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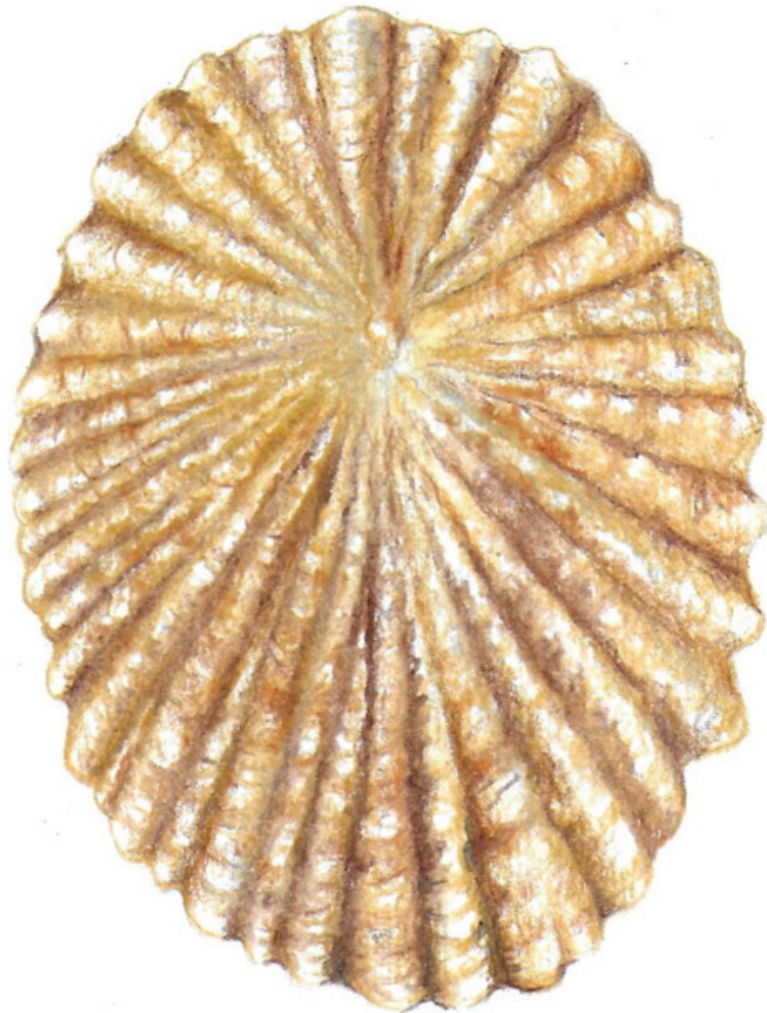
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Cover illustration: A colored-pencil illustration by Harry Witmore of the holotype of *Lottia edmittchelli* (Lipps).

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The extinct limpet *Lottia edmittchelli* (Lipps, 1963) from the Southern California Bight, U.S.A.

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New specimens of the extinct limpet *Lottia edmittchelli* (Lipps, 1963) (Mollusca: Gastropoda: Lottidae) collected during a geologic survey of the northern-most California Channel Islands by United States Geological Survey personnel and examination of museum collections record previously unreported occurrences of this species on San Miguel, Santa Rosa and San Clemente Islands in the Southern California Bight. Previously this species was reported as Late Pleistocene to Holocene in age with occurrences on San Nicolas Island and the Palos Verdes Peninsula. The single specimen identified from the California mainland (Palos Verdes Peninsula) of Holocene age is regarded as an atavism in the *L. scabra* population. Eliminating this single specimen results in *L. edmittchelli* being a strictly fossil species with occurrences reported here from San Clemente, San Miguel, San Nicolas, and Santa Rosa Islands in deposits of possibly Calabrian Stage of the International Commission on Stratigraphy (=early Pleistocene) to Middle Pleistocene.

Keywords: Mollusca, Gastropoda, California Channel Islands, Pleistocene, Calabrian Stage, fossil

INTRODUCTION

Lottia edmittchelli (Lipps, 1963) (Figure 1) was first recognized on San Nicolas Island as *Acmaea* Eschscholtz (1833) n. sp.? by Jack Vedder in Vedder and Norris (1963) and described from the Pleistocene terrace deposits on the island later that year by Jere Lipps as *Acmaea mitchelli* Lipps (1963). Lipps later renamed his species *A. edmittchelli* Lipps (1966), as *A. mitchelli* was preoccupied by *A. striata mitchelli* Oldroyd (1933) from the Philippine Islands. Working on the higher terraces on Palos Verdes Peninsula Marinovich (1976) found what he thought was this species, but at the time it was attributed to *Collisella* (Dall, 1871). He states "...[*Collisella*] *edmittchelli*... intergrades completely with specimens of *C. scabra* (Gould)..." however, he lists *L. edmittchelli* as separate from *L. scabra* and the former only from the 7th and 12th terraces, Los Angeles County. Later, Lindberg (1978) referred all Marinovich's specimens to the Pleistocene and Holocene species *L. scabra* (Gould, 1846). Lindberg (1978) used shell structure instead of shell or radular morphology to show that *L. edmittchelli* is closely related to *L. scabra*, and that these two species are distinct from all other eastern Pacific Lottidae, which have different shell structure. Lindberg (1984) discussed the single specimen he identified as *L. edmittchelli* collected in San

Pedro by J.G. Cooper in 1861 mixed with two typical *L. scabra* noting differences and discussed the ecology of the former species. However, Lindberg (email correspondence, 12/2014) now considers that the single *L. edmittchelli* specimen from San Pedro to be an atavism in the *L. scabra* population, although there is no way to determine this. Atavism here refers to a modification of a biological structure whereby ancestral trait(s) reappear after having been lost through evolution (Tomic and Meyer-Rochow 2011). Carlton (1993), based on Lindberg's *L. edmittchelli* specimen, attributed its modern extinction to "...vast alterations of the California coastal zone that accompanied the rapidly increasing human population at that time...". However, removing J. G. Cooper's single specimen from *L. edmittchelli* results in it no longer being considered a recently extant species and therefore no longer a valid record from mainland southern California. Edward Mitchell, for whom this species is named recently passed away (Summer 2019) and this paper is in his honor (<https://onlinelibrary.wiley.com/doi/abs/10.1111/mms.12668>).

MATERIAL AND METHODS

Collections—In reviewing fossil collections from the Channel Islands for abstracts and a paper on the

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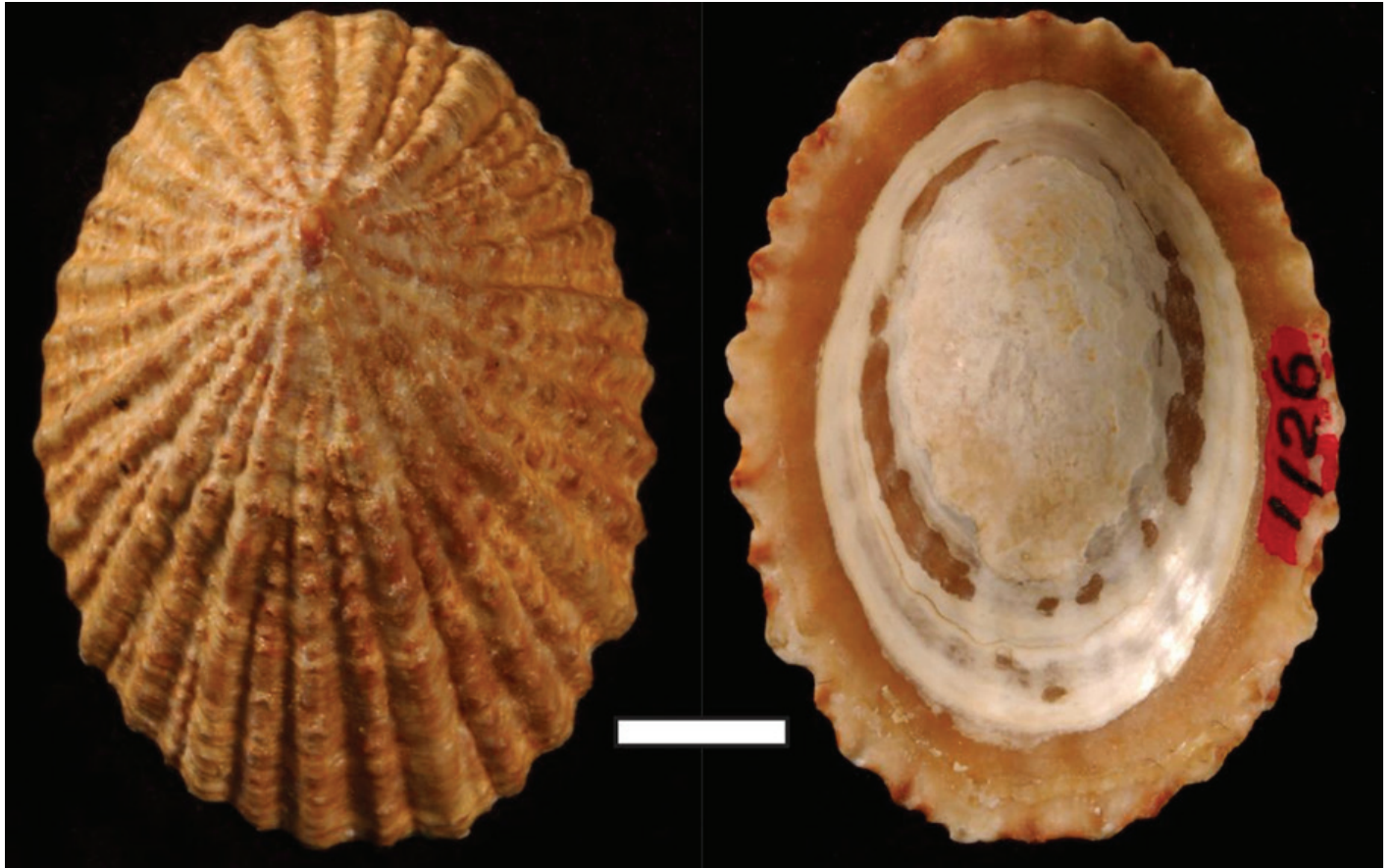


Figure 1. Holotype of *Lottia edmittchelli* (Lipps, 1963)(LACMIP 1126) from San Nicolas Island, Ventura County (locality LACMIP 4658). **A.** Dorsal view. **B.** Ventral view. Photographs thanks to many people at the Natural History Museum of Los Angeles County. White bar=1 cm.

occurrence of the gastropod genus *Architectonica* (Röding 1798) and its chronostratigraphic significance in coastal southern and central California Pliocene (Powell et al. 2008a, 2008b, 2009), I noted new occurrences of *Lottia edmittchelli* on San Clemente Island. Later, while identifying Santa Barbara Museum of Natural History and USGS collections from Santa Rosa Island, I again noted additional new occurrences of this extinct limpet. In preparation for this paper, I examined Pleistocene fossil collections at the California Academy of Sciences, Natural History Museum of Los Angeles County, San Diego Museum of Natural History, and the University of California Museum of Paleontology for other occurrences. After finding a few new occurrences I spoke with David Lindberg regarding its occurrence on the Palos Verdes Peninsula, Los Angeles and found that he believes the single specimen from the Palos Verdes Peninsula should be identified as *L. scabra* (D. Lindberg, email correspondence, 12/2014). Given these observations I decided to update the geographic and geologic record of *L. edmittchelli* in the Southern California Bight towards using it as

a biostratigraphic significant species in the California Channel Islands.

Institutional Abbreviations—LACMIP, Invertebrate Paleontology, Natural History Museum of Los Angeles County, California; LACMVP, Vertebrate Paleontology, Natural History Museum of Los Angeles County, California; SBMNH, Santa Barbara Museum of Natural History; UCMP, University of California Museum of Paleontology; USGS, United States Geological Survey.

Measurements—Defined here as follows: **height**, greatest distance between dorsal and ventral termini; **length**, greatest distance between anterior and posterior termini; **width**, greatest distance between left and right termini.

DISCUSSION

Occurrence

Lottia edmittchelli occurs exclusively in the Southern California Bight on San Clemente Island, Los Angeles County, San Miguel and San Nicolas islands, Ventura

County, and Santa Rosa Island, Santa Barbara County, on these islands' higher terraces. It has not been found in Pleistocene terrace deposits on Anacapa Island on or below the 76 m (250') terrace (Valentine and Lipps 1963, Lipps 1964), nor on the 24 m (80') terrace on San Clemente Island (Lipps 1967), nor on Santa Barbara Island up to and including the 40 m (130') terraces (Lipps et al. 1968). Prominent marine terraces are not found on Santa Catalina Island (Schumann et al. 2012) although terraces of Middle Pleistocene age are known from below sea-level around Santa Catalina Island (Castillo et al. 2018). However, *L. edmitchelli* has not been found from these submarine terraces (Castillo et al. 2018, Powell, personal observation). These data help to confirm that even within the Channel Islands *L. edmitchelli* does not occur in younger deposits.

Museum collections of *L. edmitchelli* in the Southern California Bight are listed below, those not previously reported in the literature are marked with an asterisk [*]. Sites for all occurrences are illustrated in Figure 2. Locality data for the institutions above not listed in the Appendix should be obtained from those institutions. General locality descriptions for UCMF and associated USGS field numbers are listed in the Appendix.

San Clemente Island*: Localities LACMIP 2642, 2643, 2649, 12577.

San Miguel Island*: Locality UCMP IP16548.

San Nicolas Island: Type locality LACMVP 1085 [=USGS 21666]. Also occurring on the island at locality LACMIP 5620, UCMP and equivalent USGS localities D9919, IP6587 (=USGS 21654), IP6588 (=USGS 21655), IP6589 (=USGS 21657), IP6594 (=USGS 21662), IP10511, IP10514, IP10518, IP10522, and IP10913

Santa Rosa Island*: Localities UCMP IP16545 (=B13S-RI-37, KSSR 13-37, SRI 17019A, SRI 17019B), IP16546.

Five of California Channel Islands (San Miguel, Santa Rosa, Santa Cruz, Anacapa, and Santa Barbara) are part of the United States National Park Service Channel Islands National Park and collecting without permits is not allowed. Collecting permits are also required for San Clemente Island as it is owned and operated by the United States Navy.

Age

Recently the Pleistocene has been expanded and its internal divisions changed (<http://www.stratigraphy.org/ICSchart/ChronostratChart2017-02.pdf>, retrieved 1/2018). It is now divided, from older to younger, into the Gelasian (2.58–1.80 Ma), Calabrian (1.80 Ma–781 ka), Middle (781–126 ka), and Late (126–11.7 ka) stages. Middle and Late (or their lithostratigraphic equivalents Middle and Upper) are formally defined and written in upper case, whereas early and part of the middle (or

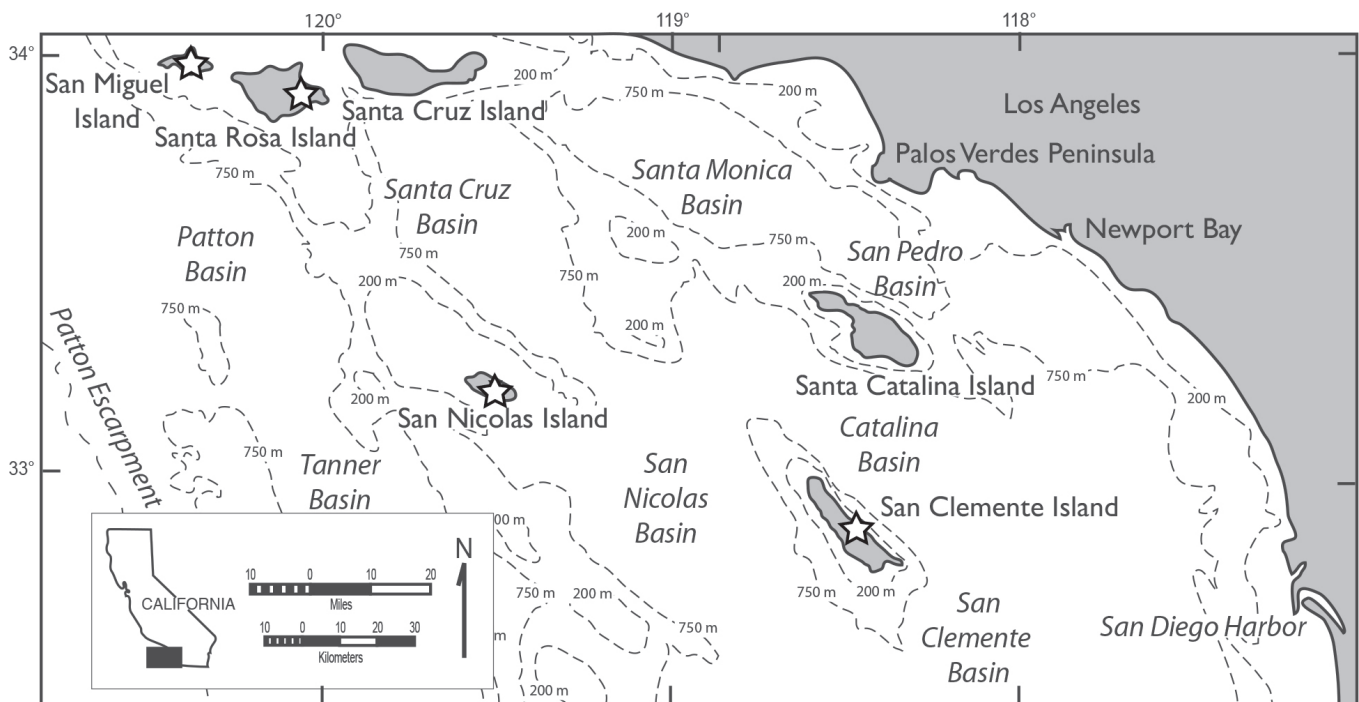


Figure 2. Map of the Southern California Bight with occurrences of *Lottia edmitchelli* marked with a star.

lower and middle) stages have been named: Gelasian and Calabrian, so early and middle Pleistocene (or lower and middle) in these cases are not capitalized.

The age range of *L. edmittchelli* was reported as Late Pleistocene by Lipps (1963). Insightfully, Kanakoff (Howard 1955:137) considered the molluscan assemblage from the type locality (locality LACMVP 1085) equivalent to the cool-water faunas of the “lower” Pleistocene in the Palos Verdes Peninsula (Timms Point Silt and Lomita Marl, which are now considered Middle Pleistocene; Lajoie et al. 1991). Lindberg (1984) discerningly reported an age range of 770 ± 100 to 400 ± 100 ka, or middle Pleistocene, on San Nicolas Island citing Lajoie, et al. (1980; George Kennedy, personal communication).

Although previously reported from the Late Pleistocene (Lipps 1963, Lindberg 1978) and Holocene (Lindberg 1984), a review of its occurrences indicate it has an age range of early Pleistocene to Middle Pleistocene with no specimens occurring in the Late Pleistocene or Holocene. The geologically oldest records of *L. edmittchelli* appear to be those on San Clemente Island, where it is found in a small quarry near the airfield (now defunct) near the top of the island (see http://www.airfields-free-man.com/CA/Airfields_CA_PacificIslands.htm, retrieved 1/2018) at an elevation of about 260 m. Collections from this site include localities LACMIP 2649 and LACIMP 12577, which contain the extinct gastropod *Pusio fortis* (Carpenter, 1866). *Pusio fortis* first appears in the late Miocene to early Pliocene (Pancho Rico Formation; Durham and Addicott 1965) and became extinct sometime during the middle Pleistocene based on age determinations of the lithostratigraphic units in which it occurs on the Palos Verdes Peninsula, Los Angeles County (Lomita Marl, 600 to 300 ka; Lajoie et al. 1991) indicating a minimum age of Middle Pleistocene. However, an older early Pleistocene age for these collections is possible based on extrapolating from uplift rates on other California Channel Islands to the elevation of locality LACMIP 12577 and using Muhs (2018) who reports this locality could be over 1.0 Ma, or early Pleistocene.

Dating marine terraces by determining the age of the lowest marine terraces on an island and extrapolating upward using a common uplift rate for the Channel Island (D. Muhs, written communication, 3/2020) has determined ages for *L. edmittchelli* occurrences on the Channel Islands (Table 1). These data give a minimum age between 667 and 590 (late oxygen isotope stage 15, see <http://www.gly.uga.edu/railsback/Fundamentals/SFMGSubstages01.pdf>, retrieved 3/2020) for the 89–95 m terrace on the Santa Rosa Island (633 to 590 ka) and

Table 1. Elevation and age estimates of occurrences of *Lottia edmittchelli* on islands in the Southern California Bight. **ka**=kiloannum or thousand years, **Ma**=megaannum or million years. D. Muhs (written communication, 2020).

California Channel Islands	Elevation of <i>Lottia edmittchelli</i> occurrences	Age estimates from terrace elevations (D. Muhs, personal communication, 3–4/2020)
San Clemente Island	260 m (D. Muhs, personal communication, 3/2020)	1.4 Ma
San Miguel Island	100-155m (herein)	560 ka–1.0 Ma
San Nicolas Island	220-255 m (Vedder and Norris 1963), 270m(?)	980 ka to possibly 1.0 Ma
Santa Rosa Island	89-175 m (herein)	590 ka to 1.2 Ma

667 ka for the 100 m terrace on San Miguel Island. An intermediate age of about 1.2 Ma was determined for the 175 m terrace on Santa Rosa Island. The oldest determinate was from the 260 m terrace, mentioned above, on San Clemente Island where Muhs determined an age of approximately 1.4 Ma (probably oxygen isotope stage 40). These data give an age range between 1.4 Ma to 630 ka for occurrences of *L. edmittchelli* on the California Channel Islands, or early to Middle Pleistocene. It should be noted that there are significant assumptions and errors built into this method and the age determinations are approximations.

Ecology

Lipps (1963) gives an excellent interpretation of the ecology of *Lottia edmittchelli* as “representing the exposed rocky shore association: *Mytilus californianus*–*Littorina planaxis* community” of Valentine (1961). Citing Test (1945), Lipps states that “it is possible to determine the ecologic niche of a species of *Acmaea* by ... certain adaptive features of the shell.” These shell characters (Lipps 1963) include: 1) the restriction of the aperture in many specimens, an adaptation to prevent desiccation in limpets subject to exposure; 2) a thick, heavy shell and prominent sculpture, which serve to withstand the impact of ocean waves; 3) an irregular margin caused by conformation to the substrate where the animal lived; and 4) a relatively high spire, the latter Test (1945) attributed to exposure or other unfavorable conditions, but which Shotwell (1950) considered a result of growth. The first two favor an environment of long-term exposure and wave action, while the latter two may instead favor an abundant food source.

According to Vedder and Norris (1963), *Acmaea*

mitchelli [= *L. edmitchelli*] occurs most abundantly near the paleo-shoreline, as inferred from geologic field relations of the terrace platform. This supplemented with Valentine and Lipps (1963) observations suggest that *A. mitchelli* occupied an ecologic niche in the intertidal zone possibly somewhat above the average mean tidal level where wave impact and exposure were important factors affecting marine life. Many specimens of *A. mitchelli* have distorted or irregular margins; such features occur in modern limpets living on rocks in the high intertidal...". Lindberg (1984) postulated based on the presence of a borehole in one specimen of *L. edmitchelli*, presumably made by the muricid gastropod *Nucella* Röding, 1798, which does not occur above the middle intertidal, an indicator of it occurring lower in the intertidal zone. He also reported the closely related species *L. scabra* reaches its highest densities in the mid-intertidal on San Nicolas Island.

Abundant molluscan species associated with *L. edmitchelli* occurring on San Clemente Island (LACMIP 12577; n=94) allow for water temperature interpretation of the terrace deposit. Accompanying taxa have overlapping geographic range zones between 32° and 33°N (the latitude of San Clemente Island), with the exception of the bivalve *Nutricula confusa* (Gray, 1982) (36–43°N; Coan et al. 2000), and gastropods *Alvania montereyensis* Bartsch (1911) (35–57°N; LACM collections), and *Styliidium eschrichtii* (Middendorff, 1849) (48–57°N; LACM collections), which all occur to the north. These northern extralimital species indicate cooler water temperatures during at least part of the year when they were alive than exists around San Clemente Island today. Whether these changes are due to lowering of the local water temperature, upwelling, or changes in the ecological tolerances of these species cannot be determined. Overlapping water depth ranges of molluscan species from this site indicate deposition somewhere between the intertidal zone to shallow subtidal water depths. Michael Vendrasco (personal communication, 1/21/2009) considers the chiton fauna from this collection to also represent cooler water at intertidal to shallow subtidal depths.

CONCLUSION

Lottia edmitchelli is here determined to be of early to Middle Pleistocene (1.4 Ma to about 560 ka) in age as opposed to the Late Pleistocene to Holocene age suggested by earlier authors. In addition, its geographic distribution is expanded from one to four islands in the southern California Bight (i.e., San Clemente, San Miguel, San Nicolas, and Santa Rosa Islands), and not on the

California mainland. It is believed to have lived in the intertidal zone in slightly cooler water temperatures, either seasonally or due to upwelling, than those in the Southern California Bight today. Further collecting on Anacapa, San Nicolas and Santa Barbara islands may, in the future, recover mollusk specimens from the terrace deposits of these islands that with the use of Sr age dating will likely refine the age range of this species.

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APPENDIX. USGS field collections now housed at UCMP and cataloged with UCMP numbers. (Latitudes and longitudes rounded to four significant figures).

UCMP IP16545 (Field no. B13SRI-37). Terrace exposure on NNW side of Santa Rosa Island, Santa Barbara County, California. Latitude 34.0051°, longitude -120.2350°, 89 m elevation. Collected by David R. Bedford, August 2013. Additional USGS field numbers under this UCMP locality include BWP 964, and KSSR 13-37 with the following description: Numerous sandstone boulders from terrace deposits with pholad borings as float capped by 2 m of eolianite on the edge of Pocketfield Road, on the NNW side of Santa Rosa Island, Santa Barbara County, California. Latitude 34.0051°, longitude -120.2353°, circa. 95 m (probably ± 5 m, determined on Google Earth).

UCMP IP16546 (Field no. B13SRI-38). Terrace exposure on NNW side of Santa Rosa Island, ENE of B13SRI-37, Santa Barbara County, California. Latitude 34.0054°, longitude -120.2324°, circa. 90 m (probably ± 5 m, determined on Google Earth). Collected by David R. Bedford, August 2013.

UCMP IP16547 (Field no. KSSM 18-2). Terrace deposit up small canyon from beach at Tyler Bight, San Miguel Island, California. Latitude: 34.0339°, longitude: -120.4113, circa. 100 m (probably ± 5 m, determined on Google Earth). Collected by Kevin Schmidt, August 2018.

UCMP IP16548 (Field no. SMI 16091). Terrace exposure in canyon gully about 5000' NE of Crook Point, on S side of San Miguel Island, California. Latitude: 34.0278°, longitude: -120.3502°, circa. 155 m (probably ± 5 m, determined on Google Earth). Collected by Kevin M. Schmidt, July 2016.

UCMP IP16549 (Field no. SRI 17019A). Coquina collected in the first secondary canyon off major canyon (Bee Canyon) from SW coast of Santa Rosa Island, California. Latitude: 33.9645°, longitude: -120.1886°, circa. 95 m (probably ± 5 m, determined on Google Earth). Collected by Kevin M. Schmidt, July 2019. Additional USGS field numbers under this UCMP locality include B13SRI-37, BWP 964, and KSSR 13-37.

UCMP IP16550 (Field no. SRI 17019B). A little further up canyon from SRI 17019A, off major canyon (Bee Canyon) from SW coast of Santa Rosa Island, California. Latitude: 33.9645°, longitude: -120.1886°, circa. 95 m (probably ± 5 m, determined on Google Earth). Collected by Kevin M. Schmidt, July 2017. Additional USGS field numbers under this UCMP locality include B13SRI-37, BWP 964, and KSSR 13-37.