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An Eocene sea turtle from the eastern North Pacific fills a Paleogene gap

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Sea turtles (Testudines: Chelonioidea) represent a monophyletic group with a global distribution in the fossil record, although most of our knowledge of their diversity and morphology comes from the Atlantic Ocean and Tethyan Sea (Evers and Benson 2019; Gentry et al. 2019). By contrast, the record of their evolution in the vast Pacific Basin prior to the Neogene is paltry. Late Cretaceous chelonioids are known from northern California (Parham et al. 2003), British Columbia (Nicholls 1992; Nicholls and Meckert 2002), Japan (Hirayama and Chitoku 1996), Australia (Kear et al. 2003; Kear 2006; Kear and Lee 2006), and New Zealand (Wiffen 1981), indicating they occupied at least portions of both the North and South Pacific Oceans at this time. Pacific Paleocene specimens are entirely unknown, and to date the Eocene record has been limited to chelonioids and dermochelyids (Köhler 1995a, b; Grant-Mackie et al. 2011) from New Zealand, and an informal report of a sea turtle from Oregon (Orr and Orr 2009). Here, we describe a new sea turtle fossil from the middle Eocene of California which demonstrates that members of this clade were indeed present in the North Pacific at this time.

Institutional abbreviations.—IRSNB, Royal Belgian Institute of Natural Sciences, Brussels, Belgium; SDNHM, San Diego Natural History Museum (run and operated by SDSNH, San Diego Society of Natural History), San Diego, USA.

Geologic setting

Stratigraphy.—SDSNH 103374 was recovered from middle Eocene strata during 2004 construction of the Bressi Ranch planned community in Carlsbad, San Diego County, California, USA (Fig. 1A). The upper estuarine/lagoonal stratigraphic unit of the Santiago Formation that produced SDSNH 103374 is an ~18 meter-thick complex sequence of cross-bedded sandstone, siltstone, and mudstone beds in a ~110 meter-thick Eocene section (Fig. 1B). Ripple cross-stratification, trough cross-stratification, graded bedding, and bioturbation were all observed in this unit. Several beds contained abundant carbonaceous horizons (e.g., SDSNH locality 5560) with leaf compressions of terrestrial plants, and others (e.g., SDSNH localities 5550, 5555, and 5561) had dense concentrations of estuarine mollusks. Typically, thicker cross-bedded strata were composed of yellow to yellowish-orange, lenticular, well-cemented sandstone bodies, which were fine- to medium-grained and shelly at the base and graded upwards into siltstone or greenish-gray massive mudstone. One mudstone stratum (SDSNH locality 5567) produced well-preserved remains of stomatopod crustaceans (Haug et al. 2013). Another, (SDSNH locality 5570, dubbed the "fish bed") contained partial and complete skeletons of bony fishes and produced the chelonioid fossil described below.

The "fish bed" is a localized, thin stratum of bluish-gray, organic-rich, ripple-laminated and bioturbated siltstone. Roughly cylindrical burrows, about 1 cm in diameter, penetrate the siltstone both vertically and horizontally. The burrows are filled with medium- to coarse-grained sandstone with dispersed shells and shell hash derived from the immediately overlying stratum. The fish skeletons, as well as whole and fragmentary leaves occur concordant to bedding, closely packed, and often stacked. The fish assemblage includes haemulids (grunts), soleids (soles), clupeids (herrings and shads), ariids (catfish), and *Genartina* sp. (bony-tongued fish). Plant fossils are dominated by leaves of the cocoplum, *Chrysobalanus* sp. Also occurring in this horizon are fragments of carbonized wood, spotty occurrences of pyrite/marcasite, mollusk and barnacle shells, and shark and crocodile teeth.

Depositional environment.—Invertebrates from the "fish bed" include the gastropods *Ampullella schencki*, *Nerita triangulata*, *Neverita globosa*, *Potamides carbonicola*, *Umpquaia oregonensis*, and the bivalves *Cuneocorbula torreyensis*, *Ostrea idrianensis*, and *Pelecyora aequilateralis* (Givens and Kennedy 1978; Squires 1992, 1999). These faunal elements are typical of Eocene lagoonal intertidal marsh flat and tidal creek facies reported elsewhere in coastal San Diego County (Boyer and Warme 1975; Clifton 1979; Eisenberg and Abbott 1985; Warme 1991). In the Bressi Ranch area, these lagoonal facies directly overlie steep, irregular paleotopography suggesting a proximal depositional setting within a broader lagoonal habitat protected by adjacent headlands.

Correlation and geologic age.—The age of the Santiago Formation is based on biochronological evidence from mammalian fossils, collected from its component members B and C and correlated with portions of the Uintan and Duchesnean North American Land Mammal Ages (Golz 1976; Golz and Lillegraven 1977; Walsh 1996), and limited paleomagnetic work indicating correlation with Chron C20R through Chron C18R (Prothero 2001).

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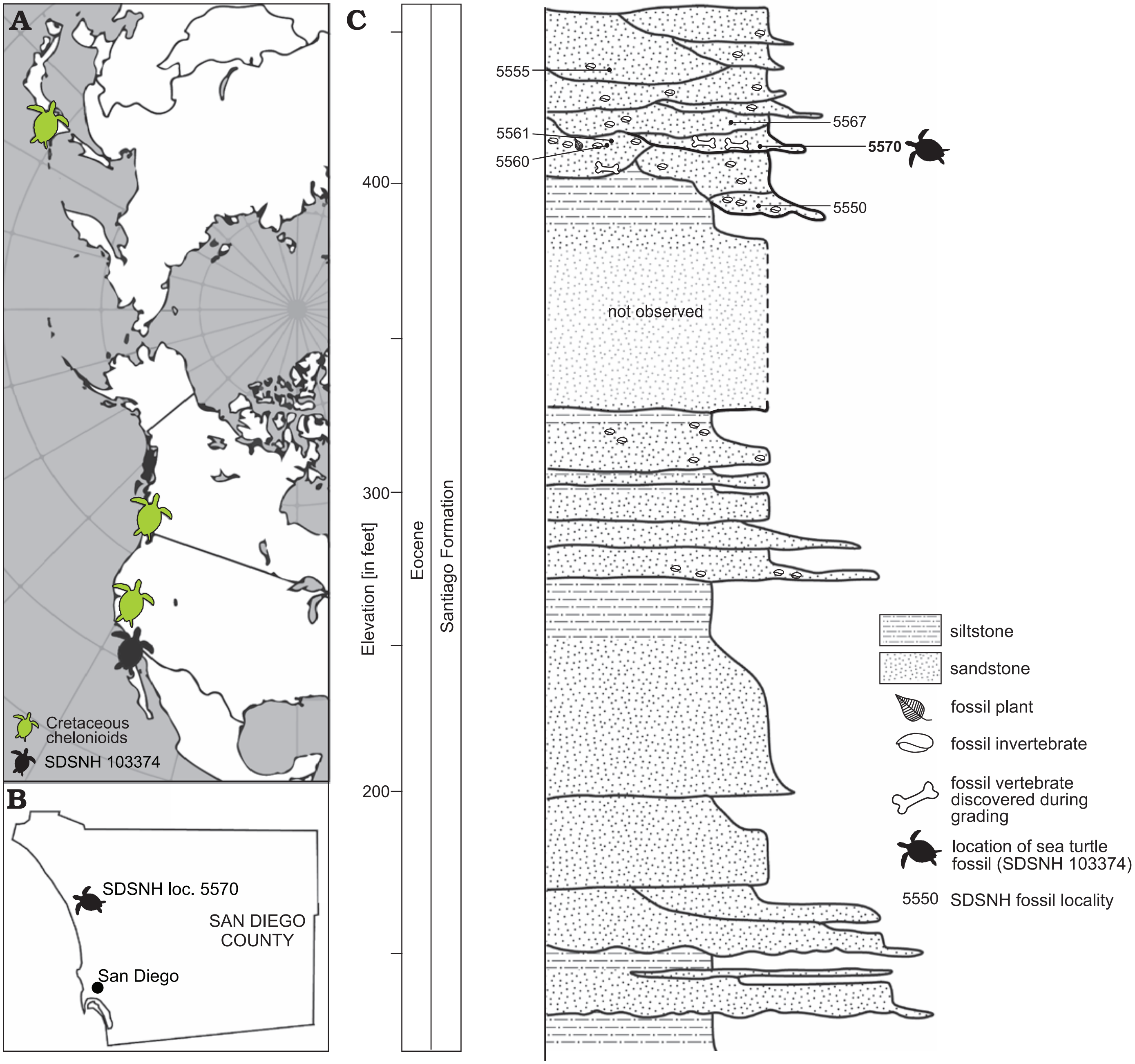

Fig. 1. Geographic and geologic context of sea turtle fragments (Chelonioidea gen. et sp. indet.). **A**. Map of northern Pacific showing sea turtle localities. **B**. Position of Bressi Ranch locality of the Santiago Formation (SDSNH loc. 5570) in Southern California, USA. **C**. Stratigraphic column of the Bressi Ranch.

Member B contains index fossils for Uintan biochron Ui1 and Ui2 (~45–43 Ma; Robinson et al. 2004). Mammals from the lower part of member C are correlated to Uintan biochron Ui3 (~42–41 Ma), whereas those from the upper part of member C are correlated with Uintan biochron Ui3 and the Duchesnean biochron (~39–40 Ma; Robinson et al. 2004). No terrestrial mammals were recovered from the Bressi Ranch stratigraphic sequence. However, the topographic and stratigraphic position of the Bressi Ranch "fish bed" relative to nearby Santiago Formation outcrops strongly suggest a correlation with member B. This position for the deposit allows us to assign the sea turtle fossil a likely age of middle Eocene (Lutetian, 45–43 Ma).

Systematic palaeontology

Testudines Batsch, 1788

Cryptodira Cope, 1868

Chelonioidea Baur, 1893

Gen. et sp. indet.

Fig. 2.

Material.—SDSNH 103374, a partial nuchal and right and left first peripherals (collected by Gino Calvano, March, 2004) from SDSNH locality 5570 ("fish bed"), middle Eocene (Lutetian, 43–45 Ma), San Diego County, California, USA.

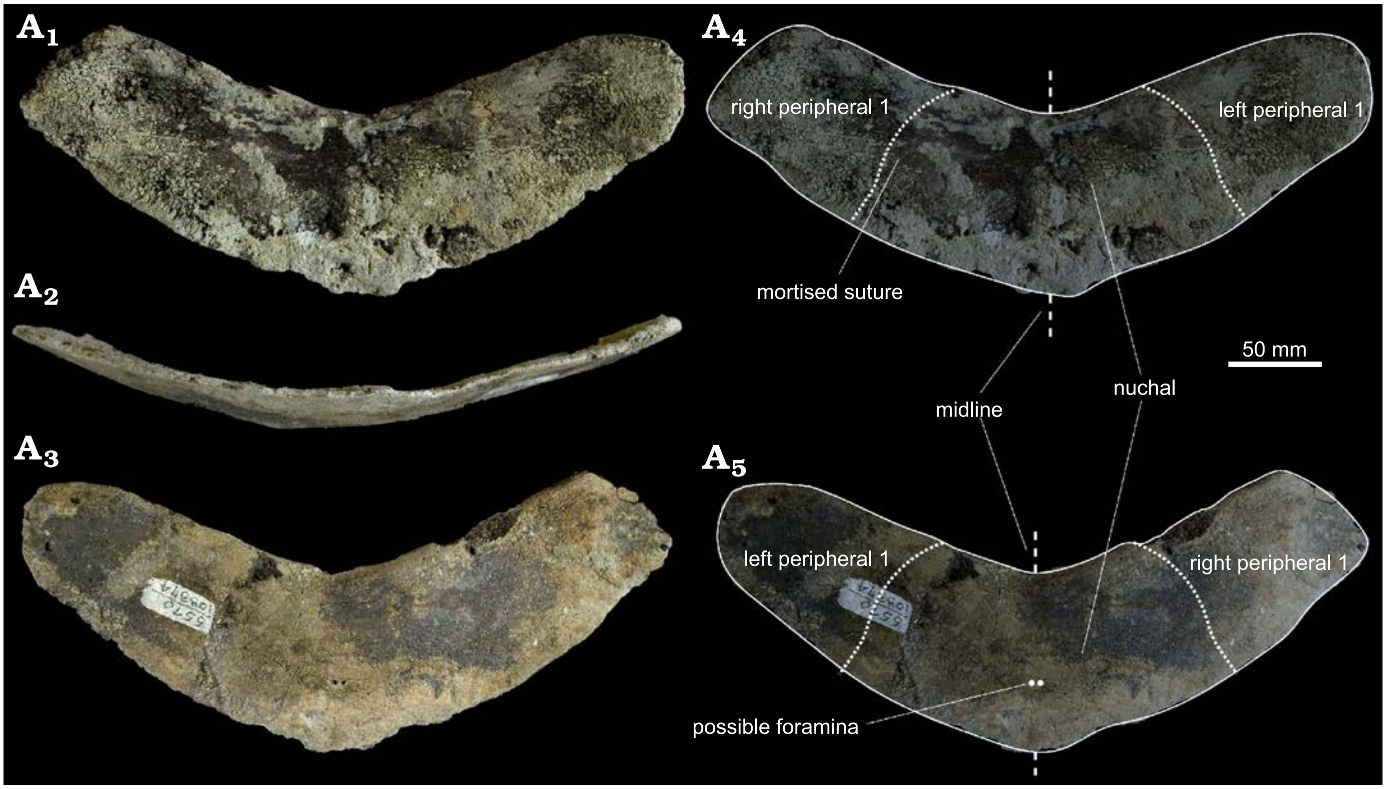

Fig. 2. Photographs of sea turtle nuchal and peripherals of Chelonioidea gen. et sp. indet. (SDSNH 103374) from the Eocene Santiago Formation of California, USA (SDSNH loc. 5570). Ventral (A_1, A_4), anterior (A_2), and dorsal (A_3, A_5) views.

This locality occurred within informal member B of the Santiago Formation. Additional locality information is available on request from SDNHM.

Measurements (in mm).—Width 120.6; ant/post height, lateral 21.2; ant/post height, midline 33.7; maximum thickness 6.7; width of "keel" 14.6.

Description.—SDSNH 103374 is a thin, "boomerang"-shaped fossil 6.7 mm at its thickest point, tapering to 2 mm at the acute anterior edge. The nuchal and partial right and left first peripherals are preserved, together forming what would have been a slightly dorsoventrally arched embayment extending concavely into the anterior portion of the carapace. The sutures are poorly expressed, but a complex suture is visible 22.1 mm from the midline on the visceral surface (equivalent to ventral view) of the left side of the nuchal embayment. The concave anterior opening measures 91.9 mm in width. The dorsal surface is subtly sculptured, and no sulci indicating the position of the scales are visible. The external cortical bone is thin and spongy; cancellous internal bone (diploe) with large pore spaces was exposed by erosion. This bone structure is typical in cryptodiran marine turtles, in contrast to marine or freshwater pleurodires and more pelagic cryptodires which generally have a thicker external cortical wall and thinner internal diploe (Scheyer 2009; Scheyer et al. 2014). On the visceral surface a thickened and slightly raised midline ridge is present for articulation with the 8th cervical vertebra. Due to erosion, it is not possible to determine whether the articular surface was formed as a blunt facet or raised pedestal (see e.g., character 120 of Cadena and Parham 2015; or characters 62 and 126 of Anquetin 2012). The posterior edge of the preserved nuchal is worn, so it is not possible to determine whether it was sutured to adjacent bones or separated by fontanelles. Two minute foramina are located bilaterally close to the midline of the nuchal. These structures are rimmed with intact cortical bone and are not taphonomic artefacts. The transverse torus is well expressed, and there is no costiform process. The first peripherals are facultatively fused to the nuchal, although a small indentation in the surface of the nuchal opening and faint impressions in the dorsal surface indicate where the bones meet. The first peripherals are incomplete, but the exterior outline would have been angled or "elbow-shaped" as seen in some other chelonioids (Lapparent de Broin et al. 2018).

The wider-than-long nuchal is dissimilar in shape and dimensions to that of dermochelyids, but consistent with that seen in other chelonioids with marked nuchal embayments. The curvature of the nuchal embayment is less than in many Cretaceous chelonioids (e.g., ctenochelyids; Zangerl 1953; Gentry 2018) and greater than in Eocene stem-cheloniids (e.g., European *Puppigerus* Cope, 1970 [Moody 1974], *Ashleychelys* Weems and Sander, 2014, *Procolpochelys* Hay, 1908, and *Carolinochelys* Hay, 1923 [Weems and Sanders 2014]). In thinness and degree of the nuchal embayment, SDSNH 103374 is most similar to *Eochelone brabantica* Dollo, 1903, and to a lesser extent *Eochelone monstigris* Grant-Mackie, Hill, and Gill, 2011, and/or *Argillochelys* sp. (Grant-Mackie et al. 2011; Lapparent de Broin et al. 2018). It differs from *E. monstigris* in lacking an acute corner at the edge of the nuchal embayment. SDSNH 103374 is more strongly curved and emarginate than similarly thin-shelled forms such as *Erquelinessia gosseleti* (IRSNB 1628; Lapparent de Broin et al. 2018).

The phylogenetic placement of incomplete carapacial specimens is challenging, due to both a paucity of characters and a lack of Paleogene taxa in most recent phylogenetic analyses of chelonioids. When included, Paleogene taxa are basal to extant taxa (e.g., Evers and Benson 2019). Weems and Brown (2017) provide the most comprehensive recent phylogenetic analysis (including multiple Paleogene taxa) based largely on cranial characters, and consistently recovered several weakly-supported clades among Paleogene and Neogene chelonioids. Notably, they recognized a clade comprising Eocene *Erquelinessia gosseleti* and the Miocene Californian and Peruvian taxon *Pacifichelys*. This phylogenetic hypothesis suggests a long ghost lineage for the origin of *Pacifichelys*.

Lapparent de Broin et al. (2018) informally grouped several thin-shelled Eocene–Oligocene species, including European *Eochelone* spp., *Puppigerus camperi*, and *Glarichelys* spp., united in part by the shape of the nuchal region, i.e., having a slight protrusion of the anterior carapacial border delimited by an “elbowed” peripheral 1 and an “anterior transversal” or slightly notched nuchal border. These authors did not consider *Eochelone monstigris* from New Zealand, but both it and SDSNH 103374 would appear to fall within this informal group. However, it is not clear if this is a monophyletic group, or whether it corresponds to one or more of the clades recognized by Weems and Brown (2017) as the closest Paleogene sister group to crown Cheloniidae.

Concluding remarks

Middle Eocene marine vertebrates of the northeastern Pacific Ocean are poorly known compared with the rich record of the North American Gulf Coast or Atlantic Coastal Plain. Marine fish scales were reported from California’s Central Valley (David 1946). Isolated chondrichthyan teeth were noted from the Scripps Formation of San Diego County (Walsh 1991), the Llajas Formation of Ventura County, California (Squires 1984, 2001), the Coaledo, Nestucca, and Spencer formations of west-central Oregon (Welton 1972), and Tukwila Formation of northwestern Washington (Nesbitt 1998). The only substantive marine microvertebrate assemblage is the Lake Miramar fauna from the Mission Valley Formation in northern San Diego County, comprising 15 families of bony fish and 9 families of chondrichthyans (Roeder 1991). Bressi Ranch is unique in preserving macro-vertebrate remains and in the preservation of a marine reptile, providing a rare glimpse of the middle Eocene Pacific Coast vertebrate fauna. The chelonioid appears to belong to a geographically widespread group of thin-shelled forms that reached both the southwestern and northern Pacific during the middle Eocene. It has not escaped our notice that the macrotaphonomic biases hitherto limiting our knowledge of turtles in the eastern North Pacific may similarly be obscuring the true geographic extent of other successful marine vertebrates during the Paleogene.

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