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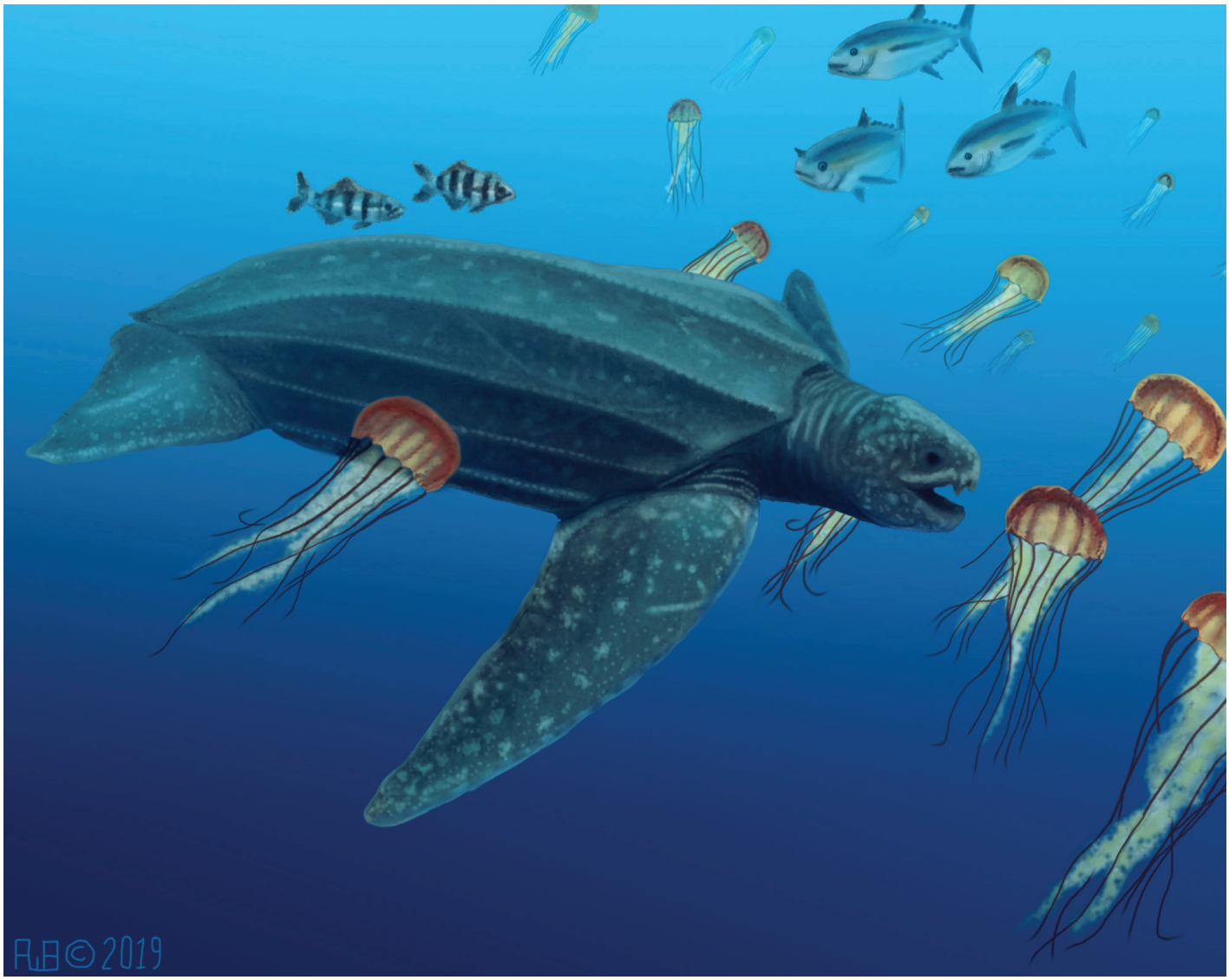

BAILEY R. FALLON & ROBERT W. BOESSENECKER (2019). First record of a leatherback sea turtle (Dermochelyidae) from the Mio-Pliocene Purisima Formation of northern California, USA.

Cover: Life restoration by R.W. Boessenecker of the archaic leatherback turtle, cf. *Psephophorus*, from the lower Pliocene Purisima Formation of northern California feeding on sea nettles (*Chrysaora*).
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First record of a leatherback sea turtle (Dermochelyidae) from the Mio-Pliocene Purisima Formation of northern California, USA

BAILEY R. FALLON[1*] and ROBERT W. BOESSENECKER[1,2]

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

The leatherback sea turtle family Dermochelyidae has an extensive evolutionary history, though it is represented by only one living species today, *Dermochelys coriacea*. Dermochelyid fossils occur worldwide from upper Cretaceous to Pliocene marine strata. Herein described is the first occurrence of a sea turtle from the lowermost Pliocene Purisima Formation of northern California, a single carapacial non-ridge ossicle. The ossicle exhibits external morphological and internal structural characteristics (ossicle thickness, internal layering, serrate margins) that are comparable to both the extinct genus *Psephophorus* and to the extant genus *Dermochelys*. Identification of the ossicle as cf. *Psephophorus* is based on examination of its thickness, internal structure, surface textures and geochronological age. This paper reports the third occurrence of leatherback sea turtle fossils from the western coast of the United States.

Keywords: *Psephophorus*, *Dermochelys*, Testudines, marine, Santa Cruz

INTRODUCTION

Dermochelys coriacea Vandelli, 1761 is the only extant species of the leatherback sea turtle family, Dermochelyidae. The leatherback sea turtle is so named because its carapace is comprised of thousands of bony ossicles covered in thick, leathery tissue (Chen et al. 2015). Growing to nearly 3.0 m long and weighing up to over 900 kg, *D. coriacea* is one of the largest living reptiles, and is the largest turtle species (Matthews et al. 1994). Found in temperate, tropical, and even subarctic waters, *D. coriacea* has the widest distribution of all sea turtles, and feeds almost exclusively on jellyfish (Fossette et al. 2010, Heaslip et al. 2012, Curtis et al. 2015). Listed as endangered in the United States and as vulnerable internationally, *D. coriacea* faces anthropogenic threats from fishery bycatch and plastic pollution (Wallace et al. 2013).

Though it is represented by only a single living species, the family Dermochelyidae has a long evolutionary history (Wood et al. 1996). Leatherback sea turtle fossils have been reported from Cretaceous through Pliocene strata from the North Sea, Tethys Sea, Mediterranean Sea, Equatorial Atlantic Ocean, Western North Atlantic Ocean, Southern Ocean, Eastern South Pacific Ocean, Eastern North Pacific and Western North Pacific Ocean (Andrews 1919, Gilmore 1937, Packard 1940, de la Fuente et al. 1995, Köhler 1996, Wood et al. 1996, Tong et al. 1999, Karl 2002, Lynch and Parham 2003, Chesi et al. 2007, Karl et al. 2012). With only one species reported from the Paleocene, *Arabemys crassiscutata* (Tong et al. 1999), leatherback sea turtles were most diverse during the Eocene, from which seven species have been reported: *Cosmochelys dolloi* Andrews, 1919, *Egyptemys oregonensis* Packard, 1940, *Eg. eoceanus* Andrews, 1901, *Eosphargis gigas* Owen, 1880, *Eo. breineri* Nielsen, 1959, and two species of *Psephophorus* Meyer, 1847, *Psep. terrypratchetti* Köhler, 1995, and an unnamed *Psephophorus* species by de la Fuente et al. 1995 (Andrews 1919, Wood et al. 1996, Tong et al. 1999). Dermochelyid richness diminished over time, with three species likely occurring in the Oligocene: *Natemys peruvianus* Wood et al., 1996, *Pseudosphargis rupeliensis sensu* Karl, 2014 and *Psephophorus* sp.; two in the Miocene, *Psep. polygonus* Meyer, 1847 and *Psep. calvertensis* Palmer, 1909; and one from the Pliocene, *Psephophorus* sp. (Dodd and Morgan 1992,

*author for correspondence

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Köhler 1996, Wood et al. 1996). This global and historical distribution suggests ancestors of *D. coriacea* were both cosmopolitan and more species rich than present.

The extinct genus *Psephophorus* has historically acted as a taxonomic waste basket in which most fossil leatherback material was classified, until Wood et al. (1996) reexamined the leatherback record and identified two new genera, concluding that *Psephophorus* should no longer be used as a waste basket genus. Wood et al. (1996) also suggested that the extant species *D. coriacea* did not derive from the genus *Psephophorus* as previously suggested by Broin and Pironon (1980), but rather is sister to the extinct genus. The study proposed five morphological trends in the evolution of shell structure, one of which is the decrease in shell thickness over time. Delfino et al. (2013) followed this study with a reexamination of the neotype and topotype materials of *Psep. polygonus*, and compared these materials with those of the extant genus *Dermochelys*. This study provided parameters by which the two genera may be distinguished, including the presence or absence of an internal diploic structure and the presence or absence of sharply serrated sutural margins in the shell ossicles (Delfino et al. 2013). These findings, along with descriptions of other leatherback material, allow for newly discovered leatherback fossils to be taxonomically classified. The present study describes the first occurrence of a sea turtle from the Miocene-Pliocene Purisima Formation of northern California, an ossicle with features similar to those of *Psephophorus* and *Dermochelys*.

MATERIALS AND METHODS

Geological setting and available fossil record

UCMP 293839 is a single carapacial ossicle. It currently represents the only known remains of a sea turtle collected from the Purisima Formation near Santa Cruz, Santa Cruz County, California. The Purisima Formation consists mainly of lightly consolidated to unconsolidated mudrock, diatomites, sandstones and shell beds dating from the late Miocene to the late Pliocene, and is located in the counties of San Mateo, Marin, and Santa Cruz (Norris 1986, Powell et al. 2007, Boessenecker et al. 2014). The Purisima Formation is richly fossiliferous and preserves abundant mollusks, crustaceans, echinoderms and vertebrates (Norris 1986, Powell 1998, Boessenecker et al. 2014). Marine vertebrates reported from this unit in Santa Cruz County include approximately 70 taxa of bony fish, sharks, sea birds, fur seals, walruses, dolphins, porpoises, sperm whales, baleen whales, a sea cow and terrestrial mammals (Boessenecker et al. 2014).

UCMP 293839 was collected in 2015 from coastal cliffs near Santa Cruz from the "Lower Shell Bed facies" of Perry (1988), otherwise referred to as "Bonebed 5" (Boessenecker et al. 2014). This stratum is located approximately 102 m above the base of the formation (Fig. 1). Bonebed 5 is a 10–30 cm thick clast-supported conglomerate dominated by phosphate pebbles, phosphatic steinkerns, teeth, bone fragments, rare mollusks and terrigenous clasts with occasional tabular calcareous siltstone nodules present. The lower contact is sharp and expresses up to 20 cm of relief (Boessenecker et al. 2014). Bonebed 5 has not yet been overprinted by bioturbators and maintains a clast-supported fabric and sharp lower erosional surface, and is approximately 50 cm above hummocky cross-stratified sandstone, all pointing towards bonebed genesis occurring in the lower shoreface, between fair weather and storm weather wave base (Boessenecker et al. 2014). Bonebed 5 occurs approximately 20 m above the Miocene-Pliocene boundary as identified by Powell et al. (2007), and is 25 m below Bonebed 6, which marks a depositional hiatus corresponding to Chrons C2Ar through C3N.3n (4.89–3.59 Ma, Madrid et al. 1986, Gradstein et al. 2012). These age data indicate that Bonebed 5 is earliest Pliocene in age (Zanclean correlative) and age control is 5.33–4.89 Ma. Detailed locality information is available on request from UCMP or the authors.

Measurements of maximum diameter and thickness of UCMP 293839 and of the ossicles of a partial fossil leatherback carapace (ChM PV 4892; cf. *Psephophorus*) located at the Charleston Museum were taken using digital calipers. UCMP 293839 was photographed with a Canon Rebel EOS DSLR camera with a 100 mm lens. When collected, UCMP 293839 was broken in half and photographed prior to reassembly.

Institutional abbreviations—ChM, Charleston Museum, Charleston, South Carolina, USA; **UCMP**, University of California Museum of Paleontology, Berkeley, California, USA.

SYSTEMATIC PALEONTOLOGY

TESTUDINES Linnaeus, 1758 (sensu Joyce et al., 2004)
CRYPTODIRA Duméril & Bibron, 1835
CHELONIOIDEA Baur, 1893
DERMOCHELYIDAE Gray, 1825
CF. *PSEPHOPHORUS* Meyer, 1847
Fig. 2

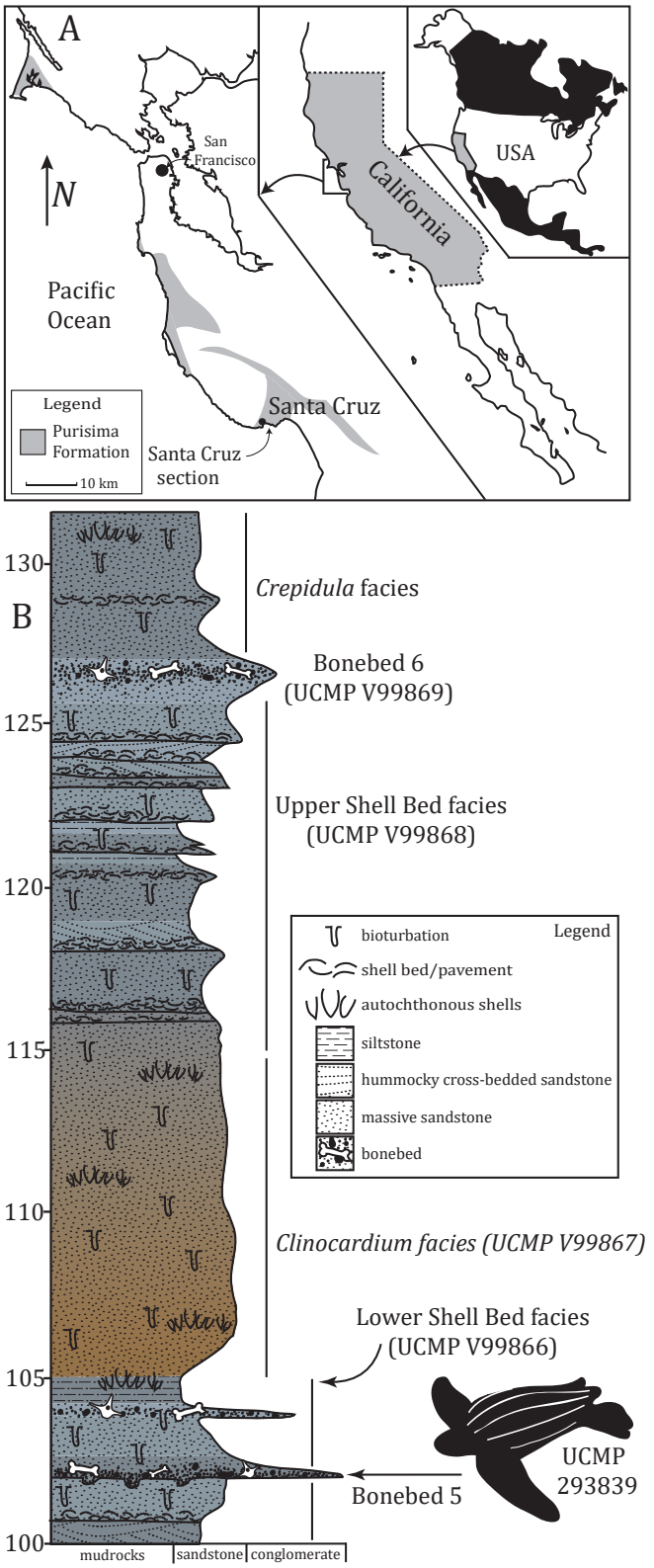

Figure 1A, B. The Purisima Formation and geologic context of UCMP 293839. **A**. Map of Purisima Formation exposures in northern California (modified from Boessenecker 2013). **B**. Stratigraphic column of the middle part of the Purisima Formation (modified from Boessenecker et al. 2014 and Boessenecker 2017).

Referred specimen—UCMP 293839, an isolated carapacial ossicle.

Occurrence—Bonebed 5 of the Purisima Formation near Santa Cruz, California.

Description—UCMP 293839 is polygonal, slightly longer than wide, and measures 22.61 mm long, 16.35 mm wide, and 5.56 mm thick. It is approximately tabular in cross section, but has a very slight concavity and convexity on the dorsal and visceral surfaces, respectively. The dorsal surface is scattered with shallow, circular pits ranging in size from ~ 0.50–0.91 mm in diameter, which are weakly radially oriented (Fig. 2A). The pits become increasingly elongated toward the edges of the dorsal surface, ranging in size from ~ 2.24–2.62 mm in length, and are also radially oriented. The visceral surface is scattered with slightly larger, more irregularly-shaped pits ranging in size from ~ 0.68–1.67 mm and are not radially oriented (Fig. 2B). Two different textures comprise the sutural surface. A groove with rounded, worn projections runs parallel to the dorsal and visceral surfaces, essentially dividing the ossicle in half. The groove ends with an X-shaped depression. The non-groove sutural surface is rugose with peaks and troughs that potentially indicate the original presence of finger-like projections (Fig. 2C). The internal structure of the ossicle, as revealed by a fracture, is comprised of a compact layer extending from the dorsal surface to just over half the thickness of the ossicle. A porous, more vascularized layer extends from this point to the visceral surface (Fig. 2D).

Remarks—UCMP 293839 is tentatively referred to *Psephophorus* based on its morphological and internal structural differences as compared to extant *Dermochelys* and other Cenozoic dermochelyids. Its stratified internal structure is characterized by dense dorsal bone and porous visceral bone when viewed in cross section. These features are unlike the thinner, non-stratified bone structure found in the ossicles of extant *Dermochelys*. UCMP 293839 is thinner than the ossicles of other Cenozoic dermochelyids (e.g., *Natemys*, *Egyptemys*), and thus may be distinguished from these genera.

DISCUSSION

Identification of UCMP 293839 is challenging because it is a disarticulated non-ridge ossicle. It is identifiable as a non-ridge ossicle based on its tabular shape (Table 1). UCMP 293839 has a thickness that falls within the range recorded for *Psephophorus* (4.8–19.2 mm thick), and that is close to the maximum thickness recorded for *Dermochelys* (1.5–4.0 mm thick) (de la Fuente et al. 1995, Wood et al. 1996, Chesi et al. 2007, Karl et al. 2012,

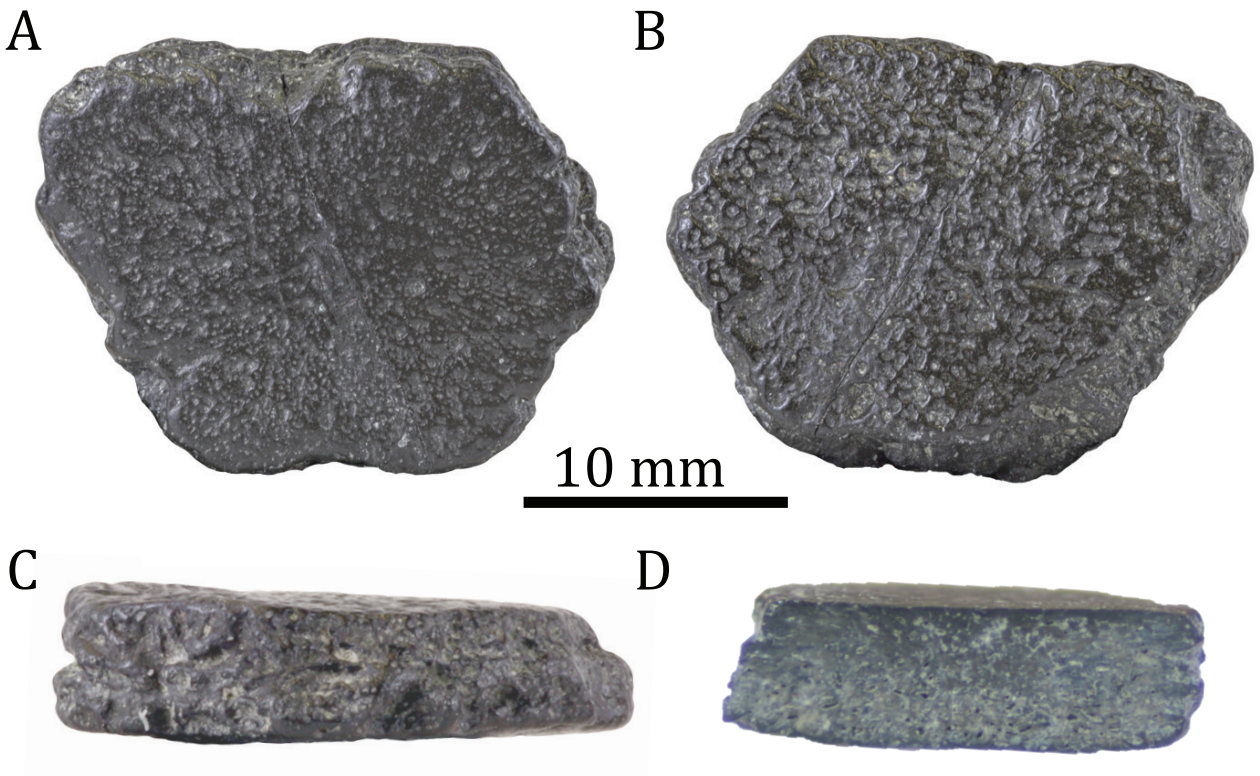

Figure 2A–D. The **A**. dorsal, **B**. visceral, **C**. sutural, and **D**. internal surfaces of the carapacial ossicle (UCMP 293839) from the Purisima Formation.

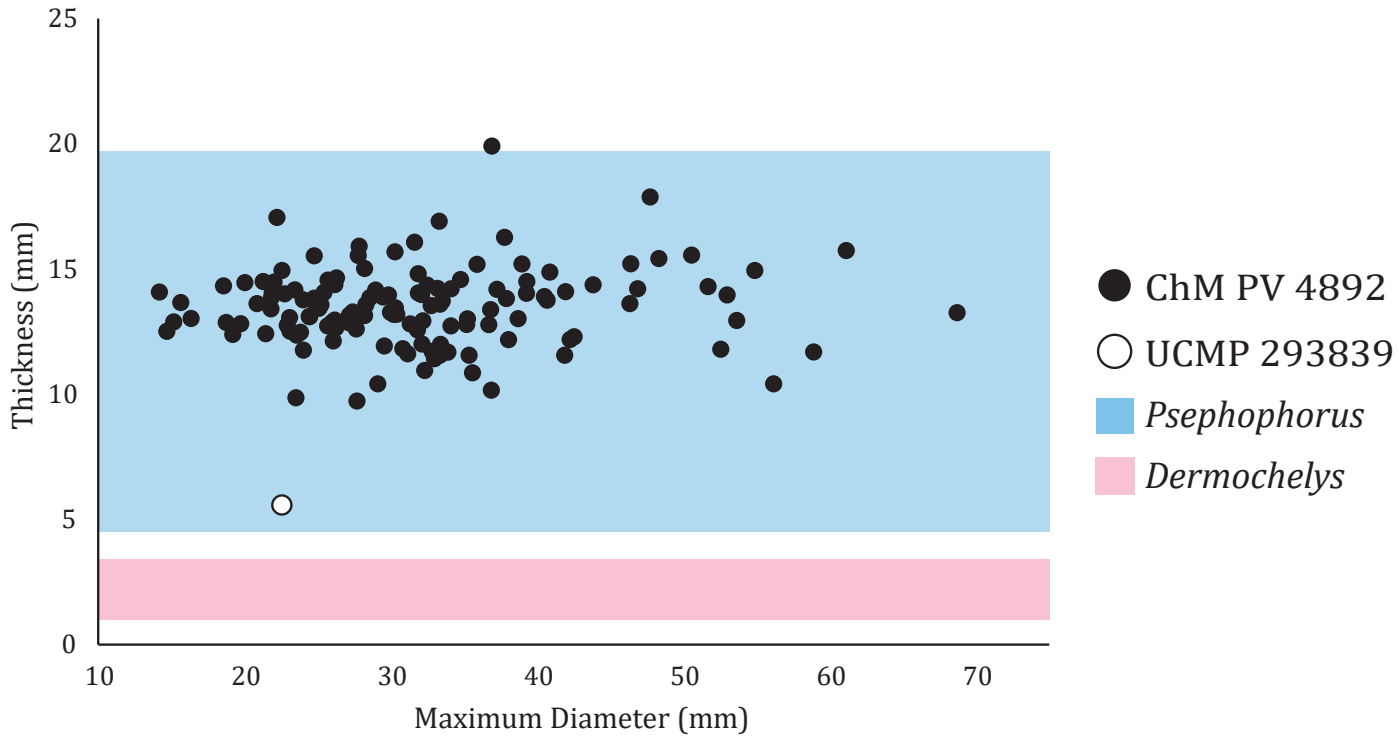

Figure 3. Thickness and maximum diameter measurements for the non-ridge carapacial ossicles of Oligocene cf. *Psephophorus* (ChM PV 4892) and those for UCMP 293839. The blue and pink bands depict the reported ranges of non-ridge ossicle thicknesses for *Psephophorus* and *Dermochelys*, respectively.

Delfino et al. 2013).

Thickness

With a thickness of 5.56 mm, UCMP 293839 falls within the range currently documented for non-ridge ossicles of *Psephophorus polygonus* described by Delfino et al. (2013), 4.8–19.2 mm, but is thinner than the *Psephophorus* non-ridge ossicles described by Köhler (1995), Chesi et al. (2007), and Karl et al. (2012): 10–12, 10.5 and 6–11 mm, respectively (Table 1). However, Chesi et al. (2007) described one specimen that is only 4.2 mm thick. UCMP 293839 is also thinner than the non-ridge ossicles of *Arabemys* (6–20 mm), *Cosmochelys* (7–10 mm), and *Egyptemys* (7 mm) (Andrews 1919, Wood et al. 1996, Tong et al. 1999), and the Antarctic specimens tentatively referred to *Psephophorus* (6–18 mm) described by de la Fuente et al. (1995). UCMP 293839 is significantly thinner than the non-ridge ossicles measured for a partial dermochelyid carapace tentatively referred to *Psephophorus*, ChM PV 4892 from the Oligocene Chandler Bridge Formation of South Carolina, which range between 9.72 and 19.90 mm thick (Fig. 3). It is thicker than the non-ridge ossicles reported for *Dermochelys*, which range between 1.5 and 4.0 mm thick (Wood et al. 1996, Delfino et al. 2013, Frazier et al. 2018). Though much thinner than most extinct dermochelyid ossicles, UCMP 293839 has a thickness that is most comparable to the range reported for *Psephophorus* (Table 1).

Internal structure

UCMP 293839 demonstrates an internal structure that is most comparable to *Psephophorus*. It clearly exhibits a diploic structure that is characteristic of *Psephophorus* as described by Delfino et al. (2013), being divided approximately in half by one layer that is very dense near the dorsal surface and another that is markedly more porous near the visceral surface. Karl et al. (2012) also describes an ossicle tentatively referred to as *Psephophorus* that has an internal basal compact layer, a middle porous layer, and a dorsal cortical layer. However, Karl et al. (2012) identifies this ossicle as *Psephophorus*, along with two other specimens from a carapacial fragment they describe as having a "sunflower pattern." This carapacial pattern is characterized by a series of enlarged ossicles surrounded by smaller, radiating elongated ossicles (Wood et al. 1996). Wood et al. (1996) argues this "sunflower pattern" is characteristic of only *Natemys peruvianus* and *Pseudosphargis rupeliensis* (syn. *Psephophorus rupeliensis* and *Pseu. ingens* according to Karl 2014). Thus, we tentatively compare the internal

Table 1. Thicknesses of non-ridge ossicles reported for leatherback genera to date.

Geologic Age	Genus	Thickness (mm)	Source
Late Paleocene – Early Eocene	*Arabemys crassiscutata*	6–20	Tong et al. 1999
Eocene	*Cosmochelys dolloi*	7–10	Andrews 1919
Eocene	*Psephophorus* sp.	6–18	de la Fuente et al. 1995
Eocene	*Psephophorus terrypratchetti*	10–12	Köhler 1995
Late Eocene	*Egyptemys eoceanus*	7	Wood et al. 1996
Late Oligocene	cf. *Psephophorus*	9.7–19.9	ChM PV 4892
Miocene	*Psephophorus polygonus*	10.5	Chesi et al. 2007
Miocene	*Psephophorus polygonus*	6–11	Karl et al. 2012
Middle Miocene	*Psephophorus polygonus*	4.8–19.2	Delfino et al. 2013
Early Pliocene	*Psephophorus* sp.	12.2	Dodd and Morgan 1992
Mid-Late Holocene	*Dermochelys coriacea*	3–4	Frazier et al. 2018
Modern	*Dermochelys coriacea*	3–4	Wood et al. 1996
Modern	*Dermochelys coriacea*	1.5–5.0	Delfino et al. 2013

structure of UCMP 293839 with that of the *Psep. rupeliensis* ossicle reported by Karl et al. (2012). *Dermochelys* does not exhibit any stratification of internal structure, having relatively uniform vascularization throughout (Delfino et al. 2013, Frazier et al. 2018). Thus, UCMP 293839 may be aligned with the genus *Psephophorus* based on examination of its internal structure.

Surfaces

The dorsal surface of UCMP 293839 is comparable to that of *Egyptemys*, *Natemys*, *Cosmochelys* and *Psephophorus* regarding its scattered dimpling (Andrews 1919, Wood et al. 1996, Karl et al. 2012). The dorsal surface does not compare well with *Arabemys* as the ossicles of this genus are described as having deep wrinkles and a bulging exterior surface (Tong et al. 1999), whereas UCMP 293839 has shallow dimples with an approximately flat surface. The elongation and faint radiation of the dorsal dimples on UCMP 293839 is also described in *Cosmochelys*, *Psephophorus* and *Dermochelys* ossicles, whereas its visceral dimples are also reported in these genera except for *Cosmochelys* (Andrews 1919, de la Fuente et al. 1995, Wood et al. 1996, Karl 2002, Karl et al. 2012, Delfino et al. 2013). The sutural surface of UCMP 293839 is comparable to *Psephophorus* and *Dermochelys*. It demonstrates reduced sutural structures similar to the *Psephophorus* ossicles described by Delfino et al. (2013), with all edges being roughly uniform and not deeply scalloped. However, this sutural reduction may be due to abrasion of the specimen, as the edges are rounded and smooth, which is typical of preserved vertebrate specimens from Bonebed 5 of the Purisima Formation. The rugosity of the sutural surface is comparable to that of *Dermochelys* (Delfino et al. 2013). This texture, along with the groove present along half of the surface, may indicate the original presence of finger-like projections characteristic of *Dermochelys* ossicles. Though the dorsal and visceral surfaces of UCMP 293839 do not align it directly with any one genus, the morphology of the sutural surface is intermediate between *Psephophorus* and *Dermochelys*.

Pliocene Dermochelyidae

Few records of leatherback sea turtles have been reported from the Pliocene (Wood et al. 1996, Karl 2002), and all are from the eastern coast of the United States. Remains of *Psephophorus* and *Dermochelys* have been reported from the Pliocene Yorktown Formation of the Lee Creek Mine in North Carolina in a thesis by Köhler (1996), though there is disagreement regarding the classification of these specimens and they might represent both taxa, a single undescribed species of *Dermochelys*, or perhaps a leatherback distinct from *Dermochelys* (Frazier et al. 2018: Supplemental Information 2). Regardless, these specimens from the Lee Creek Mine have yet to be formally published, hindering informed discussion of late Neogene leatherback evolution. However, a single *Psephophorus* ossicle has been reported from the lower Pliocene Bone Valley Formation of Florida (Dodd and Morgan 1992).

The ossicle reported herein, UCMP 293839, is earliest Pliocene in age (5.33–4.89 Ma) and therefore one of the geochronologically youngest dermochelyid specimens reported to date, inviting comparison with extant *Dermochelys* (see above). This specimen is best identifiable as cf. *Psephophorus*, suggesting late survival of archaic dermochelyids. Pending formal study of the material from the Yorktown Formation, two dermochelyid genera appear to be present in the Pliocene, and this study suggests a late Cenozoic decrease in leatherback richness compared to the high richness of the Paleogene (Dodd and Morgan 1992, Köhler 1996, Wood et al. 1996). Improved sampling of Pliocene assemblages worldwide is needed in order to elucidate the murky origin of *Dermochelys* and the extinction of *Psephophorus*.

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LITERATURE CITED

Andrews, C.W. 1901. Preliminary note on some recently discovered extinct vertebrates from Egypt. (Part II). *Geological Magazine* 8:436–444.

Andrews, C.W. 1919. A description of a new species of zeuglodont and of leathery turtle from the Eocene of Southern Nigeria. *Proceedings of the Zoological Society* 18:309–319.

Baur, G. 1893. Notes on the classification of the Cryptodira. The *American Naturalist* 1893:672–674.

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

35(4):815–940.
Boessenecker, R.W. 2017. A new early Pliocene record of the toothless walrus *Valenictus* (Carnivora, Odobenidae) from the Purisima Formation of northern California. *PaleoBios* 34(0):1–6.
Boessenecker, R.W., F.A. Perry, and J. G. Schmitt. 2014. Comparative taphonomy, taphofacies, and bonebeds of the Mio-Pliocene Purisima Formation, Central California: strong physical control on marine vertebrate preservation in shallow marine settings. *PLoS ONE* 9(3):e91419.
Broin, F., and B. Pironon. 1980. Découverte d'une tortue dermochélyidée dans le Miocène d'Italie Centro-Méridionale (Mátese oriental), Province de Benevento. *Rivista Italaliana di Paleontologia* 86(3):589–604.
Chen, I.H., W. Yang, and M.A. Meyers. 2015. Leatherback sea turtle shell: A tough and flexible biological design. *Acta Biomaterialia* 28:2–12.
Chesi, F., M. Delfino, A. Varola, and L. Rook. 2007. Fossil sea turtles (Chelonii, Dermochelyidae and Cheloniidae) from the Miocene of Pietra Leccese (Late Burdigalian – Early Messinian) of Southern Italy. *Geodiversitas* 29(2):321–333.
Curtis, K.A., J.E. Moore, and S.R. Benson. 2015. Estimating limit reference points for western pacific leatherback turtles (*Dermochelys coriacea*) in the U.S. West Coast EEZ. *PLoS ONE* 10(9):e0136452.
de la Fuente, M.S., S.N. Santillana, and S.A. Marenssi. 1995. An Eocene leatherback turtle (Cryptodira: Dermochelyidae) from Seymour Island, Antarctica. *Stvdia Geològica Salmanticensia* 31:21–34.
Delfino, M., T.M. Scheyer, F. Chesi, T. Fletcher, R. Gemel, S. Macdonald, M. Rabi, and S.W. Salisbury. 2013. Gross morphology and microstructure of type locality ossicles of *Psephophorus polygonus* Meyer, 1847 (Testudines, Dermochelyidae). *Geological Magazine* 150:767–782.
Dodd, C.K. Jr., and G.S. Morgan. 1992. Fossil sea turtles from the early Pliocene Bone Valley Formaton, Central Florida. *Journal of Herpetology* 26(1):1–8.
Duméril, C., and G. Bibron. 1835. Erpétologie Générale, ou, Histoire Naturelle Complète des Reptiles. Roret, Paris.
Fossette, S., V.J. Hobson, C. Girard, B. Calmettes, P. Gaspar, J. Georges, and G.C. Hays. 2010. Spatio-temporal foraging patterns of a giant zooplanktivore, the leatherback turtle. *Journal of Marine Systems* 81:225–234.
Frazier, J.G., V. Azzarà, O. Munoz, L.G. Marcucci, E. Badel, F. Genchi, M. Cattani, M. Tosi, and M. Delfino. 2018. Remains of leatherback turtles, *Dermochelys coriacea*, at mid-late Holocene archaeological sites in coastal Oman: Clues of past worlds. *PeerJ* 6:e6123.
Gilmore, C.W. 1937. A new marine turtle from the Miocene of California. *Proceedings of the California Academy of Sciences, 4th series* 23(10):171–174.
Gradstein, F.M., J.G. Ogg, M. Schmitz, and G. Ogg. 2012. The Geologic Time Scale 2012. Elsevier, Oxford. 1144 pp.
Gray, J.E. 1825. A synopsis of genera of Reptiles and Amphibia, with a description of some new species. *Annals of Philosophy* 2(10):193–217.
Heaslip, S.G., S.J. Iverson, W.D. Bowen, and M.C. James. 2012. Jellyfish support high energy intake of leatherback sea turtles (*Dermochelys coriacea*): Video evidence from animal-borne cameras. *PLoS ONE* 7(3):e33259.
Joyce, W.G., J.F. Parham, and J. Gauthier. 2004. Developing a protocol for the conversion of rank-based taxon names to phylogenetically defined clade names, as exemplified by turtles. *Journal of Paleontology* 78(5):989–1013.
Karl, H.-V. 2002. Übersicht über die fossilen marinen Schildkrötenfamilien Zentraleuropas (Reptilia, Testudines). *Mauritiana* 18(2):171–202.
Karl, H.-V. 2014. Die fossilen Schildkröten vom Doberg bei Bünde. Pp. 90-102 *in* M. Kaiser and R. Ebel (eds.). Der Doberg bei Bünde: Eine klassische Fundstelle der Paläontologie. Verlag Dr. Friedrich Pfeil, Munchen.
Karl, H.-V., B.E.K. Lindow, and T. Tütken. 2012. Miocene leatherback turtle material of the genus *Psephophorus* (Testudines: Dermochelyoidea) from the Gram Formation (Denmark). *Studia Palaeocheloniologica* 4(9):205–216.
Köhler, R. 1995. A new species of the fossil turtle *Psephophorus* (Order Testudines from the Eocene of the South Island, New Zealand. *Journal of The Royal Society of New Zealand* 25(3):371–384.
Köhler, R. 1996. Eocene turtles and whales from New Zealand. Ph.D. diss. University of Otago, Dunedin, New Zealand.
Linnaeus C. 1758. Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Impensis Laurentii Salvii, Holmiae.
Lynch, S.C., and J.F. Parham. 2003. The first report of hard-shelled sea turtles (Cheloniidae sensu lato) from the Miocene of California, including a new species (*Euclastes hutchisoni*) with unusually plesiomorphic characters. *PaleoBios* 23(3):21–35.
Madrid, V.M., R.M. Stuart, and K.L. Verosub. 1986. Magnetostratigraphy of the late Neogene Purisima Formation, Santa Cruz County, California. *Earth and Planetary Science Letters* 79:431–440.
Matthews, P., M.D. McCarthy, and M. Young. 1994. The Guinness Book of Records. Facts on File, New York. 39 pp.
Meyer, H. von 1847. Mittheilungen an Professor Bronn gerichtet. *Neues Jahrbuchfiir Mineralogie, Geognosie, Geologie und Petrefactenkunde* 1847: 572–580.
Nielsen, E. 1959. Eocene turtles from Denmark. *Meddelelser fra Dansk Geologisk Forening* 14(2):96–114.
Norris, R.D. 1986. Taphonomic gradients in shelf fossil assemblages: Pliocene Purisima Formation, California. *Palaios* 1:256–270.
Owen, R. 1880. Monography on the first Reptilia of the London clay. *Monograph of the Palaeontographical Society* 2:1.
Packard, E.L. 1940. A new turtle from the marine Miocene of Oregon. *Oregon State College Studies in Geology* 2:1–31.
Palmer, W. 1909. Description of a new species of leatherback turtle from the Miocene of Maryland. *Proceedings of the United States National Museum* 36:369–373.
Perry, F.A. 1988. Fossil invertebrates and geology of the marine cliffs at Capitola, California. Santa Cruz City Museum Association, Santa Cruz, California. 30 pp.
Powell, C.L. II. 1998. The Purisima Formation and related rocks (Upper Miocene-Pliocene), greater San Francisco Bay area, central California – Review of literature and USGS collections (now housed at the Museum of Paleontology, University of California, Berkeley). *U.S. Geological Survey* Open-File Report 98-594:1–101.
Powell, C.L. II, J.A. Barron, A.M. Sarna-Wojcicki, J.C. Clark, F.A. Perry, E.E. Brabb, and R.J. Fleck. 2007. Age, stratigraphy, and correlation of the late Neogene Purisima Formation, central California coast ranges. *U.S. Geological Survey Professional*

Paper 1740:1–32.

Tong, H., E. Buffetaut, H. Thomas, J. Roger, M. Halawani, A. Memesh, and P. Lebret. 1999. A new dermochelyid turtle from the late Paleocene-early Eocene of Saudi Arabia. *Earth and Planetary Sciences* 329:913–219.

Vandelli, D. 1761. Epistola de holothurio, et testudine coriacea ad celeberrimum Carolum Linnaeum equitem naturae curiosum Dioscoridem II. Padua, Conzatti.

Wallace, B.P., M. Tiwari, and M. Girondot. 2013. *Dermochelys coriacea*, leatherback. *The IUCN Red List of Threatened Species* 2013: e.T6494A43526147.

Wood, R.C., J. Johnson-Gove, E.S. Gaffney, and K.F. Maley. 1996. Evolution and phylogeny of leatherback turtles (Dermochelyidae), with descriptions of new fossil taxa. *Chelonian Conservation and Biology* 2(2):266–286.