Paludicola 11(1):8-30 October 2016

NEW RECORDS OF *EPIHIPPUS* (EQUIDAE) AND A RHINOCEROTOID PERISSODACTYL FROM THE MIDDLE EOCENE SANTIAGO FORMATION OF SOUTHERN CALIFORNIA

Thomas S. Kelly[1] and Paul C. Murphey[2]

[1]Research Associate, Vertebrate Paleontology Department, Natural History Museum of Los Angeles County,
900 Exposition Blvd., Los Angeles, California 90007
[2]Research Associate, Department of Paleontology, San Diego Museum of Natural History,
1788 El Prado, San Diego, California 92101

ABSTRACT

Records of the middle Eocene equid *Epihippus* from the West Coast of North America are extremely rare. Previously, only one specimen was reported from California in a faunal list of the Mission del Oro Local Fauna from the Santiago Formation of San Diego County, but this specimen was never described or illustrated and its specific status remained undetermined. Subsequently, additional specimens of *Epihippus* from southern California have been discovered as the result of paleontological mitigation programs conducted for commercial development projects. Here we provide detailed accounts of all of the *Epihippus* specimens currently known from California, wherein we recognize the occurrence of two species, *E. gracilis* and *E. uintensis*. A rhinocerotoid, which likely represents either *Uintaceras* or *Teletaceras*, is also recorded from the Santiago Formation of San Diego County. In addition, a new middle Eocene fauna is documented, the Rancho Mission Viejo Local Fauna, which is the first fauna of the early Uintan North American Land Mammal Age recorded from Orange County.

INTRODUCTION

Contrary to the early and late Eocene faunas of North America, horses are a relatively rare component in middle Eocene faunas of the Bridgerian, Uintan and Duchesnean North American Land Mammal Ages, primarily being known from the western interior and Gulf Coast Plain (Granger, 1908; Matthew, 1929; McGrew, 1953; Gazin, 1976; MacFadden, 1980,1998; Rasmussen, et al., 1999a, 1999b; Froehlich, 2002; Kelly et al., 2012). During the early Eocene Wasatchian North American Land Mammal Age, horses were common and diverse, including at least six genera and 13 species (Froehlich, 2002). By the beginning of the Bridgerian, horse diversity had rapidly declined with only one genus, *Orohippus* Marsh, 1872, being recognized (MacFadden, 1998). *Orohippus* gave rise to *Epihippus* in the earliest Uintan and the latter gave rise to *Duchesnehippus* Peterson, 1931, in the Duchesnean. During the late Duchesnean *Duchesnehippus* gave rise to *Mesohippus* Marsh, 1875, which became abundantly represented by numerous species during the early Chadronian (late Eocene) through earliest Arikareean (early late Oligocene) North American Land Mammal Ages (MacFadden, 1998).

Occurrences of middle Eocene horses are extremely rare in southern California. Walsh (1996b) reported the first record of *Epihippus* in a faunal list of the Mission del Oro Local Fauna from the Santiago Formation of San Diego County, but did not provide a description or illustration of the specimen. Extensive, ongoing paleontological mitigation programs have been conducted since 1996 in southern California, which have resulted in new records of *Epihippus* from three additional localities in the Santiago Formation (Figure 1). A rhinocerotoid specimen, which was not described or illustrated, was previously recorded from the Santiago Formation of San Diego County and misidentified as *Hyracodon* sp. (Tomiya, 2012). These perissodactyl records are highly significant to our understanding of the middle Eocene biostratigraphy of southern California. The purpose of this report is to provide detailed accounts of all of the known specimens of *Epihippus* from California and reevaluate the taxonomic status of the rhinocerotoid specimen.

METHODS

Measurements of teeth were made with an optical micrometer to the nearest 0.01 mm. Equid dental terminology follows Froehlich (2002) and that

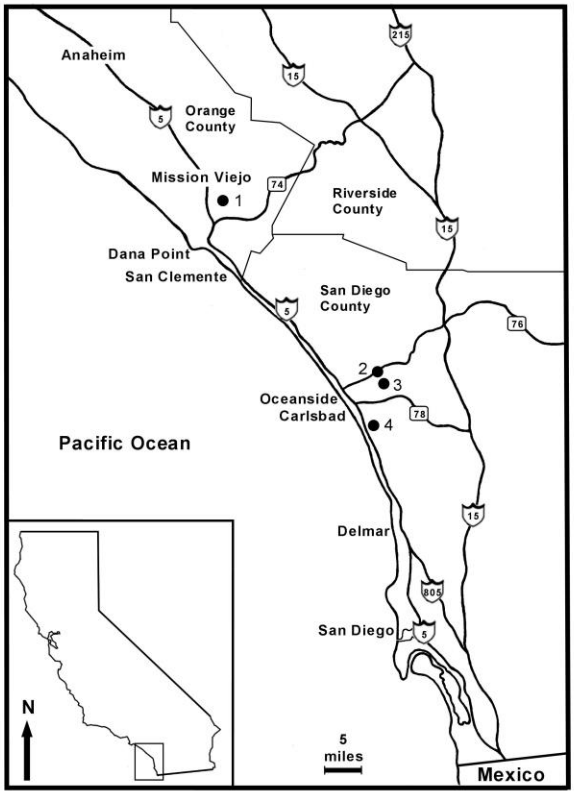

FIGURE 1. Map of southern California coastal area showing geographic locations of middle Eocene localities that yielded *Epihippus*. 1, Rancho Mission Viejo (locality OCPC 03976), Orange County. 2, Mission del Oro (locality SDSNH 3574), San Diego County. 3, Ocean Ranch (locality SDSNH 4730), San Diego County. 4, Legoland (locality SDSNH 4131), San Diego County. Insert map shows area covered by map.

for Rhinocerotoidea follows Dashzeveg and Hooker (1997) except that we prefer the term cristid obliqua instead of metalophid for the cristid that extends anterolingually from the hypoconid to protolophid. Upper and lower teeth are designated by uppercase and lowercase letters, respectively. Open nomenclature qualifiers follow Bengtson (1988). All specimens described here are curated in the research collections at the Department of Paleontology at the San Diego Museum of Natural History, San Diego, California and the Orange County Paleontological Collection at the Dr. John D. Cooper Archaeological and Paleontological Center, Orange County, California. Detailed locality data are available at these institutions.

Subzones or biochrons of the Bridgerian and Uintan North American Land Mammal Ages (e.g., Br3, Ui1a, Ui1b, Ui2, and Ui3) follow Gunnell et al. (2009).

Abbreviations are: ap, greatest anteroposterior length; CV, coefficient of variation; L, left; Ma, megannum (one million years in the radioisotopic time scale); N, number of specimens; R, right; SD, standard deviation; tr, greatest transverse width; tra, anterior transverse width; trp, posterior transverse width. Abbreviations for institutions and specimens cited in text are: OCPC, Orange County Paleontological Collection at the Dr. John D. Cooper Archaeological and Paleontological Center, Orange County, California; SDNHM, San Diego Natural History Museum; SDSNH, San Diego Society of Natural History.

GEOLOGIC SETTING

The type Santiago Formation was first named by Woodring and Popenoe (1945) for outcrops on Santiago Creek to the east of Irvine Park in the Santa Ana Mountains of Orange County, California. The Santiago Formation unconformably overlies the Paleocene Silverado Formation and unconformably underlies the middle Eocene (late Uintan) to Miocene Sespe Formation and/or the informal unit referred to by Whistler and Lander (2003) as the Sespe-Vaqueros Formations undifferentiated (see also Woodring and Popenoe, 1945; Morton, 1974; Schoellhamer et al., 1981; Prothero, 2001). In the type area, the formation is divided into two informal units, the lower and upper beds (Schoelhammer et al., 1981). The lower beds are characterized by medium to coarse grained, cross-bedded sandstones, greenish-gray to reddish mudstones and conglomerate lenses near the base, whereas the upper beds are characterized by medium to fine grained, poorly bedded sandstones, greenish-gray to reddish variegated sandy siltstones and claystones (Woodring and Popenoe, 1945; Morton, 1974).

In northern San Diego County, outcrops have also been referred to the Santiago Formation by Wilson (1972), wherein he recognized three informal members (members A, B and C). Based upon early Uintan mammal faunas from the upper part of member B and correlation with Calcareous Nannoplankton Zones, Planktonic Foraminiferal Zones, Benthic Foraminiferal Stages and West Coast Molluscan "Stages," Walsh (1996b) regarded member B of the Santiago Formation in northwestern San Diego County to span the late Bridgerian to early Uintan North American Land Mammal Ages, or about 48-45.5 Ma, and a correlative to the La Jolla Group of southwestern San Diego County. Member C of the Santiago Formation is separated from member B by an unconformity in northwestern San Diego County and has yielded middle Eocene mammal faunas of late Uintan and early Duchesnean Ages (Walsh, 1996b; Walsh et al., 1996; Prothero, 2001; Mihlbachler and Deméré, 2009). Based on magnetostratigraphy, Walsh et al. (1996) correlated the La Jolla Group to Chron C21n and the lower third of Chron C20r of the Global Polarity Time Scale, or about 47.9-45.5 Ma. Prothero (2001) reported that the lower part of the type Santiago Formation in Orange County was entirely within a paleomagnetic normal zone, which he correlated to Chron C21n. Prothero (2001) was unable to sample the magnetostratigraphy of the upper part of the type Santiago Formation, so its polarity has not been determined. The Bridgerian-Uintan transition is regarded by most recent investigators as occurring within Chron C21n at about 47 Ma (e.g., Walsh, et al., 1996; Robinson et al., 2004; Gunnell, et al., 2009; Kelly and Murphey, 2016).

LOCALITIES AND FAUNAS

Mission del Oro—Walsh (1996b) named the Mission del Oro Local Fauna based on a fauna from three localities (SDSNH 3570, 3572, 3574) in member C of the Santiago Formation that were discovered during the grading of the Mission del Oro housing project, Oceanside, California (Figure 2, Table 1). The localities occur in brownish, gritty mudstones interbedded within coarse-grained, arkosic channel sandstones, about 9 to 10 m above the disconformity that separates members B and C. Locality SDSNH 3574 yielded the first record of *Epihippus* from California. Based primarily on the presence of *Protylopus* sp., cf. *P. robustus* Golz, 1976, in the fauna, Walsh (1996b) regarded the Mission del Oro Local Fauna to be a correlative of the Laguna Riviera Local Fauna from member C at the Laguna Riviera housing district, Carlsbad, and latest Uintan or earliest Duchesnean in age. *Protylopus robustus* is also known from the late Uintan Brea Canyon Local Fauna of the Sespe Formation of Ventura County, California (Kelly, 1990; Kelly et al., 1991; Kelly and Whistler, 1994). Walsh (1996b) also noted that another locality (SDSNH 3235) at Mission del Oro, which occurs in an exposure that is separated from the section that yielded the Mission del Oro Local Fauna by a covered portion and estimated to be about 30 to 35 m stratigraphically higher, yielded *Duchesneodus uintensis* and *Amynodontopsis bodei*, species which are generally regarded as characteristic taxa of the early Duchesnean (Rasmussen et al., 1999b; Robinson et al., 2004; Kelly et al., 2012). Based upon a partial left dentary with m1-3 (SDSNH 43478), Tomiya (2012) listed the occurrence of *Hyracodon* sp. from locality SDSNH 3574, a genus that is generally considered as having its first appearance in the late Duchesnean (Krishtalka et al., 1987; Prothero, 1998; Kelly et al., 2012). However, this specimen was originally cataloged as *Triplopus*, and Tomiya (2012) did not describe or illustrate the specimen. In order to clarify the systematic status of SDSNH 43478, we reexamined it and provide a detailed description below, which indicates that it cannot be assigned to either *Triplopus* or *Hyracodon*.

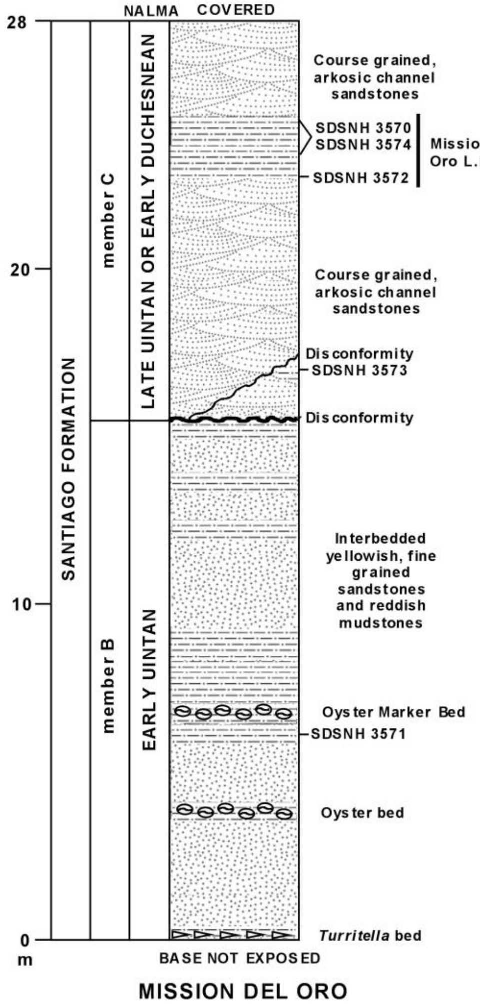

FIGURE 2. Generalized stratigraphic column of Santiago Formation at Mission del Oro housing project showing localities that yielded the Mission del Oro Local Fauna. Stratigraphic column modified after Walsh (1996b).

Rancho Mission Viejo—A small paleontological mitigation program was conducted in 2010 at Rancho Mission Viejo during the excavation and grading for a substation, which resulted in the discovery a single locality (SDSNH 6407) that yielded a small sample of fossil mammals. Subsequently, Kelly (2015) reported on the fossil mammals recovered from two additional localities (OCPC 03976 and OCPC 03988) at Rancho Mission Viejo that were discovered during an ongoing paleontological mitigation program for Rancho Mission Viejo Planning Area 2, conducted by Archaeological Resource Management Corporation of Rancho Palos Verdes, California (Figure 3). Planning Area 2 included the major excavation and grading of a large area of the foothills along the north side of San Juan Creek, adjacent to the substation and between the mouths of Cañada Chiquita and Cañada Gobernadora, Orange County, California. The paleontologic program at Rancho Mission Viejo has also resulted in the recovery of plant fossils, including leaf and seed impressions, silicified logs and palynomorph assemblages. In a mitigation report for the program, Fisk et al. (2015) documented a plant assemblage from Rancho Mission Viejo consisting of ferns, cedars, alders, palms, magnolias, wild avocados, evergreen oaks and cattails, which they interpreted to represent a lowland to montane rain-forest community that was significantly wetter and warmer than the present day climate.

The section exposed during excavation at the Rancho Mission Viejo substation included about 6.6 m of Santiago Formation and about 3.2 m of unconformably overlying Quaternary terrace deposits. The stratigraphy of the Santiago Formation at the substation consisted of the following, in ascending order: 1) a basal 0.61 m yellowish-grey sandy siltstone containing locality SDSNH 6407; 2) about 5 m of light gray, coarse grained sandstone; and 3) about 1 m of yellowish-green siltstone.

The two new vertebrate localities discovered during excavation activities in 2013 and 2014, along with SDSNH 6407, occur on the east side of Planning Area 2. The lithology on the east side of Planning Area 2 differs from that of the west side, which yielded most of the plant fossils. The west and east sides cannot be directly correlated because of local faulting, inconsistent small scour-filled channel cuts, the lack of marker beds that can be traced from one side to the other, and the fact that a major fissure zone separates them. However in both sides of Planning Area 2, a series of fining up cycles (12 on the east side and 15 on the west side), each consisting of a sandstone unit and overlying claystone unit, were recognized by Patrick Riseley (per. communication, 2015). Patrick kindly provided us with his stratigraphic sections of the east and west sides of Planning Area 2, of which that of the east side containing the vertebrate fossil localities is shown in Figure 4.

Except for locality OCPC 03988, most of the fossil mammals from Rancho Mission Viejo were recovered from bulk samples of screen-washed matrix, yielding small fossil containing concretions that were then dissolved using peroxide. The concretions often contained a mixture of iron oxide and green waxy claystone, which made preparation difficult. Many of the mammalian fossils recovered were fragmentary, consisting of isolated teeth, partial isolated teeth and appendicular elements, some of which were articulated. Some taxa are represented by either a single specimen or a few specimens, so confident taxonomic allocation at the species level could not always be made with confidence. Furthermore, generic level identifications were also difficult for some taxa due to the lack of intact dentitions. Considering these facts, most generic referrals presented here are conservative (Table 2), wherein they are often only compared to (cf.) a genus, indicating that they either actually represent the genus or a closely related genus (after Bengtson, 1988). Nevertheless, the mitigation programs have resulted in the recognition of a relatively diverse mammalian fauna containing at least 18 taxa representing seven orders from the Santiago Formation at Rancho Mission Viejo (Table 2). This fauna is referred to the Rancho Mission Viejo Local Fauna. The presence of *Palaeictops*, *Patriolestes davisi*, *Achaenodon robustus*, *Leptoreodon marshi*, *Protoreodon* sp., cf. *P. parvus*, *Merycobunodon* and possibly *Hesperolemur*, taxa that have been previously recorded from the early Uintan Poway Fauna of the Friars Formation of southwestern San

TABLE 1. Faunal list of Mission del Oro Local Fauna from localities SDSNH 3570, 3572, and 3574, Oceanside, San Diego County, California, member C, Santiago Formation, latest Uintan or earliest Duchesnean (Walsh,1996b; Tomiya, 2012; this paper).

- Mammalia
  - Didelphomorphia
    - Peradectidae
      - *Peradectes californicus* Stock, 1936
  - Lipotyphla
    - Sespedectidae
      - *Sespedectes singularis* Stock, 1935a
      - *Proterixoides davisi* Stock, 1935a
  - Rodentia
    - Ischyromyidae
      - *Microparamys* sp.
      - *Mytonomys* sp
      - *Eohaplomys* sp., cf. *E. serus* Stock, 1935b
    - Cylindrodontidae
      - *Pareumys* sp.
    - Eomyidae
      - *Metanoiamys* sp.
    - Geomyidae?
      - *Griphomys* sp.
    - Simimyidae
      - *Simimys simplex* (Wilson, 1935)
  - Perissodactyla
    - Rhinocerotoidea
      - genus and species undetermined (probably *Uintaceras* or *Teletaceras* sp., not *Hyracodon* sp. vide Tomiya [2012])
    - Brontotheriidae
      - cf. *Duchesneodus* sp.
    - Equidae
      - *Epihippus uintensis* (Marsh, 1875)
  - Artiodactyla
    - Agriochoeridae
      - *Protoreodon* sp.
    - Oromerycidae
      - *Protylopus* sp., cf. *P. robustus* Golz, 1976

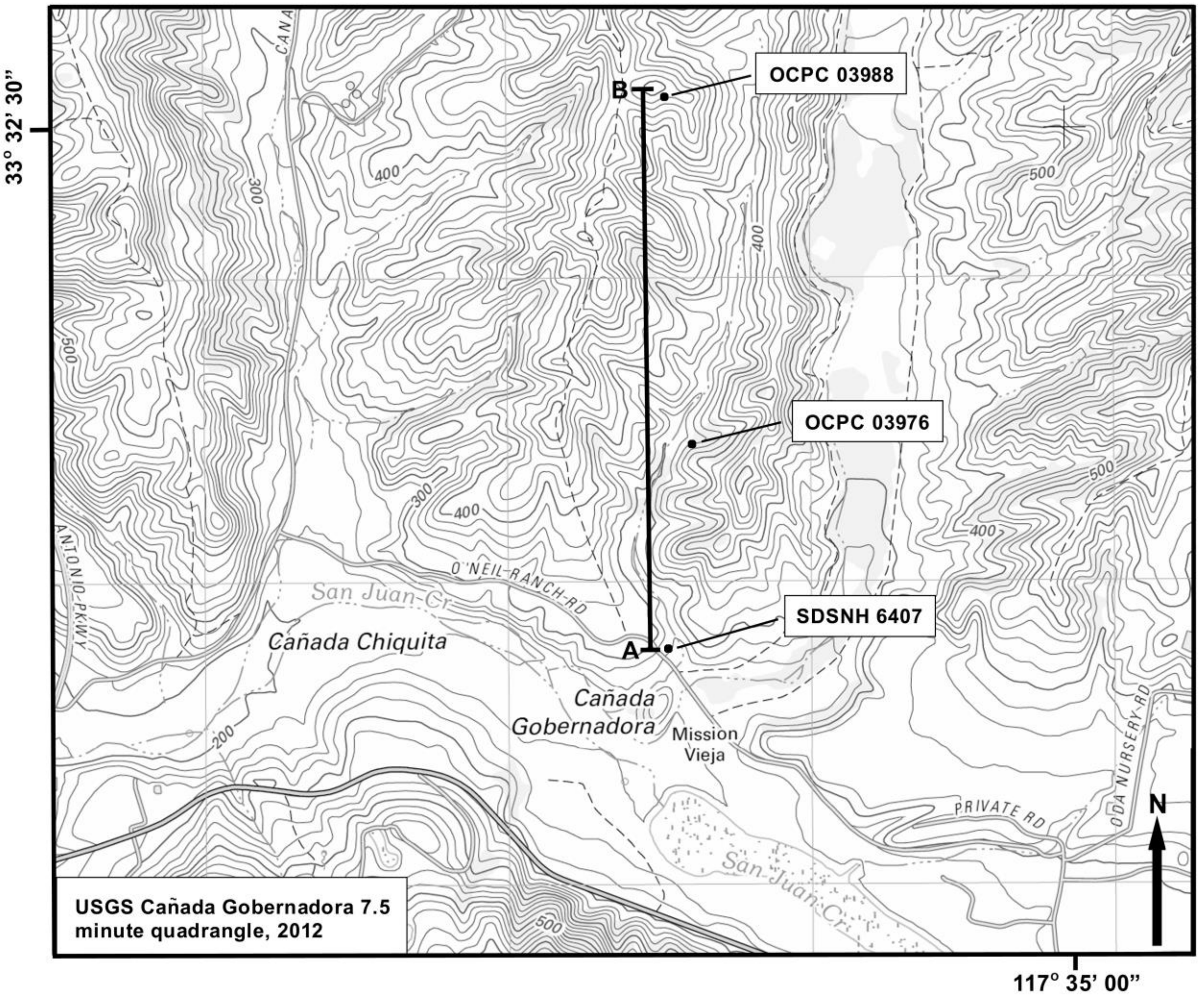

FIGURE 3. Map showing the geographic locations of the three fossil localities (SDSNH 6407, OCPC 03976, and OCPC 03988) that yielded the Rancho Mission Viejo Local Fauna of Orange County, California. Details of section A-B shown in Figure 4.

Diego County and/or from the early Uintan portion of member B of the Santiago Formation of northwestern San Diego County (Walsh, 1996b), indicate a similar age for the Rancho Mission Viejo Local Fauna. The fauna is highly significant because it includes the largest sample of *Epihippus* from southern California and is the first early Uintan North American Land Mammal Age assemblage (biochron Ui1b) from the Santiago Formation of Orange County.

Morton (1974) provided a geologic map of the Gobernadora 7.5 minute Quadrangle, which included Planning Area 2 at Rancho Mission Viejo. He mapped the Santiago Formation in Planning Area 2 as the lower beds of the formation (= lower part of Schoellhamer et al., 1981) and regarded them as marine because one locality in the Santiago Formation, which occurs outside and south of the mapped area, yielded the oyster, *Ostrea stewartii*. However, some portions of the Santiago Formation exposed on the east side of Rancho Mission Viejo are more probably non-marine because of the following: 1) the stratigraphy consists of sequences of channel sandstones, some with rip up clasts, and interbedded siltstones and claystones that form a series of weakly fining up units that appear to represent multiple flood events; and 2) only land mammals have been recovered (marine vertebrates and invertebrates are lacking). Furthermore, Schoellhamer et al. (1981) regarded the upper part of the Santiago Formation in the type area along the north side of Santiago Creek as non-marine because silicified wood is commonly present, which is also true for the exposures at Rancho Mission Viejo. In addition, the upper part of member B of the Santiago Formation in San Diego County, which is regarded as a correlative of the upper part of the formation in Orange County (Wilson, 1972), contains early Uintan mammals (Walsh, 1996b), which is also true for the section at

TABLE 2. Faunal list for Ranch Mission Viejo Local Fauna from localities OCPC 03976, OCPC 03988, and SDSNH 6407, Rancho Mission Viejo substation and Planning Area 2 (subareas 2.1 and 2.2), Orange County, California, Santiago Formation, early Uintan (Ui1b).

- Reptilia
  - Squamata
    - Anguidae, genus undetermined.
- Mammalia
  - Leptictida
    - Leptictidae
      - *Palaeictops* sp.
  - Lipotyphyla
    - Geolabididae
      - *Centetodon* sp.
    - Erinaceomorpha
      - Sespedectidae
        - *Patriolestes davisi* Walsh, 1998
  - Primates
    - Notharctidae
      - cf. *Hesperolemur* sp.
  - Canivoramorpha (sensu Bryant, 1996)
    - Viverravidae
      - cf. *Viverravus* sp.
    - Carnivoriformes (sensu Flynn, Finarelli and Spaulding, 2010)
      - Miacidae
        - *Miacis* spp.
        - cf. *Procyondictis* sp.
  - Rodentia
    - Ischyromyidae
      - cf. *Thisbemys* sp.
      - cf. *Pseudotomus* sp. A
      - cf. *Pseudotomus* sp. B
      - *Microparamys* sp.
    - Eomyidae
      - *Metanoiamys* sp.
  - Perissodactyla
    - Brontotheriidae
      - brontothere, genus undetermined
    - Equidae
      - *Epihippus gracilis* (Marsh, 1871)
  - Artiodactyla
    - Helohyidae
      - *Achaenodon robustus* Osborn, 1883
    - Oromerycidae
      - *Merycobunodon* sp.
    - Protoceratidae
      - *Leptoreodon marshi* Wortman, 1898
    - Agriochoeridae
      - *Protoreodon* sp. cf. *P. parvus* Scott and Osborn, 1887
    - artiodactyl, family undetermined

TABLE 3. Faunal list for localities SDSNH 4730 (= *Harpagolestes* Quarry) and 5721, which are laterally equivalent, but 73 m apart on lot 18 of Phase 1B of the Ocean Ranch Commercial Development Project, San Diego County, California, member C, Santiago Formation, early Duchesnean (Deméré and Murphey, 2005; Mihlbachler and Deméré, 2009; Tomiya, 2012; this paper).

- Reptilia
  - Testudines
    - Trionychidae
      - *Trionyx* sp.
- Mammalia
  - Didelphomorphia
    - Herpetotheriidae
      - *Herpetotherium* sp.
    - Peradectidae
      - *Peradectes* sp.
  - Pantolesta
    - Pantolestidae
      - *Simidectes* sp.
  - Lipotyphla
    - Sespedectidae
      - *Sespedectes* sp.
      - *Proterixoides* sp.
    - Oligoryctidae
      - *Oligoryctes* sp.
  - Primates
    - Omomyidae
      - *Dyseolemur* sp.
      - *Ourayi*a sp.
  - Carnivoramorpha (sensu Bryant, 1996)
    - Carnivoraformes (sensu Flynn, Finarelli and Spaulding, 2010)
      - *Lycophocyon hutchinsoni* Tomiya, 2011
      - *Tapocyon* sp.
      - *Plesiomiacis* sp.
      - *Miocyon* sp.
  - "Condylartha"
    - Mesonychidae
      - *Harpagolestes* sp.
  - Rodentia
    - Ischyromyidae
      - *Microparamys* sp.
      - *Eohaplomys* sp., cf. *E. serus* Stock, 1935b
    - Cylindrodontidae
      - *Pareumys* sp.
    - Eomyidae
      - *Metanoiamys marinus* Chiment and Korth, 1996
    - Simimyidae
      - *Simimys simplex* (Wilson, 1935)
    - Geomyidae?
      - *Griphomys* sp.
    - Amynodontidae
      - amynodont, genus undetermined
    - Brontotheriidae
      - cf. *Parvicornus occidentalis* Mihlbachler and Deméré, 2009
    - Equidae
      - *Epihippus uintensis* (Marsh, 1875)
  - Artiodactyla
    - Dichobunidae
      - *Tapochoerus* sp.
    - Agriochoeridae
      - *Protoreodon walshi* Theodor, 1999
    - Oromerycidae
      - *Protylopus* sp.
    - Protoceratidae
      - *Leptoreodon* sp.

Rancho Mission Viejo. In a mitigation report, Rugh (2016) identified fossil invertebrates from another locality in the Santiago Formation at Rancho Mission Viejo, including the following: 1) a few tropical land snails; 2) a few species of gastropods and bivalves characteristic of marine estuary mudflats; 3) two species of snails characteristic of freshwater lakes or ponds; and 4) one species of brackish water snail. The freshwater snails were the most common invertebrates at this locality. Rugh (2016) suggested that the invertebrate fossils may have been

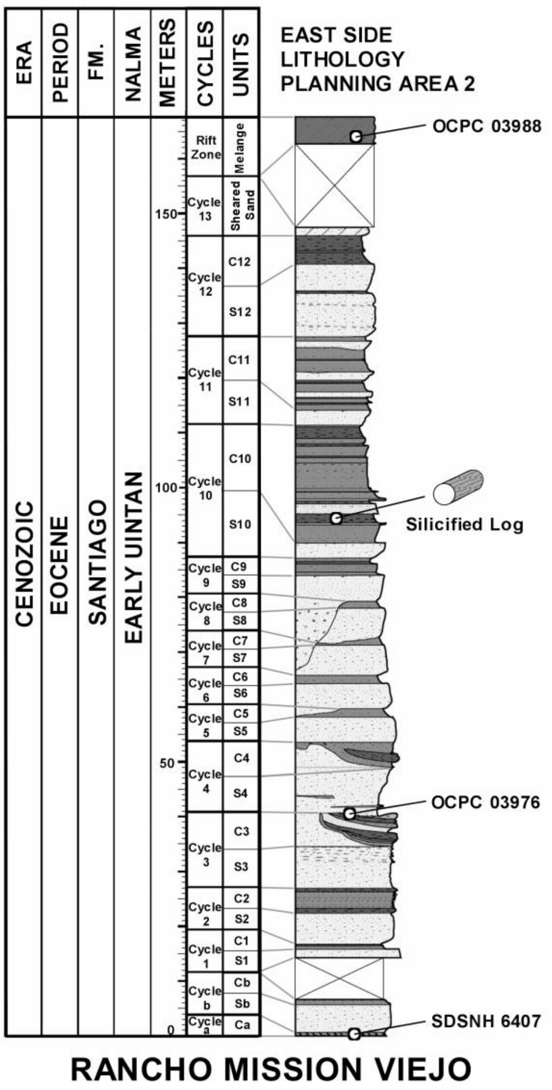

FIGURE 4. Generalized stratigraphic column of section on east side of Planning Area 2 (see section A-B, Figure 3) at Rancho Mission Viejo showing relative stratigraphic positions of vertebrate fossil localities that yielded the Rancho Mission Viejo Local Fauna (modified section courtesy of Patrick Riseley, per. communication, 2015). Abbreviations are: C, claystone; Fm., Formation; NALMA, North American Land Mammal Age; S, sandstone.

transported a short distance from land and/or freshwater lakes or ponds by monsoonal rains or connecting channels to their final deposition along an estuary shoreline or mudflat. Thus, another possible scenario that cannot be ruled out to explain the occurrence of land mammals, terrestrial plants, silicified tree logs at the other Rancho Mission Viejo localities along with the lack of deep water marine invertebrates or marine vertebrates in the section, is that the fossils were, at least in part, deposited in a non-marine environment that may have been subject to repeated flooding into a near shore estuarine embayment or intertidal mudflat. Contrary to Morton (1974), the presence of early Uintan land mammals indicates that the exposures of Santiago Formation at Rancho Mission Viejo most likely represent some portion of the upper part of the formation rather than the lower part.

TABLE 4 . Faunal list for SDSNH 4131, site 6 at Legoland project, Carlsbad, San Diego County, California, member C, Santiago Formation.

- Mammalia
  - Lipotyphla
    - Sespedectidae
      - cf. *Proterixoides* sp.
  - Primates
    - Omomyidae
      - omomyid, genus undetermined
  - Rodentia
    - Ischyromyidae
      - cf. *Microparamys* sp.
    - Cylindrodontidae
      - *Pareumys* sp.
    - Eomyidae
      - *Metanoiamy*s sp.
    - Geomyidae?
      - *Griphomys* sp.
    - Simimyidae
      - *Simimys* sp.
  - Perissodactyla
    - Hyracodontidae
      - *Triplopus* sp.
    - Equidae
      - *Epihippus uintensis* (Marsh, 1875)
  - Artiodactyla
    - Agriochoeridae
      - *Protoreodon* sp.

Ocean Ranch—In a report for a paleontological mitigation program conducted at the Ocean Ranch Commercial Development Project at Oceanside, San Diego County, California, Deméré and Murphey (2005) documented the discovery of numerous superposed localities in the Santiago Formation that yielded fossils that span the early Uintan through the early Duchesnean North American Land Mammal Ages. The section at Ocean Ranch consists of about 76 m of the Santiago Formation, including members B and C, and unconformably overlying Quaternary stream terrace deposits. A detailed stratigraphic framework was provided by Mihlbachler and Deméré (2009, figure 2) for the localities at Ocean Ranch and is summarized as follows, in ascending order: 1) about 21 m of member B of the Santiago Formation, which yielded mammal fossils of early Uintan Age and marine invertebrates (see also Schweitzer and Feldman, 2002); 2) 12 m of member C that is separated from member B by an unconformity and characterized by a maroon sandstone unit that yielded mammals of late Uintan Age; 3) about 40 m of

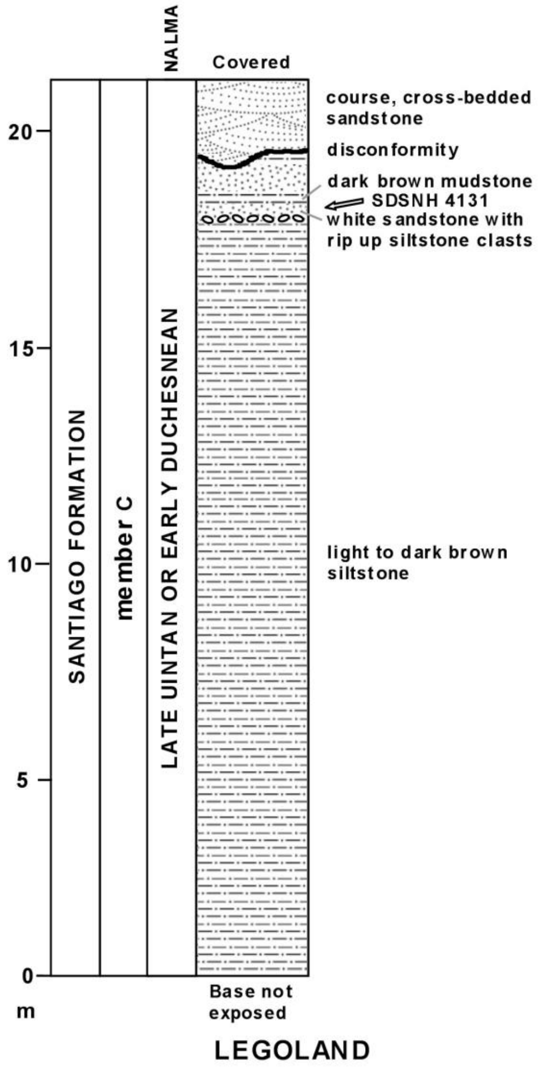

FIGURE 5. Generalized stratigraphic column of exposed section containing locality SDSNH 4131 at site 6, Legoland.

interbedded siltstones and sandstones, which are separated from the maroon sandstone unit by a disconformity, that yielded early Duchesnean mammals from two localities (SDSNH 4730 = *Harpagolestes* Quarry, and SDSNH 5721) within a 0.3 m thick siltstone layer and overlying 0.6 - 1 m muddy sandstone bed near the middle of the unit that represent an undulating channel deposit; 4) 10 to 15 m of channel filled sandstone sequences, referred to as the Bone Sands, which yielded mammals of early Duchesnean age; and 4) about 16 to 17 m of stream terrace deposits, which unconformably overlie the Santiago Formation, that yielded mammal fossils of Pleistocene age. Although most of the fossil mammals from Ocean Ranch have not been formally described, Mihlbachler and Deméré (2009) documented a new genus and species of brontothere, *Parvicornis occidentalis*, from the Bones Sands localities and referred an associated partial skull and skeleton to cf. *P. occidentalis* from the *Harpagolestes* Quarry. Subsequently, Tomiya (2011) described a new basal carnivoramorphan, *Lycophocyon hutchisoni*, from member C of the Santiago Formation of San Diego County, which included specimens from the Bone Sands at Ocean Ranch. Although Mihlbachler and Deméré (2009) reported that *Epihippus* occurred in the Bone Sands, only a single specimen of *Epihippus* was recovered at Ocean Ranch, which actually came from locality SDSNH 4730. Also, it should be noted that Mihlbachler and Deméré (2009) mistakenly listed locality SDSNH 5721 as the *Harpagolestes* Quarry, but in fact the quarry occurred at locality SDSNH 4730, which is laterally equivalent to SDSNH 5721. A faunal list for localities SDSNH 4730 and 5721 is provided in Table 3.

Legoland—Locality SDSNH 4131 was discovered in 1997 during grading for the development of the theme park Legoland in Carlsbad, California. The locality occurred approximately 244 m West of Hidden Valley Road in Legoland at an elevation of about 23 m and is now a landscape covered area within the park. The fossils were recovered by quarrying the fossiliferous horizon along with wet screen washing of 400 lbs of bulk matrix from the site.

The exposed section at locality SDSNH 4131 was identified as member C of the Santiago Formation and is composed of the following units, in ascending stratigraphic order (Figure 5): 1) 15 to 17 m of light to dark brown siltstones; 2) a 1.6 m unit consisting of a basal white sandstone with siltstone rip up clasts containing locality SDSNH 4131 and an overlying 0.17 m thick dark brown mudstone; 3) a second 1.6 m fining up unit, which has an erosional disconformity at its top of up to 0.9 m, consisting of a basal white sandstone and overlying dark brown siltstone; and 4) 3.6 m of course, cross-bedded sandstone. The mammals recovered from locality SDSNH 4131 include taxa that are known from both the late Uintan and early Duchesnean, so the fauna could be either age (Table 4).

SYSTEMATIC PALEONTOLOGY

Class Mammalia Linnaeus, 1758
Order Perissodactyla Owen, 1848
Family Equidae Gray, 1821
Genus *Epihippus* Marsh, 1878
Epihippus gracilis (Marsh, 1871)
Figures 6A-H, Table 7

Referred Specimens—From locality OCPC 03976 (Mission Rancho Viejo): RM1 or 2, OCPC

76439, 80084; LM1 or 2, OCPC 76440, 80097; partial right upper cheek teeth, OCPC 80087, 85391; partial Rp4?, OCPC 73188; partial lower right cheek tooth, OCPC 73198.

Description—The four complete upper molars exhibit posterior appression facets, eliminating the possibility that any of them represent M3. Based on their occlusal outlines and relative sizes, they most likely represent M1 or 2. The tooth positions for the partial upper and lower cheek teeth are less certain, but, based on relative size, OCPC 73198 probably represents m1 or 2 and OCPC 73188 probably represents p4.

The upper cheek teeth are relatively low-crowned with a quadrate occlusal outline. The parastyle is moderately robust. A distinct mesostyle is present between the paracone and metacone. The four primary cusps (paracone, metacone, protocone and hypocone) are distinct, with the paracone taller and slightly larger than the metacone, and the protocone slightly larger and positioned slightly more lingually than the hypocone. The protoloph is moderately tall, extending anterolabially from the protocone to a distinct protoconule and then continues to the anterolingual base of the paracone. The metaloph is moderately tall, extending anterolabially from the hypocone to a moderately distinct metaconule and then continues to the anterolingual base of the metacone. The anterior and posterior cingula are robust. A distinct lingual cingulum is present between the protocone and hypocone that commonly extends anteriorly across the lingual base of the protocone to connect with the anterior cingulum (4 of 6 specimens), but only extends posteriorly across the lingual base of the hypocone to connect with the posterior cingulum in half of the specimens.

The two lower cheek teeth are broken. OCPC 73188 is missing the labial portion of the protoconid and the anterior wall of the tooth, including the paralophid, and OCPC 73198 is missing the posterolabial corner of the hypoconid and much of the lingual edge of the tooth, including most of the entoconid. Also, in OCPC 73198, the lingual portion of the protolophid is displaced (folded) anteriorly. Even in their broken state, certain characters, which are typical of early equids, can still be discerned. The teeth are moderately low-crowned, with length greater than width. The paraconid and metaconid are transversely compressed, while the hypoconid and metaconid are robust and conical. A distinct paracristid (or paralophid) descends anteriorly from the protoconid apex and then turns lingually. The protolophid is moderately tall, connecting the protoconid to the metaconid. A tall cristid obliqua extends anterolingually from the hypoconid, terminating relatively high on the posterior wall of the protolophid, just below and posterolabially of the metaconid apex. The posthypocristid is short, extending posterolabially from the hypoconid to a small hypoconulid. A moderately strong, continuous cingulid composed of the anterior, labial and posterior cingulids is present, which extends around the tooth from the anterolabial base of the protoconid to the posterolabial base of the entoconid.

TABLE 5. Combined dental measurements (in mm) and statistics of middle Eocene specimens of *Epihippus gracilis* and *Epihippus uintensis* showing large observed ranges (OR) and high coefficients of variation (CV>10) for most all dental measurements, which, contrary to Hanson (1996), does not appear to support a single species scenario. Measurements from Peterson (1931) Gazin (1956), Bjork (1967), Forstén (1971), MacFadden (1980), Westgate (1990), McCarrol et al. (1996) and this paper.

Position/ dimension		N	Mean	OR	SD	CV
P2	ap	5	6.86	6.0-8.4	0.971	14.2
	tr	5	5.54	5.1-6.5	0.611	11.0
P3	ap	6	6.90	6.2-8.5	0.817	11.8
	tr	6	6.93	6.6-7.5	0.399	5.6
P4	ap	6	7.62	6.2-9.3	1.241	16.3
	tr	6	8.92	7.6-10.4	1.070	12.0
M1	ap	6	8.50	7.0-9.6	0.938	11.0
	tr	6	10.08	8.0-11.6	1.440	14.3
M2	ap	6	8.38	7.0-9.3	0.926	11.1
	tr	6	10.72	9.2-12.3	1.290	12.0
M3	ap	4	8.93	7.5-10.1	1.110	12.4
	tr	6	10.82	8.7-12.3	1.570	14.5
p2	ap	9	7.16	5.3-8.4	0.967	13.5
	tr	11	3.67	2.9-4.5	0.578	15.8
p3	ap	30	7.53	6.2-9.1	0.848	11.3
	tr	26	4.82	3.6-6.0	0.667	13.8
p4	ap	26	7.72	6.4-9.1	0.745	9.7
	tr	25	5.47	4.3-6.5	0.702	12.8
m1	ap	21	8.08	6.3-9.3	0.747	9.3
	tr	20	5.65	4.2-6.8	0.760	13.4
m2	ap	19	8.56	6.8-9.8	0.781	9.1
	tr	17	5.84	4.7-6.8	0.572	9.8
m3	ap	16	11.15	9.6-12.9	1.203	11.2
	tr	16	5.44	4.5-6.2	0.534	10.2

Discussion—Unlike early Eocene equids, *Epihippus* is a relatively rare component of middle Eocene faunas (Granger, 1908; Peterson, 1931; Stirton, 1940; Gazin, 1956, 1976; Bjork, 1967; Forstén, 1971; MacFadden, 1980, 1998; Hanson, 1996; McCarroll et al., 1996). In the first major revision of North American Eocene equids, Granger (1908) recognized two species of *Epihippus* from the Uintan; *E. gracilis* (Marsh, 1871) with *E. uintensis* (Marsh, 1875) as its junior synonym, and a new species, *E. parvus*. Peterson (1931) described *Duchesnehippus intermedius* from the middle Duchesnean Lapoint Fauna of the Duchesne River Formation of Utah. MacFadden (1980) reevaluated the taxonomy of *Epihippus* and provided several conclusions. He regarded the characters used by Granger (1908) to distinguish *E. parvus* from *E.*

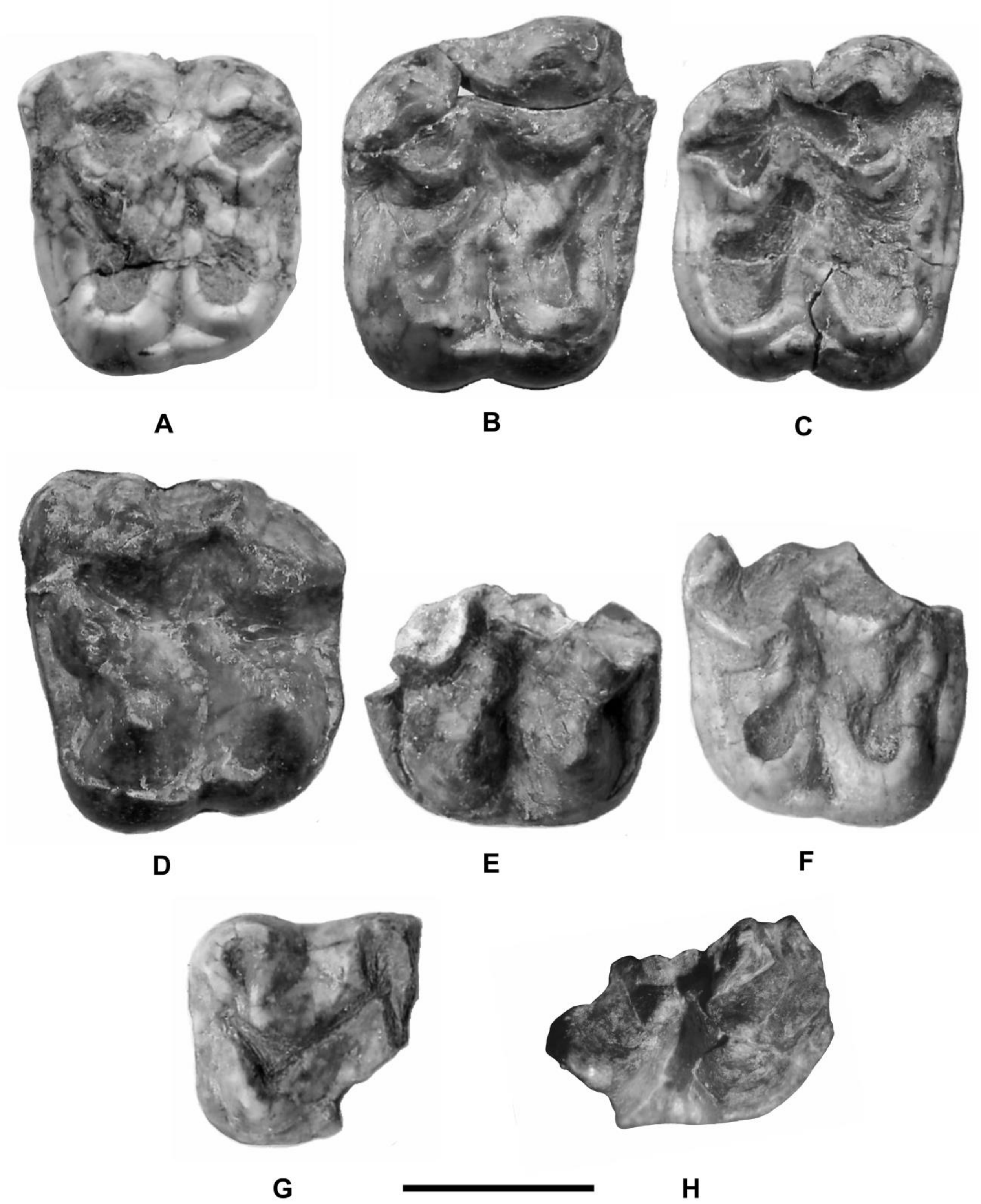

FIGURE 6 . *Epihippus gracilis* from Rancho Mission Viejo. A, LM1 or 2, OCPC 76440. B, RM1 or 2, OCPC 76439. C, RM1 or 2, OCPC 80084. D, LM1 or 2, OCPC 80097. E, partial right upper cheek tooth, OCPC 80087. F, partial right upper cheek tooth, OCPC 85391. G, partial Rp4?, OCPC 73188. H, partial right lower cheek tooth, OCPC 73198. All occlusal views. Bar scale = 5 mm.

TABLE 6. Measurements (in mm) of *Epihippus gracilis*, *E. uintensis* and *Duchesnehippus intermedius* (from Peterson, 1931; Gazin, 1956; Bjork, 1967; Forstén, 1971; MacFadden, 1980; Westgate, 1990; McCarrol et al., 1996; this paper). Contrary to Hanson (1996), we tentatively recognize *E. uintensis* as distinct from *E. gracilis* and consider the two specimens from the Hancock Quarry, Clarno Formation, Oregon, that he referred to *E. gracilis* as representing *E. uintensis* instead. N = number of specimens; OR = observed range; SD = standard deviation.

Position/		*E. gracilis*				*E. uintensis*				*D. intermedius*		
dimension		N	Mean	OR	SD	N	Mean	OR	SD	N	Mean	OR
P2	ap	4	6.48	6.0-7.1	0.519	1	8.4	-	-	-	-	-
	tr	4	5.30	5.1-5.8	0.337	1	6.5	-	-	-	-	-
P3	ap	5	6.58	6.2-6.9	0.259	1	8.5	-	-	-	-	-
	tr	5	6.94	6.6-7.5	0.378	1	6.9	-	-	-	-	-
P4	ap	3	6.63	6.2-7.5	0.751	3	8.60	8.1-9.3	0.624	1	8.8	-
	tr	3	8.03	7.6-8.6	0.513	3	9.80	9.4-10.4	0.529	1	10.6	-
M1	ap	2	7.40	7.0-7.8	-	4	9.05	8.7-9.6	0.387	1	10.1	-
	tr	2	8.35	8.0-8.7		4	10.95	10.4-11.6	0.592	1	13.4	-
M2	ap	3	7.60	7.0-8.0	0.529	3	9.17	9.0-9.3	0.153	1	11.2	-
	tr	2	9.40	9.2-9.6	-	3	11.60	11.2-12.3	0.608	1	12.9	-
M3	ap	1	7.5	-		3	9.40	8.7-10.1	0.700	-	-	-
	tr	2	8.95	8.7-9.2	-	4	11.75	10.6-12.3	0.777	-	-	-
p2	ap	5	6.66	5.3-7.7	0.888	4	7.76	7.1-8.4	0.723	1	9.0	-
	tr	6	3.23	2.9-3.8	0.327	5	4.20	3.9-4.5	0.255	1	4.5	-
p3	ap	15	6.82	6.2-7.6	0.434	15	8.19	7.3-9.1	0.562	1	8.5	-
	tr	13	4.27	3.6-5.5	0.541	13	5.28	4.6-6.0	0.406	1	6.0	-
p4	ap	14	7.02	6.4-7.7	0.464	12	8.37	7.5-9.1	0.485	2	8.85	8.7-9.0
	tr	13	4.90	4.3-6.0	0.550	12	6.00	5.5-6.5	0.323	2	6.35	6.0-6.7
m1	ap	11	7.49	6.3-8.2	0.523	10	8.58	8.0-9.3	0.492	2	9.20	9.0-9.4
	tr	10	4.99	4.2-5.8	0.537	10	6.04	5.4-6.8	0.461	2	6.35	6.0-6.7
m2	ap	7	7.78	6.8-8.7	0.698	12	8.70	7.6-9.8	0.644	2	9.25	9.0-9.5
	tr	5	5.15	4.7-5.7	0.420	12	5.94	5.3-6.4	0.374	2	6.35	6.0-6.7
m3	ap	7	10.34	9.6-11.5	0.602	9	11.90	10.8-12.9	0.804	-	-	-
	tr	7	5.09	4.5-5.6	0.472	9	5.53	4.8-6.2	0.544	-	-	-

gracilis as unjustified and placed *E. parvus* in synonymy with *E. gracilis*. Based primarily on size, he regarded *E. uintensis* as specifically distinct from *E. gracilis*, with the former being larger than the latter. MacFadden (1980) further considered that the characters used by Peterson (1931) to distinguish *D. intermedius* from *E. uintensis* did not rise to the level of generic or specific separation and placed *D. intermedius* in synonymy with *E. uintensis*. Hanson (1996) followed MacFadden (1980) and regarded *Duchesnehippus* as a junior synonym of *Epihippus*, but considered *D. intermedius* a valid species. Hanson (1996) also regarded *E. uintensis* as a junior synonym of *E. gracilis*. Contrary to Hanson (1996), MacFadden (1998) continued to recognize *E. uintensis* as specifically distinct from *E. gracilis*. Rasmussen et al. (1999b, p. 424) resurrected *Duchesnehippus* as generically distinct from *Epihippus*, based on a partial lower molar from the Lapoint Member, Duchesne River Formation, that agrees "in size, robustness and crown height with the teeth of the holotype of *D. intermedius*" from the Dry Gluch Creek Member, Duchesne River Formation. Kelly et al. (2012) also regarded *Duchesnehippus* as generically distinct from *Epihippus* based its greater molarization of the lower premolars (especially p2), greater hypsodonty and increased size. Robinson et al. (2004) tentatively included the first appearance of *Duchesnehippus intermedius* in their characterization of the beginning of the Duchesnean.

No large samples of *Epihippus* from a single quarry or stratigraphic horizon are available, so the amount of individual variation in dental size for either *E. gracilis* or *E. uintensis* cannot be confidently determined. If one accepts Hanson's (1996) proposal that *E. gracilis* and *E. uintensis* are conspecific and the measurements of all the specimens of both species previously reported in the literature are combined with those documented here (Table 5), then the resulting observed ranges for the dental dimensions are much larger and their respective coefficients of variation are much higher than one would expect for a single species (Simpson et al., 1960; Gingerich, 1974, 1979; Freudenthal and Bescos, 1984; Carrasco, 1998). However, based on size, the dental measurements of a number of small samples from different middle Eocene localities do appear to support separating *E. gracilis* from *E. uintensis* even though there is some overlap in their dental dimensions (Table 6). Thus, we follow MacFadden (1980, 1998) and tentatively recognize *E. uintensis* as specifically distinct from *E. gracilis*. However, we recognize that if a single, large sample of *Epihippus* is discovered that exhibits the observed range of dental measurements of both species, then synonymy would be justified with *E. gracilis* having priority.

The early Uintan sample of *Epihippus* from Rancho Mission Viejo agrees well in size to *E. gracilis* and is referred to the species.

TABLE 7. Measurements (in mm) of *Epihippus gracilis* specimens from Rancho Mission Viejo (b = broken dimension; lct = lower cheek tooth; p = partial; uct = upper cheek tooth).

Specimen	Position	ap	tra	trp
OCPC 76439	RM1 or 2	8.19	9.75	9.05
OCPC 76440	LM1 or 2	7.36	8.60	7.95
OCPC 80097	LM1 or 2	8.50	9.50	8.30
OCPC 80084	RM1 or 2	7.95	9.83	8.70
OCPC 80087	p. R uct	7.60b	-	-
OCPC 85391	p. R uct	7.50b	-	7.26b
OCPC 73188	p. Rp4?	5.65b	-	5.58
OCPC 73198	p. R lct	7.04b	5.35b	-

Epihippus uintensis (Marsh, 1875)

Figures 7A-G, 8A-C and 9A-D, Table 8

Referred Specimens—From locality SDSNH 3574 (Mission del Oro): partial left dentary with partial p2-3, complete p4-m1, partial m2 and associated partial upper cheek tooth, SDSNH 43476. From locality SDSNH 4730 (Ocean Ranch): associated partial fragmented skull with complete RP1-M1, partial RM2-3, LP1, partial LP2-M2, complete LM3, partial dentaries with complete Rp2-m3 and complete Lp3-m3, isolated Li2 or 3, Lc, Lp1, and bone fragments, SDSNH 105765. From locality SDSNH 4131 (Legoland): Lm2, SDSNH 65006.

Description—The skull is highly fragmented so little can be said for its morphology, except that the infraorbital foramen occurs above the anterolabial root of P4.

To the best of our knowledge, the P1 of *E. uintensis* has not been previously described. It has an oval occlusal outline, two distinct roots and a single, tall central cusp. The anterior crest sharply declines from the central cusp to terminate at the anterolabial base of the tooth. The posterior crest first declines rapidly from the central cusp, but then slows its declination as a more gentle slope resulting in it being longer than the anterior crest, and ends at the posterior base of the tooth. A very weak lingual cingulum is present.

The P2 has a triangular occlusal outline and is submolariform with a distinct paracone, metacone and protocone. The mesostyle is small, but distinct. A very small parastyle is present at the anterior terminus of the premetacrista. Anterior and posterior cingula are present, with the anterior cingulum joined to and continuous with a distinct lingual cingulum that ends at the anterior base of the protoconid.

The P3 has a quadrate occlusal outline and is fully molariform, with four robust primary cusps (paracone, protocone, metacone and hypocone). The parastyle is relatively tall and cuspate. The mesostyle is large, connected to the paracone and metacone by a strong centrocrista, which along with the preparacrista and postmetacrista, give the ectoloph a wide W-shaped occlusal pattern. The paraconule is robust. The metaconule is distinct, but smaller and less cuspate than the paraconule. The anterior and posterior cingula are prominent, whereas the lingual cingulum is weak and does not extend across the lingual bases of the protocone or hypocone.

The P4 is similar to the P3, but differs in being larger and more transverse, that is, relatively less expanded anteroposteriorly due to a relatively more closely positioned parastyle. The P4 also differs from the P3 by having a slightly more distinct protoconule and metaconule and slightly stronger anterior and posterior cingula.

Of the upper molars of SDSNH 105765, only the LM3 is complete. The M2s on both sides of SDSNH 105765 are damaged, missing most of their labial portions, so little can be said of their occlusal morphology. The RM1 has a small portion of the parastyle broken away, but it is assumed that it had a similarly developed one as those of the P4 and M3. The occlusal morphology of the RM1 of SDSNH 105765 is similar to those of the four M1 or 2s of *E. gracilis* from Rancho Mission Viejo, but is larger in size. The M1 of SDSNH 105765 has a quadrate occlusal outline with four large primary cusps (paracone, protocone, metacone, and hypocone). A robust mesostyle is present between the paracone and metacone. The protoloph extends from the protocone to a distinct protoconule and then continues, terminating just anterior of the anterior base of the paracone. The metaloph extends from the hypocone to a weak metaconule and then continues, terminating near the anterolingual base of the metacone. The anterior and posterior cingula are prominent, whereas the lingual cingulum varies from being weak on M1, not extending anteriorly or posteriorly across the labial bases of the protocone and hypocone, respectively, to moderately strong on M2, extending across their labial bases. The occlusal morphology of the M3 is very similar to that of the M1 except for being relatively narrower posteriorly. The M3 lingual cingulum is also stronger than those of P3-M2.

The sample of lower teeth associated with the skull from Ocean Ranch include the i2 or 3, canine, and p1-m3. The partial dentary from Mission del Oro includes a partial p2-3, p4-m1 and partial m2, whereas only an isolated lower molar (probably m2) was recovered from Legoland. Based on their similar sizes and the fact that no distinguishing dental characters can be discerned among these specimens, they are all regarded as conspecific. The two partial dentaries associated with the skull from Ocean Ranch are the most complete, but are distorted anteriorly.

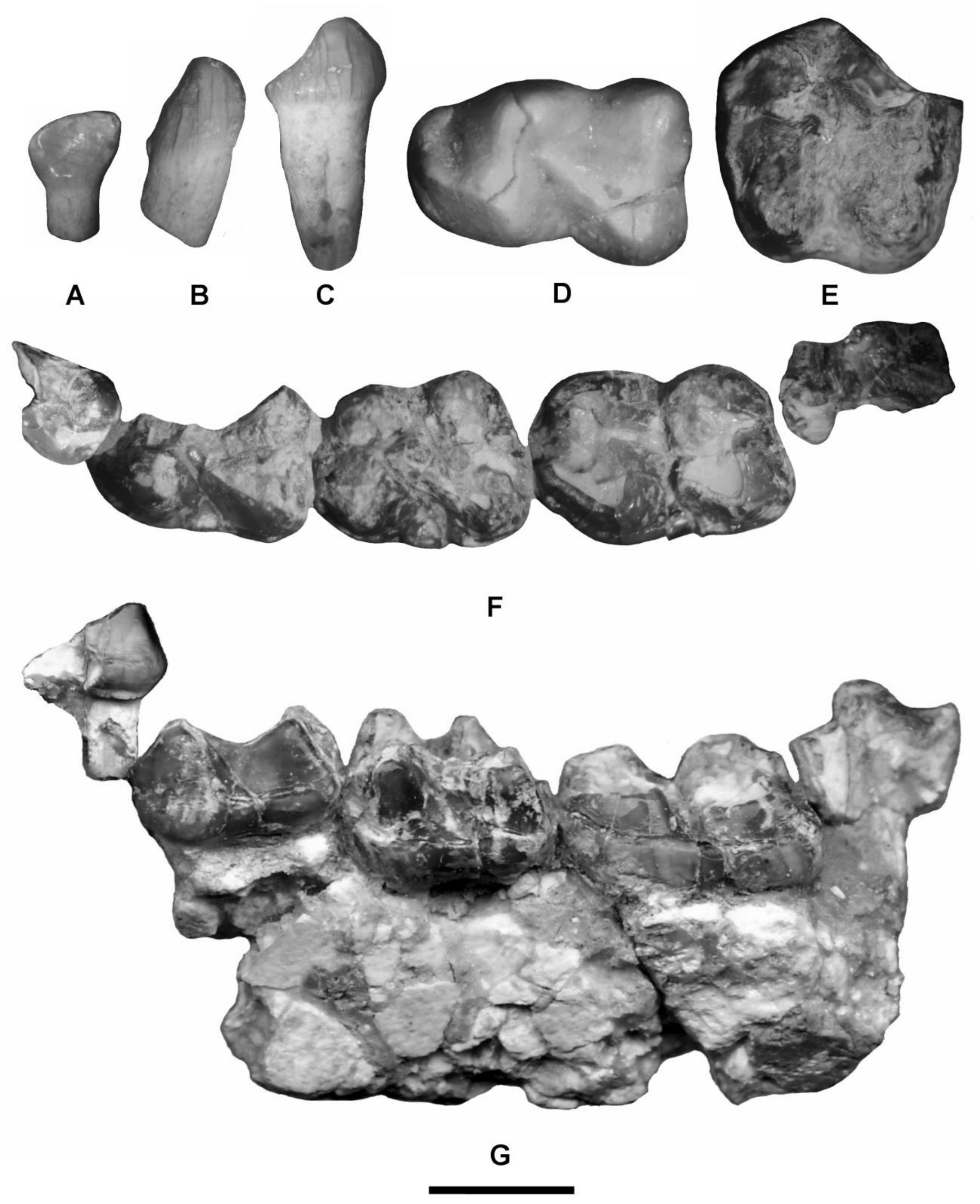

FIGURE 7. *Epihippus uintensis* from Mission del Oro, Legoland and Ocean Ranch. A-C, antemolar teeth associated with SDSNH 105765: A, Li2 or 3; B, left canine; C, Lp1. D, Lm2, SDSNH 65006. E, partial right upper cheek tooth and F-G, associated partial left dentary with partial p2-3, p4-m1 and partial m2, SDSNH 43476. A-C and G, labial views. D-F, occlusal views. Bar scale = 5 mm.

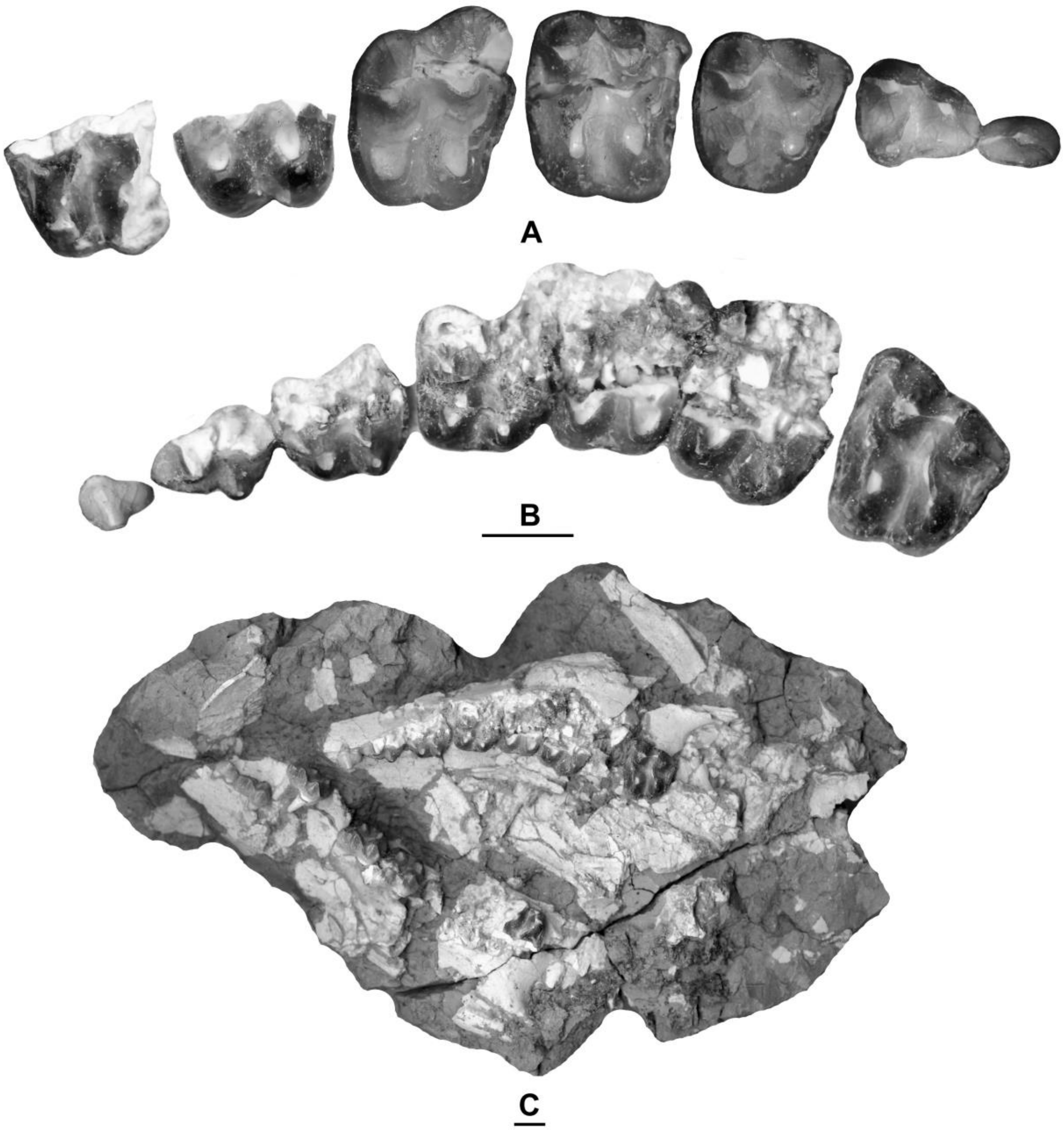

FIGURE 8 . *Epihippus uintensis* from Ocean Ranch. A-C, partial skull with LP1, partial LP2-M2, LM3, RP1-M1 and partial RM2-3, SDSNH 105765: A, close up occlusal views of RP1-M3; B, close up occlusal views of LP1-M3; C, ventral view of fragmented partial skull. Bar scales = 5 mm.

They are moderately robust with the depths below the center of m1 being 17.6 and 17.7 mm. An associated fragment preserving the anterior portion of the right dentary of SDSNH 105765 has a c-p1 alveolar diastema length of 8.5 mm.

The lower incisor has a typical hyracothere morphology. The occlusal outline is triangular. A small cuspid is present at the anterolabial corner of the tooth that has a ridge or crest extending posteriorly from it in a gentle arc to the posterolabial corner of the tooth, which then turns lingually and continues, terminating at about the middle of the labial base of the tooth. The central labial portion has

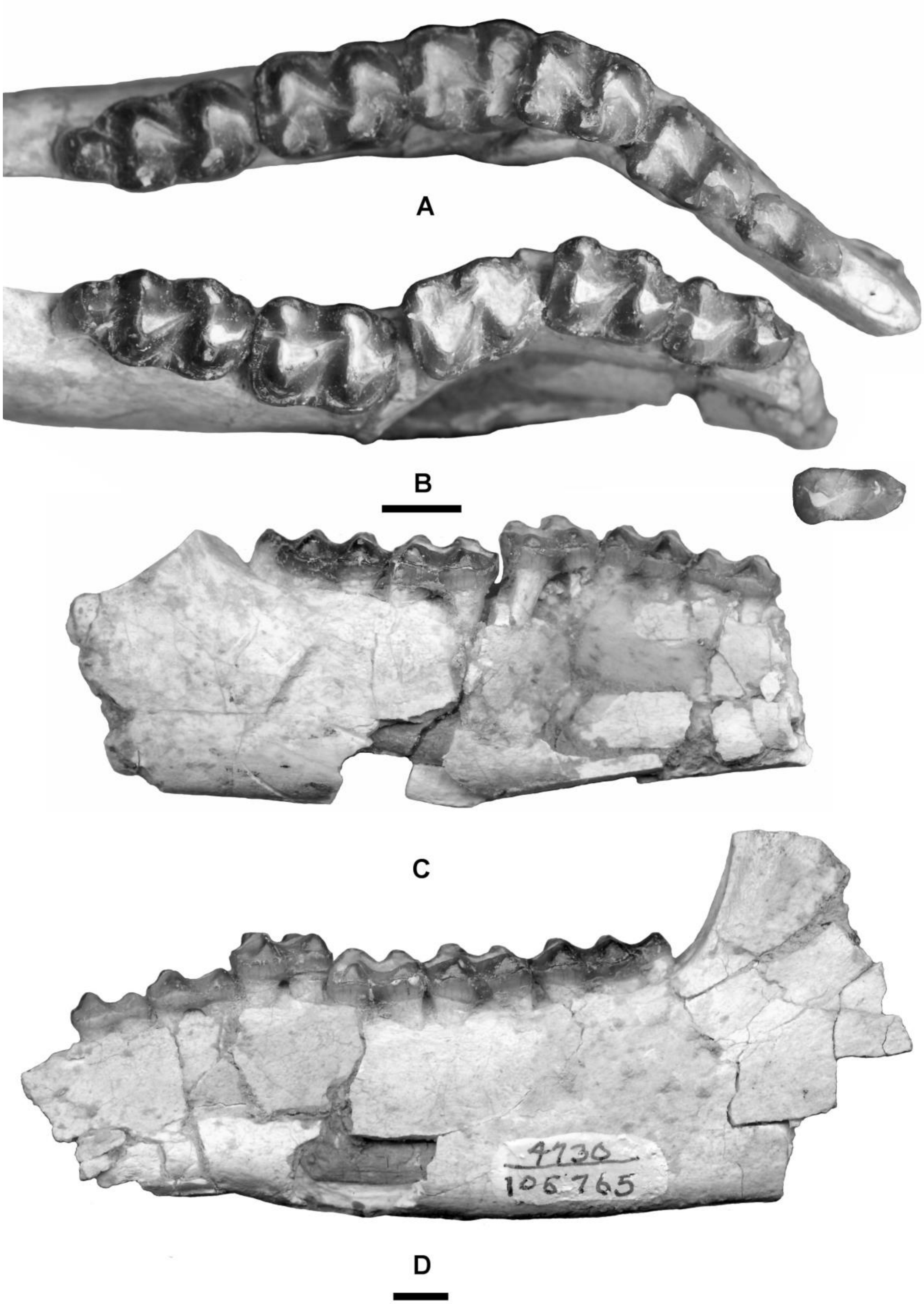

FIGURE 9. *Epihippus uintensis* from Ocean Ranch. A-D, partial dentaries associated with partial skull, SDSNH 105765: A and D, partial left dentary with p2-m3; B and C, partial right dentary with p2-m3. A-B, occlusal views. C-D, labial views. Bar scales = 5 mm.

TABLE 8. Measurements (in mm) of *Epihippus uintensis* from southern California (a = approximate; b = broken dimension; p = partial; uct = upper cheek tooth).

Fauna (Locality)	Specimen	Position	ap	tra	trp
Mission del Oro L.F. (SDSNH Loc. 3574)	SDSNH 43476	p. R uct	8.09b	-	8.37
		p. Lp2	-	-	3.55
		p. Lp3	7.21	-	5.45
		Lp4	7.45	5.85	5.99
		Lm1	8.70	6.46	6.54
Legoland (SDSNH Loc. 4131)	SDSNH 65006	Lm2	9.83	5.85	6.23
Ocean Ranch (SDSNH Loc .4730, *Harpagolestes* Quarry)	SDSNH 105765	LP1	4.40	2.74	-
		RP1	4.42	2.65	-
		p. LP2	7.37b	-	-
		RP2	7.40	4.30	5.81
		RP3	8.34	8.31	7.85
		RP4	8.70	-	9.0a
		RM1	8.89a	11.85a	10.85a
		LM3	9.50	11.02	9.35
		Li2 or 3	3.09	1.70	-
		Lc	3.33	2.15	-
		Lp1	4.14	2.35	-
		Lp2	6.75	2.95	3.47
		Rp2	6.72	2.93	3.46
		Lp3	7.76	4.59	5.20
		Rp3	7.75	4.57	5.37
		Lp4	8.09	5.55	5.80
		Rp4	8.02	5.66	5.96
		Lm1	8.54	6.48	6.50
		Rm1	8.45	6.32	6.35
		Lm2	9.01	6.56	6.65
		Rm2	9.30	6.50	6.76
		Lm3	12.17	5.97	6.08
		Rm3	12.20	6.08	5.95
		Lp2-p4	22.2	-	-
		Lm1-3	29.7	-	-
		Rm1-3	29.9	-	-

a concave, shallow, triangular basin and cingulids are lacking.

The canine is simple in structure, with a single, robust root and a central primary cuspid. An anterior, centrally positioned ridge extends anteriorly in a gentle arc from the central cuspid to the base of the crown and a posterior, centrally positioned ridge descends rapidly from the central cuspid, terminating at the posterior base of the crown. The canine is relatively small compared to the associated lower incisor and p1, suggesting that SDSNH 105765 probably represents a female (following Gingerich, 1981).

The p1 has a single, relatively tall primary cuspid, which is positioned slightly anteriorly, and a single, straight root that has a slight crease along the center of its labial surface. A weak, anterior ridge is present that descends rapidly from the primary cuspid, terminating at the base of the crown, along with a weak posterior ridge that descends from the primary cuspid in a gentle arc, terminating at an incipient cuspid (slight bulge) at the posterior edge of the tooth.

The p2 is submolariform, with the length considerably longer than the width. A small, low paraconid is positioned at the anterior margin of the tooth. The protoconid is tall, with its apex slightly expanded lingually, resulting in slight bulge that could be regarded as an incipient metaconid. The hypoconid is large with a low cristid obliqua extending anterolingually from its apex to the base of the protoconid. The entoconid is small, but distinct, whereas the hypoconulid is minute. Anterior, posterior and labial cingulids are lacking.

The p3 is fully molariform. The paracristid (= paralophid) is low, descending rapidly from the protoconid to a very weak paraconid and then turns lingually, terminating at the anterolingual corner of the tooth. A robust, tall protoconid and slightly transversely expanded, tall metaconid are present, connected by a distinct protolophid. The hypoconid is robust, wide and slightly larger than the protoconid. A prominent entoconid is present that is connected to the hypoconid by a moderately strong hypolophid. The hypoconulid is very small, positioned at about the center of the posterior cingulid and connected to the hypolophid by a short, low cristid (postcristid). The cristid obliqua is robust, but low, extending anterolingually from the hypoconid to the base of the protolophid, just slightly lingual of its center. The anterior and posterior cingulids are relatively weak. A moderately strong lingual cingulum is present that is continuous with the posterior cingulid and crosses the labial base of the hypoconid, but does not continue anteriorly across the labial base of the protoconid.

The p4-m2 are very similar in occlusal morphology to that of the p3, but several differences can be seen. The metaconid is more expanded transversely with an incipient metastylid often present on the anterolabial edge of the metaconid (an incipiently twinned metaconid). The cristid obliqua is slightly more robust and relatively taller in height. The labial cingulum is stronger and continuous across the labial bases of the protoconid and hypoconid, connecting anteriorly and posteriorly with the anterior and posterior cingulids, respectively.

The occlusal morphology of the m3 is essentially identical to those of p4-m2 except that it possesses a large, lobed, posteriorly projecting hypoconulid.

Discussion—The primitive equid, *Haplohippus texanus* McGrew, 1953, is known from the late Duchesnean Porvenir Local Fauna of Texas and the latest Uintan or earliest Duchesnean Clarno Formation of Oregon (Hanson, 1996). Although the p1 of SDSNH 105765 has a slight crease along the labial face of the root, which might be a remnant from the fusion of two roots, it can be easily distinguished from *H. texanus* by lacking the primitive hyracothere state of two distinct roots on p1, being smaller in size, and having a significantly shorter c-p1 diastema and greater molarization of the p2-3. All of the above differences are diagnostic characters of *Epihippus* (McGrew, 1953; MacFadden, 1976, 1980, 1998; Hanson, 1996). Based on size, the samples of *Epihippus* from Mission del Oro, Ocean Ranch and Legoland are referred to *E. uintensis*.

Superfamily Rhinocerotoidea Owen, 1845
family and genus undetermined
Figures 10A-C , Table 9

Referred Specimen—From locality SDSNH 3574: partial left dentary with partial m1, m2, and partial m3, SDSNH 43478.

Description—SDSNH 43478 was cataloged as a partial left dentary with p4-m2. However, a series of radiographs were taken of the dentary posterior to the last tooth (Figure 10C), which demonstrated that no hidden unerupted tooth was present, indicating the last tooth is actually m3, so only m1-3 are present. The m2 is relatively complete, but the m1 is fragmented and missing the hypoconid and a portion of the metalophid, while the m3 has portions of the entoconid and lingual hypolophid broken off. The lower molars have typical rhinocerotoid occlusal patterns with two primary transverse lophids (protolophid and hypolophid) connecting the protoconid to the metaconid and the hypoconid to the entoconid, respectively. They are moderate in height (ratio of m3 protoconid height/m3 ap = 0.43). The paralophid descends anteriorly from the protoconid apex to an indistinct paraconid (slight widening) and then turns sharply lingually to end at a point just labial of the metaconid apex. The cristid obliqua (= metalophid of some authors; e.g., Radinsky, 1969; Hanson, 1989) descends rapidly from the hypoconid apex, terminating near the base of the protolophid, just lingual of the protoconid apex. On m2, the anterior and posterior cingulids are moderately strong, but do not extend beyond the anterolabial base of the protoconid or posterolabial base of the hypoconid, respectively, whereas on m3, the anterior and posterior cingulids are slightly more robust and join a very weak labial cingulum that extends across the labial bases of the protoconid and hypoconid.

TABLE 9. Measurements (in mm) of Rhinocerotoidea, genus undetermined (probably *Uintaceras* or *Teletaceras*) from Mission del Oro Local Fauna, locality SDSNH 3574 (a = approximate; b = broken dimension; p. = partial).

Specimen	Position	ap	tra	trp
SDSNH 43478	p. Lm1	22.1b	-	10.1b
	p. Lm2	27.20	16.42	17.33
	Lm3	27.30	17.53	17.80
	Lm1-3	77a	-	-

Discussion—SDSNH 43478 was originally cataloged as a partial left dentary with p4-m2 of *Triplopus*. Tomiya (2012) reidentified SDSNH 43478 as *Hyracodon* sp. without explanation. This assignment may have been due to the previous identification of the teeth of SDSNH 43478 as being p4-m2, wherein the putative p4 would be regarded as fully molariform, similar to those of *Hyracodon*, and the fact that its molars are significantly larger than those of *Triplopus*. If this referral was correct, it would have been highly significant because the previous

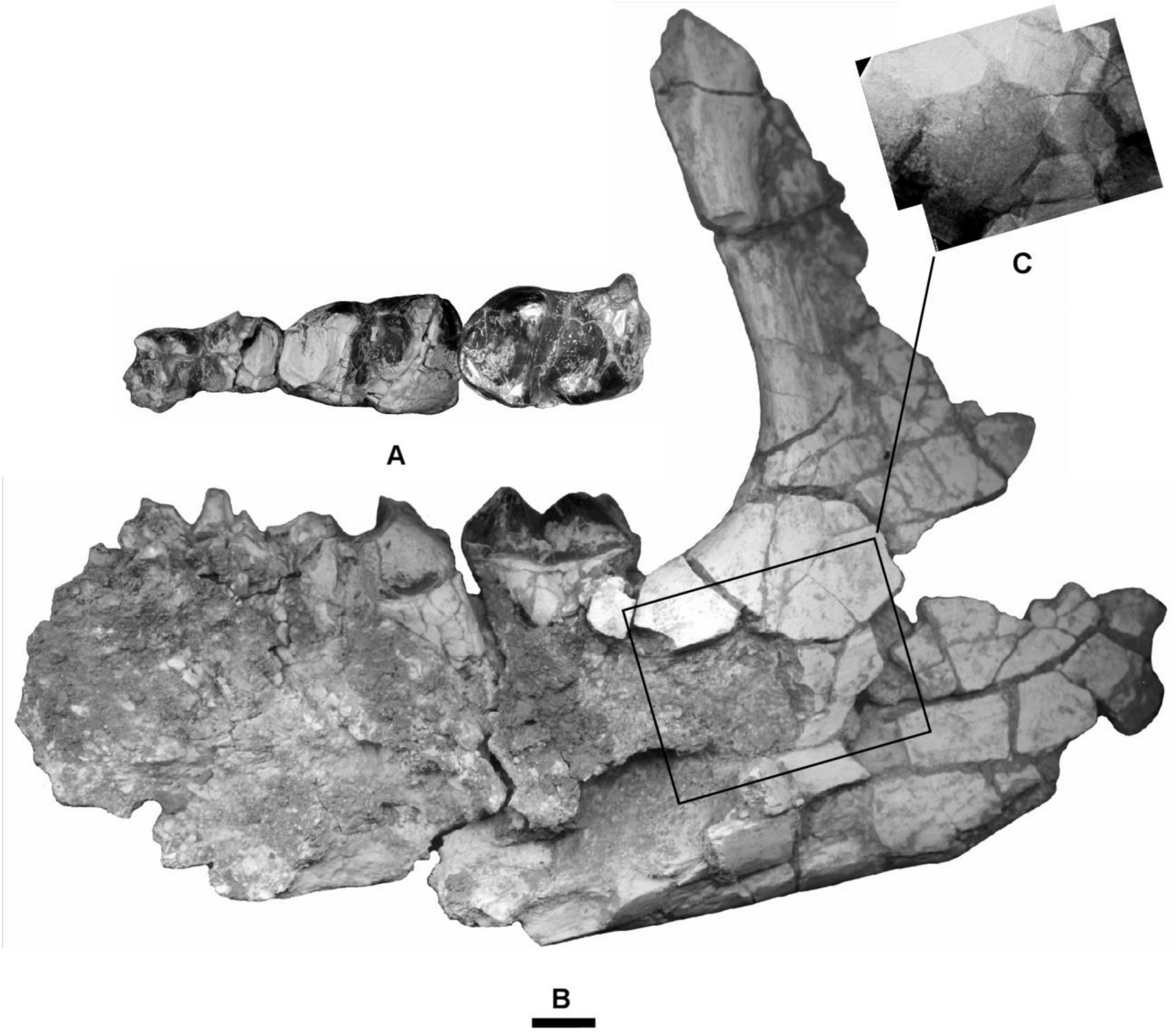

FIGURE 10. Rhinocerotoidea, genus and species undetermined (probably *Uintaceras* or *Teletaceras* sp.) from Mission del Oro. A-B, partial left dentary with partial m1, m2-3, SDSNH 43478. A, occlusal view. B, labial view. C, example of one of the radiographs taken of dentary posterior to last molar showing that no unerupted tooth is present. Bar scale = 10 mm.

earliest record of *Hyracodon* is from the middle Duchesnean Halfway/Lapoint Fauna of Utah (Radinsky, 1967; Prothero, 1998; Rasmussen et al., 1999b; Kelly et al., 2012). However, SDSNH 43478 can be easily distinguished from *Hyracodon* by the following: 1) relatively lower crowned; 2) a slightly weaker, relatively lower paralophid, not extending as far lingually; 3) a rapidly descending cristid obliqua, terminating near the posterior base of the protoconid; and 4) larger size. The lower molars of SDSNH 43478 are most similar in occlusal morphology to those of the rhinocerotoid *Uintaceras* and the primitive rhinocerotid *Teletaceras* (Hanson, 1989; Holbrook and Lucas, 1997; Prothero, 2005). They differ from those of *Hyrachyus* by being significantly larger. Although the familial status of *Uintaceras* has not been determined, it is generally regarded as the closest sister taxon to the Rhinocerotidae (Holbrook and Lucas, 1997; Prothero, 2005). SDSNH 43478 is intermediate in size between *Teletaceras radinskyi* Hanson, 1989, and *Uintaceras radinskyi* Holbrook and Lucas, 1997, wherein its lower molar lengths are about 9% larger than the largest specimen of *T. radkinskyi* and about 9-14% smaller than those of the smallest specimens of *U. radkinskyi*. Unfortunately, besides size, knowledge of the morphologies of the upper cheek teeth, lower premolars, incisors and manus are needed to distinguish *Teletaceras* from *Uintaceras*; these characters are unknown for the Mission del Oro form. It is likely that SDSNH 43478 represents either *Uintaceras* or *Teletaceras* and its intermediate size between *U. radkinskyi* and *T. radinskyi* suggests that it may be a new species. Thus, contrary to Tomiya (2012), SDSNH 43478 does not represent *Hyracodon*, so the currently accepted first appearance of the genus (Radinsky, 1967; Prothero, 1998; Rasmussen et al., 1999b; Kelly et al. 2012) remains unchanged.

CONCLUSIONS

Unlike early Eocene equids, *Epihippus* is a relatively rare component of middle Eocene faunas in North America. After more than 80 years of collecting land mammals from Eocene strata in southern California by various investigators, the first specimen of *Epihippus* was discovered in 1991 at Mission del Oro by Stephan Walsh during a paleontological mitigation program. Walsh (1996b) included this specimen as *Epihippus* sp. in a faunal list of the Mission del Oro Local Fauna, but did not describe or illustrate the specimen. Since 1996, numerous paleontological mitigation programs have been conducted in California for the commercial development of properties, which have resulted in the discovery of additional specimens of *Epihippus* from three localities in the Santiago Formation. Here we provide detailed descriptions of the specimens, which we refer to two different species. The smaller *Epihippus gracilis* is recorded from a new early Uintan fauna, the Rancho Mission Viejo Local Fauna, of Orange County (Table 2). The larger *E. uintensis* is recorded from the late Uintan or early Duchesnean? Mission del Oro Local Fauna and locality SDSNH 4131 at Legoland, and the earliest Duchesnean *Harpagolestes* Quarry (SDSNH 4730) at Ocean Ranch in San Diego County. These are the only specimens of *Epihippus* so far known from California and extend the geographic range of *E. gracilis* and *E. uintensis* to the southern part of the West Coast. We also document the occurrence of a rhinocerotoid from locality SDSNH 4131, whose taxonomic status is uncertain, but likely represents either *Uintaceras* or *Teletaceras*.

Although some investigators regard *Duchesnehippus* from the middle Duchesnean of Utah and Wyoming as a junior synonym of *Epihippus* (e.g., MacFadden,1980; Hanson, 1996), we follow Rasmussen et al. (1999b), Gunnell et al. (2009) and Kelly et al. (2012) and consider it a valid genus. *Epihippus gracilis* has been previously recorded from the early to late Uintan of Utah, Wyoming and Texas (Forstén, 1971; MacFadden, 1980, 1998; Eaton, 1985; Westgate, 1990; Gunnell et al., 2009). *Epihippus uintensis* has been previously recorded from the early to late Uintan of Utah, Wyoming, Montana and Texas (MacFadden, 1980, 1998; Eaton, 1985; Gunnell et al., 2009). Storer (1984) referred eight isolated teeth from the late Uintan Swift Current Creek Local Fauna of Saskatchewan to *Epihippus* sp., cf. *E. gracilis*. However, based on Storer's (1984) measurements of these teeth, they appear to represent *E. uintenisis* instead. Hanson (1996) regarded *E. uintensis* as a junior synonym of *E. gracilis* and referred two specimens from the Hancock Quarry of the Clarno Formation of Oregon to *Epihippus* sp., cf. *E. gracilis*. However, we believe that this synonymy is premature until much larger samples of each species are available for further comparison and, based on differences in size and following MacFadden (1980, 1998), we recognize both species as valid. Thus, based on the measurements provided by Hanson (1996) for the two *Epihippus* specimens from the Hancock Quarry, we believe they should be referred to *E. uintensis* instead of *E. gracilis*. The age assignment of the Hancock Quarry has been debated, for example Hanson (1989, 1996) and Lander and Hanson (2006) regarded it as early Duchesnean in age, but most other investigators have regarded it as latest Uintan in age (e.g., Lucas et al., 2004; Mihlbachler, 2007; Kelly et al., 2012). As noted above, if *Duchesnehippus* is regarded as generically distinct from *Epihippus* and the age assignment by Mihlbachler and Deméré (2009) for the *Harpagolestes* Quarry is correct, then the new record of *E. uintensis* from Ocean Ranch would confirm a geochronologic range extension of the species into the earliest Duchesnean.

AKNOWLEDGMENTS

We are thankful to the Rancho Mission Viejo (RMV) and, in particular, Steven Shea and Laura Coley Eisenburg of RMV, for their considerate support of the paleontological impact mitigation program that lead to the discovery of the Rancho Mission Viejo Local Fauna. We are grateful to Thomas Deméré and Kesler Randall of the SDMNH for providing loans of specimens for this study. Special thanks are given to Mark Roeder of the SDMNH and the Archeological Resource Management Corporation (ARMC), Carol Demcak, Patrick Riseley and Hugo Lozano of the ARMC for providing geologic and locality data from the paleontological mitigation program at Rancho Mission Viejo, and Michaela Adler and Crystal Cortez of the Cooper Center, Orange County, California, for their help in the curation of the specimens from Rancho Mission Viejo. Dr. Richard Klein and Brent Klein of Sierra Cosmetic Dental Center, Carson City, Nevada, graciously allowed access to their radiographic equipment for analysis of the rhinocerotoid specimen. William W. Korth of the Rochester Institute of Vertebrate Paleontology and Eric Scott of the California State University, Fullerton, provided constructive comments and advice on the original draft of this report.

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