known p4s of *Protoselene*, p4 lacking metaconid and anterior basal cusp in contrast to *P. opisthacus*, paraconid of m1 more lingual than *P. opisthacus* or *P. novissimus*, relative length and width of m1 talonid shorter and wider than *P. novissimus*, and m1 larger than *P. griphus*.

DESCRIPTION: The distinctive features of the p4 of RAM 9047 are its greatly swollen protoconid and the lack of both an anterior basal cusp and metaconid (fig. 7A–C). On the anterior face of the protoconid is a small, but distinct ridge, that defects posterolabially as it traces the midline of the crown and extends to the apex. A well-developed cristid obliqua extends to the posterior edge of the p4, where it defects lingually and lessens in height. Thus, a small talonid basin is present that opens lingually. Talonid enamel is rugose, in contrast to the faintly crenulated protoconid enamel.

The m1 of RAM 9047 has a low, lingually positioned paraconid connected by a well-developed paracristid with a large protoconid. The metaconid and protoconid are subequal in size and height. The talonid basin of m1 opens lingually and is deep, and broad. The cristid obliqua extends posteriorly to the hypoconid, which is larger than the entoconid and the slightly smaller hypoconulid, which are closely appressed. A well-developed precingulid is present anterior to the trigonid, as is a small postcingulid posterior to the hypoconid. The p4 of RAM 9047 is 5.99 mm in length and 4.08 mm in width, and the m1, 5.63 mm in length, with trigonid and talonid widths of 4.13 mm and 4.33 mm respectively.

DISCUSSION AND COMPARISONS: *Protoselene* is a relatively rare component in Torrejonian and Tiffanian mammalian faunas from western North America. Found at many Torrejonian localities in the San Juan Basin of New Mexico (Matthew, 1937; Williamson, 1996), *P. opisthacus* is the best-known species. Another Torrejonian species is *Protoselene* (“*Dracoclaenus*”) *griphus* known from a few specimens collected at the early Torrejonian Dragon Canyon site in central Utah (Gazin 1939, 1941; Robison, 1986) and a single P4 from the lowest Torrejonian part of Kimbeto Wash in the San Juan Basin (Williamson, 1996). The third species is *P. novissimus* from early Tiffanian strata in the Bison Basin of southwest Wyoming (Gazin, 1956). A few other specimens of *Protoselene* have been identified from Tiffanian strata, including fragmentary teeth of *P.* cf. *P. opisthacus* from the Torrejonian–Tiffanian overlap zone and early Tiffanian of the Hanna Formation of southern Wyoming (Higgins, 2003), and a dentary with m1–3 of *P. opisthacus* from Ray’s Bonebed (middle Tiffanian) from the Big Bend area of Texas (Schiebout, 1974).

The massive and swollen p4 protoconid of *P. ashtoni* is its most distinctive feature and separates it from *P. opisthacus* whose protoconid is only slightly inflated. Also, the p4 of *P. opisthacus* usually has an anterior basal cusp and a small metaconid, features absent in RAM 9047. The p4 is not known for either *P. griphus* or *P. novissimus*, so comparisons of these species to *P. ashtoni* are limited to the m1. The only known m1 of *P. novissimus* (USNM 21023) is an isolated tooth (Gazin, 1956) with a relatively longer and narrower talonid than the m1 of *P. ashtoni*. Also, the m1 paraconid of *P. ashtoni* is positioned more lingually than in either *P. novissimus* or *P. opisthacus*. The only known m1 of *P. griphus* (USNM 15773) has a lingually positioned paraconid like the m1 of RAM 9047, but the m1 of *P. ashtoni* is larger than the m1 of *P. griphus* as the length and width of USNM 15773 are 5.3 mm and 4.0 mm, compared to 5.63 mm and 4.33 mm for RAM 9047. Also, a slight accessory cusp is present on the anterior

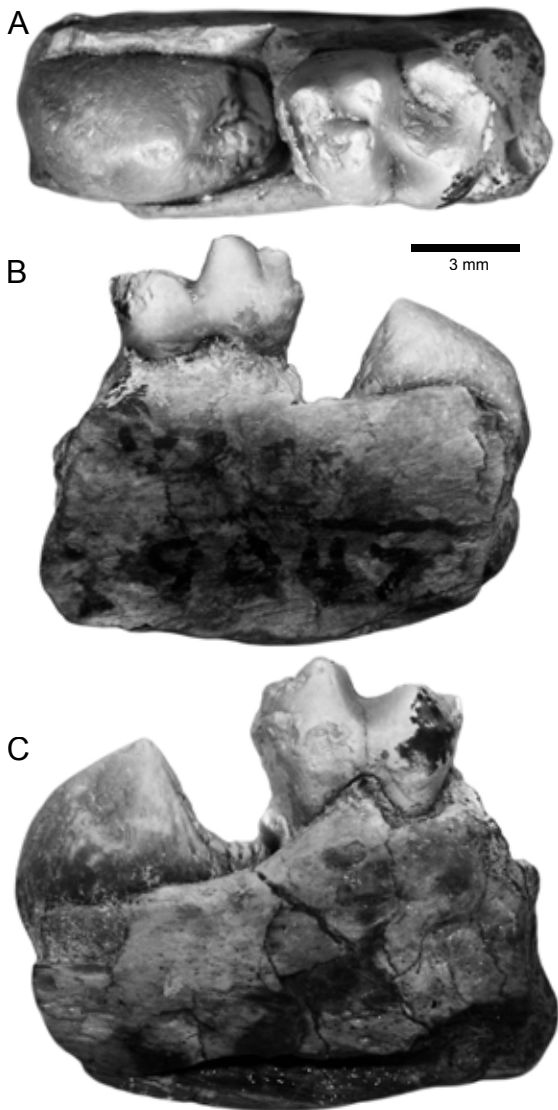


FIGURE 7. Dentition of the holotype of *Protoselene ashtoni*, new species, RAM 9047, left dentary fragment with m1 and partially erupted p4 from RAM locality V200702; **A.** occlusal view; **B.** lingual view; **C.** labial view.

crest of the entoconid in *P. griphus* (Gazin, 1941), a cusp absent in the only known m1 of *P. ashtoni*.

Species of *Protoselene* are poorly known except for *P. opisthacus*, which can be easily distinguished from *P. ashtoni* by its lack of a massive p4 protocoenid. Based on the single m1s known for *P. ashtoni*, *P. griphus*, and *P. novissimus*, differences in size or the position of the paraconid indicate they are distinct species, but the evidence is less robust. The recovery of more complete material of *P. ashtoni*, as well as, of *P. griphus*, and *P. novissimus*, is needed to fully diagnose the three species.

Promioclænus Trouessart, 1904

***Promioclænus walshi*, new species**

HOLOTYPE: RAM 9098, left m1–3 with lingual half of m1 and anterior part of trigonid of m2 missing, and right dentary fragment with m2–3 with m2 missing all of the trigonid except the basal portion of the posterior wall from RAM locality V200510, member 4a, Goler Formation, California (fig. 8B–E).

REFERRED SPECIMENS: RAM 6724, dentary fragment with m2 and talonid of m1 (fig. 8A), and RAM 6926, right maxilla fragment with M2–3 (referral questionable) (fig. 8F–G) from RAM locality V200001, member 4a.

ETYMOLOGY: Named in honor of the late Steven Walsh, whose enthusiastic leadership of Goler Formation screenwashing efforts significantly increased the sample of Tiffanian vertebrates from southern California.

DIAGNOSIS: Significantly larger than all other described species of *Promioclænus*.

DESCRIPTION: Lower premolars of *Promioclænus walshi* are unknown. The m1 of the holotype (RAM 9098) is broken, with only the labial half present, which preserves part of the tal-

onid basin and a large hypoconid and protoconid. A complete but worn m1 talonid is present in RAM 6724 (fig. 8A) and the hypoconid is large and the talonid basin is well developed and opens lingually through a deep talonid notch. A distinct entoconid and hypoconulid are present, with the hypoconulid slightly smaller than the entoconid and placed medially, while the entoconid is positioned on the posterolingual tooth margin. The hypoconulid is positioned closer to the entoconid than the hypoconid and a small postcingulid is developed between the hypoconid and hypoconulid.

RAM 6724 has a slightly worn, but well preserved, quadrate shaped m2 (fig. 8A). The trigonid is anteroposteriorly short because the large metaconid and small paraconid are closely appressed and the paraconid is slightly shifted labially. The paracristid is faintly visible while the protocristid is distinct. The talonid of m2 is very similar to m1, with a large hypoconid and smaller hypoconulid and entoconid, with the entoconid the larger of the two. The partial m2s of the holotype (fig. 8B–E) have the same features as the complete m2 of RAM 6724.

Left and right m3s of the holotype are identical in size and morphology (fig. 8B–E). The protoconid is the largest trigonid cusp and the paraconid and metaconid are subequal in size, with a slight labial shift of the paraconid. The paracristid is more distinct in m3 than in m2. The m3 talonid has a large hypoconid, broad hypoconulid and a smaller ridgelike entoconid positioned directly adjacent to the hypoconulid, separated by a slight constriction in the talonid wall. The talonid basin is narrow, but deep, and opens lingually through a small talonid notch.

A maxilla fragment with right M2–3 (RAM 6926) was found in a concretion at the same site as RAM 6724 and may represent the upper dentition of *Promioclænus walshi*. The maxilla fragment is crushed making it difficult to photograph M2–M3 in occlusal view (fig. 8F), so a drawing is provided (fig. 8G). The M2 is quadrate in outline and has moderate to heavy wear on all major cusps. The protocone is the largest cusp and the paracone is slightly larger than the metacone. A centracrista wear facet connects the metacone and paracone, as do preparacrista and postprotocrista wear facets connect the protocone with the paraconule and metaconule. The precingulum and postcingulum are both present, and a well-developed hypocone is positioned on the postcingulum. Before wear, it appears that the apex of the hypocone was positioned directly posterior to the apex of the protocone or slightly labial to it. The lingual cingulum is not developed across the lingual face of the protocone and the labial cingulum is developed only adjacent to the ectoflexus and paracone. A minute parastyle and weak ectoflexus are present, but the metastyle is absent.

The M3 of RAM 6926 has a rectangular shape and is significantly smaller than M2. The protocone is the largest cusp, with the metacone and paracone subequal in size. The metacone of M3 is shifted lingually in comparison to its position in M2. The paraconule and metaconule are also relatively smaller in M3 compared to M2. A distinct hypocone is not evident on the postcingulum of M3.

DISCUSSION AND COMPARISONS: The lower dentition of *Promioclænus walshi* is essentially a larger version of the morphology seen in *P. lemuroides* from the Nacimiento Formation of

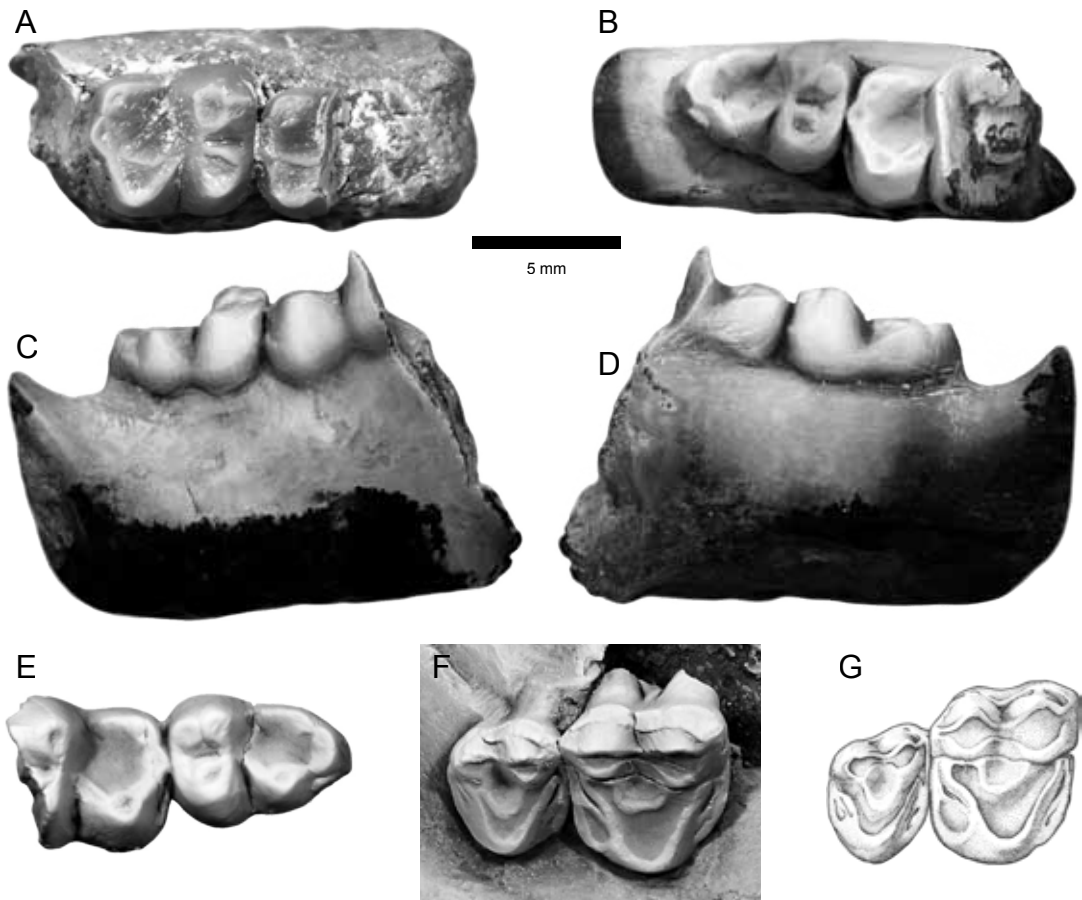


FIGURE 8. Dentition of *Promioclænus walshi*, new species. **A.** Occlusal view of RAM 6724, right dentary fragment with m2 and talonid of m1 from RAM locality V200001. **B–E.** Holotype of *Promioclænus walshi*, RAM 9098, partial right and left lower dentitions from RAM locality V200510: **B.** occlusal view, **C.** labial view, and **D.** lingual view of RAM 9098, right dentary fragment with m3 with damaged m2; **E.** occlusal view of RAM 9098, left m2–3 with anterior part of m2 trigonid missing. **F.** Oblique occlusal view of RAM 6926, right maxillary fragment with M2–3, from RAM locality V200001; **G.** drawing of RAM 6926 in occlusal view.

New Mexico described by Matthew (1897, 1937). Compared to the holotype of *P. lemuroides*, lower molars of *P. walshi* are consistently larger (table 9). In addition to the holotype, 12 dentary and three maxillary fragments of *P. lemuroides* at the AMNH, were also measured to document the range in dimensions of premolars and molars of *P. lemuroides*. These results also indicate that *P. walshi* is significantly larger than *P. lemuroides*, particularly in lower molar width (table 9). *Promioclænus walshi* is also larger than *P. pipiringosi*, a poorly known species described by Gazin (1956) from early to middle Tiffanian strata in the Bison Basin of Wyoming. The holotype of *P. pipiringosi* (USNM 20571) is a partial dentary whose molars are similar in morphology and size to those of *P. lemuroides* (table 9). However, Gazin (1956) also referred a dentary fragment with p2–4 (USNM 21021) from the type locality to *P. pipiringosi*. If this referral is correct, *P. pipiringosi* has smaller and less inflated premolars than *P. lemuroides*.

(table 9). The lower premolars of *P. walshi* are unknown, so no comparison can be made with *P. pipiringosi* or *P. lemuroides*. *Promioclænus acolytus* is the only other species of *Promioclænus*. The size of its lower dentition, based on the large sample from Swain Quarry (Rigby, 1980: table 46), is much smaller than *P. walshi* (table 9).

A second species of *Promioclænus*, that is larger than *P. pipiringosi*, may occur in the Bison Basin. A fragmentary dentary with the posterior portion of m2 and part of the trigonid and roots of m3 (USNM 21020) was noted as possibly representing *Litaletes* or another species of *Promioclænus* (Gazin, 1956). The talonid of the m2 in USNM 21020 has an entoconid, hypoconulid, and hypoconid that have about the same relative size and positioning as those cusps in *Promioclænus*. The size of the m2 in USNM 21020 (based on a photograph with scale) shows a length and width of approximately 4.75 mm and 4.00 mm, respectively, 0.3–0.4 mm larger than *P. pipiringosi* and 0.4–0.5 mm smaller than *P. walshi* (table 9). Gazin (1956) surmised that if USNM 21020 represented *Promioclænus*, it was too large to be *P. pipiringosi*. USNM 21020 is too fragmentary for detailed comparison to *P. walshi*, but its smaller size suggests it is not the Goler Formation species.

A partial maxilla with M2–3 (RAM 6926) from RAM locality V200001, the same site that yielded a partial dentary of *P. walshi* (RAM 6724) could represent the upper dentition of *P. walshi*. RAM 6926 was compared to the M2–3 of *P. lemuroides* and similarities include the relative size and position of the protocone, metacone, paracone, and conules, and cingulum development. However, there are significant differences, as RAM 6926 has a more quadrate shaped M2 (like the M1 of *P. lemuroides*), a relatively larger M2 hypocone, an M3 closer in size to M2 compared to the significantly smaller M3 relative to M2 in *P. lemuroides*, and an anteroposteriorly broad, rectangular M3, compared to the narrow M3 in *P. lemuroides*. Thus, M2–M3 of *P. lemuroides* and RAM 6926 have the same cusp construction and arrangement, but proportional differences in certain cusps and tooth shape cast doubt on whether RAM 6926 represents *P. walshi*, although these differences might represent characters that distinguish *P. walshi* from other species of *Promioclænus*.

A maxilla with heavily worn M2–3 (USNM 21022) from the Bison Basin that was tentatively referred to *P. pipiringosi* (Gazin, 1956) has some bearing on this issue. The M2 of USNM 21022 is complete and has a distinct rectangular shape, measuring about 3.2 mm in length and 5.0 mm in width. Although heavily worn, the wear facets indicate that the paracone of USNM 21022 was slightly larger than the metacone and a distinct hypocone was present on the posterior cingulum. Thus, two discernible features of the M2 of USNM 21022 resemble features present in the M2 of RAM 6926, but the shape of the M2 of USNM 21022 is rectangular like *P. lemuroides*, unlike the quadrate-shaped M2 of RAM 6926. Also, the M3 of USNM 21022 is nearly as large as the M2, more so than in either *P. lemuroides* or *P. walshi*. It is uncertain whether USNM 21022 even represents *P. pipiringosi*, but if it does, then upper molar morphology of *Promioclænus* would exhibit significant variation. The two molars preserved in RAM 6926 are about the correct size to represent the upper dentition of *P. walshi*. But based on differences in upper molar morphology evident in RAM 6926, *P. lemuroides*, and USNM 21022 (*P. pipiringosi*?), referral of RAM 6926 to *P. walshi* is tentative.

TABLE 9. Measurements of *Promioclænus walshi*, new species from the Goler Formation compared to *P. pipiringosi*, *P. lemuroides*, and *P. acolytus*.¹

Tooth Site		<i>P. walshi</i>	<i>P. pipiringosi</i>	<i>P. lemuroides</i>	<i>P. lemuroides</i> Holotype	<i>P. acolytus</i>
P ₂	L	—	2.7	3.65–3.70	3.90	—
	W	—	1.6	1.90–1.97	2.09	—
P ₃	L	—	3.3	4.50–4.79	4.55	3.60–3.90
	W	—	2.1	2.52–2.84	2.83	2.10–2.40
P ₄	L	—	3.8	4.55–4.85	4.62–4.72	3.45–4.35
	W	—	2.8	3.16–3.47	3.36–3.45	2.55–3.15
M ₁	L	5.10	4.1	4.07–4.80	4.19–4.36	3.15–4.05
	WTri	—	—	3.23–4.22	3.67–3.87	2.40–3.45
	WTal	4.05	3.4	3.35–4.01	3.77–3.78	2.55–3.45
M ₂	L	4.96*–5.50	4.4	4.23–4.73	4.26–4.38	3.45–4.50
	WTri	4.65–4.82*	—	3.92–4.49	4.05–4.22	2.85–3.90
	WTal	4.40–4.42	3.7	3.48–4.34	3.77–3.82	2.85–3.75
M ₃	L	5.42–5.43	—	4.12–4.81	4.49	3.15–4.35
	WTri	4.08–4.14	—	2.94–3.50	3.33	2.40–3.15
	WTal	3.35–3.36	—	2.11–3.09	2.64	—
M ¹	L	—	—	3.75–4.30	—	—
	W	—	—	5.16–5.91	—	—
M ²	L	5.37	—	3.88–4.34	—	—
	W	6.65	—	5.68–6.49	—	—
M ³	L	3.70	—	2.60–2.95	—	—
	W	5.52	—	3.81–4.64	—	—

* Estimate.
¹ Measurements of *P. pipiringosi* from Gazin (1956) and *P. acolytus* from Rigby (1980: table 46). The holotype of *P. lemuroides* is AMNH 2421. Other specimens of *P. lemuroides* measured were: AMNH 15952, 15953, 15955, 15957, 15958, 15959, 16631, 16632, 16633, 16634, 16645 (lower dentitions) and AMNH 16636, 16644, 17045 (upper dentitions).

PHENACODONTIDAE Cope, 1881a

Phenacodus Cope, 1873

Phenacodus cf. *P. bisonensis* Gazin, 1956

HOLOTYPE: USNM 20564, right maxilla with P4–M2, and a left maxilla with M1 and M2 thought to be from the same individual from the Bison Basin, Fort Union Formation, Wyoming.

REFERRED SPECIMENS: UCMP 69122, parts of both dentaries with right m2 and left p4–m2 from UCMP locality V65710, member 4b(?); RAM 9659, RM1 from RAM locality V98012, member 4b (fig. 11C); RAM 6722, right M1 (fig. 11D), RAM 7205, right dP4 (fig. 11I), RAM 7245, maxilla fragment with left dP3–4 (fig. 11H), RAM 7208, left dP4, RAM 9725, right dP4, RAM 6721, damaged right m2, RAM 6723, right dentary fragment with m2–3 (fig. 9E) from RAM locality V200001, member 4a; RAM 7248, left maxilla fragment with P4–M1 and damaged M2 from RAM locality V200304, member 4a (fig. 11B); RAM 9019, right m3 from RAM locality

V200508, member 4a; RAM 9022, left dentary with damaged dp4 and erupting m1, RAM 9672, left maxillary with P3-4 (fig. 11A) from RAM locality V200510, member 4a; RAM 9025, right m1, RAM 9021, right M2 (fig. 11F), RAM 9046, left dentary fragment m1-3 (fig. 9D) from RAM locality V200603, member 4a; RAM 9020, associated left M2 and M3 (fig. 11G); RAM 9024, left dentary with m2-3 (fig. 9F), RAM 9023, right dentary with p3-m2 and anterior portion of m3 trigonid (fig. 9A-C) from RAM locality V200612, member 4a; RAM 9045, left dp4 from RAM locality V200704, member 4b (fig. 9G); RAM 10290, right dentary fragment with m1 and m2 trigonid and partial talonid, RAM 10291, left m3, RAM 10292 left dentary with c-m3 and right dentary with i1-2, and c-m1 from RAM locality V200802, member 4a (fig. 10A-C); RAM 15000 right maxilla fragment with dP4-M2 from RAM locality V201122, member 4a (fig. 11E).

DESCRIPTION AND DISCUSSION: This medium-sized phenacodontid, referred to *Phenacodus* cf. *P. bisonensis*, is the most common mammalian species found by surface collecting in the Goler Formation. Included in *P.* cf. *P. bisonensis* is UCMP 69122, a concretion with parts of both dentaries previously referred to *Tetraclaenodon puercanensis* (West, 1970, 1976: pl. 120, 1-2). Found by a hiker in 1954, exact provenance of UCMP 69122 is uncertain, but based on general location information (West, 1970), it likely came from member 4b. In the past two decades, multiple specimens of the upper dentition of *Phenacodus* were recovered from member 4a and member 4b and these specimens have well-developed molar mesostyles and large P4 metacones, features that distinguish *Phenacodus* from *Tetraclaenodon* (Thewissen, 1990). Lower dentitions of *Phenacodus* and *Tetraclaenodon* are often difficult to distinguish (Thewissen, 1990), but if all upper dentition specimens from member 4a and member 4b are *Phenacodus*, UCMP 69122 almost certainly represents *Phenacodus* as well.

Features of the lower dentition of *Phenacodus* cf. *P. bisonensis* are shown in RAM 9023 (fig. 9A-C), RAM 9046 (fig. 9D), RAM 6723 (fig. 9E), RAM 9024 (fig. 9F) and RAM 10292, an extraordinary complete specimen for the sparsely fossiliferous Goler Formation, with the left and right dentaries of a single individual within a concretion (fig. 10A-C). Based on RAM 10292, crowns of the canines and incisors are missing due to breakage, but these teeth were single rooted. Smaller than i3, i2 probably had a circular-shaped crown based on its root, while the crown of i3 was anteroposteriorly elongate, based on the same line of evidence. Small diastemas separate i2 and i3, and i3 from the much larger canine, which has a circular root in cross section. The p1 is single rooted and its crown is elongate anteroposteriorly, exhibiting a single tall cusp and a miniscule posterior basal cusp on a weakly developed posterior cingulid. In contrast, the posterior basal cusp and posterior cingulid are well developed on the two-rooted p2. Diastemas are small between c1 and p1, and p1 and p2, and minute between p3 and p4. The p3 lacks a metaconid, but has a large protoconid and small paraconid positioned low and directly anterior to the protoconid, and a very small talonid basin. The p4 metaconid is smaller than the protoconid, and a paralophid connects the small and low paraconid to the protoconid. The talonid of p4 has a relatively narrow basin and a large hypoconid and small entoconid. The m1-m3 of *P.* cf. *P. bisonensis* are of basic phenacodontid morphology, as they lack paraconids, but have well-developed metaconids, protoconids, and hypoconids, and smaller entoconids and hypoconulids, and wide talonid basins. The m3 of *P.* cf. *P. bisonensis* is significantly smaller than the m2, but it has a larger hypoconulid.

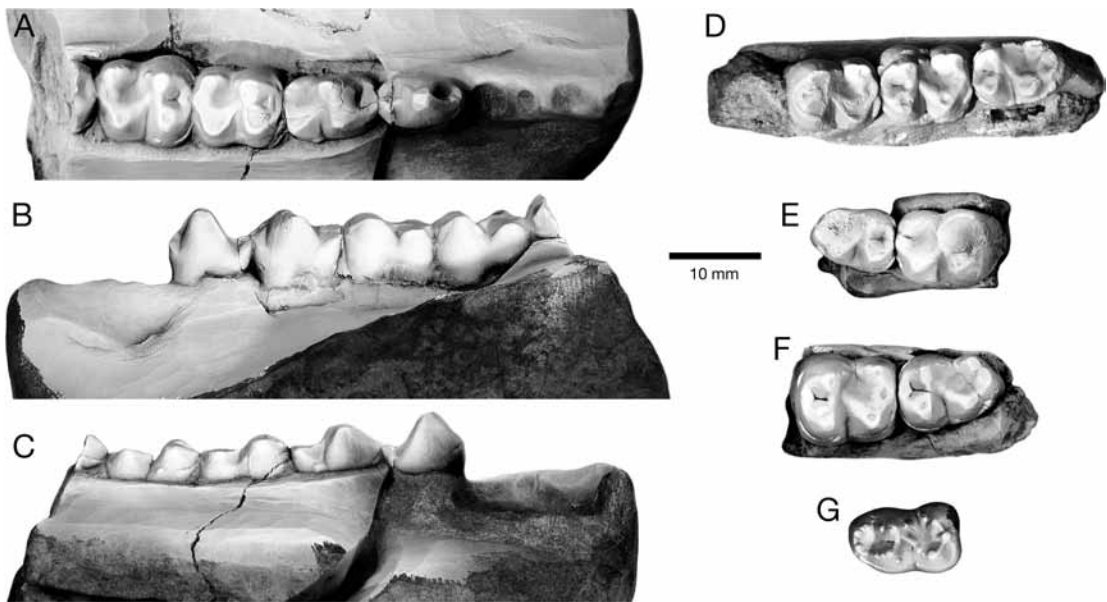


FIGURE 9. Lower dentition of *Phenacodus* cf. *P. bisonensis*. **A.** Occlusal view of RAM 9023, right dentary with p3–m2 and anterior portion of m3 trigonid from RAM locality V200612; **B.** lingual view of RAM 9023; **C.** labial view of RAM 9023. **D.** Occlusal view of RAM 9046, left dentary with m1–3 from RAM locality V200603. **E.** Occlusal view of RAM 6723, right dentary fragment with m2–3 from RAM locality V200001. **F.** Occlusal view of RAM 9024, left dentary fragment with m2–3 from RAM locality V200612. **G.** Occlusal view of RAM 9045, left dp4 from RAM locality V200704.

The upper dentition of *Phenacodus* cf. *P. bisonensis* consists of two M1s (RAM 9659, RAM 6722), an M2 (RAM 9021), maxillary fragments with P4–M2 (RAM 7248) and dp4–M2 (RAM 15000), an associated M2–3 (RAM 9020), and a maxillary fragment with heavily worn P3–4 (RAM 6972). The P3 of *P. cf. P. bisonensis* has a large paracone and protocone and smaller metacone and the P4 has a large paracone, metacone, and protocone, and a small parastyle (fig. 11A–B). All upper molars of *P. cf. P. bisonensis* have well-developed mesostyles and parastyles (fig. 11B–G). The single M3 of *P. cf. P. bisonensis* (RAM 9020) has a small hypocone (fig. 11G).

The dentition of this mid-sized species of *Phenacodus* from the Goler Formation is too small to be *P. grangeri*, *P. magnus*, or *P. intermedius*, and too large to be *P. matthewi* or *Ectocion* (tables 10–11) (see Thewissen, 1990: tables A4–A14, A18–A20, A26–A29), and *Ectocion* lacks a hypocone on M3 (Thewissen 1990). Direct comparison of specimens from member 4a and member 4b to the Bison Basin sample of *Phenacodus bisonensis* at the USNM, indicates they are more similar to *P. bisonensis* than any other phenacodontid. *Phenacodus vortmani* and *P. bisonensis* are both similar in size to the Goler specimens (table 10) (Thewissen, 1990: tables A15–A17, A21–A25), but the p4 of the Goler sample is more aligned with *P. bisonensis*. The entoconid is present in 59% of p4s of *P. bisonensis*, but is absent in all Tiffanian and early Clarforkian p4s of *P. vortmani*, and *P. bisonensis* has a relatively narrower talonid basin than *P. vortmani* (Thewissen, 1990). Goler p4s from member 4a and member 4b have entoconids and relatively narrow talonid basins (figs. 9A–C, 10A–C), which indicates they are not *P. vortmani*. Goler lower molars are also very similar to those of *P. bisonensis* from the Bison Basin.

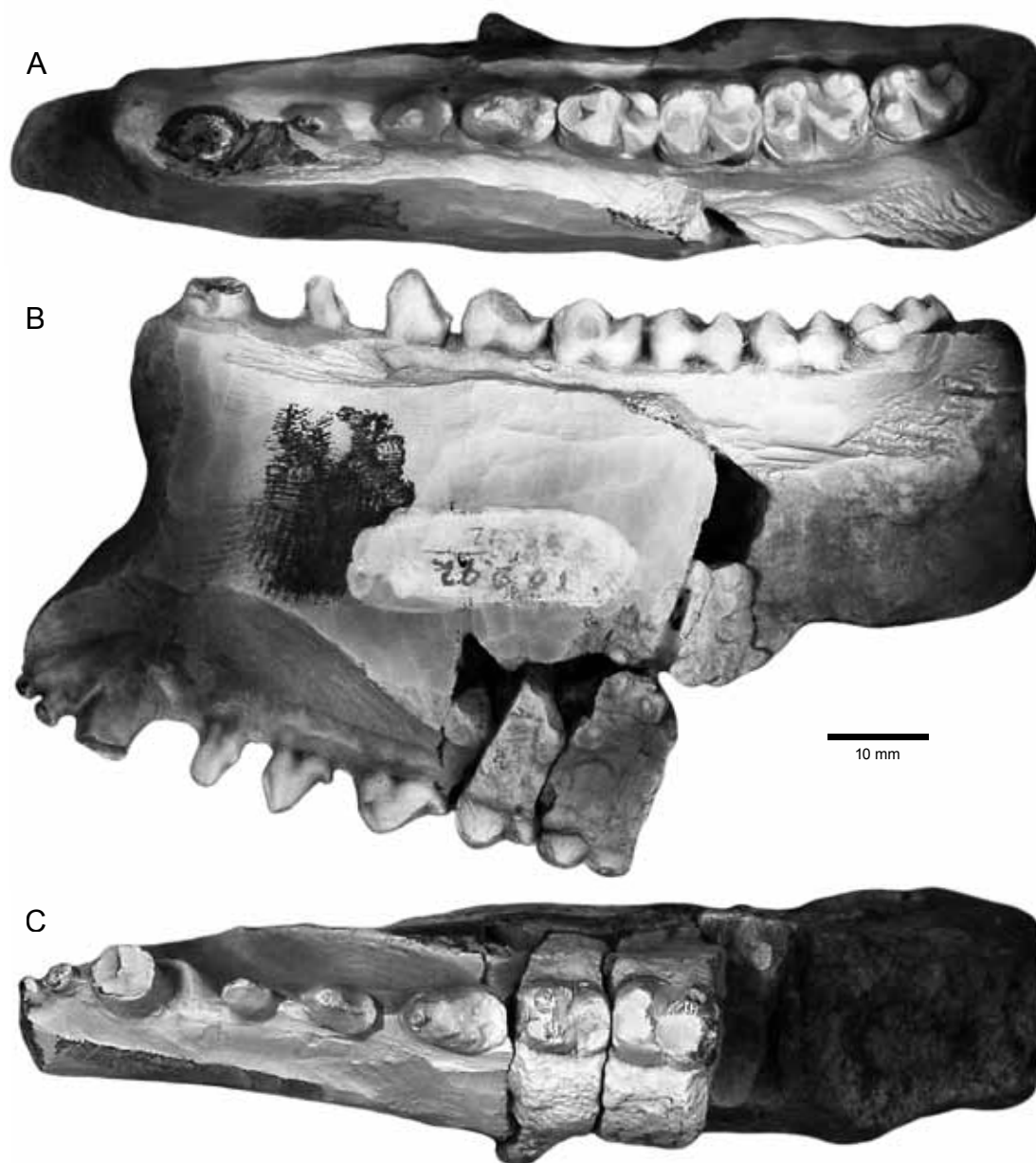


FIGURE 10. RAM 10292, left and partial right dentaries of *Phenacodus* cf. *P. bisonensis* from RAM locality V200802: A. occlusal view of left dentary with c–m3; B. labial view of RAM 10292; C. occlusal view of right dentary with i1–2, and c–m1.

One notable difference between Goler p4s and those from the Bison Basin is paraconids of *P. bisonensis* are slightly larger and more anteriorly positioned relative to the protoconid in comparison to Goler p4s. The only consistent difference between Goler upper molars and those of *P. bisonensis* is the mesostyle is usually shifted posteriorly, so part of it is positioned labial to the metacone in *P. cf. P. bisonensis* (fig. 11B–G), and in *P. bisonensis* the mesostyle

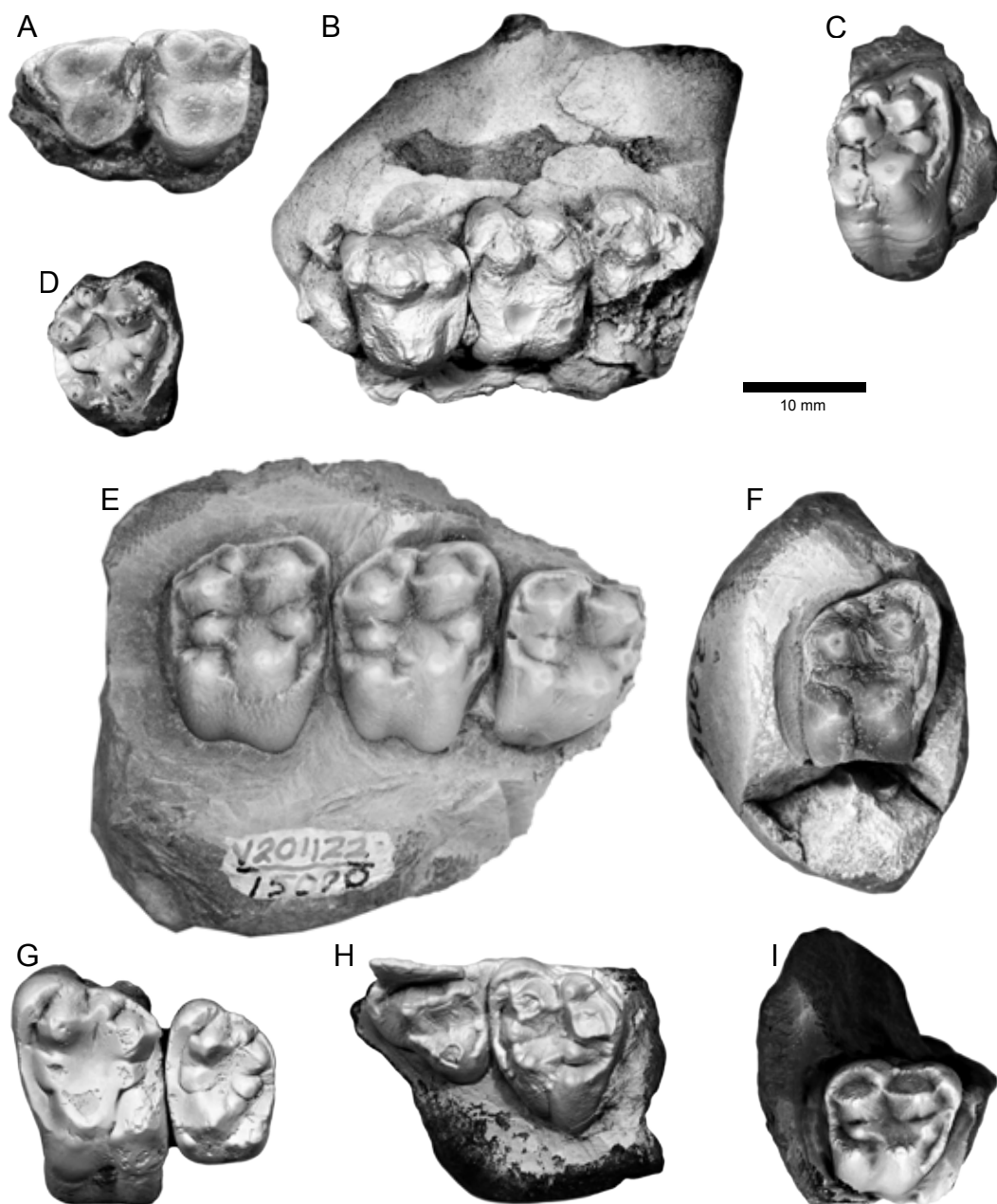


FIGURE 11. Upper dentition of *Phenacodus* cf. *P. bisonensis*. **A.** Occlusal view of RAM 9672, left maxillary fragment with P3–4, from RAM locality V200510. **B.** Occlusal view of RAM 7248, left maxillary fragment with P4–M1 and damaged M2, from RAM locality V200304. **C.** Occlusal view of RAM 9659, right M1 from RAM locality V98012. **D.** Occlusal view of RAM 6722, right M1 from RAM locality V200001. **E.** Occlusal view of RAM 15000, right maxilla fragment with dP4–M2 from RAM locality V201122. **F.** Occlusal view of RAM 9021, right M2 from RAM locality V200603. **G.** Occlusal view of RAM 9020, associated left M2 and M3 from RAM locality V200612. **H.** Occlusal view of RAM 7245, maxillary fragment with left dP3–4 from RAM locality V200001. **I.** Occlusal view of RAM 7205, right dP4 from RAM locality V200001.

is positioned close to the metacone, but not partly labial to it. Also, the postparacrista and premetacrista usually intersect with the mesostyle at its lingual base in *P. cf. P. bisonensis* (fig. 11C–G), while the postparacrista and premetacrista intersect with the mesostyle at its apex in *P. bisonensis*. Because of these differences, the Goler specimens are referred to *Phenacodus cf. P. bisonensis*.

Seven specimens of the deciduous dentition of *Phenacodus* were also recovered from the Goler Formation and RAM 15000, a maxilla fragment with dP4–M2 (fig. 11E), is particularly informative as it preserves part of the permanent and deciduous dentition. The M1–M2 of RAM 15000 are identical to M1s and M2s referred to *P. cf. P. bisonensis*, indicating that the dP4 of RAM 15000 must also be this taxon, which facilitated identification of four isolated dP4s (RAM 7245; fig. 11H, RAM 7205; fig. 11I, RAM 7208, and RAM 9725) as representing *P. cf. P. bisonensis*. Two dp4s (RAM 9022 and RAM 9045) also represent *P. cf. P. bisonensis* as the specimens are closely comparable to dp4s of *P. bisonensis* described by West (1971) and RAM 9022 is from a site that yielded a specimen of the permanent dentition (RAM 9672).

West (1971) described two specimens of the deciduous dentition of *P. bisonensis*, a dp4 from Bison Basin (USNM 26325; Fort Union Formation, Wyoming) and a dP4 from Douglas Quarry (PU 14634b; Lebo Formation, Montana). Estimates of their dimensions based on graph plots by West (1971: figs. 14, 15) are comparable in size to deciduous teeth of *P. cf. P. bisonensis* (tables 10–11). RAM 9022 is a partial dentary with dp4 that is missing its crown, so only its approximate size is known (table 10). RAM 9045 is an unworn dp4 that is anteroposteriorly elongate, with a metaconid and protoconid of equal size, a linguallly positioned and smaller paraconid, a miniscule cusp labial to the paraconid, and a well-developed and cuspidate cristid obliqua (fig. 9G). The talonid basin of RAM 9045 is large and the talonid has a large entoconid and hypoconid and smaller hypoconulid. RAM 9045 is most similar in morphology and size to USNM 26325 (table 10), the single dp4 referred to *P. bisonensis* by West (1971).

RAM 7245, a maxillary fragment with dP3–dP4, represents the only known dP3 of *P. cf. P. bisonensis* (fig. 11H). Triangular in shape, dP3 has a large paracone and protocone, smaller metacone, and a parastyle, paraconule and metastyle, but lacks a metaconule. A dP3 of *P. bisonensis* was not identified (West, 1971), so the dP3 of RAM 7245 serves as a close proxy. Five dP4s of *P. cf. P. bisonensis* all have well-developed paraconules and hypocones (fig. 11E, H–I). The single dP4 (PU 14634b) referred to *P. bisonensis* does not have a paraconule and hypocone, but these cusps are present on deciduous dP4s of the similar sized phenacodontid, *P. vortmani* (West, 1971). Goler dP4s are similar in approximate dimensions to dP4s of *P. bisonensis* and *P. vortmani*, but Goler dP4s are wider than long, unlike both *P. bisonensis* and *P. vortmani* (table 11). Also, the mesostyle, and postmetacrista and premetacrista in Goler dP4s are positioned as they are in molars of *P. cf. P. bisonensis*, while these features in the only known dP4 of *P. bisonensis* (PU 14634b) have the same orientation as molars of *P. bisonensis*. These differences are further evidence that this mid-sized Goler phenacodontid referred to *Phenacodus cf. P. bisonensis* is not conspecific with *P. bisonensis*, although it resembles it in many ways.

TABLE 10. Measurements of the lower dentition of *Phenacodus* cf. *P. bisonensis* from the Goler Formation. All are RAM specimens except 69122 (UCMP). USNM 26325, a dp4 of *P. bisonensis*, has an approximate length of 10.6 mm and width of 7.7 mm.

ID	Tooth Site	L	W	W Tri	W Tal
10292	Lc	5.70	5.10	—	—
	lp1	3.55	2.43	—	—
	lp2	6.30	3.96	—	—
	lp3	8.22	5.18	—	—
	lp4	8.93	6.05	—	—
	lm1	9.00	—	7.50	7.50
	lm2	9.25	—	8.77	8.35
	lm3	9.55	—	9.69	5.88
	Rc	5.28	4.92	—	—
	rp1	3.51	2.60	—	—
	rp2	6.02	3.86	—	—
	rp3	8.50	5.19	—	—
	rp4	7.45*	5.88	—	—
	rm1	8.70	—	7.18	7.19
9023	p3	8.43	5.38	—	—
	p4	9.89	6.98	—	—
	m1	9.21	—	8.11	8.17
	m2	9.57	—	9.14	8.38
	m3	—	—	7.52*	—
69122	p4	8.1	—	—	—
	m1	8.5	—	—	—
	lm2	8.6	—	—	—
	rm2	9.0	—	7.7	7.2
	m3	8.6	—	—	—
9025	m1	8.85	—	7.24	7.31
9046	m1	8.94	—	7.17	7.18
	m2	9.32	—	8.36	7.80
	m3	9.70	—	6.92	6.26
6721	m2	9.05	—	7.06*	6.93
10290	m1	9.10	—	7.13	7.22
	m2	8.27*	—	8.15	7.70*
6723	m2	9.49	—	8.05	7.35
	m3	9.10	—	6.51	5.74
9024	m2	9.99	—	8.98	8.42
	m3	10.43	—	7.60	6.67
10291	m3	10.22	—	7.03	6.08
9019	m3	9.00	—	6.50	6.47
9045	dp4	11.25	—	6.78	7.41
9022	dp4	9.76*	6.52	—	—
	m1	8.43*	—	7.11*	6.96*

* Estimate.

TABLE 11. Measurements of the upper dentition of *Phenacodus* cf. *P. bisonensis* from the Goler Formation. PU 14634b (dP4 of *P. bisonensis*) is approximately 9.2 mm in length and 8.2 mm in width. The five dP4's of *P. vortmani* have lengths of 8.3–9.9 mm and widths of 7.9–9.7 mm.

Specimen	Tooth Site	Length	Width
RAM 9672	P3	6.86	7.26
	P4	7.49	8.50
RAM 7248	P4	8.14	9.33
	M1	8.21	10.78
	M2	9.15*	11.99*
RAM 9659	M1	8.37	11.42
RAM 6722	M1	8.53	10.99
RAM 9021	M2	8.70	11.21
RAM 9020	M2	9.27	13.19
	M3	7.11	10.78
RAM 15000	dP4	7.74	9.37
	M1	9.68	11.36
	M2	8.97	11.58
RAM 7245	dP3	8.11	7.40
	dP4	9.19	9.95
RAM 7205	dP4	8.86	9.03
RAM 7208	dP4	8.41*	8.88*
RAM 9725	dP4	7.39*	8.00

* Estimate.

Phenacodus cf. *P. matthewi* Simpson, 1935

HOLOTYPE: AMNH 17191, right dentary with m2–3 from Mason Pocket, Animas Formation, Colorado; see Thewissen (1990) for alternative interpretation of type locality.

REFERRED SPECIMEN: RAM 7210, right dentary fragment with p4 and outline of base of p3 from RAM locality V200001, member 4a (fig. 12A).

DESCRIPTION: RAM 7210 represents a small phenacodontid with a p3 broken off at the gum line and a well-preserved p4. The p3 was approximately 6.37 mm in length and 3.52 mm in width, and the p4 is 7.62 mm in length and 5.30 mm in width. The paraconid of p4 is low and small and is shifted labially to the midline of the tooth (fig. 12A) and the metaconid and protoconid are well developed with the protoconid positioned more anterior than the metaconid. Trigonid enamel is crenulated only on the labial side of p4 and is slight. The talonid basin of p4 is well developed and a large hypoconid and slightly smaller entoconid are present.

DISCUSSION: The paraconid and size of the p3 and p4 of RAM 7210 are significantly smaller than Goler Formation p3s and p4s referred to *Phenacodus* cf. *P. bisonensis* (table 10), indicating that RAM 7210 may represent *Phenacodus matthewi*, the smallest species of *Phenacodus*. The holotype of *P. matthewi* is a dentary with m2–3 (AMNH 17191) which can't be compared directly with RAM 7210, but two other specimens from the type locality (AMNH

56284, AMNH 17193) each have a heavily worn p4. The p4 of AMNH 56284 is 8.02 mm in length and 5.17 in width, similar in dimensions to RAM 7210, but the paraconid of RAM 7210 is significantly smaller than the p4 paraconid of AMNH 56284, which is equal in size to the metaconid or protoconid. Also, trigonid enamel is distinctly crenulated on the labial side and slightly crenulated on the lingual side of the p4 in AMNH 56284, while trigonid enamel is crenulated only on the labial side of the p4 in RAM 7210. AMNH 17193 (right p4, m1, and m3), the holotype of "*Phenacodus gidleyi*" (Simpson, 1935) now referred to *P. matthewi* (Delson, 1971; West, 1976; Thewissen, 1990), has a p4 that is 6.91 mm in length and 4.76 mm in width, smaller than either AMNH 56284 or RAM 7210. The paraconid is well developed in AMNH 17193, indicating a closer affinity to AMNH 56284 than RAM 7210. The only other reported p4 of *P. matthewi* is CM 34292 from the Fort Union Formation in the Wind River Basin of Wyoming (Thewissen, 1990). CM 34292 is about the same size as RAM 7210, but has a large paraconid, like AMNH 17193 and AMNH 56284. Thus, RAM 7210 is similar in size to p4s referred to *P. matthewi*, but its small paraconid makes referral to the species uncertain.

Phenacodus cf. *P. grangeri* Simpson, 1935

HOLOTYPE: AMNH 17185, right maxilla with M1–2 and labial fragment of M3 from Mason Pocket, Animas Formation, Colorado.

REFERRED SPECIMEN: RAM 7172, left m3 from RAM locality V94014, member 4a (fig. 12B).

DESCRIPTION AND DISCUSSION: RAM 7172 is a slightly worn m3 whose paraconid is absent, but whose protoconid, metaconid, hypoconid, entoconid, and hypoconulid are large (fig. 12B). RAM 7172 is 12.87 mm in length and has trigonid and talonid widths of 8.72 mm and 7.99 mm, respectively.

RAM 7172 is almost identical to the m3 of USNM 21025, a dentary fragment with m3 from the Bison Basin. When describing *P. bisonensis*, Gazin (1956) noted the presence of a larger phenacodontid and described it as *Phenacodus?* sp. (large), and included USNM 21025 in it. Later, Thewissen (1990) referred USNM 21025 to *P. grangeri*. RAM 7172 appears to represent *P. grangeri*, but m3s of *P. grangeri* cannot be reliably distinguished from *P. intermedius* based on size or morphology, or from *P. magnus* based on size (m3 of *P. magnus* is unknown) (Thewissen, 1990). Thus, RAM 7172 is referred to *Phenacodus* cf. *P. grangeri* until more complete material of this taxon is recovered.

Phenacodus cf. *P. vortmani* Cope, 1880

HOLOTYPE: AMNH 4824, left dentary with p4 and fragment of m1, roots of p3 and m3, and alveoli for p1–2 from Alkali Creek, Wind River Basin, Wyoming.

REFERRED SPECIMEN: RAM 7253, rp4 from RAM locality V200307, member 4d (fig. 12C).

DESCRIPTION: RAM 7253 is a slightly worn p4 (fig. 12C), that is 10.2 mm in length, with trigonid and talonid widths of 6.5 mm and 6.4 mm respectively. RAM 7253 has a large protoconid

and metaconid that are the same size and height, but has two smaller cusps in the position of the paraconid. The labially positioned paraconid cusp is twice the size of the lingually positioned cusp. The talonid of RAM 7253 is wide, and a large hypoconid and small entocoid are present.

DISCUSSION: An isolated p4 of *Phenacodus* is difficult to identify to species, but size is helpful as RAM 7253 is too small to be *P. intermedius*, *P. magnus*, or *P. grangeri*, and too large to be *P. matthewi*. The length and width of RAM 7253 approach the maximum length (10.3 mm) and width (6.8 mm) of p4s of *P. bisonensis* (Thewissen, 1990: tables A15–A17). RAM 7253 is also similar to *P. vortmani*, as p4s of *P. vortmani* from late Paleocene strata range from 9.1–9.8 mm in length and 5.7–7.1 mm in width (Thewissen, 1990: table A–21). *Phenacodus bisonensis* differs from *P. vortmani* in having a narrower talonid basin on p4 with an entoconid commonly present, a cusp commonly absent in *P. vortmani* (Thewissen, 1990). The p4 of RAM 7253 has a wide talonid and a small entoconid (fig. 12C). Presence or absence of the p4 entoconid does not distinguish *P. vortmani* and *P. bisonensis*, but the broad talonid basin of RAM 7253 shows a greater affinity to *P. vortmani*. Thus, RAM 7253 is tentatively referred to *Phenacodus* cf. *P. vortmani* based on its wide p4 talonid.

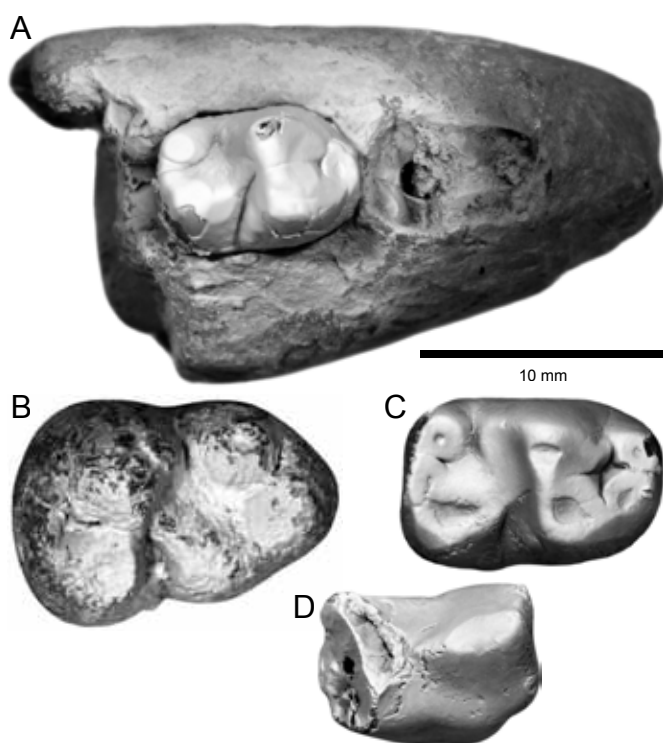


FIGURE 12. Specimens of *Phenacodus* cf. *P. matthewi*, *Phenacodus* cf. *P. grangeri*, *Phenacodus* cf. *P. vortmani*, and *Dissacus*. **A.** Occlusal view of RAM 7210, right dentary fragment with p4 and base of p3 of *Phenacodus* cf. *P. matthewi* from RAM locality V200001. **B.** Occlusal view of RAM 7172, left m3 of *Phenacodus* cf. *P. grangeri* from RAM locality V94014. **C.** Occlusal view of RAM 7253, rp4 of *Phenacodus* cf. *P. vortmani* from RAM locality V200307. **D.** Occlusal view of RAM 6507, talonid of m1 (possibly m2) of *Dissacus* sp. from RAM locality V94014.

Family PERIPTYCHIDAE Cope, 1882

Goleroconus McKenna, Honey, and Lofgren, 2008

Goleroconus alfi McKenna, Honey, and Lofgren, 2008

HOLOTYPE: RAM 7171, right dentary with p4–m2 and part of trigonid of m3 from RAM locality V200120, member 4b, Goler Formation, California.

REFERRED SPECIMENS: RAM 6506, rm2, RAM 6417, lp3, UCMP 131790, lm2, UCMP 44761, left dentary fragment with m3, UCMP 49487, rm3 fragment from RAM locality V94014, member 4a.

DISCUSSION: UCMP 44761 was the first mammalian specimen described from the Goler Formation and was referred to cf. *Conacodon entoconus* (McKenna, 1955). Study of additional isolated teeth of this taxon recovered from the same site as UCMP 44761 resulted in revised referrals: “unnamed genus and species of anisonchine peripitychid” (McKenna, 1960: 12) and “unnamed genus and species of conacodontine peripitychid” (McKenna et al., 1987: 36). In 2001, J. Honey collected a partial dentary with multiple teeth (RAM 7171) that served as an adequate holotype for description of the new genus and species, *Goleroconus alfi* (McKenna et al., 2008: figs. 3–6), which is only known from the Goler Formation.

MESONYCHIA Van Valen, 1969

MESONYCHIDAE Cope, 1875

Dissacus Cope, 1881b

Dissacus sp.

REFERRED SPECIMEN: RAM 6507, talonid of m1 (possibly m2) from RAM locality V94014, member 4a (fig. 12D).

DESCRIPTION AND DISCUSSION: Mesonychids are among the rarest mammals in North American Paleogene faunas (O’Leary and Rose, 1995) and the only specimen recovered from the Goler Formation (RAM 6507) is a well-preserved talonid of a lower molar of *Dissacus*, probably an m1 (fig. 12D), which is 5.50 mm in width. Based on size, RAM 6507 cannot be referred to a specific species with confidence as *Dissacus navajovius*, *D. argenteus*, *D. willwoodensis*, and *D. serior* are about the same size, and *D. praenuntius* is only about 15% larger than the other four (O’Leary and Rose, 1995). The only morphological feature present in RAM 6507 that may be taxonomically significant is the nearly symmetrical shape of the talonid caused by equal sloping of its labial and lingual surfaces (as seen in distal view). This condition is similar to m1s of *D. navajovius* (O’Leary and Rose, 1995: fig. 3).

BIOSTRATIGRAPHY

Members 1 and 2 of the Goler Formation lack fossils of any kind and member 3 has yielded only fragmentary turtle remains that are not age diagnostic, so development of a biostratigraphic framework for much of the Goler Formation is not possible at this time. The lower part of member 4 (member 4a and member 4b) contain all the presently known mammal localities of the Goler Formation, except for a single tooth from member 4d in the uppermost part of the formation (table 12) (Lofgren et al., 2004a; Lofgren et al., 2010). Member 4 strata are mostly covered and when exposed are composed of sequences of often repeated lithologies that lack distinct marker beds, making precise physical correlation of

sites difficult to impossible. The only widely recognizable lithologic horizon for member 4 is the mappable contact between member 4a and overlying member 4b. Assuming that the contact is not significantly time transgressive, this lithologic horizon serves as a biostratigraphic marker from which a comparison can be made of the composite mammalian faunas from member 4a and member 4b. Of the six taxa known from member 4b, four also occur in member 4a (table 13), with the other two occurrences consisting of the endemic Goler metatherian *Golerdelphys* and *Ignacius frugivorus*, a widely distributed taxon and that has a broad temporal range (Lofgren et al., 2008). Thus, the mammalian fauna from member 4b is not distinguishable from that of member 4a based on the sample sizes available, even though sites from the middle part of member 4a and lower part of member 4b are separated by as much as 500 m of strata (Cox, 1987: fig. 3).

The approximate stratigraphic distance below or above the member 4a and member 4b lithologic horizon can also be determined for the most productive member 4a and member 4b localities. Employing this methodology, the ascending stratigraphic order of these sites is Grand Canyon/Land of Oz, Laudate Discovery Site, and Edentulous Jaw Site, as Grand Canyon and Land of Oz are within the middle part of member 4a, the Laudate Discovery Site high in member 4a, and the Edentulous Jaw Site low in member 4b (fig. 13). Mammalian assemblages from the four localities consist of three to seven eutherian taxa at a single site (table 12), with four of these taxa shared in some combination between sites (fig. 13). Similar to the comparison of the composite assemblages from member 4a and member 4b, significant faunal differences between these four sites are also not evident. Alternative explanations for this faunal similarity are deposition of member 4a and the lower part of member 4b occurred over a short time interval, or the available faunal data is too sparse to record differences in mammalian assemblages within this stratigraphic interval. Recovery of the plesiadapid *Nannodectes lynasi*, from three sites spanning this stratigraphic interval (fig. 13), suggests deposition rates were high because plesiadapids from Western Interior Paleocene sedimentary basins are employed in defining biozones (Archibald et al., 1987; Lofgren et al., 2004b; Secord et al., 2006) as rapid rates of evolution for this clade are well documented (Gingerich, 1976). Single specimen occurrences at sites from the middle part of member 4b (sites 9–11, in fig. 13) add little to this discussion, although occurrences of *Goleroconus alfi* at the Laudate Discovery Site and Honey Pot site (sites 6 and 10, in fig. 13), separated by as much as 585 m of strata, provide support for rapid deposition (McKenna et al., 2008). In any case, the eutherian mammalian fauna from member 4a and lower part of member 4b is discussed as a single biochronologic assemblage when compared to Tiffanian mammalian faunas from the Western Interior of North America. This assemblage is informally termed the Goler Assemblage to signify that it is composed of mammals from multiple sites that must differ somewhat in age based on their relative stratigraphic positions and that recovery of additional specimens may eventually allow recognition of discrete faunal units within this stratigraphic interval.

Comparison of the Goler Assemblage to Tiffanian biozone ranges of mammalian taxa from the northern Bighorn Basin and sites elsewhere in the Western Interior, indicate a probable Ti3–Ti4a age, based on the revised geochronologic framework for Tiffanian strata of Secord et

TABLE 12. Eutherian and metatherian mammalian taxa from RAM localities in the Goler Formation with sites organized by member (4a, 4b, 4d) and listed left to right in approximate ascending stratigraphic order; (1) Red Flat area (V201014, V201122); (2) Grand Canyon area (V200508, V200510, V200706, V200802, V200804); (3) Land of Oz (V200001); (4) Phenacodus Pocket area (V200603, V200612); (5) R-Z Zone area (V200303, V200304, V200702); (6) Laudate Discovery Site area (V94014, V94133); (7) Edentulous Jaw Site (V98012); (8) Primate Gulch (V200202); (9) Lone Tooth (V200704); (10) Butte Tooth (V200613); (11) Honey Pot (V200120); (12) Shark Site (V200307).

	Member 4a						Member 4b					4d
Taxon	1	2	3	4	5	6	7	8	9	10	11	12
<i>Peradectes</i> sp.	—	—	X	—	—	—	X	—	—	—	—	—
<i>Golerdelphys stocki</i> .	—	—	—	—	—	—	X	—	—	—	—	—
<i>Taeniodonta</i>	—	—	—	X	—	—	—	—	—	—	—	—
<i>Bessoecetor septentrionalis</i>	—	X	—	—	—	—	—	—	—	—	—	—
<i>Protictis paralus</i>	—	—	X	—	—	—	—	—	—	—	—	—
<i>Protictis</i> cf. <i>P. agastor</i>	—	—	X	—	—	—	—	—	—	—	—	—
<i>Paromomys depressidens</i>	—	—	—	—	—	X	—	—	—	—	—	—
<i>Ignacius frugivorus</i>	—	—	—	—	—	—	X	—	—	—	—	—
<i>Nannodectes lynasi</i>	—	X	—	—	—	X	X	X	—	—	—	—
<i>Thryptacodon</i> sp.	—	X	—	—	—	—	—	—	—	—	—	—
<i>Mimotricentes tedfordi</i>	X	X	X	—	—	—	—	—	—	—	—	—
<i>Lambertocyon</i> cf. <i>L. gingerichi</i>	—	—	X	—	—	—	—	—	—	—	—	—
<i>Arctocyondidae?</i>	—	—	—	—	—	—	—	—	—	X	—	—
<i>Protoselene ashtoni</i>	—	—	—	—	X	—	—	—	—	—	—	—
<i>Promioclauenus walshi</i>	—	X	X	—	—	—	—	—	—	—	—	—
<i>Phenacodus</i> cf. <i>P. bisonensis</i>	X	X	X	X	X	—	X	—	X	—	—	—
<i>Phenacodus</i> cf. <i>P. matthewi</i>	—	—	X	—	—	—	—	—	—	—	—	—
<i>Phenacodus</i> cf. <i>P. grangeri</i>	—	—	—	—	—	X	—	—	—	—	—	—
<i>Phenacodus</i> cf. <i>P. vortmani</i>	—	—	—	—	—	—	—	—	—	—	—	X
<i>Goleroconus alfi</i>	—	—	—	—	—	X	—	—	—	—	X	—
<i>Dissacus</i> sp.	—	—	—	—	—	X	—	—	—	—	—	—

al. (2006), where the previous Ti4 biozone was subdivided into Ti4a (new) and Ti4b, and the Ti5a biozone was revised (Secord, 2008). Of the 15 Goler Assemblage taxa, 14 have ranges that overlap in the Ti3–Ti4a biozones (fig. 14). A Ti3–Ti4a age for the Goler Assemblage requires only a range extension for *Paromomys*, a taxon not previously known from strata younger than Ti1 (Lofgren et al., 2004b; Lofgren et al., 2008). Also, cooccurrence of three species of *Phenacodus* (*P.* cf. *P. bisonensis*, *P.* cf. *P. grangeri*, *P.* cf. *P. matthewi*) and taxa with restrictive biozone ranges from the Goler Assemblage, including *Lambertocyon* cf. *L. gingerichi*, *Protictis paralus*, *P.* cf. *P. agastor*, and the large species of *Nannodectes*, *N. lynasi*, add further support for a Ti3–Ti4a age (fig. 14). *Lambertocyon gingerichi* is known only from Ti4a strata in the northern Bighorn Basin (Secord, 2008) and from the Chappo Type Locality of southwest Wyoming, considered by Gunnell (1994) to be a transitional Ti3–Ti4 fauna. *Protictis paralus* and *Protictis*

TABLE 13. Eutherians and metatherians from member 4a and member 4b of the Goler Formation. In parentheses are the number of specimens per taxon; taxa without numbers are one single specimen occurrences. Presence of metatherians, *Peradectes* sp., and *Golerdelphys stocki*, based on Williamson and Lofgren (in press).

Member 4a	Member 4b
<i>Peradectes</i> sp.	<i>Peradectes</i> sp. (2)
<i>Nannodectes lynasi</i> (6)	<i>Nannodectes lynasi</i> (15)
<i>Phenacodus</i> cf. <i>P. bisonensis</i> (21)	<i>Phenacodus</i> cf. <i>P. bisonensis</i> (3)
<i>Goleroconus alfi</i> (4)	<i>Goleroconus alfi</i>
	<i>Golerdelphys stocki</i> (5)
	<i>Ignacius frugivorus</i>
Taeniodonta	
<i>Bessoecetor septentrionalis</i>	
<i>Protictis paralus</i>	
<i>Protictis</i> cf. <i>P. agastor</i>	
<i>Paromomys depressidens</i>	
<i>Thryptacodon</i> sp.	
<i>Mimotricentes tedfordi</i> (5)	
<i>Lambertocyon</i> cf. <i>L. gingerichi</i> (2)	
<i>Protoselene ashtoni</i>	
<i>Promioclaenus walshi</i> (3)	
<i>Phenacodus</i> cf. <i>P. matthewi</i>	
<i>Phenacodus</i> cf. <i>P. grangeri</i>	
<i>Dissacus</i> sp.	

agastor are known only from Ti3–Ti4a strata (Lofgren et al., 2004b; Secord, 2008) and both species are present at the Land of Oz locality in member 4a and Cedar Point Quarry, the latter of which is a well-sampled Ti3 fauna from the northern Bighorn Basin (Rose, 1981; Secord, 2008). Also, *Protictis paralus* is a rare taxon that occurs at both the Brisbane and Judson localities from the Tongue River Formation of North Dakota (Holtzman, 1978), sites Ti3 and Ti4a in age, respectively (Kihm and Hartman, 2004). *Nannodectes* is known from Ti1–Ti5 strata (Lofgren et al., 2004b), but *Nannodectes lynasi* is most similar in morphology and size to *N. gidleyi* from Mason Pocket in Colorado (Simpson, 1935; Gingerich, 1976) and *Nannodectes* aff. *N. gidleyi* from Joe’s Bonebed in Big Bend, Texas. Both Mason Pocket and Joe’s Bonebed were considered to be Ti5 in age (Lofgren et al., 2004b), but Mason Pocket was recently reinterpreted as Ti4a or the older part of Ti4b in age (Secord et al., 2006), and Joe’s Bonebed may also correlate to the Ti4a or Ti4b biozone (see discussion below). Finally, cooccurrence of three species of *Phenacodus* in the Goler Assemblage (*P.* cf. *P. bisonensis*, *P.* cf. *P. grangeri*, *P.* cf. *P. matthewi*) adds support for a middle Tiffanian age (fig. 14), because *P. bisonensis* and *P. grangeri* also cooccur at the Ti3 Ledge Locality from the Bison Basin in southern Wyoming (Gazin, 1956; Thewissen, 1990) and *P. matthewi* is best known from the Mason Pocket site (Simpson, 1935), which is Ti4a or Ti4b in age (Secord et al., 2006). In summary, taxa of restricted biochronologic

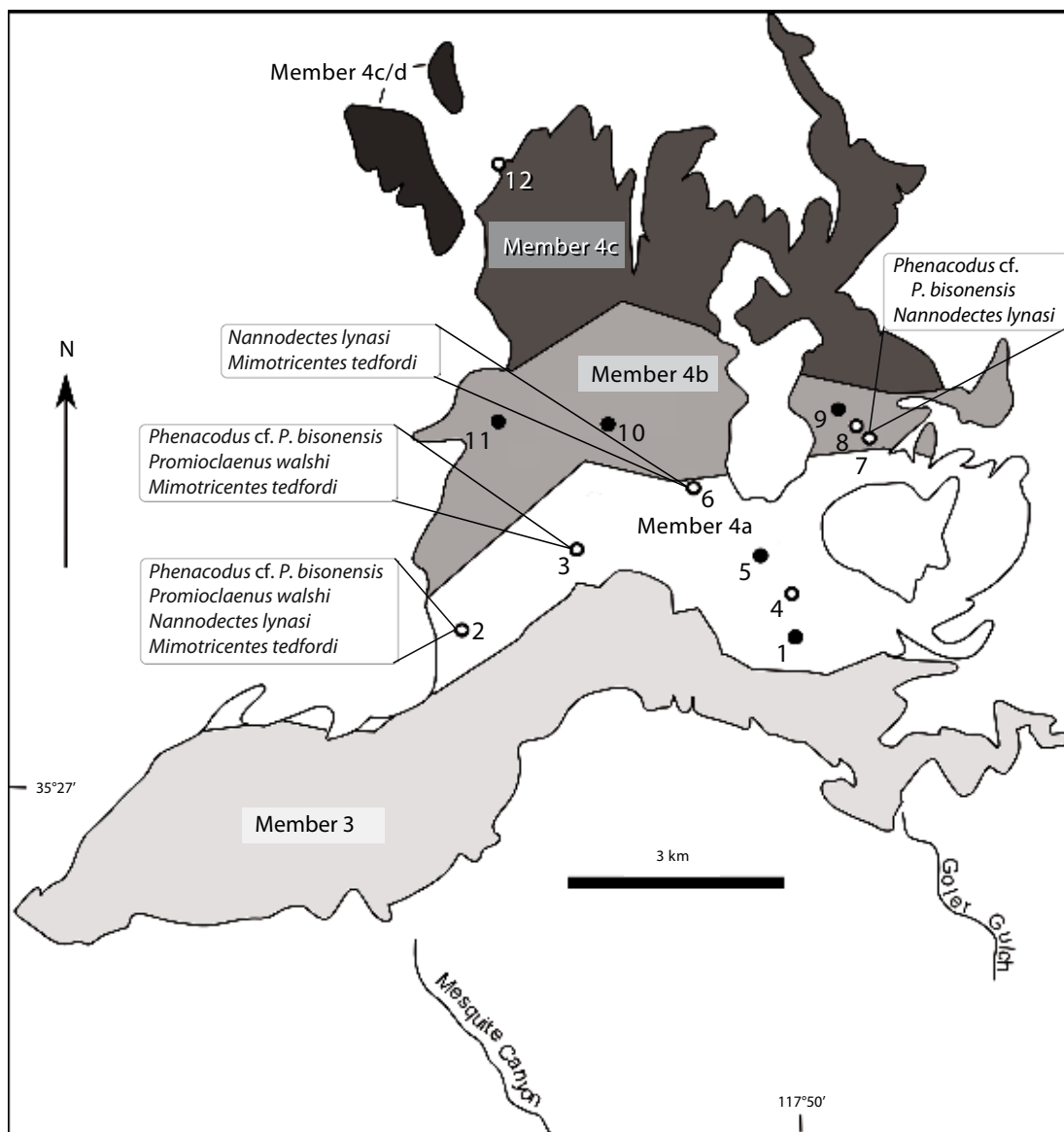


FIGURE 13. Outcrop map of member 3 and member 4 of the Goler Formation (adapted from Cox, 1982; Cox and Diggles, 1986) showing location of the most productive mammal yielding sites, with shared taxa listed in text boxes: Grand Canyon site (no. 2, V200510), Land of Oz (no. 3, V200001), Laudate Discovery Site (no. 6, V94014), and Edentulous Jaw Site (no. 7, V98012). Other sites as numbered in figure 1.

age and the overlap in range zones of 14 of 15 Goler taxa, both support a Ti3–Ti4a age for the Goler Assemblage (fig. 14).

There is also support for a Ti5a age for the Goler Assemblage as nine of 15 taxa are also known from strata correlated to the Ti5a biozone (fig. 14). A Ti5a correlation would significantly alter the known ranges of *Paromomys*, *Protoselene*, *Promioclauenus*, *Phenacodus* cf. *P. bisonensis*, *Protictis paralus*, and *P. cf. P. agastor* (fig. 14) and thus appears less plausible than a

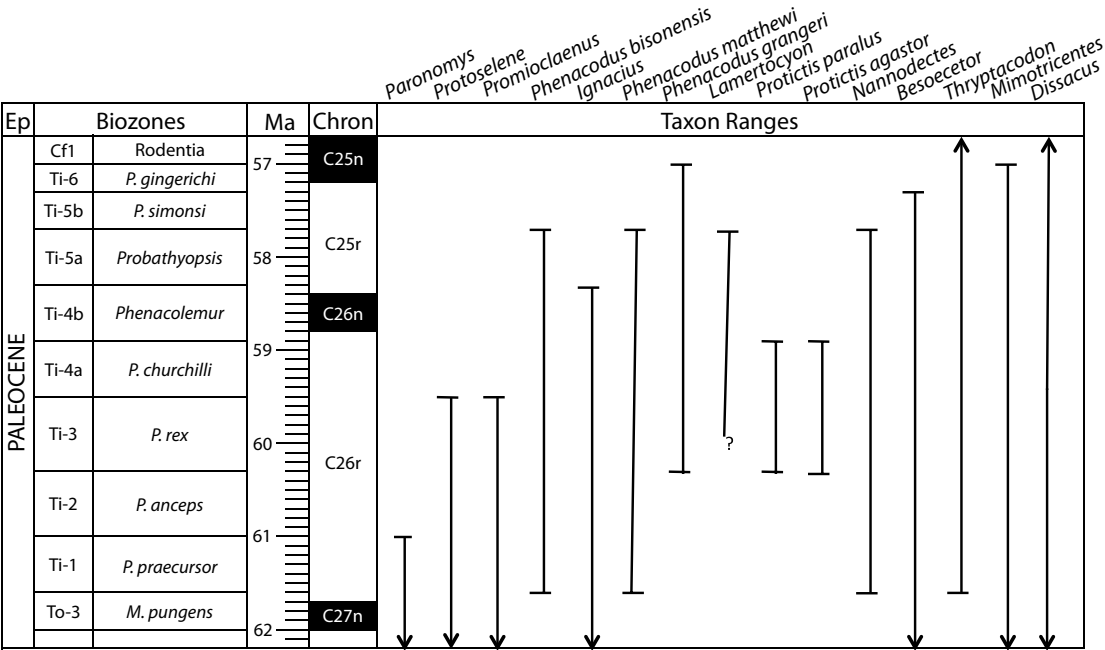


FIGURE 14. Presently known temporal ranges of eutherian mammals from the Western Interior that are also found in the Goler Assemblage. Biochronology and geochronology adapted from Albright et al. (2009: fig. 4), but based on Secord et al. (2006: fig. 3).

Ti3–Ti4a correlation. Also, the presence of *Lambertocyon*, *Nannodectes*, *Phenacodus bisonensis*, and *Phenacodus matthewi* in the Ti5a biozone is based only on their occurrence at Joe’s Bonebed in Big Bend, Texas, a site that may be Ti4a or early Ti4b in age (see below). However, preliminary analysis of multituberculates from member 4a and the lower part of member 4b indicate the presence of *Neoliotomus conventus* and a species of *Parectypodus* similar to *P. laytoni* (Albright et al., 2009), taxa not known from strata older than Ti5a (Lofgren et al., 2004b; Secord et al., 2006).

Magnetostratigraphic sampling of selected localities that yielded mammals from member 4a and the lower part of member 4b (sites 2–4 and 6–8, in fig. 13) were all of reversed polarity except for a normal sample bracketed by reversed samples within a 9 m sequence at the Land of Oz site (Albright et al., 2009). Analysis of these samples in their biostratigraphic context results in multiple magnetostratigraphic correlations. If the normal at the Land of Oz site is interpreted to represent a short normal within a thick interval of reversed polarity, then a correlation to C26r is in agreement with a Ti3–Ti4a age of the Goler Assemblage (fig. 14). Similarly, correlation to C25r would lend support for a Ti5a age for the Goler Assemblage, a less likely scenario based on the presently known eutherian fauna from the Goler Formation. If the magnetostratigraphic sequence at Land of Oz is interpreted to represent a three chron sequence, there are two choices that conform to the Tiffanian age for member 4a and the lower part of member 4b of the Goler Formation, C27r–C27n–C26r or C26r–C26n–C25r. The C27r–C27n–C26r correlation would indicate that the member 4 and lower part of member 4b spans the

Torrejonian-Tiffanian boundary, an interpretation not well supported by the mammalian faunal data (fig. 14), as *Lambertocyon*, *Protictis paralus*, *P. cf. P. agastor*, *Nannodectes lynasi*, *Phenacodus cf. P. bisonensis*, and *P. cf. P. matthewi* would all occur in the late Torrejonian, large range extensions for most of these taxa (fig. 14), a very unlikely scenario. A C26r–C26n–C25r correlation would require a less dramatic change in taxon ranges, but would still significantly alter the known ranges of *Paromomys*, *Protoselene*, *Promioclaenus*, *Phenacodus cf. P. bisonensis*, *Protictis paralus*, and *P. cf. P. agastor* (fig. 14). Also, the C26r–C26n–C25r correlation would indicate that strata representing member 4a and the lower part of member 4b span parts of three biozones (Ti4a, Ti4b, Ti5a). The Goler Assemblage, as currently known, does not support that interpretation as eutherian taxa from member 4a and member 4b are very similar and only a single species of plesiadapid primate (*Nannodectes lynasi*) is known from that stratigraphic interval. The interpretation favored here is that the normal polarity sample at the Land of Oz site represents a short normal within a reversed chron, most likely C26r, a hypothesis in agreement with biochronologic data supporting a probable Ti3–Ti4a age for the Goler Assemblage.

Reassignment of Mason Pocket, from strata correlated to C25r of Ti5 age, to strata correlated to C26r of Ti4a or earliest Ti4b age (Secord et al., 2006) was necessitated by the strong affinity of the Mason Pocket mammalian fauna to the Ti4a biozone fauna from the northern Bighorn Basin (Secord et al., 2006), a change that places *Nannodectes gidleyi* and other taxa formerly indicative of Ti5 within Ti4a or earliest Ti4b. The reassignment of Mason Pocket limits the Ti5a occurrence of *Lambertocyon*, *Nannodectes*, *Phenacodus bisonensis*, and *Phenacodus matthewi* to Joe's Bonebed from the Blacks Peak Member of the Tornillio Formation in Big Bend, Texas. The original correlation of Joe's Bonebed was based on the close affinity of its mammalian assemblage to the Tiffany fauna (Mason Pocket is the primary site) from southern Colorado (Schiebout, 1974) and the cooccurrence of *Nannodectes* aff. *N. gidleyi* and *Chiromyoides potior* (Gingerich, 1976). Since the original description of the Joe's Bonebed mammalian fauna (Schiebout, 1974), some taxa were reassigned; *Plesiadapis gidleyi* became *Nannodectes* aff. *N. gidleyi* (Gingerich, 1976), undescribed arctocyonid genus and species became *Lambertocyon eximus* (Gingerich, 1979), *Phenacodus matthewi* became *P. bisonensis* (Thewissen, 1990), and *Ectocion* cf. *E. montanensis* became *Phenacodus matthewi* (Thewissen, 1990) and all specimens of *Chiromyoides potior* previously identified in the UM collections from the northern Bighorn Basin have been referred to *C. gingerichi* (Secord, 2008). Precise correlation of the mammalian fauna from Joe's Bonebed to Tiffanian biozones is important for Goler Formation biochronology because re-evaluation of this mammalian assemblage might result in a Ti4a or earliest Ti4b correlation, similar to the reassignment of the Mason Pocket site (Secord et al., 2006). If so, then the youngest records of *Phenacodus matthewi*, *P. bisonensis*, *Nannodectes*, and *Lambertocyon* would be Ti4a or earliest Ti4b, not Ti5a, a development that would provide additional support for a Ti3–Ti4a age for the Goler Assemblage, as these taxa or closely related forms also occur in the Goler Formation.

An isolated tooth (RAM 7253) referred to *Phenacodus* cf. *P. vortmani* is the only mammal specimen known from member 4d in the uppermost part of the Goler Formation (site 12 in fig. 13). RAM 7253 was found in deltaic deposits mapped as a nonmarine unit of member 4c

(Cox and Diggles, 1986), which contains abundant marine invertebrates and a few teeth of the shark *Striatolamia* (Lofgren et al., 2004a; Lofgren et al., 2010). Member 4d was tentatively dated as late Paleocene (CP8) based on cocoliths (Reid and Cox, 1989), late Paleocene to early Eocene based on mollusks (Squires et al., 1988), and early Eocene (P8 and ?P9) based on forams (McDougall, 1987). If RAM 7253 does represent *Phenacodus vortmani*, its occurrence would indicate a Ti5 or younger age for member 4d as *P. vortmani* first occurs in Ti5 strata in the northern Bighorn Basin (Secord et al., 2006; Secord, 2008). *Phenacodus vortmani* is known from late Tiffanian to early Bridgerian strata in the Western Interior (Thewissen, 1990), and the dimensions of RAM 7253 (length 10.2 mm, maximum width 6.5 mm) match the size of specimens of *P. vortmani* from sites of late Tiffanian to Wastachian age (Thewissen, 1990: tables A21–A25). Thus, the tooth from member 4d referred to *P. cf. P. vortmani* supports a late Paleocene or early Eocene age for these strata, but does not refine earlier age estimates based on cocoliths, forams, and mollusks. All sites sampled in the new member 4d marine section for paleomagnetic analysis where RAM 7253 was found, were reversed polarity (Albright et al., 2009). Together with the presence of *P. cf. P. vortmani*, these strata could correlate to C25r (Albright et al., 2009) or C24r.

PALEOBIOGEOGRAPHY

Strata that comprise the Goler Formation were deposited within a tectonically active area, just east, and inland from a complex forearc basin developed during subduction of the Farallon Plate, when plutonism driven by subduction had largely terminated in California (Nilsen, 1987). There is no consensus on what tectonic forces controlled development of the Goler Basin. Hypotheses range from a supradetachment basin formed when the southernmost Sierra Nevada Batholith was unroofed by extensional faulting during the Late Cretaceous–Paleocene (Wood and Saleeby, 1997, 1998), to a fault-bounded basin formed within a northeast-trending tectonic trough that lay on the northern edge of the Mojave Desert block (Cox, 1987; Nilsen, 1987). As the Goler Basin formed, locally derived sediments (member 1 and member 2) covered parts of the basin floor and then were overlain by strata (member 3) deposited on a southern sloping piedmont from a source located within a mountainous region on the basin's northern margin (Cox, 1987). Members 1–3 overlie Cretaceous intrusives (Cox 1982, 1987), and are overlain by member 4 sediments that yield mammals indicative of the Tiffanian NALMA (Lofgren et al., 2002; Lofgren et al., 2008; Albright et al., 2009). Member 4a and the lower part of member 4b were deposited primarily in the middle Tiffanian (this report) by westward-flowing braided and meandering streams, in a river system whose mouth was an embayment of the Pacific Ocean not far to the west (Cox, 1987). Eastward transgression of the Pacific Ocean eventually filled the Goler Basin as evidenced by strata that yield late Paleocene to early Eocene marine invertebrates, shark teeth, and foraminifers in member 4d (Cox and Diggles, 1986; McDougall, 1987; Lofgren et al., 2010). Other evidence that the Goler Basin may have been in close proximity to the Pacific Ocean throughout much of its existence are a fish from member 3 and a turtle from member 4a, both with presumed marine affinities (McKenna

et al., 1987). If so, the Goler Formation was deposited at fairly low elevation in a near coastal setting. These factors would have significantly influenced the local climate, as well as the composition of the vertebrate fauna. Paleosol profiles of member 3 and member 4 of the Goler Formation may indicate a climate with highly seasonal precipitation, possibly indicating an important rain shadow effect caused by regional topography (Torres and Gaines, 2011, 2013), presumably highlands further inland.

Terrestrial Paleocene strata are rarely preserved throughout the Great Basin so little information is available concerning highlands or other barriers that might limit dispersal of Paleocene vertebrates between the Western Interior and the Goler Basin, especially during the Tiffanian. However, a north-south mountain chain is presumed to have been located in southern and eastern California and western Nevada during the Paleocene (Nilsen and McKee, 1979), just east of the Goler Basin. Support for isolation of the Goler Basin from the Western Interior is also provided by detrital zircons from member 4 of the Goler Formation. Paleoproterozoic zircon ages dominate Neoproterozoic and Paleozoic quartzite rich strata in the central Great Basin (Nevada and western Utah) and the relative lack of Paleozoic or older zircons recovered from member 4 suggest that the fluvial system that deposited these strata was isolated from the continental interior during the early Paleogene (Lechler and Neimi, 2011). Also, study of detrital zircons in Paleogene fluvial strata in coastal southern California (moved 300 km postdepositionally by dextral displacement along the San Andreas Fault) by Ingersoll et al. (2013), indicate that this fluvial system had a source within the eastern Mojave Desert, Sonoran Desert, and Mogollon Highlands (eastern California and western Arizona), but not the Colorado Plateau (northern Arizona, southern Utah, western Colorado, and northwest New Mexico). Abundant silicic metavolcanic and quartzite clasts in member 4 also suggest a local source, as these lithologies were probably derived from sources located near the Panamint/Slate ranges and/or Avawatz/Soda Mountains, areas only 50 km to the east of the Goler Basin during the Paleocene (Cox, 1982; Cox and Diggles, 1986). Thus, the Goler Basin was probably separated from the continental interior by one or more topographic divides as the primary source for member 4 sediments was local, mostly within California.

The Goler Basin is situated on the east side of the San Andreas Fault and this region of California has probably not moved significantly north or south in the last 55 million years (Engelbreton et al., 1985). Thus, paleolatitude of the Goler Basin relative to Western Interior basins with Tiffanian strata has not changed greatly since the Paleocene. In contrast, the Goler Basin was displaced westward (with a minor northwest component) at least 140 km, and perhaps as much as 300 km during movement of the Sierran–Great Valley block relative to the Colorado Plateau, driven by Basin and Range extensional tectonics in the latter half of the Tertiary (Wernicke et al., 1982; Wernicke and Snow, 1998). Currently, the Goler Basin is over 1000 km southwest of the Bison and northern Bighorn basins, over 900 km west of the northeastern San Juan Basin, and over 1500 km northwest of Big Bend, Texas, the closest regions where diverse middle Tiffanian faunas are located (fig. 15). Reversal of the 300 km westward displacement of the Goler Basin would position the Goler mammalian fauna much closer to the Tiffany Fauna from the northeastern San Juan Basin, but less so for middle Tiffanian faunas

from Big Bend (Texas) and the Bison and northern Bighorn basins (Wyoming) (fig. 15).

Eutherian mammalian assemblages from well-known middle Tiffanian faunas, such as those from Cedar Point Quarry (34 taxa) and Divide Quarry (32 taxa) from the northern Bighorn Basin of Wyoming (Secord, 2008), have nearly twice the number of species as the entire eutherian fauna from member 4 of the Goler Formation (19 taxa) (table 12). Species richness is apparently not affected by latitude in the Paleocene of western North America (Rose et al., 2011), so the true diversity of the Goler Assemblage was very likely to have been significantly more than 18 species. Notably absent from the Goler Assemblage are representatives of some large-bodied (Pantodonta) and small-bodied mammal groups (Leptacidae, Palaeoryctidae, Cimolestidae, Apatemyidae, Erinaceomorpha, and Sorciomorpha) often found in Western Interior basins. Small fragmentary teeth recovered by screenwashing from the Edentulous Jaw Site have features suggesting alignment with one of more representatives of these smaller-bodied groups, but these broken teeth could not be identified to genus.

Even at this stage of recovery of the Goler Assemblage, significant endemism is evident, as 40% of eutherian and metatherian taxa currently known from the Goler Formation (eight of 20) are not found in Tiffanian faunas from the Western Interior. Endemic taxa are the metatherian, *Golerdelphys stocki* (Williamson and Lofgren, in press) and eutherians *Goleroconus alfi*, *Nannodectes lynasi*, *Mimotricentes tedfordi*, *Protoselene ashtoni*, and *Promioclauenus walshi*. *Phenacodus* cf. *P. bisonensis* and *Lambertocyon* cf. *L. gingerichi* are represented in the Goler Assemblage by specimens similar to *Phenacodus bisonensis* and *Lambertocyon gingerichi*, but can't be assigned to those species because of significant character differences. Also, Goler specimens referred to *Protictis* cf. *agastor*, *Thryptacodon*, *Phenacodus* cf. *P. vortmani*, *Phenacodus* cf. *P. grangeri*, *Phenacodus* cf. *P. matthewi*, *Dissacus*, *Taeniodonta*, and *Peradectes* are undiagnostic or too fragmentary to determine whether they represent previously described species. Thus, only four of 20 Goler Formation metatherian or eutherian taxa (*Bessoecetor septentrionalis*, *Protictis paralus*, *Ignacius frugivorus*, and *Paromomys depressidens*) can be referred to species from the Western Interior of North America with confidence. Turtles from member 4 of the Goler Formation also reflect significant endemism (Hutchison, 2004) and the remains of gars, a type of fish commonly found in Paleocene strata in the Western Interior have not been recovered from the Goler Formation (Lofgren et al., 2008). In total, these data indicate that the Goler

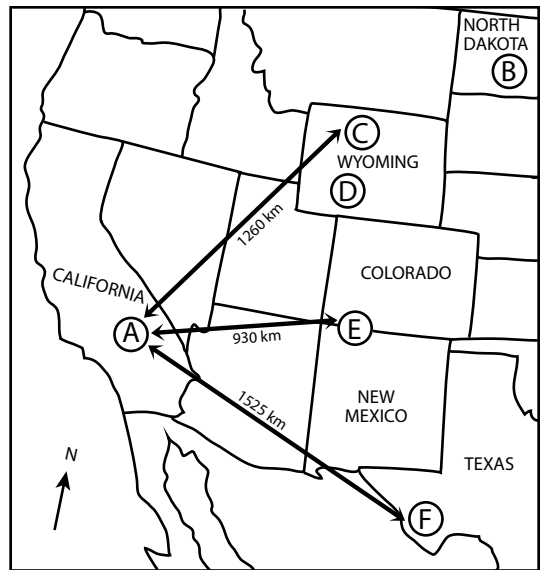


FIGURE 15. Present geographic relationship of the Goler Basin to the selected Western Interior Paleocene basins that yield middle Tiffanian eutherian assemblages most similar to the Goler Assemblage. A. Goler Basin. B. Williston Basin. C. northern Bighorn Basin. D. Bison Basin. E. northeast San Juan Basin. F. Big Bend.

TABLE 14. Genus and species level comparison of the Goler Assemblage to selected middle Tiffanian mammalian assemblages from basins in figure 15. Faunal data from Secord (2008) for the northern Bighorn Basin, Gazin (1956) and Thewissen (1990) for Bison Basin, Simpson (1935) and Thewissen (1990) for northeast San Juan Basin, Schiebout (1974), Gingerich (1976, 1979), and Thewissen (1990) for Big Bend, and Holtzman (1978) and Kihm and Hartman (1994) for Williston Basin.

California	Wyoming			Colorado	Texas	North Dakota	
Goler Basin	Northern Bighorn Basin		Bison Basin	NE San Juan Basin	Big Bend Area	Williston Basin	
Goler Assemblage	Cedar Point Quarry	Divide Quarry	Ledge Locality	Tiffany Fauna	Joe's Bonebed	Brisbane	Judson
Ti3-Ti4a (18)	Ti3 (35)	Ti4a (32)	Ti3 (14)	Ti4a (17)	Ti5a (Ti4a?) (15)	Ti3 (22)	Ti4a (20)
<i>Peradectes</i>	<i>P. elegans</i>			<i>P. elegans</i>		<i>P. elegans</i>	
<i>Golerdelphys stocki</i>							
<i>Bessoecetor septentrionalis</i>	<i>B. cf. B. ptilondontus</i>	<i>B. ptilondontus</i>				<i>Bessoecetor</i>	<i>Bessoecetor</i>
<i>Protictus paralus</i>	<i>P. paralus</i>					<i>P. paralus</i>	<i>P. paralus</i>
<i>Protictus cf. P. agastor</i>	<i>P. agastor</i>						
<i>Paromomys depressidens</i>							
<i>Ignacius frugivorus</i>	<i>I. frugivorus</i>	<i>I. frugivorus</i>		<i>I. frugivorus</i>	<i>I. frugivorus</i>	<i>I. frugivorus</i>	<i>I. frugivorus</i>
<i>Nannodectes lynasi</i>			<i>N. simpsoni</i>	<i>N. gidleyi</i>	<i>N. aff gidleyi</i>	<i>Nannodectes sp.</i>	
<i>Thryptacodon sp.</i>	<i>T. australis</i>	<i>T. australis</i>	<i>T. orthogonius</i>	<i>T. australis</i>		<i>T. australis</i>	<i>T. australis</i>
<i>Mimotricentes tedfordi</i>	<i>M. fremontensis</i>		<i>M. fremontensis</i>				
<i>Lambertocyon cf. L. gingerichi</i>		<i>L. gingerichi</i>			<i>L. eximius</i>		
<i>Protoselene ashtoni</i>							
<i>Promioclaenus walshi</i>			<i>P. pipiringosi</i>				
<i>Phenacodus cf. P. bisonensis</i>			<i>P. bisonensis</i>		<i>P. bisonensis</i>		
<i>Phenacodus cf. P. matthewi</i>				<i>P. matthewi</i>	<i>P. matthewi</i>		
<i>Phenacodus cf. P. grangeri</i>	<i>P. grangeri</i>		<i>P. grangeri</i>	<i>P. grangeri</i>	<i>P. grangeri</i>		<i>P. grangeri</i>
<i>Goleroconus alfi</i>							
<i>Dissacus sp.</i>	<i>D. cf. D. navajovius</i>	<i>D. cf. D. navajovius</i>	<i>Dissacus sp.</i>				
18/18 = 100%	9/35 = 26%	5/32 = 16%	7/14 = 50%	6/17 = 35%	6/15 = 40%	6/22 = 27%	5/20 = 25%

Basin was geographically isolated from Paleocene sedimentary basins of the Western Interior by significant distances, as well as barriers that limited dispersal of terrestrial vertebrates, and a unique paleogeographic province probably existed during the Paleocene adjacent to the Pacific Ocean in what is now southern California. The occurrence of new species in the Goler Formation, such as *Nannodectes lynasi*, is not unexpected as sediments that formed the Goler Formation were deposited much farther west than any other plesiadapid site by hundreds of kilometers, in a near coastal setting, a habitat that may have not been preserved in strata from the Western Interior. This isolation and possibly unique habitat provided excellent opportunity for further diversification of the Plesiadapidae and other Goler taxa.

Similar to the successful recovery of new records of eutherians and metatherians, recent collecting efforts in member 4a and member 4b of the Goler Formation have yielded significant multituberculate remains, including partial skulls, dentaries, and isolated teeth. These specimens await description, as does a comprehensive statistical comparison of the entire Goler Assemblage to Tiffanian mammalian faunas from the Western Interior. In the meantime, the faunal similarity of the Goler Assemblage and selected middle Tiffanian sites from the Western Interior can be roughly estimated based on the percentage of genera or species in common. This comparison indicates that Goler metatherians and eutherians have the greatest taxonomic affinity (50%) to taxa from the Ledge Locality in the Bison Basin of southern Wyoming (table 14). The Tiffany fauna of Colorado and Joe's Bonebed from Texas have affinities of about 35% to 40%, while those from the Williston and northern Bighorn basins are less than 30% (table 14); metatherians and eutherians described thus far from middle Tiffanian sites in southern Canada (not shown in either fig. 15 or table 14) are even less similar. Based on latitude and proximity, one would expect that the Tiffany Fauna of southern Colorado would have the greatest affinity with the Goler Assemblage, and that middle Tiffanian mammalian faunas from the Bison and northern Bighorn basins would be more similar to each other than to the Goler Assemblage. However, our preliminary results suggest otherwise, a disparity that warrants further investigation, keeping in mind that these results are tenuous as they are based on assemblages that sometimes consist of fewer than 20 eutherian/metatherian taxa, where any newly reported taxon may significantly affect similarity percentages.

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