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

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ABSTRACT

The Miocene to Pliocene Purisima Formation crops out in multiple transform fault bounded structural blocks in central California. As a result of poor exposure, strike slip fault offset, and uncertain intraformational correlations, some exposures of the Purisima Formation are not well dated. The San Gregorio section of the Purisima Formation occurs in the Pigeon Point Block, west of the San Gregorio Fault, along the coast of southern Halfmoon Bay. Ages based on invertebrate and diatom biostratigraphy support a Late Miocene to Early Pliocene age, while ash correlations indicate a much younger Middle to Late Pliocene (3.3-2.5 Ma) age. Abundant remains of marine vertebrates occur in the Purisima Formation. Recent fieldwork in the San Gregorio section identified a modest assemblage of 26 taxa, including sharks (*Carcharodon carcharias, Carcharodon* sp., *Cetorhinus maximus,* cf. *Hexanchus, Isurus oxyrinchus, Pristiophorus* sp., *Squatina* sp., and *Sphyrna* sp.), skates (*Raja* sp., cf. *R. binoculata*), bony fish (*Paralichthys* sp., *Thunnus* sp.), birds (*Mancalla diegensis, Morus* sp.), and 13 marine mammal taxa, including several new records for the Purisima Formation. The non-mammalian vertebrates of this assemblage are described herein. The vertebrate assemblage is utilized to evaluate previous biostratigraphic and tephrochronologic age determinations for the San Gregorio section. The stratigraphic range of *Carcharodon carcharias, Raja* sp., cf. *R. binoculata, Mancalla diegensis,* and some of the marine mammals strongly indicate a Middle to Late Pliocene age for the upper and middle parts of the section, while a Late Miocene or Early Pliocene age is probable for the base of the section.

Introduction

In 1827, the surveyor of the HMS Blossom, Lt. Edward Belcher, reported "petrified bones of a cylindrical form" from coastal cliffs near modern day Santa Cruz, California (Vanderhoof, 1951: 109-110). These were probably cetacean vertebrae from exposures of the Purisima Formation and constitute one of the earliest records of fossil vertebrates collected from the west coast of North America (Powell, 1998). Several decades later, a partial odontocete rostrum was designated as the holotype of *Lonchodelphis occiduus* by the preeminent anatomist Joseph Leidy (1868). The specimen was collected from Miocene rocks near 'Halfmoon Lake' (a probable corruption of Halfmoon Bay), suggesting this fossil likely originated from the Purisima Formation (Barnes, 1976; Powell, 1998). Aside from a few isolated cetacean and pinniped bones mentioned by Repenning and Tedford (1977) and Barnes (1976), few other marine vertebrate fossils have been reported from the extensive exposures around Halfmoon Bay. Much richer vertebrate assemblages have been collected from the Purisima Formation at Point Reyes and Santa Cruz (see Palaeontologic Background).

In August 2004 the author and T. Palladino investigated exposures of the Purisima Formation near Halfmoon Bay, based on reports of whale bones by local surfers. Multiple prolific bonebeds were discovered during fieldwork in 2005 and 2006. A diverse vertebrate assemblage comprising 26 taxa (table 1) of sharks (*Carcharodon carcharias*, *Cetorhinus maximus*, cf. *Hexanchus*, *Isurus oxyrhincus*, *Pristiophorus* sp., *Squatina* sp., and cf. *Sphyrna*), skates (*Raja* sp., cf. *R. binoculata*), bony fish (*Paralichthys* sp., *Thunnus* sp.), birds (*Mancalla diegensis*, *Morus* sp.), pinnipeds (*Dusignathus* sp., Otariidae indet.), and cetaceans (*Parapontoporia* sp., Phocoenidae new genus, Phocoeninae indet., Globicephalinae indet., Odontoceti indet., Balaenidae sp. indet.1, Balaenidae sp. indet. 2, Balaenopteridae indet., Balaenopteridae, new species, *Herpetocetus bramblei*, *Herpetocetus* sp.) was established. These include several new vertebrate records for the Purisima Formation, and potentially new cetacean taxa (Boessenecker, 2006). These

▶ Table 1. List of fossil vertebrate taxa preserved in the San Gregorio section of the Purisima Formation, Halfmoon Bay, California.

- Chondrichthyes
  - Hexanchidae
    - cf. *Hexanchus*
  - Pristiophoridae
    - *Pristiophorus* sp.
  - Squatinidae
    - *Squatina* sp.
  - Cetorhinidae
    - *Cetorhinus maximus*
  - Lamnidae
    - *Carcharodon carcharias*
    - *Carcharodon sp.*
    - *Isurus oxyrinchus*
  - Sphyrnidae
    - cf. *Sphyrna*
  - Rajidae
    - *Raja* sp., cf. *R. binoculata*
- Osteichthyes
  - Scombridae
    - *Thunnus* sp.
  - Paralichthyidae
    - *Paralichthys* sp.
- Aves
  - Sulidae
    - *Morus* sp.
  - Alcidae
    - *Mancalla diegensis*
- Mammalia
  - Pinnipedia
    - Otariidae
      - Otariidae indet.
    - Odobenidae
      - *Dusignathus* sp.
  - Odontoceti
    - Odontoceti indet.
    - Delphinidae
      - Globicephalinae indet.
    - Lipotidae
      - *Parapontoporia* sp, cf. *P. sternbergi*
    - Phocoenidae
      - New genus and species
      - Phocoeninae indet.
  - Mysticeti
    - Balaenidae
      - Balaenidae sp. indet. 1
      - Balaenidae sp. indet. 2
    - Balaenopteridae
      - Balaenopteridae indet.
      - Balaenopteridae, new species
    - Cetotheriidae *sensu stricto*
      - *Herpetocetus bramblei*
      - *Herpetocetus sp.*

localities are within the San Gregorio section of the Purisima Formation (Powell *et al.*, 2007), an informal name applied to Purisima Formation strata on the west side of the San Gregorio Fault (and therefore in the Pigeon Point Structural Block), in the southern part of Halfmoon Bay, San Mateo County, California (figure 1). This section was initially mapped as the Late Miocene Tahana Member (Cummings *et al.*, 1962) on lithologic grounds. However, conflicting age data exist for this section, including a Late Miocene age based on previous biostratigraphy (Durham & Morgan, 1978; Gavigan, 1984), and a Middle Pliocene age supported by tephrochronologic correlations and recent molluscan biostratigraphy (Sarna-Wocjicki *et al.*, 1991; Powell *et al.*, 2007). The aim of this paper is to describe the non-mammalian marine vertebrates, and discuss the age of the San Gregorio section of the Purisima Formation in light of this new marine vertebrate assemblage.

Materials and Methods

The fossils described herein were collected in 2005 and 2006 from coastal exposures, specimens were recovered from the cliff face as well as screen washing of sediment. Specimens were prepared at Montana State University Department of Earth Sciences and the Museum of the Rockies in Bozeman, MT. Terminology for chondrichthyan teeth follows Purdy *et al.* (2001). Terminology for batoid cranial morphology follows Dean & Motta (2004). Terminology for avian osteology follows Howard (1929). Detailed locality data are available to qualified researchers upon request.

Although the Pliocene-Pleistocene boundary has recently been changed from 1.806 Ma to 2.588 Ma due to inclusion of the Gelasian Stage within the Pleistocene and modification of the Quaternary (Gibbard *et al.*, 2009), this change is based on chronostratigraphy and does not reflect the biostratigraphic integrity of the traditionally defined Pleistocene epoch (Aubry *et al.*, 2009). Thus, for the purposes of this paper, the traditional definition as delineated in Gradstein *et al.* (2004) of the Pliocene-Pleistocene boundary at the 1.806 Ma Gelasian-Calabrian stage boundary is retained along with a threefold division of the Pliocene epoch (Lower, Middle and Upper, equivalent with the Zanclean, Piacenzian, and Gelasian stages, respectively).

Institutional Abbreviations

SCMNH, Santa Cruz Museum of Natural History, Santa Cruz, California, USA;
SDNHM, San Diego Natural History Museum, San Diego, California, USA;
UCMP, University of California Museum of Paleontology, Berkeley, California, USA.

Palaeontologic Background

Despite the abundance of vertebrate fossils in the San Gregorio section of the Purisima Formation, only three previous studies have addressed them. In 1907 D. S. Jordan reported a single tooth of the shark *Carcharodon* "*arnoldi*" (identified as *Carcharodon carcharias* in this report) from the 'Pliocene of Pescadero.' A fragmentary, putative physeteroid rostrum collected by R.M. Touring was mentioned by Packard (1962). In their description of the Purisima Formation in the Halfmoon Bay region, Cummings *et al.* (1962) noted the presence of cetacean bones at the base of the San Gregorio section. Additional studies regarding other Purisima Formation vertebrates include mention, discussions, or descriptions of sharks (Stewart & Perry, 2002), pinnipeds (Kellogg, 1927; Mitchell, 1962; Repenning & Tedford, 1977; Barnes & Perry, 1989; Boessenecker & Perry, 2011), sirenians (Domning, 1978), and cetaceans (Leidy, 1868; Glen, 1959; Packard, 1962; Barnes, 1976, 1985; Pyenson & Brudvik, 2007; Boessenecker & Geisler, 2008; Whitmore & Barnes, 2008; Boessenecker *et al.*, 2009; Goodwin *et al.*, 2009). With the exception of fossil material described by Kellogg (1927), Mitchell (1962), Repenning & Tedford (1977), Barnes (1985) and Whitmore & Barnes (2008), very few vertebrate fossils from the Purisima Formation have been described in sufficient detail.

Geologic Background

The upper Neogene Purisima Formation in central California is a grouping of Miocene and Pliocene marine sandstones, siltstones and mudstones representing deposition in shoreface to outer shelf and continental slope settings (Norris, 1986). The Purisima Formation occurs in four distinct structural blocks (and subblocks) west of the San Andreas Fault (figure 1), and scattered exposures exist with significant fault displacement (Powell *et al.*, 2007). Exposures of

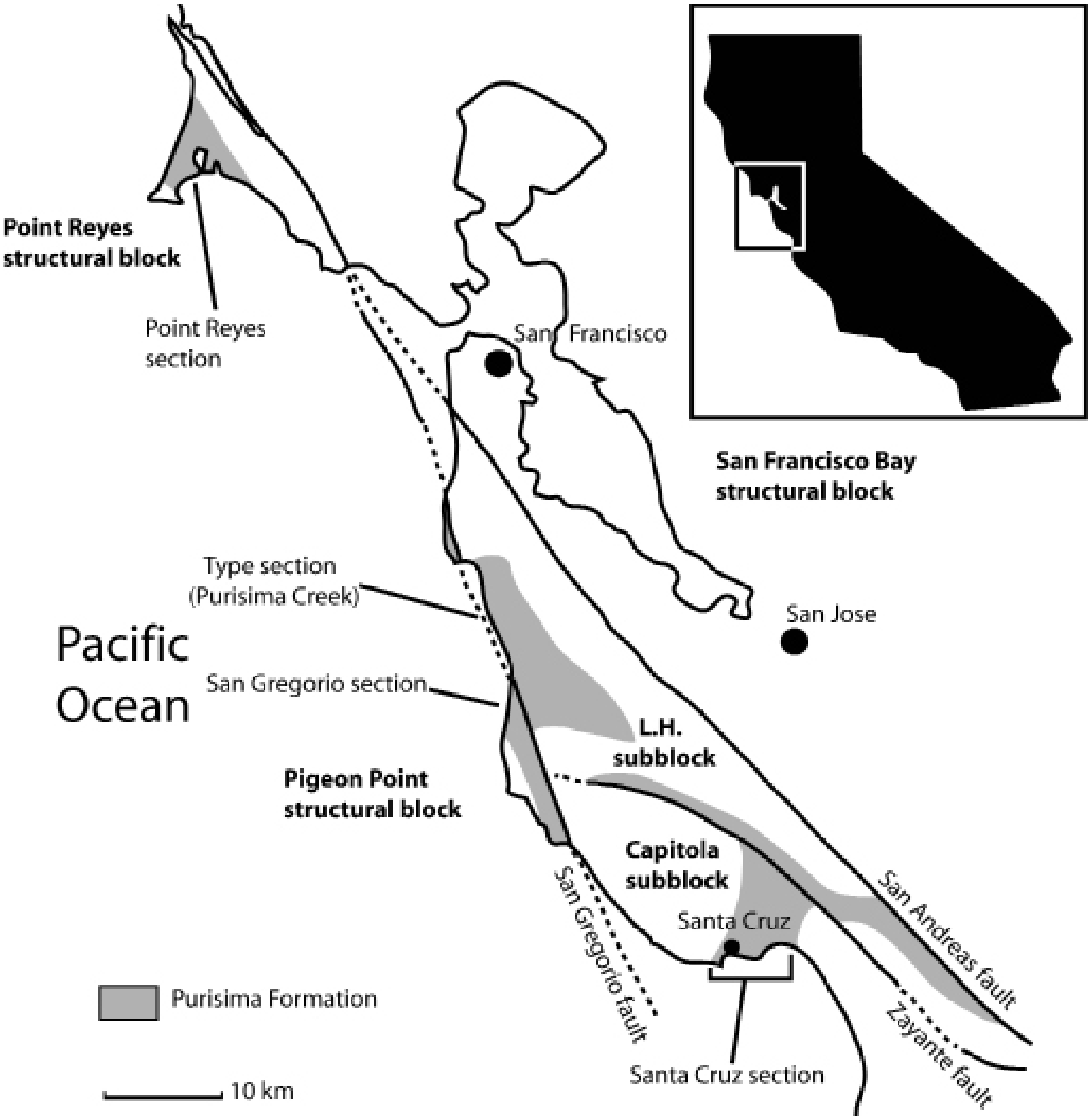

Figure 1. Generalized geologic map of part of central California, showing relevant tectonic features, and major localities and exposures of the Purisima Formation. Inset shows California and box showing location of map. L.H. subblock = La Honda subblock of the Santa Cruz structural block; Capitola subblock is also part of the Santa Cruz structural block. Faults are shown as black lines, or dashed where uncertain.

the Purisima Formation vary in terms of their stratigraphic succession, lithology, thickness, outcrop quality, fossil occurrence, fossil preservation and abundance, which have impeded attempts at intraformational correlations. The Purisima Formation crops out in four primary areas in central California: 1) Point Reyes (Point Reyes Structural Block); 2) the Halfmoon Bay region (La Honda subblock of the Santa Cruz Structural Block, and Pigeon Point Structural Block); 3) southern Santa Cruz County (Capitola subblock of the Santa Cruz Structural Block), and 4) in the Santa Cruz Mountains (between the San Andreas and Zayante faults in the La Honda subblock of the Santa Cruz structural block). The northernmost exposures at Point Reyes (figure 1) in Marin County (65 km north of San Francisco) were originally named the Drakes Bay Formation (Galloway, 1977), but later recognized as including the Santa Margarita Sandstone, Santa Cruz Mudstone, and Purisima Formation (Clark *et al.*, 1984). The exposures of the Purisima Formation in coastal Santa Cruz County (approximately 100 km south of San

Francisco; figure 1) range from 6.9 to about 2.5 Ma, are the best exposed, best studied, and most accurately dated Purisima Formation exposures. Additionally, they were recently designated as a supplementary reference section (Powell *et al.*, 2007). Localities from the lower and middle portions of this section have yielded diverse vertebrate assemblages (see Palaeontologic Background, above) that are currently under study (Perry & Boessenecker, unpublished data).

In central San Mateo County (the La Honda subblock), the Purisima Formation is divided into five distinct members (Cummings *et al.*, 1962). The type section of the Purisima Formation is exposed south of Halfmoon Bay (figure 1) near Purisima Creek (Haehl & Arnold, 1904), which is now accessible only by boat. The stratigraphic relationships of the type section and the five members named by Cummings *et al.* (1962) remain unclear. These members are, from oldest to youngest, the Tahana Sandstone, Pomponio Mudstone, San Gregorio Sandstone, Lobitos Mudstone, and Tunitas Sandstone. The San Gregorio section (figure 1) has previously been mapped as the Tahana Member (Upper Miocene; Cummings *et al.*, 1962), and these coastal cliffs were even designated as an alternative type section for the Tahana Member (Cummings *et al.*, 1962). However, Powell *et al.* (2007) concluded that these strata should not be mapped as the Tahana Member, because ash correlations and and the occurrence of the mollusk *Patinopecten healyi* suggested a Pliocene age, younger than the Upper Miocene Tahana Member.

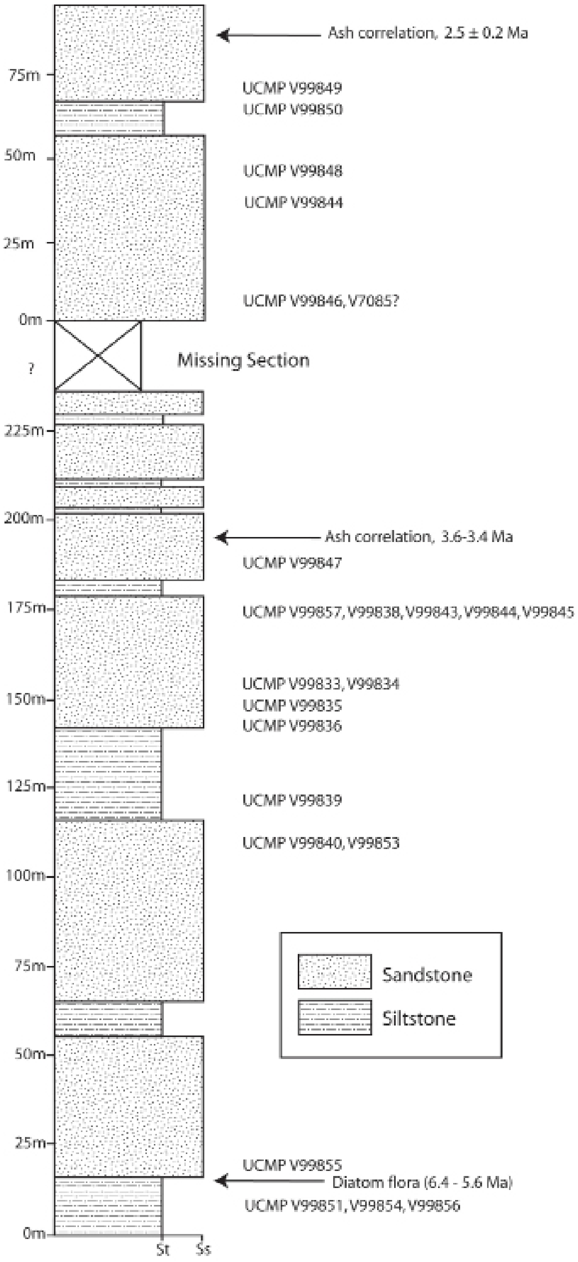

Figure 2. Simplified stratigraphic column of the San Gregorio section, showing approximate stratigraphic positions of UCMP vertebrate localities, ash beds, and diatom assemblages. Because the thickness of missing section is undetermined, the upper part of the San Gregorio section is measured separately.

The strata composing the San Gregorio section (figure 2) are gently folded into an easterly dipping syncline-anticline pair. Rocks from the entire section are light-brown to tan, fine to very fine-grained sandstones and coarse siltstone. The sandstones are massively bedded due to pervasive bioturbation that has homogenized the sediment. However, in certain horizons distinct burrows (*Ophiomorpha*, *Teichichnus pescaderoensis*) have been preserved. The uppermost San Gregorio section is punctuated by several 1-100 cm thick white tephra beds. Body fossils and molds of mollusks are restricted to the upper third of the San Gregorio section, where they sporadically occur as isolated bioclasts or (more commonly) within laterally extensive, thin shell-rich beds. Rare phosphatized crustacean remains, often in phosphate nodules, occur in these shell beds. Vertebrate fossils are typically confined to bonebeds in the middle of the section, although isolated bones and partial, disarticulated skeletons occur near the base of the section. Bonebeds in the middle of the section contain a mix of unabraded complete and fragmented bones, mollusk shells, and prismatically calcified batoid cartilage. Vertebrate skeletal concentrations that exhibit more evidence of time-averaging and reworking contain rare, abraded bone fragments, pebbles, molluscan steinkerns, crustacean fragments, and phosphatic nodules, and lack calcareous mollusk elements. Shark and mammal teeth are rare in these concentrations, as well as all other Purisima Formation deposits. Rare vertebrate fossils occur within occasional shellbeds in the uppermost San Gregorio section.

Age

The age of the Purisima Formation varies from one tectonic block to another and incidentally inter-block correlations have proven difficult (Clark & Brabb, 1978; Powell, 1998; Powell *et al.*, 2007). The San Gregorio section was initially mapped as the Tahana Member, and considered to be Late Miocene in age (supported by Durham & Morgan, 1978). Based on invertebrate fossils, Cummings *et al.* (1962) suggested that the Tahana Member was probably correlative with the Upper Miocene Jacalitos Formation of central California, although it is not clear if invertebrate fossils from localities west or east (or both) of the San Gregorio fault were used for this determination (since the Tahana Member was mapped on both sides of the fault). Microfossils from the Tahana Member in the La Honda subblock (east of the San Andreas Fault) indicate a latest Miocene age of 6.4-5.3 Ma, while the Pomponio, San Gregorio, Lobitos, and Tunitas Members are of younger, undetermined Pliocene age (Powell *et al.*, 2007).

Based on mollusks and echinoids, Purisima Formation strata were correlated with the upper Jacalitos Formation by Durham & Morgan (1978). The presence of three species of *Lituyapecten* led Durham & Morgan (1978) to correlate the 'Tahana Member' in the San Gregorio section with Upper Miocene strata of the Falor Formation (now known to be latest Pliocene to Pleistocene in age; Nilsen & Clarke, 1989) of northern California, and the Ohlson Ranch and 'Merced' (= Wilson Grove Formation; Powell *et al.*, 2004) Formations north of San Francisco. These correlations indicated a Late Miocene to Early Pliocene age for the San Gregorio section (Durham & Morgan, 1978; Powell *et al.*, 2007). Gavigan (1984) correlated the San Gregorio section with an Upper Miocene portion of the Wilson Grove Formation north of San Francisco due to the occurrence of *Lituyapecten turneri*. Powell *et al.* (2007) reported the Pliocene bivalve *Patinopecten healyi* from the San Gregorio section. While the molluscan fossils reported thus far (Cummings *et al.*, 1962; Durham & Morgan, 1978; Gavigan, 1984) were collected from the upper part of the San Gregorio section, Powell *et al.* (2007) reported a diatom flora from the base of the San Gregorio section (figure 2) that was correlative with the Late Miocene *Nitzchia reinholdii* zone (6.4-5.6 Ma).

Naeser (in Gavigan, 1984) reported a 5.2 ±1.2 Ma fission track date from zircon grains within a rhyolitic tuff unit in the uppermost San Gregorio section. Sarna-Wocjicki *et al.* (1991) chemically correlated this upper tephra unit (figure 2) in the uppermost San Gregorio section with the 2.5 Ma Ishi Tuff Member of the Tuscan Formation, in contrast to the numerous Late Miocene age determinations mentioned above. Recently Powell *et al.* (2007) reported additional tephra correlations; the aforementioned upper unit was again correlated with the 2.5 Ma Ishi Tuff, while another tephra unit in the middle of the San Gregorio section (figure 2) was correlated with the 3.35 Ma Putah Tuff Member of the Tuscan and Tehama Formations. These dates (3.35-2.5 Ma) led Powell *et al.* (2007) to conclude that the San Gregorio section of the Purisima Formation is Pliocene in age and should not be mapped as the Tahana Member, as opposed to the Late Miocene determinations of Durham & Morgan (1978) and Gavigan (1984). The discordance between age determinations derived from biostratigraphy and tephrochronology can be further investigated by utilizing the fossil vertebrates (and their known stratigraphic ranges) from this section as an independent test.

Systematic Palaeontology

Class Chondrichthyes Huxley, 1880
Order Hexanchiformes Buen, 1926
Family Hexanchidae Gray, 1851
Genus *Hexanchus* Rafinesque, 1810
cf. *Hexanchus*

Figures 3.1-3.2

Material examined – One tooth, UCMP 219010, from UCMP Locality V99851.

Discussion – This specimen is an upper anterior hexanchid tooth (figures 3.1-3.2). It bears an incomplete, but robust root with a distinct triangular mesial lobe. The root is robust lingually, flat labially, and is nearly flush with the labial surface of the primary cusp. The distally inclined, elongate primary cusp is robust basally, and is labially recurved in mesial view. The cutting edge continues smoothly to its termination at the root mesially and distally. No cusplets are present on the mesial or distal heels of the primary cusp.

The primary cusp of this specimen differs from *Heptranchias* by being more robust and not as distally inclined and recurved (Kemp, 1978). This specimen differs from *Notorhynchus* in lacking a square-shaped mesial root lobe, and a cutting edge that continues smoothly to its termination rather than in a cusplet or a small shoulder (Kemp, 1978). Reported fossil occurrences of *Hexanchus* in California include the Paleocene Lodo Formation (Welton, 1974), the Lower Miocene Skooner Gulch Formation (Phillips *et al.*, 1976), the Lower Miocene Jewett Sand Member of the Temblor Formation (Mitchell & Tedford, 1973), the Middle Miocene Round Mountain Silt (Mitchell, 1965), the Upper Miocene Santa Margarita Sandstone (Perry, 1993), and from the Mio-Pliocene Santa Cruz section of the Purisima Formation (Perry, 1977). Other Northeast Pacific records include the Lower Miocene Nye Mudstone and the Lower Miocene Astoria Formation of coastal Oregon (Welton, 1972), and the Upper Miocene Almejas Formation of Baja California (Stewart, 1997; Barnes, 2008). Fossils of *Hexanchus* are known from the Early Jurassic to the Holocene and occur worldwide (Cappetta, 1987). Extant sixgill sharks inhabit continental shelves, slopes, and the abyssal plain along oceanic margins in temperate, cold temperate, and some tropical waters worldwide (Compagno *et al.*, 2005). Sixgill sharks are large, typically deep water predators that feed on fish and invertebrates (Compagno, 1984).

Order Pristiophoriformes Berg, 1958
Family Pristiophoridae Bleeker, 1859
Genus *Pristiophorus* Müeller & Henle, 1837
Pristiophorus sp.

Figures 3.3-3.4

Material examined – One rostral tooth, UCMP 219026, from UCMP locality V99847.

Discussion – The dorsoventrally flattened, narrow crown identifies this as a sawshark rostral tooth (figures 3.3-3.4). The characteristically smooth cutting edges of the tooth makes the specimen referable to *Pristiophorus*, as it lacks the barbs typical of the genera *Pliotrema* and *Ikamauius* (Keyes, 1979). The crown gradually tapers apically, has a straight posterior margin, and a convex anterior margin. The crown is about 10 mm long. Most of the root is not preserved. The length of this specimen overlaps fossil specimens of *Pristiophorus lanceolatus* and extant specimens of *P. nudipinnus* and *P. cirratus*. The rostral tooth morphology of these species is very similar (Keyes, 1982); therefore, a specific identification is not possible.

Pristiophorus has previously been reported from several northeast Pacific Tertiary formations. Welton (1972) reported *Pristiophorus* from several geologic units in Oregon, including the Lower Oligocene Keasey Formation, the Lower-Middle Oligocene Pittsburg Bluff Formation, and the Upper Oligocene-Lower Miocene Nye Mudstone. *Pristiophorus* fossil occurrences in California include the Lower Miocene Skooner Gulch Formation (Phillips *et al.*, 1976), the Lower-Middle Miocene Jewett and Olcese Sand Members of the Temblor Formation (Olson & Welton, 1986), and the Lower Pliocene Lawrence Canyon Local Fauna of the San Mateo Formation (Barnes *et al.*, 1981). As the San Gregorio section is herein determined to be Late Pliocene, this is the youngest record of a sawshark from the northeast Pacific Ocean. This indicates that sawsharks became extinct in this region no earlier than the Late Pliocene. Extant sawsharks do not currently inhabit the northeastern Pacific (Compagno *et al.*, 2005). Fossil *Pristiophorus* have been reported from Upper Cretaceous through Pliocene strata in North America, Europe, Africa, Asia, Australia, Antarctica, and New Zealand (Keyes, 1982; Cappetta, 1987; Long, 1992; Gottfried & Rabarison, 1997). Extant *Pristiophorus* species inhabit the Indian Ocean, northwest Pacific Ocean, and the northern Carribbean Sea (Compagno *et al.*, 2005). Sawsharks inhabit inner shelf through continental slope environments (>100-630 m depth), and are small (1-1.5 m long) epibenthic predators that consume invertebrates and small fish (Compagno, 1984).

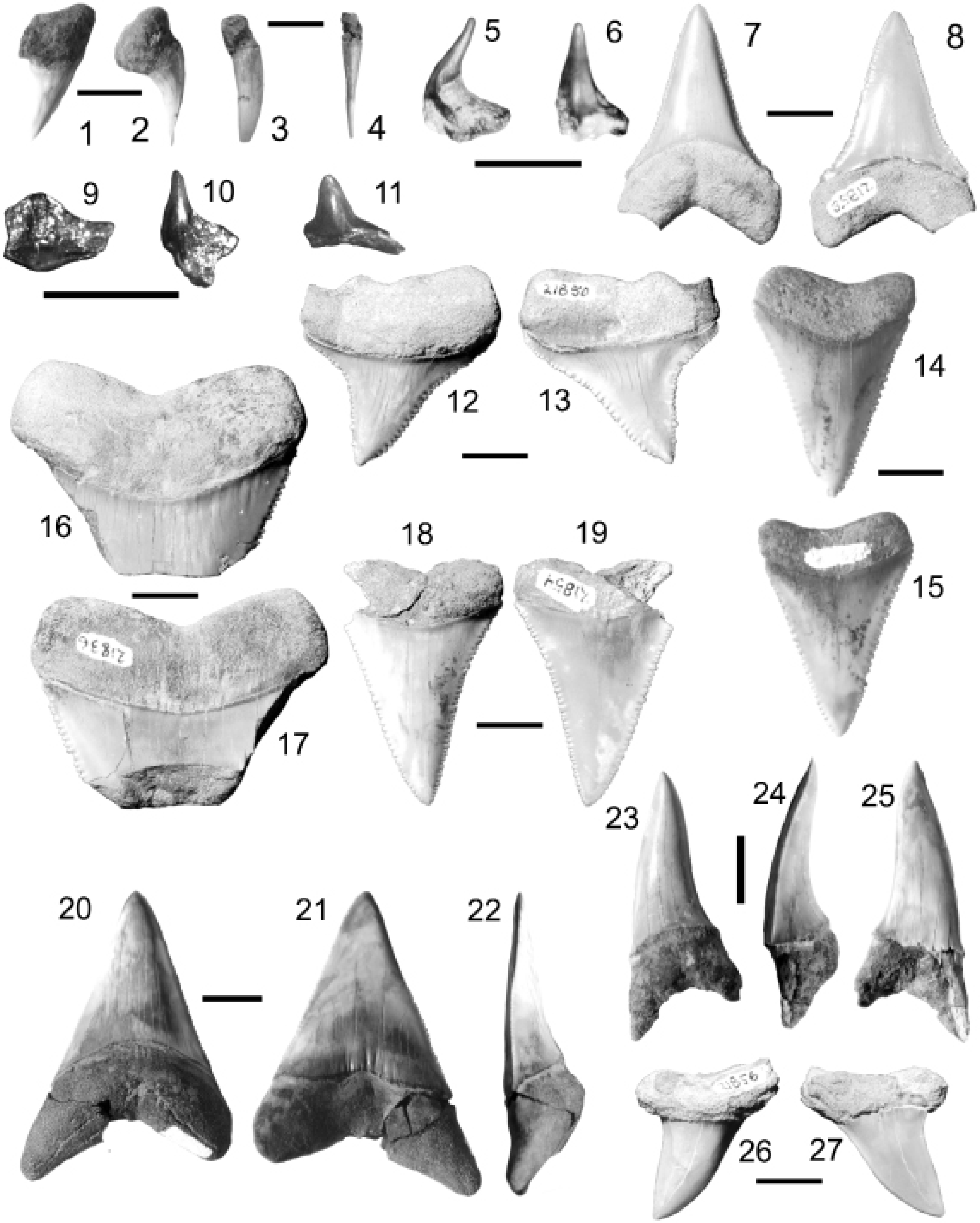

Figure 3. Elasmobranch teeth from the San Gregorio section of the Purisima Formation. 1-2, UCMP 219010, tooth of cf. *Hexanchus* (Rafinesque, 1810), in lingual and medial aspect (respectively); 3-4, UCMP 219026, rostral tooth of *Pristiophorus* sp. (Müller & Henle, 1837), in dorsal and distal aspect (respectively); 5-6, UCMP 219029, tooth of *Squatina* sp. (*Dumeril*, 1806), in lateral and labial aspect (respectively); 7-8, UCMP 212861, tooth of *Carcharodon carcharias* (Linnaeus, 1758), in lingual and labial aspect (respectively); 9-10, UCMP 219055, tooth of *Squatina* sp., in apical, lateral, and labial aspect (respectively); 12-13, UCMP 212860, tooth of *Carcharodon carcharias* in lingual and labial aspect (respectively); 14-15, UCMP 219025, tooth of *Carcharodon carcharias* in lingual and labial aspect (respectively); 16-17, UCMP 212863, tooth of *Carcharodon carcharias* in lingual and labial aspect (respectively); 18-19, UCMP 219011, tooth of *Carcharodon carcharias* in lingual and labial aspect (respectively); 20-22, UCMP 219022, tooth of *Carcharodon* sp. in lingual, labial, and mesial aspect (respectively); 23-25, UCMP 219023, tooth of *Isurus oxyrinchus*, in lingual, labial and mesial view (respectively); 26-27, UCMP 219024, tooth of *Isurus oxyrinchus* in lingual and labial aspect (respectively). Scale bar = 5 mm for 1-6 and 9-11, and 10 mm for 7-8 and 12-26.

Order Squatiniformes Buen, 1926
Family Squatinidae Bonaparte, 1838
Genus *Squatina* Dumeril, 1806
Squatina sp.

Figures 3.5-3.6, 3.9-3.11

Material examined – Two teeth (UCMP 219029 and 219055) from UCMP localities V99836 and V99837.

Discussion – The narrow cusps with wide heels, and wide-based, diamond shaped roots oriented perpendicularly to the cusp identify these teeth as the angel shark, *Squatina* (figures 3.5-3.6, 3.9-3.11). The narrow crown is 6.1 mm long. Additional features of *Squatina* exhibited in these specimens include enameloid 'pegs' protruding linguobasally from the base of the crown, narrow mesial and distal extensions of the crown foot onto the sides of the root, and lingual curvature of the crown. The equidimensional roots are much wider labiolingually than the teeth of many species of *Squatina,* which often possess labiolingually compressed roots; this is exemplified by UCMP 219055. A slight bulge occurs on the lingual portion of the root. The crown feet are oriented more steeply apically (figures 3.6, 3.11), differing from extant *Squatina dumeril*, *Squatina tergocellata*, and similar to *Squatina californica*, *Squatina japonica*, *Squatina nebulosa*, and *Squatina australis*. In terms of the root narrowness (figure 3.6), this tooth compares best with *S. californica* and *S. japonica*. Teeth of fossil species of *Squatina* are very similar, and isolated teeth can be difficult to confidently identify (Cappetta, 1987); given the similarity to several extant taxa and small sample, this specimen is identified only to the genus level. Teeth of *Squatina* sp. are also present elsewhere in the Purisima Formation, in the Middle portion of the Santa Cruz section (UCMP and SCMNH collections).

The genus *Squatina* has previously been reported from several other localities in California, including the Paleocene Lodo Formation (Welton, 1974), the Lower Miocene Jewett and Olcese Sand Members of the Temblor Formation (Mitchell & Tedford, 1973; Olson & Welton, 1986), the Lower Miocene Skooner Gulch Formation (Phillips *et al.*, 1976), the Middle Miocene Round Mountain Silt (Mitchell, 1965), the Upper Miocene Santa Margarita Sandstone (Domning, 1978; Perry, 1993), the Upper Miocene Almejas Formation of Baja California (Stewart, 1997; Barnes, 2008), the Lower Pliocene Lawrence Canyon local fauna of the San Mateo Formation (Barnes *et al.* 1981), and the Upper Pleistocene Palos Verdes Sand (Long, 1993b). Additional records from Baja California include the Middle Miocene Rosarito Beach Formation (Deméré *et al.,* 1984). *Squatina* is known from Jurassic through Pleistocene strata worldwide (Cappetta, 1987; Long, 1993b; Purdy *et al.*, 2001). One extant species, *Squatina californica*, currently inhabits waters off California (Ebert, 2003); other species of *Squatina* inhabit continental shelf and upper slope environments (0-400 m depth) worldwide (Compagno *et al.*, 2005). In general, angel sharks have dorso-ventrally compressed bodies convergent with skates and rays, inhabit inner to outer shelf settings, and are small (1-2 m) epibenthic ambush predators that prey on crustaceans, cephalopods, bony fish, and small elasmobranchs (Compagno, 1984).

Order Lamniformes Berg, 1958
Family Cetorhinidae Gill, 1862
Genus *Cetorhinus* Gunnerus, 1765
Cetorhinus maximus Gunnerus, 1765

Figures 5.1-5.6, 5.9-5.14

Material examined – Three teeth (UCMP 219015, 219020, and 219021), and gill raker fragments (UCMP 219016-219018, 219050, 219073, 219074) from UCMP localities V99833, V99840, V99845, V99849, V99854.

Discussion – The referred teeth are small, with tetrahedral roots lacking a nutrient groove (figures 5.5-5.6, 5.9-5.14). The crowns are teardrop-shaped, lack crown feet, are not lingually-curved, and are basally narrower than the oral teeth of the genera *Rhincodon*, *Megachasma* and *Squatina*. The largest specimen (UCMP 219015) has a 6.9 mm long crown, while the smallest specimen (UCMP 219020) has a 4.3 mm long crown. These teeth bear a single, weakly developed lateral cusplet (*e.g.* figure 5.6). These teeth differ from the extinct species *Cetorhinus parvus* by having teeth without distinct root lobes and nutrient grooves; Miocene teeth referable to *Cetorhinus* have traditionally been referred to *C. parvus*, and Pliocene teeth to *C. maximus* (Cappetta, 1987; Long, 1993a). Extant *Cetorhinus maximus* display a wide variety of tooth

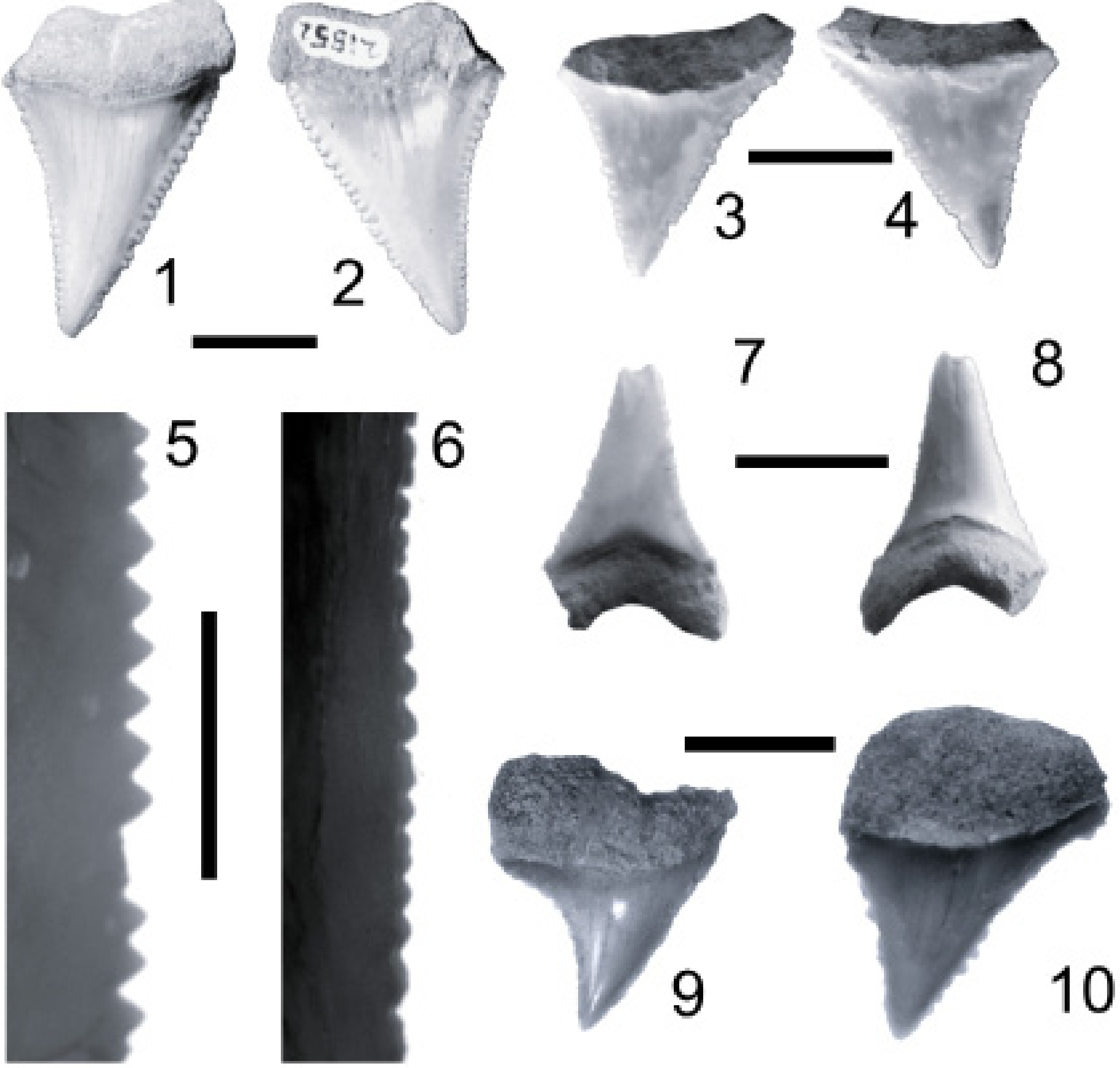

Figure 4. *Carcharodon* teeth from the San Gregorio section of the Purisima Formation, and a comparison of serration size between *Carcharodon carcharias* and *Carcharodon* sp. 1-2, UCMP 212862, tooth of *Carcharodon carcharias*, in lingual and labial aspect (respectively); 3-4, UCMP 219013, tooth of *Carcharodon carcharias* in lingual and labial aspect (respectively); 5, cutting edge of fossil *Carcharodon carcharias* (UCMP 212863); 6, cutting edge of *Carcharodon* sp. (UCMP 219022); 7-8, UCMP 219014, tooth of *Carcharodon carcharias* in labial and lingual aspect (respectively); 9, UCMP 219064, tooth of *Carcharodon carcharias* in lingual aspect; 10, UCMP 219012, tooth of *Carcharodon carcharias* in lingual aspect. Scale bar = 10 mm for 1-4 and 7-10, and 5 mm for 5-6.

morphologies (Shimada, 2002), and *C. parvus* teeth should be reanalyzed in light of recent observations of dental variation in *C. maximus*.

The gill raker fragments from the San Gregorio section are long (up to 21 mm; UCMP 219016) and less than one mm in width except at the anterior end, where the filament expands in width, curves, and connects to a hatchet-shaped osteodentine root (figures 5.1-5.4). The roots exhibit a minor anterior extension, and a long posterior extension. The raker 'crown' is covered in smooth enameloid. These specimens are morphologically identical to those of extant *Cetorhinus maximus*. Gill rakers of *C. parvus* are similar to *C. maximus*, albeit smaller (Herman, 1979; Long, 1993a). *Cetorhinus* fossils from California have been reported from the Lower Miocene Jewett and Olcese Sands (Mitchell & Tedford, 1973; Olson & Welton, 1986), the Middle Miocene Round Mountain Silt (Mitchell, 1965), the Upper Miocene Monterey Formation (Domning, 1978). Additional records from Baja California include the Middle Miocene Ysidro Formation (Domning, 1978) and the Upper Miocene Almejas Formation (Stewart, 1997; Barnes, 2008). *Cetorhinus* has an Eocene to Pliocene, worldwide fossil record (Cappetta, 1987; Cione & Reguero, 1998). The extant basking shark

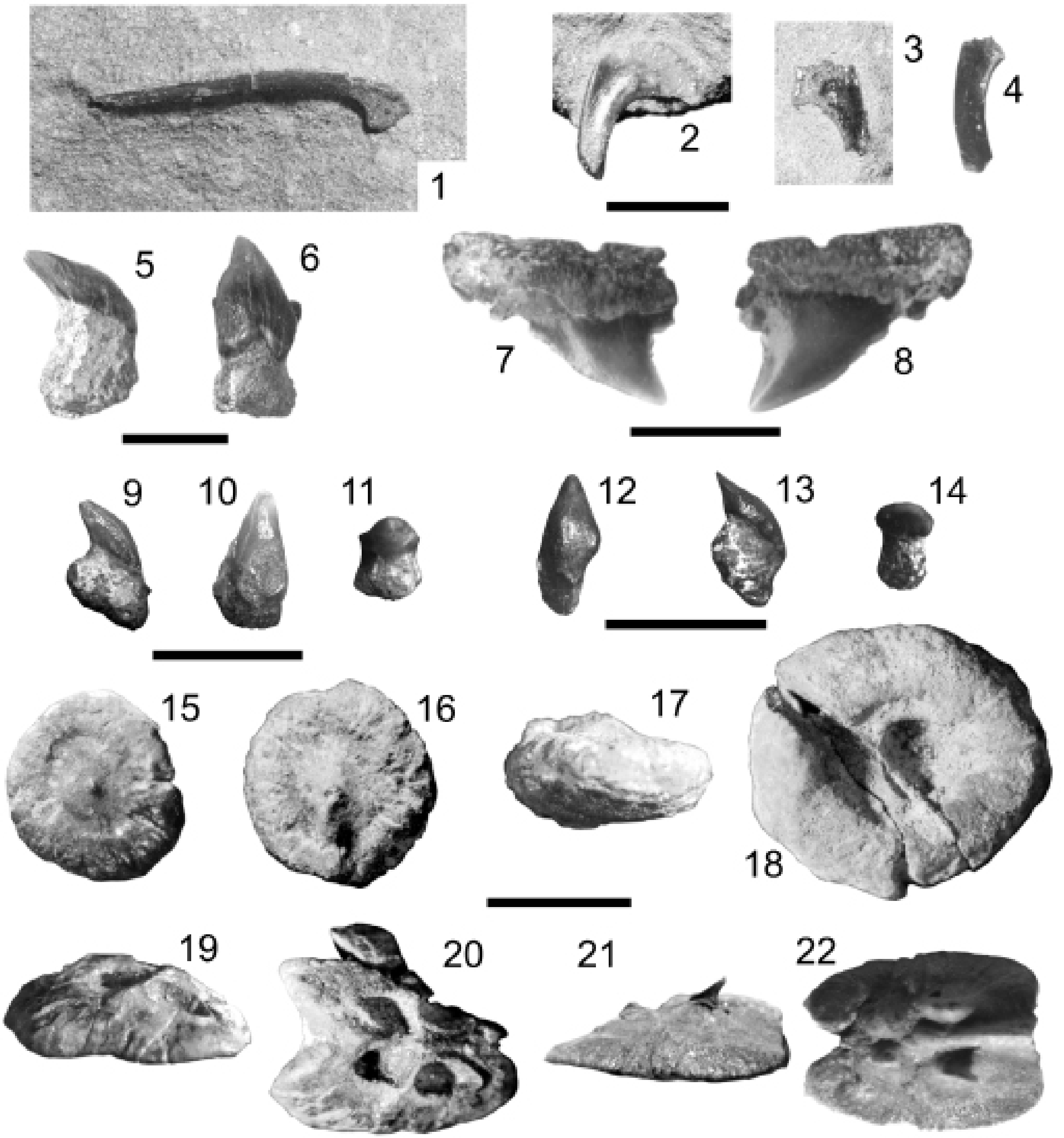

Figure 5. Elasmobranch teeth, gill rakers, and dermal denticles from the San Gregorio section of the Purisima Formation. 1, UCMP 219016, partial gill raker of *Cetorhinus maximus* (Gunnerus, 1765); 2, UCMP 219073, partial gill raker of *Cetorhinus maximus*; 3, UCMP 219074, partial gill raker of *Cetorhinus maximus*; 4, UCMP 219018, partial gill raker of *Cetorhinus maximus*; 5-6, UCMP 219015, tooth of *Cetorhinus maximus*, in lateral and labial aspect (respectively); 7-8, UCMP 219028, tooth of *Sphyrna* sp. (Rafinesque, 1810), in lingual and labial aspect (respectively); 9-11, UCMP 219021, tooth of *Cetorhinus maximus*, in lateral, labial, and lingual aspect (respectively); 12-14, UCMP 219020, tooth of *Cetorhinus maximus*, in lateral, labial, and lingual aspect (respectively); 15, UCMP 219044, dermal buckler of *Raja* sp., cf. *R. binoculata* (Girard, 1855), in external aspect; 16-17, UCMP 219041, dermal buckler of *Raja* sp., cf. *R. binoculata*, in lateral aspect; 18, UCMP 219072, dermal buckler of *Raja* sp., cf. *R. binoculata*, in external aspect; 19-20, UCMP 219047, dermal buckler of *Raja* sp., cf. *R. binoculata*, in lateral and external aspect (respectively); 21-22, UCMP 219063, dermal buckler of *Raja* sp., cf. *R. binoculata*, in lateral and external aspect (respectively). Scale bar = 10 mm for 1-4, and 15-22, and =5 mm for 5-14.

Cetorhinus maximus has an antitropical temperate distribution in the Pacific and Atlantic Oceans, including California waters (Ebert, 2003; Compagno *et al.*, 2005). *Cetorhinus maximus* is a gigantic (5-10 m long), epipelagic filter feeder that feeds on planktonic invertebrates, and inhabits continental shelf and slope waters (Compagno, 1984; Compagno *et al.*, 2005).

Family Lamnidae Müller & Henle, 1838
Genus *Carcharodon* Smith *in* Müller & Henle, 1838
Carcharodon carcharias Linnaeus, 1758

Figures 3.7-3.8, 3.12-3.22, 4.1-4.10

Material examined – Eleven teeth (UCMP 212860-21863, 219011-219014, 219025, 219027, and 219064) from UCMP localities V99833, V99834, V99838, and V99857.

Discussion – Jordan (1907) described and figured a tooth he referred to *Carcharodon arnoldi* from the San Gregorio section; *Carcharodon arnoldi* and other species of *Carcharodon* named from the Neogene of California were considered invalid by Cappetta (2006). The teeth reported here are broad and triangular, and are labiolingually compressed with irregular, coarse serrations on a cutting edge that continues to the crown foot (figures 3.7-3.8, 3.12-3.22). In smaller teeth (UCMP 212862, 219013; figures 4.1-4.4, 4.7-4.10) the serrations are very minute, and largest in larger teeth (UCMP 212863). Serrations are largest basally, and decrease in size towards the apex of the tooth crown. These teeth exhibit roughly 29-38 serrations on each cutting edge. Serrations of these specimens range from 10.5 to 16.6 serrations/cm; the largest serrations occur on UCMP 212863 (figure 4.5). The root lobes are wide and flat and lack a nutrient groove or torus (lingual protuberance) like in extant *Carcharodon carcharias*. Root lobes of lower anterior teeth (UCMP 212861, 219014) are labiolingually robust; in UCMP 212861, the root tips are tapered (figures 3.7-3.8). In upper anteriors (UCMP 212863, 219011) and upper laterals (UCMP 212860, 212862, 219013), the root lobes are labiolingually flattened and rectangular (figures 3.12-3.13, 3.16-3.17, 3.18-3.19). These teeth differ from *Carcharocles* by lacking a chevron-shaped neck (*sensu* Cappetta, 1987), lacking a lingually convex crown, lacking a torus, and having coarse, irregular serrations. These teeth differ from *Cosmopolitodus hastalis* by possessing serrations and from other species of *Isurus* by exhibiting wide, triangular crowns that are not distally inclined. The smallest tooth (UCMP 219064) has a crown height of 8.8 mm; the largest specimen (UCMP 212863) is broken and has a crown width of 46 mm, and originally probably measured approximately 50 mm in crown height.

Recent studies have indicated that the extant great white shark evolved directly from *Cosmopolitodus hastalis* through a number of character changes, which includes the development of serrations (Muizon & DeVries, 1985; Nyberg *et al.*, 2006; Ehret *et al.*, 2009). Unserrated *Cosmopolitodus hastalis* teeth occur in the Oligocene and Miocene, and persist through the Late Miocene in the Pacific Basin, while teeth with small serrations identified as *Carcharodon* sp. first occur in rocks of latest Miocene age (Yabe, 2000; Ehret *et al.*, 2009). The serrations of these teeth increase in size through time, with Late Pliocene teeth having large serrations of identical size to extant *Carcharodon carcharias* (Muizon & DeVries, 1985). This transition has been observed in strata in Peru, Japan, and California (Muizon & DeVries, 1985; Yabe, 2000; Stewart & Perry, 2002; Ehret *et al.*, 2009) and possibly Australia (*Carcharodon* sp. tooth, misidentified as *Isurus escheri* in Kemp, 1991: 151, Plate 19), suggesting that the *Cosmopolitodus-Carcharodon* transition was a Pacific Ocean-wide phenomenon.

The *Cosmopolitodus-Carcharodon* transition has been observed in the Santa Cruz section of the Purisima Formation. Teeth of *Cosmopolitodus hastalis* occur within the basal strata of the Purisima Formation near Santa Cruz; where glauconitic sand from the base of the Purisima Formation has yielded a K/Ar date of 6.9 ± 0.5 Ma (Clark, 1966; Madrid *et al.*, 1986). *Carcharodon* sp. teeth with minute serrations occur in a bed dated at 5.3 Ma (the 'crab marker bed' of Madrid *et al.*, 1986, which was identified as the Mio-Pliocene boundary by Powell *et al.*, 2007). *Carcharodon* sp. teeth with slightly larger serrations occur in the 'concretionary bed' of Perry (1989), which records a depositional hiatus ranging from 4.5 to 3.47 Ma (Madrid *et al,* 1986). These *Carcharodon* teeth have serrations that are intermediate in size between *Carcharodon* sp. from the lower bed and extant *Carcharodon carcharias* (Stewart & Perry, 2002); this increase in serration size is similar to and appears to be contemporaneous with the transition observed in the Pisco basin in Peru (Muizon & DeVries, 1985) and the Capistrano Formation in southern California (Stewart & Raschke, 1999).

Fossils of *Carcharodon* have previously been reported from several other localities in California, including the Pliocene Deguynos Formation (Mitchell, 1961), the Lower Pliocene

Lawrence Canyon Local Fauna of the San Mateo Formation (Domning, 1978; Barnes *et al.* 1981) the Upper Miocene-Lower Pliocene Capistrano Formation (Stewart & Raschke, 1999), the Plio-Pleistocene San Diego Formation (Deméré & Cerutti, 1982), and an unnamed Upper Pleistocene unit near Newport Bay, California (Long, 1993b; originally mapped to as the Palos Verdes Sand). *Carcharodon* has also been recorded in the Mio-Pliocene Almejas Formation of Baja California (Barnes, 1991, 2008; Stewart, 1997). Other fossils of *Carcharodon* have been reported from latest Miocene, Pliocene, and Pleistocene fossil localities worldwide (Cappetta, 1987; Yabe, 2000; Purdy *et al.*, 2001; Ehret *et al.*, 2009). The extant great white shark, *Carcharodon carcharias*, currently inhabits temperate waters worldwide, including coastal waters of California (Ebert, 2003; Compagno *et al.*, 2005). *Carcharodon carcharias* is a large (3-6 m long), macrophagous predator that feeds on fish, elasmobranchs, sea turtles, birds, and small marine mammals, and frequents temperate epipelagic and continental waters worldwide (Compagno, 1984; Compagno *et al.*, 2005).

Carcharodon sp.

Figures 3.20-3.22, 4.6

Material examined – UCMP 219022, a tooth from UCMP locality V99851.

Discussion – A specimen from the base of the San Gregorio section is a large lower second anterior tooth, and represents a different, earlier taxon than *Carcharodon carcharias*. The crown is broadly triangular and symmetrical (figures 3.20-3.22), with a flat labial surface with slight longitudinal enameloid wrinkles near the root, and a lingual surface of the crown which is strongly convex. The root lobes are elongate, and the mesial root lobe is slightly longer than the distal. A slight lingual protuberance is manifested on the strongly convex lingual portion of the root (figure 3.22). The crown height of this tooth is 59 mm. This tooth differs from the teeth from higher in the section referred above to *Carcharodon carcharias* in the possession of minute serrations. This tooth has 46 serrations on the distal cutting edge, and 11.5 serrations/cm (figure 4.6). Although the number of serrations per centimeter is similar to those reported above for *Carcharodon carcharias*, this specimen exhibits a much higher absolute number per cutting edge, and the height of individual serrations is smaller than in comparably sized teeth of *Carcharodon carcharias* (figures 4.5-4.6). The serration size is similar to teeth of *Carcharodon* sp. from the 'crab marker bed' of the Santa Cruz section, and to teeth of *Carcharodon* sp. from the Pisco Formation (Muizon & DeVries, 1985; Ehret *et al.*, 2009). UCMP 219022 was collected from the base of the San Gregorio section, which has yielded a diatom flora (figure 2) correlative with the Late Miocene (6.4-5.6 Ma) *Nitzchia reinholdii* zone (Powell *et al.*, 2007). The occurrence of teeth of *Carcharodon carcharias* in the middle and upper parts of the San Gregorio section with Pliocene mollusks and Late Pliocene ash correlations (3.5 and 2.5 Ma; Powell *et al.*, 2007) suggests that part of the *Cosmopolitodus*-*Carcharodon* transition is represented by *Carcharodon* fossils within the San Gregorio section, in addition to the Santa Cruz section. 'Transitional' teeth identified as *Carcharodon* sp. that possess minute serrations have been reported from the Lower Pliocene of Japan (Yabe, 2000), the Upper Miocene of Peru (Ehret *et al.*, 2009), the Upper Miocene Capistrano Formation (Stewart & Raschke, 1999), and the 'crab marker bed' of the Santa Cruz section of the Purisima Formation (Stewart & Perry, 2002).

Genus *Isurus* Rafinesque, 1810
Isurus oxyrinchus Rafinesque, 1810

Figures 3.23-3.27

Material examined – Two teeth (UCMP 219023 and 219024) from UCMP locality V99853.

Discussion – Specimens include one upper lateral tooth (UCMP 219024), and a lower second anterior tooth (UCMP 219023). The upper lateral tooth lacks lateral cusplets, has an unusually wide, gracile root, and a robust, wide, smooth, and distally inclined crown (crown height of 30.2 mm) with a flat labial surface and moderately convex lingual surface (figures 3.26-3.27). The smooth cutting edges of the crown are convex mesially, and nearly straight distally. This tooth is superficially similar to *Isurus planus*, due to the wide, relatively flat, distally inclined crown. The lower anterior tooth (UCMP 219023) exhibits more typical morphology for *Isurus oxyrinchus*, and has an elongate crown (crown height of 25.6 mm) with a slightly convex labial surface and a strongly convex lingual surface (figures 3.23-3.25). In distal aspect, the crown is curved lingually for most of its length, and is labially curved at its apex (figure 3.24). In labial aspect, the apex of the crown is mesially inclined, unlike *Isurus paucus*; this tooth also exhibits a much labiolingually thicker crown than *I. paucus*, *Isurus hastalis*, and *I. planus*, which typically have flattened crowns.

While the upper lateral tooth (UCMP-219024) superficially resembles the Miocene taxon *Isurus planus*, it differs by having narrower root lobes and a more convex lingual surface of the crown. Additionally, *I. planus* is only confidently known from Oligocene through lowermost Upper Miocene strata around the Pacific rim. Records of *I. planus* in California include the Middle Miocene Round Mountain Silt (Mitchell, 1965), the Middle Miocene Topanga Canyon Formation (Howard & Barnes, 1987), the Middle to Upper Miocene Santa Margarita Sandstone (Domning, 1978; Perry, 1993), and the upper Miocene Monterey Formation (Domning, 1978). Further south, *I. planus* has also been reported from the Middle Miocene Rosarito Beach Formation (Deméré *et al.*, 1984), and the Plio-Pleistocene San Diego Formation in Baja California (Ashby & Minch, 1984). Ashby & Minch (1984) also recorded *Carcharocles megalodon* from this locality, although neither *C. megalodon* nor *I. planus* have been found in the San Diego Formation since, and it is likely that these specimens were actually collected from the older Rosarito Beach Formation (the *I. planus* specimen, SDNHM 29744, is now labeled as having been collected from this older unit). Records from Oregon include the Lower Miocene Astoria Formation (Welton, 1972), and the Upper Miocene (8.5-6.5 Ma; Prothero *et al.,* 2001) Empire Formation of Oregon (Arnold & Hannibal, 1913). Other records indicate *I. planus* was restricted to the Pacific Ocean, with reports from the Late Oligocene and Middle Miocene of Australia (Fitzgerald, 2004; Kemp, 1991), and the Middle and Late Miocene of Japan (Kuga, 1985; Nakano, 1999).

Californian records of *Isurus oxyrinchus* include the Upper Miocene Santa Margarita Sandstone in Santa Cruz County (Perry, 1993), and the Miocene/Pliocene San Mateo Member of the Capistrano Formation (Barnes *et al.*, 1981). *Isurus oxyrhinchus* was also reported by Stewart (1997) from the Upper Miocene Almejas Formation of Baja California. Many other published records simply list "*Isurus* sp." from Neogene strata on the west coast of North America; many of these in all likelihood represent additional records of this species. *Isurus* has a Paleocene to Pleistocene fossil record worldwide (Cappetta, 1987; Long, 1993b). The extant shortfin mako (*I. oxyrinchus*) inhabits temperate and tropical waters worldwide, including the California coast (Ebert, 2003). Modern mako sharks are large (2-4 m) epipelagic, macrophagous predators that feed on cephalopods, fish, and small marine mammals, and are the fastest swimming sharks (Compagno, 1984; Compagno *et al.*, 2005).

Order Carchariniformes <u>Compagno</u>, 1973
Family Sphyrnidae <u>Gill</u>, 1872
Genus *Sphyrna* <u>Rafinesque</u>, 1810
cf. *Sphyrna* sp.

Figures 5.7-5.8

Material examined – One tooth, UCMP 219028, from UCMP locality V99836.

Discussion – This specimen is tentatively referred to *Sphyrna* due its robust, distally inclined crown with convex margins, strong distal notch differentiating the cusp from the distal crown foot, and minute serrations (figures 5.7-5.8), the combination of which identifies it as a hammerhead shark (Cappetta, 1987). The crown height of this specimen is 6.3 mm; it also has a large root with a shallow nutrient groove that does not reach the base of the crown. This specimen differs from *Rhizoprionodon* by having a broader primary cusp. UCMP 219028 exhibits similarities with extant *Sphyrna mokarran* and *Sphyrna zygaena*, with its robust, distally inclined primary cusp and minute serrations; however, the incompleteness of this specimen precludes a specific identification. Fossil teeth of *Carcharhinus* are often misidentified as hammerhead shark teeth (Cappetta, 1987). Welton (1972) reported a single occurrence of *Sphyrna* in the Upper Eocene Spencer Formation of Oregon. *Sphyrna* has previously been reported in California and Baja California from the Lower Miocene Jewett Sand (Mitchell & Tedford, 1973), the Middle Miocene Rosarito Beach Formation (Deméré *et al.*, 1984), the Middle Miocene Round Mountain Silt (Mitchell, 1965) and the Mio-Pliocene Capistrano Formation (Bonner & Gilmour, 1988). Additionally, Welton (1972) reported a single occurrence of *Sphyrna* in the Late Eocene Spencer Formation of Oregon. Three extant species of *Sphyrna* can be found in California waters, including *Sphyrna lewini*, *Sphyrna tiburo*, and *Sphyrna zygaena* (Ebert, 2003). Extant hammerhead sharks inhabit temperate and tropical continental shelves and slopes (0-275 m depth) worldwide, and are medium sized (1-6 m) epipelagic predators that feed on invertebrates, bony fish, and other elasmobranchs (Compagno, 1984; Compagno *et al.*, 2005).

Order Rajiformes Berg, 1940
Family Rajidae Blainville, 1816
Raja Linnaeus, 1758
Raja sp., cf. *R. binoculata* Girard, 1855

Figures 5.15-5.22, 6.3-6.14

Material examined – Multiple palatoquadrate (UCMP 219068-219070) and mandibular cartilages (UCMP 219033, 219034, 219071), and dermal denticles (UCMP 219036-219054, 219056-219059, and 219063) from UCMP localities V99833, V99834, V99835, V99840, V99842, V99843, V99844, V99847, and V99854.

Discussion – Four palatoquadrate cartilages and eleven mandibular cartilages were collected from the San Gregorio section, in varying states of completeness. These are prismatically calcified elements, and preserved in bonebeds alongside bones and teeth as distinct, competent bioclasts; with the exception of cetacean bones, these elements locally constitute the most abundant type of vertebrate fossil. The palatoquadrate cartilages lack an orbital process and instead have a labiolingually compressed, tabular-shaped mesial projection, which in life bore the upper dentition (figures 6.3-6.8). Short ridge-like otic processes occur labially on the dorsolateral margin of the palatoquadrate. The most proximal portion is developed into a subspherical palatoquadrate condyle, which articulates with the concave mandibular articular fossa (Dean & Motta, 2004). Immediately mesial to the commissural process is the shallow palatoquadrate cavity, which in turn receives the mandibular knob (Dean & Motta, 2004). The palatoquadrate exhibits faintly visible prismatic cartilage, which is often exposed in areas of slight abrasion and in cross section. The surface texture is primarily fibrous, concealing the underlying prismatic cartilage. The mandibular cartilages (figures 6.9-6.14) bear a dorsoventrally compressed mesial portion that is curved anteriorly toward the symphysis. This portion has subparallel anterior and posterior margins, and is wider toward the quadratomandibular joints. An elongate, shallow fossa is oriented diagonally in an anterolateral direction across the lingual surface of the mandibular cartilage (figure 6.13). Rough surface texture characterizes the fossa, often with parasagittal striations; this region corresponds to the dental file-bearing portion of the mandibular cartilage. On the posterolabial margin of the element lies the sustentaculum, which forms a parasagittal ridge, as well as a dorsolaterally oriented process, the dorsal flange of the sustentaculum. In extant batoids, the dorsal flange articulates with the hyomandibula, the sole cranial connection of the jaws (Dean & Motta, 2004). Immediately posterior to this is the mandibular articular fossa, which receives the palatoquadrate condyle. Mesial to this lies the mandibular knob, which articulates with the palatoquadrate concavity; batoids bear a unique dual quadratomandibular joint that restricts lateral movement of the mandibular arch (Dean & Motta, 2004). The mandibular cartilage is also constructed from prismatic cartilage, obvious in cross section and abraded portions, and rarely visible along the posterolateral margin of the element. The mesial morphology of these elements indicates the symphysis was unfused, unlike many extant durophagous batoids, such as myliobatids.

Among Rajidae that currently inhabit the temperate northeast Pacific Ocean these elements compare best with those of extant *Raja binoculata* in size and morphology (figures 6.1-6.2). These elements differ from Dasyatidae by having less robust otic processes and sustentaculi, and comparatively more slender mesial portions of palatoquadrate and mandibular cartilages. The genus *Rhinobatos* exhibits significantly smaller otic processes, and much larger sustentaculi, but lacks such a posterolateral projection of the dorsal flange. These elements differ from those of Myliobatidae and Rhinopteridae by not having a widely expanded mesial surface with a fused symphysis. This taxon differs from the genera *Torpedo* and *Gymnura* by having more robust palatoquadrate and man-

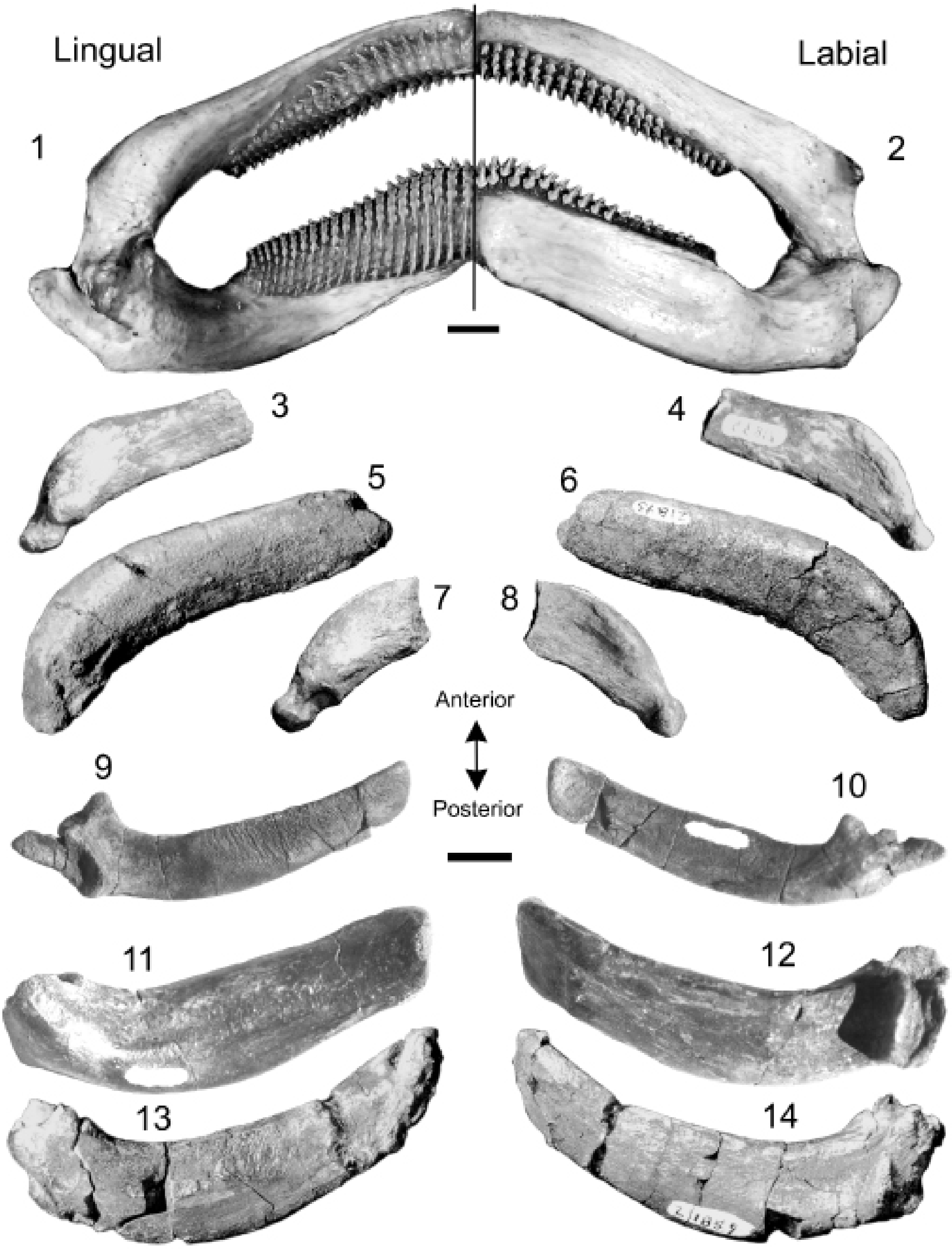

Figure 6. Cranial elements of modern and fossil *Raja* from the San Gregorio section of the Purisima Formation. 1-2, UCMP 83662, articulated palatoquadrate and mandibular cartilages of modern *Raja binoculata*.; 3-4, UCMP 219069, proximal palatoquadrate cartilage of *Raja* sp., cf. *R. binoculata* (reversed); 5-6, UCMP 219068, palatoquadrate cartilage of *Raja* sp., cf. *R. binoculata* (reversed); 7-8. UCMP 219070, proximal palatoquadrate cartilage of *Raja* sp., cf. *R. binoculata*; 9-10, UCMP 219034, complete mandibular cartilage of *Raja* sp., cf. *R. binoculata* (reversed); 11-12, UCMP 219022, complete mandibular cartilage of *Raja* sp., cf. *R. binoculata* (reversed); 13-14, UCMP 219071, complete mandibular cartilage of *Raja* sp., cf. *R. binoculata*. Scale bar is 10 mm.

dibular cartilages. Wedgefish and guitarfish (Rhinidae) differ from this taxon by exhibiting laterally expanded sustentaculi and associated dorsal flanges, in addition to subspherical expansions of the tooth pad portion near the symphysis of either element. Mobulidae possess a very gracile, straight, and extremely labiolingually flattened mesial portion of both jaw elements, differing strongly from these fossil cartilages. Pristidae have much less robust otic flanges and sustentaculi than the fossil taxon. Prismatically calcified mandibular and palatoquadrate cartilages preserved in this manner have not been reported for any other batoid from the Neogene of the Northeast Pacific. Extensive examination of Neogene museum collections (SCMNH, SDNHM, UCMP) have not yielded similar specimens from other batoid taxa.

Additional elements tentatively referred to *Raja* sp. cf. *R. binoculata* include a large assortment of dermal denticles or bucklers (figures 5.15-5.22), and are nearly as abundant as the calcified cartilage specimens. These denticles are similar to dorsal and ventral 'bucklers' of Rajidae, which have smooth to slightly striated, conical to disc-shaped osteodentine roots, with variously shaped enameloid cusps. The specimens reported here are disc-shaped, with very small enameloid cusps positioned in a slight depression just below the level of the rim of the denticles. A hollow cavity in the middle of the denticle is visible when the enameloid cap is missing (figure 5.18). The morphology of these elements is very similar to ventral bucklers of *Raja clavata* (Reynat & Brito, 1994). Additionally, some specimens (UCMP 219047, 219053, and 219063) appear to represent four coalesced denticles (figures 5.19-5.22). The enameloid caps are missing on most of these specimens, and each denticle has taken on a quadrilateral shape, and the region of the enameloid cap has migrated toward the center of the element, so that all four caps abut each other. One specimen (UCMP 219063) is preserved with the caps in place, which bear small, obliquely oriented enameloid spines (figures 5.21-5.22). Similar examples of coalesced denticles were described from fossil denticles of the stingray *Dasyatis centroura* from the Pliocene of North Carolina (Purdy *et al.,* 2001). Although no teeth referable to this taxon have been identified from this locality, teeth of *Raja* sp. have been collected from the Santa Cruz section of the Purisima Formation (F.A. Perry, personal communication, 2006). As only a limited amount of screening was conducted at this locality, most microvertebrate specimens were recovered from the outcrop surface, and small specimens like *Raja* teeth are easily overlooked.

Fossils of *Raja* have been reported in Oregon from the Upper Eocene Nestucca Formation, the Middle Oligocene Pittsburg Bluff Formation, and the uppermost Oligocene-Lower Miocene Nye Mudstone (Welton, 1972). *Raja* is known in California from the Lower Miocene Jewett Sand (Olson & Welton, 1986), the Upper Miocene Almejas Formation (Stewart, 1997; Barnes, 2008), and from an unnamed Upper Pleistocene unit near Newport, California (Long, 1993b). Prismatically calcified palatoquadrate and mandibular cartilages have been observed in museum collections from the Pliocene portion of the Santa Cruz section of the Purisima Formation, the Middle Pleistocene Moonstone Beach Formation of Humboldt County, California, the Pliocene to Lower Pleistocene Falor Formation of Humboldt County, California, and the Middle Pleistocene Port Orford Formation of southwestern Oregon (Boessenecker, unpublished data). Extant Rajidae are small (1-2 m) epibenthic predators that feed on invertebrates and fish and live on continental shelves and slopes; several extant species of *Raja* inhabit temperate waters of the northeast Pacific (Ebert, 2003).

Order Perciformes Bleeker, 1859
Family Scombridae Rafinesque, 1815
Genus *Thunnus* South, 1845
Thunnus sp.

Figures 7.1-7.2

Material examined – One vertebra, UCMP 219066, from UCMP locality V99849.

Discussion – Tuna vertebrae are rather common in some late Neogene deposits (Purdy *et al.* 2001). However, there are few known from the Purisima Formation. This specimen possesses typical scombrid features including a simple overall morphology, with a single lateral septum that is broadly convex and dorsoventrally thick anteriorly and posteriorly, which is somewhat narrow and 'pinched' toward the middle (figures 7.1-7.2). A pair of septa occurs on the dorsal and ventral sides of the centrum, and possesses the broken bases of the neural and haemal arches.

Deep fossae occur dorsal and ventral to the lateral septa. On the anteriormost portion of each lateral septum is a small foramen adjacent to the broken base of the intramuscular process. In anterior and posterior view of extant *Thunnus* vertebrae and the fossil specimen, the dorsal margin of the centrum has a slight concavity at the midline (figure 7.1). The scombrid morphology and the large size of UCMP 219066 identify this specimen as *Thunnus*. Although unidentified scombrid fossils were reported by Stewart (1997) from the Almejas Formation of Baja California, *Thunnus* has not been reported from the Neogene of the northeast Pacific, and occurs in the Pliocene of North Carolina (Purdy *et al.*, 2001). Extant species of tuna are medium sized (1-2 m), epipelagic predators that inhabit tropical and temperate oceans worldwide, and are among the fastest of all marine vertebrates (Eschmeyer *et al.*, 1999).

Order Pleuronectiformes Bleeker, 1859
Family Paralichthyidae Hensley & Ahlstrom, 1984
Genus *Paralichthys* Girard,1858
Paralichthys sp.

Figures 7.3-7.4

Material examined – One vertebra, UCMP-219067, from UCMP locality V99839.

Discussion – A single small, partial vertebra, exhibits lateral paper-thin septa characteristic of *Paralichthys*, which converge in the middle of the centrum, but diverge anteriorly and posteriorly; where the septa diverge, deep interstitial dossae occur (figure 7.4). Although broken, the centrum exhibits the oval shaped cross section (figure 7.3), which can become nearly circular or hexagonal in fossil and modern specimens. Deep fossae occur dorsal and ventral to the lateral septa. A second specimen (UCMP 219075) is more complete, has a circular centrum, and a small portion of the base of the neural arch preserved, which appears to be pathologic and swollen, shifting the neural canal laterally. Deep recesses occur dorsolaterally, and two lateral septa occur, again with the anteriorly and posteriorly diverging morphology. However, the septa of this specimen are thicker and exhibit less branching anteriorly and posteriorly. This vertebra is tentatively referred to *Paralichthys*, but may actually represent another pleuronectiform. Fossils of *Paralichthys* have previously been reported from the Upper Miocene of Baja California (Stewart, 1997; Barnes, 2008), and the Pleistocene of southern California (Long, 1993b). Extant *Paralichthys* or large-tooth flounders are small to medium-sized (1-1.5 m) epibenthic ambush predators that feed on fish and invertebrates, have both eyes on the left side of their body, live in water to 200 m depth on the continental shelf and upper slope. Several species currently live in temperate waters of the northeast Pacific (Eschmeyer *et al.*, 1999).

Class Aves Linnaeus, 1758
Order Pelecaniformes Sharpe, 1891
Family Sulidae Reichenbach, 1849
Morus Vieillot, 1816
Morus sp.

Figures 8.1-8.2

Material examined – UCMP 130134, one left humerus from UCMP locality V7085.

Discussion – This specimen is a nearly complete, well preserved humerus with some minor damage to the proximal end (figures 8.1-8.2). Features that identify this humerus as a gannet (*Morus*) rather than a booby (*Sula*) include a longer deltoid crest than bicipital crest, gradually rounded internal margin of the bicipital crest, and an apneumatic olecranon fossa, the medial margin of which is not overhanging (Chandler, 1990). In addition, a large partial phalanx (UCMP 219031, figures 8.5-8.6) may also be referable to *Morus* sp.

Morus humeralis and *M. recentior* have been reported from the Plio-Pleistocene San Diego Formation by Chandler (1990). The humerus of *M. humeralis* is evidently much smaller than the San Gregorio specimen. This specimen is within the size range of extant *Morus bassanus*. Additionally, the much smaller size of the pneumatic opening precludes referral to *M. humeralis*. The large size of this specimen excludes it from all fossil species of *Morus* except *M. magnus* and *M. lompocanus* (Chandler, 1990), both of which are known from the Upper Miocene Monterey, Sisquoc, and Santa Margarita Formations of California (Domning, 1978; Howard, 1978). Humeri of *Morus peninsularis* differ from this specimen in their smaller size, and having a deeper brachial fossa. Specific

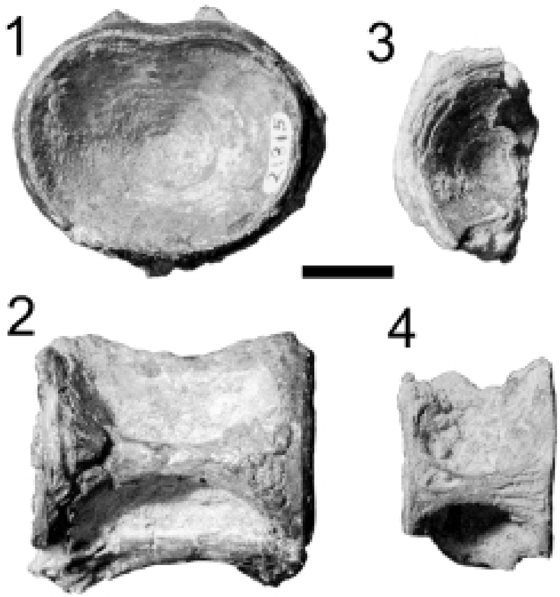

Figure 7. Vertebrae of teleost fish from the San Gregorio section of the Purisima Formation. 1-2, UCMP 219066, vertebral centrum of *Thunnus* sp. (South, 1845), in anterior and lateral aspect (respectively); 3-4,UCMP 219067, partial vertebral centrum of *Paralichthys* sp. (Girard, 1858), in anterior (or posterior) and lateral aspect (respectively). Scale bar is 10 mm.

identification of this well-preserved specimen should await discovery and study of additional humeri of *Morus* from the late Neogene of the northeast Pacific. Specimens of *Morus* have previously been collected from the Santa Cruz section of the Purisima Formation (F.A. Perry, personal communication, 2006). Although gannets are extinct in the northeast Pacific Ocean, fossils of *Morus* have been reported from the middle Miocene Sharktooth Hill Bonebed (Miller, 1961), the Upper Miocene Monterey and Sisquoc Formations (Miller, 1925; Howard, 1978), the Upper Miocene Santa Margarita Sandstone (Domning, 1978), the Upper Miocene Almejas Formation (Howard, 1971), the Middle to Upper Pliocene San Diego Formation (Chandler, 1990), and from Upper Pleistocene Palos Verdes Sand (Howard, 1936; Miller, 1971). This find demonstrates that gannets inhabited much of the California coast prior to their extirpation during the Pleistocene. Three species of *Morus* currently inhabit the Atlantic and the southeast Pacific Ocean (Nelson, 1978). Extant gannets are large, diving seabirds that feed on pelagic fish and breed on rocky shores and islands (Nelson, 1978).

Order Charadriformes Huxley, 1867
Family Alcidae Vigors, 1825
Genus *Mancalla* Lucas, 1902
Mancalla diegensis Miller, 1937

Figures 8.3-8.4

Material examined – One humerus (UCMP 219060) from UCMP locality V99833.

Discussion – The robust morphology, shaft curvature, and thick cortex identify this humerus as the extinct flightless auk *Mancalla*. The humeral shaft of *Mancalla* is dorsoventrally flattened and laterally broad, and curved medially relative to other Alcidae (figures. 8.3-8.4). This specimen differs from *Praemancalla* by having a less compressed shaft and distal end, and a mediolaterally more expanded shaft (Howard, 1966). UCMP 219060 differs from *Mancalla milleri* in its larger size, by possessing a well-developed ligamental attachment on the bicipital crest, and having a more convex distal margin of the bicipital crest, both of which are characteristics of *Mancalla diegensis* (Howard, 1970). Unlike *Mancalla californiensis*, this specimen has a straighter shaft and a muscle scar in the pneumatic fossa with edges that converge anteriorly, as seen in *M. diegensis*, and which are parallel in *M. californiensis* (Howard, 1970). *Mancalla cedrosensis* differs from UCMP 219060 in lacking a well developed ligamental scar on the bicipital crest, and having a relatively straight distal margin of the bicipital, which in this specimen (and other *M. diegensis*) is very convex, nearly forming a 90° angle (Howard, 1970; 1971). Additionally, this specimen differs from *M. cedrosensis* by having a more laterally oval-shaped triceps insertion distal to the humeral head. This specimen differs from *Mancalla emlongi* and a new species of *Mancalla* from the Mio-Pliocene Capistrano Formation and San Mateo Member (of the Capistrano Formation) by its smaller size and less robust morphology. A complete tibiotarsus from the San Gregorio section (UCMP-219030, figures 8.7-8.8) may represent *Mancalla diegensis*, but is only identified to the family Alcidae.

The large size of the humerus, breadth of the tricipital insertion, relatively straight shaft, presence of a muscle scar with converging margins within the pneumatic fossa, and a well-developed ligamental attachment on the strongly convex bicipital crest all indicate that this hu-

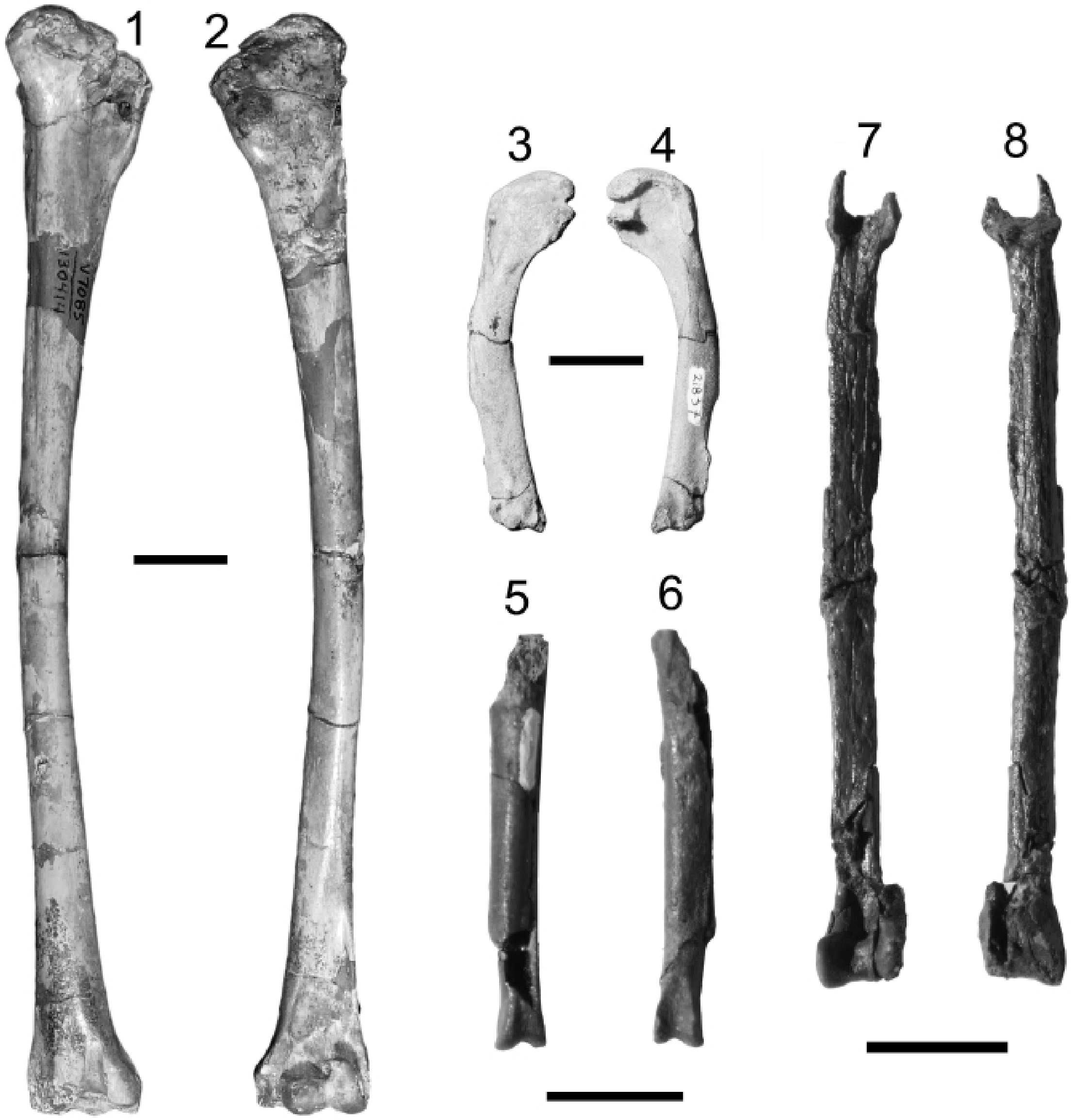

Figure 8. Avian bones from the San Gregorio section of the Purisima Formation. 1-2, UCMP 130414, humerus of *Morus* sp. (Viellot, 1816), in ventral and dorsal aspect (respectively); 3-4, UCMP 219060, humerus of *Mancalla diegensis* (Miller, 1937), in dorsal and ventral aspect (respectively); 5-6, UCMP 219031, partial phalanx, Aves indet. in dorsal and plantar aspect (respectively); 7-8, UCMP 219030, tibiotarsus of Alcidae indet., in anterior and posterior aspect (respectively). Scale bars = 20 mm.

merus is identifiable as *Mancalla diegensis*, previously recorded from the Plio-Pleistocene San Diego Formation (Chandler, 1990), the Lower Pliocene Lawrence Canyon Local Fauna of the San Mateo Member of the Capistrano Formation (Howard, 1982), and the Lower Pleistocene Moonstone Beach Formation (Kohl, 1974). Additional records from the Purisima Formation include a new large species of mancalline alcid (N.A. Smith, personal communication, 2008), and *Mancalla milleri*, both from the Santa Cruz section of the Purisima Formation. *Mancalla* was a small, penguin-convergent, piscivorous wing-propelled, flightless diving bird that inhabited the northeast Pacific from Baja California to northern California during the latest Miocene, Pliocene, and Pleistocene (Howard, 1970, 1971, 1982; Kohl, 1974).

Marine Mammals

Abundant bones and teeth of various marine mammals were collected from the San Gregorio section (representing 13 taxa of marine mammals; table 1), and will be described in a separate publication. However, as some of the marine mammals have implications for the age of this deposit (see below) a brief discussion of the mammalian assemblage is pertinent. An unidentified otariid fur seal is represented by several elements including a tooth, temporal bone, and some postcrania. An odobenid walrus (*Dusignathus* sp.) is represented by a partial radius and isolated vertebrae. Five odontocete cetaceans are potentially represented by 1) a cranium and lower jaws that is congeneric (or conspecific) with an undescribed genus and species of bizarre phocoenid from the San Diego Formation (Racicot *et al.*, 2007); 2) a partial skull of a phocoenine porpoise; 3) a tympanic of a large, pilot whale-like globicephaline; 4) a juvenile skull with tympanoperiotics of *Parapontoporia* sp., cf. *P. sternbergi* and 5) a large squamosal of an possible physeteriod. Mysticetes are represented by a large suite of bones and abundant bone fragments, including tympanic bullae of a large balaenid and the smaller right whale, *Balaenula*. Balaenopterids are represented by several tympanics of a small balaenopterid, fragments of a very large petrosal, a well preserved cranium (Balaenopteridae new species). The bizarre dwarf cetotheriid mysticete *Herpetocetus bramblei* is represented by a single, large lower jaw, while a separate taxon (*Herpetocetus* sp.) is represented by two petrosals, a posterior process of a petrosal, a tympanic bulla, and a partial dentary.

Discussion

This study reports several first occurrences for the Purisima Formation. The only previously recorded non-mammalian marine vertebrates from this unit are the sharks *Isurus hastalis*, *Carcharodon*, *Hexanchus*, the bat ray *Myliobatis*, and the booby *Sula*, from the Santa Cruz section of the Purisima Formation (Perry, 1977; Stewart & Perry, 2002). *Cetorhinus maximus*, *Morus* sp., *Pristiophorus* sp., *Raja* sp., cf. *R. binoculata*, and *Squatina* sp., constitute new published records for the Purisima Formation, although unpublished specimens of these taxa are currently under study from the Santa Cruz section of the Purisima Formation (F.A. Perry and R.W. Boessenecker, unpublished data). New records for the Purisima (including unpublished material) include *Sphyrna* sp., *Thunnus* sp., and *Mancalla diegensis*. In addition to these specimens, several marine mammals including a fur seal, a walrus, porpoises, a pilot whale like odontocete, a large odontocete, and four baleen whales occur at this locality. Altogether, 26 taxa are represented by the San Gregorio assemblage (table 1). In comparison, nearly 80 taxa have been identified from the Santa Cruz section of the Purisima Formation, although this higher number is likely due to more intensive collecting and pooling of multiple assemblages (F.A. Perry and R.W. Boessenecker, unpublished data).

Age of the San Gregorio Section

As outlined above, the precise age of the Purisima Formation west of the San Gregorio Fault has been modified by various researchers over time. Previous authors (Cummings *et al.*, 1962; Durham & Morgan, 1978; Gavigan, 1984) have concluded a latest Miocene (ca. 8-5 Ma) age for these outcrops based on invertebrate fossils from the upper San Gregorio section. Powell *et al.* (2007) reported a Late Miocene (6.4-5.6 Ma, *Nitzchia reinholdii* zone) diatom flora from the base of the San Gregorio section (figure 2). However, Sarna-Wocjicki *et al.* (1991) and Powell *et al.* (2007) utilized chemical fingerprinting of ash beds in the Purisima Formation to yield ash correlations of 3.35-2.5 Ma (figure 2), indicative of a Middle Pliocene age. Vertebrate fossils outlined above may help evaluate previously made age determinations. Many taxa described herein have chronologic ranges that are too long or are too poorly known to be of use; these include *Cetorhinus maximus*, cf. *Hexanchus*, *Isurus oxyrinchus*, *Morus* sp., *Paralichthys* sp., *Pristiophorus* sp., cf. *Sphyrna*, *Squatina* sp., and *Thunnus* sp.; however, the age implications of the remaining taxa are discussed below.

Fossil teeth of the shark *Carcharodon* have only been reported from the Quaternary, Pliocene, and latest Miocene. Weakly serrated *Carcharodon* teeth are typical of latest Miocene and earliest Pliocene strata (Muizon & DeVries, 1985; Stewart & Perry, 2002; Ehret *et al.*, 2009), while coarsely serrated teeth occur in Pliocene and younger sediments, and are typical of the extant great white shark, *Carcharodon carcharias* (Muizon & DeVries, 1985; Ehret *et al.*, 2009). The teeth of *Carcharodon carcharias* described herein (figures 3.7-3.8, 3.12-3.22) have larger serrations than those of latest Miocene *Carcharodon* sp. from Peru (Ehret *et al.*, 2009) and Japan (Yabe, 2000), as well as *Carcharodon* teeth from the 'crab marker bed' in the Santa Cruz section; this bed approximates the 5.33 Ma Miocene/Pliocene boundary (Powell *et al.*, 2007). The teeth reported herein have serrations as large as extant *Carcharodon carcharias*, as well as *Carcharodon* teeth from the Plio-Pleistocene San Diego Formation (Deméré & Cerutti, 1982). Therefore, the presence of *Carcharodon carcharias* teeth indicates a Middle Pliocene (or younger) age for the upper and middle parts of the San Gregorio section. However, the occurrence of a weakly serrated 'transitional' *Carcharodon* sp. tooth (figures 3.20-3.22), in concert with a Late Miocene diatom flora, suggests a latest Miocene age for the base of the San Gregorio section.

Numerous calcified palatoquadrate and mandibular cartilages of *Raja* sp., cf. *R. binoculata* were recovered from the San Gregorio section (figures 5.15-5.22). The only other known occurrences of these cartilaginous cranial elements are in Pliocene strata of the Santa Cruz section of the Purisima Formation, the Lower Pleistocene Falor Formation and Moonstone Beach Formation of northern California, and the Middle Pleistocene Port Orford Formation of southwestern Oregon; these all appear to represent one species (Boessenecker, personal observation). Although fossil teeth of *Raja* are known from Eocene through Pleistocene strata in western North America (Welton, 1972; Long, 1993b; Stewart, 1997), these cranial elements only occur in Middle Pliocene through Lower Pleistocene strata in California and Oregon. The occurrence of these cranial elements strongly indicates a Middle Pliocene to Pleistocene age for the upper and middle San Gregorio section. The occurrence of the flightless auk *Mancalla diegensis* (figures 8.3-8.4) is significant as this taxon is only known from Pliocene and Pleistocene sediments of California (see Systematic Palaeontology). The presence of *Mancalla diegensis* indicates a Middle Pliocene to Pleistocene age for the upper and middle San Gregorio section.

Additionally, undescribed marine mammal fossils from this locality are also indicative of a Middle to Late Pliocene age. A phocoenid cranium and lower jaw from the San Gregorio section is congeneric with a new genus recently reported by Racicot *et al.* (2007) from the Plio-Pleistocene (4-2 Ma) San Diego Formation. A dentary and several periotics and tympanics of *Herpetocetus* sp. are also from this locality. Similar fossils (*Herpetocetus bramblei*, *Herpetocetus* sp.) occur in the 'crab marker bed' and younger strata (5.3-3.5 Ma; Pliocene) in the Santa Cruz section and the Pliocene/Pleistocene San Diego Formation (Deméré & Cerutti, 1982). *Herpetocetus*-like fossils (previously identified as *Nannocetus*; Barnes, 1976; Barnes *et al.*, 1981) occur in the Upper Miocene (9-6 Ma) San Luis Rey River Local Fauna of the San Mateo Member (of the Capistrano Formation) and Upper Miocene (12-10 Ma) Santa Margarita Sandstone (Boessenecker, 2011). This older taxon exhibits different dentary morphology from the younger Purisima and San Diego specimens, which are morphologically most similar to the *Herpetocetus* sp. specimen from the San Gregorio section. Although significantly more work is needed for *Herpetocetus*, this occurrence also indicates a Pliocene age for the San Gregorio section.

While the longevity of many of the fossil taxa reported herein preclude their usefulness for determining a Late Miocene age or a younger Pliocene age (or otherwise) for the San Gregorio section of the Purisima Formation, several identified above (including *Carcharodon*, *Raja* sp., cf. *R. binoculata*, *Mancalla diegensis*, Phocoenidae new genus, and *Herpetocetus* sp.) can help elucidate the age relationships of this locality. Taken in full, these taxa indicate a Pliocene age for the upper and middle parts of the San Gregorio section, and several of these strongly indicate a Middle to Late Pliocene age, correlative with the 4-2 Ma San Diego Formation of southern California. This is in accordance with the ash correlation dates for the two tephra units (3.35 Ma, and 2.5 Ma) reported by Sarna-Wojcicki *et al.* (1991) and Powell *et al.* (2007). While the upper and middle parts of the San Gregorio section are most likely Middle to Late Pliocene, the combined presence of a *Carcharodon* sp. tooth with a Late Miocene diatom flora suggests a somewhat older age for the base of the San Gregorio section (figure 2), which is also in accordance with the Late Miocene correlations by Cummings *et al.* (1962), Durham & Morgan (1978), and Gavigan (1984). However, it is important to note that all of the invertebrates examined by these authors were collected from the upper and middle parts of the San Gregorio section, herein determined to be Middle Pliocene or younger. Interestingly, Gavigan (1984) correlated the San Gregorio section with the Falor Formation which was then considered to be Late Miocene; the Falor Formation is now known to be latest Pliocene and Pleistocene in age (Nilsen & Clarke, 1989). The invertebrate assemblages and correlations of Durham & Morgan (1978) and Gavigan (1984) should be investigated further, and reevaluated in light of modern advances in biostratigraphy of Neogene marine strata in California.

Conclusions

The Purisima Formation near Halfmoon Bay, California, has yielded a diverse assemblage of 26 taxa, including sharks (*Carcharodon carcharias*, *Carcharodon* sp., *Cetorhinus maximus*, cf. *Hexanchus*, *Isurus oxyrhincus*, *Pristiophorus* sp., cf. *Sphyrna*, *Squatina* sp.) skates (*Raja* sp., cf. *R. binoculata*), bony fish (*Paralichthys* sp., *Thunnus* sp.), birds (*Mancalla diegensis*, *Morus* sp.), and marine mammals including pinnipeds and cetaceans. A Late Miocene age for this locality was previously proposed based on lithologic correlations and supported by early molluscan biostratigraphy, while a Middle to Late Pliocene age was indicated by ash correlations. The stratigraphic range of some of these vertebrate taxa supports a Middle to Late Pliocene age for the upper and middle parts of the San Gregorio section, supporting the ash correlations. However, the presence of *Carcharodon* sp. in concert with a diatom flora at the base of this section indicates a Late Miocene to Early Pliocene age for the lower part of the San Gregorio section. In this study, the utilization of the vertebrate assemblage to evaluate the age of these strata demonstrates that both the biostratigraphic and tephrochronologic age determinations are correct. Future studies utilizing a holistic approach to other vertebrate assemblages may help resolve age determinations for other Neogene marine deposits in California.

Note Added In Proof

During the period in which this article was in review, two studies relevant to this article have been published (or accepted for publication). Both of these studies concern fossil birds of the San Gregorio vertebrate assemblage, or the taxonomy of the bird fossils reported herein. The first is Boessenecker & Smith (In press), which reports a large humerus of a gigantic bony-toothed bird, *Pelagornis* sp. The fossil was properly identified after this article was submitted for publication. This fossil represents one of the largest flying birds ever in North America and one of the youngest pelagornithid fossils worldwide, and adds another taxon to the San Gregorio assemblage, bringing the total to 27. The second article is Smith (2011), which included a taxonomic revision of mancalline auks from California, and descriptions of several new species of Mancallinae. The holotype of *Mancalla diegensis* is a femur, and because alcid femora are not diagnostic to the species level, Smith (2011) considered this taxon to be Pan-Alcidae incertae sedis. A new species, *Mancalla lucasi*, was erected for diagnostic material formerly referred to *Mancalla diegensis* (Smith, 2011), and the fossil specimen identified above as *Mancalla diegensis* should now be regarded as a referred specimen of *Mancalla lucasi*.

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