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Terrestrial Soldier Crab (Coenobita clypeatus, Fabricius 1787) and Cerion spp. (Röding 1798) shell relationship on San Salvador Island, Bahamas

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We hereby approve the thesis of

Terrestrial Soldier Crab (*Coenobita clypeatus*, Fabricius 1787) and *Cerion* spp. (Röding 1798) shell relationship on San Salvador Island, Bahamas

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TABLE OF CONTENTS

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Harley Hunt

Abstract –

The Caribbean terrestrial soldier crab, *Coenobita clypeatus* (Fabricius 1787), coexist and utilize the shells of numerous species of land and marine gastropods. Soldier crabs rely on gastropod shells for protection as the crabs have a soft abdomen, leaving them vulnerable for predation and desiccation, threatening their survival. This creates a strong pressure to obtain well-fitting shells that provide adequate protection against water loss. *Cerion* of Röding 1798 shells are one of the most commonly used shells among living colonies of *C. clypeatus* on San Salvador Island. This study is interested in the frequency of shell use by *C. clypeatus* crabs based on several colonies and associated assemblages of discarded shells on San Salvador. In this study, unoccupied shells from the areas inhabited by *C. clypeatus* crabs were collected and measured to determine preference for shell type. Additionally, this study examined how discarded shells from three colonies of *C. clypeatus* crabs are modified and highly adapted for a better fit. Percentages of cerionids collected in the assemblages of discarded shells ranged from 75% to 89.5%. The following shell modifications were included in this study: aperture lip modifications, inner aperture ridge modifications, hollowing out the columella, umbilicular region modifications, and exterior holes. This study provides insights regarding shell locations, shell sizes, and shell modifications that can determine *C. clypeatus* population demographic and location. Additionally, this present study also provides a means for those using electron spin resonance dating of terrestrial quaternary shells to recognize if shells were used by soldier crabs and were transported into a depositional environment.

Introduction –

At least five major lineages within Crustacea have made evolutionary transitions from marine to terrestrial life (Harzsch and Hansson 2008). Members of the genus *Coenobita* are likely the best-known terrestrial crustaceans (Latreille 1829) and are abundant throughout tropical and subtropical regions (Burggren and McMahon 1988, Walker et al. 2003). Known as hermit crabs in the United States, or soldier crabs in the Bahamas, all 16 species of the genus are fully terrestrial as adults. Coenobitans have an ability to survive several kilometers inland because of several physiological adaptations involving gas exchange, chemoreception, and photoreception (De Wilde 1973, Harzsch and Hansson 2008, Krång et al. 2012) along with their ability to store water in their shells, preventing desiccation (Morrison and Spiller 2006, Walker 1994, Walker et al. 2003). Shells are a limiting factor for terrestrial hermit crabs (Abrams 1978, Morrison and Spiller 2006, Ragagnin et al. 2016, Seyfabadi et al. 2014, Shih and Mok 2000), thus providing another requirement to live in addition to those (e.g. area, food resources) of other organisms. Coenobitans use enhanced chemosensory cues to pick-up on death scents from recently deceased gastropods to retrieve intact shells (Krång et al. 2012, Small and Thacker 1994, Vannini and Ferretti 1997). Finding and maintaining a suitable shell is of paramount importance for survival from the time crabs metamorphosize to death. Without shells, terrestrial hermit crabs are incapable of surviving the heat of the day (De Wilde 1973). They also forage at night and reside in cracks and crevices of limestone during the day to limit changes exposure to the highest daily temperatures (De Wilde 1973, Morrison and Spiller 2006, Provenzano Jr. 1962). Shells are therefore important in establishing a tolerable micro-climate for Coenobitans.

Members of *Coenobita* utilize both marine and land gastropod shells as a resource (DeVore et al. 2016, Morrison and Spiller 2006, Nieves-Rivera and Williams 2003, Walker

1994). Their ability to choose suitable shells has been widely studied in both the field and laboratory settings (Abrams 1978, Bartmess-LeVasseur and Freeburg 2015, Ragagnin et al. 2016, Sallam 2012). Coenobitans examine potential gastropod shells thoroughly to obtain a combination of fit, low weight, and strength (Bartmess-LeVasseur and Freeberg 2015, Elwood et al. 1998, Ragagnin et al. 2016, Reese 1969, Shih and Mok 2000). Members of *Coenobita* have shown preferences for shells of specific species because of their fit, based on shape and size (Abrams 1978, Mitchell 1975, Reese 1969, Scully 1983, Shih and Mok 2000, Seyfabadi et al. 2014). If a suitable sized shell is not available, coenobitans tend to select a relatively larger shell in order to retract deeper into it for protection from predators (Abrams 1978, Briffa and Elwood 2005, Osorno et al. 2006, Ragagnin et al 2016, Vance 1972).

Fully mature female hermit crabs who have a larger/better fitting shell, which increases internal volume, typically exhibit higher reproduction potential (Thacker 1994, Sallam 2012, Vermeij 2012). Shell volume allows reproductive females, who mate inland, to store more eggs and larvae around their abdomen before transporting and washing larvae into the surf (De Wilde 1973). This results in selection for larger internal shell volume in mature female coenobitans to ensure a higher fitness. It is also beneficial to have a shell which permits the female to have stability while transferring larvae into the surf. Shell selection has the potential to impact the fitness of individuals of *Coenobita* (Thacker 1994); however, there is a tradeoff in transporting a shell that is affiliated with mobility.

Shell choice is linked with mobility and shell weight. As opposed to marine hermit crabs, where buoyancy provides some compensation, shell mass affects coenobitan's shell choice (Vermeij 2010, 2012). For example, marine hermit crabs often collect encrusting corals and other cnidarians, adding to their weight and providing a protective advantage with camouflage and strength that terrestrial hermit crabs cannot afford (Vermeij 2010, 2012).

Another important physical characteristic is strength, or durability of the shell. Terrestrial hermit crabs balance a set of trade-offs including, but not limited to shell fit, weight, and strength. Strength of shells and resistance to breakage and wear are important to hermit crabs. Over time, strength will diminish in shells whether it is because of hermit crab wear/dragging the shell, or because the crab only had access to shells which were abraded from physical agents like burial, tidal movement, or decomposition (Hazlett 1981, Laidre 2011, Ragagnin et al. 2016). Because of this, coenobitans have to constantly rely on a fresh supply of vacant shells in the area (Chase et al. 1988).

Hermit crabs obtain shells in two ways: asynchronously and synchronously (Rotjan et al. 2010). Asynchronous shell acquisition is when a hermit crab randomly comes across a lone shell to potentially use. Finding a shell in this way, there is a lower chance of finding a suitable shell, but it allows for easy reversal. Synchronous shell acquisition is created by a sequential shell exchange between two or more individual hermit crabs. This type of shell acquisition is called the vacancy chain (Lewis and Rotjan 2009, Rotjan et al. 2010). The vacancy chain increases the potential of obtaining a suitable shell, but also increases the risk of injury, predation, and individuals have a greater chance of being stranded in an unsuitable shell as well (Rotjan et al. 2010).

Coenobita species are well known for the way they modify both the inside and outside of their shell to make it more suitable for wear (Vermeij 2012). Laidre (2012) has documented that individuals of *Coenobita* depend on modifications made to shells. Marine hermit crab species are less prone to modify shells as they are less reliant on its fit and weight (Vermeij 2010). Over time, shells do wear and incentivize terrestrial hermit crabs to discard them, so modifying the shells for a select period of time could prove advantageous for coenobitans compared to marine hermit species. Modifications noted from some species in the *Coenobita* genus include: cleaning and thinning the interior shell wall (Abrams 1978, Ragagnin et al. 2016, Vermeij 2012), removing the columella (interior spiral structure in a shell; Abrams 1978, Ragagnin et al. 2016, Vermeij 2012, Walker 1994), clipping the aperture of the shell (outer opening; Abrams 1978, Walker 1994), and wearing down the outside of the shell (Ragagnin et al. 2016, Walker 1994).

The Caribbean terrestrial soldier crab, *Coenobita clypeatus* (Fabricius 1787), is the only terrestrial hermit crab in the tropical western Atlantic. *Coenobita clypeatus* is a communal species distributed in north Florida, the Bahamas and Bermuda to the Gulf of Mexico, and northern South America and are listed as vulnerable in Bermuda (Bermuda Protected Species 2012), but not mentioned on the International Union for the Conservation of Nature site (IUCN; IUCN 2020). This species is a generalist scavenger/decomposer, with a diet comprising plant and animal matter, fungi, feces, and even other dead hermit crabs (Brodie 1998, Thacker 1996). *Coenobita clypeatus* crabs undergo six marine larval stages (Provenzano Jr. 1962) and can grow up to a length of 10cm (Bermuda Protected Species 2012).

Larval terrestrial hermit crabs use marine gastropod shells as they emerge from the water, but once fully terrestrial they tend to choose readily available marine or terrestrial gastropod shells (DeVore et al. 2016, Morrison and Spiller 2006, Provenzano Jr. 1962, Walker et al. 2003). On 19 islands of the Bahamas, Morrison and Spiller (2006) observed shells originating from tidal gastropod species and did not observe any shells from terrestrial gastropod species. Similarly, in Bermuda, Walker (1994) observed that shells occupied by *C. clypeatus* originated from four species of gastropod shells that were all shallow water to intertidal species. On San Salvador

Island, Bahamas, DeVore et al. (2016) observed 67% of gastropod shells being used are from terrestrial gastropod species while the remaining shells represented taxa from tidal habitats.

Fossil trackways of the ichnotaxon *Coenobichnus currani* (Walker et al. 2003), show that terrestrial hermit crabs have occupied the Bahamas since the early Holocene (11,700 years ago; Carew and Mylroie 1995, Walker et al. 2003). San Salvador Island is a small isolated island on the northeastern perimeter of the Bahamian archipelago (Baldini et al. 2007, Harasewych and Tenorio 2018, Yanes 2012). The island is an 11 km wide by 19 km long carbonate platform that has seen little change in land area since Pleistocene era sea level changes (Harasewych and Tenorio 2018, Hearty and Schellenberg 2008). The island consists of eolian ridges up to 40 m tall and low interdune lakes filled with fresh rainwater or saltwater due to close proximity to the ocean (Hearty and Schellenberg 2008). Dating the accretion of aeolian sediments and clarifying absolute dates for stratigraphic sequences can be challenging to paleontologists, requiring the use of the terrestrial gastropod record. Understanding the natural history of terrestrial soldier crabs and terrestrial gastropods is essential for assuring that the shells were deposited on site, as opposed to being transported by crabs.

One means of obtaining absolute dates is applying electron spin resonance (ESR) dating to fossil shells. Yanes (2012) documented 12 genera of terrestrial gastropods on San Salvador Island with shells of *Cerion* spp. (Roding 1798) accounting for 59% of all individuals identified in pristine locations. Members of *Cerion* have been utilized to exam evolutionary processes because of the range of morphological variation present within the species (Baldini et al. 2007, Dall 1905, Goodfriend and Gould 1996, Gould 1988, Gould 1997, Gould and Woodruff 1978, Gould and Woodruff 1986, Hearty et al. 1993, Hearty and Schellenberg 2008, Mayr and Rosen 1956, Walker and Hearty 1993, Walker 1994, Woodruff and Gould 1980). *Cerion* is represented by six species on San Salvador Island; *C. eximium fraternum* (Pilsbry 1902), *C. watlingense* (Dall 1905), *C. inconspicuum* (Dall 1905), *C. inconspicuum lacunorum* (Dall 1905), *C. coloni* (Bartsch 1924), *C. rodrigoi* (Gould 1997). Morphology within the genus can be vastly different because of a number of evolutionary mechanisms at play. Due to the risk of taxonomic misidentification as a result of interbreeding, hybridization, and morphological variability within species, *Cerion* will henceforth be referred to by the genus name.

Cerionid snails have occupied San Salvador Island for the past 140,000 years and have been relatively isolated due to the geography of San Salvador Island (Harasewych and Tenorio 2018, Hearty and Schellenberg 2008). Cerionid snails are not limited to San Salvador as they have populations throughout the Florida Keys, Bahamas, Cuba, Cayman Islands, Hispanola, Puerto Rico, and the Virgin Islands (Woodruff 1978). Generally, cerionids live close to shore in areas of open vegetation within 1km of seawater, but a few colonies may live inland near a freshwater lens (Harasewych and Tenorio 2018, Woodruff 1978). Densities within colonies can reach 10 adults/m^2 and colonies of up to 10,000 individuals have been reported (Woodruff 1978). *Cerion* shells go through three major phases of growth based on the direction of the shell whorls (Gould 1989, Stone 1996). In phase one, the button phase (Stone 1996), shells are triangular in shape due to length and width of the shell increasing simultaneously. In phase two, the barrel phase (Stone 1996), the direction of the whorl changes to increase shell length while keeping shell width steady. Phase three, the recurved phase (Stone 1996), shell width decreases shell while increasing shell length and a clearly protruding and thickened aperture lip (Gould 1989, Stone 1996).

Coenobita clypeatus has coexisted with land snails of the genus *Cerion* in a comparable range (Bahamas, south Florida, Puerto Rico, Greater Antilles, Dutch Antilles, Cayman Islands, the western Virgin Islands) for at least the past 11,700 years (Carew and Mylroie 1995, Harasewych and Tenorio 2018, Hearty and Schellenberg 2008, Nieves-Rivera and Williams 2003, Walker et al. 2003). Both *C. clypeatus* and *Cerion* snails have high densities in their respective areas and interact often but their ecological relationship has not been widely studied. On Mona Island, Puerto Rico, *Cerion* shells are among the most occupied shells by *C. clypeatus* (Nieves-Rivera and Williams 2003). Given the high abundance of both *C. clypeatus* and *Cerion* snails on San Salvador Island, it is hypothesized that small to intermediate sized *C. clypeatus* crabs may prefer *Cerion* shells. Live *C. clypeatus* crabs from North Point were observed occupying 62.5% *Cerion*, 9.4% *Tectarius* (Valenciennes 1832), 6.35% *Cittarium* (Linnaeus 1758), 5.95% *Nerita* (Linnaeus 1758), and 4.85% *Echininus* (Pfeiffer 1839) (DeVore et al. 2016). *Cerion* shells were used over 50% of the time in North Point, San Salvador is the only terrestrial gastropod genus *C. clypeatus* individuals occupied. This suggests an intricate relationship between *C. clypeatus* crabs and *Cerion* shells in their overlapping habitats, however the relationship between *C. clypeatus* crabs and *Cerion* shells have not been studied in depth.

Within literature, Walker's (1994) study was the only one that included *C. clypeatus'* modifications to shells. This study was based in Bermuda and focused on modifications to just one species of shell, the West Indian Topshell (*Cittarium pica*, Linnaeus 1758). The study focused on the importance of the *C. pica* to *C. clypeatus*. Similar to Walker's (1994) study, this study hopes to draw attention to the modifications made to *Cerion* shells by coenobitans, which is largely unknown. Understanding the modification patterns can help distinguish shells used by crabs versus those representing death assemblages of the gastropods themselves. Obviously, the movement of shells by crabs, even the use of fossil gastropod shells, would confound the use of shells for obtaining accurate dates.

Objectives –

Based on a previous observation on San Salvador Island, we hypothesize that *C. clypeatus* crabs use a variety of gastropod shells but rely mainly on terrestrial gastropod shells available to them. The assessment of shell use is made from discarded vacant shells in different communities of *C. clypeatus* crabs on San Salvador Island, Bahamas. Shells included were unfavorable and damaged shells that were discarded from the vacancy chain. Shell origin will be noted to determine the difference between each location based on their vicinity to a rocky shoreline. We also hypothesize that *Cerion* shells will be the most abundant in our sample locations. A high abundance of *Cerion* shells allow an analysis of modifications to determine if *C. clypeatus* crabs do modify *Cerion* shells for better fit, lighter weight, and have favorable strength. There were also shells that had a range of modifications which may have rendered them unsuitable for *C. clypeatus* crabs.

This study will highlight modifications *C. clypeatus* individuals make to *Cerion* shells in North Point, San Salvador. In this study we will be exploring several questions surrounding the relationship between *C. clypeatus* crabs and *Cerion* shells; including what is altered, how shells are altered, and consider potential reasons why they are altered. This research will provide insight into steps taken in the modification process of *Cerion* shells and find a pattern undertaken by the crab. Modified shells and their location can determine *C. clypeatus* crab's accessibility to shell resources. The present study also provides a means for those using ESR dating of terrestrial quaternary shells to recognize if shells were used by crabs and were transported into a depositional environment (Deely et al. 2011, Skinner and Shawl 1994). Identifying whether a shell has been moved by a hermit crab can greatly reduce the potential for an incorrect stratigraphic age reading, since hermit crabs can move shells from stratigraphic layer to layer.

Methods –

Vacant shells were collected over three days (May 18, May 24, and May 27) in 2018 from three *C. clypeatus* colonies, each less than 50m of the shore at North Point, San Salvador (**Figure 1**). North Point, San Salvador has been noted as having dense *C. clypeatus* colonies with a high selectivity of *Cerion* shells (DeVore et al. 2016). The locations are: Grahams Harbour (GH; 24.1230°N, -74.4575°W), road slab (RS; 24.1209°N, -74.4599°W), and North Point trail (NPT; 24.1239°N, -74.4567°W) (**Figure 1)**. Two locations, GH and NPT are located above a rocky shoreline while RS is located inland of a sandy shoreline.

Once collected, gastropod shells were identified to genus to determine location of shell origin, similar to the six shell habitats (shallow water, mangrove roots, subtidal, intertidal, high intertidal, and supratidal) of Morrison and Spiller (2006) (**Figure 2**). Shell genera were compared within each location as well as the total number of shells found in North Point. Observed shell origin frequency for each location was compared to expected values based on a Fisher's Exact Test using the software R (version 4.0.3).

To determine shell size and modifications performed, shells were measured and examined for taphonomic overprints fabricated by *C. clypeatus* crabs (modifications made by *C. clypeatus* crabs on the desired gastropod shell; Walker 1994). Size measurements taken were shell length (SL), shell width (SWI), shell weight (SWE), shell density (SD), and aperture width (AWI). Shell length and shell width measurements were taken by digital calipers to the nearest 0.01mm. Shell length was measured from the apertural end (nearest the opening of the shell) to the apex of the spire (tip of the shell posterior), which is typically the longest portion of the shell. Twenty shell length categories were determined to visualize the shell size discrepancy found within North Point and give an insight into the allometric shift through growth phases among collected *Cerion* shells, as described by Gould (1989). Shell width was measured perpendicular to shell length at the widest portion of the shell, typically toward the apertural end. Shell weight was determined on a digital scale to the nearest 0.1g. Shell density was calculated using the formula SD = SWE/(SL*SWI*SWI). Density serves as a proxy for relative strength of the shell making it an important value to assess the trade-off *C. clypeatus* crabs have to consider.

Along with shell measurements, taphonomic overprints are examined. Modifications include aperture lip modifications, inner aperture ridge modifications, columella modifications, umbilicular region abrasion (Walker 1994), exterior holes, and boring holes. The aperture lip (ALIP) surrounding the opening of the entrance is noted as fully modified, partially modified, or not modified at all. Fully modified is an instance with no portion of the original, natural outer aperture lip present while partially modified shows a portion of the natural outer lip paired with some obvious aperture lip clipping. Inner aperture ridge (ARID) is a ridge on the inside ventral portion of the opening to the shell, classified as present or absent. The columella is the interior spiral structure of the shell. Modifications of the columella (COL) can be interior columella holes, or absence of the columella, which both increase interior area and decrease shell weight. The outside, apertural portion of the columella is the umbilicular region (UMB), which can show abrasion and develop holes as noted in Walker's (1994) study on *C. clypeatus* modifications to *Cittarium* shells. Exterior wear is easily explained using exterior holes (EH) which does not include boring holes (BH) that were likely made by predators.

Measurement and taphonomic overprint data were compiled for each shell and analyzed. Shell measurements for each taphonomic overprint were averaged along with the standard deviation, minimum, all quartiles, and maximum size to distinguish what size is preferred for each modification. To assess the relative size of the shell, shell weight and shell length are the two best measurements representative of occupying hermit crab size. Shell length will be used as the shell size reference following Abrams (1978), Shih and Mok (2000), and Walker (1994).

To determine if *C. clypeatus* crabs are more likely to modify shells of a certain size range, a t-test was run in Microsoft Excel (version 16.30) between modified and unmodified shells. Shell length was used as the shell size reference in the t-test. A Cohen's *d* effect size test was run to determine if the difference in means of modified and unmodified shells were statistically large enough.

Lastly, shell images were taken on unmodified and modified shells using a Canon EOS 5DSR camera with a 65mm lens and a DynaLite Power Pack controlled lighting system. The programs involved in capturing the image are Visionary Digital P-51 Camlift controller and Capture One Pro (version 10.1.2). To stack the images of shells, Zerene Stacker (version 1.04) was used while Adobe Photoshop (version 20.0.0) was used to add scale bars to the completed image.

Results –

The number of collected shells in North Point, San Salvador totaled 399 individuals of 12 genera: 106 from GH, 160 from RS, and 133 from NPT. All shells collected originated from four habitats (subtidal, intertidal, supratidal, and terrestrial; Figure 2). Subtidal shells found belong to genera of *Cittarium* (Linnaeus 1758) and *Cerithium* (Bruguiere 1789), intertidal shells were identified as *Echininus* (Pfeiffer 1839), *Thais* (Röding 1798), *Callistoma* (Herrmannsen 1846), *Nerita* (Linnaeus 1758), and *Purpura* (Linnaeus 1758), supratidal shells found were identified as *Tectarius* (Valenciennes 1832), and *Semicassis* (Mörch 1852), and terrestrial shells were *Cerion*, *Hemitrochus* (Swainson 1840), and *Bulimulus* (Leach 1814). Of the 399 discarded shells, 325 (81.5%) were of the genus *Cerion* (Figure 2). To compare, the Yanes (2012) study of live-dead gastropod assemblages showed individuals of *Cerion* made up 59% of all gastropods on pristine portions of the island, including North Point.

Cerion shells made up 81.1% of all shells at GH, 75% of all shells at RS, and 89.5% of the total shells collected at NPT. Terrestrial shells made up 91.2% (n = 364) of all shells found in North Point while intertidal shells comprised 4.3% (n = 17), supratidal made up 2.5% (n = 10), and subtidal made up 2% (n = 8). *Cerion* is the most abundant shell genus in the collection while the next most abundant is *Hemitrochus* with 38 shells. Shells of the genus *Hemitrochus* were found in only one location, RS. Outside of the two most abundant shell genera, which are both terrestrial in origin, the most frequent shell genus found consists of nine shells and is supratidal: *Tectarius*.

Shell frequency focused on shell origin rather than shell genera because of the absence of many shell genera in some locations. The shell origin frequency in the three locations of our study was significantly different in a Fisher's Exact test, resulting in 0.00002142. Two locations of *C. clypeatus* colonies are above a rocky shoreline (GH and NPT) while one location (RS) is on the inland side of a sandy shoreline 300 yards from the nearest rocky shore. Grahams Harbour (GH) and NPT had 13 and 17 shells that were not from terrestrial gastropods while RS had only two shells that were not from terrestrial gastropods. Road slab (RS) hosted two genera of terrestrial gastropods (*Cerion* and *Hemitrochus*) while the other two locations hosted only one (*Cerion*) genus of terrestrial gastropods.

Given the large sample size of *Cerion* shells, modifications and measurements can be accurately depicted. *Cerion* shells collected were assigned to one of three phases, similar to Gould (1989) and Stone (1996). The three phases in this study varied in shell length (5.84mm-29.42mm) and weight (0.1g-2.3g; **Table 1**). At location GH, nine phase one *Cerion* shells, 11 phase two, and 66 phase three *Cerion* shells were collected for a total of 86 collected *Cerion* shells. Road Slab had 68 phase one *Cerion* shells, 29 phase two, and 23 phase three *Cerion* shell creating a total of 120 collected *Cerion* shells. Location NPT hosted 50 phase one *Cerion* shells, 18 phase two, and 51 phase three *Cerion* shells with a total of 119 collected *Cerion* shells. The three locations included in the study held significantly different ratios of phase one, phase two, and phase three *Cerion* shells (chi-square: $1.5774*10^{-14}$).

Average, standard deviation, minimum, quartiles, and maximum sizes of all *Cerion* shells (SL, SWI, SWE, SD, AWI) are shown in **Table 1**. *Cerion* shells collected had an average length of 16.96mm with a standard deviation of +/-6.06mm. *Cerion* shell length ranged from 5.84mm to 29.42mm and were separated into twenty categories between the minimum and maximum shell length values (**Figure 4)**. This histogram shows an uneven distribution and high variability of *Cerion* shells that were found in this study. All *Cerion* shells that weigh 0.5g or less (n = 176) have a density of less than $0.00040g/mm^3$ with the exception of 7 shells while all *Cerion* shells weighing 1.5g (n = 18) or greater have a density of more than $0.00040g/mm^3$.

Shells had from zero to five modifications (**Figures 3, 5-7**). Twenty-four (7.4%) *Cerion* shells were not modified and 301 (92.6%) *Cerion* shells were modified in the sample set. The 301 shells that were modified had several combinations of modifications (**Table 2**). The average unmodified *Cerion* shell had a length of 23.70mm, weight of 1.23g, and a density of 0.000403g/mm^3 while an average modified *Cerion* shell had a length of 16.41mm, weighs 0.61g and has a density of 0.000306g/mm^3. A t-test comparing modified and unmodified shells showed that modified shells are significantly smaller than unmodified shells ($p = 1.343*10^{-26}$). A Cohen's *d* test to compare means between modified and unmodified shells showed that the two groups differ by 1.236 standard deviations. Within the two groups, 89.13% of modified shells are smaller than the unmodified shell's average.

Aperture lip and the inner aperture ridge had the most modifications with 286 and 287 out of 325, respectively. An aperture lip modification was the only modification in five circumstances including both fully and partially modified aperture lips. There were 277 shells with a fully modified aperture lip (**Figure 5**) and nine shells with a partially modified aperture lip (**Figure 6**). Seven of the nine shells with partially modified aperture lips were not modified in any other way while the other two had just an inner aperture ridge modification and no other modification. Aperture lip and inner aperture ridge were the only two modifications performed in 222 shells, or 68.3% of the total number of *Cerion* shells. The inner aperture ridge is the only modification in six shells and is represented in **Figures 3, 5 and 6**.

Shells with a modified columella (n = 48; **Figure 7**) were on average 6.65mm larger in length, 0.95mm larger in width, 0.41g heavier, 0.0000396g/mm^3 ($3.96*10^{-5}$g/mm^3) denser, and 1.33mm larger in aperture width compared to those with no columella modification. Shells with a modified columella were significantly larger in shell length than those with no columella modification (p-value = $1.5676*10^{-15}$). Modifications on the columella were made only on shells with a shell length above 8.82mm and only six columella modifications in shells below 21.04mm in length. Shells with a columella modification were found to be 1.0752 standard deviations greater than shells with no columella modification. Four shells had a columella modification without any aperture lip or aperture ridge modification. Thirty-three shells were shown to have an umbilicular region modification (**Figure 7**), all being above average in shell length (22.80mm), shell width (10.98mm), shell weight (1.00g), and aperture width (7.22mm).

Exterior holes were present in 25 shells (**Figure 7**). Four holes were present in one shell, three holes were present in one shell, two holes were present in six shells, and there was only one hole in 17 shells. In three shells, (the four-holed shell, a two-holed shell, and a one-holed shell) all exterior holes were clogged with sediment. Shells with exterior holes ranged from 8.99mm in shell length to 29.42mm with an average of 19.78mm and a standard deviation of +/-5.93mm.

Discussion –

Shell middens, a collection of shells, play an important role in the fossil record as they indicate where gastropods die, or where predators/shell-users reside. In studies dating stratigraphy using gastropod fossils, the determining factor of the fossil location is important. In this study, shells found across three *C. clypeatus* colonies were used to determine the effect *C. clypeatus* crabs have on *Cerion* gastropod shells. Because vacant shells were found within these colonies and were previously observed both being exchanged and modified by individuals of *C. clypeatus* (DeVore obs. 2018), there is a strong likelihood that most, if not all, shells collected have been used. Shells collected from each location originated from a gastropod in a subtidal, intertidal, supratidal, or terrestrial habitat. Shells originating from subtidal, intertidal, or supratidal zones were used by *C. clypeatus* crabs as gastropods found in those habitats will not travel to terrestrial habitats on their own. Terrestrial gastropod shells were the most abundant in each location similar to the DeVore et al. (2016) study that observed gastropod shell genera occupied by live *C. clypeatus* crabs.

Locations adjacent to rocky shorelines (GH and NPT) had significantly more subtidal, intertidal, and supratidal gastropod shells while RS, located adjacent to a sandy shoreline, had significantly less subtidal, intertidal, and supratidal gastropod shells than what was expected based on a Fisher's Exact test. *Coenobita clypeatus* crabs, when using tidal gastropods, tend to use gastropods that come from rocky tidal areas (Morrison and Spiller 2006) which typically hold a wide diversity of gastropods (Lumeran 2019). Similar to the Morrison and Spiller (2006) study, this study recognizes that all tidal shells (subtidal, intertidal, and supratidal shells) came from rocky tidal zones except for one shell of *Semicassis*. However, Morrison and Spiller (2006) did not find any *C. clypeatus* individuals occupying terrestrial gastropod shells. The high abundance of terrestrial gastropod shells in this study contradicts the results of Morrison and Spiller (2006) from several other islands in the Bahamas.

The lack of variability of gastropod shells in our study may mean the location is short on shell resources with *C. clypeatus* crabs continuously rejecting *Cerion* shells in the vacancy chain. However, it can also mean that *Cerion* shells are suitable for young *C. clypeatus* crabs to wear as protection, otherwise soldier crabs would inhabit and discard a greater amount of other shell genera. *Cerion* (terrestrial gastropod) shells were the focus of this study given their abundance within samples, as well as observations of *C. clypeatus* crab usage of *Cerion* shells by DeVore et al. (2016) on San Salvador Island, Bahamas. The abundance of *Cerion* shells is a result of *Cerion* snail availability around each of the three locations that *C. clypeatus* colonies occupy. A study using geometric morphometric analysis of *Cerion* shells on San Salvador narrows down the species at North Point to *C. coloni* and *C. rodrigoi* (probability >99.9%; Harasewych and

Tenorio 2018), which have high hybridization potential. Abundance of *Cerion* shells in *C. clypeatus* colonies at North Point was much higher in percentage than *Cerion*'s presence on San Salvador Island. Yanes (2012) searched San Salvador Island for any live or dead gastropods and concluded that individuals of *Cerion* makes up 59% of all gastropods on the island.

Cerion gastropod shells that were found in shell middens can give insight into *C. clypeatus* crab population demographics. The process in this study for determining *C. clypeatus* population demographics using shells can be implemented across shell middens with any *Coenobita* species throughout terrestrial tropical and subtropical regions. Location of shell middens, discarded shell sizes, and shell modifications can give an insight into terrestrial hermit crab populations. Location of *C. clypeatus* colonies may be a factor in determining population dynamics. Since coenobitans are known for traveling miles inland in search of shells, food, or water (Walker 1994, Randall 1964, De Wilde 1973, Vannini 1975). Major treks like this are typically accomplished by older, larger individuals while smaller, younger individuals that have just emerged from the marine habitat reside close to shore (De Wilde 1973, Walker 1994). In this case, all three shell midden locations are very close to shore (**Figure 1**)**.** *Coenobita clypeatus* crabs rely on their water source while they are young and cannot retain enough water in their relatively small *Cerion* shells to travel far inland. This begins the selective choice for smaller shells near the coast and begins the shell vacancy chain. The vacancy chain, described as a sequential distribution of resources across multiple individuals (Lewis and Rotjan 2009, Rotjan et al. 2010), in this case, sequential use of vacant shells, is an observation in regard to all hermit crabs.

Studies have shown a strong correlation between shell length and hermit crab size (Abrams 1978, Shih and Mok 2000, Walker 1994) as well as shell width and hermit crab size

(Abrams 1978). Shell length was used more often in studies, therefore shell "size" references shell length. In this study, *Cerion* shells were found in three phases, showing a range of *C. clypeatus* crab sizes present in each location. Analysis of shell length of all *Cerion* shells show that the population distribution is bimodal and has a high variability (**Figure 4**). Two peaks are clearly shown in the figure as the majority of shell lengths are within two length categories. Three locations of this study vary in their ratio of phase one through three of discarded *Cerion* shells. The three *Cerion* shell phases were significantly different (P-value = $1.5774*10^{-14}$) than what was expected within each sampling location via chi-squared statistic.

Shell size is a good indication of *Coenobita* crab size and had an R^2 value of 0.92 in a study measuring individuals of *C. clypeatus* major chela length and *Cittarium* shells (Walker 1994). Unfortunately, there were not enough *Cittarium* shells present (n = 5) to perform an analysis of population structure nor does this study have a formula for *Cerion* shells to predict *C. clypeatus* crab size. However, analyzed shell size can infer relative *C. clypeatus* crab size; phase one *Cerion* shells housed the smallest *C. clypeatus* crabs, while phase two and three *Cerion* shells housed *C. clypeatus* crabs that are slightly larger but still juvenile.

Shell choice is important for *C. clypeatus* individuals as they will spend their whole life in countless numbers of shells, each just as important as the last. Shells need to balance fit, light weight, and strength. To choose a shell, there must be an evaluation process to determine size and strength of vacant shells (Elwood et al. 1998). Coenobitans will select for specific species of gastropod shells as the most important variable in the selection process with shell size and shell condition as the second and third most important variable (Abrams 1978). Based on this selection process, *C. clypeatus* crabs prefer *Cerion* shells as they emerge from the ocean and proceed to the fitting process. Young *C. clypeatus* crabs choose smaller, lighter shells, which is expected as they arrive on land, but these shells have a consistently low density. Smaller, phase one *Cerion* shells tend to be weaker than those that are larger. Young individuals of *C. clypeatus* may not have much of a choice but to use these low-density shells as they emerge from the ocean, but if other shell genera/species were better suited for protection, they would have a stronger presence in these discarded shell locations.

Coenobita species tend to choose shells large enough so they are able to retract into the shell, only exposing the major chela to seal the opening to protect from predators and water loss (Abrams 1978). If shell fit is suitable, *C. clypeatus* crabs may omit modifications. That is the case in 24 shells that were collected, but there is no guarantee they were worn. The 24 shells that were unmodified were significantly larger in size than the 301 shells that showed modifications.

If the shell does not fit perfectly, the shell aperture lip and inner aperture ridge can be modified to effectively seal the opening. These aperture modifications are likely the first to be created because it involves the simplicity of clipping the shell with their major chela (DeVore obs. 2018) or friction on rocks and other objects. Collected shells have noticeable clipping and abrasion marks as shown by small chips in modified apertures (**Figures 3, 5, and 6**). The high number of these modifications in the collection (ALIP = 88%, ARID = 88.3%) support the hypothesis that the shells showing these modifications were worn and modified by *C. clypeatus* crabs. All shells below 19.72mm in shell length (n = 192) had a modified aperture lip suggesting that aperture clipping is a necessity for shells of this size. The average width of modified aperture lips is much smaller than those with unmodified aperture lips, mainly because smaller shells have more of these modifications. However, *C. clypeatus* crabs may prefer smaller apertures and clip the aperture lip accordingly. Once the aperture is modified, the shell is then reassessed for suitability. If the shell is suitable, *C. clypeatus* crabs will continue their modifications until they either outgrow or degrade the shell.

Columella modifications (**Figure 7**) occur in 14.8% (n = 48) of all collected *Cerion* shells. Noted in other studies, the modified columella thins the inner walls (Ragagnin et al. 2016), increases area to retract into the shell, increases self-defense effectiveness (Greenaway 2003, Imafuku and Ikeda 1990), increases area for females to house eggs (Laidre 2012, Sallam 2012), and increases water volume storage (Laidre 2012). Alternatively, the removal of the columella reduces structure and may result in a broken shell. Columella modifications are likely created by clipping with the chela paired with friction from constant movement and chemical abrasion (Kinosita and Okajima 1968). In this study, columella modifications are more present in larger shells than smaller ones. Columella modifications are also much more abundant in shells with an aperture lip or ridge modifications than those without aperture lip or ridge modifications.

As *C. clypeatus* crabs mature and increase in size, there is more need for weight reduction and interior volume increase. Since larger shells are heavier and denser, removing the columella may significantly decrease weight. Once the columella is removed, *C. clypeatus* crabs use the space for self-defense by enabling their full body to retract and create a self-defense method of communication by snapping and croaking their chela (Greenaway 2003, Imafuku and Ikeda 1990). Absence of the columella also creates more room for females to house their eggs, which can increase fecundity of individuals of *Coenobita* species (Laidre 2012, Sallam 2012). As *C. clypeatus* crabs grow, without the opportunity to exchange for a larger shell, a columella modification is a suitable option.

Compared to the 58% of shells with a columella modification reported by Walker (1994), the smaller percentage of columella modifications (4.8%) found herein have two explanations;

interior space for eggs is not needed for juvenile *C. clypeatus* crabs and an abundance of suitable vacant shells are present. If *C. clypeatus* crabs find a larger, more suitable shell, they will likely exchange shells instead of creating more interior space. Abundant shells in the area may reduce the need for modifications such as these, while discarded shells with a high percentage of columella modifications may not have an ideal shell selection for *C. clypeatus* individuals to choose from.

Umbilicular modifications and exterior holes make up 7.1% (n = 23) and 7.7% (n = 25) of all *Cerion* shells collected, respectively. Umbilicular modifications show no obvious advantage other than weight reduction and may actually decrease the suitability of the shell as modifications to the umbilicular region result in a hole shown in **Figure 7**. However, some umbilicular modifications allow for a larger aperture width, thus possibly achieving a better fit and seal for the major chela. Exterior holes are a result of lack of suitable vacant shells paired with extreme use by *C. clypeatus* crabs. Holes can also be a result of natural weathering such as burial, waves, tides, or predators/large animals crushing shells. Holes can also be created by constant friction by *C. clypeatus* from dragging the shell along rocks, cement, or other rough substrates (Walker 1994). Hermit crabs find no use for shells with holes in a study by Abrams (1978), reported 1-2% of hermit crabs having holes in their shells, whereas in this study, only 7.7% (n = 25) of collected *Cerion* shells had holes and three of them (12%) had sand clogging the holes. *Coenobita clypeatus* may not continue to use these holed shells, but if they are limited to using them, they effectively seal holes with resources around them like sand. In Curaçao, Gould (1971) noted damage on the apical whorl (tip), resulting in a hole, in over 80% of *Cerion* (*Cerion uva*, Linnaeus 1758) shells collected on the island. Gould's interpretations of this damage are noted as the following: natural removal, or artificial removal such as use of shells as ornaments, or shells were broken, and gastropods were sucked out. Something Gould (1971) did not mention, was the presence of hermit crabs. Interpretations that involve unknown damage to a high percentage of discarded shells should always include hermit crabs as a suspect. Holes in this specific shell species, *Cerion uva* (a much larger species of *Cerion* gastropod than our subjects), could be made to reduce significant weight then plugged with sand to decrease water loss. Although we did not note any apical whorl damage, this study does not rule it out as a modification by *C. clypeatus* crabs.

Coenobita clypeatus is a species that has been documented once for manipulating shells to obtain a better fit (Walker 1994). This study, compounded with results reported by Walker (1994), support the notion that shells of any size that were worn can be modified by *C. clypeatus* crabs. The hypothesis states that, once a shell is chosen, modifications are performed for a better fit, decreased weight, and increased strength. Both fit and weight hypotheses are supported as aperture lip, inner aperture ridge, columella, and umbilicular modifications are performed. However, there is no evidence that modifications can increase the density or strength of the shell. Removing the columella may have a negative impact on the strength of the shell as the interior structure of the shell is absent. *Coenobita clypeatus* rarely modified the columella on shells shorter than 21.04mm (n=6), likely because they could not afford to lose density on already low-density shells.

Each modification takes time to create, thus making it a step-by-step process from one modification to the other. The earliest modifications are modifications that occur more often in discarded shells, while later modifications show less of an occurrence in discarded shells. Aperture lip and inner aperture ridge modifications are likely created using the major chela and are the most abundant modifications among shells collected, making those modifications the first to occur. Likely, the second modification is a modified columella, created by the major chela, abdomen friction, and chemical abrasion (Kinosita and Okajima 1968), followed by an umbilicular region modification. Lastly, holes are made from friction and will likely deem the shell unsuitable to wear, which is supported by Abrams (1978). Once individuals of *C. clypeatus* find a shell unsuitable or too small, they will discard it and replace it with a more suitable shell. This cycle, called the vacancy chain, is repeated until the *C. clypeatus* individual dies.

This study shows that young *C. clypeatus* crabs have a high reliance on terrestrial gastropods, including cerionids, because of their abundance on San Salvador Island. In Bermuda, the decrease of once abundant suitable *Cittarium* shells, which is the most used shell genus, led to the decline of the *C. clypeatus* population (Walker 1994). The relationship between *C. clypeatus* and *Cerion* shells are similar to *C. clypeatus* and *Cittarium* in Bermuda. With more ecological research on the relationship of *C. clypeatus* and *Cerion* gastropods, predictions can be made for the fate of *C. clypeatus* crabs on the island. In the future using clues from this study, researchers may be able to tell the duration that a hermit crab has occupied the shell using only the modification stages shown on that shell. In general, more studies should be conducted to show shell use throughout the *C. clypeatus* crab lifespan. Morrison and Spiller (2006) used pitfall traps to monitor *C. clypeatus* crabs and the shells they inhabit. The pitfall traps collected *C. clypeatus* individuals using solely marine and tidal gastropod shells, differing from the results of this study despite both studies being on Bahamian Islands. Inland pitfall traps are likely to capture more mature *C. clypeatus* in comparison to pitfall traps near the coast, but the locations of pitfall traps were not mentioned in the study. This may be a reason for finding no terrestrial gastropods because pitfall traps may not be so reliable to represent the full lifespan of *C. clypeatus* nor the full spectrum of shells used.

Aperture lip modifications and inner aperture ridge modifications are overwhelmingly the favorite modification performed on the shells. Columella modifications are also an important modification to have done, but for smaller *C. clypeatus* and their shells, this modification does not happen so often compared to larger *C. clypeatus'* shells. In order to establish that *C. clypeatus* crabs have transported a shell from its original resting place, the aperture and columella should be analyzed before conclusions can be made for the location of the vacant shell. With more research, modifications shown in this study can be used to determine time it takes to modify each step, paired with the duration of wear by *C. clypeatus* crabs. Modified shells, paired with their location, can determine population structure of *C. clypeatus*.

A group of modified fossil shells in the Caribbean or other terrestrial tropical and subtropical locations can determine general *Coenobita* population make-up. This study will also be useful for ESR dating of terrestrial Quaternary aged shells to recognize if shells were transported into a depositional environment by *C. clypeatus* individuals or any other *Coenobita* species across the globe. Shell modifications convey that shells were likely transported by a hermit crab from its original resting place. Modifications should not be limited to what is found in this study and may vary between gastropod species. As shells are used for relative dating, they become essential for absolute dating purposes throughout the world, this study should bring attention to modification assessments and their importance with determining the final location of the shell. Stratigraphy on San Salvador Island should not be dated using shells unless the shells have been inspected for hermit crab modifications. The potential for hermit crabs to transport a fossil shell from one stratigraphic layer to another is high and will result in misleading dating results if not analyzed properly.

In conclusion, shells are modified by *C. clypeatus* from any size. This study shows that shells can be modified as soon as *C. clypeatus* comes on land. Paired with other studies, it is known that they modify shells in a similar way, no matter the shell type, throughout their life. *Coenobita clypeatus* can also wear and modify fossil shells and deposit them into a different stratigraphic layer, resulting in stratigraphic time-skewing if shells are not carefully analyzed for modifications. Implications from this study can be used in tropical and subtropical locations where terrestrial hermit crabs are present around the world.

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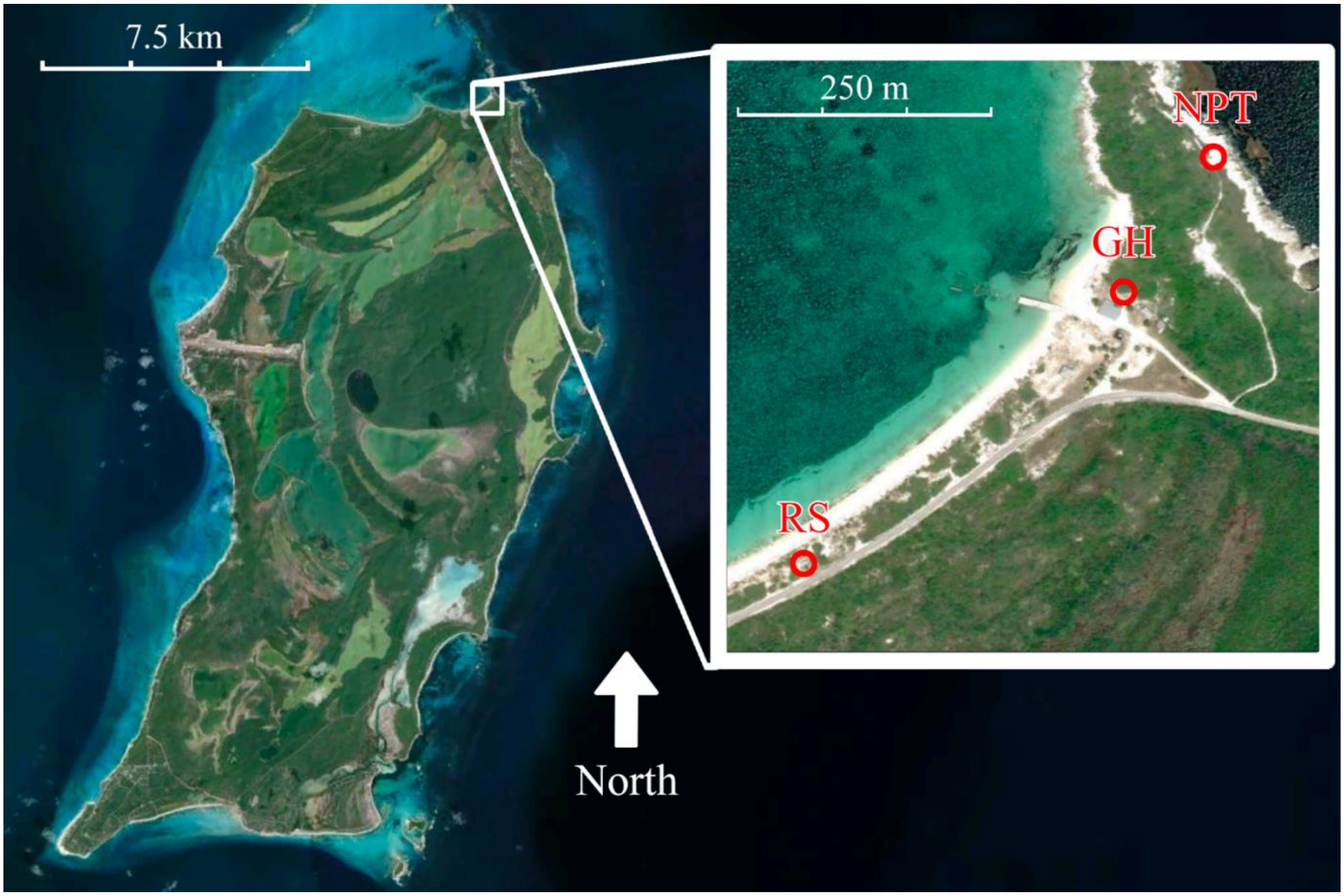
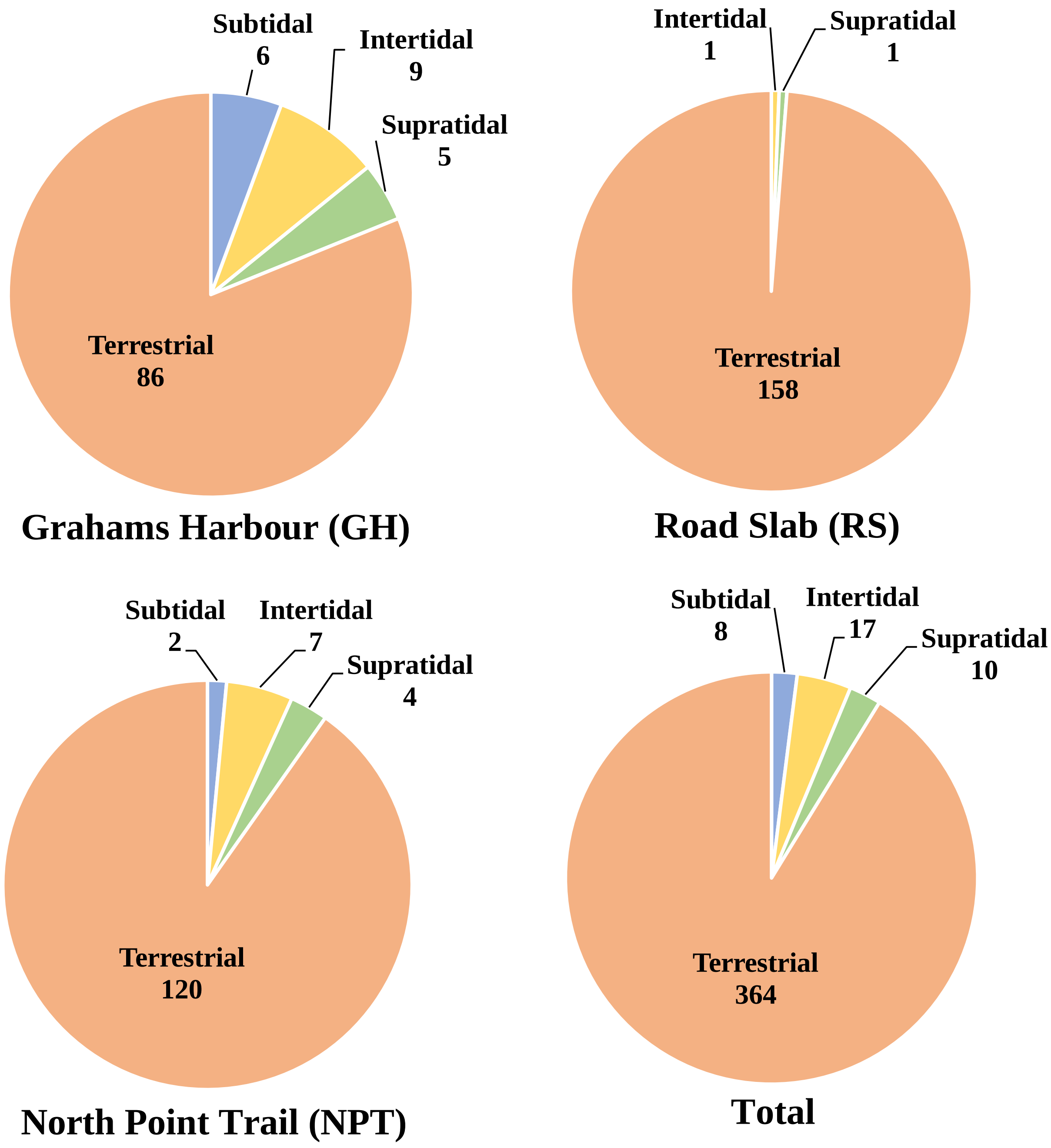


Figure 1: Map of San Salvador Island, Bahamas indicating sampling locations. North Point is enlarged to show greater detail of each location (in red circles); Grahams Harbour (GH; 24.1230°N, -74.4575°W), Road Slab (RS; 24.1209°N, -74.4599°W), and North Point Trail (NPT; 24.1239°N, -74.4567°W).



Grahams Harbour (GH)

Road Slab (RS)

North Point Trail (NPT)

Total

Figure 2: Pie charts showing the frequency of gastropod shell origin in each location as well as the total.

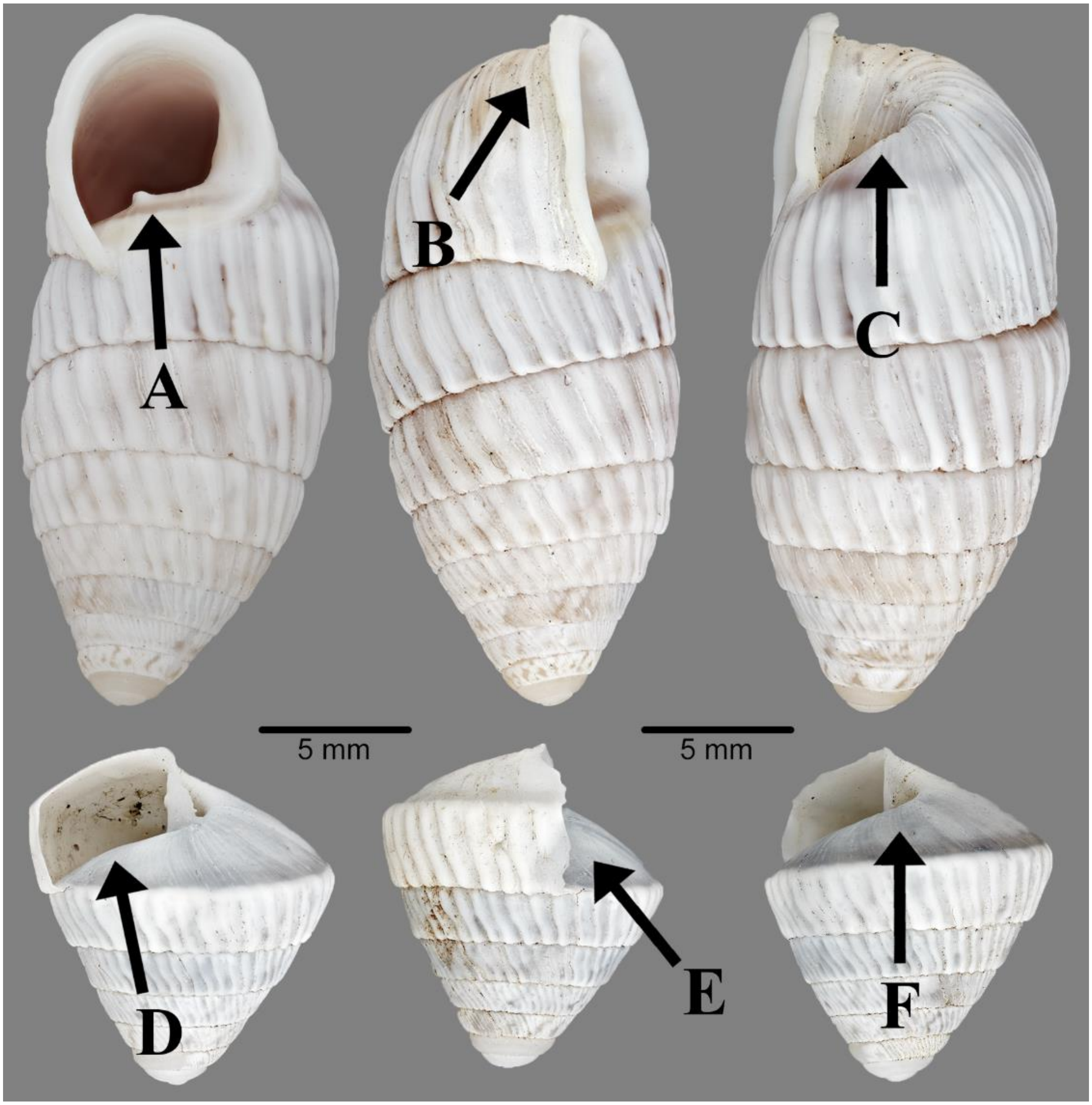


Figure 3: A phase three *Cerion* shell (top three) is shown from three different angles to represent an unmodified shell as a control. Arrow "A" shows an unmodified inner aperture ridge. Arrow "B" shows an unmodified aperture lip. Arrow "C" shows an unmodified umbilicular region. A phase one *Cerion* shell (bottom three) is shown from three different angles to show its rectangular aperture, to differentiate from the rounded aperture of the phase three *Cerion* shell, as well as its lack of inner aperture ridge (D), modified aperture lip (E), and an unmodified umbilicular region (F).

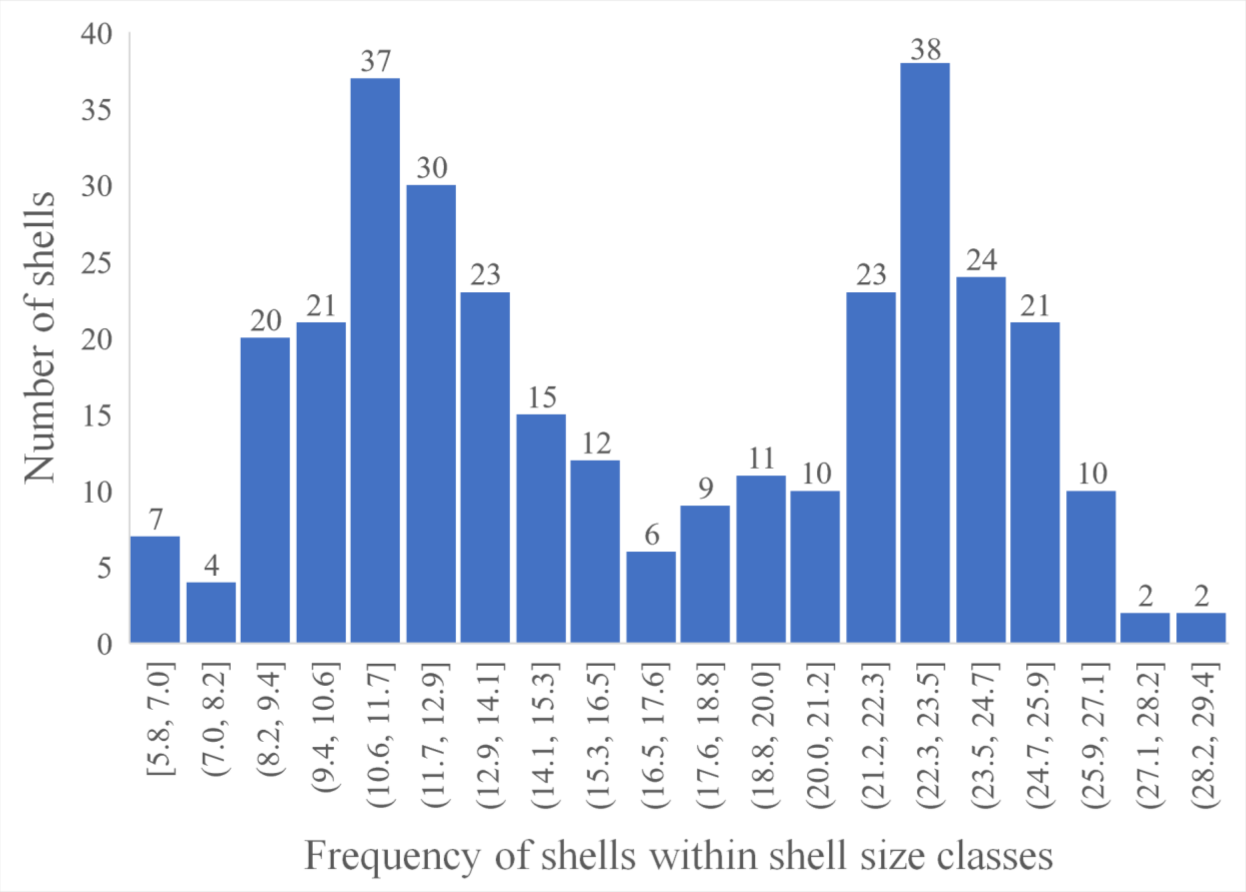


Figure 4: Collected *Cerion* shell frequencies within 20 shell length categories are shown to visualize the *Cerion* size range and frequency in North Point, San Salvador.

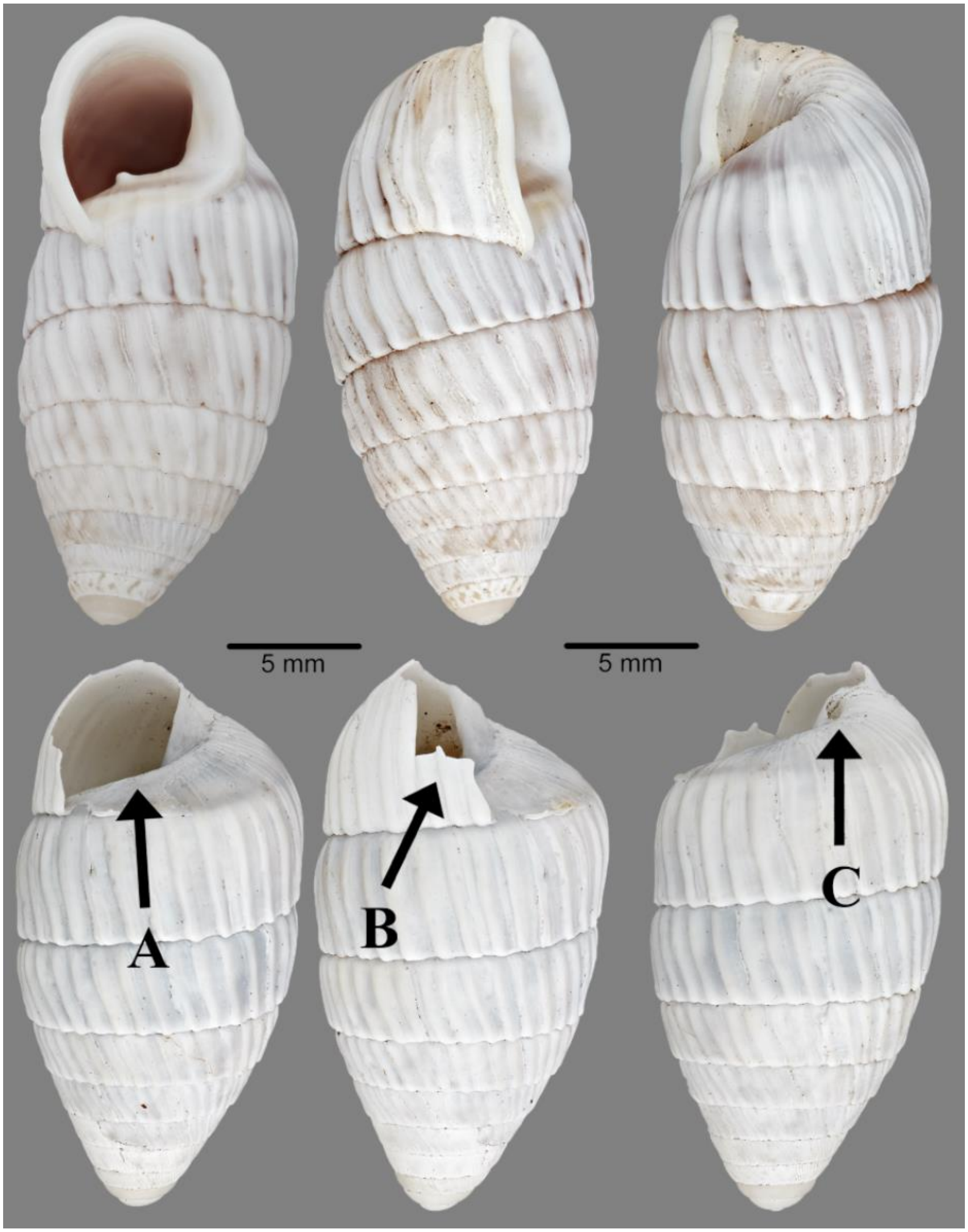


Figure 5: A phase three *Cerion* shell (top three) is shown from three different angles to represent an unmodified shell as a control. Below, a *Cerion* shell is shown from three different angles to represent a shell with an absent inner aperture ridge (A), fully modified aperture lip (B), and an unmodified umbilicular region (C).

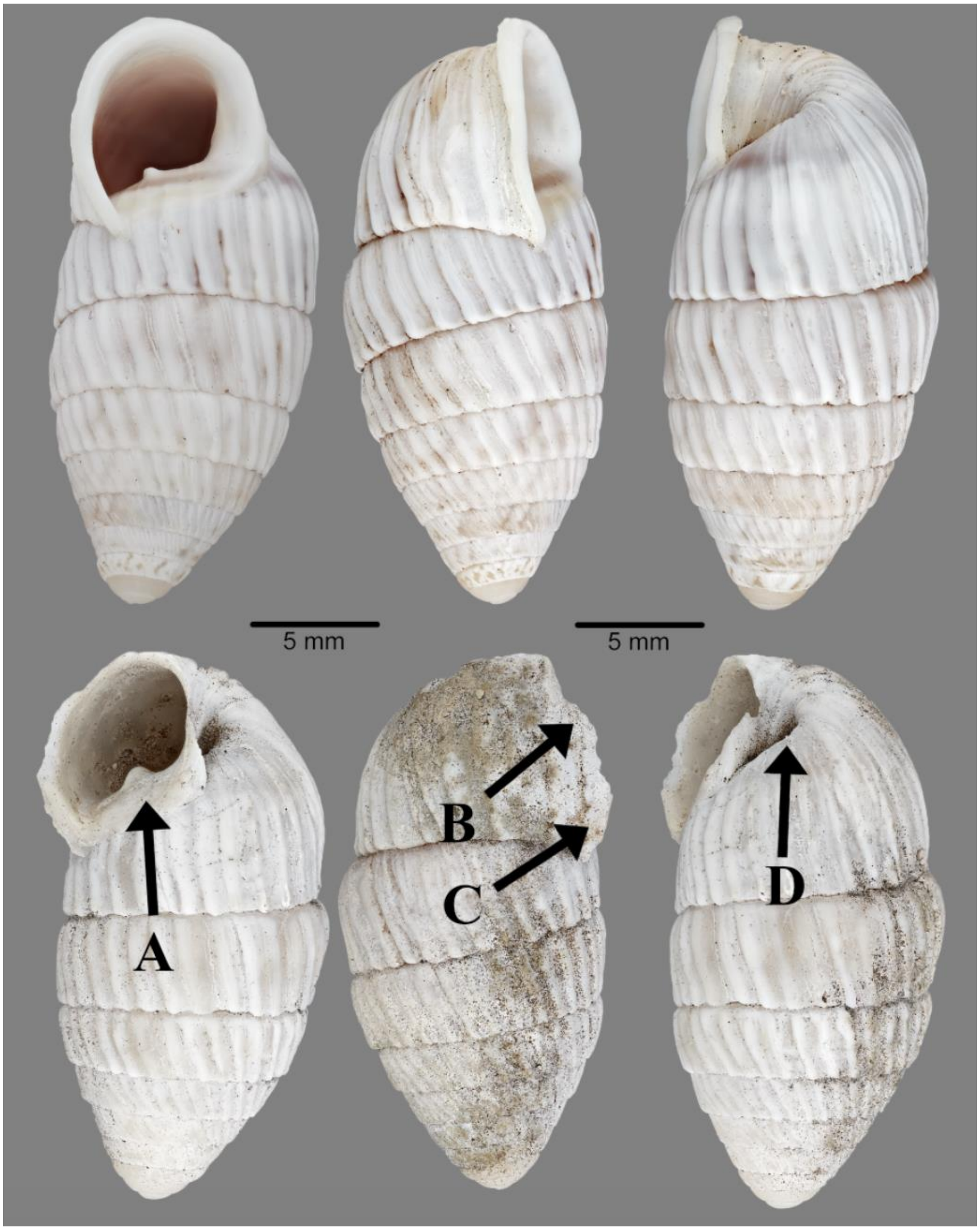


Figure 6: A phase three *Cerion* shell (top three) is shown from three different angles to represent an unmodified shell as a control. Below, a *Cerion* shell is shown from three different angles to represent a shell with a present inner aperture ridge (A), a partially modified aperture lip, and an unmodified umbilicular region (D). Arrow "B" shows the modified portion of the aperture lip while arrow "C" shows the unmodified portion of the aperture lip.

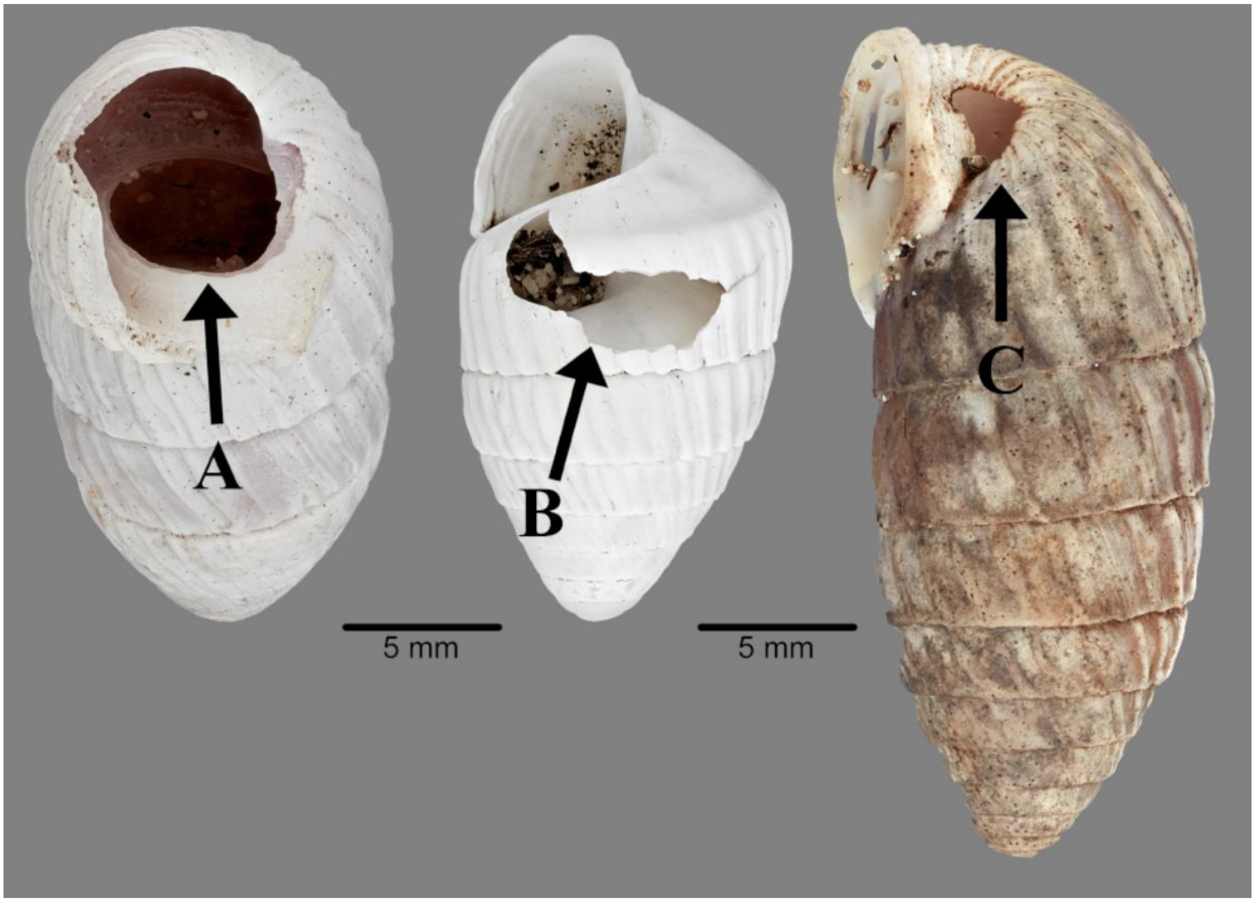


Figure 7: Three *Cerion* shells are shown to represent three different modifications to shells. Arrow “A” shows an absent (modified) columella as well as an absent umbilicular region. Arrow “B” shows an exterior hole in the shell of a phase two *Cerion* shell. Arrow “C” shows a hole (modified) in the umbilicular region of the shell.

Table 1: Average, standard deviation, minimum, quartiles, and maximum mearurements are shown for all collected *Cerion* shells; SL, SWI, SWE, SD, AWI.

	Shell Length (SL, mm)	**Shell Width (SWI, mm)**	**Shell Weight (SWE, g)**	**Shell Density (SD, g/mm^3)**	**Aperture Width (AWI, mm)**
Average	16.96	10.30	0.65	0.0003130	6.21
Standard Deviation (+/-)	6.06	1.12	0.48	0.0001141	1.25
Minimum	5.84	6.17	0.1	0.0001074	2.73
Quartile 1	11.50	9.66	0.3	0.0002329	5.36
Quartile 2	16.16	10.41	0.5	0.0002899	6.24
Quartile 3	22.95	11.06	1.0	0.0003739	7.03
Quartile 4	29.42	12.70	2.3	0.0007199	9.96
Maximum	29.42	12.70	2.3	0.0007199	9.96

Table 2: The number of *Cerion* shells for each modification is shown along with the percentage of *Cerion* shell modifications out of the total number of *Cerion* shells (325) collected in North Point.

	Columella (COL)	**Umbilicular region (UMB)**	**Aperture Lip (ALIP)**	**Inner Aperture Ridge (ARID)**	**Exterior Holes (EH)**
# of *Cerion* Shells	48	33	286	287	25
% of *Cerion* Shells	14.8%	7.1%	88.0%	88.3%	7.7%