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

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

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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.

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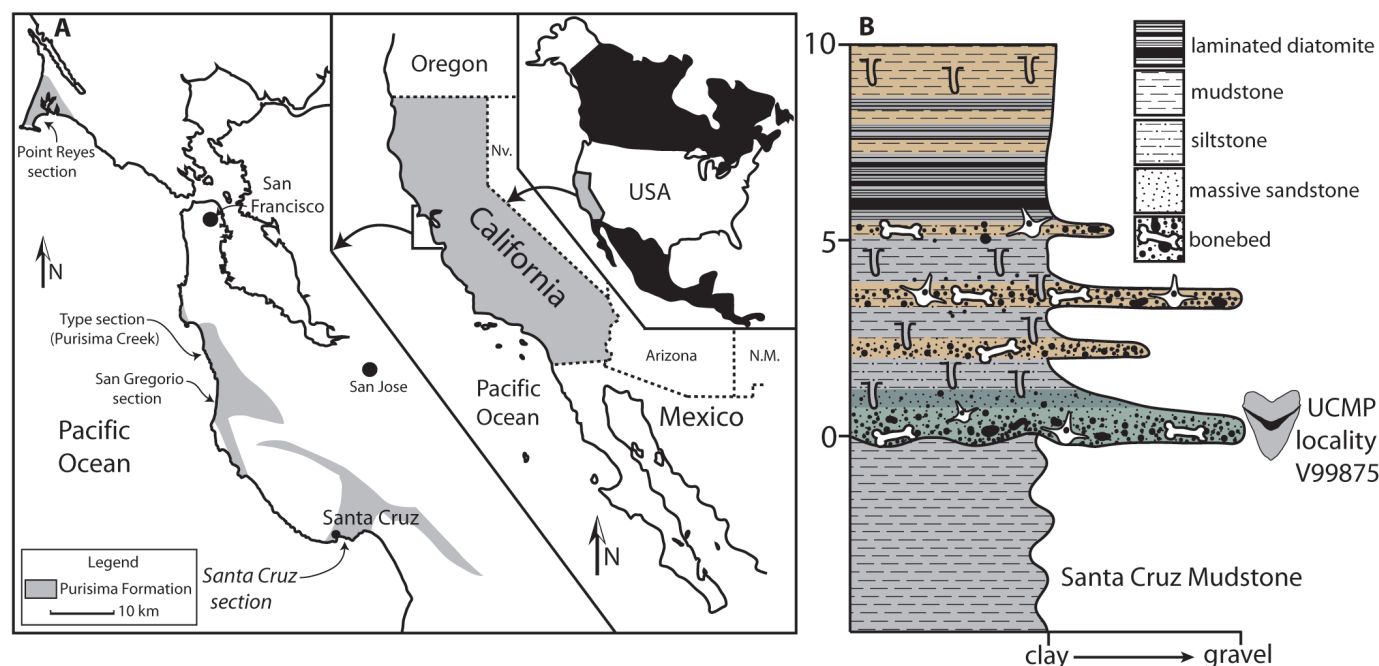
GEOLOGIC BACKGROUND

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 a 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. Linnaeus, 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, Phaseteroidea 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

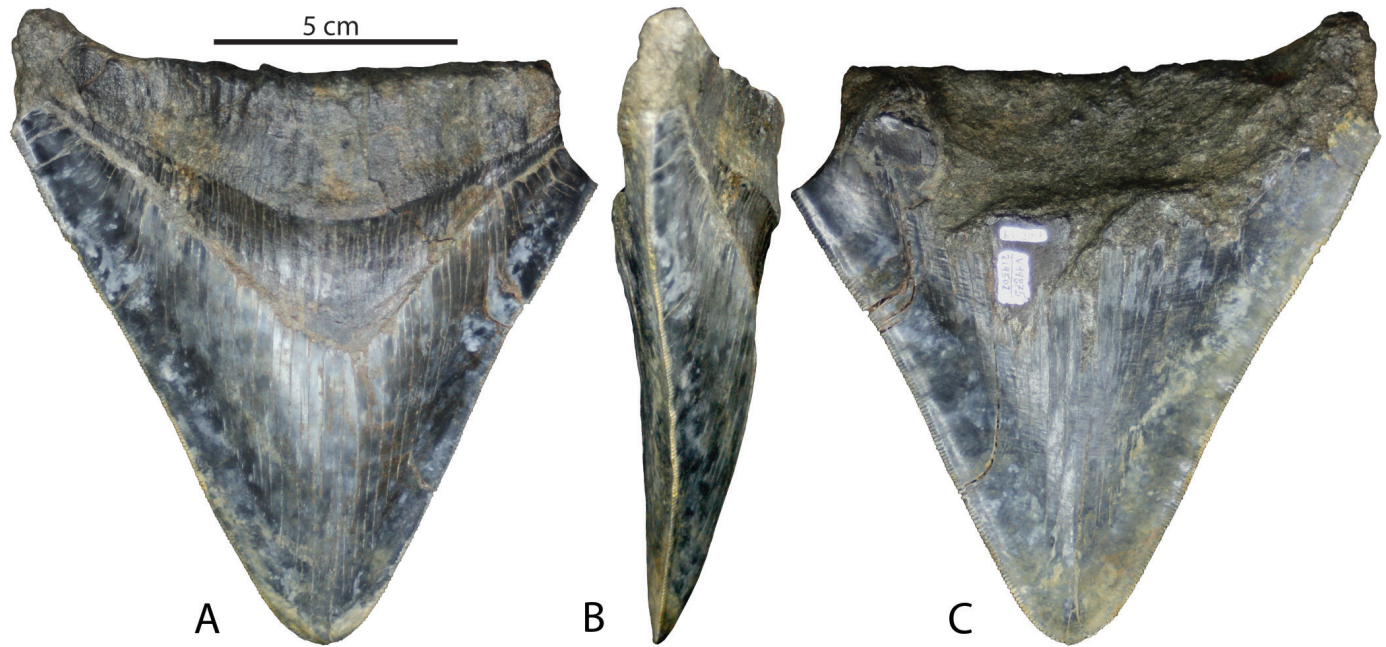


Figure 2. *Carcharocles megalodon* (UCMP 219502) from the Purisima Formation in lingual (A), ?distal (B) and labial (C) view.

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) non-serrated *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.

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