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ABSTRACT

Fossil mammal and other vertebrate remains from the Lomas Las Tetas de Cabra in Baja California Norte, Mexico, provide an opportunity to examine the utility of continental scale geochronologies based on land mammal faunas. Early reports proposed a late Paleocene to early Eocene age for this fauna. Recent fieldwork and considerations of cumulative fossil discoveries strongly indicate that the Baja fauna represents the Wasatchian Land Mammal Age (early Eocene) and is strikingly similar to faunas of this age from the western interior of the United States. Wasatchian-age taxa represented in the Baja assemblage include *Hyracotherium, Hyopsodus, Meniscotherium* (also possibly from Clarkforkian assemblages), *Diacodexis,* and *Prolimnocyon.* Also present in the fauna are excellent specimens of *Wyolestes* and *Esteslestes,* a new genus of didelphid marsupial, as well as a badly distorted skull of a pantodont. An early Eocene age assignment is supported by analysis of the marine section adjacent to the Tetas de Cabra sequence. The marine organisms are consistent with a middle Ypresian (early Eocene) age assignment. Paleomagnetic analyses of both the terrestrial and marine sections also corroborate this age assignment. These new results substantiate the validity of the Wasatchian as a discrete temporal interval that can be applied at a continental scale. The Wasatchian thus fulfills the expectations for a mammal-based chronology. Similarities, rather than differences, between the Baja assemblage and other Wasatchian-age faunas is the dominant pattern. A choice among dispersal theories for the sources of Wasatchian mammals is not clearly indicated by the faunal evidence.

INTRODUCTION

Intensive studies of Wasatchian-age (early Eocene) mammal faunas (Gingerich et al., 1980) provide a rich and fascinating chapter in Cenozoic history. The Wasatchian is now defined, and separated from the earlier Clarkforkian Land Mammal Age, by the first appearance of true horses (*Hyracotherium* and other perissodactyls), artiodactyls, more advanced primates, carnivorelike forms, and a few specialized lineages of the "stem" ungulate radiation (Gingerich and Gunnell, 1979; Gingerich et al., 1980; Gingerich and Haskin, 1981; Rose, 1980, 1981; Gingerich, 1989; Krause and Maas, 1990). Nevertheless, these distinctions are based on comparisons of assemblages in intermontane basins of the Rocky Mountain region of the United States (fig. 1). Hence, the Wasatchian, though clearly defined taxonomically, applies to interior faunas of relatively restricted latitudinal and longitudinal distribution.

New insights on the utility of the Wasatchian Land Mammal Age have come from recent documentation of a fossil vertebrate fauna from Baja California. This assemblage fulfills two important requirements for a test of a Land Mammal Age. First, the Baja fauna is geographically far removed from the cluster of Wasatchian-age localities in the Rocky Mountains (fig. 1).[1] Second, the terrestrial sequence at the Baja site intertongues with marine coastal sediments having rich macroinvertebrate and microorganism assemblages. This situation, as well as the opportunity for paleomagnetic sampling, shows the potential of the Baja assemblage for refinement of the Early Cenozoic time scale and for development of a broader picture of mammalian history in North America.

Recent extensive field collecting as well as synthesis of results from earlier exploration of the Baja locality (Flynn and Novacek, 1984) demonstrate the utility of the Wasatchian Land Mammal Age for broad, continental-scale age correlation. In addition, the Baja

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[1] It is noteworthy that during the Early Tertiary, Baja California was sutured to the Mexican mainland. The peninsula and its entombed faunas have either remained at the same latitude or were slightly shifted northward (about 2.5°) with the opening of the Gulf approximately 20 Ma (figs. 1, 2). Results of recent paleomagnetic analyses (Flynn et al., 1989) contradict proposals for a 10–15° northward translation for the Baja peninsula during post-Eocene times.

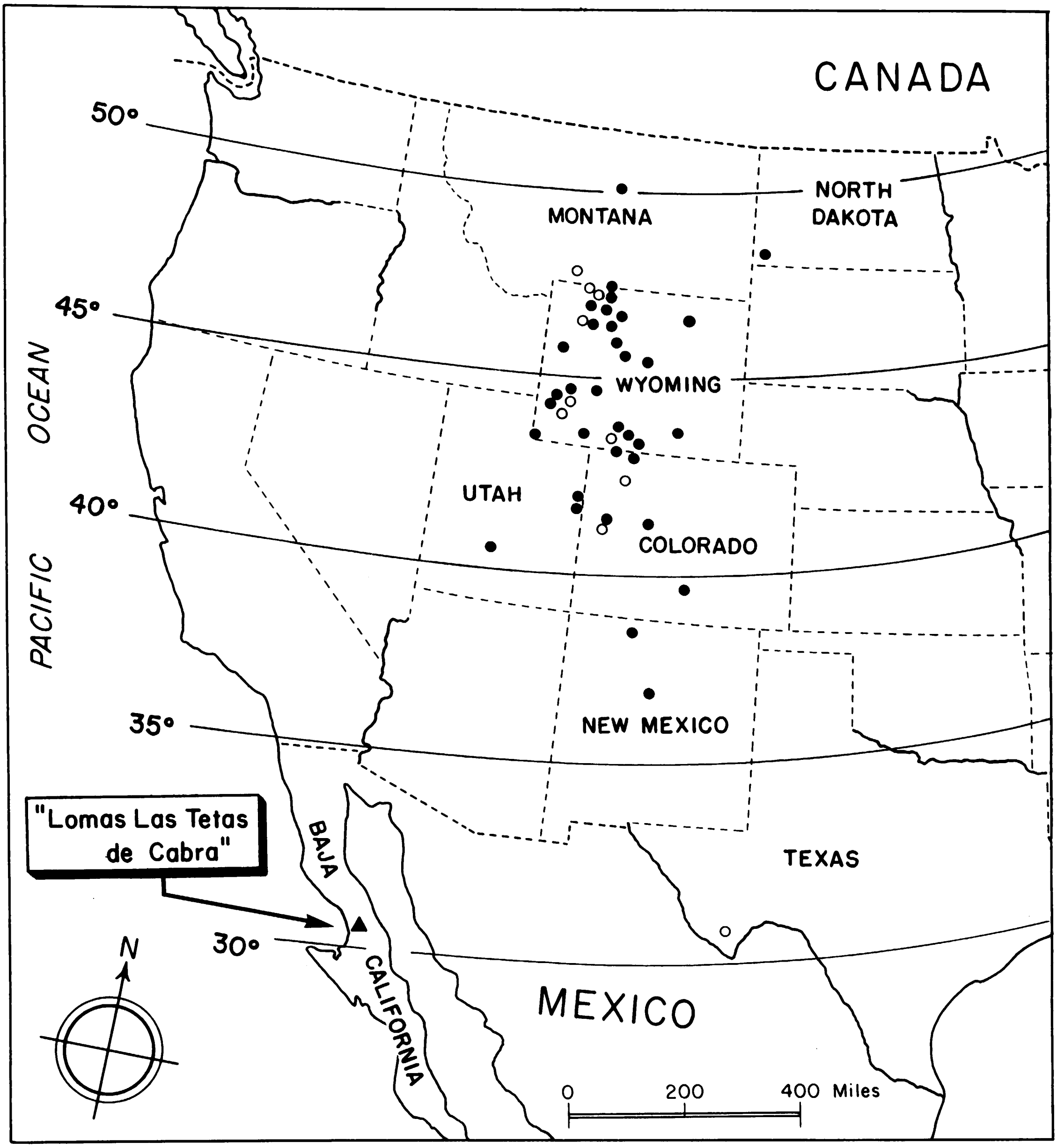

Fig. 1. Distribution of North American Wasatchian (●) and Clarkforkian (O) faunas. Location of Las Tetas de Cabra fauna is indicated). This locality was designated "Punta Prieta" on former maps (e.g., Flynn and Novacek, 1984). Paleolatitudes are based on the time-averaged 50 million-year pole position (83.1°N, 178.2°E) for North America (see Flynn and Novacek, 1984).

fauna adds another dimension to the biogeographic history of North America during this interesting time interval. This paper is a comprehensive account of the mammalian taxa in the fauna and a synopsis of the geochronologic and geographic implications reviewed in several other papers (Ferrusquía-Villafranca, 1978; Flynn and Novacek, 1984; Novacek et al., 1987; Flynn et al., 1989).

ACKNOWLEDGMENTS

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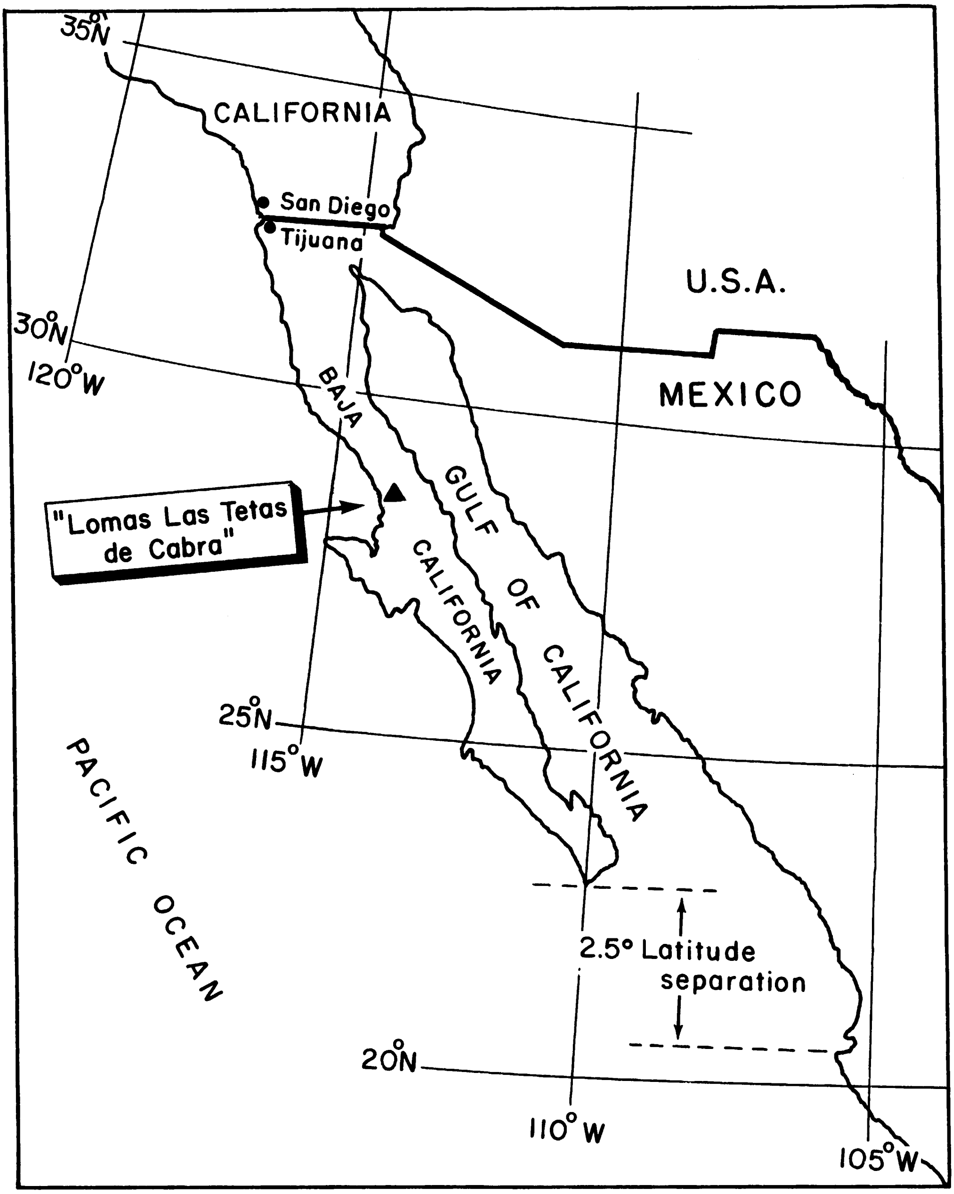

Fig. 2. Map of Baja Peninsula showing location of Lomas Las Tetas de Cabra site. Also shown are present-day latitudes and longitudes. Possible 2.5° latitudinal separation was caused by opening of the Gulf of California in the Neogene (but see Flynn et al., 1989).

Victor Torres Roldan, Margarito Alvarez-Montes, Harley J. Garbani, Shelly P. Applegate, William J. Morris, Jeanne Kelly, Lawrence Flynn, Nancy Olds, Steve Rudman, and S. Rodriguez. Figures were expertly prepared by Ray Gooris, Chester Tarka (photographs), and Ed Heck. Lorraine Meeker was helpful in preparing layouts for the illustrations. Alejandra Lora prepared the translation for Appendix 10.

For their critical reviews of the manuscript, we thank Philip D. Gingerich, David W. Krause, and Ken D. Rose.

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ABBREVIATIONS

AC	Adelphi College
AMNH	American Museum of Natural History
IGM	Instituto de Geología, Universidad Nacional Autonoma de Mexico (Mexico City)
PU	Princeton University (now accessioned by Yale Peabody Museum, YPM)
UM	University of Michigan, Museum of Paleontology
USNM	United States National Museum of Natural History

PREVIOUS INVESTIGATIONS

A small, localized assemblage of Early Tertiary vertebrates on the Baja Peninsula (fig. 2) has been known to exist for more than 20 years. On May 2, 1965, Shelton P. Applegate, then at the Los Angeles County Museum of Natural History (LACM), H. Garbani, and P. Royce prospected a small area of badlands about 30 km south of the town of Punta Prieta and 625 km south of the United States–Mexico border. The badlands, which lay just a few kilometers west of Highway 1, are marked by two prominent buttes, known locally as Lomas Las Tetas de Cabra (figs. 3, 4), a name that appears on official Mexican geological and topographic maps (Hoja Rosarito, HII D69, 1:50,000; CETENAL [=INEGI], 1977). A single day of prospecting by the Applegate crew produced a damaged skull and associated fragmentary skeleton of a pantodont.

Further study of the area was conducted by W. J. Morris (Research Associate, LACM; Professor, Occidental College) in 1965 and 1966. This work, supported by grants from the National Geographic Society, resulted in several important discoveries, including an isolated jaw fragment and molar of the earliest genus of horse, *Hyracotherium* (Morris, 1966, 1968). Morris (ibid.) tentatively assigned the Baja fauna a Clarkforkian age (roughly equivalent to a latest Paleocene–early Eocene time interval [see Rose, 1980, 1981]). He acknowledged, however, that the fauna was only incompletely known and might eventually be assigned a Tiffanian (late Paleocene) or Wasatchian age. Morris named the locality Occidental Buttes, a term used in another published map of Baja (Gastil et al., 1975). We prefer, however, the locally familiar name for the area, Lomas las Tetas de Cabra, as presented by the Mexican publications (see above citation).

In 1974, Morris transferred the pantodont material to I. Ferrusquía-Villafranca of the Instituto de Geologia, Mexico City (IGM), for study. Two years later, Ferrusquía-Villafranca and Applegate joined in a paleontological reconnaissance of the whole Baja peninsula, including Las Tetas de Cabra badlands. This phase of fieldwork ended in 1978 and it was not until the spring of 1983 that field parties from the American Museum of Natural History, New York City (AMNH), led by M. J. Novacek and J. J. Flynn, returned to Las Tetas. This effort yielded preliminary results that suggested a Wasatchian rather than Clarkforkian age for the Baja locality (Flynn and Novacek, 1984).

Somewhat later in 1983, the area was independently prospected by I. Ferrusquía-Villafranca, V. Torres Roldan, and S. Rudman as a joint venture by IGM and the University of Michigan Museum of Paleontology. Subsequently, Ferrusquía-Villafranca and Novacek agreed on a cooperative study of the Baja site to account for both earlier and more recent discoveries. AMNH field parties returned to Las Tetas in 1984 and 1985, the latter season with support from the National Geogrphic Society. Goals were expanded to detailed paleomagnetic sampling by J. J. Flynn and coordinated study of invertebrate paleontology and stratigraphy of the adjacent marine section by R. M. Cipolletti (Rutgers University). Results of these activities, with special emphasis on the systematics of the fauna, are provided in this paper (see also Novacek et al., 1987).

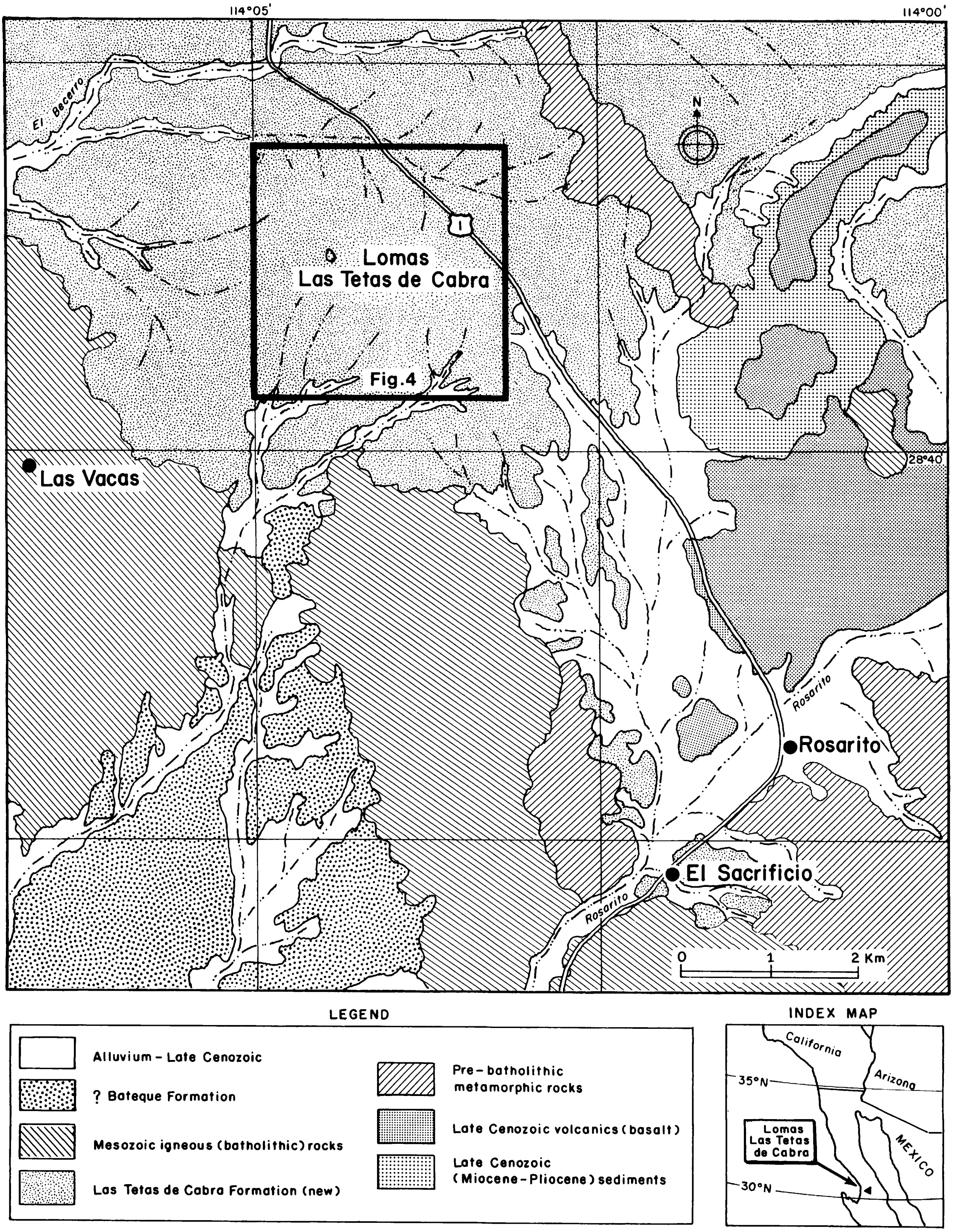

Fig. 3. Region in Baja Peninsula north of the town of Rosarito, encompassing the study area (outlined square, see fig. 4). Extent of units recognized in this paper are shown. Inset map shows paleolatitudes for early Eocene (see fig. 1).

GEOLOGY

Early studies of the Baja California peninsula include the pioneering work of Gabb (1869) and early reconnaissance studies of Darton (1921), Heim (1922), and Santillan and Barrera (1930). Beal (1948) and Gastil et al. (1975) presented the most complete summaries of the geology of the peninsula. Recent stratigraphic and biochronologic studies include those of Mina (1956, 1957), Durham and Allison (1960), Fife (1968, 1969), Flynn (1970), Minch (1970), Cipolletti (1986), Novacek et al. (1987), and Flynn et al. (1989). Previous studies of the vertebrate paleontology of northern and central Baja California include Morris (1966), Lillegraven (1972), Ferrusquía-Villafranca (1978), Flynn and Novacek (1984), and Novacek et al. (1987). Much of the previous geologic work has focused on the northern part of Baja California Norte; relatively few studies have concentrated on the southern part of Baja California Norte, or on the central part of the peninsula.

Stratigraphic nomenclature of Early Cenozoic units in the study area is quite confused. Early Cenozoic strata on the Baja Peninsula variably have been assigned to the (1) Tepetate Formation (Heim, 1922; Beal, 1948; Mina, 1956, 1957; thought to be Eocene by Heim, Paleocene/Eocene by Mina, and Paleocene by Beal, 1948; Gastil et al., 1975), (2) Santo Domingo Formation (Heim, 1922; Paleocene), (3) Sepultura Formation (Santillan and Barrera, 1930; Fife, 1968, 1969; considered Paleocene/Eocene by Santillan and Barrera, and Paleocene by Fife), (4) Malarrimo Formation (Mina, 1956, 1957; considered Cretaceous by Gastil et al., 1975), (5) Bateque Formation (Mina, 1957; Eocene). Based both on age and lithology, Fife (1968; followed by Gastil et al., 1975) assigned all Paleogene marine strata of the Santa Rosalia Quadrangle, which encompass the study area, to the Sepultura Formation. Cipolletti (1986) followed requirements of the North American Code of Stratigraphic Nomenclature (1983) and argued that, based on lithology only and excluding age information, most of these marine strata could be better assigned to the Bateque Formation. The fossiliferous terrestrial strata of the Lomas las Tetas de Cabra region (Santa Rosalia Quadrangle) have been assigned to an "unnamed formation" by Morris (1966) and Novacek et al. (1987). Below, we propose a new formation for this "unnamed formation." The major units recognized in the vicinity of the study area are shown in figure 3.

LAS TETAS DE CABRA FORMATION

We name a new formation, the "Las Tetas de Cabra Formation" for terrestrial strata cropping out in the area surrounding the Lomas las Tetas de Cabra. Although the formation is restricted areally, we feel the distinct lithology, terrestrial environment of deposition, and confusing nomenclature of strata in this region require formal designation of the new unit. Included within the new formation are strata that had been assigned previously to the Tepetate Formation (Beal, 1948), Bateque Formation (Mina, 1957), Sepultura Formation (Fife, 1968), and an "unnamed" formation (Morris, 1966; Gastil et al., 1975; Flynn and Novacek, 1984; Novacek et al., 1987). It is advisable to trace a formation physically from its type area to any new area where the same formation is recognized. In Baja, lithologic units are variable and discontinuous laterally, making direct physical correlation extremely difficult.

The exposures of the Las Tetas de Cabra Formation cannot be traced laterally to the type areas of any previously named formation. Exposures of the nearest formation, the ?Bateque Formation, clearly are distinct and differentiable from the Las Tetas de Cabra Formation.

Strata of the Las Tetas de Cabra Formation are distinct from the Bateque Formation, and all other previously described Paleogene formations in Baja, in the predominance of "oxidized" red and brown sandstones and siltstones; low abundance of "reduced" gray, green, or blue claystones; lack of sedimentologic/paleontologic indicators of marine deposition; abundance of sedimentologic/paleontologic indicators of terrestrial deposition; and presence of possible paleosols.

Strata underlying and intertonguing with Las Tetas de Cabra Formation may be assigned tentatively to the Bateque Formation

(Cipolletti, 1986). Contact between the Las Tetas de Cabra Formation and the underlying ?Bateque Formation is not sharp, and tentatively is set around the 100 m contour line. The contact crops out in the western portion of the study area, rather away from the buttes and the fossil localities. It was not practical to measure a section between these portions of the area because there is very low relief here and outcrop is poor. We define the lower boundary of Las Tetas de Cabra Formation as the first occurrence of extensive red and brown sandstones; unambiguous recognition of this formation requires the presence of indicators of subaerial deposition (e.g., terrestrial snails or plants, root casts, paleosols, etc.). Although formational definitions require precise, albeit occasionally arbitrary, boundaries, we note that a few red and brown sandstone/siltstone interbeds occur to the south of the formational outcrops within the marine strata of the ?Bateque Formation (see map). These interbeds contain *Celtis* seeds, terrestrial snails, and mammals (*Hyracotherium* and several nondiagnostic specimens), and probably represent the terrestrial "facies" in an area in which the Las Tetas de Cabra and ?Bateque Formations intertongue.

The line of the type section starts some 460 m S 83°E of the western butte, nearly at the junction of a north-south trending gully coming from the eastern slope of this butte and an east-west trending gully close to the southern slope of the eastern butte. From here it proceeds about 50 m due east (up to unit 12), then it turns due north for a 100 m detour, and finally, it turns due east again, up to the eastern butte summit, where the section ends. This type section was measured with a 50 m steel tape, and its trace is plotted in figure 4. Additional measured stratigraphic sections are presented in appendices 2 and 3. Fossil vertebrate localities are numbered (see appendix 1 for description). The field description of the type section follows (see also figs. 5, 6):

Las Tetas de Cabra Formation
Type Section

Unit	Thickness (m)	Description
01	1.54	Quaternary alluvium on the channel floor of the north-south trending gully. Las Tetas de Cabra Formation at the eastern channel wall. The measured section starts at its bottom. Chocolate brown, fine grained, medium bedded, tuffaceous sandstone that shows spheroidal weathering.
02	0.82	Light red, medium grained, friable, thickly bedded, feldspathic sandstone.
03	1.54	Brown, silty to clayey, medium bedded, fine sandstone.
04	0.25	Similar to unit 2.
05	0.70	Brown, silty to clayey, friable, medium bedded fine sandstone.
06	0.60	Red, medium grained, well indurated, thickly bedded, feldspathic sandstone. 20 m detour north (to pick up a better outcrop), then line of section proceeds due east
07	1.40	Red, medium grained, well indurated, medium to thickly bedded, feldspathic sandstone, interbedded with a lens of granule-pebble, friable conglomerate made up of metamorphic and plutonic rock clasts.
08	0.27	Red, medium grained, friable, medium bedded tuffaceous sandstone.
09	0.42	Red, fine to medium grained, friable, medium bedded feldspathic sandstone; this unit makes up the plain surrounding the buttes area.
10	3.36	Light to dark brown, thickly bedded, clayey siltstone, that shows spheroidal weathering; top meter is darker.
11	2.42	Light red, medium grained, thickly bedded, feldspathic sandstone, that shows spheroidal weathering. 100 m detour north (to pick up a better outcrop), then line of section proceeds again due east to the slope of the eastern Teta (butte).
12	5.55	Red, clayey to silty, fine to medium grained, friable, thickly bedded, feldspathic sandstone that forms the lower part of the eastern butte; the pantodont, other vertebrates, and some snails were found in this unit. It shows some polyhedric fragments 2 to 6 cm in diameter.

Continued

Unit	Thickness (m)	Description
13	4.65	Light red, medium grained, friable, feldpsathic sandstone, interbedded with five layers of red, 6 to 8 cm thick silty sandstone; these interbeds are more indurated.
14	0.40	Brown to red (upward), thickly bedded, clayey siltstone.
15	1.90	Alternatively red to brown, thin to medium bedded, clayey siltstone.
16	1.50	Red, coarse grained, thickly bedded, feldspathic sandstone; it shows poorly developed cross bedding.
17	1.30	Light green, fine grained sandstone that shows spheroidal weathering.
18	1.40	Light red, coarse grained, well indurated, micaceous feldspathic sandstone.
19	3.14	Light green, coarse grained, thickly bedded moderately indurated feldspathic sandstone.
20	3.36	Light green, pebble, brecciated, thickly bedded conglomerates made up of metamorphic rock fragments.
21	6.60	Red, fine to medium grained, thinly bedded, indurated, feldspathic sandstone that makes three bed-sets, 0.70, 0.20, and 1.00 m thick respectively (upward), interbedded with brown, medium grained, medium bedded, feldspathic sandstone.
22	0.70	Brown, thickly bedded, silty claystone that shows spheroidal weathering, grades upward to fine to medium sandstone.
23	0.70	Brown, coarse grained, thickly bedded, well indurated feldspathic sandstone.
24	1.11	Similar to unit 22, although more clayey.
25	0.25	Similar to unit 23.
26	2.20	Light to cream color, medium grained, thickly bedded feldspathic sandstone that shows spheroidal weathering, covered by light red to cream color, well indurated tuffs (or tuffaceous sandstones) that also show spheroidal weathering. (This unit makes the upper end of the slope.)
Unconformity		
27	2.50	Unnamed, ?Miocene formation that makes up the cliff-bound, nipple-like cap of the (eastern) Teta(s) butte(s). Light pink to white to cream color, coarse grained, well indurated, thickly bedded feldspathic sandstone; interbedded with two thin conglomeratic lenses.
Unconformity		
28	1.00	White to cream color, pebble to cobble, well indurated, thickly bedded conglomerate made up of metamorphic clastics.
29	2.50	White to cream color, coarse grained, well indurated, medium to thickly bedded, litharenitic sandstone.
30	2.50	White to cream color, pebble to cobble, moderately indurated to friable, thickly bedded conglomerate made up of metamorphic clastics. Eastern Tetas (butte) summit.
		End of section
	56.68	*Total measured thickness*

MARINE UNITS

To the southwest of Las Tetas de Cabra badlands are extensive outcrops consisting of variegated siltstones, mudstones, and sandstones (fig. 3). These beds contain abundant oysters and molluscs, and appear to be a series of marine near-shore and lagoonal deposits. Fife (1968, fide Gastil et al., 1975: 50) identified these marine rocks as ?Tepetate Formation, following Heim (1922) and Beal (1948) and designated them as Paleocene in age based on the common occurrence of *Turritella pacheocoensis.* Cipolletti's (1986) study in conjunction with this project, however, documents the presence of numerous gastropod and bivalve species that indicate a "Capay" marine stage (see Givens, 1974; Squires, 1984) and a Ypresian age assignment for these beds. (The Ypresian is a marine invertebrate-based age developed from studies of molluscan faunas in the Paris Basin and generally equated with early Eocene time, see Berggren et al., 1985, fig. 5; Aubrey et al., 1988.) The stratigraphically important species include

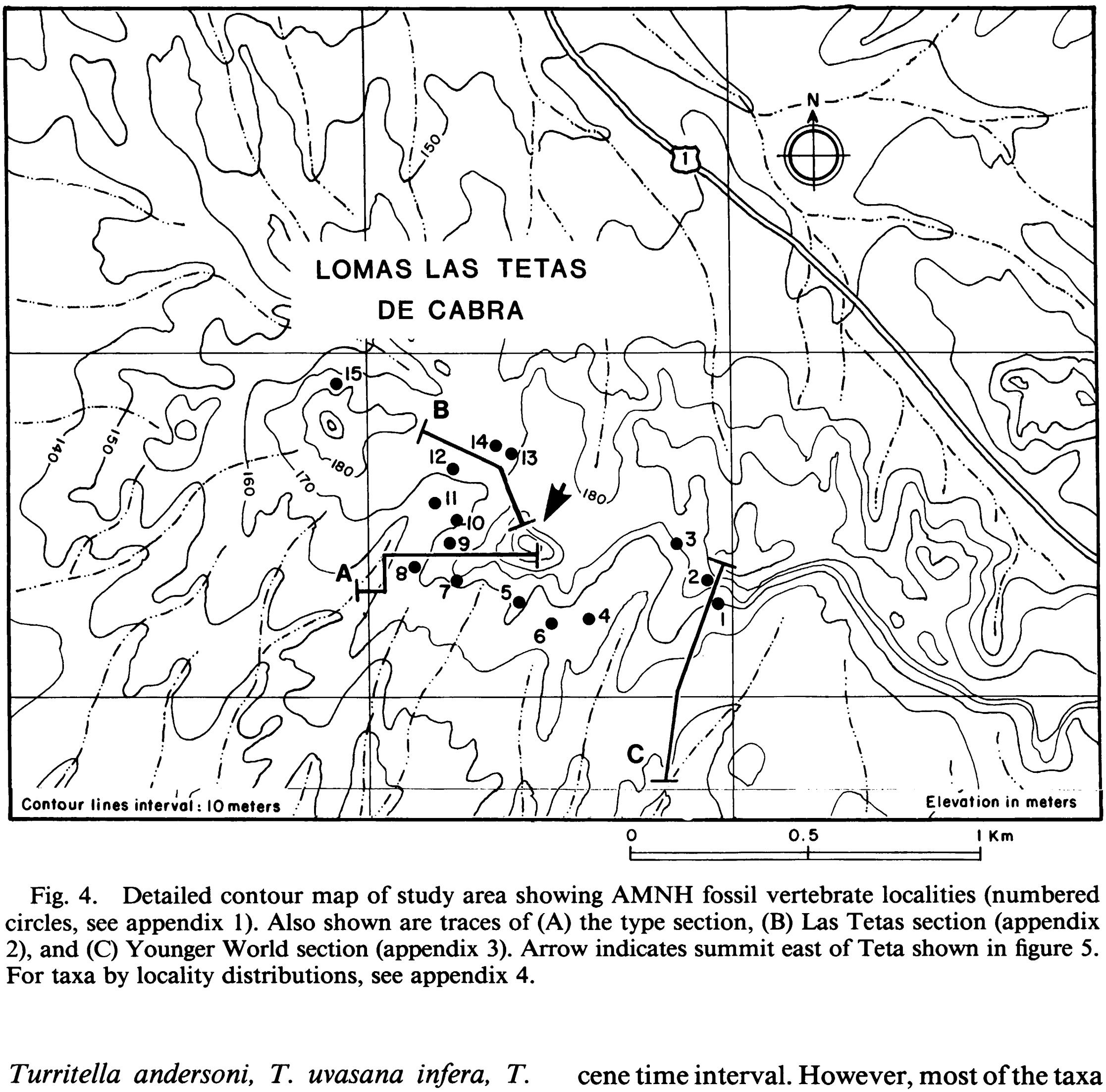

Fig. 4. Detailed contour map of study area showing AMNH fossil vertebrate localities (numbered circles, see appendix 1). Also shown are traces of (A) the type section, (B) Las Tetas section (appendix 2), and (C) Younger World section (appendix 3). Arrow indicates summit east of Teta shown in figure 5. For taxa by locality distributions, see appendix 4.

Turritella andersoni, T. uvasana infera, T. meganosensis protumescens, Venericardia (*Pacifer*) *hornii lutmani, V.* (*P.*) *durhami,* and *Crassatella* cf. *uvasana matthewsonii.* In addition, three molluscan taxa (*Tympanotonus* cf. *papalis, Ostrea rarilamella,* and *O.* cf. *angusta*) are very similar to taxa previously identified from the Ypresian of the Paris Basin.

The Early Eocene age of the marine sequence near Las Tetas is further substantiated by six benthic (bottom-dwelling) foraminifera found in these units. Where these taxa occur elsewhere in Paleogene strata of western North America, their ranges are limited to marine stages (Ynezian to Narizian) that indicate a latest Paleocene to early Eocene time interval. However, most of the taxa in the Baja sequence only occur in early Eocene or younger strata and this age assignment seems appropriate for this benthic assemblage. *Buntonia,* an ostracod recovered from the Baja marine units, also has its first occurrence in the Eocene. The cumulative evidence from marine organisms, then, suggests an assignment for the Baja strata of middle Ypresian (early Eocene) age. More precise correlation (Flynn et al., 1989) with revised time scales (Berggren et al., 1985; Aubrey et al., 1988) indicates an approximate correlation with early P7 to late P8 (planktonic foraminiferal zones) and mid-CP 9b to early CP 11 (calcareous nannoplankton zones).

Because these marine units provide signif-

Fig. 5. Panorama of study area showing exposure of Las Tetas de Cabra Formation. View is southeastward toward the higher (eastern) Teta (summit indicated by arrow). Localities 7–11 (see fig. 4) are in the ravines in foreground. The butte is capped by an unnamed ?Miocene coarse grained sandstone and conglomerate. Hill in the distance (horizon) is composed of Late Cenozoic basalts and related volcanics.

icant independent evidence of age, their stratigraphic relationships with the terrestrial sequence must be established. Contact between the marine and terrestrial units in the study area is discontinuous and difficult to trace. This problem is due to postdepositional erosion and discontinuity at the time of deposition controlled by prominent hills of pre-Eocene age (fig. 3). Nevertheless, an approximate stratigraphic correlation between the marine and nonmarine strata is indicated because both sequences are nearly horizontal and at the same elevations, and there is no evidence of postdepositional faulting between the two sections. Moreover, lagoonal to nonmarine facies that contain numerous *Celtis* seeds and the horse *Hyracotherium* (an important indicator of Early Eocene age—see discussion below) directly intertongue with "Capay" stage marine strata about 6 km south of the main buttes (fig. 3). (See also appendix 8.)

FOSSIL VERTEBRATE FAUNA

Fossil vertebrates in the study area were usually preserved as partial jaws with dentitions. However, specimens showed considerable abrasion and surface weathering, and edentulous jaws were most commonly found. Well preserved jaws, dentitions, and skeletons (e.g., *Wyolestes iglesius*) were very rare. Specimens were not concentrated in distinct-

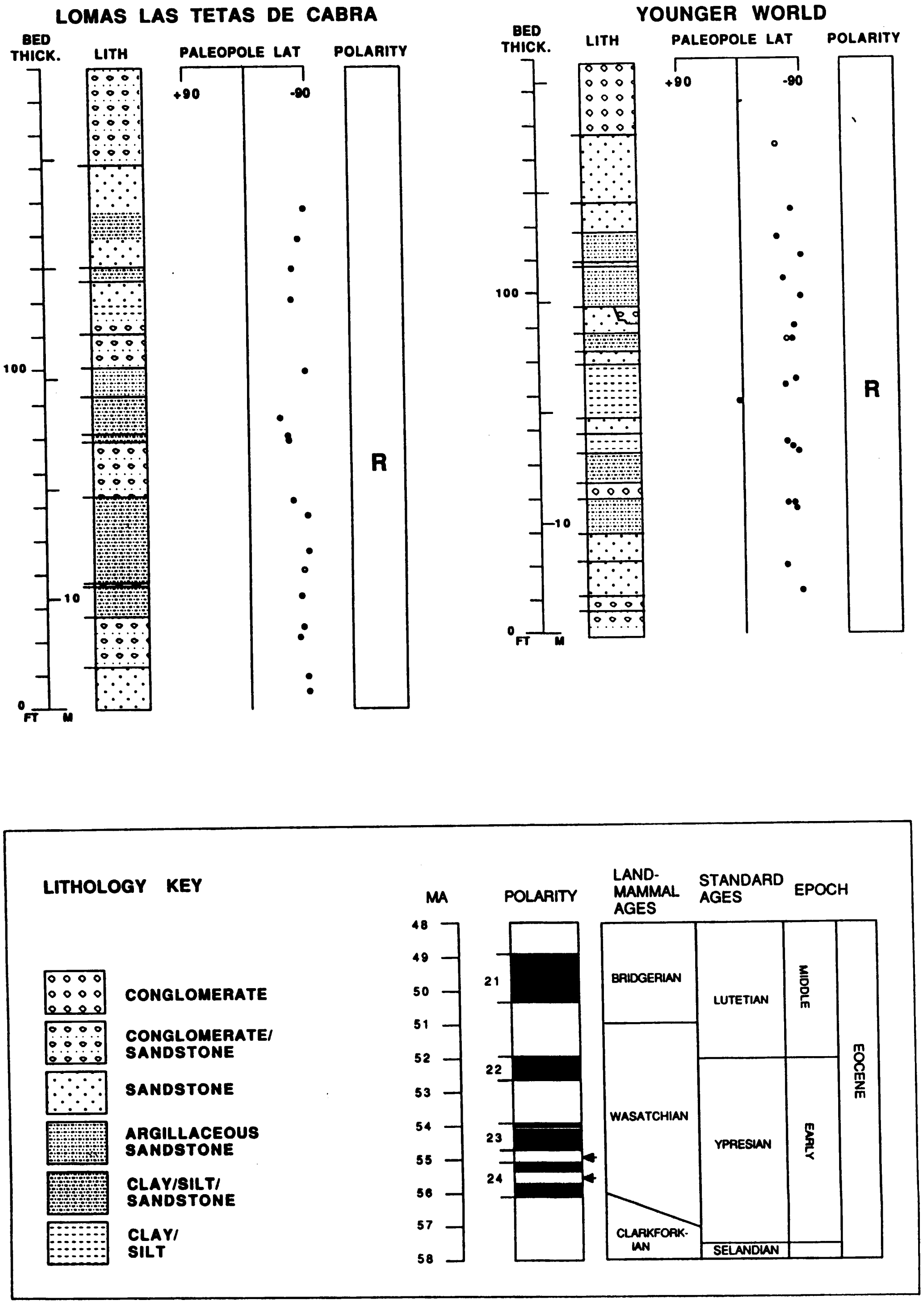

Fig. 6. Lomas Las Tetas de Cabra and Younger World sections showing lithologic units, paleomagnetic readings, and age correlations (from Flynn et al., 1989). See also appendix 9.

ly richer horizons, but were scattered throughout the fossiliferous section. Localities shown in figure 4 in many cases indicate sites where only one or two specimens were recovered, primarily through surface prospecting. A few localities (e.g., 13 and 14 in fig. 4) provided fragmentary bone through quarrying. The yield from a test sample taken from locality 5 for screen-washing was very poor.

The following systematic section on the mammalian fauna from Las Tetas de Cabra covers essentially all the identifiable material collected. The only major omission is the postcranial skeleton of *Wyolestes iglesius* (see remarks below). A small sample representing the fossil herpetofauna is also described (see appendix 7). The treatment of the mammals here emphasizes description and comparison with relevant early Tertiary taxa but does not provide broader revisions of genera and higher taxa which, in several cases, are greatly needed.

SYSTEMATICS

CLASS MAMMALIA LINNAEUS, 1758

SUBCLASS THERIA PARKER AND HASWELL, 1897

INFRACLASS METATHERIA HUXLEY, 1880

ORDER MARSUPIALIA ILLIGER, 1811

FAMILY DIDELPHIDAE GRAY, 1821

SUBFAMILY DIDELPHINAE (GRAY, 1821) SIMPSON, 1927

TRIBE DIDELPHINI CROCHET, 1979

Esteslestes, new genus

Table 1, Figures 7, 8

ETYMOLOGY: Named in honor of vertebrate paleontologist Richard Estes, a member of the 1983 AMNH field party in Baja California; *lestes* is a common suffix for names of small predaceous marsupials and insectivores.

TYPE AND ONLY SPECIES: *Esteslestes ensis.*

DIAGNOSIS: The new genus is distinctive in having the following combination of characters: Shares with Didelphini the flattened, posteriorly salient hypoconulid in proximity to a much higher entoconid, but differs from recognized Early Tertiary Northern hemisphere Didelphini (*Peratherium, Amphiperatherium, Herpetotherium*) in having a relatively much deeper jaw and a somewhat weaker entoconid notch, and a slightly more labially positioned hypoconulid. Unlike *Herpetotherium* in having a relatively much broader talonid on m3. Like modern Didelphini (*Didelphis*), in having the proportionally deeper jaw and more labially positioned hypoconulid, but unlike this genus in its much smaller size, more trenchant p3 and less expanded m2 precingulid, and less swollen entoconid. Like *Mirandotherium* and *Microbiotherium* (Early Tertiary, South America) in some of the characters noted for Didelphini but differs from these genera in having a more salient and flattened hypoconulid and a broader m3 talonid. Differs from Peradectini (*Peradectes* [including *Nanodelphys*], *Mimoperadectes,* and *Armintodelphys*) in lacking the subequally high, closely twinned hypoconulid-entoconid that forms the lingual shearing wall of the talonid basin. Like Peradectini and Didelphini but unlike the Cretaceous didelphines *Alphadon* and *Albertatherium* in having lower molars with shorter talonids and a cristid obliqua that meets the posterior wall of the trigonid labial to the protocristid notch.

Esteslestes ensis, new species

Table 1, Figures 7, 8

ETYMOLOGY: *ensis,* Latin, a sword.

TYPE AND ONLY SPECIMEN: IGM 3688, left lower ramus with p3, m3–4, roots of m1–2, and fragment of posterior dentary, collected by AMNH field party, 1983.

LOCALITY: "Marsupial Hill" (see fig. 4, appendix 1), Las Tetas de Cabra Formation, Punta Prieta region, Baja California Norte, Mexico. Wasatchian (early Eocene).

DIAGNOSIS: As for genus.

DESCRIPTION: IGM 3688 is a partial left dentary with p3 and m3–4; roots for m1–2 are present. p3 is high and trenchant with a caniniform outline; there is a short heel with a row of three(?) worn cuspules that form a posterolabially trending arc in occlusal view. The main cutting cusp is marked by low vertical ridges along its posterolingual face. There is no cusp anterior to the main cusp.

m3 has a trignoid with a salient, anterolingually positioned, somewhat conical paraconid. The protoconid is broken to the level of the trignoid basin. The metaconid is also damaged; it is separated from the protoconid by a distinct protocristid notch. There is a narrow precingulid that rises obliquely at a high angle up the outer face of the protoconid-paraconid wall. The cristid obliqua joins the posterior trigonid labial to the protocristid notch.

The ectoflexid is well excavated and has within it a distinct ellipitical wear facet. The talonid basin is broad and shallow. The entoconid is the highest talonid cusp, just slightly exceeding the elevation of the hypoconid. Both these cusps are somewhat conical, though the faces that border the talonid basin are planed with wear. By contrast, the hypoconulid is not erect; rather it is worn flat nearly level to the posterior talonid basin and it projects posteriorly to nearly contact the anterior trigonid (prevallid) wall of m4, just labial to its paraconid. The hypoconulid is close and posterolabial to the entoconid, being separated from the latter by a weak notch. There is a very narrow postcingulum that descends obliquely on the posterior hypoconid face.

The above description also applies to m4 except that the talonid is relatively narrower and more elongated, and the entoconid notch is more incised. The hypoconulid, hypoconid, protoconid, and metaconid are badly damaged.

A fragment of the posterior left ramus shows a very deep masseteric fossa but little else.

DISCUSSION: The relationships of this marsupial pose some intriguing problems. The species is most like northern hemisphere (and North African—see Bown and Simons, 1984) members of the didelphine tribe Didelphini. These taxa are distinguished (Setoguchi, 1973; Crochet, 1979; Krishtalka and Stucky, 1983) by features of the hypoconulid and entoconid noted above, as well as features of the upper molars not relevant here. The diverse Peradectini, by contrast, share a condition wherein the more erect hypoconulid is closely twinned with, and nearly as high as (or even higher than—e.g., *Mimoperadectes*), the entoconid, so that in worn molars these cusps nearly merge to form a cutting blade lingual to the talonid basin. This distinction suggests a closer alliance between the Baja form and Didelphini. Nevertheless, ambiguity remains concerning the relative degree of specialization represented by these entoconid-hypoconulid conditions. Krishtalka and Stucky (1983, fig. 6) imply that both conditions are "equally" but divergently derived from some undisclosed condition. This is a critical matter, since there is some variation in talonid structure within the Cretaceous genus *Alphadon* (ibid., pp. 255–256), a taxon excluded by the same authors from either Peradectini or Didelphini. Making the reasonable assumption that the Didelphini hypoconulid condition is, to some degree, specialized, assignment of the Baja species to this tribe seems preferable.

TABLE 1
Dental and Jaw Measurements (in mm) of *Esteslestes ensis*, IGM 3688 (Type), and *Peratherium comstocki*, AMNH 4252 (Type)

Element	Length	Anterior width	Posterior width
IGM 3688 (depth of jaw below m2 (est.) 7.68)			
Lp3	2.59	1.26	1.42
Lm3	3.10	1.66	1.42
Lm4	3.11	1.69	1.49
AMNH 4252 (depth of jaw below m2 4.08)			
Lm2 (broken)	—	—	1.91
Lm3 (broken)	3.26	—	1.79

In addition to these distinctions, there is one remarkable difference between the Baja form and all other Early Tertiary "Holarctic" didelphines; namely, the jaw is much deeper and more robust in the former. For example, the teeth in this species are slightly smaller than those of the type (AMNH 4252) of *Peratherium comstocki* (the largest North American Eocene species of that genus), but the jaw is significantly deeper (table 1). Indeed, the *relative* proportions of the jaw and cheek teeth are more reminiscent of those in modern *Didelphis* (though that genus is overall much larger) than in early Tertiary members of the subfamily. The phylogenetic implications of this unusual condition are unclear, other than suggesting that the Baja form represents a distinct lineage of the Didelphini; a larger sample of the Baja form would provide a more meaningful basis for comparison.

Other features of the lower molar crowns in the Baja form seem somewhat conservative in comparison to those of most Didelphini. The entoconid is less inflated and the entoconid notch less pronounced, although the latter feature must surely be affected by the heavy wear on the molars. The basic argument would be that *Esteslestes* is dentally more primitive than most Didelphini but more derived than the latter in the more robust proportions of the jaw.

Comparisons with South American forms cannot be excluded. *Esteslestes* seems closest to *Mirandotherium* from the Riochican-age fauna of Itaborai, Brazil (see Paulo Couto, 1952; Marshall, 1982), but differs from the latter in its larger size, deeper jaw, more labially positioned hypoconulid, and more obliquely oriented entocristid. Resemblance between the two taxa is nevertheless striking, once again raising the possibility of close relationships among certain early members of the Northern Hemisphere and South American Didelphinae. It is unfortunate that the incomplete material representing the Baja taxon fails to elucidate this question.

Esteslestes ensis is endemic to Baja and not particularly indicative of an age correlation for the Tetas fauna. It is noteworthy, however, that the Didelphini, the tribe that includes this genus, is unrecorded prior to the early Eocene in "Holarctica" (Crochet, 1979; Krishtalka and Stucky, 1983).

INFRACLASS EUTHERIA GILL, 1872

GRANDORDER FERAE (LINNAEUS, 1758) McKENNA, 1975

ORDER INDET.

Table 2, Figure 9

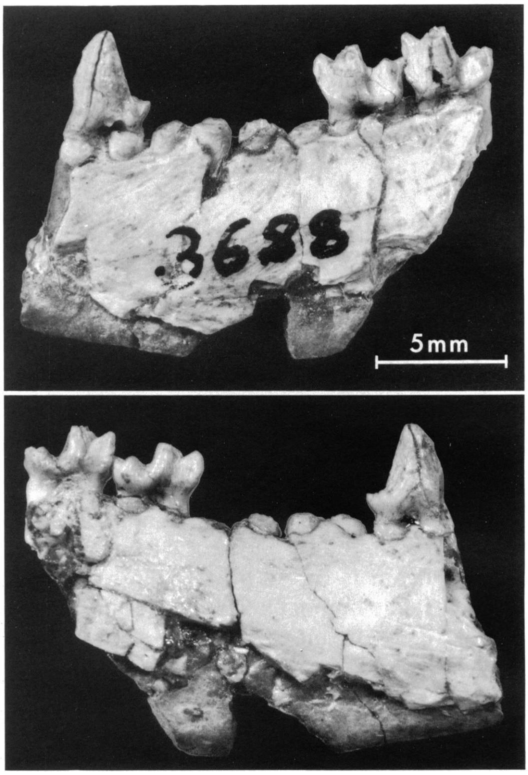

Fig. 7. *Esteslestes ensis*. Labial (above) and lingual (below) views of IGM 3688, left mandible with p3, m3–4.

REFERRED SPECIMEN: IGM-4047, body of a left astragalus lacking the capitulum, collected by Ismael Ferrusquía-Villafranca in 1983.

LOCALITY: Small ravine located some 600 m due west of the western Tetas hill, stratigraphically about 50 to 60 m below its summit. Las Tetas de Cabra Formation, Punta Prieta region, Baja California Norte, Mexico. Wasatchian (Early Eocene).

DESCRIPTION: The specimen is heavily weathered so that the dorsal surface of the trochlea and the sustentacular facet show pitting, and a small part of the medial trochlear ridge is missing. The trochlea is well developed; its medial ridge is larger than the lateral one and shows pitting. The trochlear sulcus is almost complete and well preserved; it narrows anterolaterally and shows the dorsal astragalar foramen (=foramen astragalar superior) in the anterior part. The surface of the sulcus anterior to the foramen is not preserved. Just beyond the end of this surface

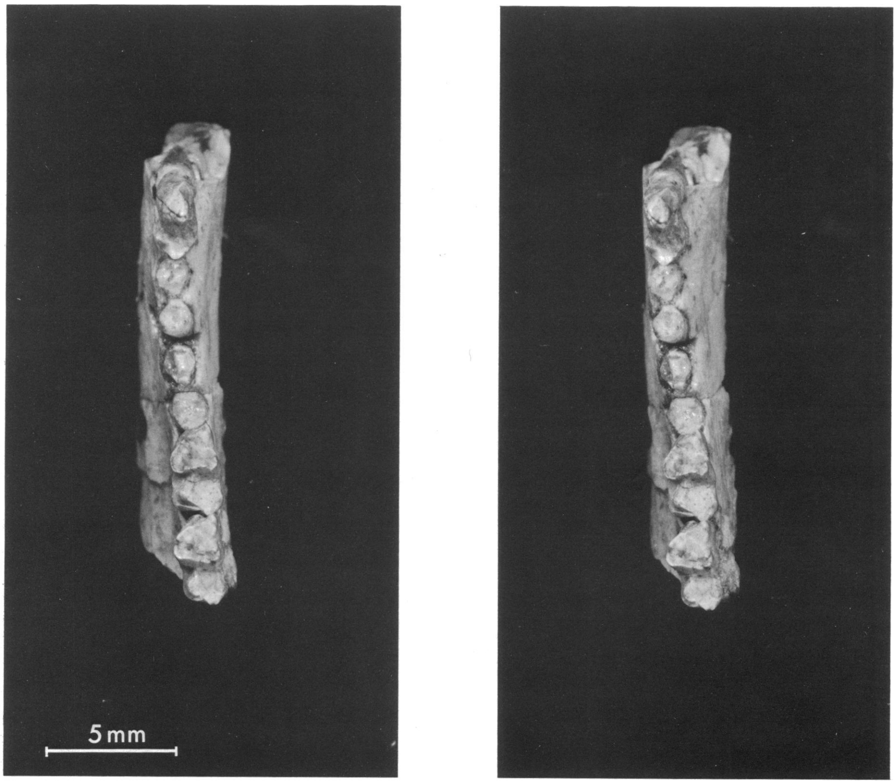

Fig. 8. *Esteslestes ensis.* Stereo pairs of occlusal aspect of IGM 3688, left mandible with p3, m3–4.

there is a shallow fossa, probably corresponding to a small prominence in the internal tibial malleolus.

The lateral wall of the trochlea bears a fibular facet; it is relatively triangular in outline. Its dorsal border is convex, and its posteroventral border is almost straight. A broad sulcus extends the length of this straight part of the border, separating the fibula from the ectal facet in this region. The distal half of the fibular facet border is not preserved.

The plantar surface shows a large, triangular ectal facet (fig. 9B); it is apparently much larger than the sustentacular facet from which it is separated by a wide (astragalar) interarticular sulcus (=sulcus for the calcaneoastragalar interossous ligament). The interarticular sulcus meets the trochlear sulcus at nearly a right angle; near this juncture there is a small ventral astragalar foramen. The sustentacular facet is broken distally; the portion preserved is rectangular. It touches the plantar projection of the internal trochlear condyle.

Medially on the astragalar head, there is a shallow oval depression, the malleolar tibial facet, surrounded by the (medial) trochlear ridge. The medial face of this astragalus is set at an oblique (some 130°) angle to the plantar plane, so that it is mesiodorsally oriented.

The capitulum is missing; the cross section of its base is asymmetrically bilobed, with the medial lobe much larger than the lateral one.

TABLE 2

Measures of IGM 4047 (in mm), Left Astragalus, Referred to Ferae indet.

Anteroposterior length (excluding capitulum)	7.5
Transverse width	7.0
Trochlear-sulcus width	2.3
Interosseal ligament-sulcus	2.3

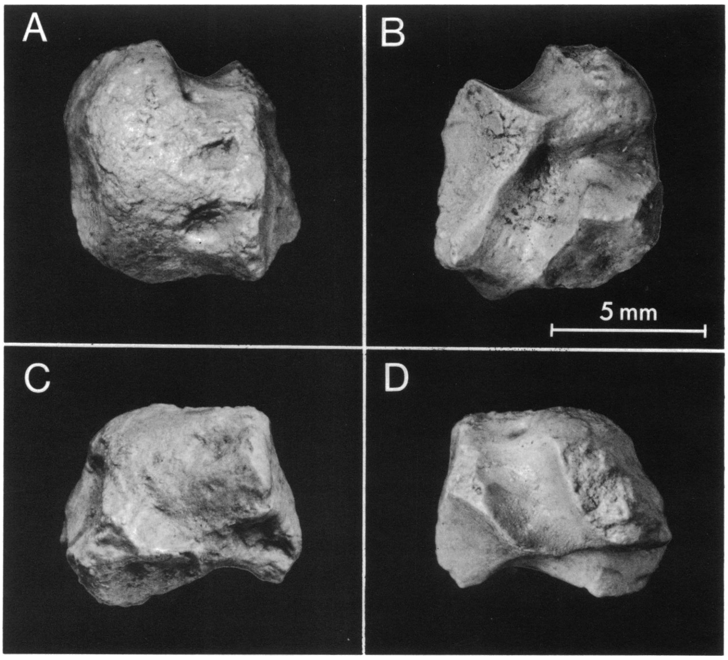

Fig. 9. Ferae indet. (**A**) dorsal, (**B**) plantar, (**C**) anteroventral, (**D**) posterodorsal views of IGM 4047, trochlea of left astragalus.

DISCUSSION: According to Gingerich (1983: 220 et seq.) the astragali of "miacids" are distinctive in having: (1) a relatively flat capitulum; (2) an arched, shallowly grooved trochlear tibial facet that (3) is confluent with a smoothly curved malleolar tibial facet; (4) an astragalar canal perforating the body; and (5) a deep, slightly oblique posterior trochlear groove for the flexor hallucis longus tendon. It should be pointed out, however, that most of these features are also found in creodonts (e.g., *Thinocyon, Limnocyon*) and therefore are not strictly diagnostic of the "miacid" carnivorans.

The specimen IGM-4047 shows four of the above noted five characters (2 to 5); the other (1) is not determinable. Further (table 2), the proportions and morphological features (such as a broad interarticular sulcus, ample contact between the sustentacular facet and the medial trochlear condyle, narrow trochlear sulcus—no wider than the interarticular one—and the relatively small sustentacular and ectal facets) correspond most closely to the ferean (miacid or creodont) astragalar morphology as described or figured by Matthew (1915), MacIntyre (1966), and Gingerich (1983). We assign this specimen conservatively to the Ferae; it is not diagnostic at the ordinal or lower taxonomic levels.

Among the other taxa from the Baja fauna, the identity of IGM-4047 might most likely be confused with those for taxa (e.g., *Hyopsodus, Meniscotherium*) with rather generalized astragali. However, *Hyopsodus* astragali have a wide, flat trochlea without a sulcus (proper), as ascertained from Gazin (1965a: 67 and pl. 12, fig. 8 cf. USNM-23740). *Meniscotherium* astragali differ from those of IGM-4047 in having a trochlear sulcus that is shallow and broad, an ectal facet with a beaklike projection, and a facet for a fibular articulation. The configuration of the sustentacular facet is also different (cf. Gazin, 1965b: 70–72 and pl. 10, figs. 4 and 6, specimens USNM-22918 and 18283, referred to *Meniscotherium robustum*). The general condylarthran morphology of the astragalus is discussed in Cifelli (1983), wherein *Arctocyon* was used as the standard reference in comparisons with South American ungulates. IGM-4047 is clearly different from *Arctocyon* in particular and from the

TABLE 3
Measurements (in mm) for m2-3 in Selected *Prolimnocyon*

	P. atavus	*P. elisabethae*			*P. antiquus*		Baja
	AMNH 16816	AC 2576	AC 4328	USNM 19350	USNM 22452	Mean	IGM 3673
m2 L	6.4	6.6		6.8	7.0	7.73	*5.96
W	4.2	4.0		3.5	4.0	3.78	*3.32
m3 L	2.6		3.3			1.90	3.65
W	1.7		1.8			1.55	*1.94

* Damaged tooth, measurement approximate.

"condylarths" in general. *Wyolestes,* judging from the size of its molars, probably had much larger astragali than IGM 4047, and hence is also ruled out.

ORDER CREDONTA Cope, 1875

FAMILY HYAENODONTIDAE LEIDY, 1869

Prolimnocyon sp. Matthew, 1915

Table 3, Figure 10

Referred Specimen: IGM 3673, a fragmentary right dentary with posterior root of m1, broken m2–3, and the anterior part of the masseteric fossa and ascending ramus. Collected by AMNH field party, 1984.

Locality: East Hill Cairn (see fig. 4, appendix 1), Las Tetas de Cabra Formation, Punta Prieta Region, Baja California Norte, Mexico. Wasatchian (early Eocene).

Description: The preserved portion of the posterior root of m1 is generally circular in outline, and appears to be smaller than the posterior root of m2.

m2 is a robust tooth that is much larger than m3. m2 is anteroposteriorly elongate, and somewhat rectangular in outline. The trigonid, although broken, is longer and wider than the talonid. The anterior border of the trigonid is straight and transverse; there is a broad and well-developed articular facet on the anterior surface of the m2 trigonid, indicating significant contact with the m1 talonid. A very weak anterobuccal cingulum is present at the base of the trigonid. The dorsal and lingual surfaces of the trigonid are broken, but it is clear that the trignoid is much higher than the talonid. There is a slight buccal constriction of the crown at the trignoid/talonid junction. The hypoconid is low and broad; a weak, crenulated cingulum runs lingually from the hypoconid at the posterior talonid margin. There is no distinct hypoconulid. The weak cristid obliqua is broad and runs anteroposteriorly in the center of the talonid; it contacts the posterior trigonid wall buccal to the midline. The hypoflexid slopes steeply, and is excavated by a broad, deep, and rounded wear facet. The lingual margin of the talonid is broken, the posterior margin is transverse, and the buccal margin curves anterobucally from the base of the hypoconid. The posterior margin of the crown slopes steeply anteroventrally to connect to the dorsal margin of the tooth root. There is little or no contact between the m2 talonid and the m3 trigonid. The lingual talonid basin is broad and worn, and slopes gently lingually from the cristid obliqua.

m3 is much smaller than m2, and the m3 trigonid is relatively narrower. It is anteroposteriorly elongate, and ovoid in outline. The trigonid is slightly wider than the talonid, and a buccal constriction is present at the trigonid/talonid junction. The anterior margin of the trigonid is angled anterolingually to posterobucally. Most of the m3 trigonid crown surface is broken. The morphology of the m3 talonid is similar to the m2 talonid, except in m3 the hypoflexid wear facet is not as broad or deeply excavated, the lingual talonid basin is more heavily worn and more steeply lingually sloping, there is no posterior talonid cingulum, and the posterior margin of the tooth is more rounded. m3 is double rooted and relatively large.

The dentary is transversely narrow, ovoid in cross section, and moderately deep below the molars. The masseteric fossa is moderately deeply excavated. Two small foramina are present at the anterior margin of the masseteric fossa and a small foramen is presently slightly posterior to m3 on the dorsal surface of the ramus. The ascending ramus is robust.

Size measurements for species of *Prolimnocyon* are given in table 3.

DISCUSSION: IGM 3673 is clearly referable to *Prolimnocyon,* as it differs significantly from Carnivora, and from all other Creodonta. In comparison to primitive Carnivora (caniform "miacines") in the Baja specimen: the m2–3 trigonids are relatively much larger, and more robust, and longer anteroposteriorly, and, what is preserved of the trigonid-Vs suggests a more open outline; the m2–3 talonid basins are less well developed and the cristid obliqua are more central; m3 is relatively more elongate anteroposteriorly and narrower; and the posterior root of m1 is much smaller than that of caniforms. The primitive caniform *Oodectes* is much smaller, has a more oblique cristid obliqua and better developed talonid basins on m2–3, the talonid and total length of m2 is relatively much smaller, and m3 is more triangular in outline (talonid narrower and triangular) than IGM 3673. If one hypothesizes that the teeth in the Baja specimens are m1–2 rather than m2–3, IGM 3673 lacks the derived enlargement of the "m2" hypoconulid; lacks distinct talonid cusps; and has larger trigonids, a more central cristid obliqua, and less well-developed talonid basins than in early Cenozoic feliform Carnivora ("viverravines").

The last molar (either m3 primitively, or m2 in the Creodonta [Oxyaenidae] that lose m3) is large in all Creodonta, except *Prolimnocyon* and *Galecyon* (see Gingerich and Deutsch, 1989). In *Prolimnocyon* m3 is much smaller than m2 and the m3 trigonids are greatly reduced relative to those in m2. In all other creodonts the trigonid of the last molar is very large and robust, and the last molar is similar in size or larger than the preceding molar. IGM 3673 differs from oxyaenids, as in the Oxyaenidae m3 is lost, m2 is typically extremely large, molar trigonids are much more deeply basined and narrower, molar trigonid-Vs are more open and the paralophids are aligned more anteroposteriorly, molar trigonids are relatively much broader, the teeth are much more robust and bulbous, and the enamel generally is crenulated.

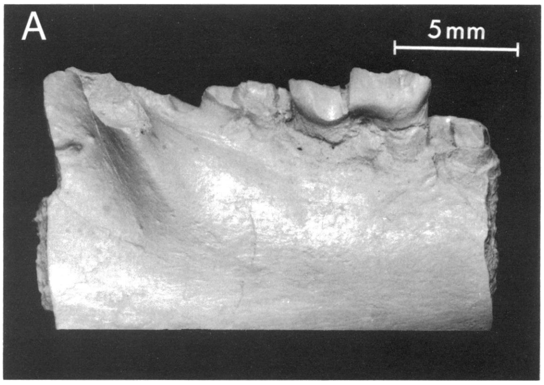

Fig. 10. *Prolimnocyon* sp. **(A)** lateral view, **(B)** stereo pairs of occlusal aspect of IGM 3673, right dentary with part of m1, m2–3.

In comparison to all other hyaenodontids that retain an m3 (e.g., *Hyaenodon, Proviverra, Prototomus, Tritemnodon,* etc.), IGM 3673 has a much smaller m3, which in these other hyaenodontids (proviverrins and hyaenodontines) is equal to, or greater than m2 in size. Several other hyaenodontids (e.g., limnocyonines *Limnocyon* and *Thinocyon*) can be distinguished from IGM 3673 in their loss of m3, although m2 in these taxa and in IGM 3673 is similar in morphology (as well as size, in *Thinocyon*). In any case, the last molar in these taxa is much larger than the last molar in IGM 3673.

The Baja *Prolimnocyon* is most similar in size (see table 3) and morphology to *P. atavus* from the "Greybull" of the Big Horn Basin, Wyoming (see Gazin, 1962; Guthrie, 1967, 1971). In particular, the depth and shape of the ramus, the development of the cristid obliqua, the m2 trigonid shape, and the m3 shape and crown morphology are very similar in *P. atavus* and IGM 3673. *P. elisabethae* and *P. antiquus* have slightly larger m2s and smaller m3s than does IGM 3673. The Baja specimen differs from all other *Prolimnocyon* in its shallower lingual talonid basin on m2–3, more deeply excavated m2–3 hypoflexid, straight transverse anterior and posterior borders of the m2 crown, and larger m3. IGM 3673 is much larger than *P. iudei* (*Oödectes iudei* in

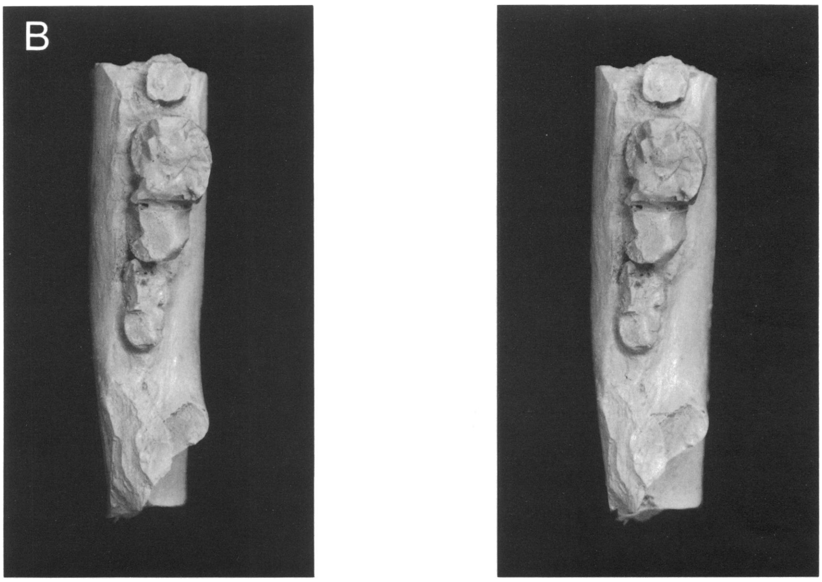

Fig. 10. Continued.

Gingerich and Deutsch, 1989: 330) from the Lysite Member, Wind River Formation, Wyoming (Guthrie, 1967), although m3 in *O.* (*P.*) *iudei* is relatively slightly larger than in IGM 3673. *O.* (*P.*) *iudei* also differs from all other *Prolimnocyon* in the constriction of the m2–3 talonid, and the relatively large size of m3. The m3 of IGM 3673 is larger and better developed than in all other *Prolimnocyon,* other than *O.* (*P.*) *iudei.* Many specimens of *Prolimnocyon* have a greatly reduced single-rooted m3.

FAMILY OXYAENIDAE COPE, 1877

?*Oxyaena* Cope, 1874
cf. *Oxyaena* sp.
Table 4, Figure 11

REFERRED SPECIMEN: IGM 4051, left p3, collected by IGM–University of Michigan field party in 1983.

LOCALITY: A small ravine, some 450 m south of the southeastern Tetas Butte, stratigraphically about 50 m below its summit. Las Tetas de Cabra Formation, Punta Prieta region, Baja California Norte, Mexico. Wasatchian (early Eocene).

DESCRIPTION: The tooth is trenchant, with a prominent, tuberculo-sectorial protoconid whose anterior border is slightly convex and the posterior one gently concave, thus conferring a triangular outline to the tooth, with the apex turned slightly posteriorly. Unlike other oxyaenids, *Oxyaena* shows a paraconid (albeit small), which is located more lingually than the protoconid. The metaconid is low and blunt, larger than the paraconid. The tooth is ovoid in cross section, elongated anteroposteriorly, and its labial side is gently concave. The lingual side is nearly straight. The roots are not preserved.

The anatomical identification of IGM 4051 as p3 is justified on the following grounds: p4 is larger (in oxyaenids) and has a large, high metaconid (separated from the protoconid by a deep, narrow cleft), and a less oblique (nearly vertical) posterior margin of the protoconid than p3 (cf. Matthew, 1915, figs. 44, 46, 48, 49; Rose, 1981, figs. 55–57).

DISCUSSION: In size (table 4) and morphology, IGM 4051 is a typical oxyaenid p3, corresponding best to *Oxyaena* and *Dipsalidictis.* The differences between these genera are very slight (cf. Denison, 1938; Simpson, 1945; Van Valen, 1966; Bown, 1979), and their diagnoses do not involve p3 (Cope, 1874; Jepsen, 1930; Denison, 1938). However, Bown (1979: 87) mentioned that *Dipsalidictis*

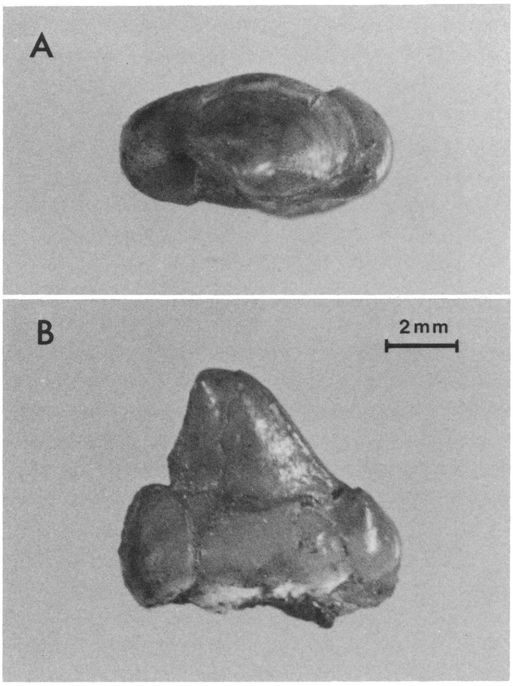

Fig. 11. *Oxyaena* sp. **(A)** occlusal, **(B)** labial views of IGM 4051, left p3.

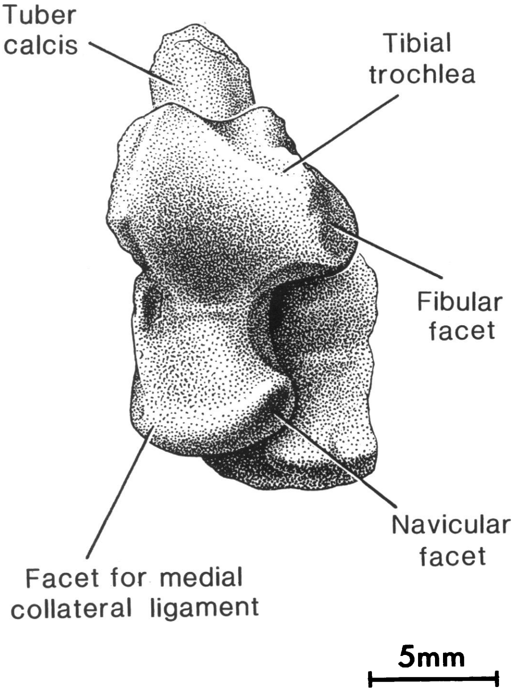

Fig. 12. *Hyopsodus* sp. Anterodorsal view of IGM 3674, left calcaneum and astragalus.

differs from *Oxyaena* in having relatively more slender p3–4 with more trenchant protoconids. Bown (1979) provides measurements for p3 (length = 7.4 mm, width = 3.8 mm) that are slightly smaller than those of IGM 4051. On these criteria, the Baja specimen is closer to *Oxyaena*. Therefore, the tooth is tentatively assigned to *Oxyaena*, the most common member of the family in North America.

The specific allocation of the Baja specimen is not possible because p3 is not involved in the diagnosis of the various *Oxyaena* species. Moreover, IGM 4051 shows a well-defined (albeit small) spur anterior to the protoconid (interpreted as a paraconid) that is not present in other species of *Oxyaena* (Matthew, 1915; Rose, 1981; 104, et seq.). In this regard, p3 in IGM 4051 approaches the morphology of p4 more closely than in any known species of *Oxyaena* and resembles PU 17846, the holotype of *Dipsalodon churchillorum*, and UM 71172, referred by Rose (1981) to cf. *Dipsalodon* ?undescribed species. Unlike most specimens referred to *Oxyaena*, IGM 4051 does not show enamel pitting or corrugation. The significance of such a feature is, however, moot.

The differences noted above suggest that IGM 4051 may represent a new species, but the material is too fragmentary for a formal designation.

ORDER CONDYLARTHRA COPE, 1881a

FAMILY HYOPSODONTIDAE LYDEKKER, 1889

Hyopsodus Leidy, 1870

cf. *Hyopsodus* sp.

Figure 12

REFERRED SPECIMEN: IGM 3674, partial skeleton, consisting of associated hind limb elements, pelvis, axial skeleton, and left proximal calcaneum and astragalus. Collected by AMNH field party, 1983.

LOCALITY: Windy Gap (see fig. 4, appendix 1), Las Tetas de Cabra Formation. Punta Prieta region, Baja California Norte, Mexico. Wasatchian (early Eocene).

TABLE 4
p3 Measurments (in mm) of Specimens Referred to *Oxyaena* and *Palaeonictis* Species[a]

Taxon	Anteroposterior length	Transverse width
IGM 4051 referred cf. *Oxyaena* sp.	8.1	4.0
UM 69331, type of *O. transiens*	8.0	5.0
AMNH 15857, type of *O. platypus*	7.0 alv	3.6 alv
PU 21215, referred to *O. platypus*	6.0	3.4
UM 7615, referred to *O. platypus*	7.4 alv	4.0 alv
UM 74144, referred to *O. gulo*	7.7	5.0
UM 821145, referred to *O. gulo*	9.0 e	4.7 e
UM 76920, referred to *O. aequidens*	9.8	6.3
UM 76929, referred to *O. intermedia*	10.0 e	5.4
UM 74558, referred to *O. forcipata*	11.2 a	5.6 a
UM 77221, referred to *Paleonictis occidentalis*	13.3	8.7

[a] a, measured at alveolus; alv, alveolus only; e, estimate.

DISCUSSION: This skeleton is badly weathered, fragmented, and incomplete. The skull, pectoral girdle, and forelimb are missing. Nevertheless, the astragalus and calcaneum are strongly similar to those of *Hyopsodus walcottianus* (AMNH 14654) from Alkali Creek, Wind River Formation of Wasatchian age. The specimens are virtually the same size and proportions and cannot be distinguished qualitatively, except that the astragalar neck is slightly more flared distally in the Baja specimen. The badly weathered bone surface of IGM 3674 impedes closer comparison.

The Baja tarsus is clearly not referable to *Hyracotherium*. It does not show the elongate, deeply grooved, spoollike astragalar trochlea of the latter, nor does it have the distinctly concave naviculo-astragalar facet typical of *Hyracotherium* and other equids.

IGM 3674 does not seem referable to the small *Meniscotherium* species from the Baja assemblage because the astragalus lacks the distinctive swelling of the lateral trochlear ridge and very broad, deeply concave and semi-rectangular ectal facet characteristic of *Meniscotherium*. IGM 3674 is easily distinguished from the tarsus of *Esthonyx* by its much smaller size and more elongate trochlea on the astragalus. IGM 3674 differs from the tarsus of creodonts in having a less elongate medial malleolar facet and a sustentacular facet distinctly isolated from the (distal) navicular facet. The specimen is too small to be assigned to *Wyolestes*.

This partial skeleton may belong to a primitive hyopsodontid poorly known from skeletal anatomy. The resemblance to *Hyopsodus* is, however, so strong that we favor this identification for the Baja tarsus and associated skeleton.

FAMILY PHENACODONTIDAE COPE, 1881a

GENUS *ECTOCION* COPE, 1882a

Ectocion ignotum, new species

Table 5, Figure 13

ETYMOLOGY: *ignot,* Latin, unknown, ignored.

HOLOTYPE: IGM 3675, maxillary fragment with left P2–4, partial M1, and worn M2–3; right crown of partial M1, M2, and M3, and associated bone fragments. Collected by AMNH field party, 1984.

LOCALITY: Manly Man locality in Las Tetas de Cabra Formation. Punta Prieta region, Baja California Norte, Mexico. Wasatchian (early Eocene).

TABLE 5
Measurements of Cheek Teeth (in mm) of *Ectocion ignotum* Holotype IGM 3675

Specimen element	Length	Anterior width	Posterior width
LP2	5.77	4.15*	—
LP3	7.42	7.39*	—
LP4	7.35	8.59	—
LM2 (est.)	8.15	11.09	9.64
LM3 (est.)	7.50	—	—
RM2	8.33	10.83	9.99
RM3	7.52	—	—

* Maximum width.

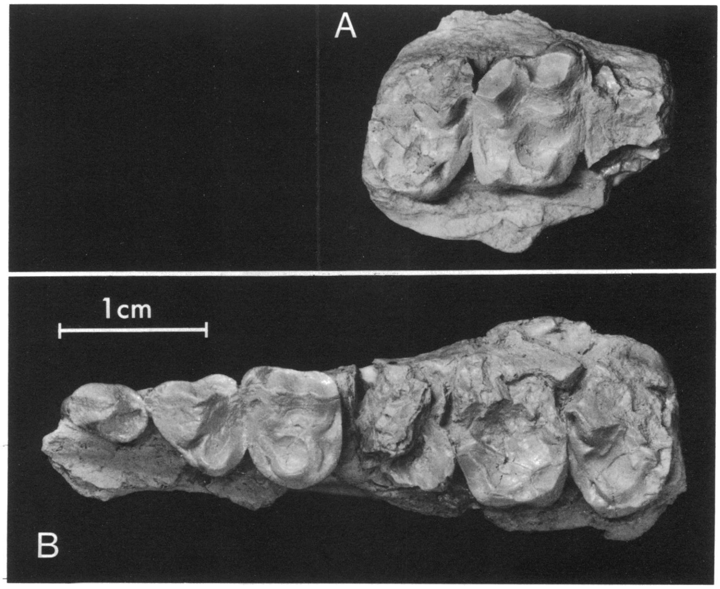

Fig. 13. *Ectocion ignotum* n. sp. Occlusal views of **(A)** fragment of right M1, M2–3 (above), and **(B)** left P2–4, partial M1, M2–3; both referable to holotype IGM 3675.

DIAGNOSIS: Phenacodontid distinguished by strong development of the mesostyle and prominent ectoloph on M2. Differs from *Phenacodus* in the above features and in having less bulbous, conical cusps, a metaconule anterior (rather than aligned or posterior) to the axis between the hypocone and the metacone, M3 with a postcingulum instead of a well-developed hypocone, and P3 with a more projecting parastylar region. Significantly larger than all other species of *Ectocion* except *E. superstes.* Upper dentition differs from that of other *Ectocion* (including specimens referred to *E. superstes,* see comments below) in the strong mesostyle, flat (rather than convex) labial surfaces of M2 metacone and paracone, anteroposteriorly broader M1–3, and less crenulated pre- and postcingula on M2–3. Unlike *Prosthecion* in having a P3 with a more projecting parastylar region, a less distinctly isolated metacone, and a cingulum that is not continuous around the lingual base of the protocone. Differs from *Desmatoclaenus* and *Tetraclaenodon* in those characters noted above for *Phenacodus.*

DESCRIPTION: The left maxillary fragment of IGM 3675 preserves P3 through M3. However, M1 is essentially destroyed and M2 badly broken. The remaining teeth show heavy wear or partial breakage (M3). M2 from the right maxillary fragment is the least damaged of the molars, but it too shows heavy wear.

P2 is double rooted. The crown is oval in outline with a large anterior cusp and a short posterior heel. A distinct ridge runs from the apex of the main cusp to the apex of the heel. The lingual side of this ridge is excavated as a shallow basin.

P3 is three-rooted and triangular in outline. The parastylar area is well developed and transversely broadened. The protocone is shifted somewhat posteriorly rather than centrally aligned with the labial cusps. The protocone, though badly worn, is well developed and swollen or bulbous in form. Both a paracone and metacone were probably present as indicated by slight convexities along the labial margin of the crown. These cusps were likely in close apposition, although wear in this area of the tooth is extreme. There is no evidence of conules. The weak pre- and postcingula are not continuous around the base of the protocone. The stylar shelf is extremely narrow and the labial border shows a slight inflexion.

P4 is semimolariform with a well-developed metacone, paracone, and protocone. Para- and metaconules are weakly preserved. The parastyle is well developed and connected via a prominent ridge to the paracone. The pre- and postcingula are well developed but do not merge lingual to the base of the protocone. There is no evidence of a hypocone.

The right M2 shows the most detail of any preserved upper molar. The tooth is semirectangular with a parastyle that projects anterolabially. The metacone and protocone are joined by a distinct W-shaped ectoloph formed by prominent ridges. There is a well-developed mesostyle. The labial faces of the paracone and metacone are flattened rather than convex outward. The paraconule and metaconule are heavily worn, and situated labially, near the base of the paracone and metacone, respectively. The paraconule is aligned slightly anterior to the position of the protocone apex. The precingulum is weak, but the postcingulum is strong with a well-developed hypocone. The metaconule is located opposite a point between the hypocone and protocone. The cusp thus is anterior to the transverse axis between the metacone and hypocone. An extensive wear facet joins the apices of the protocone, hypocone, and metaconule.

M3 has a somewhat heart-shaped crown. The labial region on both right and left M3 is badly damaged, although the teeth appear to have a prominent ectoloph as in M2. There are well-developed conules and lingual cingula. The hypocone, if present, has been obliterated by wear, although the postcingulum is extensive enough to accommodate a hypocone. There is also a slight rise on the postcingulum just posterolingual to the metaconule.

DISCUSSION: Despite the heavy wear and damage to the holotype, recognition of this species is warranted. The new species seems most closely comparable to other species of *Ectocion*. However, the differences cited in the above diagnosis seem sufficient to keep *E. ignotum* apart, as these differences pertain to all species with upper dentitions referable to *Ectocion*. The Baja form also exceeds the upper size limits previously described for *Ectocion* (see West, 1976: fig. 38). In shape as well there is a distinct difference. The molars of *E. ignotum* are proportionally more elongate anteroposteriorly. This is well illustrated by comparisons with upper dentitions (AMNH 15325) referred to *Ectocion superstes*[2] by Granger (1915: 353). The right M2 of this specimen is closely similar to that tooth in *E. ignotum* with respect to maximum width (10.90 and 10.83 mm, respectively), but is significantly shorter anteroposteriorly than the Baja form (7.37 and 8.33 mm, respectively).

The above distinctions seem valid in spite of the rather vague concept of *Ectocion* as a generalized "small phenacodont" (see diagnosis in West, 1976: 46). The Baja species is larger than the Paleocene *E. collinus* (=*E. montanensis,* see Gingerich, 1982: 489) and *E. wyomingensis,* where values for mean length of M2 are 6.71 and 6.45 mm, respectively (see West, 1976: tables 19, 20). *Ectocion ignotum* is also notably larger than the late Paleocene, early Eocene *E. osbornianus* Cope, 1882a, and the much smaller *E. parvus* (known from a jaw with m1–3). *E. osbornianus* is known by large samples from the Polecat Bench area and Willwood Formation that show mean M2 lengths of 6.61 and 6.67 mm, respectively (West, 1976: tables 22, 23). Although a few individuals from the early Wasatchian approach the Baja species in M2 dimensions (West, 1976: fig. 38) only the upper dentition originally referred to *E. superstes* is, as noted above, comparable in transverse width (but not in anteroposterior length). Qualitative differences given in the above diagnosis also distinguish *E. ignotum* from *Prosthecion.*

Separation of *Ectocion ignotum* from *Phenacodus, Desmatoclaenus,* and *Tetraclaenodon* is more obvious, as the former lacks the swollen molar cusps and the large M3 hypocone characteristic of the latter three taxa, and has a more salient mesostyle and ectoloph. The mesostyle-ectoloph pattern in *Ectocion ignotum* is, in fact, reminiscent of *Meniscotherium.* However, the development of these structures as well as the selenodont loph pattern is much more pronounced in

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[2] The status of *Ectocion superstes* remains problematic. There is valid concern that the type lower jaw (AMNH 233A) may be an aberrant individual of *Phenacodus vortmani* (McKenna, 1960: 102; Guthrie, 1971: 81). Moreover, West (1976: 58) placed dentitions of AMNH 15324 and 15325 within *Ectocion osbornianus.* Nonetheless, the upper dentition (15325) compared above seems aberrantly large for *E. osbornianus* whether or not it is referable to the species.

TABLE 6
m2 Measurements (in mm) (observed range) of *Phenacodus* and *Ectocion* Species and Selected Specimens*

	Total length	Trigonid length	Trigonid width	Talonid length	Talonid width
Ph. matthewi	7.2–7.8	–	6.6–6.8	–	–
Ph bisonensis	9.2–9.7	–	7.2–8.1	–	7.1–7.9
Ph. grangeri	10.4–11.0	–	8.4–10.4	–	8.4–11.0
	11.6–12.4	–	9.4–10.6	–	9.3–10.1
Ph. brachypternus	6.4–7.3	–	5.0–6.1	–	4.4–6.0
Ph. vortmani	7.4–10.7	–	6.2–9.2	–	5.4–8.8
Ph. primaevus	10.4–15.9	–	9.1–13.9	–	8.7–13.3
E. montanensis	6.8–7.3	–	5.6–6.4	–	5.3–5.8
E. wyomingensis	5.8–7.2	–	4.6–5.7	–	4.2–5.5
E. osbornianum	5.7–8.0	–	4.5–6.6	–	4.3–6.1
IGM 4034, *Ph.* cf. *vortmani*	9.4	4.0	6.1	5.4	5.3
UM 74602, *Ph. ?brachypternus*	7.3	4.0	5.9	3.3	5.9
UM 76269, *Phenacodus* sp.	9.4	5.4	8.0	4.0	6.2 (a)
UM 761274, *Phenacodus* sp.	8.9	4.8	7.8	3.0	7.3
UM 76945, *Phenacodus* sp.	11.9	5.0	10.0	6.9	10.0
UM 76176, *Phenacodus* sp.	7.0	3.8	6.0	3.2	5.5
UM 75723, *Ectocion* sp.	7.0	3.6	6.0	3.4	5.6

* Observed range data from West, 1976.

Meniscotherium. The crown of M3 of *Meniscotherium*, with its vaguely triangular outline and centrally positioned protocone, is not at all like the M3 of *E. ignotum*. Nonetheless, the "*Meniscotherium*-like tendencies" of the Baja taxon are intriguing in light of Cope's (1882a) original suggestions for a close relationship between phenacodontids and meniscotheriids.

Phenacodus Cope, 1873a
Phenacodus cf. *P. vortmani* (Cope, 1880)

Table 6, Figure 14

REFERRED SPECIMEN: IGM 4034, left dentary fragment bearing m3, collected by the late Mr. Margarito Alvarez-Montes, a member of IGM field party, 1976. Mr. Alvarez-Montes was a preparator at the Instituto de Geologia.

LOCALITY: A small ravine located midway between the Tetas Buttes, stratigraphically about 40 m below the summit of the eastern butte. Las Tetas de Cabra Formation. Punta Prieta region, Baja California Norte, Mexico. Wasatchian (early Eocene).

DESCRIPTION: This posterior jaw fragment is badly damaged and its ventral edge is entirely missing. m3 is abraded and the anterolingual portion of the trigonid and the posterolingual part of the talonid are missing. The trigonid is relatively low and slightly wider (transversely) than the talonid; the paraconid, paracristid, and trigonid basin are missing, but what remains of the tooth suggests that the paracristid extended to the anterolingual corner and then curved (?sharply) posteriorly, thus partly closing the trigonid basin. However, the para- and metaconid must have been relatively separated. The protocristid is nearly complete and meets the anteroposterior axis at an angle of 72°. The hypoflexid is wide and deep, and the talonid has a wide basin that opens lingually through a large sulcus located behind the metaconid. The cristid obliqua is relatively short and gently curved. The postcristid is straight and the entocristid is very weak. Part of the postcristid is broken, so that the presence of a hypoconulid cannot be determined. Only a weak precingulid is present (no other cingulids are discernible). Finally, it should be noted that the tooth was abraded more heavily lingually, since the enamel on the labial wall is higher than on the lingual one. Judging by the wear, the specimen belonged to a mature individual.

DISCUSSION: IGM 4034 clearly resembles m3s of *Ectocion* and *Phenacodus,* showing stronger similarities to the latter. *Ectocion* has the following m3 features that distinguish it from *Phenacodus*: It is less elongated (hence its length/width ratio is smaller), the talonid is nearly as long as the trigonid, and there is a faint ectocingulid and a well-developed shelf at the base of the hypoflexid. IGM 4034 does not show these features, and it is slightly larger than *Ectocion osbornianus,* the larger of the more common *Ectocion* species (see remarks above regarding *Ectocion superstes*). IGM 4034 lies within the lower size range of *Phenacodus vortmani* (cf. West, 1976: tables 22, 23; Bown, 1979: table 30; Rose, 1981: tables 19, 20). Bown (1979) noted the difficulties of identifying the intergrading morphs of *Phenacodus,* even when large, stratigraphically controlled samples were available. Reference of IGM 4034 to *P. vortmani* is therefore tentative.

FAMILY MENISCOTHERIIDAE
COPE, 1882b

Meniscotherium Cope, 1874
Meniscotherium cf. *priscum*
(Granger, 1915)

Table 7, Figures 15, 16, 17

REFERRED MATERIAL: IGM 3676, right maxillary fragment with M2–3, broken crown base of M1, left maxillary fragment with (badly damaged) M1, M2, anterolabial crown base of M3; right and left m3, isolated postcranial skeletal fragments. IGM 3677, right maxillary fragment with damaged P4, M1–2, crown base of M3. IGM 3678, left maxillary fragment with partial M1, complete M2. IGM 3679, left M3. IGM 3680, partial right M2? IGM 3681, associated fragments of dentaries and maxillaries with tooth roots and damaged crowns; collected by AMNH field parties, 1983–1985. IGM 4035, right dentary fragment with m1–2; collected by IGM field party, 1976.

LOCALITIES: Danger Bird Quarry (IGM 3678, 3680), Quieter West (IGM 3677, 3679, 3681), Lil' Buddy (IGM 3676), Ferrusquia Locality D (IGM 4035). Las Tetas de Cabra Formation. Punta Prieta region, Baja California Norte, Mexico. Wasatchian (early Eocene).

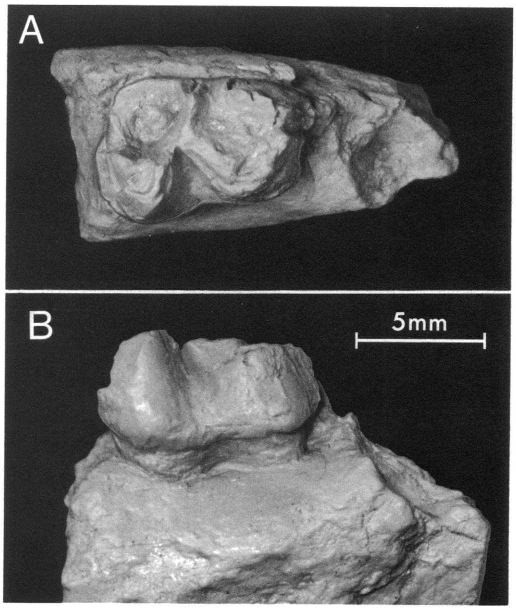


Fig. 14. *Phenacodus* cf. *vortmani.* (**A**) occlusal and (**B**) lateral views of IGM 4034, left dentary fragment with m3.

DESCRIPTION: The above hypodigm is largely a series of maxillary fragments with molars. Only in IGM 3677 is there a partial P4. This tooth is broken badly in its labial region and only the faces of the paracone and metacone are preserved. These faces drop steeply into the deep clefts labial to the conules. Both the paraconule and metaconule are prominent with crescent-shaped wear facets. There appears to be a "twinning" of two small cusps on the apex of the metaconule (as in *Meniscotherium chamense*). The apex of the swollen, very large protocone lies on an axis directly between the paraconule and metaconule. The protocone shows little wear so it is not joined to the conules by a large wear facet, as is common in older individuals of *M. chamense.* A small shelf (precingulum?) lies at the foot of the anteriorly concave wall joining the protocone and the paraconule. There is a rise on this shelf that forms a small cuspule. The posterolingual corner of the crown is badly damaged. No other premolars are preserved in this specimen or other *Meniscotherium* specimens from the Baja locality.

M1, best preserved in IGM 3678, has the strong crescentic ectoloph characteristic of this taxon. Unfortunately, the labial region

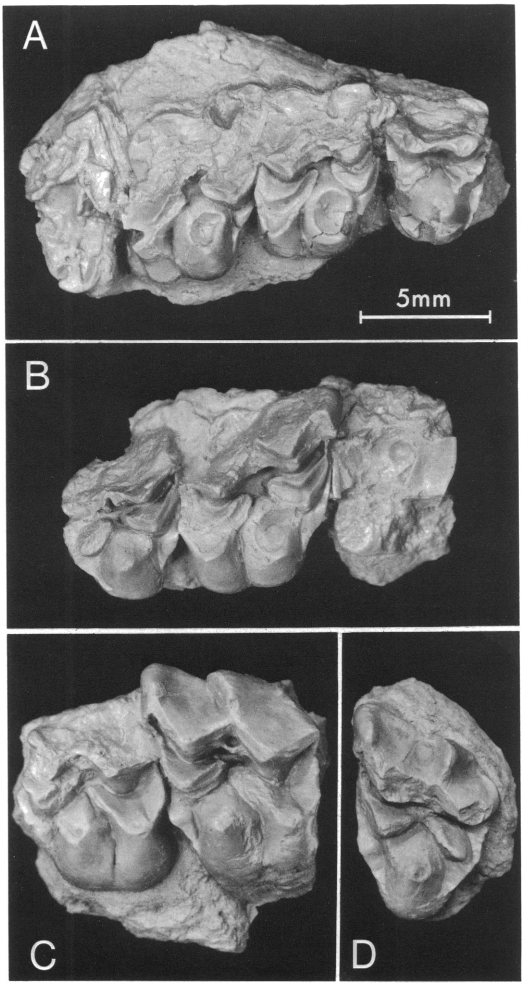


Fig. 15. *Meniscotherium* cf. *priscum*. Occlusal views of **(A)** IGM 3677, right maxillary fragment with P4, M–12, crown base of M3. **(B)** IGM 3676, right maxillary fragment with fragmentary crown base of M1, M2–3. **(C)** IGM 3678, left maxillary fragment with partial M1, complete M2. **(D)** IGM 3679, left M3.

of this tooth in both IGM 3678 and 3677 is badly damaged. In the latter specimen the outline remaining at the base of the crown shows that M1 has a weaker parastylar spur than does M2. The paraconule on M1 is very prominent with a strong V-shaped wear facet. The apex of this cuspule lies on the axis well anterior to the apex of the protocone. At early stages of wear (IGM 3678) the metaconule is separated from the protocone by a very deep obliquely trending cleft. By contrast, the metaconule, if present at all, is indicated only by a swelling on the anterolabial trending crest that leads from the hypocone. In later stages of wear (IGM 3677), a large, confluent facet joins the "metaconule" with the apex of the hypocone. The "metaconule" lies on a transverse axis nearly between the apices of the protocone and hypocone.

The protocone is, as in P4, a large swollen bulbous cusp that wears to very low relief with a distinctive circular wear facet (IGM 3677). In less worn specimens the precingulum at the foot of the protocone-paraconule wall develops a cuspule that is somewhat larger than that in P4. The hypocone shows extreme development, being as robust and even slightly higher than the protocone. Two prominent crests flare labially from the apex of the hypocone. These mark the boundaries of a broad V-shaped depression that floors the lingual wall of the metacone. The wear pattern on the hypocone (seen in IGM 3677) differs from that of the protocone, as the former shows the V-shaped wear facet noted above.

M2 resembles M1 in most of the above features except that the tooth is somewhat more transversely broad and anteroposteriorly narrow, with a stronger parastylar spur and a somewhat larger cusp on the precingulum. In addition, the labial region of M2 is well preserved in several specimens. In these we observe the distinctive, deep bicrescentric ectoloph and the indented, flattened walls of the labial paracone and metacone. The mesostyle is also very prominent and it protrudes labially nearly as far as the parastyle. The crest leading to the mesostyle shows a strong, anteriorly concave curvature. Similarly, a strong curved buttress sweeps down the labial face of the crown from the apex of the mesostyle. Accordingly, the labial crown is distinguished by two prominent (parastylar and mesostylar) vertical ribs and a much weaker crest leading from the metastyle to the posterolabial corner of the tooth. Worn M2s (IGM 3676, 3677) show the wear pattern described above for M1 except that the circular wear facet on the protocone is somewhat smaller.

M3 shares with the more anterior molars the strong bicrescentric ectoloph, salient mesostyle, and well-developed paraconule and

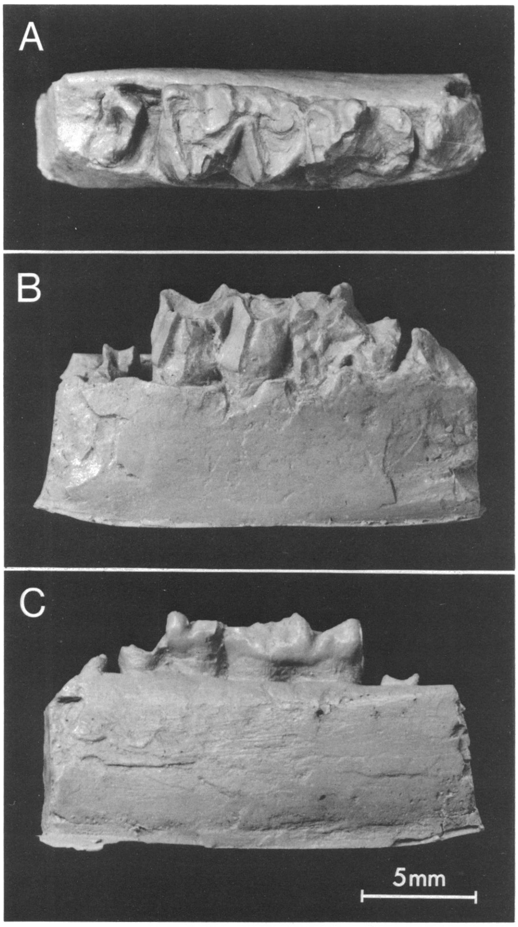


Fig. 16. *Meniscotherium* cf. *priscum.* **(A)** occlusal, **(B)** lateral, **(C)** lingual views of IGM 4035, right dentary with m1–2.

protocone. In addition, M3 is distinctive for its complete lack of a hypocone, lending to the crown a vaguely triangular outline. There is also a large, elongate metaconule, well isolated from the protocone by an oblique furrow and a distinct postcingulum that rises from the base of the protocone to the metaconule. The best preserved M3 (IGM 3679) shows little wear. In IGM 3676 the degree of wear on (the partial) M3 is exceeded by that in M2; the protocone retains a blunt apex, whereas this cusp in M2 shows a characteristic circular facet noted above.

Lower teeth of *Meniscotherium* from the Baja fauna are poorly represented. A jaw fragment with a posterior root of p4, heavily worn and damaged m1–2, and an anterior root of m3 (IGM 4035) has the following characteristics: m1 is severely damaged with only the posterolingual corner of the talonid preserved. A small metastylid is adjacent to the damaged metaconid. m2 is, by estimate, anteroposteriorly longer and transversely wider than m1. The crests of the trigonid and talonid show the characteristic selenodont pattern, although the crowns are heavily worn and the cristids are not prominent. A heavily worn metastylid is present. Damage to the tooth is most pronounced in the region of the protoconid and hypoconid. The hypoflexid is very deep, as the cristid obliqua contacts the posterior trigonid crest (protocristid) in the region of the metaconid. The talonid has a well-developed entoconid but no distinct hypoconulid; the hypoconid is damaged. There is a small cuspule (entoconulid?) on the anterolingual wall of the entoconid. The cuspule lies just posterior to a well-developed lingual basin that separates the metaconid and entoconid.

Both right and left m3s are well preserved as isolated teeth in IGM 3676. These show the strongly selenodont crests of the trigonid and talonid noted above for m2. The paracristid is strongly curved with a posterior deflection in its lingual region. The metaconid is easily the highest cusp of the crown, whereas the protoconid is worn level to an extensive wear facet. There is no rise on the paracristid to indicate the presence of a paraconid. As in m1–2, the hypoflexid is very deep and narrow, ending directly at the labial face of the metaconid. As a result the cristid obliqua is sharply angled and leads to the ridge just posterior to the metaconid apex. The posterior talonid crest (postcristid) is also strongly oblique, and the talonid is broadly open lingually, contributing to the crescentic outline of the crests in this portion of the crown. The hypoconid is not well differentiated from the wear facet comprising the talonid crests, but the entoconid shows a distinct rise, nearly equaling the height of the metaconid-cristid obliqua junction. As in other species of *Meniscotherium,* there is no hypoconulid. There is a distinct, but small metastylid at the back of the metaconid and just anterior to the notch outlet of the talonid basin. This notch is bordered by an even smaller cuspule (an entoconulid?) that is developed at the base of the

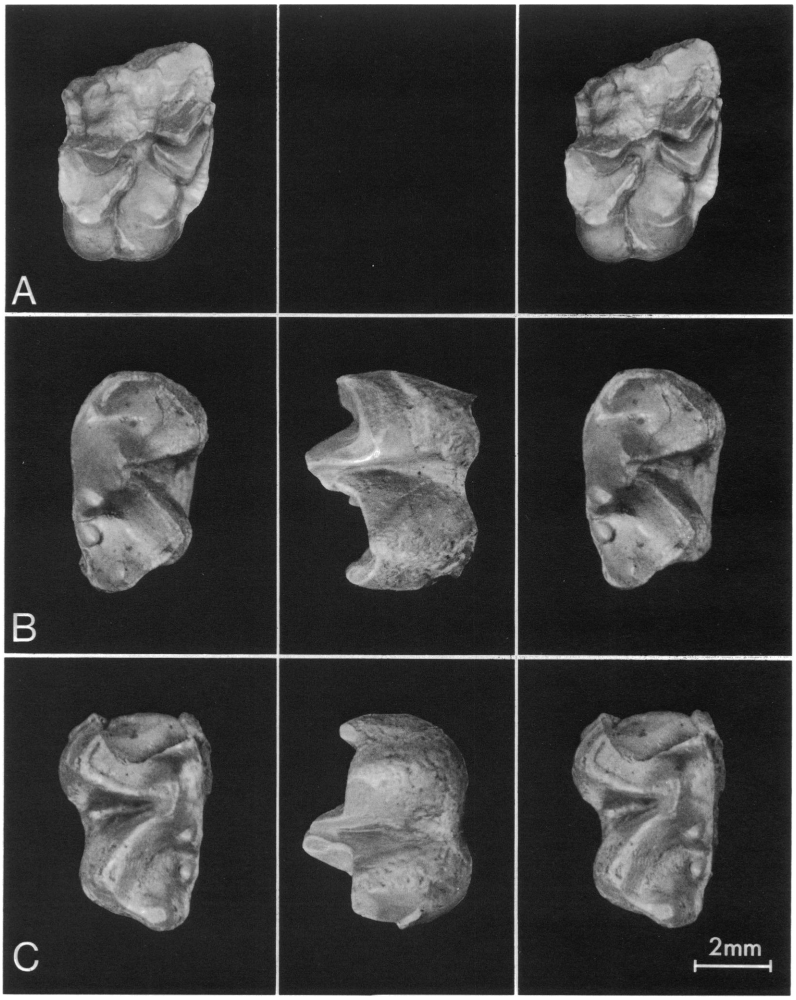


Fig. 17. *Meniscotherium* cf. *priscum.* **(A)** Stereo pairs of occlusal surface of IGM 3680, partial right M2. **(B, C)** lateral aspect and stereo pairs of occlusal surface of IGM 3676, right (B) and left (C) m3.

anterolingual face of the entoconid. Both the metastylid and this additional cusp are typically present in m3s of *M. chamense.* Unfortunately, m3s are not represented in the types of *M. tapiacitis* or *M. priscum.*

DISCUSSION: *Meniscotherium* is the most common mammal from the Tetas de Cabra beds. Accordingly, the small hypodigm of the genus described above gives an indication of the rarity of fossil vertebrate remains in this area. Several edentulous jaws may also be referable to *Meniscotherium,* but their identity is by no means certain and they are not listed here or under any other taxon.

Meniscotherium is represented by the species *M. chamense, M. robustum, M. tapiacitis, M. semicingulatum,* and *M. priscum.* In his review of the genus, Gazin (1965b) argued that only the first three of these species are valid. This conclusion has geochronologic implications because all species except *M. semicingulatum* are from early Eocene faunas. *M. semicingulatum* was described by Russell (1929) from the Cochrane II fauna of Alberta, an assemblage regarded as either Tiffanian (late Paleocene) or Torrejonian (middle Paleocene) in age (see Russell, 1929; Russell, 1967; Krause, 1978)—or earliest Tiffanian (see Archibald et al., 1987). However, Gingerich (1982) convincingly argued that *M. semicingulatum* known only from an isolated dp4 is a junior synonym of the Tiffanian *Ectocion collinus* (=*E. montanensis*). Gingerich (ibid.) also rejected West's (1976) synonymy of *E. collinus* with *Phenacodus vortmani.*

Of the remaining species, the Baja *Meniscotherium* compares most closely with *M. tapiacitis* and *M. priscum,* being significantly smaller than *M. chamense* and *M. robustum.* Unfortunately, there is some uncertainty over the relationships of *M. priscum.* This species was synonymized with *Ectocion parvus* by Van Valen (1978) but Rose (1981) enumerated several distinctive traits in p4 and lower molar morphology (no hypoconulid, high entoconid, large metastylid, deep hypoflexid) that support the continued recognition of *Meniscotherium priscum.* One feature overlooked in his comparison is the relative depth of the jaw. Despite the comparable size of cheek teeth in both taxa, the ramus of *E. parvus* is nearly twice as deep as that of the type of *M. priscum.* The latter species has a jaw of basically the same dimensions as that in AMNH 4425, the type of *Meniscotherium tapiacitis.* Moreover, the p4 and m1 of *M. tapiacitis* closely resemble these teeth in *M. priscum.* The only significant difference is the presence of an accessory cusp (metastylid) posterior to the metaconid in *M. priscum,* a feature lacking or very weakly developed or obscured by wear in *M. tapiacitis.* Gazin (1965b: 21) noted, however, that the development of the metastylid is somewhat variable in other species of *Meniscotherium.* Granger (1915) and Rose (1981) provided no other characters that separate *M. priscum* from *M. tapiacitis* and our observations of the original material have not uncovered any additional differences.

Comparison of the smaller species of *Meniscotherium* with the Baja taxon is difficult because the types of the former are lower dentitions and the material of the latter is well represented primarily by upper dentitions. A lower jaw with m1–2 (IGM 4035) and m3s (IGM 3676) from the Baja locality show a well-developed metastylid (fig. 17), as in the type of *M. priscum.* The measurements of the teeth in IGM 4035 (table 7) are closer to those of the holotype of *M. tapiacitis* (AMNH 4425), but are well within a range that would allow reference to either this species or *M. priscum.* A maxilla with P3, M1–2 (USNM 22431) from the Wasatchian Bitter Creek fauna identified as *Meniscotherium tapiacitis* (Gazin, 1965b: 97) is very close in size and morphology to upper cheek teeth of *Meniscotherium* from Las Tetas de Cabra. The only difference of note is the slightly deeper concavity of the ectoloph between the metastyle and the parastyle in the Baja form. There is thus little justification for the separation of the latter from individuals with upper teeth identified as *M. tapiacitis.* It remains uncertain, however, whether the dentitions figured by Gazin (1965b) are actually referable to *M. tapiacitis* or *M. priscum* since the distinction between these two species is based entirely on lower cheek teeth. Identification of the Baja *Meniscotherium* hinges entirely on the validity of this distinction, an unfortunate conundrum given the poor samples available. The few lower teeth known from the site show the presence of a meta-

TABLE 7
Measurements (in mm) of Cheek Teeth of *Meniscotherium* cf. *priscum*, Las Tetas de Cabra

Specimen element	Length	Anterior width	Posterior width
	IGM 3676		
RM2*	6.39	7.84	–
RM3	5.39	–	–
LM2	6.34	7.71	5.49
Rm3	6.50	3.88	3.51
Lm3	–	3.80	3.43
	IGM 3677		
RP4*	4.15	–	–
RM1	5.24	–	–
RM2	6.05 (est.)	–	–
	IGM 3678		
LM1	5.61	–	–
LM2	6.67	7.91	5.09
	IGM 3679		
LM3	5.29	8.47	5.09
	IGM 3680		
RM2?*	6.42	–	–
	IGM 4035		
Rm1	4.7	4.0	3.4
Rm2	6.1	4.4	4.8

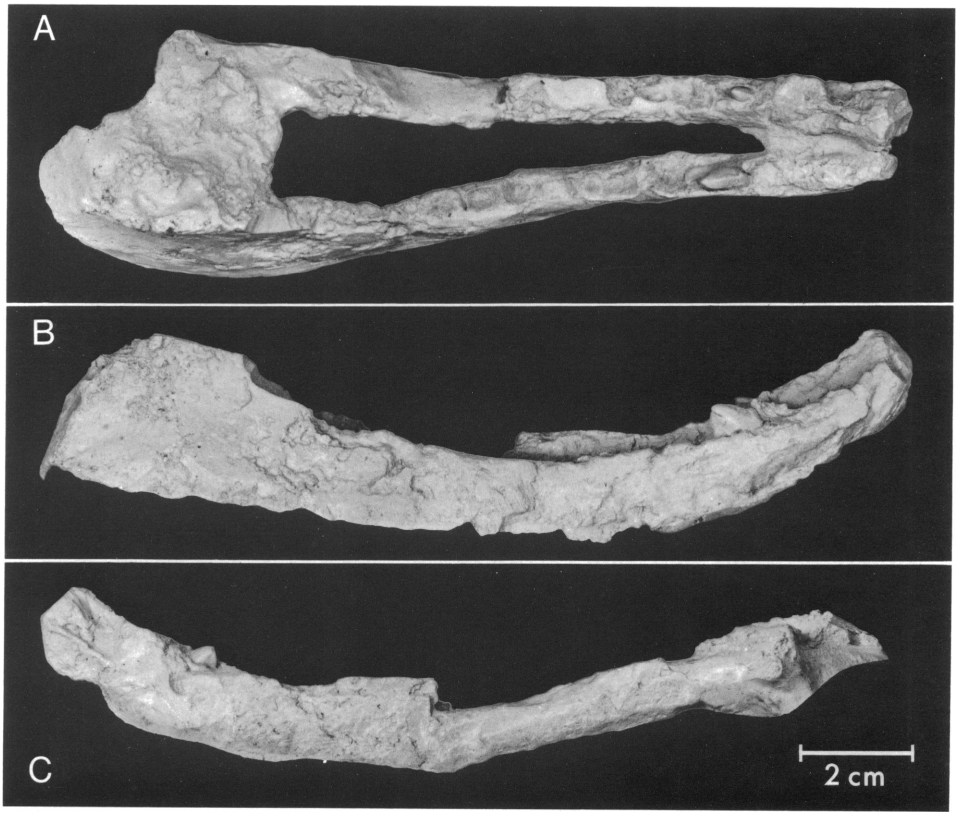


Fig. 18. *Dissacus* sp. **(A)** occlusal, **(B)** right lateral, and **(C)** left lateral views of IGM 4038, left and right rami with canine, p2.

stylid, as in the type of *M. priscum.* We thus tentatively refer the Baja material to this species and, at the same time, share Gazin's (1965b) doubts concerning the separation of *M. priscum* from *M. tapiacitis.*

Although *Meniscotherium priscum* has been cited as a taxon of Clarkforkian age (Gazin, 1965b; Rose, 1981), Gingerich (1982) proposed that both this species and *Ectocion parvus* are from a level in the Polecat Bench sequence above the boundary between the Clarkforkian and Wasatchian land mammal ages. (The precise localities for these species were never recorded.) This suggests that *Meniscotherium* is restricted to Wasatchian-age faunas in the Rocky Mountain region. However, Gingerich (1989) has subsequently listed *Meniscotherium* as an element of the late Clarkforkian.

The smaller species of *Meniscotherium* appear to be rare elements in more midcontinental faunas of early Eocene age. In contrast, large species are often abundant, as documented by the rich samples of *Meniscotherium chamense* from the San Juan Basin faunas of New Mexico. The absence of these larger forms and the relative dominance of a small "*M.* cf. *priscum*" species in the Baja fauna therefore represent an interesting environmental or biogeographic distinction from higher-latitude Wasatchian faunas. This southernmost occurrence of *Meniscotherium* has bearing on a variety of biogeographic scenarios for Wasatchian faunas (Godinot, 1981; Flynn and Novacek, 1984; discussion below).

ORDER ACREODI (MATTHEW, 1909) MCKENNA, 1975

FAMILY MESONYCHIDAE COPE, 1875

Dissacus Cope, 1881d

Dissacus sp. cf. *D. navajovius*

Table 8, Figures 18, 19

REFERRED SPECIMEN: IGM 4038, left and right horizontal rami with the canine and p2 in each ramus and the alveoli for right p1, right p3–m2, and left p1, p3–m2. IGM 4040, damaged right ?m1 (or m2). IGM 4041, three isolated cheek teeth fragments interpreted as cusps and/or cuspids (questionably referred). Collected by H. J. Garbani, a member of W. J. Morris' field party, 1966.

LOCALITY: Precise localities within the Tetas de Cabra Formation unknown.

DESCRIPTION: IGM 4038 consists of both horizontal rami (fig. 18); they are slender, gently curved, and show extensive pitting and cross fracturing, as well as having most alveoli matrix-filled.

The left ramus is broken off behind the posterior alveolus of m1. The slender right ramus is more complete, and curved so that the upper border is concave (subtending a 9.0 mm arc between the canine and the m2 posterior alveolus), and the lower border is convex.

Lower canines from both rami are present, they are broken close to the aveolus and are conical, compressed laterally, and ovoid in cross section; the enamel is very thin. The lower incisors were probably minute and crowded or even absent, as the canines are positioned far forward and near the jaw symphysis.

There is a small diastema between the lower canine and the anterior aveolus of p1. p1 is not preserved, but the left ramus shows two alveoli before p2, indicating that p1 was birooted.

Both left and right p2s were erupted at the time of death. The right p2 is more exposed; it is bladelike. The main cusp is stout and blunt, the anterior margin of the tooth is convex, and the broken posterior margin is slightly concave. There is a minor cingular spur on the anterior border.

p3s are not preserved; their alveoli are ovoid, and anteroposteriorly elongated.

m1 and m2 are not preserved in IGM 4038, their alveoli are larger than those of the premolars, and elongated anteroposteriorly.

Other material possibly referable to *Dissacus* sp. are isolated ?upper tooth fragments (IGM 4041) and, very provisionally, IGM 4040, a badly damaged lower molar fragment (fig. 19). This lower molar sustained much breakage on the lingual rim of the talonid and the posterior half of the labial trigonid. There is a very small paraconid and a labially trending paracristid. The talonid shows a shallow ectoflexid. The ridge joining the hypoconid to the posterior trigonid wall descends steeply in an anterior direction. The hypoconid and hypoconulid are small but distinct. An entoconid is not preserved. The smallest of these is a unicuspid tooth. The cusp is somewhat conical with the anterior border convex, and the posterior border concave. The other specimens are cusp fragments that are blunt, but show no wear.

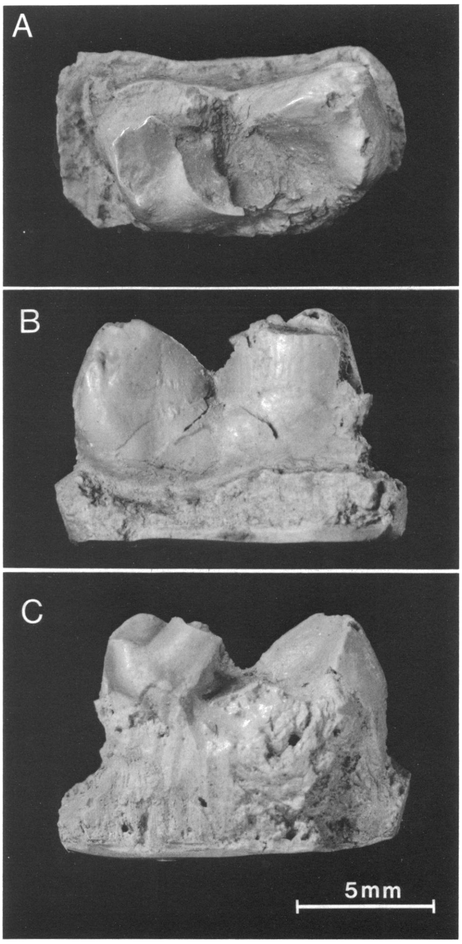


Fig. 19. *Dissacus* sp. (A) occlusal, (B) labial, (C) lingual views of IGM 4040, partial right m1 (or m2).

DISCUSSION: The long and slender dentaries and the blunt cusps are typically mesonychid and the size (table 8) and other dental characters are similar to those of *Dissacus* (cf. Matthew, 1915: 84 et seq.). Species allocation of the Baja specimens cannot be made because the material is so poor. The specimens are 20 to 40 percent smaller than UM 77182, UM 75677, and other specimens referred to

TABLE 8
Dental Measurements (in mm) of Selected Mesonychid Species

	A	B	C	D	E
Rp2					
Anteroposterior length	7.9e	13.8	—	—	—
Transverse length	4.5	5.7			
Rm1					
Anteroposterior length	11.0	15.7	14.0	14.0	20.0
Trigonid width	5.3e	7.3	7.0	7.5	9.3
Talonid width	5.0	6.5	6.6	—	8.5
Crown height	4.0e	6.0	5.6	—	10.0

A, Baja specimens referred to *Dissacus* sp.: Rp2 (IGM 4038) Rm1, or m2 (IGM 4040).

B, UM 76563 referred to *Dissacus praenuntius.*

C, UM 75677 referred to *D. praenuntius.*

D, *D. praenuntius,* data from Rose, 1981: 87.

E, UM 77182 referred to *Pachyaena* sp.

e, estimated.

Dissacus praenuntius from the Sand Coulee area, Clark's Fork Basin (*Plesiadapis cookei* and *Plesiadapis gingerichi* zones). This is the same order of magnitude that separates *D. saurognathus,* the largest species of the genus, from *D. navajovius longaevus,* a named subspecies of *D. navajovius,* the smallest species of the genus (cf. Matthew, 1915). Therefore, the Tetas de Cabra specimens actually may fall within the observed range of *D. navajovius.*

Dissacus is known from western North American Torrejonian, Tiffanian, Clarkforkian and Wasatchian (Graybullian) horizons (cf. Cope, 1881b,c,d; Matthew, 1915; Simpson, 1937a,b; Rose, 1981: 87). The Baja California record of *Dissacus* sp. is the southernmost one of this genus in North America, as well as the first definitive record of the order Acreodi in Mexico and Central America.

Outside North America, *Dissacus* has been recorded from the Early Tertiary of Mongolia (Dashzeveg, 1976), the Paleocene of China (Yan and Tang, 1976; Russell and Zhai, 1987), the Paris Basin (Lemoine, 1891; Stehlin, 1926), and from Spain (Crusafont and Golpe, 1968). The genus was therefore widespread in the Northern Hemisphere.

ORDER PANTODONTA COPE, 1873b

FAMILY PANTOLAMBDIDAE COPE, 1883a

SUBFAMILY ?TITANOIDEINAE SIMONS, 1960

New? genus and species

Tables 9–12, Figures 20, 21

Referred Specimen: IGM 4043, cranium and dentaries crushed and weathered, bearing left I3–M3 and left p2–m3, plus associated postcranial material including the left scapula, some caudal vertebrae and miscellaneous fragments. Collected by S. P. Applegate and H. J. Garbani, 1965.

Locality: The site is 120 m SSW of the northwestern Tetas (Butte) about 35 m below its summit, in the upper part of Las Tetas de Cabra Formation. Punta Prieta region, Baja California Norte, Mexico. IGM Locality 48.

Description: The skull is deformed (fig. 20), so that the sagittal plane is tilted some 30° and the left half is set at a different horizontal plane than the right one. The poor preservation suggests extensive preburial weathering and surface erosion. The articulated condition of the cranium, dentaries, and postcranial skeleton suggests little transport.

The cranium consists of the facial region and the braincase (fig. 20); both zygomatic arches are missing, and the palate and basicranium are largely gone. The facial region is broad, deep, and rather short. The anterior root of the zygomatic arch is above M1. There is a small infraorbital foramen. What remains of the snout indicates that it was blunt because of the anterointernal position of I3 relative to the upper canine, which suggests a strong medial curve of the premaxilla. The braincase is low and narrow and the sagittal and lambdoidal crests are moderately developed (fig. 20). The occipital region is narrow and high (in part because of secondary deformation) and both occipital condyles are present. These condyles are broad, triangular-shaped as seen posteriorly, gently convex, and project posteriorly beyond the occipital plane (again a feature exaggerated by deformation). The sutures cannot be distinguished because of poor preservation.

The dentary is short and deep and each horizontal ramus has its lower border nearly straight and parallel to the upper border (fig.

21). The anterior end of the ramus is not fully preserved, but the symphysial region starts at a point below p2, thus indicating that the symphysis is short (and probably unfused). The posterior end of the horizontal ramus meets the ascending one nearly at a right angle. The posterior margin of the ascending ramus is nearly straight up to the beginning of the coronoid process. The mandibular condyle is relatively small, apparently as large transversely as anteroposteriorly, and separated from the coronoid process by a small V-shaped valley. The coronoid process is relatively short and triangular in lateral outline, with a convex anterior border and a gently concave posterior border. The apex of the coronoid process is 1.0 cm (i.e., roughly one-third the height of the process) above the mandibular condyle.

Only the left sides of the dentitions remain. I3–M3 and p2–m3 are present; all are fully erupted and extensively worn and eroded. I3 is broken at the alveolus; it is ovoid in cross section, wider transversely, and the enamel is very thin. I3 is separated from the upper canine by a small diastema (nearly as large as the alveolous itself). There is a trace of the I2 alveolus.

The upper canine is broken off close to the root; it is ovoid in cross section and transversely compressed. The canine is oblique, directed anteroventrally, and the enamel is also very thin.

P1 is represented by a peglike structure broken off at the alveolus, ovoid in cross section, elongated anteroposteriorly, and isolated from the canine by a very small (2.0 mm long) diastema, and from P2 by a much larger (9.0 mm) diastema. The enamel is thicker than that of the canine. The description of the alveolus is problematical because the maxilla is partly broken in this region. This structure may represent the only root of a small, single-rooted tooth, as is strongly indicated by the lack of any trace of the alveolus for the posterior root.

P2 is very distinctive; its cross-sectional outline is that of an obtuse triangle, where the protocone is placed further anteriorly than the paracone, and the metacone is located further externally than the paracone, so that the posterointernal margin of the tooth is the longest side of this triangle. The proto-paracone margin is nearly straight, the para-metacone margin is very gently concave (posterointernally). Most of the crown is severely damaged and few features are clearly discernible.

P3 is also lacking most of its crown. The occlusal outline is again an obtuse triangle where the protocone, the largest cusp, is placed even further anteriorly to the paracone than in P2. The para- and metacones are nearly of equal size; the labial (external) margin is V-shaped, suggesting the presence of large, well-developed para- and metastyles.

P4 is a damaged tooth showing the condition described above. However, the protocone seems to have been placed posteriorly more nearly level to the paracone, thus defining a less obtuse angle.

M1 has a well-preserved labial margin that shows a deeply concave outline and strong para- and metastyles. The protocone area is very narrow with respect to those of the paracone and metacone. This tooth is slightly shorter (anteroposteriorly) than wide.

M2, the best preserved tooth, is broad, squarish, and nearly as long as wide. Its anterior margin is convex, and shows traces of a large precingulum. The labial margin is broadly and deeply concave, denoting the presence of large para- and metastyles. The posterior margin is gently concave and shows traces of a modest postcingulum. The protocone area is very wide and shows a large pear-shaped prominence surrounded by a narrow rim. The prominence may represent what remains of the protocone and the rim is probably the base of the lingual wall of the crown.

M3 is also broad, irregularly trapezoidal, and smaller than M2. Its paracone area projects externally much farther than the metacone. The labial border is moderately concave; it shows medium-size para- and metastyles, the protocone area is broad; anterior and posterior cingula seem to have been present.

The lower incisors, canine, and p1 are missing; the remaining teeth are heavily but unevenly worn so that the occlusal surface is inclined ventrointernally. Unfortunately no tooth preserves the lingual part of the crown intact. The teeth are moderately hypsodont.

p2 is double-rooted. Only the protoconid

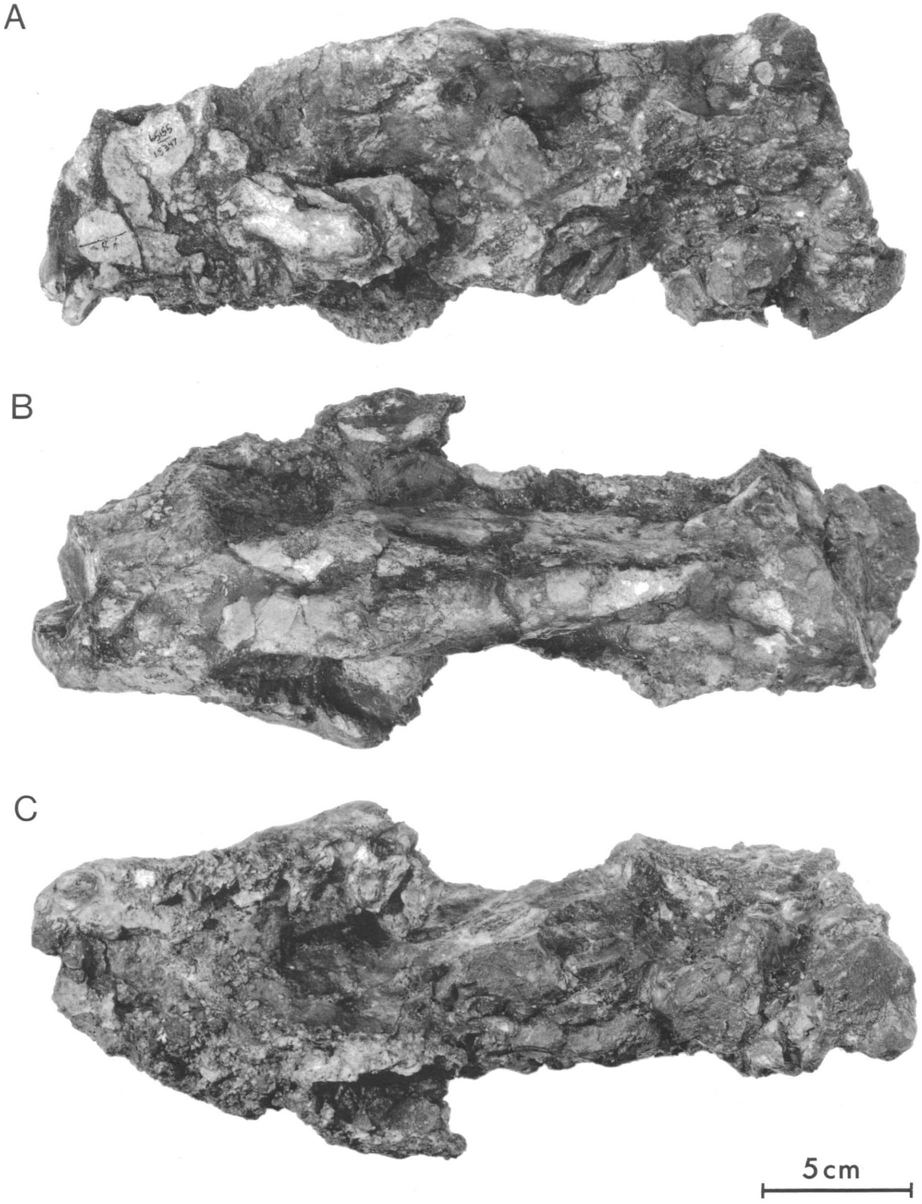


Fig. 20. Pantolambdidae ?new genus. **(A)** left lateral, **(B)** dorsal, **(C)** ventral views of IGM 4043, heavily eroded cranium.

area and traces of a short talonid are discernible.

p3 is double-rooted, nearly the same size as p2, and has a distinct trigonid with protoconid, metaconid, and paraconid. There is a short (?basined) talonid.

p4 is slightly larger than p2 and p3. The protoconid is relatively larger than in p3 and

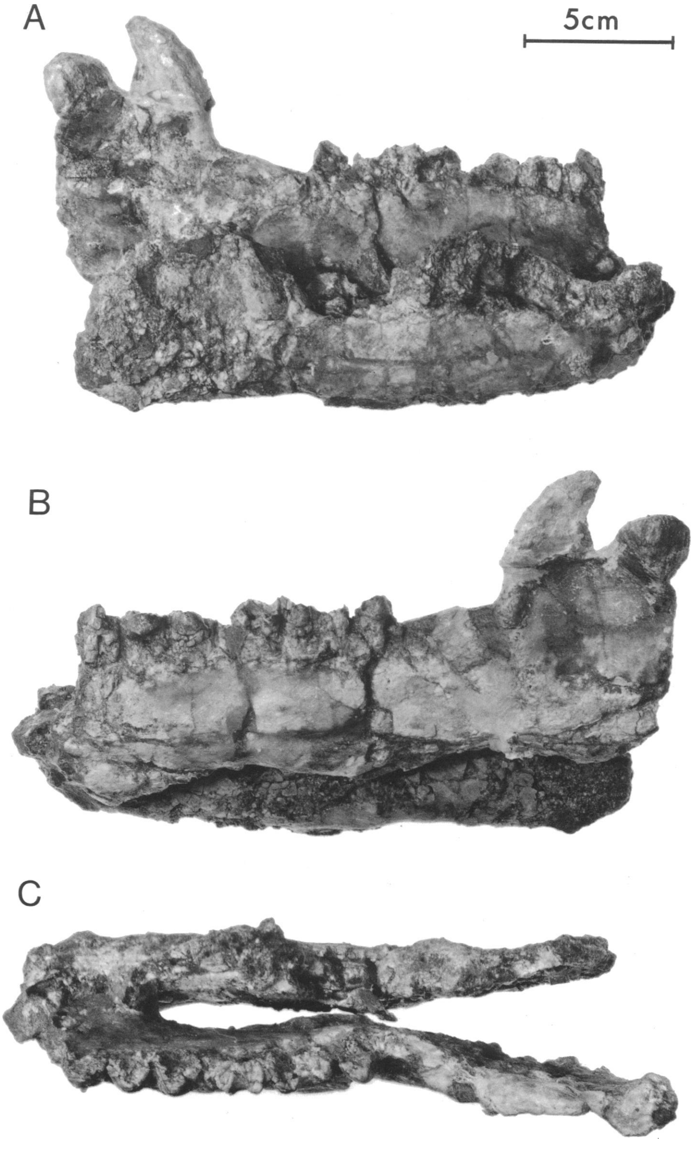


Fig. 21. Pantolambdidae ?new genus. **(A)** right lateral, **(B)** left lateral, **(C)** occlusal views of IGM 4043, heavily eroded lower jaw, IGM 4043.

the paracristid is distinctly straight (rather than gently curved as in p3). The trigonid is relatively shorter anteroposteriorly than in p2, but the talonid is relatively larger.

What remains of ml suggests that both trigonid and talonid were of the same size; the latter was very broad and basined, with its cristid obliqua straight and its postcristid gently curved.

m2 is represented by part of the trigonid and the posterior margin of the talonid. The protoconid is very broad and the paracristid trends anterolingually in a distinctly oblique line.

TABLE 9
IGM 4043, Pantolambdidae, ?New Genus Tetas de Cabra Formation Cranial and Mandibular Measurements (mm)

Cranium	
Anteroposterior length	322
Transverse width at M3	140
Greatest width at occipital condyles	70
Foramen magnum width	35
Height at canine	76
Height at M3	88
Height at midpoint of foramen magnum	90
Mandible	
Total length	105
Depth at p2	57
Depth at p4	54
Depth at m3	57
Height at ascending ramus tip	105
Height at articular condyle	95
Articular condyle transverse width	23
Articular condyle height	22

m3 consists only of the trigonid labial half. The tooth is strongly hypsodont, the paracristid is oblique, and the protocristid is nearly transverse to the anteroposterior axis. The metaconid is thus closer to the paraconid than if both cristids were oblique. A faint cingulum is present on the anterior and posterior walls of the trigonid.

The postcranial material is very fragmentary and is not discussed here.

DISCUSSION: In a comprehensive revision of the North American Pantodonta, Simons (1960) recognized four families and eight genera: Pantolambdidae, including *Pantolambda* and *Caenolambda*; Barylambdidae, including *Barylambda, Haplolambda, Leptolambda,* and *Ignatiolambda*; Titanoideidae, including only *Titanoides*; and Coryphodontidae, including only *Coryphodon* (see also updated treatment of Lucas, 1982). Recently Rose and Krause (1982) erected a new family, the Cyriacotheriidae, for the highly specialized pantodont *Cyriacotherium* (but see Lucas, 1982, for an opposing argument). Gingerich and Childress (1983) proposed to reduce the number of families and genera of pantodonts because of the close morphological similarity among several taxa. They retained Coryphodontidae and Cyriacotheriidae and combined the other genera into a single family, for which the name Pantolambdidae Cope, 1883a, has priority. This family includes *Barylambda, Haplolambda,* and possibly *Caenolambda*; and Titanoideinae, as well as *Pantolambda* (Gingerich and Childress, 1983). The other genera were synonymized: *Leptolambda* with *Barylambda* and *Ignatiolambda* (tentatively) with *Haplolambda.*

Gingerich and Childress (1983) briefly characterized the pantolambdid subdivisions as follows: (1) *Pantolambda* includes middle Paleocene species of moderate body size, simple conical canines, and generalized pantodont cheek teeth; (2) *Caenolambda, Haplolambda,* and *Barylamba* include late Paleocene and early Eocene species of moderate to large body size that have specialized canines, moderate para- and metastylar crests on rectangular upper molars, and relatively short, broad, high-crowned lower molars; (3) *Titanoides* includes late Paleocene to earliest Eocene species of moderate to large body size that have specialized canines, exaggerated crestlike para- and metastyles on triangular upper molars, and relatively long, narrow low-crowned lower molars. Gingerich and Childress (ibid.) further distinguished *Barylambda* from *Haplolambda* as follows: *Barylambda* has large body size, more nearly equidimensional upper molars, and relatively broader, more hypsodont lower molars than *Haplolambda. Caenolambda* was conditionally accepted as valid, but not characterized.

The overall skull morphology and dental characters of the Baja pantodont suggest its assignment to the Pantolambdidae. While size is hardly indicative of familial relationship, it is worth nothing that the Baja pantodont is significantly larger than Cyriacotheriidae (cf. Rose and Krause, 1982), significantly smaller than Coryphodontidae (cf. Simons, 1960), and within the observed range of Pantolambdidae. The Baja form also has a short, blunt, and deep snout, a moderate-size upper canine, broad upper molars, narrow, hypsodont lower cheek teeth, and premolars that increse in size from p2 to p4. These traits readily fall within the observed size range and morphologic spectrum of the Pantolambdidae.

To assess the position of the Baja taxon within the Pantolambdidae requires the careful application of the criteria used by Gingerich and Childress (1983), namely: absolute body size, canine development, upper molar shape, upper molar stylar development, lower molar hypsodonty, and lower molar transverse and longitudinal dimensions. The application of such criteria, however, is subjective and very difficult in the case of this poorly preserved skull.

Tables 9 through 12 summarize the dentalmetric information on the North American Pantolambdidae species; tables 11 and 12 are percentage comparisons of the linear measurements, using the Baja specimen as the standard of reference. The results of the comparisons, as discussed below, are only tentative pending better preserved material.

The canine size shows an overlap with the large canines of *Pantolambda cavirictus,* small canines of *Haplolambda barnesi,* and both small and large canines of *Barylambda.* Canine development may be sexually dependent, as Gingerich and Childress (1983) convincingly argued.

In the Tetas de Cabra specimen the m1 length/width ratio is low and the m2 length/width ratio is high (1.54), thus being closer to *Titanoides* than to the other pantolambdids (table 12).

The upper molar shape criterion used by Gingerich and Childress (1983) pertains to the triangular versus rectangular outline of the crown in occlusal view. The crown is triangular in *Titanoides* and rectangular in other Pantolambdidae (Simons, 1960: fig. 10; Gingerich and Childress, 1983: p. 142). The occlusal outline is hardly discernible in M2–3 of the Baja specimen, but it seems more rectangular than triangular. In this regard the Baja form is closer to other Pantolambdidae than to *Titanoides.*

Stylar development of the upper molars does not seem as discriminating as Gingerich and Childress (1983) maintained. Para- and metastyles are well developed not only in *Titanoides* but also in *Barylambda* (*B. faberi, B. churchilli = Leptolambda schmidti*) and *Haplolambda* (*H. barnesi = Ignatiolambda barnesi*) (cf. Simons, 1960). The preservation in the Baja specimen suggests remnants of prominent para- and metastyles: a feature unlike that in *Pantolambda* and *Caenolambda.*

The lower molar hypsodonty or brachydonty could not be objectively compared since relevent metric data previously have not been provided for the Pantodonta (cf. Simons, 1960; Gingerich and Childress, 1983). The Baja specimen shows relatively hypsodont lower molars, thus being closer to the Barylambdinae (*Barylambda, Haplolambda,* and *Caenolambda*) than to *Titanoides.* It should be noted that in the Baja form hypsodonty is only apparent in the labial region of the crown.

TABLE 10
Dental Measurements (mm) of IGM 4043, Pantolambdidae ?New Genus Las Tetas de Cabra Formation

Element	Length	Width
I3	7.4	7.5
C	13.3	9.0
P1	15.0	–
P2	15.3 (est.)	15.0
P3	16.6	23.5
P4	15.6 (est.)	21.2
M1	21.0	28.0
M2	24.0	28.0
M3	71.0	22.0
C-M3	150.0	–
p2	16.5 (est.)	14.4
p3	17.0	15.6
p4	18.3	15.6 (est.)
m1	19.5 (est.)	15.4 (est.)
m2	24.0	15.5 (est.)
m3	25.0 (est.)	–

Absolute size, as analyzed by Gingerich and Childress (1983), distinguished only between the small *Pantolambda bathmodon* and the following larger taxa: *Pantolambda cavirictus, Caenolambda,* and *Haplolambda* (of approximately equal size); *Barylambda churchilli* (lower observed range), *Titanoides gidleyi,* and *T. zeuxi* (population from Wyoming) which are slightly (about 10%) larger than the previous group; and *B. faberi* and *T. primaevus* which are significantly larger (over 20%) than *P. cavirictus, Caenolambda,* and *Haplolambda.* The Baja specimen falls within the size range of the last group.

The above discussion shows the limited value of the six criteria so far considered. None of them produces a clear distinction between pantolambdid genera. Taken together these criteria cannot be used effectively for designation of the poorly preserved Baja skull.

TABLE 11

Summary of Pantodont Upper Teeth Measurements Expressed as Percentages Compared with Pantolambdidae ?New Genus from Baja California (A)*

			B		C					G		H		I				L	
		A	min	max	min	max	D	E	F	min	max	min	max	min	max	J	K	min	max
I3	L	100	71.6	–	110	–	–	–	122.9	118.9	122.9	139.1	162.1	135.1	–	–	–	–	–
	W	100	–	–	100	–	–	–	90.6	90.6	120.0	146.6	169.3	77.3	–	–	–	–	–
C	L	100	64.6	67.6	114.2	141.3	214.2	104.5	81.9	81.9	109.0	135.3	157.8	225.5	–	–	–	95.4	–
	W	100	90.0	–	156.6	158.8	171.0	137.7	97.7	97.7	166.6	188.8	222.2	166.6	214.4	–	–	138.8	–
P1	L	100	40.0	40.0	60.6	–	98.0	–	98.0	92.0	104.6	105.3	120.0	81.3	82.0	–	–	80.6	–
P2	L	100	43.7	53.5	78.4	–	94.1	67.9	118.9	104.5	118.4	116.3	141.8	71.8	–	66.6	–	72.5	–
	W	100	48.0	52.0	81.3	–	140.0	111.3	170.0	158.6	173.3	154.6	210.0	126.0	–	120.0	–	94.6	–
P3	L	100	53.0	54.8	78.3	–	90.3	74.0	104.8	102.4	123.4	114.4	133.7	69.8	–	66.2	–	86.1	–
	W	100	50.2	54.4	72.3	–	102.5	91.4	110.6	106.3	125.5	123.4	140.4	97.8	95.5	89.3	–	71.4	–
P4	L	100	57.6	59.6	82.6	91.0	96.1	88.4	–	108.9	115.3	128.2	153.8	75.6	81.4	76.2	73.7	75.0	120.0
	W	100	65.5	66.0	84.4	94.8	115.0	111.7	–	132.0	150.9	143.8	177.8	113.2	130.1	108.4	72.1	82.0	85.8
M1	L	100	49.0	52.3	74.7	80.9	–	84.7	109.5	102.3	123.8	119.0	147.6	69.0	74.2	69.0	61.9	63.3	78.5
	W	100	53.9	57.1	70.7	85.7	–	85.3	114.6	100.0	118.5	110.7	135.0	79.2	89.2	78.5	66.0	52.5	70.0
M2	L	100	45.4	50.8	65.8	72.9	77.9	75.0	100.0	95.0	112.5	108.3	125.0	74.1	77.1	67.9	58.7	62.9	80.0
	W	100	60.7	63.5	78.9	90.7	93.5	96.4	122.2	114.2	139.2	117.7	151.7	100.7	111.0	98.2	73.2	65.7	83.2
M3	L	100	51.1	58.8	76.4	79.4	–	100.0	108.4	105.8	123.5	117.6	135.2	111.7	147.7	102.9	65.2	71.1	91.1
	W	100	75.0	80.9	106.8	116.8	–	127.2	143.3	131.8	151.8	152.2	190.0	145.9	147.2	147.7	89.0	97.2	110.4

A, Pantolambdidae, n. gen.; B, *Pantolambda bathmodon*; C, *P. cavirictus*; D, *Caenolambda jepseni*; E, *Haplolambda quinni*; F, *H. barnesi* (=*Ignatiolambda barnesi*); G, *Barylambda churchilli*; H, *B. churchilli–B. faberi* complex (=*Leptolambda schmidti*, small range probably represents *B. churchilli*, and higher range probably represents *B. faberi* as redefined by Gingerich and Childress, 1983); I, *B. faberi*; J, *Titanoides primaevus*; K, *T. gidleyi*; L, *T. simpsoni*.

* Measurement and percentage analysis by I. Ferrusquía-Villafranca.

TABLE 12

Summary of Pantodont Lower Teeth Measurements Expressed as Percentages Compared with Pantolambdidae ?New Genus, Baja California (A)

			B								I		J		K				N		
		A	min	max	C	D	E	F	G	H	min	max	min	max	min	max	L	M	min	max	O
p2	L	100	46.0	—	66.6	83.6	—	96.9	82.4	123.2	115.1	130.3	106.0	133.3	87.2	—	81.8	116.9	78.7	90.3	76.3
	W	100	45.6	—	79.8	109.6	—	96.4	80.7	118.6	100.0	137.7	126.3	136.8	99.1	—	100.0	124.5	88.5	89.4	72.8
p3	L	100	—	—	69.4	91.4	96.4	97.0	80.5	117.6	111.7	132.3	112.9	126.4	94.1	—	89.4	114.7	87.0	—	68.8
	W	100	—	—	69.2	89.7	91.0	83.3	73.7	105.3	96.1	117.3	103.2	116.6	89.7	92.9	75.5	100.0	75.6	—	57.6
p4	L	100	44.8	—	71.0	87.4	94.5	93.9	97.2	110.3	98.3	120.2	98.3	115.8	94.5	—	98.3	—	81.9	—	74.3
	W	100	48.0	51.9	76.2	92.3	108.9	96.1	86.5	114.6	108.9	125.0	105.7	126.2	103.8	—	98.0	—	76.9	—	136.5
m1	L	100	48.7	53.8	89.7	85.1	87.6	93.3	85.6	113.4	97.4	128.2	120.5	136.4	100.5	—	111.2	—	89.7	—	—
	W	100	49.3	51.9	94.1	92.2	93.5	98.7	97.4	114.9	97.4	126.6	116.2	142.8	99.3	101.2	97.4	—	87.6	—	—
m2	L	100	42.9	45.8	81.2	83.3	82.5	79.1	83.3	97.6	89.5	111.2	105.0	123.3	100.0	116.2	96.6	—	99.1	—	—
	W	100	45.8	56.1	96.7	101.1	111.6	96.7	96.7	112.1	109.6	135.4	116.1	148.3	113.5	121.2	101.2	—	90.3	90.0	—
m3	L	100	53.2	58.0	89.6	100.0	102.0	90.0	94.0	111.5	100.0	126.0	126.0	145.2	124.0	130.0	—	—	104.4	104.8	89.6

A, Pantolambdidae n. gen.; B, *Pantolambda bathmodon*; C, *P. cavirictus*; D, *Caenolambda jepseni*; E, "*Caenolambda jepseni*" (=*Barylambda jackwilsoni*); F, *Haplolambda quinni*; G, *H. barnesi* (*Ignatiolambda barnesi*); H, *Barylambda churchilli*; I, *B. churchilli–B. faberi* complex (=*Leptolambda schmidti* of Simons, 1960, lower range probably represents *B. churchilli* and higher range probably represents *B. faberi* as redefined by Gingerich and Childress, 1983); J, *B. faberi*; K, *Titanoides primaevous*; L, *T. gidleyi*; M, *T. majus*; N, *T. zeuxis*; O, *T. zeuxis*.

This specimen has (1) a similar size to *Pantolambda cavirictus, Caenolambda,* and *Haplolambda*; (2) an unspecialized (i.e., small) canine as is seen in *Haplolambda barnesi* and *Barylambda churchilli* (although this character has been interpreted as sexually dependent, with females having smaller canines than males; Gingerich and Childress, 1983); (3) rectangular upper molars as in *Pantolambda, Caenolambda, Haplolambda,* and *Barylambda*; (4) prominent para- and metastyles as in *Titanoides, Barylambda faberi, B. churchilli,* and *Haplolambda barnesi*; (5) hypsodont lower molars as in *Caenolambda, Haplolambda,* and *Barylambda*; and (6) an m2 that is relatively narrow as in *Titanoides* (m1 and m3 are not diagnostic in this regard).

Further analysis (tables 11 and 12) discloses that the Baja specimen has upper premolar and molar dimensions that are similar to those of the other pantolambdids (except *P. cavirictus,* whose molars are narrower); the lower premolars are similar in shape (and allometric proportions) to those of *Caenolambda* and some *Titanoides zeuxis* (Texas population), and narrower than those of other pantolambdids; the lower molars in general are relatively wider than in *Pantolambda* and similar to those of the other pantolambdids (except in *Titanoides gidleyi,* whose m1 is narrower).

From these comparisons it is apparent that the distinctions among pantolambdid genera are not sharply drawn. Moreover, the Baja taxon shares allegedly distinguishing characters with all the pantolambdid genera, making it impossible to unequivocally assign it to any one of these. Nonetheless, the surface details of this skull and dentition are so poorly preserved that a formal name for the Baja taxon is not appropriate. This conservatism also seems justified by the lack of consistent criteria for recognizing different pantolambdid genera. The Baja form does, however, differ from other pantolambdids in the following features: (1) it is unlike *Pantolambda* in being significantly larger (20 to 30% greater in most dental measurements than *P. cavirictus,* the largest *Pantolambda* species), and in having transversely narrower upper canines, upper premolars where the protocone is set further anteriorly than the paracone, thus shaping the premolars as obtuse triangles, upper molars with prominent para- and metastyles, and labially hypsodont lower cheek teeth; (2) it is unlike *Caenolambda* in having specialized upper molars with prominent para- and metastyles, mandible without extensive symphysis, relatively narrower lower cheek teeth, lower premolars with relatively longer (anteroposteriorly) trigonids, and m2 significantly narrower (length/width ratio of 1.54 versus 1.14 to 1.26 in *Caenolambda*); (3) it is unlike *Haplolambda* in having transversely narrower upper canines separated from P1 by a small diastema, specialized upper premolars, all upper molars with prominent para- and metastyles, large, nearly square M2, relatively narrower lower cheek teeth, and significantly narrower m2 (length/width ratio 1.54 versus 1.26 to 1.33 in *Haplolambda*); (4) it is unlike *Barylambda* in being moderately to significantly smaller (20 to more than 50% in most linear dimensions of the cheek teeth), in having narrower upper canines (length/width ratio 1.47 versus 0.96 to 1.23 in *Barylambda*), relatively narrower upper and lower cheek teeth, specialized upper premolars, upper molars with prominent para- and metastyles, M2 nearly square and larger than M1, p3 with anteroposteriorly longer trigonid, and m2 narrower (length/width ratio 1.54 versus 1.26 to 1.40 in *Barylambda*); (5) it is unlike *Titanoides* in having a wider upper canine (length/width ratio 1.47 versus 2.0 in *Titanoides*), specialized upper premolars, broad, more rectangular upper molars and (labially) hypsodont lower premolars and molars.

The position of the Baja genus with respect to one of the pantolambdid subfamilies is also open to question. In absolute size it seems closest to *Haplolambda* and *Caenolambda.* Canine development is rather moderate, again being closest to that of *Haplolambda* and *Caenolambda.* (Although, alternatively, it could be interpreted as being comparable to that of putative females of *Barylambda* and *Titanoides*; cf. Gingerich and Childress, 1983.) The broad upper molars and hypsodont lower molars (and premolars) would suggest affinity within the Barylambdinae plus *Pantolambda,* thus excluding the Titanoideinae. However, the possible presence of prominent para- and metastyles in the upper molars, of the relatively narrow lower cheek teeth, and more significantly, the presence of the upper premolar protocone located anterior to the transverse midline of the teeth (cf. Simons, 1960: 31) suggest affinities to the Titanoideinae. The latter characters seem more compelling than the others, suggesting assignment of the Baja genus to this subfamily.

ORDER TILLODONTIA MARSH, 1875

FAMILY ESTHONYCHIDAE COPE, 1883b

Esthonyx Cope, 1874

Esthonyx sp. indet.

Table 13, Figures 22, 23

Referred Material: IGM 4044, rostral tip bearing the right and left I1–3 and associated right P3, M1–2, right p4, m1, m2 (root), m3 (base of crown), and left m3, all presumably representing the same individual. IGM 4045, left edentulous dentary fragment bearing the alveoli of i3, c, and p2–3. IGM 4046, right dentary fragment bearing the roots of m3. These were collected by Victor Torres-Roldan in 1983.

Localities: The precise provenance of IGM 4044 and 4045 within the Tetas de Cabra area is unknown. IGM 4046 was found in a site some 850 m SSW of the northwestern Tetas butte in a small ravine, about 60 to 75 m below the summit of this hill. Tetas de Cabra Formation. Baja California Norte, Mexico. Wasatchian (early Eocene).

Description: IGM 4044, the snout includes both left and right premaxillae (up to the suture), and includes part of the mesial border. The premaxillae are not fused. The upper incisors in IGM 4044 are crowded and notably different in structure from each other. I1 is gently curved, conical, and ovoid (transversely compressed) in cross section. The enamel covers only the anterolateral face; the mesial face is flat and meets that of the opposite tooth. The root is closed. The alveolus of I1 is set higher (i.e., further from the occlusal plane) and more anteriorly than that of the other incisors; thus it is the longest upper incisor.

I2 has a greater occlusal surface than I1, and its enamel is eroded. I2 is posterointernal to I1.

The crown of I3, the smallest incisor, is peglike, ovoid, transversely compressed, and completely surrounded by enamel.

P3 is of triangular outline in occlusal view, although the crown is partly broken. The metacone is nearly as large as the protone (which is the largest cusp), thus differing from other *Esthonyx* species; the paracone is very small, a faint anteroexternal cingulum is discernible, but no anterostyle (=parastyle) is present.

M1 is transversely wide and anteroposteriorly very short. The protocone is by far the largest cusp while the para- and metacones are nearly equal in size. Only the posteroexternal cingulum is clearly discernible, although a more extensive cingulum is vaguely outlined.

M2 is only slightly smaller than M1. Much of the crown labial to and including the paracone and metacone is missing. There are strong cingula anterior and posterior to the protocone (fig. 22D).

The crown of p4 is broken; it is rectangular in outline and faintly bilobed.

m1 (fig. 23) shows most of the trigonid, which is U-shaped, and has very small, badly damaged para- and metaconids. The talonid is shorter anteroposteriorly than the trigonid. The occlusal surface of the talonid is broken, and only a narrow hypoconid is vaguely discernible.

m2 is only represented by the posterior half of the trigonid root.

m3 is elongated anteroposteriorly and is much wider anteriorly than posteriorly. The crown is broken nearly at the alveolus, but the outlines of the trigonid, talonid, and the accessory lobe are discernible.

IGM 4045, the left edentulous dentary fragment (fig. 23), is robust, with a heavily eroded ventral border. The lingual side is twisted anterointernally, and the external side is correspondingly twisted anteroventrally. There is a well-developed mental foramen below the alveolus for p2.

The alveoli of IGM 4045 are as follows: that of I3 is very small, oval, and elongated anteroposteriorly. The canine alveolus is much larger, ovoid, and also elongated anteroposteriorly. There is no diastema; the remaining four alveoli are interpreted as belonging to two double-rooted premolars, p2 and p3. The circular alveolus for the anterior root of p2 is much larger than that for the posterior root. The alveolus for the anterior root of p3 is nearly as wide transversely as that of p2, but is shorter anteroposteriorly.

IGM 4046, a right dentary fragment, rep-

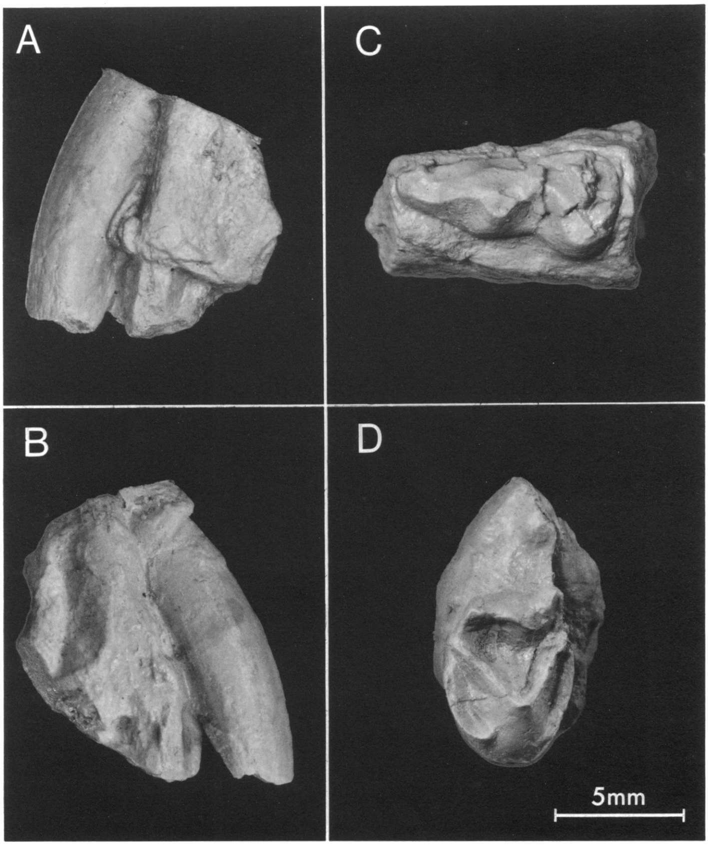


Fig. 22. *Esthonyx* sp., IGM 4044. Lateral views of **(A)** left and **(B)** right maxillary fragments with I1–3. **(C)** occlusal view of right dentary fragment with m3. **(D)** occlusal view of fragmentary right M2.

resents part of the horizontal and ascending rami; it is thick and its lower border is missing. The alveolar outline shows a wider trigonid and talonid, followed posteriorly by a very narrow accessory lobe. The external side shows a large pierced mark, probably resulting from the bite of a carnivore. Reference of this fragment to *Esthonyx* is tentative.

DISCUSSION: The Baja specimens are only fragmentary remains of at least one species of *Esthonyx*. Estimates of size depend largely on the alveolar dimensions. IGM 4045 bears the alveoli for i3, C, and p2–3; none could be directly compared with IGM 4044. Indirect comparions using the p3 alveolus and p4 dimensions indicate that the p3 alveolus of IGM 4045 is some 10 to 20% smaller than the occlusal dimensions of IGM 4044, thus suggesting a p3 smaller than its corresponding p4 by at least that much, as observed in the species of *Esthonyx* (see table 13). The alveolar dimensions of m3 in IGM 4046 are similar to those of IGM 4044. Finally, the morphology of both IGM 4045 and IGM 4046 matches that of *Esthonyx* dentaries. This is most apparent in the case of IGM 4045, where there is a small i3 alveolus, crowded teeth, lack of diastema, and a relatively stout dentary (see Gazin, 1953; Gingerich and Gunnell, 1979). The morphology of IGM 4046 also corresponds to that of *Esthonyx* in size, and the alveoli suggest the presence of molars with comparable proportions. It should be noted that *Hyracotherium, Phenacodus,* and *Oxyaena,* already identified in the Tetas de Cabra fauna, have specimens of roughly similar size to IGM 4046; therefore it is necessary to compare them. *Hyracotherium* differs from IGM 4046 in having m3 with the trigonid and talonid nearly equally

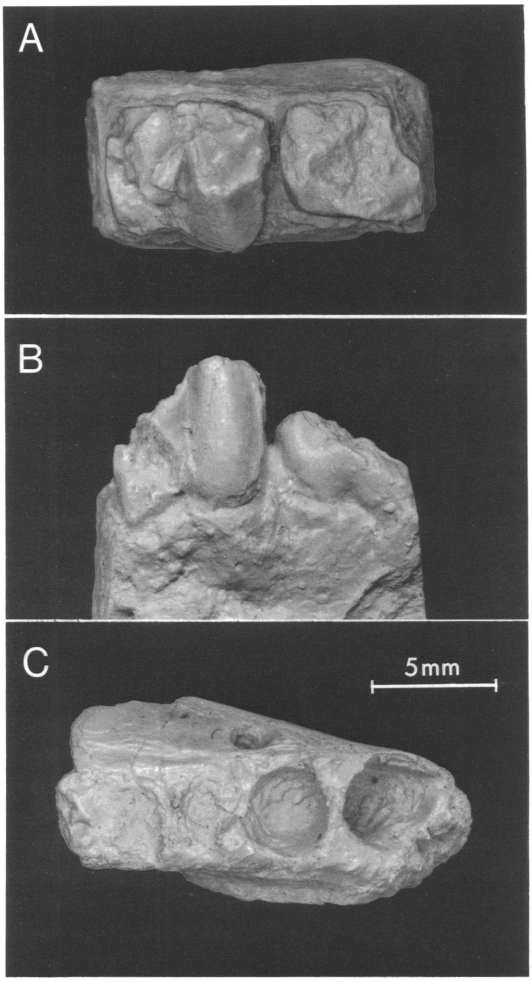


Fig. 23. *Esthonyx* sp. **(A)** occlusal and **(B)** lateral view of IGM 4044, right jaw fragment with P4–m1. **(C)** occlusal view of IGM 4045, left edentulous jaw fragment with alveoli of i3, c, p2–3.

wide, a much wider accessory lobe, and a relatively (thinner) narrower ramus. *Phenacodus* differs from IGM 4046 in having an anteroposteriorly shorter m3, and a (thinner) narrower ramus.

Assuming that the three specimens actually belong to the same *Esthonyx* species, this material can be compared with the *Esthonyx* species already recognized. However, such comparisons are impeded by a lack of consensus concerning the species-level taxonomy of this genus (cf. Gazin, 1953; Gingerich and Gunnell, 1979; Bown, 1979; Stucky and Krishtalka, 1983). For purpose of evaluation, we here recognize *Esthonyx xenicus, E. ancylion, E. grangeri, E. spatularius, E. bisulcatus,* and *E. acutidens* (see Gingerich and Gunnell, 1979) as well as *E. munieri.* Recently, Gingerich (1989) proposed a new genus, *Azygonyx,* for "*E.*" *xenicus, ancylion,* and *grangeri* species. It should also be noted that Bown's (1979) *E. spatularius* seems not diagnostically different from *E. bisulcatus.* Bown was skeptical of the mensurate data used to separate these species. These concerns were further emphasized by Stucky and Krishtalka (1983), who regarded both *E. spatularius* and *E. acutidens* as junior synonyms of *E. bisulcatus.* They also questioned the separation of *E. xenicus* and *E. ancylion.* The differences here pertain to the criteria for recognition of taxa. Stucky and Krishtalka (1983) accept the designations by Gingerich and Gunnell (1979) of the lineage *E. xenicus–E. ancylion–E. grangeri* as separate from the lineage *E. spatularius–E. bisulcatus–E. acutidens.* Stucky and Krishtalka (1983), however, recognized most of the involved species as arbitrarily designated members of two or three species lineages. The meager material from the Baja fauna does not justify our analysis of this issue and reference to the taxa designated by Gingerich and Gunnell (1979) is applied in the following comparisons.

The Baja specimens (table 13) are the smallest referable to *Esthonyx.* The significance of this distinction is, however, not at all clear, given the poor sample available for the Baja species.

p2 is double-rooted in the Baja specimens, as in *E. xenicus, E. ancylion,* and *E. grangeri,* but unlike *E. spatularius,* and *E. bisulcatus* (cf. Gingerich and Gunnell, 1979; Stucky and Krishtalka, 1983).

In IGM 4044, m1 is a tranversely narrow tooth with a large protoconid that leaves little room for the para- and metaconids. Hence the metaconid probably was not inflated, but was small and moderately separated from the paraconid. Should this inference be correct, then the Tetas de Cabra specimens resemble those of *E. spatularius, E. bisculatus,* and *E. acutidens* in having uninflated metaconids, and are unlike those of *E. xenicus, E. ancylion,* and *E. grangeri.*

The Tetas de Cabra specimens hence show one feature (the double-rooted p2) that would

TABLE 13
Dental Measurements Summary of the North American *Esthonyx* Species

		A		B			D		E		F	
		left	right	min	max	C	min	max	min	max	min	max
I1	L	2.1e	3.2	—	—	7.0	—	—	—	—	—	—
	W	2.3	2.5	—	—	5.2	—	—	—	—	—	—
I2	L	5.3e	4.8	—	—	6.1	—	—	—	—	—	—
	W	4.0e	4.3	—	—	4.5	—	—	—	—	—	—
I3	L	1.7	1.5	—	—	—	—	—	—	—	—	—
	W	2.3	1.6	—	—	—	—	—	—	—	—	—
P3	L	5.8	—	—	—	8.5	9.4	—	8.55	—	6.8	—
	W	6.4	—	—	—	8.4	9.4	—	8.57	—	5.5	—
M1	L	6.3	—	—	—	8.8	9.6	10.6	9.95	—	6.9	8.2
	W	9.4	—	—	—	10.8	9.1	16.1	12.42	—	9.7	12.6
M3	L	5.6e	—	—	—	6.9	—	—	—	—	6.0	—
	W	—	9.9e	—	—	10.8	—	—	—	—	10.2	—
i3	L	(1.1)	—	—	—	2.2	—	—	—	—	—	—
	W	(0.9)	—	—	—	1.0	—	—	—	—	—	—
C	L	(4.9)	—	—	—	6.0	—	—	—	—	—	—
	W	(3.3)	—	—	—	4.2	—	—	—	—	—	—
p2	L	(5.9)	—	—	—	5.0	—	—	—	—	—	—
	W	(4.2)	—	—	—	3.5	—	—	—	—	—	—
p3	L	(4.3)	—	6.0	—	7.2	—	—	6.92	—	5.4	5.7
	W	(4.4)	—	4.1	—	5.0	—	—	5.45	—	3.5	3.7
p4	L	—	5.4e	6.6	7.4	7.5	8.4	9.2	8.78	9.86	6.6	7.1
	W	—	4.6	5.3	5.8	5.9	6.5	6.7	7.0	7.18	4.9	5.3
m1	L	—	6.1	7.4	7.5	8.5	9.9	10.7	9.85	11.30	6.5	7.8
	W	—	6.0	6.5	6.5	7.7	8.0	9.9	8.0	8.60	5.5	6.2
m3	L	8.8	8.6	8.0	9.4	11.2	15.2	—	—	—	9.6	10.3
	W	4.8	4.2a	5.1	5.8	7.2	9.0	—	—	—	5.1	5.7

e, estimated. Numbers in parentheses for alveolar measurements. A, Baja specimens referred to *Esthonyx* sp., IGM-4044, I1–3, P3, M1, and M3, p4, m1, and m3; IGM 4045, mandibular fragment bearing the alveoli of i3–p3. B, *Esthonyx xenicus*, data from Gingerich and Gunnell, 1979, table 4. C, *E. ancylion*, holotype, data from Gingerich and Gunnell, ibid., table 5. D, *E. grangeri*, ibid., table 6. E, *E. grangeri*, data from Bown, 1979, table 17. F, *E. spatularius*, data from Gingerich and Gunnell, 1979, table 1. G, *E. spatularius*, data from Gazin, 1953: 24. H, *E. bisulcatus*, data from Gingerich and Gunnell, 1979, table 2. I, *E. bisulcatus*, data from Bown, 1979, tables 18 and 19. J, *E. bisulcatus*, data from Stucky and Krishtalka, 1983, tables 1 and 3. K, *E. acutidens*, data from Gingerich and Gunnell, 1979, table 9. L, *E. acutidens*, data from Stucky and Krishtalka, 1983, tables 2 and 3.

seem to relate them to the *E. xenicus–ancylion–grangeri* lineage (species belonging to *Azygonyx*, Gingerich, 1989), together with other inferred features (unswollen metaconids) that seem to relate them to the *E. spatularius–bisculatus–acutidens* lineage. In size, the Baja species may be smaller than younger members of either lineage. The Tetas de Cabra sample may represent yet another species of *Esthonyx*, but that conclusion is tentative based on the scanty evidence available.

The Baja specimen IGM 4044 is, however, important in providing the first record of an *Esthonyx* specimen having three upper incisors (cf. Gingerich and Gunnell, 1979: 132). IGM 4044 is best described as a young adult; all teeth are erupted but show little wear. I1 and I2 are well developed and of nearly equal size, thus contrasting with I3 which is vestigial.

Gazin (1953: 14) characterized the Esthonychidae as having I2i3-1?, C1c1, P3p3, M3m3. I2 and i2 were thought to have been progressively enlarged in esthonychid lineages. I2 is either rooted (*Esthonyx* and *Megalesthonyx*) or may have grown from persistent pulp (*Trogosus* and *Tillodon*). I3 became progressively enlarged, but remained

TABLE 13—(*Continued*)

G		H		I		J		K		L	
min	max	min	max	min	max	min	max	min	max	min	max
—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	6.67	—	—	—	—	—	—	—
—	—	—	—	6.27	—	—	—	—	—	—	—
—	—	—	—	7.26	10.20	—	—	—	—	8.2	9.5
—	—	—	—	6.81	9.20	—	—	—	—	12.3	13.9
—	—	—	—	6.22	6.62	7.0	7.2	—	—	7.2	8.0
—	—	—	—	10.20	11.30	12.4	12.7	—	—	12.9	15.6
—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—
—	4.2	—	—	—	—	—	—	—	—	—	—
—	2.5	—	—	—	—	—	—	—	—	—	—
5.3	6.0	6.7	—	5.18	5.62	6.1	—	6.4	—	—	—
3.7	4.1	4.3	—	3.40	3.77	3.8	—	3.9	—	—	—
—	7.4a	6.6	7.5	6.23	6.94	7.8	8.7	8.5	8.6	8.1	9.0
—	—	4.8	5.6	4.16	5.40	5.3	5.7	5.5	5.9	5.2	6.2
—	7.8	7.1	8.3	6.75	7.55	7.5	8.0	8.2	8.6	8.6	8.9
—	—	5.5	6.7	5.00	6.17	6.0	6.5	6.0	6.8	6.5	7.0
8.8	9.4	9.0	11.2	8.61	10.0	10.0	—	11.1	13.1	10.8	11.5
—	—	4.8	6.0	4.35	4.95	5.2	5.4	5.9	6.6	5.7	7.6

rooted, whereas i1 and i3 became relatively reduced as in *Trogosus* (although i1 would appear to have become rootless) or were lost as in *Tillodon*.

Further, Gazin (1953: 16) characterized the Esthonychinae as including tillodonts having relatively large, rooted incisors above and below; these teeth have the enamel of the anterior surface restricted to an elongate crown portion.

Finally, Gazin (ibid.: 17) characterized *Esthonyx* as having rooted second incisors of oval cross section at the alveolar level. Gingerich and Gunnell (1979: 131) added that the enamel is limited to the anterior, lateral, and a narrow band of the medial surfaces of the crown.

It is apparent that IGM 4044, undoubtedly referred to *Esthonyx* (or possibly *Azygonyx*, see Gingerich, 1989), preserves structures that call for a revision of the generic and familial diagnoses. The presence of a small I3 indicates that I1 is not lost in some members of this group, as was presumed. Therefore, all the attributes of I2 sensu Gazin (1953) and Gingerich and Gunnell (1979) actually pertain to I1 and those of I3 of these authors refer to I2.

Gingerich and Gunnell (1979: 132) mentioned that no specimen known to them has three upper incisors; therefore IGM 4044 is the first specimen that shows the full incisor set. They also noted, following Gazin (1953), that the "I3" (actually I2) was much smaller than "I2" (actually I1). IGM 4044 shows that the alveolar diameter is greater for the true I2 than for the true I1, but the latter is exposed beyond the alveolar margin at a higher point than I2, thus accounting for the observed difference. It is warranted, then, to add this information on the upper incisors to the generic diagnosis of *Esthonyx*.

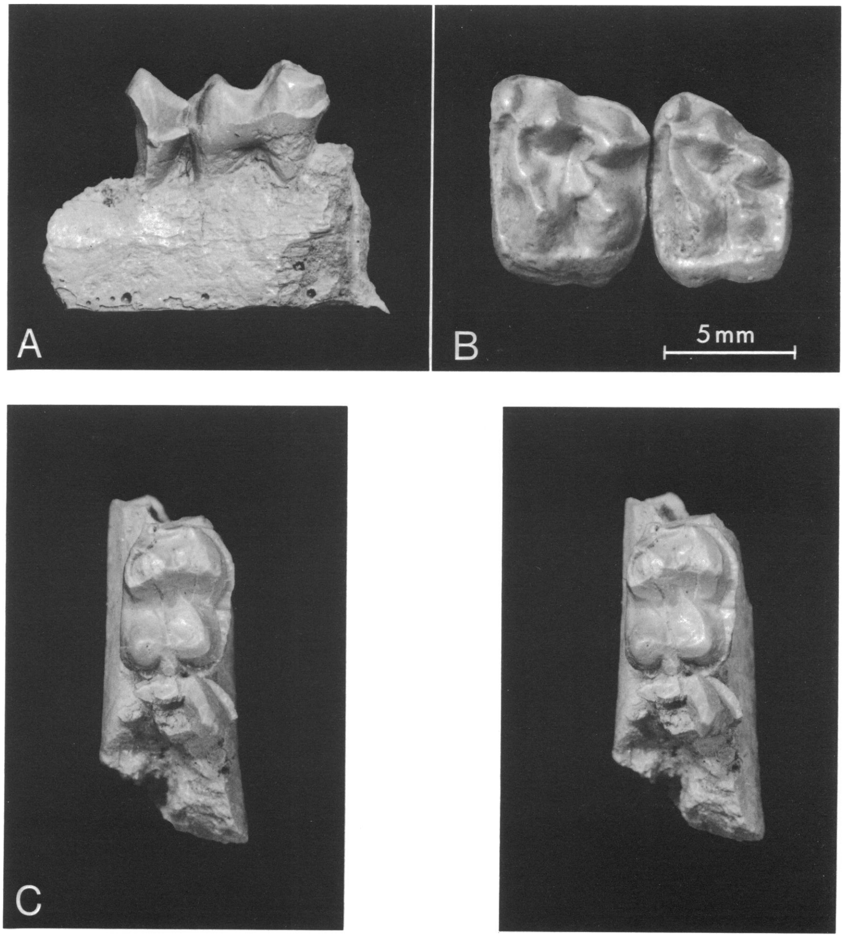


Fig. 24. *Hyracotherium seekinsi.* **(A)** lateral view of IGM 3685, right dentary fragment with m1 (or m2) and trigonid of m2 (or m3). **(B)** occlusal view of holotype LACM 15349, left M2–3. **(C)** Stereo pairs of occlusal aspect of IGM 3685.

ORDER PERISSODACTYLA OWEN, 1848

FAMILY EQUIDAE GRAY, 1821

Hyracotherium Owen, 1840

Hyracotherium seekinsi Morris, 1968

Table 14, Figure 24

Holotype: LACM 15349, left M2, M3, and right M2, M3.

Referred Specimen: IGM 3685, right m1 or m2, fragmentary trigonid of m2 or m3. Collected by AMNH field party, 1983.

Locality: Near Danger Bird Quarry, Tetas de Cabra Formation. Punta Prieta region, Baja California Norte, Mexico. Wasatchian (early Eocene).

Description: IGM 3685 consists of a partial right dentary with a complete molar and a fragmentary trigonid of the next posterior molar. The following description applies only to the complete molar.

The trigonid is anteroposteriorly compressed and squarish in outline. The most strongly developed arm of the paralophid is directed anteriorly away from the protoconid crest, while the remainder of the paralophid is weakly developed and transversely short, forming a slight ridge along the anterior base of the trigonid parallel to the tooth margin. This parallelism of the paralophid and metalophid results in a relatively closed trigonid basin. Although slightly broken, the metaconid appears to be a single cusp that lies lingual and slightly posterior to the protoconid. The metaconid and protoconid are similar in size and are relatively closely appressed. A shallow but distinct valley separates the metaconid and protoconid; the metalophid is weak and is oriented transversely.

The talonid is slightly narrower than the trigonid; it is widest at the trigonid/talonid juncture and becomes narrower toward the posterior margin of the tooth. The cristid obliqua is moderately well developed. It contacts the posterior wall of the trigonid low on the crown and buccal to the midline of the tooth, resulting in a somewhat anteroposterior alignment. A buccal ectocingulid is developed continuously around the base of the hypoconid. In outline the buccal margin of the tooth is straight, without a transverse construction at the trigonid/talonid junction. There is a smooth, shallow talonid basin.

The hypoconulid is a weak, rounded cusp that connects to the posterior margin of the entoconid. A shallow groove separates the closely appressed hypoconid and entoconid lingually. The hypolophid is weak and is oriented transversely.

All cusps are bulbous and rounded. They are generally conical rather than angular or sharp. Enamel crenulations are developed weakly on the buccal cingulum but not on the dorsal crown. The tooth crown is low and relatively square; the ratio of anteroposterior length to transverse width is 1.39; tooth dimensions are presented in table 14.

DISCUSSION: Morris (1968) originally described this species on the basis of upper molars only. The new lower molar specimen provides significant information concerning the size and morphology of the lower dentition of *H. seekinsi.* This specimen articulates well with the upper molars of the holotype and clearly represents the same species. A definitive identification of the tooth described above as m1 or m2 is not possible although the length/width proportions, trigonid basin closure, very weak paralophid, hypoconulid morphology, relatively narrow posterior tooth margin, and small size, suggest that it is almost certainly m1.

From table 14 it is clear that m1 of *H. seekinsi* is smaller than in most other species of the genus. The tooth is smaller than the observed ranges of m1–2 for almost all the *Hyracotherium* species recorded by Kitts (1956), McKenna (1960), and for various European specimens (see table 14). Noteworthy here (see below) is that the Baja specimen falls within the size range observed for *H.* sp. from Rians, France (Godinot, 1981). The upper molars as well, are smaller than, or fall at the low end of the observed size ranges of other known species of *Hyracotherium.*

The species-level systematics of *Hyracotherium* are badly in need of revision—a task which far exceeds the scope of the present paper. Here we go only as far as presenting morphological comparisons with *H. seekinsi* and specimens representing many of the previously named species and subspecies. Detailed comparisons were made between IGM 3685 and representative specimens of *H. angustidens* (New Mexico, Wyoming); *H. a. grangeri* and *H. a. etsagicum* (Wyoming); *H. vasacciense* (Texas); *H. vassaciense vassaciense* and *H. v. venticolum* (Wyoming, Colorado); *H. craspedotum* (Wyoming, Colorado, New Mexico); *H. index* (New Mexico, Wyoming); *H.* sp. (France); and *H. vulpiceps* (England). Although considerable morphological variation within species and subspecies obfuscates these comparisons, *H. seekinsi* does appear to maintain several distinctive features. These are listed below; taxa in which some representatives exhibit similar morphologies are given in parentheses.

1) The high degree of trigonid closure and appression of the paralophid/protolophid (*H. angustidens etsagicum, H. craspedotum, H. index*);

2) cristid obliqua contacts posterior wall of the trigonid buccal to the midline, rather than at, or lingual to, the midline (*H. vasacciense vasacciense, H. index*);

3) the protoconid and metaconid, and particularly the hypoconid and entoconid, are closely appressed;

4) the metaconid is not divided into two separate cusps in contrast to the double metaconid cusp present in some *H. a. angustidens, H. craspedotum, H. index, H. vulpiceps*;

5) crown enamel not crenulated in contrast to the crenulated enamel in some *H. a. angustidens*;

TABLE 14

Comparative Measurements (in mm) on the Dentition of *Hyracotherium*

(after Kitts, 1956; Savage et al., 1965; Hooker, 1980)
Asterisks indicate overlap in size with *H. seekinsi.*

	M1		M2		M3		m1	
	W	L	W	L	W	L	W	L
Hyracotherium seekinsi	7.8	5.8	7.67	6.42	7.43	5.36	4.37	6.07
H. angustidens angustidens & *H. a. estagicum,* Almagre Mbr., San Jose Fm.								
Range	8.0–9.9	7.0–7.5	7.8–10.9	*6.4–8.8	*7.2–11.2	6.8–9.6	*3.8–5.6	*5.7–7.6
N	3		11		21		16	
H. a. angustidens Powder River Basin								
Range	*7.2–8.6	6.7–7.6	8.4–9.5	7.1–8.3	8.2	8.0	4.7	7.1
N	2		2		1		1	
H. a. estagicum Willwood Fm. (Gray Bull)								
Range	8.8–9.9	6.9–8.5	95.–12.0	7.8–10.8	8.8–12.9	7.4–10.3	5.0–5.4	7.3–8.8
N	7		14		11		13	
H. vasacciense vasacciense Largo Mbr., San Jose Fm.								
Range	7.9–8.5	6.5–7.0	7.9–9.2	6.7–7.6	8.2–9.0	7.1–7.2	*4.2–5.0	6.4–7.2
N	4		4		3		7	
H. v. vasacciense La Barge local fauna								
Range	*6.5–9.1	6.0–7.5	7.3–9.7	6.2–7.5	7.5–9.1	7.1–7.7	4.2–6.3	*5.8–8.1
N	5		3		4		17	
H. v. v. & *H. craspedotum* Willwood Fm. (Lysite Equiv.)								
Range	*6.9–8.2	6.2–6.9	8.2–10.0	7.0–8.3	8.0–11.3	7.0–8.8	4.4–4.9	6.9–8.7
N	3		7		10		23	
Hyracotherium sp. (Rians)								
Range	7.6	5.9–6.3	7.8–8.6	6.5–7.0	8.0	6.1–7.0	*4.2–4.5	*5.7–6.2
N	2		2		2		4	

TABLE 14—(*Continued*)

	M1		M2		M3		m1	
	W	L	W	L	W	L	W	L
H. sp., or *Propachynolophus* (Palette)								
Range	6.7	5.7	7.5	6.0	7.0	5.7	—	—
N	1		1		1			
H. cuniculus								
Range	*6.4–8.1	6.3–7.5	*6.4–8.1	*6.3–7.5	7.6	6.4	[a]3.9	—
N	4 (same as M2)		4 (same as M2)		1		1	
H. vulpiceps								
Range	9.0–9.5	7.2–7.6	10.1–10.2	8.2–8.9	8.9–9.5	7.5–7.6	5.5	7.4
N	2		2		2		1	
H. aff. *vulpiceps*								
Range	8.9–9.2	7.5–7.7	[b]*6.4–8.1	*6.3–7.5	8.8–9.8	7.8–8.4	5.1–5.3	7.2
N	3		2/3		3		2	
H. leporinum								
Range	9.7–10.3	7.7–8.0	10.5–11 .0	8.5–8.6	10.0–10.4	8.1–8.5	—	—
N	2		2		2			

[a] m1 or m2.
[b] M1 or M2.

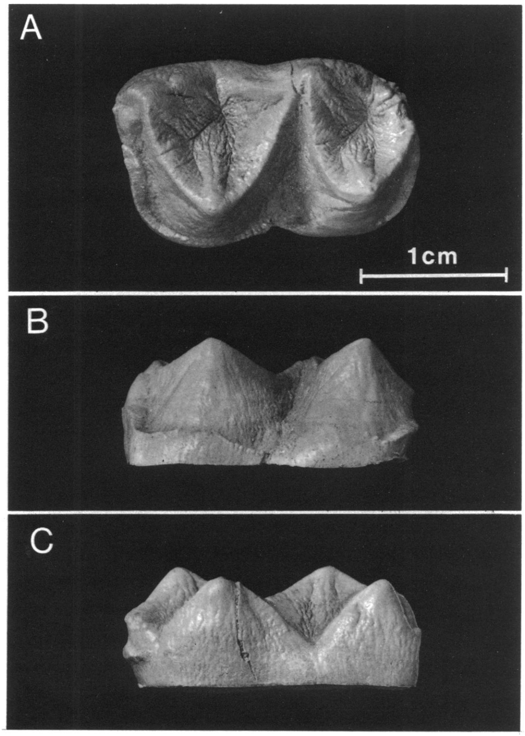


Fig. 25. *Eotitanops* sp. **(A)** occlusal, **(B)** labial, **(C)** lingual views of IGM 4048, right m2.

6) lophids weak (some *H. v. venticolum, H. craspedotum*);

7) cusps bulbous and rounded, not conical and sharp or angular;

8) hypoconulid connects to posterior margin of entoconid rather than to the hypoconid or hypolophid (some *H. a. etsagicum* and possibly some *H. index*);

9) talonid narrower than trigonid, rather than equal to or wider than trigonid (some *H. a. etsagicum,* type of *H. index*).

Recently the absolute sizes of *Hyracotherium* molars have been used (although in our view not justifiably so) as a criterion for estimating their level of evolutionary development (Godinot, 1981). Such assessments have in turn been used in geochronologic studies including intercontinental correlation. Godinot (ibid.) argued that, partly on the basis of its small size, the *Hyracotherium* specimen present at Rians, France, is more primitive—and hence occurred earlier—than any known population of the genus in North America. This, he argued (Godinot, 1981), is suggestive of a western European origin of perissodactyls (as well as several other major mammal lineages) with subsequent migration to North America. This scheme, however, appears to be contradicted by the *Hyracotherium* from Mexico. In terms of morphology, *H. seekinsi* is more primitive than the Rians form (and coincidentally is extremely small). Its primitive features include a poorly developed hypocone on M3, more bunodont cusps, and poorly developed lophodonty. This has obvious implications for hypotheses concerning centers of origin, direction and timing of migrations, and stratigraphic correlation.

FAMILY BRONTOTHERIIDAE MARSH, 1873

Eotitanops Osborn, 1907
Eotitanops princeps Osborn, 1913
Eotitanops cf. *E. princeps*
Table 15, Figure 25

REFERRED MATERIAL: IGM 4048, right m2, collected by IGM field party in 1977.

LOCALITY: A small ravine, some 700 m SSE of the southeastern Tetas hill, stratigraphically about 50 to 60 m below its summit.

DESCRIPTION: The specimen (fig. 25) is an isolated, unworn crown of m2. Its occlusal pattern is bicrescentic, with the trigonid anteroposteriorly shorter than the talonid. The paraconid is the lowest cusp, and is located just anterior to the trigonid basin outlet. Lingually, the paraconid is "twinned" with two closely apposed cuspules. The paracristid is gently convex, and the protoconid is as high as the hypoconid, and higher than the meta- and entoconids, and shows a lingual ridge. The protocristid is longer than the paracristid, concave, and descends gently toward the metaconid, meeting it at the lingual border of the tooth. The metaconid has faint pre- and postmetacristids, and a small anterolingual ridge, but shows no metastylid. The cristid obliqua is nearly straight, starting at the metaconid (on the lingual border), and its occlusal surface is gently concave. The hypoflexid is deep, nearly reaching the lingual border. The hypoconid also has a lingual ridge (as with the protoconid). The postcristid is shorter than the cristid obliqua. The entoconid is as high as the metaconid; it has a central ridge directed anterolabially, a faint entoconulid, and an incipient entostylid. The cingulum is nearly complete, so the precingulid, the ectocingulid, and the postcingulid are present.

TABLE 15
Measurements (in mm) of m2 Specimens Referred to *Eotitanops, Lambdotherium,* and *Paleosyops*

	A	B	C	D	E
Anteroposterior length	21.8	11.1	18.0	21.0	24.0–29.0
Trigonid width	12.3	8.0 ef	10.8	—	—
Talonid width	13.0	8.5 ef	11.7 ef	14.0*	15.0–19.0*
Trigonid length	8.9	3.5 ef	7.6	—	—
Talonid length	13.2	7.5 ef	10.2	—	—
Crown height	10.0	—	—	—	—

ef, measured from the figure. * Originally given as transverse width.

A, IGM 4048, right m2, referred to *Eotitanops* sp.

B, AMNH 14889, referred to *Lambdotherium popoagicum,* data from Osborn, 1929: 280 and fig. 236C2.

C, AMNH 1488, referred to *Eotitanops borealis,* data from Osborn, 1929: 290, and fig. 249A (about 10% larger than the actual specimen, measurements from figure have been corrected).

D, AMNH 296, holotype of *E. princeps,* data from Osborn, 1929: 290.

E, *Paleosyops* sp., observed range for m1 (since m2 is not reported), data from Osborn, 1929: 316.

The occlusal surface shows numerous crenulations and pitting, and the talonid basin is wide and deep, defining a V-shaped valley that opens lingually.

DISCUSSION: From the onset it should be noted that both the taxonomic identity and the unusually fine preservation of this specimen raise doubts concerning its provenance. Dr. Ismael Ferrusquía, who led the 1977 IGM field team that collected this specimen, provided the locality information noted above. It is described here as part of the Tetas assemblage, but it is possible that the specimen may have been weathered out of the higher stratigraphic unit capping the Butte (see comments on Geology, above). The size (table 15) and morphology of the Baja specimen conform best to the m2 of *Eotitanops* (cf. Osborn, 1929: 292 and 294, fig. 249, and plates XXVI and LIV), especially to those of *E. princeps.* It differs from *Lambdotherium* in being nearly twice as large (cf. Osborn, ibid.: 280), and in having well-developed cingulids (cf. Osborn, ibid.: figs. 236 and 240). IGM 4048 differs also from *Paleosyops, Limnohyops,* and *Telmatherium* in being significantly smaller (at least 20%, cf. Osborn, ibid.: 297–358, and table 14 herein), although it resembles *Paleosyops* in having complex parallel striations on the main cusp (Osborn, ibid.: 315).

This specimen is therefore identified as *Eotitanops* cf. *E. princeps. Eotitanops* is known from the late Wasatchian (Lostcabinian) and early Bridgerian from Wyoming. Thus this taxon implies a somewhat later time than most of the other mammals from the fauna. Nonetheless, the possibility that this specimen is a contaminant from younger strata cannot be ruled out.

Recently, Stucky (1984) proposed the *Paleosyops borealis* Assemblage Zone, synonymizing *Eotitanops* with *Paleosyops.* If his argument is correct, the Baja specimen would be referred to *Paleosyops.* Although Stucky's (1984) argument is less than compelling, the exhaustive revision necessary to evaluate it is beyond the scope of this paper.

Eotitanops is the first large Eocene perissodactyl, a taxon that approaches the size of the small to medium-size pantodonts. Hence, it is possible that IGM 4048 could represent a milk premolar of a pantodont. Comparisons to AMNH 15797, a dp4, referred to the pantodont *Coryphodon* (Simons, 1960: 44, fig. 4A), rule against this possibility. IGM 4048 is 20% smaller than AMHH 15797, has a much less robust metaconid, paraconid, and entoconid, and also shows the lingual ridges associated to the proto- and paraconids, as well as crenulations, lacking in AMNH 15797.

ORDER ARTIODACTYLA OWEN, 1848

FAMILY DIACODEXIDAE, GAZIN 1955,

emended Krishtalka and Stucky, 1985
Diacodexis Cope, 1882c
Diacodexis cf. *D. gracilis*
Krishtalka and Stucky, 1985
Table 16, Figure 26

REFERRED SPECIMENS: IGM 3684, partial left dentary with m2–3 collected by AMNH field party, 1985. IGM 4049, right dentary

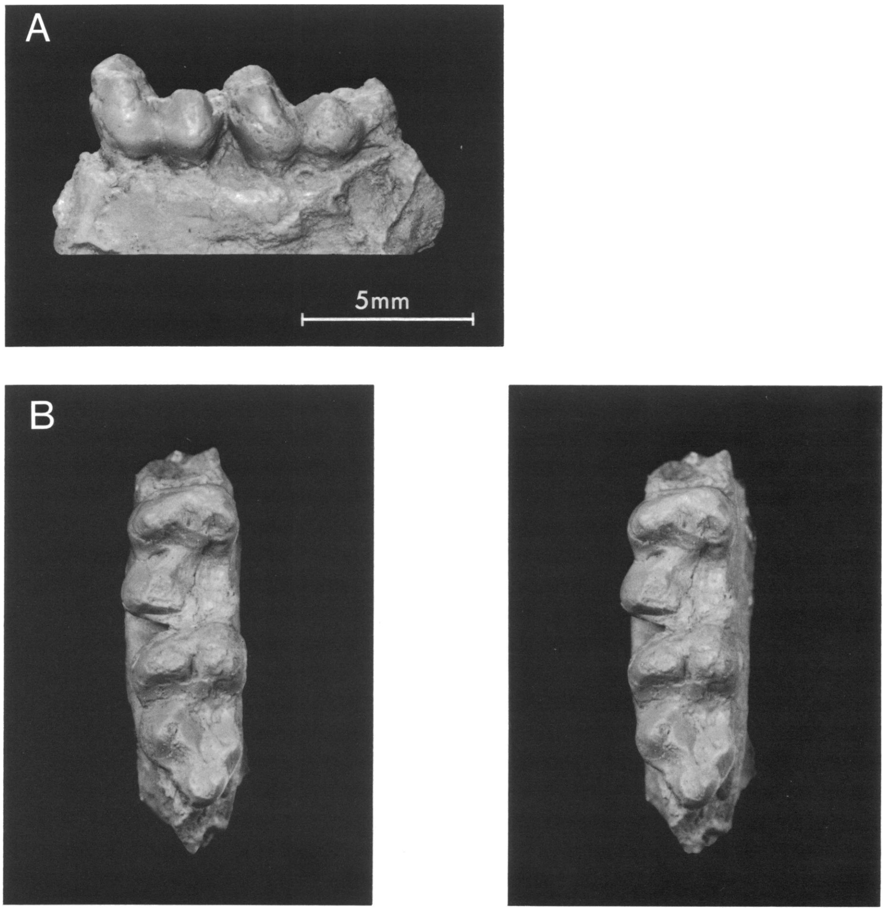


Fig. 26. *Diacodexis* cf. *gracilis.* **(A)** lateral and **(B)** stereo pairs of occlusal aspects of IGM 3684, partial left mandible with m2–3.

with roots of p4–m1; and IGM 4050, isolated cusps; collected by W. J. Morris field party, 1966.

Locality: Two Years (IGM 3684), Las Tetas de Cabra Formation. Baja California Norte, Mexico. Wasatchian (early Eocene).

Description: IGM 3684 consists of a partial left dentary that is broken beneath the anterior end of m2 and just posterior to m3. The teeth are moderately worn, making comparison with other members of the genus difficult. m2 is roughly rectangular in outline, the talonid being slightly broader than the trigonid. The trigonid is weak and narrow. The metaconid is the largest cusp on the tooth; a faint vestige of the paraconid may be inferred from a shallow groove present on its anteromedial edge. The protoconid lies buccal to the closely appressed paraconid and metaconid. A broad anteroposteriorly oriented valley separates the metaconid and protoconid. The cristid obliqua joins the trigonid directly below this depression at the midline of the tooth. The hypoflexid is deep and lacks a basal cingulum at its buccal edge. A short cingulum extends buccally from the hypoconulid region to the base of the hypoconid. Wear obscures the entoconid and hypoconulid. The talonid basin is moderately deep and open lingually; a low smooth ridge rims its lingual margin. The m2 talonid weakly interlocks with the m3 trigonid.

m3 is almost triangular in outline; the trigonid is broader and considerably shorter than the talonid. The morphology of m3 is very similar to that of m2 except that in m3 the

TABLE 16
Comparison of Linear Dimensions of IGM 3684 to the Species of *Diacodexis* Recognized by Krishtalka and Stucky (1985)
Asterisks indicate instances of overlap between IGM 3684 and the information taken from *Diacodexis*

	m2		m3	
	L	W	L	W
D. secans secans				
Range	4.3–5.3	3.4–5.3	5.6–7.1	3.7–4.9
N	53	54	47	52
Mean	4.79	4.41	6.36	4.35
D. secans kelleyi				
Range	4.0–4.9	3.5–4.5	5.1–6.4*	3.1–4.5
N	58	56	50	52
Mean	4.47	3.97	5.73	3.72
D. secans metsiacus				
Range	4.0–4.7	3.3–4.2*	4.6–5.8*	3.1–4.0
N	50	52	34	38
Mean	4.36	3.73	5.17	3.43
D. secans primus				
Range	4.0–5.0	3.5–4.2	5.0–6.7*	3.5–4.1
N	40	41	39	39
Mean	4.51	3.89	5.83	3.75
D. woltonensis				
Range	4.1–4.3	3.5–4.0	4.9–5.6*	3.4–4.0
N	7	7	7	7
Mean	4.21	3.76	5.27	3.70
D. minutus				
Range	3.7–4.4*	3.1–3.6*	4.5–5.4*	2.9–3.6
N	34	34	26	27
Mean	4.02	3.40	4.82	3.22
D. gracilis				
Range	3.7–3.9	3.3–3.8*	4.5–4.8	3.0– –
N	3	3	2	2
Mean	3.83	3.44	4.65	3.00
IGM 3684				
	3.92	3.35	5.14	3.35
N	1	1	1	1

hypoconulid is large, bulbous, and projects posteriorly as a lobe that lies lingual to the midline. A shallow notch separates the hypoconulid and entoconid, and a sharp valley at the posterior end of the talonid basin separates the entoconid and hypoconid. IGM 4049, an edentulous jaw, and IGM 4050, isolated tooth fragments, are poorly preserved and only tentatively referred here to *Diacodexis.*

Discussion: Krishtalka and Stucky (1985) have recently completed an excellent and much needed revision of the North American members of *Diacodexis.* We base the comparisons presented here on their analysis. These workers (ibid.) recognize four species of the genus: *D. secans* (divided into four lineage segments, *D. s. primus, D. s. metsiacus, D. s. kelleyi, D. s. secans*), *D. woltonensis, D. minutus,* and *D. gracilis.* Krishtalka and Stucky (ibid.) discussed at length, however, difficulties stemming from various degrees of morphological overlap encountered when stratigraphically and geographically disjunct samples were added to the comparisons. In view of this high degree of variation and of our limited material, we make here only the tentative allocation of IGM 3684 to *Diacodexis gracilis.* This is based on the following observations.

Krishtalka and Stucky's (1985) comparisons indicate that *D. gracilis* differs from all other species of *Diacodexis,* except the *D. s. primus* lineage segment of *D. secans,* in lacking a postmetacristid and a talonid notch. Both of these features are also lacking in IGM 3684. Unlike *D. s. primus,* however, IGM 3684 lacks a pre-entocristid that closes the talonid basin lingually. Of course, the certainty of our identification rests on how frequently these characters occur in unrelated clades. Although size does not uniquely support the pairing of IGM 3684 and *D. gracilis,* this alliance is the one most consistent with known size variations of members of the genus. These are presented in table 16, where the numerous instances of size overlap are denoted by asterisks.

ORDER RODENTIA BOWDICH, 1921

?FAMILY PARAMYIDAE MILLER AND GIDLEY, 1918

Gen. and sp. indet.

Figure 27

Referred Specimen: IGM 3686, right dentary fragment with broken incisor and alveoli with roots for p4–m2. Collected by AMNH field party, 1984.

Locality: The Way (see fig. 4, appendix

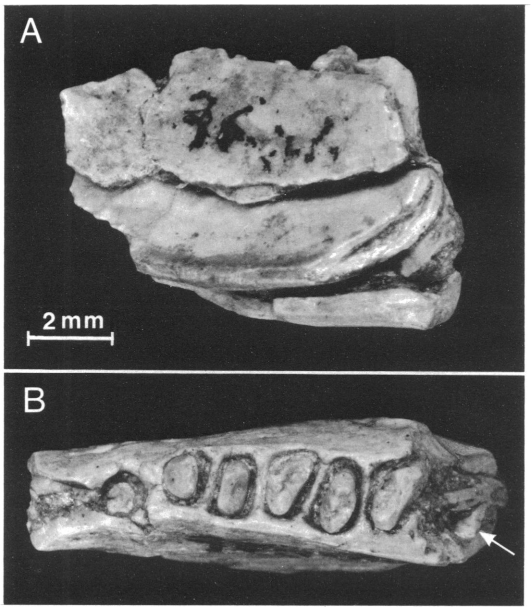


Fig. 27. ?Paramyidae indet. **(A)** lateral and **(B)** occlusal views of IGM 3686, right mandible fragment with broken incisor and alveoli with roots for p4–m2.

1) in Las Tetas de Cabra Formation, Punta Prieta region, Baja California Norte, Mexico. Wasatchian (early Eocene).

DESCRIPTION: The dentary fragment shows two small mental foramina below the p4 anterior alveolus and p4 posterior alveolus, respectively. The depth of the jaw below m2 at its deepest measurable aspect is 6.7 mm. The dentary is convex on its lateral surface, flattened on its lingual surface. Due to damage on the lingual surface of the dentary, the unerupted portion of the incisor is exposed. A distinct enamel band is restricted to its convex ventral surface. The arrangement of the root-filled alveoli suggests the close apposition of p4, m1, and m2.

DISCUSSION: This poorly preserved specimen does little but demonstrate the presence of rodents in the Tetas de Cabra sequence. Rodent affinities are indicated by the restricted enamel band on the incisor and the close apposition of p4, m1, and m2 suggested by the alveoli (in contrast to taeniolabidoid multituberculates). The size of IGM 3686 suggests alliance with small paramyines (e.g., *Paramys huerfanensis*) but other affinities cannot be ruled out. Paramyids (and rodents, for that matter) appear in the North American fossil record at least as early as Clarkforkian time (Rose, 1981).

INFRACLASS EUTHERIA INCERTAE SEDIS

Genus *Wyolestes* Gingerich, 1981
Type Species *Wyolestes apheles*
Gingerich, 1981

Wyolestes iglesius, new species
Table 17, Figures 28–30

HOLOTYPE: IGM 3669, partial skeleton including nearly complete right and left rami with complete, well-preserved dentition (excepting right p1 and right and left incisors, if present) found in occlusion with snout fragment containing left and right P3–M3, left C-P2, isolated incisors, and fragmentary postcranial remains. Collected by AMNH field party in 1984.

LOCALITY: Manly Man locality, Las Tetas de Cabra Formation, Punta Prieta region, Baja California Norte, Mexico. Wasatchian (early Eocene).

REFERRED SPECIMENS: IGM 3670, right dentary with c, p2, m1, and m3 intact and alveoli for p1, p3–4, and m2. IGM 3671, fragments of left and right dentary rami, the left bearing broken m1 talonid, intact m2, partial m3 trigonid, the right containing badly fractured m1 and partial m2 trigonid; left maxillary fragment with fractured but intact M1–2. IGM 3672, two skull fragments probably in association (found within 20 cm of one another in same block of matrix), one consisting of left and right dentary fragments with the right p2 and anterior half of p3 intact, and left maxillary fragment with poorly preserved P3?, the other skull fragment is a left maxillary fragment with intact P4 in occlusion with isolated trigonid of left m1. Collected by AMNH field parties, 1984–1985.

LOCALITY: Younger World (IGM 3670, 3671) and Too Much Hot (IGM 3672). Las Tetas de Cabra Formation, 40 km south of Punta Prieta. Baja California Norte, Mexico. Wasatchian (early Eocene).

ETYMOLOGY: Iglesius, Spanish, *iglesia,* in allusion to the church or cathedrallike form of the eastern butte near which the type specimen was discovered.

DIAGNOSIS: Differs from other species of the genus in having anterior ridge of p3 smooth and two posterior cuspules present, M2–3 lacking buccal cingulae and being anteroposteriorly narrower, M1 being longer than M2 anteroposteriorly, parastyle projecting buccal and anterior to the paracone, not falling on a line joining paracone and metacone, two anterior and two posterior conules bordering the trigon of M1, a diastema separating p1–2, and a small gap between p2–3. Differs from *W. dioctes* (known only from lower dentitions) in having a p1 with a single root and an anteriorly canted crown.

DESCRIPTION: The holotype of *Wyolestes iglesius,* IGM 3669, described here represents the most complete material known for the genus. It consists of a poorly preserved partial skeleton and skull; the dentition, however, is nearly complete and in excellent condition. As noted above, the tooth rows were found in occlusion. The snout and palate are badly fractured and reveal no details of cranial anatomy. The following descriptions apply to the morphology of all the referred material preserving the element described except where noted.

Both premaxillae and right P1–2 are missing. Three associated but isolated incisors are preserved. These are small, blunt, and ovoid in cross section.

The upper canine is a long, posteriorly curved tooth that is oval in cross section. It projects considerably further ventrally than any other tooth of the upper tooth row.

P1 is a relatively large, double-rooted tooth located almost directly behind the canine. It is laterally compressed and tilts slightly forward. The tip of the large central cusp and the lingual face of the crown are missing. There is a crest on the steeply sloping posterior portion of the tooth.

In general size and shape, P2 appears to be almost identical to P1. It too is double-rooted; however, unlike P1, the posterior root of P2 projects posterodorsally. The apex of the central cusp is missing. A small oval wear facet is present at the posterior end of the posterior crest.

P3 is double-rooted and much larger than P1–2. Like these anterior teeth, P3 is laterally compressed and is characterized by a central cusp. In contrast to P1–2, the anterior and posterior portions of the crown of P3 are better developed. The most steeply inclined posterior margin of the central cusp forms a weak ridge lingual to the midline that flattens markedly posteriorly. Two cuspules lie near the base of this ridge. The posterolingual edge of the tooth slopes steeply while the posterobuccal edge forms a shallow shelf.

P4 is three-rooted and triangular in occlusal outline. The paracone is robust and by far the largest cusp on the tooth. The metacone is very small, forming little more than an accessory cusp on the paracone. The protocone also is small and lies directly lingual to the paracone. A broad parastylar wing extends anterobuccally. Sharp notches separate the metastyle from the metacone and the metacone from the paracone. The base of the paracone extends to the buccal margin of the tooth.

M1 is tritubercular. The paracone is the largest cusp on the tooth and is separated from the metacone by a notched valley. Distinct anterior and posterior ridges project from the apex of each cusp. In outline the buccal edge of the tooth is emarginated near the base of the paracone, resulting in the discontinuity of the large parastylar and metastylar wings. In IGM 3671 the metastylar wing is less broad and flat than in the holotype. There is a small, tranversely compressed metastylar cusp posterobuccal to the metaconal base. The well-developed protone lies lingual and slightly anterior to the paracone. Lingually, the tooth is compressed anteroposteriorly. The trigon basin is shallow and is bordered on the edges of the crown by two anterior and two (? or three) posterior conules. A moderately developed cingulum extends from the anterior trigon conules to the parastylar shelf.

M2 is a transverse, three-rooted tooth. The crown morphology is similar to that of M1, but the paracone and metacone are more closely appressed and the metastylar spur does not project as far posterobuccally as in M1. M2 exhibits buccal emargination and lingual compression similar to M1. The posterior edge of the trigon basin bears three distinct cuspules. The posterior margin of M2 is transverse and concave rather than oblique and straight as it is in M1.

M3 is much smaller than M1–2. Both the anterior and buccal edges are straight and oriented obliquely to the sagittal plane. The

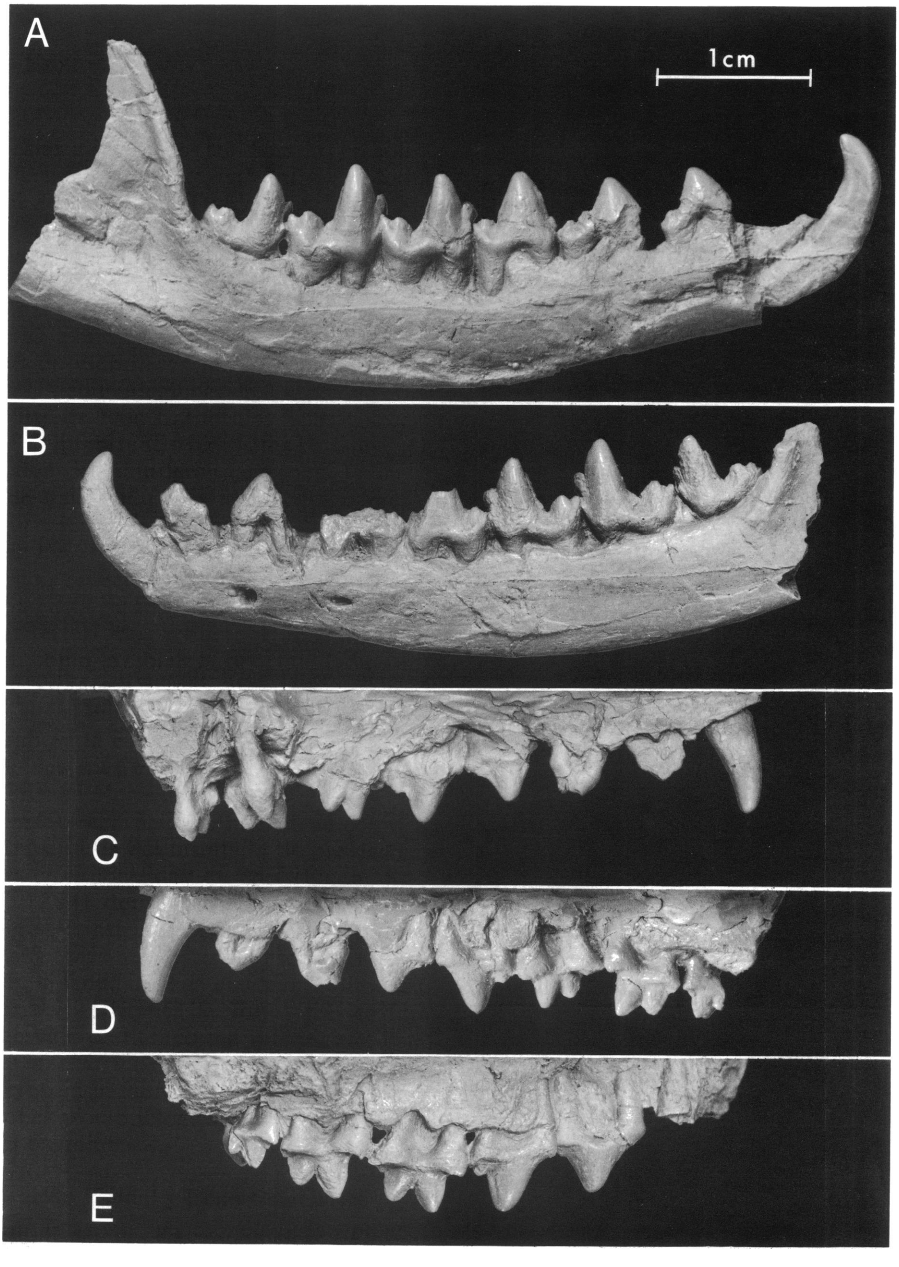


Fig. 28. *Wyolestes iglesius,* new species. Holotype, IGM 3669. **(A)** lateral view of right dentary with c, p2–m3, and **(B)** left dentary with c–m3. **(C)** lingual and **(D)** labial views of left maxilla with C–M3. **(E)** labial view of right maxilla with P3–M3.

metacone is reduced in relation to M1–2. The metastyle is absent; the parastyle is well developed and projects anterobuccally. The parastyle, paracone, and metacone are arranged in an oblique arc. The lingual portion of the tooth is similar in disposition to that seen in M1–2. The anterior edge of the trigon basin has two cuspules; the posterior edge is not preserved. The cingulum connecting the trigon and parastyle in M1–2 is absent.

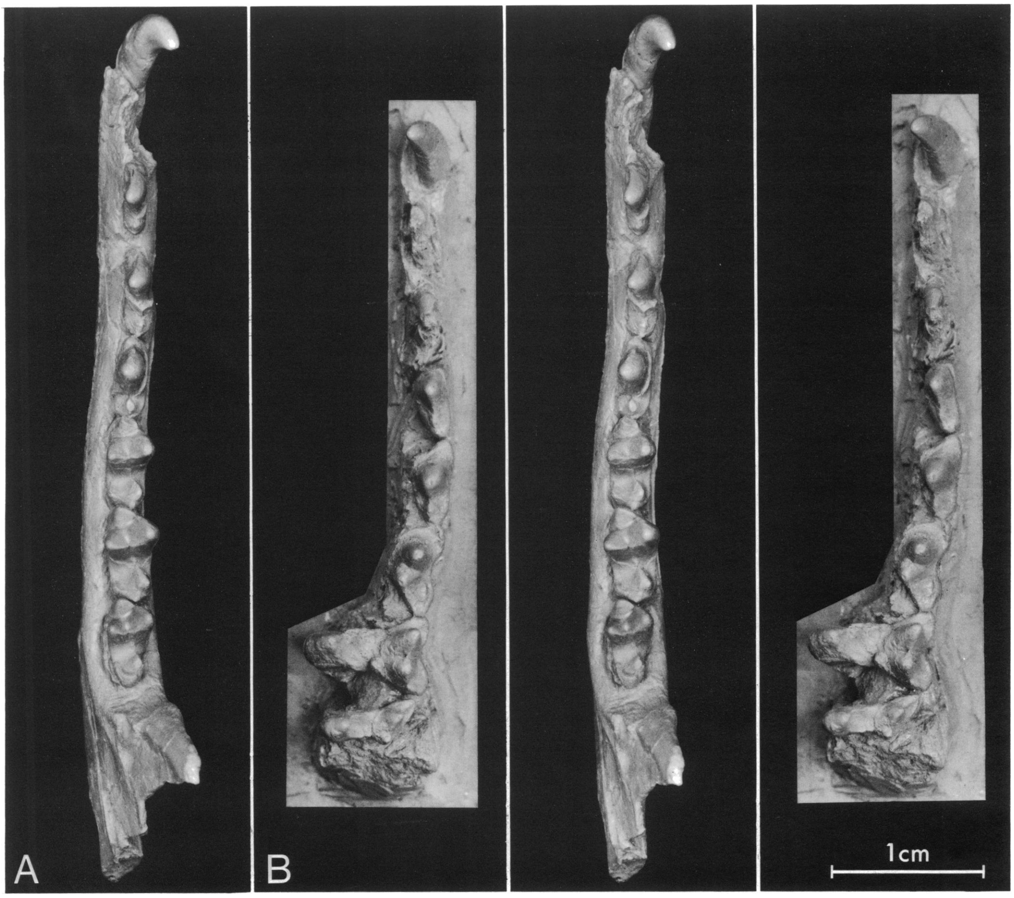


Fig. 29. *Wyolestes iglesius,* new species. Holotype, IGM 3669. Stereo pairs of occlusal aspects of **(A)** right mandible with c, p2–m3, **(B)** left maxilla with C–M3.

The dentary is long and slender. The anterior mental foramen is below the anterior root of the p2 and a smaller posterior mental foramen is below the anterior root of p3. The anterosuperior border of the ascending ramus is broad at its base and narrow dorsally. The coronoid process is relatively broad and the apex recurves posteriorly and appears to flatten dorsally. The mandibular condyle lies at the same level as the apex of the lower canine. The buccal surface of the condyle is anteroposteriorly narrow, triangular in outline, and faces dorsolingually. The lingual articular surface is very broad, projects far medially, and curves posterobuccally. The masseteric fossa is deeply excavated. The ventral border extends from the condyle anteriorly and ventrally to below the m3 talonid; the anterior border forms a pronounced ridge paralleling the border of the ascending ramus.

Except for the right p1 and the incisors (if there were, in fact, any), the lower dentition is complete. The lower canines are high, robust, and strongly curved. They are single rooted and project anteriorly. They are ellipsoidal in cross section, being slightly compressed transversely. The poorly preserved mandibular symphysis extends at least as far anteriorly as p2.

Although it is damaged below the crown, p1 appears to be single rooted. The root is anteroposteriorly elongate. A single, anteroposteriorly elongate p1 alveolus is present in IGM 3670. The tooth tilts sharply forward and bears anterior and posterior ridges and a single blunt anteriorly placed cusp. The cusp

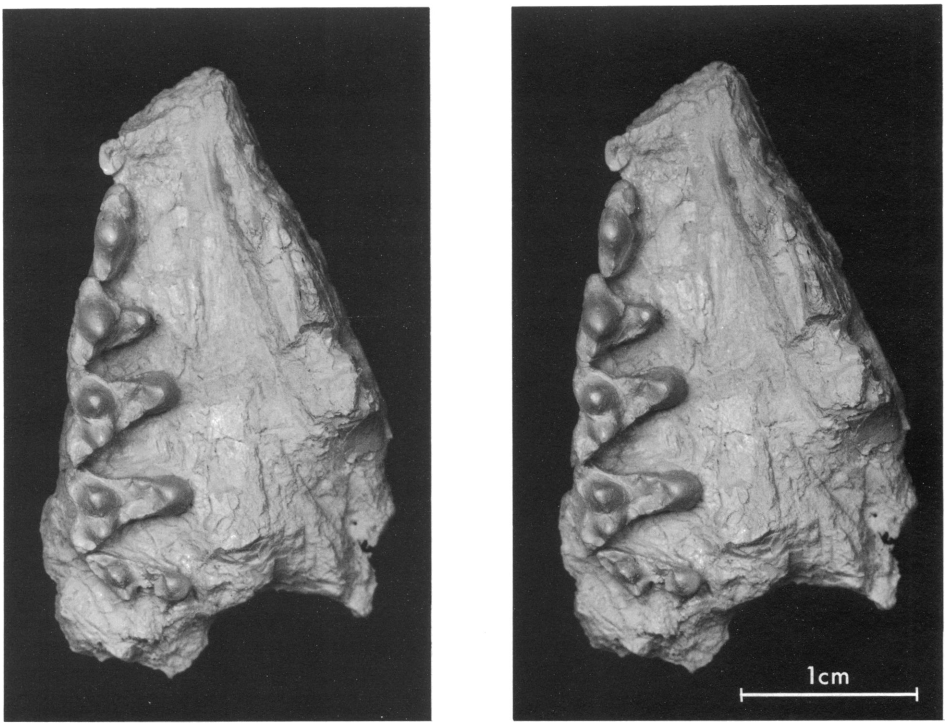


Fig. 30. *Wyolestes iglesius,* new species. Holotype, IGM 3669. Stereo pairs of occlusal aspect of right maxilla with P3–M3.

itself curves markedly lingually. There is a broad, steeply inclined posterolingual shelf.

A short diastema separates p1 from p2. The crown of p2 is dominated by a single anterior cusp. This cusp curves lingually and its apex lies over the juncture of the two roots. The posterior root tilts slightly anteriorly but the tooth does not tilt forward. A low ridge curves down the posterior edge of the central cusp, forming an inclined heel near the base of the tooth. A small cuspule is present near the posterior edge of this heel in the holotype, but is absent in IGM 3672.

In general form p3 is very similar to p2, but the heel of p3 is slightly longer and the posterior cuspule is better developed. A small valley separates this cuspule from the main cusp and a second extremely small cuspule sits on the posterior part of the heel.

In comparison to p1–3, the central cusp of p4 is much larger and does not curve lingually. At the expense of the enlarged main cusp, the posterior heel is reduced. The posterior margin of the tooth consists of a medial basal cusp separated from the main cusp by a notch. This cusp is bordered posteriorly by a short narrow cingulum that slopes lingually and buccally from the midline. A small anterolingually placed cusp is present near the base of the main cusp.

The three lower molars are all elongate teeth with well-developed talonids and typical tricuspid trigonids. On m1 the protoconid is the largest and highest cusp. The metaconid is slightly smaller but considerably lower and projects posterolingually. The posterior surface of this cusp bears a small wear facet on its posterior flank. The paraconid, the smallest and lowest of the trigonid cusps, projects anterolingually but lies more labially than the metaconid. A wear facet is present along its anterior surface. The lower anterior margin of this cusp is marked by an indentation for the reception of the heel of the p4. The trigonid leans slightly anterodorsally and lingually. The hypoconid forms the major cusp of the talonid and is flanked posteriorly by a smaller, lower, medial hypoconulid. Lower still is the small entoconid that lies directly opposite the hypoconid on the lingual margin of the tooth. The deep, narrow, lingual talonid basin is open lingually. IGM 3670, although showing a comparable or slightly greater degree of wear than the type, has the m1 talonid basin closed lingually by a distinct ridge joining the entoconid and the posterolingual ridge of the metaconid; the type shows only faint indications of this ridge. The talonid interlocks weakly with the trigonid of M2 by means of a small indentation present near the base of the paraconid of the posterior tooth. The trigonid and talonid widths are approximately equal. The cristid obliqua touches the posterior wall of the trigonid base slightly labial to its midpoint, thus forming a deep hypoflexid constriction that separates the trigonid and talonid.

m2 (although slightly larger) is very similar in appearance to m1. The protoconid of m2 is better developed. As in m1 the talonid forms a weak connection with the trigonid of the tooth behind it. No wear facets are present on the trigonid. Narrow notches separate the protoconid from the metaconid and the protoconid from the paraconid. These notches appear also to have been present but less developed in m1. The entoconid is positioned slightly further posteriorly and is smaller relative to the entoconid of m1. The talonid is slightly shorter and narrower relative to that of m1.

m3 maintains the same general form as the preceding molars; it is the smallest of the three. Compared to the talonid of the two anterior teeth its talonid is distinctly narrower and elongated, giving the tooth a more triangular outline. The hypoconid and hypoconulid are more equal in size. The entoconid is not developed.

DISCUSSION: This exquisite material represents a new species of *Wyolestes*, an enigmatic genus known from the early Eocene of North America. The affinities of *Wyolestes* are problematic. Although Gingerich (1981) has argued persuasively for an assignment to the Didymoconidae, relationships with other Early Tertiary mammals (e.g., hyaenodontids) cannot be excluded. We have opted for recognition of the genus merely as Eutheria incertae sedis. The postcranial skeletal fragments of the holotype could be informative in this regard. The material is under study by Jin Meng (personal commum.) as part of his analysis of new didymoconids.

TABLE 17
Dental Measurements of *Wyolestes iglesius*, New Species and Other *Wyolestes* Species

		W. iglesius Type, IGM 3669	IGM 3670	*W. apheles* UM 74642	*W. dioctes* USNM 22456
P1	L	4.02	–	–	–
	W	1.5 (est.)	–	–	–
P2	L	3.89	–	–	–
	W	1.63	–	–	–
P3	L	6.38	–	6.3	–
	W	2.30	–	2.9	–
P4	L	5.68	–	–	–
	W	4.85	–	–	–
M1	L	6.28	–	5.9*	–
	W	7.04	–	7.1	–
M2	L	5.49	–	7.4	–
	W	8.07	–	8.6	–
M3	L	3.87	–	5.4	–
	W	6.69	–	8.1	–
p1	L	3.39	–	–	3.9
	W	1.45	–	–	1.9
p2	L	5.02	5.45	6.0	5.5
	W	1.75	1.85	2.1	2.2
p3	L	5.27	–	–	6.1*
	W	2.23	–	–	2.4*
p4	L	5.92	–	6.8*	5.9
	W	2.61	–	3.2	2.7
m1	L	6.50	6.16	–	5.9
	W	3.47	3.50	–	3.4
m2	L	6.52	–	7.4*	6.0
	W	3.99	–	4.0*	3.7*
m3	L	5.84	6.21	6.2*	5.4
	W	3.39	3.77	–	3.3

* Tooth damaged, measurement approximate.

Apart from the size differences illustrated in table 17, *Wyolestes iglesius* differs significantly from the Wyoming taxa in several respects. The Wyoming species of *Wyolestes* lack well-preserved upper premolars and M1 (*W. dioctes* is only known from lower dentition) precluding detailed comparisons for some features. P3 in *W. apheles* is characterized by small basal cusps anterior and posterior to a large central cusp. In the Baja species two posterior cuspules are present but the anterior edge of this tooth is smooth. M2–3 in the Baja *Wyolestes* lack complete buccal cingulae, and are anteroposteriorly narrow relative to transverse width. In *W. apheles* M2 exceeds M1 in anteroposterior length whereas in *W. iglesius* M2 is anteroposteriorly shorter than M1. In the Baja *Wyolestes* M2 the paracone and metacone are more closely appressed and situated more posteriorly on the crown; the external tooth margin is more curved, with a central invagination; and the parastyle and metastyle project more buccally than in *W. apheles*. The paracone, metacone, and parastyle of M2 in *W. apheles* lie along a parasagittal line. In *W. iglesius* the parastyle projects buccal and anterior to the paracone, disrupting this line. The M3 of the Baja *Wyolestes* is anteroposteriorly narrower; the buccal margin is oriented more posteromedially; the anterior edge is sharper and straight, and is directed posterolingually rather than directly lingually.

Both the Baja *Wyolestes* and *W. apheles* possess the distinctive features of two anterior and three posterior conules bordering the trigon on M2 and two anterior conules on M3. The Baja *Wyolestes* has two anterior and two posterior conules bordering the trigon on M1; this tooth is not known for *W. apheles*.

p1 of *W. iglesius* is canted much more strongly forward than in *W. dioctes*. *W. dioctes* is unique in having a double-rooted p1. *W. iglesius* has a closed lower tooth row with a diastema between p1–2 and a short gap between p2–3. *W. apheles* displays sizable gaps between p2–3 and p3–4, whereas *W. dioctes* has a short diastema between the canine and p1. Aside from minor size variations and the exceptions noted above, the morphology of the lower molars and mandibular condyles (not known in *W. apheles*) is similar in all three species of *Wyolestes*. Size comparisons between IGM 3669 and IGM 3670 are also presented in table 17. IGM 3670 has a significantly anteroposteriorly more elongate p2, shorter m1, and more robust m3 trigonid.

FAUNAL COMPARISON AND AGE CORRELATION

The geochronologic and biogeographic implications of the Baja fauna have been considered elsewhere (Flynn and Novacek, 1984; Cipolletti, 1986; Novacek et al., 1987; Flynn et al., 1989) and are briefly summarized here. The dominant pattern represented by the mammalian fauna is one of strong similarity to Wasatchian-age faunas from the western interior. This is significant because the older Clarkforkian Land Mammal Age is now clearly discriminated from the Wasatchian (Rose, 1980, 1981). Resemblances to Wasatchian age are clearly favored over Clarkforkian. Several taxa (*Hyracotherium, Hyopsodus, Diacodexis, Wyolestes, Prolimnocyon,* and *Eotitanops*) making their first appearance in the Wasatchian are also known from Las Tetas de Cabra. Taxa from the Baja locality with older first occurrences elsewhere (*Esthonyx, Oxyaena, Meniscotherium*—see Gingerich, 1989, *Phenacodus*) are not a contradiction to our age assignment, as these taxa are known from Wasatchian faunas as well. Recognition of a Land Mammal Age depends on first occurrence (Flynn and Novacek, 1984) and under this criterion the Wasatchian age assignment for the Baja fauna is clearly established. (See also appendices 5 and 6.)

As noted above, corroboration of an early Eocene rather than later Paleocene age for the Baja locality is provided by independent evidence of the adjacent marine units containing invertebrate fossils and benthic foraminifera. Cipolletti (1986) documented several molluscan species that indicate a "Capay" marine stage and a Ypresian age assignment for these beds. The Ypresian is currently equated with early Eocene time (Berggren et al., 1985). (See also appendix 8.)

A third line of evidence for this age assignment relies on paleomagnetic analysis (appendix 9). All paleomagnetic sites from two sections (both marine and terrestrial) are reversely magnetized, and the above biochronologic relationships suggest correlation of this reversed polarity with Chron 23R or the reversed polarity interval within Chron 24N. These are intervals that correlate with middle Ypresian planktonic foram biozones P7 to late P8 and calcareous nannoplankton biozones middle CP9b to early CP11. Hence, paleomagnetics do not provide a strictly independent time scale but these results do corroborate an early Eocene age assignment based on biostratigraphic evidence (Flynn et al., 1989).

Biogeographic conclusions are less certain. A variety of hypotheses regarding the biogeographic origin of Wasatchian faunas have implicated the Baja assemblage. Morris (1966, 1968) and also Ferrusquía-Villafranca (1978) favored the idea that *Hyracotherium* appeared in the "Clarkforkian-age" Baja fauna and subsequently migrated to "Wasatchian-age" faunas in the Rocky Mountain region. A more complicated scenario is one wherein ancestors of Wasatchian taxa were displaced southward during a phase of late Paleocene climatic deterioration, but their descendants reinvaded the north during the phase of increased tropicality in the latest Paleocene and early Eocene (Sloan, 1969; Gingerich, 1976; Krause and Maas, 1990). Although these reconstructions differ in pattern, both theories converge on the proposal that a tropical community was the immediate source of the North American Wasatchian fauna.

Other sources for this continental fauna have, however, been proposed. Godinot (1981) noted that typical Wasatchian taxa were present from the Sparnacian of France. He recognized a correlation between the basal Sparnacian and the North American Clarkforkian. Citing this correlation and other evidence, Godinot argued for the large-scale migration of mammals from Europe to North America during the late Paleocene–early Eocene interval. Yet another variation is provided by Hickey et al. (1983) who claimed that the Arctic Ellesmere Island fauna, although strongly similar to Wasatchian faunas, is better regarded as later Paleocene in age. These authors accordingly propose the southward migration of typical Wasatchian mammals from the Arctic to both North America and Europe. Dispersal of these faunal elements from Asia and Africa has also been considered (Gingerich, 1976). More extensive review of these biogeographic arguments is provided by Krause and Maas (1990).

Thus a wide variety of hypotheses involving dispersal events as an explanation for the Wasatchian North American fauna has been put forth. We note at this juncture that we regard most such "directional theories" as unrealistic. That is, we doubt that the control and resolution provided by the vertebrate fossil record allow one to identify a preferred direction of dispersal with any consistency. It is, however, acknowledged that any clear and independent evidence of heterochroneity for two or more faunas of similar composition does suggest that large-scale migration may explain this similarity (Huxley's 1862 "homotaxis" problem). In this regard, none of the above theories is very compelling because evidence for asynchrony is based on the mammals themselves (e.g., the more primitive "stage of evolution" of a given taxon suggests an earlier age). Only one argument, that of Hickey et al. (1983), purports to identify an earlier age for typical Wasatchian mammals in the Arctic on a "nonmammalian" (paleomagnetic) time scale. The magnetostratigraphic evidence for these temporal correlations is, however, poorly documented and does not conclusively provide an independently defined geochronology (Kent et al., 1984).

In a biogeographic context, new information on the Baja fauna documented here has further implications. Because this fauna is now known to be so typically Wasatchian in composition, its similarity to—rather than differences from—other early Eocene North American faunas is the dominant pattern. There is nothing to indicate that the Baja fauna is older than any of these faunas—i.e., is equivalent to Clarkforkian-age faunas elsewhere. Hence, there is no reason to argue that Baja was a staging area for the northward dispersal of Neotropical mammals during the late Paleocene–early Eocene. Moreover, independent evidence that might demonstrate asynchrony for widely separated Wasatchian faunas simply fails to do that. Correlations of the marine biochrons and magnetostratigraphic results from Baja clearly identify an early Eocene interval, and not a later Paleocene one, as theories for dispersal from the neotropics would predict. There is, in fact, no convincing evidence for asynchrony for any subset of Wasatchian faunas.

The foregoing discussion has, then, addressed two important goals of paleontology. The first of these is to establish a useful geochronology based on fossils; the second is to reconstruct paleobiogeographic patterns. It may seem ironic that the realization of one of these goals may not always complement the other. In this case, we demonstrate that widely separated North American faunas show strong similarities and that these faunas can be equated with early Eocene time through correlation with marine biochrons and magnetostratigraphy. Thus it can be argued that the North American Wasatchian Land Mammal Age is useful on a continental scale as a geochronological unit (Flynn and Novacek, 1984), and fulfills the correlations with early Eocene intervals originally predicted for this Land Mammal Age (Flynn et al., 1989). Such refinement, however, does nothing to illuminate the preferred source and direction of migration of Wasatchian mammals.

Given this situation, it seems fair to ask whether further refinement of faunal correlations will necessarily clarify such dispersal patterns. It is difficult for us to imagine how such a clarification would come about. If it is eventually recognized from independent geochronologic evidence that some Wasatchian faunas are not time-equivalent, then the possibility of dispersal among these faunas can be entertained. The circularity here is that such a discovery would destroy the basic Land Mammal Age system upon which mammalian faunal history is calibrated. Without such calibration, refined theories of dispersal lack any framework. Over a century of work has established the argument that most North American Land Mammal Ages are roughly synchronous and thus useful for geochronology. A corollary is that higher-level dispersal events—namely those that are meant to explain the origin of characteristic genera for a Land Mammal Age—cannot be detected once a geochronology based on these Land Mammal Ages is accepted. Such dispersal events must be expressed at a finer scale (e.g., species-level patterns) than the faunal change that documents discrete Land Mammal Ages. Alternatively, theories for dispersal events involving mammalian genera would have to abandon a mammal-based time calibration—an action required by the demonstration of asynchrony among mammal faunas of similar composition. This seems particularly evident for any theory that proposes a direction of dispersal. In such a case, the demonstration of asynchrony is a minimum—but not the only—requirement for the argument that certain organisms moved in a certain direction from one place to another.

REFERENCES

Archibald, J. D., P. D. Gingerich, E. H. Lindsey, W. A. Clemens, D. W. Krause, and K. D. Rose
1987. First North American Land Mammal Ages of the Cenozoic Era. *In* M. Woodburne (ed.), Cenozoic mammals of North America, pp. 24–76. Berkeley: Univ. California Press.

Aubrey, M. P., W. A. Berggren, D. V. Kent, J. J. Flynn, K. D. Klitgord, J. D. Obradovich, and D. R. Prothero
1988. Paleogene geochronology: an integrated approach. Paleoceanography 3: 707–742.

Beal, C. H.
1948. Reconnaissance of the geology and oil possibilities of Baja California, Mexico. Geol. Soc. Am. Mem. 31: 1–138.

Berg, D. E.
1967. Aquitane Krokodile vom "Hessler" (Wiesbaden-Biebrich) und anderen Fundstellen. Ber. deutsch. geol. Ges. Geol. Wiss., A (Geol. Paläont.) 12: 653 (abstr.).
1969. Characteristic crocodiles of the Paleogene in Europe. Mem. Bur. Rech. Geol. Min. 69: 73–75.

Berggren, W. A., D. V. Kent, J. J. Flynn, and J. A. van Couvering
1985. Cenozoic geochronology. Geol. Soc. Am. Bull. 96: 1407–1418.

Bowdich, T. E.
1921. An analysis of the natural classification of Mammalia for use of students and travellers. Paris: J. Smith, 115 pp.

Bown, T. M.
1979. Geology and mammalian paleontology of the Sand Creek Facies, lower Willwood (lower Eocene), Washakie County, Wyoming. Geol. Surv. Wyoming Mem. 2: 1–151.

Bown, T. M., and E. L. Simons
1984. First record of marsupials (Metatheria: Polyprotodonta) from the Oligocene in Africa. Nature 308(5958): 447–449.

Cifelli, R. L.
1983. The origin and affinities of the South American Condylarthra and early Tertiary Litopterna (Mammalia). Am. Mus. Novitates 2772: 49 pp.

Cipolletti, R. M.
1986. Age determination and paleoecology of marine Paleogene strata, Baja Califor-

nia Norte. Unpubl. Master's Thesis, Rutgers University, 147 pp.

Cope, E. D.

1873a. Fourth notice of extinct Vertebrata from the Bridger and Green River Tertiaries. Palaeontol. Bull. 17: 3 pp.

1873b. On the short-footed Ungulata of the Eocene of Wyoming. Proc. Am. Philos. Soc. 13: 38–74.

1873c. Extinct vertebrata from the Eocene of Wyoming. Hayden Annu. Rep. USGS of the Territories for 1872. Washington.

1874. Report upon vertebrate fossils discovered in New Mexico, with description of new species. Geogr. Expl. Surv. W. of 100th Merid., Appendix FF, Ann. Rept. Chief of Engineers for 1874, 18 pp.

1875. On the supposed Carnivora of the Eocene of the Rocky Mountains. Proc. Acad. Nat. Sci. Philadelphia 27: 444–448.

1877. Report upon the extinct Vertebrata obtained in New Mexico by parties of the expedition of 1874. Rept. U.S. Geogr. Surv. 4(2): 370 pp.

1880. The badlands of the Wind River and their fauna. Am. Naturalist 15: 610–611.

1881a. A new type of Perissodactyla. Am. Naturalist 15: 1017–1018.

1881b. Mammalia of the lower Eocene beds. Am. Naturalist 15: 337–338.

1881c. On some Mammalia of the lowest Eocene beds of New Mexico. Proc. Am. Philos. Soc. 19: 484–495.

1881d. Notes on Creodonta. Am. Naturalist 15: 1018–1020.

1882a. Notes on Eocene Mammalia. Am. Naturalist 16: 522.

1882b. New characters of the Perissodactyla Condylarthra. Am. Naturalist 16: 334.

1882c. Two new genera of Mammalia from the Wasatch Eocene. Am. Naturalist 16: 1029.

1883a. The ancestor of *Coryphodon*. Am. Naturalist 17: 407–408.

1883b. On the mutual relations of the bunotherian Mammalia. Proc. Acad. Nat. Sci. Philadelphia 34: 77–83.

Crochet, J.-Y.

1979. Diversité systématique des Didelphidae (Marsupiala) Européens Teriaires. Géobios 12: 365–378.

Crusafont, P. M., and P. J. Golpe

1968. *Dissacus progressus* nova sp. el primor creodonto de Espana. Bol. Geol. Min. Espana 79(4): 354–357.

Darton, N. H.

1921. Geologic reconnaissance in Baja California. J. Geol. 29: 720–748.

Dashzeveg, D.

1976. New mesonychids (Condylarthra, Mesonychiadae) from the Paleogene of Mongolia. Trans. Joint Soviet-Mongolian Paleontol. Exped. 3: 14–31.

De Broin, F.

1977. Contribution à l'étude des Chéloniens. Chéloniens continentaux du Crétacé et du Tertiare de France. Mém. Mus. Natl. Hist. Nat. Paris, Ser. C, 38: I–IX, 1–366.

Denison, R. H.

1938. The broad-skulled Pseudocreodi. Ann. New York Acad. Sci. 37: 163–256.

Durham, J. W., and E. C. Allison

1960. The geologic history of Baja California and its marine faunas. Syst. Zool. 9(2): 47–91.

Estes, R.

1983a. Sauria terrestria, Amphisbaenia. Handbuch der Paleoherpetol. Part 10A. New York, Stuttgart: Gustav Fischer Verlag.

1983b. The fossil record and the early distribution of lizards. *In* G. Anders, J. Rhodin, and K. Miyata (eds.), Advances in Herpetology and Evolutionary Biology. Essays in Honor of Ernest E. Williams, pp. 365–398. Cambridge, MA: Harvard Univ. Press.

Estes, R. and J. H. Hutchinson

1980. Eocene lower vertebrates from Ellesmere Island, Canadian Arctic Archipelago. Palaeogeogr., Palaeoclimatol., Palaeoecol. 30: 325–347.

Estes, R., K. de Queiroz, and J. Gauthier

1988. Phylogenetic relationships within squamata. *In* R. Estes and G. Pregill (eds.), Phylogenetic relationships of the lizard families, pp. 119–282. Stanford, CA: Stanford Univ. Press.

Ferrusquía-Villafranca, I.

1978. Distribution of Cenozoic vertebrate faunas in Middle America and problems of migration between North and South America. Univ. Natl. Auton. Mexico, Inst. Geol., Bol. 101: 193–321.

Fife, D. L.

1968. Geology of the Bahia Santa Rosalia quadrangle, Baja California, Mexico. Unpubl. Master's Thesis, San Diego State Univ., 100 pp.

1969. Reconnaissance geology of the Bahia Santa Rosalia quadrangle, Baja California, Mexico. Geol. Soc. Am. Spec. Pap. 121: 505–506 (abs.).

Flynn, J. J.

1970. Post batholithic geology of the La Gloria Presa Rodriguez Area, Baja Califor-

nia, Mexico. Geol. Soc. Am. Bull. 81: 2409–2430.
1986. Faunal provinces and the Simpson coefficient. *In* K. M. Flanagan and J. A. Lillegraven (eds.), Vertebrates, phylogeny, and philosophy. Univ. Wyoming, Spec. Pap. 3: 317–388.

Flynn, J. J., and M. C. Novacek
1984. Early Eocene vertebrates from Baja California: evidence for intracontinental age correlations. Science 224: 151–153.

Flynn, J. J., R. M. Cipolletti, and M. J. Novacek
1989. Chronology of early Eocene marine and terrestrial strata, Baja California, Mexico. Geol. Soc. Am. Bull. 101: 1182–1196.

Gabb, W. M.
1869. Description of new species of American Tertiary and Cretaceous fossils. J. Acad. Nat. Sci. Philadelphia 4(4): 375–406.

Gastil, R. C., R. P. Phillips, and E. C. Allison
1975. Reconnaissance geology of the state of Baja California. Geol. Soc. Am. Mem. 140: 1–140.

Gazin, C. L.
1953. The Tillodontia: an early Tertiary order of mammals. Smithson. Misc. Collect. 121: 1–110.
1955. A review of the upper Eocene Artiodactyla of North America. Smithson. Misc. Collect. 128: 1–96.
1962. A further study of the lower Eocene mammalian faunas of southwestern Wyoming. Smithson. Misc. Collect. 144: 1–98.
1965a. Early Eocene mammalian faunas and their environment in the vicinity of the Rock Springs Uplift, Wyoming. Wyoming Geol. Assoc. 19th Ann. Field Conf. Guide book. pp. 171–180.
1965b. A study of the early Tertiary condylarthran mammal *Meniscotherium*. Smithson. Misc. Collect. 149: 1–98.

Gill, T.
1872. Arrangement of the families of mammals with analytical tables. Smithson. Misc. Collect. 11: 1–98.

Gingerich, P. D.
1976. Cranial anatomy and evolution of early Tertiary Plesiadapidae (Mammalia, Primates). Univ. Michigan, Pap. Paleontol. 15: 1–141.
1981. Radiation of the early Cenozoic Didymoconidae (Condylarthra, Mesonychia), in Asia, with a new genus from the early Eocene of western North America. J. Mammal. 62: 526–538.
1982. Paleocene "*Meniscotherium semicingulatum*" and the first appearance of Meniscotheriidae (Condylarthra) in North America. J. Mammal. 63: 488–491.
1983. Systematics of early Eocene Miacidae (Mammalia, Carnivora) in the Clark's Fork Basin, Wyoming. Univ. Michigan, Contrib. Mus. Paleontol. 26: 197–225.
1989. New earliest Wasatchian mammalian fauna from the Eocene of northwestern Wyoming: Composition and diversity in a rarely sampled high-floodplain assemblage. Univ. Michigan Pap. Paleontol. 28: 1–97.

Gingerich, P. D., and G. F. Gunnell
1979. Systematics and evolution of the genus *Esthonyx* (Mammalia, Tillodontia) in the early Eocene of North America. Univ. Michigan, Contrib. Mus. Paleontol. 25: 125–153.

Gingerich, P. D., K. D. Rose, and D. W. Krause
1980. Early Cenozoic mammalian fauna of the Clark's Fork Basin-Polecat Bench area, northwestern Wyoming. *In* P. D. Gingerich (ed.), Early Cenozoic paleontology and stratigraphy of the Bighorn Basin, Wyoming. Univ. Michigan Pap. Paleontol. 24: 51–68.

Gingerich, P. D., and R. A. Haskin
1981. Dentition of early Eocene *Pelycodus jarrovii* (Mammalia, Primates) and the generic attribution of species formerly referred to *Pelycodus*. Univ. Michigan, Contrib. Mus. Paleontol. 25: 327–337.

Gingerich, P. D., and C. G. Childress
1983. *Barylambda churchilli*, a new species of Pantolambdidae (Mammalia, Pantodonta) from the late Paleocene of western North America. Univ. Michigan, Contrib. Mus. Paleontol. 26: 141–155.

Gingerich, P. D., and H. A. Deutsch
1989. Systematics and evolution of early Eocene Hyaenodontidae (Mammalia, Creodonta) in the Clarks Fork Basin, Wyoming. Univ. Michigan, Contrib. Mus. Paleontol. 27: 327–391.

Givens, C. R.
1974. Eocene molluscan biostratigraphy of the Pine Mt. area, Ventura County, California. Univ. California, Publ. Geol. Sci. 109: 1–107.

Godinot, M.
1981. Les mammifères de Rians (Eocène inférieur, Provence). Palaeovertebrata 10(2): 43–126.
1982. Aspects nouveaux des echanges entre les faunas mammaliennes d'Europe et d'Amerique du Nord a la base de l'Éocene. Geobios, mem. spec. 6: 403–412.

Granger, W. D.

1915. Part III—Order Condylarthra. Families Phenacodontidae and Meniscotheriidae. *In* W. D. Matthew and W. D. Granger (eds.), A revision of the lower Eocene Wasatch and Wind River faunas. Bull. Am. Mus. Nat. Hist. 37: 821–830.

Gray, J. E.
1821. On the natural arrangement of vertebrose animals. London Med. Reposit. 15(1): 296–310.

Guthrie, D. A.
1967. The mammalian fauna of the Lysite Member, (early Eocene) of Wyoming. Mem. South. California Acad. Sci. 5: 1–53.
1971. The mammalian fauna of the Lost Cabin Member, Wind River Formation (lower Eocene) of Wyoming. Ann. Carnegie Mus. 43: 47–113.

Hecht, M. K.
1959. Amphibians and reptiles. *In* P. O. McGrew et al., The geology and paleontology of the Elk Mountain and Tabernacle Butte area, Wyoming. Bull. Am. Mus. Nat. Hist. 117(3): 130–146.

Heim, A.
1922. Notes on the Tertiary of southern Lower California (Mexico). Geol. Mag. 59: 529–647.

Hickey, L. J., R. M. West, M. R. Dawson, and D. K. Choi
1983. Arctic terrestrial biota: paleomagnetic evidence of age disparity with mid-northern latitudes during the late Cretaceous and early Tertiary. Science 221: 1153–1156.

Hoffstetter, R., and J.-P. Gasc
1969. Vertebrae and ribs of modern reptiles. *In* C. Gans, T. S. Parsons, and A. d'a Bellairs (eds.), Biology of the reptilia, Vol. 1, morphology, pp. 201–310. London: Academic Press.

Hooker, J. J.
1980. The succession of *Hyracotherium* (Perissodactyla, Mammalia) in the English early Eocene. Bull. Br. Mus. Nat. Hist. (Geol.) 33: 101–114.

Hutchison, J. H.
1980. Turtle stratigraphy of the Willwood formation, Wyoming: preliminary results. *In* P. D. Gingerich (ed.), Early Cenozoic paleontology and stratigraphy of the Bighorn Basin. Univ. Michigan. Pap. Paleontol. 24: 115–118.
1982. Turtle, crocodilian, and champsosaur diversity changes in the Cenozoic of the north-central region of Western United States. Palaeogeogr., Palaeoclimatol., Palaeoecol. 37: 149–164.

Huxley, T. H.
1862. The anniversary address. Proc. Geol. Soc. 1862: xl–liv.
1880. On the application of the laws of evolution to the arrangement of the Vertebrata and more particularly of the Mammalia. Proc. Zool. Soc. London, 1880: 649–662.

Illiger, C.
1811. Prodomus systematis mammalium et avium additis terminis zoographicis utriudque classis. Berlin: C. Salfeld, 301 pp.

Jepsen, G. L.
1930. New vertebrate fossils from the lower Eocene of the Big Horn Basin, Wyoming. Proc. Am. Philos. Soc. 69: 117–131.

Kent, D. V., M. C. McKenna, N. D. Opdyke, J. J. Flynn, and B. J. MacFadden
1984. Arctic biostratigraphic heterochroneity. Science 224: 173–174.

Kitts, D. B.
1956. American *Hyracotherium* (Perissodactyla, Equidae). Bull. Am. Mus. Nat. Hist. 110(1): 1–60.

Krause, D. W.
1978. Paleocene primates from western Canada. J. Earth Sci. 15: 1250–1271.
1980. Early Tertiary amphibians from the Bighorn Basin. *In* P. D. Gingerich (ed.), Early Cenozoic paleontology and stratigraphy of the Bighorn Basin, Wyoming. Univ. Michigan Pap. Paleontol. 24: 69–72.

Krause, D. W., and M. C. Maas
1990. The biogeographic origins of late Paleocene–early Eocene mammalian immigrants to the Western Interior of North America. *In* T. M. Bown and K. D. Rose (eds.), Dawn of the age of mammals in the north part of the Rocky Mountain Interior, North America. Geol. Soc. Am., Spec. Pap. 243: 71–105.

Krishtalka, L., and R. K. Stucky
1983. Paleocene and Eocene marsupials of North America. Ann. Carnegie Mus. 42(10): 229–263.
1985. Revision of the Wind River faunas, early Eocene of central Wyoming. Part 7. Revision of *Diacodexis* (Mammalia, Artiodactyla). Ann Carnegie Mus. 54(14): 413–486.

Leidy, J.
1869. The extinct mammalian fauna of Dakota and Nebraska including an account of some allied forms from other local-

ities, together with a synopsis of the mammalian remains of North America. J. Acad. Nat. Sci. Philadelphia 7: 1–472.

1870. Remarks on a collection of fossils from the western territories. Proc. Acad. Nat. Sci. Philadelphia 1870: 109–110.

Lemoine, V.

1889. Considérations générales sur les vertébrés fossiles des environs de Reims et specialement sur les mammifères de la fauna cernaysienne. C. R. des Séances, Congr. Internatl. Zool., Paris, pp. 233–279.

1891. Etude d'ensemble sur les dents des mammifères fossiles des environs de Reims. Bull. Soc. Geol. France 19: 263–290.

Lillegraven, J. A.

1972. Preliminary report on late Cretaceous mammals from the El Gallo Formation, Baja California del Norte, Mexico. Nat. Hist. Mus. L. A. County, Contrib. Sci. 232: 11 pp.

Linnaeus, C.

1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus differentiis, synonymis, locis. Editio decima, reformata. Stockholm: Laurentii Salvii, 1: 824 pp.

Lucas, S. G.

1982. The phylogeny and composition of the Order Pantodonta (Mammalia, Eutheria). 3rd N. A. Paleont. Convention, Proc. 2: 337–342.

Lydekker, R.

1889. Paleozoology—Vertebrata. *In* H. A. Nicholson and R. Lydekker (eds.), A manual of paleontology, 3rd. ed. Edinburgh and London: W. Blackwood 2(3): 889–1474.

MacIntyre, G. T.

1966. The Miacidae (Mammalia, Carnivora). Part 1. The systematics of *Ictidopappus* and *Proctictis*. Bull. Am. Mus. Nat. Hist. 131: 119–209.

Marsh, O. C.

1873. Notice on new Tertiary mammals. Am. J. Sci. 5: 407–410, 485–488.

1875. New order of Eocene mammals. Am. J. Sci. 9: 221.

Marshall, L. G.

1982. Systematics of the South American marsupial family Microbiotheriidae. Fieldiana: Geol. 10: 1–75.

Matthew, M. D.

1909. The Carnivora and Insectivora of the Bridger Basin, middle Eocene. Mem. Am. Mus. Nat. Hist. 9(6): 289–567.

1915. A revision of the lower Eocene Wasatch and Wind River faunas. Part 1.—Order Ferae (Carnivora), suborder Creodonta; part 4.—Entelonychia, Primates, Insectivora (part). Bull. Am. Mus. Nat. Hist. 34: 4–103; 429–483.

McKenna, M. C.

1960. Fossil Mammalia from the early Wasatchian Four Mile fauna, Eocene of northwest Colorado. Univ. California, Publ. Geol. Sci. 37: 1–130.

1972. Was Europe connected directly to North America prior to the Middle Eocene? Evol. Biol. 6: 179–188.

1975. Toward a phylogenetic classification of the Mammalia. *In* W. P. Luckett and F. S. Szalay (eds.), Phylogeny of the primates, pp. 21–46. New York: Plenum.

1984. Cenozoic paleogeography of North Atlantic land bridges. *In* M. H. P. Bott, S. Saxov, M. Talwani, and J. Thiede (eds.), Structure and development of the Greenland-Scotland Ridge, pp. 351–399. New York: Plenum Press.

Miller, G. S., and J. W. Gidley

1918. Synopsis of supergeneric groups of rodents. J. Washington Acad. Sci. 8(13): 431–448.

Mina, U. F.

1956. Bosquejo geologico de la parte sur de la peninsula de Baja California. 20th Internatl. Geol. Congr., Excursion A-7, pp. 1–79.

1957. Bosquejo geologico del territoria sur de la Baja California. Assoc. Mexicana Geol. Petrol. Bol. 9: 139–269.

Minch, J. A.

1970. Early Tertiary paleogeography of a portion of the northern Peninsular Ranges. *In* E. C. Allison et al. (eds.), Pacific slope geology of northern Baja California and adjacent Alta California. Am. Assoc. Petrol. Geol. (Pac. Sec.), Field Trip Guide Book, pp. 4–9.

Mook, C. C.

1933. A skull of *Crocodilus clavis* Cope in the United States National Museum. Am. Mus. Novitates 678: 7 pp.

Morris, W. J.

1966. Fossil mammals from Baja California: new evidence on early Tertiary migrations. Science 135(3742): 1376–1378.

1968. A new early Tertiary perissodactyl, *Hyracotherium seekinsi,* from Baja California. L. A. County Mus. Contrib. Sci. 151: 1–11.

Norell, M. A.

1989. The higher level relationships of the extant Crocodylia. J. Herp. 23(4): 325–334.

Norell, M. A., and J. M. Clark
1990. A reanalysis of *Bernissartia fagesii*, with comments on its phylogenetic postion and its bearing on the origin and diagnosis of the Eusuchia. Bull. Inst. R. Sci. Nat. Belg. (sci. Terre) 60: 115–128.

North American Commission on Stratigraphic Nomenclature (NACSN)
1983. North American stratigraphic code. Am. Assoc. Petrol. Geol. Bull. 67: 841–875.

Novacek, M. J., J. J. Flynn, I. Ferrusquía-Villafranca, and R. M. Cipolletti
1987. An early Eocene (Wasatchian) mammal fauna from Baja California. Natl. Geogr. Res. 3(3): 376–388.

Osborn, H. F.
1907. Tertiary mammal horizons of North America. Bull. Am. Mus. Nat. Hist. 23: 237–253.
1913. Lower Eocene titanotheres. Genera *Lambdotherium* and *Eotitanops*. Bull. Am. Mus. Nat. Hist. 32: 407–415.
1929. The titanotheres of ancient Wyoming, Dakota and Nebraska. U.S. Geol. Surv. Monogr. 55: 1–701.

Owen, R.
1840. Description of fossil remains of a mammal, a bird, and a serpent from the London Clay. Proc. Geol. Soc. London 3: 162–166.
1848. Description of teeth and portions of jaws of two extinct anthracotherioid quadrupeds discovered in the Eocene deposits on the N.W. coast of the Isle of Wight. Q. J. Geol. Soc. London 4: 103–141.

Parker, T. J., and W. A. Haswell
1897. A text-book of zoology. London: Macmillan, vol. 2, 683 pp.

Paula Couto, C. de
1952. Fossil mammals from the beginning of the Cenozoic in Brazil. Marsupialia: Didelphidae. Am. Mus. Novitates 1567: 26 pp.

Rage, J.-C.
1973. Presence de *Dunnophis* (Reptilia: serpentes) dans l'Eocene et l'Oligocene European. Bull. Soc. Geol. France 15(3–4): 76–78.
1974. Les serpents des phosphorites du Quercy. Palaeovertebrata 6(3–4): 274–303.
1977. An erycine snake (Boidae) of the genus *Calamagras* from the French Lower Eocene with comments on the phylogeny of the erycinae. Herpetologica 33(4): 459–463.
1984. Handbuch der Paleoherpetologie, Part 10. Stuttgart, New York: Gustav Fischer Verlag.

Rose, K. D.
1980. Clarkforkian Land Mammal Age: revised definition, zonation, and tentative intercontinental correlations. Science 208: 744–746.
1981. The Clarkforkian Land Mammal Age and mammalian faunal composition across the Paleocene-Eocene boundary. Univ. Michigan, Pap. Paleontol. 26: 1–196.

Rose, K. D., and D. W. Krause
1982. Cyriacotheriidae, a new family of early Tertiary pantodonts from western North America. Proc. Am. Philos. Soc. 126: 26–50.

Russell, D. E.
1967. Le Paléocène continental d'Amérique du Nord. Mém. Mus. Natl. d'Hist. Nat., Sér. C, 16: 39–99.

Russell, D. E., and R.-J. Zhai
1987. The Paleogene of Asia: mammals and stratigraphy. Mém. Mus. Natl. d'Hist. Nat., Sci. de la Terre 52: 1–488.

Russell, L. S.
1929. Paleocene vertebrates from Alberta. Am. J. Sci. 5: 162–178.

Santillan, M., and T. Barrera
1930. Las posibilidadas petroliferas en la costa occidental de la Baja California, entre los paralelos 30 y 32 de latitud norte: Mexico. Inst. Geol. An. 5: 1–37.

Savage, D. E., D. E. Russell, and P. Louis
1965. European Eocene Equidae (Perissodactyla). Univ. Calif. Publ. Geol. Sci. 56: 1–94.

Setoguchi, T.
1973. Late Eocene marsupials and insectivores from the Tepee Trail Formation, Badwater, Wyoming. Unpubl. Ph.D. Thesis, Texas Tech Univ., Lubbock, 101 pp.

Simons, E. L.
1960. The Paleocene Pantodonta. Trans. Am. Philos. Soc. 50(6): 1–99.

Simpson, G. G.
1937a. The Fort Union of the Crazy Mountain Field, Montana and its mammalian faunas. Bull. U.S. Natl. Mus. 169: 1–287.
1937b. Additions to the upper Paleocene fauna of the Crazy Mountain Field. Am. Mus. Novitates 940: 15 pp.
1945. The principles of classification and classification of mammals. Bull. Am. Mus. Nat. Hist. 85: 1–350.
1947. Holarctic mammalian faunas and continental relationships during the Cenozoic. Bull. Geol. Soc. Am. 58: 613–687.

Sloan, R. E.
1969. Cretaceous and Paleocene terrestrial communities of western North America. Proc. N. A. Paleontol. Convention 1(E): 427–453.

Squires, R. L.
1984. Megapaleontology of Eocene Llajas Formation, Simi Valley, California. Nat. Hist. Mus. L. A. County, Contrib. Sci. 350: 1–76.

Stehlin, H. G.
1926. Une espece lutétienne de *Dissacus*. Bull. Soc. Geol. France 26(4): 185–189.

Stucky, R. K.
1984. Revision of the Wind River faunas, early Eocene of central Wyoming. Part 5. Geology and biostratigraphy of the upper part of the Wind River Formation, northeastern Wind River Basin. Ann. Carnegie Mus. Nat. Hist. 53(9): 231–294.

Stucky, R. K., and L. Krishtalka
1983. Revision of the Wind River faunas, early Eocene of central Wyoming. Part 4. The Tillodontia. Ann. Carnegie Mus. Nat. Hist. 52(7): 375–391.

Van Valen, L.
1966. Deltatheridia, a new order of mammals. Bull. Am. Mus. Nat. Hist. 132: 1–126.
1978. The beginning of the age of mammals. Evol. Theory 4: 45–80.

Wassersug, R. J., and M. K. Hecht
1967. The status of the crocodylid genera *Procaimenoidea* and *Hassiacosuchus* in the New World. Herpetologica 23: 30–34.

West, R. M.
1976. The North American Phenacodontidae (Mammalia, Condylarthra). Contrib. Biol. and Geol., Milwaukee Publ. Mus. 6: 1–78.

Yan Defa, and Tang Yingjun
1976. Mesonychids from the Paleocene of Anhui. Vert. Palas. 14: 252–258. [in Chinese]

APPENDIX 1

AMNH Locality Descriptions

For location, see figure 4; for unit designation see Type Section (above). Also see Las Tetas Section (appendix 2) and Younger World Section (appendix 3).

1. EAST HILL CAIRN:

In stratigraphic unit 10 of Younger World Section (directly within measured section). Brown, nonresistant siltstone. Directly above red resistant marker sandstone (unit 9) 8 ft above contact with unit 9.

2. YOUNGER WORLD:

In stratigraphic unit 12 (Younger World Section), reddish brown contact with unit 13. Reddish-brown silts. Note: "white layer" in this section seems equivalent to unit 13 to 14 or 15.

3. TOO MUCH HOT:

In stratigraphic unit 12 of Younger World Section (see above).

4. MUTANT HILL:

20½ ft below base of White Sand. 3 ft below resistant gray-brown sand. Within a nonresistant brown, poorly sorted, sandy siltstone. Approximately 2½ ft above distinctive, resistant, gray, red, poorly sorted, coarse sandstone.

5. LIL' BUDDY:

Brownish-gray, poorly sorted, sandy siltstone, mottled with green. Approximately 6 ft above contact with darker brown sandy siltstone to silty sandstone. Approximately 4 ft below the White Marker Sand (white layer).

6. QUIETER LOCALITY:

In brownish gray, nonresistant, well sorted, sandy siltstone. Approximately 5 ft below a resistant pinkish red and gray coarse chunky sandstone. Approximately 29 ft below White Marker Beds.

7. WINDY GAP:

In brownish-gray, nonresistant, poorly sorted, sandy siltstone with small mottled green clays and silts. *Hyopsodus* pelvis and pes found here by M. J. Novacek in 1983. Locality is 7 ft below base of white layer.

8. MANLY MAN:

Corresponds with unit 5 in Type Section. Seminonresistant, gray, brownish green, poorly sorted, sandy siltstone with sand—about 5 ft below unit 6, resistant pinkish red coarse ledge, chunky sandstone.

9. MARSUPIAL HILL:

Corresponds with unit 5 in Type Section. Brownish gray-green, mottled, nonresistant sandy siltstone about 4½ ft above unit 4, a reddish resistant poorly sorted sand. Marsupial jaw with m2–3 (IGM 3688).

10. TWO YEARS:

Corresponds with unit 5 in Type Section. Brownish gray-green, mottled sandy siltstone. Locality in north side of wash opposite Marsupial Hill.

11. THE H-WORD:

In Unit 5 (see description for Marsupial Hill).

12. GENERIC LOCALITY:

Scattered occurrence in northwest edge of a small amphitheatre known collectively as the Generic Locality or "Reptile Saddle." All fossils appear to occur at roughly the same horizon in unit 1 in the Type Section, varying 10–12 ft below resistant pink-gray sandstone (unit 2).

13. DANGER BIRD:

Mottled brown and green clays, in nonresistant grayish brown well-sorted siltstone. Approximately 21 ft below white marker sand (white layer).

14. EEEYI-HA:

Approximately 18 ft NNW of Danger Bird Quarry in small bank. Adjacent to wash, approximately 1 ft lower stratigraphically than Danger Bird Locality.

15. THE WAY:

In a ravine on north side of northwest Tetas. In buffy-brown well-sorted siltstones. Approximately 18 ft below white marker sand (white layer).

APPENDIX 2

Las Tetas Section

Unit	Thickness	Description
01	12′5″	Red-brown, fine to medium sandstone, poorly resistant, poorly sorted, massive, micaceous.
02	6′7″	Bright red-brown, medium sandstone to pebble conglomerate, massive, resistant, multicolored grains.
03	8′6″	Dark brown, sandy siltstone to very fine sandstone, brown weathering, massive, poorly sorted, deeply weathered.
04	8′6″	Tan to brown, fine sandstone at base to sandy siltstone at top, poorly to moderately resistant, massive, micaceous, mottled near base.
05	9″	Gray weathering, matrix supported pebble conglomerate, very resistant, subangular to subrounded clasts, multicolored grains.
06	26′8″	Variegated sequence, poorly resistant.
6A	(12′4″)	Brown, fine sandstone, poorly sorted, massive.
6B	(6′0″)	Light brown, medium sandstone with some fine sandstone and silt, very poorly sorted, some red and green surface mottling.
6C	(2′6″)	Brown, silty sandstone, poorly to moderately sorted, mottled on fresh surfaces, sharp contact with 6B.
6D	(2′0″)	Gray to brown, fine to medium sandstone, distinctive, gray weathering, subangular grains.
6E	(3′10″)	Mottled green and red sandy siltstone, poorly sorted, gradational contact with 6D.
07	15′5″	Green-gray, medium sandstone to pebble conglomerate, sandstone and conglomerate lenses poorly sorted, gray to white weathering, contact with unit 6 undulating to erosional, generally massive (but x-bedding on south side of butte), relatively resistant, conglomerates matrix supported with subrounded to rounded clasts. Distinctive marker bed!
08	2′0″	Green and red, silty claystone (red layers) to fine sandstone (green layers), yellow ?limonitic staining on sandstone, wavy laminae in claystone, gradational contact with unit 9.
09	11′4″	Brown to tan-brown interbedded siltstone and fine to medium sandstone, variegated, predominantly gray-green weathering with some red weathering interbeds, gradational contact with unit 10.
10	9′0″	Brown (base) to red-brown (top) interbedded sandy siltstone to fine sandstone (base) to medium to coarse sandstone (top); brown (base) to reddish (top) weathering, micaceous.
11	10′4″	Gray to brown; coarse sandstone to pebble conglomerate; two prominent ledges 4.5′ above base and at top of unit, with slightly finer brown sandstone to conglomerate between ledges; micaceous, quartzose, some red staining, gradational contact with unit 10.
12	15′0″	Brown, nonresistant unit consisting of: (a) coarse sandstone to pebble conglomerate at base, very poorly sorted; (b) siltstone with some sandy inclusions, poorly to moderately well sorted; (c) 3′ below top of unit—red medium to coarse sandstone, distinctive, nonresistant, poorly sorted.
13	4′6″	Distinctive unit of 3 bright red weathering resistant ledges in brown, nonresistant interval; (1) red ledges are coarse sandstone, very poorly sorted, with mica/feldspar/lithics, each ledge about 0.5′ thick; (2) interbeds are red-brown, sandy siltstone, brown weathering, poorly sorted.
14	30′6″	Nonresistant variegated unit; (a) basal 8.5′ is brown, coarse sandstone; (b) next 8′ is a red interval consisting of (bottom to top): (i) brown siltstone, well sorted; (ii) pink, medium to coarse sandstone, moderately well sorted, micaceous/feldspathic/?hematitic; (iii) red, coarse sandstone, poorly sorted, micaceous; (c) top is red-brown to tan, coarse sandstone to pebble conglomerate, brown to buff-gray weathering, poorly sorted, isolated cobble-size clasts, matrix supported. Top of unit forms N base of butte cap.
15	30′0″	Interbedded lenses of (1) the base—pink to buff, coarse sandstone interbedded with thin lenses of very poorly sorted cobble to boulder conglomerate, and (2) the top—gray cobble conglomerate, thickly bedded, with minor sandstone interbeds; erosional contact with unit 14.

APPENDIX 3
Younger World Section

Unit	Thickness	Description
01	6′6″	Brownish green, fine to medium sandstone, moderately sorted, nonresistant, weathers dull brown.
02	6′0″	Red-brown, medium to coarse sandstone, well sorted, resistant, weathers red, finely laminated (may be cross-laminated).
03	10′0″	Tan, fine sandstone, nonresistant, well sorted.
04	8′0″	Red-brown, medium to coarse sandstone, lithic fragments, micaceous, weathers dull red-brown, resistant.
05	10′6″	Dark brown, fine to medium sandstone, lithics, fines upward, dark brown silty fine sandstone on top, forms less resistant hills, weathers dull tan, gradational contact with unit 4.
06	5′0″	Channel unit; dull gray pebble conglomerate, very resistant weathers buff gray, poorly sorted, angular to rounded clasts, lithic fragments, quartz sand matrix, undulating contact with unit 5.
07	8′6″	Tan to light brown, siltstone to fine sandstone, slightly micaceous, nonresistant, weathers dull brown, unit contains brown medium sandstone (lithics) stringers, abrupt contact with unit 6.
08	5′0″	Dark earth brown, clayey silt, some mica and ?fine sand, nonresistant, forms slopes, unit coarsens upward, getting sandier toward contact with unit 9.
09	5′2″	Light pinkish-gray, very coarse sandstone, lithic fragments and mica, blocky type weathering, weathers gray, forms resistant ridge, good marker bed, undulating contact with unit 8.
10A	4′8″	Dark brow-yellow siltstone to fine sandstone, very nonresistant, forms slopes, poorly sorted, some lithic fragments, fines upward, gradational contact with unit 10B.
10B	10′8″	Dark brown siltstone, slightly more resistant than unit 10A, ?root casts, gray weathering band through middle of unit, lateral variation in color.
11	4′0″	Forms a resistant ridge—marker bed; coarsens upward, base of unit is brown, medium sandstone, biotite and lithics, well sorted with angular to subrounded grains, gradational contact with unit 10B; grades upward into red-brown, very coarse sandstone, with pebbles, very poorly sorted, angular to subrounded grains, top of unit fines upward to gradational contact with unit 12.
12	4′6″	Brown, clayey fine sandstone, poorly sorted, subrounded to angular grains, nonresistant, heavily indurated on fresh surface, weathers dull brown, green sandy stringers, rapidly grades into unit 13A.
13A	7′0″	Brown-red, fine to medium sandstone, multicolored lithics, well sorted, grains rounded.
13B	1′0″	Red, coarse sandstone to pebble conglomerate, disappears laterally to the west, eastward grades into a gray pebble conglomerate, not very resistant.
14A	4′0″	Dark brown, clayey fine sandstone, feels greasy on fresh surface, nonresistant, indurated, weathers light brown, amount of sand varies laterally and vertically, grades into unit 14B.
14B	7′6″	Dark brown, fine sandstone, indurated, weathers light brown; eastward: becomes coarser, more indurated, and lighter brown to pink, medium sandstone, multicolored grains, fairly well sorted, some mica and lithic fragments, grains subrounded; farther east unit becomes very coarse sandstone, multicolored, poorly sorted, more mica and lithics, subangular to subrounded grains, abrupt contact with unit 15.
15	2′0″	Red-brown, medium sandstone, marker bed, resistant ledge, well sorted, subrounded grains, spheroidal weathering, buff-pink weathering.
16	9′0″	Light gray-brown, silty fine sandstone, weathers grayish green, very indurated, varies slightly in grain size laterally and vertically.
17	8′10″	Light brown, medium to coarse sandstone, indurated, well sorted, some mica and multicolored grains (lithics?), grains subangular to rounded, becomes lighter gray-red upward and forms resistant ridges, abundant mica and lithics.
18	9′0″	Brown-red, medium to coarse sandstone, moderately well sorted, grains subrounded, multicolored grains and mica, varies laterally to a channel pebble conglomerate, also finer laterally in places.
18B	10′8″	Gray-pink, coarse sandstone, moderately poorly sorted, very resistant, ridge-forming, some mica and lithic fragments.
19	13–19′6″	Boulder conglomerate, channels up to 6.5′ into unit 18B in places.

APPENDIX 4
Distribution of Vertebrate Taxa by Locality

Taxa	Catalog numbers	Localities (see text and Appendix 1)
Amphibia	IGM 3660	AMNH loc. 12
Anguidae	IGM 3665–3667	AMNH loc. 13
Varanidae	IGM 3661, 3662	AMNH locs. 12, 13
Serpentes, Boidae?	IGM 3663	AMNH loc. 12
Crocodylia	IGM 3664	"SB Hill" (see Cipolletti, 1986)
Mammalia		
Esteslestes ensis, n. gen. & sp.	IGM 3688	AMNH loc. 9
Ferae, indet.	IGM 4047	IGM loc. (see text)
Prolimnocyon sp.	IGM 3673	AMNH loc. 1
Oxyaena sp.	IGM 4051	IGM loc. (see text)
Hyopsodus sp.	IGM 3674	AMNH loc. 7
Ectocion ignotum, n. sp.	IGM 3675	AMNH loc. 8
Phenacodus cf. *P. vortmani*	IGM 4034	IGM loc. (see text)
Meniscotherium cf. *priscum*	IGM 3676–3681, 4035	AMNH locs. 5, 1 "Quieter West," IGM loc. D (see text)
Dissacus sp.	IGM 4038, 4040, 4041	IGM loc. (see text)
?Pantolambdidae, ?n. gen.	IGM 4043	IGM loc. 48 (see text)
Esthonyx sp.	IGM 4044–4046	IGM loc. (see text)
Hyracotherium seekinsi	LACM 15349, IGM 3685	LACM loc. (see Morris, 1968), AMNH loc. 13
Eotitanops cf. *E. princeps*	IGM 4048	IGM loc. (see text)
Diacodexis cf. *D. gracilis*	IGM 3684, 4049, 4050	AMNH loc. 1, IGM locs. (see text)
Paramyidae, gen. and sp. indet	IGM 3686	AMNH loc. 15
Wyolestes iglesius, n. sp.	IGM 3669–3672	AMNH locs. 2, 3, 8

APPENDIX 5

Mammalian Faunal Comparisons

Genera taken from Gingerich (1989, table 27) that occur in 20 localities in the Bighorn and Clark's Fork basins of northwestern Wyoming. According to Gingerich (1989), these localities comprise an earliest Wasatchian mammal fauna (Wa_0) that correlates with earliest Sparnacian faunas of Europe. Zones, in order of decreasing age, are Clarkforkian (Cf_2, Cf_3) and Wasatchian (Wa_0, Wa_1, Wa_2) subdivisions based on faunas discussed in Gingerich (ibid.) and other references cited therein. Genera and orders from Lomas las Tetas de Cabra are indicated in boldface.

Taxa	Cf_2	Cf_3	Wa_0	Wa_1	Wa_2
Multituberculata					
Ectypodus	X	X	X	X	X
Marsupialia					
Mimoperadectes			X	X	X
"Proprimates"					
Cf. *Niptomomys*	X	X	X	X	X
Arctodontomys	X		X	X	X
Phenacolemur	X	X	X	X	X
Primates					
Cantius			X	X	X
Tillodontia					
Azygonyx	X	X	X	X	X
Esthonyx			X	X	X
Pantodonta					
Coryphodon	X	X	X	X	X
Taeniodonta					
Ectoganus			X		
Creodonta					
Dipsalidictis	X	X	X	X	X
Palaeonictis	X	X	X	X	X
Acarictis			X	X	X
Prototomus			X	X	X
Arfia			X	X	X
Prolimnocyon			X	X	X
Carnivora					
Viverravus	X	X	X	X	X
Didymictis	X	X	X	X	X
Miacis			X	X	X
Rodentia					
Acritoparamys	X	X	X	X	X
Paramys	X	X	X	X	X
Condylarthra					
Thryptacodon	X	X	X	X	X
Chriacus	X	X	X	X	X
Hyopsodus			X	X	X
Ectocion	X	X	X	X	X
Phenacodus	X	X	X	X	X
Copecion		X	X	X	X
Meniscotherium		X	X		
Acreodi					
Dissacus	X	X	X	X	X
Pachyaena			X	X	X
Artiodactyla					
Diacodexis			X	X	X
Perissodactyla					
Hyracotherium			X	X	X
Edentata					
Palaeanodon	X	X	X	X	X
Mammalia incertae sedis					
Cf. *Asiabradypus*			X		

APPENDIX 6

Simpson Coefficients of Faunal Similarity

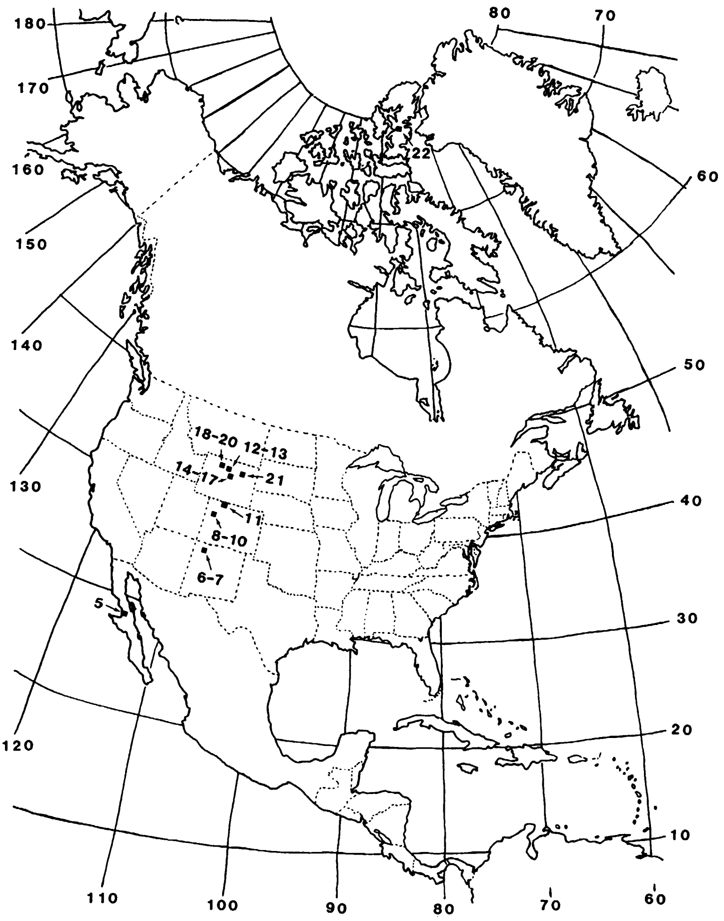
Table of coefficients of resemblance (below) for 34 Eocene faunas (including the Tetas de Cabra fauna) from North America, Europe, and Asia. The index of similarity, the Simpson coefficient, is $C/N_1 \times 100$, where C is the number of taxa (at a specified taxonomic level) in common between the two samples (faunas) compared, and N_1 is the total number of taxa (at the same taxonomic level) in the smaller of the samples. Data shown here are derived from table 8 in J. J. Flynn (1986). Numbers in map 1 and table 1 of this appendix correspond to the following localities or faunas (for original references, see Flynn ibid.).

NORTH AMERICA

1. Composite Clarkforkian Land Mammal Age
2. Composite Graybull (Wasatchian Land Mammal Age)
3. Composite Lysite (Wasatchian Land Mammal Age)
4. Composite Lost Cabin (Wasatchian Land Mammal Age)
5. Tetas de Cabra Fauna, Baja, California
6. San Juan Basin, New Mexico—Almagre
7. San Juan Basin, New Mexico—Largo
8. Piceance Basin, Colorado—Early Wasatchian
9. Piceance Basin, Colorado—Late Wasatchian
10. Piceance Basin, Colorado—Middle Wasatchian
11. Four Mile Local Fauna, NW Colorado
12. Willwood Fm., Wyoming—No Water Fauna, Sand Creek Facies
13. Willwood Fm., Wyoming—No Water Fauna, Elk Creek Facies
14. Wind River Fm., Wyoming—Lysite
15. Wind River Fm., Wyoming—Lost Cabin
16. Wind River Fm., Wyoming—*Lambdotherium* Zone
17. Wind River Fm., Wyoming—*Palaeosyops borealis* Zone
18. Willwood Fm., Wyoming—*Haplomylus*-Ectocion Zone
19. Willwood Fm., Wyoming—*Bunophorus* Zone
20. Willwood Fm., Wyoming—*Heptodon* Zone
21. Powder River Basin, Wyoming
22. Eureka Sound Formation, Ellesmere Island, Canada

LOC	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	LOC
1	--	65	44	31	64	56	52	55	48	43	58	60	65	45	29	32	18	59	59	47	65	50	32	25	33	38	41	33	32	28	24	36	35	8	1
2	85	--	75	59	82	82	78	90	83	71	80	85	81	82	52	55	40	89	91	77	87	50	50	43	53	66	82	50	45	48	42	55	65	13	2
3	74	83	--	75	73	80	85	76	80	86	69	62	71	98	58	68	48	66	85	83	68	50	42	43	56	59	76	50	41	38	44	51	60	13	3
4	74	84	94	--	83	78	89	76	83	93	58	55	60	86	78	72	66	57	88	81	61	75	37	40	47	55	71	50	36	34	38	43	50	18	4
5	75	83	92	92	--	73	73	64	73	64	64	64	73	64	73	55	45	64	73	64	55	13	64	45	36	55	45	18	27	36	36	45	27	27	5
6	79	96	**	**	92	--	93	76	70	64	64	67	82	64	62	51	42	78	76	73	74	38	49	42	44	48	65	50	36	34	38	44	55	11	6
7	78	94	**	**	75	**	--	52	70	56	56	67	85	74	70	52	52	78	70	78	44	25	44	37	30	37	47	50	18	22	30	37	30	11	7
8	68	91	**	**	83	91	78	--	83	64	83	79	90	69	72	59	48	83	66	72	62	50	55	41	34	38	47	33	27	24	41	55	35	14	8
9	73	92	**	**	92	92	89	95	--	82	60	65	83	68	68	50	43	73	74	70	61	50	48	40	36	48	65	50	27	31	38	45	40	13	9
10	68	86	**	**	75	91	83	86	91	--	57	61	79	82	82	68	57	68	68	86	46	50	50	39	29	43	53	42	18	18	36	46	35	18	10
11	82	96	93	93	83	86	78	86	85	77	--	76	80	50	53	47	36	80	65	62	94	50	51	42	50	48	65	42	36	38	40	49	60	11	11
12	83	**	93	93	83	89	89	86	85	82	93	--	91	57	47	47	32	82	71	60	84	50	45	38	47	59	76	50	41	41	36	47	60	8	12
13	82	97	89	91	83	96	94	91	96	91	96	97	--	84	55	62	46	92	94	83	94	50	47	42	50	59	71	50	41	48	42	53	70	16	13
14	75	89	**	**	75	82	89	91	85	95	75	82	93	--	73	55	43	70	79	84	52	50	43	39	36	48	65	50	36	34	36	41	50	13	14
15	71	81	92	94	92	**	**	**	**	**	89	90	86	**	--	74	76	51	74	64	61	75	30	32	36	38	47	42	36	38	34	38	45	21	15
16	67	83	90	93	83	79	83	86	85	91	79	79	87	79	90	--	70	55	59	60	42	63	45	40	50	45	59	33	36	34	38	43	55	13	16
17	65	81	90	94	83	82	83	86	85	82	75	79	84	82	94	87	--	42	53	44	35	63	32	30	39	34	41	42	23	28	28	32	50	16	17
18	79	94	88	91	83	93	94	91	88	91	93	97	94	93	85	83	81	--	88	72	90	50	45	43	53	55	71	50	41	41	42	53	65	8	18
19	81	**	92	96	75	88	83	86	85	92	**	88	92	88	92	77	81	**	--	94	55	50	59	50	38	45	59	50	32	34	44	50	45	9	19
20	75	88	97	97	92	93	94	95	96	**	86	90	91	**	97	83	84	91	96	--	65	63	40	36	42	48	65	50	32	31	34	40	50	16	20
21	78	**	91	91	67	91	72	68	78	68	96	91	**	74	91	78	78	95	78	87	--	38	52	42	42	41	53	42	27	34	39	48	50	13	21
22	67	67	83	**	50	83	67	83	83	83	67	67	67	67	**	83	**	67	67	83	67	--	38	38	25	25	25	13	13	25	38	38	13	25	22
23	70	82	79	76	83	82	83	82	81	77	86	86	79	75	73	77	71	79	81	72	83	67	--	74	97	97	**	**	91	90	76	94	**	11	23
24	56	62	62	62	75	64	67	59	62	59	68	69	62	57	62	67	62	62	62	56	65	67	82	--	86	62	71	58	59	52	94	74	85	5	24
25	70	81	78	74	67	67	67	59	62	59	70	74	78	59	70	74	70	78	62	67	70	50	**	93	--	59	71	67	55	48	81	83	80	6	25
26	80	95	95	95	67	90	67	75	80	80	90	95	95	90	90	90	80	95	85	90	75	67	95	85	80	--	**	**	50	48	62	76	65	10	26
27	76	**	**	**	58	94	65	76	82	82	94	**	**	94	94	94	82	**	88	94	76	67	**	88	82	**	--	50	35	47	59	65	47	18	27
28	67	92	92	92	42	92	67	83	83	92	83	92	92	92	92	92	83	92	92	92	83	33	92	75	75	**	75	--	42	67	50	67	50	25	28
29	87	93	93	93	58	93	60	53	73	60	87	93	93	73	93	87	80	93	73	87	80	17	**	93	87	80	67	67	--	95	59	68	30	0	29
30	82	**	**	**	75	**	65	65	82	65	94	**	**	82	**	88	88	**	82	94	82	33	**	82	76	76	71	75	93	--	55	62	45	10	30
31	57	67	63	63	67	57	61	55	58	50	61	62	63	50	63	60	60	63	54	53	56	67	80	**	81	75	76	67	80	71	--	79	85	5	31
32	79	90	83	79	83	75	83	77	77	68	82	83	86	68	76	72	72	86	77	76	78	67	97	83	89	85	88	75	87	88	79	--	85	5	32
33	75	94	94	94	50	88	56	63	75	63	88	94	94	75	88	94	88	94	69	81	75	33	94	94	94	81	69	67	60	63	94	94	--	10	33
34	25	33	42	46	42	33	33	36	38	36	29	25	38	33	46	38	42	25	25	38	30	67	33	25	21	30	29	50	27	35	25	21	25	--	34

Appendix 6, table 1. Simpson coefficients of similarity for genera (upper half) and families (lower half) for Eocene North American, European, and Asian faunas. Localities corresponding to numbers on margins of matrices are listed above and correspond to numbers shown in the map. Double asterisk (**) denotes similarity of 100. From Flynn (1986).



Appendix 6, map 1. North American localities compared using Simpson coefficients. Key to numbers is given on opposite page. From Flynn (1986).

EUROPE

23. Composite Sparnacian
24. Composite Cuisian
25. Mutigny Local Fauna (Sparnacian) France
26. Abbey Wood and Suffolk Pebble Beds (Sparnacian), England
27. Blackheath Beds, England
28. Suffolk Pebble Beds, England
29. Dormaal, France
30. Dormaal = Upper Landenian, NW Europe
31. Sable a Unios et Teredines, France
32. Argile a lignites and Argiles Plastique, France
33. Rians, France

ASIA

34. Early Eocene of Asia (composite)

APPENDIX 7

Notes on the Herpetofauna from Lomas las Tetas de Cabra

A few reptilian remains were collected from Lomas las Tetas de Cabra. Although extremely fragmentary, these specimens represent five taxa. Most of the reptilian fossils were collected at the Danger Bird and Generic localities (see appendix 1); however, a few elements were collected as float in other localities.

Following is a list of reptilian and amphibian specimens with comments on their affinities.

AMPHIBIA

MATERIAL: IGM 3660, proximal end of a right femur.

LOCALITY: Generic Locality.

COMMENTS: Judging by the breadth of the proximal end and the width of the shaft, the femur was about 1.5 cm long when complete.

Not enough of the specimen is preserved to refer it to a less inclusive taxon than Caudata. The presence of amphibian taxa in the Lomas las Tetas de Cabra fauna is potentially interesting because amphibian remains are very rare in late Paleogene North American faunas. In fact, no amphibian remains have been reported for late Paleogene localities in the Bighorn basin despite extensive collecting (Krause, 1980).

REPTILIA

SQUAMATA

ANGUIDAE

MATERIAL: IGM 3665, 3666, 3667, several isolated osteoderms.

LOCALITY: Danger Bird.

COMMENTS: Several isolated, small, subrectangular osteoderms were encountered during the quarrying operation at the Danger Bird Quarry. These osteoderms measure approximately 7 mm on the long axis and 4 mm on the short axis. Their dorsal surface is covered with small, evenly spaced tubercles. A short, smooth lappet is present along the anterodorsal surface.

The osteoderms resemble those of a host of different glyptosaurine anguids. Unfortunately, isolated and disassociated body osteoderms are not sufficient to adequately differentiate these taxa. Glyptosaurine anguid reptile remains are among the most common elements in similarly aged faunas in North America and Europe.

VARANIDAE

MATERIAL: IGM 3661, caudal vertebra; IGM 3662, trunk vertebra.

LOCALITY: Generic Locality, Danger Bird.

COMMENTS: The caudal vertebra is small (1 cm) in length and relatively complete. Although the intervertebral articulations are weathered, the specimen shares derived characters with *Lanthanotus* and the Varanidae. These include a constriction anterior to the vertebral condyle (Hoffstetter and Gasc, 1969), the presence of zygantra and zygosphenes (albeit poorly developed), and an absence of autotomic septa (Estes et al., 1988). The elongate centrum of the vertebra is very reminiscent of extant Varanidae. The trunk vertebra is somewhat less complete, but shows the development of zygantra and zygosphenes as well as a constriction anterior to the vertebral condyle. The trunk vertebra is comparable in size to the aforementioned caudal one. Varanids (i.e., the genus *Saniwa*) are common elements of North American early and middle Eocene faunas.

SERPENTES

BOIDAE?

MATERIAL: IGM 3663, trunk vertebra.

LOCALITY: Generic Locality.

COMMENTS: This medium-size vertebra (7 mm in length) is nearly complete. It is wider than long, and no hypapophysis is present, although a poorly developed hemal keel is preserved. The neural spine, although broken, was restricted to the posterior part of the vertebra and was thick and tubular as can be inferred from its base. The neural arch is upswept posteriorly and the paradiapophysis is not distinctly divided.

All of these characteristics are consistent with assignment to the Boidae; however, determination of snake vertebrae, especially those from broken single specimens, is extremely tenuous. Boids are very common elements of North American and European Eocene faunas.

ARCHOSAUROMORPHA

CROCODYLIA

MATERIAL: IGM 3664, a broken tooth

LOCALITY: "Snake Butt Hill," described in Cippoletti (1986).

COMMENTS: The single broken tooth is 2 cm in length and represents the area above the shaft. Unfortunately, crocodylian teeth are notoriously uninformative for identification to low-level taxa.

APPENDIX 7—TABLE 1

Number of Genera Occurring in the Late Paleocene and Eocene of Europe and North America[a]

	Europe	North America	Both		Europe	North America	Both
Late Paleocene				Middle Eocene			
Crocodylians	0	2	0	Crocodylians	8	8	3
Snakes	0	0	0	Snakes	2	18	0
Lizards	1	3	0	Lizards	10	6	0
Amphisbaenians	0	1	0	Amphisbaenians	0	2	0
Turtles	1	2	0	Turtles	3	3	0
Total	**2**	**8**	**0**	**Total**	**23**	**36**	**3**
Early Eocene				Late Eocene			
Crocodylians	4	3	1	Crocodylians	3	3	1
Snakes	4	0	1	Snakes	7	3	0
Lizards	4	8	0	Lizards	9	4	0
Amphisbaenians	0	2	0	Amphisbaenians	0	0	0
Turtles	6	2	0	Turtles	3	2	0
Total	**18**	**15**	**2**	**Total**	**22**	**12**	**1**

[a] Data from: turtles—DeBroin, 1977; snakes—Rage, 1983; lizards and amphisbaenians—Estes, 1983a; crocodylians—Norell, 1989.

The tooth is slightly recurved with distinct fluting. Such fluting is present on several extant *Crocodylus* and in many fossil Crocodylia (sensu Norell and Clark, 1990). It is relevant that this specimen is found in a marine estuarine deposit, because today only members of the crocodylid group (sensu Norell, 1989) occupy marine or estuarine environments.

INDETERMINATE

Several other extremely fragmentary specimens were collected that are undoubtedly reptilian. Included are an edentulous lizard jaw fragment from Danger Bird Quarry and a few fragments of snake vertebra. These materials were so fragmentary that they do not deserve further comment.

DISCUSSION

The Lomas las Tetas de Cabra fauna is unusually depauperate for Wasatchian reptile faunas, which typically contain a diversity of lizards, snakes, turtles, and crocodylians. Most notable is the absence of turtles. At other Wasatchian localities, turtles make up a high percentage of vertebrate fossils encountered. Also noticeably absent are crocodylian remains. Only a single tooth was found, and this was collected in the marine/estuarine locality of "Snake Butt (SB) Hill." Absent are the common alligatorids typical of most North American Wasatchian localities.

Because the fauna is so depauperate, comparison with other Wasatchian faunas is difficult. However, comparisons between typical North American Early Eocene reptile faunas, and syntemporal European ones, are interesting because they show a different pattern than the associated mammal faunas.

During the Late Paleocene and Early Eocene, many of the European mammalian faunas show increasing taxonomic similarity with North American faunas—suggesting a close faunal relationship between the two areas during the Early Tertiary (McKenna, 1972; Godinot, 1982; Simpson, 1947; Flynn, 1986). Similarity in mammalian faunas between the Paleogene of North America and Europe has been well documented. This interchange, reviewed in McKenna (1972), Godinot (1982), and Simpson (1947), began in the Late Clarkforkian/Early Sparnacian and culminated in the Wasatchian/Late Sparnacian Eocene. By Middle Eocene times these mammalian faunas are approximately 60% identical at the generic level (Godinot, 1982), causing Flynn (1986) to suggest that "High similarities for Early Eocene faunal comparisons indicate presence of a single North American–European faunal realm" (Flynn, 1986: 317). The extensive mammalian interchange increases likelihood that reptilian faunas would also show increased similarity during this time period.

APPENDIX 7—TABLE 2
Occurrences of Selected Paleocene and Eocene Crocodylian Taxa in Europe and North America

Asterisks indicate taxa with additional distributions outside Europe and North America

Europe	North America	Both
Late Paleocene		
	Leidyosuchus	
	Ceratosuchus	
	Allognathosuchus	
Early Eocene		
Kentisuchus	*Orthogenysuchus*	*Allognathosuchus*
Eosuchus		
*Asiatosuchus**		
Middle Eocene		
*Asiatosuchus**	*Brachyuranochampsa*	*Allognathosuchus*
Caimanosuchus	"*Crocodilus*" *afinis*	*Pristichampsus*
Dollosuchus	"*Crocodilus*" *acer*	*Diplocynodon*
Eocenosuchus	*Procaimanoidea*[a]	
Hassiacosuchus[a]	*Leidyosuchus*	
Late Eocene		
Arambourgia	*Procaimanoidea*	*Pristichampsus*
Diplocynodon	*Allognathosuchus*	

[a] *Procaimanoidea* and *Hassiacosuchus* were considered synonymous by Wassersug and Hecht, 1967, and *Hassiacosuchus* and *Allognathosuchus* were considered synonymous by Berg, 1967.

Table 1 of appendix 7 displays the Early Tertiary occurrence of reptilian (lizard, turtle, snake, amphisbaenian, and crocodylian) genera between North America and Europe. In general, reptile faunas do not display levels of faunal resemblance equivalent to those of mammals. This lack of similarity is in direct contrast to high levels of mammalian faunal similarity reported during this interval (Flynn, 1986; Godinot, 1982) and has not been previously documented. The following comments pertain to specific phylogenetic groups.

LIZARDS

Estes' (1983a) monograph of the fossil record of lizards and amphisbaenians of the world indicates that none of the 32 Late Paleocene and Eocene genera listed occur contemporaneously in North America and Europe. Two lizard genera, *Tinosaurus* and *Saniwa,* occur during this general time span on both continents. These taxa do not have overlapping transcontinental temporal ranges. *Tinosaurus* also occurs in the Late Eocene and Paleocene of central Asia. One lizard genus (*Melanosaurus*) has a doubtful joint European–North American occurrence, and another Eocene European taxon (*Ophisaurus*) has congeners occurring in North America from the Oligocene to the Recent (Estes, 1983a); however, European and North American *Ophisaurus* may not constitute a monophyletic group (Estes, personal commun.). North American and European Middle Paleogene lizard faunal assemblages are virtually incomparable because no genera and only 5 of 12 European and North American families known from relevant fossils occur on both continents. Estes (1983b) indicated that the pattern of modern lizard distribution reflects ancient continental splitting events. The reasons for the maintenance of this pattern in the face of massive translocation of associated mammals is not clear.

SNAKES

A similar pattern is indicated by snake faunas. No genera of Paleocene snakes common to North America and Europe have been identified (Rage, 1984). During the Eocene, when the record is better, only the genus *Palaeophis* is found on both continents contemporaneously. This genus is a circum-Atlantic marine taxon found only in marine or near shore deposits. Two other taxa have a shared geographic range; their occurrence, however, is not contemporaneous. *Calamagras* occurs in the Middle Eocene of North America (Hecht, 1959) and the Early Eocene of Europe (Rage, 1977). The *Calamagras-Ogmophis* group of primitive erycine boids is poorly defined; the genera are not demonstrably monophyletic and are in need of complete revision (Rage, 1984).

Dunnophis, a tropidopheine snake, occurs in the Late and Early Eocene of Europe (Rage, 1973, 1974) but is restricted to the Middle Eocene of North America (Hecht, 1959). In North America, the published occurrence of this taxon is limited to a single vertebra, although an undescribed form apparently exists in the Late Eocene (Rage, 1984), and Estes (1976) questionably referred a Paleocene specimen to this genus.

TURTLES

Turtles occur commonly in most Eocene and Paleocene fossiliferous deposits, in some cases permitting their usage as stratigraphic indicators (Hutchison, 1980). Yet, even though they are abundantly preserved, their provincial distribution pattern is similar to other "reptilian" taxa. None of the genera listed by DeBroin (1977) is definitively common to North America and Europe during the Late Paleocene and Early Eocene. The genus *Palaeotrionyx*, well known in North America and reported in the Paleogene of Europe, is problematic and may not constitute a monophyletic group (Meylan, personal commun.); the North American forms may be referred to *Conchochelys* (DeBroin, 1977). Hutchison (1982) indicated higher turtle diversities for the North American Early Eocene (15 genera). Unfortunately, he did not list these genera and it is not possible to make direct comparison with the European record. He also stated that "tabulations are based upon numerous taxonomic decisions which may or may not follow the published literature" (1982: 151). It is probable that Paleogene turtle generic diversity approaches these values (Meylan, personal commun.); until these taxa are explicitly documented, however, DeBroin's (1977) tabulation is the best available. The genera listed for the Early Eocene Willwood Formation of the Bighorn Basin by Hutchison (1980) do not increase generic similarity between North America and Europe.

CROCODYLIANS

Crocodylians are more difficult to compare, because many taxa have been lumped into the genus *Crocodylus* by earlier workers. The monophyly of this genus is difficult to establish and it is unlikely that Early Tertiary specimens are assignable to a monophyletic group containing only extant *Crocodylus*. Pending phylogenetic revision, we consider the Bridgerian North American taxa "*Crocodylus*" *clavis* and "*Crocodylus*" *affinis* equivalent to generic-level taxa. A synopsis of valid North American and European Eocene crocodylian taxa is presented in table 2 of this appendix. These recommendations are reflected in the following comments.

Berg (1969) suggested that the Bridgerian "*Crocodilus*" *clavis* (Cope, 1873c; Mook, 1933) was referable to the European and Asian genus *Asiatosuchus*. If this suggestion is accepted, faunal similarity is increased and the distribution of this taxon is extended to all of the Northern Hemisphere continents. Berg, however, provided no basis for the inclusion of "*C.*" *clavis* in an expanded *Asiatosuchus*. Restudy of the two taxa indicates that they are not a demonstrably monophyletic unit. The extensive curved retroarticular process and the undivided retroarticular fossa in *Asiatosuchus* are not present in the type specimen of "*Crocodylus*" *clavis*.

If comparisons are restricted to well-documented material, Europe and North America possess distinct crocodylian faunas in the Early Tertiary, with no unequivocal species, and three genera (*Allognathosuchus*, *Pristichampsus*, and *Diplocynodon*) common to both areas. Fossil crocodylian genera show a stable pattern of European–North American similarity from the Early to the Late Eocene.

The rich Middle Eocene crocodylian faunas of both Europe and North America appear to be endemic units that did not respond in kind to the changes promoting the mixing of mammalian faunas. Crocodylian taxa display a typical reptilian pattern of faunal provinciality with little taxonomic resemblance between European and North American continental faunas; they do not increase in similarity during the Eocene.

CONCLUSIONS

Compared with mammalian faunas, the lower degree of taxonomic similarity between Eocene reptilian faunas of Europe and North America is perplexing. This discontinuity may be the result of different factors influencing the spread and proliferation of mammalian communities as opposed to reptilian ones. High-latitude climatic barriers seem unlikely, however, because a characteristic reptilian fauna including large lizards, turtles, and crocodylians has been documented from the Early Eocene of Ellesmere Island (Estes and Hutchison, 1980). This occurrence is north of, or equal in latitude to, the hypothesized Early Eocene intercontinental land connection (McKenna, 1984) and represents an interval of tropicality.

Substantive differences between reptilian and mammalian genera and their fossil records are difficult to express. An obvious difficulty is that reptilian and mammalian genera are recognized on different criteria. For instance, unlike mammals, reptiles have dental remains that are usually useful only in recognizing high-level groups. Complete cranial material, necessary for diagnosis of low-level taxa, is rarely preserved.

The pattern of faunal similarity seen in generic comparisons, however, is also present at higher levels. If reptile and mammal faunas are compared at the family level, similarities among reptiles do not increase to levels comparable with those of mammals. Transcontinental family similarities among squamates (phylogenetically the best known of reptilian groups) do not increase dramatically during the Eocene, during which only 4 of 12 lizard families are shared between Europe and North America. One of these (Agamidae) also occurs in the Asian Eocene. Levels of similarity do not increase appreciably from Late Paleocene (1 shared occurrence) to Middle Eocene (2 families) and Late Eocene (1 shared family) horizons. Thus, even at more inclusive taxonomic levels, the similarity of North American and European Eocene reptile faunas is less than that displayed by mammals.

APPENDIX 8

Faunal Composition and Correlations, Marine Strata, Rosarito Quadrangle

Taxa from marine units adjacent to the terrestrial section represented at Lomas las Tetas de Cabra (see text) followed by charts showing correlations between bivalve and molluscan range zones and calcareous nannoplankton zones, planktonic foraminifera zones, and standard ages. Data are from Flynn et al. (1989).

"Snake Butt (SB) Hill" Locality

For description, see Flynn et al. (1989).

BIVALVIA

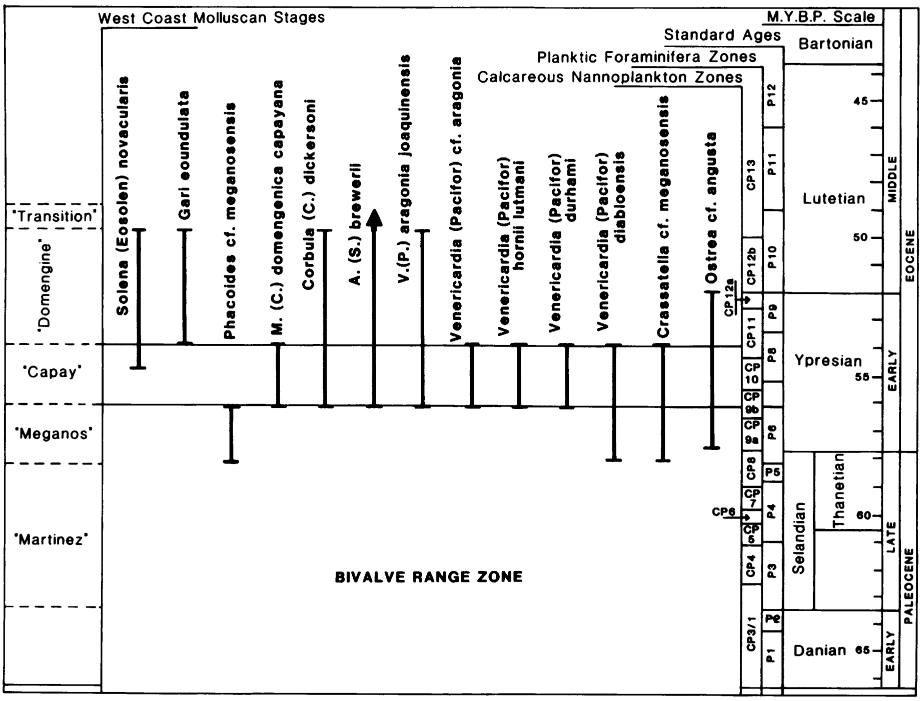
Solena (*Eosolen*) *novacularis*
Venericardia (*Pacifor*) *durhami*
V. (*P.*) *diabloensis*
V. (*P.*) cf. *aragonia*
V. (*P.*) *aragonia lutmani*
V. (*P.*) *aragonia joaquinensis*
Corbula (*Carycorbula*) *dickersoni*
Phacoides cf. *meganosensis*
Crassatella cf. *meganosensis*
Crassatella sp.
Gari eoundulata
Ostrea cf. *angusta*
Acanthocardia (*Shedocardia*) *brewerii*
Macrocallista (*Costocallista*) *domengenica capayana*

GASTROPODA

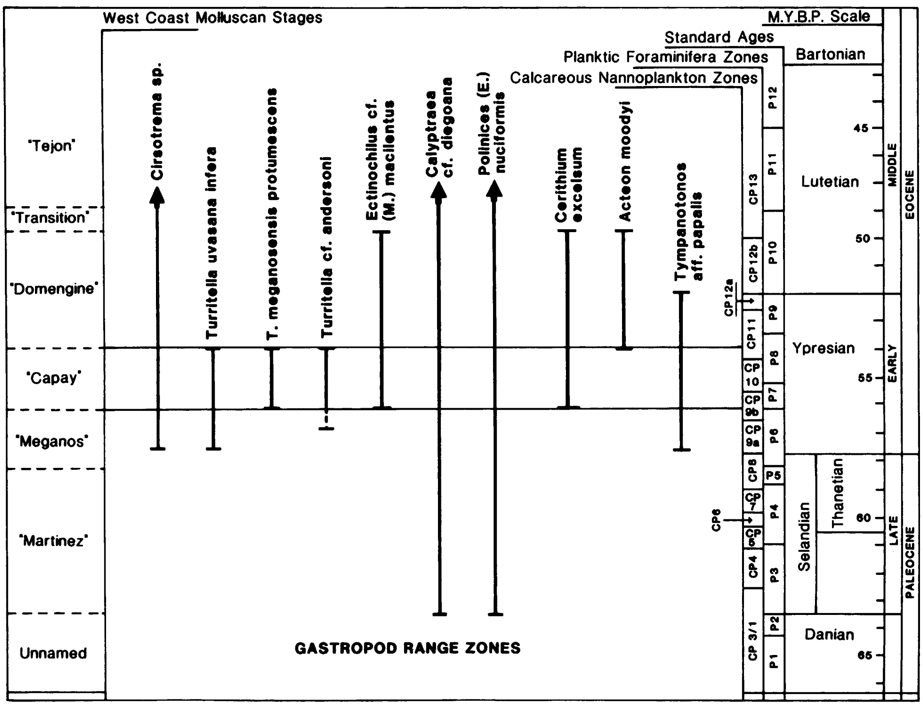
Cirsotrema sp.
Turritella uvasana infera
Cerithium excelsum
Polinices (*Euspira*) *nuciformis*
Calyptraea cf. *diegoana*
Tympanotonos aff. *papalis*
Acteon moodyi
Ectinochilus cf. (*Macilentos*) *macilentus*

BENTHIC FORAMINIFERA

Elphidium californicum
Quinqueloculina cf. *josephina*



Appendix 8, fig. 1. Standard biostratigraphic range zones of bivalve taxa present in "SB Hill" and "Slump Hill" sections. For explanation and sources see Flynn et al. (1989).



Appendix 8, fig. 2. Standard biostratigraphic range zones of gastropod taxa present in "SB Hill" and "Slump Hill" sections. For explanation and sources see Flynn et al. (1989).

Quinqueloculina triangularis
Cibicides cf. *cushmani*
Discorbis cf. *coalingensis*
Amphistegina sp.

"Slump Hill" (SH) Locality

For description, see Flynn et al. (1989).

BIVALVIA

Pholadomya sp.
Macrocallista n. sp.
M. (*C.*) *domengenica capayana*

GASTROPODA

Turritella cf. *andersoni*
T. meganosensis protumenscens
Cerithidea?

APPENDIX 9

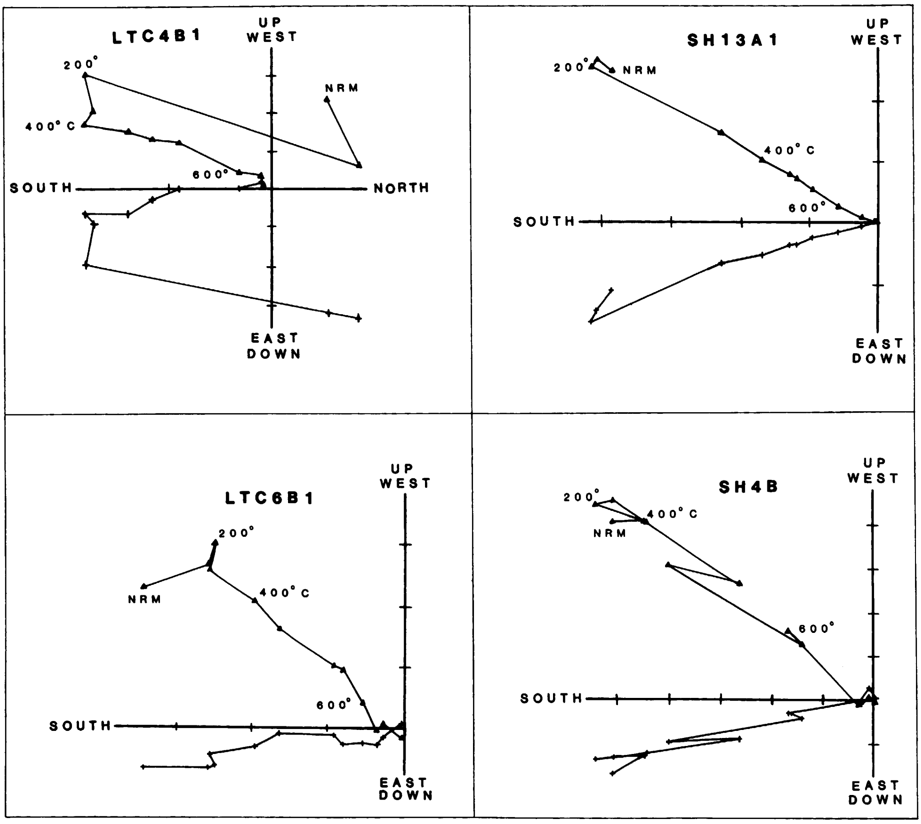
Paleomagnetic Results

Lomas las Tetas de Cabra Section (LTC)/GTXX Section (GTXX)

Site #	DEC	INC	N	K	CofC	R	PLNG	PLAT
GTXX 1	188.0	-49.1	3	20.33	28.1	2.902	142.8	-82.9
GTXX 2*	183.0	-39.3	3	3.27	83.7	2.388	222.2	-83.1
GTXX 3	206.9	-63.4	4	48.35	13.4	3.938	111.2	-63.2
GTXX 4*	25.5	-64.3	3	1.08	>90	1.151	48.2	11.8
GTXX 5	158.3	-49.1	3	113.91	11.6	2.982	345.5	-71.1
GTXX 6	187.2	-54.4	3	30.49	22.7	2.934	108.2	-81.2
LTC 1	175.2	-42.8	4	60.05	12.0	3.950	295.9	-84.3
LTC 2	172.1	-51.9	3	90.61	13.0	2.980	7.9	-82.2
LTC 3	159.9	-46.8	4	40.69	14.6	3.926	339.0	-72.3
LTC 4	164.7	-47.8	3	38.48	20.2	2.948	340.9	-76.6
LTC 5	169.6	-36.3	3	17.25	30.6	2.884	296.6	-77.3
LTC 9*	178.2	-33.8	2	12.06	79.7	1.917	255.7	-79.8
LTC 6	179.2	-43.8	3	87.75	13.2	2.977	259.6	-86.9
LTC 7	173.7	-52.2	3	304.21	7.1	2.993	15.4	-83.1
LTC 8	176.0	-70.8	4	5.21	44.6	3.424	60.9	-63.3
LTC 10	145.4	-36.8	3	156.15	9.9	2.987	329.4	-57.6
LTC 11	144.4	-40.0	3	14.99	33.0	2.867	334.0	-57.5
LTC 12	135.8	-28.7	3	342.97	6.7	2.994	327.6	-47.2
LTC 13	181.0	-52.4	3	136.21	10.6	2.985	76.8	-85.5
LTC 14	178.7	-70.0	3	26.11	24.6	2.923	64.2	-64.6
LTC 15	154.1	-47.1	3	39.37	19.9	2.949	341.5	-67.3
LTC 16	165.5	-51.4	3	42.45	19.2	2.953	355.1	-77.0
LTC 17	176.7	-41.7	3	12.43	36.6	2.839	279.6	-84.5
Mean	167.5	-50.0	16	30.25	6.8	15.504	343.1	-76.2
"Slump Hill" Section (SH)								
SH 14	131.4	-29.5	3	5.72	57.2	2.650	330.9	-43.6
SH 15*	124.2	-7.3	3	4.33	68.4	2.538	321.6	-31.6
SH 1	174.0	4.5	3	5.67	57.5	2.647	257.7	-58.7
SH 2	143.3	-33.4	3	136.13	10.6	2.985	327.2	-55.0
SH 3	155.8	-48.7	3	51.42	17.4	2.961	344.9	-68.9
SH 4	156.1	-41.7	4	71.62	10.9	3.958	329.7	-68.2
SH 5	143.4	-48.5	4	6.04	40.8	3.503	346.9	-58.1
SH 6	153.3	-49.4	4	24.81	18.8	3.879	346.9	-66.7
SH 7	155.3	-41.3	4	208.96	6.4	3.986	346.7	-68.5
SH 8	155.0	-47.7	5	451.63	3.6	4.991	342.8	-68.1
SH 9*	180.9	-48.6	3	4.62	65.5	2.567	102.4	-88.7
SH 16	160.0	-14.4	3	152.00	10.0	2.987	291.6	-61.6
SH 12	155.8	-38.8	4	16.49	23.3	3.818	324.7	-67.2
Mean 1	153.5	-36.2	11	18.09	11.0	10.447	322.7	-64.5
Mean 2	153.3	-40.7	9	45.79	7.7	8.825	329.8	-65.5
Younger World Section (YW)								
YW 1	165.2	-41.2	4	45.94	13.7	3.935	318.9	-75.8
YW 2	153.3	-32.6	4	26.30	18.3	3.886	317.9	-63.2
YW A3	168.0	-41.6	3	65.53	15.4	2.969	315.3	-78.3
YW B3	152.1	-50.0	3	48.77	17.9	2.959	348.1	-65.7
YW C3	162.5	-56.0	3	42.47	19.2	2.953	8.9	-73.3
YW 4	170.0	-53.8	3	27.55	24.0	2.927	12.5	-79.7
YW 5	195.1	-57.4	3	80.78	13.8	2.975	115.3	-74.3
YW 6	149.1	-45.9	3	5.50	58.6	2.637	340.7	-62.8
YW 7	23.9	-70.2	5	2.69	58.1	3.512	52.3	4.6
YW 8	151.5	-51.7	3	233.78	8.1	2.991	351.8	-65.2
YW 9	161.6	-36.9	4	103.49	9.1	3.971	314.5	-71.5
YW 10*	160.2	-64.1	3	4.58	65.9	2.564	29.3	-66.8
YW 11	166.7	-51.4	3	12.23	36.9	2.837	356.1	-78.0
YW 12	171.4	-60.7	4	18.10	22.2	3.834	40.2	-75.2
YW 13	182.9	-46.7	3	23.85	25.8	2.916	169.6	-87.4
YW 14	205.0	-62.4	4	23.81	19.2	3.874	112.2	-65.0
YW 15	177.6	-45.9	4	28.18	17.6	3.894	304.9	-87.5
YW 16	141.1	-56.4	4	4.86	46.6	3.383	0.7	-56.5
YW 17	170.7	-54.4	4	23.50	19.4	3.872	17.1	-79.9
YW 18*	218.5	-61.9	3	1.61	>90	1.756	120.3	-56.0
Mean	165.0	-53.4	18	20.65	7.8	17.177	2.3	-76.1
Composite section mean								
	161.4	-48.2	3	93.39	12.8	2.979	342.7	-73.7
Composite individual site mean								
	162.5	-49.3	48	23.04	4.4	45.960	346.1	-74.7

Mean, section mean; Mean 1 includes SH1 and SH14, Mean 2 excludes SH1 and SH14 (marginally significant); Composite section mean, mean of LTC/GTXX, YW, and SH (Mean 2) section means; Composite individual site mean, mean of all statistically significant sites; DEC, site mean declination; INC, site mean inclination; N, number of samples; K, kappa, magnetic precision parameter; CofC, angular radius of the 95% cone of confidence about the observed mean; R, resultant vector (giving unit values to each N vector); PLNG, PLAT, paleopole longitude and latitude calculated from the mean direction; *, mean direction not statistically significant at [illegible]

Appendix 9, table 1. Paleomagnetic site—mean directions for Lomas las Tetas de Cabra from Flynn et al. (1989). For further explanation, see Flynn et al. (1989).



Appendix 9, fig. 1. Vector demagnetization diagrams for representative pilot samples from the Lomas las Tetas de Cabra (LTC) and "Slump Hill" (SH) paleomagnetic sections. Progressive thermal demagnetization from NRM to 650°C. Crosses, horizontal component of magnetization vector; triangles, vertical component of vector. Scale divisions are in $10^{-3}/4\pi$.amps/meter. For original source and further explanation, see Flynn et al. (1989).

APPENDIX 10

Abstract and Summary (in Spanish)

Resumen

Mamíferos fósiles y restos de otros vertebrados de Lomas Las Tetas de Cabra en Baja California Norte, México nos dan la oportunidad de examinar la escala geocronológica continental basada en faunas de mamíferos terrestres. Reportes anteriores indican que estas faunas son del Paleoceno tardío a Eoceno temprano. Recientes campañas de terreno y una gran acumulación de fósiles descubiertos, indican que la fauna de Baja representa la edad Wasatchian de mamíferos terrestres (Eoceno temprano) y es parecida a las faunas de esta edad del Oeste interior de los Estados Unidos. Los taxa de edad Wasatchian representados en la colección de Baja, incluyen *Hyracotherium, Hyopsodus, Meniscotherium* (muy posible también de la colección Clarkfordian), *Diacodexis,* y *Prolimnocyon.* También en la fauna hay excelentes muestras de *Wyolestes* y *Esteslestes,* un nuevo género de marsupiales didélfidos, como también un cráneo de pantodonte en muy mal estado. Una asignación al Eoceno temprano es sostenida por un análisis en la sección marina adyacente a la secuencia de Tetas de Cabra. Los organismos marinos son consistentes con la asignación a la edad Ypresian media (Eoceno temprano). Un análisis paleomagnético en secciones terrestres y marinas también comprueban la asignación a esta edad. Nuevos resultados solidifican la validez de Wasatchian como un intervalo temporal discreto que puede ser aplicado en la escala continental. La Wasatchian, así, llena las expectaciones cronológicas basadas en mamíferos. Semejanzas, más que differencias, entre las colecciones de Baja y otras faunas de edad Wasatchian son el patrón dominante. Preferencias entre teorías de dispersión para el orígen de los mamíferos Wasatchian no están claramente indicadas con la evidencia de la fauna.

Introducción

Estudios intensivos de faunas de mamíferos (Eoceno anterior) de edad Wasatchian (Gingerich et al., 1980) proporcionan un rico y fascinante capítulo en la historia del Cenozoico. La edad Wasatchian es ahora definida, y separada del Clarkfordian temprano de mamíferos terrestres, por la primera aparición de caballos puros (*Hyracotherium* y otros perisodáctilos), arctiodáctilos, primates mas desarrollados, algunas formas parecidas a los carnívoros, y algunos linajes especializados de la radiación del tronco de los ungulados (Gingerich and Gunnell, 1979; Gingerich et al., 1980; Gingerich and Haskin, 1981; Rose, 1980, 1981; Gingerich, 1989; Krause and Maas, 1990). Sin embargo, estas distinciones son basadas en colecciones de formaciones geológicas entre las Montañas Rocosas de los Estados Unidos (fig. 1). Por lo tanto, la edad Wasatchian, aunque claramente definida taxonómicamente, se aplica a la fauna inferior con una distribución relativamente restricta latitudinal y longitudinalmente.

Nuevos estudios profundos de la edad Wasatchian de mamíferos terrestres, han salido de recientes documentaciones de faunas de vertebrados fósiles de Baja California. Estas colecciones llenan dos importantes requisitos para un exámen de la edad de mamíferos terrestres. Primero, la fauna de Baja está removida geográficamente de las agrupaciones de la localidad de edad Wasatchian en las Montañas Rocosas (fig. 1). Segundo, la sucesión de Baja está intrincada, con sedimentos de la costa marina con una gran colección de macroinvertebrados y microorganismos. Esta situación, como también la oportunidad de muestreos paleomagnéticos, indican el potencial de la colección de Baja de perfeccionar el Cenozoico temprano en la escala del tiempo y el desarrollo de una idea más comprensiva de la historia de mamíferos en Norte América.

Recientes excavaciones intensivas como también una síntesis del resultado de previas exploraciones en la localidad de Baja (Flynn and Novacek, 1984) demuestran la utilidad de los mamíferos terrestres de edad Wasatchian para una correlación más amplia en la escala continental. Además, la fauna de Baja añade otra dimensión a la historia biogeográfica de Norte América durante este intervalo de tiempo tan interesante. Este reporte es un informe extensivo de la taxonomía de mamíferos en la fauna y una sinopsis de las implicaciones geocronológicas y geográficas en otros reportes examinados.

Comparación Faunal y Edad Correlativa

Las implicaciones geocronológicas y biogeográficas de la fauna de Baja han sido consideradas por otros (Flynn and Novacek, 1984; Cipolletti, 1986; Novacek et al., 1987; Flynn et al., 1989) y están resumidas brevemente aquí. El modelo dominante representado por la fauna de mamíferos es de gran similaridad con las fauna de edad Wasatchian del oeste interior. Esto es de gran importancia porque los mamíferos terrestres anteriores a la Clarkfordian están ahora claramente distinguidos de los Wasatchian. Semejanzas a la edad Wasatchian están distinguidas claramente sobre Clarkfordian. Algunos taxa (*Hyracotherium,* *Hyopsodus, Diacodexis, Wyolestes, Prolimnocyon,* y *Eotitanops*) que hacen su primera aparición en Wasatchian son también conocidos en Las Tetas de Cabra. Los taxa provenientes de Baja, con primeras apariciones anteriores en otros lugares (*Esthonyx, Oxyaena, Meniscotherium*-ver Gingerich, 1989, *Phenacodus*) no contradicen la asignación de edad, como se sabe que estos taxa son de la fauna Wasatchian también. Reconocimiento de la edad de mamíferos terrestres depende de la primera ocurrencia (Flynn and Novacek, 1984) y bajo este criterio la asignación a la edad Wasatchian para la fauna de Baja está claramente establecida. Como antes mencionado, una confirmación al Eoceno temprano es preferible que al Paleoceno tardío para las localidades de Baja es proporcionada por pruebas independiente de las unidades marinas adyacentes que contienen fósiles de invertebrados y foraminíferos bentónicos. Cipolletti (1986) documentó varias especies de moluscos que indican a "Capay" como representante marino y a la edad Ypresian asignados para estas capas. La edad Ypresian es actualmente igualada al Eoceno temprano (Berggren et al., 1985).

Una tercera fuente de prueba para esta asignación de edad se basa en análisis paleomagnéticos. Todas las localidades paleomagnéticas de las secciones (marinas y terrestres) están invertidas magnéticamente y la ya mencionada relación biocronológica sugiere correlatividad a esta polaridad invertida con Crono 23R o el intervalo de polaridad invertida dentro del Crono 24N. Estos son intervalos correlativos con biozonas de foraminíferos planctónicos Ypresian medio P7 a P8 tardío y biozonas calcáneas no planctónicos medio CP9b a temprano CP11. Por lo tanto, paleomagnéticos no proporcionan una independencia estricta de la escala del tiempo, pero estos resultados sí confirman Eoceno temprano asignado a base de pruebas bioestratigráficas (Flynn et al., 1989).

Más de un siglo de trabajo ha establecido el argumento de que la edad de la mayoría de mamíferos terrestres de Norte América está severamente sincronizada y por lo tanto provechosa para la geocronología. Un corolario es que eventos de dispersión de alto grado—aquellos que intentar explicar el orígen de géneros característicos de la edad de los mamíferos terrestres—no se puede detectar hasta que una cronología basada en esta edad de mamíferos terrestres sea aceptada. Enfáticamente los eventos de dispersión deben ser expresados en una escala maas fina (e.g., modelos nivel-especie) que el cambio de fauna que documenta discretamente la edad de mamíferos terrestres. Recíprocramente, teorías de los eventos de dispersion incluyendo los géneros de mamíferos, tendrían que abandonar el tiempo-calibre-mamífero—una acción requerida por la demostración de asincronismo entre faunas mamíferas de igual composición. Esto parece particularmente evidente por cualquier teoría que proponga a una dirección de dispersión. Es este caso la demostración de asincronismo es mínima—pero no el único requisito para el argumento de ciertos organismos que se movieron en cierta dirección de un lugar a otro.

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