Review of Paleogene vertebrates and invertebrates from the Goler Formation of California and their biostratigraphic and paleogeographic significance

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ABSTRACT—The Goler Formation is the only Paleocene rock unit in North America west of the Rocky Mountains that has yielded a diverse assemblage of vertebrates. Exposed in the El Paso Mountains in the northern Mojave Desert, the formation is composed of 4,000 m of strata subdivided into four members that represent nonmarine sediments capped by marine strata. Members 1-2 have not yielded fossil remains of any type, and the sparse fauna from Member 3 composed of only three partial turtles and a fish skeleton have limited utility in determining the age of the formation. Strata representing Member 4a-4b have yielded numerous specimens of vertebrates, primarily mammals, turtles, lizards, and crocodilians, as well as a partial avian humerus, a ray tooth, and a few gastropod shells. New taxa based on specimens from these strata include three new genera and seven new species of mammals and two new genera and species of turtles. Based primarily on its mammalian assemblage, Member 4a-4b is middle Tiffanian (late Paleocene) when compared to Paleocene mammal assemblages in the Western Interior, an age supported by magnetostratigraphic correlation of Member 4a-4b to Chron 26r. Based on the age of overlying Member 4 strata, Member 3 is middle Tiffanian (late Paleocene) or older. The late Paleocene or early Eocene Member 4d marine section contains cocoliths, planktic and benthic foraminifera, marine mollusks, shark teeth and a terrestrial mammal tooth, and probably represents a near shore marine facies of a river delta. Marine section paleomagnetic samples are of reversed polarity that probably correlate to either Chron 25r or Chron 24r. The non-marine fauna of the Goler Formation exhibits significant endemism as more than 45% of mammalian taxa are not found elsewhere and only five mammal taxa can be confidently referred to species from the Western Interior. Turtles reflect similar endemism and the remains of gars, a common fish in Paleocene strata from the Western Interior have yet to be found in Goler strata. The high degree of endemism reflected in the vertebrate fauna of the Goler Formation strongly suggests geographic isolation, which led to the formation of a unique west coast faunal province in what is now southern California during the late Paleocene.

Introduction

The Goler Formation is composed of about 4000 meters of mostly nonmarine sediments (Cox and Diggles, 1986) that crop out within the El Paso Mountains in the northern Mojave Desert (Figure 1). The formation is divided into four members (numbered 1-4), with Member 4 consisting of four informal units, listed in ascending stratigraphic order as 4a, 4b, 4c and 4d (Cox 1982, 1987) with 4d containing marine sediments (Cox and Edwards, 1984; Cox and Diggles, 1986). Member 1-3 consist of locally derived fluvial and debris-flow deposits that accumulated mostly on alluvial plains and fans on a southward sloping piedmont while the majority of Member 4 strata consist of distally derived fluvial deposits that accumulated in the axial region of the Goler Basin south of the piedmont slope until an eastward transgression of the Pacific Ocean eventually invaded it (Cox, 1982; Cox and Diggles, 1986; Cox, 1987).

The age of the Goler Formation is based mostly on vertebrate and invertebrate fossils recovered since 1950, although Members 1-2 and 4c have yet to yield fossils of any type. The earliest reports of Goler fossils were leaf impressions recovered from mudstones now mapped as Member 3 that were thought to indicate an Eocene age (Fairbanks, 1896; Axelrod, 1949). In 1952, R. Tedford and M. McKenna found a crocodilian tooth in Member 4, higher in the formation than where the "Eocene" plant fossils were recovered and McKenna returned to the site in 1954 and found a mammal jaw of Paleocene age (McKenna, 1955). Subsequent discoveries of mammal

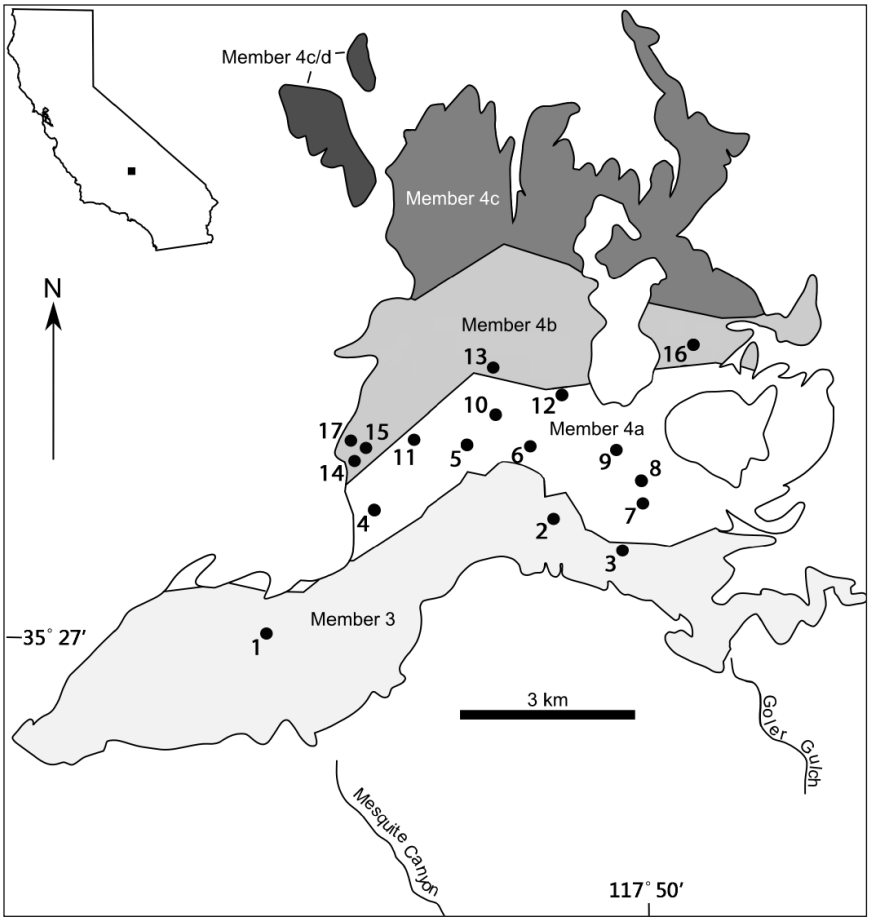

Figure 1. Map of California with the location of the study area shaded and outcrop map of Member 3 and Member 4 of the Goler Formation (adapted from Cox, 1982; Cox and Diggles, 1986) showing location of non-mammalian vertebrate sites in Table 1.

teeth and jaws in Member 4a and 4b confirmed the Paleocene age which was further refined based on the similarity of the Goler mammals to Torrejonian (middle Paleocene) mammals from the Rocky Mountain states (McKenna, 1960; West, 1970; McKenna et al., 1987). About the same time, late Paleocene or early Eocene foraminifera, marine mollusks, and cocoliths were recovered above the mammal sites in strata mapped as Member 4d (Cox and Edwards, 1984; Cox and Diggles, 1986; McDougall, 1987; Squires et al. 1988; Reid and Cox, 1989).

A renewed phase of collecting in Member 4a and Member 4b began in the early 1990s and resulted in the recovery of a numerous specimens of vertebrates, primarily mammals, turtles, lizards, and crocodilians, as well as a partial avian humerus and a ray tooth (Lofgren et al., 2002, 2008, 2009, 2014, 2018; McKenna and Lofgren, 2003; McKenna et al., 2008; Nydam and Lofgren, 2008; Stidham et al., 2014; Williamson and Lofgren, 2014). The eutherian mammalian assemblage from Member 4a and Member 4b indicates that these strata are middle Tiffanian (late Paleocene) (Lofgren et al., 2014) rather than Torrejonian (middle Paleocene). Also, a nonmarine mammal tooth, shark teeth and additional marine mollusks were recovered from previously unknown sites in Member 4d (Lofgren et al., 2010).

The Goler Formation is the only Paleocene rock unit in North America west of the Rocky Mountains that has yielded a diverse assemblage of vertebrates and we review the entire vertebrate and invertebrate fauna of the Goler Formation for the first time.

Abbreviations, materials, and methods

RAM: Raymond M. Alf Museum of Paleontology, Claremont, California; **UCMP**: University of California Museum of Paleontology, Berkeley, California. The RAM and UCMP record each vertebrate locality by using a V followed by numbers (e.g. V98012 or UCMP 5250) and specimens are each given a unique number following RAM or UCMP (e.g. RAM 9044 or UCMP 81603). RAM localities in the text will be referred to only by number (e.g. V98012), while UCMP localities will carry the UCMP designation to avoid confusion. Screen-washing of approximately 12 tons of sediment at RAM localities V98012 and V94014 yielded over 200 specimens identifiable to taxon; all others were found as surface float. Images of many mammal specimens listed here were provided in McKenna et al. (1987), West (1970), McKenna and Lofgren (2003), McKenna et al. (2008), Lofgren et al. (2014, 2018), and Williamson and Lofgren (2014). Published images for non-mammalian taxa listed here are noted in the text. Site numbers in Figure 1 refer to localities and non-mammalian taxa identified from them listed in Table 1. Similarly, Figure 4 numbers refer to localities and mammalian taxa identified from them listed in Table 2.

Member 3

The first vertebrate fossils reported from the Goler Formation were a mammal tooth and a partial turtle carapace found in 1950 by R. Tedford and R. Schultz from sediments (#1 in Figure 1) mapped as Member 3 by Cox (1982, 1987). These specimens were given to C. Stock at the California Institute of Technology so they could be studied, but soon thereafter, Stock died unexpectedly and apparently the fossils were discarded (McKenna et al. 1987; Lofgren et al., 2009). This was a great loss because intense prospecting of outcrops of Member 3 over the last six decades has not yielded additional mammalian

Figure 2. Macrobaenid carapace (RAM 14538) as found in 2010 in Member 3.

specimens. However, three partial turtle shells and a partial skeleton of a fish were recovered. A concretion containing the dorsal and pelvic fins of a bass-shaped osteichthyan (UCMP 81603, UMCP V5250) was found in 1952, about one km east of the Tedford-Schultz site and was tentatively identified as a beryciform or peciform (spiny-rayed fishes) (McKenna et al., 1987; Table 1). If UCMP 81603 does indeed represent a beryciform (extant beryciforms are marine), it suggests a marginal marine environment might have been preserved in Member 3 (McKenna et al., 1987).

In 1996, M. McKenna found turtle shell fragments about .5 km south of the Tedford-Schultz site and these specimens housed at the UCMP have yet to be studied. Just over a decade later, two partial shells were found a few km east of the Tedford and Schultz site. RAM 14538 (Figure 2) is a nearly complete carapace of a macrobaenid from V201001 (#3 in Figure 1) and RAM 9958 is a fragmentary carapace from V200916 (#2 in Figure 1) that has not been identified to taxon. Extensive prospecting of Member 3 over the last two decades did not yield additional vertebrate specimens, a testament to the rarity of fossils in Member 3. The few known specimens from Member 3 have limited utility in determining the age of these strata; based on the age of overlying Member 4 strata, Member 3 is middle Tiffanian (late Paleocene) or older (Albright et al., 2009; Lofgren at al., 2014).

Member 4a and Member 4b

Locating fossils in Member 4a and Member 4b is difficult, but concentrated efforts over the last three decades yielded a surprisingly diverse assemblage of vertebrates and a small number of gastropod shells (Lofgren et al., 2014, 2018, and references therein). The fauna from these strata (Figure 1, Table 1) includes:

Gastropods: The few gastropods recovered represent a single nonmarine taxon, but they lack anatomical details, so could only be confidently identified as representing the Order Stylommatophora (McKenna et al., 1987).

Birds: A proximal humerus of *Lithornis* (RAM 15530) was found at V200001 (#5) in 2013 and it represents the oldest Cenozoic bird from the west coast of North America (Stidham et al., 2014, fig. 2); lithornithids were ground dwellers that foraged with their slender bills.

Table 1. Types of vertebrates (excluding mammals) recovered from RAM and UCMP sites in the Goler Formation with turtles broken into four groups. Sites organized by member and listed left to right 1-17 based on approximate ascending stratigraphic order; (1) UCMP V5250; (2) RAM V200916; (3) RAM V201001; (4) RAM V200509, V200510, V200803; (5) RAM V200001; (6) RAM V200602; (7) RAM V200302; (8) RAM V200603, V200203; (9) RAM V200304, 200303;(10) UCMP V81035; (11) RAM V200048; (12) RAM V94014, UCMP V5252, V67158, V5870, V99042; (13) UCMP V6516; (14) RAM V201301; (15) RAM V201302; (16) RAM V94015, V98012; (17) UCMP V5251.

	Member 3			Member 4a									Member 4b				
Taxon	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**
Trionychid	-	-	-	-	-	X	-	X	-	-	X	X	X	-	-	-	X
Macrobaenid	-	-	X	-	-	-	X	-	-	X	-	X	-	-	-	-	-
Baenid	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-
Turtle indet.	-	X	-	X	X	-	-	-	X	-	-	X	-	X	X	X	-
Crocodylia	-	-	-	X	X	-	-	-	-	-	-	X	-	-	-	X	-
Lacertilia	-	-	-	X	-	-	-	-	X	-	-	X	-	-	-	X	-
Fish	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ray teeth	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-
Lithornis		-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-

Rays: The single ray tooth (RAM 7180, V98012, #16) has a flat rombic crown with paired roots and resembles the anterior teeth of *Hypolophodon*. Ray teeth are commonly found in marginal marine and nonmarine fluvial deposits of Paleocene age.

Crocodilians: Teeth, osteoderms, and a skull fragment were recovered from four sites (#4, #5, #12, #16) and are similar in morphology to the Paleogene alligator *Allognathosuchus*. These specimens are a skull fragment (RAM 9173) from V200803, teeth (RAM 18279, 6985, 6982) and osteoderms (RAM 6983, 18280) from V94014, a single tooth from V98012 (RAM 1823) and UCMP V67158 (UCMP 55402), and three teeth (RAM 18278, 9724, 9723) from V200001.

Lizards: Osteoderms were commonly recovered from screen-washing at V98012 (#16) and there are two main morphotypes: (1) non-keeled, imbricating osteoderms with shallow pits/grooves (RAM 10018, 10022, 10030-31, 10033-36) that are most similar to the anguid *Proxestops* (but might also represent *Odaxosaurus*), a frontal fragment with ornamentation (RAM 10028) also represents this taxon; (2) keeled, imbricating osteoderms with prominent rugose ornamentation (RAM 10019-10021, 10023-24) similar to the anguid *Exostinus* (Nydam and Lofgren, 2008). Six lizard jaws are also recovered from V98012 and they represent anguids (RAM 7187, 7182), xantusiids (RAM 7183, 7186), a scincomorphan (RAM 7181) and an indeterminate taxon (RAM 7188). A second scincomorphan (RAM 7213) was found at V200203 (Nydam and Lofgren, 2008). Unstudied specimens are a jaw (RAM 7190) from V94014 and a jaw (RAM 9702) and osteoderm (RAM 9705) from V200510. Anguids are alligator lizards, scincomorphans are relatives of skinks (leaf litter dwellers) and xantusiids are relatives of night lizards (rock/tree bark dwellers) (Nydam and Lofgren, 2008; Lofgren et al. 2009). These Goler Formation specimens represent the western-most Paleocene lizards in North America (Nydam and Lofgren, 2008).

Turtles: Shell fragments are commonly found in Member 4a and Member 4b strata. In addition to these fragmentary remains, partial shells, skulls, and postcranial material have also been recovered. These specimens represent three families, Baenidae, Macrobaenidae and Trionychidae. Baenids are known from two specimens, a hypoplastron fragment (UCMP 131765, UCMP V6516, #13) and a skull (UCMP 179519, UCMP V99042, #12) which is the holotype of *Goleremys mckennai* (Hutchison, 2004). UCMP 179519 is the first specifically identifiable record of a baenid from the Pacific slope of North America (Hutchison, 2004). Baenids are river turtles found in Cretaceous to late Eocene strata.

Figure 3. Trionychid carapace (RAM 9967) from Member 4a.

There are a few specimens of macrobaenids, the most complete a partial plastron and carapace with postcranial elements (RAM 7214, V200302, #7). In 1952, a tibia of *Trionyx* (UCMP 55403) was found at UCMP V5251 (#17) and is now identified as a probable marcobaenid. Similarly, a phalange of a large unspecialized eucryptodire (UCMP 55401; McKenna et al. 1987, fig. 2) from UCMP V5252 (#12) is now tentatively identified as a macrobaenid metatarsal. Other specimens are more fragmentary and include two peripherals (UCMP 124941, UCMP V81035, #10; McKenna et al., 1987, fig. 1), bridge peripherals (UCMP 131764, UCMP V5870, #12) (McKenna et al., 1987), and shell fragments (RAM 15956, V94014 and RAM 15959, V94015). Macrobaenids are nonmarine turtles that range in age from Late Cretaceous to late Paleocene in North America and are unknown elsewhere on the Pacific slope.

Trionychids are the most common turtle in the Goler Formation and most of their occurrences are shell fragments: RAM 15951, V200602 (#6); RAM 6989, RAM 6992, RAM 6994 RAM 6999, RAM 7001, RAM 9360, RAM 15952, RAM 6995, RAM 9966, RAM 15953, V94014; RAM 6978, RAM V20001; UCMP 81605, UCMP 149164, UCMP 149165, UCMP V5252; UCMP 81609, UCMP V5870 (#12); UCMP 69580, UCMP V6516 (#13). A skull (RAM 7004) of an undescribed new genus of trionychid was found in 2000 at V200048 (#11). Also, a partial carapace (RAM 9967; Figure 3) from V200603 (#8) with thirteen costals and five neurals represents a new species (probably the same one as the skull RAM 7004).

Other records of turtles from the Member 4a and Member 4b are shell fragments that can't be referred to a specific group. These specimens are: RAM 9968, V200916;

RAM 15957, V200509; RAM 6979, RAM 6980, RAM 7206, V200001; RAM 15954, V200304, RAM 6988, RAM 6990, RAM 6991, RAM 6993, RAM 6996, RAM 7000, RAM 7002, RAM 15955, V94014; RAM 16018, RAM 16019, V201301; RAM 16020, V201302; UCMP 81606, UCMP V5252 (turtle indeterminate in Table 1).

Mammals: The record of mammals in the Goler Formation is represented by multituberculate, metatherian, and eutherian specimens that consist almost entirely of dental remains. Initial efforts in the 1950s to 1980s to recover fossils yielded a sparse mammalian assemblage (McKenna, 1955, 1960; McKenna et al., 1987). A renewed phase of collecting in the 1990s resulted in recovery of a few hundred mammalian specimens (Figure 4, Table 2) (Lofgren et al., 2014, 2018, and references therein).

Multituberculates: The early sample of three incisors (McKenna, 1960; McKenna et al., 1987) was augmented by 33 additional teeth listed below that include a new genus and species, *Golercosmodon mylesi* (Lofgren et al., 2018). Two skulls to be described later utilizing μCT technology represent *Neoliotomus*? (RAM 9663, V200014) and a new species of *Parectypodus* (RAM 9048, V200001) (Lofgren et al., 2018).

—*Neoliotomus conventus*: UCMP 49490, incisor fragment, UCMP 55399, incisor root, UCMP V5870 (#6 in Figure 4); RAM 7237, P4 fragment, V98012, (#7); RAM 7204, questionable referral p4, V200001 (#3). RAM 7237 exhibits the diagnostic P4 morphology of *Neoliotomus conventus* and confirms the presence of this rare taxon in California (Lofgren et al., 2018).

—*Golercosmodon mylesi* (new genus and species): RAM 6968, P4 (holotype), RAM 6965, P4 and RAM 9656 partial P4, V98012 (#7); RAM 9685, P4, V200510 (#2). The P4s of *Golercosmodon mylesi* differ from other microcosmodontids in the development of the labial cusp row and the number of medial row cusps (Lofgren et al., 2018). cf. *Golercosmodon mylesi*: these isolated molars are a tentative referral; RAM 7232, RAM 6969, RAM 6970, RAM 6971, RAM 6434, RAM 9999, RAM 9988, RAM 7230, RAM 6483, RAM 6731, RAM 6975, RAM 7235, RAM 6463, RAM 9993, RAM 9971, RAM 9995, RAM 6967, RAM 9990, RAM 9974, RAM 9975, RAM 9972, V98012 (#7); RAM 6980, RAM 9676, V200510 (#2); RAM 6447, RAM 6422, V94014 (#6); RAM 9722, V200001 (#3).

—Microcosmodontid genus indeterminate: This heavily worn P4 (RAM 9987, V98012, #7) is not *G. mylesi*, so it represents a second microcosmodontid species in the Goler Formation.

Multituberculates from Member 4a and Member 4b increase the known taxonomic diversity of microcosmodontids and confirm the previously proposed geographic range extension of *Neoliotomus* and microcosmodontids to the west coast of North America (McKenna, 1960; McKenna et al., 1987) during the late Paleocene (Lofgren et al., 2018).

Metatherians: Specimens listed below include seven teeth that represent *Golerdelphys stocki*, a new genus and species of herpetotheriid, and a maxilla and two partial teeth identified as *Peradectes* (Table 2) (Williamson and Lofgren, 2014).

—*Peradectes* sp.: RAM 12403 maxilla with M1, M3-4, V200001 (#3); RAM 6476 partial M1 and RAM 9989 molar trigonid, V98012 (#7). These specimens are too fragmentary to be identified to species but are similar to peradectids from the Western Interior (Williamson and Lofgren, 2014).

—*Golerdelphys stocki* (new genus and species): RAM 6432 right M2

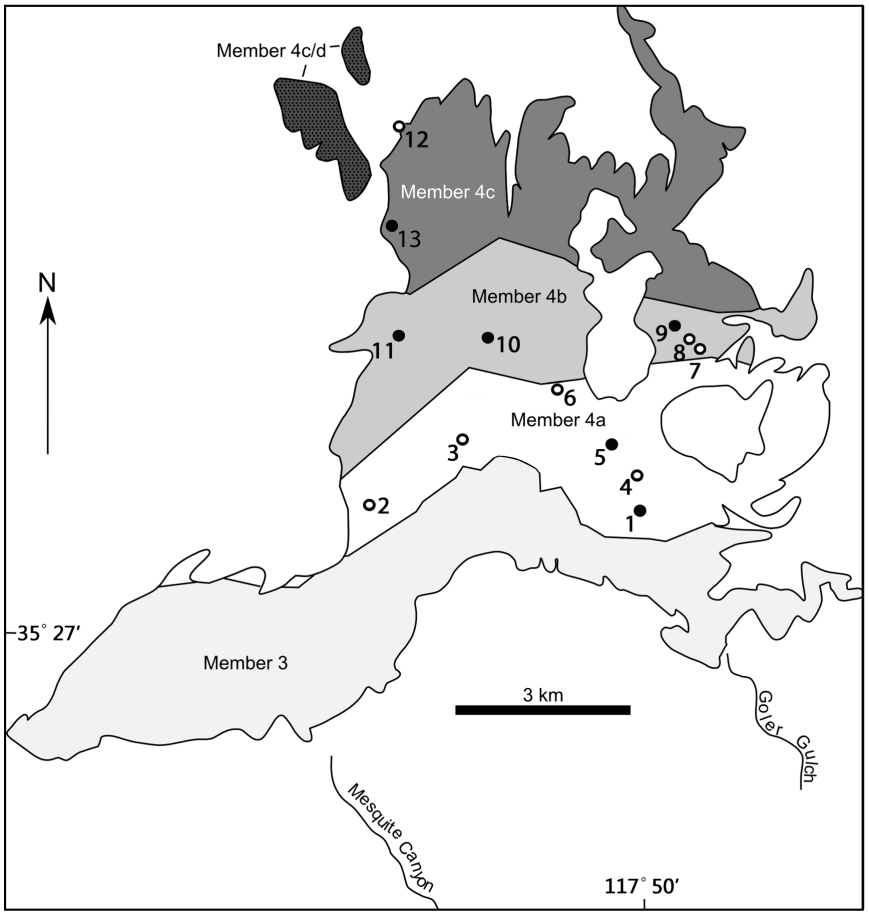

Figure 4. Outcrop map of Members 3 and 4 of the Goler Formation (adapted from Cox, 1982; Cox and Diggles, 1986) showing location of mammalian and invertebrate sites in Table 2 (except #13 which is the Squires Mollusk Site). Open circles are sites that underwent paleomagnetic analysis (results presented in Albright et al., 2009).

Table 2. Eutherians, metatherians, and multituberculates (* new taxon) from RAM localities in the Goler Formation with sites organized by member and listed 1-12 in approximate ascending stratigraphic order; 1) V201014, V201122; 2) V200508, V200510, V200706, V200802, V200804; 3) V200001, V201346, V201481; 4) V200603, V200612 V201211, V201757; 5) V200303, V200304, V200702; 6) V91014, V94133, UCMP 5251, 5870; 7) V98012; 8) V200202; 9) V200704; 10) V200613, UCMP V65170; 11) V200120; 12) V200307, I200306, I200305.

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

(holotype), RAM 6404 molar talonid, RAM 6471 molar trigonid, RAM 6699 m2 or m3, RAM 6470 partial M3, V98012 (#7). These specimens represent the only known herpetotheriid from the late Paleocene of North America (Williamson and Lofgren, 2014).

Eutherians: This sample consists of over eighty specimens, representing seventeen species, including five new taxa; *Nannodectes lynasi*, *Promioclaenus walshi*, *Protoselene ashtoni*, *Goleroconus alfi*, *Mimotricentes tedfordi*. These and the other eutherian taxa (Table 2) were described by McKenna and Lofgren (2003), McKenna et al. (2008), and Lofgren et al. (2014).

—*Bessoecetor septentrionalis*: RAM 9099, dentary with m2-3, V200510 (#2). This pantolestid is well known from the Rocky Mountain states.

—*Protictis paralus*: RAM 6927, dentary with c, p1-2, p4-m1, and *Protictis* cf. *P. agastor*: RAM 7246, dentary with partial m1, both from V200001 (#3). These specimens constitute the oldest known mammalian carnivores from the west coast of North America.

—Taeniodont: RAM 15328 is a canine fragment from V200612 (#4) and represents the only known taeniodont from California.

—*Paromomys depressidens*: RAM 6426, P4, V94014 (#6), and Ignacius frugivorus: RAM 6433, m3, V98012 (#7). These primate-like species are well-known from the Rocky Mountain states.

—*Nannodectes lynasi*: RAM 9044 (holotype), dentary with p3-m3, RAM 9668, maxilla fragment with C, P4-M1, RAM 9669, skull fragment with broken I1, P4, M1-2 and associated p3, V200510 (#2); RAM 9429, dentary with p3-m3, V200706 (#2); RAM 10029, dentary with p4-m3, V200804 (#2); six m3s (RAM 6960, RAM 6963, RAM 6700, RAM 6961, RAM 6934, RAM 6963), m2 (RAM 6446), mx (RAM 6935), mx trigonid (RAM 6946), M3 (RAM 6957), M2 (RAM 6962), P3 (RAM 6931), 2 I1s (RAM 6431, RAM 6929) from V98012 (#7); RAM 7193, dentary with p4-m1, broken m2, V200202 (#8); RAM 6925, m3, V94014 (#6). These specimens represent a new species of plesiadapid primate only known from the Goler Formation.

—*Thryptacodon* sp: RAM 9041, m1, V200510 (#2). RAM 9041 is the only oxyclaenid from the Goler Formation.

—*Mimotricentes tedfordi*: RAM 6908 (holotype), maxilla with P4-M3, V94133 (#6); RAM 15622, dentary with p4 talonid and m1-2, V201014 (#1); RAM 6928, dentary with m3 talonid, RAM 15333, M2, V200001 (#3); RAM 9670, dentary with p4-m1, V200510 (#2); *Lambertocyon* cf. *L. gingerichi*: RAM 9040, M1 and RAM 9043, p3 fragment, V200001 (#3); RAM 19622, M1, V2006012 (4); ?Arctocyonidae: RAM 9660, px or PX, V200613 (#10). Most of these arctocyonid specimens represent *Mimotricentes tedfordi*, which is only known from the Goler Formation. The three specimens of *Lambertocyon* cf. *L. gingerichi* may represent a new species of *Lambertocyon* as RAM 9040 has a large mesostyle and RAM 19622 has a distinct metaconule and an incomplete posterior cingulum, unlike *Lambertocyon gingerichi*. But

more complete specimens are needed before a new species of *Lambertocyon* can be erected.

—*Protoselene ashtoni*: RAM 9047 (holotype), dentary with p4-m1, V200702 (#5); and *Promioclaenus walshi*: RAM 9098 (holotype), dentaries with left m1-3 and right m2-3, V200510 (#2); RAM 6724, dentary with m2 and talonid of m1, RAM 6926, maxilla fragment with M2-3 (referral questionable), V200001 (#3). These specimens represent two new species of hyposodontid condylarths only known from the Goler Formation and they significantly increase the known diversity of hyopsodontids in North America.

—*Phenacodus* cf. *P. bisonensis*: UCMP 69122, dentaries with right m2 and left p4-m2, UCMP V65710; RAM 9659, M1 from V98012 (#7); RAM 6722, M1, RAM 7205, dP4, RAM 7245, maxilla with dP3-4, RAM 7208, dP4, RAM 9725, dP4, RAM 6721, damaged m2, RAM 6723, dentary with m2-3, RAM 18562, m3, V200001 (#3); RAM 7248, maxilla with P4–M1 and damaged M2, V200304 (#5); RAM 9019, m3, V200508 (#2); RAM 9022, dentary with dp4-m1, RAM 9672, maxilla with P3-4, RAM 18564 p4, RAM 18617, M3, RAM 18569, M3, V200510 (#2); RAM 9025, m1, RAM 9021, M2, RAM 9046, dentary with m1-3, RAM 18563, m2, V200603 (#4); RAM 9020, M2 and M3; RAM 9024, dentary with m2-3, RAM 9023, dentary with p3-m3, RAM 20874 DP3-DP4 and M1, V200612 (#4); RAM 9045, dp4, V200704 (#9); RAM 10290, dentary with m1-2, RAM 10291, m3, RAM 10292 left dentary with c–m3 and right dentary with i1-2, and c-m1, V200802 (#2); RAM 15000 maxilla with dP4-M2, V201122 (#1); RAM 15620, m1 or m2, V2012011 (#4); RAM 18567 M1 or M2, RAM 18565, P3, RAM 18568 P4, RAM 18566, left p2-3 and right p2 and p4, RAM locality V201014 (#1); RAM 20875, M1, V2017057 (#4). This mid-sized phenacodontid is the most common mammal recovered from the Goler Formation. *Phenacodus* cf. *P. bisonensis* resembles *Phenacodus bisonensis* in most ways, but a few minor differences in the upper molars and the size of the dentition indicate the Goler sample is not *Phenacodus bisonensis* (Lofgren et al., 2014). Twelve additional specimens were found between 2014 and 2018 and these fossils inspired a re-analysis of the entire Goler sample of *Phenacodus* cf. *P. bisonensis*. However, the Goler sample still does not exhibit the consistent diagnostic features needed to erect a new species of phenacodontid.

—*Phenacodus* cf. *P. matthewi*: RAM 7210, dentary with p4, V200001 (#3). RAM 7201 is very similar to the smallest species of *Phenacodus*, *P. matthewi*, but has a smaller p4 paraconid (Lofgren et al., 2014). Additional specimens of this small phencodontid are needed to determine if a new species is present.

—*Phenacodus* cf. *P. grangeri*: RAM 7172, left m3, RAM locality V94014 (#6); RAM 18570 m1 or m2, V201481 (#3); RAM 18571, canine, left and right p4, and m1, V201346 (#3). Referral of these large specimens to *Phenacodus* cf. *P. grangeri* is tentative because *P. grangeri* is difficult to distinguish from *P. intermedius* (Thewissen, 1990).

—*Goleroconus alfi* (new genus and species): RAM 7171 (holotype), dentary with p4-m2 and part of m3, V200120 (#11); RAM 6506, m2, RAM 6417, p3, UCMP 131790, m2, UCMP 44761, dentary with m3, UCMP 49487, m3, V94014 (#6) (equals UCMP V5252). Specimens referred to *Goleroconus alfi* are only known from the Goler Formation and include the first mammal (UCMP 44761) identified from the formation (McKenna, 1955). A suitable holotype (RAM 7171) for this new periptychid was not found until 2001 (McKenna et al., 2008).

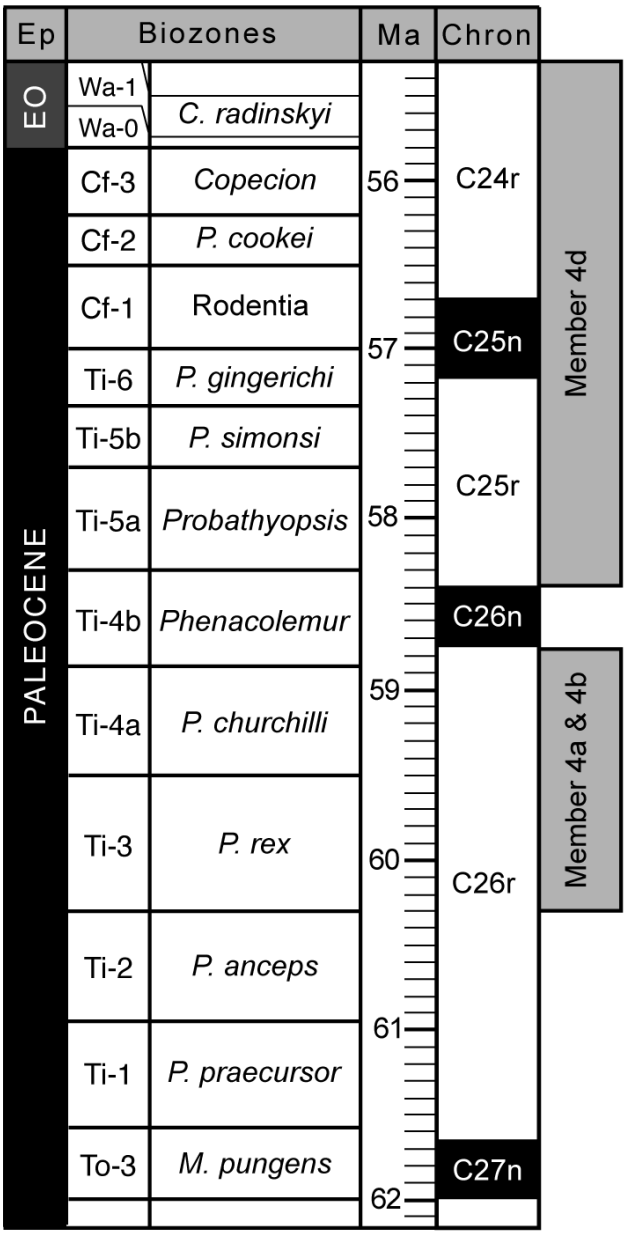

Figure 5. Biochronology and geochronology of the late Paleocene and early Eocene after Secord et al. (2006, fig. 3). Correlation of Member 4a and Member 4b based on mammalian biochronology and magnetostratigraphy and correlation of Member 4d based on vertebrate and invertebrate biostratigraphy and magnetostratigraphy (Albright et al., 2009; Lofgren et al., 2010, 2014, and references therein).

—*Dissacus* sp: RAM 6507, talonid of m1 or m2, V94014 (#6). Mesonychids are rare mammals that may be related to ancestors of whales and RAM 6507 is the oldest mesonychid known from the west coast of North America.

The stratigraphic interval that represents Member 4a and the lower part of Member 4b is about 500 m thick and cannot be subdivided into discrete biostratigraphic units based on mammalian biochronology, so mammals from this interval are referred to as the Goler Assemblage (Lofgren et al., 2014). The Goler Assemblage was compared to Tiffanian assemblages from the Western Interior and indicate a middle Tiffanian (late Paleocene) age for this part of the Goler Formation (Figure 5) (Lofgren et al., 2014, 2018). The middle Tiffanian age is supported by magnetostratigraphic correlation of Member 4a and Member 4b to C26r (Albright et al., 2009; Lofgren et al., 2014).

Member 4D

In the 1980's, an interval of marine sediments was discovered in the uppermost part of the Goler Formation in Member 4d (Cox and Edwards 1984; Cox and Diggles, 1986; Cox 1987). Initial collections of marine invertebrates from Member 4d indicated that these strata (northwest of #12) were late Paleocene (CP8) based on cocoliths (Reid and Cox, 1989) and early Eocene (P8 and ?P9) based on foraminifera (McDougall, 1987). Another small outcrop of Member 4d (#13) yielded fifty-one specimens of late Paleocene–early Eocene mollusks (Squires et al., 1988).

In 2003, RAM crews identified an additional section of fossil-bearing marine strata (#12) situated roughly between the previously identified marine outcrops and three sites (V200305, V200306, V200307) from this newly discovered section yielded abundant and well-preserved marine invertebrates along with shark teeth and the tooth of a terrestrial mammal (Lofgren et al., 2004, 2010). These RAM localities are within a series of cobble-pebble conglomerate and sandstone lenses where gastropods and shark teeth are rare and whole valves and shell fragments of oysters are common. Surprisingly, a tooth of the terrestrial mammal was found at V200307. Also, oysters and other mollusks with original shell material are present at V200305. Specimens listed below from the three RAM marine sites were briefly described by Lofgren et al. (2010).

Pelecypoda: Six taxa were identified and all were previously described by Squires et al. (1988) from site #13, but these RAM specimens are more numerous and complete.

—*Acutostrea idriaensis*: This oyster is the most common mollusk and over 100 whole and fragmentary valves were recovered from V200306 and V200307 (#12).

—*Barbatia biloba*: One specimen (RAM 9633) was collected at V200306 (#12).

—*Corbula* aff. *C. dickersoni:* Eight specimens were recovered, seven from V200305 (RAM 9567, 9593-94, 9563, 9610-11, 9576) and one from V200306 (RAM 9626).

—*Ledina duttonae*: One specimen (RAM 9627) was found at V200306.

—*Nemocardium linteum*: Twelve specimens were recovered from V200305 (RAM 9573, 9614, 9565, 9582, 9585, 12248-12254).

—*Thracia* aff. *T. condoni*: Five specimens were identified, three from V200305 (RAM 9601, 9615, 9586) and two from V200306 (RAM 9619, 9625).

Gastropoda: In contrast to pelecypods, only two (*Calyptraea diegoana, Turritella buwaldana*) of the eight gastropod species recovered from the RAM marine sites were previously described by Squires et al. (1988), but the six new records remain unidentified to taxon. Three specimens of *Calyptraea diegoana* were recovered from V200305 (RAM 9584, 9599, 9613), as well as 27 specimens of *Turritella buwaldana* including complete shells; V200305 yielded 22 and V200306/V200307 five. The six additional gastropod morphotypes are from V200305 except three specimens of morphotype A from V200306. These morphotypes (A-F) are: A) RAM 9621-22 (V200306) and RAM 9600 (V200305); B) RAM 9592 resembles *Admete*; C) RAM 9591 has seven whorls and well-defined costa; D) RAM 9616 resembles *Gyrodes*; E) RAM 9602 has strong ribbing and costae; F) RAM 9604 has four whorls.

Chrondrichthyes: Sharks are represented by isolated striated teeth (RAM 7256, 7255, 7254) from V200307 which are similar in morphology to those of *Striatolamia*, a shark widespread in late Paleocene and Eocene strata in North America.

Mammals: A p4 of *Phenacodus* cf. *P. vortmani* (RAM 7253) was found at V200307. If RAM 7253 does represent *Phenacodus vortmani*, its occurrence would indicate a late Paleocene or early Eocene age (Thewissen, 1990; Secord et al., 2006; Secord, 2008).

The RAM marine localities (#12) extended the known area of the marine transgression that deposited a large part of Member 4d. The older known marine sequence consists of sandstones and conglomerates with marine mollusks, overlain by a marine siltstone unit with planktic and benthic forminifera (indicating water depths of 50–150 m) which was interpreted to represent a braided river delta (Cox, 1987; McDougall, 1987). The RAM marine section probably represents a more proximal delta facies because the well-preserved mollusks, shark teeth and a nonmarine mammal tooth (both nonmarine and marine vertebrates and marine invertebrates) suggest a near shore marine facies where nonmarine fossils were deposited in a delta lobe with oysters and other marine invertebrates (Lofgren et al., 2010).

Strata at the RAM marine section was sampled for paleomagnetic analysis and all samples were of reversed polarity (Albright et al., 2009). Correlation to Chron 25r or Chron 24r (Figure 5) is the most plausible based on the correlation of Member 4a and Member 4b strata to Chron 26r (Albright et al., 2009; Lofgren et al., 2014) and the late Paleocene to early Eocene age of Member 4d based on

invertebrates (McDougall, 1987; Squires et al., 1988; Reid and Cox, 1989).

Paleobiogeography and prospectus

The non-marine fauna of the Goler Formation exhibits significant endemism as more than 45% of mammalian taxa (ten of twenty-one) are not found in middle Tiffanian faunas from the Rocky Mountain states. Endemic taxa are the metatherian, *Golerdelphys stocki* (Williamson and Lofgren, 2014), the multituberculate *Golercosmodon mylesi* (Lofgren at al., 2018) and eutherians *Goleroconus alfi*, *Nannodectes lynasi*, *Mimotricentes tedfordi*, *Protoselene ashtoni*, and *Promioclaenus walshi* (McKenna and Lofgren, 2003; McKenna et al., 2008; Lofgren et al., 2014). In addition, *Phenacodus* cf. *P. bisonensis*, *Lambertocyon* cf. *L. gingerichi*, and *Phenacodus* cf. *P. matthewi* are represented in the Goler Assemblage by specimens that have significant character differences compared to their respective species from the Western Interior and likely represent new species that require more complete specimens for confirmation. Also, only five Goler mammalian taxa can be confidently referred to species from the Western Interior of North America (i.e. *Neoliotomus conventus*, *Bessoecetor septentrionalis*, *Protictis paralus*, *Ignacius frugivorus*, *Paromomys depressidens*), a strong indication of endemism.

Turtles from Member 4a and Member 4b also reflect significant endemism (Hutchison, 2004) and the remains of gars, a type of fish commonly found in Paleocene strata in the Rocky Mountain states, have yet to be found in the Goler Formation (Lofgren et al., 2008). This degree of vertebrate endemism strongly suggests that the Goler Basin was geographically isolated from Paleocene sedimentary basins of the Western Interior and this isolation provided excellent opportunity for the formation of a unique west coast faunal province in what is now southern California during the late Paleocene.

There is much yet to accomplish with respect to Goler Formation paleontology. Very little prospecting of finer grained strata of Member 2 with the potential to yield vertebrates or invertebrates has occurred. Also, the extensive outcrops of Member 3 still could yield additional vertebrate specimens which could provide a more precise age determination for these strata. Finally, detailed analysis of invertebrates from the RAM marine sites in Member 4d would be productive as the original study of these specimens was cursory (Lofgren et al., 2010) and many more specimens have been collected since 2010.

Outcrops of the Goler Formation extend for many kilometers north–south and east–west, and prospecting this very broad geographic area would likely yield unexpected results. Plant fossils are extremely rare, but there is potential to discover identifiable specimens because sedimentary facies that commonly preserve floral material are common in Member 3 and Member 4. By the 1980s, the Goler Formation had developed a reputation of being too sparsely fossiliferous to be worthy of further prospecting. That all changed in the last three decades when numerous specimens were recovered representing new taxa and some incredibly rare fossils were found (i.e. mammal and turtle skulls). Thus, more treasures await the meticulous researcher.

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