The Early Pliocene extinction of the mega-toothed shark *Otodus megalodon*: A view from the eastern North Pacific

Robert W Boessenecker Corresp., [1] , **Dana J Ehret** [2] , **Douglas J Long** [3] , **Evan Martin** [4] , **Sarah J Boessenecker** [1]

[1] Department of Geology and Environmental Geosciences, College of Charleston, Charleston, South Carolina, United States
[2] New Jersey State Museum, Trenton, New Jersey, United States
[3] Department of Biology, Mount St. Mary's College California, Moraga, California, United States
[4] San Diego Natural History Museum, San Diego, California, United States

Corresponding Author: Robert W Boessenecker
Email address: boesseneckerrw@cofc.edu

The extinct giant shark *Otodus megalodon* is the last member of the predatory megatoothed-lineage and is reported from Neogene sediments from nearly all continents. The timing of the extinction of *O. megalodon* is thought to be Pliocene, although reports of Pleistocene teeth fuel speculation that *O. megalodon* may still be extant. The longevity of the *Otodus* lineage (Paleocene to Pliocene) and its conspicuous absence in the modern fauna begs the question: when and why did this giant shark become extinct? Addressing this question requires a densely sampled marine vertebrate fossil record in concert with a robust geochronologic framework. Many historically important basins with stacked *Otodus*-bearing Neogene marine vertebrate fossil assemblages lack well-sampled and well-dated lower and upper Pliocene strata (e.g. Atlantic Coastal Plain). The fossil record of California, USA, and Baja California, Mexico, provides such an ideal sequence of assemblages populated with age determinations. This study reviews all records of *O. megalodon* from post-Messinian marine strata from Western North America and evaluates the reliability of each. All post-Zanclean *O. megalodon* occurrences exhibit clear evidence of reworking or lack reliable provenance. The youngest reliable records of *O. megalodon* are Early Pliocene, suggesting a late Zanclean (3.6 Ma) extinction, corresponding with youngest occurrences of *O. megalodon* in Japan, the North Atlantic, and Mediterranean. This estimate is somewhat earlier than a recently proposed late Pliocene extinction date. Post-middle Miocene oceanographic changes and cooling sea surface temperature may have resulted in range fragmentation, while competition with the newly evolved great white shark (*C. carcharias*) during the Pliocene is a probable determinant in the demise of the megatoothed shark. Alternatively, these findings may also suggest a globally asynchronous extinction of *O. megalodon*.

The Early Pliocene extinction of the mega-toothed shark *Otodus megalodon*: A view from the eastern North Pacific

Robert W. Boessenecker[1,2,3], Dana J. Ehret[4], Douglas J. Long[5,6], Evan Martin[7], and Sarah J. Boessenecker[3,8]

[1]Department of Geology and Environmental Geosciences, College of Charleston, 66 George Street, Charleston, SC, 29424, USA

[2]University of California Museum of Paleontology, University of California, 1101 Valley Life Sciences Building, Berkeley, CA, 94720, USA

[3]Mace Brown Museum of Natural history, College of Charleston, 66 George Street, Charleston, SC, 29424, USA

[4]New Jersey State Museum, P.O. Box 530, Trenton, NJ 08625-0530, USA

[5]Department of Ichthyology, Institute for Biodiversity Science and Sustainability; California Academy of Sciences, 55 Music Concourse Dr., San Francisco, CA, 94118, USA

[6]Current address: Department of Biology, St. Mary's College, 1928 St. Mary's Rd., Moraga, CA, 94575, USA

[7]San Diego Natural History Museum, P.O. Box 1211390, San Diego, CA 92112, USA

[8]School of Museum Studies, University of Leicester, 19 University Road, Leicester, LE1 7RF, UK

Corresponding author:

Robert W. Boessenecker[1,2,3]

Abstract

The extinct giant shark *Otodus megalodon* is the last member of the predatory megatoothed-lineage and is reported from Neogene sediments from nearly all continents. The timing of the extinction of *O. megalodon* is thought to be Pliocene, although reports of Pleistocene teeth fuel speculation that *O. megalodon* may still be extant. The longevity of the *Otodus* lineage (Paleocene to Pliocene) and its conspicuous absence in the modern fauna begs the question: when and why did this giant shark become extinct? Addressing this question requires a densely sampled marine vertebrate fossil record in concert with a robust geochronologic framework. Many historically important basins with stacked *Otodus*-bearing Neogene marine vertebrate fossil assemblages lack well-sampled and well-dated lower and upper Pliocene strata (e.g. Atlantic Coastal Plain). The fossil record of California, USA, and Baja California, Mexico, provides such an ideal sequence of assemblages populated with age determinations. This study reviews all records of *O. megalodon* from post-Messinian marine strata from Western North America and evaluates the reliability of each. All post-Zanclean *O. megalodon* occurrences exhibit clear evidence of reworking or lack reliable provenance. The youngest reliable records of *O. megalodon* are Early Pliocene, suggesting a late Zanclean (3.6 Ma) extinction, corresponding with youngest occurrences of *O. megalodon* in Japan, the North Atlantic, and Mediterranean. This estimate is somewhat earlier than a recently proposed late Pliocene extinction date. Post-middle Miocene oceanographic changes and cooling sea surface temperature may have resulted in range fragmentation, while competition with the newly evolved great white shark (*C. carcharias*) during the Pliocene is a probable determinant in the demise of the megatoothed shark. Alternatively, these findings may also suggest a globally asynchronous extinction of *O. megalodon*.

Keywords: *Otodus megalodon*, *Otodus*, Otodontidae; Extinction; Lamniformes; California; Baja California; North Pacific; Miocene; Pliocene

Introduction

The giant predatory shark *Otodus megalodon* has been reported from Miocene and some Pliocene age sediments from all continents except Antarctica, indicating a near worldwide distribution (Cappetta, 2012). Although some controversy exists regarding the generic allocation of this species (Purdy et al., 2001; Ehret et al., 2009a; Cappetta, 2012; Ehret et al., 2012; and references therein), *O. megalodon* appears to represent the terminal chronospecies of a Paleocene to late Neogene lineage including *Otodus obliquus* and earlier species fomerly placed within *Carcharocles* such as *Otodus angustidens*, generally characterized by steadily increasing body size through time (Ward and Bonavia, 2001; Ehret et al., 2009a; Cappetta, 2012; Ehret et al., 2012). *Otodus megalodon* is estimated to have attained a body length of 16 m (Gottfried et al., 1996), representing one of the largest sharks to ever exist, and one of a few marine superpredators in the Miocene, alongside macrophagous sperm whales (Bianucci and Landini, 2006; Lambert et al., 2010) and the less well known giant shark *Parotodus benedeni* (Kent, 1999; Kent and Powell, 1999; Purdy et al., 2001). Although some aspects of the morphology, evolution, and paleoecology of *O. megalodon* and other members of the *Otodus* lineage have been investigated, including phylogenetic affinities (Applegate and Espinosa-Arrubarrena, 1996; Gottfried and Fordyce, 2001; Nyberg et al., 2006; Ehret et al., 2009a; Ehret et al., 2012), body size (Gottfried et al., 1996; Gottfried and Fordyce, 2001), tooth histology (Bendix-Almgreen, 1983), vertebral morphology and growth (Gottfried and Fordyce, 2001; MacFadden et al., 2004), physiology (Ferrón, 2017) and reproductive behavior and habitat preference (Purdy et al., 2001; Pimiento et al., 2010), little attention has been directed at causes for the extinction of this predator or even the timing of its extinction. A recent study (Pimiento and Clements, 2014) utilized an optimal linear estimation to estimate a late Pliocene (terminal Piacenzian; 2.58 Ma) extinction for *O. megalodon*. However, the dataset utilized by Pimiento and Clements (2014) is rife with problems including incorrectly identified specimens, use of specimens with poor provenance, and use of specimens with unclear or poor geochronologic dates. Examples of these problems, illuminated below, indicate that rigorous reevaluation of the provenance of late Neogene *O. megalodon* specimens worldwide and their geochronologic age is necessary.

Few rigorous attempts have been made to identify the youngest known records of *O. megalodon* (Pimiento and Clements, 2014), and in many regions the lack of continuous fossiliferous strata of late Neogene age, abundance of specimens with poor or dubious provenance, and stratigraphic confusion have contributed to difficulty in assessing the age and manner of occurrence of reported *O. megalodon* records. The stratigraphic record of the eastern North Pacific, primarily in California and Baja California, includes fossiliferous marine strata with abundant marine vertebrates and excellent age control, essentially preserving a near continuous record of middle Miocene through Pleistocene marine vertebrate assemblages (Boessenecker, 2016). Other regions with abundant Neogene marine vertebrate assemblages including fossils of *O. megalodon* either lack well-sampled Pliocene intervals (e.g. Peru; the youngest assemblages such as Sacaco and Sud-Sacaco are late Messinian in age (Ehret et al., 2012; di Celma et al., 2017) or lack well-sampled Upper Pliocene intervals (Neogene marine deposits of the Atlantic coastal plain; e.g. Ward, 2008). We review previously reported occurrences of *O. megalodon* from the densely-sampled and well-dated Miocene and Pliocene stratigraphic record of California and Baja California (Messinian-Gelasian equivalent), historically renowned for extensive assemblages of Cenozoic marine vertebrates (Jordan, 1922; Jordan and Hannibal, 1923; Mitchell, 1966; Barnes, 1977; Repenning and Tedford, 1977; Domning, 1978; Welton, 1979; Warheit, 1992; Barnes, 1998; Deméré et al., 2003; Boessenecker, 2011b, 2013a, 2016), and report several new specimens (Fig. 1; Table 1). We further reevaluate some specimens that appear to be reworked from underlying strata, or which have dubious provenance.

Materials and methods

We examined collections from several institutions (CAS, LACM, RMM, SDNHM, UCMP) housing large collections of Neogene marine vertebrate fossils from the Pacific coast of North America. From these collections we identified a total of 145 *Otodus megalodon* teeth from Miocene and Pliocene deposits; this study (Fig. 1; Table 1) only focuses on those specimens of Messinian (latest Miocene) or younger age (n=40). Teeth of *O. megalodon* were examined for evidence of reworking (e.g. abrasion, enameloid cracking, phosphatization, fragmentation), and details of provenance (collector, collection date, locality description, similarity of preservation with other material from the same locality) to evaluate the likelihood of specimens being taphonomically autochthonous or allochthonous, or mistakenly attributed to an incorrect locality. We also reviewed relevant literature on late Neogene occurrences of *O. megalodon* to interpret the youngest known occurrences in other ocean basins for comparison with the late Neogene record of *O. megalodon* in the eastern North Pacific. Because this study relied upon existing collections of fossil specimens in museum collections and did not involve field study, no permits for field collection were required.

Geochronologic framework

The traditional threefold division of the Pliocene and Plio-Pleistocene boundary set at 1.806 Ma (Gradstein et al., 2004) has recently been modified by the inclusion of the Gelasian stage within the Pleistocene and designation of the Zanclean and Piacenzian stages as Early and Late Pliocene (respectively), and a new Plio-Pleistocene boundary at 2.566 Ma (Gibbard et al., 2009), which we follow herein. Stages of international usage are generally referred to throughout (e.g. Messinian, Zanclean, Piacenzian, Gelasian) to alleviate confusion between late Pliocene *sensu lato* (=Gelasian stage) and late Pliocene *sensu stricto* (=Piacenzian stage); references to North American Land Mammal Ages (e.g. Clarendonian, Hemphillian, Blancan) and local New Zealand stages (e.g. Opoitian) are also made. Note that other recent studies in Plio-Pleistocene marine vertebrate paleontology followed the compromise of Hilgen et al. (2012) in maintaining the Gelasian as the late Pliocene (e.g. Boessenecker 2011b, 2013a, 2013b).

Institutional abbreviations

CAS, California Academy of Sciences, San Francisco, California, USA; **LACM**, Natural History Museum of Los Angeles County, Los Angeles, California, USA; **RMM**, Riverside Municipal Museum, Riverside, California, USA; **SDNHM**, San Diego Natural History Museum, San Diego, California, USA; **UCMP**, University of California Museum of Paleontology, Berkeley, California, USA

Results

Systematic Paleontology

Chondrichthyes Huxley, 1880

Lamniformes Berg, 1958

Otodontidae Glikman, 1964

Otodus Agassiz, 1838

Otodus megalodon Agassiz, 1843

Referred material

LACM 59836, 59837, 115989, 129982, and SDNHM 53167, Capistrano Formation (LACM localities 4437, 5792, 61520, and SDNHM locality 3842); LACM 148311, 148312, and 149739, Fernando Formation (LACM localities 7321 and 7481); RMM A597-1, A597-9A, A597-9B, and A597-12, Lomita Marl (no locality number); LACM 59065 and SDNHM 73462, Niguel Formation (LACM locality 65187 and SDNHM locality 4080, respectively); LACM 10141, LACM 159028, Palos Verdes Sand (LACM locality 1066 and 7971); UCMP 219502, Purisima Formation (UCMP locality V-99875); LACM 10152, LACM 103448, LACM 156334, and SDNHM 29742, San Diego Formation (LACM localities 1080, 1095, 4875 and SDNHM locality 3253); LACM 131149, SDNHM 23056, 23959 (four teeth with same number), 24448, 77430, and 77343, “upper” San Mateo Formation (Lawrence Canyon local fauna; LACM locality 4297 and SDNHM locality 3161); CAS 72799.00, Santa Cruz Mudstone (no locality number); and LACM 29065-29067, 29069-29070, and 29073-29075, Tirabuzón Formation (LACM locality 6579).

Diagnosis

Crowns broad, triangular and erect, being broader and more vertical in anterior teeth and with increasing posterior inclination distally; labial crown face relatively flat or mildly convex, often showing short vertical infoldings of the enameloid at base of crown, lingual crown face moderately convex; crown enameloid relatively thick; chevron-shaped band of thinner enameloid on lingual crown face between base of crown and root (lingual neck), thicker in medial section becoming thinner laterally and showing fine vertical striations; cutting edge with fine, even, rounded serrations along entire margin, averaging 12-17 serrations per cm; lateral cusplets lacking in adult teeth; root is labiolingually thick with two laterally divergent but apicobasally shallow lobes, usually similar in size and not extending much laterally beyond the lower margin of the crown; labial root face is relatively flat while the lingual root face is laterally convex and thicker in the center with a pronounced nutritive foramen medially.

Taxonomic Note

The taxonomy of the megatoothed sharks is a topic that has been subject to much controversy and debate. In the original description of the taxon, Agassiz (1843) referred *Otodus megalodon* to the genus *Carcharodon* based on superficial morphological similarities in tooth shape and the presence of serrations. In 1923, Jordan and Hannibal recognized a difference between the extant great white shark (*Carcharodon carcharias*) and the fossil serrated-edged megatoothed sharks, erecting the genus *Carcharocles* for the latter. However, this taxonomic change was not adopted into the literature until the late 1980s (Cappetta, 1987). Other generic names proposed for *Otodus megalodon* include *Procarcharodon* Casier, 1960 and *Megaselachus* Glikman, 1964. Usage of *Carcharodon* and *Procarcharodon* were challenged in the literature based on tooth morphology, the fossil record, and taxonomic priority (Cappetta, 1987; Ehret et al., 2009a; Pimiento et al., 2010; Ehret et al., 2012). Instead, *Carcharocles* is broadly accepted for the assignment *O. megalodon* in many recent studies (Ehret et al., 2009; 2012; Pimiento and Clements, 2014; Boessenecker, 2016; Pimiento and Balk, 2016; Pimiento et al., 2010, 2017; Collareta et al., 2017). Some recent publications have proposed uniting all megatoothed shark taxa included within *Otodus* and *Carcharocles* in the genus *Otodus*. In this scenario, all non-serrated forms would belong to the genus *Otodus*, whereas Eocene-Oligocene serrated forms *C. auriculatus* and *C. angustidens* are designated to the subgenus *Carcharocles*, and *Carcharocles chubutensis* and *O. megalodon* belong to their own subgenus *Megaselachus* (Zhelezko and Kozlov, 1999; Cappetta and Carvallo, 2006; Cappetta, 2012). Recently, Shimada et al. (2017) further argued from a cladistic standpoint that *Carcharocles* should be synonymized within *Otodus* in order to make the latter genus monophyletic. We follow the reassignment of *Isurus hastalis* (or alternatively, *Cosmopolitodus hastalis*) to the genus *Carcharodon* (Ehret et al., 2012) for similar reasons, and thus adopt the reassignment of *Carcharocles* to *Otodus*. However, because subgenera are generally not used as a taxonomic convention in vertebrate paleontology, we do not use the subgeneric taxonomy of Cappetta (2012).

Occurrence Data

Pliocene-aged teeth of *Otodus megalodon* have been recovered or reported from several formations in California and Baja California (Fig. 1), including the Capistrano, Fernando, Lomita Marl, Niguel, Purisima, San Diego, San Mateo, and Tirabuzón formations, the ages of which are summarized below. These specimens exhibit a combination of morphological characters including: a large overall size and thickness, triangular shape, fine serrations, and a v-shaped chevron on the lingual surface between the crown and root. These characters, when observed together, indicate that the specimens undoubtedly belong to *O. megalodon*. The only other sharks that could be confused with *O. megalodon* during the late Miocene and Early Pliocene are those belonging to *Carcharodon* (*C. hubbelli* and *C. carcharias*), which have significantly smaller and labiolingually flatter teeth lacking v-shaped chevrons and have coarser serrations. Therefore, we are confident in assigning these specimens to *O. megalodon*. Additionally, this survey found that relatively few *O. megalodon* teeth from eastern North Pacific Neogene sediments are present in museum collections; for example, a total of 145 teeth are represented in total from LACM, SDNHM, and UCMP collections from Neogene west coast deposits, primarily from California. In comparison, Purdy et al. (2001:131) referred 82 specimens in addition to "several hundred isolated teeth" from the Pungo River Limestone and Yorktown Formation at the Lee Creek mine alone, and countless additional teeth exist in other collections and from other Neogene stratigraphic units from the Atlantic coastal plain. Intense collecting at eastern North Pacific localities like the Sharktooth Hill Bonebed suggests that this is not simply a case of collection bias and likely reflects genuine rarity (whether biogenic or taphonomic in origin) of *O. megalodon* teeth from west coast deposits. An alternative hypothesis is a geochronologically earlier extinction of *O. megalodon* in the Pacific basin than the Atlantic.

Capistrano Formation

A thick section of late Neogene mudrock exposed in Orange County, California, are divided into the Monterey Formation (early late Miocene) and the Capistrano Formation (latest Miocene to Early Pliocene). In southern Orange County, the Capistrano Formation is between 300-650 m thick, and includes a basal turbidite unit composed of breccia, sandstone, and siltstone, and an upper micaceous siltstone unit (Vedder, 1972; Ingle, 1979). The Oso Member of the Capistrano is a coarse clastic tongue within the finer grained parts of the Capistrano (not formally named as member) interpreted as the distal deposits of a delta within a shallow embayment (Vedder et al., 1957; Barboza et al., 2017).

Specimens recovered from the Capistrano Formation (latest Miocene – Early Pliocene) include SDNHM 53167, LACM 59836, 58937, 115989, and 129982 (Fig. 2). SDNHM 53167 is an incomplete upper left anterior tooth and represents the largest specimen from the Capistrano Formation (Fig. 2 A-B). The other specimens from the Capistrano Formation represent both anterior and posterolateral teeth and range from nearly complete (LACM 129982, Fig. 2C-D; LACM 115989, Fig. 2G-H) to highly fragmented (LACM 59837, Fig. 2E-F; LACM 59836, Fig. 2I-J). SDNHM 53167 was collected from the upper siltstone unit of the Capistrano Formation (SDNHM locality 3842) from a horizon approximately 30 m below a marker bed which yielded diatoms of the earliest Pliocene *Thalassiosira oestruppi* zone (T.A. Deméré, pers. comm., 11/2012; Deméré and Berta, 2005), approximately 5.6-3.7 Ma in age (Barron and Gladenkov, 1995; Barron and Isaacs, 2001). This occurrence of *Otodus megalodon* can be best summarized as latest Miocene to earliest Pliocene in age (latest Messinian to Zanclean equivalent, 5.6-3.7 Ma). Other Capistrano Formation specimens within LACM collections (LACM 58936, 59837, 115989, 129982) were collected from unknown horizons within the Capistrano Formation. A record of *Otodus megalodon* was listed by Pimiento and Clements (2014: table S1) from the Capistrano Formation and dated to 11.6-3.6 Ma, without explanation or an accompanying Paleobiology Database entry. Specimens reported from the Oso Member of the Capistrano Formation by Barboza et al. (2017) are 6.6-5.8 Ma in age (Messinian) based on the occurrence of the horse *Dinohippus interpolatus*.

Fernando Formation

The Fernando Formation is a poorly defined unit of Pliocene marine sediments in the Ventura and Los Angeles basins of southern California (Eldridge and Arnold, 1907; Woodring et al., 1946; Vedder, 1972; Squires, 2012). The Fernando Formation unconformably overlies several Miocene units, including the terrestrial Sycamore Canyon Member of the Puente Formation and the marine Capistrano and Monterey Formations (Vedder, 1972). The Fernando Formation was defined only on biostratigraphic age and includes numerous lithologies (Eldridge and Arnold, 1907; Squires, 2012); because of confused relationships with other late Neogene marine rocks in southern California (e.g. Pico, Towsley, and Repetto formations), poor exposure, subsequently overlain by suburban sprawl in by the late 20th century, the stratigraphy and age of this formation at many localities remains inaccessible and uncertain.

Eldridge and Arnold (1907) listed a single occurrence of *Otodus megalodon* (as *Carcharodon rectus*, a junior synonym of *Otodus megalodon*, Jordan 1910:182) from the Shatto Estate locality; however, no photograph, specimen number, or repository information was given and thus it is not possible to unambiguously interpret this record. However, Eldridge and Arnold (1907) also reported the shark *Isurus planus* (as *Oxyrhina plana*) in addition to numerous mollusks indicating a Late Pliocene to Middle Pleistocene age (C. L. Powell, II, pers. comm., 6/2013). However, *I. planus* is only represented in upper Oligocene through lower upper Miocene sediments (Tortonian equivalent; (Boessenecker, 2011b):14). The lack of reliable provenance and reported presence of *I. planus* casts doubt on the validity of this record, and it will not be considered further.

Three teeth are recorded from the Fernando Formation (Fig. 3), including two specimens (LACM 148311 and 148312) from Eagle Glen in Riverside County (LACM locality 7321) and a single specimen (LACM 149739) from nearby LACM locality 7481. LACM 148311 and 148312 are fragmentary with thin and abraded enameloid, and the serrations have been eroded away. LACM 149739 is now missing, but an existing photograph shows this specimen is fragmented, but exhibits unabraded cutting edges. However, owing to poor understanding of the lithostratigraphy and age of the Fernando Formation, the age of these specimens – whether reworked or not – is equivocal, and the age of the Fernando Formation is best summarized as Pliocene to Pleistocene.

Lomita Marl

The Lomita Marl consists mostly of unconsolidated calcareous mudrocks and sandstones exposed in the Los Angeles basin in the vicinity of Torrance and Lomita northeast of the Palos Verdes Hills (Grant and Gale, 1931; Woodring et al., 1946). The Lomita Marl is, in part, a lateral and temporal equivalent of the Timms Point Silt and the San Pedro Sand (Woodring et al., 1946). The Lomita Marl is widely considered to be early to middle Pleistocene in age based on molluscan biostratigraphy (Woodring et al., 1946) and amino acid racemization (Dupré et al., 1991), but has yielded a 3 Ma K/Ar date from glauconite (Obradovich, 1965) potentially indicating a Late Pliocene age. *Otodus megalodon* is represented from this unit by teeth of "*Carcharodon branneri*" Jordan, 1922 (RMM A597-1, A597-12) and "*Carcharodon leviathan*" Jordan, 1922 (RMM A597-9A, A597-9B), both junior synonyms of *Otodus megalodon*. These specimens are fragmented, abraded, with polished enameloid and phosphatic matrix adhering in cracks. Mount (1974) noted that several marine vertebrate fossils appear to be reworked from underlying Miocene rocks. In summary, these specimens appear to have been reworked or anthropogenically mixed with Pleistocene sediment approximately 650 to 350 Ka in age (See Purported Pleistocene and Holocene records of *Otodus megalodon*).

Niguel Formation

The Niguel Formation is a unit of unconsolidated conglomerates, sandstones, and siltstones exposed in the San Joaquin Hills in Orange County, California deposited along the southeastern margin of the Los Angeles Basin; it unconformably overlies the Capistrano Formation and other strata (Vedder, 1972). At SDNHM locality 4080, the Niguel Formation unconformably overlies the lower-middle Miocene "Topanga" Formation (T.A. Deméré, pers. comm., 2013). The base of the Niguel Formation is a conglomerate lag deposit (Vedder, 1972). The Niguel Formation is rich in fossils and mollusks suggesting a Pliocene age (Vedder, 1972) possibly between 3.3 and 3.15 Ma (Powell et al. 2008). Ehlig (1979) considered the Niguel Formation to be Late Pliocene to Pleistocene in age, estimating it to be 1-3 Ma (Kem and Wicander, 1974; Powell et al., 2008). An abraded tooth fragment identifiable as *Otodus megalodon* (SDNHM 73462) was collected from the basal conglomerate, along with teeth of other sharks including *Carcharhinus* sp., *Carcharodon carcharias*, *Carcharodon hastalis*, *Galeocerdo* sp., *Hemipristis* sp., *Isurus planus*, and *Myliobatis* sp. Also recovered from this locality were fragments of *Desmostylus* sp. teeth, earbones of a delphinid dolphin and a balaenid mysticete, and a pharyngeal tooth plate of *Semicossyphus*. Another *O. megalodon* specimen, LACM 59065 from Capistrano Highlands (LACM locality 65187), likely represents an upper anterior tooth (Fig. 4A-B) and exhibits longitudinal cracks, abraded cutting edges, and a fragmented root.

Although certain marine vertebrates from SDNHM locality 4080 such as *Carcharodon carcharias* and Delphinidae indet. are consistent with a Pliocene age for the Niguel Formation, several other taxa are typical of older Miocene age. For example, the youngest records of desmostylians occur in the Tortonian equivalent Santa Margarita Sandstone in Santa Cruz County, and the Monterey Formation in Orange County, California (Mitchell and Repenning, 1963; Barnes, 1978; Domning, 1978; Barnes, 2013). Other Miocene vertebrates from this locality include *Carcharodon hastalis* and *Isurus planus*; *Carcharodon hastalis* is replaced by *Carcharodon hubbelli* at approximately 8-7 Ma (Ehret et al., 2012), whereas confirmable records of *Isurus planus* are Tortonian and older (Boessenecker, 2011b:14). The taphonomic condition of these *Otodus megalodon* specimens and presence of strictly Miocene marine vertebrates, and the occurrence of these specimens in the basal conglomerate of the Niguel Formation all indicate they were reworked from the early middle Miocene “Topanga” Formation.

Purisima Formation

The Purisima Formation comprises a series of lightly consolidated sandstones, mudrocks, and diatomites of latest Miocene and Pliocene age representing shoreface to offshore sedimentation, and is exposed west of the San Andreas fault in the vicinity of Santa Cruz, Halfmoon Bay, and Point Reyes in Central and Northern California (Cummings et al., 1962; Norris, 1986; Powell, 1998; Powell et al., 2007; Boessenecker et al., 2014). The Purisima Formation is richly fossiliferous, including fossils of sharks, bony fish, marine birds, and marine mammals (see Boessenecker, 2011b, 2013b; Boessenecker et al., 2014, and references therein). A single nearly complete upper anterior tooth of *O. megalodon* (UCMP 219502; Fig. 5) was reported by Boessenecker (2016) from the basal bonebed of the Miocene to Pliocene Purisima Formation near Santa Cruz, California (UCMP locality V99875). Only the root lobes and a small portion of the crown base are missing, and longitudinal enameloid cracks are evident lingually and labially.

The basal meter of the Purisima Formation is composed of glauconitic sandstone and a matrix-supported conglomerate with abundant vertebrate skeletal elements mantling an erosional surface with ~1 m of relief, unconformably overlying the upper Miocene Santa Cruz Mudstone (Clark, 1981; Boessenecker et al., 2014). Glauconite from the base of the Purisima Formation has yielded a K/Ar date of 6.9 ± 0.5 Ma (Clark, 1966; Powell et al., 2007). A tuff bed approximately 30 m above the base of the Purisima Formation has been tephrochronologically correlated with 5.0 ± 0.3 Ma tephra in the Pancho Rico Formation (Powell et al., 2007). Therefore, this locality (UCMP locality V99875) can be summarized as 6.9-5.3 Ma in age, or latest Miocene (Messinian equivalent).

San Diego Formation

The San Diego Formation comprises approximately 85-90 m of unconsolidated Pliocene and Pleistocene sandstones, mudrocks, and conglomerates of terrestrial and marine origin deposited via extensional tectonics within a graben in the vicinity of San Diego, California between Pacific Beach and northern Baja California (Deméré 1982, 1983; Wagner et al., 2001; Vendrasco et al., 2012). The San Diego Formation is informally divided into two members: a “lower” sandstone member that is entirely marine in origin, and an “upper” sandstone and conglomeratic member that is marine and terrestrial (Deméré 1982, 1983). Although earlier studies concluded that the San Diego Formation was approximately 3-1.5 Ma in age (Late Pliocene to Early Pleistocene; Deméré 1983), more recent estimates based on paleomagnetism and correlation with patterns of eustatic sea level change suggest an Early Pliocene age (Zanclean equivalent) for parts of the “lower” member of the San Diego Formation (Wagner et al., 2001). Furthermore, Vendrasco et al. (2012) reported the San Diego Formation to be 4.2-1.8 Ma in age. A single upper right anterior or anterolateral tooth missing part of the root and crown (SDNHM 29742; Fig. 6A-B) was reported from the basal San Diego Formation near La Joya in Baja California (SDNHM locality 3253; Ashby and Minch, 1984). The tooth is almost equilateral, with a slight curvature to the right. A v-shaped chevron, fine serrations, and three small nutrient foramina are present on the lingual surface of the root. Three additional specimens (Fig. 6C-H) are recorded from LACM collections from San Diego County: LACM 156334 (LACM locality 1095), a broken tooth with thinned and longitudinally cracked enameloid, abraded surfaces and broken edges; LACM 10152 (LACM locality 4875), a broken but unabraded tooth with longitudinally cracked enameloid; LACM 103448 (LACM locality 1080), a fragment of enameloid shell missing the orthodentine core. These other specimens are less complete than SDNHM 29742 and come from unknown horizons within the San Diego Formation.

Recent studies suggest an Early Pliocene to Early Pleistocene age for the San Diego Formation (Wagner et al., 2001; Vendrasco et al., 2012). The only specimen with precise stratigraphic data (SDNHM 29742) was collected from the basal unconformity of the San Diego Formation. This occurrence can be summarized as approximately 4.2 Ma in age (Early Pliocene), approximately contemporaneous with teeth of *O. megalodon* from the upper unit of the San Mateo Formation (Lawrence Canyon local fauna) and the Tirabuzón Formation.

San Mateo Formation

The San Mateo Formation is a thin package of unconsolidated sandstones and conglomerates, which crop out in the vicinity of Oceanside in San Diego County, California. It is considered a temporal equivalent of the Oso Member of the Capistrano Formation (Barnes et al., 1981; Domning and Deméré 1984), and represents a coarse clastic tongue within the Capistrano

Formation (Vedder, 1972). It consists of a lower unit composed of massive, fine-grained sandstones with occasional muddy lenses, sparse pebbles and cobbles, and an upper unit of complexly bedded sandstones and conglomerates; a sharp erosional surface at the base of the upper unit divides the formation (Barnes et al., 1981; Domning and Deméré 1984). Fossil assemblages from the lower and upper units have been termed the San Luis Rey River and Lawrence Canyon local faunas, respectively (Barnes et al., 1981). Domning and Deméré (1984) interpreted the lower unit to represent middle or inner shelf deposition, and the upper unit to represent the distal margin of a submarine fluvial delta system. A diverse marine vertebrate assemblage including sharks, bony fish, marine birds, and marine mammals is now known from the San Mateo Formation at Oceanside (Barnes et al., 1981; Domning and Deméré 1984; Long, 1994). Due to the lack of macroinvertebrates or microfossils, age estimates for the San Mateo Formation have been established based on vertebrate biochronology, including terrestrial mammals and mancalline auks (Domning and Deméré 1984). Barnes et al. (1981) considered both the lower and upper units to be correlative with the Hemphillian North American Land Mammal Age (NALMA). However, Domning and Deméré (1984) reported that the presence of *Aepycamelus* indicated the lower unit is slightly older, perhaps Late Clarendonian to Early Hemphillian in age (approximately 10-7 Ma; Tedford et al., 2004), and correlated the upper unit with the Late Hemphillian NALMA (7 Ma to 4.9-4.6 Ma; Tedford et al., 2004). Based on the presence of mancalline auks found in other rocks of Early Pliocene age (and the lack of Late Pliocene mancalline taxa as from the San Diego Formation), Domning and Deméré (1984) indicated an Early Pliocene age for the upper unit of the San Mateo Formation. Teeth of *Otodus megalodon* occur in both the lower and upper units of the San Mateo Formation (Domning and

Deméré 1984; Barnes and Raschke, 1991), and occurrences from the upper unit are here summarized as earliest Pliocene in age (5.33 to 4.9-4.6 Ma).

The San Mateo Formation has yielded a number of partial *O. megalodon* teeth including: SDNHM 23056, 23959, 24448, 77430, 77343, and LACM 131149 (Fig.7). One specimen catalogued in the lot SDNHM 23959 (Fig. 7I-J) and another tooth (SDNHM 24448, Fig. 7C-D) represent the most complete teeth recovered from the San Mateo Formation. SDNHM 23959 represents an upper right anterolateral tooth consistent with *O. megalodon* despite missing the apex, having worn and chipped mesial and distal cutting edges, and broken root lobes. SDNHM 24448 represents an upper left posterolateral tooth (Fig. 7C-D). The specimen is missing a portion of the right root lobe and is missing some enameloid on the lingual surface of the crown.

Santa Cruz Mudstone

At the type section west of Santa Cruz (Santa Cruz County) the Santa Cruz Mudstone is a monotonous succession of jointed, indurated, and siliceous mudrocks (siltstone and porcelanite); this unit conformably overlies the Santa Margarita Sandstone and is in turn unconformably overlain by the Purisima Formation. In the vicinity of Point Reyes thick, massively bedded, indurated and fractured siliceous mudrocks were originally considered by Galloway (1977) to represent both the Monterey and Drakes Bay formations, but were remapped by Clark et al. (1984) as the somewhat younger Santa Cruz Mudstone. Near Bolinas, foraminifera representative of the Delmontian California benthic foraminiferal stage (~7-5 Ma; Barron and Isaacs, 2001) has been recorded, in addition to a diatom flora typical of Diatom Zone X (Clark et al., 1984), which was later refined to subzone A of the *Nitzschia reinholdii* zone by Barron (*in* Zeigler et al., 1997), equivalent to 7.6-6.5 Ma (Barron and Isaacs, 2001). Fossil bivalves from the

Santa Cruz Mudstone at Bolinas indicate deposition at about 500+ m (Zeigler et al., 1997). Fossil vertebrates from the Santa Cruz Mudstone include the baleen whale *Parabalaenoptera baulinensis* (Zeigler et al., 1997), the sea cow *Dusisiren dewana* (initially reported as *Dusisiren* species D by Domning, 1978), a herpetocetine baleen whale (Boessenecker, 2011a:8), and a number of unpublished marine mammals (Boessenecker, pers. obs.) including a phocoenid porpoise (cf. *Piscolithax*), an albireonid dolphin, fragmentary odobenid and otariid bones, and earbones of indeterminate balaenopterid mysticetes.

A single tooth of *O. megalodon* was reported from "Bolinas Bay" by Jordan and Hannibal (as the holotype specimen of "*Carcharodon branneri*"; Jordan and Hannibal, 1923). Figure 15; Page 116 in Jordan, 1907). Unfortunately, searches for additional locality information at California Academy of Sciences were unsuccessful, and it is possible that some of these Stanford University specimens were never transferred to California Academy of Sciences (S. Mansfield, pers. comm., 2013; D. Long, pers. obs., 2013). Ransom (1964) published township and range coordinates for this locality, suggesting that the type was collected near the west shore of the Bolinas Lagoon in the vicinity of the Bolinas County Park. However, this area is covered by Quaternary alluvium with nearby exposures of sparsely fossiliferous Pliocene to Pleistocene Merced Formation. It is more likely that this locality information is incorrect, and that the type specimen was collected from exposures (or as float) of the Santa Cruz Mudstone along the northwestern shore of Bolinas Bay (as initially reported by Jordan and Hannibal, 1923; also see Jordan, 1907) or possibly from as far west as Duxbury Reef (where the majority of twentieth and twenty-first century vertebrate collections have been made). This specimen was erroneously assigned to the Purisima Formation by Pimiento and Clements (2014: table S) and assigned an age of 5.3-2.6 Ma without explanation; the Purisima Formation does not crop out anywhere within 25 km of Bolinas (Clark et al. 1984). Bones and bone fragments of fossil marine mammals are often collected as float from these beaches. If this specimen was collected from the Santa Cruz Mudstone near Bolinas, then it likely represents a 7.6-6.5 Ma record.

Tirabuzón Formation

The Tirabuzón Formation consists of unconsolidated fossiliferous sandstone exposures in the vicinity of Santa Rosalia along the eastern side of the northern Baja California Peninsula (Applegate, 1978; Applegate and Espinosa-Arrubarrena, 1981; Wilson, 1985). Formerly mapped as the Gloria Formation, it was renamed the Tirabuzón Formation by Carreno (1982) after abundant spiral burrows of the ichnogenus *Gyrolithes* which leant the locality the name "Corkscrew Hill". Paleodepth estimates for this unit range from 200-500 m (outer shelf to slope) based on foraminifera (Carreno, 1982) to 55-90 m (middle shelf) based on ichnology (Wilson, 1985). The Tirabuzón Formation unconformably overlies the upper Miocene Boleo Formation, and is in turn unconformably overlain by the upper Pliocene Infierno Formation (Holt et al., 2000). Holt et al. (2000) reported an $^{40}Ar/^{39}Ar$ date of 6.76 ± 0.9 Ma from an andesitic interbed within the Boleo Formation, constraining a lower limit for the age of the Tirabuzón Formation. The age of the Tirabuzón Formation was considered Pliocene by Applegate (1978) and Applegate and Espinosa-Arrubarrena (Applegate and Espinosa-Arrubarrena, 1981), and approximately 4-3 Ma (Zanclean equivalent) by Barnes (1998). Shark and marine mammal fossils have previously been reported from the Tirabuzón Formation near Santa Rosalia, including 34 shark taxa (including *Otodus megalodon*), an indeterminate otariid, two balaenopterid mysticetes, a small Fransicana-like dolphin (aff. *Pontoporia*), an indeterminate phocoenid, two delphinids (*Delphinus* or *Stenella* sp., aff. *Lagenorhynchus* sp.), two kogiids (aff.

Kogia sp. and cf. *Scaphokogia* sp.), and an indeterminate physeterid (Applegate, 1978; Applegate and Espinosa-Arrubarrena, 1981; Barnes, 1998). This occurrence of *O. megalodon* is estimated to be early Pliocene (Zanclean equivalent; 5.33-3.6 Ma).

Small *Otodus megalodon* teeth are fairly abundant in the Tirabuzón Formation (Fig. 8), and include 14 partial teeth: LACM 29064-29065, 29067, 29069-29070, and 29072-29077. Most of these teeth, except for smaller fragments, exhibit the characteristic v-shaped chevron and most still retain their fine serrations. The most complete specimens are two left posterolateral upper teeth, LACM 29065 (Fig. 8I-J), missing portions of the root lobes, and LACM 29076 (Fig. 8G-H), missing the apex of the crown and parts of the root lobes.

Discussion

Purported Pleistocene and Holocene records of Otodus megalodon

The record of *Otodus megalodon* from the Lomita Marl (Jordan, 1922) is substantially younger than many other records from California. However, as noted by Mount (1974), numerous sharks and marine vertebrates from the Lomita Quarry locality are only found elsewhere in middle and late Miocene localities, such as *Allodesmus* (Jordan and Hannibal, 1923: plate 9J) and *Carcharodon hastalis* (Jordan and Hannibal, 1923: plate 9E-F). Furthermore, shark teeth including *O. megalodon* teeth were collected by quarry manager H. M. Purple (Anonymous, 1921, Mount 1974), without accompanying stratigraphic information and it is unclear where in the Lomita Quarry these specimens were collected. Hanna (*in* Jordan and Hannibal, 1923) notes that the base of the Lomita Marl within the Lomita Quarry was a glauconitic sandstone with abundant abraded whale bones, and that in addition to Miocene marine mammals and sharks, Pleistocene terrestrial mammals and a single Pleistocene pinniped were present in the quarry. This curious mix suggests stratigraphic reworking of older fossil material; indeed, the holotype specimen of the gastropod *Mediargo mediocris* was considered by Wilson and Bing (1970:7) to be reworked from Pliocene sediments into the Lomita Marl. Woodring et al. (1946) report that the Lomita Marl includes "beds of gravel consisting chiefly or entirely of limestone pebbles and cobbles derived from the Monterey Shale. Locally huge boulders of soft Miocene mudstone and Pliocene siltstone are embedded in calcareous strata." These specimens of *O. megalodon* (RMM A597-1, A597-9A, and A597-9B) are fragmented, strongly abraded, with polished enameloid, suggestive of reworking. Only RMM A597-12 showed little evidence of abrasion, although experiments by Argast et al. (1987) noted that abrasion is not a guaranteed outcome of transport or reworking. Lastly, anthropogenic mixing of multiple strata during mining operations is also a likely possibility for seeming older taxa in younger beds. Dynamite was used for mining in the quarry, which apparently “[brought] down bones of whales, sea lions, land animals, chipped flints, pieces of charcoal, sea shells, shark’s teeth, arrowheads, all mixed together” (Anonymous, 1921). The report of *O. megalodon* from the Pleistocene Lomita Marl could be due to reworking from the Monterey Formation, anthropogenic mixing from mining operations, collection from underlying rocks, poor record keeping, or any combination of the above. In this context, *O. megalodon* teeth from the Lomita Marl are considered to be allochthonous (either by sedimentologic or anthropogenic reworking) and thus not relevant to the consideration of the timing of the extinction of the species.

Three teeth of *Otodus megalodon* (LACM 11194, 10141, and 159028) are questionably recorded from the upper Pleistocene Palos Verdes Sand (Fig. 9). The first, LACM 11194, is now missing, but was collected by an unknown collector prior to 1915 from the N. Pacific Avenue and Bonita Avenue intersection in northern San Pedro, California. The locality is now built over, but was mapped as Palos Verdes Sand by Woodring et al. (1946). The second specimen, LACM 10141, is a fragmentary tip of a tooth with longitudinally cracked enameloid and abraded serrations (Fig. 9c-d), and was collected from unnamed strata along the Newport Bay Mesa formerly considered to belong to the Palos Verdes Sand (collector and collection date unknown). The third specimen (LACM 159028; Fig. 9a-b) possesses the following dubious locality information: "Rosecranz Ave. Long Beach, Orange Co.?". We note that Rosecrans Avenue is far from the Palos Verdes Hills and from Long Beach, and that both Rosecrans Avenue and Long Beach are located within Los Angeles County. It is also possible that this specimen is reworked from the underlying Puente Formation (L.G. Barnes, pers. comm., 2015). It is not possible to unambiguously recognize either of these specimens as genuine Pleistocene records of *O. megalodon*, given that LACM 11194 is missing (raising the possibility that it may represent a misidentified *Carcharodon carcharias*), and the lack of provenance for the other specimens. We also note the similarity in preservation (chiefly color) between LACM 159028 and teeth of *O. megalodon* from some localities at Sharktooth Hill (middle Miocene, Kern County). Kanakoff (1956) only listed *Carcharodon carcharias* from this unit. Furthermore, a comprehensive study of the ichthyofauna of this unit by Fitch (1970) only recorded *C. carcharias*. We hypothesize that LACM 11194 was a misidentified or mistranscribed specimen of *C. carcharias* and that the other two specimens originated from a separate locality. Therefore, we conclude that no reliable records of *O. megalodon* exist for the Palos Verdes Sand.

Several studies have reported teeth of *O. megalodon* dredged from the seafloor and considered to be Pleistocene or even Holocene in age (Tschernezky, 1959; Seret, 1987; Roux and Geistdoerfer, 1988). Dredged specimens from the south Pacific were reported by Tschernezky

(1959) and Seret (1987), whereas Roux and Geistdoerfer (1988) reported numerous specimens from the Indian Ocean seafloor off the coast of Madagascar. Tschernezky (1959) and Roux and Geistdoerfer (1988) both attempted to determine the age of the teeth by measuring the thickness of adhering manganese dioxide nodules and applying published rates of MnO_2 nodule growth. Tschernezky (1959) reported a range of 24,406-11,333 years for the MnO_2 nodule formation for these teeth, and Roux and Geistdoerfer (1988) reported specimens with nodules with the equivalent of 60-15 Ka of MnO_2 growth. However, both studies assumed a constant rate of nodule development and interpreted these dates as indicating a latest Pleistocene-Early Holocene extinction of *O. megalodon* (Tschernezky, 1959; Roux and Geistdoerfer, 1988). Tschernezky (1959) argued that even if *O. megalodon* went extinct during the Middle Pleistocene ca. 500 Ka, his dredged *O. megalodon* teeth should have had MnO_2 coatings approximately 75 mm thick. It is possible that the conditions favoring the formation and growth of MnO_2 nodules were not constant over geologic time (Purdy et al., 2001). It is further possible, if not probable, that these specimens were concentrated on the seafloor via submarine erosion, winnowing, or depositional hiatus (or a combination thereof). Collections of numerous resistant vertebrate hardparts from these dredgings (shark teeth, cetacean ear bones) support this suggestion. A more parsimonious scenario is that these specimens are Pliocene (or older) in age and were deposited in areas of slow sedimentation with intermittent erosion, concentrating nodules and resistant marine vertebrate skeletal elements (typically teeth and cetacean skull fragments) on the seafloor. Intermittent periods of favorable chemistry fostered the formation and growth of MnO_2 nodules and coatings, and it is possible that these specimens have experienced numerous burial-exhumation cycles. Lastly, because no extrinsic absolute or biostratigraphic age data exist for these specimens, the maximum age of these specimens is ultimately unknown and cannot be considered to represent robust post-Pliocene occurrences (Applegate and Espinosa-Arrubarrena, 1996; Purdy et al., 2001).

Timing of the extinction of **Otodus megalodon** *in the eastern North Pacific*

Although numerically less abundant than in deposits of the Atlantic Coastal Plain, fossil teeth of *Otodus megalodon* have been reported from numerous middle Miocene localities in California and Baja California (Jordan and Hannibal, 1923; Mitchell, 1966; Deméré et al., 1984). Late Miocene occurrences of this species in this region include the Almejas (Barnes, 1992), Monterey (Barnes, 1978), (this study), and "lower" San Mateo Formations (Domning and Deméré 1984), Capistrano Formation (Barboza et al., 2017; this study), Purisima Formation (Boessenecker, 2016; this study), Santa Cruz Mudstone (Jordan and Hannibal, 1923; this study), and Santa Margarita Sandstone (Barnes, 1978; Domning, 1978). Pliocene occurrences in California (reviewed above) are restricted to the Capistrano, Fernando, "upper" San Mateo, basal San Diego, and the Tirabuzón Formations (Fig. 10). In the context of dubious provenance or clear evidence of reworking for specimens younger than these, we do not consider post-Early Pliocene records of *O. megalodon* to be reliable; putative Quaternary specimens are particularly dubious. Several specimens of *O. megalodon* are now recorded from the basal San Diego Formation, which is as old as 4.2 Ma (Wagner et al., 2001; Vendrasco et al., 2012), and we interpret these records as earliest Pliocene (Zanclean equivalent; Fig. 10). The lack of *O. megalodon* specimens and abundant *Carcharodon carcharias* teeth in younger sections of the San Diego Formation is paralleled in the Purisima Formation at Santa Cruz. Although *Carcharodon carcharias* teeth are common within well-sampled bonebeds, no *O. megalodon* teeth have been discovered from the Pliocene section of this unit. However, teeth of *O.*

megalodon are rare within established Miocene marine vertebrate collections relative to *Carcharodon hastalis* or *C. carcharias* (e.g., Sharktooth Hill Bonebed). With the exclusion of the Niguel and San Diego Formation specimens, the remainder of specimens discussed herein are entirely latest Miocene or earliest Pliocene in age (Messinian-Zanclean equivalent; Fig. 10).

The fossil record of *O. megalodon* in California thus indicates extinction of this taxon during the Early Pliocene, perhaps during the Zanclean stage or near the Zanclean-Piacenzian boundary (ca. 4-3 Ma; Fig. 10). This differs from the somewhat younger quantitative determination made by Pimiento and Clements (2014), who found evidence for a latest Pleistocene extinction at 2.6 Ma. Rather than use numerical dates from the literature, much of their dataset (88% of data consists of dates artificially stretched to fit stage 'bins'. Several problems arise from this; for example, many Piacenzian stage occurrences in New Zealand, Australia, and Europe are based on outdated stratigraphic determinations (see above). In many other cases (n=15, 34% of the dataset), poorly dated specimens dated to "Pliocene" are given an age of 5.3-2.6 Ma despite lacking concrete minimum dates, perhaps artificially inflating the number of true Piacenzian-age occurrences. Further confounding matters is the apparent treatment of "late Pliocene" reports in older literature published prior to the transfer of the Gelasian to the Pleistocene (e.g. Gibbard et al., 2009) as belonging to the Piacenzian stage. Pimiento and Clements (2014) marks an excellent advance in the study of megatoothed sharks, but great care must be taken in order to properly interpret the history of lithostratigraphic terminological changes and age determinations for fossil localities (Parham et al., 2012). Stratigraphic and geochronologic auditing and reanalysis of the Pimiento and Clements (2014) dataset may indeed support an earlier 'mid' Pliocene extinction.

A worldwide view of **Otodus megalodon** *extinction*

The fossil record of *Otodus megalodon* in other regions lends support to an Early Pliocene (Zanclean) extinction (Fig. 10). Previously described records of Pliocene age possibly relevant to temporally constraining the extinction of *O. megalodon* include occurrences from the eastern U.S.A., Japan, Australia, New Zealand, western Europe (Belgium, Spain, United Kingdom, Denmark), southern Europe (Italy), Africa (Libya), and South America (Chile, Ecuador, Peru, Venezuela).

In deposits around the North Sea, *O. megalodon* has been reported from the Miocene (Bendix-Almgreen, 1983). A tooth from the upper Miocene Gram Formation of Denmark was interpreted by Bendix-Almgreen (1983:23-24) as representing the youngest record of *O. megalodon* from the eastern North Atlantic. A tooth of *O. megalodon* from the Pliocene to Pleistocene Red Crag Formation of eastern England was mentioned by Donovan (1988), although the majority of marine vertebrate remains – marine mammals in particular – are typically abraded and phosphatized and often consisting of dense elements with relatively high preservation potential (e.g. cetacean tympanoperiotics, teeth and tusks, and osteosclerotic beaked whale rostra; Owen, 1844, 1870; Lydekker, 1887). This evidence suggests that marine vertebrate material has been reworked from preexisting strata predating the Red Crag Formation; indeed, the Red Crag unconformably overlies the Eocene London Clay and the Lower Pliocene Coralline Crag Formation (Zalasiewicz et al., 1988), and marine vertebrate remains may date to the Eocene-Pliocene depositional hiatus (or erosional lacuna) between the London Clay and overlying Red Crag Formation, or may have been reworked from the Coralline Crag Formation. A single record from the Piacenzian of France is cited by Cappetta (2012) from Gervais (1852), but no locality information is given by Gervais (1852):173) and this record cannot be evaluated.

In a review of the stratigraphic range of Pliocene to Pleistocene elasmobranchs from Italy, Marsili (2008) indicated that *O. megalodon* disappeared from the record during the Zanclean (~4 Ma) and that no Piacenzian records existed, *contra* Pimiento and Clements (2014: table S1). In their discussion of the shark fauna of Malta, Ward and Bonavia (Ward and Bonavia, 2001) considered *O. megalodon* to have become extinct in the Early Pliocene (but without further comment). Other Early Pliocene (Zanclean equivalent) records of *O. megalodon* from western Europe and the Mediterranean region include the Huelva Formation of Spain (Garcia et al., 2009) and unnamed strata in the Sabratah Basin of northwestern Libya (Pawellek et al., 2012). Elsewhere in Africa, *O. megalodon* is recorded from the Early Pliocene of Angola (Antunes, 1978).

In a summary of Mesozoic and Cenozoic ichthyofaunas from Japan, Yabumoto and Uyeno (1995) reported that *O. megalodon* is widely known from Miocene strata and occurs in the Lower Pliocene, but not from younger Upper Pliocene and Pleistocene rocks. Subsequently, a review by Yabe et al. (2004) reported widespread occurrences of *O. megalodon* in the earliest Pliocene (Zanclean) and a few late Early Pliocene records (Piacenzian), and considered *O. megalodon* to have gone extinct in the late Early Pliocene or Late Pliocene. Three post-Zanclean occurrences were listed by Yabe et al. (2004); one is uncertainly Piacenzian, another is Zanclean or Piacenzian in age, and only one is strictly Piacenzian in age. However, these specimens were not figured by Yabe et al. (2004) and it is unclear whether or not they are reworked.

An Early Pliocene (Zanclean or Piacenzian) extinction of *Otodus megalodon* seems to be reflected in the fossil record of Australia and New Zealand. Late Miocene occurrences of *O. megalodon* are common from both landmasses (Keyes, 1972; Kemp, 1991; Fitzgerald, 2004). Several Early Pliocene records of *O. megalodon* have been reported from Australia (Kemp, 1991; Fitzgerald, 2004), including a single specimen from the Lower Pliocene Cameron Inlet Formation (Zanclean-Piacenzian correlative; Kemp, 1991; Fitzgerald, 2004). However, judging from Kemp's (Kemp, 1991: plate 30C) illustration, this specimen from the Cameron Inlet Formation is almost certainly a misidentified *C. carcharias* tooth owing to its small size, lack of a preserved chevron, and relatively large serrations. Although Keyes (1972) reported several specimens ranging in age from Early Pliocene to Pleistocene age, many of these have tenuous provenance. For example, one such specimen (included in the analysis by Pimiento and Clements 2014) can only be pinpointed to a 200 km section of coastline. Only a single published Pliocene tooth of *O. megalodon* from New Zealand has robust provenance, a specimen collected from Patutahi Quarry on the North Island. According to Keyes (1972), strata at the quarry correspond to the local New Zealand Opoitian Stage (5.33-3.6 Ma); accordingly, this tooth represents the youngest demonstrable record of *O. megalodon* from New Zealand.

In South America, *O. megalodon* is known continuously from at least the middle Miocene to the lowermost Pliocene in the Pisco Basin of Peru (Muizon and de Vries, 1985; Ehret et al., 2012). However, owing to the absence of well-sampled younger marine vertebrate assemblages, it is unclear if this simply reflects an artifact of preservation. *Otodus megalodon* has also been reported from the latest Miocene-Early Pliocene of Ecuador (Longbottom, 1979). Although *O. megalodon* has been reported from the well-sampled uppermost Miocene to Lower Pliocene Bahia Inglesa Formation of Chile (Long, 1993), the exact age of this occurrence is imprecisely known (Walsh and Hume, 2001; Walsh and Naish, 2002). On the Caribbean coast of South America, *O. megalodon* is continuously known from middle Miocene through Lower Pliocene deposits, with the youngest specimens occurring in the lowermost Pliocene (Zanclean-correlative; Aguilera et al., 2004).

Paralleling the record in Venezuela, abundant Miocene records of *O. megalodon* exist in the western North Atlantic and West Indies, with the youngest specimens consistently being earliest Pliocene in age (Iturralde-Vinent et al., 1996; Flemming and McFarlane, 1998; Purdy et al., 2001; Ward, 2008). In deposits of the Atlantic coastal plain of the United States, teeth of *O. megalodon* are abundant within the lower Pliocene Sunken Meadow Member of the Yorktown Formation (Purdy et al., 2001; Ward, 2008), but absent from the Upper Pliocene Rushmere and Moore House members of the Yorktown Formation (Ward, 2008). The extinction of *O. megalodon* was interpreted by Ward (2008) to have occurred during the time recorded by the unconformity and depositional hiatus of uncertain duration between the Sunken Meadow and Rushmere members. A number of possible Pleistocene occurrences of Otodus megalodon from Florida are present in FLMNH collections, but originate from temporally mixed fossil assemblages and quarry spoil piles (Ehret, pers. obs. 2015).

We interpret the absence of *O. megalodon* in the Rushmere and Moore House members of the Yorktown Formation, upper San Diego Formation, and “upper” parts of the Purisima Formation to be biochronologically real and reflect the genuine absence of this taxon. Given the intense collecting of these localities by amateur and professional paleontologists alike, collection bias is not likely a factor in determining the stratigraphic occurrence of *O. megalodon*. Lastly, agreement between well-sampled stratigraphic intervals in the North and South Pacific, western North Atlantic, and Mediterranean on the termination of the *O. megalodon* lineage during the earliest Pliocene ~~suggests~~ a globally synchronous ~~extinction~~.

***Possible causes for the extinction of* Otodus megalodon**

Determination of the timing of the extinction of *Otodus megalodon* is a necessary step in identifying potential causal factors contributing to its demise. Although testing various hypotheses in a quantitative manner is beyond the scope of this article, some comments regarding potential biotic and physical drivers are appropriate. Abiotic drivers such as changes in climate, upwelling, currents, sea level, and paleogeography are possible determinants in the decline of the otodontid lineage. Physical events coincident with an Early Pliocene extinction include: 1) a decrease in upwelling in the eastern North Pacific (Barron, 1998), 2) increased seasonality of marine climates (Hall, 2002); 3) a period of climatic warming and permanent El-Niño like conditions in the equatorial Pacific (Wara et al., 2005; Fedorov et al., 2013), 4) followed by Late Pliocene global cooling (Zachos et al., 2001), 5) initiation of closure of the Panama seaway and restriction of currents and east-west dispersal among marine organisms (Collins et al., 1996; Haug et al., 2001), and 6) stable eustatic sea level during the Early Pliocene, 7) followed by eustatic sea level fall related to initial glaciation during the Late Pliocene (Miller et al., 2005). Some of these changes in oceanic circulation and upwelling were regional, and therefore do not represent likely causes in the extinction of *O. megalodon* (if the extinction was indeed globally synchronous; e.g. Pimiento and Clements, 2014); however, these events may have been, in part, responsible for range fragmentation. Long term cooling following the middle Miocene Climatic Optimum (Zachos et al., 2001) cannot be excluded as a contributing factor and certainly may have reduced the geographic range of this species (Purdy, 1996; Dickson and Graham, 2004; but see Pimiento and Balk, 2016; Ferrón, 2017). Within the eastern North Pacific (ENP), many "archaic" marine mammal taxa became extinct towards the end of the Pliocene (~2 Ma; Boessenecker, 2013b, 2013a), but the extinction of *O. megalodon* predated this (~5-4 Ma;

but see Pimiento et al., 2017). However, the appearance of the modern marine mammal fauna appears to have occurred by the Early Pliocene in the North Atlantic and western South Pacific (Whitmore, 1994; Fitzgerald, 2005), suggesting globally asymmetric origination of modern marine mammal genera and species (Boessenecker, 2013a), in contrast with an apparently synchronous extinction of *O. megalodon* (Pimiento and Clements, 2014). Other biotic effects have been hypothesized to have affected or been driven by *O. megalodon*. Recently described macrophagous sperm whales appear to have been diverse worldwide in the middle and late Miocene, were similar in size to *O. megalodon*, and were likely competing apex predators (Lambert et al., 2010). A high diversity of small-bodied baleen whales during the middle Miocene is implicated in supporting such an assemblage of gigantic predators (Lambert et al., 2010; Collareta et al., 2017). Similarly, Lindberg and Pyenson ~~(Lindberg and Pyenson,~~ 2006~~)~~ noted that the extinction of *O. megalodon* is roughly contemporaneous with the earliest fossil occurrences of killer whales (*Orcinus*) in the fossil record, and perhaps competition with killer whales during the Pliocene could have acted as a driver in the extinction of *O. megalodon*. However, the Neogene fossil record of *Orcinus* is limited to two occurrences: an isolated tooth from Japan (Kohno and Tomida, 1993), and the well-preserved skull and skeleton of *Orcinus citoniensis* from the Late Pliocene of Italy (Capellini, 1883). Furthermore, *Orcinus citoniensis* was small in comparison to extant *Orcinus orca* (est. 4 m body length; Heyning and Dahlheim, 1988) and possessed a higher number of relatively smaller teeth and narrower rostrum (Bianucci, 1996), and was probably not an analogous macrophagous predator. Because fossils of *Orcinus* are not widespread during the Pliocene, ~~competition~~ with *Orcinus* is problematic. Furthermore, the decline and loss of cosmopolitan macrophagous physeteroids (Tortonian-Messinian; Lambert et al., 2010) appears to have predated the Early Pliocene extinction of *O. megalodon* by several million years.

Evolutionary interactions with baleen whales have also been implicated for the *Otodus* lineage. Lambert et al. (2010) implicated increased diversity of mysticetes during the middle Miocene to have driven the evolution of killer sperm whales; similarly, this could have driven body size increases in *O. megalodon*. Cetacean diversity peaked in the middle Miocene and began to decrease in the late Miocene (Lambert et al., 2010; Marx and Uhen, 2010), and maximum body length amongst fossil mysticetes increased during the late Miocene and Pliocene (Lambert et al., 2010), heralding the appearance of modern giants such as *Balaenoptera*, *Megaptera*, *Eschrichtius*, *Balaena*, and *Eubalaena*. Despite the increase in maximum body size among mysticetes and coincidental extinction of *O. megalodon* during the Pliocene, numerous small-bodied archaic mysticetes persisted into the Pliocene (Bouetel and Muizon, 2006; Whitmore and Barnes, 2008; Collareta et al., 2017) and even Pleistocene (Boessenecker, 2013a), complicating this relationship (but see Collareta et al., 2017). Many extant genera of cetaceans first appeared during the Pliocene (Fordyce and Muizon, 2001), apparently temporally coincident with the extinction of *O. megalodon*, but with uncertain relevance.

Another potential biotic factor in the extinction of *Otodus megalodon* is the evolution of the modern great white shark, *Carcharodon carcharias* (Pimiento and Balk, 2016). It gradually evolved from the non-serrated *Carcharodon hastalis* during the late Miocene, transitioning first into the finely serrated *Carcharodon hubbelli* approximately 8-7 Ma, then evolved into the coarsely serrated *C. carcharias* approximately 6-5 Ma (Ehret et al., 2009a; Ehret et al., 2012; Long et al. 2014). However, in the western North Atlantic, *C. carcharias* is absent in the Early Pliocene Sunken Meadow Member of the Yorktown Formation (Purdy et al., 2001; Ward, 2008), and in its place is *C. hastalis* (=*Isurus hastalis* and *Isurus xiphodon* in Purdy et al., 2001). *Carcharodon carcharias* instead occurs higher in the Rushmere Member of the Yorktown Formation (Müller, 1999). This suggests that the appearance of *C. carcharias* in the Atlantic may have been delayed relative to the Pacific. Pawellek et al. (2012) reported an earliest Pliocene fish assemblage on the Mediterranean coast of Libya that included *C. carcharias* and *O. megalodon*; clarifying the timing of first appearance of *C. carcharias* in ocean basins outside the Pacific is necessary, but beyond the scope of this study. Nevertheless, the timing of *O. megalodon* extinction appears to overlap with the final widespread global occurrence of *C. carcharias* in the Early Pliocene. It is necessary to note that a single putative tooth of *C. carcharias* has been reported from the middle Miocene Calvert Formation and has been identified as evidence supposedly disproving the *Carcharodon hastalis-hubbelli-carcharias* transition (Purdy, 1996; Gottfried and Fordyce, 2001), although Ehret et al. (2012) indicated this specimen is a misidentified juvenile *O. megalodon* tooth.

The development of serrations in *Carcharodon hubbelli* suggests a refined ability to prey upon warm-blooded prey relative to other large lamnid and carcharhinid sharks (Frazzetta, 1988; Ehret et al., 2009a; Ehret et al., 2009b; Ehret et al., 2012). Perhaps trophic competition with the newly evolved *C. carcharias* contributed to the extinction of *O. megalodon*, in which adult *C. carcharias* would have been in the same size range and likely would have competed with juvenile *O. megalodon*. Owing to its global scope, the first appearance of modern *C. carcharias* during the Early Pliocene is a likely candidate for the driver behind the extinction of *O. megalodon*. Further investigations regarding body size trends in the *Otodus*and *Carcharodon* lineages, the *Carcharodon hastalis-hubbelli-carcharias* anagenetic lineage in the Pacific basin and elsewhere, and the timing of *C. carcharias* first appearances and *O. megalodon* last appearances in the Atlantic and other ocean basins are necessary to evaluating these hypotheses of extinction drivers of *O. megalodon*.

On a final note, this entire discussion, and most discussions of the extinction of *Otodus megalodon*, presuppose a globally synchronous extinction (Pimiento and Clements, 2014; Pimiento and Balk, 2016; Collareta et al., 2017; Pimiento et al., 2017). An alternate hypothesis that bears testing is that there may have been a globally asynchronous extinction, with *O. megalodon* becoming extinct in the eastern North Pacific earlier than other basins. Greater faunal provinciality amongst Pliocene marine mammal assemblages in comparison to today (Boessenecker, 2013a), and the earlier appearance of *Carcharodon carcharias* in the North Pacific relative to the North Atlantic (Ward, 2008; Boessenecker, 2011; Long et al., 2014) lend some support to this idea. Evaluation of this hypothesis will require careful ~~examination~~ of the geologic range of *O. megalodon* occurrences in other ocean basins with similarly well-established assemblages and framework of age determinations.

Conclusions

Fossil teeth of *Otodus megalodon* have been reported or recorded from Miocene, Pliocene, and Pleistocene aged strata in the eastern North Pacific. Critical examination of Pleistocene specimens and their stratigraphic context clearly indicate that they are reworked, have poor provenance, or are missing specimens (or combination thereof). Specimens of Late Pliocene age, such as those from the Niguel Formation, also appear to be reworked from older strata. Early Pliocene specimens from the lowermost San Diego Formation, upper San Mateo Formation, and Tirabuzón Formation appear to represent the youngest autochthonous (or parautochthonous) records of *O. megalodon* in this region, whereas numerous *Otodus megalodon* records of middle and late Miocene age have been reported. These revised and refined interpretations of the *Otodus megalodon* fossil record ~~suggest~~ that within the eastern North Pacific, it became extinct during the Early Pliocene (end-Zanclean, approximately 4-3 Ma), corresponding well with the youngest known specimens in the North Atlantic (Yorktown Formation, North Carolina) and Mediterranean (Pliocene of Italy). This ~~predates~~ Plio-Pleistocene faunal turnover of marine mammals, and the extinction of *O. megalodon* may instead be related to range fragmentation resulting from post-middle Miocene paleoceanographic changes and decreasing sea surface temperature, and perhaps more importantly by the evolution of modern *Carcharodon carcharias*. Alternatively, a globally asynchronous extinction of *O. megalodon* may also be possible. This study dispels publicly held opinions that *Otodus megalodon* may still be extant, and that *Otodus megalodon* did not survive ~~to the Late Pliocene, and certainly not~~ to the end of the Pliocene.

Acknowledgments

This study benefited from discussions with J. Ashby, M. Balk, M. Churchill, M. DeJong, T.A. Deméré, J. Duran, R.E. Fordyce, M.D. Gottfried, S. Mansfield, F.A. Perry, C. Pimiento, and K. Shimada. We thank the following, who expedited access to collections under their care: L.G. Barnes, J. Bryant, T.A. Deméré, J. El Adli, M. Goodwin, P. Holroyd, S. McLeod, F.A. Perry, K. Randall, and V. Rhue. Thanks to S. McLeod, V. Rhue, and J. Velez-Juarbe for curatorial assistance. We are grateful for the careful comments of C.L. Powell, II and K. Shimada, whose detailed comments improved the quality of an earlier draft of this study. RWB was supported by a University of Otago Doctoral Scholarship during this study.

References

Agassiz LJR. 1843. *Recherches sur les poissons fossiles. Tome III (livr. 15-16)*. Neuchatel: Imprimerie de Petitpierre.

Aguilera OA, Garcia L, and Cozzuol MA. 2004. Giant-toothed white sharks and cetacean trophic interaction from the Pliocene Caribbean Paraguana Formation. *Paläontologische Zeitschrift* 82:204-208.

Anonymous. 1921. Life extension bulletin. *Advertising supplement to the Torrance Herald, Torrance, California* 1:1.

Antunes MT. 1978. Faunes ichthyologiques du Néogène supérieur d'Angola, leur age, remarques sur le Pliocéne marin en Afrique australe. *Ciênces da Terra (UNL)* 4:59-90.

Applegate SP. 1978. Phyletic studies. Part 1. Tiger sharks. *Universidad Nacional Autonoma de Mexico, Instituto de Geologia, Revista* 2:55-64.

Applegate SP, and Espinosa-Arrubarrena L. 1981. The geology and selachian paleontology of Loma del Tirabuzon (Corkscrew Hill), Santa Rosalia, B.C.S. In: Ortlieb L, and Roldan J, eds. *Geology of northwestern Mexico and Arizona*. Hermosillo, Mexico: Universidad Nacional Autonoma Mexico, Instituto de Geologia, Estacion de Noroeste, 257-263.

Applegate SP, and Espinosa-Arrubarrena L. 1996. The fossil history of *Carcharodon* and its possible ancestor, *Cretolamna*: a study in tooth identification. In: Klimley AP, and Ainley DG, eds. *Great white sharks: the biology of Carcharodon carcharias*. San Diego, California: Academic Press, 19-36.

Argast S, Farlow JO, Gabet RM, and Brinkman DL. 1987. Transport-induced abrasion of fossil teeth: Implications for the existence of Tertiary dinosaurs in the Hell Creek Formation, Montana. *Geology* 15:927-930. 10.1130/0091-7613(1987)15<927:TAOFRT>2.0.CO;2

Ashby JR, and Minch JA. 1984. The Upper Pliocene San Diego Formation and the occurrence of *Carcharodon megalodon* at La Joya, Tijuana, Baja California, Mexico. In: Minch JA, and Ashby JR, eds. *Miocene and Cretaceous Depositional Environments, Northwestern Baja California, Mexico*. Los Angeles, California: American Association of Petroleum Geologists, Pacific Section, 19-28.

Barboza MM, Parham JF, Santos GP, Kussman BN, and Velez-Juarbe J. 2017. The age of the Oso Member, Capistrano Formation, and a review of fossil crocodylians from California. *PaleoBios* 34:1-16.

Barnes LG. 1977. Outline of eastern North Pacific fossil cetacean assemblages. *Systematic Zoology* 25:321-343.

Barnes LG. 1978. A review of *Lophocetus* and *Liolithax* and their relationships to the delphinoid family Kentriodontidae (Cetacea: Odontoceti). *Natural History Museum of Los Angeles County Science Bulletin* 28:1-35.

Barnes LG. 1992. The fossil marine vertebrate fauna of the latest Miocene Almejas Formation, Isla Cedros, Baja California, México. In: Carrillo-Cha´vez A, and Alvarez-Arellano A, eds. *Primera Reunión Internacional sobre Geología de la Península de Baja California, Memorias*. La Paz, Baja California Sur, Mexico: Universidad Autónoma de Baja California Sur, 147-166.

Barnes LG. 1998. The sequence of fossil marine mammal assemblages in Mexico. *Avances en Investigacion: Paleontologia de Vertebrados, publicacion especial* 1:26-79.

Barnes LG. 2013. A new genus and species of late Miocene paleoparadoxiid (Mammalia, Desmostylia) from California. *Contributions in Science, Natural History Museum of Los Angeles County* 521:51-114.

Barnes LG, Howard H, Hutchison JH, and Welton BJ. 1981. The vertebrate fossils of the marine Cenozoic San Mateo Formation at Oceanside, California. In: Abbott PL, and O'Dunn S, eds. *Geologic Investigations of the coastal plain, San Diego County, California*. San Diego, California: San Diego Association of Geologists, 53-70.

Barnes LG, and Raschke RE. 1991. *Gomphotaria pugnax*, a new genus and species of late Miocene dusignathine otariid pinniped (Mammalia: Carnivora) from California. *Natural History Museum of Los Angeles County Contributions in Science* 426:1-27.

Barron JA. 1998. Late Neogene changes in diatom sedimentation in the North Pacific. *Journal of Asian Earth Sciences* 16:85-95.

Barron JA, and Gladenkov AY. 1995. Early Miocene to Pleistocene Diatom Stratigraphy of Leg 145. *Proceedings of the Ocean Drilling Program, Scientific Results* 145:3-19.

Barron JA, and Isaacs CM. 2001. Updated chronostratigraphic framework for the California Miocene. In: Isaacs CM, and Rullkötter J, eds. *The Monterey Formation - from rocks to molecules*. New York, New York: Columbia University Press, 393-395.

Bendix-Almgreen SE. 1983. *Carcharodon megalodon* from the Upper Miocene of Denmark, with comments on elasmobranch tooth enameloid: coronoin. *Bulletin of the Geological Society of Denmark* 32:1-32.

Bianucci G. 1996. The Odontoceti (Mammalia, Cetacea) from Italian Pliocene systematics and phylogenesis of Delphinidae. *Palaeontolographia Italica* 83:73-167.

Bianucci G, and Landini W. 2006. Killer sperm whale: a new basal physeteroid (Mammalia, Cetacea) from the Late Miocene of Italy. *Zoological Journal of the Linnaean Society* 148:103-131.

Boessenecker RW. 2011a. Herpetocetine (Cetacea: Mysticeti) dentaries from the Upper Miocene Santa Margarita Sandstone of Central California. *PaleoBios* 30:1-12.

Boessenecker RW. 2011b. A new marine vertebrate assemblage from the Late Neogene Purisima Formation in central California, Part I: Fossil sharks, bony fish, birds, and implications for the age of the Purisima Formation west of the San Gregorio Fault. *PalArch's Journal of Vertebrate Paleontology* 8:1-30.

Boessenecker RW. 2013a. A new marine vertebrate assemblage from the Late Neogene Purisima Formation in Central California, Part II: Pinnipeds and cetaceans. *Geodiversitas* 35:815-940.

Boessenecker RW. 2013b. Pleistocene survival of an archaic dwarf baleen whale (Mysticeti: Cetotheriidae). *Naturwissenschaften* 100:365-371.

Boessenecker RW. 2016. First record of the megatoothed shark *Carcharocles megalodon* from the Mio-Pliocene Purisima Formation of Northern California. *PaleoBios* 33.

Boessenecker RW, Perry FA, and Schmitt JG. 2014. Comparative taphonomy, taphofacies, and bonebeds of the Mio-Pliocene Purisima Formation, Central California: strong physical control on marine vertebrate preservation in shallow marine settings. *PLoS ONE* 9:e91419.

Bouetel V, and Muizon Cd. 2006. The anatomy and relationships of *Piscobalaena nana* (Cetacea, Mysticeti), a Cetotheriidae s.s. from the early Pliocene of Peru. *Geodiversitas* 28:319-395.

Capellini G. 1883. Di Un'Orca fossile scoperta a cetona in Toscana. *Memorie dell'Accademia delle Scienze dell'Instituto di Bologna* 4:1-25.

Cappetta H. 1987. *Handbook of Paleoichthyology, Volume 3B. Chondrichthyes II, Mesozoic and Cenozoic Elasmobranchii.* Stuttgart: Gustav Fisher Verlag.

Cappetta H. 2012. *Handbook of Paleoichthyology. Chondrichthyes (Mesozoic and Cenozoic Elasmobranchii: Teeth), vol. 3B.* Stuttgart, Germany: Gustav Fisher.

Cappetta H, and Carvallo O. 2006. Les selaciens du Pliocene de la region d'Alba (Piemont, Italie Nordouest). *Rivista Piemontese di Storia Naturale* 27:33-76.

Carreno AL. 1982. Biostratigraphy at the Loma del Tirabuzón (Corkscrew Hill), Santa Rosalia Baja California Sur, Mexico. *Third North American Paleontological Convention, Proceedings* 1:67-69.

Clark JC. 1966. Tertiary stratigraphy of the Felton-Santa Cruz area, Santa Cruz Mountains, California Ph.D. Stanford University.

Clark JC. 1981. Stratigraphy, paleontology and geology of the central Santa Cruz mountains. *United States Geological Survey Professional Paper* 1168:1-51.

Clark JC, Brabb EE, Greene HG, and Ross DC. 1984. Geology of Point Reyes Peninsula and implications for San Gregorio Fault history. In: Crouch JK, and Bachman SB, eds. *Tectonics and sedimentation along the California margin*. Los Angeles, California: Pacific Section SEPM, 67-86.

Collareta A, Lambert O, Landini W, Di Celma C, Malinverno E, Varas-Malca RM, Urbina M, and Bianucci G. 2017. Did the giant extinct shark *Carcharocles megalodon* target small prey? Bite marks on marine mammal remains from the late Miocene of Peru. *Palaeogeography, Palaeoclimatology, Palaeoecology* 469:84-91.

Collins LS, Coates AG, Berggren WA, Aubry MP, and Zhang J. 1996. The late Miocene Panama isthmian strait. *Geology* 24:687-690.

Cummings JC, Touring RM, and Brabb EE. 1962. Geology of the Northern Santa Cruz Mountains. *California Division of Mines Geology Bulletin* 181:179-220.

Deméré TA. 1982. Review of the lithostratigraphy, biostratigraphy and age of the San Diego Formation. In: Abbott PL, ed. *Geologic studies in San Diego*. San Diego: San Diego Association of Geologists, 127-134.

Deméré TA. 1983. The Neogene San Diego Basin: a review of the marine Pliocene San Diego Formation of southern California. In: LaRue DK, and Steel RJ, eds. *Cenozoic Marine Sedimentation, Pacific Margin, USA*. Los Angeles, California: Society of Economic Paleontologists and Mineralogists, 187-195.

Deméré TA, and Berta A. 2005. New skeletal material of *Thalassoleon* (Otariidae:Pinnipedia) from the Late Miocene–Early Pliocene (Hemphillian) of California. *Bulletin of the Florida Museum of Natural History* 45:379-411.

Deméré TA, Berta A, and Adam PJ. 2003. Pinnipedimorph evolutionary biogeography. *Bulletin of the American Museum of Natural History* 279:32-76.

Deméré TA, Roeder MA, Chandler RM, and Minch JA. 1984. Paleontology of the middle Miocene Los Indios Member of the Rosarito Beach Formation, Northwestern Baja California, Mexico. In: Minch JA, and Ashby JR, eds. *Miocene and Cretaceous Depositional Environments, Northwestern Baja California, Mexico*. Los Angeles: Pacific Section A.A.P.G., 47-56.

Di Celma C, Malinverno E, Bosio G, Collareta A, Gariboldi K, Gioncada A, Molli G, Basso D, Varas-Malca RM, Pierantoni PP, Villa IM, Lambert O, Landini W, Sarti G, Cantalamessa G, Urbina M, and Bianucci G. 2017. Sequence stratigraphy and paleontology of the upper Miocene Pisco Formation along the western side of the lower Ica Valley (Ica Desert, Peru). *Rivista Italiana di Paleontologia e Stratigrafia* 123:255-273.

Dickson KA, and Graham JB. 2004. Evolution and consequences of endothermy in fishes. *Physiological and Biochemical Zoology* 77:998-1018.

Domning DP. 1978. Sirenian evolution in the North Pacific Ocean. *University of California Publications in Geological Sciences* 18:1-176.

Domning DP, and Deméré TA. 1984. New material of *Hydrodamalis cuestae* (Mammalia; Dugongidae) from the Miocene and Pliocene of San Diego County, California. *Transactions of the San Diego Society of Natural History* 20:169-188.

Donovan SK. 1988. Palaeoecology and taphonomy of barnacles from the Plio-Pleistocene Red Crag of East Anglia. *Proceedings of the Geologists' Association* 99:279-289.

Dupré WR, Morrison RB, Clifton HE, Lajoie KR, Ponti DJ, Powell CL, II, Mathieson SA, Sarna-Wojcicki AM, Leithold EL, Lettis WR, McDowell PF, Rockwell TK, Unruh JR, and Yeats RS. 1991. Quaternary geology of the Pacific margin. In: Morrison RB, ed. *Quaternary nonglacial geology: conterminous US*. Boulder, Colorado: Geological Society of America, 141-213.

Ehlig P. 1979. The late Cenozoic evolution of the Capistrano Embayment. *Geologic Guide of the San Onofre Nuclear Generating Station and Adjacent Regions of Southern California: Pacific Sections AAPG, SEPM, and SEG Guide Book* 46:A36-A46.

Ehret DJ, Hubbell G, and MacFadden BJ. 2009a. Exceptional preservation of the white shark *Carcharodon* (Lamniformes, Lamnidae) from the Early Pliocene of Peru. *Journal of Vertebrate Paleontology* 29:1-13.

Ehret DJ, MacFadden BJ, Jones DS, DeVries TJ, Foster DA, and Salas-Gismondi R. 2012. Origin of the white shark *Carcharodon* (Lamniformes: Lamnidae) based on recalibration of the upper Neogene Pisco Formation of Peru. *Palaeontology* 55:1139-1153.

Ehret DJ, MacFadden BJ, and Salas-Gismondi R. 2009b. Caught in the act: trophic interactions between a 4-million year old white shark (*Carcharodon*) and mysticete whale from Peru. *Palaios* 24:329-333.

Eldridge GH, and Arnold R. 1907. The Santa Clara Valley, Puente Hills, and Los Angeles oil districts, Southern California. *US Geological Survey Bulletin* 309:1-266.

Fedorov AV, Brierley CM, Lawrence KT, Liu Z, Dekens PS, and Ravelo AC. 2013. Patterns and mechanisms of early Pliocene warmth. *Nature* 496:44-49.

Ferrón HG. 2017. Regional endothermy as a trigger for gigantism in some extinct macropredatory sharks. *PLoS ONE* 12:e0185185.

Fitch JE. 1970. Fish remains, mostly otoliths and teeth, from the Palos Verdes Sand (late Pleistocene) of California. *Los Angeles County Museum Contributions in Science* 199:1-41.

Fitzgerald EMG. 2004. A review of the Tertiary fossil Cetacea (Mammalia) localities in Australia. *Memoirs of the Museum of Victoria* 61:183-208.

Fitzgerald EMG. 2005. Pliocene marine mammals from the Whalers Bluff Formation of Portland, Victoria, Australia. *Memoirs of Museum Victoria* 62:67-89.

Flemming C, and McFarlane DA. 1998. New Caribbean locality for the extinct great white shark *Carcharodon megalodon*. *Caribbean Journal of Science* 34:317-318.

Fordyce RE, and Muizon Cd. 2001. Evolutionary history of cetaceans: a review. In: Mazin JM, and Buffrenil Vd, eds. *Secondary Adaptations of Tetrapods to Life in Water*. Munich, Germany: Verlag Dr. Friedrich Pfeil, 169-233.

Frazzetta TH. 1988. The mechanics of cutting and the form of shark teeth (Chondrichthyes, Elasmobranchii). *Zoomorphology* 108:93-107.

Galloway AJ. 1977. Geology of the Point Reyes Peninsula, Marin County, California. *California Division of Mines and Geology Bulletin* 202:1-72.

Garcia EXM, Antunes MT, Caceras-Balbino A, Ruiz-Munoz F, and Civis-Llovera J. 2009. Los tiburones Lamniformes (Chondrichthyes, Galeomorphii) del Pliocene inferior de la Formación Arenas de Huelva, suroeste de la cuenca del Guadalquivir, España. *Revista Mexicana de Ciencias Geologicas* 26:674-686.

Gervais P. 1852. *Zoologie et paléontologie française (animaux vertébrés)*. Paris: Arthus Bertrand.

Gibbard PL, Head MJ, Walker MJ, and Stratigraphy SoQ. 2009. Formal ratification of the Quaternary System/Period and the Pleistocene Series/Epoch with a base at 2.58 Ma. *Journal of Quaternary Science* 25:96-102.

Gottfried MD, Compagno LJV, and Bowman SC. 1996. Size and skeletal anatomy of the giant "megatooth" shark *Carcharodon megalodon*. In: Klimley AP, and Ainley DG, eds. *Great White Sharks: the biology of Carcharodon carcharias*. San Diego: Academic Press, 55-66.

Gottfried MD, and Fordyce RE. 2001. An associated specimen of *Carcharodon angustidens* (Chondrichthyes, Lamnidae) from the Late Oligocene of New Zealand, with comments on *Carcharodon* interrelationships. *Journal of Vertebrate Paleontology* 21:730-739.

Gradstein FM, Ogg JG, Smith AG, Agterberg FP, Bleeker W, Cooper RA, Davydov V, Gibbard P, Hinnov L, House MR, Lourens L, Luterbacher HP, McArthur J, Melchin MJ, Robb LJ, Shergold J, Villeneuve M, Wardlaw BR, Ali J, Brinkhuis H, Hilgen FJ, Hooker J, Howarth RJ, Knoll AH, Laskar J, Monechi S, Powell J, Plumb KA, Raffi I, Röhl U, Sadler P, Sanfilippo A, Schmitz B, Shackleton NJ, Shields GA, Strauss H, Van Dam J, Veizer J, van Kolfschoten T, and Wilson D. 2004. *A geologic timescale 2004*. Cambridge: Cambridge University Press.

Grant US, IV, and Gale HR. 1931. Catalogue of the marine Pliocene and Pleistocene Mollusca of California. *San Diego Society of Natural History Memoir* 1:1-1036.

Hall CA. 2002. Nearshore marine paleoclimatic regions, increasing zoogeographic provinciality, molluscan extinctions, and paleoshorelines, California: Late Oligocene (27 Ma) to Late Pliocene (2.5 Ma). *Geological Society of America Special Paper* 357:1-489.

Haug GH, Tiedemann R, Zahn R, and Ravelo AC. 2001. Role of Panama uplift on oceanic freshwater balance. *Geology* 29:207-210.

Heyning JE, and Dahlheim ME. 1988. *Orcinus orca*. *Mammalian Species* 304:1-9.

Hilgen FJ, Lourens LJ, Van Dam JA, Beu AG, Boyes AF, Cooper RA, Krijgsman W, Ogg JG, Piller WE, and Wilson DS. 2012. The Neogene Period. In: Gradstein FM, Ogg JG, Schmitz M, and Ogg G, eds. *The Geologic Time Scale 2012*. Amsterdam: Elsevier, 923-978.

Holt JW, Holt EW, and Stock JM. 2000. An age constraint on Gulf of California rifting from the Santa Rosalía basin, Baja California Sur, Mexico. *Geological Society of America Bulletin* 112:540-549.

Ingle JC. 1979. Biostratigraphy and paleoecology of early Miocene through early Pleistocene benthonic and planktonic Foraminifera, San Joaquin Hills–Newport Bay–Dana Point area, Orange County, California. In: Stuart CJ, editor. A guidebook to Miocene Lithofacies and Depositional Environments, Coastal Southern California and Northwestern Baja California: Pacific Section of Society of Economic Paleontologists and Mineralogists. p 53-77.

Iturralde-Vinent M, Hubbell G, and Rojas R. 1996. Catalogue of Cuban fossil Elasmobranchii (Paleocene to Pliocene) and paleogeographic implications of their lower to middle Miocene occurrence. *The Journal of the Geological Society of Jamaica* 31:7-21.

Jordan DS. 1907. The fossil fishes of California, with supplementary notes on other species of extinct fishes. *University of California Publications Bulletin of the Department of Geology* 5:95-144.

Jordan DS. 1910. Notes on ichthyology. *American Midland Naturalist* 519:178-191.

Jordan DS. 1922. Some shark's teeth from the California Pliocene. *The American Journal of Science, fifth series* 2:338-342.

Jordan DS, and Hannibal H. 1923. Fossil sharks and rays of the Pacific Slope of North America. *Bulletin of the Southern California Academy of Science* 22:27-63.

Kanakoff GP. 1956. Fish records from the Pleistocene of southern California. *Bulletin of the Southern California Academy of Science* 55:47-49.

Kem JP, and Wicander ER. 1974. Origin of a bathymetrically displaced marine invertebrate fauna in the upper part of the Capistrano Formation (Lower Pliocene), southern California. *Journal of Paleontology* 48:495-505.

Kemp NR. 1991. Chondrichthyans in the Cretaceous and Tertiary of Australia. In: Vickers-Rich P, Monaghan JM, Baird RF, and Rich TH, eds. *Vertebrate Palaeontology of Australasia*. Melbourne: Pioneer Design Studio in cooperation with the Monash University Publications Committee.

Kent BW. 1999. Speculations on the size and morphology of the extinct lamnoid shark, *Parotodus benedeni* (le Hon). *The Mosasaur* 6:11-15.

Kent BW, and Powell GW, Jr. 1999. Reconstructed dentition of the rare lamnoid shark *Parotodus benedeni* (le Hon) from the Yorktown Formation (Early Pliocene) at Lee Creek Mine, North Carolina. *The Mosasaur* 6:1-10.

Keyes IW. 1972. New records of the elasmobranch *C. megalodon* (Agassiz) and a review of the genus *Carcharodon* in the New Zealand fossil record. *New Zealand Journal of Geology and Geophysics* 15:228-242.

Kohno N, and Tomida Y. 1993. Marine mammal teeth (Otariidae and Delphinidae) from the early Pleistocene Setana Formation, Hokkaido, Japan. *Bulletin of the National Science Museum, Tokyo* 19:139-146.

Lambert O, Bianucci G, Post K, Muizon Cd, Salas-Gismondi R, Urbina M, and Reumer J. 2010. The giant bite of a new raptorial sperm whale from the Miocene epoch of Peru. *Nature* 466:105-108.

Lindberg DR, and Pyenson ND. 2006. Evolutionary patterns in Cetacea: fishing up prey size through deep time. In: Estes JA, DeMaster DP, Doak DP, Williams TM, and Brownell RL, eds. *Whales, Whaling, and Ocean Ecosystems*. Berkeley, California: University of California Press, 67-81.

Long DJ. 1993. Late Miocene and Early Pliocene fish assemblages from the north central coast of Chile. *Tertiary Research* 14:117-126.

Long DJ. 1994. Historical biogeography of sharks from the eastern North Pacific Ocean Ph.D. University of California, Berkeley.

Long DJ, Boessenecker RW, and Ehret DJ. 2014. Timing of evolution in the *Carcharodon* lineage: Rapid morphological change creates a major shift in a predator's trophic niche. 2nd Annual Sharks International Conference. Durban, South Africa. p 123.

Longbottom AE. 1979. Miocene shark's teeth from Ecuador. *Bulletin of the British Museum (Natural History) Geology* 32:57-70.

Lydekker R. 1887. The Cetacea of the Suffolk Crag. *Quarterly Journal of the Geological Society* 43:7-18.

MacFadden BJ, Labs-Hochstein J, Quitmyer I, and Jones DS. 2004. Incremental growth and diagenesis of skeletal parts of the lamnoid shark *Otodus obliquus* from the early Eocene (Ypresian) of Morocco. *Palaeogeography, Palaeoclimatology, Palaeoecology* 206:179-192.

Marsili S. 2008. Systematic, paleoecologic and paleobiogeographic analysis of the Plio-Pleistocene Mediterranean elasmobranch fauna. *Atti Della Societa Toscana Di Scienze Naturali Memorei Serie A* 113:81-88.

Marx FG, and Uhen MD. 2010. Climate, critters, and cetaceans: Cenozoic drivers of the evolution of modern whales. *Science* 327:993-996.

Miller KG, Kominz MA, Browning JV, Wright JD, Mountain GS, Katz ME, Sugarman PJ, Cramer BS, Christie-Blick N, and Pekar SF. 2005. The Phanerozoic record of global sea-level change. *Science* 310:1293-1297.

Mitchell ED. 1966. *History of research at Sharktooth Hill, Kern County, California.* Bakersfield, California: Kern County Historical Society.

Mitchell ED, and Repenning CA. 1963. The chronologic and geographic range of desmostylians. *Contributions in Science, Natural History Museum of Los Angeles County* 78:1-20.

Mount JD. 1974. Type vertebrates from Lomita, California, in the Municipal Museum, Riverside, California. *Journal of Paleontology* 48:198-199.

Muizon Cd, and de Vries TJ. 1985. Geology and paleontology of late Cenozoic marine deposits in the Sacaco area (Peru). *Geologische Rundschau* 74:547-563.

Müller A. 1999. Ichthyofaunen aus dem atlantischen Tertiär der USA. *Leipziger Geowissenschaften, Leipzig* 9/10:1-360.

Norris RD. 1986. Taphonomic gradients in shelf fossil assemblages: Pliocene Purisima Formation, California. *Palaios* 1:256-270. 10.2307/3514689

Nyberg KG, Ciampaglio CN, and Wray GA. 2006. Tracing the ancestry of the great white shark, *Carcharodon carcharias*, using morphometric analyses of fossil teeth. *Journal of Vertebrate Paleontology* 26:806-814.

Obradovich JD. 1965. The potential use of glauconite for Late-Cenozoic geochronology. *Proceedings of the International Association for Quaternary Research* 8:267-279.

Owen R. 1844. Appendix to Professor Henslow's paper, consisting of a description of the fossil tympanic bones referable to four distinct species of *Balaena*. *Proceedings of the Geological Society of London* 4:283-286.

Owen R. 1870. *Monograph on the British fossil Cetacea from the Red Crag*. London: The Palaeontographical Society.

Parham JF, Donoghue PCJ, Bell CJ, Calway TD, Head JJ, Holroyd PA, Inoue JG, Irmis RB, Joyce WG, Ksepka DT, Patane JSL, Smith ND, Tarver JE, Tuinen Mv, Yang Z, Angielczyk KD, Greenwood JM, Hipsley CA, Jacobs L, Makovicky PJ, Muller J, Smith KT, Theodor JM, Warnock RCM, and Benton MJ. 2012. Best practices for justifiying fossil calibrations. *Systematic Biology* 61:346-359.

Pawellek T, Adnet S, Cappetta H, Metais E, Salem M, Brunet M, and Jaeger JJ. 2012. Discovery of an earliest Pliocene relic tropical fish fauna in a newly detected cliff section (Sabratah

Basin, NW Libya). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 266:93-114.

Pimiento C, and Balk MA. 2016. Geographical distribution patterns of *Carcharocles megalodon* over time reveal clues about extinction mechanisms. *Journal of Biogeography* 43:1645-1655.

Pimiento C, and Clements CF. 2014. When did *Carcharocles megalodon* become extinct? A new analysis of the fossil record. *PLoS ONE* 9:e11086.

Pimiento C, Ehret DJ, MacFadden BJ, and Hubbell G. 2010. Ancient nursery area for the extinct giant shark Megalodon from the Miocene of Panama. *PLoS ONE* 5:e10552.

Pimiento C, Griffin JN, Clements CF, Silvestro D, Varela S, Uhen MD, and Jaramillo C. 2017. The Pliocene marine megafauna extinction and its impact on functional diversity. *Nature Ecology & Evolution* 1:1100-1106.

Powell CL, II. 1998. The Purisima Formation and related rocks (upper Miocene–Pliocene), greater San Francisco Bay area, central California—Review of literature and USGS collections (now housed at the Museum of Paleontology, University of California, Berkeley):. *United States Geological Survey Open-File Report* 98-594:1-101.

Powell CL, II, Barron JA, Sarna-Wojcicki AM, Clark JC, Perry FA, Brabb EE, and Fleck RJ. 2007. Age, stratigraphy, and correlation of the late Neogene Purisima Formation, central California coast ranges. *US Geological Survey Professional Paper* 1740:1-32.

Powell CL, II, Stanton RJ, and Liff-Grier P. 2008. Architictonica (Gastropoda) and associated warm-water mollusks used to correlate and date scattered outcrops in the Pliocene of south and central California. *The Western Society of Malacologists, Annual Report* 41:36.

Purdy RW. 1996. Paleoecology of fossil white sharks. In: Klimley AP, and Ainley DG, eds. *Great White Sharks: The Biology of Carcharodon carcharias*. San Diego: Academic press, 67-78.

Purdy RW, Schneider VP, Applegate SP, McLellan JH, Meyer RL, and Slaughter BH. 2001. The Neogene sharks, rays, and bony fishes from Lee Creek Mine, Aurora, North Carolina. *Smithsonian Contributions to Paleobiology* 90:71-202.

Ransom JE. 1964. *Fossils in America*. New York: Harper and Row.

Repenning CA, and Tedford RH. 1977. Otarioid seals of the Neogene. *US Geological Survey Professional Paper* 992:1-87.

Roux C, and Geistdoerfer P. 1988. Dents de requins et bulles tympaniques de cétacés: noyaux de nodules polymétalliques récoltés dans l'océan Indien. *Cybium* 12:129-137.

Seret B. 1987. Découverte d'une faune à *Procarcharodon megalodon* (Agassiz, 1835) en Nouvelle-Calédonie (Pisces, Chondrichthyes, Lamnidae). *Cybium* 11:389-394.

Shimada K, Chandler RM, Lam OLT, Tanaka T, and Ward DJ. 2017. A new elusive otodontid shark (Lamniformes: Otodontidae) from the lower Miocene, and comments on the taxonomy of otodontid genera, including the 'megatoothed' clade. *Historical Biology* 29:704-714.

Squires RL. 2012. Late Pliocene megafossils of the Pico Formation, Newhall area, Los Angeles County, Southern California. *Los Angeles County Museum Contributions in Science* 520:73-93.

Tedford RH, Albright LB, III,, Barnosky AD, Ferrusquia-Villafranca H, R.M. Jr., Swisher CC, III,, Voorhies MR, Webb SD, and Whistler DP. 2004. Mammalian biochronology of the Arikareean through Hemphillian interval (Late Oligocene through Early Pliocene epochs). In: Woodburne MO, ed. *Late Cretaceous and Cenozoic Mammals of North*

America: Biostratigraphy and Geochronology. New York: Columbia University Press, 169-231.

Tschernezky W. 1959. Age of *Carcharodon megalodon*? *Nature* 184:1331-1332.

Vedder JG. 1972. Review of stratigraphic names and megafaunal correlation of Pliocene rocks along the southeast margin of the Los Angeles basin, California. In: Stinemeyer EH, ed. *Proceedings of the Pacific Coast Miocene Biostratigraphic Symposium*. Los Angeles, California: Society of Economic Paleontologists and Mineralogists, Pacific Section, 158-172.

Vedder JG, Yerkes RF, and Schoellhamer JE. 1957. Geologic map of the San Joaquin Hills-San Juan Capistrano area, Orange County, California. US Geological Survey Oil and Gas Investigation Map.

Vendrasco MJ, Eernisse DJ, Powell CL, II, and Fernandez CZ. 2012. Polyplacophora (Mollusca) from the San Diego Formation: a remarkable assemblage of fossil chitons from the Pliocene of Southern California. *Los Angeles County Museum Contributions in Science* 520:15-72.

Wagner HM, Riney BO, Deméré TA, and Prothero DR. 2001. Magnetic stratigraphy and land mammal biochronology of a nonmarine facies of the Pliocene San Diego Formation, San Diego County, California. *SEPM Pacific Section Book* 91:359-368.

Walsh SA, and Hume JP. 2001. A new Neogene marine avian assemblage from north-central Chile. *Journal of Vertebrate Paleontology* 21:484-491.

Walsh SA, and Naish D. 2002. Fossil seals from late Neogene deposits in South America: a new pinniped (Carnivora, Mammalia) assemblage from Chile. *Palaeontology* 45:821-842.

Wara MW, Ravelo AC, and Delaney ML. 2005. Permanent El Nino-like conditions during the Pliocene warm period. *Science* 309:758-761.

Ward DJ, and Bonavia CG. 2001. Additions to, and a review of, the Miocene shark and ray fauna of Malta. *Central Mediterranean Naturalist* 3:131-146.

Ward LW. 2008. Synthesis of paleontological and stratigraphic investigations at the Lee Creek Mine, Aurora, N.C. *Virginia Museum of Natural History Special Publication* 14:325-436.

Warheit KI. 1992. A review of the fossil seabirds from the Tertiary of the north Pacific: plate tectonics, paleoceanography, and faunal change. *Paleobiology* 18:401-424.

Welton BJ. 1979. Late Cretaceous and Cenozoic Squalomorphii of the Northwest Pacific Ocean Ph.D. University of California.

Whitmore FC. 1994. Neogene climatic change and the emergence of the modern whale fauna of the North Atlantic Ocean. *Proceedings of the San Diego Society of Natural History* 29:223-227.

Whitmore FC, and Barnes LG. 2008. The Herpetocetinae, a new subfamily of extinct baleen whales (Mammalia, Cetacea, Cetotheriidae). *Virginia Museum of Natural History Special Publication* 14:141-180.

Wilson EC. 1985. The spiral trace fossil *Gyrolithes* de Saporta, 1884 in the Pliocene Tirabuzon Formation near Santa Rosalia, Baja California Sur, Mexico. *Bulletin of the Southern California Academy of Science* 84:57-66.

Wilson EC, and Bing DE. 1970. Type specimens of fossil Invertebrata in the Los Angeles County Museum of Natural History, exclusive of Paleoentomology. *Los Angeles County Museum Contributions in Science* 181:1-20.

Woodring WP, Bramlette MN, and Kew WSW. 1946. Geology and Paleontology of Palos Verdes Hills, California. *US Geological Survey Professional Paper* 207:1-145.

Yabe H, Goto M, and Kaneko N. 2004. Age of *Carcharocles megalodon*: a review of the stratigraphic records. *Fossils* 75:7-15.

Yabumoto Y, and Uyeno T. 1995. Late Mesozoic and Cenozoic fish faunas of Japan. *The Island Arc* 3:255-269.

Zachos J, Pagani M, Sloan L, Thomas E, and Billups K. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* 292:686-693.

Zalasiewicz JA, Mathers SJ, Hughes MJ, Gibbard P, Peglar SM, Harland R, Nicholson RA, Boulton GS, Cambridge P, and Wealthall GP. 1988. Stratigraphy and paleoenvironments of the Red Crag and Norwich Crag Formations between Aldeburgh and Sizewell, Suffolk, England. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences* 322:221-272.

Zeigler CV, Chan GL, and Barnes Lg. 1997. A new late Miocene balaenopterid whale (Cetacea: Mysticeti), *Parabalaenoptera baulinensis*, (new genus and species) from the Santa Cruz Mudstone, Point Reyes Peninsula, California. *Proceedings of the California Academy of Sciences* 50:115-138.

Zhelezko V, and Kozlov V. 1999. Elasmobranchii and Palaeogene biostratigraphy of Transurals and Central Asia. *Materials on Stratigraphy and Palaeontology of the Urals* 3:1-324.

Figure 1. Map of California and Baja California showing genuine late Miocene and Early Pliocene records of *Otodus megalodon*, and dubious Late Pliocene and Pleistocene records.

Figure 2. *Otodus megalodon* teeth from the Capistrano Formation. SDNHM 53167 in lingual (a) and labial (b) view; LACM 129982 in lingual (c) and labial (d) view; LACM 59837 in lingual (e) and labial (f) view; LACM 115989 in lingual (g) and labial (h) view; LACM 59836 in lingual (i) and labial (j) view.

Figure 3. *Otodus megalodon* teeth from the Fernando Formation. LACM 148312 in lingual (a) and labial (b) view; LACM 148311 in lingual (a) and labial (b) view.

Figure 4. *Otodus megalodon* tooth from the Niguel Formation. LACM 59065 in lingual (a) and labial (b) view.

Figure 5. *Otodus megalodon* tooth from the Purisima Formation. UCMP 219502 in lingual (a) and labial (b) view.

Figure 6. *Otodus megalodon* teeth from the San Diego Formation. SDNHM 29742 in lingual (a) and labial (b) view; LACM 156334 in lingual (c) and labial (d) view; LACM 10152 in lingual (e) and labial (f) view; LACM 103448 in lingual (g) and labial (h) view.

Figure 7. *Otodus megalodon* teeth from the San Mateo Formation. LACM 131149 in lingual (a) and labial (b) view; SDNHM 24448 in lingual (c) and labial (d) view; SDNHM 23959 in lingual (e) and labial (f) view; SDNHM 77343 in lingual (g) and labial (h) view; SDNHM 23959 in lingual (i) and labial (j) view; SDNHM 23959 in lingual (k) and labial (l) view; SDNHM 23959 in lingual (m) and labial (n) view.

Figure 8. *Otodus megalodon* teeth from the Tirabuzón Formation. LACM 29067 in lingual (a) and labial (b) view; LACM 29064 in lingual (c) and labial (d) view; LACM 29077 in lingual (e) and labial (f) view; LACM 29076 in lingual (g) and labial (h) view; LACM 29065 in lingual (i) and labial (j) view; LACM 29074 in lingual (k) and labial (l) view; LACM 29069 in lingual (m) and labial (n) view; LACM 29073 in lingual (o and labial (p) view; LACM 29075 in lingual (q) and labial (r) view; LACM 29072 in lingual (s) and labial (t) view.

Figure 9. *Otodus megalodon* teeth of purported Pleistocene age. LACM 159028 in lingual (a) and labial (b) view, supposedly from Palos Verdes Sand; LACM 10141 in lingual (c) and labial (d) view, supposedly from unnamed strata at Newport Bay Mesa.

Figure 10. Geochronologic age range of *Otodus megalodon*-bearing strata and occurrences in the eastern North Pacific. Age control of latest Miocene and Pliocene *O. megalodon*-bearing stratigraphic units represented by thick vertical gray bars. Stratigraphic range of autochthonous and parautochthonous *Otodus megalodon* occurrences (allochthonous records excluded) depicted as thin vertical black bars. Abbreviations: NALMA, North American Land Mammal Age.

Figure 1

Figure 1. Map of California and Baja California showing genuine late Miocene and Early Pliocene records of *Otodus megalodon*, and dubious Late Pliocene and Pleistocene records.

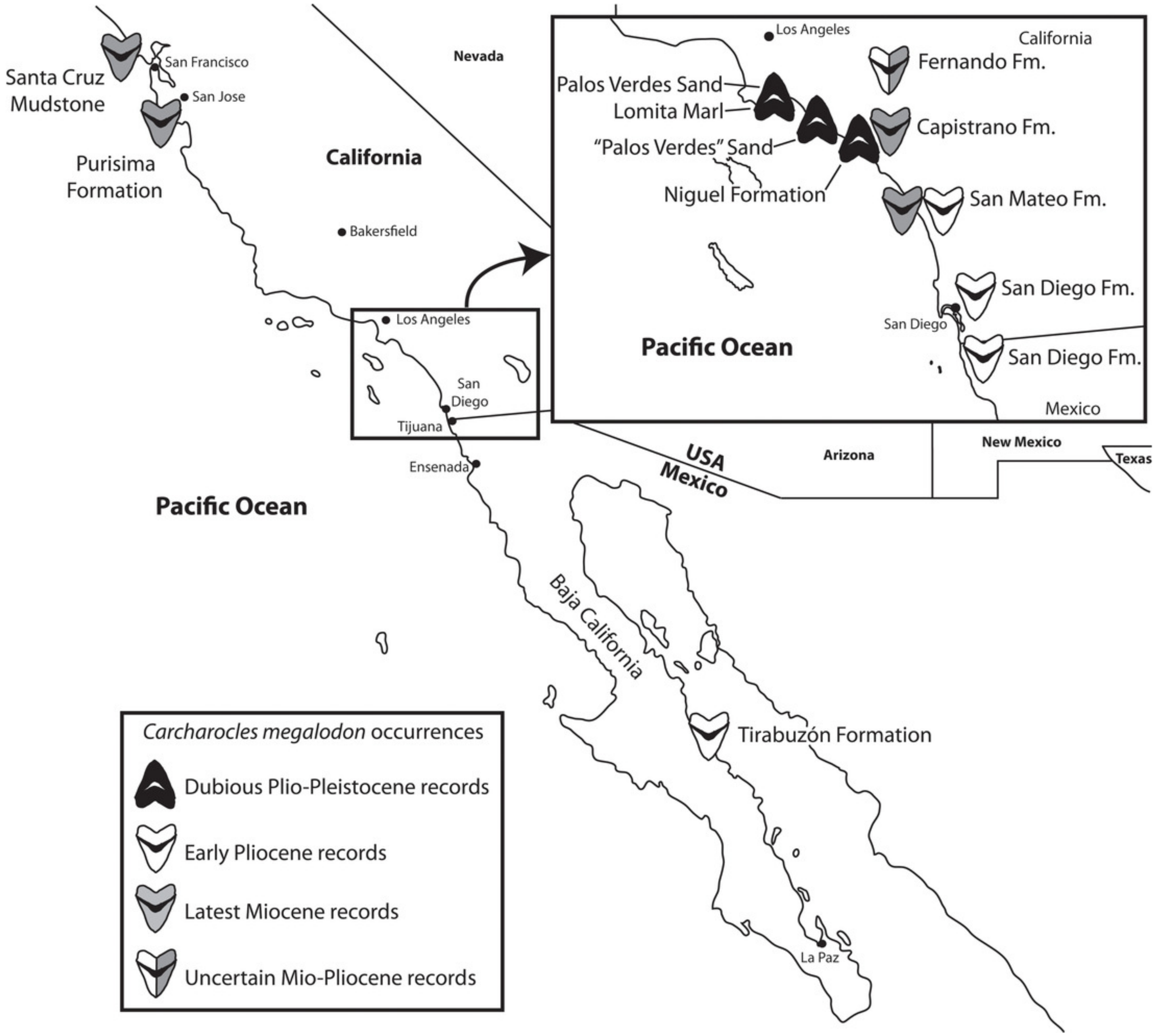

Figure 2

Otodus megalodon teeth from the Capistrano Formation.

SDNHM 53167 in lingual (a) and labial (b) view; LACM 129982 in lingual (c) and labial (d) view; LACM 59837 in lingual (e) and labial (f) view; LACM 115989 in lingual (g) and labial (h) view; LACM 59836 in lingual (i) and labial (j) view.

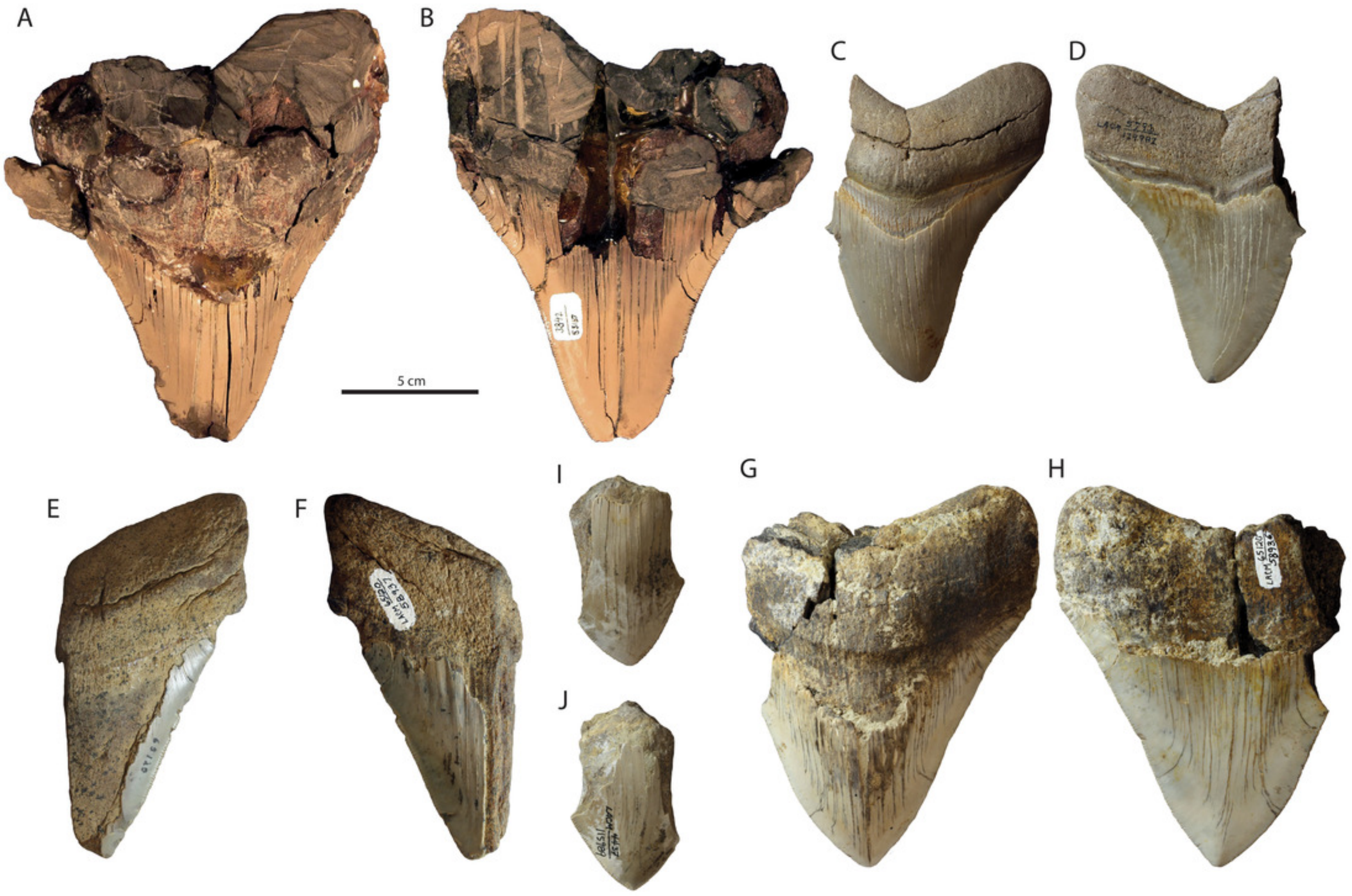

Figure 3

Otodus megalodon teeth from the Fernando Formation.

LACM 148312 in lingual (a) and labial (b) view; LACM 148311 in lingual (a) and labial (b) view.

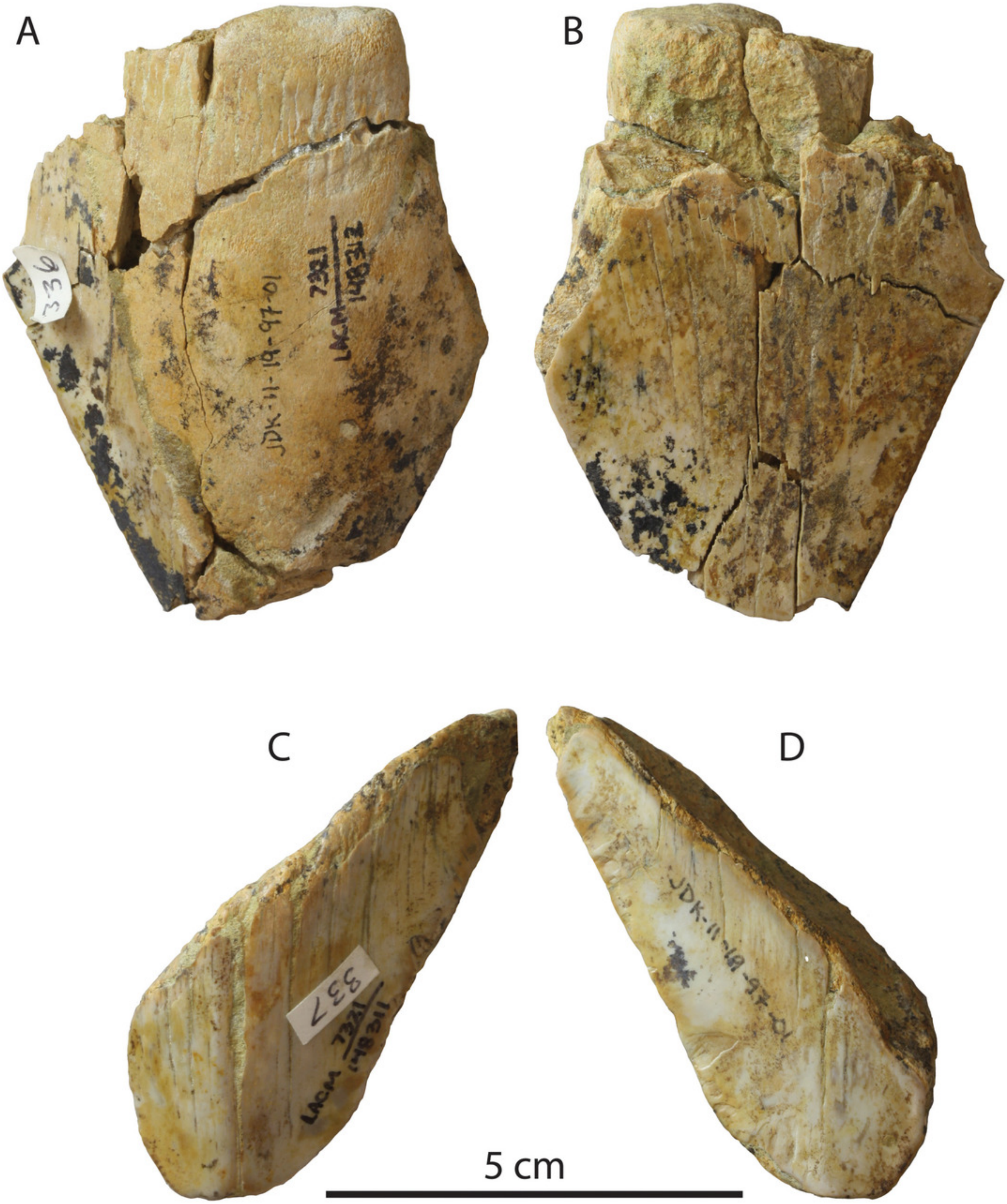
A
B
C
D
5 cm
336
JDK-11-19-97-01
LACM 7321 148312
337

Figure 4

Otodus megalodon tooth from the Niguel Formation.

LACM 59065 in lingual (a) and labial (b) view.

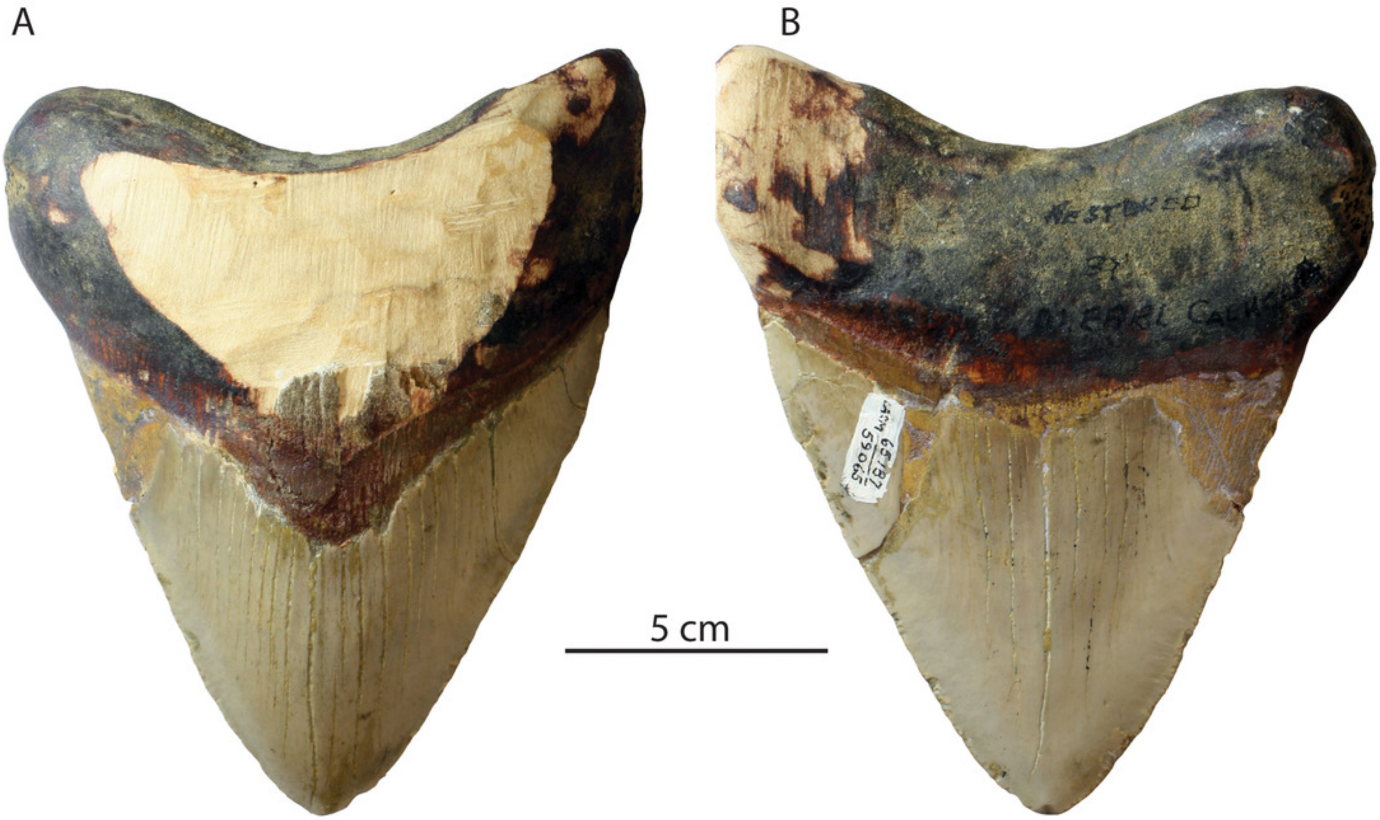

Figure 5

Otodus megalodon tooth from the Purisima Formation.

UCMP 219502 in lingual (a) and labial (b) view.

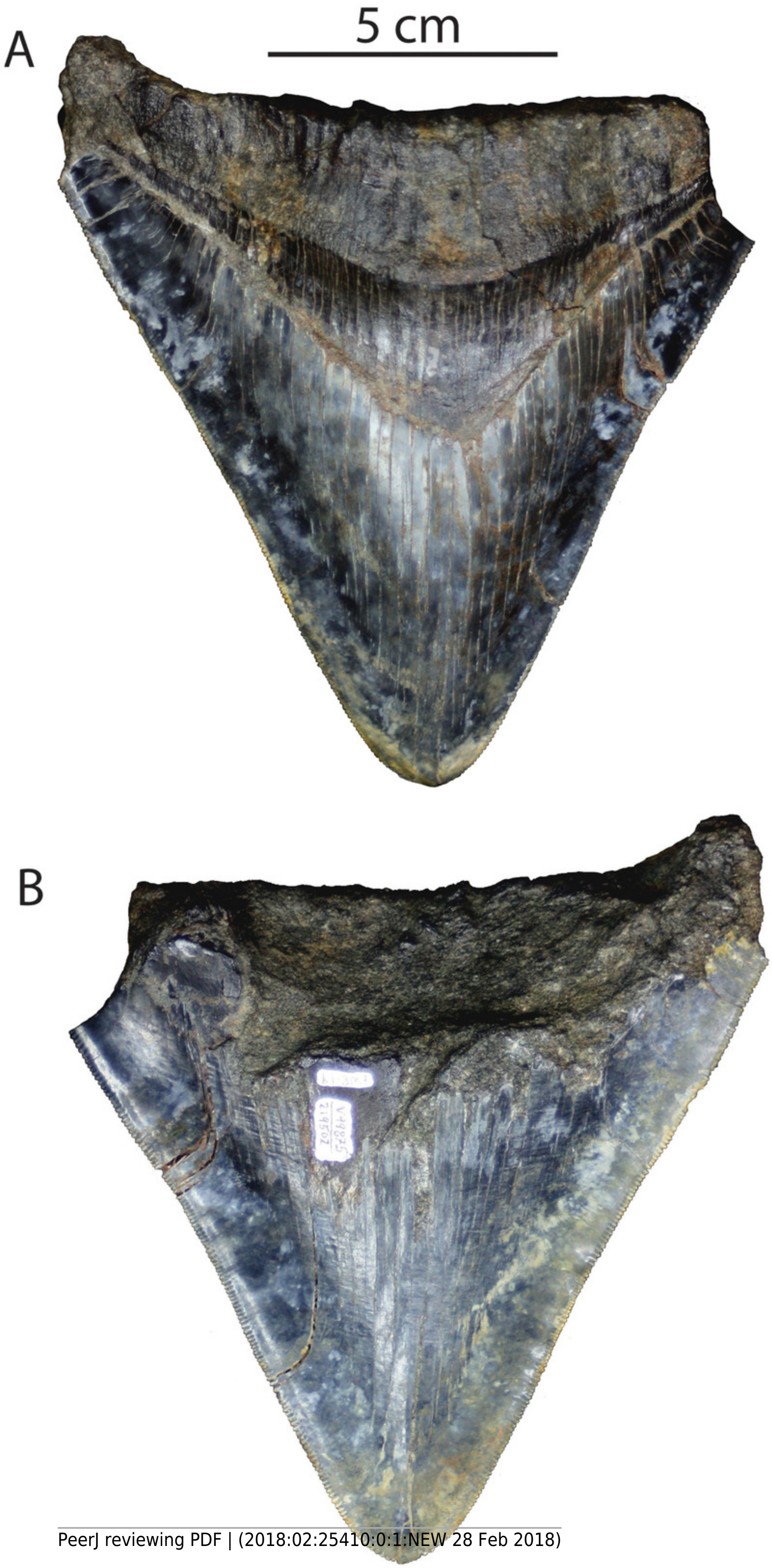
A
5 cm
B
V49875
219502

Figure 6

Otodus megalodon teeth from the San Diego Formation.

SDNHM 29742 in lingual (a) and labial (b) view; LACM 156334 in lingual (c) and labial (d) view; LACM 10152 in lingual (e) and labial (f) view; LACM 103448 in lingual (g) and labial (h) view.

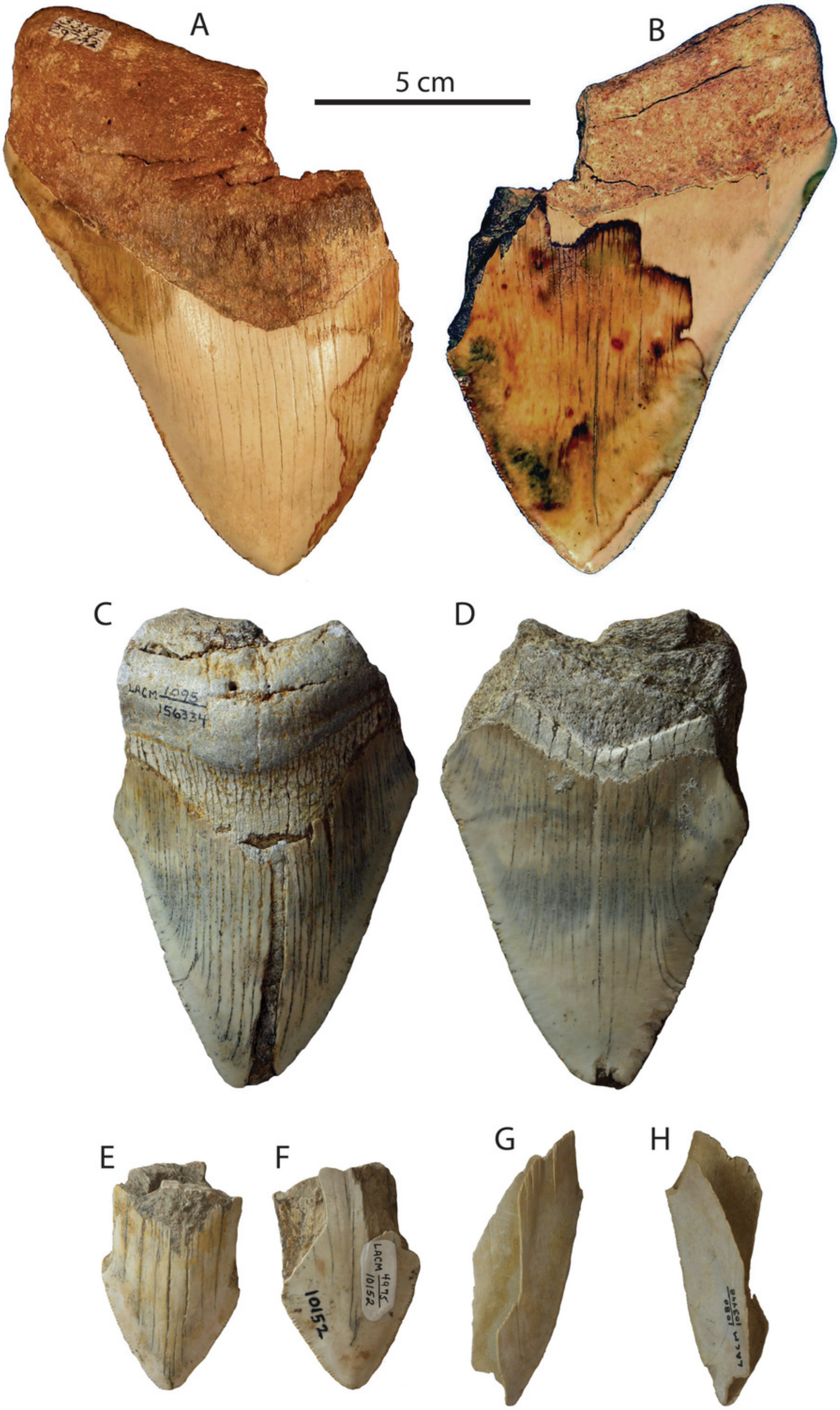
A
B
5 cm
C
D
LACM 1095
156334
E
F
G
H
LACM 4975
10152
10152
LACM 1080
103448

Figure 7

Otodus megalodon teeth from the San Mateo Formation.

LACM 131149 in lingual (a) and labial (b) view; SDNHM 24448 in lingual (c) and labial (d) view; SDNHM 23959 in lingual (e) and labial (f) view; SDNHM 77343 in lingual (g) and labial (h) view; SDNHM 23959 in lingual (i) and labial (j) view; SDNHM 23959 in lingual (k) and labial (l) view; SDNHM 23959 in lingual (m) and labial (n) view.

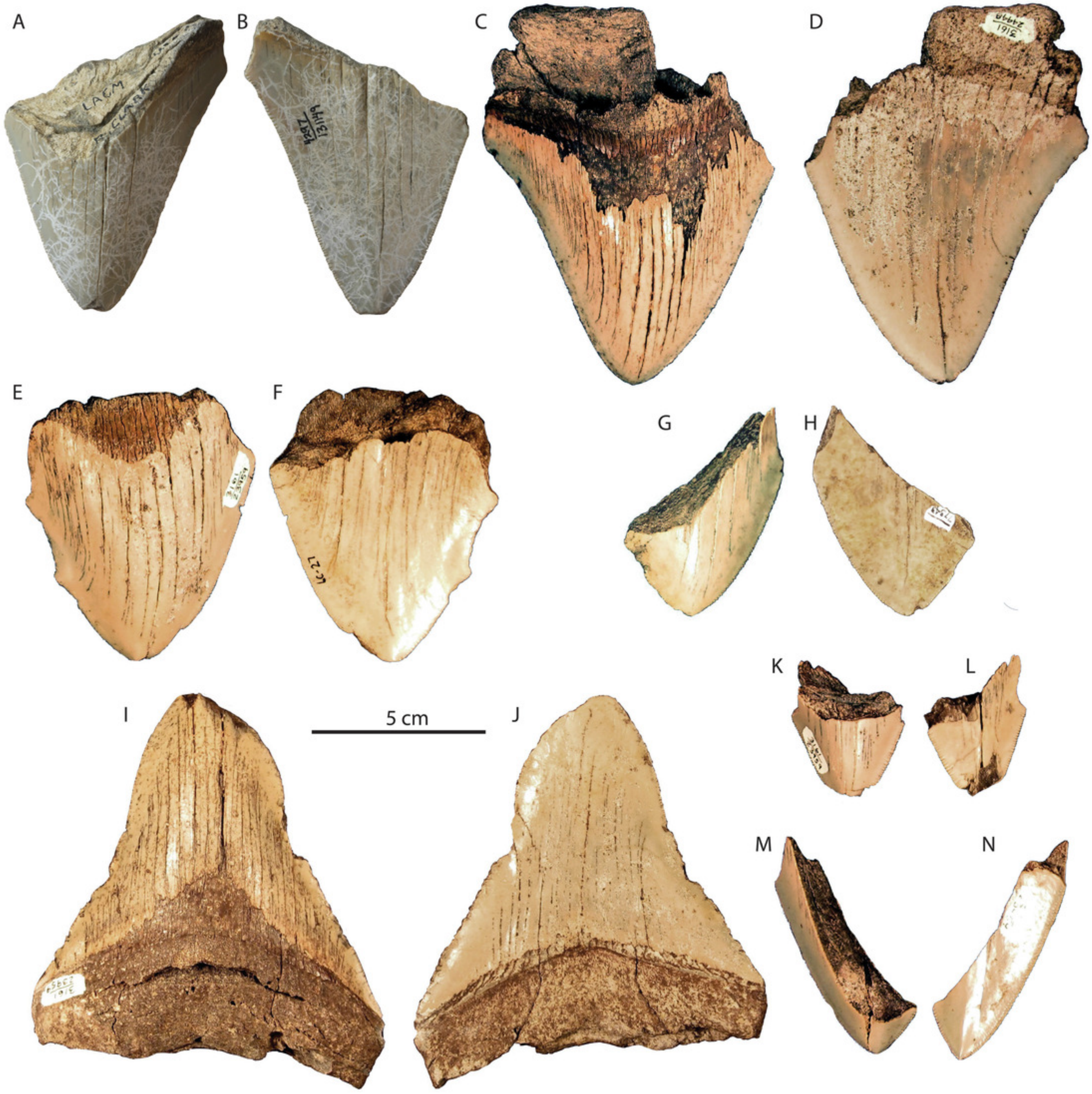
A
B
C
D
E
F
G
H
K
L
I
5 cm
J
M
N

Figure 8

Otodus megalodon teeth from the Tirabuzón Formation.

LACM 29067 in lingual (a) and labial (b) view; LACM 29064 in lingual (c) and labial (d) view; LACM 29077 in lingual (e) and labial (f) view; LACM 29076 in lingual (g) and labial (h) view; LACM 29065 in lingual (i) and labial (j) view; LACM 29074 in lingual (k) and labial (l) view; LACM 29069 in lingual (m) and labial (n) view; LACM 29073 in lingual (o and labial (p) view; LACM 29075 in lingual (q) and labial (r) view; LACM 29072 in lingual (s) and labial (t) view.

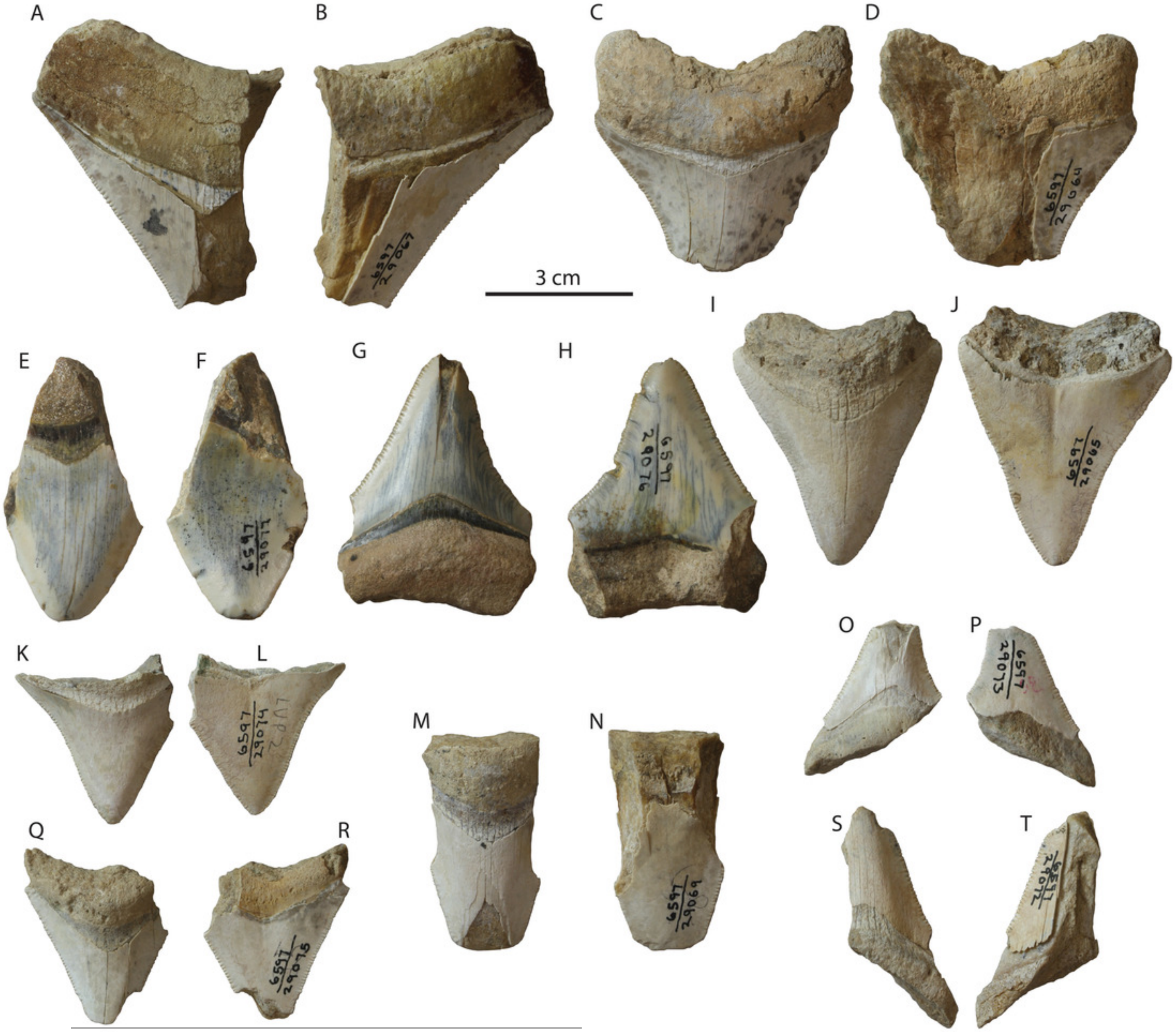

Figure 9

Otodus megalodon teeth of purported Pleistocene age.

LACM 159028 in lingual (a) and labial (b) view, supposedly from Palos Verdes Sand; LACM 10141 in lingual (c) and labial (d) view, supposedly from unnamed strata at Newport Bay Mesa.

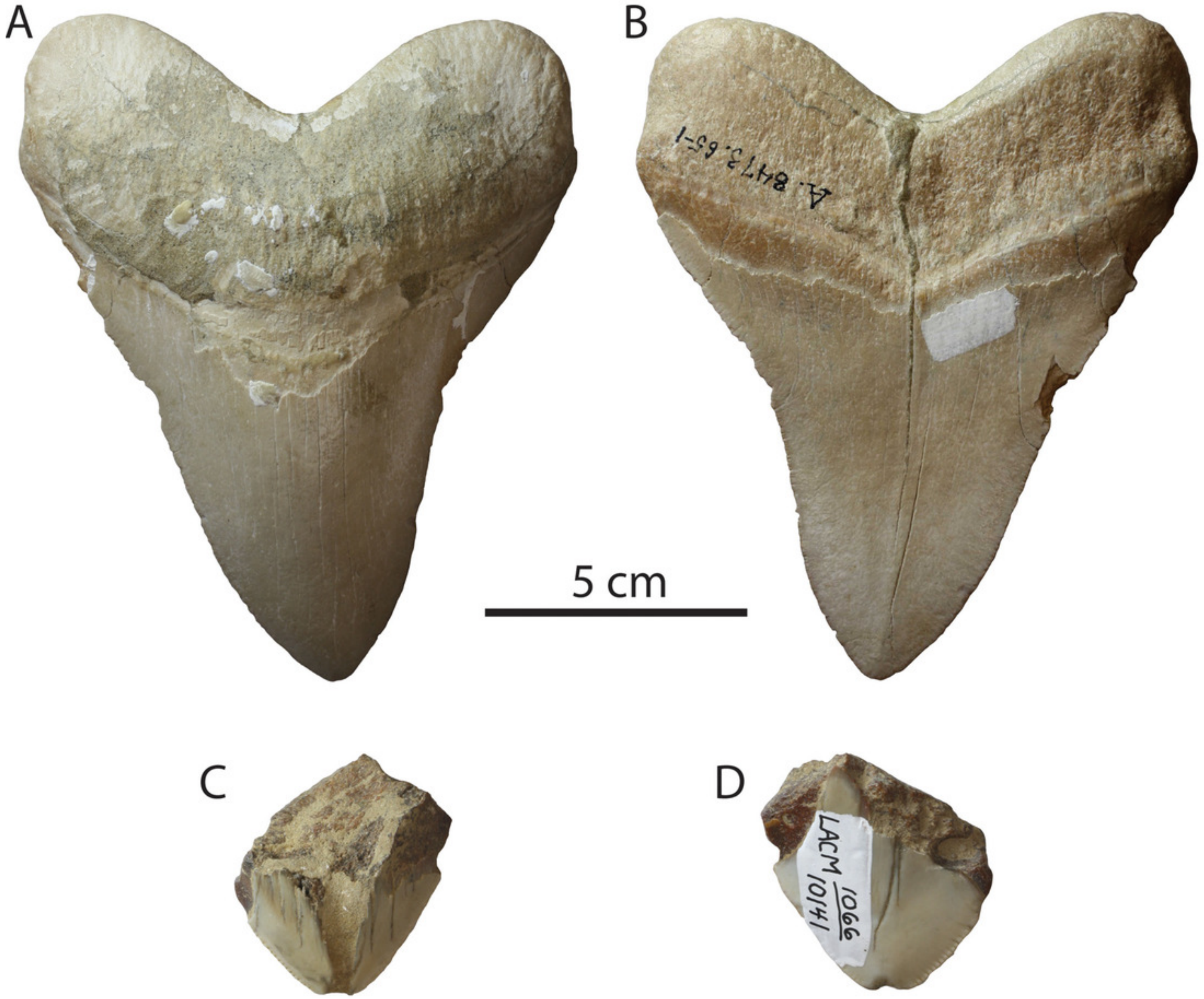

Figure 10

Geochronologic age range of *Otodus megalodon*-bearing strata and occurrences in the eastern North Pacific.

Age control of latest Miocene and Pliocene *O. megalodon*-bearing stratigraphic units represented by thick vertical gray bars. Stratigraphic range of autochthonous and parautochthonous *Otodus megalodon* occurrences (allochthonous records excluded) depicted as thin vertical black bars. Abbreviations: NALMA, North American Land Mammal Age.

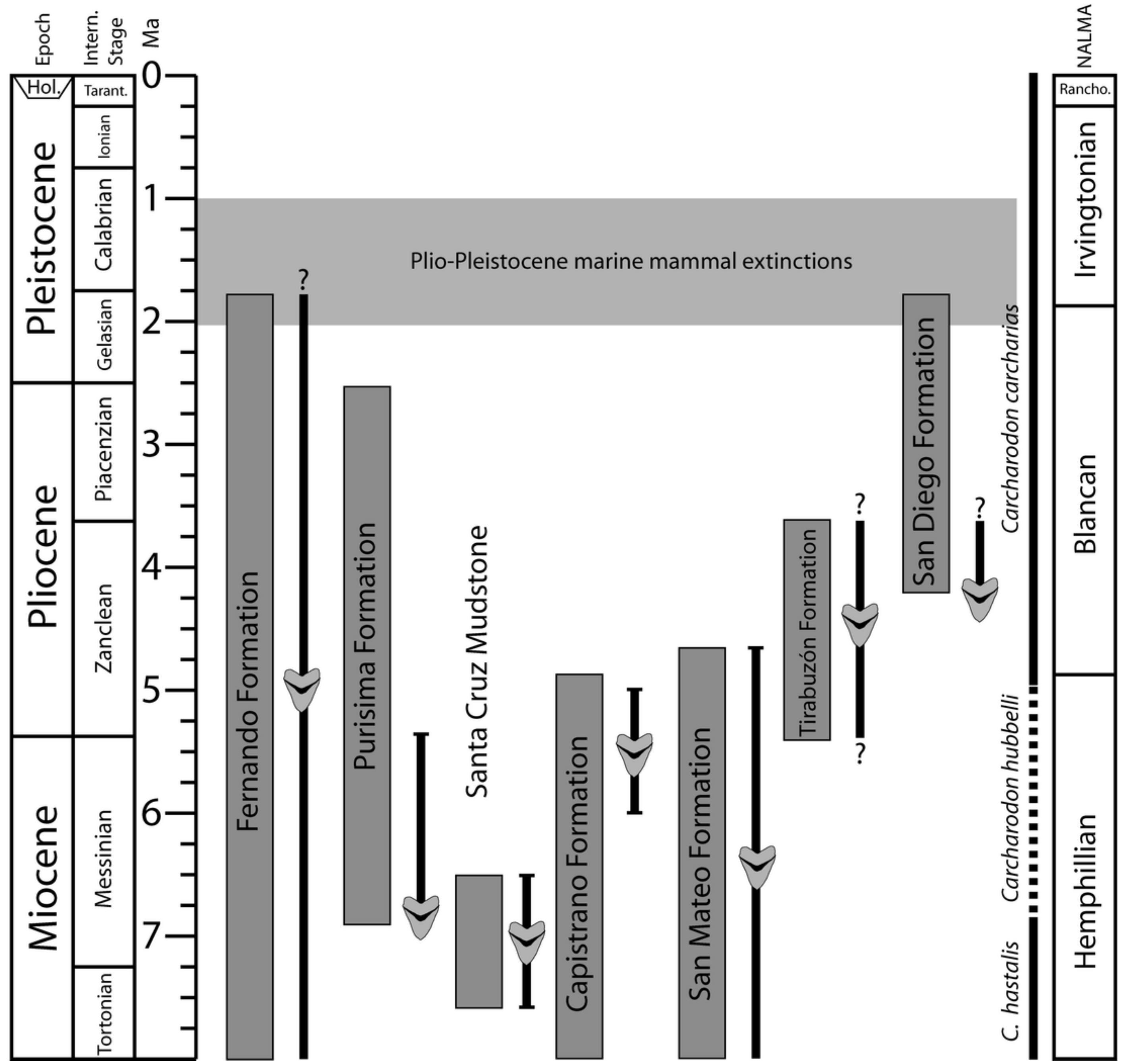
Epoch
Intern. Stage
Ma
NALMA
Hol.
Tarant.
Ionian
Calabrian
Gelasian
Piacenzian
Zanclean
Messinian
Tortonian
Pleistocene
Pliocene
Miocene
0
1
2
3
4
5
6
7
Plio-Pleistocene marine mammal extinctions
Fernando Formation
Purisima Formation
Santa Cruz Mudstone
Capistrano Formation
San Mateo Formation
Tirabuzón Formation
San Diego Formation
?
C. hastalis
Carcharodon hubbelli
Carcharodon carcharias
Rancho.
Irvingtonian
Blancan
Hemphillian

Table 1(on next page)

Table 1. Measurements (in mm), age, and occurrence of *Otodus megalodon* teeth examined during this study.

Measurements after Pimiento et al. (2010). Asterisks (*) denote incomplete measurements; specimens without measurements are incomplete tooth fragments. Note that SDMHN 23959 consists of four partial teeth; a measurement is provided for the only tooth complete enough to measure.

Table 1. Measurements (in mm), age, and occurrence of *Otodus megalodon* teeth examined during this study. Measurements after Pimiento et al. (2010). Asterisks (*) denote incomplete measurements; specimens without measurements are incomplete tooth fragments. Note that SDMHN 23959 consists of four partial teeth; a measurement is provided for the only tooth complete enough to measure.

Specimen	Formation	Age	Occurrence	Crown width	Crown height
LACM 29064	Tirabuzón Fm.	Zanclean, 5.33-3.6 Ma	Autochthonous	48.55	-
LACM 29065	Tirabuzón Fm.	Zanclean, 5.33-3.6 Ma	Autochthonous	42.9	45.1
LACM 29066	Tirabuzón Fm.	Zanclean, 5.33-3.6 Ma	Autochthonous	-	-
LACM 29067	Tirabuzón Fm.	Zanclean, 5.33-3.6 Ma	Autochthonous	-	-
LACM 29069	Tirabuzón Fm.	Zanclean, 5.33-3.6 Ma	Autochthonous	-	-
LACM 29070	Tirabuzón Fm.	Zanclean, 5.33-3.6 Ma	Autochthonous	-	-
LACM 29071	Tirabuzón Fm.	Zanclean, 5.33-3.6 Ma	Autochthonous	-	-
LACM 29072	Tirabuzón Fm.	Zanclean, 5.33-3.6 Ma	Autochthonous	-	-
LACM 29073	Tirabuzón Fm.	Zanclean, 5.33-3.6 Ma	Autochthonous	22.3*	18.15*
LACM 29074	Tirabuzón Fm.	Zanclean, 5.33-3.6 Ma	Autochthonous	31.7	32.45
LACM 29075	Tirabuzón Fm.	Zanclean, 5.33-3.6 Ma	Autochthonous	28.3*	29.5*
LACM 29076	Tirabuzón	Zanclean,	Autochthonous	33.4	36.75

	Fm.	5.33-3.6 Ma			
LACM 29077	Tirabuzón Fm.	Zanclean, 5.33-3.6 Ma	Autochthonous	-	-
LACM 29078	Tirabuzón Fm.	Zanclean, 5.33-3.6 Ma	Autochthonous	-	-
LACM 10141	“Palos Verdes” Ss.	Pleistocene	Poor provenance	-	-
LACM 10152	San Diego Fm.	Pliocene	Autochthonous	-	-
LACM 103448	San Diego Fm.	Pliocene	Autochthonous	-	-
LACM 115989	Capistrano Fm.	Messinian-Zanclean, 5.6-3.7 Ma	Autochthonous	-	-
LACM 129982	Capistrano Fm.	Messinian-Zanclean	Autochthonous	-	-
LACM 131149	San Mateo Fm.	Zanclean, 5.33-4.6 Ma	Autochthonous or parautochthonous	57.6*	73.8
LACM 148311	Fernando Fm.	Pliocene-Pleistocene	Autochthonous	-	-
LACM 148312	Fernando Fm.	Pliocene-Pleistocene	Autochthonous	57.1*	-
LACM 156334	San Diego Fm.	Pliocene	Autochthonous	67.5	-
LACM 159028	Palos Verdes Ss.	Pleistocene	Poor provenance	101.5	97.1
SDNHM 23056	San Mateo Fm.	Zanclean, 5.33-4.6 Ma	Autochthonous or parautochthonous	-	-
SDNHM 23959	San Mateo Fm.	Zanclean, 5.33-4.6 Ma	Autochthonous or parautochthonous	90.07	82.6
SDNHM 24448	San Mateo Fm.	Zanclean, 5.33-4.6 Ma	Autochthonous or parautochthonous	77.39*	74.1
SDNHM 29742	San Diego Fm.	Zanclean, ~4.2 Ma	Autochthonous or parautochthonous	86.71*	96.89
SDNHM 53167	Capistrano Fm.	Messinian-Zanclean, 5.6-3.7 Ma	Autochthonous	103.86	89.83
SDNHM	Niguel Fm.	Pliocene	Allochthonous	-	-

73462					
SDNHM 77343	San Mateo Fm.	Zanclean, 5.33-4.6 Ma	Autochthonous or parautochthonous	-	-
SDNHM 77430	San Mateo Fm.	Zanclean, 5.33-4.6 Ma	Autochthonous or parautochthonous	27.53	23.82
UCMP 219502	Purisima Fm.	Messinian, 6.9-5.33 Ma	Autochthonous or parautochthonous	114.1*	112.2