

**EXPLORING SIZE AND BRYOZOAN ENCRUSTATION OVER TIME IN SOUTHERN CALIFORNIA
CREPIPATELLA LINGULATA (GASTROPODA: CALYPTRAEIDAE):
PLEISTOCENE TO PRESENT DAY**

A Thesis By

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**California State University, Fullerton
Fall, 2021**

In partial fulfillment of the degree:

Master Science, Biological Science

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DOI:

10.5281/zenodo.5717382

Keywords:

fossil, bryozoan, gastropod, Calyptraeidae, symbiosis, epibiont

Abstract:

This study examines the bryozoan fauna encrusting on the common Pacific half-slippersnail, *Crepidatella lingulata*. This suspension-feeding calyptraeid gastropod is common at shallow depths off the coast of California and is also common in the fossil record. The shell lengths of *C. lingulata* specimens dating back to the late Pliocene-early Pleistocene were examined, as well as the area of shells encrusted with bryozoans. Holocene shells were significantly larger than other shells, and modern (specimens collected in the present day) encrusted shells were significantly shorter than encrusted shells from the ancient past, but the latter could reflect collection bias. I also determined that modern shells are more fully covered with bryozoans than fossil shells. However, there was significant statistical interaction in the Holocene and modern data; thus, if more specimens were to be added that were relatively less prone to sampling biases from these time periods, the observed patterns could change. Finally, I identified bryozoan species encrusting on modern *C. lingulata* shells: 34 of the 41 specimens examined were found to be the species *Rhynchozoon rostratum* and, because one bryozoan species seems to dominate the encrustation, this implies a symbiotic association between *C. lingulata* and *R. rostratum*.

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ACKNOWLEDGMENTS

I would like to thank my advisor, Dr. Douglas Eernisse, for his support and patience throughout this process, and for allowing me to use his many specimens he has collected over the years. I would also like to thank my two other committee members, Dr. Danielle Zacherl and Dr. Nicole Bonuso, for their guidance and suggestions regarding my research and analyses. I would like to thank Dr. Austin Hendy, Shawn Wiedrick, and the staff of the Natural History Museum of Los Angeles County's Invertebrate Paleontology Collections for graciously allowing me to work with and study their fossil specimens, and for providing locality data for the fossils. I would like to thank Megan McCuller of the North Carolina Museum of Natural Sciences for her tips in working with and identifying bryozoans. Lastly, I would like to thank Dr. Henry Chaney of the Santa Barbara Museum of Natural History for providing helpful knowledge, for giving me a hard copy of Volume 13 of *The Taxonomic Atlas of Benthic Fauna*, for allowing me to use images from that book, and for allowing me to tour the museum's molluscan collections, an experience which ultimately helped decide the direction that my research would go.

CHAPTER 1

INTRODUCTION

Organisms of the phylum Bryozoa are small, colonial animals that often encrust onto hard surfaces. Several bryozoan species are among the most prolific invasive organisms, including for the California rocky shores (Zabin et al., 2019), as many species can be transported in the larval stage via ship ballast or by encrusting on the ships themselves (Wostenberg, 2015). Once established in an area, invasive bryozoans can damage local ecosystems such as kelp beds (Scheibling & Gagnon, 2009) and can also foul equipment used by the aquaculture industry (Loxton et al., 2017). The southern California fauna is also changing through time due to global warming, with species shifting to higher latitudes in California and elsewhere (Hughes, 2000). Winston and Håkansson (1986) found a variable number of bryozoan species encrusting on shells in Capron Shoal, Florida, dependent on shell size, and a study by Tilbrook (2012) in Australia revealed two invasive bryozoans that had been previously unseen at the time of publication.

The most common bryozoans worldwide tend to belong to one of four bryozoan orders, Cheilostomatida, which includes the calcified species that encrust onto hard surfaces, even shells of mollusks such as gastropods (Ryland, 2001; Soule et al., 1996). Associations between bryozoans and gastropod shells are well known but appear to be mostly limited to bryozoans encrusting on empty gastropod shells inhabited by pagurid hermit crabs (Aguierre-Urreta & Olivero, 1992; López-Gappa et al., 2018). Associations between bryozoans and actual gastropods (rather than simply on hermit-inhabited gastropod shells) are much rarer, but are not unheard of (Gray et al., 2005; Ryland, 2001). Such relationships have also been noted to occur in the fossil record (Kidwell & Gyllenhaal, 1998; McNamara, 1978).

In this paper I examine the common Pacific half-slippersnail, *Crepidatella lingulata* (Gould, 1846), and bryozoans that typically encrust on its dorsal shell surface. Examining the species encrusting on *C. lingulata* could reveal some bryozoans that are present in southern California that will encrust on the shells of living gastropods. Interestingly, Dr. Eernisse has noted that many of the

specimens he has collected are encrusted with an orange, previously unidentified bryozoan (Eernisse, pers. obs.; Figure 1). Collin (2019) also noted in her study of northeastern Pacific calyptraeids that such a bryozoan is often seen encrusting *C. lingulata*. One primary goal of this study includes examining or documenting the bryozoans encrusting on this gastropod to reveal the identity of this mystery bryozoan. Doing so will lay groundwork for a potential future study to determine if this bryozoan has a symbiotic relationship with *C. lingulata*. A finding of a symbiotic relationship between a bryozoan and *C. lingulata* would therefore be significant and would be the first known association between a bryozoan and a calyptraeid gastropod. As part of my analyses, I conduct a chi-squared test on bryozoans that I identify to determine if one species (such as the mystery bryozoan) is statistically overrepresented in the encrusting bryozoan fauna. However, because there is a diversity of encrusting bryozoan species common in southern California (Soule et al., 1996), I also hypothesized that no single bryozoan species will be significantly more common than others and not especially more common than it is observed to be on other hard substrates. Additionally, this research could be useful in the event of any future introduction of one or more invasive bryozoan species with an encrusting habit in southern California. By taking a census of species currently encrusting on *C. lingulata*, my research will provide a baseline faunal reference for any future studies that might include documentation of newly invasive species or faunal or productivity shifts due to climate change. Such studies could involve chi-squared tests similar to those I perform here as well as those performed in similar scenarios by other authors (Almeida et al., 2018).



Figure 1. *Crepidatella lingulata* encrusted by “mystery bryozoan”, *Rhynchozoon rostratum* (Busk, 1855). Photo credit: D. Eernisse.

I was also interested in observing potential changes in the average shell length and area of this gastropod over geologic time; any changes could potentially affect how much of the gastropod's shell bryozoans may encrust, as well as hint at environmental conditions affecting the size and dimensions of this gastropod. I hypothesized that bryozoans colonize and spread much faster than shell growth, so that encrustation should cover available shell area, independent of shell size, and that this habit is consistent through geologic time. It was assumed that a bryozoan colony would take advantage of any free area on a shell; a deviation in the data from this assumption could signify that a bryozoan colony was somehow prevented from expanding onto the entire shell (although there is some potential deviation due to individuals being buried prior to full shell colonization). Some prehistoric bryozoan taxa have been shown to have fully encrusted their contemporary gastropods (McNamara, 1978), so I wanted to determine if a such a phenomenon could be observed in *C. lingulata* over geologic time.

Separately, I hypothesized that the average shell length of *C. lingulata* would change significantly over this comparatively brief geologic time. Significant change in shell length could

coincide with environmental changes or could be a product of the immediate environment where the animals lived. A study of the suspension-feeding South American bivalve *Tawera elliptica* (Lamarck, 1818) showed a significant difference in dimensions of modern individuals of this bivalve and fossils dating back 4,500 years (Gordillo et al., 2011). An examination of the southern African tick shell, *Nassarius kraussianus* (Dunker, 1846) revealed a decrease in shell size linked to rising temperatures from the Pleistocene to the Holocene (Teske et al., 2007). It has also been suggested that increased productivity could result in size changes in bivalves (Vermeij, 1990) and gastropods (Teusch et al., 2002). An observed increase in size could imply that a period or periods of increased productivity took place in the ancient past. Alternatively, significant change could signify taphonomic effects on these fossils (i.e., smaller shells being more prone to destruction by the environment).

Because our current interglacial interval has a relatively high sea level, terrestrial accumulation of marine fossils is most commonly found from previous interglacial intervals (DeDiego-Forbis et al., 2004) when sea level was at its highest, including the last interglacial interval about 125,000 years ago (Dahl-Jensen et al., 2013). A few others originate from periods of glacial expansion. However, it is often difficult to pinpoint a specific age for fossils, and this is the case for many of the fossils that I studied. Such fossils were typically assigned age ranges that encompass parts of both interglacial and glacial intervals. Thus, determining if the Earth's Pleistocene "Ice Age" cycles of glaciation may have caused changes in the size of this gastropod over geologic time is challenging, but it is something I explore in this thesis.

CHAPTER 2

METHODS

To examine changes in shell length, and to attempt to determine if there is a relationship between bryozoan colony area and shell area, I photographed various *C. lingulata* specimens in a dorsal orientation and measured shell length and area using the digital image tools in ImageJ v. 1.53a (Wayne Rasband, 1997).

I was granted access to the Invertebrate Paleontology Collection of the Natural History Museum of Los Angeles County (LACMIP) in 2019. In the pre-pandemic time I spent there, I retrieved almost every *C. lingulata* specimen in the catalog and sorted them into two groups: bryozoan-free (also referred to as unencrusted) and encrusted. I made sure to choose shells that were found in my target range (from Point Conception in Santa Barbara County to the San Diego-Mexico border). I used the on-site mounted Canon EOS 5D Mark IV camera with Canon MP-E 65mm f/2.8 1-5x macro lens to photograph every specimen in dorsal view with an included scale bar.

In the spring and summer of 2019, I visited several intertidal sites in Los Angeles and Orange counties to collect some living *C. lingulata*. I visited White Point, the Seal Beach Jetty, and the Newport Coast Guard beach. Unfortunately, my efforts were not fruitful, as I collected only one living specimen (from the Coast Guard beach near the entrance to Newport Bay, Orange Co.; empty shells were plentiful at all sites). To make up for the lack of my own collected specimens, I examined the specimens that Dr. Eernisse had previously collected. Most of these specimens were collected from either the Coast Guard beach (among the tubes of the vermetid gastropod, *Thylacodes squamigerus* (Carpenter, 1857)), or they were collected by biological dredge from a rockpile of 25m depth near San Pedro in Los Angeles County. Similar to my treatment of fossils, I used our lab's mounted Canon EOS 5D Mark IV camera with Canon MP-E 65mm f/2.8 1-5x macro lens to photograph each specimen (Figure 2A).

In ImageJ, I used the "Measure" function of the program to measure each shell's length down its longitudinal median defined by the apex position. This was a little challenging, as not every

specimen was symmetrical, so I attempted to make measurements as close to the shell median as possible; therefore, some of the measurements may not have been of the maximum shell length. In taking measurements of shell length, I assumed that shells that were longer were also “larger” overall (shell length is therefore used as a proxy for shell size). I also measured the surface area of the encrusted shells as approximated in the two-dimensional image, as well as the area of the bryozoan colonies encrusting them. Both values were measured in two dimensions. Because the shell has some three-dimensional attributes, underestimation of the surface area is expected from this method; however, this is expected to be slight because the shells are quite flat, and thus any differences between my methods and a method involving three-dimensional calculations should be small. However, I calculated the approximate surface area using a formula for an idealized conical three-dimensional object across a range of height values, and given realistic height values, I noted that the surface area should be underestimated by less than 10% of the actual surface area. For example, if the shell was assumed to be a perfect cone with a 1 cm diameter base, the underestimation of the shell surface is expected to be equivalent to a ratio of the cone’s basal surface area (the gastropod’s aperture) divided by the remaining surface area of the cone (the dorsal shell surface), or about 98, 92, or 72% of the actual surface area for a cone of height 1, 2, or 5 mm height, respectively. Moreover, any underestimation of the ratio of bryozoan coverage to total dorsal shell surface should be even less. Similar methods have been conducted on the valves of brachiopod shells (Bordeaux & Brett, 1990), and these are relevant because individual brachiopod valves often have a shape somewhat similar to the shells of *C. lingulata*.

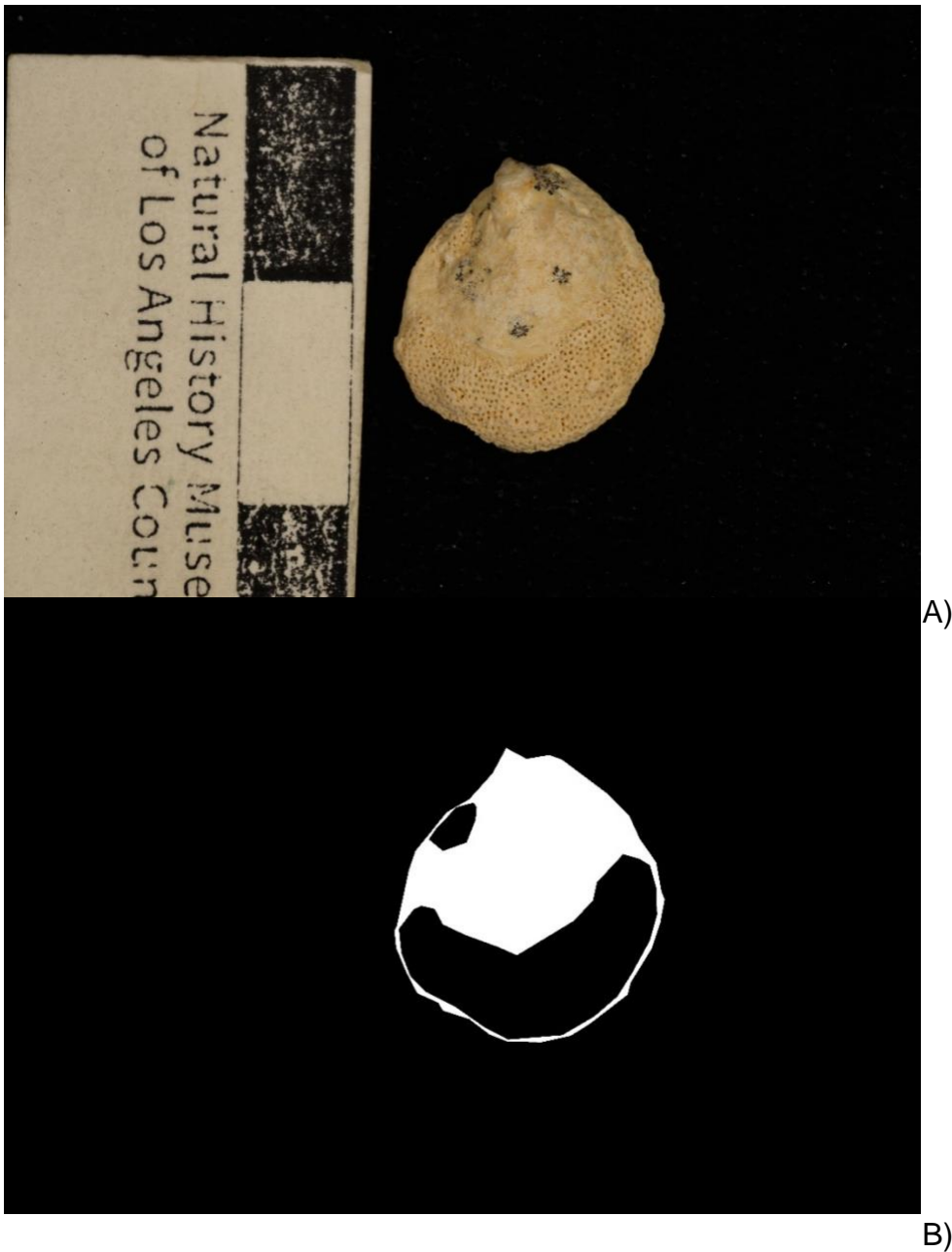


Figure 2. A) a photograph of an encrusted *Crepipatella lingulata* shell, and B) an image mask created from the photo. The bryozoan colonies in the image mask are represented as black spaces within the shell. The boxes on the scale bar on the left of figure 2A are 1.0 by 0.5 cm.

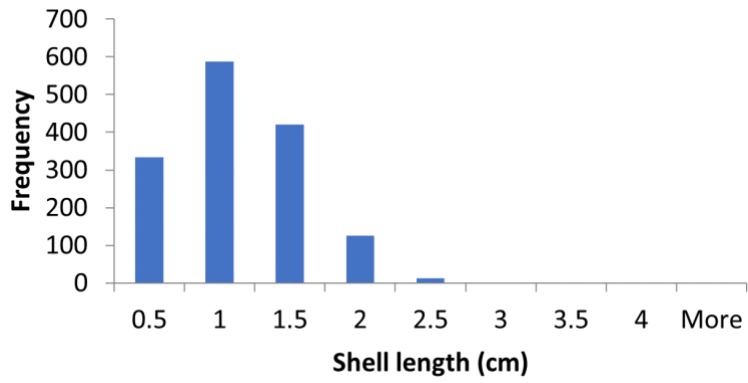
To conduct surface area measurements, I used ImageJ's polygon selection tool; I chose this tool because of its ease of use compared to the freehand selection tool. Outlining the shells and bryozoan colonies using ImageJ's freehand selection tool would have taken up a large amount of time, and when using such a tool, once a mistake is made, the only way to correct it is to reselect the area of interest. The polygon selection tool allows the user to place multiple points around an area of interest; it is much faster to use. While only straight lines are created between points, enough points

can be created that the resulting area has enough lines that the edges of the area are almost round. Through use of the polygon selection tool, I do not believe a lot of area from the original image is lost. For each image, once I had selected the shell, I used the same polygon selection tool to deselect the bryozoan colonies to leave empty areas representing them. Once that was finished, I created image masks of each image and made these image masks binary in order to make them fully black and white images (Figure 2B). I used ImageJ's "Measure" tool (with automated calculations given by the program's provided "Wand Auto-Measure Tool" macro) to determine the total area of the shell in a dorsal two-dimensional view, as well as the area of the bryozoan colonies in the same view.

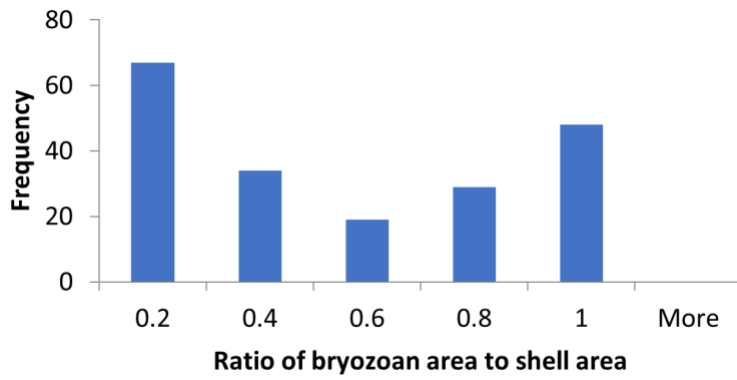
I entered the data into several Excel spreadsheets. The LACMIP staff personnel were kind enough to send me detailed information about the origins of my specimens (see Appendix): this information included numeric age range (e.g., 100 kA), locality age range (hereafter referred to as "time period"; not as specific as numeric age range), formation, and (when available) member (more specific than formation). I assigned each specimen to one of the following conventional time periods for convenience: late Pliocene-early Pleistocene, early Pleistocene, middle Pleistocene, middle-late Pleistocene, late Pleistocene, and Holocene. Assembling individual records allowed me to tally the percentage of specimens from each time period that were encrusted (Table 1).

Table 1. Summary of numbers of *Crepipatella lingulata* specimens imaged for each time period.

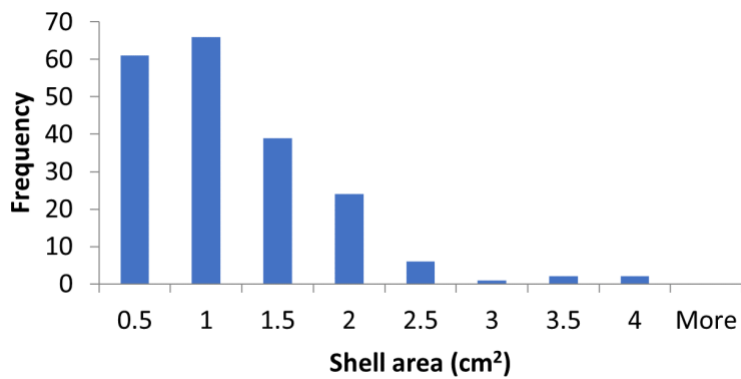
Age	Total Number	Number of Encrusted	Number of Bryozoan-free	% Encrusted
Late Pliocene-Early Pleistocene	1	1	0	100
Early Pleistocene	11	1	10	9.09
Middle Pleistocene	367	21	346	5.72
Middle-Late Pleistocene	36	1	35	2.78
Late Pleistocene	681	56	625	8.22
Holocene	238	65	174	27.20
Modern	147	62	85	42.18



A)



B)



C)

Figure 3. Distribution graphs of A) lengths of all studied *Crepipatella lingulata* shells, B) ratios of bryozoan colony area to shell area, and C) areas of encrusted shells.

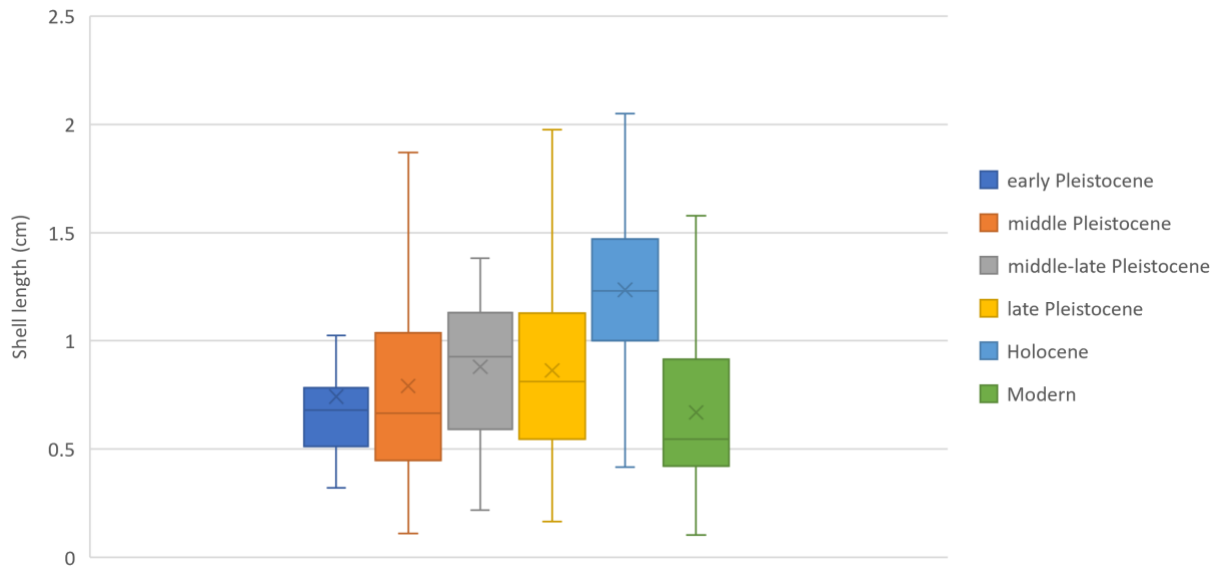


Figure 4. Box-and-whisker plot of shell length of *Crepipatella lingulata* throughout different geological time periods. The late Pliocene-early Pleistocene was excluded due to low sample size.

After I photographed shells, estimated their dimensions, and computed estimates of dorsal shell and bryozoan surface areas, I used the computer program, JMP v. 15.2.1 (SAS Institute Inc. 2019), to conduct Steel-Dwass nonparametric analyses (Neuhäuser and Brett, 2001) on the data, as well as Tukey post-hoc tests. I additionally performed a two-way ANOVA on shell length data in order to determine the effects of encrustation status, time period, and their interaction on shell length. I grouped my data into the previously listed time periods both for convenience and to allow evaluations of trends through time. For living specimens collected by myself or Dr. Eernisse, I labeled the time period as “modern”. Once I grouped the data, I checked whether each grouping had normal a distribution and equal variance using JMP and by creating distribution graphs of the data (Figure 3), and because in general the distributions and variances did not meet these conditions, I rank transformed the data and conducted several nonparametric analyses. For all the tests of shell length, I excluded one time period for which there was only a single specimen: late Pliocene-early Pleistocene. When I examined shell lengths of encrusted vs bryozoan-free shells, I excluded the early Pleistocene and middle-late Pleistocene data for similar reasons. Additionally, for the encrusted shells, I took the ratios of bryozoan area to shell area and conducted analyses on those as well.

Lastly, I used Excel (v. 2104, Microsoft Office 365) to create a box-and-whisker plot of the shell length data to better visualize the range of the data (Figure 4).

I additionally found that certain shells were dated to particular glacial or interglacial intervals- these specifically were the Marine Isotope Stage 5e interglacial interval (dating from 130,000 to 115,000 years ago), the last glacial interval (from 115K to around twelve thousand years ago), and the current interglacial interval starting around twelve thousand years ago. To compare average shell lengths across glacial and interglacial intervals, I conducted a t-test with the data in JMP. I JMP was also used to create a plot of the results.

I examined the encrusted modern shells under a microscope; I used a field guide by Soule et al. (1996) to find diagnostic features of the bryozoans to accurately identify them. Once bryozoan taxa were identified, I conducted a chi squared analysis on the data to determine if any of the taxa identified were statistically overrepresented.

CHAPTER 3

RESULTS

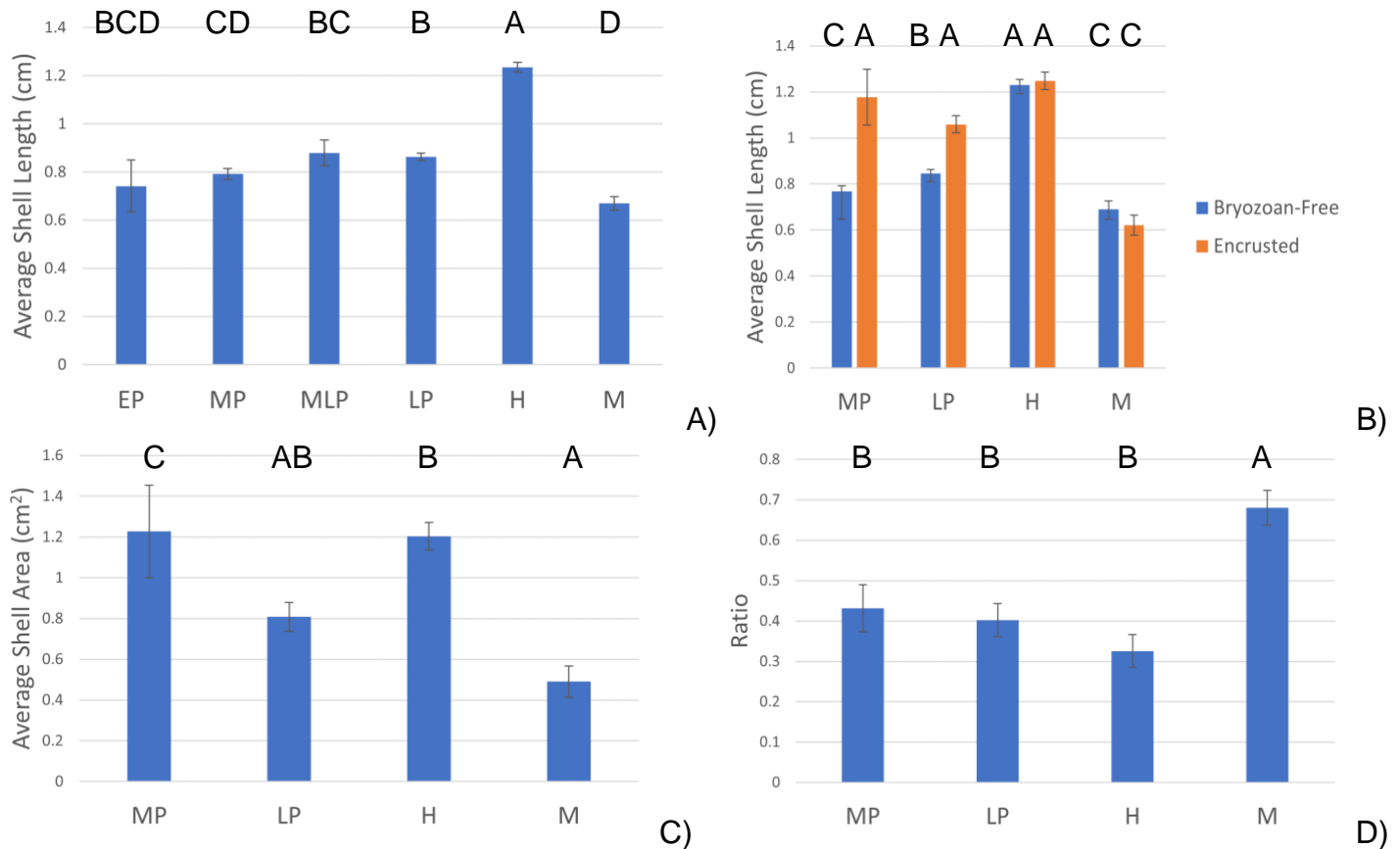
When all shell lengths were compared, I found that the Holocene shell lengths were on average significantly higher ($p < 0.01$) than shell lengths from the other groups (Figure 5A). When I examined the shell lengths of bryozoan-free vs encrusted shells and performed a two-way ANOVA on the data, I found that the effect of encrustation on shell length was not the same across all time periods (Figure 5B, Table 2). These results interestingly showed that shell length in the Holocene and modern specimens was not affected by encrustation status, but in the middle and late Pleistocene shells, there was an association between shorter shell length and being free of bryozoans. I additionally found that the average shell lengths of bryozoan-free modern shells were not significantly different from bryozoan-free middle Pleistocene shells, and encrusted modern shells were significantly smaller on average ($p < 0.01$) than encrusted shells from all prior time periods.

Table 2. Two-way ANOVA statistics for effect of time period on *Crepidatella lingulata* shell encrustation status.

Source	df	Sum of Squares	F ratio	P
Bryozoan-Free vs Encrusted	1	2318752	16.67	<.0001
Time Period	3	26162526	62.70	<.0001
Bryozoan-Free vs Encrusted X Time Period	3	3544378	8.49	<.0001

The analyses of the shell area data show that the modern encrusted shells have a significantly smaller area than encrusted shells from prior time periods; this pattern matches up with the results of the shell length analyses (Figure 5C). This also affirms my earlier assumption that shell length can be used as a proxy for overall shell size. The results also show that the average shell area of the Holocene shells is significantly higher than the average shell area of the modern and late Pleistocene shells, but not the middle Pleistocene shells. When the ratio of bryozoan colony area to total shell area is analyzed, the data shows that this ratio was significantly higher in the modern shells than it

was in shells from prior time periods (Figure 5D); this means that the modern encrusted shells were covered with bryozoans more extensively than encrusted shells from prior time periods.



Abbreviations: EP: Early Pleistocene; MP: Middle Pleistocene; MLP: Middle-Late Pleistocene; LP: Late Pleistocene; H: Holocene; M: Modern

Figure 5. Graphs of A) average shell length of *Crepipatella lingulata* over time, B) average lengths of bryozoan-free and encrusted shells over time, C) average area of encrusted shells over time, and D) the ratio of bryozoan colony area to area of encrusted shells over time. Groups in each graph that do not share a letter above the bar are significantly different, as determined via Tukey's post-hoc tests.

I additionally conducted a t-test on certain shell lengths where I was able to determine if the specimen originated from an interglacial or glacial interval (Figure 6). My analysis shows that the average shell length from Marine Isotope Stage 5e (also known as the Eemian stage), the interglacial interval from 130K to 115K years ago (Dahl-Jensen et al., 2013), was longer than the average shell length of fossils dating back to the Last Glacial Period (115K to 11.5K years ago). Interestingly, the average shell length of the Holocene fossils is higher than both of those previous averages, while the average shell length of the modern shells is only higher than the average shell length of shells dating back to the last glacial interval.

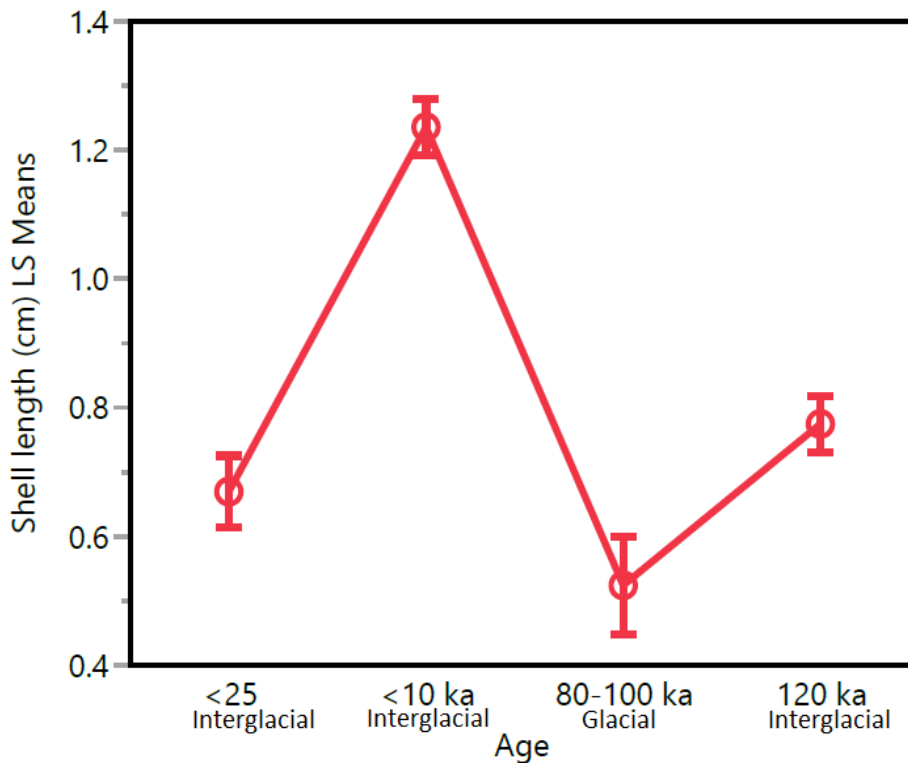


Figure 6. Plot of averages of *Crepipatella lingulata* shell length at different points of the Earth's glacial cycle.

After examining the modern encrusting bryozoan fauna, I found that one species of bryozoan, *Rhynchozoon rostratum* (Busk, 1855) was exclusively found on thirty-four of the forty-one *C. lingulata* specimens I examined that had encrusting bryozoans. Another species, *Cauloramphus californiensis* Soule, Soule & Chaney, 1995, was the second-most common bryozoan, occurring exclusively on six specimens. I did see one other bryozoan species, *Microporella catalinensis* Soule, Soule & Chaney, 1995, but I was only able to find it on a single specimen. None of the shells studied ever had more than one bryozoan taxa encrusting on it. The results of my chi-squared analysis revealed that *Rhynchozoon rostratum* was statistically overrepresented in my samples, $\chi^2 (2, N = 41) = 43.13, p < 0.01$.

In summary, the most striking findings of my research were that average shell length of Holocene shells was significantly higher than the average shell lengths from the other studied points in time, and that encrusted modern shells were significantly smaller both in terms of shell length and shell area than shells from earlier points in time. The modern shells also have a higher ratio of

bryozoan colony area to shell area, meaning that on average they are the most encrusted shells out of the studied specimens. Additionally, the effect of bryozoan encrustation on shell length is not the same across all time periods, with no effect observed in the Holocene and modern shells, and an association between unencrusted shells and shorter shell lengths. Finally, I was able to positively identify bryozoan species on forty-one modern shells, thirty-four of which were identified as *Rhynchozoon rostratum*.

CHAPTER 4

DISCUSSION

The fluctuation in shell length and area, especially regarding modern *C. lingulata*, is rather interesting. My results provide no evidence for a directional change over time in average shell length since the early Pleistocene, but the average shell length does seem to fluctuate from time period to time period. Sometimes the pattern of fluctuation is statistically significant, in comparisons between adjacent time periods, and at other times it is not. The most notable pattern from my data is how shell length changes after the late Pleistocene. My data show a significant increase in average shell length in the Holocene fossils, but specimens collected in the present day are significantly smaller than all specimens except for those from the early and middle Pleistocene. Additionally, the significant presence of the bryozoan *R. rostratum* on most of the encrusted modern shells is interesting because it could point to an association between this bryozoan and *C. lingulata* that likely extends into the fossil record, an association that could perhaps be based on, for example, bryozoans camouflaging the gastropod, or the gastropod providing refuge for the bryozoans from their predators. Alternatively, it could be due to collection bias. I will explore potential biases in the following sections and explore alternative explanations for patterns seen in my data.

Possible Causes of Fluctuations in Average Shell Size

There are several possible explanations for the significant changes seen in the late Pleistocene onward. The simplest explanation is a sampling bias. Many of the modern specimens collected by Dr. Eernisse near San Pedro were found living inside the burrows of date mussels (*Mytilidae*); living inside of these burrows could restrict the gastropod size, or they might migrate out of these burrows as they mature. If this is the case, these individuals would be elongate in order to fit inside of the burrows ("burrow morphs"). However, while there are a few specimens that could be considered "elongate", they are not common enough for me to consider them "burrow morphs". If such a phenomenon is common among the modern shells collected from date mussel burrows, I would expect to see more elongate individuals at a higher frequency. This is not the case.

The other large group of modern specimens, collected from the Coast Guard Beach, were found among vermetid tubes. I believe that this could have also restricted the size of the specimens, due to a lack of space. It has been noted that the shell size of *C. lingulata* seems to be influenced by the animal's choice of substrate. Eighty-five percent of the specimens that Goodwill (1975) observed were found living under rocks, and it was noted that there was, in one location (northern Cantilever Pier, San Juan Island, Washington), a correlation between rock size and shell size. Therefore, it is possible that the shorter shell length in the modern specimens is due to the shells being collected from places where their size is restricted, although in this case the substrate involved is vermetid tubes rather than the undersides of rocks. Measuring a greater range of specimens in collections of modern shells would be a way to test whether Dr. Eernisse had collected smaller than average shells.

The relatively small average size of the modern shells does not explain why the Holocene fossil shells exhibited significantly longer shell length than the fossils examined in every other time period. The nature of any collection bias for Holocene fossils seems obscure, because not only is there a high number of Holocene specimens (238), but there are also large numbers of both middle Pleistocene and late Pleistocene specimens (367 and 681, respectively), and the Holocene samples show a significantly greater average shell length than these earlier time periods. From such a high number of samples, one might expect there to be a similar wide range of shell lengths and a similar average, but this was not the case.

I suspect that the most likely explanation for the larger average shell size of the Holocene fossil shells is that these fossils were subjected to higher levels of destruction due to erosional or tectonic geological processes (Gilluly, 1949) than the fossils from earlier time periods. All the Holocene specimens were collected from Venice Beach and Marina del Mar, both in Los Angeles County. Both localities are roughly in the same area. Fossil shells that are smaller are generally more delicate and are more easily destroyed by taphonomic processes, which can lead to a lack of smaller specimens in the fossil record (Cooper et al., 2006; Puchalski and Johnson, 2008; Valentine, 1989). In a locality in New Zealand, for example, fossil mollusks measuring less than five millimeters long

are depleted in the fossil record (Cooper et al., 2006). It is possible that the localities where these Holocene fossils were found had experienced relatively greater erosional activity that could have destroyed smaller, more fragile, fossils and made preservation of smaller organisms much more difficult. This sort of preservational bias could have affected which shells survived, and ultimately could have led to a higher-than-normal average shell length observed later. More study on this specific locality would be needed to determine the ancient Holocene environment and its possible effect on preservation of organisms there.

An alternative explanation is that the greater average Holocene shell length corresponds to (for an unknown reason) a more female-biased sex ratio in Holocene samples. Female *C. lingulata* are generally larger than their male counterparts in this species (Collin, 2000; Goodwill, 1975) and for members of Calyptraeidae in general, as these taxa will generally change sex from male to female at a larger size (Brante et al., 2016; Holtheuer et al., 2018). However, there is much overlap between the sizes of the sexes, with individuals who measure between 1 and 1.5 cm being members of either sex (Collin, 2000). Out of the 238 Holocene specimens I examined, fifty-three of them are over 1.5 cm in length. Additionally, the work of Collin (2000) suggests that it is not body size but instead the presence or absence of females in a male's vicinity that triggers a male *C. lingulata* to change sex. Therefore, I find the possibility of a sex-based explanation to be unlikely, because such a bias is expected to lead to selection for a balancing of the sex ratio (Conover & Van Voorhees, 1990), and be impossible to document given that soft parts would be needed to determine the gender.

Another explanation might be that Holocene *C. lingulata* were larger than their past or future counterparts due to another factor such as differing temperature. For example, it is known that species of the abalone genus *Haliotis* Linnaeus, 1758 living in cold waters are larger than *Haliotis* living in the tropics. North Pacific *Haliotis* are likely larger than in other regions worldwide because of the unusual abundance of kelp and other macroalgae, their primary food sources in this region (Estes et al., 2005), whereas the plankton diet of suspension-feeding *C. lingulata* would seem to require a different explanation, such as the prevalence of upwelling and thus greater planktonic productivity

during cooler periods (Hughes 2000). Additionally, there have been observations that the body size of polyplacophoran mollusks increases in relation to latitude, which was further linked to sea surface temperature (Ibáñez et al., 2021), although the authors that made these observations did not note any mechanism for body size increase. Future studies utilizing museum collections could test for associated predictions that size should increase with latitude or upwelling frequency in *C. lingulata*.

In addition, the effects of preservational biases on the bryozoans need to be addressed. In my examinations of the fossil shells, I noticed that there were many shells that showed evidence of being encrusted by bryozoans, but the skeletons of the epibionts had been quite eroded and damaged. Based on my observations, I believe it unlikely that an encrusting bryozoan colony would be removed from a shell by taphonomic processes without leaving a trace of its prior presence behind. However, this damage would make any future attempts to identify these bryozoans quite difficult due to the destruction of many of their diagnostic physical features.

There was no significant difference in average shell length between the middle and late Pleistocene. As stated above, there many specimens were available from both time periods; these specimens were also collected from a wider variety of areas than the late Holocene specimens. If there is some unknown bias of preservation that accounts for the greater size of fossil Holocene *C. lingulata*, and because middle and late Pleistocene seem to match the present-day size distribution more closely, this would imply that the middle and late Pleistocene more faithfully approximates its average shell length. If more Holocene and modern specimens were to be collected from a greater variety of localities and substrates, and average shell lengths were observed to be more like those of the middle and late Pleistocene, this could implicate the one or more Holocene localities sampled as biased toward larger individuals. Alternatively, if the larger size average were to be upheld, this implies some other explanation is required, such as a relationship to sea water temperature or occurrence of upwelling.

Interpreting Interaction Effect

When I analyzed the data to determine the effects of encrustation status, time period, and their interaction on shell length, the results show that the effect of encrustation status is not the same across geologic time. In other words, shell length does not seem to be statistically affected by encrustation status in the Holocene and modern samples, but there is an effect in the middle and late Pleistocene samples. I believe these observations may be due to the potential biases already discussed. If more specimens were to be collected, I would expect the effect of encrustation status on shell length to change; perhaps the interaction effect would also be observed in the Holocene and modern data if the sample set was expanded?

If, however, the patterns that the data are showing are not influenced by biases, and reflect patterns of significant shell length variation, then the most likely explanation would be related to environmental stressors. There are several interlinked stressors that can be considered, such as salinity and temperature. Salinity, for example, is known to negatively affect another congeneric species, *Crepidatella peruviana* (Lamarck, 1822), in western South America; periods of heavy rainfall in parts of this species' native range can lower the salinity of its aquatic environment (Montory et al., 2016). It was found that juveniles in the veliger stage who were exposed to lower salinity for several hours will metamorphose at a lower shell length than individuals who did not experience the stress of lower salinity (Montory et al., 2016). Although the study concluded that lower salinity did not affect the growth rate of the gastropod, any juveniles that metamorphose at a lower shell length will still be smaller than their unstressed counterparts of the same age. However, rainfall is not the only factor that could create conditions of lowered salinity. Current studies suggest that the Pacific Ocean is experiencing decreasing levels of salinity (referred to as "freshening") that is linked to global warming (Boyer et al., 2005; Durack & Wijffels, 2010). If the significantly short shell length of the modern specimens is not an artifact of collecting bias, then perhaps it is a result of the gastropods being exposed to an ocean that is currently undergoing a freshening phenomenon caused by anthropogenic climate change.

Nutrient Availability

A likely alternative, but related, explanation for differences in shell size could be related to nutrient availability. In southern California, the local upwelling of the California Current provides nutrients to many organisms (Hughes, 2000; Poloczanska et al., 2016), including *C. lingulata*. Studies of the California Current have shown that sea water temperatures warmed during interglacial intervals and were cooler during glacial intervals (Lyle et al., 2010). A study by Teusch et al. (2002) on turritellid gastropods in Chile indicated that periods of increased cooler upwelling intensity and increased food availability are correlated with periods of increased shell size, and this observation by the authors extended to fossil specimens. Turritellid gastropods are suspension feeders, like calyptraeids, so if we assume that calyptraeids are similarly affected by upwelling currents, it would be expected that *C. lingulata* would have a larger average shell size during glacial intervals, when the California Current is stronger, leading to upwelling processes that result in cooler water and more nutrients (Hughes, 2000). However, if I have accurately interpreted the associations between fossil size and associated sea water temperatures, my results suggest that this is not the case. After determining which shells confidently date back to interglacial and glacial intervals, I found that average shell size of *C. lingulata* is lower during glacial intervals and higher during interglacial intervals. This does not, however, rule out nutrient upwellings driven by the California Current influencing the shell size of *C. lingulata*. More data and research are needed to better determine how environmental conditions are linked to changes in the shell size of *C. lingulata*.

Climate Change

In addition to changes in salinity, climate change also affects oceanic pH and temperature (Du et al., 2018). A study on the effect of increased temperature and lower pH on the gastropod *Littorina littorea* (Linnaeus, 1758) found that these conditions result in reduced growth rates for this gastropod (Melatunan et al., 2013). As global oceanic temperature has been increasing due to anthropogenic climate change, it is possible that these conditions could have a similar effect on *C. lingulata* as they do on *L. littorea*. Data from alkenone samples, as well as isotopic studies of molluscan and

foraminiferal taxa help reconstruct Pleistocene ocean temperatures off of the coast of California; these proxies have helped determine warmer or cooler oceanic temperatures. Muhs et al. (2002) report oceanic temperatures warmer than the present day within southern California dating back to 120K years ago suggests oceanic temperatures warmer than the present day, followed by cooler than present oceanic temperatures 105K or 80K years ago. Fossil faunas from San Nicolas Island suggested the same conclusion (Muhs, 2012), and its more western location subjects it to the cooling influence of the California Current.

As previously considered, some of the fossils I examined date back to the Marine Isotope Stage 5e interglacial interval (the interglacial interval prior to the one that is currently taking place), and others date back to the last glacial interval. I found that shells dated specifically to the Marine Isotope Stage 5e interglacial interval are on average significantly larger than the modern specimens collected by Dr. Eernisse, and the fossils dating back to the last glacial interval are on average significantly shorter than these modern specimens. Interestingly, the Holocene fossils are significantly larger than the shells both from Marine Isotope Stage 5e and the last glacial interval, as well as the modern specimens (Figure 6). More importantly, the average shell length of *C. lingulata* from the last glacial interval is significantly less than the average shell length from the prior interglacial interval. This finding is relevant as it seems to suggest that the average shell length of *C. lingulata* changes with the Earth's natural cycle of glaciation.

Change in Ratio of Bryozoan Colony Area to Total Shell Area

When examining the change in ratio of bryozoan colony area to total shell area, I found that this ratio was significantly higher in the modern samples than in previous three time periods examined. In other words, the modern shells were more encrusted with bryozoan colonies than more ancient shells. The ratios in the other three time periods examined were not significantly different from each other. However, I believe that this is due to how small the modern shells are on average, based on both the shell length data and the shell area data. If more samples were to be collected, I would expect this ratio to change so that it would not be significantly different from this ratio in the previous

time periods. In any case, this finding signifies that it appears to be easier for bryozoans to entirely encrust a small shell than for them to encrust a larger shell. If this were not the case, then we would expect the ratios to not be significantly different from each other, even given how the modern shells are significantly smaller than their older counterparts. Again, a collection bias that favored collection of those individuals that were both smaller and more encrusted than average would provide an alternative explanation.

Identification of Bryozoan Taxa

I was able to determine the identity of the modern bryozoans through important diagnostic features, such as the aperture (the opening of the external zooid structure) and avicularia (beaklike zooids with a defensive purpose). Avicularia was specifically important in helping me determine the identity of *Rhynchozoon rostratum*- the avicularia of this are often oriented in random directions (Figure 7). My identification of this species was also aided by the shape of the apertures of the zooids (which are round with a dip, or sinus, along the margin), and the presence of globular ovicells in many specimens. These features are very striking and diagnostic with respect to any other co-occurring bryozoan and led to my identification of this species as *R. rostratum*.

On six specimens, I found a completely different species of bryozoan. The most obvious notable trait of this species is that the frontal part of the zooid was uncalcified; this is the diagnostic trait of the bryozoan suborder Anasca. This particular bryozoan also had a plethora of spines, and I was able to find an intact avicularium on one specimen. The avicularium, unlike the avicularia of *R. rostratum*, is attached to the colony by a stalk. The shape of the avicularium has led me to identifying this species as *Cauloramphus californiensis* (Figure 8). Interestingly, Soule et al. 1996 states that this species is only found in the California Channel Islands. There is, however, another species in this genus that is native to the California coast, *Cauloramphus echinus* (Hincks, 1882), which differs from *C. californiensis* in having less spines, and in having avicularia that are more hooked than those of *C. californiensis*. I learned of *C. echinus* after I had examined the specimen that Dr. Eernisse had collected, but I do not recall the avicularium I observed to be very hooked, nor do I recall the colony

as having a large number of spines as in *C. echinus*. Therefore, I do believe that my earlier identification as *C. californiensis* is correct, but more study will be needed in order to further confirm that the species is *C. californiensis*. In either case, I am confident that the bryozoan is a member of the genus *Cauloramphus*.

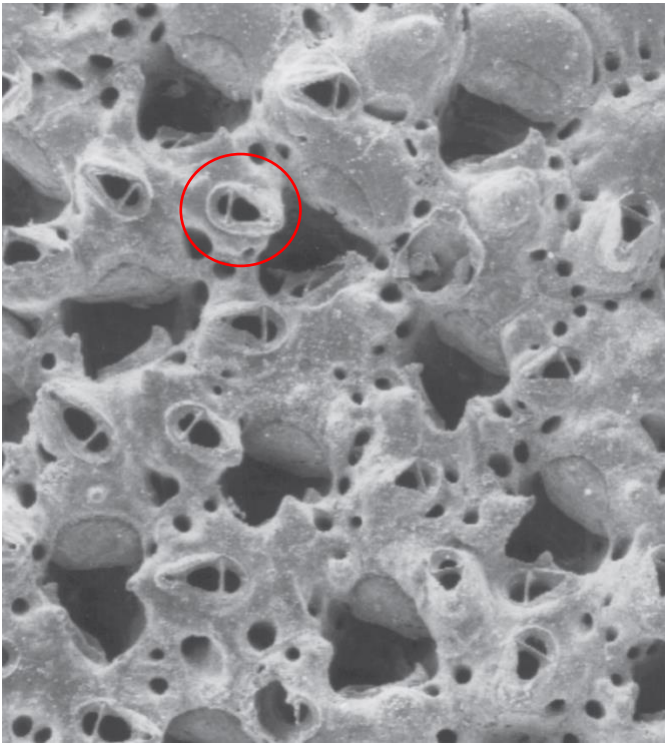


Figure 7. Scanning electron microscope (SEM) image of a *Rhynchozoon rostratum* colony. An example avicularium is circled in red. Photo taken with permission from Soule et al. (1996).

One specimen of *Crepidatella lingulata* had a bryozoan that I did not find on any other shell. As in *R. rostratum*, the frontal portion of the zooids was calcified, putting it as a member of suborder Ascophora. This bryozoan was also noted to have an opening known as the ascopore that is situated on the frontal wall. This trait is characteristic of bryozoans in the family Microporellidae. Due to features such as the shape of the aperture, I was able to determine that the bryozoan is a member of the genus *Microporella* Hincks, 1877. There are at least eight species of *Microporella* that are native to southern California, and many species look very similar to each other. I however realized that I could not find any avicularia on this particular specimen, allowing me to tentatively identify it as *M. catalinensis* (Figure 9), as *M. catalinensis* are the only southern Californian species of *Microporella*.

that are known to sometimes lack avicularia. However, this species, much like *Cauloramphus californiensis*, is only known from the California Channel Islands, and this bryozoan was found on a gastropod collected off the coast of San Pedro. It is possible that this is a different species of *Microporella*, and more study is needed to determine if my identification is correct.

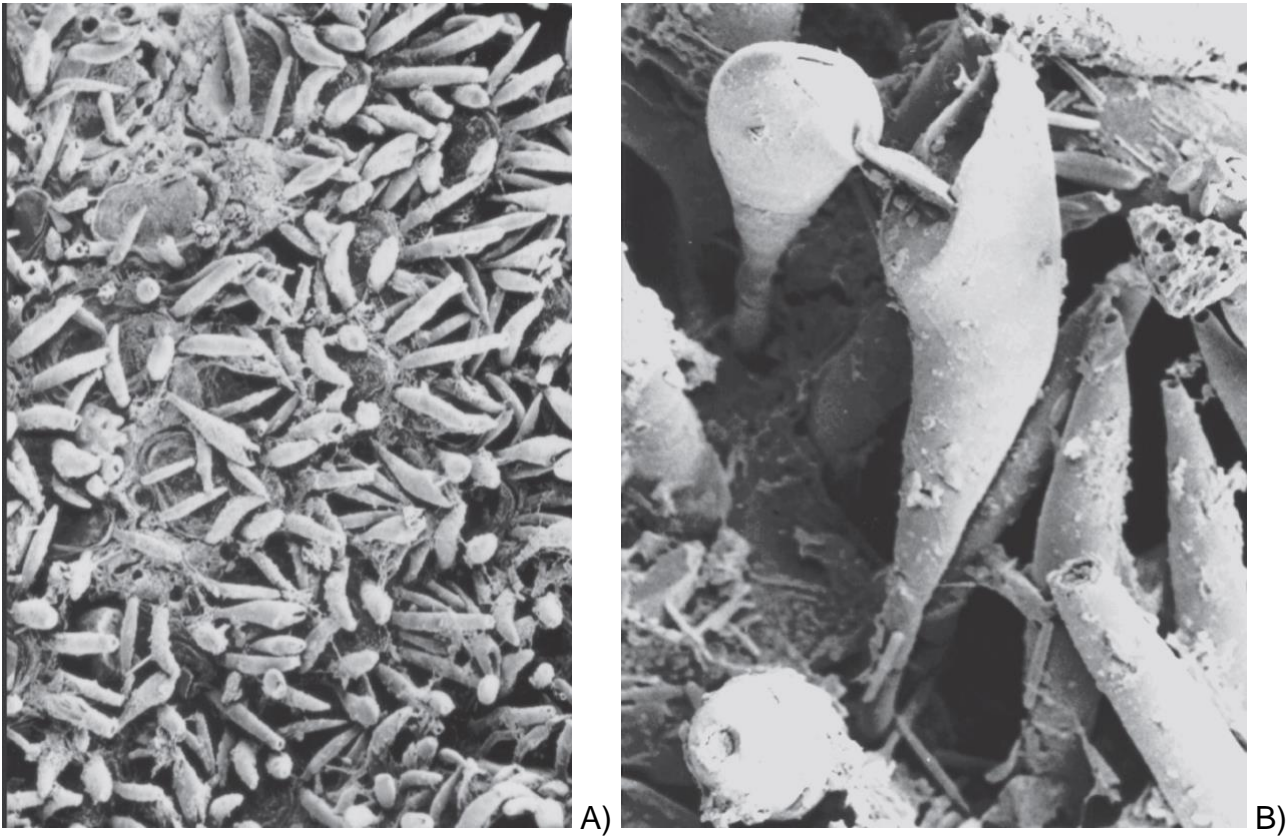


Figure 8. SEM images of A) a *Cauloramphus californiensis* colony, and B) a *C. californiensis* avicularium. Photos taken with permission from Soule et al. (1996).

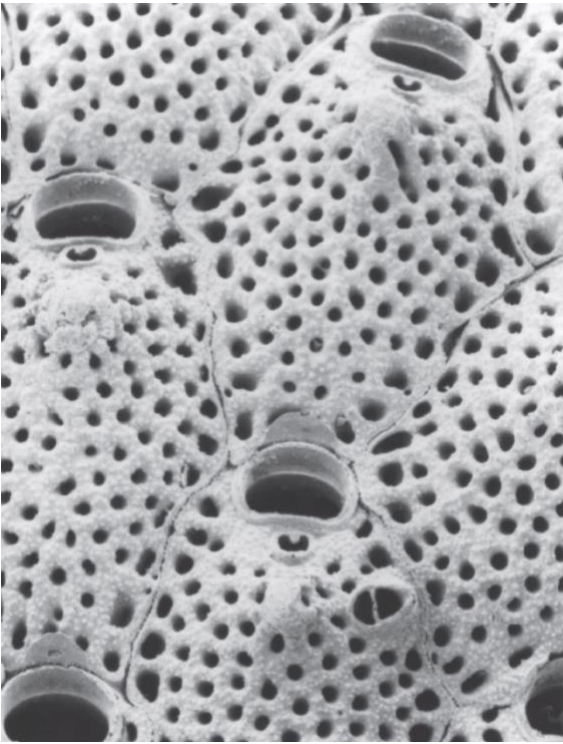


Figure 9. SEM image of *Microporella catalinensis* colony. Photo taken with permission from Soule et al. (1996).

Bryozoan-Gastropod Relationship

It is highly unusual that one species of bryozoan has been noted to be much more common on the shell of *C. lingulata* than other encrusting bryozoan species, especially when a diversity of bryozoans with such a lifestyle co-occur in southern California (Soule, et al., 1996). I have considered that this apparent relationship may be a result of possible collecting bias in the modern specimens; however, a previous examination of *C. lingulata* has noted that it is often encrusted with an orange-pink bryozoan (Collin, 2019; Eernisse, pers. obs.). *R. rostratum* is an orange-pink color, so it is likely that most of these observations are of this bryozoan.

There are a few possibilities as to why this bryozoan was observed on this gastropod. The simplest explanation is that there is no specific relationship at all, and that it is by pure chance that most of my samples were encrusted with *R. rostratum*. However, there are many cheilostome bryozoans that live off the coast of California that encrust shells (Soule et al., 1996), so why would there not be a higher variety of bryozoans encrusting on *C. lingulata*? The results of my chi-squared

analysis affirmed that *R. rostratum* occurs in significantly higher numbers on the shell of *C. lingulata* than other bryozoans; this, in addition to this bryozoan having been observed separate to my own analyses encrusting on *C. lingulata*, suggests so that the high amount of *R. rostratum* colonizing shells of *C. lingulata* is unlikely to reflect a chance association.

Symbiotic relationships between bryozoans and gastropods have been noted many times in the fossil record (McNamara, 1978). One hypothesis regarding symbiotic relationships between bryozoans and gastropods is that the bryozoans add a layer of physical protection to the gastropod's shell, while the bryozoans benefit by being slightly higher up in the water, affording them more absorbable oxygen (McNamara, 1978). It has been noted that *C. lingulata* has little in the way of periostracum (Collin, 2019); the periostracum of mollusks has a variety of functions, including physically protecting the shell from decalcification by acids (Nakayama et al. 2013; Taylor & Kennedy, 1968). It is entirely possible that the presence of bryozoans on the shell of *C. lingulata* can act as a replacement of sorts for the periostracum, preventing the gastropod's shell from being eroded away.

The potential benefit of increased exposure to oxygen that bryozoans may obtain by encrusting on a gastropod might not necessarily apply in this situation. Unlike most gastropods, calyptraeids such as *C. lingulata* are generally flatter and lower in profile in contrast to typical snails that are also known to have encrusting bryozoans on their shells, e.g., the Kellet's whelk (*Kelletia kelletii* (Forbes, 1852)). Thus, bryozoans encrusting on *C. lingulata* would not seem to benefit as much in terms of increasing their available oxygen. If an encrusted gastropod were to move up in the water column, however, then this would be a way for bryozoans to benefit from increased oxygen exposure.

A likely alternative to this hypothesis is that bryozoans encrusting on *C. lingulata* can obtain more food. It has been suggested that bryozoans from the Ordovician period that encrusted on gastropods were able to obtain more food by forming colonies on the shells of gastropods. Encrusting on a shell may have increased water flow over the colony, and with it, increased food availability (McNamara, 1978). It is possible this is the primary benefit that bryozoans like *R. rostratum* receive

when they encrust on the shells of *C. lingulata* individuals; if the gastropods were to move up in the water column, this would increase the amount of food available to the bryozoans.

Another theory is that the bryozoans act as a sort of camouflage for whatever organism they are encrusting on (Key et al., 1996). Predators of bryozoans are generally grazing organisms (Carte & Faulkner, 1986), while *C. lingulata* is preyed upon by organisms such as drilling gastropods, sea stars, crabs (Goodwill, 1975) and fishes (Ellison et al., 1979). Additionally, at least one species of bryozoan that has a symbiotic relationship with a gastropod can produce foul-tasting chemicals that may serve to deter predators (Gray et al., 2005), so this may also account for this apparent bryozoan-gastropod relationship. Dr. Eernisse has also suggested the alternative explanation that the mucus produced by *C. lingulata* may deter grazing predators of bryozoans. Mucus of some gastropods have been found to alter the behavior of other species of gastropods living in the same area (Putnam & Peckol 2018; Raw et al., 2015). It may be possible that the mucus of *C. lingulata* has a deterring effect. This would allow *R. rostratum* and other bryozoans to find refuge from grazers on the shell of the gastropod. However, *R. rostratum* is currently not known to produce any chemicals, and the mucus of *C. lingulata* is currently not known to be noxious to grazing organisms, so testing would be needed in order to affirm or reject these hypotheses.

These hypotheses are made under the assumption that the relationship between *C. lingulata* and *R. rostratum* is mutualism. There is, of course, a possibility that this relationship is commensal, or even parasitic in nature. The aforementioned hypothesis on *C. lingulata* providing a refuge for *R. rostratum* with noxious mucus could be an example of commensalism, if the gastropod does not benefit from the encrustation. Additionally, there is the matter of competition that needs to be addressed. Bryozoans are filter-feeding organisms (Key et al., 1996), as is *C. lingulata* (Collin, 2000; Collin, 2019; Goodwill, 1975). It is strange that two organisms that compete for the same food would form a mutualistic relationship with each other. If their relationship is indeed mutualistic, then perhaps the bryozoans competing with the gastropod for the same food would be outweighed by whatever benefit the bryozoans may offer, whether that is in the form of chemical deterrents or camouflage. If

this relationship is commensal or parasitic, then the bryozoans could reap all the potential benefits of encrusting the shell of *C. lingulata* (increased food and oxygen availability, protection via deterring mucus, etc.) while the gastropod is either unaffected by the bryozoans' presence or is negatively affected by the competition with the colony for food. More study into this relationship needs to be done to determine its nature.

The research I have presented here strongly supports an association between a specific bryozoan and a particular gastropod. It also lays the groundwork for future studies. In particular, *C. lingulata* fossils can now be examined in order to determine if their relationship with *R. rostratum* is an ancient one or perhaps is restricted to present day, in an age when multiple bryozoans have been transported around the world by humans. Additionally, my research highlights the need for more data on and natural history studies both *C. lingulata* and *R. rostratum*. More Holocene fossils and modern specimens need to be collected to determine if there have been truly significant patterns of change in shell length of *C. lingulata* over geologic time. More *R. rostratum* specimens will need to be collected to determine what benefits this species could give and receive in its relationship with *C. lingulata*. The modern data I have collected can also serve as a baseline for any studies in the coming years and decades. As the world's climate and oceans change, what will become of *C. lingulata*, *R. rostratum*, and their apparent association? Studies in a future decade could help shed light on how, if at all, these two species will be affected by anthropogenic climate change.

APPENDIX

FOSSIL LOCALITY INFORMATION

Loc. N.	Locality Name	numeric age range	Locality Age Range	Formation	Member
17	Deadman Island, San Pedro, Los Angeles Co., CA	300-600 ka	middle Pleistocene	unknown	
58	Capistrano Beach, Orange Co., CA	120 ka	late Pleistocene	unknown	
59	Lincoln Ave, NE of Playa del Rey, LA Co., CA	<125 ka	late Pleistocene	Palos Verdes Sand	
64	Hilltop Quarry, San Pedro, LA Co., CA	500-700 ka	middle Pleistocene	Lomita Marl	
66	Newport Bay Mesa, Newport Beach, Orange Co., CA	<125 ka	late Pleistocene	Palos Verdes Sand	
68	Newport Bay Mesa, Newport Beach, Orange Co., CA	<125 ka	late Pleistocene	Palos Verdes Sand	
72	Portero Canyon, LA Co., CA	120 ka	late Pleistocene	unknown	
97	General St. & Gaffey St., San Pedro, LA Co., CA	<125 ka	late Pleistocene	Palos Verdes Sand	
98	3rd St. & Mesa St., San Pedro, LA Co., CA	~300 ka	middle Pleistocene	San Pedro Sand	
129	Lomita St. & Broad St., Los Angeles, LA Co, CA	<125 ka	late Pleistocene	Palos Verdes Sand	
131	Bonita St. & Pacific St., San Pedro, LA Co., CA	~300 ka	middle Pleistocene	San Pedro Sand	
136	Newport Beach bluff, Newport Beach, Orange Co., CA	<125 ka	late Pleistocene	Palos Verdes Sand	
183	Santa Barbara General Hospital, Santa Barbara Co., CA	450 ka	middle Pleistocene	Santa Barbara Formation	
224	Crawfish George's, San Pedro, LA Co., CA	<125 ka	late Pleistocene	Palos Verdes Sand	
226	8th St. & Palos Verdes St., San Pedro, LA Co., CA	~300 ka	middle Pleistocene	San Pedro Sand	
229	Lomita, LA Co., CA	<125 ka	late Pleistocene	Palos Verdes Sand	
300	Nob Hill, San Pedro, LA Co., CA	~300 ka	middle Pleistocene	San Pedro Sand	
332	Miraflores St. & Gaffey St., San Pedro, LA Co., CA	~300 ka	middle Pleistocene	San Pedro Sand	
416	Isla Vista, Santa Barbara Co., CA	47 ka	late Pleistocene	Quaternary Terrace	Goleta Terrace
435	Park Western Dr. & Coralmount St., San Pedro, LA Co., CA	500-700 ka	middle Pleistocene	Lomita Marl	
1210	Westmont St. & Gaffey St., San Pedro, LA Co., CA	<125 ka	late Pleistocene	Palos Verdes Sand	
1304	San Pedro Hill, Ranchos Palos Verdes, LA Co., CA	800 ka-1 Ma	early Pleistocene	Quaternary Terrace	12th Terrace
1305	San Pedro Hill, Ranchos Palos Verdes, LA Co., CA	800 ka-1 Ma	early Pleistocene	Quaternary Terrace	12th Terrace

Loc. N.	Locality Name	numeric age range	Locality Age Range	Formation	Member
1307	Crest Rd., Ranchos Palos Verdes, LA Co., CA	300-500 ka	middle Pleistocene	Quaternary Terrace	7th Terrace
2657	Tourmaline St., San Diego, San Diego Co., CA	80-120 ka	late Pleistocene	Quaternary Terrace	
2687	15th St. & Leland Ave., San Pedro, LA Co., CA	120 ka	late Pleistocene	Quaternary Terrace	
2697	Crawfish George's, San Pedro, LA Co., CA	<125 ka	late Pleistocene	Palos Verdes Sand	
4521	Pacific Coast Highway, Santa Monica, LA Co., CA	120 ka	late Pleistocene	unknown	
5060	23rd St. & Panorama St., Signal Hill, LA Co., CA	<125 ka	late Pleistocene	Palos Verdes Sand	
5062	Costa Mesa, Orange Co., CA	<125 ka	late Pleistocene	Palos Verdes Sand	
5100	Point Vincente, Palos Verdes Estates, LA Co., CA	120 ka	late Pleistocene	Quaternary Terrace	3rd Terrace
5129	San Clemente Island Naval Reservation, California Channel Islands, CA	80-300 ka	middle-late Pleistocene	Quaternary Terrace	
5138	Point Loma, San Diego, SD Co., CA	80-120 ka	late Pleistocene	Quaternary Terrace	
5574	Camp Pendleton Marine Corps Base, SD Co., CA	120 ka	late Pleistocene	Quaternary Terrace	
6153	La Rotonda St., Rancho Palos Verdes, LA Co., CA	120-300 ka	middle Pleistocene	Quaternary Terrace	4th Terrace
6961	Timms Point, San Pedro, LA Co., CA	400-600 ka	middle Pleistocene	Timms Point Silt	
6962	2nd St. & Pacific St., San Pedro, LA Co., CA	400-600 ka	middle Pleistocene	Timms Point Silt	
6963	Timms Point, San Pedro, LA Co., CA	400-600 ka	middle Pleistocene	Timms Point Silt	
6964	Timms Point, San Pedro, LA Co., CA	400-600 ka	middle Pleistocene	Timms Point Silt	
6999	Timms Point, San Pedro, LA Co., CA	400-600 ka	middle Pleistocene	Timms Point Silt	
7007	Timms Point, San Pedro, LA Co., CA	400-600 ka	middle Pleistocene	Timms Point Silt	
7008	Timms Point, San Pedro, LA Co., CA	400-600 ka	middle Pleistocene	Timms Point Silt	
7013	Timms Point, San Pedro, LA Co., CA	400-600 ka	middle Pleistocene	Timms Point Silt	
7014	Timms Point, San Pedro, LA Co., CA	400-600 ka	middle Pleistocene	Timms Point Silt	
7018	Hilltop Quarry, San Pedro, LA Co., CA	500-700 ka	middle Pleistocene	Lomita Marl	
7205	Potero Canyon, Los Angeles, LA Co., CA	120 ka	late Pleistocene	unknown	
10032	Dana Point, Orange Co., CA	120 ka	late Pleistocene	Quaternary Terrace	
10033	Monarch Beach, Dana Point, Orange Co., CA	120 ka	late Pleistocene	Quaternary Terrace	
10034	Monarch Beach, Dana Point, Orange Co., CA	120 ka	late Pleistocene	Quaternary Terrace	

Loc. N.	Locality Name	numeric age range	Locality Age Range	Formation	Member
10035	Monarch Beach, Dana Point, Orange Co., CA	120 ka	late Pleistocene	Quaternary Terrace	
10036	Monarch Beach, Dana Point, Orange Co., CA	120 ka	late Pleistocene	Quaternary Terrace	
10167	Point Loma, San Diego, SD Co., CA	80-120 ka	late Pleistocene	Quaternary Terrace	
10440	Palos Verdes Drive South, Ranchos Palos Verdes, LA Co., CA	120-300 ka	middle Pleistocene	Quaternary Terrace	4th Terrace
10725	Eel Point, San Clemente Island, San Clemente Island Naval Reservation, California Channel Islands, CA	80-120 ka	late Pleistocene	Quaternary Terrace	Eel Point Terrace
11923	Cayucos Point, Estero Bluffs State Park, San Luis Obispo Co., CA	120 ka	late Pleistocene	Quaternary Terrace	
12007	Eel Point, San Clemente Island, San Clemente Island Naval Reservation, California Channel Islands, CA	80-120 ka	late Pleistocene	Quaternary Terrace	Eel Point Terrace
12575	Portugese Bend, Rancho Palos Verdes, LA Co., CA	80-100 ka	late Pleistocene	Quaternary Terrace	2nd Terrace
12576	Gibson Blvd., San Pedro, LA Co., CA	<125 ka	late Pleistocene	Palos Verdes Sand	
13031	Palos Verdes Hills, Palos Verdes, LA Co., CA	80-100 ka	late Pleistocene	Quaternary Terrace	2nd Terrace
17650	Timms Point, San Pedro, LA Co., CA	400-600 ka	middle Pleistocene	Timms Point Silt	
20146	Deadman Island, San Pedro, LA Co., CA	400-600 ka	middle Pleistocene	Timms Point Silt	
20147	Deadman Island, San Pedro, LA Co., CA	400-600 ka	middle Pleistocene	Timms Point Silt	
20151	Deadman Island, San Pedro, LA Co., CA	~300 ka	middle Pleistocene	San Pedro Sand	
20214	Signal Hill, LA Co., CA	120-300 ka	Pleistocene	unknown	
20651	Sun Lumber Company, San Pedro, LA Co., CA	<125 ka	late Pleistocene	Palos Verdes Sand	
21191	Signal Hill, LA Co., CA	120-300 ka	Pleistocene	unknown	
21458	Crawfish George's, San Pedro, LA Co., CA	<125 ka	late Pleistocene	Palos Verdes Sand	
22413	Lincoln Blvd. & Jefferson St., Playa del Rey, LA Co., CA	120-300 ka	middle-late Pleistocene	unknown	
22774	San Clemente State Park, Orange Co., CA	120 ka	late Pleistocene	Quaternary Terrace	
23175	Border Fields State Park, San Diego Co., CA	120 ka	late Pleistocene	Quaternary Terrace	
23225	Portero Canyon, Santa Monica Mountains National Recreation Area, LA Co., CA	120 ka	late Pleistocene	unknown	
23440	8th St. & Palos Verdes St., San Pedro, LA Co., CA	~300 ka	middle Pleistocene	San Pedro Sand	
23457	Torrey Pines State Park, San Diego Co., CA	80-120 ka	late Pleistocene	Quaternary Terrace	

Loc. N.	Locality Name	numeric age range	Locality Age Range	Formation	Member
23459	Torrey Pines State Park, San Diego Co., CA	80-120 ka	late Pleistocene	Quaternary Terrace	
23605	Sunset Cliffs, San Diego, SD Co., CA	80-120 ka	late Pleistocene	Quaternary Terrace	
24216	Venice Beach, LA Co., CA	<10 k	Holocene	unknown	
24242	Flatrock Point, Palos Verdes Estates, LA Co., CA	120-300 ka	middle Pleistocene	Quaternary Terrace	5th Terrace
25839	Newport Bay Mesa, Newport Beach, Orange Co., CA	<125 ka	late Pleistocene	Palos Verdes Sand	
25917	Gaffey St., San Pedro, LA Co., CA	<125 ka	late Pleistocene	Palos Verdes Sand	
31255	Goleta, Santa Barbara Co., CA	47 ka	late Pleistocene	Quaternary Terrace	Goleta Terrace
31263	Hawthorne Blvd. & Rolling Hills Rd., Torrance, LA Co., CA	500-700 ka	middle Pleistocene	Lomita Marl	
31276	Upper Newport Bay, Newport Beach, Orange Co., CA	<125 ka	late Pleistocene	Palos Verdes Sand	
31439	Newport Bay, Newport Beach, Orange Co., CA	<125 ka	late Pleistocene	Palos Verdes Sand	
41649	Vista Entrada, Newport Beach, Orange Co., CA	1.5-2.5 Ma	late Pliocene - early Pleistocene	Niguel Formation	
41651	Marina Del Mar, LA Co., CA	<10 ka	Holocene	unknown	
41652	Marina Del Mar, LA Co., CA	<10 ka	Holocene	unknown	

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