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Cover photo: Temporal and geographical distribution of fossil crocodylians in California.

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The age of the Oso Member, Capistrano Formation, and a review of fossil crocodylians from California

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Fossils from the late Miocene Oso Member of the Capistrano Formation in Orange County, California, are underreported in the scientific literature. Mitigation activities in the Oso Member have resulted in collections of fossils in museums. We provide a preliminary list of identified faunal elements from the Oso Member and determine its age using biostratigraphy. The presence of the fossil horse *Dinohippus interpolatus* allows us to constrain the age of the Oso Member to the early late Hemphillian (Hh3, 6.6–5.8 Ma). We provide a review of other Hemphillian terrestrial vertebrate sites from Southern California. Our age assessment for the Oso Member allowed us to recognize a significant temporal range extension for crocodylians on the Pacific Coast of the United States. Including the Oso Member, the fossil record of crocodylians in California is based on fragmentary material from 13 formations ranging from the Paleocene to the late Miocene (including seven Eocene units). Of these records, the Oso Member fossils represent the youngest record of fossil crocodylians in California. Fossil crocodylians from Orange County extend the record of crocodylians in California ~10 million years from the middle Miocene to the late Miocene.

Keywords: Oso Member, Capistrano Formation, California, Orange County, Crocodylia, horse

INTRODUCTION

The vertebrate paleontology of Orange County, California has received increased attention in recent years, providing insights on the biogeography (Hunt and Stepleton 2015), temporal distribution (Boessenecker and Churchill 2015), and paleobiology (Santos et al. 2016) of extinct mammals. One of the more significant vertebrate-bearing rock units in Orange County is the Oso Member of the Capistrano Formation (Fig. 1). Mitigation activities in the Oso Member

from 1984 to 1994 and again in 2011 (e.g., Maher 1984, Minch and Hull 1993, Minch and Leslie 1994, Gust and Glover 2011) placed fossils in four museum collections in Southern California (Los Angeles County Museum, Ralph B. Clark Regional Park, John D. Cooper Center, and San Diego Natural History Museum). A full accounting of the rich but largely unpublished vertebrate assemblage from this unit is beyond the scope of this paper, but a preliminary list of identified material is provided in Table 1. For this study we set out to determine the age of the Oso Member by reviewing specimens of this unit from museum collections to identify biostratigraphically useful taxa. We determined that horse fossils provide the most precise chronostratigraphic

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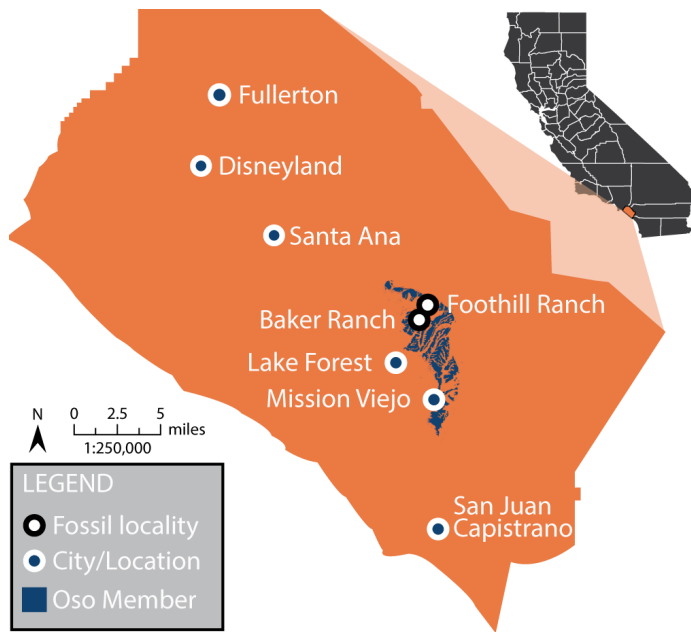


Figure 1. Map of Orange County (orange) showing the location of major cities, fossil sites and extent of the Oso Member.

information (MacFadden 1992) and so describe and identify horse teeth to constrain the age of the Oso Member.

Our age assessment for the Oso Member allowed us to recognize a temporally significant range extension (~10 million years) for crocodylians on the Pacific Coast of the United States. Including the Oso Member, the fossil record of crocodylians in California is based on fragmentary material from 13 formations ranging from the Paleocene to the late Miocene (including seven Eocene units). Until now only a single fossil specimen has ever been figured, a specimen from the upper Eocene Scripps Formation of San Diego County (Brochu 2013). There are dozens of additional specimens of late Eocene crocodylians from California in museum collections, but the non-Eocene crocodylians from California are represented by very few (one to four) fragmentary specimens from each unit. We take this opportunity to figure non-Eocene specimens from California for the first time, including previously unreported specimens from four formations (Skooner Gulch, Jewett Sand, Monterey, Capistrano [Oso Member]). Of these records, the Oso Member fossils represent the youngest record of fossil crocodylians in California.

GEOLOGIC SETTING

The Capistrano Formation is a heterogeneous marine unit exposed in Orange and San Diego Counties, California. The Capistrano Formation was named by Woodford (1925) for exposures in the San Juan Capistrano area of southern

Table 1. Preliminary list of fossil vertebrate taxa recorded from the Oso Member, Capistrano Formation, Orange County, California housed at LACM, LC, and OCPC. For information on vouchers and localities, see Appendix 1.

Chondrichthyes

Carcharocles megalodon
Carcharodon hastalis
Myliobatis sp.

Osteichthyes

Acipenseridae indet.
Makaira nigricans
Oncorhynchus rastrosus

Testudines

Dermochelyidae indet.
 Testudinidae indet.

Crocodylia

Aves

Mancallinae indet.

Mammalia

Afrotheria

Desmostylia
Desmostylus sp.
 Proboscidea indet.
 Sirenia
Hydrodamalis cuetae

Artiodactyla

Antilocapridae indet.
 Camelidae indet.
 Tayassuidae indet.
 Cetacea
 Odontoceti
 Delphinidae indet.
 Lipotidae
Parapontoporia sp.
 Physeteroidea Species A
 Physeteroidea Species B

Mysticeti

Cetotheriidae indet.
 Balaenopteridae
 cf. *Balaenoptera* sp.

Carnivora

Borophagus
 Mustelidae indet.
 Pinnipedia
 Odobenidae
Gomphotaria pugnax
 Odobenidae sp. A
 Odobenidae sp. B
 Otariidae indet.

Lagomorpha

Leporidae indet

Perissodactyla

Equidae
Dinohippus interpolatus
 Rhinocerotidae indet.

Orange County. The formation is located at the northern end of the Peninsular Ranges, a province that includes the Los Angeles Basin and extends 125 miles southward into Baja California. The ranges are composed of Late Jurassic and Cretaceous plutonic and metamorphic rocks (Demouthe 1994). Covering this core are Paleogene–Neogene marine and nonmarine deposits. In Orange County, these deposits reflect a significantly complete, fossil-bearing stratigraphic record.

The Capistrano Formation is composed of two distinct members: 1) the nearshore facies known as the Oso Member (Fig. 1), an arkosic sandstone, and 2) the deeper marine, unnamed siltstone member. The units are laterally equivalent and interfinger at the southwestern extent of the Oso Member (Fife 1974). Vedder et al. (1957) named the Oso Member for its type locality, which is located four kilometers east of El Toro between Agua Chinon Wash and Oso Creek (Morton and Miller 2006). The member is exposed at multiple localities throughout Orange County as a white to tan, crudely bedded to massive, and medium to coarse grained sandstone (Schoellhamer et al. 1981). In Foothill Ranch, the Oso Member sediments conformably overlie the deepwater shales of the Soquel Member of the Puente Formation (Sundberg 1991). In this case, the Oso Member may be correlative with part of the Yorba Member and Sycamore Canyon Member of the Puente Formation (Schoellhamer et al. 1981: page D53, but see fig. 3). In other areas, the Oso Member rests unconformably over the Miocene Monterey Formation and is unconformably overlain by the Pliocene Niguel Formation (Schoellhamer et al. 1981, Morton and Miller 2006).

The depositional environment of the Oso Member is interpreted as a submarine delta deposit in a shallow marine embayment (Minch and Hull 1993). Based on the occurrence of the fossil marlin *Makaira nigricans* Lacépède, 1802, Fierstine (2008) proposes that the Oso Member was deposited at upper bathyal depths. However, occurrence of pelagic fishes in marine sediments is not always a reliable indicator of depositional depth and in at least one case a marlin fossil has been found in a supratidal deposit (e.g., Pyenson et al. 2014).

PALEONTOLOGY AND AGE

The paleontology of the Oso Member is poorly documented despite the existence of extensive fossil collections. Vedder (1972) reported that benthonic and planktonic microfossils were found at a few localities in the Oso Member, but that macrofossils were rare. Barnes (1976) reported that marine mammals are present in the Capistrano Formation, but did not state in which member the fossils were found. Schoellhamer et al. (1981) stated that fossils other than shark teeth and whale bones were rare in the Oso Member. In some cases, papers reporting fossils from the siltstone member of

the Capistrano Formation mentioned that the Oso Member also contained fossils. Barnes and Rashke (1991) commented that the Oso Member had produced horses, rabbits, and other fossils of the Hemphillian North American Land Mammal Age. Deméré and Berta (2005) mentioned that the Oso Member contained marine mammals. Only a single paper dedicated to a paleontological find from the Oso Member has been published so far; the description of a marlin (*Makaira nigricans*) skull (Fierstine 2008).

In the Foothill Ranch area, the Oso Member conformably overlies the Soquel Member of the Puente Formation, which contains diatoms representative of the *Thalassiosira antiqua* Biozone Subzone B, 7.9–7.7 Ma (Barron and Isaacs 2001, Barron 2003, Gradstein 2004). This maximum age is consistent with age assessments for the Oso Member as Hemphillian (9.0–4.9 Ma) based on undescribed terrestrial fossils (Barnes and Raschke 1991, Deméré and Berta 2005). Taken together this would give an age range for the Oso Member of 7.7–4.9 Ma. Vedder (1972) and Schoellhamer et al. (1981) suggest that the Oso Member is the equivalent of the lower part of the unnamed silty member of the Capistrano Formation, and is no younger than Miocene (i.e., >5.3 Ma). Combined with the evidence stated above, restricting the Oso Member to the Miocene would give an age range of 7.7–5.3 Ma.

SYSTEMATIC PALEONTOLOGY

Institutional Abbreviations—LACM, Vertebrate Paleontology Collection, Natural History Museum of Los Angeles County, Los Angeles, California, USA; LC, Ralph B. Clark (formerly “Los Coyotes”) Regional Park, Interpretive Center, Buena Park, CA, USA; OCPC, Orange County Paleontological Collection [John D. Cooper Center], Santa Ana, California, USA; RAM, Raymond M. Alf Museum of Paleontology, Claremont, California, USA; SDNHM, San Diego Natural History Museum, San Diego, California, USA; UCMP, University of California Museum of Paleontology, Berkeley, California, USA. USNM PAL Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, District of Columbia, USA.

REPTILIA LAURENTI, 1768

CROCODYLIFORMES HAY, 1930 (SENSU BENTON AND CLARK, 1988)

EUSUCHIA HUXLEY, 1875 (SENSU BROCHU, 1999)

CROCODYLIA GMELIN, 1789 (SENSU BENTON AND CLARK, 1988)

FIGS. 2, 3

Referred specimens—The crocodylian material reported

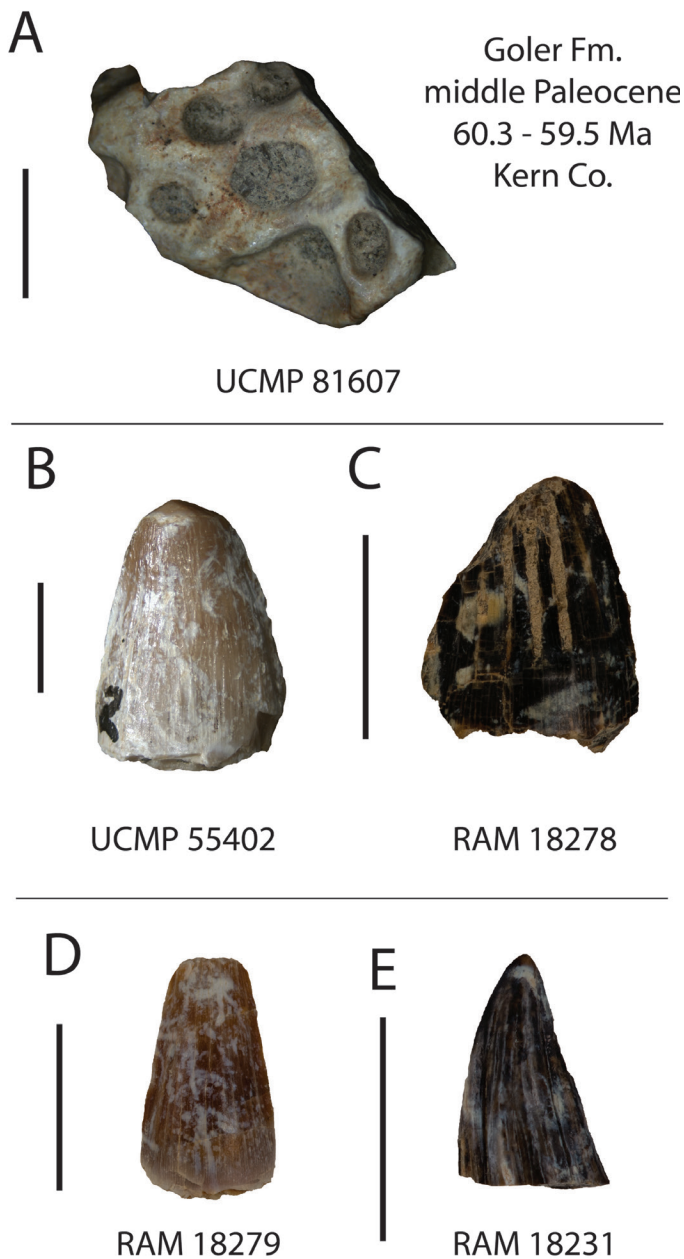


Figure 2. Fossil crocodylians from the Goler Formation, Kern Co., California. **A.** Osteoderm fragment, dorsal view. **B.** Tooth, lingual view. **C, D.** Teeth, labial view. **E.** Tooth, mesial or distal view. Age justification in Appendix 3. Scale bar = 5 mm.

here is from six formations in California. Museum specimen numbers are listed before their locality numbers: 1) Goler Formation (Paleocene), Kern County: one osteoderm (Fig. 2A; UCMP 81607, V5252,) and four teeth (Fig. 2B–E; RAM 18278, V94014; RAM 18279, V200001; RAM 18231, V98012; UCMP 55402, V67158); 2) Jewett Sand Formation,

Pyramid Hill Sand Member (late Oligocene), Kern County: a tooth (Fig. 3I; LACM 72262, Loc. 1626); 3) Skooner Gulch Formation (early Miocene), Mendocino County: a tooth (Fig. 3H; LACM 117889, Loc. 4460); 4) Caliente Formation (middle Miocene), San Luis Obispo County: 13 teeth (Fig. 3G; USNM PAL 619511, Loc. USGS M1005; 5) Monterey Formation (middle Miocene), Orange County: one osteoderm (Fig. 3C–F; LACM 48016, Loc. 3209) and six isolated teeth (LACM 48010, 48012, 48013, 48015, 48017, 48018; Locs. 3209, 3210); 6) Capistrano Formation, Oso Member (late Miocene), Orange County: one osteoderm (Fig. 3A; LC 2380, LC locality 73) and one tooth (Fig. 3B; LACM 48019, Loc. 65122).

Remarks—All of the osteoderms from the Goler (Fig. 2A), Monterey (Fig. 3C) and Capistrano Formations (Fig. 3A) display typical crocodylian ornamentation consisting of suboval to rounded pits. LACM 48016 (Fig. 3A) from the Capistrano Formation (Oso Member) is the most complete, missing only a fragment on the right side. LACM 48016 has a rectangular outline, with a longitudinal mid-dorsal keel, its long axis oriented diagonally. The preserved margins of the scute are sculpted to varying degrees, with one of the corners having shallower pits, which can be interpreted as representing the anterior border. In many taxa, the anterior edge of dorsal osteoderms bear a smooth articular surface (e.g., the tomistomine *Penghusuchus pani* Shan, Wu, Cheng, and Sato, 2009, and caimanines such as *Tosabichi greenriv-erensis* Brochu, 2010). The keel is relatively low (~10 mm maximum height) and slopes gently towards its anterior border and more abruptly posteriorly. The keel extends almost the entire anteroposterior length of the scute, as in alligatoroids and *Crocodylus* Laurenti, 1768, and unlike the keel-less dorsal osteoderms of the tomistomine *Thecachampsia* Cope, 1867 (reported from the Neogene of North America [Myrick 2001]) and the anteroposteriorly short keels of gryposuchines (reported from the Neogene of South America [Brochu et al. 2007]).

The teeth all are all very similar in their general morphology, differing mainly in their size (Figs. 2B–E, 3B, D–I). The teeth are conical, with marked fluting on the lingual and buccal surfaces; distal and mesial carinae are present on all teeth, reaching nearly to the apex of the crown. At their base, the teeth are almost rounded in outline, and the crowns are curved lingually. The relatively stout and wide shape of the teeth is more consistent with alligatoroids and crocodyloids, than the more slender and elongated teeth observed in gavialoids or tomistomines. However, the large specimens of the tomistomine *Thecachampsia* have stout teeth (Myrick, 2001) and so we cannot rule out that taxon.

Taken together, morphology of the osteoderms and teeth

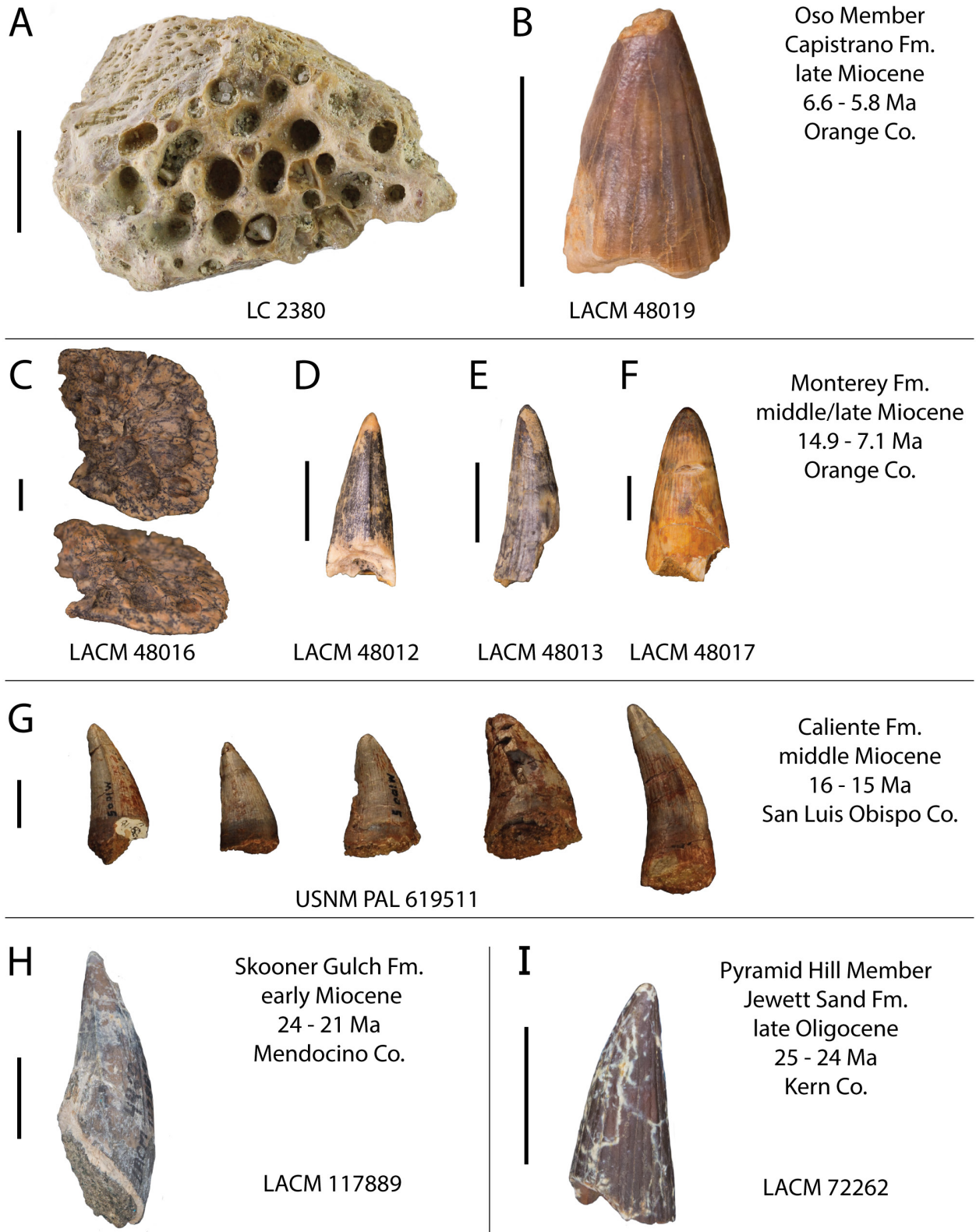


Figure 3. Post-Eocene fossil crocodylians from California. **A.** Osteoderm fragment, dorsal view. **B.** Tooth, labial view. **C.** Osteoderm fragment, dorsal and oblique views. **D-F.** Teeth, labial view. **G-I.** Teeth, mesial or distal view. Age justification in Appendix 3. Scale bar = 1 cm..

are consistent with Brochu's (1999) tentative identification of part of this material as representing alligatoroids, although we cannot rule out the possibility that the teeth (Fig. 3B, D-I) or the osteoderm that lacks a keel (LC 2380, Fig. 3A) could be *Thecachampsa* as proposed by Myrick (2001).

MAMMALIA LINNAEUS, 1758
 PERISSODACTYLA OWEN, 1848
 EQUIDAE GRAY, 1821
 DINOHIPPIUS QUINN, 1955
 DINOHIPPIUS INTERPOLATUS (COPE, 1893)

FIG. 4

Referred specimens—The horse material reported here is from the Oso Member of the Capistrano Formation in the area of Baker Ranch (Fig. 1; LC localities 73, 74). The Oso Member has 11 identifiable isolated upper and lower cheek teeth of *Dinohippus interpolatus* (Cope 1893): left lower m3 (LC 2159, LC locality 73); right lower m2 (LC 2165, LC locality 73; Fig. 4A); right lower m2 or m3 (LC 2331, LC locality 73; Fig. 4C); left lower m3 (LC 2341, LC locality 73); right lower p3 (LC 2411, LC locality 73); right lower m2-m3 (LC 2443, LC locality 73); right upper (LC 2568, LC locality 74); right lower m1 or m2 (LC 2659, LC locality 74; Fig. 4B); right upper P2 (LC 2692) LC locality 74; Fig. 4D); right lower (LC 2727, LC locality 74); left upper (LC 2726, LC locality 74).

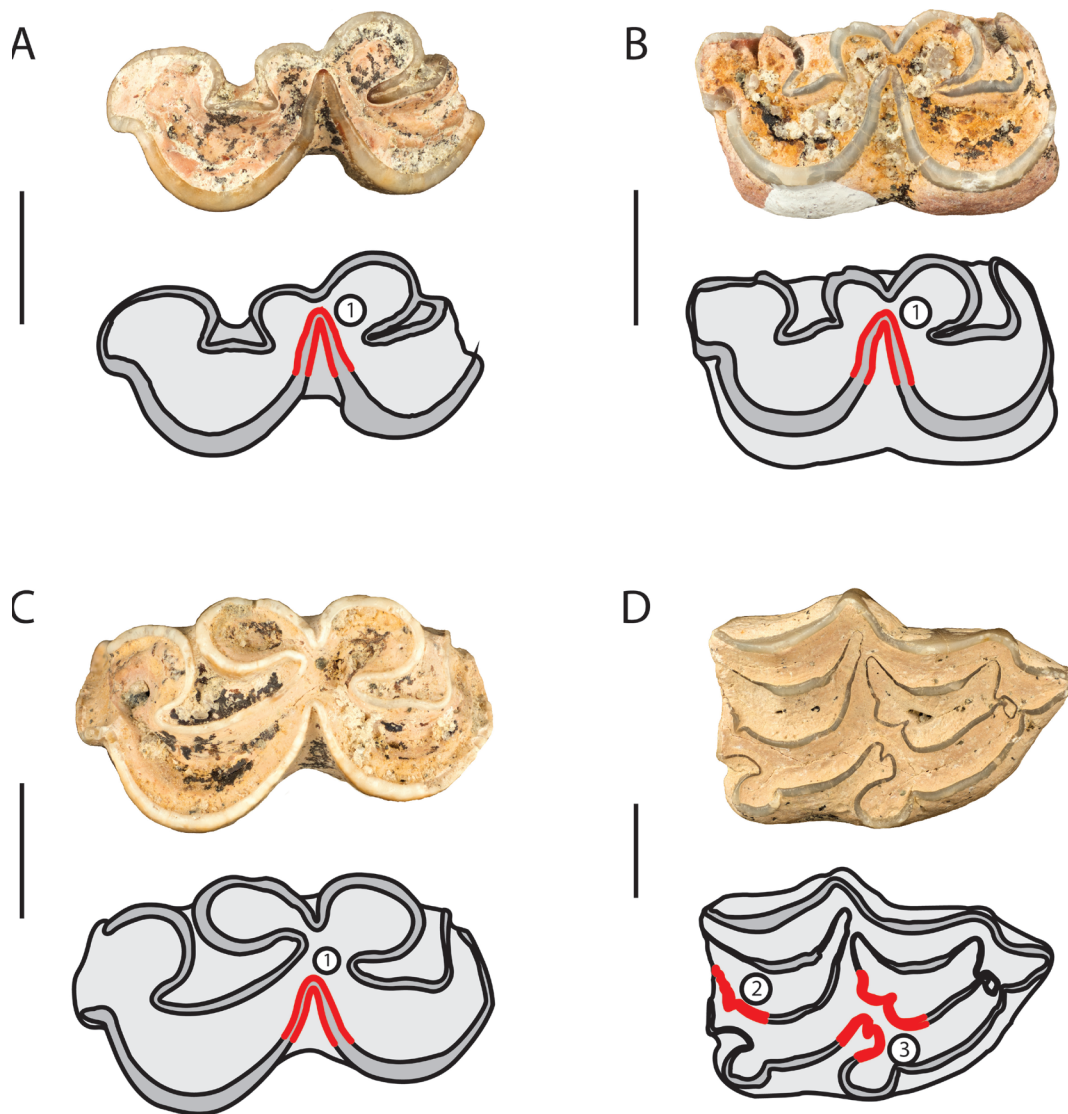


Figure 4. Right lower cheek teeth of *Dinohippus interpolatus*. Drawings illustrate: 1=ectoflexid, 2=fossette borders, 3=pli cabalin. A. m2; LC 2165. B. m1 or m2; LC 2659. C. m2 or m3 exhibiting a relatively deep ectoflexid; LC 2331. D. Right upper cheek tooth of *Dinohippus*. P2 exhibiting simple fossette borders and a pli cabalin; LC 2692. Scale bar = 1 cm.

Remarks—The equid teeth from the Oso Member are compared to specimens of *Dinohippus interpolatus* from the Mehrten Formation in Stanislaus County, California (LACM 61662, LACM 61653), and a specimen of *Dinohippus mexicanus* (Lance, 1950) from Yepomera, Mexico, housed at the LACM (LACM [CIT] 3723, Loc. 275) as well as descriptions of *Pliohippus* Marsh, 1874 and *Dinohippus* from Kelly (1998) and figures and descriptions of *Astrohippus* Stirton, 1940 and *Dinohippus* from MacFadden (1986: figs. 2, 3, 5).

The teeth collected from the Oso Member are large (worn crown height of m1-2 ~50–60 mm) compared to *Pliohippus* or *Astrohippus* and exhibit moderately curved upper dentition (relative to *Pliohippus*). They all display a pli caballin and hypoconal groove (e.g., Fig. 4D), which is usually absent in *Astrohippus*. In addition, *Pliohippus* and *Astrohippus* have very simple enamel patterns on the upper cheek teeth, whereas the equid teeth from the Oso Member exhibit enamel plications on the fossette borders. In the lower cheek teeth (Fig. 4A–C), the ectoflexid is deep, which is characteristic of *Dinohippus* (all lower cheek teeth from referred material display this feature). *Astrohippus* and *Pliohippus* exhibit a moderate to shallow ectoflexid. From these features, the Oso Member specimens are identified as *Dinohippus*, which is known from the late Miocene to early Pliocene.

Upper teeth (Fig. 4D) demonstrate characters diagnostic of *D. interpolatus*. The patterns on the upper cheek teeth differ from those of *D. mexicanus* (latest Hemphillian, Hh4), by exhibiting a simple plication on the fossette borders relative to the moderately developed plications of *D. mexicanus*. The protocones of *D. mexicanus* are significantly elongated, but those of the upper cheek teeth from the Oso Member are oval in shape, which occurs in *D. interpolatus*. Based on this feature, the upper cheek teeth can be confidently assigned to *D. interpolatus*.

DISCUSSION

The age of the Oso Member

The best indication of a Hemphillian age of the Oso Member is the presence of *Dinohippus interpolatus* which is characteristic of the early late Hemphillian stage (Hh3, Tedford et al. 2004). Other Hh3 faunas containing *D. interpolatus* include: the Edson Local Fauna, Ogallala Formation, Sherman County, Kansas (Harrison 1983); the Coffee Ranch Local Fauna, Goodnight Beds Formation, Hemphill County, Texas (Dalquest 1983); the Mehrten Formation in Stanislaus County, California (LACM 61662, LACM 61653). We did not find any evidence of either older (Hh 2 or earlier) or younger (Hh 4 or later) taxa and so we provisionally restrict the Oso Member to Hh3, 6.6–5.8 Ma (Tedford et al. 2004, Hilgen et

al. 2012). This proposed age range for the Oso Member is narrower than the 7.7–5.3 Ma proposed by previous studies (see Introduction).

It is important to note that this proposed age of the Oso Member does not apply to the Capistrano Formation as a whole. Parts of the unnamed silty member of the Capistrano Formation are younger than the Oso Member, extending even into the Pliocene, as summarized in Blake (1991) and also later reported by Deméré and Berta (2005). Vedder (1972) and Schoellhamer et al. (1981) suggest that the Oso Member is the equivalent of the lower part of the Capistrano unnamed silty member. If this is the case it may be possible to restrict the maximum age of the Capistrano Formation as a whole to 6.6 Ma.

Once more material from the Oso Member is described, the refined age we provide here will allow for more detailed comparisons to other late Neogene faunas in California. Based on our age estimate, the Oso Member terrestrial fauna is older than the Warren Local and Mount Eden Local Faunas and younger than the Sequence Canyon Local Fauna. Parts may correlate with all other known Hemphillian units around Southern California (Fig. 5, Appendix 2).

The early late Hemphillian stage (Hh3) is correlative to part of the Messinian stage of the Miocene. Most Neogene strata from California are summarized by Boessenecker (2013, fig. 51). The lower vertebrate fauna of the San Mateo Formation (The San Luis Rey River Local Fauna, SLRRLF, of Barnes et al. 1981) of nearby San Diego County might be as young as the early Messinian (early Hemphillian fide Domning and Deméré 1984); Smith (2011) provides a range estimate of 10.0–6.7 Ma for the SLRRLF, which would predate our estimate for the Oso Member (6.6–.8 Ma). The close geographic proximity and temporal succession of the SLRRLF and the Oso Member invites further comparisons, especially since both assemblages are relatively diverse (see Domning and Deméré 1984, and Table 1). Other Messinian marine strata in Southern California include parts of both the Modelo (Powell et al. 2007) and Puente Formations (Pajak. 1992, Santos et al. 2016), the latter of which contains both marine and terrestrial vertebrates. Neither of these units has well-characterized vertebrate faunas, with just two taxa (a kentriodontid dolphin and a sulid bird) described from the Messinian part of the Modelo (Barnes 1985, Howard 1958) and the presence of “cetaceans, sirenians, pinnipeds, sharks, and fish” mentioned by Pajak (1992) for the Sycamore Canyon Member of the Puente Formation. Our data confirm the assertion by Schoellhamer et al. (1981) that the Oso Member is correlative to the Sycamore Canyon Yorba Members of the Puente Formation. Pending the description of that fauna, the Oso Member probably has the best fossil record of Messinian

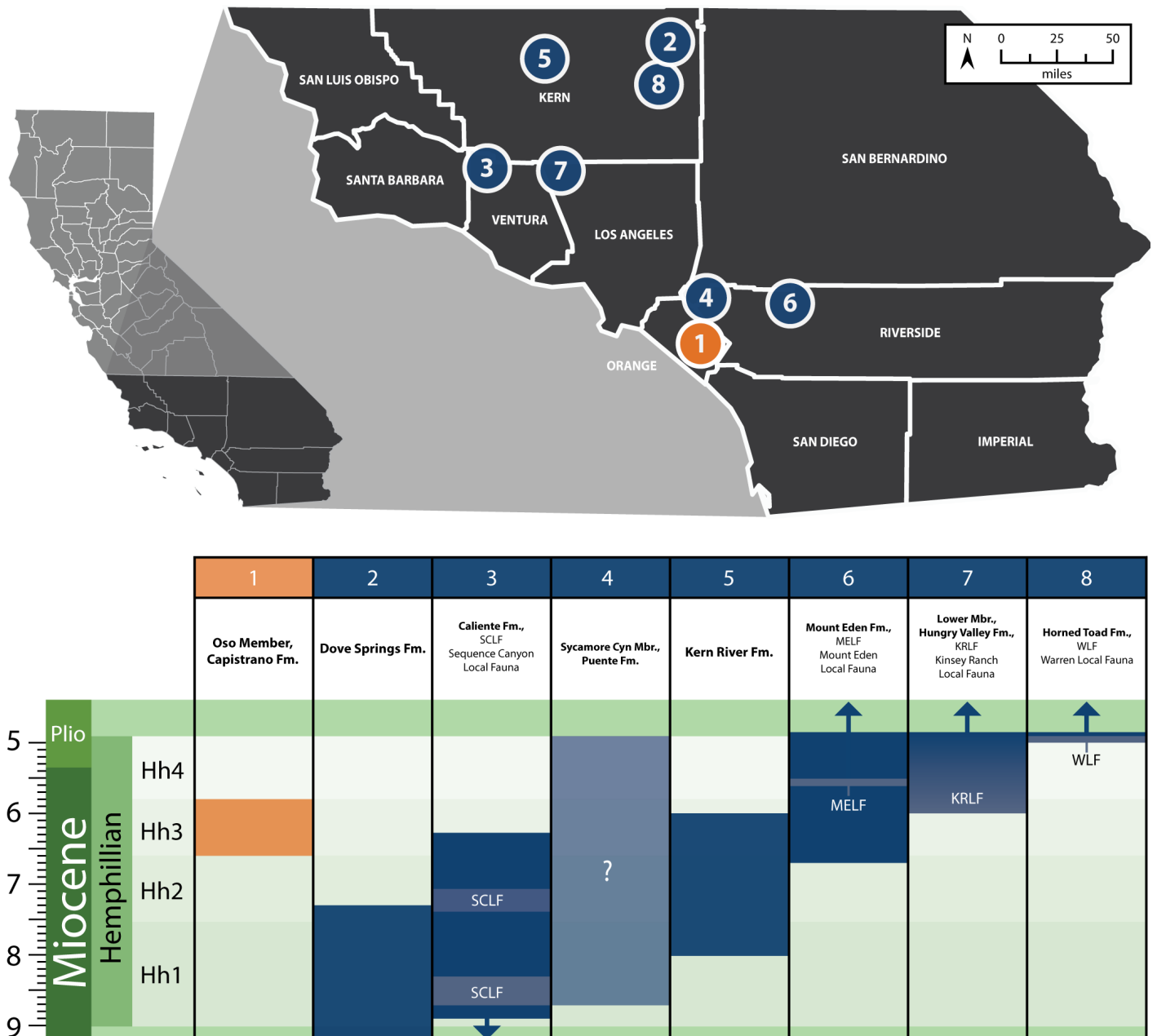


Figure 5. Temporal and geographical distribution of Hemphillian terrestrial mammal sites in Southern California. Abbreviation for local faunas given at top of each column. The two ages given for SCLF refer to uncertainty to its age. Age justifications are given in Appendix 2.

marine vertebrates in Southern California. Ultimately, the most important comparisons for the Oso Member fauna will likely come from the basal 10 m of the Purisima Formation of Northern California, which has a recently refined age of 6.9–5.6 Ma (Boessenecker 2016), which nearly matches the age of the Oso Member presented here (6.6–5.8 Ma) and has a relatively well known fauna (Boessenecker 2011, 2013, Boessenecker et al. 2014, Boessenecker 2016).

Fossil crocodylians from California

The oldest published records of crocodylians from California, both in terms of stratigraphic age and publication date, are from the Paleocene Goler Formation of Kern County (Fig. 2; Appendix 3; Savage et al. 1954, Mckenna et al. 1987). The Goler Formation was deposited at low elevation in a near coastal setting (Torres and Gaines 2011, Lofgren et al. 2014), and all younger records are from a similar topographic setting

(e.g., Caliente Formation) or else further offshore (e.g., Jewett Sand and Monterey Formations).

The next oldest crocodylians are from six Eocene formations in San Diego County (Ardath Shale, Scripps Formation, Friars Formation, Stadium Conglomerate, Mission Valley Formation, Santiago Formation) and one in Ventura County (Sespe Formation) first mentioned by [Golz and Lillegraven \(1977\)](#). There are dozens of undescribed specimens of Eocene crocodylians from California at OCPC, LACM, SDNHM, and UCMP that likely represent more than one taxon of

crocodylian. A thorough treatment of Eocene crocodylians from California is outside the scope of the present paper as there is enough material to warrant a standalone study. After being listed by [Golz and Lillegraven \(1977\)](#), Eocene crocodylians from California are mentioned just two additional times in the peer reviewed literature ([Busbey 1986](#), [Brochu 2013](#)). [Brochu \(2013\)](#) figures one specimen from the Scripps Formation assigned to the Planocraniidae [Li, 1976](#) (formerly *Pristichampsus Gervais, 1853*).

Published records of post-Eocene fossil crocodylians from



Figure 6. Temporal and geographical distribution of fossil crocodylians in California. Age justifications are given in Appendix 3.

California are limited. Whistler and Lander (2003) include a mention of crocodiles from the “Vaqueros” lithofacies that are either upper Oligocene or lower Miocene, but they do not list specimens. Here we report specimens from the late Oligocene Pyramid Hill Member of the Jewett Sand Formation of Kern County and the early Miocene Skooner Gulch Formation of Mendocino County.

Before this study, the only slightly specific record of a Neogene crocodylian from California is from the Caliente Formation, San Luis Obispo County (Repenning and Vedder 1961) that was also discussed by Brochu (1999) and Myrick (2001). This specimen, 13 associated teeth, have now been accessioned as USNM PAL 619511. These fossils represent the youngest fossil Californian crocodylians mentioned in the literature until now, and are between 16–15 Ma (Fig. 6, Appendix 3). In addition to clarifying this record, we can extend the record of fossil crocodylians to younger formations, both from Orange County. We report middle/late Miocene records from the marine Monterey Formation of Orange County (Figs. 3C–F, 6). The age of the Monterey Formation crocodylians is not well constrained, highlighting the need for much further work on the stratigraphy of that unit (Appendix 3). The youngest crocodylian fossils from California are from the Oso Member of the Capistrano Formation in Orange County (Figs. 3A, B, 6).

Given the sparse published record, until now, and the fragmentary nature of the material, it is too soon to speculate on the precise timing of crocodylian extirpation from the California coast. After all, this study extends the record of fossil crocodylians in California by 10 million years and so later records may still appear. In fact, Pliocene fossils referable to the extant genus *Crocodylus* are known from nearby Baja California Sur, Mexico (Miller 1981, Brochu 2003 and Brochu et al. 2007). Although it is unlikely that the California crocodylians are related to the *Crocodylus*, ultimately, it may be possible to correlate the latitudinal distribution of crocodylians in California with climate change, as we would expect records to shift southward as the climate cools in the late Neogene. Together with data from other large ectotherms (e.g., giant tortoises, Biewer et al. 2016), additional records of crocodylians may help correlate the paleobiogeography and eventual extinction of California’s megaherpetofauna with late Neogene cooling (Zachos et al. 2001).

Finally, additional description can help answer questions about the diversity of California crocodylians through time. For example, the only Eocene taxon known thus far is a planocraniid, but there may be adequate material in collections to expand the known diversity for that time period. Beyond the Eocene, we have figured the best specimens but were unable to generate precise identifications. Therefore, more

complete material is needed to determine patterns of crocodylian faunal change such as the temporal and geographic distribution of tentatively identified alligatoroids (Brochu 1999) and crocodyloids (Brochu 2003, Brochu et al. 2007) on the California coast.

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Appendix 1. Voucher list for taxa identified from the Oso Member, Capistrano Formation. Order as in Table 1 with specimen number and locality number given in parentheses: **Chondrichthyes:** *Carcharocles megalodon* (LC 2686, LC locality 74), *Carcharodon hastalis* (LC 2410, LC locality 73), *Myliobatis* sp. (LACM 148836, Loc. 7371); **Osteichthyes:** Acipenseridae (LACM 115956, Loc. 4436), *Makaira nigricans* (OCPC 31001, Loc. 3101); *Oncorhynchus rastrosus* (LACM 115971-3, Loc. 4436); **Testudines:** Dermochelyidae (LC 2001, LC locality 73), Testudinidae (LACM 103281, Loc. 3221); **Crocodylia:** this paper; **Aves** Mancallinae (LACM 39560, Loc 3221); **Mammalia, Afrotheria:** Desmostylia - *Desmostylus* (LC 2135, LC locality 73), Proboscidea: (LC 2399, LC locality 73), Sirenia - *Hydrodamalis cuestae* (OCPC 43618, Loc. 3214); **Mammalia, Artiodactyla, non-Cetacea:** Tayassuidae (LACM 145061, Loc. 3186); Camelidae (LC 2161 and LC 2146, LC locality 73) Antilocapridae (LC 2678, LC locality 74); **Mammalia, Artiodactyla, Cetacea, Odontoceti:** Delphinidae (LACM 115975, Loc. 4436), Lipotidae - *Parapontoporia* (LACM 150921, Loc. 7546), Physteroidea Species A (LACM 115979, Loc. 4436), Physteroidea Species B (LACM 39561, Loc. 3221); **Mammalia, Artiodactyla, Cetacea, Mysticeti:** Cetotheriidae (LACM 148854, Loc. 7372), Balaenopteridae - cf. *Balaenoptera* sp. (LACM uncat., Loc. 4093); **Mammalia, Carnivora, non-Pinnipedia:** *Borophagus* (LC 2676, LC locality 74), Mustelidae (LACM 50665, Loc. 3221); **Mammalia, Carnivora, Pinnipedia:** Odobenidae - *Gomphotaria pugnax* (LACM 105151, Loc. 4177), Odobenidae sp. A (OCPC 11141, Loc. 721), Odobenidae sp. B (LACM 118967, Loc. 3866); Otariidae (LACM 150914, Loc. 7539); **Mammalia, Lagomorpha:** Leporidae (LACM 123712, Loc. 3186); **Mammalia, Perissodactyla:** Equidae - *Dinohippus interpolatus* (see text); Rhinocerotidae (LACM 39590, Loc. 3221).

Appendix 2. Age estimates for Hemphillian vertebrate sites in Southern California appearing in Fig. 5. Although Hemphillian fossils have been reported from the Bedrock Springs Formation (Woodburne 1991), we do not include it here or in Fig. 5 because Smith et al. (2002) show that the formation may be Clarendonian in age. Similarly, we exclude the Chanac Formation, which is considered Hemphillian by Whistler and Burbank (1992) but Clarendonian by Wilson and Prothero (1997). **1. Oso Member, Capistrano Formation:** See text. **2. Dove Springs Formation:** The Dove Springs Formation ranges from the Barstovian to the Hemphillian, with the upper age estimate for the fossiliferous layers estimated to be at about 7.3 Ma (Whistler 1991, Whistler and Burbank 1992). **3. Caliente Formation:** The Caliente Formation ranges from the early Miocene (Hemingfordian) until the late Miocene (late Hemphillian) and includes eight described local faunas (Prothero et al. 2008). The top of the Caliente Formation is marked by the Lockwood Clay which is in Chron C3An, the top of which is 6.3 Ma (Hilgen et al. 2012). The youngest described local fauna is the Sequence Canyon Local Fauna which can be assigned to chron C4r (8.7–8.3 Ma) or C3Br (7.4–7.1 Ma, Prothero et al. 2008, Hilgen et al. 2012). **4. Sycamore Canyon Member, Puente Formation:** Pajak (1992) reports undescribed terrestrial mammals assigned to the Hemphillian from the Sycamore Canyon Member as well as foraminifera from the Mohnian and Delmontian stages from the Puente Formation overall. Blake (1991) correlates the base of the Sycamore Canyon Member to be the base of the Delmontian benthic foraminifera stage, and this has been followed by later authors (Saul and Stadum 2005, Santos et al. 2016). More work on the age of the mammal fauna from the Sycamore Canyon Member is needed, but for now we accept the Hemphillian age of the unit with a base equivalent to that of the Delmontian. The boundary of the Mohnian and Delmontian is known to be time transgressive but is never considered older than chron C4, planktonic foraminiferal zone N17, or the middle of the *Thalassosira antiqua* subzone B Diatom zone (e.g., Blake, 1991, Hosford-Scheirer and Magoon 2007). Conservatively using the oldest possible date for the Delmontian from the preceding list would place it at the base of chron C4, which is 8.7 Ma (Hilgen et al. 2012). **5. Kern River Formation:** Hosford-Scheirer and Magoon (2007) and assume the deposition of the Kern River Formation occurred between 8 and 6 Ma based on well data acquired for a petroleum systems/geologic assessment of oil and gas in the San Joaquin Basin Province. **6. Mount Eden Formation:** The top of the formation extends into the Blancan, and Albright (1999) gives the base of the lower arkose member, and the base of the formation, at 6.3 Ma. The formation begins in Chron C3An.2n, which begins at 6.7 Ma (Hilgen et al. 2012) and we use that as the conservative age for the base of the formation. Albright (1999) provides a precise age for the Mt. Eden Local Fauna at 5.6 Ma. **7. Hungry Valley Formation:** The Hemphillian Kinsey Ranch Local Fauna was originally considered to be in the Hungry Valley and Peace Valley Formations, the boundary of which was uncertain (Miller and Downs 1974). May et al. (1993) restricted Kinsey Ranch Local Fauna to Hungry Valley Formation. The age of the base of the Hungry Valley Formation is uncertain, but is no older than the base of chron C3r which has maximum age of 6.0 Ma. The Hungry Valley Formation extends into the Blancan. **8. Horned Toad Formation:** Most of the mammal fossils from the Horned Toad Formation are assigned to the Warren Local Fauna, which is precisely dated to the latest Hemphillian (5.0–4.8 Ma) through a combination of magnetostratigraphy and the age of the Lawlor Tuff (May et al. 2011).

Appendix 3. Ages estimates for California strata with crocodylian fossils appearing in Figs. 2, 3, 5: **1. Capistrano and Monterey Formation in Orange County:** For the age of the Oso Member, Capistrano Formation, see text. For the Monterey Formation in Orange County, [Barnes \(2013: figure 2\)](#) provides an age estimate of 13.5–8 Ma but it is not clear how these dates were determined. [Velez-Juarbe \(in press\)](#) uses a more conservative age range of 14.9–7.1 based on the benthic foraminifera listed in [Blake \(1991\)](#) and the age ranges of [Barron and Isaacs \(2001\)](#). Unpublished data show that diatoms from vertebrate sites of the Monterey Formation of Orange County can, so far, be assigned from as low as the Denticulopsis subzone B (UCMP locality V99593 analyzed by Micropaleontology Consultants; 14.9–13.1 Ma, [Berggren et al. 1995](#)). Therefore, we conservatively use an age range of 14.9–7.1 for the Monterey Formation in Orange County. **2. Caliente Formation:** The crocodylian specimen (USNM PAL 619511) is from locality USGS M1005 (Fig. 3G), which is assigned to the early Barstovian ([Wang et al. 1999](#)). The early Barstovian is 16–15 Ma according to [Hilgen et al. \(2012\)](#). **3. Pyramid Hill Member, Jewett Sand Formation:** The Pyramid Hill Member is well constrained at 25–24 Ma ([Hosford-Scheirer and Magoon 2007](#)). **4. Skooner Gulch:** The Skooner Gulch is variably reported as Oligocene ([Shimada et al. 2014](#), [Thomas and Barnes 2015](#)), Miocene ([Boessenecker 2011](#)), or either ([Clark 1991](#)). [Miller \(1981\)](#) shows that the Skooner Gulch lacks diagnostic Oligocene nannofossils whereas [Phillips et al. \(1976\)](#) place the Skooner Gulch Formation the Zemorrian Californian stage which is primarily Oligocene, but extends into the very earliest Miocene. Therefore we propose an earliest Miocene age of 23–22 Ma for the Skooner Gulch Formation. **5, 6. Eocene Formations:** The Eocene record of crocodylians in California could stretch back as far as 47.4 Ma, the oldest estimated age of the Ardath Shale (C21n, [Walsh et al. 1996](#), [Vandenberghe et al. 2012](#)). The youngest Eocene occurrence would be from locality CIT 150 ([Golz and Lillegraven 1977](#)) which is part of the Pearson Ranch Local Fauna of the Sespe Formation ([Lander 2013](#)) in chron C18r, the top of this chron is 40.5 Ma ([Whistler and Lander 2003](#), [Vandenberghe et al. 2012](#)). **7. Paleocene Goler Formation:** The entire age range of the Goler Formation is 61.6–57.7 Ma ([Albright et al. 2009](#), [Lofgren et al. 2014](#)). All crocodylian specimens from the Goler Formation are from strata that assigned to Tiffanian Biozone 3 or 4a, giving an age range of 60.3–58.9 Ma ([Lofgren et al. 2014](#)).