The Delray Beach, Florida, colony of *Cerion (Paracerion) tridentatum costellata* Pilsbry, 1946 (Gastropoda: Pulmonata: Cerionidae): Evidence for indirect Cuban origins

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ABSTRACT

A large colony of *Cerion* has recently been reported from Delray Beach, Florida, far north from the ranges of both native and introduced species of *Cerion*. Specimens correspond morphologically to the type series of *Cerion (Paracerion) tridentatum costellata* Pilsbry, 1946, which no longer survives at its type locality (Fort Jefferson, Garden Key, Dry Tortugas, Florida.) Historical data indicate that this taxon is a hybrid of two or more of the five Cuban species of *Cerion* introduced to Fort Jefferson by Bartsch in June, 1924. Museum records document that a propagule of this hybrid taxon was transplanted to Boynton Beach in the late 1940s and proliferated to give rise to the Delray Beach colony. Partial cytochrome c oxidase I sequences reveal the Delray colony to be monophyletic, and of exclusively Cuban ancestry. Limited sampling confirms the presence of mitochondrial genes from two (*C. tridentatum* and *C. sculptum marielinum*) of the five Cerion taxa introduced to Fort Jefferson in 1924. A larger sample size, together with data from nuclear genes, will be needed to rule out the presence of rare alleles from other taxa. Transplantation of this newly formed hybrid propagule to an area distant from either parent population has allowed it to evolve in isolation and provides a unique opportunity to study the origins and persistence of genetic diversity within the genus *Cerion*.

Additional keywords: Native species, introduced species, cytochrome c oxidase I

INTRODUCTION

The fossil history of the Genus *Cerion* in Florida dates from the Oligocene/early Miocene (Petuch, 2004: 73), yet the Recent fauna is limited to a single native species with four subspecies or varieties, and to survivors of a series of experimental introductions during the early 20th Century. These introductions and the fates of the resulting colonies were documented in detail by Bartsch (1913–1931), summarized by Pilsbry (1946: 165–169), and reviewed by Harasewych and Strauss (2006: table 1.C., fig. 1).

Harasewych and Strauss (2006) also detailed the occurrence of a well-established yet previously unreported colony of *Cerion* in Delray Beach, Florida, far north from the ranges of either the native or any of the introduced species. These authors conjectured that, “whether transported by a hurricane or intentionally introduced, the most proximal sources for the Delray Beach colony are the *Cerion* faunas of the Little Bahama Bank or of the Bimini Islands.” However, comparisons of the shells of both mottled and unpigmented phenotypes from the Delray Beach colony with the primary types of each of the named *Cerion* from the Bimini Islands (5 taxa) and the Little Bahamas Bank (9 taxa) failed to produce a close match, leading Harasewych and Strauss (2006) to speculate that the Delray Beach colony may be a hybrid population descended from two or more propagules introduced some time near the middle of the 20th Century.

In the present study, we investigate more broadly the potential sources of the Delray Beach colony of *Cerion*. Historical records of the various transplantation experiments and relevant museum collections were examined. In addition, partial sequences of the mitochondrial cytochrome c oxidase I gene derived from examples of both white (Figure 1) and mottled (Figure 2) phenotypes were compared against representative *Cerion* taxa spanning the current range of the genus, including the Bimini Islands and Little Bahamas Bank. These molecular data, supplemented by morphological comparisons and archival records, are used to ascertain the identity and sources for this introduced colony.

Figures 1–15. Species of *Cerion* treated in this study. **1–6.** *Cerion* (*Paracerion*) *tridentatum costellata* Pilsbry, 1946. **1.** White and **2.** mottled morphotypes, USNM 1123779. Between highway A1A and the Ocean, at northern limit of public beach, Delray Beach, Florida, Florida (26°28.032' N, 80°3.382' W). On vegetation on seaside sand dunes, within 0.5 m of the ground. M.G. Harasewych coll., July 7, 2008. **3.** Lectotype (here designated), specimen figured in Pilsbry, 1946:fig. 80d. ANSP 179274. **4.** Paralectotype, specimen figured in Pilsbry, 1946: fig. 80c. ANSP 426010. Both from Garden Key, Dry Tortugas, Florida, Bales and McGinty coll., 1941. **5.** White and **6.** mottled morphotypes, ANSP 192703, from the McGinty lawn, Boynton Beach, Florida, Pilsbry coll., April 1954. **7–11.** Taxa introduced to Fort Jefferson, Garden Key, Dry Tortugas, by Paul Bartsch in June, 1924. **7.** *Cerion* (*Paracerion*) *tridentatum* Pilsbry and Vanatta, 1895, USNM 392820, Rincon de Guanaba at Playa, Cuba. Bartsch coll., May 29, 1924. **8.** *Cerion chrysalis* Férrusac, 1832, USNM 361745, Cabañas Fort, Havana Cuba, Bartschcoll., May 27, 1924. **9.** *Cerion sculptum* Poey, 1858, USNM 361763, near Light House, Mariel, Cuba. Bartsch coll., May 29, 1924. **10.** *Cerion mumia* Bruguiere, 1792. USNM 391821, the point at Miramar, Cuba. Bartsch coll., 1924. **11.** *Cerion* "species". USNM 361766, east of the point at Mariel, Cuba, Bartsch coll., 1924. **12–15.** Dried museum specimens of *Cerion* used for DNA extraction. **12–13.** *Cerion* (*Paracerion*) *tridentatum* Pilsbry and Vanatta, 1895, USNM 392820, Rincon de Guanaba at Playa, Cuba. Bartsch coll., May 29, 1924. **14.** *Cerion* (*Paracerion*) *tridentatum costellata* Pilsbry, 1946, USNM 487438a. **15.** *Cerion sculptum* Poey, 1858, USNM 487438b, both from, Garden Key, Dry Tortugas, Florida. G.R. Bales coll., May 3, 1947. Abbreviations: **e,** epiphragm, **t,** dried tissue used for DNA extraction.

MATERIALS AND METHODS

With the exception of the *Cerion* samples from Cuba and Fort Jefferson in the Dry Tortugas, which were available only as dried museum specimens, DNA from each of the taxa listed in Table 1 was extracted from a portion of the digestive gland and gonad dissected from living specimens using a Qiagen DNeasy extraction kit according to manufacturer's protocol.

In order to obtain DNA from older museum specimens, individuals with intact epiphragms were selected, and the dorsum of the shell removed using a Wizard Model 100 Saw (Diamond Pacific Tool Corp.) with a diamond lapidary blade. This usually revealed second, and occasionally third, epiphragms, as well as desiccated tissues (Figure 15). Small fragments of dried digestive gland and gonad were extracted using the Qiagen DNeasy kit. The initial lysis step was extended to 48 hours at 65°C with continuous agitation, until the tissues completely disintegrated. Subsequent steps were according to manufacturer's protocol.

A portion of the mitochondrial cytochrome oxidase I gene was amplified using Sigma Jumpstart Red Taq Ready Mix and Folmer et al. (1994) primers. Resulting PCR products were purified using AMPure magnetic beads (Agencourt, manufacturer's protocol) and sequenced using either ABI 3130xl or Spectrumedix 9600 fluorescent sequencers. Sequences were manually checked and assembled using Sequencher 4.6 (Gene Codes Corp.), and aligned against the cytochrome *c* oxidase 1 gene of *Albinaria caerulea* (Deshayes, 1835) (1529 bp) derived from its complete mitochondrial genome (Hatzoglou et al., 1995; GenBank NC 001761) using ClustalX 2.1 (Larkin et al., 2007). The ends and primers were trimmed, yielding an alignment of 655 bases corresponding to positions 39 to 693 of the COI gene in *Albinaria caerulea*. Aligned sequences were reviewed and translated to 218 amino acid sequences using McClade Version 4.08 (Maddison and Maddison, 1992) and the extended *Drosophila* mtDNA genetic code. Relationships among the taxa based on nucleotide and amino acid sequences were analyzed using PAUP 4.0b10 (Swofford, 2002).

RESULTS

Comparative Morphology and Historical Review: Specimens of the Delray Beach colony of *Cerion* (Figures 1, 2) were compared against samples of each of the native and non-native taxa introduced to Florida (Harasewych and Strauss, 2004: Table 1) as well as with *Cerion tridentatum costellata* Pilsbry, 1946, a form that Pilsbry described from Garden Key (Dry Tortugas). The Delray Beach *Cerion* matched closely the type series *Cerion tridentatum costellata*, which also includes both white (Figure 3) and mottled (Figure 4) phenotypes.

There were no native *Cerion* species in the Dry Tortugas prior to Bartsch's introductions during the first quarter of the twentieth century (Bartsch, 1913–1931). The majority of these transplantation and hybridization experiments were conducted on Loggerhead Key, where the Carnegie Institution of Washington maintained its Marine Biology Laboratory from 1903 until 1939. However, *Cerion* were also introduced onto Garden Key, Man Key, Boy Key, and Bird Key in the Dry Tortugas.

Cerion species were introduced onto Garden Key on two occasions. On June 8, 1912, 138 specimens of a species later to be named *Cerion viaregis* Bartsch, 1920 were planted in the "back of a small unpainted house on the northeast side of the Fort, Garden Key, Tortugas." (Bartsch, 1913: 130). Bartsch visited this planting on May 2, 1913, and found 60 of the *Cerion* still living. He concluded that the site was unsuitable for the colony and transplanted the living specimens to the inside of the fort, near the center (Bartsch, 1914a: 170–171). He revisited this colony on April 27, 1914, and discovered that "the second planting inside the fort had been burned over; 28 dead shells were found, but the rest had disappeared. A visit to the original planting showed 6 living specimens, but no young." On January 16, 1919, "a careful search was made both within and without the fort, but not a trace of *Cerion* was discovered, so it is feared that this colony has disappeared." (Bartsch, 1920a: 19–20)

On June 5–20, 1924, Bartsch (1924b: 187) introduced 2,125 specimens of Cuban *Cerion* onto the west and north side of the parapet at Fort Jefferson on Garden Key. These included: 500 specimens of *Cerion tridentatum* Pilsbry and Vanatta, 1895, from Rincon de Guanabon (Figure 7); 500 specimens of *Cerion chrysalis* Férrusac, 1832, from near Cabanas Fort (Figure 8); 500 specimens of *Cerion sculptum* Poey, 1858, from near the lighthouse at Mariel (Figure 9); 500 specimens of *Cerion mumia* Bruguière, 1792, from the point at Miramar (Figure 10); and 125 young specimens of a species of *Cerion* that Bartsch considered to be undescribed (similar to *C. johnsoni*) from east of the point at Mariel (Figure 11). Upon revisiting these colonies the following year, Bartsch (1925a: 222) reported that "the colonies which we introduced on the top of Fort Jefferson last year also showed considerable mortality, also considerable living specimens." In August 1927, the colonies on the parapet were reported to be "holding their own" (Bartsch, 1927: 216). By August 1931, *Cerion mumia, C. chrysalis,* and *C. tridentata* were "thriving", while *C. sculptum*, and *C*. n. sp. "seemed not to have survived" (Bartsch, 1931: 373).

In his treatment of the genus *Cerion*, Pilsbry (1946) discussed Bartsch's transplantation experiments in the Florida Keys. Citing a letter from Bartsch, Pilsbry (1946: 166) reported that specimens of *Cerion striatellum* (Guérin, 1829) from Balena Point, near Guanica Bay, Puerto Rico, were also introduced to the parapet at Fort Jefferson in 1924. This species was not

Table 1. Taxa, locality data, voucher specimen information and GenBank Accession information for the samples used in this study. USNM = National Museum of Natural History, Smithsonian Institution.

TAXON	LOCALITY	Voucher Specimen	GenBank Accession Number [CO I]
DUTCH WEST INDIES			
Cerion uva arubanum (Baker, 1924)	Baranca Alto, Aruba	USNM 1073039	JN 038138
Cerion uva arubanum (Baker, 1924)	Baranca Alto, Aruba	USNM 1073039	JN 038139
FLORIDA			
Cerion Delray White 1	Delray Beach, FL	USNM 1123779	JN 038140
Cerion Delray White 2	Delray Beach, FL	USNM 1123779	JN 038141
Cerion Delray White 3	Delray Beach, FL	USNM 1123779	JN 038142
Cerion Delray White 4	Delray Beach, FL	USNM 1123779	JN 038143
Cerion Delray Mottled 1	Delray Beach, FL	USNM 1123779	JN 038144
Cerion Delray Mottled 2	Delray Beach, FL	USNM 1123779	JN 038145
Cerion Delray Mottled 3	Delray Beach, FL	USNM 1123779	JN 038146
Cerion Delray Mottled 4	Delray Beach, FL	USNM 1123779	JN 038143
Cerion incanum incanum (Binney, 1851)	Key West, FL	USNM 1116902	JN 038147
Cerion incanum incanum (Binney, 1851)	Key West, FL	USNM 1116902	JN 038148
Cerion casablancae Bartsch, 1920 32	Indian Key, FL (*ex* Andros Bahamas)	USNM 1158942	JN 038149
Cerion casablancae Bartsch, 1920 33	Indian Key, FL (*ex* Andros Bahamas)	USNM 1158942	JN 038150
Cerion tridentatum costellatum Pilsbry and Vanatta, 1895	Garden Key, Dry Tortugas, FL 1947	USNM 487438a	JN 038151
Cerion sculptum (Poey, 1858)	Garden Key, Dry Tortugas, FL 1947	USNM 487438b	JN 038152
CUBA			
Cerion tridentatum Pilsbry and Vanatta, 1895	Rincon de Guanaba at Playa, Cuba, 1924	USNM 392820a	JN 038153
Cerion tridentatum Pilsbry and Vanatta, 1895	(source of Garden Key introduction)	USNM 392820b	JN 038153
PUERTO RICO			
Cerion striatellum (Guerin, 1829) 1	Tamarindo Beach, Puerto Rico	USNM 1158944	JN 038154
Cerion striatellum (Guerin, 1829) 2	Tamarindo Beach, Puerto Rico	USNM 1158944	JN 038154
LITTLE BAHAMA BANK			
Cerion bendalli Pilsbry and Vanatta, 1896	Great Abaco, Bahamas	USNM 1158941	JN 038155
Cerion bendalli Pilsbry and Vanatta, 1896	Great Abaco, Bahamas	USNM 1158941	JN 038156
GREAT BAHAMA BANK			
BIMINI			
Cerion biminiense Henderson and Clapp, 1913	Bimini, Bahamas	USNM 1080860	JN 038157
Cerion biminiense Henderson and Clapp, 1913	Bimini, Bahamas	USNM 1080860	JN 038158
Cerion eximium lerneri Clench, 1956	Bimini, Bahamas	USNM 1080858	JN 038159
Cerion eximium lerneri Clench, 1956	Bimini, Bahamas	USNM 1080858	JN 038160
ANDROS			
Cerion pepperi Bartsch, 1913 192	Somerset Pt., Andros, Bahamas	USNM 1080841	JN 038161
Cerion pepperi Bartsch, 1913 193	Somerset Pt., Andros, Bahamas	USNM 1080841	JN 038162
ELEUTHERA			
Cerion uniformis Maynard, 1913	Eleuthera, Bahamas	USNM 1158933	JN 038163
Cerion uniformis Maynard, 1913	Eleuthera, Bahamas	USNM 1158933	JN 038163
Cerion glans Küster, 1844	Eleuthera, Bahamas	USNM 1158937	JN 038164
Cerion glans Küster, 1844	Eleuthera, Bahamas	USNM 1158937	JN 038164
LONG ISLAND			
Cerion malonei Clench, 1937	Long Island, Bahamas	USNM 1083081	JN 038165
Cerion malonei Clench, 1937	Long Island, Bahamas	USNM 1083081	JN 038166
Cerion fernandina Clench, 1937	Long Island, Bahamas	USNM 1083076	JN 038167
Cerion fernandina Clench, 1937	Long Island, Bahamas	USNM 1083076	JN 038167
Cerion josephinae Clench, 1935	Long Island, Bahamas	USNM 1083062	JN 038168
Cerion josephinae Clench, 1935	Long Island, Bahamas	USNM 1083062	JN 038168

(Continued)

Table 1. (Continued)

TAXON	LOCALITY	Voucher Specimen	GenBank Accession Number [CO I]
SAN SALVADOR			
Cerion watlingense Dall, 1905	San Salvador, Bahamas	USNM 1110080	JN 038169
Cerion watlingense Dall, 1905	San Salvador, Bahamas	USNM 1110080	JN 038170
TURKS AND CAICOS			
Cerion regina Pilsbry and Vanatta, 1895 1	Conch Cay, Middle Caicos Island	USNM 1080843	JN 038171
Cerion regina Pilsbry and Vanatta, 1895 2	Conch Cay, Middle Caicos Island	USNM 1080843	JN 038171
Cerion lewisi Clench, 1961 1	Blue Hill, Providenciales	USNM 1080845	JN 038172
Cerion lewisi Clench, 1961 2	Blue Hill, Providenciales	USNM 1080845	JN 038173

mentioned in Bartsch's (1924b: 187) published account of the introductions, and Pilsbry (1946: 166) noted that *C. striatellum* was not represented in the collections made in the Tortugas in 1941 by Dr. Bales and Mr. McGinty.

Working with the 1941 collections from the Tortugas, Pilsbry (1946: 168) reported that no specimens of *C. viaregis* or *C. mumia* were present, and questioned the identity of the species that Bartsch referred to as *C. mumia*. Pilsbry revised the nomenclature for the surviving taxa introduced to Garden Key to: *C. chrysalis fastigatum* Maynard, 1896 and *C. sculptum marielinum* Pilsbry, 1927, commenting that both were abundant on Garden Key in 1941, as was *Cerion tridentatum*. He also noted that the typical smooth form of *C. tridentatum* was rare on Garden Key, and went on to name the prevalent, ribbed form as *Cerion tridentatum costellata*, illustrating three specimens (Pilsbry, 1946: fig. 80, b, c, d) that included both white and mottled phenotypes. The unpigmented specimen (Figure 3) illustrated in (Pilsbry, 1946: fig. 80, d) is selected here as the lectotype (ANSP 179274). The remaining syntypes (Figure 4) become paralectotypes and have been recatalogued as ANSP 426010.

Additional specimens of living *Cerion tridentatum costellata* and *C. sculptum marielinum* sampled from Garden Key on May 3, 1947, are represented in the collections of the National Museum of Natural History (USNM 487438). A survey of Garden Key by the senior author in July 2006 revealed numerous dead *Cerion* on the parapets of Fort Jefferson, but no living *Cerion* were found anywhere on Garden Key.

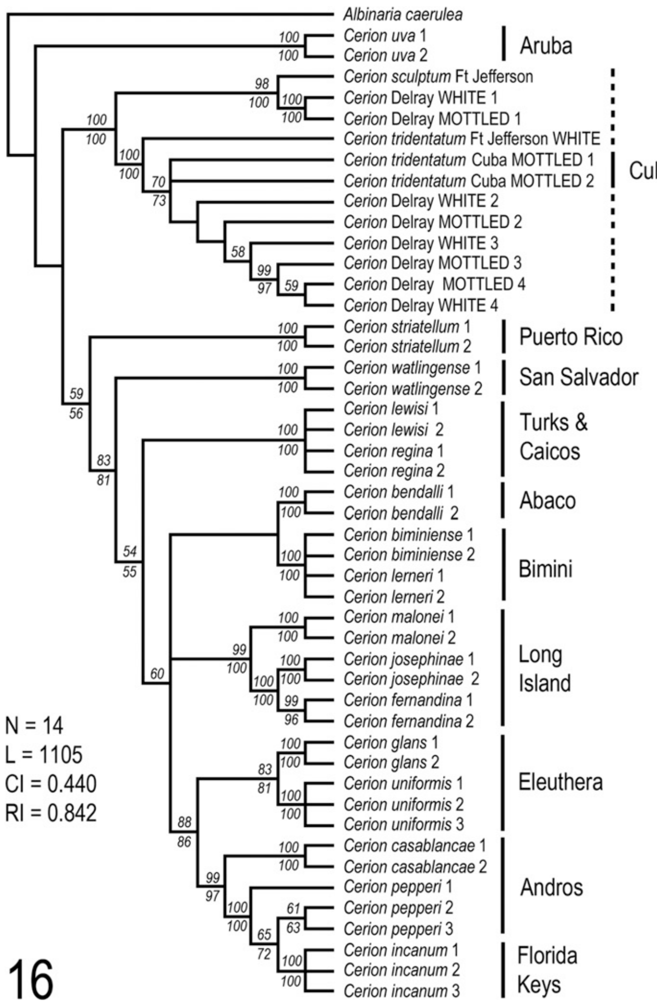
The collections of the Academy of Natural Sciences contain a lot (ANSP 192703) of several specimens corresponding to *Cerion tridentatum costellata* collected by Pilsbry in 1954. The label, hand written by Pilsbry, identifies the specimens only as *Cerion*, but states that they are from Boynton Beach, Florida, "from the McGinty lawn, April, 1954. Imported from Andros + the Keys 5 or 6 years before." The "McGinty lawn", on Old Ocean Boulevard in Boynton Beach, was roughly 3 kilometers north of the Delray Beach population of *Cerion* (Harasewych and Strauss, 2006: 94).

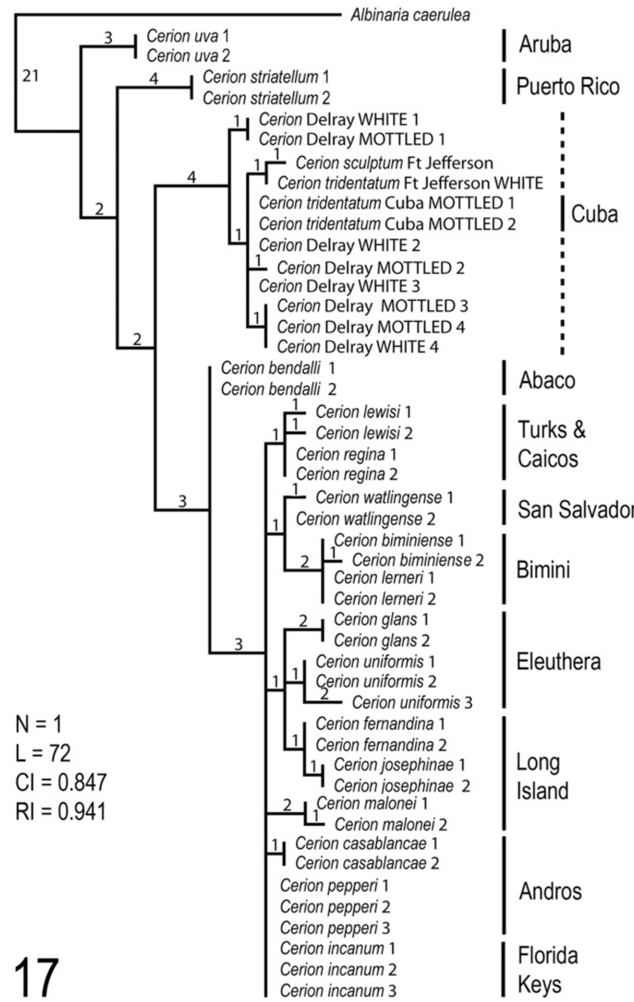
The phenotype *Cerion tridentatum costellata*, which presently inhabits Delray Beach, traces its origin to Fort Jefferson, on Garden Key, and may be a hybrid of two or more of five Cuban taxa introduced there by Bartsch in 1924: *Cerion tridentatum*, *Cerion mumia* (identity questioned by Pilsbry), *Cerion chrysalis* (revised by Pilsbry to *C.chrysalis fastigatum*), *Cerion sculptum* (revised by Pilsbry to *C. sculptum marielinum*), and an undescribed taxon of *Cerion* similar to *C. johnsoni*. There are conflicting reports as to whether the Puerto Rican *Cerion striatellus* was among the species that were introduced to Fort Jefferson, and may have thus contributed to the genotype.

During the 1940s, propagules of *Cerion* from "the Florida Keys and Andros" Island in the Bahamas were introduced to the McGinty's lawn. While it seems certain that a sample of *Cerion* from Fort Jefferson was among those introduced to Boynton Beach, it is less clear how many, if any, of the four native and 13 introduced species from the Florida Keys (Harasewych and Strauss, 2006: Table 1) or the 26 named species from Andros Island (see Harasewych, 2009) were also introduced to Boynton Beach, and thus may have contributed to subsequent hybridizations.

Evidence From Partial Cytochrome c Oxidase I Sequences: The strict consensus of six most parsimonious trees based on maximum parsimony analyses of a 655 bp segment of the cytochrome c oxidase I gene (Figure 16) groups individuals from the same taxon, as well as taxa inhabiting the same island (e.g., Long Island, Eleuthera) or island group (e.g., Bimini Islands, Turks and Caicos Islands) with a high level of support.

All Delray specimens, both mottled and white, emerged in a single, highly supported clade that also included two Cuban specimens of *Cerion tridentatum* (Figures 12, 13) from the same 1924 sample as the 500 individuals of this species that were introduced to Fort Jefferson, as well as a specimen of *C. tridentatum*





Figures 16–17. Relationships of the Delray Beach population of *Cerion*, based on maximum parsimony analyses of a 665 bp segment of the cytochrome c oxidase I gene (CO I) using representative taxa spanning the geographic range of the genus. **16.** Strict consensus of 6 most parsimonious trees, bootstrap proportions given in % above, and jackknife proportions given in % below nodes supported at levels above 50%. **17.** Single most parsimonious tree based on amino acid sequences translated using the *Drosophila* mtDNA (extended) genetic code.

costellata (Figure 14) and of *Cerion sculptum marielinum* (Figure 15) that were collected on Garden Key in 1947. This clade is comprised of two subclades, each also highly supported. One includes the specimen of *Cerion sculptum marielinum* and two Delray specimens, one white, the other mottled. The other subclade includes the two 1924 specimens of *Cerion tridentatum*, the 1947 specimen of *C. tridentatum costellata*, and the remaining six Delray specimens, three white and three mottled. These data indicate that both *C. tridentatum* and *C. sculptum marielinum* have contributed to the genotype of *C. tridentatum costallata* at Fort Jefferson, and that traces of both parent taxa persist in the mitochondrial genomes of the Delray Beach population in a 3:1 ratio after more than 60 years. As none of the Delray specimens (n = 8) appeared elsewhere in the tree, there is no evidence to indicate that other Floridian or Andros Island taxa have contributed to, or persist in, the genotype of the Delray Beach population. However, a substantially larger sample size, and data from nuclear genes would be needed to rule out the presence of rare alleles from other taxa.

The nucleotide sequences were translated to amino acids, and the maximum parsimony analysis repeated, resulting in a single most parsimonious tree (Figure 17).

Neither individuals of the same taxon, nor taxa inhabiting the same island or island group, were well resolved. However, coarser patterns were detected. Amino acid sequence data were sufficient to segregate taxa inhabiting each of the following island groups: Dutch Leeward Islands, Puerto Rico, Cuba, Little Bahama Bank, and Grand Bahama Bank, with San Salvador and Turks and Caicos Islands grouping with the Grand Bahama Bank.

As with the nucleotide sequence data, all Delray specimens emerged in a single, highly supported clade that also included the Cuban *C. tridentatum* and the two Fort Jefferson specimens. These results support an exclusively Cuban ancestry for all specimens in the clade. This clade was subdivided into two weakly supported subclades identical in composition to those based on nucleotide data, except that the two specimens from Fort Jefferson (*C. tridentatum costellata* and *C. sculptum*) were grouped together within the large clade. These two specimens shared a single tyrosine (TAT) to serine (TCG) substitution not present in any other *Cerion* studied.

It is interesting to note that *Cerion incanum* (Binney, 1851), from the Florida Keys, consistently grouped with the samples from Andros Island, Bahamas in both analyses, contradicting early hypotheses of a Cuban origin for this species (e.g., Binney, 1851: 153; Pilsbry, 1902: 213; 1907: 193; 1946: 162; Dall, 1905: 30).

DISCUSSION

The transplantation experiments conducted by Bartsch in the early 20th Century and subsequent, less well-documented intentional introductions by others (e.g., Krieger and Austin, 1975), are anathema to modern conservation biologists. Nevertheless, the survivors of Bartsch's diligently recorded experiments provide insights into the processes by which many of the numerous phenotypes within the genus *Cerion* (> 600 named species level taxa) may have arisen, and how they persist through time.

The original objective for the transplantations of propagules of *Cerion* from Andros Island to a number of the Florida Keys was to determine if their morphology would be altered over several generations by exposure to different environments (Bartsch, 1913). Years of careful measurement and segregation of multiple generations of progeny revealed that their morphology remained unaffected by habitat (Bartsch, 1920; Woodruff and Gould, 1987: 1023). However, in two instances the Andros Island *Cerion* hybridized with the native *Cerion incanum* to produce phenotypes that differed markedly from either parent species. This led Bartsch to redirect subsequent experiments to the production of hybrids. The majority of these efforts were focused on controlled, pairwise combinations of species (e.g., Bartsch, 1923a, 1924b), but some, such as those conducted on the parapets of Fort Jefferson, were simply the comingling of multiple species (Bartsch, 1924b).

The hypothesis that hurricanes play an important role in dispersing propagules of *Cerion* among neighboring islands has been widely accepted (e.g., Pilsbry, 1907; Mayr and Rosen, 1956; Clench, 1957). These infrequent, stochastic events are major factors determining biogeographic patterns within *Cerion*, and must have contributed to populating the Florida Keys and the islands of the Bahamas that had been completely submerged during Pleistocene interglacial high stands (Hearty et al., 1999). Subsequent introductions of propagules into the range of established populations of *Cerion* result in the formation of narrow hybrid zones in which the phenotypic variation exceeds that of either parent (Gould and Woodruff, 1986: 435–440), and that are characterized by the presence of unexpected alleles (hybrizymes) that do not occur in either parent taxon (Woodruff, 1989).

Gould and Woodruff (1990:78) showed that, whether the product of hurricane transport or human activity, such hybrid zones produce distinctive populations with sharply demarcated boundaries and are the results of "happenstances of history rather than forces of local adaptation." Such area effects are generally ephemeral, with both the genotype and phenotype of the hybrid subsumed into that of the numerically dominant parent taxon over time. Goodfriend and Gould (1996) documented that phenotypic traits in hybrid zones may persist for periods on the order of thousands to tens of thousands of years.

Very few of Bartsch's introductions survive to this day. The propagule of 500 adult *Cerion casablancae* introduced to Indian Key on June 1, 1912 (Bartsch, 1913: 130) has proliferated, and, in the continued absence of the native *Cerion incanum*, remains unchanged in its morphology, and presumably its genotype. On Bahia Honda Key, a surviving propagule of 55 *Cerion casablancae* hybridized with *Cerion incanum*, which reappeared on that Key between 1926 and 1931. The resulting hybrid phenotype and genotype continue to be assimilated into those of *C. incanum*. Based on allozyme studies, Woodruff and Gould (1987: 1040) calculated that "we may be unable to detect *C. casablancae* genes on Bahia Honda Key 350 years from now."

While these examples of Bartsch's transplantations can be expected to endure fates similar to those of hurricane introduced propagules, finding a parallel in nature for the Delray Beach colony is more difficult. Five Cuban taxa were introduced simultaneously into a small isolated area on the parapets of Fort Jefferson in June of 1924. The taxon *Cerion tridentatum costellata* was described based on specimens collected in 1941. This phenotype, not present in any of the five introduced Cuban taxa, was produced in 17 years, roughly 3–5 generations, based on estimates of a generation time of 4–5 years (Woodruff, 1978: 229). A propagule from Fort Jefferson of unknown size and composition (Pilsbry [1946] reported that *C. chrysalis fastigatum*, *C. sculptum marielinum*, *Cerion tridentatum* [rare] and *Cerion tridentatum costellata* were all present on Fort Jefferson in 1941) was introduced to the "McGinty lawn" in Boynton Beach in the late 1940s, and possibly admixed with one or more propagules of other *Cerion* from Florida and/ or Andros Island. After 60 + years, this population has expanded geographically, and is estimated to exceed 10^5 individuals. Specimens are fairly uniform in morphology (Figures 1, 2; Harasewych and Strauss, 2006: figs. 1–8), with the exception that some are white and others are mottled. Limited genetic sampling (n = 8) indicates the presence of mitochondrial genes from two (*C. tridentatum* and *C. sculptum marielinum*) of the five species originally introduced onto the parapets at Fort Jefferson in a 3:1 ratio that does not correlate with the presence of mottling. The possibility of as yet undetected rare alleles from other taxa cannot be ruled out. The Delray Beach colony of *Cerion tridentatum costellata* is more than 100 km distant from the nearest neighboring population of *Cerion*. Thus, this "happenstance of history" has placed a newly formed hybrid propagule in an area far removed from either parent population. Rather than being subsumed, it will continue to evolve in isolation for the foreseeable future and provides a unique opportunity to study the origins and persistence of genetic diversity within the genus *Cerion*.

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