

**PROCEEDINGS OF THE
EIGHTH SYMPOSIUM
ON THE GEOLOGY
OF THE BAHAMAS AND
OTHER CARBONATE REGIONS**

Edited by
James L. Carew

Production Editors
Daniel R. Suchy
Nicole G. Suchy

**Bahamian Field Station, Ltd.
San Salvador, Bahamas
1997**

Front Cover: View to the SSE on White Cay in Grahams Harbour off the north coast of San Salvador, Bahamas. At this spectacularly scenic site one can see that marine erosion has removed the entire windward portion of these early Holocene eolianites (North Point Member, with an alocchem age of ~5000 radiocarbon years B.P.) that were deposited when sea level was at least 2 meters below its present position.

Back Cover: Stephen Jay Gould, keynote speaker for this symposium, holds a *Cerion rodregoi* at the Chicago Herald Tribune's 1891 monument to the landfall of Christopher Columbus, which is located on the windward coast of Crab Cay on the eastern side of San Salvador Island, Bahamas. The monument consists of an obelisk constructed from local limestone which houses a carved rock sphere depicting the globe with the continents. The inscription carved in a marble slab, reads: "On this spot, Christopher Columbus first set foot upon the soil of the New World."

© Copyright 1997 by Bahamian Field Station, Ltd.

All Rights Reserved

No part of this publication may be reproduced or transmitted in any form or by any means, electronic or mechanical, including photocopy, recording, or any information storage and retrieval system, without permission in written form.

Printed in USA by Don Heuer

ISBN 0-935909-63-X

THE TAXONOMY AND GEOGRAPHIC VARIATION OF *CERION* ON SAN SALVADOR (BAHAMA ISLANDS)

Stephen Jay Gould
Museum of Comparative Zoology
Harvard University
Cambridge, MA 02138

ABSTRACT

The complex geographic distribution of variation in the protean land snail *Cerion* had long been viewed as incoherent and without sensible pattern. But field work on all major Bahamian islands, combined with morphometric and genetic studies of collected specimens with known geographic and ecologic positions, has led to a recognition of sensible order correlated with locations and histories of sea level. Application of these rules to the highly confusing variation of *Cerion* on San Salvador leads to a resolution based on the island's peculiarities of isolation and stable size and habitats during ice-age eustatic fluctuations, and the island's position right between the two major geographic domains of Bahamian *Cerion*. Two species of *Cerion* inhabit San Salvador today: the conventional ribby morphotype of the northern Bahamas, called *C. wallingense* on San Salvador and the only taxon heretofore named; and the (herein) newly designated *Cerion rodrigo*, for populations of the southeastern Bahamian triangular morphotype. Each species lives in its characteristic habitats and varies with geography and habitat in its usual ways. The two species also hybridize extensively, more so than on most islands, given San Salvador's long stability, isolation from invasion, and lack of geographic barriers separating the habitats of the two species. Both species are well represented in the Pleistocene fossil record, often in the same places and indistinguishable in form from modern populations -- another example of unprecedented stability in the history of San Salvador *Cerion*.

THE BACKGROUND OF BAHAMIAN *CERION*

The recent history of land snails on

oceanic islands has provided some of the most famous evolutionary studies of our literature (Gulick, 1905 on the Hawaiian achatinellids; Crampton, 1917. 1932 on *Partula* from Tahiti and adjacent islands) -- and these themes have been further developed in modern investigations (Murray and Clarke, 1980 on *Partula*; Gould, 1969 on Bermudian *Poecilozonites*; Gould and Woodruff, 1978, 1986, on Bahamian *Cerion*). This concentration of attention is no mystery, for the conjunction of such a variable and rapidly evolving group (land snails) with the most noted locale for fast and extensive phyletic change (oceanic islands) provides a combination of maximal interest for biologists.

The West Indian land snail *Cerion*, with centers of diversity in Cuba and the Bahama Islands (Figure 1), and with outlying populations in the Florida Keys (northwest), Virgin Islands (east) and Curaçao, Aruba and Bonaire (south), is unmatched for diversity of shell form among the world's pulmonate genera. Ranging in size of the adult shell from 7 to 71 mm (Gould, 1984), and in shape from pencils to golf balls to virtual cubes (Gould, 1992), *Cerion* has been divided into hundreds of species by overenthusiastic naturalists (see especially Maynard, 1889). Most of the names do not mark true biological species, but rather identify recognizable populations within the range of geographic variation for such protean taxa. Nonetheless, the previous designation of so many species does record a primary reality about the biology of this fascinating genus: variability in shell form is so great, and geographic patterns in variation so regular and predictable, that each local population develops and maintains a recognizable form. Earlier biologists misconstrued such populations as true species, but these scientists were correct in noting the distinctiveness of each local form. (Interestingly, despite the

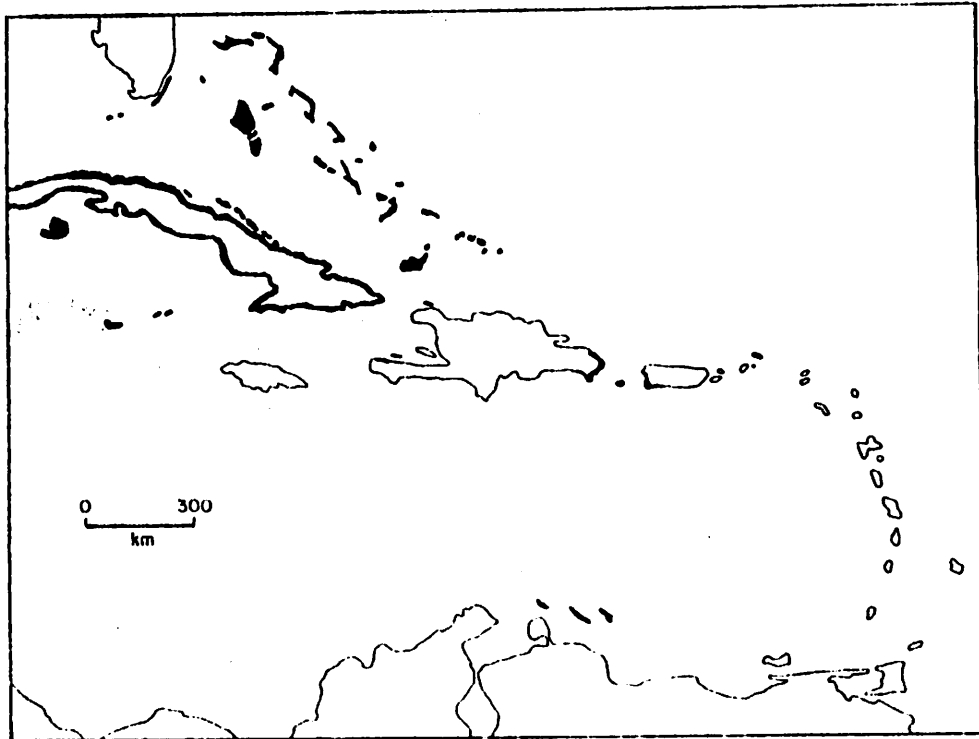


Figure 1: The geographic distribution of the genus *Cerion* in the West Indies. from Woodruff and Gould, 1980.

great differences in average shell form among local populations, the variation for individual shells within any local population tends to be restricted and quite unremarkable -- another feature of *Cerion* that enhances the uniqueness of each local population.)

Older studies of Bahamian *Cerion* tended to work by "hit or miss" collecting -- that is, one landed a boat in a few accessible places, sampled the local population; and, then, in the absence of any feel for patterns of continuous variation across long stretches of coastline, named each distinctive sample as a new species. This technique gave rise to the old consensus that *Cerion*'s geographic variation could be represented as a "crazy quilt" of purely local distinctions, with no sensible match to environments and no continuity of transformation along geographic gradients (see Clench, 1957). This conclusion further suggested a controlling cause for the absence of spatial pattern -- that most *Cerion* populations had been founded by specimens adventitiously transported by hurricanes or some other rarely acting and effectively

random mode of transport.

However, following some hints in earlier literature (particularly Plate, 1907), and a pioneering study based on denser collecting and more contemporary theory (Mayr and Rosen, 1956), S.J. Gould and D.S. Woodruff have devoted 20 years of field work and laboratory study to reassessing the patterns of geographic and temporal variation in Bahamian *Cerion*. By walking out the complete ranges of taxa on nearly all major islands (*Cerion*'s distribution is effectively coastal and therefore basically linear, although interior populations often exist, particularly on islands with little topographic relief), we have reversed the older consensus and documented almost invariably recurring patterns of sensible geographic variation on all Bahamian islands (see Gould and Woodruff, 1978, 1986, 1987, 1990 and earlier references cited therein). We have proceeded by applying both morphometric and genetic analysis to specimens personally collected in the field. This new conclusion provides, for the first time, an operational framework for assessing the taxonomy and

variation of *Cerion* on islands previously unstudied -- including San Salvador, one of the few substantial Bahamian islands with no previous systematic survey of *Cerion* populations in the light of this new model.

Thanks to the good offices and previous work of Drs. James Carew, John Mylroie and their colleagues, I was able to do a preliminary survey of *Cerion* on San Salvador in conjunction with the Eighth Symposium on the Geology of the Bahamas held from May 30 to June 3, 1996 at the Bahamian Field Station, San Salvador. Although this report focusses primarily on the geographic variation of living *Cerion*, the results have important implications for interpreting the excellent Pleistocene and Holocene record of fossil *Cerion* on San Salvador (where shells are common in protosols, *terra rossa* paleosols, and, to a lesser extent, in colianites of all recorded ages). *Cerion* holds special importance for any potential Bahamian biostratigraphy. Marine species evolve too slowly for any realistic hope of recognizable paleontological differences during the half million years or so of recorded Bahamian geology. But local *Cerion* faunas change substantially on this time scale -- more by extinction and migration of populations, and by hybridization, than by conventional selective transformation, but representing potentially recognizable evolution nonetheless. The paleontology of *Cerion* has provided reliable temporal guides on other Bahamian islands (Gould and Woodruff, 1990; Goodfriend and Gould, 1996 on Great Inagua; Gould, 1988, on the major islands of Great Bahama Bank; Gould and Woodruff, 1986, on the three successive faunas of New Providence Island).

THE COHERENT GEOGRAPHICAL PATTERNS OF OTHER ISLANDS, AND PREDICTIONS FOR SAN SALVADOR

In our survey of all large Bahamian islands (with the exception of Crooked-Acklins), Woodruff and I have documented two major patterns of geographic variation that conform both with modern environments and the history of sea levels on the island banks. San Salvador, lying at the junction of these two regions, and having a different

history of continual isolation with little variation in island size during eustatic fluctuations, yields some interesting novelties upon a basic pattern of conformity with regularities noted elsewhere (Figure 2).

The Northern Pattern

The basic pattern of diversity for *Cerion* on all islands of both Little and Great Bahama Bank can be understood as a contrast between two morphotypes in consistent relation to the nature of coastlines. With this basic key, Woodruff and I have been able to reduce more than 100 named species to these two predictable forms, thereby disproving the false impression of a "crazy quilt" distribution. One form -- we call it the "ribby" morphotype -- lives along coastlines that abut the bank edges; that is, along shores that have been effectively coastal throughout the glacial ages, for the full extent of eustatic fluctuation does not match the rapid falloff to oceanic depths. The other form -- we call it the "mottled" morphotype -- lives along coastlines that now abut an interior region of the larger island bank; that is, along coasts that were inland when eustatic falls of glacial ages exposed the larger banks.

Shells of the ribby morphotype tend to be wider and more robust (although both morphotypes can become strongly dwarfed, particularly in unfavorable habitats), either white or solid brown in color, ornamented with fairly strong and distinct ribs, and discordant in outline, with juvenile shells triangular in cross-section and the adult whorls parallel-sided as they add height to the shell without increasing width. By contrast, shells of the mottled morphotype tend to be narrower and thinner, strongly mottled in color with alternating patches of white and brown, either smooth or ornamented with a large number of very fine and indistinct ribs, and "barrel-shaped" or evenly changing in outline throughout growth, as the whorls continue to expand gently with no marked transition from juvenile to adult form.

We do not know whether these differences should be explained primarily as results of current adaptation, or as products of history. The "modernist" alternative holds that the stouter and ribbier bank-edge shells are

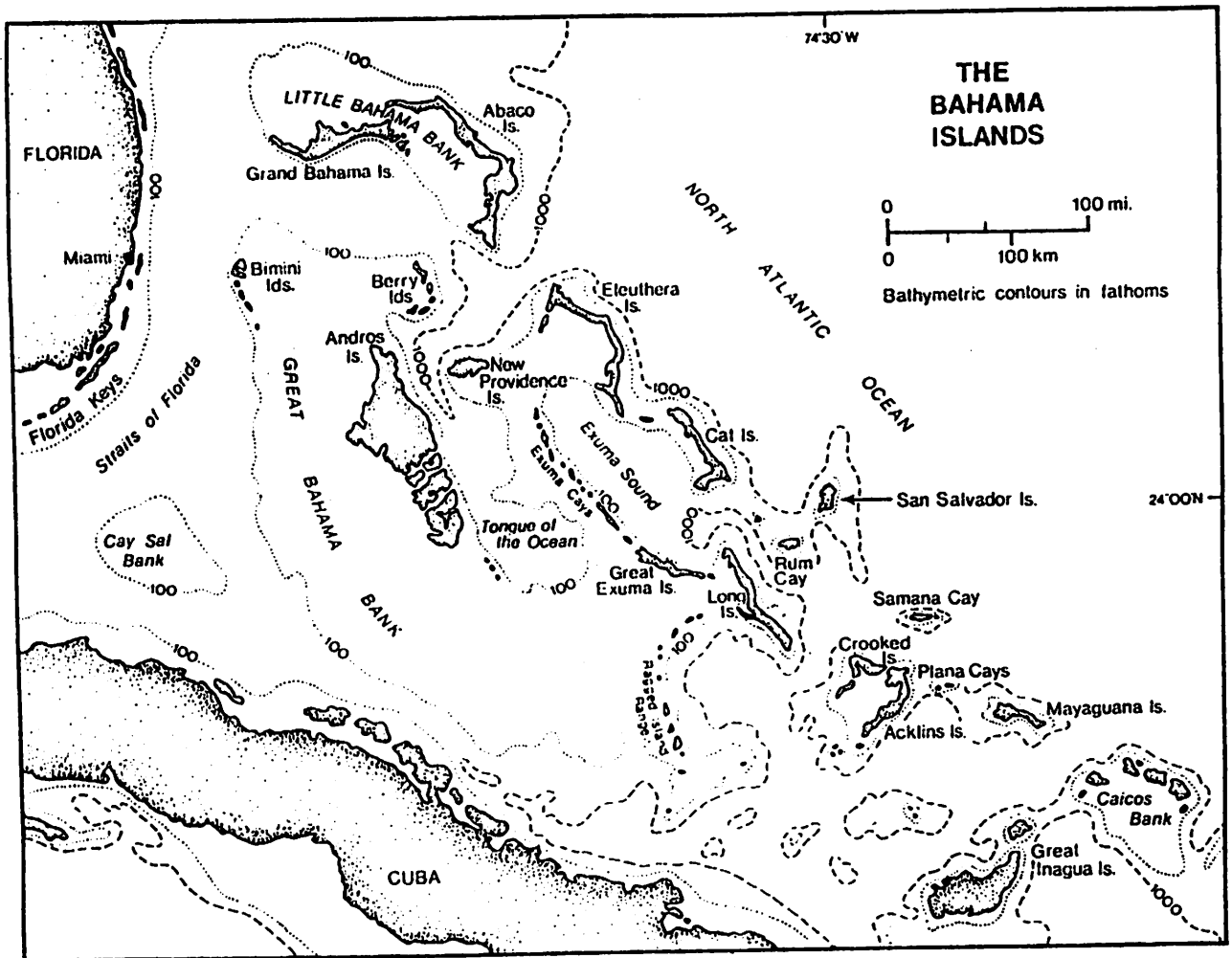


Figure 2: The Bahama Islands showing 100 and 1000 fathom contours, and the resulting degrees of isolation of islands and banks. From Curran and White, 1995.

adapted to more open, harsher environments of windward coasts (where shells often attach to low shrubs growing on windswept terraces) -- whereas the more delicate mottled shells, living in the calmer and more densely vegetated environments of bank-interior (usually leeward) coasts, do not require the protection of added weight and ribs, and may also become less conspicuous to potential predators, as the mottled color makes them difficult to see (at least to human observers) in their usual environment, where sunlight filters through a complex tangle of vegetation. On the historical alternative, mottled forms have always lived in island interiors, and ribby forms on bank-edge coasts. At eustatic minima, ribby shells surrounded the island peripheries, and mottled populations dwelled in the interior. As sea levels rose, the two

forms simply kept their positions. (The coastal populations of modern mottled shells still inhabit the former island interiors of glacial times.) Of course, these two explanations mesh well and do not contradict, for the original distinction of ribby at bank edges, and mottled on island interiors, matches the adaptive correlations still noted in present environments.

Two additional features of *Cerion*'s unique and complex biology have established our taxonomic approach to this primary distinction, and to the naming of *Cerion* species in general:

1. We do not know whether these two adaptive complexes -- the ribby and mottled morphotypes -- represent discrete and monophyletic lineages, separate since common ancestry long ago, or whether the same set of

features can arise independently, again and again, from the set of possible forms easily generated within the flexibilities of *Cerion*'s general allometric growth (Gould, 1989), and as adaptations to environments commonly encountered on nearly every Bahamian island. (This issue will ultimately be decided by comparing geographic and morphometric orderings with molecular cladograms -- but the molecular studies have not yet been done.) Pending the resolution of this issue, we have adopted the strategy of giving different names to the same morphotypes on each major bank, while using the same names for the islands of a single bank. Thus, on Little Bahama Bank, the mottled form is *Cerion bendalli*, the ribby *Cerion abacoense* (see Gould and Woodruff, 1978); whereas, on Great Bahama Bank, the mottled form is *Cerion gubernatorium*, the ribby *Cerion glans* (see Gould and Woodruff, 1986). As one tentative item of evidence favoring this solution as a potential biological reality (and not just a current expedient), preliminary study of genital anatomy indicates that both mottled and ribby forms of Little Bahama Bank share one set of features, while both mottled and ribby on Great Bahama Bank have evolved different states of the same characters -- an indication that the coordinated features of ribby and mottled shell form may arise independently on banks separated by deep waters and considerable distances. Since San Salvador occupies its own bank, we will use distinct names for the morphotypes of *Cerion* living there today.

2. In a feature that defines both the frustration and the unusual interest of *Cerion* as an evolutionary subject, *Cerion* species violate the most important criterion of distinctness and definition for their status -- for nearly any two populations will hybridize at their geographic borders. (In fact, the only clear case of recorded sympatry without extensive interbreeding occurs between a "Chihuahua" and "Great Dane" for the genus -- the dwarf *C. rehderi* and the large *C. columna* on Great Inagua.) On noting this fact, one must raise the obvious question of whether we should call these populations species at all, if they hybridize so readily wherever they meet. Should we not, despite the enormous differences in modal shell form between some adjacent populations, include all hybridizing

forms within a single, albeit remarkably variable, species?

First of all, we often do include quite different populations within a single species (note the 57 named species that we synonymized into *Cerion glans* for the New Providence ribbies -- see Gould and Woodruff, 1986). If variation is gradually and continuously graded in geographic expression, and when we find no signs of active discreteness for subregions within a spatially unbroken set of samples, then we use only a single species name, whatever the extent of morphological variation. However, we define separate species (following generally accepted procedure for populations that can produce fertile hybrids) when we find evidence for any of three situations indicating the existence of discrete and discordant sets of samples, rather than a smoothly varying unity:

1. When hybrid zones are distinct and narrow, however continuous the variation in modal form along the geographic transect: Often -- as for the well documented zone between ribby and mottled on the southeastern coast of Abaco (Gould and Woodruff, 1978), the various interactions between *C. glans* and *C. gubernatorium* on New Providence (Gould and Woodruff, 1986), and the Cuban zone analyzed by Galler and Gould (1979) -- parental forms are stable for tens of kilometers along the coast, while hybrid interactions are confined to a narrow, apparently stable, and discrete area, always less than a kilometer in length, and often only tens of meters in total extent. This pattern indicates limited interaction at the border of two different taxonomic entities.

2. When hybrid zones show an explosion of variation far in excess of that noted in any parental population -- the well known phenomenon of hybrid "release," and also an indication of the discordant merging between two different entities. This is not a common pattern in *Cerion* (where most hybrid zones do not show enhanced variation within local patches), but we have documented a remarkable case at the contact of coastal ribby with interior mottled populations on the north coast of New Providence island at the airport road (Gould and Woodruff, 1986).

3. When a genetic analysis of putative hybrid zones reveals unique alleles found in

neither parental form: Such different and restricted alleles are now generally called "hybrizymes" to honor this mode of formation. (Woodruff, in our joint work on *Cerion*, was among the original discoverers of this phenomenon, now generally recognized in many groups of organisms.) Our geographic and morphometric evidence of hybridization has been corroborated by the discovery of hybrizymes on Abaco, New Providence, and Great Inagua (see Gould and Woodruff, 1990).

We have found hybridization to be most thorough on relatively small islands that have been geographically stable for substantial time -- a situation best expressed by San Salvador among the Bahamas. In extreme cases, mixing can become so extensive that "pure" centers of distribution for discrete taxa become very hard to identify -- and the whole island may convey a first impression of one incoherent jumble of *Cerion* variation. I shall show later that this apparent situation on San Salvador can be resolved into a sensible and satisfactory order by noting an unusually high degree of mixing (but entirely in the context of standard expectations for correlation of form and geography), and then recognizing that *Cerion* populations of San Salvador have moved further in the direction of homogenization than has been possible on most Bahamian islands.

Another feature of *Cerion*'s distribution on the northern banks of the Bahama Islands becomes crucial for unravelling the fauna of San Salvador. Although the distinction and interaction of ribby and mottled morphotypes sets the basic pattern of *Cerion* throughout this region, two additional factors must also be taken into account, both relevant to the situation on San Salvador:

1. Small islands may be effectively all "edge" and no "interior" -- thus favoring the ribby morphotype in all environments and leading to exclusion of mottled populations. For example, in both the Exumas and the Abacos, small cays tend to house only ribby populations, while the two large islands (Great Abaco and Great Exuma) include extensive interiors that feature large populations of mottled *Cerion*. At its intermediate size, San Salvador could fall into either category.

2. Other taxa of *Cerion* make an

occasional entry into the northern islands. None ever becomes as extensive in geographic range as either indigenous ribby or mottled species, but these migrants can displace local species from part of their usual territory. Two morphotypes have been most successful as colonizers on several islands. First, the highly distinct subgenus *Cerion* (*Umbonis*), with its high triangular shell, prominent wavy ribs, and unique transverse shell striations, has managed to form geographically restricted but substantial populations on several islands -- for example, as *Cerion felix* on Cat Island, and *Cerion stevensoni* on Long Island (see Woodruff and Gould, 1980 for an account of the full extent of *C. (Umbonis)*, which is not found on San Salvador). Second, the characteristic morphotype of the southeastern Bahama Islands (discussion just below), has also established restricted but successful populations on several islands of the northern banks -- particularly on islands adjacent to the southeastern group. This distinctive morphotype of large, thick, generally smooth, usually entirely white shells, with a triangular cross-section and a large aperture, bears a different name on each of the distinct regions of the southeastern Bahamas -- *Cerion columna* on Great Inagua, *C. piratarum* on Mayaguana, *C. regina* on the Turks and Caicos (politically separate from the Bahamas, but part of the same region in more appropriate geographic and geological terms). On these islands, shells of this triangular morphotype dominate large regions, and may be the only living *Cerion* on several islands (as on Mayaguana).

Populations of this morphotype have become established on several islands of the northern banks, but always in small regions, and never as prominent as the indigenous ribby or mottled forms. These migrants are called *C. fernandina* on Long Island, *C. fordii* on Cat Island, and *C. eleutherae* on Eleuthera. A similar population has recently become extinct on New Providence (Gould and Woodruff, 1986). Since San Salvador, like Long and Cat (both with populations of this morphotype), lies at the boundary between the northern banks and the southeastern islands, this island also becomes a good candidate for finding populations of the southeastern morphotype. I shall document below that such

populations do, indeed, exist -- and that their location, in exactly the region anticipated, provides the key for unravelling the distribution of *Cerion* on San Salvador.

The Southeastern Pattern.

As noted above, and therefore only briefly reviewed here, the separate islands of the southeastern Bahamas -- Inagua, Mayaguana, Crooked-Acklins, Samana, Turks and Caicos -- all separated by deep waters (and therefore not subject to easy coalescence of populations during glacial times of low sea levels and general emergence), feature a quite different *Cerion* fauna. None of these islands maintains an extensive population of either the ribby or mottled morphotype (although small populations of these northern migrants may live on some of the southeastern islands -- just as the southeastern morphotype has invaded several northern islands to a limited extent). Instead, every island of the southeastern region features the same morphotype of *Cerion* as its locally dominant form -- the distinctive triangular morphotype, as defined above.

Some southeastern islands (notably, Mayaguana) contain only this morphotype of *Cerion*; other islands have been colonized by additional forms, although the triangular morphotype always ranks first or second in abundance and geographic range. On the largest island of Great Inagua, for example, the triangular morphotype, called *Cerion columna*, dominates nearly 80 km of the northern coast, whereas the southern coast and island interior features the distinct red-tipped form, *Cerion rubicundum* (while the dwarf, *Cerion (Umbois) rehderi*, occurs at lower density throughout the island, though mostly in the interior, living sympatrically with both other species in their predominantly coastal locales).

This fundamental difference -- northern banks dominated by an interaction of ribby and mottled morphotypes, each in distinctive areas, but with predictable places and styles of interaction; the southeastern islands dominated by the quite different triangular morphotype -- places San Salvador in an interesting position, both literally and conceptually. For San Salvador forms its own small and separate bank, located at the eastern

edge of the Bahama platform, but squarely in between the northern and southeastern regions with their distinct *Cerion* faunas. What should we expect for *Cerion* in such an intermediate geography -- an interesting test case, at the very least, for an interaction between the two generalities that define *Cerion*'s distribution in the Bahama Islands. And what special features might arise from the relatively small size, the isolation, the relative stability, and the lack of bank-interior coasts -- a set of distinctions that should imply important consequences for *Cerion*. In short, San Salvador becomes a lovely natural experiment for testing and extending all the generalities that we have learned about this most fascinating object of evolutionary study.

THE LIVING *CERION* FAUNA OF SAN SALVADOR

Predictions

As outlined in the last paragraph, the intersection of San Salvador's particularities with the generalities of *Cerion*'s distribution yields an array of expectations for the fauna of this crucial island. First of all, San Salvador's intermediary position between the two great Bahamian realms of *Cerion* (northern with ribby and mottled morphotypes, and southeastern with the triangular morphotype) leads us to expect representative taxa of both realms. We can also predict the probable location of these morphotypes from the map of San Salvador alone (Figure 3). The bank-edge ribby morphotype should dominate because San Salvador is a small island with no bank-interior coastlines at all. That is, the entire modern coastline lies near the edge of this independent bank. The mottled morphotype would, if present at all, therefore inhabit the island's interior. (I say "if present at all" because many small Bahamian islands, particularly the cays of the Exuma chain, are effectively "all" bank-edge coast and therefore exclude the mottled morphotype.) The triangular morphotype of the southeastern region, if present, should live on the most exposed and windward regions of bank-edge coasts, effectively displacing the ribby morphotype from this habitat (as on Long Island, where triangular *C. fernandina*

**SAN SALVADOR,
THE BAHAMAS**

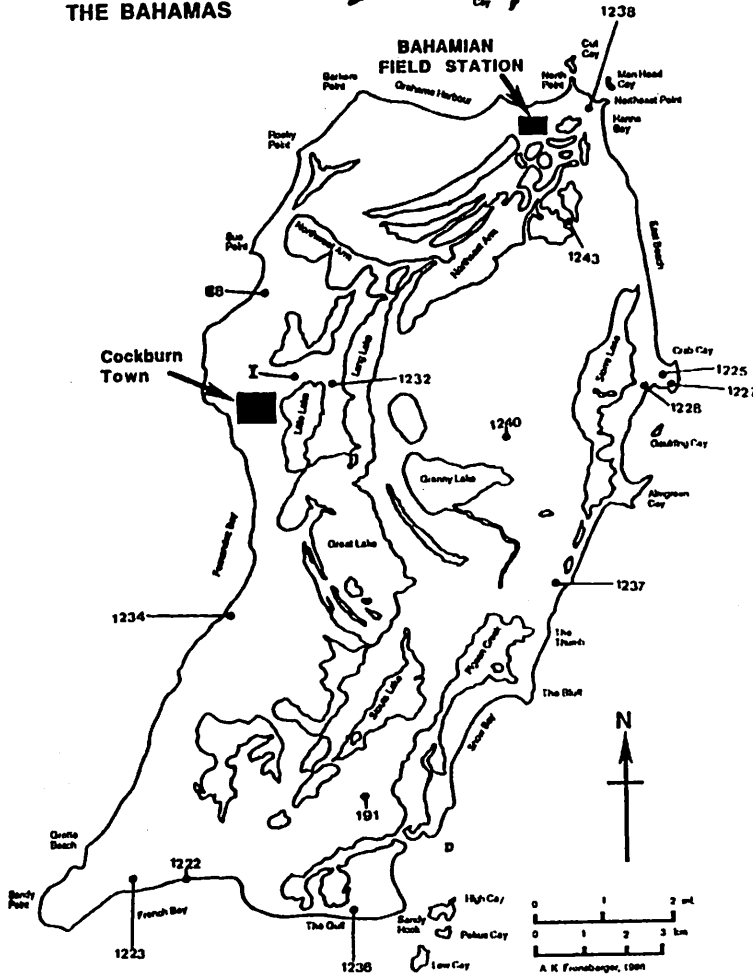


Figure 3: Outline map of San Salvador, showing all places, and all *Cerion* localities, mentioned in the text of this article.

supplants ribby *C. glans* on part of the windward east coast; and on Great Inagua where triangular *C. columna* occupies the more rocky and windward northern coast, while *C. rubicundum* dominates the lower and more leeward southern coast).

Previous Work

Only one study has ever been published on the formal taxonomy of *Cerion* from San Salvador. In 1905, the great malacologist William H. Dall began an article on Bahamian land and fresh water snails both by citing the

great opportunity offered by such creatures for evolutionary study and by apologizing for the cursory collecting (by others) that had provided his material. Dall wrote (1905, pp. 433-434): "So far, little advantage has been taken of these opportunities and the work which has been done... has been chiefly hurried collecting at as many localities as possible, rather than the patient study of conditions and results, exhaustively applied to any single locality."

Dall proposed three taxa, based on little or no geographic data, for the *Cerion* of San Salvador. He designated, as the type of *Cerion wallingense*, a shell that could not be a more typical representative of the ribby morphotype (Dall, 1905, Plate 58, Figure 7) -- and of a large size indicating probable location at the north or south ends of the western coast (Dall provided no locality information). Dall then identified, as *Cerion inconspicuum* (and also without locality information), a smaller and lighter shell of the ribby morphotype, probably either from the middle portion of the western coast or from the island's interior (as modern patterns of variation in size imply -- see next section). Finally, Dall named a subspecies of this second taxon as *Cerion inconspicuum lacunorum*, this time citing a locality as "on the shores of the lagoon" (1905, p. 439). This interior shell is larger and heavier than *C. inconspicuum*, but not so strong or ribby as *C. wallingense*.

We may, I think, be confident that Dall's three taxa only represent variants within the single ribby morphotype, and therefore all belong to the same species, which must bear Dall's first cited name, *Cerion wallingense*. The variation in size and form among Dall's three taxa falls well within the range of ribby populations on San Salvador today (see next section). Therefore, only one morphotype (and one species) has ever been formally named on San Salvador. Do either of the other anticipated morphotypes also inhabit this island (mottled of the northern region and triangular of the southeastern region)? Did Dall's cursory collectors miss these taxa, or is San Salvador truly a one-species island?

Morphology and Geographic Variation of *Cerion's* Two Species on San Salvador

Variation within *Cerion wallingense*, the ribby morphotype

Cerion populations are nearly ubiquitous on San Salvador, at high density in nearly all coastal areas, and at much lower densities, but still locally abundant, in the island's interior. Most populations clearly belong to the island's most prominent species, the ribby morphotype named *Cerion wallingense* by Dall in 1905.

In May, 1996, I spent several days collecting *Cerion* samples throughout the island (with special thanks to James L. Carew and John Mylroie for advice, local arrangements, geological expertise, and for collections from localities I was not able to visit, and to Sally Walker and Kem Fronabarger for helping with the field work). I combined these samples with others collected over the years and given to me -- by Daniel Fisher in 1970, Richard Allen in 1978, and Donald T. Gerace in the 1980's (and provided to me by Jane Rose). I also benefited greatly from the biometric studies of Fronabarger *et al.* (this volume) displayed at the 1996 conference as a poster accompanied by several small collections of specimens. His results, while differently expressed as continuous variation along mathematical axes, are in perfect accord with the conclusions reached here. I therefore believe that I have collected or seen samples from all major populations on the island.

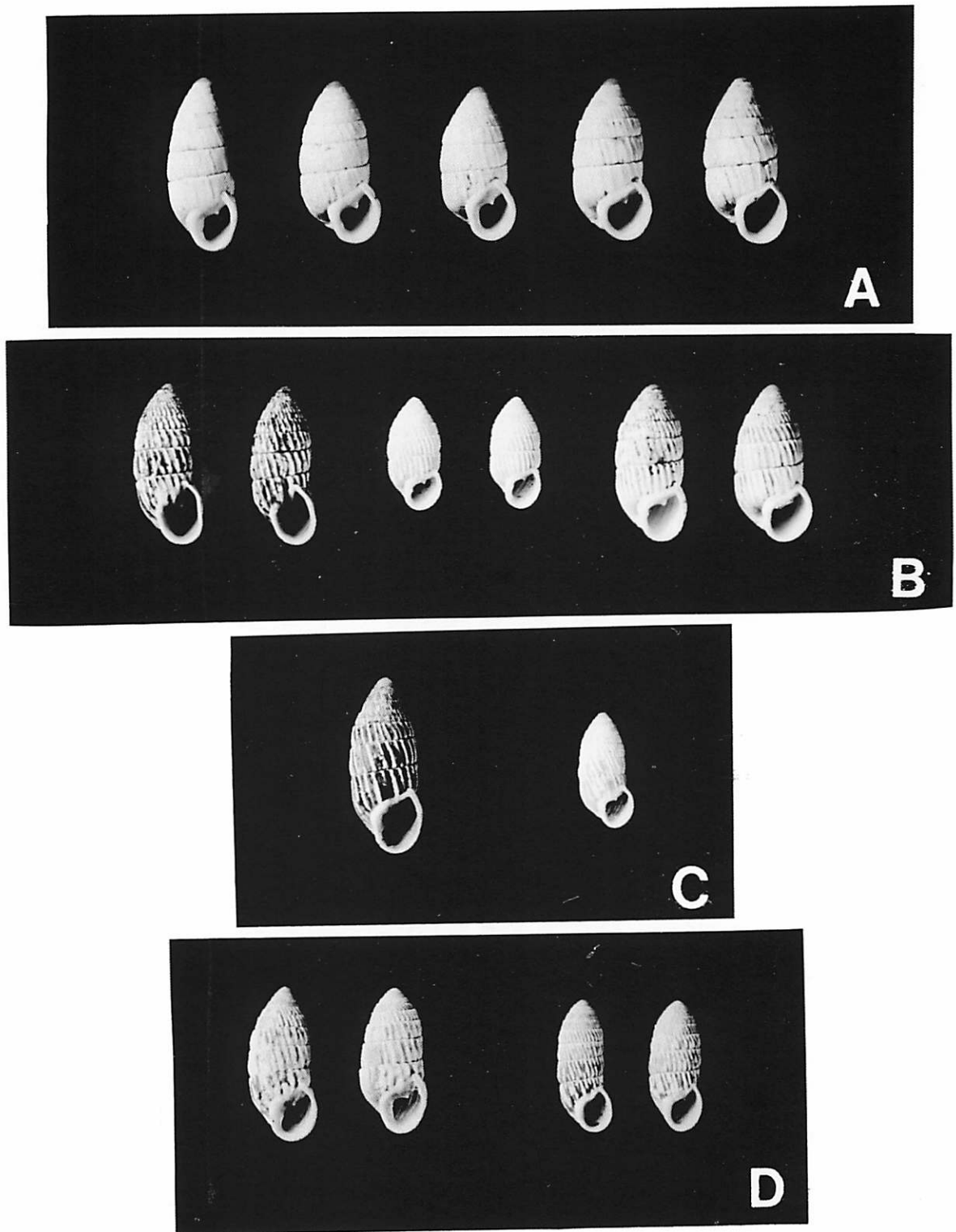
As a primary and immensely satisfying result, *C. wallingense*, although highly variable (as usually noted for the ribby morphotype), presents an entirely coherent pattern (rather than a haphazard hodgepodge) based on continuous gradation, and with characteristic forms in expected regions. All our previous studies on variation within the ribby morphotype indicate two primary patterns -- (1) larger and ribbier shells on more rocky and windward coasts, with smaller and finer ribbed shells on lower and calmer coasts; and (2) a general decrease in shell size, thickness and ribbiness in interior as opposed to coastal localities. Both patterns clearly exist on San Salvador, defining the primary variation within *C. wallingense*. Moreover, continuous gradients in shell morphology connect

endpoints of the patterns along geographic transects -- as I observed and as Fronabarger found in his biometric work -- thus establishing both the sensibility and stability of phenotypic variation in *C. wallingense*.

Plate 1, Figure B (all shells are photographed at their actual size) shows the coastal variation. Shells are smallest along the calm, low and leeward central portion of the island's western coast -- the probable first landing site of Christopher Columbus (who may well have seen a *Cerion* as his first New World land animal -- see Gould, 1996). The middle pair of shells comes from Long Bay, right at the Columbus monument, marking his probable landing site -- my locality 1234. (All locality numbers are marked on Figure 3. I have kept a running tally of Bahamian localities for all my work over twenty years. High numbers in the 1200's represent collections made in 1996; the much lower numbers refer to Fisher's earlier collections.)

From this predicted minimal size on the calmest and most leeward section of coastline, *C. wallingense* becomes larger and more robust as we proceed both north and south from this minimum. The largest shells come from populations along the windier and rockier northern and southern coasts -- the southern coast at French Bay (site 1222) for the left pair in Plate 1, Figure B; and the northern coast at Northeast Point (site 1238) for the right pair of shells in the same Figure B of Plate 1. (This right hand pair probably shows some hybrid influence with the second *Cerion* species, described in the next section.)

The similar gradation from larger and more robust coastal shells to thinner and finer ribbed interior specimens is shown in Figure D, Plate 1 -- contrasting the left pair of coastal shells from Bonefish Bay (labelled BB on Figure 3, and collected by Richard Allen and not therefore in my numbered list of localities) with the narrow and finer-ribbed right pair of shells from the island's interior east of the airport (labelled I on Figure 3, and also from Allen's collection). Finally, I show the maximal difference in size between coastal and interior samples in Figure C of Plate 1 -- contrasting a large shell from the eastern coast at 1237 with a small and delicate shell from interior sample 1232, collected even further east from the airport.



*Plate I: Variation in modern Cerion on San Salvador (see text for details of localities and varieties; all photos show shells at their actual size). A represents variation at the type locality of the new species, *Cerion rodrigoii*; B is coastal variation in size for *C. watlingense*; C shows largest and smallest forms of *C. watlingense* coastal and interior; D contrasts more robust coastal, with more delicate interior, populations of *C. watlingense*.*

This variation, covering most of the island, raises the obvious question of the status of the second northern form, the mottled morphotype. This issue cannot yet be settled, for two possibilities are consistent with current observations. I found no "pure" populations of the mottled morphotype -- that is, effectively ribless, narrow and strongly mottled shells. This might mean that the mottled species does not inhabit San Salvador -- a conclusion consistent with the island's relatively small size and absence of bank-interior coastlines (the favored habitat of the mottled morphotype).

However, San Salvador is surely large enough to support the mottled morphotype at interior localities (one taxon islands of the ribby morphotype are usually much smaller than San Salvador). Some interior populations -- with the right pair of shells on Figure D, Plate 1 as a primary example -- display several key features of the mottled morphotype, particularly the small size and relatively narrow shell with a continuous, barrel-shaped outline in cross-section. But even these shells remain fairly ribby (though finer than in coastal samples), and therefore may be expressing a common extreme of variation within the ribby morphotype.

Two interpretive possibilities therefore exist: either (1) the interior samples all belong to the ribby morphotype at one predictable extreme of its variation; or (2) interior samples represent the greatest expression of influence for the mottled morphotype, which does not exist in "pure" form on San Salvador, but has hybridized extensively with ribby *C. wallingense* throughout its interior range of habitation. Since the two species do hybridize readily (see Gould and Woodruff, 1978 and 1986), and since hybridization reaches maximal extent on relatively small islands without clear geographic barriers between characteristic habitats of the two species, this second possibility may well hold. However, and tentatively (pending a resolution that may require molecular phylogenetic analysis), I will adopt the more conservative first solution and recognize all northern-derived populations on San Salvador as members of the ribby morphotype, *Cerion wallingense*.

Cerion rodrigo -- A new species representing the southeastern triangular morphotype.

Despite the foregoing tentative decision not to recognize a separate taxon for the mottled morphotype, I do not think that all the *Cerion* populations of San Salvador belong to a single species. San Salvador lies adjacent to the southeastern islands with their characteristic species of the triangular morphotype. These more robust, thicker, white, ribless or very finely ribbed shells invariably live on the most exposed windward coasts of all islands that include this morphotype among two or more *Cerion* species. If the triangular morphotype inhabits San Salvador, it should therefore be found on the projecting headlands of the exposed and windward eastern coast -- particularly on Crab Cay and Almgreen Cay (see Figure 3), not true islands, but called cays for their projecting, nearly peninsular status.

I was delighted to find effectively pure triangular populations of *Cerion* in these two places -- see Figure A, Plate 1 for a sample from the top of the windswept terrace of Crab Cay, locality 1225, adjacent to the Columbus monument erected by the Chicago Herald in 1891 to mark a possible site for Columbus's landing -- almost surely incorrect, for no harbor exists here, and the good admiral would not have attempted a landing on a rocky, windward coast. Such "pure" populations live only in these most auspicious places for the triangular morphotype. Proceeding both north and south from the region between Crab and Almgreen Cay, the triangular morphotype hybridizes with populations of the ubiquitous ribby morphotype, *C. wallingense*. The influence of the triangular morphotype may also be traced into eastern interior regions, where the basic form can still be detected in populations hybridized with *C. wallingense* at locality 1240, well east of Storrs Lake.

The patterns of hybridization between this new triangular form and *C. wallingense* are complex, especially along the eastern coastline, and I have not yet traced the details. But the presence of large, prosperous, and effectively pure populations in the expected areas on Crab and Almgreen Cays requires the formal naming of a new species for the triangular morphotype on San Salvador. (In so doing I follow our standard procedure of using

different species names for the basic morphotypes on each separated and isolated Bahamian Bank.) The formal description appears below:

Cerion rodrigo sp. nov.

Cerion rodrigo is the first member found on San Salvador of the characteristic *Cerion* species complex of the southeastern Bahamian islands -- the "triangular" or "tapering" morphotype of Gould and Woodruff (1987, 1990, characterized by a smooth and thick white shell with a triangular outline in cross-section because the later adult whorls continue to increase in width (rather than stabilizing or constricting to produce the barrel shape so characteristic of other *Cerion* taxa).

Cerion rodrigo is the largest of San Salvador *Cerion*. At the type locality (1225 of Figure 3), ten randomly chosen specimens yield a mean shell height of 26.02 mm, a mean width of 11.64 mm, and grow an average (to the nearest 1/8 whorl) of 7 1/2 postprotoconch whorls. (By contrast, shells at Dall's type locality for *C. wailingense* range from 22-25 mm in height.) These ten shells range from 24.6-28.4 mm in height, from 11.0 to 12.1 mm in width, and grow from 6 7/8 to 8 1/8 postprotoconch whorls.

Cerion rodrigo has a translucent protoconch followed by one or two finely ribbed juvenile whorls showing mottled coloring on part of the first whorl, after which the shell becomes entirely white and uncolored for the rest of growth. The shell, as is typical for this morphotype, is white, thick, and triangular in cross-section; the aperture is strongly recurved but only modestly thickened. The adult whorls vary in expression of ribs from entirely smooth and ribless, through occasional and erratically spaced ribs, to a few individuals with weak but persistent ribbing, though always widely spaced in the paucicostate pattern noted in other species of the morphotype (as on Eleuthera -- see Gould, 1988).

Geographic distribution: On the most exposed and rocky windward coasts of the eastern shore of San Salvador. Pure populations have been found only on Crab and Almgreen Cays. Populations hybridized with *C. wailingense* occur both to the north and south along the coast and westward into the island's interior.

Derivatio nominis: The type locality, on the windswept summit of Crab Cay, lies right next to the Columbus monument erected by the *Chicago Herald* in 1891. Although Columbus surely didn't land on this windward and rocky coast, his ships first spotted the New World on the early morning of October 12, 1492. Probably, the ships then lay east of the island, and the first sight of land may well have been (according to Morison and others) the reflection of moonlight off the rocky headlands of the highest points on the eastern coast. If so, then Crab Cay is an excellent candidate for the first bit of the New World spotted by Columbus's men. I therefore name this species of *Cerion* for Rodrigo de Triana, the watchman of the Pinta who first saw land and shouted the cry of "Tierra" on that fateful night. This sailor received little or none of the promised reward, and this posthumous trophy of a snail's name must be cold comfort, while still seeming appropriate.

Holotype (central specimen of Figure A, Plate 1, actual size. The topotype specimens to the left show variation towards greater height and smoothness of shell; and to the right towards greater squatness and ribbiness. These five specimens provide a good idea of the total range). Department of Invertebrate Paleontology, Museum of Comparative Zoology, Harvard University, Locality number 1225 of Gould and Woodruff, on the windswept terrace of Crab Cay adjacent to the Columbus monument. Height of holotype, 25.2 mm; width, 11.5 mm; 7 3/8 postprotoconch whorls.

Summary statement

I have recognized two species of *Cerion* on San Salvador. Dall's *C. wailingense*, the only name previously available for *Cerion* from this island, applies to the characteristic form of the ribby morphotype, found as expected along the bank-edge coasts and more sparsely over the island's interior. I found no pure samples of the mottled morphotype, a potential resident of interior areas. Either the mottled morphotype has so extensively hybridized with *C. wailingense* that well-defined populations no longer exist, or the mottled morphotype never inhabited San Salvador (or died out long ago), and the large range of variation in *C. wailingense* includes some populations

(particularly from interior areas) with strong resemblance to some key features of mottled shells. However, the large, ribless (or sparsely ribbed), entirely white and triangular shells, living on the most exposed parts of the windward eastern coast (Crab and Almgreen Cays), do belong to a second species representing the triangular morphotype of the southeastern islands. I have designated this new species as *Cerion rodrigo*.

Unlike most other Bahamian Islands, which vary extensively in size and degree of connectivity with neighboring islands during Pleistocene eustatic fluctuations, San Salvador lies on its own independent bank, and was neither connected with any other island, nor even very different in size, throughout the extensive sea-level fluctuations of ice age times. This stability in size and isolation may well explain the greatest peculiarity of the current *Cerion* fauna -- the extensive and continuous variation in shell form among populations throughout the island. *Cerion wallingense* and *Cerion rodrigo* do show centers of relatively "pure" form -- and in the expected places based on our knowledge of *Cerion*'s distribution throughout the Bahamas (see section 1 of this paper). But populations are extensively and evenly mixed by hybridization throughout the island, forming a virtual blanket of fairly continuous variation in shell morphology -- and thus explaining the biometric results of Fronabarger and Carew in finding mappable patterns of continuous variation throughout the island based on a set of characters measuring shell and aperture size and shape.

This unusual continuity of variation -- a probable product of both the relatively small size of the island (with absence of strong geographic barriers to movement), and, especially, of San Salvador's longterm geographic stability -- does make the taxonomy of San Salvador *Cerion* quite difficult, and is responsible for previous impressions of confusing and intractable variability within a single entity. But when we apply to San Salvador our knowledge of *Cerion* patterns throughout the Bahamas, we may then infer the existence of two taxa in their characteristic places, but with extensive and thorough mixture by hybridization (given the opportunities of time and geography

mentioned above) throughout the island.

THE FOSSIL *CERION* OF SAN SALVADOR

Since *Cerion* has an extensive fossil record (primarily in protosols, but also in terra rossa soils and eolianites) in Pleistocene and Holocene deposits of the Bahama Islands, and since no other taxon evolves with enough rapidity to provide potential signals for biostratigraphic resolution, the paleontology of *Cerion* assumes special importance for geologists (Gould and Woodruff, 1986; Gould, 1984 and 1988). Fossil *Cerion* are especially well represented on San Salvador, given the density of coastal and road cut exposures, and the context of extensive geological work already done (Carew and Mylroie, 1994, 1995, and references therein).

A survey of paleontological data from other islands illustrates two basic themes. First, and even over so short a time as that elapsing between the ca. 120,000 BP highstands (the source of major geological deposits on most Bahamian islands) and the present day, we often note substantial changes in prevailing faunas -- mostly by local extinction and immigration of new species from elsewhere, rather than by *in situ* evolutionary transformation (but see Gould and Woodruff, 1990, and Goodfriend and Gould, 1996 for local transitions by hybridization). Most impressively (and eminently usefully), the *Cerion* faunas of New Providence Island display three distinct and successive temporal stages (Gould and Woodruff, 1986, pp. 478-483): *C. clenchi* from interglacial deposits prior to the 120,000 BP highstand; the entirely different 120,000 year highstand fauna itself, including *C. agassizi* of the triangular morphotype, and dwarf *C. universa*; and the modern fauna (also in Holocene eolianites) of *C. glans* (ribby) and *C. gubernatorium* (mottled). In a second example, the extensive Pleistocene *C. excelsior* fauna of Inagua, Mayagua and Samana has been entirely replaced by modern representatives of the triangular morphotype on all these islands.

Second, we also note patterns of stability on single islands, at least through a full glacial cycle from the 120,000 BP highstand, through the last glaciation, to modern times. Most unexpectedly, I was able

to trace persistence throughout this long interval of small, supposedly transient and idiosyncratic features in the morphology of *C. agassizi*, the triangular morphotype on Eleuthera and Cat Island (paucicostate ribbing on Eleuthera, characteristic adult shapes on Cat) -- even though the islands were joined during intervening glacial times! (see Gould, 1988).

I can only include a few notes on fossil *Cerion* in this paper on taxonomy and geography of the modern fauna, but I can assert that the second theme of stability dominates, and that some conserved features are both striking and surprising. (This theme of stability also affirms Fronabarger's biometric results -- continuity in variation and inability to distinguish fossils from moderns on basic measurements of overall shell form. A more detailed biometric study might, however, pick up more subtle but consistent temporal differences in features of ribbing and, particularly, sizes and shapes at standardized whorl numbers -- as most previous studies have detected, while also failing to find differences in overall measures.)

Plate 2 shows fossil specimens in comparison with adjacent modern populations. I have been most struck by a stability of place, not noted before on any Bahamian island, between Pleistocene and modern times. In most cases, the modern situation of *C. rodrigo* on the windward eastern coast, and *C. wallingense* on western, northern, and southern coasts, has apparently persisted in detail at least from the 120,000 BP highstand until today -- for fossils are indistinguishable from modern samples found in the same place. This unprecedented stability in details of geographic position can probably only occur on an island like San Salvador where eustatic fluctuations, even through the maxima and minima of a full glacial cycle, do not alter the basic ecologies and habitats of particular places. Such stability could have no meaning, for example, on an island like Eleuthera, where the current bank-interior west coast habitats of the mottled morphotype lay in the interiors of large islands during maximal sea level lowerings of glacial times, and where, at the same time, neighboring islands of New Providence and Cat were all joined together, potentially sharing their *Cerion* faunas. But on

San Salvador, by maximal contrast, windward east coasts and leeward west coasts, have retained their position and status throughout the past 120,000 years, while the island has been persistently isolated from all others.

Thus, for example, modern *C. rodrigo* of Crab Cay (the left pair of specimens from locality 1227 on Plate 2, Figure A) cannot be distinguished from Pleistocene fossils from locality 1228 on Plate 2, Figure A). Similarly, *C. wallingense* can show similar stability of form and place -- as the left pair of modern specimens from locality 1236 on the southern coast (Plate 2, Figure B) cannot be distinguished from Pleistocene fossil *C. wallingense* from the same coast (the right pair of specimens in Plate 2, Figure B, from locality 1223, also on the south coast).

These unique stabilities may help us to explain the major peculiarity of modern *Cerion* faunas on San Salvador -- the extensive admixture and hybridization of the two taxa across the entire island, forming a pattern of continuous variation radiating from "pure" centers in expected places. If the geographic centers of distribution for the two species have remained stable for 120,000 years, then ample time for extensive and uninterrupted mixture of populations has been available. In this context, I find it striking (and illustrative of *Cerion*'s subtle and predictable patterning) that the basic separation of triangular and ribby morphotypes can still clearly be made, even in the light of such extensive hybridization of populations.

Stability, however, does not exhaust the message of fossil *Cerion* on San Salvador. Not all Pleistocene fossils mirror the detailed form of modern populations in the same areas. In particular, a small, finely-ribbed and narrow-shelled species occurs extensively in Pleistocene deposits throughout the island, often in regions where modern shells are much larger, and much closer to "pure" *C. wallingense* or *C. rodrigo*. Plate 2, Figure C, for example, shows a suite of such specimens from locality 191, a Pleistocene protosol exposed on the main road. These protosols outcrop in several places along the road in this region -- and the small shells differ substantially from the larger *C. wallingense* now living in this habitat.

I do not know how these extensive

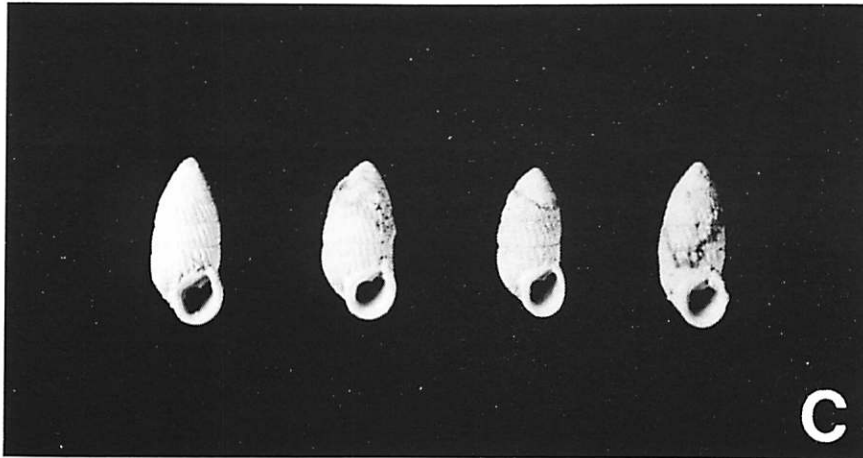
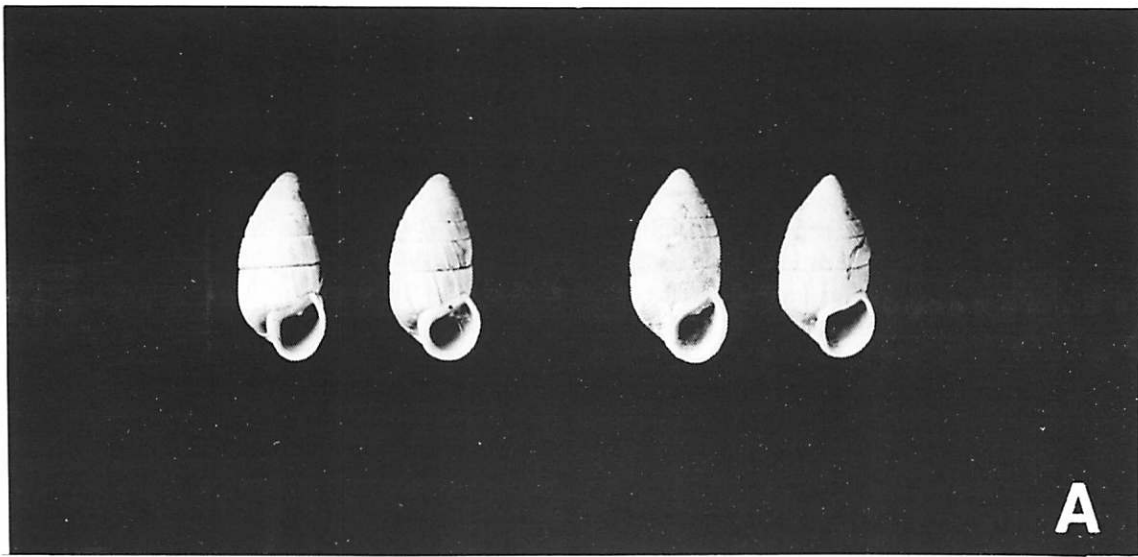


Plate 2: Variation in fossil *Cerion* of San Salvador and comparison with modern populations (see text for details of localities and varieties; all photos show shells at their actual size). A shows that both fossil (right) and living populations of *Cerion rodrigoii* on Crab Cay are indistinguishable; B shows the same phenomenon for *C. watlingense* (living left, and fossils right) on the southern coast; C shows a sample of the small ribby fossil shells found at many localities.

samples of small-shelled fossil *Cerion* should be treated taxonomically. They certainly lie within the range of variation of modern *C. wallingense* -- compare the fossils of Plate 2, Figure C with indistinguishable modern shells of the interior sample on Plate 1, Figure D. Thus, these fossils may just represent small-shelled and probably interior (or leeward coast) samples of *C. wallingense*. But I am impressed with the geographic spread and limited variation among fossil samples of this small-shelled form -- and I would not be surprised if these fossils represent an additional taxon, now either extinct or extensively hybridized with *C. wallingense* (and perhaps responsible in part for the wide range of variation among samples of the modern ribby morphotype).

CONCLUSIONS AND SUGGESTIONS FOR FUTURE WORK

I believe that this study has successfully defined the basic (and entirely sensible) pattern of taxonomy, paleontology, and geography for *Cerion* from San Salvador. But the observations have been too broad and cursory for the fine-scale resolution that a full account would require. I wish, therefore, to conclude with a list of questions and suggestions for further study -- for nothing would bring me greater satisfaction than if this preliminary work provided a basis for additional studies that might both refine and substantially alter the conclusions here reached. The following questions about the modern faunas seem most in need of resolution or most potentially fruitful for further results:

1. What is the detailed geographic distribution of the new species, *Cerion rodrigo*? Are pure populations confined to Crab and Almgreen Cays? Are they continuous between the two cays? What are the patterns of hybridization with *C. wallingense* to the north and south? Do any narrow and discrete hybrid zones exist (as on most other islands), or is hybridization so ancient and extensive that all patterns are broadly continuous?

2. *C. wallingense* inhabits most (more than 90 percent) of the island. How can we characterize detailed patterns of geographic variation within the island? Is the variation always broad and continuous (small shells on

the low and calm west-central coast grading to larger shells northwards and southwards, for example) -- or would a detailed survey show much more complicated and mosaic patterns of local differentiation? (I have the impression, for example, that variation in *C. wallingense* along the northern coast is not so continuous). How much of the pattern arises from hybridization with other taxa (surely with *C. rodrigo*, and perhaps with an unnamed mottled species, or with the small-shelled fossil form if it turns out to be a discrete taxon); and how much from localized adaptation to, or ecophenotypic modification by, immediate habitats? The general pattern and residuals from a multivariate morphometric technique like trend surface analysis might help to resolve such questions (see Gould and Woodruff, 1978, for application to variation within the mottled species on Grand Bahama Island).

3. Does a hybridized remnant (or even an undiscovered relatively pure population) of the mottled morphotype exist anywhere on San Salvador, or does all the variation within *C. wallingense* arise from the potentials of a single taxon?

I suggest the following questions as intriguing or important for further study of fossil samples:

1. Several excellent examples do not make a generality. Do Pleistocene fossils usually belong to the same species (and even to the same variant form) as modern populations living in the same place -- thus illustrating striking stability of both form and place over at least 120,000 years? In what percentage of cases, and under what circumstances, do fossils and moderns from the same region differ? In particular, are differences more likely when fossils come from the older, pre-120,000 year deposits of the Owl's Hole Formation -- and do most similarities occur when fossils come from the 120,000 year old sediments of the later Grotto Beach Formation (Carew and Mylroie, 1994, 1995)?

2. Are the small and finely ribbed fossil shells, widely distributed without substantial variation in Pleistocene deposits, representatives of a separate and unnamed fossil species, or just small-shelled variants within *C. wallingense*?

3. Do fossils from the oldest deposits

on the island (Owl's Hole from locality 1243, collected by John Mylroie from a coarse and friable eolianite from Lighthouse Cave) differ in any distinctive way from later samples? At first glance, these shells seem no different from the small finely-ribbed fossils found throughout the island (and mentioned in point 2 above), though they may be a bit larger and more strongly ribbed?

In conclusion, although the list of unresolved questions exceeds the roster of conclusions (a situation always to be cherished in science), we can specify a well-documented framework that both emphasizes some interesting peculiarities of San Salvador, and also places this fascinating island well within the general patterns predicted from knowledge of *Cerion's* spread and variation on other Bahamian islands. Most satisfactorily, the two taxa of San Salvador represent expected forms based on the island's geographic position -- and also live in the predicted habitats and regions of the island. *C. wallingense*, the mottled morphotype representing the northern region of the Bahamas, lives along the bank-edge coast and at lower density throughout the interior; while *C. rodrigo*, the triangular morphotype representing the southeastern region of the Bahamas, inhabits the most rocky and windward parts of the eastern coast. Patterns of geographic variation within the two taxa match the distribution of habitats and potentials for interaction through hybridization.

The *Cerion* of San Salvador also display two unusual features consistent with the island's status as continually isolated from all others, and effectively invariant in size and distribution of habitats during Pleistocene and Recent eustatic fluctuations. First, the two taxa are much more extensively and continuously mixed by hybridization (leading to the false impression of a single, highly variable entity) than on any other island previously studied -- a sensible consequence of biology on a relatively small island lacking strong geographic barriers between centers of distribution for the two taxa, and with greater temporal stability and isolation acting as protection from easy migration of other taxa on adjacent islands. A longer time for uninterrupted interaction may therefore explain the degree of homogenization and

continuous variation among San Salvador's *Cerion* populations.

Secondly, the fossil record of *Cerion* on San Salvador shows more stability than for any other Bahamian island studied so far. No old faunas become extinct, and no new faunas migrate in -- as has occurred twice on New Providence during the same interval. Both taxa occur as Pleistocene fossils. Moreover, if the small finely-ribbed fossil species (Plate 2, Figure C) is a variant within *C. wallingense*, and not a distinct form, then no taxonomic changes have occurred at all during the recorded history of *Cerion* on San Salvador. Most impressively, Pleistocene fossils often represent not only the same species, but even the same variant form, as modern populations now living in the same place -- an unprecedented geographic stability not observed before, but sensible in the light of San Salvador's isolation and temporal stability of habitats on this small scale.

In short, *Cerion's* established patterns of broad scale variation throughout the Bahamas can be applied to resolve, in a fully sensible and satisfactory way, the basic order of taxonomy, geography and time in the history of *Cerion* on San Salvador. The results lie in a happy middle ground of scientific interest: familiar enough for clear interpretation, yet sufficiently different (in response to San Salvador's unusual features of geography and history) to provide both extended insight and puzzles for future resolution.

REFERENCES

- Carew, J.L. and Mylroie, J.E., 1994, Geology and Karst of San Salvador Island, Bahamas: Bahamian Field Station, 32 pp.
- Carew, J.L. and Mylroie, J.E., 1995, Depositional model and stratigraphy for the Quaternary geology of the Bahama Islands, in Curran H.A. and White B., eds., Terrestrial and Shallow Marine Geology of the Bahamas and Bermuda: Geological Society of America Special Paper 300, P. 5-32.
- Clench, W.J., 1957, A catalogue of the

- Cerionidae (Mollusca-Pulmonata). *Bulletin of the Museum of Comparative Zoology*, v. 116, p. 121-169.
- Crampton, H.E., 1917, Studies on the variation, distribution and evolution of the genus *Partula*. The species inhabiting Tahiti: Carnegie Institute of Washington Publications, v. 228, p. 1-311.
- Crampton, H.E., 1932, Studies on the variation, distribution and evolution of the genus *Partula*. The species inhabiting Moorea: Carnegie Institute of Washington Publications, v. 410, p. 1-335.
- Curran, H.A. and White B., 1995, Introduction: Bahamas geology, in Curran H.A. and White B., eds., Terrestrial and shallow marine geology of the Bahamas and Bermuda: Geological Society of America Special Paper No. 300, p. 1-3.
- Dall, W.H., 1905, Report on land and fresh water shells collected in the Bahamas in 1904, by Mr. Owen Bryant and others: Smithsonian Miscellaneous Collections, v. 47, p. 433-452.
- Galler, L. and Gould, S.J., 1979, The morphology of a "hybrid zone" in *Cerion*: Variation, clines, and an ontogenetic relationship between two "species" in Cuba: *Evolution*, v. 33, p. 714-727.
- Goodfriend, G. and Gould, S.J., 1996, Paleontology and chronology of two evolutionary transitions by hybridization in the Bahamian land snail *Cerion*: *Science*, v. 274, p. 1894-1897.
- Gould, S.J., 1969, An evolutionary microcosm: Pleistocene and Recent history of the land snail *P. (Poecilozonites)* in Bermuda: *Bulletin of the Museum of Comparative Zoology*, v. 138, p. 407-532.
- Gould, S.J., 1984, Morphological channeling by structural constraint: Convergence in styles of dwarfing and gigantism in *Cerion*, with a description of two new fossil species and a report on the discovery of the largest *Cerion*: *Paleobiology*, v. 10, p. 172-194.
- Gould, S.J., 1988, Prolonged stability in local populations of *Cerion agassizi* (Pleistocene-Recent) on Great Bahama Bank: *Paleobiology*, v. 14, p. 1-18.
- Gould, S.J., 1989, A developmental constraint in *Cerion*, with comments on the definition and interpretation of constraint in evolution: *Evolution*, v. 43, p. 516-539.
- Gould, S.J., 1992, Constraint and the square snail: life at the limits of a covariance set. The normal teratology of *Cerion disforme*: *Biological Journal of the Linnaean Society*, v. 47, p. 407-437.
- Gould, S.J., 1996, A *Cerion* for Christopher: *Natural History*, v.105, no.10, p. 22-29, 78-79.
- Gould, S.J. and Woodruff, D.S., 1978, Natural history of *Cerion*. VIII: Little Bahama Bank -- a revision based on genetics, morphometrics, and geographic distribution: *Bulletin of the Museum of Comparative Zoology*, v. 148, p. 371-415.
- Gould, S.J. and Woodruff, D.S., 1986, Evolution and systematics of *Cerion* (Mollusca: Pulmonata) on New Providence Island: A radical revision: *Bulletin of the American Museum of Natural History*, v. 182, p. 389-490.
- Gould, S.J. and Woodruff, D.S., 1987, Systematics and levels of covariation in *Cerion* from the Turks and Caicos: *Bulletin of the Museum of Comparative Zoology*, v. 151 p. 321-363.
- Gould, S.J. and D.S. Woodruff, 1990, History as a cause of area effects: An

illustration from *Cerion* on Great Inagua, Bahamas: *Biological Journal of the Linnaean Society*, v. 40, p. 67-98.

Gulick, J.T., 1905, Evolution, radical and habitudinal: Carnegie Institute of Washington Publications, v. 25, p. 1-269.

Maynard. C.J., 1889, Monograph of the genus *Strophia*, in Contributions to science, v. 1, Newtonville, MA.

Mayr, E. and Rosen, C.B., 1956, Geographic variation and hybridization in populations of Bahama snails (*Cerion*): American Museum Novitates No. 1806, 48 p.

Murray, J. and Clarke B., 1980, The genus *Partula* on Moorea: speciation in process: Proceedings of the Royal Society of London, v. 211, p. 83-117.

Plate, L. 1907, Die Variabilität und die Artbildung nach dem Prinzip geographischer Formenkette bei den *Cerion*-Landschnecken der Bahama-Inseln: Arch. Rassen Gesell. Biol. v. 4, p. 433-470, 581-614.

Woodruff, D.S. and Gould, S.J., 1980, Geographic differentiation and speciation in *Cerion* -- a preliminary discussion of patterns and processes. *Biological Journal of the Linnaean Society*, v. 14, p. 389-416.