PaleoBios 33:1-7, August 16, 2016

PaleoBios

OFFICIAL PUBLICATION OF THE UNIVERSITY OF CALIFORNIA MUSEUM OF PALEONTOLOGY

Boessenecker, Robert W. (2016). First record of the megatoothed shark *Carcharocles megalodon* from the Mio-Pliocene Purisima Formation of Northern California.

Cover photo: The only known specimen of the megatoothed shark *Carcharocles megalodon* from the basal Purisima Formation (late Miocene) near Santa Cruz, California.

Citation: Boessenecker, Robert W. 2016. First record of the megatoothed shark Carcharocles megalodon from the Mio-Pliocene Purisima Formation of Northern California. *PaleoBios,* 33. ucmp_*paleobios*_32076

First record of the megatoothed shark *Carcharocles megalodon* from the Mio-Pliocene Purisima Formation of Northern California

ROBERT W. BOESSENECKER[1,2]
[1]Department of Geology and Environmental Geosciences, College of Charleston, Charleston, SC 29424; boesseneckerrw@cofc.edu
[2]University of California Museum of Paleontology, University of California, Berkeley, CA 94720

Megatoothed sharks (Family: Otodontidae) are among the most widely reported sharks in Cenozoic marine sediments worldwide, and certain species such as the famed *Carcharocles megalodon* are particularly abundant in Neogene deposits on the Atlantic margin of the United States. Cenozoic marine strata on the Pacific margin of North America have yielded one of the most densely sampled marine vertebrate records anywhere, but published occurrences of shark assemblages are uncommon. Rarer yet are published occurrences of *C. megalodon* from this region with unambiguous provenance and robust age control — critical data required for the study of recent marine vertebrate faunal evolution in the eastern North Pacific. A tooth of *C. megalodon* from near Santa Cruz, California, represents the first record of this species from the Purisima Formation and the geochronologically youngest occurrence (6.9–5.6 Ma, uppermost Miocene; late Messinian) of this species from northern California.

Keywords: Purisima Formation, Santa Cruz, California, Miocene, Otodontidae, *Carcharocles megalodon*

INTRODUCTION

Neogene marine rocks along the California coast have yielded large assemblages of marine vertebrates from stratigraphically separated localities, chronicling patterns of faunal change over the past 20 million years (Barnes 1977, Boessenecker 2011, 2013, Warheit 1992). Although generally less numerically abundant than in contemporaneous strata on the Atlantic coastal plain (e.g. Calvert, Pungo river, Yorktown, Bone Valley formations), teeth, vertebrae, and other elements of sharks and rays are commonly found in fossiliferous Miocene and Pliocene marine strata in California and are extremely abundant at some localities like the middle Miocene Sharktooth Hill bonebed (Jordan and Hannibal 1923, Mitchell 1965) and the basal gravels of the upper Miocene Santa Margarita Sandstone (Clark 1981, Perry 1993). Despite such a well-sampled fossil record consisting of dozens of taxonomically-rich shark assemblages, few have been published in the literature. A notable exception is the Sharktooth Hill Bonebed (Jordan and Hannibal 1923, Mitchell 1965, Welton 2014), but even this most well-documented shark assemblage in California is largely undescribed (Welton 2014:29).

The timing of major events in recent marine faunal history such as the appearance and evolutionary origin of the modern great white shark *Carcharodon carcharias* Linnaeus, 1758 and the extinction of the megatoothed shark *Carcharocles megalodon* Agassiz, 1843 have been the focus of recent research (Ehret et al. 2012, Pimiento and Clements 2014). Published reports of these sharks with robust stratigraphic provenance and age determinations are rare in the California Neogene but nonetheless imperative for studies relying on such data. This study reports a new well-dated specimen of *C. megalodon* from the Purisima Formation near Santa Cruz in Northern California. The shark assemblage from the San Gregorio section of the Purisima Formation near Halfmoon Bay, California, has been described in its entirety (Boessenecker 2011) but the larger sample from the Santa Cruz section of the Purisima Formation near Santa Cruz is largely unpublished.

METHODS

This study follows the classification of Cappetta (1987) with *Carcharocles megalodon* within the genus *Carcharocles* and family Otodontidae; see Purdy et al. (2001) and Cappetta (2012) for alternative taxonomic frameworks.

Institutional Abbreviations: **UCMP**, University of California Museum of Paleontology, Berkeley, CA.

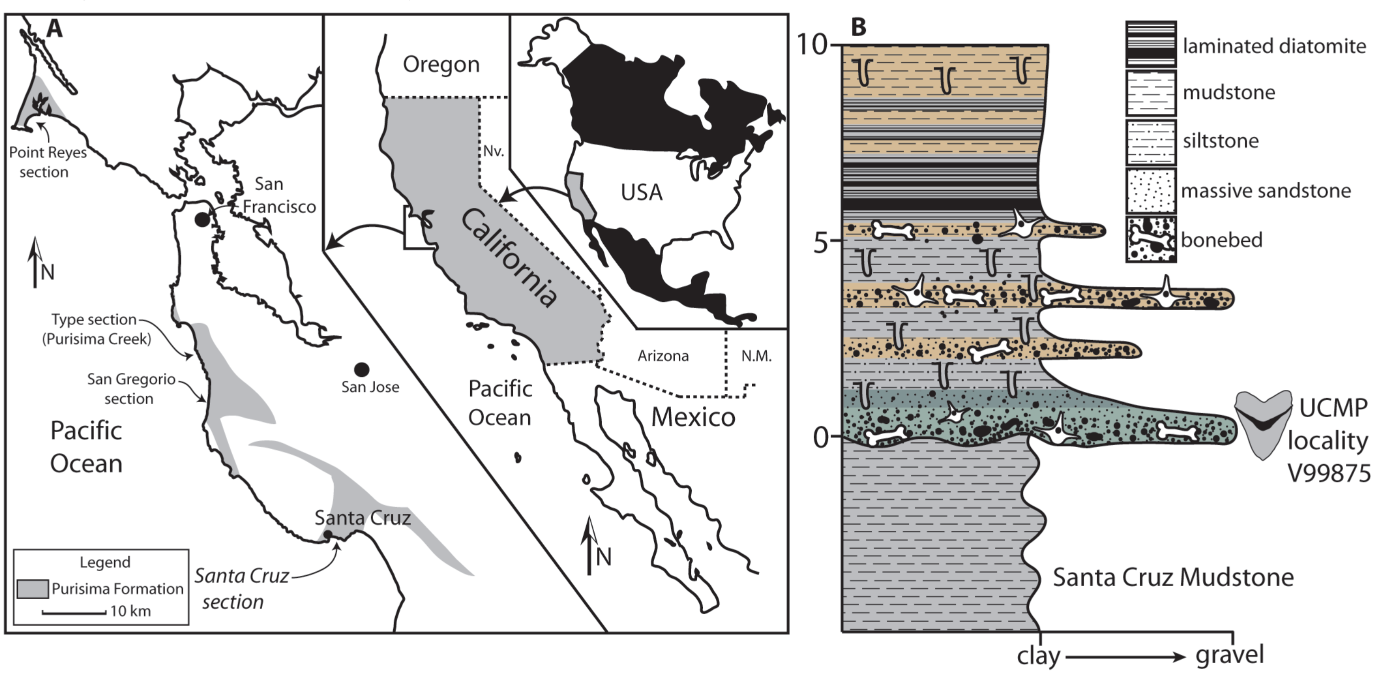
Citation: Boessenecker, Robert W. 2016. First record of the megatoothed shark *Carcharocles megalodon* from the Mio-Pliocene Purisima Formation of Northern California. *PaleoBios,* 33. ucmp_*paleobios*_32076
Permalink: http://escholarship.org/uc/item/0bs400v3

GEOLOGIC BACKGROUND

The Purisima Formation is a shallow marine unit of late Neogene age comprising a series of mostly unconsolidated sandstones and mudrocks with occasional conglomeratic bonebed lags and thick coquina shell beds exposed in the vicinity of Halfmoon Bay, Santa Cruz, and Point Reyes in northern California (Fig. 1A, B; Cummings et al. 1962, Clark 1981, Powell et al. 2007, Boessenecker et al. 2014). The Purisima Formation reflects deposition from nearshore and estuarine settings to offshore and the upper slope within one or more basins via wrench tectonics (Norris 1986, Dickinson et al. 1987, Powell et al. 2007, Boessenecker et al. 2014). The Purisima Formation is richly fossiliferous and has yielded an extensive micro- and macroinvertebrate assemblage including diatoms, foraminifera, mollusks, echinoderms, and crustaceans (Powell 1998, and references therein; Feldmann et al. 2015). A composite assemblage of 70+ types of vertebrates has been established for the Santa Cruz section of the Purisima Formation, including sharks, rays, skates, bony fish, sea birds, pinnipeds, odontocetes, mysticetes, and rare sirenians and land mammals; for a complete faunal list of fossil vertebrates from the Santa Cruz section of the Purisima Formation, see Boessenecker et al. (2014: table 1, and references therein).

A large tooth of *Carcharocles megalodon* (UCMP 219502) was collected from the basal bonebed of the Purisima Formation (Fig. 1B; UCMP locality V99875; =Bonebed 1 of Boessenecker et al. 2014) near Santa Cruz, California. In the vicinity of Santa Cruz, the Purisima Formation unconformably overlies the upper Miocene Santa Cruz Mudstone and the contact is marked by a sharp but irregular erosional surface with approximately 20 cm of relief (Clark 1981, Boessenecker et al. 2014). The basal ten meters of the Purisima Formation consists of massive sandstone grading up into sandy siltstones and diatomaceous siltstones, and eventually diatomite approximately five meters above the base; a second major bonebed containing abundant phosphatic nodules (=UCMP locality V99877 and Bonebed 2 of Boessenecker et al. 2014) punctuates pervasively bioturbated diatomaceous siltstones 3.5–4 meters above the basal unconformity. The basal bonebed lacks invertebrate fossils but contains abundant fragmented and lightly abraded vertebrate bones and teeth. *Gastrochaenolites* Leymerie, 1842 borings attributable to pholad clams occur on the erosional surface and within reworked porcelanitic clasts of the Santa Cruz Mudstone and indicate high energy conditions during bonebed formation. The basal 50 cm of the Purisima Formation here is richly glauconitic, indicating a period of slow or non-deposition (Boessenecker et al. 2014). This basal glauconite has yielded an K/Ar date of 6.9 ± 0.5 Ma (Madrid et al. 1986), and the depositional lacuna between the Purisima Formation and Santa Cruz Mudstone represents a period of 700–500 Ka based upon diatom biostratigraphy (Barron 1986). The uppermost strata of the Santa Cruz Mudstone include a diatom flora indicative of subzone A of the *Thalassiosira antiqua* zone (Barron 1986) corresponding to an age of 7.8–8.5 Ma

Figure 1. **A**. Index map of Purisima Formation exposures near Santa Cruz and San Francisco (modified from Powell et al. 2007 and Boessenecker 2013). **B**. Generalized stratigraphy of the basal ten meters of the Santa Cruz section of the Purisima Formation showing the position of UCMP locality V99875.



(Barron and Isaacs 2001). UCMP 219502 does not appear to be reworked from the underlying Santa Cruz Mudstone, as all adhering matrix consists of glauconitic sandstone matching the entombing lithology of the basal Purisima Formation. Only one vertebrate specimen (UCMP 236054, recently collected by A. Poust) from UCMP locality V99875 exhibits adhering porcelanitic siltstone indicating reworking from the Santa Cruz Mudstone. Nearly all vertebrates from this stratum — UCMP 219502 (*C. megalodon*) included – appear to date to the depositional hiatus, during which the glauconite dated to 6.9 Ma (Madrid et al. 1986) was formed. A maximum age of 6.9 Ma can be assigned to UCMP 219502. A minimum age is provided by an ash layer 30 m above the base of the Purisima Formation which has been correlated with tephra elsewhere in California dated to 5.6 to 5.0 Ma (Powell et al. 2007). The age of UCMP 219502 can thus be summarized as 6.9–5.6 Ma, latest Miocene (Messinian correlative). This contrasts with the incorrect age of 11.6–5.3 Ma assigned to this specimen without explanation by Pimiento and Balk (2015: supplementary dataset).

Other vertebrate fossils (Domning 1978, Repenning and Tedford 1977, Boessenecker 2013: appendix, Boessenecker et al. 2014: table 1) from the basal 10 meters of the Purisima Formation near Santa Cruz include sharks and rays (*Carcharodon hastalis* Agassiz, 1843, *Hexanchus* sp. Rafinesque, 1810, *Isurus oxyrinchus* Rafinesque, 1810, *Myliobatis* sp. Cuvier, 1816), bony fish (*Acipenser* sp. Linneaus, 1758, *Paralichthys californicus* Ayres, 1859), pinnipeds (*Thalassoleon macnallyae* Repenning and Tedford, 1977, *Dusignathus santacruzensis* Kellogg, 1927, cf. *Imagotaria* sp. Mitchell, 1968), odontocetes (Albireonidae indet., Delphinidae indet., *Parapontoporia wilsoni* Barnes, 1985, cf. *Piscolithax* sp. Muizon, 1983, Physeteroidea indet.), mysticetes (*Eubalaena* sp. Gray, 1864, *Nannocetus* sp. Kellogg, 1929, *"Megaptera" miocaena* Kellogg, 1922, cf. *Balaenoptera* sp. Lacépède, 1804) and a sea cow (*Dusisiren dewana* Takahashi et al., 1986).

SYSTEMATIC PALEONTOLOGY

CHONDRICHTHYES Huxley, 1880
LAMNIFORMES Berg, 1958
OTODONTIDAE Glikman, 1964
Carcharocles Jordan & Hannibal, 1923
Carcharocles megalodon Agassiz, 1843
Fig. 2A–C

Referred specimen—UCMP 219502, a single large tooth collected (December 23, 2007) and prepared by R.W. Boessenecker from UCMP locality V99875. Field number RWB 19.

Locality—UCMP locality V99875, basal bonebed of the Purisima Formation, Santa Cruz County, California. Detailed locality information available on request to qualified researchers from UCMP or the author.

Description—UCMP 219502 is a large symmetrical tooth (Fig. 2) measuring 112.2 mm in crown height, approximately 114 mm in crown width, and estimated to 150–160 mm in tooth height (crown and root) when complete, well within the upper size range of *Carcharocles megalodon* teeth (Purdy et al. 2001, Pimiento et al. 2010). Referral of UCMP 219502 to *C. megalodon* is unequivocally supported by the combination of 1) large size, 2) chevron-shaped band of thin enameloid present lingually at base of crown, and 3) regular fine serrations (10–14 serrations per 10mm). UCMP 219502 cannot unequivocally be shown to lack lateral cusplets owing to damage, but the geochronologically youngest megatoothed shark with lateral cusplets as an adult is *C. subauriculatus* Agassiz, 1843 (=*C. chubutensis* Ameghino, 1901) from the lower Miocene.

UCMP 219502 has a flattened labial face of the crown with a slight median bulge (Fig. 2C); the lingual face is convex and exhibits a well-preserved chevron-shaped dental band as in all Otodontidae. In mesial or distal view, the crown is faintly labially curved. In labial and lingual view the crown bears no distal inclination and thus the tooth is nearly symmetrical, precluding unequivocal identification of mesial or distal and hence whether UCMP 219502 is a right or left upper anterior tooth. One cutting edge is slightly more concave than the other and is tentatively identified as the distal cutting edge, therefore tentatively identifying the tooth as an upper left anterior. The large size and symmetrical shape of the crown further suggest identification of this tooth as one of the mesialmost upper anterior teeth (upper A2 *sensu* Purdy et al. 2001). The supposed distal cutting edge is pathologic and exhibits a subtle wavy edge along the apicobasal midpoint of the crown (Fig. 2C); a less-strongly developed wavy cutting edge is also present mesially. The root of UCMP 219502 is incomplete and completely missing labially; lingually the root is flattened and lacks a strongly convex lingual protuberance. The root lobes are completely missing, and the preserved portion of the root exhibits unabraded fracture edges, suggesting limited transport and sediment abrasion after initial fragmentation.

DISCUSSION AND CONCLUSIONS

UCMP 219502 represents the first record of *Carcharocles megalodon* from the Purisima Formation. The basal part of the Santa Cruz section of the Purisima Formation, consisting of UCMP localities V99875, V99876, and V99877 (=Bonebeds 1 and 2 of Boessenecker et al. 2014, and intervening strata) have yielded a meager shark assemblage, including

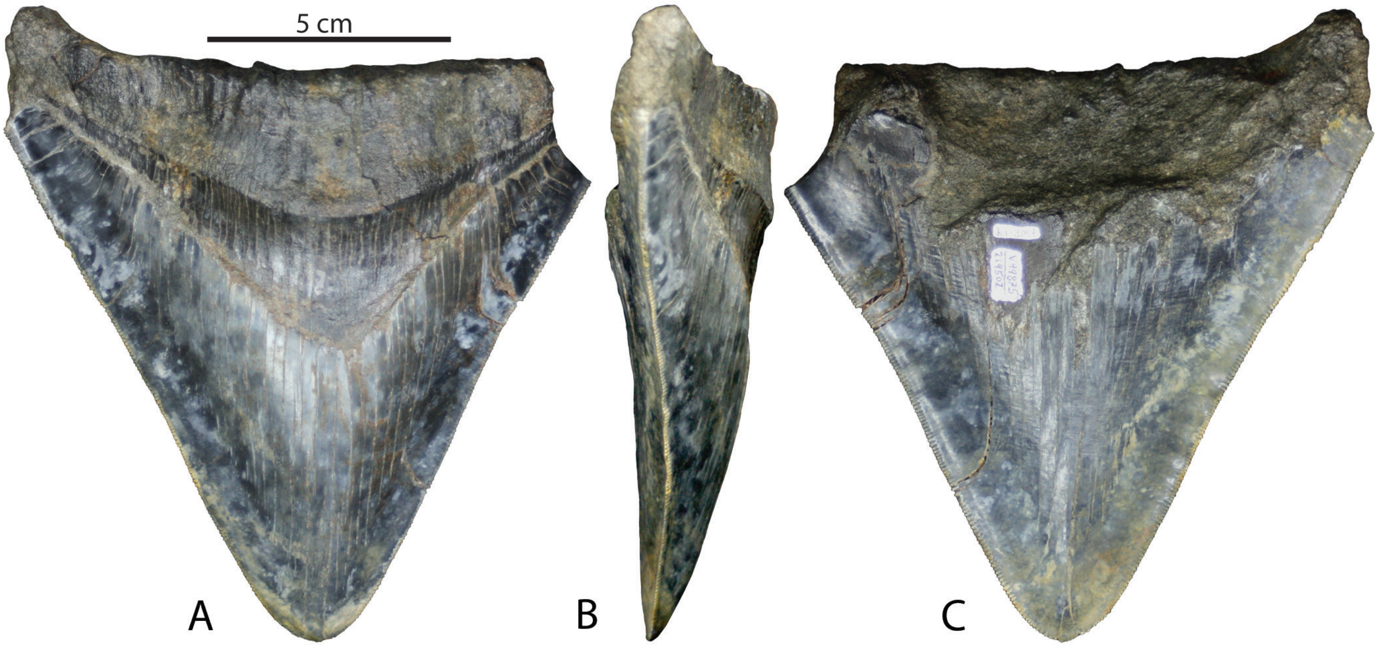


Figure 2. *Carcharocles megalodon* (UCMP 219502) from the Purisima Formation in lingual (**A**), ?distal (**B**) and labial (**C**) view.

a mako *C. hastalis*, a large cowshark *Hexanchus* sp., and a bat ray, *Myliobatis* sp. All prior sampling at these localities consisted of surface collecting which favors discovery of larger specimens; screenwashing of bonebed sediment may yield smaller teeth and reveal a more diverse fauna, though moderate consolidation of the Purisima Formation tends to preclude disaggregation of sediment. Such screenwashing for microvertebrate material in younger Purisima Formation strata in the Santa Cruz section (chiefly UCMP locality V99866) has been more successful and produced remains of a number of additional chondrichthyans (*Cetorhinus maximus* Gunnerus, 1765, *Dasyatis* sp. Rafinesque, 1810, *Galeorhinus* sp. Blainville, 1816, and *Raja* sp. Linnaeus, 1758).

Teeth of true *Carcharodon* are some of the most common shark fossils in the Purisima Formation, and hundreds of teeth have been recovered from several localities. These three species are stratigraphically separated within the Purisima Formation (Domning 1978, Clark 1981, Stewart and Perry 2002, Boessenecker 2011, 2013, Long et al. 2014): 1) nonserrated *C. hastalis* occur only in the basal ten meters of the Purisima Formation near Santa Cruz (Messinian correlative, 6.9-5.6 Ma); 2) lightly serrated *C. hubbelli* Ehret et al., 2012 teeth are reported from slightly younger rocks at the base of the San Gregorio section of the Purisima Formation near Halfmoon Bay (Messinian correlative, 6.4–5.6 Ma); 3) coarsely serrated *C. carcharias* are found in younger Pliocene intervals of the San Gregorio and Santa Cruz sections of the Purisima Formation (Zanclean-Piacenzian correlative, 5.3 Ma and younger). This biochronologic pattern records the "*Isurus-Carcharodon*" transition in the Purisima Formation (Stewart and Perry 2002, Boessenecker 2011, Long et al. 2014), originally reported from the Mio-Pliocene Pisco Formation of Peru (Ehret et al. 2009, 2012). The abundance of *Carcharodon* spp. teeth suggests that *C. megalodon* is truly rare in the Purisima Formation and not simply a taphonomic artifact. Recent studies suggest an extinction of *C. megalodon* at the end of the Pliocene (Pimiento and Clements 2014), though few North Pacific records with well-substantiated dates were utilized for this study. Few post-Miocene occurrences of *C. megalodon* from the eastern North Pacific exist but include a Pliocene specimen from the basal San Diego Formation of Baja California (Ashby and Minch 1984) and several specimens from the lower Pliocene Lawrence Canyon local fauna in the San Mateo Formation of southern California (Barnes et al. 1981). Further complicating matters is the lack of accurate, up-to-date and readily auditable stratigraphic and geochronologic ranges (see Parham et al., 2012:351-352) for many specimens in their sample (Pimiento and Clements, 2014: tables S1-S2) and problems with stage identification and the Plio-Pleistocene boundary for literature published prior to the 2009 transfer of the Gelasian stage to the Pleistocene. Other studies with finer stratigraphic detail suggest extinction of *C. megalodon* earlier at the end of the Zanclean (North Carolina, Ward 2008; Italy, Marsili 2008), contrasting strongly with a Plio-Pleistocene extinction. Reevaluation of the extinction date of *C. megalodon* requires further analysis of *C. megalodon* records from better dated regions such as the eastern North Pacific and geochronologic reassessment of published records using modern age determinations. Accurate geochronologic dates are the framework for properly understanding faunal evolution of Plio-Pleistocene marine vertebrates (e.g., Boessenecker 2013).

The majority of the chondrichthyan assemblage from the Santa Cruz section of the Purisima Formation — and the majority of Cenozoic strata on the west coast, for that matter — remains unpublished. Lack of published information on chondrichthyan occurrences hinders the study of faunal change in the eastern North Pacific, and as a result little is known regarding evolutionary interactions between chondrichthyans and other marine vertebrate groups in the eastern North Pacific including birds (Warheit 1992, Ando and Fordyce 2014), sea turtles (Parham and Pyenson 2010), or marine mammals (Boessenecker 2013). Further study of eastern North Pacific fossil fish assemblages already present in museum collections will elucidate the recent evolution of particular sharks and fish viz. *Cetorhinus* (Welton 2014), *Carcharodon* (Ehret et al. 2012) and the dating and causes of the extinction and extirpation of others such as *C. megalodon*, *Pristiophorus* Müller and Henle, 1837, *Oncorhynchus rastrosus* Cavender and Miller, 1972 (Boessenecker 2011, Eiting and Smith 2007, Pimiento and Clements 2014). Continued field study of the Santa Cruz section of the Purisima Formation, including screenwashing, has the potential to further expand the chondrichthyan fauna.

ACKNOWLEGEMENTS

First and foremost I thank F.A. Perry for advising me on the stratigraphy and paleontology of the Purisima Formation near Santa Cruz. This study benefited from discussions on chondrichthyan paleontology and stratigraphy with L.G. Barnes, T.A. Deméré, D.J. Ehret, D.J. Long, and C.L. Powell, II. Thanks to S. Boessenecker and C. Pirrone for field assistance, and M.B. Goodwin and P.A. Holroyd for curatorial assistance. Constructive comments from reviewers T.A. Deméré and S.J. Godfrey and editor D. M. Erwin improved the quality of this manuscript. Field research resulting in this find was generously funded by a graduate research grant from the Geological Society of America.

LITERATURE CITED

Agassiz, L. 1843. Recherches sur les poisons fossiles. Tome III. Imprimérie de Petitpierre, Neuchatel. 390 pp.

Ameghino, F. 1906. Les formations sédimentaires du Crétacé supérieur et du Tertiare de Patagonie avec un parallele entre leurs faunes mammalogiques et celles de l'ancien continent. *Anales del Museo Nacional de Buenos Aires* 3:15:8:1–508.

Ando, T., and R.E. Fordyce. 2014. Evolutionary drivers for flightless, wing-propelled divers in the Northern and Southern Hemispheres. *Palaeogeography, Palaeoclimatology, Palaeoecology* 400:50–61.

Ashby, J.R., and J.A. Minch. 1984. The Upper Pliocene San Diego Formation and the occurrence of *Carcharodon megalodon* at La Joya, Tijuana, Baja California, Mexico. Pp. 19–28 *in* J.A. Minch and J.R. Ashby (eds.). Miocene and Cretaceous Depositional Environments, Northwestern Baja California, Mexico. American Association of Petroleum Geologists, Pacific Section, Los Angeles, California.

Ayres, W.O. 1859. On new fishes of the Californian coast. *Proceedings of the California Academy of Sciences* 2:25–32.

Barnes, L.G. 1977. Outline of eastern North Pacific fossil cetacean assemblages. *Systematic Zoology* 25:321–343.

Barnes, L.G., H. Howard, J.H. Hutchison, and B.J. Welton. 1981. The vertebrate fossils of the marine Cenozoic San Mateo Formation at Oceanside, California. Pp. 53–70 *in* P.L. Abbott and S. O'Dunn (eds.). Geologic Investigations of the coastal plain, San Diego County, California. San Diego Association of Geologists, San Diego, California.

Barnes, L.G. 1985. Fossil pontoporiid dolphins (Mammalia: Cetacea) from the Pacific Coast of North America. *Natural History Museum of Los Angeles County Contributions in Science* 363:1–34.

Barron, J.A. 1986. Updated diatom biostratigraphy for the Monterey Formation of California. Pp. 105–120 *in* R.E. Casey and J.A. Barron (eds.). Siliceous Microfossil and Microplankton of the Monterey Formation and Modern Analogs. Pacific Section SEPM, Los Angeles, CA.

Barron, J.A., and C.M. Isaacs. 2001. Updated chronostratigraphic framework for the California Miocene. Pp. 393–395 *in* C.M. Isaacs and J. Rullkötter (eds.). The Monterey Formation - from rocks to molecules. Columbia University Press, New York, New York.

Berg, L.S. 1958. System der Rezenten und fossilien fischartigen und fische. VEB Deutscher Verlag der Wissenschaften, Berlin, Germany. 310 pp.

Blainville, H.M.D. de. 1816. Prodrome d'une distribution systématique du regne animal. *Bulletin des Sciences par la Société Philomatique de Paris* 8: 105–124.

Boessenecker, R.W. 2011. 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, R.W. 2013. A new marine vertebrate assemblage from the Late Neogene Purisima Formation in Central California, Part II: Pinnipeds and cetaceans. *Geodiversitas* 35:815–940.

Boessenecker, R.W., and N.A. Smith. 2011. Latest Pacific basin record of a bony-toothed bird (Aves, Pelagornithidae) from the Pliocene Purisima Formation of California, U.S.A. *Journal* *of Vertebrate Paleontology* 31:652–657.

Boessenecker, R.W., F.A. Perry, and J.G. Schmitt. 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.

Cappetta, H. 1987. Handbook of Paleoichthyology, Volume 3B. Chondrichthyes II, Mesozoic and Cenozoic Elasmobranchii. Gustav Fisher Verlag, Stuttgart. 193 pp.

Cappetta, H. 2012. Handbook of Paleoichthyology. Chondrichthyes (Mesozoic and Cenozoic Elasmobranchii: Teeth), vol. 3B. Gustav Fisher, Stuttgart, Germany. 512 pp.

Cavender, T. and R.R. Miller. 1972. *Smilodonichthys rastrosus*, a new Pliocene salmonid fish from western United States. *Bulletin of the Museum of Natural History, University of Oregon* 18:1-44.

Clark, J.C. 1981. Stratigraphy, paleontology and geology of the central Santa Cruz mountains. *US Geological Survey Professional Paper* 1168:1–51.

Cummings, J.C., R.M. Touring, and E.E. Brabb. 1962. Geology of the Northern Santa Cruz Mountains. *California Division of Mines Geology Bulletin* 181:179–220.

Cuvier, G.L. 1816. Le Règne Animal distribué d'après son organisation pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Avec Figures, dessinées d'après nature. Tome II. Contenant Les reptiles, les poissons, les mollusques et les annélides. Deterville, Paris. 532 pp.

Dickinson, W.R., R.A. Armin, N. Beckvar, T.C. Goodlin, S.U. Janecke, R.A. Mark, R.D. Norris, G. Radel, and A.A. Wortman. 1987. Geohistory analysis of rates of sediment accumulation and subsidence for selected California basins. Pp. 2–23 *in* R. V. Ingersoll and W. G. Ernst (eds.). Cenozoic Basin Development of Coastal California. Englewood Cliffs, New Jersey.

Domning, D.P. 1978. Sirenian evolution in the North Pacific Ocean. *University of California Publications in Geological Sciences* 18:1–176.

Ehret, D.J., G. Hubbell, and B.J. MacFadden. 2009. Exceptional preservation of the white shark *Carcharodon* (Lamniformes, Lamnidae) from the Early Pliocene of Peru. *Journal of Vertebrate Paleontology* 29:1–13.

Ehret, D.J., B.J. MacFadden, D.S. Jones, T.J. DeVries, D.A. Foster, and R. Salas-Gismondi. 2012. Origin of the white shark *Carcharodon* (Lamniformes: Lamnidae) based on recalibration of the upper Neogene Pisco Formation of Peru. *Palaeontology* 55:1139–1153.

Eiting, T.P., and G.R. Smith. 2007. Miocene salmon (*Oncorhynchus*) from Western North America: gill raker evolution correlated with plankton productivity in the eastern Pacific. *Palaeogeography, Palaeoclimatology, Palaeoecology* 249:412–424.

Feldmann, R.M., C.E. Schweitzer, and R.W. Boessenecker. 2015. A new squat lobster (Decapoda: Anomura: Galatheoidea) from the Pliocene Purisima Formation, California. *Annals of the Carnegie Museum* 83:1–9.

Glikman, L.S. 1964. Sharks of the Paleogene and their stratigraphic significance. Nakua Press, Moscow. 266 pp.

Gray, J.E. 1864. On the Cetacea which have been observed in the seas surrounding the British Islands. *Proceedings of the Scientific Meetings of the Zoological Society of London* 1864:195–248.

Gunnerus, J.E. 1765. Brugden (Squalus maximus), Beskrivenen Gunnerus. Beskrevnen ved. Norway, Kongelige norske Videnskabers selskab Skrifter Trondheim 3: 33–49.

Huxley, T.H. 1880. On the application of the laws of evolution to the arrangement of the vertebrata and more particularly of the mammalia. *Proceedings of the Zoological Society of London* 43:649–662.

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

Kellogg, R. 1922. Description of the skull of *Megaptera miocaena*, a fossil humpback whale from the Miocene diatomaceous earth of Lompoc, California. *Proceedings of the United States National Museum* 61:1–18.

Kellogg, R. 1927. Fossil Pinnipeds from California. Contributions to Palaeontology from the Carnegie Institution of Washington 27–37.

Kellogg, R. 1929. A new cetothere from southern California. *University of California Publications in Geological Sciences* 18:449–457.

Lacépède, B.G.E., (1804) Histoire naturelle des cétacés. Histoire naturelle, Paris. Vol. 37. Imprimerie de la Republique, Paris, 329 p.

Leymerie, M.A. 1842. Suite de mémoire sur le terrain Crétacé du département de l'Aube. *Mémoire de la Société Géologique de France* 5:1–34.

Linnaeus, C. 1758. Systema naturae. Vol.1. Regnum animale. Laurentius Salvius, Stockholm, 824 pp.

Long, D.J., R.W. Boessenecker, and D.J. Ehret. 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. Program and Abstracts, p. 123.

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.

Mitchell, E.D. 1965. History of research at Sharktooth Hill, Kern County, California. Kern County Historical Society, Bakersfield, California, 45 pp.

Mitchell, E.D. 1968. The Mio-Pliocene pinniped Imagotaria. *Journal of the Fisheries Research Board of Canada* 25:1843–1900.

Muizon, C. de. 1983. Un nouveau Phocoenidae (Cetacea) du Pliocene inferieur du Perou. *Comptes Rendus de l'Academie des Sciences Paris Serie II* 296:1203–1206.

Müller, J., and F.G.J. Henle. 1837. Hr. Muller las über die 'gattungen der Haifische and Rochen', nach einer von ihm mit Hrn. Henle unternommenen gemeinschaftlichen arbeit: 'über die naturgeschichte der knorpelfische'. *Berichte über die zur Bekanntmachung geeigneten der K. Preuss Akademie der Wissenschaften zu Berlin* 2: 111–118.

Norris, R.D. 1986. Taphonomic gradients in shelf fossil assemblages: Pliocene Purisima Formation, California. *Palaios* 1:256–270.

Parham, J.F., and N.D. Pyenson. 2010. New sea turtle from the

Miocene of Peru and iterative evolution of feeding ecomorphologies since the Cretaceous. *Journal of Paleontology* 84:231–247.

Parham, J.F., Donoghue, P.C.J., Bell, C.J., Calway, T.D., Head, J.J., Holroyd, P.A., Inoue, J.G., Irmis, R.B., Joyce, W.G., Ksepka, D.T., Patané, J.S.L., Smith, N.D., Tarver, J.E., van Tuinen, M., Yang, Z., Angielcsky, K.D., Greenwood, J.M., Hipsley, C.A., Jacobs, L., Makovicky, P.J., Müller, J., Smith, K.T., Theodor, J.M., Warnock, R.C.M., and M.J. Benton. 2012. Best practices for justifying fossil calibrations. *Systematic Biology* 61:346–359.

Perry, F.A. 1993. Fossil Sharks and Rays of the Southern Santa Cruz Mountains, California. Santa Cruz Museum Association, Santa Cruz, California, 48 pp.

Pimiento, C., and M.A. Balk. 2015. Body-size trends of the extinct giant shark *Carcharocles megalodon*: a deep-time perspective on marine apex predators. *Paleobiology* 41:479–490.

Pimiento, C., and C.F. Clements. 2014. When did *Carcharocles megalodon* become extinct? A new analysis of the fossil record. *PLoS ONE* 9:e111086.

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

Powell, C.L., 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.

Purdy, R.W., V.P. Schneider, S.P. Applegate, J.H. McLellan, R.L. Meyer, and B H. Slaughter. 2001. The Neogene sharks, rays, and bony fishes from Lee Creek Mine, Aurora, North Carolina. *Smithsonian Contributions to Paleobiology* 90:71–202.

Rafinesque, C.S. 1810. Caratteri di alcuni nuovi generi e nuove specie di animali e piante delta Sicilia. Nessuno, Palermo, 105 pp.

Repenning, C.A., and R.H. Tedford. 1977. Otarioid seals of the Neogene. *US Geological Survey Professional Paper* 992:1–93.

Stewart, J.D., and F.A. Perry. 2002. First paleomagnetic framework for Isurus-Carcharodon transition in the Pacific basin: the Purisima Formation, central California. *Journal of Vertebrate Paleontology* 22:111A.

Takahashi, S., Domning, D.P., and T. Saito. 1986. *Dusisiren dewana*, n. sp. (Mammalia: Sirenia), a new ancestor of Stellers sea cow from the upper Miocene of Yamagata prefecture, northeastern Japan. *Transactions and Proceedings of the Palaeontological Society of Japan* 141:296–321.

Warheit, K.I. 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, B.J. 2014. A new fossil basking shark (Lamniformes: Cetorhinidae) from the middle Miocene Sharktooth Hill Bonebed, Kern County, California. *Los Angeles County Museum Contributions in Science* 522:29-44.